REVIEW ARTICLE

Species and genetic diversity in the genus *Drosophila* inhabiting the Indian subcontinent

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Abstract

Biodiversity is the sum total of all living things on the earth with particular reference to the profound variety in structure, function and genetic constitution. It includes both number and frequency of species or genes in a given assemblage and the variety of resulting ecosystems in a region. It is usually considered at three different levels: genetic, species and ecological diversities. Genus *Drosophila* belongs to the family Drosophilidae (class Insecta, order Diptera), characterized by rich species diversity at global level and also in India, which is a megadiverse country. At global level, more than 1500 species have been described and several thousands estimated. Hawaiian Islands are particularly rich in species diversity with more than 500 species which provides a unique opportunity to study evolution in genus *Drosophila*. About 150 species of *Drosophila* have been reported from India. Certain species of *Drosophila* found in India have been investigated for genetic diversity within the species. In this regard, *Drosophila ananassae* is noteworthy. It is a cosmopolitan and domestic species with common occurrence in India and is endowed with many genetic peculiarities. Population genetics and evolutionary studies in this species have revealed as to how genetic diversity within a species play an important role in adaptation of populations to varying environments. In addition, the work carried on *D. melanogaster*, *D. nasuta*, *D. bipectinata* and certain other species in India has shown that these species vary in degree and pattern of genetic diversity, and have evolved different mechanisms for adjusting to their environments. The ecological adaptations to various kinds of stress studied in certain species of *Drosophila* inhabiting the Indian subcontinent are also discussed.

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Introduction

Genus *Drosophila* belongs to the family Drosophilidae (class Insecta, order Diptera). For the first time *Drosophila melanogaster* was described by Meigen in 1830 and was used for experimental studies by Carpenter in 1905. Since the pioneering genetical studies by T. H. Morgan in 1909, *D. melanogaster* has been used as the best biological model for the studies in areas such as genetics, behaviour, evolution, development, molecular biology, ecology and population biology. Advantages of using *Drosophila* as a model organism in laboratory studies include: cosmopolitan distribution, short generation time, easy handling, small size, easy rearing, high fecundity, clear morphology, small number of chromosomes and presence of polytene chromosomes. In addition, it is neither a pest nor a vector.

D. melanogaster is the most extensively used species in the genus. It belongs to the family Drosophilidae, commonly known as Drosophilids. The most important genus of the family is *Drosophila* which has rich species diversity at global level. More than 1500 species are known to occur at global level and estimates run to several thousands (Brake and Bachli 2008). Hawaiian Islands have rich species diversity where more than 500 species are known to occur. They have been divided into eight species groups based largely upon sexually dimorphic characters possessed by males and thought to be used mainly in courtship and mating. There are about 100 species possessing dark patches on wings called picture wing *Drosophila* which have been used in evolutionary studies by Carson and others (for references, see Carson 2002). In India, about 150 species of genus *Drosophila* are known to occur (Gupta 2005; R. S. Fartyal 2014 Recent checklist of genes *Drosophila* from India, unpublished data; A. Naskar, K. K. Bhattacharya and D. Banerjee 2014 Checklist of Indian Drosophilidae (Insecta: Diptera: Drosophilidae), unpublished data) and research on *Drosophila* taxonomy began in 1921, when Bezzi reported *D. repleta* from Kolkata (Sturtevant 1921) which was then a new record from India. Brunetti (1923) described a new

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species of *Drosophila* from Kolkata and named it as *D. prashadi* Duda (1923, 1924) described two species, namely, *D. bipectinata* and *D. fruhstorferi* from Darjeeling, also recording *D. meijerei* at the same time (named *D. nigra* Meijere). Malloch (1924) described a new species, *D. biarmipes* from Coimbatore. Sturtevant (1927) reported four species of *Drosophila* from Chennai: *D. melanogaster*, *D. ananassae*, *D. montium* and D. *tristipennis.* Ray-Chaudhuri and Mukherjee (1941), the first Indian workers, reported two new species, *D. emulata* and *D. brunettii* from Kolkata. These two new species closely resembled *D. melanogaster* and *D. bipectinata* (Gupta 2005). Thus, all the three species of *Drosophila* described from India are considered as invalid species (*D. prashadi*, *D. emulata* and *D. brunettii*). Later, *Drosophila* taxonomy research was carried out in Punjab University, Banaras Hindu University, Mysore University and Pune University, which resulted in description of a large number of new species as well as new records from India (see Gupta 2005; Fartyal *et al.* 2012; A. Naskar, K. K. Bhattacharya and D. Banerjee 2014 Checklist of Indian Drosophilidae (Insecta: Diptera: Drosophilidae), unpublished data). This research continued for a number of years, but suddenly declined. At present, the work on *Drosophila* taxonomy is being carried out only in Uttarakhand by B. K. Singh, R. S. Fartyal and their coworkers who have described a number of new species as well as new records from that region (personal communication). Several species of *Drosophila* found in India have been investigated to know the genetic diversity within the species in Indian natural populations. These species are *D. ananassae*, *D. melanogaster*, *D. bipectinata*, *D. nasuta* and a few others. The work done was with particular reference to inversion and allozyme polymorphisms and ecological adaptations. In this regard, *D. ananassae,* a cosmopolitan and domestic species commonly found in India is noteworthy. Population genetics and ecological studies carried out by the present author and his students in Indian populations of this species furnishes a very good example of genetic diversity within the species which plays an important role in adaptations of populations to varying environments (Singh 2010). In this review, the species diversity of the genus *Drosophila* in the Indian subcontinent and genetic diversity within *D. ananassae* are briefly considered. Further, the work on genetic diversity in Indian populations of *D. melanogaster*, *D. nasuta*, *D. bipectinata* and certain other species is also briefly presented as evidence for intraspecific genetic diversity in the genus *Drosophila* inhabiting the Indian subcontinent. Further, ecological adaptations to various kinds of stress have also been discussed in certain species to provide evidence for the role of natural selection.

