

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. bipectinata* 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 heterozygotes¹. 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*²⁻⁸. 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 reported⁷. Dobzhansky and coworkers^{9,10} 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 Donzhansky 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 Carson¹¹ in *D. robusta*. Carson¹¹⁻¹³ 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 adaptedness¹³. In certain species, frequencies of inversions are higher in urban populations than in rural ones¹⁴. 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 frequencies¹⁵. 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 heterozygotes². 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*^{16,17}, 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* group¹⁸. Kikkawa¹⁹ 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 Tobari²⁰; Singh²¹⁻²³; Tobari²⁴).

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 recombination²⁵⁻²⁸. 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 Singh²¹). 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 heterozygous²⁹.

A number of investigations have been carried out on chromosomal polymorphisms in *D. ananassae*^{19,24,30-50}. A total of 70 paracentric inversions have been described in *D. ananassae*^{24,49}. 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*²⁴. One pericentric inversion and 4 translocations were detected in laboratory stocks of *D. ananassae*⁴⁶. 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-Maia³⁵ 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 Futch³⁷ 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 as cosmopolitan inversions³⁷. These three inversions were originally described by Kaufman³⁰ 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 CIIL, CIIL and CIIR inversions of Kikkawa¹⁹, 2LA, 3LA and 3RA inversions of Futch³⁷, the alpha (AL), delta (DE) and eta (ET) inversions of Ray-Chaudhuri and Jha³⁸ and the In (2L) A, In (3L) A and In(3R) A inversions of Hinton and Downs⁴⁶. The present author has adopted the terminology of Ray-Chaudhuri and Jha³⁸. 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^{19,22,30-32,37,38,51}. Tomimura and Tobari (Unpublished, cited in Tobari²⁴) analysed isofemale lines of *D. ananassae* established from wild

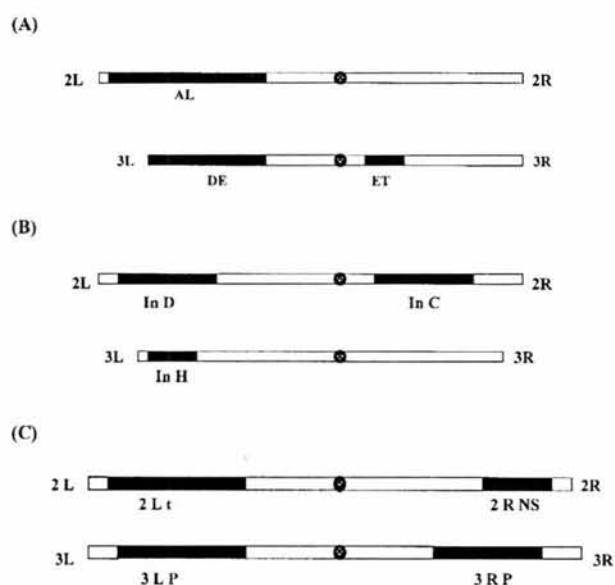


Fig. 1—(A) Location of three cosmopolitan inversions (AL, DE and ET) in different chromosomes of *D. ananassae*. (B) Location of three common inversions (In D, In C and In H) in different chromosomes of *D. bipectinata*. (C) Location of four common cosmopolitan inversions (2Lt, 2RNS, 3LP and 3RP) in different chromosomes of *D. melanogaster*.

caught females derived from 39 geographical localities ranging from Africa, India, Southeast Asia, Micronesia, Melanesia and Polynesia to Brazil. A total of 52 paracentric inversions were found and 32 of them were previously undescribed. The three cosmopolitan inversions were found in almost all the localities surveyed. These three inversions have been found in a large number of localities in India^{22,51-55}. Thus it is apparent that the three cosmopolitan inversions are of frequent occurrence in natural populations and have become coextensive with the species. The results have been considered from view point of monophyletic origin of these inversions, wherever the species flourishes in China, Japan, Hawaii, America and India, these three inversions are found^{37,51}. An inversion has more chance to spread and become established in the populations if it has selective advantage. It is possible that a chromosome inversion has a selective advantage primarily because it captures a highly heterotic combination of genes which buffer the organism¹². Therefore, Singh⁵⁶ suggested that the three cosmopolitan inversions in *D. ananassae* could spread and become established in most geographic populations because of heterotic combination of genes occurring within the inverted segments and that they are a part of the adaptive machinery in natural populations of this species.

Singh^{52,57-61} 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 Singh^{52,57-61} 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-south cline 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^{48,52,62,63}. 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 3L⁶⁴⁻⁶⁷. 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 sample⁶⁷.

Chromosomal polymorphism due to cosmopolitan inversions often persists in laboratory stocks established from flies collected from nature^{56,68,69}. 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^{47,68,70}. Inversion frequency may also change due to random genetic drift in small populations^{69,71}.

