Patterns of inversion polymorphism in three species of the *Drosophila melanogaster* species group

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In *Drosophila*, chromosomal polymorphism due to paracentric inversions is very common and constitutes an adaptive character. The degree of chromosomal variability varies in different species and also in different populations of the same species. Chromosomal polymorphism in Indian natural populations of three species, *D. melanogaster*, *D. ananassae* and *D. bippinata* which belong to the *melanogaster* species group has been studied and the quantitative data on frequency of inversions have been reported. Behaviour of chromosome inversions has also been studied in laboratory conditions. The present review summarises the work done on inversion polymorphism in Indian populations of three species which clearly demonstrates that these three species vary in their patterns of inversion polymorphism and have evolved different mechanisms for adjustment to their environments although they belong to the same species group.

The first inversions were detected in *Drosophila melanogaster* through the suppression of crossing-over in inversion heterozygotes. Since flies with different karyotypes produced by inversions are externally indistinguishable, many investigators including Dobzhansky believed inversion karyotypes to be adaptively neutral traits. This proved to be wrong. A large number of investigations have been carried out on inversion polymorphism in numerous *Drosophila* species which have demonstrated that chromosomal polymorphism due to paracentric inversions is very common in the genus *Drosophila*. It has also been demonstrated that inversion polymorphism in *Drosophila* is subject to natural selection and is an adaptive trait. The species which have been studied in detail are: *D. pseudoobscura*, *D. willistoni*, *D. persimilis*, *D. robusta*, *D. subobscura*, *D. melanogaster*, *D. ananassae*, *D. funebris*, *D. pavani*, *D. rubida*, *D. nasuta*, *D. flavopilosa* and others. The degree of inversion polymorphism varies in different species and also in different populations of the same species. The most convincing evidence for the selective control of inversion frequencies comes from observations on inversion frequencies in geographic populations of different *Drosophila* species. The inversion frequencies showed seasonal, geographic, latitudinal and altitudinal variations. In certain species, north south clines in inversion frequencies (increase towards equator) have been reported. Dobzhansky and coworkers found a good correspondence between the mean number of heterozygous inversions and an index expressing environmental heterogeneity in natural populations of *D. willistoni*. Marginal populations showed a lower degree of chromosomal polymorphism than the populations at the centre of geographical distribution. This led Dobzhansky and coworkers to suggest that chromosomal polymorphism is a device to cope with the diversity of environments. This hypothesis has been supported by observations in different species. The same pattern has been found by Carson in *D. robusta*. Carson suggested that the amount of recombination is an essential adaptive factor and that the low level of polymorphism in marginal population where homoselection predominates, gives a high potential for free recombination from which adaptive novelties can be synthesized. In geographically central populations, there is a high level of inversion polymorphism and heteroselection predominates. The marginal populations have more adaptability whereas the central ones have more adaptedness. In certain species, frequencies of inversions are higher in urban populations than in rural ones. It has been suggested that high degree of urbanization probably leads to increase in the number of ecological niches and consequently the high chromosomal variability. Studies on inversion polymorphism in natural populations of *D. pseudoobscura* have shown annual cyclic changes in inversion frequencies. In *D. pseudoobscura* and other species, inversion polymorphism has also been studied in experimental populations maintained under laboratory conditions. Persistence of inversion polymorphism in these populations could be explained by an advantage of...
inversion heterozygotes over corresponding homozygotes. Thus inversion polymorphism is adaptive and balanced due to higher Darwinian fitness of inversion heterozygotes. Chromosomal polymorphism has also been studied in certain Drosophila species found in India. These species are: D. ananassae, D. melanogaster, D. bipectinata and D. nasuta. The first three species belong to the melanogaster species group of the Sophophora subgenus. However, D. nasuta belongs to the immigrans species group of the Drosophila subgenus. Although inversion polymorphism has also been studied in Indian populations of D. nasuta, the present review summarises the work done on inversion polymorphism in Indian populations of D. melanogaster, D. ananassae, and D. bipectinata to compare the pattern of inversion polymorphism in the species of the same species group.

