Drosophila ananassae: A species characterized by several unusual genetic features

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Drosophila ananassae **Doleschall is a cosmopolitan and domestic species. It occupies a unique status among the *Drosophila* species due to certain peculiarities in its genetic behaviour and is of common occurrence in India. The most unusual feature of this species is spontaneous male meiotic recombination in appreciable frequency. The other unusual features are varied chromosomal polymorphism, high mutability, Y-4 linkage of nucleolus organizer, segregation, distortion, parthenogenesis, absence of genetic coadaptation in different geographical populations and extrachromosomal inheritance. The optic morphology (*Om*) hypermutability system is unique in *D. ananassae* and there is an involvement of *tom* retrotransposon for the generation of *Om* mutations. There is a positive correlation between sternopleural bristle number, mating propensity and fertility in *D. ananassae*. The existence of sexual isolation has been reported within *D. ananassae* and the degree of sexual isolation is stronger in isofemale lines than in natural populations. Behavioural studies also have revealed several interesting features in *D. ananassae*. A spontaneous bilateral genetic mosaic for autosomal genes resulting from mitotic recombination has been reported in *D. ananassae*. Another unusual feature attributed to *D. ananassae* is its pattern of chromosomal polymorphism. There are remarkably high levels of chromosomal polymorphism in natural populations. Although 70 paracentric inversions have been detected so far in this species, only three paracentric inversions (AL, DE, and ET) have become coextensive with the species. Most of the inversions have localized distribution and have been detected from a few individuals. Indian populations have undergone a considerable degree of genetic divergence at the level of inversion polymorphism. A large number of pericentric inversions and translocations which ordinarily do not exist in other species of *Drosophila* are present here.**

DROSOPHILA ananassae was first described by Doleschall[1] in 1858 from Indonesia. It belongs to the *ananassae* species complex of the *ananassae* subgroup of the *melanogaster* species group[2]. It has been recorded from all six biogeographic zones, although absent in some areas, and is of frequent occurrence in human habitats[3]. Although it is cosmopolitan in distribution, it is largely circumtropical and is of common occurrence in India. Genetical investigations on *D. ananassae* were started in the 1930s by Japanese workers. Kikkawa[4] selected *D. ananassae* 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* has been used for genetic studies by Japanese, Indian, North American and French workers[5–10], and about 400 papers have been published on the genetical and biological aspects of this species[10,11]. Moriwaki[12] writes: 'In conclusion, I am happy to report that *D. ananassae* has secured a position as a unique and valuable organism for genetic research, especially characterized by male recombination and high mutability, both involving chromosomal and extra chromosomal determinants, and by the *Om–tom* system'. *D. ananassae* has been extensively used for genetical studies including population genetics, behaviour genetics and recombination by Indian workers[6–9]. In the present review, the unusual genetic features of *D. ananassae* which make it a special case in the genus *Drosophila* have been documented.

Spontaneous male recombination

Since the discovery of absence of male recombination in *D. melanogaster*[13], this phenomenon has been investigated in several species resulting in reports of male recombination in *D. melanogaster*, *D. ananassae*, *D. simulans*, *D. virilis*, *D. littoralis*, *D. willistoni* and *D. bipectinata*[14]. However, it occurs at a very low rate in all the species showing spontaneous male recombination except *D. ananassae* which exhibits an appreciable level of crossing-over in males. Spontaneous male recombination in *D. ananassae* was observed for the first time by Japanese workers[4,15-17]. Since then it has been investigated by various workers[18]. Thus *D. ananassae* is

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unique in the whole of genus *Drosophila* due to the presence of spontaneous male recombination in appreciable frequency[6]. In certain strains, the total recombination frequency in males was found to approach the recombination frequency in females[19]. Spontaneous male recombination in *D. ananassae* is meiotic in origin[20,21] and is influenced by various genetic factors such as enhancers, suppressors, polygenes and inversions[4,15,19,20,22,23]. Some response was seen to selection for crossing-over frequency in males[23–25] and there is evidence for polygenic control of male recombination. The findings of intra- and interchromosomal effects of heterozygous inversions on spontaneous male recombination lend support to a previous suggestion that spontaneous crossing-over in males of *D. ananassae* is meiotic in origin[22,26]. The presence of chiasmata at a frequency capable of accounting for the observed recombination values in *D. ananassae* has also been reported[27].

