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EXPERIMENTS ON SEXUAL ISOLATION IN *DROSOPHILA*. III.  
GEOGRAPHIC STRAINS OF *DROSOPHILA STURTEVANTI*

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When females of different geographic strains of the same species are confined with males of one of these strains, the matings may occur either at random or preferentially, one kind of females being inseminated more frequently than the other. Relatively slight mating preferences have been observed in Brazilian and Guatemalan *Drosophila willistoni*,<sup>1</sup> and some quite striking preferences have been found in Brazilian, Guatemalan and Mexican strains of *D. prosaltans*.<sup>2</sup> Most of these intra-specific mating preferences are one-sided: greater proportions of females of one than of the other strain are inseminated by males of both strains. Data reported in the present article show, however, that two-sided preferences for homogamic matings, which are, in general, characteristic of interspecific crosses, occur also within the species *D. sturtevanti* Duda (= *D. biopaca* Sturtevant).

The strains of *Drosophila sturtevanti* came from Tamazunchale, state of San Luis Potosi, Mexico (obtained through the courtesy of Professor J. T. Patterson), Quiriguá, Guatemala (obtained through the courtesy of Professor A. H. Sturtevant), Belem, state of Pará, Rio de Janeiro, Federal District, and Bertioga, state of São Paulo, Brazil. The flies from all these strains are morphologically similar, intercross readily and give rise to fertile  $F_1$  and  $F_2$  progenies. The technique used in the experiments with *D. sturtevanti* is identical with that used for *D. prosaltans*,<sup>2</sup> except that *D. sturtevanti* females are dissected on the sixth or the seventh day after the making of the crosses. Sexual activity in this species starts late, in fact later than in other species of *Drosophila* with which the writer is familiar. Before the sixth day scarcely any females are inseminated, but on the eighth day only few remain not fertilized. The tubular (ventral) receptacle in *D. sturtevanti* is an extremely long tube, much longer than the body, resembling a skein of wool that is twisted, as a whole, into paired spirals lying on both sides of the vagina. Live spermatozoa can be seen in some, but usually not in all, coils. The large but transparent chitinous

spermathecae are, in inseminated females, only partly filled with a tangled mass of sperm.

The data are summarized in table 1. In every one of the 20 crosses a positive isolation index has been obtained, which suggests that males of all strains inseminate more of their own females than of those of other strains. The statistical significance of the observed deviations from random mating is measured by the  $\chi^2$ 's; values higher than 6.6 (corresponding to the 0.01 probability level) have been observed in 10 crosses, and values smaller than 2.7 (corresponding to the 0.10 probability level) in only 5 crosses. The highest isolation indices are found in the crosses of strains from the two geographically most remote localities (Tamazunchale in Mexico and Bertioga in Brazil), but localities nearly as remote (Tamazunchale and Rio de Janeiro) fail to show statistically significant isolation indices. Strains from geographically relatively close localities may either interbreed at random (Rio de Janeiro and Bertioga) or may display a considerable isolation (Tamazunchale and Quiriguá). Strains which show no isolation from each other (Rio de Janeiro and Bertioga) may behave very differently with respect to other strains (Tamazunchale, Belem, or Quiriguá).

TABLE 1  
NUMBERS OF FEMALES DISSECTED ( $n$ ) AND PER CENT CARRYING SPERM (%) IN VARIOUS  
CROSSES OF *Drosophila sturtevantii*

FEMALES	MALES	HOMOGAMIC $n$	%	HETEROGAMIC $n$	%	$\chi^2$	ISOLATION INDEX
Tamazunchale, Quiriguá	Tamazunchale	194	60.3	192	37.0	21.0	0.24
Tamazunchale, Quiriguá	Quiriguá	104	46.2	107	24.3	11.1	0.31
Tamazunchale, Belem	Tamazunchale	111	54.1	109	32.1	10.7	0.25
Tamazunchale, Belem	Belem	86	65.1	82	41.5	9.5	0.22
Tamazunchale, Rio	Tamazunchale	104	52.9	112	46.4	0.9	0.06
Tamazunchale, Rio	Rio	124	61.3	130	49.2	3.7	0.11
Tamazunchale, Bertioga	Tamazunchale	115	73.9	104	35.6	32.6	0.35
Tamazunchale, Bertioga	Bertioga	108	58.3	108	24.1	26.2	0.42
Quiriguá, Belem	Quiriguá	106	48.1	97	25.8	10.9	0.30
Quiriguá, Belem	Belem	94	54.3	99	24.2	18.3	0.38
Quiriguá, Rio	Quiriguá	99	56.6	96	43.8	3.2	0.13
Quiriguá, Rio	Rio	116	50.0	113	35.4	5.0	0.17
Quiriguá, Bertioga	Quiriguá	99	49.5	103	32.0	6.4	0.21
Quiriguá, Bertioga	Bertioga	106	59.4	109	26.6	23.7	0.38
Belem, Rio	Belem	160	55.6	157	49.0	1.4	0.06
Belem, Rio	Rio	98	65.3	106	39.6	14.5	0.24
Belem, Bertioga	Belem	101	50.5	100	39.0	2.7	0.13
Belem, Bertioga	Bertioga	91	41.8	88	31.8	2.0	0.14
Rio, Bertioga	Rio	106	51.9	106	50.0	0.1	0.02
Rio, Bertioga	Bertioga	101	50.5	106	48.1	0.1	0.02

