Population and behaviour genetics of *Drosophila ananassae*

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Received 16 August 1994 Accepted 17 September 1995

**Key words:** *Drosophila ananassae*, population and behaviour genetics

**Abstract**

*Drosophila ananassae* is a cosmopolitan and domestic species. It occupies a unique status among the *Drosophila* species due to certain peculiarities in its genetic behaviour. The most unusual feature of this species is spontaneous male recombination in appreciable frequency. The present review summarises the work done on population and behaviour genetics of *D. ananassae* from India. Population dynamics of three cosmopolitan inversions has been studied in Indian populations of *D. ananassae* and it is evident from the results that there is a considerable degree of genetic divergence at the level of inversion polymorphism. In general, the populations from south India show more differentiation than those from the north. These three cosmopolitan inversions, which are coextensive with the species, exhibit heterosis. Interracial hybridization does not lead to breakdown of heterosis, which suggests that evidence for coadaptation is lacking in geographic populations of *D. ananassae*. Heterosis appears to be simple luxuriance rather than populational heterosis (coadaptation). Unlinked inversions occur in random associations, indicating no interchromosomal interactions. However, two inversions of the third chromosome often show strong linkage disequilibrium in laboratory populations, which is due to epistatic gene interaction and suppression of crossing-over. Genetic variations for certain allozyme polymorphism and sternopleural bristle phenotypes in Indian populations of *D. ananassae* have also been observed.

A number of investigations have also been carried out on certain aspects of behaviour genetics of Indian *D. ananassae*. There is evidence for sexual isolation within *D. ananassae*. Significant variations in mating propensity of several isofemale strains, inversion karyotypes, the diminishing effects of certain mutations on sexual activity of males and positive response to selection for high and low mating propensity provide evidence for genetic control of sexual behaviour in *D. ananassae*. Males contribute more to variation and thus are more subject to intra-sexual selection than females. Evidence for rare male mating advantage has also been presented. Geographic strains of *D. ananassae* show variation with respect to oviposition site preference. The results of studies on pupation site preference, which is an important component of larval behaviour, suggest that larval pupation behaviour in *D. ananassae* is under polygenic control with a substantial amount of additive genetic variation.

**Introduction**

In studies of population and behaviour genetics, *Drosophila* has proved to be uniquely useful and a large body of information on this subject has been accumulated as a result of the work done on various species. The population genetics studies have mainly involved concealed genetic variability caused by deleterious genes, chromosomal variability and allozyme polymorphisms. In various species of *Drosophila*, it has been demonstrated that sexual and non-sexual behaviour of adults and behaviour of larvae are influenced by genetic factors.

*Drosophila ananassae*, a cosmopolitan and domestic species, belongs to the *ananassae* species complex of the *ananassae* subgroup of the *melanogaster* group (Bock & Wheeler, 1972). Kikkawa (1938) 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 unique among the various *Drosophila* species thus far investigated. *D. ananassae*
Drosophila ananassae occupies a unique status among the Drosophila species due to certain peculiarities in its genetic behaviour. One example is an appreciable level of spontaneous meiotic male recombination (Kale, 1969; Hinton, 1970; Moriwaki, Tobari & Oguma, 1970; Singh & Singh, 1988a). 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 Singh, 1985a). A spontaneous bilateral genetic mosaic, which was characterised by three mutant characters (cu, e, se) on the left side and all normal characters on the right side, was detected while scoring the progeny of a test cross between heterozygous males and mutant females. Its probable origin is attributed to mitotic recombination in the zygote which was genotypically heterozygous (Singh & Mohanty, 1992). A number of investigations carried out on chromosomal polymorphism in D. ananassae have revealed that it presents a high degree of chromosomal variability in its populations (for references see Singh, 1988a; Tobari, 1993). A total of 69 paracentric inversions, 17 pericentric inversions and 13 translocations have been detected in natural populations of D. ananassae (Tobari, 1993). The occurrence of pericentric inversions and translocations is rare in other species of Drosophila and reflects unusual mutational properties of D. ananassae. There is evidence for intra- and interchromosomal effects of heterozygous inversions on crossing-over in males and females of D. ananassae (Singh & Singh, 1987, 1988a; Singh & Mohanty, 1991). Crossing-over between linked inversions has also been studied cytologically and the results have indicated that there is strong suppression of crossing-over between inversions in D. ananassae (Singh, 1973; Singh & Singh, 1988; Singh & Mohanty, 1990). It has been suggested that this genetic characteristic of the species may confer advantages to it due to low levels of inversion heterozygosity in natural populations. Isozyme polymorphism has also been studied in certain populations of D. ananassae, indicating the presence of genetic variability among populations (Johnson, 1971). Multiple amylase genes in D. ananassae have also been reported by Da Lage et al. (1992). On the basis of positive response to selection, evidence for polygenic control and additive genetic variation for phototactic behaviour in D. ananassae has been presented (Markow & Smith, 1979). Transposable elements have also been reported in D. ananassae. The tom element is involved in mutations at the Om (optic morphology) locus (Hinton, 1984; Shrimpton, Montgomery & Langley, 1986; Matsubayashi et al., 1991). RFLP studies (Stephan, 1989) at the X-linked Om (1D) locus of D. ananassae populations from Burma, India and Brazil showed variation in the average heterozygosity per nucleotide and restriction sites. In the present review, the work done in India on population and behaviour genetics of D. ananassae is summarised.

Population genetics

Studies on chromosomal polymorphism in Indian populations of D. ananassae were initiated by Ray-Chaudhuri and Jha (1966, 1967) who detected several chromosomal aberrations and found geographic differentiation of inversion polymorphism. Since then a number of investigations on chromosomal polymorphism in Indian populations of D. ananassae have been carried out, reporting several chromosomal aberrations including paracentric and pericentric inversions and translocations (Singh, 1970, 1983a; Singh & Singh, 1991; Singh, Mishra & Jha, 1971; Singh, Jha & Rahman, 1972; Nirmala Sajan & Krishnamurthy, 1970, 1972; Reddy & Krishnamurthy, 1972a,b). The three cosmopolitan inversions (Fig. 1) have become coextensive with the species considering the monophyletic origin of these inversions. Extensive studies on the frequencies of these inversions in Indian populations have been reported. Reddy and Krishnamurthy (1974) observed significant changes in the frequency of inversion heterozygotes in natural populations from Nilgiri range in South India. They found significant differences in the chromosomal constitutions of D. ananassae populations inhabiting different altitudes in the western range of Nilgiri hills. In a population from Orissa, temperature related changes in the frequency of 2LA (AL) inversion were observed (Dasmoha-