Species diversity

The systematic position of the genus *Drosophila* is as follows: phylum Arthropoda, class Insecta, subclass Pterygota, division Endopterygota, order Diptera, suborder Brachycera, super family Ephydroidea, family Drosophilidae, genus *Drosophila.* All the species within the family Drosophilidae are commonly known as Drosophilids. This family is considered as most advanced diptera in terms of evolution. The family name is based on the type genus *Drosophila*. It has two subfamilies: Steganinae and Drosophilinae. There are 25 genera which comprise the Indian Drosophilid fauna and among them, genus *Drosophila* is the most important and of common occurrence. Genus *Drosophila* Fallen is further divided into subgenera. The number of subgenera found in India is described differently by different authors. As per the classification given by Gupta (2005), four subgenera of the genus *Drosophila* are found in India: *Dorsilopha*, *Dudaica*, *Drosophila* and *Sophophora.* In the checklist of Indian Drosophilidae prepared by A. Naskar, K. K. Bhattacharya and D. Banerjee 2014 Checklist of Indian Drosophilidae (Insecta: Diptera: Drosophilidae), unpublished data, the genus *Drosophila* has six subgenera: *Dorsilopha*, *Drosophila*, *Dudaica*, *Hirtodrosophila*, *Scaptodrosophila* and *Sophophora.* However, *Hirtodrosophila* and *Scaptodrosophila* are genera of the family Drosophilidae and not the subgenera of the genus *Drosophila.* B. K. Singh, R. S. Fartyal and their coworkers are exploring the Drosophilid fauna of Uttarakhand and have described a number of new species and new records from this region of the Indian subcontinent (Fartyal and Singh 2001; Sati *et al.* 2013). R. S. Fartyal has prepared a recent checklist of genus *Drosophila* from India (2014) and as per this list, the genus *Drosophila* has the following subgenera: *Dorsilopha,* one species; *Drosophila*, 71 species; *Sophophora*, 72 species; *Siphlodora*, three species; *Dudaica*, one species; *inc. sed.*, three species (ungrouped subgenera).

Unpublished data: *Drosophila* 1 + *Sophophora* 1 + *Siphlodora* 3 = 5.

Total number of species in the genus *Drosophila* found in India are 156. Thus, in India, the total number of species found in genus *Drosophila* is more than 150. The work of R. S. Fartyal has contributed significantly to the *Drosophila* fauna of this continent (Fartyal and Singh 2001; Fartyal 2014). The number of *Drosophila* species reported by Gupta (2005) is 135 and during the last 6–7 years this number has increased to 156. Moreover, this addition is only from Uttarakhand region. This number will rise further if this research is continued in other regions of the country, because the marked diversity of ecological conditions in the Indian subcontinent is an important aspect of biodiversity in this region. All the species reported from India fall into two categories: new species and new records. The species of common occurrence are: *D. melanogaster*, *D. ananassae*, *D. nasuta*, *D. bipectinata*, *D. malerkotliana*, *D. parabipectinata*, *D. pseudoananassae*, *D. biarmipes*, *D. kikkawai*, *D. jumbulina*, *D. albomicans*, *D. punjabiansis*, *D. seguyi*, *D. suzukii*, *D. takahashii*, *D. hydei*, *D. repleta*, *D. buzzatii*, *D. immigrans*, etc.