The situation found in *D. sturtevantii* is different from those in *D. willistoni*<sup>1</sup> and *D. prosaltans*.<sup>2</sup> In *D. sturtevantii* the rule seems to be that strains

from different regions show incipient sexual isolation—preference for homogamic matings and aversion from heterogamic ones. Random mating is the rule in *D. willistoni*, but both Guatemala and Brazilian males have in some crosses inseminated preferentially Brazilian females. In *D. prosaltans* there is a “hierarchy” of strains correlated with their geographic origin. Both northern and southern males inseminate preferentially northern females; therefore, in some crosses homogamic matings are more common than heterogamic ones (positive isolation indices), and in other crosses heterogamic matings are more frequent (negative isolation indices). The strains from Guatemala and Brazil show, however, a mutual aversion to interbreeding. *D. nebulosa* Sturtevant is another species in which preferences for homogamic as well as for heterogamic matings are observed. Strains of this species coming from state of San Luis Potosi, Mexico (kindly furnished by Professor J. T. Patterson), and from Belem do Pará, Brazil, have been used. The experiments on *D. nebulosa* were arranged exactly like those on *D. prosaltans* and *D. sturtevanti*; the dissections have been made on the fourth day after the crosses. A summary of the results is given in table 2. It is evident that when Brazilian and Mexican females are kept with Brazilian males, Brazilian females are inseminated preferentially; but when Mexican males are used there seems to be also an excess of inseminations of Brazilian females (a negative isolation index which is not quite significant statistically).

TABLE 2

NUMBERS OF FEMALES DISSECTED (*n*) AND PER CENT CARRYING SPERM (%) IN CROSSES OF *Drosophila nebulosa*

FEMALES	MALES	HOMOGENIC %		HETEROGENIC %		$\chi^2$	ISOLATION INDEX
		<i>n</i>		<i>n</i>			
Mexican, Brazilian	Brazilian	126	78.6	133	41.4	37.1	0.31
Mexican, Brazilian	Mexican	113	42.5	113	55.8	4.0	-0.14

Two types of preferential mating have been observed in *Drosophila*. They are sexual isolation proper and one-sided mating preferences. Strains A and B are said to be sexually isolated if males of A mate chiefly with A, and males of B chiefly with B females (positive isolation indices). If the mating preference is one-sided, A males mate more frequently with A than with B females (positive isolation index), but B males show either no preference (isolation index close to zero) or a preference for A females (negative isolation index). Situations intermediate between true sexual isolation and one-sided mating preference occur. Theoretically, two strains may also show consistent preferences for heterogamic matings (negative isolation indices), but this has never been found in experiments.

Sexual isolation reduces the rate of gene exchange between the populations concerned; when the isolation is complete the gene exchange is altogether excluded. Sexual isolation is found, as a rule, in interspecific

crosses. Rudiments of sexual isolation have been found also within a species, e.g., in crosses between certain strains of *D. miranda*,<sup>3</sup> *D. sturtevanti* and *D. prosaltans* from Brazil and Guatemala.<sup>2</sup> One-sided mating preferences are known in most geographic races of *D. prosaltans*, in *D. Willistoni*<sup>1</sup> and in *D. nebulosa*. Such mating preferences do not render the gene exchange impossible, because at least one of the two populations would continue to receive an inflow of genes from the other.

