



# Patterns and Population Dynamics of Inversion Polymorphism in different Species of *Drosophila*

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**Abstract:** The structural and numerical aberrations are known to occur in different species of plants and animals including humans. Paracentric inversions in *Drosophila*, pericentric inversions in grasshoppers, translocations in *Oenothera lamarckiana* and polyploidy in plants have been studied in detail. The genus *Drosophila* is an interesting biological model which belongs to the family Drosophilidae (Class-Insecta and Order-Diptera) characterised by rich species diversity at global level and also in India. More than 1500 species have been rereported at global level and about 150 species from India. Inversions were detected about hundred years ago in *Drosophila melanogaster* through their suppressive effects on recombination by Sturtevant. Inversion polymorphism caused due to paracentric inversions have been studied in a large number of species and about 100 species have been found to be chromosomally polymorphic. Inversions polymorphism has been studied in detail in certain species with respect to the patterns and population dynamics of inversion polymorphism. In this article, briefly the patterns and population dynamics of inversion polymorphism have been described in certain species. In several cases, it has been found that inversions are adaptive. But the precise selective mechanisms that maintain them polymorphic in natural populations remains poorly understood and it has been suggested by molecular evolutionary biologists that recent advances in the area of population genomics, modelling and functional genetics promise to greatly improve our understanding of this long standing and fundamental problem in the near future.

**Index Terms:** *Drosophila*, inversion polymorphism, pattern, population dynamics, different species.

## I. INTRODUCTION

Structural and numerical aberrations are widespread in plant and animal species including humans (for references see Dobzhansky, 1951; White, 1954, 1978; Mayr, 1966; Powell, 1997). There are well known cases of paracentric inversions in

*Drosophila*, pericentric inversions in grasshoppers, translocations in *Oenothera lamarckiana* and polyploidy in a number plant species. The genus *Drosophila* is an interesting biological model which belongs to the family Drosophilidae (Class-Insecta and Order-Diptera) characterised by rich species diversity at global level and also in India. More than 1500 species have been rereported at global level and about 150 species from India. It is interesting to mention that more than 500 species of *Drosophila* including picture winged species have been reported from Hawaiian Islands which are extensively used in evolutionary studies (Carson, 2002; Singh, 2015). Thus *Drosophila* has rich species diversity and the species which have been studied for genetic composition in their natural populations show adequate level of genetic diversity. It has been employed in different kinds of studies such as population genetics, evolutionary genetics, sexual isolation, behaviour, genetic recombination, inversion polymorphism, ecological genetics, molecular biology etc (Singh, 2010). Sturtevant (1917) detected inversions in *D. melanogaster* for the first time through the suppression of crossing-over in inversion heterozygotes. Paracentric inversion does not include the centromere. Recombination within the paracentric inversion in a heterozygote produces acentric and dicentric fragments which are eliminated through polar bodies in females and egg receives only a normal nonrecombinant chromatid. Thus crossovers are not observed. Furthermore, recombination may be strongly suppressed within inversion. In *Drosophila*, the inversions do not decrease the fertility in males because crossing-over does not occur in males (Singh 2020). Thus paracentric inversions are cytologically neutral. The heterozygous inversions may strongly influence the rate of recombination outside the inverted zone as well as heterozygous inversions in one chromosome may strongly enhance the rate of recombination in non homologous chromosomes (Singh and Singh 1987). Since the flies with different inversion karyotypes are morphologically indistinguishable, many researchers including Theodosius Dobzhansky believed that chromosome inversions are adaptively

