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## OBSERVATIONS ON TWO CASES OF INTER- SPECIFIC HYBRIDIZATION WITH *DROSOPHILA ATHABASCA*

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### INTRODUCTION

*Drosophila athabasca* Sturtevant and Dobzhansky (1936) is one of the relatively small, dark-bodied flies assigned to the *obscura* group (*affinis* subgroup) of the subgenus *Sophophora* (Sturtevant, 1942). This species has a rather wide distribution in North America. In the eastern United States it has been collected in New England and the Great Lakes region and in the mountains of North Carolina and Tennessee. In the west, collections have been made at various places along the Pacific coast (Oregon to Alaska) and in the Rocky Mountain region from New Mexico to central Alaska. It is quite possible that further collections will show the species to have a more or less continuous distribution across the northern Great Plains. (For collection points of this and the other *affinis* subgroup species used in this study, see Sturtevant and Dobzhansky, 1936; Miller, 1939; Sturtevant, 1940; Patterson, Wagner, and Wharton, 1943; and Novitski, 1946.)

In the laboratory, *Drosophila athabasca* may be made to hybridize with three other species of the *affinis* subgroup. It was reported by Sturtevant and Dobzhansky (1936) that

<sup>1</sup>The research on which this paper is based was done by the author as a student and research assistant at the California Institute of Technology.

both reciprocal crosses with *Drosophila azteca* Sturtevant and Dobzhansky (southwestern United States, Mexico, and Central America) yield hybrids. In previous publications (Miller, 1939, 1941) it was reported that *D. athabasca* males may be made to hybridize with females of *D. algonquin* Sturtevant and Dobzhansky and *D. affinis* Sturtevant (both are eastern American species overlapping the range of *D. athabasca*; they are distributed from the western Great Plains to the Atlantic coast, with *affinis* extending farther to the southeast than *algonquin*).

This paper is a presentation of additional data concerning the hybridization of *D. athabasca* males with females of *D. algonquin* and *D. affinis*.

HYBRIDIZATION BETWEEN *D. algonquin* FEMALES  
AND *D. athabasca* MALES

Hybrids were first obtained between *D. algonquin* females and *D. athabasca* males from several crosses involving wild type strains of these species. These offspring, though quite normal in general appearance, were sufficiently different from individuals of the female parent's species to raise the suspicion that they were hybrids and not the result of non-virginity. The supposition that hybrids might be obtained in this combination was confirmed by a cross between *D. algonquin* females homozygous for the recessive mutant gene rough (eyes) and wild type *D. athabasca* males of a Grey's River (Wyoming) strain. The offspring of this cross were wild type with respect to eye character.

Continued interspecific matings have shown that hybrids between *algonquin* and *athabasca* are rather difficult to obtain. In Table 1 are given insemination frequencies involving certain mutant strains of these species. (Recessive mutant strains were usually used as a source of females employed in interspecific crosses so as to have a check on the authenticity of any hybrids produced.) To obtain these data, females and males (about ten of each) were kept together in culture bottles for ten or eleven days, and at the end of this time the females were dissected and their semi-

nal receptacles examined for sperms. Frequencies of inseminated females are presented here as fractions, the denominators of which represent total numbers of females examined. As is shown in Table 1, interspecific insemination was very low in the combination of *algonquin* females and *athabasca* males and was not detected at all in the reciprocal combination.

Hybrids between *algonquin* and *athabasca* have been obtained principally from a series of group matings in each of which five *algonquin* females were kept with five *athabasca* males for about a month (longer if hybrids were being

TABLE 1  
FREQUENCIES OF FEMALES FOUND INSEMINATED AT THE END  
OF THE 10-11-DAY MATING PERIOD

Mutant strains used here were: *affinis* rugose eyes (rug); *algonquin* droop wings (dr) and cinnabar eyes (cn); and *athabasca* vermilion eyes (v) (sex-linked) and cinnabar eyes (cn).

Intraspecific matings:			
<i>affinis</i> ♀♀	× <i>affinis</i> ♂♂	("rug")	50/51 (98.0%)
<i>algonquin</i> ♀♀	× <i>algonquin</i> ♂♂	("dr")	45/51 (88.2%)
<i>athabasca</i> ♀♀	× <i>athabasca</i> ♂♂	("v")	45/53 (84.9%)
Interspecific matings involving <i>D. athabasca</i> :			
<i>algonquin</i> ♀♀	× <i>athabasca</i> ♂♂	<i>affinis</i> ♀♀	× <i>athabasca</i> ♂♂
"dr" × "v"	3/53	"rug" × "v"	56/82
"dr" × "cn"	0/54	"rug" × "cn"	34/54
"cn" × "v"	0/25		
	3/132		90/136
	(2.3%)		(66.2%)
<i>athabasca</i> ♀♀	× <i>algonquin</i> ♂♂	<i>athabasca</i> ♀♀	× <i>affinis</i> ♂♂
"v" × "dr"	0/104	"v" × "rug"	0/102
"v" × "cn"	0/36	"cn" × "rug"	0/24
	0/140		0/126

produced in this time). Various strains of both species were used in these crosses. The *algonquin* females were all from mutant strains; the following recessive characters were used singly and in combinations: dusky wings (dy) and swollen tarsi (sw), both sex-linked; brown eyes (bw) and droop wings (dr), linked to each other on one of the autosomes; and cinnabar eyes (cn) and rough eyes (ro) carried separately on two of the other autosomes. Males were taken from the following wild type *athabasca* strains:

Gravina (Alaska), two strains from Grey's River (Wyoming), Sundance (Wyoming), and Quinault (Washington). The *athabasca* mutant strain vermilion eyes (*v*) (sex-linked recessive) was also used.