An effect of Y-chromosome on male crossing over[28] and a positive correlation between minute mutation frequency and male recombination rate has been demonstrated[29], which suggests that a series of inducers and suppressors are responsible for both these traits. An extrachromosomal suppressor of male crossing-over in *D. ananassae* has also been reported by Hinton[30]. Significant variation in the rate of crossing-over among different strains provides evidence for genetic control of this phenomenon[20,31].

A number of investigations have been conducted to detect the effect of parental age on male recombination in *D. ananassae*. Kikkawa[4] reported spontaneous male crossing-over in a strain of this species in which he found that the crossover frequency in the male does not change markedly with age of the father in the tested third chromosome. Ray-Chaudhuri and Kale[32] reported that parental age has a more pronounced effect on the spontaneous crossing-over in males. Matsuda and Tobari[33] investigated the effect of aging on male recombination and found that the patterns of age effect were characteristic for specific strains. Tobari *et al.*[34] demonstrated aging effect on male recombination and mutation. Singh and Singh[22,26] also followed brooding pattern while studying male crossing-over in *D. ananassae* and observed maximum crossing-over frequency in the first brood. There was considerable decrease of crossing-over in older males. From these reports it is evident that spontaneous male crossing-over in *D. ananassae* is affected by the age of males.

The effect of temperature and X-rays on crossing-over has also been investigated in males of *D. ananassae*. Kale[35] reported spermatogonial origin of crossovers in *D. ananassae* by irradiating early developmental stages where spermatocytes were not present. He found great individual variation and inequality of complementary crossovers. Kale[36,37] studied crossing-over in males of *D. ananassae* by treating early and mid pupae, and young and 48-h-old adults with X-ray and found crossovers which appeared to have originated in treated spermatocytes. Interestingly, the frequency of crossovers in early pupal stages was much more frequent than in the later stages, which suggests that spermatocytes of early pupae are more sensitive to the induction of crossing-over. Matsuda[38] found that elevated temperature enhanced meiotic crossing-over in males of *D. ananassae*.

Lack of correlation between crossing-over and chromosome distance between linked inversions

Effects of heterozygous inversions on crossing-over in both sexes of *D. ananassae* have been tested by Singh and his coworkers[22,26,39–45] and the results have indicated the existence of intra- and interchromosomal effects of inversions on recombination in males and females of *D. ananassae*. The rate of crossing-over between linked inversion (DE- ET in the third chromosome and AL- ZE in the second chromosome) has been studied by the salivary gland smear technique[22,39,40,42,43,46]. Although the two linked inversions of the second chromosome as well as of the third chromosome are widely separated from each other, there is a strong suppression of recombination between inversions when heterozygous, in spite of a large euchromatic distance available for crossing-over between them. Thus there is a lack of correlation between the rate of crossing-over and chromosome distance between heterozygous inversions in *D. ananassae* when studied cytologically. Singh and Mohanty[46] suggested that the strong suppression of crossing-over between inversions is the genetic characteristic of *D. ananassae* and may be advantageous for a species with a considerably low level of inversion heterozygosity in its natural populations.

Segregation distortion

The phenomenon of segregation distortion (or meiotic drive) leads to unequal segregation of two alleles in a heterozygote due to certain unusual mechanisms during meiosis. This phenomenon has been studied in detail in *D. melanogaster*[47,48]. It is caused due to the *SD* gene and occurs in males only in *D. melanogaster*. Mukherjee and Das[49] reported an interesting case of aberrant segregation in a laboratory strain (*px pc*) of *D. ananassae*. In *D. ananassae*, distortion is observed in both the sexes (i.e. in heterozygous females and males) but only in the segregation of recombinants and not in the segregation of nonrecombinants. Careful experimental analysis revealed that the disproportionate recovery of the two reciprocally recombinant classes should not be attributed to differential viability, zygotic mortality and lack o

penetrance of mutation[49]. Segregation distortion observed in *D. ananassae* differs from *SD* in *D. melanogaster* in several important aspects: (i) it was detected in a laboratory stock; (ii) it occurred in both sexes; and (iii) it affected the recovery of recombinant classes without any influence on nonrecombinant classes. The hypotheses suggested to explain the mechanism of segregation distortion in *D. melanogaster* failed to explain all the properties of segregation distortion in *D. ananassae*. Mukherjee and Das[49] opine that it opens a new line of thought concerning high frequency of spontaneous male recombination in *D. ananassae* and its relation to segregation distortion.