The genus *Drosophila* has rich species diversity in this region where a high level of diversity of ecological conditions might have provided impetus to the evolution of *Drosophila* species. A large number of species of this genus is endemic to this subcontinent. Thus, this genus is quite diverse and well distributed in this subcontinent including Andaman and Nicobar Islands. Further, the distribution of species varies in different regions of the country and in different seasons of the same area (Parshad and Paika 1964; Parshad and Duggal 1966; Gupta and Ray-Chaudhuri 1970a, b; Parshad and Singh 1971; Reddy and Krishnamurthy 1971, 1973; Vaidya and Godbole 1971; Godbole and Vaidya 1972, 1973; Ranganath and Krishnamurthy 1972a, b; Singh 1972; Gupta 1974, 1981, 1993, 2005; Gowda *et al.* 1977; Hegde and Krishnamurthy 1980; Nagraj and Krishnamurthy 1980; Singh and Gupta 1981; Dasmohapatra *et al.* 1981, 1982a, b; Gai and Krishnamurthy 1983; Prakash and Reddy 1984; Shyamala *et al.* 1987; Gupta and Gupta 1988; Singh and Bhatt 1988; Singh and Negi 1989; Kumar and Gupta 1990; Sundaran and Gupta 1993; Singh and Dash 1993; Singh and Fartyal 2002). The species have been described from West Bengal, Orissa, Arunachal Pradesh, Meghalaya, Nagaland, other regions of northeast India, Sikkim, Maharashtra, Kumaun region, Uttarakhand, Punjab, Eastern and Western Ghats, Karnataka, Tamil Nadu, Jammu and Kashmir, Andaman and Nicobar Islands, Bihar, Uttar Pradesh, Kerala and other regions of the country. The cosmopolitan species of *Drosophila*, such as *D. melanogaster*, *D. ananassae*, *D. busckii*, *D. immigrans* and *D. repleta* are of common occurrence. It has been observed that their representation is poorer in wild areas than urban areas (Gupta 2005). According to Bock and Parsons (1977), resources are fully utilized in wild habitats by endemic species and thus there is a stringent competition for niches which prevents the colonization of cosmopolitan species in the wild. Most likely, they require a stable and abundant resource of food which they get from urban refuse. Similarly, the *Drosophila* species which are successful in the forest have not invaded the urban areas at all. Thus, a consideration of the existing data reveals that India possesses fairly rich species diversity in the genus *Drosophila* comprising species of many radiations, but the present picture is by no means complete as many more species may be added if the research in this area is continued in future (Gupta 2005).

Although large numbers of *Drosophila* species are known to occur in this subcontinent which provides evidence for rich species diversity, the scenario of *Drosophila* research is not very encouraging (Singh 2013a). As per *Drosophila* meeting report (Ray and Lakhotia 2014), there are more than 90 active research groups pursuing research using *Drosophila* in India. Michan *et al.* (2010) published a bibliometric analysis of global *Drosophila* research from 1900 to 2008 in *Drosophila* Information Service (USA). On the basis of data obtained from Science Citation Index and PubMed, they investigated the scientific productivity of *Drosophila* research among researchers, countries, institutions, journals and subject areas. A total of 36,486 documents were obtained by Michan *et al.* (2010). Their bibliometric analysis included 4600 institutions and 45,415 researcher names. They prepared the list of most prolific researchers at global level in terms of number of research papers and found 34 researchers as most prolific, each with more than 100 research papers. At global level, in the list of most prolific *Drosophila* researchers, there is only one name (B. N. Singh) from India at 24th position. The 10 countries with highest number of publications are: USA, France, England, Japan, Germany, Canada, Spain, Switzerland, USSR and Australia. Maximum publications are from USA (21,508) but India does not figure in this list. At global level, there are 501 different institutions. The most productive institutions being the Russian Academy of Sciences, the Centre National de la Recherche Scientifique (CNRS), France and Harvard University, USA. No institution from India figures in the list of 50 institutions given by Michan *et al.* (2010). Thus, at global level India is lagging behind as far as *Drosophila* research productivity is concerned during the last 8–9 decades. *Drosophila* is a very good biological model with relatively low cost of maintenance and experimentation. Researchers should be encouraged to employ this dipteran insect model in their research which will enhance the scientific productivity of *Drosophila* research in India.

Intraspecific genetic variability

Genetic diversity, as a concept of variability within a species (intraspecific) is quantified in terms of genetic variability. Genetic polymorphism at global level has been studied in a number of species of *Drosophila*, such as *D. melanogaster*, *D. ananassae*, *D. pseudoobscura*, *D. persimilis*, *D. robusta*, *D. pavani*, *D. nasuta*, *D. subobscura*, *D. flavopilosa*, *D. silvestris*, *D. guaramunu*, *D. rubida*, *D. paulistorum*, *D. willistoni*, *D. bipectinata*, etc. (Powell 1997; Krimbas and Powell 1992; Singh 1994, 2001, 2013b). It has been studied extensively at the level of chromosome, allozyme and DNA. Certain species of *Drosophila* found in India have been investigated for genetic diversity within the species such as *D. melanogaster*, *D. ananassae*, *D. nasuta* and *D. bipectinata* (Singh 2001, 2013b). However, in India the most extensively studied species from the genetic diversity point of view within the species in the Indian subcontinent is *D. ananassae.*

