induction of significant levels of behavioural isolation. The sexual isolation observed developed in complete allopatry and is solely due to the process of adaptation to the different regimes.

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Role of inversion system on morphometric and fitness traits in *Drosophila* ananassae.

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Introduction

The role of inversions on the fitness characters have been well demonstrated (Dobzhansky and Wallace, 1953). Many experiments have demonstrated the superiority of heterokaryotypes over homokaryotypes (Singh, 1989a; Singh and Som, 2001). *Drosophila ananassae* is one such species which exhibits high level of inversion polymorphism. It is a cosmopolitan domestic species having a unique status among *Drosophila*. Due to certain peculiarities such as male crossing over, high mutability, high level of chromosomal polymorphism it has been used for many genetic studies. This species harbors a large number of inversions. Influence of different chromosomes on sternopleural bristle number have been detected, and different genetic factors controlling sternopleural bristle number have been located in different chromosomes by using marker strains (Shrimpton and Robertson, 1988a). Genetic heterogeneity for sternopleural bristle number has been found in Indian populations of *D. melanogaster* (Singh and Das 1991; Griffiths *et al.*, 2005; Yadav and Singh, 2006).

In certain cases, association between chromosomal inversion polymorphism and morphometric characters has been reported (David *et al.*, 2003; Griffiths *et al.*, 2005; Singh and Das, 1991; Yadav and Singh, 2006). The earlier studies on inversion polymorphism in *D. ananassae* (Da Cunha, 1960; Singh, 1998) have demonstrated that most of the inversions are distributed either on second or third chromosome. Two hypotheses have been proposed to account for the concentration of inversions on single chromosome, the co-adaptation hypothesis and mechanical hypothesis.

The author in the present studies has made analysis of inversion polymorphism, comparison of morphometric traits and fitness are studied in an inversion free strain and strains carrying 2LA, 3LA and 2LA+3LA inversions of Dharwad population of *D. ananassae*.

Materials and Methods

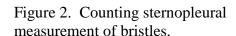
In the present study inversion strains were established from D. ananassae flies collected from wild locality of Dharwad using the procedure of Hegde $et\ al$. (1999). These flies were maintained in the vivarium at constant temperature of $22\pm1^{\circ}C$ and relative humidity of 70%. Preparations of polytene chromosomes were made to screen for the presence or absence of inversions following the procedure of Jayaramu (2009). Progenies of these inversion strains were isolated and aged for 5-6 days analyze morphometric traits (sternopleural bristles, scutellar bristles of the left side of the body, head width and wing length of the female), and fitness character fecundity and ovarioles have been measured using the procedure of Jayaramu (2009) and Prathibha (2011).

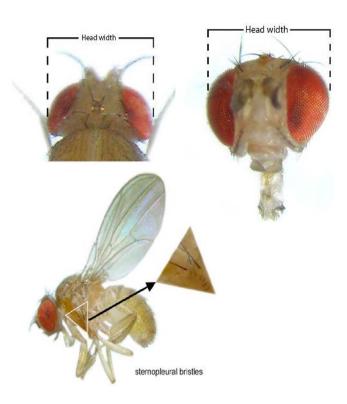
Table 4a. Morphometric traits in different inversion strains in *D. ananassae* (Values are Mean ± SE)

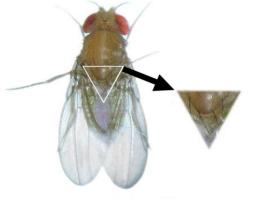
| <u>Strain</u> → | Inversion free | 2LA inversion | 3LA inversion | 2LA+3LA |
|------------------------|----------------------|----------------------|----------------------|----------------------|
| ↓Parameters | inversion nee | ZLA IIIVEISIOII | SLA IIIVEISION | inversion |
| Sternopleural bristles | 6.26 ± 0.102^{a} | 6.70 ± 0.086^{b} | 6.84 ± 0.082^{b} | 7.74 ± 0.14^{c} |
| Scutellar bristles | 4.30 ± 0.06^{a} | 4.48 ± 0.05^{b} | 4.56 ± 0.07^{b} | 4.64 ± 0.06^{b} |
| Head width | 0.72 ± 0.007^{a} | 0.75 ± 0.009^{b} | 0.77 ± 0.011^{b} | 0.82 ± 0.003^{c} |
| Wing length | 1.82 ± 0.02^{a} | 1.83 ± 0.02^{a} | 1.84 ± 0.03^{a} | 1.89 ± 0.02^{a} |

