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Cosmopolitan Inversions in a Cosmopolitan Species of *Drosophila* Commonly found in India

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Abstract: Structural and numerical aberrations are known to occur in different species of plants and animals including humans. Paracentic inversions in *Drosophila*, pericentric inversions in grasshoppers, trananslocations 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 levl 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 paracentic inversions have been studied in a lage number of species and about 100 species have been found to be chromosomally polymorphic. There are a large number of species which remain chromosomally monomorphic. Inversions polymorphism has been studied in detail in certain species with respect to the patterns, degrees and population dynamics of inversion polymorphis. In this article, briefly the patterns and population dynamics of inversion polymorphism have been described in *Drosophila ananassae,* a cosmopolitan and domestic species, commonly found in India and characterized by a number unusual genetic features. Although it contains a large number of paracentric inversions in its natural populations, three cosmopolitan inversions having monophyletic origin are distributed at global level.

Key Terms: Inversion polymorphism, *Drosophila*, cosmopolitan Inversions, Cosmopolitan Species, *Drosophila ananassae*, Indian Populations

I. INTRODUCTION

Structural and numerical abberations are widespread in plant and animal species including humans (Powell, 1997). There are well known cases of paracentic inversions in *Drosophila*, pericentric inversins in grasshoppers, translocations in *Oenothera lamarckiana* and polyploidy in a number plant species. The genus *Drosophiala* 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 levl 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 fron Hawaiian Islands which are extensively used in evolutionary studies (Krimbas & Powell, 1992). 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, 2015). 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

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within the paracentric inversion in a heterozygote produces acentric and dicentric fragments wich 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 donot decrease the fertility in males because crossing-over does not occur in males. Thus, paracentric inversions are cytologically neutral.The heterozygous inversions may strongly influemce 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. Since the flies with different inversion karyotypes are morphologically indistinguishable, many researchers including Theodosius Dobzhansky believed that chromosome inversions are adpatively neutral. However, it was proved to be wrong. Dobzhansky in 1947demontrated 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 nubmer 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, degrees and population dynamics of inversion polymorphism in natural and experimental populations: *D. pseudoobscura, D. willistoni* and related species*, D. robusta, D. subobscura, D. melanogaster, D. ananassae, D. pavani, D. bipectinata, D. nasuta, D. funebris* and Hawaiian Species. Different species show variation in the degree of inversion polymorphism and also frequencies of inversions show grographic, latitudinal, nort-south clines 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 (Krimbas & Powell, 1992) . With the help of inversion polymorphism, different phenomena such as genetic coadptation, balanced plymorphism and heterosis, linkage disequilibrium and epistasis have been studied in different species which are of considerable evolutionary significance (Singh, 2015). Chromosome inversions also persist in laboratory populations due to higher fitness of inversion heterozygotes although inversion frequencies may vary due random genetic drift involving bottleneck effects and founder principle. Singh (2001) compared the pattern of inversion polymorphism in three different species: *D. melanogaster, D. ananassae* and *D. bipectinata* which belong to the *melanogaster* 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 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 iniated 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 re-established rapidly after a new continent is colonized (Hoofman et al. 2004). 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. 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 polymorpohisms provide adapaptive advantages to their carriers in relation to diverse factors such as niche expoitation 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. In 1950's it was demonstrated by Dobzhansky and his coworkers (Dobzhansky et al., 1950; Da Cunha & Dobzhansky, 1954) that chromosomal polymorphism due to paracentric inversions in *Drosophila* is a device to cope with the diversity of environments which is known as ecological niche hypothesis. Further, there is evidence for seasonal variations, geographic differentiation, altitudinal variations, latitudinal variations, north-south gradients and rural-urban differentiation in inversion frequencies in different species (Singh, 2019). Inversion heterozygotes show superiority over corresponding homozygotes which is known as heterosis leading to balanced polymorphism which is brokendown in interracial crosses in certain species extending evidence for genetic coadaptation (Singh, 2018). In this article, a brief account is given about the inversion polymorphism in *D. ananassae* which is a cosmopolitan and domestic species commonly occurring in India endowed with a number of unusual genetic features such as presence of spontaneous male recombination which is meiotic in origin, high mutability, absence of genetic coadaptation, occurrence of spontaneous genetic mosaic, Y-4 linkage of nucleolus organizer, variation in resistance to different kinds of stress, parthenogenesis, extra chromosomal inheritance and presence of chiasmata during meiosis in males (Singh, 2000, 2020) .

II.COSMOPOLITAN INVERSIONS IN *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, 1998). 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 are called as cosmopolitan inversions (AL in 2L, DE in 3L and ET in 3R) which is based on monophyletic origin of inversins (Singh, 1970). An inversion within the AL inversion was detected (Singh, 1983, Figure 2). Hundred years of research on *Drosophila ananassae* has revealed a number of unusual features of this species (Singh, 2024).