Singh⁷²⁻⁷⁵ 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 interracial 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 Singh⁷⁶). Singh⁷⁵ 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 intra- and interchromosomal associations in natural populations and laboratory stocks of *D. ananassae*. Various combinations of unlinked inversions occurring in

Table 1—Frequencies (in percent) of three cosmopolitan inversions in Indian natural populations of *D. ananassae*

Population	Total number of chromosomes examined	AL	DE	ET	Mean no. of heterozygous inversions per individual
Jammu	262	53.40	42.80	11.80	1.18
Agra	104	65.38(45.45)	50.96(81.41)	3.85 (0.00)	0.83(0.80)
Siliguri	56	89.29	35.71	19.64	1.04
Guwahati	90	82.22	28.89	32.22	1.22
Lucknow	24	58.33(56.00)	16.67(11.00)	4.17(1.50)	0.92(0.73)
Kanpur	78	62.82(55.00)	2.56(5.50)	20.51(9.50)	1.00(0.88)
Shillong	70	84.29	30.00	32.86	1.44
Ghazipur	100	23.00(42.16)	12.00(5.88)	3.00(0.00)	0.64(0.65)
Bhagalpur	130	80.00	30.77	20.77	1.22
Varanasi	200	25.00(26.00)	8.00(0.00)	5.50(0.00)	0.53(0.44)
Jamsoti	60	0.00	21.70	0.00	0.43
Lowari	42	0.00	21.40	4.80	0.52
Ukhara	30	56.70	40.00	26.70	1.26
Calcutta	240	89.17	15.00	21.67	0.80
Birlapur	200	75.00	17.00	15.00	0.94
Bhubaneswar	104	83.65(73.66)	35.58(50.89)	37.50(2.68)	1.33(0.97)
Puri	100	89.00(96.12)	36.00(50.00)	36.00(37.86)	1.14(1.04)
Mumbai	208	96.63(100.00)	16.83(35.00)	28.37(64.50)	0.78(0.93)
Hyderabad	140	77.14	45.00	15.00	1.06
Goa	140	87.14(61.00)	64.29(45.50)	16.43(71.50)	1.04(1.36)
Chennai	100	73.00(3.50)	86.00(69.50)	35.00(0.00)	1.12(0.62)
Port Blair	122	69.70	56.60	31.20	1.40
Trichur	204	53.43(60.50)	79.90(79.00)	3.43(0.00)	0.80(0.71)
Ernakulam	210	85.2	52.86	19.52	1.00
Madurai	158	53.16(55.50)	93.67(100.00)	32.91(60.50)	0.94(0.98)
Quilon	108	76.85	85.19	14.81	1.02
Thiruvananthapuram	140	84.29	82.26	14.29	0.89
Kamorta	26	65.40	57.70	38.50	1.38
Kanniya Kumari	100	89.00	74.00	2.00	0.62

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 stocks^{78,80-86}. 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 drift⁸⁵. 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 Pacific¹⁸. This species has genetic potentiality to become cosmopolitan because of high degree of genetic similarity (0.98) between Samoan and Palawan populations⁸⁷. Panigrahy⁸⁸ prepared the detailed photomap of polytene chromosomes of *D. bipectinata* showing standard gene sequence. Bock⁸⁹ 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 Panigrahy⁹⁰ and they detected nine autosomal paracentric inversions. Of the nine inversions, two were described earlier by Bock⁸⁹. Das and Singh⁹¹ 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 Singh⁹². These three inversions were described earlier by Gupta and Panigrahy⁹⁰. 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 polymorphism⁹³. Bock⁸⁹ detected all the six inversions in heterozygous condition from laboratory stocks initiated from flies collected from Borneo, Philippines and Thailand. Gupta and Panigrahy⁹⁰ 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 inversions⁹⁰. Only three inversions-In(D)2L, In(C)2R and In(H)3L were detected in laboratory stocks as well as in natural populations of *D. bipectinata*⁹¹⁻⁹⁵ 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. Geographic distribution of these three common inversions: In(D)2L- Sarnath, Varanasi, Chakia forest, Uttar Pradesh; Panagarh, West Bengal; Arumanai, Kanniya Kumari, Tamil Nadu; Padmapur, Orissa; Delhi University campus, Delhi. In(C) 2R- Kerala, Allahabad, Rajghat, Varanasi, Uttar Pradesh, Mysore, Nepal, Arumanai, Kanniya Kumari, Tamil Nadu; Borneo, Philippines and Thailand .In(H)3L- Rajghat, BHU Campus, Varanasi and Nepal. This inversion has been detected from laboratory stocks and natural populations only in heterozygous condition. Two types of homozygotes (ST/ST, In/In) could not be

Table 2—Frequencies (in percent) of two common inversions in Indian natural populations of *D. bipectinata*