Same superscript in each row indicates that the value is non significant by DMRT.

Figure 1. Points of head width of *D. ananassae* (a = Dorsal view, b = Front view).







Wing length—

Scutellar bristles Wing length

Figure 3. Counting scutellar bristles.

Figure 4. Points of measurement of wing length.

Table 4b. One way ANOVA for morphometric traits in different inversion strains of *D. ananassae*

| Source | | Sum of squares | df | Mean squares | F value | P value |
|------------------------|--|------------------------------|-----------------|-----------------|------------|---------------------|
| Sternopleural bristles | Between groups Within groups Total | 57.895 110.460 168.355 | 3 196 199 | 19.298 0.564 | 24.243 | 0.000** |
| Scutellar bristles | Between groups Within groups Total | 03.295 46.660 49.955 | 3 196 199 | 1.098 0.238 | 4.614 | 0.004* |
| Head width | Between groups Within groups Total | 0.289 0.896 1.186 | 3 196 199 | 0.096 0.004 | 21.082 | 0.000** |
| Wing length | Between groups Within groups Total | 0.141 5.951 6.092 | 3 196 199 | 0.046 0.036 | 1.544 | 0.204 ^{NS} |

NS- non significant *P<0.05; **P< 0.001.

Results and Discussion

In the present study the relationship between different inversions with some morphometric traits such as sternopleural bristles, scutellar bristles, head width and wing length was studied (Table 4a, and Figures 1, 2, 3, and 4). Significant difference found in such an analysis suggests differential genotypic influences on these traits (Table 4b). In the present study the author has analyzed the differences in four morphometric traits in four different genetic strains of *D. ananassae* viz., inversion free strain, the second with a sub-terminal inversion on the left arm of second chromosome 2LA strain, third with a terminal inversion on the third chromosome 3LA strain and the fourth with two inversions, one on second chromosome and another on the third chromosome 2LA+3LA strain. Among the four morphometric traits analyzed, sternopleural and scutellar bristles are the polygenic traits whose expression is under the influence of the environmental conditions (Mather, 1943; Whittle, 1969), while the head width and wing lengths are polygenic traits that determine the body size of the flies (Capy *et al.*, 1994; Gracia-Vazuez *et al.*, 1989; Sokoloff, 1965, 1966; Yadav and

Singh, 2003, 2006). This study thus permits the analysis of relationship between these morphometric traits and inversions strains.

The number of sternopleural and scutellar bristles was highest in the strain with 2LA+ 3LA (double inversion strain) and lowest in the strain with inversion free. The number of sternopleural bristles was intermediate in the strain which carried 2LA and 3LA inversions. But the inversion free strain had lower number of sternopleural and scutellar bristles than inversion strains. This shows that the presence of inversion 2LA+ 3LA (double inversion strain) produces extra bristles on the sternopleural, scutellar plate. The presence of extra bristles in the inversion karyotypes of *D. melanogaster* has also been noticed by Das and Singh (1992b). Thus the study of the author confirms with the observation of these authors. The association of inversion with individuals having extra dorso-central and scutellar bristles has also been reported in certain other studies on *Drosophila* (Garcia-Vazquez and Sanchez -Refusta, 1989).

