

Discussion

My data show that antennae are important to *D. melanogaster*'s ability to detect and respond to odorants from Morinda fruit. In particular, the removal of the basiconic sensillia clearly reduces avoidance of this fruit, genetically confirming the electrophysiological data of Dekker *et al.* (2006). My data also suggest that tarsal taste receptors (*sensu* Matsuo *et al.*, 2007) may influence behavior, although not as much as antennae. Interestingly, ablation of sensory organs in *D. melanogaster* is not sufficient to engender *D. sechellia*-like behavior (Figure 1). This result suggests that the host specific behavior is not simply a loss of the ability of *D. sechellia* to perceive its host.

Acknowledgments: I thank Ian Dworkin for comments on this note and William Jeck for technical assistance. This work was supported by funds from the National Science Foundation.

References: Dekker, T., I. Ibba, et al., 2006, Curr. Biol. 16(1): 101-9; Ebbs, M.L., and H. Amrein 2007, Pflugers Arch 454: 735-47; Hallem, E.A., A. Dahanukar, et al., 2006, Ann. Rev. Entomol. 51: 113-35; Jones, C.D., 1998, Genetics 149: 1899-908; Jones, C.D., 2001, Genet. Res. 78: 225-33; Jones, C.D., 2004, Heredity 92: 235-41; Jones, C.D., 2005, Genetica 123: 137-45; Lachaise, D., and J.F. Silvain 2004, Genetica 120(1-3): 17-39; Legal, L., B. Chappe, et al., 1994, Journal of Chemical Ecology 20: 1931-1943; Louis, J., and J.R. David 1986, Acta Oecologica 7: 215-229; Matsuo, T., S. Sugaya, et al., 2007, PLoS Biol 5: e118; McBride, C.S., 2007, Proc. Natl. Acad. Sci. USA 104: 4996-5001; R'Kha, S., P. Capy, et al., 1991, Proc. Natl. Acad. Sci. USA 88: 1835-9; Tsacas, L., and G. Bächli 1981, Revue fr. Ent. NS 3: 146-150.



Chromosomal aberrations in *Drosophila ananassae*.

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Drosophila ananassae exhibits a high degree of chromosomal polymorphism. It harbors a large number of inversions in its natural populations (Singh, 1998). Out of these reported from various parts of the world, most have restricted distribution while the three cosmopolitan inversions namely, Alpha (AL) in 2L, Delta (DE) in 3L, and Eta (ET) in 3R show worldwide distribution (Singh, 1998). Population genetics of chromosomal polymorphism in Indian natural populations of *D. ananassae* has been extensively studied (for references see the review by Singh, 1998). The results have clearly shown that there is geographic differentiation of inversion polymorphism. Present communication gives the details of chromosomal aberrations detected from natural populations and laboratory stocks of *D. ananassae*. We have tried to include all detected chromosomal aberrations so far in *D. ananassae* in natural populations and laboratory populations to give the holistic picture of chromosomal variability as well as unusual mutational property.

The details of pericentric inversions and translocations detected in *D. ananassae* are given in Tables 1 and 2, respectively. The numbers of pericentric inversions and translocations are twenty one and forty eight, respectively. The occurrence of pericentric inversions (heterozygotes for pericentric inversions produce unbalanced gametes, their appearance, therefore, is opposed by natural selection) and translocations, which are rare in other species of *Drosophila*, reflect unusual mutational properties of *D. ananassae*.

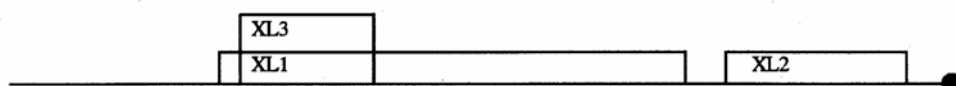
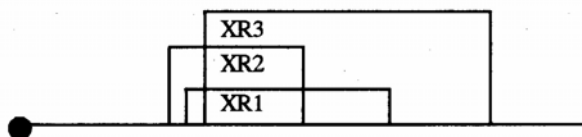
The paracentric inversions are depicted in Figures 1-6 via line diagram. We have followed the improved edition of polytene chromosome reference photomap of *D. ananassae* (Moriwaki and

Table 1. Pericentric inversions in *D. ananassae*.