Pattern of inversion polymorphism in D. ananassae

Drosophila ananassae, although a cosmopolitan and domestic species, is largely circumtropical in distribution. It belongs to the ananassae species complex of the ananassae subgroup of the melanogaster group. Kikkawa selected D. ananassae as material for genetic studies because of its excellent viability, high mutability and certain peculiarities in its cytological and genetic behaviour. It has become clear that it is a unique species among the various Drosophila species thus far investigated. D. ananassae has been used for genetic studies by Japanese, Indian, North American and French workers (for references see Moriwaki and Tobari; Singh; Tobari).

D. ananassae occupies a unique status among the Drosophila species due to certain peculiarities in its genetic behaviour. One example is an appreciable level of spontaneous meiotic male recombination. Other unusual features are varied chromosomal polymorphism, high mutability, Y-4 linkage of nucleolus organizer, segregation distortion, parthenogenesis, extrachromosomal inheritance and lack of coadaptation (for references see the review by Singh). A spontaneous bilateral genetic mosaic, which was characterized by three mutant characters (cu, e, se) on the left side and all normal characters on the right side, was detected while scoring the progeny of a test cross between heterozygous males and mutant females. Its probable origin is attributed to mitotic recombination in the zygote which was genotypically heterozygous.

A number of investigations have been carried out on chromosomal polymorphisms in D. ananassae. A total of 70 paracentric inversions have been described in D. ananassae. One of the most unusual features of natural populations of D. ananassae is the presence of pericentric inversions and translocations. In other species of Drosophila pericentric inversions and translocations are rare. Contrary to this, 17 pericentric inversions and 13 translocations have been detected in natural populations of D. ananassae. One pericentric inversion and 4 translocations were detected in laboratory stocks of D. ananassae. Thus D. ananassae presents a high degree of chromosomal polymorphism. The occurrence of pericentric inversions and translocations which are rare in other species of Drosophila reflects unusual mutational properties of D. ananassae. Freire-Maia suggested that it has developed some special mechanism through which it can retain chromosome rearrangements which are disadvantageous. Although 70 paracentric inversions have been detected so far in this species, only three paracentric inversions which have been called cosmopolitan inversions by Futch have become coextensive with the species. Most of the inversions have localised distribution and detected in a few individuals. This is a feature of the pattern of chromosomal polymorphism in D. ananassae.

Three paracentric inversions which are of common occurrence in natural populations have been called cosmopolitan inversions. These three inversions were originally described by Kaufman from Alabama and Japanese populations and designated by him as subterminal (2L), terminal (3L) and basal (3R). The same inversions were given different names by other investigators. These correspond respectively to the CIL, CIIIL and CIIIR inversions of Kikkawa, 2LA, 3LA and 3RA inversions of Futch, the alpha (AL), delta (DE) and eta (ET) inversions of Ray-Chaudhuri and Jha and the In (2L) A, In (3L) A and In(3R) A inversions of Hinton and Downs. The present author has adopted the terminology of Ray-Chaudhuri and Jha. These three cosmopolitan inversions (Fig. 1A) have been found in most geographical populations of D. ananassae: Africa, China, Hawaii, Cuba, Mexico, Japan, Formosa, Panama, Costa Rica, Porto Rico, Borneo, Malaysia, Alabama, Brazil, Texas, Majuro, India including Andaman and Nicobar Islands. Tomimura and Tobari (Unpublished, cited in Tobari) analysed isofemale lines of D. ananassae established from wild
Singh52,57-61 studied inversion polymorphism in natural populations of D. ananassae from 29 geographical localities. The results show that the frequencies of different gene arrangements vary significantly among the populations analysed. The data reported by Singh52,57-61 are presented in Table 1. Further, the level of heterozygosity (measured in terms of mean number of heterozygous inversions per individual) also varies among the populations. The degree of chromosomal variability is low in rural populations than in the urban populations57. Populations from South India particularly Tamil Nadu, Kerala and Andaman and Nicobar Islands situated near the equator maintain inversions in higher frequency than those inhabiting different localities in Uttar Pradesh and other northern states. With some exceptions in north, results in general indicate the existence of north-southcline in inversion frequencies.

