

CHROMOSOMAL VARIABILITY DUE TO INVERSIONS IN INDIAN POPULATIONS OF *Drosophila*

A. K. SINGH¹

Genetics Laboratory, Department of Zoology, Institute of Science, Banaras Hindu University, Varanasi, Uttar Pradesh, India

ABSTRACT

Every animal species possesses a fixed number of chromosomes which have their specific structural morphology. Changes in the chromosome structure may occur due to addition, deletion, inversion or translocation of a chromosome segment. Structural chromosomal aberrations can be distinctly spotted in the polytene chromosomes of *Drosophila*. One of the structural changes in the chromosomes is inversions, that occur very frequently in almost every species of *Drosophila*. Chromosomal markers like inversions, particularly paracentric inversions are very useful to know the level of genetic differentiation among different populations of a *Drosophila* species. A number of species of this genus have been chosen and analyzed for their chromosomal polymorphisms from all across the world and it has been inferred that persistence of inversions is due to their adaptive significance to the bearers. Indian population geneticists have also done ample work in this regard and have contributed substantially to the field of evolutionary genetics. Through the present article, it has been tried to review the work which have been accomplished by Indian workers with respect to chromosomal polymorphisms in different species of *Drosophila*, found in Indian subcontinent.

KEYWORDS: *Drosophila*, Chromosomal Polymorphism, Inversions, Indian Subcontinent

The normal morphology of chromosome/s may change due to change in the gene rearrangements caused by deletions, duplications, inversions and translocations. Each of these chromosomal changes can may originated due to breakage of chromosome arms. An inversion is a chromosome rearrangement in which a segment of a chromosome is reversed end to end. An inversion occurs when a single chromosome undergoes breakage and rearrangement within itself. Inversions are of two types, paracentric (that does not include centromere) and pericentric (that includes centromere). Due to easy preparations of polytene chromosomes from its larval salivary glands, a number of species of this genus available in this subcontinent were scrutinized for the cytological analysis and species identity. During such endeavors, people could see the presence of inversions, particularly paracentric inversions which are of common occurrence in *Drosophila* and are known to provide adaptive superiority to the species. Different populations of a *Drosophila* species can be examined for the presence of paracentric inversions to know the extent of chromosomal polymorphisms in them. A person working on this aspect has to first make oneself well acquainted with the banding pattern of every chromosome arm so that any variation in the arrangement of bands on a chromosome can be identified with absolute certainty. Due to after inversion in a particular segment of chromosome, three different types of karyotypes may be ascertained: ST/ST, ST/IN and IN/IN; here ST/ST stands for standard gene arrangements on both chromosomes, i.e., normal homozygotes, ST/IN for

heterozygotes and IN/IN for inversion homozygotes. Several experiments conducted in a number of species of *Drosophila* have clearly proved that the presence of paracentric inversions is an adaptive trait (Da Cunha 1955, 1960, Dobzhansky 1970, Sperlich and Pfriem 1986). The frequency of standard and inverted gene arrangements in the population can be calculated. The frequency of the two arrangements can be easily calculated by following Hardy-Weinberg equilibrium method. This method can also be used to compute the expected frequency of genotypes. Inversion polymorphism is in fact maintained by balancing selection. The degree of chromosomal variability depicts range of variation in different populations of a species. Dobzhansky was one of the pioneer workers in the field of *Drosophila* population genetics who considered inversions as gene markers, to test Hardy-Weinberg equilibrium and the role of cosmopolitan inversions in conferring adaptability to populations. His work found great attention during the first half of twentieth century. Dobzhansky and co-workers (Da Cunha, and Dobzhansky, 1954, Dobzhansky, 1970, Dobzhansky, Burla, and Da Cunha, 1950), working on *D. willistoni* explained a good correspondence between the mean number of heterozygous inversions per individual and an index expressing environmental heterogeneity in natural populations. It has been observed that populations at the centre of geographic distribution have high degree of inversion polymorphism than those inhabiting marginal areas. Based on such observations, Dobzhansky and others opined that inversion polymorphism in *Drosophila* is a device to cope with the

¹Corresponding author

diversity of environments. This is in fact referred as ecological niche hypothesis (Da Cunha and Dobzhansky, 1954; Dobzhansky et al. 1950).