Population	Total number of chromosomes examined	2L(D)	2R(C)	Mean no. of heterozygous inversions per individual
Rajghat	130	0.00(0.00)	10.00(24.50)	0.33(0.56)
Sarnath	90	7.77(32.00)	0.00(0.00)	0.15(0.48)
Mysore	100	0.00(0.00)	12.00(33.00)	0.20(0.48)
Panagarh	162	7.40(20.00)	6.97(22.50)	0.28(0.59)
Allahabad	58	0.00(0.00)	10.34(29.50)	0.20(0.43)
Arumanai	70	6.42(23.50)	8.57(24.00)	0.30(0.61)

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 inversions^{91,94,95}. Significant non-random associations between inversions (linked inversions as well as unlinked inversions) indicate epistatic interaction between inversions in *D. bipectinata*^{92,96}. 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. bipectinata*⁹². 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*

Population	Total number of chromosomes examined	2 Lt	2 RNS	3 LP	3 RP	Mean no. of heterozygous inversions per individual
Jammu	122	18.85(0.49)	12.30(0.49)	15.57(0.98)	22.95(0.98)	1.49(0.07)
Siliguri	116	3.45(1.35)	1.72(0.45)	5.17(0)	0	0.59(0.05)
Guwahatai	200	10.00(0.99)	9.50(0.50)	7.50(0)	16.00(0.99)	1.04(0.07)
Patna	118	9.32(0.50)	10.17(0.50)	0	11.86(0.50)	0.90(0.04)
Shillong	132	12.12(0.98)	9.85(1.47)	11.36(0.49)	16.67(0.49)	1.09(0.07)
Ghazipur	156	7.69(0.49)	8.33(0.49)	3.85(0)	12.82(1.46)	0.95(0.05)
Ondi	92	4.35(0.43)	3.26(0.87)	0	0	0.30(0.03)
Varanasi	334	4.49(0.47)	2.69(0.94)	0.59(0.47)	0	0.49(0.05)
Ramnagar	300	2.67(0.50)	3.33(0.50)	3.33(0)	0.67(0)	0.49(0.04)
Jamsoti	294	3.06(0.49)	1.70(0.98)	0	0	0.19(0.04)
Lowari	214	0.93(0.91)	4.21(0.91)	0	2.80(0)	0.26(0.02)
Mirzapur	146	5.48(0.96)	10.96(0.48)	2.74(0)	14.38(0.48)	0.90(0.06)
Jabalpur	156	6.41	11.54	3.85	16.03	0.86
Itarsi	126	5.56	9.52	3.17	14.29	0.90
Medinipur	122	7.38	6.56	8.20	18.03	0.98
Balasore	164	10.98	9.15	8.54	18.29	1.10
Nagpur	106	10.38	16.04	4.72	14.15	1.32
Bhubaneswar	120	12.50	13.33	6.67	19.17	1.12
Mumbai	116	13.79	16.38	8.62	24.14	1.60
Panaji	86	15.12	18.60	10.47	22.09	1.72
Tirupati	108	18.52(0.93)	18.52(0.46)	12.04(0.46)	26.85(0.46)	1.81(0.08)
Chennai	82	18.29(1.47)	19.51(0.98)	15.85(0.49)	26.83(0.49)	1.88(0.09)
Bangalore	124	16.94(1.50)	15.32(0.50)	10.48(1.50)	29.03(0.05)	1.66(0.10)
Mysore	208	18.75(1.49)	19.23(0)	6.73(0.99)	17.31(0.50)	1.41(0.06)
Ernakulum	112	9.82(0.47)	23.21(0.94)	8.93(1.42)	16.96(0.94)	1.59(0.08)
Fort Cochin	124	17.74(0.97)	18.55(1.45)	9.68(0.97)	23.39(0.49)	1.79(0.11)
Thiruvananthapuram	114	16.67(1.50)	22.81(1.00)	20.18(1.0)	24.56(0.50)	2.09(0.08)
Kanniya Kumari	110	18.18(1.50)	20.91(1.00)	11.82(0.50)	24.54(1.00)	1.98(0.11)

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*⁹⁸. 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^{99,100}. Quantitative data on the frequency of cosmopolitan inversions have been reported from various regions of the world¹⁰¹⁻¹¹². 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^{107,113}. 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 inversions¹¹¹.

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^{103,105,108,110,114-119}. When *D. melanogaster* populations are maintained in the laboratory, a decline in frequency of polymorphic inversions or total elimination of inversions was observed¹¹⁴⁻¹²⁰. A significant correlation between wing length and inversion polymorphism has been observed in *D. melanogaster* populations from Spain¹²¹. Garcia-Vazquez *et al.*¹²² 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 reported¹²³⁻¹³². A total of 28 natural populations and several laboratory stocks were analyzed to study inversion polymorphism^{123,128,130,131}. 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 detected¹³¹. 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^{123,126,130}. The data on the frequencies of 4 common cosmopolitan inversions in these populations reported by Singh and Das^{123,126,127} and Das and Singh¹³⁰ 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 generations¹²⁷. 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 Das¹²⁷ discussed these results in the light of genetic drift and founder principle¹³³ causing changes of inversion polymorphism in laboratory populations of *D. melanogaster*.