Spontaneous genetic mosaic for autosomal genes

Organisms that are composed of cells of at least two different genotypes are known as genetic mosaics. They have been detected in a number of organisms and are useful tools for studies of genetically controlled phenomena like development[50]. Morgan[51] discovered for the first time sex mosaics (gynandromorphs) in *D. melanogaster* originating from diplo X zygote by the elimination of one X chromosome during development. If it occurs at the first nuclear division of zygote (XX), bilateral mosaic will be produced. In case it occurs during later stages of zygote development, patches of male and female tissues of different sizes will be produced. Sex mosaics were also known in *D. simulans, D. virilis* and *D. funebris*[50]. Genetic mosaics originate mainly by the loss of chromosomes or by mitotic recombination. Genetic exchange during mitosis may occur in somatic cells where its consequence may be visible as somatic mosaics[52]. One mechanism for such exchange could be mitotic recombination. Singh and Mohanty[53] detected a spontaneous bilateral genetic mosaic in *D. ananassae*, which was characterized by three mutant characters (*cu e se*-II chromosome) on the left side and all normal characters on the right side (Figure 1), while scoring the progeny of a test cross between heterozygous males and mutant females[53]. This is the first report of spontaneous genetic mosaic for autosomal genes in *Drosophila*. Its probable origin is attributed to mitotic recombination in the zygote which was genolypically heterozygous, since somatic loss of chromosomes cannot be the cause of its origin because when larger autosomes are either lost or added, the resulting cells will be inviable.

High mutability

Studies on mutations in *D. ananassae* have proved that it is characterized by high mutability[10]. Several workers[4,5,54,55] described a large number of mutations in *D. ananassae* and linkage maps were also constructed.

Figure 1. Photograph showing a spontaneous genetic mosaic in *D. ananassae*[53].

A considerable increase in the frequency of certain mutations has been observed[54]. The existence of mutations and their suppressors has been suggested which control mutability in *D. ananassae*[54]. This lends support to the suggestion[56] that natural selection invokes a variety of devices to minimize mutation rate while retaining mutation potential. Hinton[54] reported mutational episodes in *D. ananassae*.

A large number of pericentric inversions and translocations have been reported in *D. ananassae*[57]. The presence of such chromosomal aberrations which ordinarily do not exist in other species of *Drosophila*, reflects unusual mutational properties of *D. ananassae*. Freire-Maia[58] suggests the development of some special mechanism through which *D. ananassae* can retain chromosome arrangements which are disadvantageous.

The optic morphology (*Om*) hypermutability system is unique in *D. ananassae* and there is an involvement of *tom* retrotransposon for the generation of *Om* mutations[59–61]. The phenomenon of *Om* mutability is of special interest because almost all the mutations obtained in this system show phenotypes affecting the structure of adult compound eye and this fact raises the important question about the mechanism and specificity of the mutagenic event[10]. Although several mutator systems have been found and studied extensively in *D. ananassae*, the *Om* hypermutability system is quite unique among them. Since all mutants of this system show defect in adult compound eye, they are called *Om* mutations[59]. They are all semidominant. The mutations arise exclusively from the female germ line and they map to at least 22 different loci in the genome. In this mutability system, dominant suppressors of the *Om* phenotypes have also been isolated[59,62]. These suppressors map to six different loci. In general, *Om* mutants show Bar-like eye phenotypes.

It has been demonstrated that *Om* mutations in *D. ananassae* are induced due to insertion of *tom* retro-

transposons[59-61,63,64]. The molecular characteristic of the tom element has been analysed[65,66]. It belongs to the gypsy group of LTR-containing retrotransposon. RFLP studies[67] 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 site.