S. No.	Pericentric inversion	Locality	Reference
1.	In (2LR)a	Brazil	Freire-Maia, 1955, 1961
2.	In (2LR)A	Niue	Futch, 1966; Seecof, 1957; Hinton and Downs, 1975
3.	In (2LR)Lo	#	*
4.	In (2LR)	India	Singh et al., 1971
5.	In (2LR)9	India	Reddy and Krishnamurthy, 1972b
6.	In (2LR)B	Guam	*
7.	In (2LR)B,Ubx	#	¶
8.	In (2LR)C	Noumea	*
9.	In (3LR)a	Brazil	Freire-Maia, 1955, 1961
10.	In (3LR)b	Brazil	Freire-Maia, 1955, 1961
11.	In (3LR)c	Brazil	Freire-Maia, 1955, 1961
12.	In (3LR)D,Bi ²	#	¶
13.	In (3LR)d	Brazil	Freire-Maia, 1955, 1961
14.	In (3LR)E,stw	#	¶
15.	In (3LR)A	Niue	Seecof, 1957; Futch, 1966
16.	In (3LR)B	Niue	Seecof, 1957; Futch, 1966
17.	In (3LR)C	Chiang Mai	*
18.	In (3LR)F	Wau	*
19.	In (3LR)G	Hyderabad	*
20.	In (3LR)H	Coimbatore	*
21.	In (3LR)I	Coimbatore	*

Note: * for references see, Tobari, 1993; # detected from various laboratory stocks; ¶ Hinton (unpublished)

inversions, followed by 2R (20), 3R (17), 3L (14), XL and XR, three each. With the exception of few cases, there has been no clustering of break points in any particular region in all the arms. So, it could be said that naturally occurring inversions in *D. ananassae* are randomly distributed in X, second, and third chromosomes.

Figure 1. Location of different inversions in XL of *D. ananassae*.Figure 2. Location of different paracentric inversions in XR of *D. ananassae*.

Although a large number of paracentric inversions are known to occur in *D. ananassae*, only three have become coextensive with the species. Most of the inversions have localized distribution and have been detected from the few individuals. This is a feature of the pattern of the chromosomal polymorphism in *D. ananassae* (Carson, 1965; Singh, 1988). A given arrangement may occur in one region but may be absent in other. An explanation to account for such disjunct distribution of gene arrangements may be that all types of arrangements did not occur simultaneously in the past history of the species. The former types, being older, had greater opportunities for migration and thereby at present they have a distribution throughout the world (Kaufmann, 1936a,b; Kikkawa, 1938; Dobzhansky and Dreyfus, 1943). On the contrary, those rearrangements of relatively recent origin and due to obvious impediments in the

Ito, 1969) by Tomimura and Tobari, Tobari (1993). As for naming different inversions, to make it uniform, we have numbered them in chronological order as given in Tobari (1993). It is difficult to know the exact number of paracentric inversions, since different investigators have named inversions independently. Also all the new inversions have not been reported or documented in relevant journals. In the present communication despite these limitations we have tried to include all possible inversions, thus, taking the total tally to seventy eight. The second and third chromosome carried the maximum number of inversions. Among these, 2L carried the maximum of twenty one

means of migration could not migrate from their respective native place to the localities where they have been found wanting (Ray-Chaudhuri and Jha, 1967).

Table 2. Translocations in *D. ananassae*.

