

Volume 64, Issue 2, 2020

**Journal of Scientific Research** 

Institute of Science, Banaras Hindu University, Varanasi, India.



## Drosophila ananassae Stands Distinct from other Species of Drosophila in its Pattern of Chromosomal Polymorphism

B. N.  $Singh^*$ 

Genetics Laboratory, Department of Zoology, Institute of Science, Banaras Hindu University, Varanasi-221005, India. bashisthsingh2004@rediffmail.com, bnsinghbhu@gmail.com, bnsingh@bhu.ac.in

Abstract: Drosophila, a genus of family Drosophilidae (Class-Insecta; Order-Diptera) is characterized by rich species diversity containing more than 1500 species. It possesses polytene chromosomes which have been mostly studied from salivary glands and polytene chromosome maps have been prepared for a large number of species. It is known that about 100 species of Drosophila contain chromosomal aberrations and thus chromosomally polymorphic. There are different types of chromosomal aberrations but paracentric inversions are more common. There are intra and interspecific variations in the frequencies of inversions and the pattern of chromosomal polymorphism varies in different cases. To explain these findings of different cases different concepts/ hypothesis/ ideas have been proposed by different researchers: ecological niche hypothesis, flexible and rigid polymorphism, homoselection vs heteroselection, genetic coadaptation hypothesis, concepts of central and marginal populations, altitudinal and latitudinal variations, inversion clines, heterosis and balanced polymorphism, linkage disequilibrium, urban and rural population differentiation, suppression of crossing-over, inversion and frequency dependent selection, inversion and rare male mating advantage, inversions, behavior and mate recognition system etc. If these findings and their interpretations are compared among different species, D. ananassae, a cosmopolitan and domestic species, stands distinct from other species and has developed its own mechanism to adjust with its environment.

*Index Terms:* Chromosomal polymorphism, different species, *Drosophila ananassae*, evolutionary significance.

Species diversity in the genus *Drosophila* is well known. More than 1500 species have been reported so far and many more may be described if the research on taxonomy of *Drosophila* continues in future (Gupta, 2005; Brake & Bachli, 2008; Singh, 2015). For tracing ancestry chromosomal sequences have been used in Hawaiian species of Drosophila (Carson, 1987). Chromosomal polymorphism has been studied extensively in numerous species of Drosophila and extensive data have been reported on inversion frequencies in natural and laboratory populations of various species such as D. pseudoobscura, D. persimilis, D. willistoni, D. robusta, D. rubida, D. subobscura, D. pavani and others, (for references see the review by Singh, 2019). The data have been interpreted in different ways by suggesting different hypotheses/concepts/ideas by numerous investigators such as Dobzhansky, da Cunha, Carson, Levitan, Stalker, Brncic, Prevosti, Krimbas, Loukas, Sperlich and others. In India also, chromosomal polymorphism has been studied in D. ananassae, D. melanogaster, D. nasuta and D. bipectinata (Ranganath & Krishnamurthy, 1975, 1978; Shyamala & Ranganath, 1988; Kumar & Gupta, 1988, 1989, 1991; Singh, 1984, 1989, 1996, 1998; Banerjee & Singh, 1996; Singh & Singh, 2007a, 2008a; Das & Singh, 1991a, b; Singh & Das, 1992). D. ananassae, a cosmopolitan and domestic species possessing numerous genetic peculiarities (Singh, 2000, 2010, 2018a), presents unique features of its chromosomal polymorphism which are briefly described below:

 A large number of chromosomal aberrations are reported in natural and laboratory populations of *D. ananassae* (Kaufman, 1936; Kikkawa, 1938; Dobzhansky & Dreyfus, 1943; Shirai & Moriwaki, 1952; Seecof, 1957; Freire-Maia, 1961; Futch, 1966; Ray-Chaudhuri & Jha, 1966; Sajjan & Krishnamurththy, 1972; Reddy & Krishnamurthy, 1972, 1974; Hinton & Downs, 1975; Singh, 1988a, 2019; Singh & Singh 2007b). There are 78 paracentric inversions, 21 pericentric inversions and 48 translocations. Thus it shows high degree of chromosomal polymorphism. The presence of highest number of pericentric inversions and translocations represents its specific feature. These

<sup>\*</sup> Corresponding Author

aberrations are rare in other species of *Drosophila* and Freire-Maia (1961) suggested that it has developed some special mechanisms to retain such disadvantageous aberrations in its populations. It also reflects its unusual mutational property.