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neutral. However, it was proved to be wrong. Dobzhansky in 1947 demonstrated for the first time that inversion polymorphism is an adaptive trait in *Drosophila* based on his work in *D. pseudoobscura*. When chromosomal polymorphism was studied in a large number of species with the help of polytene chromosome maps, about 100 species were found to be chromosomally polymorphic (Powell 1997). However, certain species have been studied in detail with respect to the patterns and population dynamics in natural and experimental populations: *D. pseudoobscura*, *D. willistoni* and related species, *D. robusta*, *D. subobscura*, *D. melanogaster*, *D. ananassae*, *D. pavani*, *D. bipunctata*, *D. nasuta*, *D. funebris* and Hawaiian Species. Different species show variation in the degree of inversion polymorphism and also frequencies of inversions show geographic, latitudinal, and seasonal variations. Further, inversion polymorphism may be rigid or flexible. Inversion heterozygotes show heterotic buffering caused due to superiority of heterozygotes referred to as heterosis. With the help of inversion polymorphism, different phenomena such as genetic coadaptation, balanced polymorphism and heterosis, linkage disequilibrium and epistasis have been studied in different species which are of considerable evolutionary significance (Singh and Ray-Chaudhuri, 1972; Singh, 1982, 2008, 2013, 2018). Chromosome inversions also persist in laboratory populations due to higher fitness of inversion heterozygotes although inversion frequencies may vary due to random genetic drift involving bottleneck effects and founder principle (Singh 1987, 1988). Singh (2001) compared the pattern of inversion polymorphism in three different species: *D. melanogaster*, *D. ananassae* and *D. bipunctata* which belong to the *Drosophila* species group. Based on the variation in the pattern of inversion polymorphism in these three species, it was suggested by Singh (2001) that these species have evolved different mechanisms to adjust to their environments though they belong to the same species group. It is interesting to mention that from 27 collections of *D. melanogaster* populations revealed the presence of 53 inversions but 27 collections of *D. simulans* from Africa, Europe, Australia and South America revealed no inversion (Ashburner & Lemeunier, 1976). This reflects the contrast between two cosmopolitan and domestic species which are sibling to each other (Singh, 2016). Anderson et al. (1991) reported data on inversion frequencies during four decades in natural populations of *D. pseudoobscura* from North America in which inversion studies were initiated by Dobzhansky in 1947. The common gene arrangements continue to be present in the frequencies similar to those described four decades ago (Anderson et al. 1991).

Singh (2019) reviewed the work done on inversion polymorphism in different species of *Drosophila* during the last hundred years. It has also been found that natural selection acting on inversion polymorphism is strong because latitudinal clines in the frequencies of inversions become reestablished rapidly after a new continent is colonized (Hoofmann et al. 2004). It has also been suggested by Hoofmann et al (2004) that a combined molecular and morphological approach may help to identify the role of inversion polymorphism in adaptive

divergence but the genes responsible for associations between traits and inversion polymorphisms remain to be identified. Chromosomal inversions have the potential to be key in the adaptation processes, as they can contribute to the maintenance of favourable combinations of the alleles which contribute to adaptation through suppressed crossing-over between individuals carrying different inversion karyotypes (Pegueroles et al. 2016). While considering the adaptive significance of chromosomal inversion polymorphism in *Drosophila melanogaster*, Kapun and Flatt (2019) have suggested that the precise selective mechanisms which maintain them polymorphic in natural populations remain poorly understood and it has also been remarked by these authors that recent advances in population genomics, modelling and functional genetics promise greatly to improve our understanding of this long-standing and fundamental problem in the near future. Results of analyses of natural and laboratory populations extend evidence that the inversion polymorphism provide adaptive advantages to their carriers in relation to diverse factors such as niche exploitation, and climatic factors. Additionally, since inversions have monophyletic origin (Singh, 1970), they also serve as genetic markers for the construction of unrooted phylogenies. With the increasing domain of molecular techniques, and genome sequencing, the factors such as reuse of breakpoints by different inversions and the mechanisms which give rise to these polymorphisms have been exploited with scientific refinement. Sequence based detection and breakpoint assembly of polymorphic inversions have been done in *D. melanogaster* by Corbett-Detig et al. (2012). Corbett-Detig & Hartl (2012) developed a method which is termed as Reference-Assisted Reassembly to assemble unbiased, highly accurate sequences near inversion breakpoints which were used by these authors to estimate the age and geographic origin of polymorphic inversions in *D. melanogaster* and found that inversions are young and mostly they are African in origins. This is consistent with the demography of *D. melanogaster*. Their results also suggest that inversions interact with polymorphism not only in breakpoint regions but also chromosome-wide. These investigators have also suggested that inversions achieve a selective advantage through the maintenance of co-adapted gene complexes (Corbett-Detig & Hartl, 2012). According to Garcia and Valente (2018), these results show the presence of regions which are hot spots for breakpoints of inversions which fits with the fragile breakage chromosomal evolution model and also the involvement of transposable elements at the origin of chromosomal inversions. An interesting study has been reported in *D. melanogaster* by sequencing orchard populations collected across multiple years by Numez et al. (2023) who found that the cosmopolitan inversion In(2L)t facilitates seasonal adaptive tracking and shows molecular footprints of selection. These authors have presented evidence for seasonal loci within the inversion are associated with behaviour, life history, physiology and morphological traits. Paracentric inversions are remarkably abundant in *Drosophila*. Since different species of this genus are paradigms for genetics, evolutionary and population studies, polymorphism analyses for chromosome inversions have provided basic knowledge for beautiful biological questions