Taxonomists explored every ecological habitat to gather information regarding the diversification of this genus. About 1500 species of this genus are known to occur from the different continents of the world and out of these more than 150 species are known to exist only in India. Indian population geneticists, who loved to work using *Drosophila*, mainly preferred studying genetic variation due to chromosomal inversions occurring in different species of *Drosophila*. Data accumulated on frequency of inversion karyotypes of a *Drosophila* species have helped to study several evolutionary phenomena like natural selection, genetic drift, behavioral and ecological aspects. *Drosophila* species which have been the subject of the chromosomal polymorphism in India are mainly *D. melanogaster*, *D. ananassae*, *D. nasuta*, and members of *bipunctinata* species complex, i.e., *D. bipunctinata*, *D. malerkotliana*, *D. parabipunctinata* and *D. pseudoananassae*. In India, two laboratories are well known where studies on *Drosophila* population genetics have been substantially undertaken. These two laboratories, Genetics Laboratory, Department of Zoology, Banaras Hindu University and *Drosophila* Stock Centre, Department of Zoology, University of Mysore recruited dozens of researchers to collect various species of *Drosophila* from different parts of India to perform population genetical work on them.

Drosophila melanogaster

D. melanogaster is one of extensively studied species for genetical, evolutionary and behavioural aspects. It is a widely distributed species found in warm as well cool countries. Its population genetical work has been done from almost every part of the world. People have reported seasonal, geographical, latitudinal and longitudinal variations in the frequency of inversions in this species (Stalker 1976, 1980; Choi 1977). The data made available from all these observations reflect the trend of inversion polymorphism conferring adaptive superiority to this species, under fluctuating environmental conditions. Lemeunier and Allard (1992) described more than 300 different inversions in worldwide populations of *D. melanogaster*. Rim et al (1986) reported 22 new inversions from flies sampled from different parts of Korea.

Work on chromosomal polymorphisms in Indian populations of *D. melanogaster* was initiated at the beginning of 1990s by Singh and Das (Das and Singh 1989,

1990; 1991 a, b, Singh and Das 1990, 1991 a, b, 1992). They screened a number of Indian populations of this species for their chromosomal inversions and also the frequency of commonly occurring inversions to obtain information on the frequency of inversions and intra and inter-chromosomal associations between inversions. Das and Singh (1991a, b) studied chromosomal polymorphism in 28 natural populations and several laboratory stocks collected from Indian subcontinent. They were able to identify 42 paracentric inversions in different autosomes and sex chromosomes (3 inversions in the X-chromosome, 13 in 2L, 11 in 2R, 7 in 3L and 8 in 3R). Based on the frequency and distributions of these inversions, they categorized them into common cosmopolitan, rare cosmopolitan, recurrent endemic and unique endemic.

Drosophila ananassae

Drosophila ananassae belongs to *melanogaster* species group. It is another prevalently occurring species in Indian subcontinent. *D. ananassae* is a cosmopolitan and domestic species. A large number of Indian biologists preferred this species for their study to understand several genetical and behavioural aspects. Chromosomal polymorphism in this species started nearly 50 years ago and so far more than 50 different natural populations and several laboratory stocks have been analysed for such studies. Population dynamics of chromosomal polymorphism of *D. ananassae* was one of the major objects of interest for Singh (Singh 2013). Singh and his research group analyzed nearly 50 Indian natural populations of this species to study various phenomenon of population genetics. The genetical studies on *D. ananassae* started during 1960s by Ray Chaudhari and his students (Ray-Chaudhuri and Jha 1966). This species is characterized with several genetical peculiarities, one of which is spontaneous male meiotic crossing over which gets distinctly influenced by the presence of inversions (Singh and Singh 1986, 1987a, b, 1988a, b, c, 1989, 1990a, b). In this species so far, 78 paracentric inversions, 21 pericentric inversions and 48 translocations have been reported (Singh 1989, 1996, 2010).

