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I. A Study of Interspecific Hybridization Between Members of the Tripunctata Group of Drosophila

J. T. PATTERSON

INTRODUCTION

At the time these tests were begun in June 1955, 31 species belonging to the tripunctata group had been described. All of these are included in the important monograph by Frota-Pessoa (1954), who established four subgroups, I, II, III, and IV. We had among our laboratory stocks eight of the 31 described forms, plus one newly described species *(D. paramediostriata)*. In addition two undescribed species were also in stock. These two have been given names as follows: *D. trapeza*, *D. trifiloides*, and they are described elsewhere in this volume. These made a total of 11 available species for this study. In Table 1 the 11 species are listed, together with the localities at which the original flies had been collected, and the names of the collectors.

TABLE 1

Subgroups and Species	Collecting Localities	Collectors
II. *medionotata* Frota-Pessoa 1954	La Palma, El Salvador	Heed
II. *mediopunctata* Dobzhansky and Pavan 1943	Itanhaen, Sao Paulo, Brazil	Nonata
II. *unipunctata* Patterson and Mainland 1943	La Palma, El Salvador	Heed
III. *crocina* Patterson and Mainland 1944	San Salvador, El Salvador	Heed
III. *mediostriata* Duda 1925	San Salvador, El Salvador	Heed
III. *paramediostriata* Townsend and Wheeler 1955	Rio Piedras, Puerto Rico	Townsend
III. *trapeza* Heed and Wheeler (this bulletin)	La Lima, Honduras	Heed
III. *trifiloides* Wheeler (this bulletin)	La Lima, Honduras	Heed
IV. *albicans* Frota-Pessoa 1954	San Salvador, El Salvador	Heed
IV. *metzii* Sturtevant 1921	San Salvador, El Salvador	Heed
IV. *tripunctata* Loew 1862	Gulfport, Mississippi	Wheeler

Past experience with hybridization tests among Drosophila species has shown that small mass matings are more effective in obtaining hybrids than are pair matings. Consequently, we used mass matings of about 20 pairs per each large food vial. Three such cultures were established for each cross, making a total of about 60 pairs per test, and since 11 species were employed, the total number of reciprocal crosses will be 110.

The males and females to be used were separated within 24 hours after the culture vials had been cleared of all flies. They were then aged for five days before making the crosses. After five days the flies were transferred to fresh food vials, and at the end of this period, 20 females from each cross were dissected and their reproductive tracts examined for the presence of sperm. All of the remaining flies were then changed to a fresh food vial and kept long enough to make it possible to determine whether the cross was fertile or incompatible. At first both the corn-meal and banana-agar media were used, but since the latter gave the better results, it was employed for all the tests.

HYBRIDIZATION TESTS

The results obtained for the 110 crosses are tabulated in Table 2, and reveal that they fall into three categories, as follows: first, crosses which produced no hybrids; second, crosses which also yielded no hybrids but the dissections revealed that some few females had been inseminated; and third, crosses which gave some form of hybridization. The first group included 97 of the 110 crosses, or slightly over 88% of the total. These 97 contained 11,644 flies, which is the equivalent of 5,822 pairs.