The data on intra- and interchromosomal associations in natural and laboratory populations of *D. melanogaster* have been reported^{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 *D. melanogaster*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 inversions¹²⁷. 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 *D. melanogaster*¹²⁴. The results of selection experiment¹³² 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.

Conclusion

The three species which have been compared with respect to their patterns of inversion polymorphism,

belong to the same species group of the subgenus *Sophophora*. It is generally considered that the *melanogaster* species group originated in south east Asia¹⁸. From this region the group has dispersed and shows secondary radiation in the adjacent biogeographic regions¹³⁴. *D. melanogaster* belongs to the *melanogaster* subgroup and the remaining two species to the *ananassae* subgroup. *D. melanogaster* is a cosmopolitan species predominantly found in domestic habitats. *D. ananassae* is also cosmopolitan and domestic species but mainly circumtropical in distribution. *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 *D. melanogaster* and lowest in *D. bipectinata* but *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 *D. melanogaster*, *D. ananassae* and *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 *Sophophora*.

References

- 1 Sturtevant A H, A crossover reducer in *Drosophila melanogaster* due to inversion of a section of the third chromosome, *Biol Zent bl*, 46 (1926) 697.
- 2 Dobzhansky Th, Genetics and the Origin of Species (Columbia Univ. Press, New York) 1951.
- 3 Dobzhansky Th, Genetics of the Evolutionary Process (Columbia University Press, New York) 1970.
- 4 Da Cunha A B, Chromosomal polymorphism in the diptera, *Adv Genet*, 7 (1955) 93.