Extrachromosomal inheritance

An extrachromosomal suppressor of male recombination in *D. ananassae* is known which is maternally transmitted and is dependent on a specific third chromosome for its maintenance[30]. In hetrozygote, *Om* mutability is stimulated by the presence of extra-chromosomally replicating elements. The mutator is found to be an extrachromosomally transmitted element whose multiplication is controlled by nuclear genes[68]. The possibility exists for an extrachromosomally transmitted element which suppresses both male recombination and mutability[69].

Y-4 linkage of nucleolus organizer

In *Drosophila*, usually X–Y linked nucleolus organizer is found but the nucleolus is associated with the pair of shortest chromosomes (chromosome 4) in both the sexes in *D. ananassae*[70]. In male, Y chromosome is also associated with the nucleolus. This cytological observation was supported by the genetic demonstration of Y-4 linkage of bobbed mutation in *D. ananassae*. The Y-4 association of nucleolus organizer suggests that a translocation of the nucleolus organizer region from X to 4 has occurred during speciation in *D. ananassae*[71].

Pattern of chromosomal polymorphism

Another unusual feature attributed to *D. ananassae* is its pattern of chromosomal polymorphism and remarkably high levels of chromosomal polymorphism. Crow[72] writes: 'This is puzzling in view of the male recombination; there is a suggestion that some mechanism restricts exchange of chromosome segments within heterozygous inversions during spermatogenesis'. A number of investigations have been carried out on chromosomal polymorphisms in *D. ananassae*[8,9,57,73–76], resulting in the detection of 70 paracentric inversions, 17 pericentric inversions and 13 translocations. One pericentric inversion and 4 translocations were detected in laboratory stocks of *D. ananassae*[71]. Although 70 paracentric inversions have been detected so far in this species, only three paracentric inversions (AL, DE and ET, Figure 2) which have been called as cosmopolitan inversions by Futch[77], have become coextensive with the species

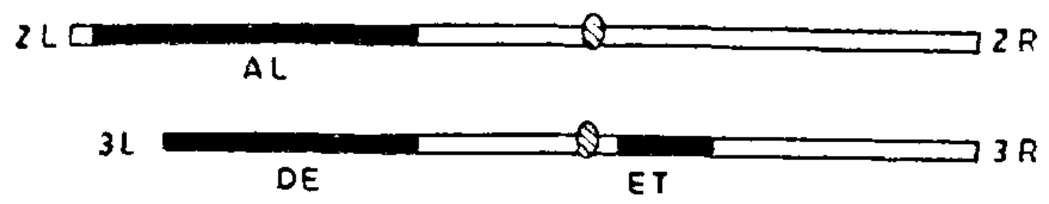

Figure 2. Location of AL (2L), DE (3L) and ET (3R) inversions in different chromosomes of *D. ananassae*.

suggesting the monophyletic origin of these inversions. Most of the inversions have localized distribution and have been detected from a few individuals. This is a feature of the pattern of chromosomal polymorphism in *D. ananassae*. Extensive studies on the frequencies of three cosmopolitan inversions in Indian populations (Figure 3) of *D. ananassae* have been reported[78–86]. The degree of genetic divergence among different populations has been quantified by calculating genetic distance (*D*) and genetic identity (*I*) on the basis of differences in the chromosome arrangement frequencies. There is strong evidence that Indian populations of *D. ananassae* have undergone a considerable degree of genetic divergence at the level of inversion polymorphism. In general, the populations from the south including Andaman and Nicobar Islands show more differentiation than those from the north. Based on the results obtained in *D. ananassae*, it has been suggested that chromosomal polymorphism may be adaptively important even in a widespread domestic species, and populations may undergo divergence as a consequence of their adaptation to varying environments.

Results of population cage experiments using different chromosome arrangements have shown that inversion polymorphism is balanced owing to adaptive superiority of inversion heterozygotes[87,88]. Inversion polymorphism due to three cosmopolitan inversions often persists in laboratory stocks established from females collected from natural populations[89–93]. Some strains maintained in the laboratory for more than a hundred generations have been found to contain these inversions[89]. This demonstrates that heterotic buffering is associated with cosmopolitan inversions. However, the degree of heterosis may vary depending upon the allelic contents of the chromosomal variants[90,91]. Inversion frequency may also change due to random genetic drift in small populations[92,93].