Singh and his students have studied inversion polymorphism in Indian populations of *D. ananassae* and the results have clearly demonstrated that there is a geogrphic differentiation of inversion pilymorphism in Indian natural populations. The results, on the whole, suggested that the 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 a population sub-structuring associated with inversions based on strong genetic differention and minimal gene flow between populations. There is a genetic similarity between natural populations of *D. ananassae* from Kerala and Andaman and Nicobar Islands(Singh, 2015, 2019). Inversion polymorphism in *D. ananassae* is balanced and often persists in laboratory populations due to adaptrive superiority of inversion heterozygotes ie heterosis. When the laboratory populations are established from the flies collected from natural populatins, inversion frequencises often fluctuate in laboratory populations due to the action of random genetic drift. *D. ananassae* is an exception to the genetic coadaptation concept of Dobzhansky who suggested that gene complexes are mutually adjusted or coadapted in natural polulations of *Drosophila* which causes superiority of imversion heterzygotes which is brokendown 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, 2018). Table 1 shows the geographic didtribution of cosmopolitan inversion at global levl. Loation of the three cosmopolitan inversions in different chromosomes are shown in Figure 1.

Table 1. Geographical distribution of three cosmopolitan inversions in *D. ananassae*.

Area	Sub-terminal	Terminal	Basal	Source
Alabama	+	+	+	Kaufmann,1936b
Texas	+	-	+	Shirai & Moriwaki 1952
Hawaii	+	+	+	Shirai & Moriwaki 1952
Majuro	+	+	+	Seecof,1957
Cuba	+	+	+	Futch,1966
Mexico	+	+	+	Shirai & Moriwaki 1952; Futch,1966
Brazil	+	+	+	Dobzhansky & Dreyfus,1943; Shirai & Moriwaki 1952; Freire-Maia,1955

China	+	+	+	Kikkawa,1938
Formosa (Taiwan)	+	+	+	Kaufmann,1936b; Kikkawa,1938
Japan	+	+	+	Kaufmann,1936b; Kikkawa,1938
India	+	+	+	Ray-Chaudhuri & Jha,1966; Sajjan & Krishnamurthy,1970; Reddy& Krishnamurthy,1972a,b; Singh, B.N.,2001; Present study
Africa	+	+	+	Shirai & Moriwaki 1952
Micronesia (Caroline Island, Marshal Island, Mariana Island)	+	+	+	Seecof (Stone et al.1957); Futch, 1966
Mauritius	+	+	+	*
Sri Lanka	+	+	+	*
Myanmer	+	+	+	*
Thiland	+	+	+	*
Malaysia	+	+	+	Singh,1983a,c *
Borneo	+	+	+	Singh,1983c*
Philippines	+	+	+	*
Singapore	+	+	+	*

*For references see Tobari (1993) + indicates presence of inversion, - indicates absence of inversion (Singh & Singh, 2007).

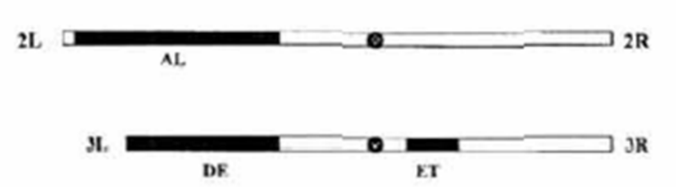

Figure 1. Three cosmopolitan inversions in *D. ananassae:* AL in 2L, DE in 3L and ET in 3R.