Singh selected *D. ananassae* as a model organism for its population genetical studies and devoted his more than four decades to explore the dynamics of its cosmopolitan inversions present all across the length and width of India (Singh 1982, 1986, 1987, 1988, 1989, 1998, 2010, 2013, Singh and Singh 2007, 2008a, b, 2010). Based on his own observations and also the results of his co-

workers, it was inferred that Indian natural populations of *D. ananassae* show geographic differentiation with respect to three autosomal, cosmopolitan inversions. He further affirmed that populations studied from south India (including Andaman and Nicobar Islands) maintain the inversion in high frequency as compared to the populations from the North Indian places. His analysis in this regard further suggested that Indian populations of this species have shown substantial genetic divergence from one ecological environment to the other only because of their adaptation in varying environmental conditions (Singh, 1998). Singh and Singh (1991a) reported the presence of a new subterminal paracentric inversion in 2R of *D. ananassae*. They also reported non random association between independent inversions in laboratory populations of this species (Singh and Singh 1991b). Singh and Singh (2007, 2008a,b, 2010) collected *D. ananassae* flies from more than forty geographical localities of India to study genetic differentiation among them, based on the chromosomal polymorphism of three cosmopolitan inversions. They were able to decipher that Indian natural populations of this species are genetically structured. Chromosomal polymorphism in natural population of *D. ananassae* derived from Sultanpur was studied (Singh, 2000; Ratnam and Singh, 2008) and it was observed that the mean heterozygous inversions per individual varied from 0.30 to 0.41 in natural population and 0.23 to 0.33 in mass culture stocks. Singh, Kumar and Ratnam (2014) reported genetic constitution with respect to three inversions of seven natural populations which came from the radius of 150 km. around Sultanpur district of Uttar Pradesh. Their observations showed a high frequency of ST arrangement than their respective inversion arrangements in all the seven natural populations analyzed. Out of three inversion arrangements, the frequency of Eta (ET) was very low in all the natural populations. These researchers also performed similar study with mass culture stocks that were raised from the flies collected from the natural populations. Study conducted in this regard indicated that the mass culture populations had not experienced significant genetic modifications in about five generations. *D. ananassae* and *D. pallidosa* are sibling species, i.e., they are morphologically very similar but reproductively isolated. *D. pallidosa* is endemic to South Pacific regions where it coexists with *D. ananassae*. The major cause of their reproductive isolation is due to difference in their behavioural pattern. Singh et al (2012) made a comparison between polytene chromosomes of these two sibling species and analyzed the chromosomes in their hybrids to know

pairing between homologous chromosomes and the presence of heterozygous loops. They did not observe any asynaptic region in the polytene chromosomes of their F1 hybrids indicating that there was normal pairing between homologous chromosomes. However, the presence of heterozygous loops in F1 hybrids in certain regions of autosomes indicated that these two species differ in the order of gene arrangements.

Drosophila nasuta

Drosophila nasuta belongs to *nasuta* subgroup of the *immigrans* species group of genus *Drosophila*. Two races of it have been identified, *Drosophila nasuta nasuta* and *D. nasuta albomicans* (Nirmala Sajjan & Krishnamurthy, 1971). The two races are fully cross fertile. However, these races differ in chromosome number and metaphase chromosome length (Ranganath and Hagele, 1982; Hagele and Ranganath, 1982, 1983). *Drosophila nasuta* has widely been studied by a number of Indian workers for its taxonomic, cytological and genetical characteristics (Shyamala and Ranganath 1988, Ranganath, and Krishnamurthy, 1974, 1975, 1978a,b, Kumar and Gupta 1986). *D. nasuta* is a known to be widely distributed species that presents a high degree of chromosomal variability particularly due to paracentric inversions in its natural populations. Its genetical and cytological characteristics have mainly been studied by Mysore group of *Drosophila* researchers and according to them this species is chromosomally most variable species in the genus *Drosophila* and ranks at the top in the list of the *nasuta* subgroup (Nirmala and Krishnamurthy 1971, 1972, 1974; Ranganath and Krishnamurthy 1975; Rajasekarasetty *et al* 1979). Chromosomal polymorphisms have been the subject of interest for this species during 1980s. Shyamala and Ranganath (1988) analysed six south Indian populations of *Drosophila nasuta nasuta* for inversion polymorphism. They recorded 28 inversions, out of which 9 were entirely new gene arrangements, reported for the first time in this species. Of the 28 inversions observed in it, they found 5 in chromosome 2 and 23 in chromosome-III. The phenomenon of linkage disequilibrium reported for linked inversions in different species of *Drosophila* has also been observed in *D. nasuta*. Kumar and Gupta (1986) studied linkage disequilibrium between two naturally occurring gene arrangements of third chromosome, III-2 and III-35 in *D. nasuta*. They observed that these two gene arrangements were most common and showed extreme non-random association. The frequencies of the coupling combinations, III-2 and III-35 were always in excess and

individuals heterozygous for one gene arrangement and the homozygous for the other gene arrangement were rarely seen in natural populations. The main reason for this happening (linkage disequilibrium) was considered to be due to natural selection and suppression of crossing over (Kumar and Gupta 1986).