There are several studies on intra- and interchromosomal associations in natural populations and laboratory stocks of *D. ananassae*. Various combinations of unlinked inversions occurring in random association indicate no interchromosomal interactions in *D. ananassae*[94–96]. Two linked inversions of the third chromosome which strongly suppress recombination between them when heterozygous often show non-random association in laboratory stocks[40,95,97–100]. This is likely to be due to epistatic interaction and suppression of crossing-over. It it also been suggested that linkage disequilibrium

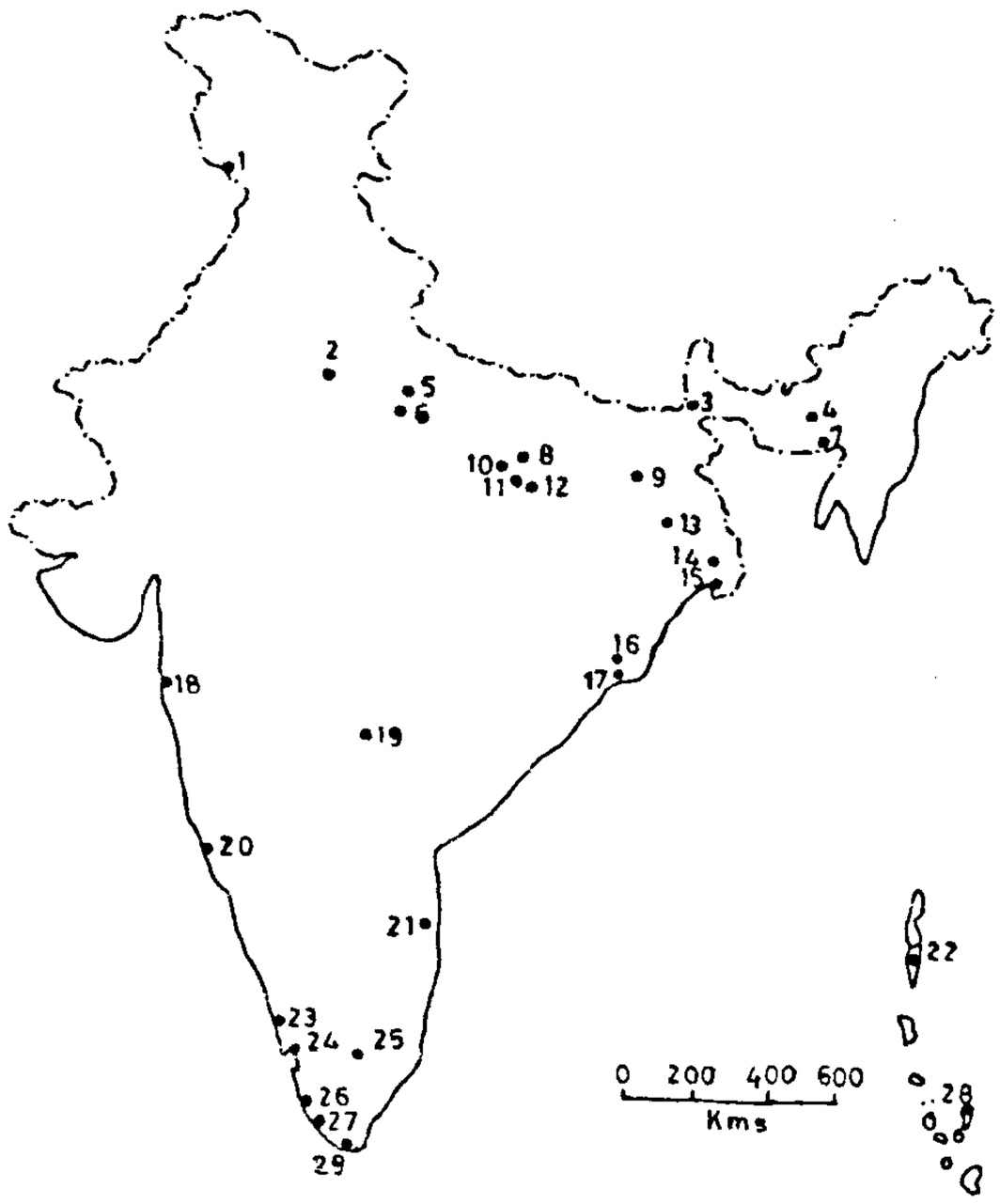

Figure 3. Map of India showing geographic localities from which *D. ananassae* flies were collected for chromosomal analysis. 1, Jammu; 2, Agra; 3, Siliguri, 4, Guwahati; 5, Lucknow; 6, Kanpur; 7, Shillong; 8, Ghazipur; 9, Bhagalpur; 10, Varanasi; 11, Jamsoti; 12, Lowari; 13, Ukhara; 14, Calcutta; 15, Birlapur; 16, Bhubaneswar; 17, Puri; 18, Mumbai; 19, Hyderabad; 20, Goa; 21, Chennai; 22, Port Blair; 23, Trichur; 24, Ernakulam; 25, Madurai; 26, Quilon; 27, Trivandrum; 28, Kamorta; 29, Kanya Kumari.

between inversions in certain isofemale strains may occur due to random genetic drift[99]. The tight linkage between the two inversions enhances the chance of drift in isofemale lines.

To test the relationship between inversions and mating propensity, Singh and Chatterjee[101,102] studied the mating ability of homo- and heterokaryotypes due to AL (2L) inversion derived from natural populations of *D. ananassae* in which the frequencies of different chromosome arrangements were known. Their main conclusions were: (i) the chromosome occurring in high frequency is associated with higher mating activity in all the populations analysed; (ii) heterokaryotypic males are superior in mating propensity to the corresponding homokaryotypes, indicating the existence of heterosis associated with AL inversion with respect to male mating activity; and (iii) males show greater variation than females, which indicates striking sex difference in *D. ananassae*. Thus inversion polymorphism in *D. ananassae* may have a partial behavioural basis as has been demonstrated in other species of *Drosophila*.

Heterosis without selectional coadaptation