- 2) It is a feature of the pattern of chromosomal polymorphism in *D. ananassae* that out of so many paracentric inversions known in this species, only three (Subterminal-AL in 2L, Terminal DE in 3L, Basal-ET in 3R) could become cosmopolitan in distribution (Carson, 1965; Futch, 1966; Singh, 1970). It is suggested that these inversions originated once and spread to different populations and thus having monophyletic origin (Singh, 1970). These inversions captured heterotic gene complexes which provided adaptive superiority to their carriers. Thus they have become coextensive with the species (Singh, 1989).
- 3) When the stocks are maintained in the laboratory, these inversions persist showing heterotic buffering is associated with these inversions (Singh, 1982a).
- 4) Singh (1972, 1981, 1985, 2018b) tested the genetic coadaptation hypothesis of Dobzhansky (1950) but his results are not in agreement to those of Dozhansky in *D. pseudoobscura*. There was persistence of superiority of inversion heterozygotes in interstrain crosses in *D. ananassae* which clearly demonstrated that there is no coadaptation of chromosomes in natural populations of *D. ananassae*. In *D. ananassae*, genetic coadaptation was also tested using body size and interchromosomal associations. Interestingly, evidence for the absence of coadaptation in *D. ananassae* has also been provided by Yadav and Singh (2003), Singh (1982b) and Singh and Singh (2010a).
- 5) Extensive data on the frequencies of three cosmopolitan inversions in Indian natural populations of *D. ananassae* have been presented by Singh and his coworkers (Singh, 1984, 1989, 1996, 1998; Singh & Singh, 2007a). Their results demonstrated that Indian populations show evolutionary divergence and populations from south show more divergence when compared with those from the north. Further, south Indian populations show genetic similarity with those from Andaman and Nicobar Islands (Singh, 1986). Genetic drift may also cause changes in the frequencies of inversions in laboratory populations (Singh, 1987, 1988b; Singh & Singh, 2008b).
- 6) There is association between rare male mating advantage and AL inversion karyotype, inversion karyotype and mate recognition system and inversion karyotypes and mating propensity (Singh & Chattedrjee, 1986, 1988; Som & Singh, 2004; Nanda & Singh, 2011).
- Linked inversions strongly suppress crossing over between them (Singh, 1973; Singh & Singh 1988; Singh & Mohanty, 1990). Tight linkage between inversions and founder effect

cause linkage disequilibrium in isofemale lines of *D. ananassae* (Singh & Singh, 1990).

- For the first time population substructuring at the level of inversion polymorphism in Indian populations has been reported (Singh & Singh, 2010b).
- Interestingly, a new inversion within the subterminal (AL) in 2L was detected in a laboratory stock showing superiority of inversion heterozygotes (Singh, 1983).
- 10) In *Drosophila*, females show crossing-over but males do not show crossing-over. So the paracentric inversions do not affect the fertility of males. However, *D. ananassae* shows male crossing over as well as the presence of paracentric inversions (Singh, 2019, 2020).

In other species of *Drosophila*, the following conclusions are briefly described in respect of chromosomal polymorphism.

- In *D. melanogaster*, more than 300 paracentric inversions have been reported (Das & Singh, 1991a; Lemeunier & Aulard, 1992). There is evidence for latitudinal clines in inversion frequencies in natural populations (Knibb, 1982; Das & Singh, 1991b; Singh & Das, 1992a). Inversions are often eliminated from laboratory populations (Singh & Das, 1992b).
- In D. pseudoobscura, D. willistoni, D. paulistorum, D. pavani, and D. bipectinata, breakdown of heterosis in interracial hybridization experiments extends evidence for genetic coadaptation in natural populations of these species (Dobzhansy 1950, Dobzhansky & Pavlovasky, 1958; Brncic, 1961; Banerjee & Singh, 1998).
- D. pseudoobscura shows seasonal variations in the frequencies of inversions in it natural poplations (Dozhansky, 1947).
- 4) In *D. robusta*, concept of heteroselection vs homoselection in central and marginal populations was suggested by Carson (1958). Central populations show heteroselection and high adaptedness in contrary to marginal populations showing homoselection and more adaptability which is correlated with rate of recombination. In the same species, Livitan (1954) reorted non- random associations of inversions in natural population for the first time.
- 5) Dobzhansky et al. (1950) proposed ecological niche hypothesis based on their work on *D. willistoni* and other species: "Inversion polymorphism is a device to cope with the diversity of environments".
- Inversion frequencies do not vary in natural populations of *D. bipectinata* extending evidence for rigid chromosomal polymorphism (Banerjee & Singh, 1996).
- 7) A large number of inversions are known in *D. subobscura* which show clines in their frequencies (Krimbas and Luokas, 1980).
- 8) *D. nasuta* shows high degree of chromosomal polymorphism in its natural populations. Evidence has been

