

## **Inversion polymorphism in natural populations of *Drosophila nasuta nasuta***

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**Abstract.** Six south Indian populations of *Drosophila nasuta nasuta* were analysed for inversion polymorphism. A total of 28 inversions were recorded. Of these, 9 are entirely new gene arrangements reported here for the first time. Various facets of the polymorphic system of these 6 populations, namely, flexibility, heteroselection, non-random distribution and linkage disequilibrium are discussed.

**Keywords.** *Drosophila nasuta*; inversions.

### **1. Introduction**

*Drosophila nasuta nasuta*, a widespread species, presents a high order structural variability due to inversions in its natural populations. It stands one among the chromosomally most variable species in the genus and tops the list in the *nasuta* subgroup (Nirmala and Krishnamurthy 1974; Ranganath and Krishnamurthy 1975; Rajasekarasetty *et al* 1979). A survey of 6 south Indian populations was made to unravel their polymorphic organization and the findings are presented.

### **2. Materials and methods**

Population samples of *D. n. nasuta* were obtained from 6 places, namely, Gangotri, Sanitorium, Mandakalli, Biligirirangana hills I and II and Kotagiri. Flies were trapped using fermenting banana seeded with yeast as the bait. Egg sample technique (Strickberger and Wills 1966) was employed to analyse the chromosomal constitution. Salivary gland chromosome preparations were made using lacto-acetoorcein stain. The nomenclature of different inversions is after Nirmala and Krishnamurthy (1974) and Ranganath and Krishnamurthy (1975).

### **3. Results and discussion**

In *Drosophila*, the absence of crossing over in males and selective elimination of dicentric and acentric chromatids during meiosis in females, created the possibility for the group to use inversion polymorphisms in structuring of their populations (Freire Maia 1961). Earlier studies of Nirmala and Krishnamurthy (1974), Ranganath and Krishnamurthy (1975) and Rajasekarasetty *et al* (1979) have revealed a total of 46 different inverted gene arrangements in different populations of *D. n. nasuta*. The present analysis of 6 populations of *D. n. nasuta* has exposed a

total of 28 different gene orders. A critical comparison of these rearrangements with those of the already described ones has shown that 19 of these correspond to the ones already recognized while 9 sequences are new. These chromosomal patterns, which are maiden reports, are shown in figure 1. By considering the present and earlier reports, the genetic system of *D. n. nasuta* is found to be highly variable with a tally of 55 inversions. Of these, 3 are located in chromosome X while 4 and 7 inversions are in the left and right arms of chromosome 2 respectively. The remaining 41 inversions are localized in chromosome 3. Eventhough there are inversions in ail chromosomes, there is a non-random distribution of inversions in the chromosomes of *D. n. nasuta* with a heavy concentration of inversion break-points in the basal region of the chromosome 3. *D. pseudoobscura*, *D. persimilis*, *D. nebulosa* and *D. busckii* also present a situation with one of its chromosomes harbouring almost all inversions; while in *D. willistoni*, *D. robusta*, *D. algonquin*, *D. sturtevantii* and *D. paramelanica* polymorphism is distributed in all chromosomes (cf. Dobzhansky 1970; Ranganath 1975). In spite of the explanations offered by Novitski (1946), Wasserman (1963), White (1973) and Ranganath and Krishnamurthy (1978), the pattern of distribution of inversions among different chromosomes is an intriguing problem that is yet to be understood adequately.

The polymorphic system of the 6 populations of *D. n. nasuta* under study is not the same. There exist both qualitative and quantitative differences among populations (tables 1–5). The Sanitorium population was most heterogeneous with 20 different inversions while the Kotagiri population had just 10 inversions. The mean number of inversions per individual varied from 2.06 of Gangothri population to 1.20 of Kotagiri population. Of the 28 inversions recorded in the present study, only 3A, 3C, 3E, 3E+3H, 3H+3K, 2RA and 2RB were found in all the 6 populations. Of these, except 3A and 3C, the frequencies of other inversions differed significantly ( $P < 0.05$ ; table 6). By judging their frequencies, it can be assumed that certain elements of the polymorphic system in *D. n. nasuta* appear to be rigid while others are flexible to the different population-environmental situations.

