Drosophila ananassae: An interesting biological model

The genus *Drosophila* belongs to the family Drosophilidae, order Diptera and class Insecta. This genus has substantial species diversity at global level and a number of species are also characterized by sufficient degree of genetic diversity when studied at different levels: chromosome, allozyme and DNA. At global level, there are more than 1500 species including Hawaiian species which are unique for evolutionary studies. In the genus, *D. melanogaster* is most commonly used in various kinds of studies beginning from T. H. Morgan in 1909. These areas include genetics, cytogenetics, behaviour, evolution, ecology, molecular biology, etc. Other than *D. melanogaster*, there are a number of species such as *D. ananassae*, *D. pseudoobscura*, *D. persimilis*, *D. simulans*, *D. robusta*, *D. subobscura*, *D. bipectinata*, *D. malerkotliana*, *D. rubida*, *D. funebris*, *D. willistoni*, *D. pavani*, *D. paulistorum*, *D. nasuta*, *D. kikkawai*, etc. that have also been employed in various kinds of investigations. Among these species, *D. ananassae* has been found to be unique based on the findings reported in this species which include: spontaneous meiotic male recombination, pattern of chromosomal polymorphism, Y-4 linkage of nucleolus organizer, presence of parthenogenesis, evolutionary relation with its sibling *D. pallidosa*, intra- and interspecific sexual isolation, hyper mutability, absence of genetic coadaptation, linkage disequilibrium, population substructuring, resistance to environmental stress, DNA polymorphism, presence of spontaneous genetic mosaic, inversion karyotype and mate recognition system, behavioural basis of inversion polymorphism, rare male mating advantage, heterosis and balanced polymorphism. These findings place *D. ananassae* in special position in the whole of genus *Drosophila*[1–4].

Drosophila ananassae was described by Doleschall in 1858 from Ambon Island, Indonesia[5]. Flies were found on ananas fruits hence the name was given *ananassae*. It belongs to the *ananassae* species complex of the *ananassae* subgroup of the *melanogaster* species group. It is a cosmopolitan and domestic species and mainly circum-tropical in distribution. Further, it is of common occurrence in India. Initially, genetical studies were initiated by Kikkawa and Moriwaki in 1930s who clearly showed that *D. ananassae* is genetically unique due to presence of spontaneous male crossing-over and hyper mutability[4,6]. In genus *Drosophila*, recombination occurs in females but not in males. However, *D. ananassae* is an exception to this generalization and is characterized by an appreciable level of male recombination[4]. This unusual phenomenon has been extensively studied in *D. ananassae* by Kikkawa, Moriwaki, Tobari, Matsuda, Hinton, Kale, Singh, Goni and others (for references see Singh[4]). Further, based on genetic data and observation of chiasmata during meiosis in males, it has been suggested that male recombination in *D. ananassae* is meiotic in origin[7,8]. Extensive study on this unique feature of this species has resulted in the discovery of different factors which influence male recombination in *D. ananassae*: suppressors, enhancers, age of males, heterozygous inversions, polygenes and strain factors (for references see Singh[4]).

During experiments on male crossing-over in *D. ananassae*, Singh and Mohanty[9] detected a spontaneous bilateral genetic mosaic for autosomal genes which was caused due to mitotic recombination in heterozygous individuals and this was the first report of spontaneous genetic mosaic for autosomal genes in the genus *Drosophila*.

Although it is a cosmopolitan and domestic species, *Drosophila* exhibits high degree of chromosomal polymorphism in natural populations. A large number of paracentric and pericentric inversions as well as translocations are known to occur in this species[10]. High occurrence of pericentric inversions and translocations in *D. ananassae* reflects its unusual mutational properties and these aberrations are rare in other species of *Drosophila*. Perhaps *D. ananassae* possesses special mechanism to counterbalance the disadvantageous effects of these aberrations[11]. A good example for hypermutability is given by optic morphology (*Om*) hypermutability system in *D. ananassae* which involves *tom* retrotransposons[12]. Although 78 paracentric inversions have been reported so far in this species, only 3: AL in 2L (subterminal), DE in 3L (terminal) and ET in 3R (basal) have become coextensive with the species and incorporated in the genetic system of the species. These three inversions have been called as cosmopolitan inversions. A new inversion was detected within the AL inversion in a laboratory stock of *D. ananassae*[3,13] and because of this new inversion, three different inversion heterozygous karyotypes are seen. Singh and his collaborators have extensively studied the population dynamics of three cosmopolitan inversions in Indian populations and extensive data have been published[14–18]. The important findings pertaining to population genetics of three cosmopolitan inversions in *D. ananassae* are: evolutionary divergence in Indian populations at the level of inversion polymorphism, north–south differentiation in inversion frequencies, persistence of inversions in laboratory populations due to heterosis, linkage disequilibrium between inversions due to founder effects, suppression of crossing over by heterozygous inversions, association between inversions and mating propensity as well as rare male effect, population substructuring, association between inversion karyotype and mate recognition system, and rural–urban differentiation in inversion frequencies. *D. ananassae* has been considered as an exception to the genetic coadaptation hypothesis of Dobzhansky because interracial hybridization does not lead to breakdown of heterosis and heterosis associated with the three cosmopolitan inversions could be explained by luxuriance hypothesis[19].