presented for flexibility, heteroselection, linkage disequilibrium, and absence of genetic coadatation (Ranganath & Krishnamurthy, 1975, 1978; Shyamla & Ranganath, 1988; Kumar & Gupta, 1988, 1989, 1991).

Thus, the comparison of features of chromosomal polymorphism observed in *D* ananassae with other species clearly shows that it stands distinct from other species. Certainly, it has developed its own mechanism to adjust with its environment.

## REFERENCES

- Brake, I., & Bachli G. (2008). Drosophilidae (Diptera)-In *World catalogue of insects*, pp 1–412. Appollo Books, St,enstup, Denmark.
- Banerjee, R., & Singh, B. N. (1996). Inversion polymorphism in natural populations of *Drosophila bipectinata*. *Cytobios*, 87, 31–43.
- Banerjee, R., & Singh, B. N. (1998). Evidence for coadaptation in geographic populations of *Drosophila bipectinata*. J. Zool. Syst. Evol. Res., 36, 1–6.
- Carson, H.L. (1958). Population genetics of *Drosophila robusta*. *Ad. Genet.*, 9, 1-40.
- Carson, H. L. (1965). Chromosomal polymorphism in geographically widespread of *Drosophila*, In:*The Genetics of Colonizing Species* (eds. H. G. Baker and G. L. Stebbins), Academic Press, NewYork, pp. 503-531.
- Carson, H. L. (1987). Tracing ancestry with chromosomal sequences. *Trends Ecol. Evol.* 2, 203–207.
- Das, A., & Singh, B.N. (1991a). Chromosomal polymorphism in Indian natural populations of *Drosophila melanogaster*. *Korean J. Genetics*, 13, 97-112.
- Das, A., & Singh, B.N. (1991b). Genetic differentiation and inversion clines in Indian natural populations of *Drosophila melanogaster*. *Genome*, 34, 618-625.
- Dobzhansky, Th. (1947). Adaptive changes induced by natural selection in wild populations of *Drosophila*. *Evolution*, 1, 1–16.
- Dobzhansky, Th. (1950). Genetics of natural populations.XIX.Origin of heterosis through selection in populations of *Drosophila pseudoobscura*. *Genetics*, 35, 288–302.
- Dobzhansky, Th., Burla H., & Da Cunha, A. B. (1950). Adaptive chromosomal polymorphism in *Drosophila willistoni*. *Evolution*, 4, 212–235.
- Dobzhansky, Th., & Dreyfus, A. (1943). Chromosomal aberrations in Brazilian *Drosophila ananassae*. *Proc. Nat. Acad. Sci. USA*, 29, 301-5.
- Dobzhansky, Th., & Pavlovasky O. (1958). Interracial hybridization and breakdown of coadapted gene complexes in *Drosophila paulistorum* and *D. willistoni*. *Proc. Natl. Acad. Sci.USA*, 44, 622–629.