S.No.	Translocation	Locality	Reference
1.	T (XL;2R) A	Niue	Seecof,1957;Futch,1966
2.	T (XR;2R)	India	Sajjan and Krishnamurthy, 1970
3.	T (XR;2L) 8	India	Reddy and Krishnamurthy, 1972b
4.	T (XL;2L) B	Nauru	*
5.	T (XR;2R)A,M Ubx ca	#	Hinton, 1979
6.	T(XL;XR)B,ca Th	#	Hinton, 1981
7.	T (1;3)A, Mo	#	¶
8.	T (Y;2L)A, ca	#	Hinton, 1979
9.	T (Y;2L)B, ca	#	Hinton, 1979; Hinton and Downs, 1975
10.	T (Y;2L)C, ca	#	Hinton, 1979, 1980, Hinton and Downs, 1975
11.	T (Y;2;3)A,M ca stw	#	Hinton, 1980
12.	T (Y;3)A.stw	#	Hinton, 1980
13.	T (Y;3R)B	#	Hinton and Downs, 1975
14.	T (Y;3L)C,e se;ru	#	¶
15.	T (Y;3L)pe ^v	#	*
16.	T (2L;3L)	Brazil	Dobzhansky and Dreyfus, 1943
17.	T (2L;3L)66	Honolulu	*
18.	T (2L;3L) 9	India	Reddy and Krishnamurthy, 1972a
19.	T (2L;3L)10	India	Sajjan and Krishnamurthy, 1972
20.	T (2L;3L)8	India	Reddy and Krishnamurthy, 1974
21.	T (2R;3R)	Brazil, India	Freire-Maia, 1961; Sajjan and Krishnamurthy, 1970
22.	T (2R;3R)AA,Ly	#	¶
23.	T (2R;3R)A,ca stw	#	Hinton, 1979; Hinton and Downs, 1975
24.	T (2R;3R)B,M ca stw	#	Hinton, 1979; Hinton and Downs, 1975
25.	T (2L;3R)C,M ca stw	#	Hinton, 1979; Hinton and Downs, 1975
26.	T (2R;3R)D,ca stw	#	Hinton, 1979, Hinton and Downs, 1975
27.	T (2L;3R)E,ca stw	#	Hinton, 1979, 1980, Hinton and Downs, 1975
28.	T (2L;3L)F,ca stw	#	Hinton, 1979
29.	T (2L;3L)G,ca stw	#	Hinton, 1979, Hinton and Downs, 1975
30.	T (2L;3R)H,ca stw	#	Hinton, 1979, 1980, Hinton and Downs, 1975
31.	T (2R;3R)J, Xa ca stw	#	Hinton, 1979, 1980, Hinton and Downs, 1975
32.	T (2L;3L)K,ca stw	#	Hinton, 1979, 1980, Hinton and Downs, 1975
33.	T (2R;3L)L,ca stw	#	Hinton, 1979, 1980, Hinton and Downs, 1975
34.	T (2L;3L)M,ca stw	#	Hinton, 1979, 1980, Hinton and Downs, 1975
35.	T (2L;3R)N,ca stw	#	Hinton, 1979, 1980, Hinton and Downs, 1975
36.	T (2R;3L)O,ca stw	#	Hinton, 1979, 1980, Hinton and Downs, 1975
37.	T (2L;3R)P,ca stw	#	Hinton, 1979, 1980, Hinton and Downs, 1975
38.	T (2R;3R)Q,ca stw	#	Hinton, 1979, 1980, Hinton and Downs, 1975
39.	T (2;3)R	#	Hinton, 1981
40.	T (2R;3R)S	#	Hinton, 1981, Hinton and Downs, 1975
41.	T (2L;3R)T	#	Hinton, 1981, Hinton and Downs, 1975
42.	T (2;3)U,ca cy	#	Hinton, 1981, Hinton and Downs, 1975
43.	T (2L;3R)V	#	Hinton and Downs, 1975
44.	T (2L;3L)W,Cy ^{EX}	#	Hinton and Downs, 1975
45.	T (2;3)Z,Mot	#	¶
46.	T (2L;3L)15	India	Singh, 1991
47.	T (3L;4)Pm	#	Kikkawa, 1938
48.	T (3L;4)	India	Ray-Chaudhuri and Jha, 1966

Note: #, Detected from various laboratory strains; *, For references see Tobari, 1993; ¶, Hinton (unpublished).

Disappearance of new sequences suggests that population, in question, might have developed a kind of resistance to acquire new gene arrangements in its genetic structure, because they could not yield adaptive values or heterotic effects to their carriers. In other words, the resistance might be

against any further increase in the amount of load of chromosomal polymorphism in natural populations of *D. ananassae*. With the same token, the existing load of chromosome polymorphism due to three cosmopolitan inversions in natural populations of *D. ananassae* might be too high to acquire any new gene arrangement as a means of adaptation of population to the extremes of the environmental conditions (White, 1958).