The inversion heterozygotes often exhibit heterosis and the adaptive function of inversions is to protect coadapted complexes of polygenes. Any two gene arrangements coming from the same populations give, as a rule, heterotic heterozygotes in *D. pseudoobscura*[103]. There is, however, evidence that higher fitness may be lost in heterozygotes for chromosomes with different gene arrangements derived from different geographic populations. This has been found in *D. pseudoobscura*[103–105], *D. paulistorum*, *D. willistoni*[106] and *D. pavani*[107]. The explanation offered by Dobzhansky[103] is that the gene complexes carried in the chromosomes are coadapted or mutually adjusted through long continued natural selection in one locality, so that inversion heterozygotes possess high adaptive values. In view of these, Singh[108–111] conducted experiments in *D. ananassae* to test the coadaptation hypothesis. Interracial hybridization experiments were carried out by employing chromosomally monomorphic as well as polymorphic strains derived from different geographic localities. It has been found that inversion heterozygotes formed by chromosomes of different geographic origins exhibit heterosis which persists in interracial crosses. Thus interracial hybridization does not lead to breakdown of heterosis in *D. ananassae*. The chief conclusion from these results is that there is lack of evidence for genetic coadaptation in geographic populations of *D. ananassae*. This situation apparently conflicts with what has been found in other species of *Drosophila* by Dobzhansky and other workers[112]. Singh[111] suggested that heterosis associated with three cosmopolitan inversions is without previous selectional coadaptation and it appears to be simple luxuriance. Thus luxuriance can function in the adjustment of organisms to their environments.

Parthenogenesis

In light and dark forms of *D. ananassae*, parthenogenesis has been reported by Futch[113]. An entirely parthenogenetic line could be established by selection. However, it occurs at a low rate. Carson *et al.*[114] reported automictic type of parthenogenesis in *D. mercatorum*. The mechanism underlying the development of unfertilized eggs in *D. ananassae* may be similar to the automictic type of parthenogenesis in *D. mercatorum*.