(Garcia & Valente, 2018). Heterozygous inversions suppress meiotic recombination and thus natural selection can act to preserve favourable gene complexes in chromosomes. Chromosomal analyses of natural and laboratory populations demonstrate that these inversion polymorphisms provide adaptive advantages to their carriers in relation to diverse factors such as niche exploitation and climatic factors. Chromosomal inversions have long fascinated evolutionary biologists due to their suppression of recombination which can protect coadapted polygenic complexes. The importance of chromosomal inversions should be better acknowledged and integrated in studies pertaining to the molecular basis of adaptation and speciation (Wallenreuther & Bernatchez, 2018).

Keeping this in view, the pattern and population dynamics of chromosomal polymorphism caused due to paracentric inversions considering the findings reported in certain species of *Drosophila* including the species found in India have been summarised in this review.

## II. PATTERNS AND POPULATION DYNAMICS OF INVERSION POLYMORPHISM IN DIFFERENT SPECIES

### A. *Drosophila pseudoobscura*

Adaptive change in inversion frequencies induced by natural selection in wild populations of *D. pseudoobscura* was demonstrated for the first time by Theodosius Dobzhansky and his interesting work was published in *Evolution* Volume 1 and issue 1 (1947) and after that studies on inversion polymorphism were initiated in other species. He for chromosome inversions have provided basic knowledge of utilized both the species: *D. pseudoobscura* and *D. persimilis*, a pair of sibling species. Both the species are chromosomally polymorphic but the level of polymorphism is more in *D. pseudoobscura* than *D. persimilis* (Dobzhansky, 1951, 1971). There is a unique feature of these species i.e. they contain a number of overlapping inversions in the third chromosome which has been used for discussing inversion phylogeny. His studies on inversion polymorphism demonstrated different phenomena of evolutionary significance such as annual cyclic changes in inversion frequencies in natural populations, role of natural selection and genetic drift, balanced polymorphism, heterosis, genetic coadaptation and maintenance of different gene arrangements in population cages at equilibrium. Anderson et al. (1991) reported data on inversion frequencies of third chromosome in natural populations of *D. pseudoobscura* in North America based on studies of Dobzhansky and others. It was observed that the common gene arrangements continue to be present in frequencies similar to those reported four decades ago. and in general the geographical patterns also remained similar. However, one change was noticed that the frequency of Tree Line arrangement of the third chromosome increased in populations of Pacific coast over time. Schaeffer et al. (2003) made evolutionary genomics analysis and their results support the hypothesis that the inversions in

*D. pseudoobscura* have emerged as suppressors of recombination to maintain the positive epistatic interaction among loci within the inversion that developed as the species adapted to a heterogeneous environment. based on pattern of higher genomic divergence and an association of reproductive isolation genes with chromosome inversions in *D. pseudoobscura* and *D. persimilis* may be a direct consequence of incomplete lineage sorting of ancestral polymorphism which forces to reconsider the role of chromosome inversions in speciation not as protectors of existing hybrid incompatibilities but as fertile ground for their formation (Fuller et al. 2018).

### B. *Drosophila willistoni* and related species

The initial studies by Dobzhansky and his coworkers in *Drosophila willistoni* and related species on inversion polymorphism made an important contribution to know the adaptive role of inversions. The results of these studies led Dobzhansky and his coworkers to advance the ecological niche hypothesis which states that "inversion polymorphism in *Drosophila* is a device to cope with the diversity of environments (Dobzhansky et al. 1950; Da Cunha & Dobzhansky, 1954). Dobzhansky et al. (1950) and Da Cunha and Dobzhansky (1994) studied inversion polymorphism in natural population of four sibling species of *Drosophila* found in Brazil: *D. willistoni*, *D. paulistorum*, *D. tropicalis*, and *D. equinoxialis*. There were intra- and interspecific variations in the degree of inversion polymorphism. Among these four species, *D. willistoni* is the commonest species, *D. paulistorum* is less common and other two species which are least common. In *D. willistoni*, 40 inversions were detected, 34 inversions in *D. paulistorum*, 4 inversions in other two species. The mean number of heterozygous inversions per individual varies in different populations of these species: from 0.8 to 9 and 10 in *D. willistoni*, 0.6 to 1.8 in *D. paulistorum*, 0.14 in *D. tropicalis*, and 0.11 in *D. equinoxialis*. These results support the ecological niche hypothesis. Interestingly, the degree of inversion polymorphism was found to be higher in geographically central populations as compared to geographically and ecologically marginal populations (Da Cunha & Dobzhansky, 1954).