The degree of genetic divergence among different populations has been quantified by calculating genetic identity (I) and genetic distance (D) on the basis of differences in chromosomal arrangement frequencies. In general, the populations from the south show more differentiation than those from the north. There is no strong positive relation between genetic differentiation and geographic distance although many pairwise comparisons show that populations separated by small geographic distance show low levels of genetic difference (high genetic identity). There is strong evidence from studies on inversion polymorphism by the present author that Indian populations of D. ananassae have undergone a considerable degree of genetic divergence. The south experiences a tropical and humid climate. Locations near the sea coast differ from those away from it. Rural populations of Jamsoti and Lowari situated in the vicinity of Chakia forest have very high frequencies of standard gene orders in all the chromosomes, the level of inversion heterozygosity remaining very low57. Thus there is genetic differentiation of inversion polymorphism in D. ananassae which suggests that chromosomal polymorphism may be adaptively important in a widespread domestic species and populations may undergo divergence as a consequence of their adaptation to varying environments.

In a number of species, it has been demonstrated that inversion polymorphism is balanced owing to higher Darwinian fitness of inversion heterozygotes. The hypothesis of balanced polymorphism has also
been verified in *D. ananassae* by the results of population cage experiments with ST and inverted gene orders in 2L and 3L. The differential mortality during larval period in a highly crowded condition of population cages favours the survival of inversion heterozygotes which was shown while comparing egg sample and adult sample.

Chromosomal polymorphism due to cosmopolitan inversions often persists in laboratory stocks established from flies collected from nature. Some strains maintained in the laboratory for more than a hundred generations have been found to contain these inversions. This demonstrates that heterotic buffering is associated with these inversions. However, the degree of heterosis may vary depending on the allelic contents of the chromosomal variants. Inversion frequency may also change due to random genetic drift in small populations.

Singh conducted interracial hybridization experiments by employing homozygous as well as chromosomally polymorphic strains of *D. ananassae* originating from different localities. It has been found that inversion heterozygotes formed by chromosomes of different geographic origins exhibit heterosis which persists in inter racial crosses involving polymorphic strains. The chief conclusion from these results is that there is lack of evidence for coadaptation in geographic populations of *D. ananassae*. This situation apparently conflicts with what has been found in other species by Dobzhansky and others (for references see Singh). Singh suggested that heterosis associated with cosmopolitan inversions in *D. ananassae* appears to be simple luxuriance rather than population heterosis (coadaptation) and thus luxuriance can function in the adjustment of organisms to their environments.

There are several studies on intraspecific and interchromosomal associations in natural populations and laboratory stocks of *D. ananassae*. Various combinations of unlinked inversions occurring in

<table>
<thead>
<tr>
<th>Population</th>
<th>Total number of chromosomes examined</th>
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<th>DE</th>
<th>ET</th>
<th>Mean no. of heterozygous inversions per individual</th>
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</thead>
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<td>28.89</td>
<td>32.22</td>
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<td>3.00 (0.00)</td>
<td>0.64 (0.65)</td>
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<td>21.67</td>
<td>0.80</td>
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<td>15.00</td>
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<td>17.00</td>
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<td>0.94</td>
</tr>
<tr>
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<td>35.58 (50.89)</td>
<td>37.50 (2.68)</td>
<td>1.23 (0.97)</td>
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<td>0.78 (0.93)</td>
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<td>64.29 (45.50)</td>
<td>16.43 (71.50)</td>
<td>1.04 (1.36)</td>
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<td>86.00 (69.50)</td>
<td>35.00 (0.00)</td>
<td>1.12 (0.62)</td>
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<td>0.80 (0.71)</td>
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<td>85.2</td>
<td>32.86</td>
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<td>1.60</td>
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<tr>
<td>Madurai</td>
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<td>53.16 (55.50)</td>
<td>93.67 (100.00)</td>
<td>32.91 (60.50)</td>
<td>0.94 (0.98)</td>
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<td>84.29</td>
<td>82.26</td>
<td>14.29</td>
<td>0.89</td>
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<td>Kamorta</td>
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<td>65.40</td>
<td>57.70</td>
<td>38.50</td>
<td>1.38</td>
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<tr>
<td>Kanniyakumari</td>
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<td>89.00</td>
<td>74.00</td>
<td>2.00</td>
<td>0.62</td>
</tr>
</tbody>
</table>