TABLE 2

Hybridization tests

Crosses		Pairs tested	Hybrids	Remarks
Females	Males			
1. *albicans*	*crocina*	57	none	incompatible cross
2. *crocina*	*albicans*	60	none	incompatible cross
3. *albicans*	*medionotata*	60	none	incompatible cross
4. *medionotata*	*albicans*	60	none	incompatible cross
5. *albicans*	*mediopunctata*	60	none	non-motile sperm in spermathecae of 1 female
6. *mediopunctata*	*albicans*	60	larvae 1♀ + 1♂	most larvae non-viable; female hybrid sterile
7. *albicans*	*mediostriata*	56	none	incompatible cross
8. *mediostriata*	*albicans*	60	none	incompatible cross
9. *albicans*	*metzii*	60	none	incompatible cross
10. *metzii*	*albicans*	60	none	inactivated sperm in V. R. of one female
11. *albicans*	*paramediostriata*	60	none	incompatible cross
12. *paramediostriata*	*albicans*	60	none	incompatible cross
13. *albicans*	*trapeza*	60	none	incompatible cross
14. *trapeza*	*albicans*	60	none	incompatible cross
15. *albicans*	*trifiloides*	60	none	incompatible cross
16. *trifiloides*	*albicans*	56	none	incompatible cross
17. *albicans*	*tripunctata*	60	none	non-motile sperm in spermathecae of one female
18. *tripunctata*	*albicans*	60	none	incompatible cross
19. *albicans*	*unipunctata*	60	none	incompatible cross
20. *unipunctata*	*albicans*	60	none	dead sperm in spermathecae of one female
21. *crocina*	*medionotata*	60	none	incompatible cross
22. *medionotata*	*crocina*	60	none	incompatible cross
23. *crocina*	*mediopunctata*	60	none	incompatible cross
24. *mediopunctata*	*crocina*	60	none	incompatible cross
25. *crocina*	*mediostriata*	60	none	incompatible cross
26. *mediostriata*	*crocina*	60	none	incompatible cross
27. *crocina*	*metzii*	60	none	incompatible cross
28. *metzii*	*crocina*	60	none	incompatible cross
29. *crocina*	*paramediostriata*	60	none	incompatible cross
30. *paramediostriata*	*crocina*	60	none	incompatible cross
31. *crocina*	*trapeza*	60	none	incompatible cross
32. *trapeza*	*crocina*	60	none	incompatible cross
33. *crocina*	*trifiloides*	63	none	1♀ with dead sperm; 1♀ with motile sperm in spth.
34. *trifiloides*	*crocina*	60	none	incompatible cross
35. *crocina*	*tripunctata*	60	none	incompatible cross
36. *tripunctata*	*crocina*	60	none	incompatible cross
37. *crocina*	*unipunctata*	60	none	incompatible cross
38. *unipunctata*	*crocina*	60	none	incompatible cross
39. *medionotata*	*mediopunctata*	60	none	incompatible cross
40. *mediopunctata*	*medionotata*	60	none	incompatible cross
41. *medionotata*	*mediostriata*	60	none	incompatible cross
42. *mediostriata*	*medionotata*	60	none	incompatible cross
43. *medionotata*	*metzii*	60	none	incompatible cross