### C. *Drosophila robusta*

*D. robusta*, with few relatives, appears to be an old, conservative, and clearly isolated member of the fauna of the eastern deciduous forest of the United States (Carson, 1958). Inversion polymorphism has been studied in natural populations of this species and geographic differentiation among the populations has been found. Certain interesting phenomena associated with inversion polymorphism has been reported in this species such as differences between central and marginal populations in the degree of chromosomal variability, measurement of free recombination rate (IFR), comparison between homoselection and heteroselection, and non-random associations of inversions due to epistatic interaction favoured

by natural selection (Carson, 1958; Levitan, 1954, 1958, 1992; Levitan & Scheffer, 1993, Levitan & Etges, 2005). In marginal populations where homoselection predominates, adaptive novelties are synthesized. Further, central populations have more adaptedness whereas marginal populations have more adaptability (Carson, 1958).

#### D. *Drosophila subobscura*

European researchers have conducted extensive study on inversion polymorphism in *D. subobscura*, which is an Old World counterpart of *D. pseudoobscura* in certain ways (Krimbas & Loukas, 1980, Prevosti et al. 1985, Sperlich & Pfriem, 1986; Krimbas, 1992; Santos, 2009). There are more than 50 paracentric inversions in five acrocentric chromosomes which are widely distributed in natural populations of *D. subobscura* and interpopulation variations occur in the frequencies of inversions. Further, there is evidence for the occurrence of clines in the inversion frequencies but it shows variation for inversion. Most likely natural selection is correlated with latitudes (Sperlich & Pfriem, 1986; Krimbas, 1999). One remarkable phenomenon occurred when *D. subobscura* was found in Chile, Argentina and USA (Beckenbach & Prevosti, 1986; Prevosti et al. 1988; Krimbas, 1992). Based on the inversion frequencies data, it was postulated that the source of north American invasion was South America by Ayala et al (1989). From the data on inversion frequencies it is evident that latitudinal gradients occurring in Old World populations have been established in South American populations in the exactly reverse order (Prevosti et al., 1988). Thus, based on these results, it is concluded that natural selection related to latitude is operating in natural populations of *D. subobscura*. In a recent study by Castaneda et al. (2013), it has been found that active behavioural thermoregulation might buffer environmental variation and reduce the potential effect of thermal selection on chromosome arrangements in *D. subobscura*. Khadem et al. (2022) have also reported that inversions based on inversion composition and frequencies have changed in marginal and isolated populations of *D. subobscura* which is in agreement with global warming expectations. Nucleotide variation in different gene regions distributed along inversion was analysed in chromosome O<sub>3</sub> using different lines of *D. subobscura* and it was found that the level of variation within arrangements was quite similar along the inversion. However, extensive genetic differentiation between arrangements in all regions was found regardless of their distance to the inversion breakpoints, along with high level of linkage disequilibrium. Further, strong genetic differentiation detected along O<sub>3</sub> arrangements may extend to other inversions and nucleotide variation would be highly structured not only in *D. subobscura* but also in the genome of other species with rich chromosomal polymorphism (Munte et al. 2005).