Values in parentheses represent the frequency of inversions and mean number of heterozygous inversions per individual in the corresponding laboratory populations. The populations for which laboratory data are not given, were not maintained in the laboratory.
random association indicate no interchromosomal interactions in *D. ananassae*77-79. Two linked inversions of the third chromosome which strongly suppress recombination between them when heterozygous often show non-random associations in laboratory stocks85-86. This is likely to be due to epistatic interaction and suppression of crossing-over. It has also been suggested that linkage disequilibrium between inversions in certain isofemale strains may occur due to random genetic drift. The tight linkage between the two inversions enhances the chance of drift in isofemale strains.

**Pattern of inversion polymorphism in *D. bipectinata***

*D. bipectinata* has wide geographical distribution ranging from India through southeast Asia and New Guinea to Fiji and Samoa in the Pacific. This species has genetic potentiality to become cosmopolitan because of high degree of genetic similarity (0.98) between Samoan and Palawan populations. Panigrahy prepared the detailed photomap of polytene chromosomes of *D. bipectinata* showing standard gene sequence. Bock detected altogether six paracentric inversions from three laboratory stocks of *D. bipectinata* established from flies collected from Borneo, Philippines and Thailand. Chromosomal polymorphism in Indian populations of *D. bipectinata* was studied for the first time by Gupta and Panigrah and they detected nine autosomal paracentric inversions. Of the nine inversions, two were described earlier by Bock, Das and Singh detected three inversions from laboratory strains of *D. bipectinata* and the same three inversions were detected from Indian natural populations of *D. bipectinata* by Banerjee and Singh. These three inversions were described earlier by Gupta and Panigrah. Thus the total number of inversions known so far in *D. bipectinata* are 13 and all are paracentric and autosomal inversions. Thus *D. bipectinata* presents low degree of chromosomal polymorphism. Bock detected all the six inversions in heterozygous condition from laboratory stocks initiated from flies collected from Borneo, Philippines and Thailand. Gupta and Panigrah presented quantitative data on the frequencies of nine heterozygous inversions in nine Indian populations of *D. bipectinata*. All the nine heterozygous inversions were found in low frequency. Maximum frequency of an inversion was 26.47%. The nine inversions from Indian populations were never present together in a single population. Some of them were confined to particular geographic localities only. Populations analysed showed qualitative and quantitative differentiation with respect to these inversions. Only three inversions—ln(D)2L, ln(C)2R and ln(H)3L were detected in laboratory stocks as well as in natural populations of *D. bipectinata* and quantitative data on the frequencies of different gene arrangements, inversion heterozygotes and level of heterozygosity have been reported in laboratory and natural populations. Location of these three inversions in different chromosomes are depicted in Figure 1B.