D. ananassae was described for the first time in Ambon island, Indonesia, by Doleschall (1858). Although *D. ananassae* is cosmopolitan in distribution, it is largely circumtropical and frequently found in domestic habitats. It is commonly distributed in the Indian subcontinent but it occurs through out the year in south, including Andaman and Nicobar Islands and towards the sea coast where climatic conditions are tropical and humid and the occurrence differs from north in this respect. Because of this reason, it is called a circumtropical species although it occurs on all the six biogeographic zones. It belongs to the *ananassae* species complex of the *ananassae* subgroup of the *melanogaster* species group. For genetical studies, *D. ananassae* was used for the first time by Japanese researchers (Moriwaki 1936; Kikkawa 1938). It occupies unique status in the genus *Drosophila* because of certain peculiarities in its cytological and genetical behaviour (Singh 1985a, 1996, 2000, 2010). The common occurrence in the Indian subcontinent coupled with genetic peculiarities attracted the attention of Indian researchers. S. P. Ray-Chaudhuri initiated research on *D. ananassae* in 1940s in Calcutta University and continued it in the Department of Zoology, BHU, where he joined as Professor and Chairman in 1960. Since that time, population genetical work on *D. ananassae* is being continued (Singh 2010). A large number of chromosomal aberrations which include inversions and translocations have been reported in this species (Singh and Singh 2007a). Out of 78 paracentric inversions, only three are cosmopolitan in distributions which have become coextensive with the species considering monophyletic origin of these inversions. Chromosomal polymorphism due to these inversions often persists in laboratory populations which demonstrates that heterotic buffering is associated with the three cosmopolitan inversions (Singh and Ray-Chaudhuri 1972; Singh 1982), which has been explained by simple luxuriance hypothesis rather than population heterosis (coadaptation) and, thus, luxuriance can function in the adjustment of organisms to their environments (Singh 1985b). These inversions are named as AL (2L), DE (3L) and ET (3R) and their locations in different chromosomes are shown in figure 1.

Genetic diversity in Indian natural populations of *D. ananassae* has been extensively studied by the present author and his students by investigating population dynamics of these three cosmopolitan inversions (Singh 1970, 1974, 1984a, b, c, 1986, 1989a, b, 1991, 1998; Singh and Anand 1995; Singh and Singh 2007b, 2008). Quantitative data on the frequencies of different gene arrangements in 2L, 3L and 3R due to occurrence of these three cosmopolitan inversions have been reported by Singh (1996, 1998) for 29 populations from India including Andaman and Nicobar Islands. Subsequently, Singh and Singh (2007b) studied 45 populations from different ecogeographic regions of the country (see figures 2 & 3 and table 1 in Singh and Singh 2007b).

Results of these investigations showed that the frequencies of different gene arrangements vary in different geographic populations. Further, the level of heterozygosity (measured in terms of mean number of heterozygous inversions per individual) also varies among the populations. There is clear difference between rural and urban populations with respect to level of inversion polymorphism and the frequencies of different arrangements with evidence for low level of

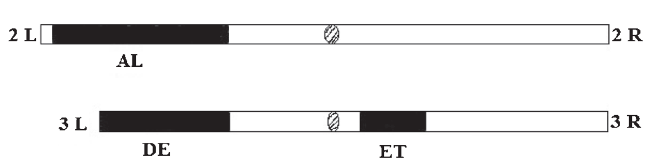

Figure 1. Location of AL (2L), DE (3L) and ET (3R) inversions in different chromosomes of *D. ananassae*.

polymorphism and high frequency of standard gene arrangements in rural populations as compared to urban populations, which has been correlated with ecological niches available for the species corroborating the ecological niche hypothesis of Dobzhansky *et al.* (1950).

The natural populations of *D. ananassae* have undergone a considerable degree of genetic divergence as a result of their adaptation to varying environments in the Indian subcontinent. Thus, natural selection operates to maintain these inversions in natural populations. With some exceptions in north, results in general indicate the existence of north–south cline in inversion frequencies. Populations from Tamil Nadu, Kerala and Andaman and Nicobar Islands situated near the equator maintain inversions in high frequency than those inhabiting different localities in north. The south experiences a tropical and humid climate. Localities near sea coast differ from those away from it. The degree of genetic divergence among natural populations has been quantified by calculating genetic identity (I) and genetic distance (D) on the basis of differences in chromosome arrangement frequencies using the formula of Nei (Singh and Anand 1995; Singh 1996; Singh and Singh 2007b). In general, the populations from the south show more differentiation than those from the north. The relationships between the populations have been shown by constructing dendrogram based on UPGMA clustering of genetic identity values. In different studies such comparison is made, but this is the only study in which 45 populations were compared (Singh and Singh 2007b). There is no strong positive correlation between the genetic distance and geographic distance. However, in many pair-wise comparisons between populations, isolated by small geographic distance, there is low level of genetic distance (high level of genetic identity). Thus, there is strong evidence that *D. ananassae* populations are genetically differentiated demonstrating genetic diversity. Further, environmental factors differing in different ecogeographic localities have influenced the genetic composition of *D. ananassae* populations in the Indian subcontinent. 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 constitution 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 (Dasmohapatra *et al.* 1982c).