Table 5a. Ovarioles and fecundity of different inversion strains of *D. ananassae* (Values are Mean ± SE)

| Strain → | Inversion free | 2LA | 3LA | 2LA+3LA |
|-------------|----------------------------|----------------------------|----------------------------|---------------------------|
| ↓Parameters | | inversion | inversion | inversion |
| Ovarioles | 14.05 ± 0.65 ^a | 18.00 ± 0.88 ^b | 20.50 ± 1.10 ^b | $24.95 \pm 1.52^{\circ}$ |
| Fecundity | 172.06 ± 3.21 ^a | 187.84 ± 4.57 ^b | 189.58 ± 2.87 ^b | $210.82 \pm 6.02^{\circ}$ |

Same superscript in each row indicates that the value is non significant by DMRT.

Table 5b. One way ANOVA for ovarioles and fecundity of different inversion strains of *D. ananassae*

| Source | | Sum of squares | df | Mean squares | F value | P value |
|-----------|--|------------------------------------|-----------------|--------------------|------------|------------|
| Ovarioles | Between groups Within groups Total | 1251.850 1426.900 2678.750 | 3 196 199 | 417.283 18.775 | 22.225 | 0.000** |
| Fecundity | Between groups Within groups Total | 38006.77 185977.10 223983.87 | 3 196 199 | 12668.92 948.86 | 13.352 | 0.000** |

^{**}P< 0.001.

Scrutiny of Table 4a and b shows that the mean head width differs in flies carrying different inversions. It was noticed that head width was larger in strains carrying both 2LA + 3LA inversion (Double inversion strain). The head width of strains carrying single inversion (either 2LA or 3LA) was lesser than the strains carrying double inversion or without inversions. Furthermore, the head width of strain without inversion was significantly different from that of the strain with double inversion. This observation on head width, on the other hand, contradicts the observations of Dobzhansky and his associates (1960) who in *D. pseudoobscura* demonstrated superiority of inversion heterozygotes over homozygotes. Thus the heterotic effect of inversions may be limited to only certain genes particularly to those concerned with fitness and need not be found in all characters of a given species.

The wing length of double inversion strain (2LA+3LA) was highest and it was not significantly different from other strains. Thus the heterotic effect of inversion could be seen with regard to this trait also. As wing length is an index of body size (Monclus and Prevosti, 1971;

Sisodia and Singh, 2001, 2004), the present study indicates that the flies of the strain carrying double inversion are larger than the others.

The maintenance of inversion polymorphism in natural populations of *D. ananassae* seems to be associated with many other adaptive functions in terms of sexual behavior, fitness and morphometric traits. This observation thus confirms earlier studies on *Drosophila* with regard to paracentric inversions (Da Cunha, 1955; Ray Chaudhuri and Jha, 1966; Singh, 1988, 1991; Singh and Das, 1990). Ovarioles and fecundity are fitness characters which determine the reproductive success of a species. In the present study (Table 5a, b) the author has noticed highest ovarioles and fecundity in the double inversion strain (2LA+3LA) and lowest in inversion free strain of *D. ananassae*. Ovarioles and fecundity is one of the fitness characters which has relevance to the reproductive success and survival of a given species (Sisodia and Singh 2004; Prathibha, 2011). The relationship between ovarioles number and fecundity were significantly stronger as compared to relationship between fecundity and female size (David and Le nobre'd, 1970; Branquart and Hemptinne, 2000). As more species are studied the number of examples where female size and fecundity (Chenoweth *et al*, 2007) and female size and ovarioles number are uncorrelated is increasing (Togashi and Life, 2007). In contrast to this, there is a strong positive relation between ovarioles number and fecundity (Branquart and Hemptinne, 2000; Wayne *et al*, 1997).

In the present study the persistence of inversion polymorphism in these populations could be explained by an advantage of inversion heterozygotes over corresponding homozygotes. The author in the present study has noticed more heterokaryotypes than homokaryotypes. This confirms the fact that the inversion polymorphism is adaptive and balanced due to higher Darwinian fitness on inversion heterozygotes (Dobzhansky, 1951).

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