<table>
<thead>
<tr>
<th>Population</th>
<th>Total number of chromosomes examined</th>
<th>2L(D)</th>
<th>2R(C)</th>
<th>Mean no. of heterozygous inversions per individual</th>
</tr>
</thead>
<tbody>
<tr>
<td>Rajghat</td>
<td>130</td>
<td>0.00(0.00)</td>
<td>10.00(24.50)</td>
<td>0.33(0.56)</td>
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<tr>
<td>Sarnath</td>
<td>90</td>
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<td>0.00(0.00)</td>
<td>0.15(0.48)</td>
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<tr>
<td>Mysore</td>
<td>100</td>
<td>0.00(0.00)</td>
<td>12.00(33.00)</td>
<td>0.20(0.48)</td>
</tr>
<tr>
<td>Panagarh</td>
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<td>7.40(20.00)</td>
<td>6.97(22.50)</td>
<td>0.28(0.59)</td>
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<tr>
<td>Allahabad</td>
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<td>10.34(29.50)</td>
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<td>Arumanai</td>
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<td>6.42(23.50)</td>
<td>8.57(24.00)</td>
<td>0.30(0.61)</td>
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</table>

Values in parentheses represent the frequency of inversions and mean number of heterozygous inversions per individual in the corresponding laboratory populations. The populations for which laboratory data are not given, were not maintained in the laboratory.
distinguished. As a consequence of this, only frequency of inversion heterozygotes is given for natural populations and laboratory stocks91-95. Out of 13 inversions reported so far in D. bipectinata, only these three inversions are commonly distributed in natural populations. These inversions are also present in laboratory stocks and there is significant excess of inversion heterozygotes which provides evidence that heterosis is associated with these three inversions91,94,95. Significant non-random associations between inversions (linked inversions as well as unlinked inversions) indicate epistatic interaction between inversions in D. bipectinata92,96. Banerjee and Singh92 analysed 7 natural populations of D. bipectinata and detected these three common inversions of which In(C)2R was most frequent. Results have shown a low level of inversion heterozygosity and inversion frequency in these populations. Further there is no evidence of genetic differentiation between populations at the level of inversion polymorphism. These findings provide evidence for rigid chromosomal polymorphism in D. bipectinata92. Behaviour of three paracentric inversions in populations of D. bipectinata transferred to laboratory conditions was studied by Singh and Banerjee95. It has been found that all the populations remained polymorphic and there was considerable increase in the frequency of inverted gene orders and the level of inversion heterozygosity in laboratory populations when compared with corresponding natural populations. Data on inversion frequency in natural and laboratory populations of D. bipectinata reported by Banerjee and Singh92 and Singh and Banerjee95 are presented in Table 2. It was suggested that inversion heterozygotes in D. bipectinata have selective advantage under stringent competition in laboratory conditions. Singh and Banerjee97 tested the effect of interracial hybridization on chromosomal variability among four polymorphic stocks of D. bipectinata by crossing these stocks with each other.

Table 3 — Frequencies (in percent) of four common cosmopolitan inversions in Indian natural populations of D. melanogaster

<table>
<thead>
<tr>
<th>Population</th>
<th>Total number of chromosomes examined</th>
<th>2 Lt</th>
<th>2 RNS</th>
<th>3 LP</th>
<th>3 RP</th>
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<tr>
<td>Jammu</td>
<td>122</td>
<td>18.85(0.49)</td>
<td>12.30(0.49)</td>
<td>15.57(0.98)</td>
<td>22.95(0.98)</td>
<td>1.49(0.07)</td>
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<td>3.45(1.35)</td>
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<td>5.17(0)</td>
<td>0</td>
<td>0.59(0.05)</td>
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<tr>
<td>Guwahati</td>
<td>200</td>
<td>10.00(0.99)</td>
<td>9.50(0.50)</td>
<td>7.50(0)</td>
<td>16.00(0.99)</td>
<td>1.04(0.07)</td>
</tr>
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<td>Patna</td>
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<td>0</td>
<td>11.86(0.50)</td>
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<td>3.33(0.50)</td>
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<td>0.67(0)</td>
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<td>18.52(0.46)</td>
<td>12.04(0.46)</td>
<td>26.85(0.46)</td>
<td>1.81(0.08)</td>
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<td>26.83(0.49)</td>
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<td>15.32(0.50)</td>
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<td>22.81(1.00)</td>
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<td>11.82(0.50)</td>
<td>24.54(1.00)</td>
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</table>

Values in parentheses represent the frequency of inversions and mean number of heterozygous inversions per individual in the corresponding laboratory populations. The populations for which laboratory data are not given, were not maintained in the laboratory.
All hybrid and parental lines remained polymorphic after ten generations and there was variation in the frequency of inversion heterozygotes among crosses involving different inversions. There was a decline in the frequency of inversion heterozygotes in certain hybrid populations of mixed geographical origin and this was due to breakdown of coadapted polygenic complexes by recombination.