TABLE 2—Continued

Hybridization tests

	Crosses Females	Males	Pairs tested	Hybrids	Remarks
44.	*metzii* × *medionotata*		60	none	incompatible cross
45.	*medionotata* × *paramediostriata*		60	none	incompatible cross
46.	*paramediostriata* × *medionotata*		60	none	incompatible cross
47.	*medionotata* × *trapeza*		60	none	incompatible cross
48.	*trapeza* × *medionotata*		60	larvae 1 ♀ + 1 ♂	most larvae non-viable both hybrids sterile
49.	*medionotata* × *trifiloides*		60	none	incompatible cross
50.	*trifiloides* × *medionotata*		60	none	incompatible cross
51.	*medionotata* × *tripunctata*		60	none	incompatible cross
52.	*tripunctata* × *medionotata*		60	none	incompatible cross
53.	*medionotata* × *unipunctata*		60	none	incompatible cross
54.	*unipunctata* × *medionotata*		60	none	incompatible cross
55.	*mediopunctata* × *mediostriata*		60	none	incompatible cross
56.	*mediostriata* × *mediopunctata*		60	none	incompatible cross
57.	*mediopunctata* × *metzii*		60	1 ♀	abnormal, sterile
58.	*metzii* × *mediopunctata*		60	none	incompatible cross
59.	*mediopunctata* × *paramediostriata*		60	none	incompatible cross
60.	*paramediostriata* × *mediopunctata*		60	none	incompatible cross
61.	*mediopunctata* × *trapeza*		62	none	non-motile sperm in spermathecae of one female
62.	*trapeza* × *mediopunctata*		56	none	incompatible cross
63.	*mediopunctata* × *trifiloides*		60	none	incompatible cross
64.	*trifiloides* × *mediopunctata*		60	none	incompatible cross
65.	*mediopunctata* × *tripunctata*		65	none	incompatible cross
66.	*tripunctata* × *mediopunctata*		64	none	incompatible cross
67.	*mediopunctata* × *unipunctata*		60	none	incompatible cross
68.	*unipunctata* × *mediopunctata*		60	5 ♀ + 5 ♂	$F_1 \times F_1$ fertile
69.	*mediostriata* × *metzii*		62	none	incompatible cross
70.	*metzii* × *mediostriata*		65	none	incompatible cross
71.	*mediostriata* × *paramediostriata*		70	larvae 26 ♀ + 22 ♂	$F_1 \times F_1$ fertile
72.	*paramediostriata* × *mediostriata*		70	larvae 5 ♀ + 4 ♂	$F_1 \times F_1$ fertile
73.	*mediostriata* × *trapeza*		60	none	incompatible cross
74.	*trapeza* × *mediostriata*		60	none	incompatible cross
75.	*mediostriata* × *trifiloides*		60	none	incompatible cross
76.	*trifiloides* × *mediostriata*		65	none	incompatible cross
77.	*mediostriata* × *tripunctata*		60	none	incompatible cross
78.	*tripunctata* × *mediostriata*		60	none	incompatible cross
79.	*mediostriata* × *unipunctata*		63	none	incompatible cross
80.	*unipunctata* × *mediostriata*		60	none	incompatible cross
81.	*metzii* × *paramediostriata*		60	none	incompatible cross
82.	*paramediostriata* × *metzii*		60	none	incompatible cross
83.	*metzii* × *trapeza*		60	none	incompatible cross
84.	*trapeza* × *metzii*		60	none	incompatible cross
85.	*metzii* × *trifiloides*		57	none	incompatible cross
86.	*trifiloides* × *metzii*		60	none	incompatible cross
87.	*metzii* × *tripunctata*		60	larvae pupae	no adults produced
88.	*tripunctata* × *metzii*		60	none	incompatible cross
89.	*metzii* × *unipunctata*		60	none	incompatible cross
90.	*unipunctata* × *metzii*		60	none	incompatible cross
91.	*paramediostriata* × *trapeza*		60	none	incompatible cross
92.	*trapeza* × *paramediostriata*		60	none	incompatible cross
93.	*paramediostriata* × *trifiloides*		60	none	incompatible cross
94.	*trifiloides* × *paramediostriata*		60	none	incompatible cross
95.	*paramediostriata* × *tripunctata*		58	none	incompatible cross
96.	*tripunctata* × *paramediostriata*		60	none	incompatible cross
97.	*paramediostriata* × *unipunctata*		60	none	incompatible cross
98.	*unipunctata* × *paramediostriata*		54	none	incompatible cross
99.	*trapeza* × *trifiloides*		60	none	incompatible cross
100.	*trifiloides* × *trapeza*		60	none	incompatible cross
101.	*trapeza* × *tripunctata*		60	none	incompatible cross

TABLE 2—Continued

Hybridization tests

Crosses		Pairs		
Females	Males	tested	Hybrids	Remarks
102. *tripunctata* × *trapeza*		60	none	incompatible cross
103. *trapeza* × *unipunctata*		60	none	incompatible cross
104. *unipunctata* × *trapeza*		60	none	incompatible cross
105. *trifiloides* × *tripunctata*		60	none	incompatible cross
106. *tripunctata* × *trifiloides*		60	none	incompatible cross
107. *trifiloides* × *unipunctata*		66	none	incompatible cross
108. *unipunctata* × *trifiloides*		60	none	incompatible cross
109. *tripunctata* × *unipunctata*		60	none	incompatible cross
110. *unipunctata* × *tripunctata*		60	none	incompatible cross

The second group included but six crosses, which are indicated in the last column of Table 2. In Cross 5 (*albicans* ♀ × *mediopunctata* ♂) a single female contained non-motile sperm in the spermathecae. Cross 10 (*metzii* ♀ × *albicans* ♂) also yielded a single female with non-motile sperm, which were located in the ventral receptacle. In Cross 17 (*albicans* ♀ × *tripunctata* ♂) one female had non-motile sperm in the spermathecae. In Cross 20 (*unipunctata* ♀ × *albicans* ♂) one female contained dead sperm in the spermathecae. In Cross 33 (*crocina* ♀ × *trifiloides* ♂) two females had been inseminated. One had dead sperm and one had motile sperm, both in the spermathecae. In Cross 61 (*mediopunctata* ♀ × *trapeza* ♂) a single female had non-motile sperm in the spermathecae.