- Freire-Maia, N. (1961). Peculiar gene arrangements in Brazilian natural populations of *Drosophila ananassae*. *Evolution*, 15, 486-495.
- Futch, D. G. 1966 A study of speciation in South Pacific populations of *Drosophila ananassae*. Univ. Tex. Publ., 6615, 79–120.
- Gupta, J. P. (2005). A monograph on Indian Drosophilidae. J. Sci. Res. (B.H.U.), 51, 1–252
- Hinton, C.W., & Downs, J.E (1975). The mitotic, polytene and meiotic chromosomes of *Drosophila ananassae*. J. Heredity, 66, 353-361;
- Kaufmann, B.P. (1936). A terminal inversion in Drosophila ananassae. Proc. Natl. Acad. Sci. USA, 22, 591-594
- Kikkawa, H. (1938). Studies on the genetics and cytology of *Drosophila ananassae. Genetica*, 20, 458-516.
- Knibb, W. R. (1982). Chromosome inversion polymorphism in Drosophila melanogaster. II. Geographic clines and climatic associations in Australasia, North America and Asia. Genetica, 58,213–221.
- Krimbas, C. B., & Loukas, M. (1980). The inversion polymorphism in *Drosophila subobscura*. Evol. Biol., 12, 163–234.
- Kumar, A., & Gupta, J. P. (1988). Linkage disequilibrium, natural selection and epistatic gene interaction in *Drosophila nasuta*. *Genome*, 30, 495–498.
- Kumar, A., & Gupta, J.P. (1989). Gene frequencies in natural and laboratory populations of *Drosophila nasuta*. *Hereditas*, 110, 1-5.
- Kumar A., & Gupta, J. P. (1991). Heterosis and lack of coadaptation in *Drosophila nasuta*. *Heredity*, 67, 275-279.
- Lemeunier, F., & Aulard, S. (1992). Inversion polymorphism in Drosophila melanogaster. In Drosophila Inversion Polymorphism (eds Krimbas, C. B. and Powell, J. R.), CRC Press, Boca Raton, Florida, USA, pp. 339–406.
- Levitan, M. (1954). Position effects in natural populations. *Am. Nat.*, 88, 419–423.
- Nanda, P., and Singh, B. N. (2011). Effect of chromosome arrangements on mate recognition system leading to behavioral isolation in *Drosophila ananassae*. *Genetica* ,139, 273-27
- Ranganath, H. A.,, & Krishnamurthy, N. B. (1975). Chromosomalpolymorphism in *Drosophila nasuta* III. Inverted gene arrangements in south Indian populations. J. *Hered.*, 66, 90–96.
- Ranganath, H. A., & Krishnamurthy, N. B. (1978). Chromosomal morphism in *Drosophila nasuta* II. Coexistence of heteroselection and flexibility in polymorphic system of south Indian populations. *Genetica*, 48, 215–221.
- Ray-Chaudhuri, S. P., & Jha, A. P. (1966). Studies on the salivary gland chromosomes of Indian *Drosophila* ananassae. Proc. Int. Cell Biol. Meet. Bombay, pp. 352-383.