- 5 Da Cunha A B, Chromosomal variation and adaptation in insects, *Ann Rev Entomol*, 5 (1960) 85.
- 6 Sperlich D & Pfriem P, Chromosomal polymorphism in natural and experimental populations. In: The Genetics and Biology of *Drosophila*, Vol 3e edited by Ashburner M, Carson H L and Thompson jr J N (Academic Press, New York) 1083, 257.
- 7 Krimbas C B & Powell J R, *Drosophila* Inversion Polymorphism, CRC Press, Boca Raton, 1992.
- 8 Singh B N, Chromosomal variability in *Drosophila*. In: Perspectives in Entomological Research, edited by Agrawal O P (Scientific Publisher, Jodhpur) 1994, 177.
- 9 Dobzhansky Th, Burla H & Da Cunha A B, A comparative study of chromosomal polymorphism in sibling species of the *willistoni* group of *Drosophila*, *Am Nat*, 84 (1950) 229.
- 10 Da Cunha A B & Dobzhansky Th, A further study of chromosomal polymorphism in *Drosophila willistoni* in its relation to environment, *Evolution*, 8 (1954) 119.
- 11 Carson H L, The population genetics of *Drosophila robusta*, *Adv Genet*, 9 (1958) 1.
- 12 Carson H L, The genetic characteristics of marginal populations of *Drosophila*. *Cold Spring Harbour Symp Quant Biol*, 20 (1955) 276.
- 13 Carson H L, Genetic conditions which promote or retard the formation of species, *Cold Spring Harbour Symp Quant Biol*, 24 (1959) 87.
- 14 Dubinin N P & Tiniakov G G, Structural chromosome variability in urban and rural populations of *Drosophila funebris*, *Am Nat*, 81 (1946) 148.
- 15 Dobzhansky Th, Adaptive changes induced by natural selection in wild populations of *Drosophila*, *Evolution* 1 (1947) 1.
- 16 Ranganath H A & Krishnamurthy N B, Chromosomal polymorphism in *Drosophila nasuta*. III. Inverted gene arrangement in south Indian populations, *J Hered*, 66 (1975) 90.
- 17 Kumar A & Gupta J P, Genetics of natural populations of *Drosophila nasuta*, *J Hered*, 79 (1988) 83.
- 18 Bock I R & Wheeler M R, The *Drosophila melanogaster* species group, *Univ Texas Publ*, 7213 (1972) 1.
- 19 Kikkawa H, Studies on the genetics and cytology of *Drosophila ananassae*, *Genetica*, 20 (1938) 458.
- 20 Moriwaki D & Tobari Y N, *Drosophila ananassae*. In: Handbook of Genetics, edited by King R C (Plenum Press, New York) 1975, 513.
- 21 Singh B N, *Drosophila ananassae* A genetically unique species, *Nucleus*, 28 (1985) 169.
- 22 Singh B N, Chromosomal polymorphism of *Drosophila ananassae*, *Indian Rev Life Sci*, 8 (1988) 147.
- 23 Singh B N, *Drosophila ananassae*: A species characterized by several unusual genetic features, *Curr Sci*, 78 (2000) 391.
- 24 Tobari, Y N (ed.) *Drosophila ananassae* – Genetical and Biological Aspects (Japan Scientific Societies Press, Tokyo) 1993.
- 25 Kale P G, The meiotic origin of spontaneous crossovers in *Drosophila ananassae* males, *Genetics*, 62 (1969) 123.
- 26 Hinton C W, Identification of two loci controlling crossing over in males of *Drosophila ananassae*, *Genetics*, 66 (1970) 663.
- 27 Moriwaki D, Tsujita M & Oguma Y, Spontaneous crossing over in male of *Drosophila ananassae*, *Cytologia*, 45 (1970) 411.
- 28 Singh A K & Singh B N, Heterozygous inversions and spontaneous male crossing-over in *Drosophila ananassae*, *Genome*, 30 (1988) 445.
- 29 Singh B N & Mohanty S, A spontaneous genetic mosaic in *Drosophila ananassae*, *Curr Sci*, 62 (1992) 372.
- 30 Kaufman B P, A terminal inversion in *Drosophila ananassae*, *Proc Natl Acad Sci USA*, 22 (1936) 591.
- 31 Dobzhansky Th, & Dreyfus A, Chromosomal aberrations in Brazilian *Drosophila ananassae*, *Proc. Natl. Acad Sci USA* 26 (1943) 301.
- 32 Shirai M & Moriwaki D, Variation of gene sequences in various strains of *Drosophila ananassae*, *Drosoph Inf Serv*, 26 (1952) 120.
- 33 Freire-Maia N, Chromosomal mutations in natural populations of *Drosophila ananassae*, *Drosoph Inf Serv*, 29 (1955) 116.
- 34 Freire-Maia N, Discusson, Cold Spring Harbour Symp Quant Biol, 20 (1955) 270.
- 35 Freire-Maia N, Peculiar gene arrangements in Brazilian natural populations of *Drosophila ananassae*, *Evolution*, 15 (1961) 486.
- 36 Seecof R.L., Cytological analysis, section III from XXII, Genetic studies of irradiated natural populations of *Drosophila*, *Univ. Texas Publ*, 5721 (1957) 269.
- 37 Futch D.G., A study of speciation in south pacific populations of *Drosophila ananassae*, *Univ. Texas Publ*, 6615 (1966) 79.
- 38 Ray-Chaudhuri S.P. & Jha A P, Studies on salivary gland chromosomes of Indian *Drosophila ananassae*, *Proc Int Cell Biol Meet Bombay*, (1966) 352.
- 39 Sajjan S N & Krishnamurthy N B, Report on two new translocations in a natural population of *Drosophila ananassae* from Hiriyur (Mysore state, India), *Drosoph Inf Serv*, 45 (1970) 166.
- 40 Sajjan S N & Krishnamurthy N B, New gene arrangements in *Drosophila ananassae*, *Drosoph Inf Serv*, 48(1972) 103.
- 41 Reddy G S & Krishnamurthy N B, Two new gene arrangements in *Drosophila ananassae* from south India, *Drosoph Inf Serv*, 48 (1972) 140.
- 42 Reddy G S & Krishnamurthy N B, Aberrant gene sequences in *Drosophila ananassae* from south India, *Drosoph Inf Serv*, 48 (1972) 139.
- 43 Reddy G S & Krishnamurthy N B, Altitudinal gradients in the frequencies of three common inversions in *Drosophila ananassae*, *Drosoph Inf Serv*, 51(1974)136.
- 44 Singh V K, Mishra M & Jha A P, A new pericentric inversion in *Drosophila ananassae*, *Drosoph Inf Serv*, 47 (1971) 97.
- 45 Singh V K, Jha A P & Rahman S M Z, A new report of paracentric inversion in the right arm of X-chromosome of *Drosophila ananassae*, *Bhagalpur Univ. J.* 1(1972) 8.
- 46 Hinton C W & Downs J E, The mitotic, polytene and meiotic chromosomes of *Drosophila ananassae*, *J Hered*, 66 (1975) 353.
- 47 Singh B N, An inversion within the subterminal inversion in *Drosophila ananassae*, *Experientia*, 39 (1983) 99.