#### E. *Drosophila melanogaster*

*Drosophila melanogaster*, a cosmopolitan and domestic species was used for genetical studies in 1909 by T H Morgan who showed for the first time that genes are linearly arranged in chromosomes and can be separated by crossing-over (theory of linkage) and discovery of first spontaneous mutation i.e. white eye which is sex-linked. Thus theory of linkage and sex-linkage was proposed by T H Morgan in *D. melanogaster*. Sturtevant was first to report the occurrence of chromosome inversions in *D. melanogaster* through their suppressive effects on recombination. After that a large number of studies were conducted on inversion polymorphism through the study of polytene chromosomes and now we know that more than 300 paracentric inversions are known to occur in natural populations of *D. melanogaster* (Das & Singh, 1991; Lemeunier & Aulard, 1992). Surprisingly, its sibling which is also cosmopolitan and domestic species, *D. simulans* has no paracentric inversions. (see Kapun & Flatt, 2019; Singh, 2019). Latitudinal clines have been reported with respect to four common cosmopolitan inversions in natural populations of *D. melanogaster* from different regions at global level (Mettler et al. 1977; Knibb et al. 1981; Das and Singh, 1991; Singh & Das, 1992; Lemeunier and Aulard, 1992). Thus inversion polymorphism in *D. melanogaster* is adaptive and shows variation in different populations (Singh 2019). *D. melanogaster* shows highest degree of inversion polymorphism in the genus *Drosophila* and paracentric inversions are adaptive and showing inversion clines in different regions of the world. When populations are maintained in the laboratory, the frequency of inversions decreases and inversions are gradually lost (Singh & Das, 1992). There is evidence for epistatic interactions between unlinked inversions in Indian natural populations of *D. melanogaster* (Singh & Das, 1991). Recently some findings have been reported in respect of inversions and molecular data and genomics. Kapun and Flatt (2019) have commented that recent advances in population genomics, modelling and functional genetics may help to improve our understanding regarding precise selective mechanisms which maintain them in natural populations. Kapun et al. (2016) presented their results that provide strong evidence that inversion clines in natural populations of *D. melanogaster* are maintained by spatially and perhaps also temporally varying natural selection. Hoofmann et al (2004) are of the view that natural selection acting on inversion polymorphisms is strong because latitudinal clines in inversion frequency become reestablished rapidly after new continent is colonized. Corbett-Detig and Hartl (2012) have suggested that with deeper sampling it would be possible to develop inferences on inversion frequencies to rigorously test selective models especially those that postulate that paracentric inversions achieve a selective advantage through the maintenance of coadapted gene complexes. Nunez et al. (2023) on the basis of sequencing orchard populations of *D. melanogaster* collected across

multiple years, characterized the genomic signals of demography and identified that the cosmopolitan inversion In(2L)t facilitates seasonal adaptive tracking and exhibits molecular prints of natural selection.

#### F. *Drosophila ananassae*

*D. ananassae* is a cosmopolitan and domestic species but it is mainly circumtropical in distribution. It is genetically unique species as it possesses a number of genetic peculiarities (Singh, 2000, 2020). It exhibits a high level of inversion polymorphism (Singh, 1989, Singh, 1998, Singh, 2019; Singh & Singh, 2007). It has been found that it has 78 paracentric inversions, 21 pericentric inversions and 48 translocations. Interestingly, out of 78 paracentric inversions, only three inversions have become widespread in geographical distribution and called as cosmopolitan inversions (AL in 2L, DE in 3L and ET in 3R) which is based on monophyletic origin of inversions (Singh, 1970). An inversion within the AL inversion was detected (Singh, 1983).

Singh and his students have studied inversion polymorphism in Indian populations of *D. ananassae* and the results have clearly demonstrated that there is a geographic differentiation of inversion polymorphism in Indian natural populations (Singh, 1989, 1996, 1998, 2015, 2019; Singh & Singh, 2007, 2008). The results on the whole suggested that cosmopolitan inversions have become integral part of genetic endowment of the species. Further, inversions occur in high frequency in south Indian populations and there is population sub-structuring associated with inversions based on strong genetic differentiation and minimal gene flow between populations (Singh & Singh, 2010). There is genetic similarity between natural populations of *D. ananassae* from Kerala and Andaman and Nicobar Islands (Singh, 1986). Inversion polymorphism in *D. ananassae* is balanced and often persists in laboratory populations due to adaptive superiority of inversion heterozygotes i.e. heterosis (Singh & Ray-Chaudhuri, 1972; Singh, 1982). When the laboratory populations are established from the flies collected from natural populations, inversion frequencies often fluctuate in laboratory populations due to action of random genetic drift (Singh, 1987, 1988). *D. ananassae* is an exception to the genetic coadaptation concept of Dobzhansky who suggested that gene complexes are mutually adjusted or coadapted in natural populations of *Drosophila* which causes superiority of inversion heterozygotes which is broken down in interracial crosses due to recombination. However, there is persistence of heterosis in interracial crosses in *D. ananassae* and thus evidence for genetic coadaptation is lacking in *D. ananassae* populations (Singh, 1972, 1985, 2018).