Freire-Maia's (1961) suggestion that that some special mechanism exists in *D. ananassae* to permit the retention of disadvantageous rearrangements in natural populations deserves exploration. Alternatively, the high incidence of such rearrangements may reflect high mutability in this species, a possibility proposed by Kikkawa (1938).

The geographical distribution of the three cosmopolitan inversions has been shown in Table 3. It is apparent from the table that the three cosmopolitan inversions are of frequent occurrence in natural populations and have become coextensive with the species.

Table 3. Geographical distribution of three cosmopolitan inversions in *D. ananassae*.

Area	Subterminal (alpha)	Terminal (delta)	Basal (eta)	Source
Alabama	+	+	+	Kaufmann, 1936
Texas	+	-	+	Shirai and Moriwaki 1952
Hawaii	+	+	+	Shirai and Moriwaki 1952
Majuro	+	+	+	Seecof, 1957
Cuba	+	+	+	Futch, 1966
Mexico	+	+	+	Shirai and Moriwaki 1952; Futch, 1966
Brazil	+	+	+	Dobzhansky and Dreyfus, 1943; Shirai and Moriwaki 1952; Freire- Maia, 1955
China	+	+	+	Kikkawa, 1938
Formosa (Taiwan)	+	+	+	Kaufmann, 1936; Kikkawa, 1938
Japan	+	+	+	Kaufmann, 1936; Kikkawa, 1938
India	+	+	+	Ray-Chaudhuri and Jha, 1966; Sajjan and Krishnamurthy, 1970; Reddy and Krishnamurthy, 1972; Singh, B.N., 2001
Africa	+	+	+	Shirai and Moriwaki 1952
Micronesia (Caroline Island, Marshal Island, Mariana Island)	+	+	+	Seecof (Stone et al. 1957); Futch, 1966
Melanesia (Papua New Guinea, Calodonia Island, Fiji)	+	+	+	Futch, 1966
Polynesia (Samoa, Cook Island)	+	+	+	Futch, 1966
Mauritius	+	+	+	*
Sri Lanka	+	+	+	*
Myanmar	+	+	+	*
Thiland	+	+	+	*
Malaysia	+	+	+	Singh, 1983a,b; *
Borneo	+	+	+	Singh, 1983b; *
Philippines	+	+	+	*
Singapore	+	+	+	*

* for references see Tobari, 1993; + indicates presence of inversion; - indicates absence of inversion.

Dobzhansky and Dreyfus (1943) pointed out that *D. ananassae* probably originated in some area of eastern and southeastern Asia and has depended on man for its present widespread distribution. *D. ananassae* certainly appears to qualify as a polytypic species. Its widespread circum-tropical distribution, especially through the scattered island groups in the Pacific ocean, has

permitted recognizable genetic differences between parts of species population to become so well developed that geographic races can be distinguished.

Relatively low number of inversions were observed in dark form *ananassae*, thus we suggest that the dark form *ananassae* was distributed around Polynesian Islands before the cosmopolitan form had a chance to expand its territory throughout the entire tropical and subtropical world. Because no reproductive isolation had developed between the two forms, the cosmopolitan form with its cosmopolitan inversions introgressed into Polynesian populations. Then these cosmopolitan inversions were distributed in many places where the dark form *ananassae* had been the precedent inhabitants. These widespread cosmopolitan inversions would be maintained in natural populations by the strong superiority of the inversion heterozygotes (Tobari, 1993).