- 48 Singh B N, Genetic similarity between natural populations of *Drosophila ananassae* from Kerala and Andaman and Nicobar Islands, *Genetica*, 69 (1986) 143.
- 49 Hegde S N & Jayashankar M, A new gene arrangement in *Drosophila ananassae* from Rewa, India, *Drosoph Inf Serv*, 71 (1992) 160.
- 50 Singh A K & Singh B N, A new inversion in Indian *Drosophila ananassae*, *Drosoph Inf Serv*, 70 (1991) 201.
- 51 Singh B N, Distribution of most common inversions of *Drosophila ananassae* in different parts of India including Andaman and Nicobar Islands, *Indian Biol*, 2 (1970) 78.
- 52 Singh B N, Inversion polymorphism in Indian populations of *Drosophila ananassae*, *Hereditas*, 110 (1989) 133.
- 53 Singh B N, Population and behaviour genetics of *Drosophila ananassae*, *Genetica*, 97 (1996) 321.
- 54 Singh B N, Population genetics of inversion polymorphism in *Drosophila ananassae*, *Indian J Exp Biol*, 36 (1998) 739.
- 55 Singh B N, Pattern of chromosomal polymorphism in *Drosophila ananassae*, *J Exp Zool*, India, 1 (1998) 3.
- 56 Singh B N, Persistence of chromosomal polymorphism in various strains of *Drosophila ananassae*, *Genetica*, 59 (1982) 151.
- 57 Singh B N, Quantitative variation of chromosomal polymorphism in natural populations of *Drosophila ananassae*, *Cytologia*, 39 (1974) 309.
- 58 Singh B N, Genetic differentiation in natural populations of *Drosophila ananassae*, *Genetica*, 63 (1984) 49.
- 59 Singh B N, High frequency of cosmopolitan inversions in natural populations of *Drosophila ananassae* from Kerala, South India, *J Hered*, 75 (1984) 504.
- 60 Singh B N, Chromosomal variability in natural population of *Drosophila ananassae* from Jammu, *Indian J Genet Plant Breed*, 49 (1989) 241.
- 61 Singh B N, Chromosomal polymorphism in *Drosophila ananassae*: Similarity between widely distant populations from India, *Korean J Genet*, 13 (1991) 27.
- 62 Singh B N, Genetic distance in inversion polymorphism among natural populations of *Drosophila ananassae*, *Genetica*, 64 (1984) 221.
- 63 Singh B N & Anand S, Genetic divergence at the level of inversion polymorphism in Indian populations of *Drosophila ananassae*, *Evol Biol*, 8&9 (1995) 177.
- 64 Moriwaki D, Shirai M & Yoshida Y N, Balanced polymorphism attained in some experimental populations of *Drosophila ananassae*, *Drosoph Inf Serv*, 29 (1955) 143.
- 65 Tobari Y N, Relation between adaptive values and composition of the population of *Drosophila ananassae*, *Evolution*, 18 (1964) 343.
- 66 Tobari Y N & Kojima K I, Selective modes associated with inversion karyotypes in *Drosophila ananassae*, *Genetics*, 57 (1967) 179.
- 67 Singh B N & Ray-Chaudhuri S P, Balanced chromosomal polymorphism in experimental populations of *Drosophila ananassae*, *Indian J Exp Biol*, 10 (1972) 301.
- 68 Singh B N, Cosmopolitan inversions in *Drosophila ananassae*, *Caryologia*, 36 (1983) 333.
- 69 Singh B N, On the degree of genetic divergence in *Drosophila ananassae* populations transferred to laboratory conditions, *Zeit Zool Syst Evol*, 25 (1987) 180.
- 70 Singh B N, Variation in the gene arrangement frequencies and the degree of heterosis in laboratory strains of *Drosophila ananassae*, *Brazilian J Genet*, 6 (1983) 407.
- 71 Singh B N, Evidence for random genetic drift in laboratory populations of *Drosophila ananassae*, *Indian J Exp Biol*, 26 (1988) 85.
- 72 Singh B N, The lack of evidence for coadaptation in geographic populations of *Drosophila ananassae*, *Genetica*, 43 (1972) 582.
- 73 Singh B N, Persistence of heterosis in crosses between geographic races of *Drosophila ananassae*, *Indian J Exp Biol* 12 (1974) 367.
- 74 Singh B N, Interracial hybridization in *Drosophila ananassae*, *Genetica*, 57 (1981) 139.
- 75 Singh B N, Heterosis without selectional coadaptation in *Drosophila ananassae*, *Theor Appl Genet*, 69 (1985) 437.
- 76 Singh B N, Genetic coadaptation in *Drosophila*, *Indian Rev Life Sci*, 11 (1991) 205.
- 77 Singh B N, The lack of evidence for interchromosomal interactions in *Drosophila ananassae*, *Naturalia*, 7 (1982) 29.
- 78 Singh B N, On intra- and interchromosomal associations in *Drosophila ananassae*, *Genetica*, 60 (1983) 231.
- 79 Singh A K & Singh B N, Further data on interchromosomal associations in *Drosophila ananassae*, *Naturalia*, 14 (1989) 19.
- 80 Singh B N, Recombination between heterozygous inversions in *Drosophila ananassae*, *Genetica*, 44 (1973) 602.
- 81 Singh B N, On the combinations of different gene arrangements in the third chromosome of *Drosophila ananassae*, *Caryologia*, 27 (1974) 285.
- 82 Singh B N, Epistatic interaction between linked gene arrangements in *Drosophila ananassae*, *Brazilian J Genet*, 7 (1984) 175.
- 83 Singh B N & Singh A K, Crossing-over between linked inversions in *Drosophila ananassae*, *Hereditas*, 109 (1988) 15.
- 84 Singh A K & Singh B N, An extreme linkage between inversions in *Drosophila ananassae*, *Curr Sci*, 57(1988)490.
- 85 Singh B N & Singh A K, Linkage disequilibrium in laboratory strains of *Drosophila ananassae* is due to drift, *Hereditas*, 112 (1990) 203.
- 86 Singh B N & Singh A K, Nonrandom associations between independent inversions in laboratory strains of *Drosophila ananassae*, *Naturalia*, 16 (1991) 11.
- 87 Yang, S Y, Wheeler L L & Bock I R, Isozyme variations and phylogenetic relationships in the *Drosophila bipectinata* species complex, *Univ Texas Publ*, 7213 (1972) 213.
- 88 Panigrahy K K, Ecogeographic differentiation of species and chromosomal inversions in Indian populations of *Drosophila*, Ph.D. thesis, Banaras Hindu University, 1984.
- 89 Bock I R, Intra- and interspecific chromosomal inversions in the *Drosophila bipectinata* species complex, *Chromosoma*, 34 (1971) 206.
- 90 Gupta J P & Panigrahy K K, Chromosomal polymorphism in Indian populations of *Drosophila bipectinata* Duda, *Genetica*, 82 (1990) 45.
- 91 Das A & Singh B N, Heterosis associated with chromosome inversions in *Drosophila bipectinata*, *Korean K Genet*, 14 (1992) 173.