**Pattern of inversion polymorphism in D. melanogaster**

*D. melanogaster* is a cosmopolitan and domestic species. It is most widespread and common *Drosophila* species. It presents a high degree of inversion polymorphism and more than 300 inversions are known in natural populations of *D. melanogaster*. On the basis of distribution and abundance, paracentric inversions in *D. melanogaster* have been classified into four types: common cosmopolitan, rare cosmopolitan, recurrent endemic and unique endemic. Quantitative data on the frequency of cosmopolitan inversions have been reported from various regions of the world. Geographic variations and latitudinal and seasonal clines have been reported in populations from north America, Japan and Australia which provide evidence that inversion polymorphism in *D. melanogaster* is subject to natural selection. However, in certain studies a north-south gradient in inversion frequencies is not evident. Further, the relationship between inversion frequency and latitude may vary between different inversions in the same region and also between different regions of the same inversions.

Data on intra- and interchromosomal associations in natural populations have been reported by numerous investigations from several parts of the world. In certain populations, interactions between linked inversions as well as between unlinked inversions is evident. When *D. melanogaster* populations are maintained in the laboratory, a decline in frequency of polymorphic inversions or total elimination of inversions was observed. A significant correlation between wing length and inversion polymorphism has been observed in *D. melanogaster* populations from Spain. Garcia-Vazquez et al. reported a significant correlation between chromosome inversion and frequency of extra dorsocentral and scutellar bristles in Spanish populations of *D. melanogaster*.

Inversion polymorphism in Indian populations of *D. melanogaster* has also been studied and results pertaining to the degree of polymorphism, geographic differentiation, north south clines, epistatic interaction, behaviour of inversions in laboratory conditions and association between inversion polymorphism and extra dorsocentral and scutellar bristles have been reported. A total of 28 natural populations and several laboratory stocks were analyzed to study inversion polymorphism. Chromosomal analysis of these populations and laboratory stocks of *D. melanogaster* revealed the presence of 42 paracentric inversions, 3 in the X chromosome, 13 in 2L, 11 in 2R, 7 in 3L, and 8 in 3R. All the four types of inversions: common cosmopolitan, rare cosmopolitan, recurrent endemic and unique endemic were found. One pair of overlapping inversions (3R) and one pair of included inversions (2L) were also detected. These observations provide evidence for high degree of inversion polymorphism in Indian populations of *D. melanogaster*. Data on the frequencies of inversions in 28 Indian populations of *D. melanogaster* have been reported. The data on the frequencies of 4 common cosmopolitan inversions in these populations reported by Singh and Das and Das and Singh are presented in Table 3. Fig. 1C depicts the location of 4 common cosmopolitan inversions in different chromosomes of *D. melanogaster*. It is evident from the results that: (i) there is a geographic differentiation among Indian natural populations, (ii) the urban population is different from rural ones, (iii) there is existence of north-south inversion clines and significant negative correlation between each of the four common cosmopolitan inversions and latitude, (iv) level of inversion heterozygosity is higher in populations from the south as compared to those from north and (v) Indian populations have undergone considerable degree of genetic divergence at the level of inversion polymorphism.