Population structure analysis in 45 Indian natural populations has been carried out by Singh and Singh (2010) by employing three cosmopolitan inversions as markers and statistical procedure suggested by Nei (1972) and Wright (1951). Population structure analysis was done for the first time by using inversions as markers. Based on F_{ST} and genetic distance estimates, a strong genetic differentiation in Indian populations of *D. ananassae* has been suggested. Although, lower most values were found for geographically closest populations, there was no significant isolation by

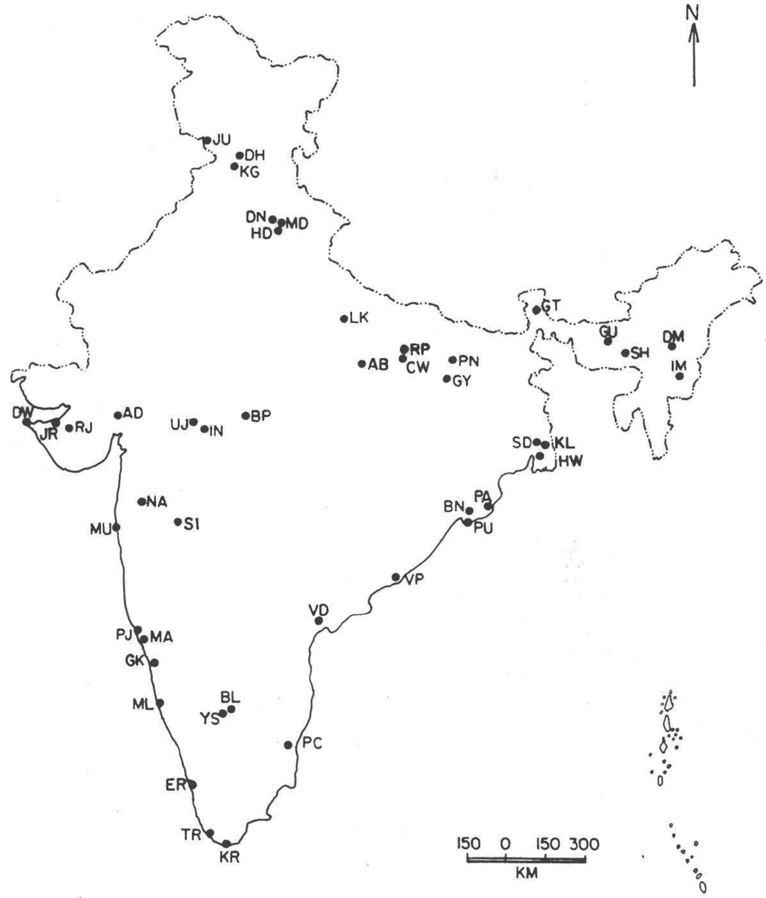

Figure 2. Map of India showing the localities from where *D. ananassae* flies were collected: JU, Jammu; DH, Dharamshala; KG, Kangra; DN, Dehradun; HD, Haridwar; MD, Mansa Devi; GT, Gangtok; LK, Lucknow; GU, Guwahati; RP, Raidopur; CW, Chowk; DM, Dimapur; SH, Shillong; PN, Patna; AB, Allahabad; IM, Imphal; GY, Gaya; UJ, Ujjain; BP, Bhopal; IN, Indore; JR, Jamnagar; HW, Howrah; SD, Sealdah; KL, Kolkata; RJ, Rajkot; DW, Dwarka; AD, Ahemdabad; PA, Paradeep; BN, Bhubneswar; PU, Puri; SI, Shirdi; NA, Nashik; MU, Mumbai; VP, Visakhapatnam; VD, Vijaywada; PJ, Panaji; MA, Madgaon; GK, Gokarna; ML, Mangalore; BL, Bengaluru; YS, Yeswantpur; PC, Pondicherry; ER, Ernakulam; TR, Thiruvananthapuram; KR, Kanniyakumari (Singh and Singh 2007b).

distance effect. Interestingly, the level of gene flow between natural populations was found to be very low (Nm < 5) which was based on F_{ST} estimates. This provides strong evidence for population substructuring in Indian natural populations of *D. ananassae* which is the first report. This is particularly important in the case of *D. ananassae* because it is frequently transported by human activities. Since the gene flow is limited, natural populations are expected to diverge genetically due to random genetic drift. Low level of gene flow coupled with high level of genetic divergence might have occurred historically and is maintained currently. Demographic properties, historical and contemporary events and other factors are more important in shaping the patterns of population substructuring, genetic differentiation and gene flow than mere terrestrial habitat characteristics (un)favourable for migration (Singh and Singh 2010). Thus, these studies provide evidence for genetic diversity within the species. In addition to inversion polymorphism, there are few reports on allozyme polymorphism in Indian populations of *D. ananassae* with evidence for latitudinal cline and ethanol tolerance (Parkash *et al.* 1993; Parkash and Shamina 1994).