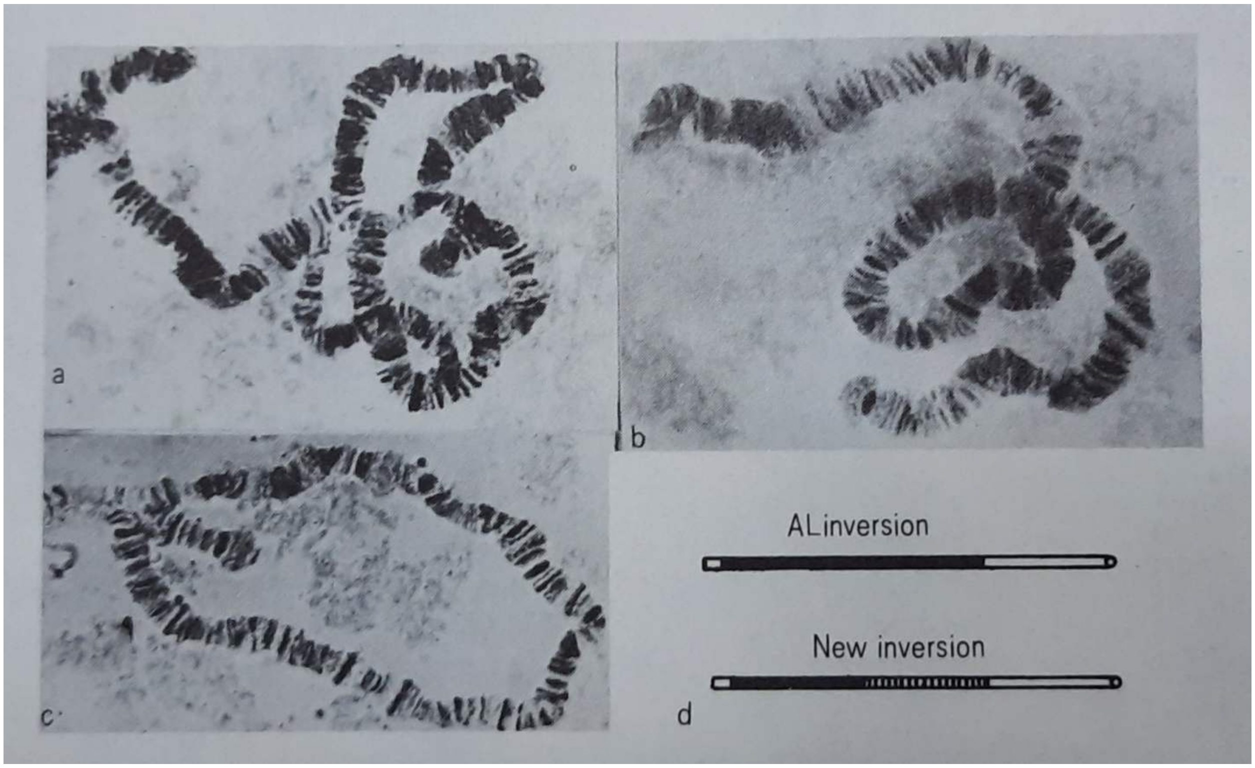

Figure 2. Photomicrographs of 2L of *D. ananassae* from larvae heterozygous for inversions and diagram of 2L showing location of inversions. (a) pairing between ST and AL^{in} chromosomes. (b) pairing between AL and AL^{in} chromosomes. and (c) pairing between ST and AL chromosomes. (d) diagram of 2L showing location of inversions. Circle indicates basal end of 2L (Singh, 1983).

In Figure 2, the occurrence of a new inversion within the Alpha inversion is shown. Three types of chromosome configuration are found:. (a) pairing between ST and AL^{in} chromosomes. (b) pairing between AL and AL^{in} chromosomes. and (c) pairing between ST and AL chromosomes. (d) diagram of 2L showing location of inversions. The three cosmopolitan inversions are paracentric: AL (subterminal-alpha in 2L), DE (terminal-delta in 3L) and ET (basal-eta in 3R). Three cosmopolitan inversions in *D. ananassae* have been considered as monophyletic in origin and migrated to different areas due to human activities because it is a domestic species occurring in human habitations. All the domestic species are characterized by a high degree of interpopulation migration because of their close association with man.

CONCLUDING REMARK

The account of chromosomal variability resulting from paracentric inversions in different species of *Drosophila* clearly shows that the pattern, degree and population dynamics of inversion polymorphism show considerable differences in different species. There are species which are chromosomally monomorphic and there are species which are highly polymorphic chromosomally. In *D. melanogaster*, more than 300 paracentric inversions have been reported. 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 polymorphis 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.

Drosophila ananassae is a genetically unique species as it possesses a number of unique genetic features and it stands distinct in the whole of genus *Drosophila.* The most important unique feature of this species is presence of spontaneous male recombination in appreciable frequency which is meiotic in origin supported by the occurrence of chiasmata during meiosis in males. It is also unique in respect of chromosomal polymorphism. In total, there are 78 paracentric inversions, 21 pericentric inversions and 48 translocations reported so far in this species (Singh & Singh, 2007). It is really remarkable feature of this species that only three paracentric inversions could become widespread and showing distribution at global level. Although the level of migration has not been studied in *D. ananassae* populations, Futch (1966) has suggested that the populations of *D. ananassae* isolated by mountains and oceans may experience gene flow because the flies are transported through the agency of human travel. It was also pointed out by Dobzhansky and Dreyfus (1943) that this species has depended on man for its present widespread distribution and coextensive distribution of three cosmopolitan inversions has been suggested as an evidence for this. In spite of this, *D. ananassae* populations show evolutionary divergence at the level of three cosmopolitan inversions which must have developed in response to ecological conditions existing in different geographic localities (Singh & Singh, 2008; Singh, 2015).

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