Since hybrids between two forms, each of which possesses a well-balanced genotype, may be ill balanced or unfit for survival, reduction or cessation of the gene exchange between populations may be adaptively important. Genetic variants which reduce the rate of the gene exchange may be favored by natural selection in populations exposed to hybridization. Reproductive isolation would be strengthened by natural selection until complete suspension of the gene exchange is attained. The development of all forms of reproductive isolation, including sexual isolation, between populations which have diverged sufficiently to make compromise genotypes unfavorable may be initiated and furthered by natural selection.<sup>4, 5</sup> On the other hand, Muller<sup>6, 7</sup> has pointed out that impediments to gene exchange may arise accidentally, as concomitants of the process of divergence of genetic systems.

These two suggestions may be complementary rather than conflicting. It is well known that natural selection operates with the genetic variants present in populations, but cannot create such variants. The variants are bound to arise, in a sense, accidentally, through mutation and recombination. The one-sided mating preferences of the kind observed in *D. prosaltans* would not, even if the geographic races involved were exposed to hybridization, constitute a barrier to gene exchange. Such mating preferences may, however, serve as raw materials from which true sexual isolation could develop by addition of genetic variants making the aversion to heterogamic matings mutual instead of unidirectional. Incipient sexual isolation is, indeed, found between strains of *D. prosaltans* from Brazil and Guatemala. Incipient sexual isolation is widespread among geographic strains of *D. sturtevanti*, but it is still neither strong enough to be a serious obstacle to gene exchange, nor ordered into a balanced system of isolation correlated with geography. One-sided mating preferences are very likely by-products of physiological racial differences, not necessarily related to the mating reactions. True sexual isolation develops if one-sided mating preferences are added up and coordinated by natural selection.

The great diversity and complexity of structures and habits connected with the search for mates, nest building, courtship and copulation in many groups of animals is very impressive. These structures and habits are often not only surprisingly complex but also constant within and characteristically different between species. Their origin in evolution seems difficult

to explain. Their orderly complexity makes accidental origin extremely improbable. Natural selection would seem to be incapable of building them because of the apparent lack of adaptive value in most of these structures and habits. Darwin's theory of sexual selection was a partially successful attempt to resolve this difficulty, but the competition for mating postulated by the theory is relatively seldom observed. It is, therefore, desirable to keep in mind the possibility that species specific courtship and mating habits and associated structures may serve as "recognition marks" of the specific identity.<sup>8</sup> If so, these habits and structures may possess adaptive value as integral parts of the mechanism of sexual isolation, and for this reason may be developed by a process of selection. Such a modification of the theory of sexual selection would, it seems, avoid most of the difficulties confronted by its original, Darwinian, version.

It should also be kept in mind that the problem of sexual structures and habits which seem to be devoid of adaptive significance is only a part of the broader problem of the origin in evolution of the so-called "neutral" characters in general. It is customary to suppose that neutral characters become established in evolution because of being physiologically correlated with some adaptively important, although less readily perceptible, characters. Unfortunately, the postulated correlations can only seldom be demonstrated to exist. For some neutral characters a reasonable alternative would be to suppose that they function as recognition marks of the species during the courtship and mating processes, and, are, therefore, susceptible of modification and development by selection.

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*Summary.*—Geographic strains of *D. sturtevantii* show incipient sexual isolation. The extent of this isolation is, however, variable and is not strictly correlated with the geographic origin of the strains; some strains coming from remote localities show less aversion to interbreeding than strains from less remote localities. The origin in evolution and the biological functions of the sexual isolation proper, as well as of other forms of preferential mating, are discussed.

<sup>1</sup> Dobzhansky, Th., and Mayr, E., these PROCEEDINGS, 30, 238-244 (1944).

<sup>2</sup> Dobzhansky, Th., and Streisinger, G., *Ibid.*, an article appearing in this issue.

<sup>3</sup> Dobzhansky, Th., and Koller, P., *Biol. Zentr.*, 58, 589-607 (1938).

<sup>4</sup> Dobzhansky, Th., *Amer. Natur.*, 74, 312-321 (1940).

<sup>5</sup> Dobzhansky, Th., *Genetics and the Origin of Species*, New York, 1941.

<sup>6</sup> Muller, H. J., *Biol. Reviews*, 14, 261-280 (1939).

<sup>7</sup> Muller, H. J., *Biol. Symposia*, 6, 71-125 (1942).

<sup>8</sup> Mayr, E., *Systematics and the Origin of Species*, New York, 1942.