Inversion polymorphism in *D. melanogaster* has been extensively studied at global level and more than 300 paracentric inversions have been detected (see Singh and Das 1990). Inversion polymorphism in Indian populations of *D. melanogaster* has also been studied and a total of 42 paracentric inversions have been detected (Das and Singh 1991a). All the four type of inversions: common cosmopolitan, rare cosmopolitan, recurrent endemic and unique endemic were found. Thus, there is high degree of inversion polymorphism in Indian populations of *D. melanogaster.* It is evident from the data on inversion frequencies (Das and Singh 1991b; Singh and Das 1992) that: (i) there is a geographic differentiation among Indian natural populations, (ii) the urban populations are different from the rural ones, (iii) there is existence of north–south inversion clines and significant negative correlation between each of the four common cosmopolitan inversions and latitude, (iv) the level of inversion heterozygosity is higher

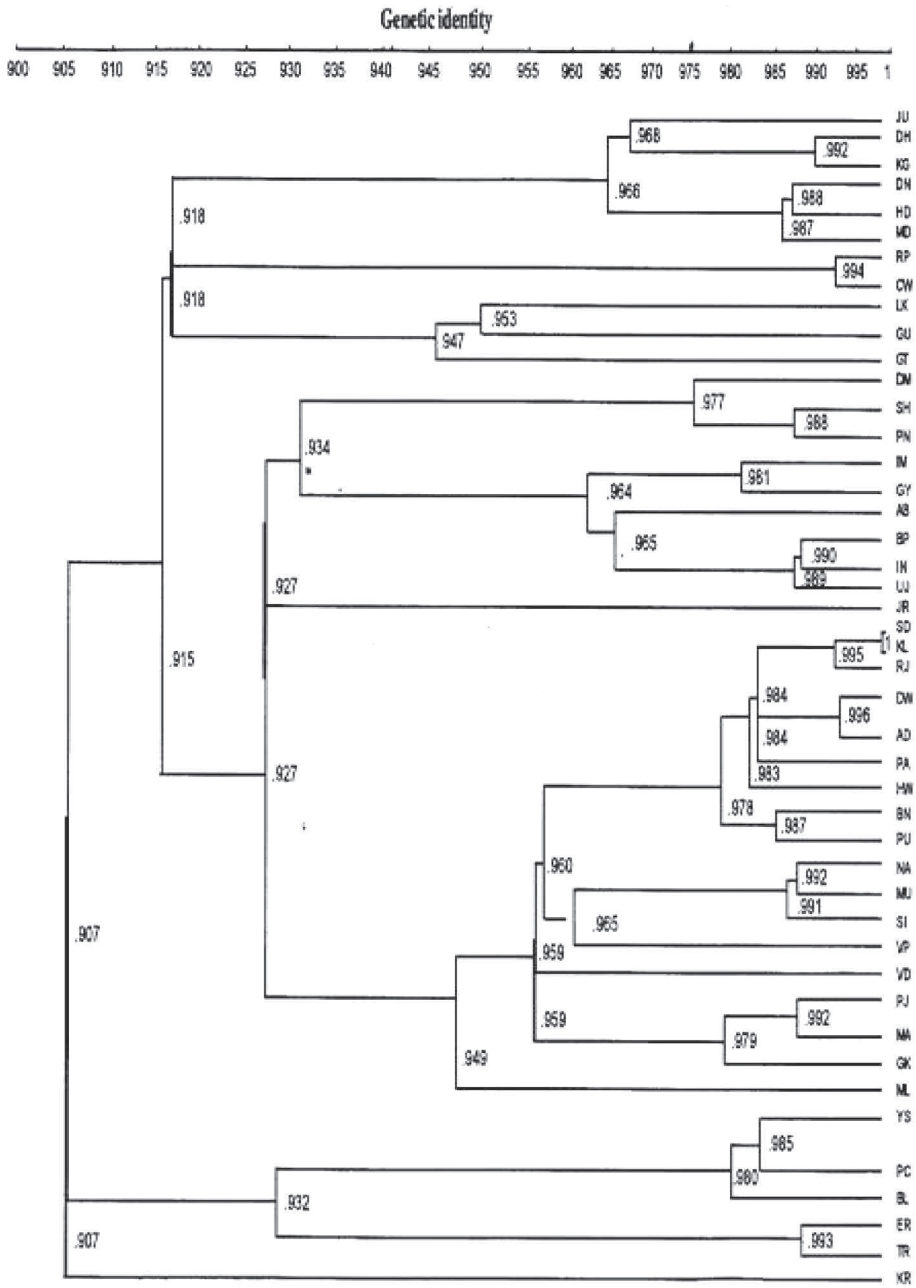

Figure 3. Dendrogram of natural populations of *D. ananassae* based on UPGMA clustering of genetic identity (I) values (Singh and Singh 2007b).

in populations from the south as compared to those from north; and (v) Indian populations have undergone considerable degree of genetic divergence at the level of inversion polymorphism.