- 92 Banerjee R & Singh B N, Inversion polymorphism in natural populations of *Drosophila bipectinata*, *Cytobios*, 87 (1996) 31.
- 93 Banerjee, R & Singh B N, Population and behaviour genetics of *Drosophila bipectinata*, *Proc Indian natn Sci Acad*, B3 (1997) 399.
- 94 Banerjee, R & Singh B N, Evidence for selection and genetic drift in laboratory populations of *Drosophila bipectinata*, *Proc Zool Soc Calcutta*, 47 (1995) 125.
- 95 Singh B N & Banerjee R, Increase in the degree of inversion polymorphism in *Drosophila bipectinata* populations transferred to laboratory conditions, *J Zool Syst Evol Res*, 35 (1997) 153.
- 96 Singh B N & Das A, Linkage disequilibrium between inversions in *Drosophila bipectinata*, *Biol Zent bl*, 110 (1991) 157.
- 97 Singh B N & Banerjee R, Chromosomal variability and interracial hybridization in *Drosophila bipectinata*, *Cytobios*, 82 (1995) 219.
- 98 Lemeunier F & Aulard S, Inversion polymorphism in *Drosophila melanogaster*. In *Drosophila Inversion Polymorphism*, edited by Krimbas C B and Powell J R (CRC Press, Boca Raton, USA) 1992, 339.
- 99 Ashburner M & Lemeunier F, Relationship within the *melanogaster* species subgroup of the genus *Drosophila* (Sophophora). I. Inversion polymorphism in *Drosophila melanogaster* and *Drosophila simulans*, *Proc R Soc London*, 193 (1976) 137.
- 100 Mettler L E, Voelker R A & Mukai T, Inversion clines in populations of *Drosophila melanogaster*, *Genetics*, 87 (1977) 169.
- 101 Watanabe, T, Chromosomal polymorphism in natural populations of *Drosophila melanogaster*, *Mem Fac Sci Kyoshu Univ Ser E*, 4 (1967) 159.
- 102 Mukai T, Watanabe T K & Yamaguchi O, The genetic structure of natural populations of *Drosophila melanogaster*. XII Linkage disequilibrium in a large local population, *Genetics*, 77 (1974) 771.
- 103 Stalker H D, Chromosome studies in wild populations of *Drosophila melanogaster*, *Genetics*, 82 (1976) 323.
- 104 Stalker H D, Chromosome studies in wild populations of *Drosophila melanogaster* II Relationship of inversion frequencies to latitude, season, wing loading and flight activity, *Genetics*, 95 (1980) 211.
- 105 Choi Y, Chromosomal polymorphism in a Korean natural population of *Drosophila melanogaster*, *Genetica* 47 (1977) 155.
- 106 Mukai T & Voelker R A, The genetic structure of natural populations of *Drosophila melanogaster*, XIII Further studies on linkage disequilibrium, *Genetics*, 86 (1977) 175.
- 107 Voelker R A, Mukai T & Johnson F M, Genetic variation in populations of *Drosophila melanogaster* from the western United States, *Genetica*, 47 (1977) 143.
- 108 Inoue Y & Watanabe T K, Inversion polymorphism in Japanese natural populations of *Drosophila melanogaster*, *Japanese J Genet*, 54 (1979) 69.
- 109 Paik Y K, Inversion polymorphism in wild populations of *Drosophila melanogaster*, *Korean J Genet*, 1 (1979) 18.
- 110 Knibb W R, Oakeshott J G & Gibson J B, Chromosome inversion polymorphism in *Drosophila melanogaster*. I. Latitudinal clines and associations between inversions in Australasian populations, *Genetics*, 98 (1981) 83.
- 111 Knibb W R, Chromosome inversion polymorphism in *Drosophila melanogaster*. II Geographic clines and climatic associations in Australasia, North America and Asia, *Genetica*, 58 (1982) 213.
- 112 Choi Y, Ha Y M & Kim S K, Further studies on chromosomal inversion polymorphism in a natural population of *Drosophila melanogaster*, *Korean J Genet*, 6 (1984) 81.
- 113 Inoue Y, Watanabe T & Watanabe T K, Evolutionary change of the chromosomal polymorphism in *Drosophila melanogaster* populations, *Evolution*, 38 (1984) 753.
- 114 Alahiotis S, Zacharopoulou A & Pelecanos M, The effect of two ecological factors upon the inversion frequency in *Drosophila melanogaster*, *Drosoph Inf Serv*, 52 (1977) 106.
- 115 Langley C H, Ito K & Voelker R A, Linkage disequilibrium in natural populations of *Drosophila melanogaster*: seasonal variations, *Genetics*, 86 (1977) 447.
- 116 Yamaguchi O, Ichinose M, Matsuda M & Mukai T, Linkage disequilibrium in isolated populations of *Drosophila melanogaster*, *Genetics*, 96 (1990) 507.
- 117 Yamasaki T, Matsuo Y, Inoue Y & Matsuo Y, Genetic analysis of natural populations of *Drosophila melanogaster* in Japan. I. Protein polymorphism, lethal gene, sterility gene, inversion polymorphism and linkage disequilibrium, *Japanese J Genet*, 59 (1984) 33.
- 118 Aulard S & Lemeunier F, Distribution et association des inversions chromosomiques dans trois populations naturelles de *Drosophila melanogaster* de France, Tunisie et Congo, *Gent Sel Evol*, 17 (1985) 311.
- 119 Afonso J M, Hernandez, M, Padron G & Gonzalez A M, Gametic nonrandom associations in north-west African populations of *Drosophila melanogaster*, *Genetica*, 67 (1985) 3.
- 120 Inoue Y, The fate of polymorphic inversions of *Drosophila melanogaster* transferred to laboratory conditions, *Japanese J Genet*, 54 (1979) 83.
- 121 Aguada M & Serra L, Spanish cellar populations of *Drosophila melanogaster*. I. Study of variability at three different levels: Quantitative, chromosomal and molecular, *Genetika*, 12 (1980) 111.
- 122 Garcia-Vazquez E, Sanchez-Refusta F & Rubio J, Chromosome inversions and frequency of extra bristles in natural populations of *Drosophila melanogaster*, *J Hered*, 80 (1989) 193.
- 123 Singh B N & Das A, Inversion polymorphism in Indian natural populations of *Drosophila melanogaster*, *Genome*, 33 (1990) 311.
- 124 Singh B N & Das A, Association of inversion polymorphism and frequency of extra bristles in Indian natural populations of *Drosophila melanogaster*, *Evol. Biol*, 5 (1991) 185.
- 125 Singh B N & Das A, Epistatic interaction between unlinked inversions in Indian natural populations of *Drosophila melanogaster*, *Genet Sel Evol*, 23 (1991) 371.
- 126 Singh B N & Das A, Further evidence of latitudinal inversion clines in natural populations of *Drosophila melanogaster* from India, *J Hered*, 83 (1992) 227.