In order to study the behaviour of chromosome inversions under laboratory conditions, a large number of laboratory populations (both mass cultures and isofemale lines) established from flies collected from natural populations were maintained in food bottles for several generations. Chromosomal analysis of the laboratory populations revealed that there was a decline in the frequency of all the polymorphic inversions detected in natural populations associated with decreasing heterozygosity (see Table 3). In some mass cultures, some of the inversions were completely lost. The degree of genetic divergence between initial and final populations was quantified by estimating genetic
distance (D) which was found to be higher in south Indian populations than in those from north which was likely to be due to high frequency of inversions in initial populations from south. Several inversions were found to persist at considerable frequency in several isofemale lines. Singh and Das\textsuperscript{27} discussed these results in the light of genetic drift and founder principle\textsuperscript{23} causing changes of inversion polymorphism in laboratory populations of \textit{D. melanogaster}.

The data on intra- and interchromosomal associations in natural and laboratory populations of \textit{D. melanogaster} have been reported\textsuperscript{125,127,129}. It has been observed that there is lack of evidence for intra- and interchromosomal interactions in several natural populations. However, in certain south Indian populations, highly significant non-random associations between unlinked inversions of second and third chromosomes were found. There was significant excess of individuals which were either doubly homozygous for ST at both unlinked loci or doubly heterozygous indicating epistatic interaction between unlinked inversions in south Indian populations of \textit{D. melanogaster}\textsuperscript{125}. Interestingly, eight inversion pairs (linked as well as unlinked) showed strong non-random association in certain isofemale lines indicating epistatic interaction between linked inversions as well as between unlinked inversions\textsuperscript{127}. An association of inversion polymorphism and individuals with extra dorsocentral and scutellar bristles has been observed in south Indian populations. The frequency of In(3R)C inversion was found to increase with the increase in the number of individuals of extra bristle phenotypes. Further, In(3R)C inversion showed a unique effect in maintaining an intermediate number of individuals with extra bristles. Thus there is a positive correlation between In(3R)C inversion and extra bristles which demonstrates that polygenic loci determining extra bristles within In(3R)C are widespread in Indian populations of \textit{D. melanogaster}\textsuperscript{125}. The results of selection experiment\textsuperscript{132} also showed an identical pattern of behaviour in the frequency of In(3R)C inversion and extra bristle phenotypes during the course of selection which was discussed in terms of balancing selection.

Conclusions

The three species which have been compared with respect to their patterns of inversion polymorphism, belong to the same species group of the subgenus \textit{Sophophora}. It is generally considered that the \textit{melanogaster} species group originated in south east Asia\textsuperscript{18}. From this region the group has dispersed and shows secondary radiation in the adjacent biogeographic regions\textsuperscript{24}. \textit{D. melanogaster} belongs to the \textit{melanogaster} subgroup and the remaining two species to the \textit{ananassae} subgroup. \textit{D. melanogaster} is a cosmopolitan species predominantly found in domestic habitats. \textit{D. ananassae} is also cosmopolitan and domestic species but mainly circumtropical in distribution. \textit{D. bipectinata} is semiwild species and less widespread than the other two species but it has genetic potentiality to become cosmopolitan. The degree of inversion polymorphism is highest in \textit{D. melanogaster} and lowest in \textit{D. bipectinata} but \textit{D. ananassae} is intermediate between the two species. Thus there is a positive correlation between the level of chromosomal polymorphism and the range of geographical distribution when the three species are compared and this relationship supports the hypothesis of Dobzhansky and coworkers that geographically widespread species are likely to be more versatile and therefore may be expected to be more polymorphic chromosomally.

From the results obtained on inversion polymorphism in Indian populations of these three species, it is evident that there is variation in the pattern of inversion polymorphism with particular reference to the degree of chromosomal variability in their natural populations, inversion frequency in natural populations, behaviour of inversions under laboratory conditions, epistatic interaction between linked inversions as well as between unlinked inversions, inversion and crossing-over, heterosis and genetic coadaptation. Thus it is concluded that \textit{D. melanogaster}, \textit{D. ananassae} and \textit{D. bipectinata} vary in their patterns of inversion polymorphism and have evolved different mechanisms for adjustment to their environments although they belong to the same species group of the subgenus \textit{Sophophora}.

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