#### G. *Drosophila pavani*

*D. pavani* is a common species in Chile and Argentina. It contains paracentric inversions which occur in natural

populations exhibiting superiority of heterozygotes over the corresponding homozygote (Brcic, 1957, 1958). Brcic (1970, 1973) reported rigid inversion polymorphism in *D. pavani* which demonstrates that inversion polymorphism does not show variation in natural populations. However, there is evidence for genetic coadaptation in geographic populations of *D. pavani* as interracial hybridization leads to breakdown of heterosis in interracial crosses which extends evidence for genetic coadaptation concept of Dobzhansky (Brcic, 1961, Singh, 2018).

#### H. *Drosophila bipectinata*

*D. bipectinata* has wide geographical distribution ranging from India through south east Asia and New Guinea to Fiji and Samoa in the Pacific (Bock & Wheeler, 1972). Inversion polymorphism has been studied in this species and several paracentric inversions are known to occur in natural populations and laboratory stocks (Bock, 1971; Gupta & Panigrahy, 1990) and all the inversions are autosomal. Inversion frequencies have been reported in its natural populations particularly in Indian populations with regard to three common inversions (Banerjee & Singh, 1996; Singh & Singh, 2021). Inversions occur at very low frequency and does not show much variation. This led Banerjee and Singh (1996) to suggest that inversion polymorphism in *D. bipectinata* is rigid. However, Singh and Singh (2021) found significant variation in inversion frequencies while comparing north and south Indian populations of this species suggesting genetic differentiation between populations. Common inversions often persist in laboratory populations due to heterotic buffering associated with these inversions (Das & Singh, 1992) and linked inversions occur in non-random association due to epistatic interaction (Singh & Das, 1991). The work on population dynamics of inversion polymorphism in this species has been reviewed by Singh (2001) and Singh and Banerjee (2016).

#### I. *Drosophila nasuta*

Inversion polymorphism has been studied in *D. nasuta* and evidence has been presented for geographic differentiation and altitudinal clines in Indian natural populations (Ranganath & Krishnamurthy, 1975; Rajasekarasetty et al., 1979; Shyamala & Ranganath, 1988; Kumar & Gupta, 1988). However, evidence for genetic coadaptation in geographic populations of *D. nasuta* is lacking since interracial hybridization does not lead to breakdown of heterosis (Kumar & Gupta, 1991). Using molecular techniques, the breakpoints of six autosomal inversions were characterized in the *D. nasuta* species group which demonstrated that repeated sequences are associated with inversion breakpoints in four of these inversions suggesting that ectopic recombination is an important mechanism in generating inversions (Mai & Bachtrog, 2021)

### J. *Drosophila funebris*

*Drosophila funebris* is widely distributed through the temperate regions of the world. It shows chromosomal variability due to presence of paracentric inversions in natural populations (Dubinin et al, 2010). Remarkable studies were conducted on population dynamics of inversion polymorphism in this species by Dubinin & Sokolowski (1945, 1946a,b) and Borisov (1970) who reported interesting findings on inversion frequencies in this species particularly from Moscow. The dependence of inversion frequencies on ecological factors discovered initially in *D. funebris* by Dubinin & Tiniakov were confirmed by Borisov (1970) following his studies on *D. funebris* populations in the Moscow regions. The existence of urban and rural races differing in karyotypic constitution were confirmed together with established evidence of spreading of rural races over a 20 years period from 25 to 800 square kms in this species, The level of chromosomal variability varies between rural and urban populations which is correlated with ecological niches available for the species (Dubinin & Tiniakov, 1945, 1946a,b). Further, inversion frequencies vary in different seasons of the year. Further, some gene arrangements are more frequent than others during the period of hibernation (Dubinin & Tiniakov, 1946b).