***Drosophila bipectinata* species complex**

D. bipectinata species complex comprises four sympatric species which have been major focus of study with regard to their phylogenetic relationships by a number of population geneticists from India (Gupta and Panigrahy 1990, Singh and Singh 2001). These four different species of *bipectinata* complex are widely distributed in Indian subcontinent and have been used for their chromosomal analysis. Bock (1971) working on these after species from different parts of the world detected twenty autosomal inversions in the larvae which were obtained by crossing inversion-free strains of the *bipectinata* complex (*D. bipectinata*, *D. parabiptectinata*, *D. malerkotliana* and *D. pseudoananassae*). Inversion polymorphism in *D. malerkotliana* was studied by Jha and Rahan (1972) and they reported five inversions from India. Naseerulla and Hegde (1993) reported a new inversion in the left arm of second chromosome, IILa, in *D. malerkotliana* collected from Varanasi (Uttar Pradesh). In their after report described a new paracentric inversion heterozygote. Comparison with the reference map of salivary gland chromosomes of *D. malerkotliana* constructed by Jha and Rahan (1972) showed that the new inversion lies between the regions 38 to 43 of the left arm of the second chromosome and involves about 16% of the euchromatic length of this arm. Singh and Singh (2015) observed an autosomal translocation in 2L of *D. malerkotliana*. Working on chromosomal polymorphisms in natural populations of *Drosophila malerkotliana*, they (Singh and Singh 2016) were able to observe more than half a dozen of inversions in the autosomal as well as sex chromosome arms of this species. These four species of *bipectinata* species complex have also been of attention to foreign workers. Tomimura et al (2005) studied chromosomal phylogeny and geographical divergence in this complex and prepared polytene chromosomes maps as a standard sequence. They reported 87 inversions in the *D. bipectinata* complex and also portrayed their breakpoints on the reference maps.

Out of these four species of *bipectinata* species complex, *D. bipectinata* is of wide distribution in Indian sub-continent. *D. bipectinata* was described by Duda in

1923 from Darjeeling town area of West Bengal state. Taxonomically this species belongs to the *bipectinata* species complex of the *ananassae* subgroup of the *melanogaster* species group. Bark and Wheeler (1972) reported that it has its distribution extending from India to Southeast Asia and New Guinea to Fiji and Samoa in the Pacific. It is one of the chromosomally polymorphic species and up to 1984 about 12 paracentric autosomal inversions were observed by some researchers (Bock 1971, Panigrahi 1984, Gupta and Panigrahy 1990). To answer whether inversions persist in the stocks being reared under laboratory conditions, Das and Singh (1992) analysed laboratory stocks for their karyotypic constitution and convincingly reported that inversions do persist in the flies being cultured in laboratory conditions. Their explanation in this regard was based on heterotic buffering, indicating that heterozygotes superiority is the consequence of their existence in the laboratory cultures. The linked inversions (inversions of the same chromosome) also occur in the non-random association (linkage disequilibrium) due to epistatic interaction in *D. bipectinata*. Singh and Das (1991) studied the phenomenon of linkage disequilibrium and reported that the two linked inversions of the second chromosome of *D. bipectinata* occur in non-random association. They found significantly excess number of coupling homozygotes and doubly heterozygous individuals in all the stocks analysed. Working on the same aspect, Das and Singh (1992) scrutinized a number of stocks of this species which were reared for a number of generations under laboratory conditions and found persistence of chromosomal polymorphisms in them. Chromosomal polymorphisms in *D. bipectinata* was also studied by Banerjee and Singh (1995) who reported the loss or absence of certain inversions from the long maintained laboratory stocks due to random genetic drift. Singh and Banerjee (1997) described the persistence of naturally occurring cosmopolitan inversions in the laboratory reared populations of *D. bipectinata*. Polytene chromosomes have been used as cytogenetical evidences to establish phylogenetic relationships among these four species of *bipectinata* species complex. However, a comparative study of these chromosomes have provided varying outlook regarding the pattern of divergence of the four species of this complex (Bock 1971; Jha and Rahman 1972, Tomimura et al. 2005). Recently Singh and Singh (2018) reported an excessive occurrence of paracentric inversions in a natural population of *Drosophila bipectinata* collected from a small town area of Moradabad

and opined that this may be due to ecological condition of the niche harboring this population.