Ethological isolation

Spieth[115] studied mating behaviour of light and dark forms of *D. ananassae* and found that various laboratory stocks developed sexual isolation but their degree varied from weak to marked. Sexual isolation between light and dark forms was reported from Samoa[77]. Later, these

forms were found to be different sibling species (*D. ananassae* and *D. pallidosa*) of the *ananassae* complex, which are potentially interfertile but are genetically distinct and their isolation is maintained by strong mating preference[116]. The existence of sexual isolation within *D. ananassae* has been reported by Singh and Chatterjee[117,118]. The degree of sexual isolation is stronger in isofemale lines than in natural populations. It has been suggested that stronger isolation in isofemale lines is likely to be via genetic bottlenecks[118]. Among the isofemale lines tested by Singh and Chatterjee[118], symmetrical and asymmetrical isolation was found and asymmetrical (one-sided) isolation was used to interpret the evolutionary sequences. The results with laboratory strains of *D. ananassae* are consistent with the hypothesis of Watanabe and Kawanishi[119] that the derived females discriminate against the ancestral males, which is the most important change for the creation of new species[120]. The pattern of mating preference between *D. nasuta nasuta* and *D. n. albomicans* fits into the hypothesis of Kaneshiro[121]. However, the results of mating propensity tests conducted by Ramachandra and Ranganath[122] in closely related strains of the *nasuta* subgroup (*D. n. nasuta*, *D. n. albomicans*, Cytorace I and Cytorace II) are nearer to the hypothesis of Watanabe and Kawanishi.

Sternopleural bristle phenotypes, mating propensity and fertility

In *D. melanogaster*, the genetics of various quantitative traits has been studied and the number of sternopleural bristles has been most extensively employed to study the effect of artificial and natural selection and to throw light on the genetic constitution of natural populations[123–127]. Singh and Mathew[128–132] studied quantitative genetics of sternopleural bristle phenotypes in *D. ananassae*. Their results have shown that there is genetic heterogeneity with respect to sternopleural bristle number in Indian populations of *D. ananassae*. Further, there was positive response to directional and stablilizing selection for sternopleural bristle number which provides evidence for genetic control of sternopleural bristle phenotypes with substantial amount of additive genetic variation in *D. ananassae* populations.

In *D. melanogaster*, Gibson and Thoday[127] found ethological isolation between flies having high and low number of sternopleural bristles resulting from disruptive selection. The lines differing in bristle number developed sexual isolation as a consequence of genetic divergence. However, no evidence of sexual isolation between high and low lines differing in bristle number was found in *D. ananassae* by Singh and Mathew[131]. The females and males with high number of bristles (collected from high line) are more successful in mating than those with low number of bristles (collected from low line). Furthermore, the flies with high number of bristles show higher fertility than those with low number of bristles[132]. Thus there is a positive correlation among sternopleural bristle number, mating propensity and fertility in *D. ananassae*[132].

Sexual and non-sexual behaviour

A number of investigations on sexual behaviour, oviposition site preference, pupation site preference and phototactic behaviour have been conducted in *D. ananassae*[101,102,133–143]. Evidence for genetic control of mating activity, oviposition site preference, pupation height and phototactic behaviour has been presented on the basis of positive response to selection. Interestingly, a Y-linked influence on mating propensity[135] and a transient maternal effect with respect to pupation height[138] were reported in *D. ananassae*. There is a positive correlation between mating activity and fertility in *D. ananassae*[134]. It has also been found that males are much more affected by selection than females. When red eye males were tested separately with *sepia* and *cardinal* mutants at nine different ratios, it was found that both types of males were equally successful in mating when present in the same ratio. However, they were more successful in mating when in a minority. This advantage disappeared when the males became common. This provides evidence for rare-male mating advantage in *D. ananassae*[136].

The results of experiments on female and male remating in *D. ananassae* provide evidence for shorter duration of copulation in second mating compared to first mating. Thus it differs from other species where it has been demonstrated that duration of copulation is shorter in first mating when compared to second mating[142]. For male remating such a comparison was made for the first time in *D. ananassae*[143]. This is the first report in the genus *Drosophila* for interstrain variation in remating time (remating latency) for both male remating as well as female remating in *D. ananassae*[142,143].

Conclusion

The work carried out so far on genetics and biology of *D. ananassae*, a cosmopolitan and domestic species commonly found in India, has clearly demonstrated that it possesses several unusual and interesting features which make it a special case in the genus *Drosophila*. Further studies may provide more information concerning genetics and biology of this species.

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