Parkash *et al.* (1999) presented evidence for geographical variation in Adh^F frequency with latitudes in Indian populations of *D. melanogaster*. Inversion polymorphism has also been studied in *D. nasuta* which shows a considerable degree of inversion polymorphism and there is existence of geographic differentiation and altitudinal clines with respect to inversion polymorphism in Indian natural populations (Ranganath and Krishnamurthy 1975, 1978; Rajasekarasetty *et al.* 1979; Kumar and Gupta 1988). *D. bipectinata* shows relatively less number of inversions (only 13 paracentric in versions) in its natural populations (Gupta and Panigrahy 1990). Only three inversions have been found to persist in laboratory stocks due to heterozygote superiority (Singh and Banerjee 1997). Inversions occur at low frequency in natural populations and there is no evidence for geographic differentiation in natural populations which lend support for rigid inversion polymorphism in *D. bipectinata* (Banerjee and Singh 1996). There is evidence for genetic

Table 1. Frequencies (in per cent) of three cosmopolitan inversions (AL, DE and ET) and level of inversion heterozygosity in Indian natural populations of *D. ananassae.*

Population	Latitude (N)	Number of chromosomes analysed	AL	DE	ET	Level of inversion heterozygosity
JU	34.08	260	61.6	16.2	15.4	0.92
DH	32.22	92	59.8	27.2	4.4	0.95
KG	32.10	130	58.5	39.3	3.1	0.87
DN	30.19	108	63.9	39.9	8.4	0.94
HD	29.98	90	48.9	35.6	6.7	0.84
MD	29.58	60	63.4	38.4	16.7	1.10
GT	27.20	68	95.6	14.8	38.3	0.70
LK	26.50	96	69.8	6.3	20.9	0.72
GU	26.17	202	92.6	11.4	36.2	0.78
RP	26.00	50	60.0	8.0	14.0	0.76
CW	26.00	142	49.3	11.3	16.2	0.88
DM	25.92	422	92.7	20.0	27.3	0.81
BN	20.27	18	88.9	38.9	16.7	0.66
PU	19.50	32	84.4	28.2	28.2	0.56
SI	19.45	206	85.5	18.5	6.8	0.58
NA	19.00	268	82.1	16.8	4.2	0.64
MU	18.96	198	84.9	10.7	20.3	0.65
VP	17.42	66	67.0	25.8	19.7	0.78
VD	16.31	52	67.4	46.2	36.6	0.76
PJ	15.25	66	92.5	45.5	15.2	0.81
MA	15.18	156	87.2	35.9	17.4	0.80
GK	14.48	160	91.3	60.0	17.5	0.82
ML	12.85	236	87.9	8.5	7.3	0.72
BL	12.58	72	68.1	45.9	25.0	1.38
YS	12.58	30	60.0	46.7	13.4	1.46
PC	11.93	42	59.6	50.0	31.0	1.85
ER	10.00	116	80.2	61.3	19.9	0.84
TR	8.53	108	85.2	58.4	14.9	0.90
KR	8.07	112	79.5	77.7	26.8	0.82

For full form of abbreviations, see figure 2 (Singh and Singh 2007b).

variations in natural populations of *D. busckii* at the level of allozyme polymorphism (Parkash *et al.* 1990). Data on allozyme variation have been reported in *D. malerkotliana*, *D. bipectinata* and *D. ananassae* (Parkash and Jyoutsna 1988).

Ecological adaptations

To study the mechanisms of adaptive evolution in animals and plants, analysis of geographical variations is often used in population genetic studies. It is clear from the foregoing that *D. ananassae* populations respond to clinal variations along the climatic gradients prevalent in the Indian subcontinent. The clinal variation along clinal gradient indicates a possible contribution of directional selection to differences among populations. Latitudinal variations for physiological and life history traits have been studied in *Drosophila*. India is a large tropical and subtropical continent covering a large range of latitude. From south to north, the seasonal thermal amplitude shows a regular increase with progressively more marked cold and warm seasons. Seasonal variations strongly increase with latitude. There is thermal stability in southern region and high humidity through out the year. However, when we move towards north, the summer becomes increasingly warmer and drier causing a progressively stronger heat desiccation stress. If natural selection really acts on stress tolerance and adaptation, such a regular clinal pattern according to latitude in the Indian subcontinent should produce clearer genetical trends (Karan *et al.* 1998).