CONCLUSION

India is very rich in Dipteran biodiversity, especially for the distribution of a large number of *Drosophila* species. The *Drosophila* flies have long been esteemed in the studies of genetics and evolution. During the present time, it has become a versatile experimental organism in nearly every discipline of biology. Its polytene chromosomes provide excellent material to study genetic diversity among the different populations of a species and also to see that to what extent different species of *Drosophila* vary chromosomally from each other. A number of geneticists from India selected this organism for the study of chromosomal polymorphisms and found that the level of polymorphism differs from population to population in a species and also from species to species. When populations of different geographical localities of a species were analyzed, it was found that populations do show varying level of chromosomal polymorphism. Seasonal, altitudinal, longitudinal and clinal variations also affect the frequency of cosmopolitan inversions found in a species. These studies in *Drosophila* clearly indicate that inversions confer adaptive significance to the species. Indian subcontinent is inhabited by some of the species of *Drosophila* that are abundantly distributed in close proximity to human habitation and kitchen gardens. Different species of *Drosophila* are known to be phylogenetically very close from each other, and therefore, perusal of their chromosome karyotypes and population genetical profile may help to draw a comprehensive idea regarding their evolutionary future fate.

Polytene chromosome inversions served to be excellent tool for twentieth century population biologists to analyse genetic profile of the species under consideration. The onset of molecular techniques during second half of 1960 revolutionized this kind of study by looking into the protein/enzyme polymorphism in different populations of a species. The discovery of amplifying a specific segment of DNA and also sequencing a segment of DNA, in later part of genetical investigations have now enabled the present day geneticists to envisage the genetic variability among the members of a population at nucleotide level. However, the results obtained by employing inversions as genetic markers do prove to be equally useful as compared with the molecular markers. It is therefore necessary to know that

the population genetical aspects can efficiently be studied by using cosmopolitan inversions as genetic markers.

ACKNOWLEDGEMENT

The author is highly thankful to Dr. Deepak Kumar Srivastav for his stimulus to write an article on population genetical aspect. Financial support in the form of UGC-CAS (Zoology) is also acknowledged.

REFERENCES

- Banerjee R. and Singh B.N., 1995. Inversion polymorphism in natural populations of *Drosophila bipectinata*. *Cytobios*, **87**: 31-43.
- Bock I.R., 1971. Intra- and interspecific chromosomal inversions in the *Drosophila bipectinata* species complex. *Chromosoma*, **34**: 206-229.
- Bock I.R. and Wheeler M.R., 1972. The *Drosophila melanogaster* species group. Univ. Texas Publ., **7213**: 1-102.
- Gupta J.P. and Panigrahy K.K., 1990. Chromosomal polymorphism in Indian populations of *Drosophila bipectinata* Duda. *Genetica*, **82**: 45-49.
- Choi Y., 1977. Chromosomal polymorphism in Korean natural population of *Drosophila melanogaster*. *Genetica*, **47**: 155-160.
- Da Cunha A.B., 1955. Chromosomal polymorphism in the Diptera. *Adv. Genet.*, **7**: 93-138.
- Da Cunha A.B., 1960. Chromosomal variation and adaptation in insects. *Annu. Rev. Entom.*, **5**: 85-110.
- Da Cunha A.B. and Dobzhansky Th., 1954. A further study of chromosomal polymorphism in *Drosophila willistoni* in its relation to the environment. *Evolution*, **8**: 119-134.
- Das A. and Singh B.N., 1989. An inversion in an Indian population of *Drosophila melanogaster*. *Dros. Inf. Serv.*, **68**.
- Das A. and Singh B.N., 1990. Chromosome inversions in Indian *Drosophila melanogaster*. *Genetica*, **81**: 85-88.
- Das A. Singh B.N., 1991a. Genetic differentiation and inversion clines in Indian natural populations of *Drosophila melanogaster*. *Genome*, **34**: 618-625.