Resistance to different kinds of stress has also been studied in *D. ananassae*[20–22]. Interestingly, it has been found that flies consuming protein-rich diets have higher desiccation and heat shock resistance. On the other hand, flies that consume carbohydrate-rich diets, have higher starvation and cold resistance. In Indian populations of *D. ananassae*, it has been found that there is a positive correlation between starvation resistance and lipid contents. Further, it was also found that desiccation and lipid contents as well as desiccation and heat resistance showed significant negative correlation. Thus the storing capacity of flies for lipids is important. It was detected that depositions of uric acid crystals in Malpighian tubules of *D. ananassae* possess a regulatory role in desiccation tolerance.

There is a unique pair of sibling species: *D. ananassae* and *D. pallidosa*. A number of investigations have been done

on this unique pair of sibling species[23–31]. Singh and Singh[32] and Singh[33,34] have suggested that *D. pallidosa* does not occupy the full status of species rather it is in *statu nascendi*. The main reason behind this suggestion is that there is no difference in male genitalia between the two species and they are crossable in the lab producing fertile hybrids lacking post-zygotic reproductive isolation. Singh[35] reviewed sibling species in the genus *Drosophila* and in all the pairs/groups, this is the only pair showing these features. In natural populations, they are sympatric and remain reproductively isolated by ethological isolation. *D. pallidosa* is still in the process of speciation and does not occupy the full status of species rather it is incipient species. Intra and interspecific sexual isolation studies between these two species have also shown that degree of isolation varies. *D. ananassae* is a cosmopolitan and domestic species. However, *D. pallidosa* is endemic to certain islands such as South Pacific Islands of Samoa and Fiji. Interestingly, *D. pallidosa* shows greater degree of intraspecific sexual isolation compared to its sibling cosmopolitan species *D. ananassae*[31]. It has also been suggested that *D. ananassae* is ancestral to *D. pallidosa* which means *D. pallidosa* is derived from *D. ananassae* in certain islands of Samoa group. This ancestral and derived relationship between these two sibling species is discussed by Singh[36] while explaining allopatric and sympatric modes of speciation. In these modes of speciation, both the factors are important: geographical component and origin and perfection of reproductive isolation.

Matsuda *et al.*[26] suggested that *D. ananassae* and its relatives have numerous advantages as a model for genetic differentiations and speciation. Based on their observations on multilocus molecular data set, pattern of reproductive isolation, morphological traits, inversion polymorphism, meiotic chromosomes, karyotypes, Y-chromosomal and mitochondrial haplotypes, and hybrid male sterility, they have found that these taxa represent a very recent evolutionary divergence and experience considerable degree of gene flow.

Analysis of DNA polymorphism and divergence data has demonstrated that there is evidence for positive selection favouring preferred codons in recent and long-term evolutionary time scale. It has also shown that strength for selection for preferred codons was stronger for X-chromosome in comparison to autosomes[37].

Thus the genus *Drosophila* is unique and having rich species diversity. If different species are compared there are differences and similarities. Even the species belonging to the same species group might have evolved different mechanisms in order to adjust to their environmental requirements[38]. The findings mentioned here clearly demonstrate that it occupies special status in the whole of genus *Drosophila*. In general, it appears to be an interesting model for different kinds of studies because of its advantages and unique genetic features which make it very suitable for studies in the area of evolutionary biology and speciation. *D. ananassae* is an important member of the *ananassae* species cluster[33] and thus by extending further studies in this cluster, the mechanisms of speciation may be elucidated.

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