In the 6 populations of *D. n. nasuta* under investigation, the incidence of individuals with one or more heterozygous inversions was always significantly more than those without any heterozygous inversion. In every population, the frequency of such heterokaryotypes was always more than 50% (table 1). Further, there was no significant difference in their frequencies among different populations (table 5). Thus, heterokaryotypy has become a part and parcel of the population structure of *D. n. nasuta* and this fits into the concept of obligate heteroselection proposed by Ranganath and Krishnamurthy (1974).

Of the 28 inversions observed in the present study, 5 were in chromosome 2 and 23 were in chromosome 3. Frequencies of individuals with inversions in only one of these chromosomes (linked) and inversions in both of these chromosomes (unlinked) in different populations are presented in table 6. It was seen that the number of individuals with only linked inversions was significantly higher than those with unlinked inversions. Possible factors which favour the dominance of individuals with linked inversions over unlinked inversions have been discussed by Anderson *et al* (1967), Copper *et al* (1955), Riles (1965) and Ranganath and Krishnamurthy (1978).

Yet another interesting feature of the polymorphic system of *D. n. nasuta* is the nature of relationship between two independent inversions namely 3A and 3C. In



Figure 1. For caption, see next page.

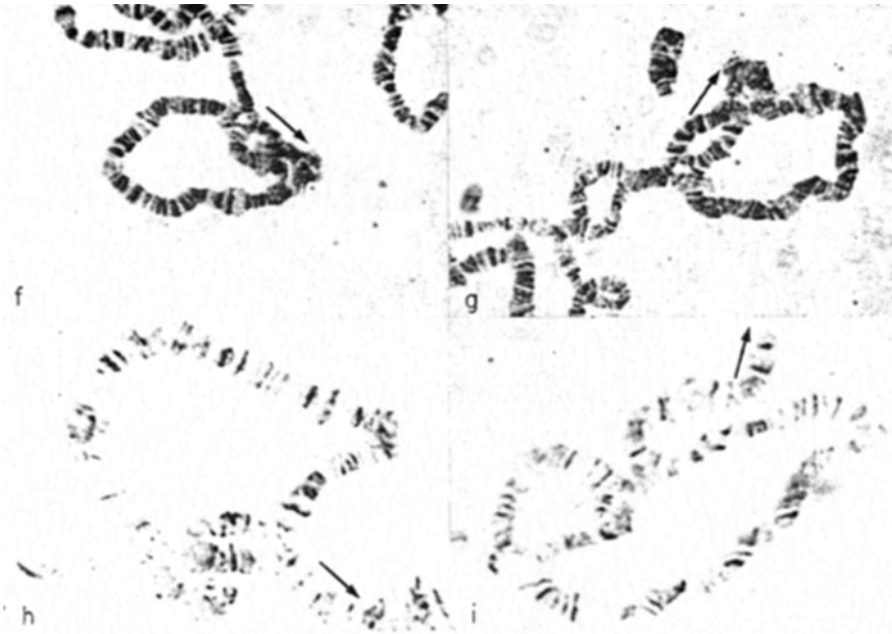


Figure 1a-i. New inverted gene arrangements in the chromosome III of *D. n. nasuta*. Arrows indicate the chromocenter end.

Table 1. Differences in number of inversions, mean number of inversions and heterokaryotypes in 6 south Indian populations of *D. n. nasuta*.

Populations	No. of larvae scored	No. of inversions	Mean No. of inversions per larva	Heterozygosity (%)
Gangothri	236	15	2.06 ± 0.08	85.59
Sanitorium	271	20	1.83 ± 0.07	79.70
Mandakalli	289	18	1.65 ± 0.06	77.50
BR hills I	218	14	1.52 ± 0.07	71.10
BR hills II	129	12	1.44 ± 0.10	65.89
Kotagiri	234	10	1.20 ± 0.06	63.24

Table 2. Frequency (in per cent) distribution of II chromosome gene arrangements in 6 south Indian populations of *D. n. nasuta*.

Populations inversions	Gangothri	Sanitorium	Mandakalli	BR hills I	BR hills II	Kotagiri
2RA	9.74	13.28	4.84	0.45	2.32	0.85
2RB	8.05	7.74	8.30	2.29	—	1.28
2RC	—	2.58	2.76	—	0.77	—
2RD	4.66	0.36	1.73	—	—	—
2RG	—	0.36	—	—	—	—
2RA + 2RB	2.11	—	1.73	2.29	0.77	0.85

**Table 3.** Frequency (in per cent) distribution of III chromosome gene arrangements in 6 south Indian populations of *D. n. nasuta*.