- Das A. Singh B.N., 1991b. Chromosomal polymorphism in Indian natural populations of *Drosophila melanogaster*. Korean J, Genet., **13**: 97-112.
- Das A. and Singh B.N., 1992. Heterosis associated with chromosome inversions in *Drosophila bipectinata*. Korean J. Genetics, **14**(3): 173-178.
- Dobzhansky Th., 1970. Genetics of the Evolutionary Process. Columbia University Press, New York.
- Dobzhansky Th., Burla H. and Da Cunha A.B., 1950. A comparative study of chromosomal polymorphism in sibling species of the *willistoni* group of *Drosophila*, Am. Nat., **84**: 229-246.
- Gupta J.P. and Panigrahy K.K., 1990. Chromosomal polymorphism in Indian populations of *Drosophila bipectinata* Duda. *Genetica*, **82**: 45-49.
- Hagele K. and Ranganath H.A., 1982. The chromosomes of two *Drosophila* races: *D. nasuta nasuta* and *D. n. albomicana*. II. Differences in their microchromosomes. *Chromosoma*, **85**: 215-220.
- Hagele K. and Ranganath H.A., 1983. The chromosomes of two *Drosophila* races: *D. nasuta nasuta* and *D. nasuta albomicans* III. Localization of nucleolar organizer regions. *Genetica*, **60**: 123-128.
- Jha A.P. and Rahman S.M.Z., 1972. Cytogenetics of natural populations of *Drosophila*. I. Role of chromosomal inversions in the evolution of the *bipectinata* species complex. *Chromosoma*, **37**: 445-454.
- Kumar A. and Gupta J.P., 1986. Linkage disequilibrium between two naturally occurring gene arrangements of *Drosophila nasuta*. *Heredity*, **57**: 1-4.
- Lemeunier F. and Allard S., 1992. Inversion polymorphism in *Drosophila melanogaster*. In *Drosophila Inversion Polymorphism* (eds. Krimbas C B and Powell J R) CRC press, Boca Raton, pp.339-406.
- A. Naseerulla M.K. and Hegde S.N., 1993. A new inversion in *Drosophila malerkotliana* from Varanasi, India. *Dros. Inf. Serv.*, **72**: 158-159.
- Nirmala S.S. and Krishnamurthy N.B., 1971. Karyotype of *Drosophila nasuta*. *Dros. Inf. Serv.*, **47**: 121-122.
- Nirmala S.S. and Krishnamurthy N.B., 1972. *Drosophila albomicans* - a race of *Drosophila nasuta*. *Dros. Inf. Serv.*, **49**: 60.
- Nirmala S.S. and Krishnamurthy N.B. 1974. Endophenotypic variability in natural populations or *Drosophila nasuta*. *Egypt. J. Genet. Cytol.*, **3**: 211-228.
- Panigrahy K.K., 1984. Ecogeographic differentiation of species and chromosomal inversions in Indian populations of *Drosophila*. Ph D thesis, Banaras Hindu University, Varanasi, India.
- Ranganath H.A. and Hegele K., 1982. The chromosomes of two *Drosophila* races: *D. nasuta nasuta* and *D. nasuta albomicana*. 1. Distribution and differentiation of heterochromatin. *Chromosoma*, **85**: 83-92.
- Rajasekarasetty M.R., Ramesh S.R. and Krishnamurthy N.B., 1979. Inversions in the natural populations of *Drosophila nasuta*. *Nucleus. Calcutta*, **22**: 992-995.
- Ranganath H.A. and Krishnamurthy N.B., 1974. Developmental studies in *Drosophila nasuta* IV. Rate of development. inversion polymorphism at constant and fluctuating temperatures. *Indian J. Hered.*, **6**: 5-11.
- Ranganath H.A. and Krishnamurthy N.B., 1975. Chromosomal polymorphism in *Drosophila nasuta* III. Inverted gene arrangements in South Indian populations. *J. Heredity*, **66**: 90-96.
- Ranganath H.A. and Krishnamurthy N.B., 1978a. Chromosomal polymorphism in *Drosophila nasuea* V. Concentration of inversions in the salivary gland chromosomes. *Nucleus. Calcutta*, **21**: 158-161.
- Ranganath H.A. and Krishnamurthy N.B., 1978b. Chromosomal morphism in *Drosophila nasuea* II. Coexistence of heteroselection and flexibility in polymorphic system of South India populations. *Genetica*, **48**: 215-221.
- Ratnam D. and Singh A.K., 2008. Quantitative distribution of the cosmopolitan paracentric inversions in mass culture and isofemale lines of *Drosophila ananassae*. *J. Exp. Zool.*, **11**: 465-468.
- Ray-Chaudhuri S.P. and Jha A.P., 1966. Studies on the salivary gland chromosomes of Indian *Drosophila ananassae*. *Proc. Int. Cell Biol Meet Bombay*, **352**.