- Reddy, G.S., & Krishnamurthy, N.B. (1972). Two new gene arrangements in *Drosophila ananassae* from south India. *Dros. Inf. Serv.*, 48, 140-142,
- Reddy, G. S., & Krishnamurthy, N.B. (1974). Altitudinal gradients in the frequencies of three common inversions in *Drosophila ananassae*. *Dros. Inf. Serv*, 51, 136-137.
- Sajjan S N & Krishnamurthy N B 1972 New gene arrangements in *Drosophila ananassae*. *Dros. Inf. Serv.*, 48, 103-104.
- Seecof, R L. (1957). Cytological analysis. Section III. From XXII . Genetic studies of irradiated natural populations of Drosophila. Univ. Texas Publs., 5721, 269-281.
- Shirai, M., & Moriwaki D. (1952). Variation of gene sequences in various strains of *Drosophila ananassae*. Dros. Inf. Serv., 26, 120-121.
- Shyamala, B.V., & Ranganath, H.A. (1988). Inversion polymorphism in natural populations of *Drosophila nasuta nasuta*. Proc Ind. Acad. Sci. (Anim. Sci.), 97, 471-477
- Singh, B.N. (1970). Distribution of most common inversions of Drosophila ananassae in different parts of India including Andaman and Nicobar Islands. Ind. Biol., 2, 78-81.
- Singh, B.N. (1972). The lack of evidence for coadaptation in geographic populations of *Drosophila ananassae*. *Genetica*, 43, 582-588.
- Singh B.N. (1973). Recombination between heterozygous inversions in *Drosophila ananassae*. *Genetica*, 44, 602-607.
- Singh, B.N. (1981). Interracial hybridization in *Drosophila* ananassae. Genetica ,57, 139-142.
- Singh B. N. (1982a). Persistence of chromosomal polymorphism in various strains of *Drosophila ananassae*. Genetica ,59, 151-156.
- Singh, B.N. (1982b). The lack of evidence for interchromosomal interactions in *Drosophila ananassae*. *Naturalia*, 7, 29-34.
- Singh, B. N. (1983). An inversion within the subterminal inversion in *Drosophila ananassae*. *Experientia*, 39, 231-235.
- Singh, B. N. (1984). High frequency of cosmopolitan inversins in natural populations of *Drosophila ananassae* from Kerala, South India. J. Hered., 75, 504-505.
- Singh, B. N. 1985 Heterosis without selectional coadaptation in Drosophila ananassae. Theor. Appl. Genet. ,69, 437-441.
- 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. (1988a). Chromosomal polymorphism of Drosophila ananassae. Ind. Rev Life Sci. ,8, 147-168.
- Singh, B. N. (1988b). 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*, 97,321-332.
- Singh, B. N. (1998). Population genetics of inversion polymorphism in *Drosophila ananassae*. Ind. J. Exp. Bio., 36, 739-748.
- Singh, B.N. (2000). *Drosophila ananassae* a species characterised by several unusual genetic features. *Curr.Sci.*,78,391-398.
- Singh B.N. (2010). Drosophila ananassae : A good model species for genetical, behavioural and evolutionary studies. Ind. J. Exp. Bio., 48,333-345.
- Singh, B.N. (2015). Species and genetic diversity in the genus *Drosophila* inhabiting the Indian subcontinent. *J. Genet.* 94,351-361.
- Singh, B.N. (2018a). *Drosophila ananassae*-Why it is considered as a unique species in the genus *Drosophila*. *Curr. Sci.*, 114, 11-12.
- Singh, B.N. (2018b). The Dobzhansky's concept of genetic coadaptation: *Drosophila ananassae* is an exception to this concept. *J. Genet.*, 97, 1039-46.
- Singh, B.N. (2019). Hundred years of research on inversion polymorphism in *Drosophila*. *Curr. Sci.*, 117, 761-775.
- Singh, B.N. (2020). Drosophila ananassae: a species characterized by spontaneous male recombination in appreciable frequency. J. Genet. ,99, 12.
- Singh B. N. & Chatterjee, S. (1986). Mating ability of homo- and heterokaryotypes of *Drosophila ananassae* from natural populations. *Heredity*, 57, 75-78.
- Singh, B.N., & Chatterjee, S.(1988). Parallelism between male mating propensity and chromosome arrangement frequency in natural populations of *Drosophila ananassae*. *Heredity*, 60, 269-272.
- Singh, B.N., &. Das, A. (1992a). Furher evidence for latitudinal inversion clines in natural populations of *Drosophila melanogaster* from India. J. Heredity, 83, 227-230.
- Singh, B.N., & Das A. (1992b). Changes of inversion polymorphism in laboratory populations of *Drosophila melanogastaer. Zeit. Zool. Syst. Evol.*, 30, 268-280.
- Singh, B. N., & Mohanty, S. 1990 Lack of correlation between crossing-over and chromosome distance between inversions in *Drosophila ananassae*. *Genome*, 33, 592 595.
- Singh, B.N., & Ray-Chaudhuri S.P. (1972). Balanced chromsomal polymorphism in experimental populations of *Drosophila ananassae*. *Ind. J. Exp. Biol.*, 10, 301-303.
- Singh, B. N., & Singh, A. K. (1988). Crossing-over between linked inversions in *Drosophila ananassae*. *Hereditas*, 109, 15-19.

- Singh, B. N., & Singh, A.K. (1990). Linkage disequilibrium in laboratory strains of *Drosophila ananassae* is due to drift. *Hereditas*, 112, 203-208.
- Singh, P., & Singh B. N. (2007a). Chromosomal aberrations in Drosophila ananassae. Dros. Inf. Serv. ,90, 49-54.
- Singh, P., and Singh, B.N. (2007b). Population genetics of Drosophila ananassae: Genetic differentiation among Indian natural populations at the level of inversion polymorphism. Genet. Res., 89, 191-199.
- Singh, P., & Singh, B.N. (2008a). Population genetics of *Drosophila ananassae. Genet. Res.* 90, 409-419.
- Singh, P., & Singh, B.N. (2008b). 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., & Singh, B.N. (2010a). Population genetics of Drosophila ananassae: chromosomal association studies in Indian populations. Genetika, 42, 210-222.
- Singh, P., & Singh, B.N. (2010b). Population genetics of *Drosophila ananassae*. Evidence for population substructuring at the level of inversion polymorphism in Indian natural populations. *Int. J. Biol.* (Canada) ,2,19-28.
- Som, A., & Singh, B.N. (2004). Rare male mating advantage for inversion karyotype in *Drosophila ananassae*. *Behav. Genet.*, 34, 335-342.
- Yadav, J.P., & Singh, B.N. (2003). Population genetics of Drosophila ananassae: inversion polymorphism and body size in Indian geographical populations. J. Zool. Syst. Evol. Res., 41, 217-226.

\*\*\*