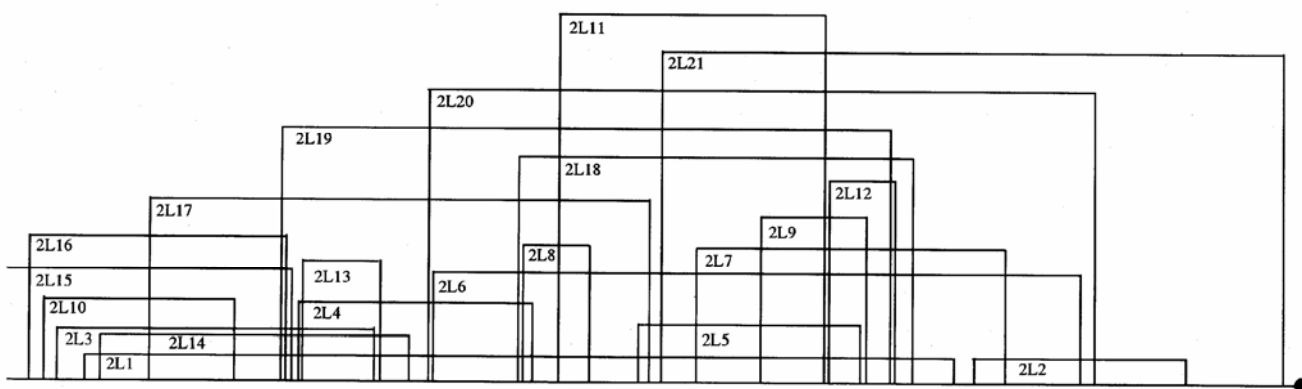


Figure 3. Location of different paracentric inversions in 2L of *D. ananassae*.

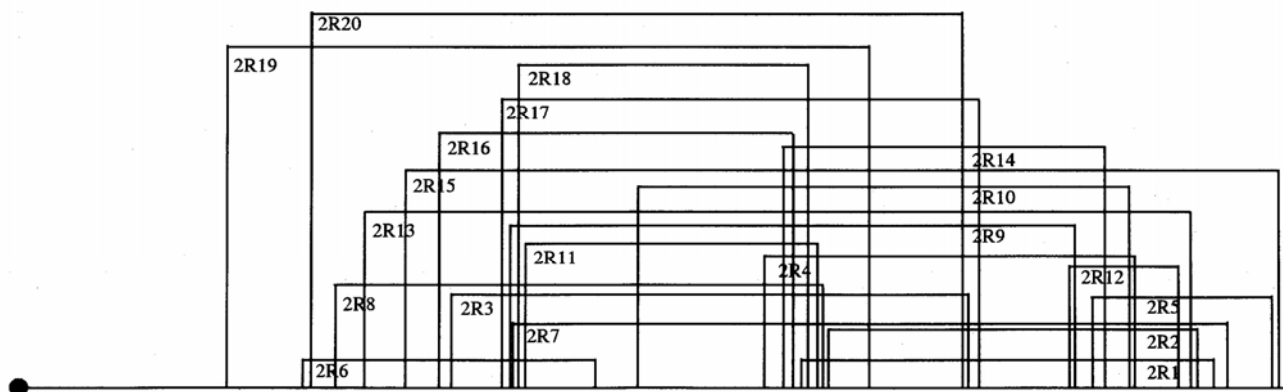


Figure 4. Location of different paracentric inversions in 2R of *D. ananassae*.

Acknowledgments: The financial support from CSIR, New Delhi, in the form of Senior Research Fellowship to PS is gratefully acknowledged.

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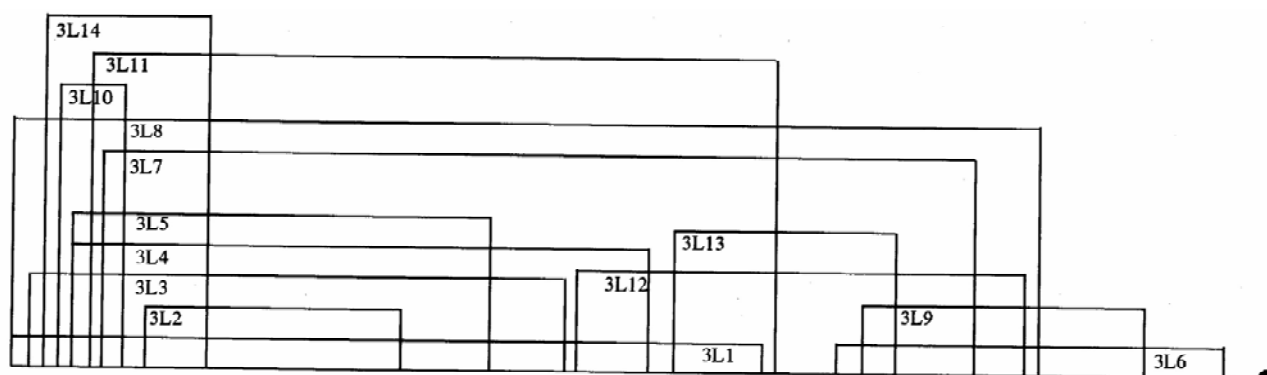


Figure 5. Location of different paracentric inversions in 3L of *D. ananassae*.