Populations inversions	Gangothri	Sanitorium	Mandakalli	BR hills I	BR hills II	Kotagiri
3A	19.91	14.39	17.99	12.84	18.62	9.82
3C	19.06	14.02	18.33	12.84	18.62	9.82
3E	12.71	20.29	20.06	13.30	22.48	11.96
3H	2.54	—	1.03	1.37	4.65	4.70
3O	—	0.36	1.03	0.91	0.77	—
3V	—	—	—	0.45	—	—
3E + 3H	31.35	27.67	23.87	33.94	17.05	24.78
3H + 3K	16.10	8.11	7.61	8.71	10.07	6.83
3E + 3N	1.69	1.00	1.38	—	—	—
3E + 3J	—	—	—	4.12	2.32	5.98
3O + 3P	0.42	2.58	1.73	0.45	2.32	2.56
3O + 3N	—	0.36	—	—	—	—
3W + 3X	5.50	4.42	3.80	2.29	—	—
3Y + 3Z	—	—	1.38	—	—	—

**Table 4.** Frequency (in per cent) distribution of the new gene arrangements of III chromosome in 6 populations of *D. n. nasuta*.

Populations inversions	Gangothri	Sanitorium	Mandakalli	BR hills I	BR hills II	Kotagiri
Complex						
I	2.54	—	—	—	—	—
II	—	1.47	—	—	—	—
III	—	1.84	—	—	—	—
IV	—	—	1.03	—	—	—
V	—	—	—	1.37	—	—
VI	—	1.84	—	—	—	—
VII	—	1.47	—	—	—	—
VIII	2.54	0.36	1.03	—	—	—
IX	—	—	—	—	3.87	—

**Table 5.** Summary of Chi square test computed to compare the frequencies of common inversions and the heterozygosity in 6 south Indian populations of *D. n. nasuta*.

Populations	No. of larvae scored	3A	3C	3E	3E + 3H	3H + 3K	2RA	2RB	No. of inversion heterozygotes
Gangothri	236	47	45	30	74	38	23	19	202
Sanitorium	271	39	38	55	75	22	36	21	216
Mandakalli	289	52	53	58	69	22	14	24	224
BR hills I	218	28	28	29	74	19	1	5	155
BR hills II	129	24	24	29	22	13	3	0	85
Kotagiri	234	23	23	28	58	16	2	3	148
	$\Sigma X^2$	11.00	10.53	13.56	11.75	14.45	56.85	29.41	10.74
df 5;	P Value	>0.05	>0.05	<0.05	<0.05	<0.05	<0.01	<0.01	>0.05

all the 6 populations, the number of double heterozygotes for both 3A and 3C was significantly higher than the number of single heterozygotes for either 3A or 3C

**Table 6.** Frequencies (in per cent) of linked and unlinked heterozygous inversions in II and III chromosomes encountered in the natural populations of *D. n. nasuta*.

Populations	II Chromosome	III Chromosome	II + III Chromosome
Gangothri	6.35	61.44	17.79
Sanitorium	5.53	17.34	9.22
Mandakalli	6.92	69.89	11.41
BR hills I	1.37	22.47	3.66
BR hills II	0.77	61.24	3.10
Kotagiri	2.13	16.66	0.85

**Table 7.** Linkage disequilibrium between 3A and 3C heterozygous inversions in 6 south Indian populations of *D. n. nasuta*.

Populations	No. of larvae	3A	3C	3A, 3C	$\Sigma X^2$	df. 1 P value
Gangothri	236	3	1	44	73.50	<0.001
Sanitorium	271	1	0	38	72.10	<0.001
Mandakalli	289	2	3	50	82.05	<0.001
BR hills I	218	0	0	28	56.02	<0.001
BR hills II	129	0	0	24	48.00	<0.001
Kotagiri	234	0	0	23	46.05	<0.001

(table 7). Out of 1377 larvae only 10 were single heterozygotes (0.72%) while 207 were double heterozygotes (15.03%). This is a clear case of linkage disequilibrium between two linked gene orders. Eventhough many species of *Drosophila* are known to have inversion polymorphism, the phenomenon of linkage disequilibrium is not frequent. It has been recorded only in a few instances (Blight 1955; Levitan and Salzano 1959; Brncic 1961; Mather 1963; Kumar and Gupta 1986).

Thus the polymorphic system of *D. n. nasuta*, featuring a wealth of inversions, flexibility, heteroselection, non-random distribution and linkage disequilibrium is unique among the members of *Drosophila*.

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