- 127 Singh B N & Das A, Changes of inversion polymorphism in laboratory populations of *Drosophila melanogaster*, *Z Zool Syst Evol Forsch*, 30 (1992) 268.
- 128 Das A & Singh B N, Chromosome inversions in Indian *Drosophila melanogaster*, *Genetica*, 81 (1990) 85.
- 129 Das A & Singh B N, The lack of evidence for intra- and interchromosomal interactions in Indian natural populations of *Drosophila melanogaster*, *Korean J Genet*, 12 (1990) 95.
- 130 Das A & Singh B N, Genetic differentiation and inversion clines in Indian natural populations of *Drosophila melanogaster*, *Genome*, 34 (1991) 618.
- 131 Das A & Singh B N, Chromosomal polymorphism in Indian natural populations of *Drosophila melanogaster*, *Korean J Genet*, 113 (1991) 97.
- 132 Das A & Singh B N, Selection for increased phenotypes of extra bristles in *Drosophila melanogaster*: Correlated response in the frequency of IN(3R)C inversion, *Evol Biol*, 6 (1992) 15.
- 133 Mayr E, *Animal Species and Evolution*, (Belknap Press, Cambridge), 1963.
- 134 Lemeunier F, David J R, Tascas L & Ashburner M, The *melanogaster* species group In: *The Generics and Biology of Drosophila*, Vol 3e edited by Ashburner M, Carson H L and Thompson jr J N (Academic Press, London) 1986, 147.