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Allopatric populations of *Drosophila ananassae*: a genetically unique species

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Abstract: **Doleschall described *Drosophila ananassae* for the first time in 1858 from Ambon Island, Indonesia. This species belongs to the *ananassae* complex of the *ananassae* subgroup of the *melanogaster* species group. It is a cosmopolitan and domestic species and mainly circumtropical in distribution. It is of common occurrence in Indian subcontinent. In 1930s, Kikkawa and Moriwaki in Japan started genetical studies on *D. ananassae* and showed that it is a genetically unique species characterized by spontaneous male recombination and hypermutability. Another unique genetic feature of this species is absence of genetic coadaptation in its geographic populations which is considered as an exception to the genetic coadaptation concept of Dobzhansky. In a recent paper published in Ethology, Ecology & Evolution, Paul et al. (2024) have presented evidence that two allopatric populations of *D. ananassae* derived from Port Blair and Mysuru exhibit different degrees of trade-offs for evolving response against bacterial infection. Based on their results, the authors have suggested that two geographically isolated populations of a given species respond differently under a given selection pressure and gradually may diverge from each other in nature to develop a species barrier. Thus, the authors believe in allopatric mode of speciation which comes under geographic speciation suggested by Mayr. The importance of these studies is two allopatric populations of *D. ananassae* exhibit different degrees of trade offs for evolving resistance against bacterial infection. These populations may diverge in nature to develop species barrier ie. may be reproductively isolated. These findings in this recent paper are briefly discussed in the light of previous findings pertaining to trade-off studies, genetic differentiation in geographic populations, allopatric mode of speciation, a pair of sibling species: *D. ananassae* and *D. pallidosa,* and speciation in south Pacific populations of *D. ananassae.***

Index Terms: Drosophila ananassae, **Allopatric Populations, Degrees of Trade-offs, Response against bacterial infection, Selection Pressure, Species Barriers, Allopatric mode of speciation.**

I. INTRODUCTION

Drosophila ananassae was described for the first time by Doleschall in 1858 from Ambon Island, Indonesia. It belongs to the *ananassae* complex of the *ananassae* subgroup of the *melanogaster* species group (Bock & Wheeler, 1972). It is a cosmopolitan and domestic species and mainly circumtropical in distribution. It is of common occurrence in Indian subcontinent (Singh, 2015). Initially, Kikkawa and Moriwaki in Japan started genetical studies on *D. ananassae* and showed that it is a genetically unique species characterized by spontaneous male recombination and hypermutability (Singh, 2000, 2010, 2020, 2024; Singh & Yadav, 2015). Another unique genetic feature of this species is absence of genetic coadaptation in its geographic populations which is considered as an exception to the Dobzhansky's genetic coadaptation concept (Singh, 1972, 1985, 2018). In a recent paper published in Ethology, Ecology & Evolution, Paul et al. (2024) have presented evidence that two allopatric populations of *D. ananassae* exhibit different degrees of trade-off for evolving response against bacterial infection.

In their experiments, these investigators have used two allopatric populations of *D. ananassae* which originated from isofemale lines collected from Port Blair, Andaman and Nicobar Islands and Mysuru, Karnataka State. Both the populations are geographically isolated (by ocean). The populations were infected by the bacterium *Pseudomonas aeruginosa* for 55 generations followed by rearing for the next 10 generations under the relaxed selection. The main findings reported by these authors are: progressive increase in immune response in selected flies, gradual increase in survival, reproductive life span, post reproductive life span, development time, fecundity rate, fat content, in contrast to body length and water content that exhibited longitudinal decrease. However, under the relaxed selection regime, the traits showed reversion of the trend but not to the basal level. There was significant difference in the response to selection when the two allopatric populations are compared. The authors have concluded that the two allopatric populations of *D. ananassae* from the Indian sub-continent show different trade-offs between evolving immune response and life history traits. Based on their results, the authors have suggested that two geographically isolated populations of a given species respond differently under a given selection pressure and gradually may diverge from each other in nature to develop a species barrier. Thus the authors believe in allopatric mode of speciation which comes under geographic speciation suggested by Mayr (1966). So the importance of these studies is two allopatric polulations of *D. ananassae* exhibit different degrees of trade offs for evolving resistance against bacterial infection. These populations may diverge in nature to develop species barrier ie. may be reproductively isolated. There is an interesting study by Matsuda et al. (2009) regarding the evolution in the *D. ananassae* species subgroup. These authors have suggested that *D. ananassae* and its relatives have many advantages as a model of genetic differentiation and speciation. They have suggested the evolutionary relationship in the *ananassae* subgroup using multi locus molecular data, karyotypes, meiotic chromosome configurations, chromosomal inversions, morphological traits, and the pattern of reproductive isolation.

There are studies on trade-offs among different life history traits (fitness traits) in *D. ananassae* (Sisodia & Singh, 2002; Yadav & Singh, 2007). There was first report of trade-off between longevity and productivity in *D. ananassae* (Sisodia & Singh, 2002). There are apparent novel trade-offs between hatching time and pupal period, pupal period and egg-pupa development time, and pupal period and larval development time (Yadav & Singh, 2007). It was also found that there was sexual dimorphism for certain trade-offs which may help in understanding the life history evolution of the species (Yadav & Singh, 2007). Sisodia and Singh (2010) presented evidence for resistance to environmental stress based on their studies on 45 Indian natural populations of *D. ananassae* collected from all over India. A significant positive correlation was found between starvation resistance and lipid contents. And also, a significant negative correlation was evident between desiccation and lipid content and between desiccation and heat resistance. Interestingly, the flies from lower latitudes have higher starvation resistance, heat resistance and lipid content but the pattern was reversed for desiccation resistance. Based on these results, Sisodia and Singh (2010) suggested that the flies from different Indian localities varied in their susceptibility to starvation because of the difference in their propensity to store lipid in the body. Experimental evidence for nutrition regulated stress resistance has also been presented in *D. ananassae* which suggests that *D. ananassae* adapts different stress tolerance and life history strategies according to the diets available to the flies (Sisodia & Singh, 2012).