- Rim N.R., Lee B.S. and Lee T.S., 1986. Chromosomal inversion studies in local populations of *Drosophila melanogaster*. Korean J. Genet., **8**: 12-22.
- Shyamala B.V. and Ranganath H.A., 1988. Inversion polymorphism in natural populations of *Drosophila nasuta nasuta*. Proceedings: Animal Sciences, **97**:471-477.
- Singh A.K., 2000. Chromosomal polymorphism in natural populations of *Drosophila ananassae* from Sultanpur, Uttar Pradesh. J. Exp. Zool., **3**: 93-96.
- Singh A.K., 2017. Perusal of genetic variation in *Drosophila* populations through various methods of genetic polymorphisms. Recent Trends in Biological Research, Global Academy Society, **8**:112-130.
- Singh A.K., Kumar S. and Ratnam D., 2014. Genetic differentiation in natural populations and their mass culture stocks of *Drosophila ananassae*. Thai. J. Genetics, **7**: 123-132.
- Singh A.K. and Singh B.N., 1986. Inversion karyotypes and crossing over in *Drosophila ananassae*. Dros. Inf. Serv., **63**: 127.
- Singh A.K. and Singh B.N., 1988a. Heterozygous inversions and spontaneous male crossing over in *Drosophila ananassae*. Genome, **30**: 445-450.
- Singh A.K. and Singh B.N., 1988b. An extreme linkage between inversions in *Drosophila ananassae*. Current Science, **57**:400-402.
- Singh A.K. and Singh B.N., 1989. Further data on interchromosomal association in *Drosophila ananassae*. Naturalia, **14**:19-29.
- Singh A.K. and Singh B.N., 1990. Recombination in *Drosophila* males. Indian Rev. Life Science, **10**: 27-53.
- Singh A.K. and Singh B.N., 1991. A new inversion in Indian *Drosophila ananassae*. Dros. Inf. Serv., **70**: 201-202.
- Singh B.N., 1982. Persistence of chromosomal polymorphism in various strains of *Drosophila ananassae*. Genetica, **59**: 151-156.
- Singh B.N., 1986. Genetic similarity between natural populations of *Drosophila ananassae* from Kerala and Andaman and Nicobar Islands. Genetica, **69**: 143-147.
- Singh B.N., 1987. On the degree of genetic divergence in *Drosophila ananassae* populations transferred to laboratory conditions, Zeit Zool. Syst. Evol., **25**: 180-187.
- Singh B.N., 1988. Evidence for random genetic drift in laboratory populations of *Drosophila ananassae*, Ind. J. Exp. Biol., **26**: 85-87.
- Singh B.N., 1989. Inversion polymorphism in Indian populations of *Drosophila ananassae*. Hereditas, **110**: 133-138.
- Singh B.N., 1996. Population and behaviour genetics of *Drosophila ananassae*, Genetica, **97**: 321-32.
- Singh B.N., 1998. Population genetics of inversion polymorphism in *Drosophila ananassae*, Ind. J. Exp. Biol., **36**: 739-748.
- Singh B.N., 2010. *Drosophila ananassae*: A good model species for genetical, behavioural and evolutionary studies. Ind. J. Exp. Biol., **48**: 333-345.
- Singh B.N., 2013. Genetic polymorphisms in *Drosophila*. Curr. Sci., **105**: 461-469.
- Singh B.N. and Banerjee R., 1997. Increase in the degree of inversion polymorphism in *Drosophila bipectinata* populations transferred to laboratory conditions J. Zool. Syst. Evol. Res., **35**: 153-157.
- Singh B.N. and Das A., 1990. Inversion polymorphism in Indian natural populations of *Drosophila melanogaster*, Genome, **33**: 311-316.
- Singh B.N. and Das A., 1991a. Changes of inversion polymorphism in laboratory populations of *Drosophila melanogaster*, Z. Zool. Syst. Evolution Forsch.
- Singh B.N. and Das A., 1991b. Epistatic interaction between unlinked inversions in Indian natural populations of *Drosophila melanogaster*. Genetique Selection Evolution, **33**: 311-316.
- Singh B.N. and Das A., 1992. Changes of inversion polymorphism in laboratory populations of *Drosophila melanogaster*. Journal of Zoological Systematics and Evolutionary Research, **30**:268-280.