The third group included seven crosses which gave some form of hybridization (Table 2). Cross 6 (*mediopunctata* ♀ × *albicans* ♂) yielded many non-viable larvae, and one female and one male hybrid. In the test for the possible fertility of these two flies, the $F_1 \times F_1$ cross failed to produce offspring. The female was backcrossed simultaneously to both types of parental males, but failed to produce progeny. But the male hybrid backcrossed in the same manner to both types of parental females yielded 12 females and 17 males. The results from these tests show that the female was sterile, while the male was fertile.

Cross 48 (*trapeza* ♀ × *medionotata* ♂) yielded many non-viable larvae and one female and one male hybrid. These hybrids proved to be completely sterile in inbred and backcross tests. Cross 57 (*mediopunctata* ♀ × *metzii* ♂) produced a single hybrid female which was highly abnormal and incapable of breeding.

In the matings between *mediopunctata* and *unipunctata* the cross was incompatible when *mediopunctata* was used as the female parent (Cross 67), but slightly fertile when *unipunctata* represented the female parent, yielding 5 female and 5 male hybrids (Cross 68). The $F_1 \times F_1$ cross was fertile and gave nine females and 14 males. The following results were obtained in the backcross tests:

F_1 female mated to *unipunctata* males failed to produce offspring;
F_1 female mated to *mediopunctata* males gave nine females and 10 males;
F_1 male mated to *unipunctata* females failed to produce offspring;
F_1 male mated to *mediopunctata* females gave 19 females and 19 males.

Crosses 71 and 72 include the reciprocal matings between the two closely related species of *mediostriata* and *paramediostriata*. The first cross (*mediostriata* ♀ × *paramediostriata* ♂) produced a total of 26 females and 22 males. The

$F_1 \times F_1$ cross was fertile. The following results were obtained from the backcross tests. The F_1 females crossed to both types of parental males were fertile and produced a total of 22 ♀ ♀ and 13 ♂ ♂, plus several non-viable larvae. The F_1 males mated to both types of parental females produced 16 ♀ ♀ and 19 ♂ ♂ to *mediostriata* females, and none to *paramediostriata* females, not even non-viable larvae. The reciprocal Cross 72 (*paramediostriata* ♀ × *mediostriata* ♂) gave many non-viable larvae and only nine adults, five ♀ ♀ and four ♂ ♂. The F_1 flies were all used for inbred tests and produced 35 pupae, from which 13 females and 11 males emerged.

In Cross 87 (*metzii* ♀ × *tripunctata* ♂) many non-viable larvae and some pupae appeared in the culture, but no adults emerged from these pupae.

In Table 3 are summarized the results of the 110 reciprocal crosses. The table was constructed in order to facilitate the discussion and conclusions. The species included in Frota-Pessoa's subgroup I were not available for study. Only three species were available from his subgroup II, five from subgroup III, and three from subgroup IV. The symbols "Hy" and "In" represent the seven cases of hybridization and six of insemination, respectively. The numbers following these symbols refer to the numbers of the crosses as given in Table 2.

Among the reciprocal crosses within subgroup II, only one yielded hybrids (Hy-68), and none gave an insemination. The matings of the females of these three species to the males of the five of subgroup III gave a single case of insemination (In-61), which was found in the cross between *mediopunctata* females to *trapeza* males. The females of subgroup II mated to the males of subgroup IV gave two cases of hybrids (Hy-6, Hy-57) and one of insemination (In-20). It is interesting to note that *medionotata* females did not cross with any of the males of the other ten species, while the females of *mediopunctata* crossed to the males of three other species, and those of *unipunctata* mated to the males of two other species.

The females of subgroup III crossed to the males of subgroup II yielded a single case of hybridization. This was from *trapeza* females to the males of *medionotata* (Hy-48). The matings within subgroup III produced two cases of hybrids and one of insemination. The hybrids were from the reciprocal crosses between the two related species *mediostriata* and *paramediostriata* (Hy-71, Hy-72). The single case of insemination was from the cross of *crocina* females to *trifiloides* males (In-33).