There is extensive study on population dynamics of inversion polymorphism in Indian natural populations of *D. ananassae* (Singh, 1970, 1974, 1984 a, b, c, 1986, 1989, 2019; Yadav & Singh, 2003; Singh & Singh, 2007). Indian populations are genetically differentiated at the level of inversion polymorphism. The populations from South including Andaman and Nicobar Islands maintain the three cosmopolitan inversions in higher frequencies as compared to the populations from north. There is genetic similarity among the populations from south and Andaman and Nicobar Islands (Singh, 1986). There is evidence for population sub-structuring at the level of three cosmopolitan inversions in Indian natural populations of *D. ananassae*. This finding is intriguing in *D. ananassae* because the flies are frequently transported via human travels. Low level of gene flow coupled with high degree of genetic divergence in geographic populations might have occurred historically and is maintained currently (Singh & Singh, 2010).

The domestic *Drosophila* species are characterized by interpopulation migration because they are closely associated with human. In *D. ananassae*, there is no such study in which the level of migration has been studied. Futch (1966) has suggested that the natural populations of *D. ananassae* isolated by mountains and oceans may experience gene exchange because the flies are frequently transported through human travels. It has also been pointed out by Dobzhansky and Dreyfus (1943) that *D. ananassae* has depended on man for its world wide distribution and the coextensive distribution of three cosmopolitan inversions (2LA, 3LA and 3RA) presents a strong support to the suggestion of these authors. In spite of this, *D. ananassae* shows geographic differentiation of inversion polymorphism which must have developed in response to ecological opportunities available to the species in different geographic areas (Singh, 1989).

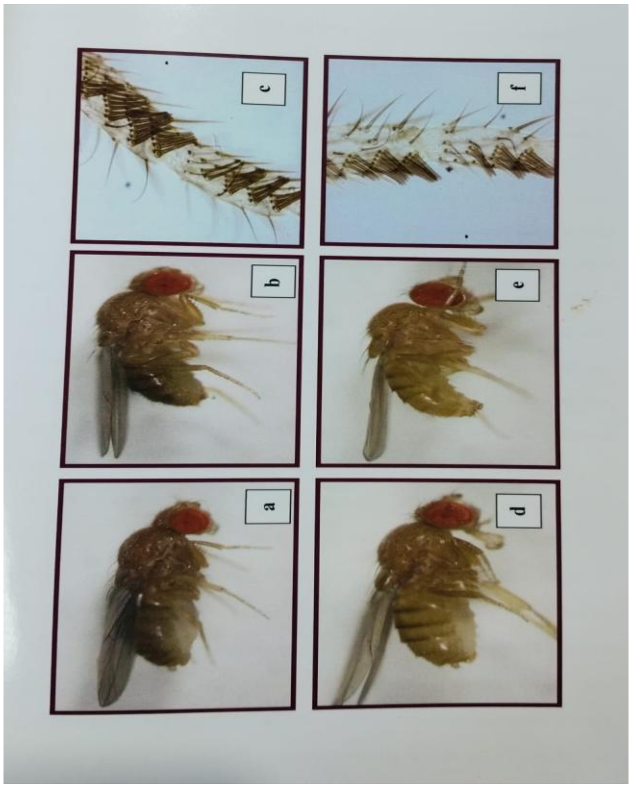

Figure 1.Two sibling species of *Drosophila:* (a) Female of *D. ananassae* (b) Male of *D. ananassae* (c) sex comb of *D. ananassae* (d) Female of *D. pallidosa* (e) Male of *D. pallidosa* (f) Sex comb of D. *pallidosa* (Singh, 2023).

Paul et al. (2024) have mentioned that the outcome of their study suggests natural populations with greater genetic diversity might exhibit greater evolutionary divergence over a given period of time and may develop stronger species barrier between the allopatric populations. This may result in the origin of reproductive isolating mechanisms which is prerequisite for speciation (Singh, 2014). However, the studies on the populations of *D. ananassae* inhabiting the Indian subcontinent have not yielded any indication of species barrier leading to speciation although asymmetric sexual isolation has been observed in laboratory populations of *D. ananassae* caused due to founder effects (Singh &Chattarjee, 1985; Nanda & Singh, 2011). An interesting example may be mentioned here which has originated from the extensive study on speciation in south Pacific populations of *D. ananassae* from Samoa by Futch (1966) who found light and dark forms of *D. ananassae*. The light form of *D. ananassae* has been identified as a new species *D. pallidosa* by Bock and Wheeler (1972). Their separation is just based on sexual isolation and differences in sex comb tooth number but they have identical male genitalia and are crossable in the lab producing fertile hybrids of both sexes. Thus, they lack postzygotic reproductive isolation (Singh, 2023). This is a unique pair of sibling species having close phylogenetic relationship (Singh 2016). *D. ananassae* is a cosmopolitan and domestic species whereas *D. pallidosa* is endemic to South Pacific Island of Samoa and Fijii where both the species are sympatric and remain reproductively isolated by ethological isolation. Figure 1 shows both the sibling species: *D. ananassae* and *D. pallidosa*. Based on the pattern of sexual isolation between these two sibling species, it has been suggested that *D. pallidosa* is derived from *D. ananassae*. Thus, these two sibling species have ancestral and derived relationship (Singh, 2023).

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