### K. Hawaiian Species

On Hawaiian Islands, about 700 species of the family Drosophilidae have been described (Kaneshiro, 1997). There are about 100 picture winged species belonging to the sub-genus *Drosophila* which are unique and have been extensively utilized for the studies related to cytogenetics, behaviour and evolution. (Carson, 1982, 1987). Studies on inversion polymorphism in these species have revealed the presence of paracentric inversions which have been subjected to intra and interspecific comparisons. One third of these species are found to be chromosomally polymorphic. These species possess certain unique features pertaining to inversion polymorphism: there are species having identical banding pattern in polytene chromosomes designated as homosequential species occurring in clusters (19 clusters of from 2 to 10 species in each). However, there are morphological and physiological differences among these species and they also distinct pertaining to other genetic measures. Phylogenetic relationship among these species have been discussed based on fixed inversions (Carson, 1973, 1987). Paracentric inversions in these species are unique and have been considered having monophyletic origin. Further, considering banding patterns in salivary gland chromosomes, chromosome breaks and fixed inversions, the chromosome phylogeny has been discussed in different species sub-groups of picture winged species found on Hawaiian Islands (Carson, 1992). Chromosomal polymorphism has been studied and the results show interpopulation variation in certain homosequential species (Cradock & Johnson, 1979). Cradock and Carson (1989)

reported eleven chromosomal polymorphism showing subdivided population structure with spatial heterogeneity in chromosome inversion distribution and frequencies with the limited geographic range of *D. silvestris*.

### CONCLUSION

The account of chromosomal variability resulting from paracentric inversions given above in different species of *Drosophila* clearly show that the pattern and population dynamics of inversion polymorphism show considerable differences if different species are compared. There are species which are chromosomally monomorphic and there are species which are highly polymorphic. The species which are chromosomally polymorphic vary in the degree of polymorphism, pattern of polymorphism and population dynamics both concerning natural and laboratory populations. Based on the variation in the pattern of inversion polymorphism in different species, it has been suggested that these species have evolved different mechanisms to adjust to their environments. There are obvious differences among the species pertaining to seasonal variation in inversion frequencies, inversion clines, latitudinal clines, geographic differentiation, changes in inversion clines with time, degree of chromosomal variability, marginal and central populations, homoselection vs heteroselection, balanced polymorphism and heterosis, genetic coadaptation, role of selection, random genetic drift and linkage disequilibrium. Chromosomal inversions have long fascinated evolutionary biologists due to their suppression of recombination which can protect coadapted polygenic complexes. The importance of chromosomal inversions should be better acknowledged and integrated in studies pertaining to the molecular basis of adaptation and speciation.

Recent work in the areas of molecular biology and genomics related to chromosome inversions in different species of *Drosophila* have certainly given new perspectives. Based on pattern of higher genomic divergence and an association of reproductive isolation genes with chromosome inversions in *D. pseudoobscura* and *D. persimilis* it has been suggested that the role of chromosome inversions in speciation is not as protectors of existing hybrid incompatibilities but as fertile ground for their formation. Nucleotide variation in different gene regions distributed along inversion was analysed in chromosome O<sub>3</sub> using different lines of *D. subobscura* and it was found that the level of variation within arrangements was quite similar along the inversion. However, extensive genetic differentiation between arrangements in all regions was found regardless of their distance to the inversion breakpoints. Further, strong genetic differentiation detected along O<sub>3</sub> arrangements may extend to other inversions and nucleotide variation would be highly structured not only in *D. subobscura* but also in the genome of other species with rich chromosomal polymorphism.

With the help of molecular techniques and genome sequencing, methods have been developed to assemble highly accurate sequences near inversion breakpoints which were used to estimate the age and origin of polymorphic inversions in *D. melanogaster*. Interestingly, it was found that chromosome inversions are young and in most of cases they originated in Africa. It has also been suggested that chromosome inversions achieve a selective advantage through the maintenance of co-adapted polygenic complexes. Using molecular techniques, the breakpoints of six autosomal inversions were characterized in the *D. nasuta* species group which demonstrated that repeated sequences are associated with inversion breakpoints in four of these inversions suggesting that ectopic recombination is an important mechanism in generating inversions. The results of evolutionary genomic analysis extend evidence for the hypothesis that the inversions in *D. pseudoobscura* have emerged as suppressors of recombination to maintain the positive epistatic interaction among loci within the inversion that developed as the species adapted to a heterogeneous environment. It has been remarked by molecular evolutionary biologists that the precise selective mechanisms which maintain the inversions polymorphic in natural populations remain poorly understood while suggesting that recent advances in population genomics, modelling and functional genetics promise greatly to improve our understanding of this long-standing and fundamental problem in the near future.

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