In subgroup IV the females of *albicans* mated to the males of *mediopunctata* produced a single case of insemination (In-5). There were no successful crosses between members of subgroups IV and III. But in crosses within subgroup IV one case of hybridization (Hy-87) and two of insemination occurred (In-10, In-17). These results indicate that the species of these two subgroups are completely isolated from each other, for in a total of thirty crosses not a single case of either hybridization or insemination was obtained.

CONCLUSIONS

One may conclude from the results obtained in the cross tests that these 11 species of the tripunctata group are rather highly isolated from one another. There are, however, two cases in which the members of two species are rather

TABLE 3

FEMALES	MALES Subgroup II			Subgroup III					Subgroup IV		
	medio-notata	medio-punctata	uni-punctata	crocina	medio-striata	paramedio-striata	trapeza	tri-filoides	albicans	metzii	tri-punctata
II. medionotata	...	0	0	0	0	0	0	0	0	0	0
II. mediopunctata	0	...	0	0	0	0	In–61	0	Hy–6	Hy–57	0
II. unipunctata	0	Hy–68	...	0	0	0	0	0	In–20	0	0
III. crocina	0	0	0	...	0	0	0	In–33	0	0	0
III. mediostriata	0	0	0	0	...	Hy–71	0	0	0	0	0
III. paramediostriata	0	0	0	0	Hy–72	...	0	0	0	0	0
III. trapeza	Hy–48	0	0	0	0	0	...	0	0	0	0
III. trifiloides	0	0	0	0	0	0	0	...	0	0	0
IV. albicans	0	In–5	0	0	0	0	0	0	...	0	In–17
IV. metzii	0	0	0	0	0	0	0	0	In–10	...	Hy–87
IV. tripunctata	0	0	0	0	0	0	0	0	0	0	...

similar morphologically, with the possibility that gene exchanges could occur. The first of these include *mediopunctata* and *unipunctata*, which show considerable resemblance to each other, but the cross was fertile only when *unipunctata* represented the female parent. The F_1 hybrids were fertile in the inbred test, and partially fertile in the backcrosses. There is one striking difference in the two species in the behavior of the larvae during pupation. The larvae of *mediopunctata* pupate at the surface of the food, while those of *unipunctata* pupate within masses of food which they had carried up on the inner surface of the vial. The second pair of species between which gene exchanges could occur includes *mediostriata* and *paramediostriata*, which are very similar morphologically. The reciprocal crosses were fertile, but went better when *mediostriata* was employed as the female parent. The F_1 flies of both crosses were fertile, as indicated above.

There is also a possibility of gene exchange in a third case. This is Cross 6 (*D. mediopunctata* ♀ × *D. albicans* ♂) in which the F_1 male was fertile in backcrosses.

The final point of interest is the degree of isolation that exists between the different species. The results obtained in the tests show that several isolating mechanisms operate to prevent the exchange of genes. The most important of these is sexual isolation, or the failure of the sexes to mate. Of the 110 reciprocal crosses, 97, or slightly more than 88%, were incompatible. The writer never observed a single copulating pair in all of these cultures. Occasionally a male would perform feeble courtship movements, but in every instance the female gave no response.

A second type of isolating mechanism is present in Crosses 5, 10, 17, 20, 33, and 61. In each cross the female had been inseminated, but in each case the sperm had become inactivated or even killed in the reproductive tract of the alien female. This type of isolation has been termed sperm or gametic mortality.

A third type of isolating mechanism is represented by crosses in which the larvae are non-viable and fail to pupate, or pupate without producing adults (Cross 87). Even when hybrids are produced the cultures may contain dead larvae (Crosses 71, 72). This form of isolation has been termed zygotic mortality.

Finally, a fourth isolating mechanism is revealed in matings producing only a few hybrids, such as seen in Crosses 6, 48, and 57, as well as in matings yielding larger numbers of progeny, in which some of the F_1 flies exhibited hybrid sterility.

Geographical isolation must be an important means of preventing gene exchanges between the different members of the group. At present we do not have enough accurate data on distribution to justify an extended discussion of the subject. However, we do know that *D. tripunctata* Loew is the only species of the group thus far collected in the United States, although Dr. W. B. Heed has collected a closely related form in Costa Rica, Panama, and Colombia.

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