- Singh B.N. and Singh A.K., 1987. Intrachromosomal effect of inversion on crossing over in *Drosophila ananassae*. Braz. J. Genet., **10**: 1-12.
- Singh B.N. and Singh A.K., 1987. The effects of heterozygous inversions on crossing over in *Drosophila ananassae*. Genome, **29**: 802-805.
- Singh B.N. and Singh A.K., 1988. Crossing over between linked inversions in *Drosophila ananassae*. Hereditas, **109**:15-19.
- Singh B.N. and Singh A.K., 1989. The suppression of crossing over between heterozygous inversions of *Drosophila ananassae*. Genetika, **21**:155-163.
- Singh B.N. and Singh A.K., 1990. Linkage disequilibrium in laboratory strains of *Drosophila ananassae* is due to drift. Hereditas, **112**: 203-208.
- Singh B.N. and Singh A.K., 1991. Non-random association between independent inversions in laboratory strains of *Drosophila ananassae*. Naturalia, **16**: 11-18.
- Singh B.N., Singh S. and Banerjee P., 2012. A comparison between polytene chromosomes of two sibling species of *Drosophila*: *D. ananassae* and *D. pallidosa*. Dros. Infor. Serv., **95**: 50-54.
- Singh P. and Singh B.N., 2007. Population genetics of *D. ananassae*: Genetic differentiation among Indian natural populations at the level of inversion polymorphism, Gent. Res. Camb., **89**: 191-199,
- Singh P. and Singh B.N., 2008a. Population genetics of *Drosophila ananassae*, Variation in the degree of genetic divergence in populations transferred to laboratory conditions. Zool. Stud., **47**: 704-712.
- Singh P. and Singh B.N., 2008b. Population genetics of *Drosophila ananassae*, Genet. Res., **90**: 409-419.
- Singh P. and Singh B.N., 2010. Population genetics of *D. ananassae*: Chromosomal association studies in Indian populations, Genetika, **42**: 210-222.
- Singh G. and Singh A.K., 2015. Chromosomal translocation at the terminal end of 2L in *Drosophila malerkotliana*. Dros. Inf. Serv., **98**: 43.
- Singh G. and Singh A.K., 2016. Chromosomal polymorphisms in a natural population of *Drosophila malerkotliana*. Dros. Inf. Serv., **99**: 49-51.
- Singh G. and Singh A.K., 2018. Excessive occurrence of paracentric inversions in a natural population of *Drosophila bipectinata*. J. Exp. Zool. India, (in press).
- Singh S. and Singh B.N., 2001. *Drosophila bipectinata* species complex. Ind. J. Exp. Biol., **39**, 835-844.
- Sperlich D. and Pfriem P., 1986. Chromosomal polymorphism in natural and experimental populations, pp. 257-309 in The Genetics and Biology of *Drosophila*, Vol. 3a, edited by M. Ashburner, L. Carson and J.N. Thompson, Jr. Academic Press, London.
- Stalker H.D., 1976. Chromosome studies in wild populations of *Drosophila melanogaster*. Genetics, **82**: 323-347.
- Stalker H.D., 1980. Chromosome studies in wild populations of *Drosophila melanogaster*, II. Relationship of inversion frequencies to latitude, season, wing loading and flight activity, Genetics, **95**: 211-223.
- Tomimura Y., Matsuda M. and Tobar Y.N., 2005. Chromosomal phylogeny and geographical divergence in the *Drosophila bipectinata* complex. Genome, **48**: 487-502.