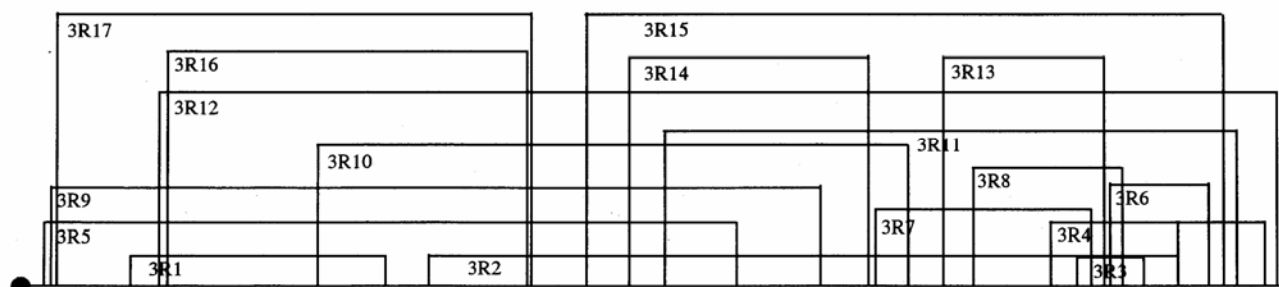


Figure 6. Location of different paracentric inversions in 3R of *D. ananassae*.

Dros. Inf. Serv. 55: 213-217; Hinton, C.W., 1981, Genetics 98: 77-90; Hinton, C.W., and J.E. Downs, 1975, J. Heredity 66: 353-361; Kaufmann, B.P., 1936a, Science 83: 39; Kaufmann, B.P., 1936b, Proc. Natl. Acad. Sci. USA 22: 591-594; Kikkawa, H., 1938, Genetica 20: 458-516; Moriwaki, D., and S. Ito 1969, Jpn. J. Genet. 44: 129-138; Ray-Chaudhuri, S.P., and A.P. Jha 1966, Proc. Int. Cell Biol. Meet. Bombay: 325-383; Ray-Chaudhuri, S.P., and A.P. Jha 1967, Nucleus 10: 81-89; Reddy, G.S., and N.B. Krishnamurthy 1972a, Dros. Inf. Serv. 48: 139-140; Reddy, G.S., and N.B. Krishnamurthy 1972b, Dros. Inf. Serv. 48: 140-142; Sajjan, S.N., and N.B. Krishnamurthy 1970, Dros. Inf. Serv. 45: 166; Sajjan, S.N., and N.B. Krishnamurthy 1972, Dros. Inf. Serv. 48: 103-104; Singh, B.N., 1983a, Experientia 39: 99-100; Singh, B.N., 1988, Ind. Rev. Life Sci. 8: 147-168; Singh, B.N., 1991a, Dros. Inf. Serv. 70: 203; Singh, B.N., 1998, Ind. J. Expt. Biol. 36: 739-748; Singh, B.N., 2001, Ind. J. Expt. Biol. 39: 611-622; Singh, P., and B.N. Singh 2005a, Dros. Inf. Serv. 88: 10-11; Singh, P., and B.N. Singh 2005b, Dros. Inf. Serv. 88: 15-16; Singh, V.K., M. Mishra, and A.P. Jha 1971, Dros. Inf. Serv. 47: 97; Tobari, Y.N. (ed), 1993, *Drosophila ananassae: Genetical and Biological Aspects*, Japan Scientific Societies Press, Tokyo; White, M.J.D., 1958, Cold Spring Harb. Symp. Quant. Biol. 23: 307-310.