In view of the above, we have investigated the resistance to different kinds of stress such as heat and cold shocks, starvation and desiccation in populations of *D. ananassae* (Sisodia and Singh 2010a, b, 2012). It is known that mild increase or decrease in temperature may result in increased resistance to temperature extremes, when flies of *Drosophila* species are exposed to varying temperatures. Sisodia and Singh (2010a) investigated cold tolerance in 45 Indian populations of *D. ananassae* from different latitudes which were also analysed for inversion polymorphism (see figure 2). The time taken by adults (males and females) to recover from chill coma after a treatment for 16 h at 4°C was monitored. Significant latitudinal differentiation was observed for chill coma recovery in *D. ananassae* populations and it was found that chill coma recovery was associated with local climatic factors of original populations. From these results, it is evident that populations of *D. ananassae* from higher latitudes show more cold resistance than those from lower latitudes. These findings suggest that cold adaptation and resistance within *D. ananassae* may vary with latitude which has resulted due to direct/indirect action of natural selection. Further, these findings also lend support to the suggestion that higher cold tolerance in north Indian populations of *D. ananassae* might have evolved during the colonization of *D. ananassae*, which supports the hypothesis of an adaptive response of plasticity to the experienced environment (Sisodia and Singh 2010a). In *Drosophila*, the traits related to fitness usually show geographical variations which is the result of adaptive evolution and the clinal variations in stress resistance traits lend support to the hypothesis that natural selection affects resistance traits either directly or indirectly. In view of this, we tested (Sisodia and Singh 2010b) multiple stress resistance traits in 45 *D. ananassae* populations derived from different latitudes. The main findings are: (i) there is a positive correlation between starvation resistance and lipid contents. (ii) There is a negative correlation between desiccation and lipid contents and between desiccation and heat resistance. (iii) Flies from lower latitudes (south) show higher starvation resistance, heat resistance and lipid contents, but the pattern is reversed for desiccation resistance. Thus, *D. ananassae* flies from different latitudes vary in their susceptibility to starvation owing to the difference in their propensity to store body lipid. This suggests a considerable degree of variation in stress resistance at the level of populations in *D. ananassae*. Thus, there is evidence for climatic selection in *D. ananassae* in the Indian subcontinent influenced by latitudinal variation in temperature and humidity (Sisodia and Singh 2010b). Further, the larval nutrition also affects the stress resistance in *D. ananassae*. It has been reported that flies consuming protein-rich diet have higher desiccation and heat shock resistance whereas flies developed on carbohydrate-rich diet have higher resistance for starvation and cold. Thus, *D. ananassae* adapts to different stress tolerance according to the quality of available diet. This is correlated with phenotypic adjustment at anatomical and physiological levels (Sisodia and Singh 2012). Thus, the findings recorded for *D. ananassae* provide evidence that the quality and quantity of nutrients consumed by organisms have strong impact on stress resistance. Studies on resistance to different kinds of stress in different species of *Drosophila* occurring in India have also been reported by Parkash and coworkers (Parkash and Shamina 1994; Parkash *et al.* 1994; Karan and Parkash 1998; Karan *et al.* 1998; Parkash and Munjal 1999; Parkash *et al.* 2005; Chahal *et al.* 2013; Chahal and Dev 2013). The desiccation tolerance and starvation resistance exhibit opposite latitudinal clines and significant differentiation among Indian geographical populations of *D. kikkawai*. In Indian populations of *D. melanogaster* and *D. ananassae*, significant opposite latitudinal clines were observed for desiccation and starvation tolerance which are fitness related traits independently selected in nature and are genetically independent. Further, there is evidence for latitudinal clines for Adh allozymic variation and ethanol tolerance in Indian populations of *D. ananassae*. Latitudinal populations of *D. ananassae* differ in slope values of clines for stress-related traits across season (Chahal and Dev 2013). Further, the evolution of clines associated with starvation and lipid content might have resulted due to specific ecological conditions, i.e. humidity gradient in the Indian subcontinent (Chahal *et al.* 2013). There is evidence for opposite clinal variation and adaptation for desiccation and starvation tolerance in certain altitudinal populations of two sympatric and cold-adapted species: *D. takahshii* and *D. nepalensis* from northern India. The high altitudinal populations are more tolerant to desiccation than those from lower altitudes whereas the reverse trend occurs for starvation tolerance. Indian geographic populations of *D. bipectinata* and *D. malerkotliana* show adaptively maintained genetic divergence for starvation and desiccation tolerance. There is significant positive latitudinal correlation for body size and desiccation tolerance, and negative correlation for starvation tolerance in *D. repleta*. Thus, ecological adaptation shows variation in different species of *Drosophila* inhabiting the Indian subcontinent. Rajpurohit *et al.* (2013) performed a meta-analysis of geographical clines in desiccation tolerance in Indian drosophilids and suggested that the latitude of the sampling sites explained most of the variability in *D. melanogaster*, *D. ananassae*, *D. kikkawai*, *D. bipectinata*, *D. repleta* and *D. immigrans.*

Conclusion

The genus *Drosophila* inhabiting the Indian subcontinent presents a considerable level of species and genetic diversity. It has a large number of species (above 150) described so far from this region as new species as well as new records. If the taxonomy research is given due emphasis then many more species may be described in future. Considering the diversity in the ecological conditions in this region, the processes of evolution and speciation might have affected this genus to a great extent. As far as genetic diversity at the species level is concerned, extensive data have been presented by the author and his group in *D. ananassae* to provide ample evidence for intraspecific genetic and ecological variations driven by ecological factors which vary to a great extent in this region resulting in marked genetic diversity within the species. In addition, the work on genetic diversity in Indian populations of *D. melanogaster*, *D. nasuta*, *D. bipectinata, D. malerkotliana* and *D. busckii* also provides evidence for intraspecific genetic diversity. The pattern and the degree of genetic diversity in the Indian populations of these species vary which shows that these species have evolved different mechanisms for adjusting to their environments. Thus, there is strong evidence for marked genetic diversity in the genus *Drosophila* inhabiting the Indian subcontinent. Ecological adaptations to various kinds of stress have also been investigated in certain species to provide evidence for the role of natural selection.

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