Of 342 such group matings 13 (3.8 per cent.) yielded adult hybrids. All the mutant genes used in the successful crosses (*algonquin* *dy*, *dr*, *cn*, and *ro*; *athabasca* *v*) proved to be recessive in the hybrids. The total numbers of hybrids obtained from these crosses were 217 females and 178 males. In 11 of the 13 cases, the sex ratio was about 1:1 (totaling 150 females and 154 males), but there was a marked excess of females in two cases (totaling 67 females and 24 males). The reason for these aberrant progenies was not investigated, but it is possible that otherwise unnoticed sex-linked lethal genes were responsible. Since the crosses were group matings, it was not possible to determine whether or not the hybrids derived from a cross were all the offspring of the same two parents, although considering the low frequency of interspecific insemination, it seems likely that in each case they were. The numbers of adult hybrids obtained in the 13 cases ranged from 1 to 77, with an average number of 25.1, which seems low in comparison to *algonquin* pair matings kept under these conditions.

*D. algonquin* and *D. athabasca* are very similar morphologically. However, certain differences between them are noticeable. As pointed out in the descriptions of these species (Sturtevant and Dobzhansky, 1936), *algonquin* is more brownish than the other *affinis* subgroup species, while *athabasca* tends to be dark brown. With respect to color the hybrids may be described as intermediate to the parent species. Another striking difference concerns the sex combs of the males: *athabasca* males have very small sex combs (4 teeth) while *algonquin* males have rather large ones (8–10 teeth). Although the sex combs of hybrid males broadly overlapped those of *algonquin* males in number of teeth, the average number of sex comb teeth was lower in hybrids than in *algonquin* ( $6.7 \pm 0.073$  in hybrids and  $7.4 \pm 0.072$  in *algonquin*; see Fig. 1, A and B). The hy-

brids of both sexes were usually quite normal in general appearance and adult viability. However, from some of the early crosses involving wild type strains (*e.g.*, *algonquin* from Aldrich, Texas, to *athabasca* from Sundance, Wyoming) there were obtained a few females with large wing cells and coarse compound eyes, suggesting polyploidy. An ovary smear from one of these showed oogonia with definitely more than the diploid number of chromosomes characteristic of both these species (ten), but an accurate chromosome count could not be made. In the later crosses such females did not appear.

In order to obtain evidence on fertility, dissections and examinations of hybrid gonads and genital tracts were made. The ovaries of the females seemed quite normal in every respect. Backcrosses of these females to *algonquin* males have shown that the female hybrids are in some cases fertile. These crosses were made as pair matings (hybrid female to male of *algonquin* parent strain) lasting about a month. Altogether 128 such backcrosses were made, and 46 of them (35.9 per cent.) produced adult offspring. The total numbers of backcross flies obtained were 378 females and 295 males (there was an excess of females in all groups of crosses), with a mean family size of 14.4, which is well below that for the crosses that produced the hybrids. Since mutant genes were involved, both mutant and wild type individuals appeared in the backcross progeny. In addition, a few of the backcross flies, both mutant and wild type, exhibited various abnormalities (rough eyes, missing or reduced bristles, wings held out, abnormal abdomen) which were not found in the hybrids. These abnormalities were not noticed early in the backcross counts, and a number of abnormal individuals were undoubtedly overlooked, but altogether 13 abnormal females (3.4 per cent.) and 23 abnormal males (7.8 per cent.) were recognized.

The testes of the male hybrids were found to be somewhat smaller than those of either species, although the rest of the male genitalia appeared to be normal. Smear preparations of hybrid testes revealed no sperms. Altogether no

extensive crossing experiment has been performed with hybrid males, it seems very likely that they are regularly sterile.

Among backcross males there was greater variation in the number of sex comb teeth than there was in the hybrids or in either of the parent species. The number of sex comb teeth in the backcross males varied from 4 through 9 (mean was  $6.4 \pm 0.094$ ), while variation was from 5 to 8 in the hybrids and 4 to 5 and 6 to 9 in *athabasca* and *algonquin*, respectively. Fig. 1, Parts A, B, and C, shows diagrammatically the distributions of numbers of sex comb teeth.

The only sex-linked mutant gene that was involved in successful backcrosses was the *athabasca* mutant vermilion. Unfortunately, the backcrosses involving vermilion also involved the *algonquin* autosomal recessive cinnabar. Both mutant genes produce bright red eyes. However, *athabasca* vermilion produced regularly a more striking deviation from wild type than *algonquin* cinnabar, which allows for a certain amount of darkening with age. In the backcrosses involving both these mutant genes it was possible to distinguish between two kinds of males with bright red eyes, one definitely more extreme than the other. The extreme type has been called vermilion, and the less extreme one, which was similar to the bright red eye class found in the females, has been called cinnabar. The kinds of offspring of these crosses are given in Table 2, A. According to expectation, the two kinds of females, wild type and cinnabar, were of equal frequencies. However, the frequencies of the classes of males deviated from expectations based on the inheritance of these mutant genes and the assumption that they would together produce bright red eyes. According to these expectations, the males with bright red eyes should have been about three times as numerous as the wild type males. Actually, the vermilion and cinnabar males taken together were only about twice as numerous (deviation significant by Chi-square test). In other backcrosses involving cinnabar (but no other mutant) there was no great deviation from a 1 : 1 ratio of wild type to cinnabar males (Table 2, B;

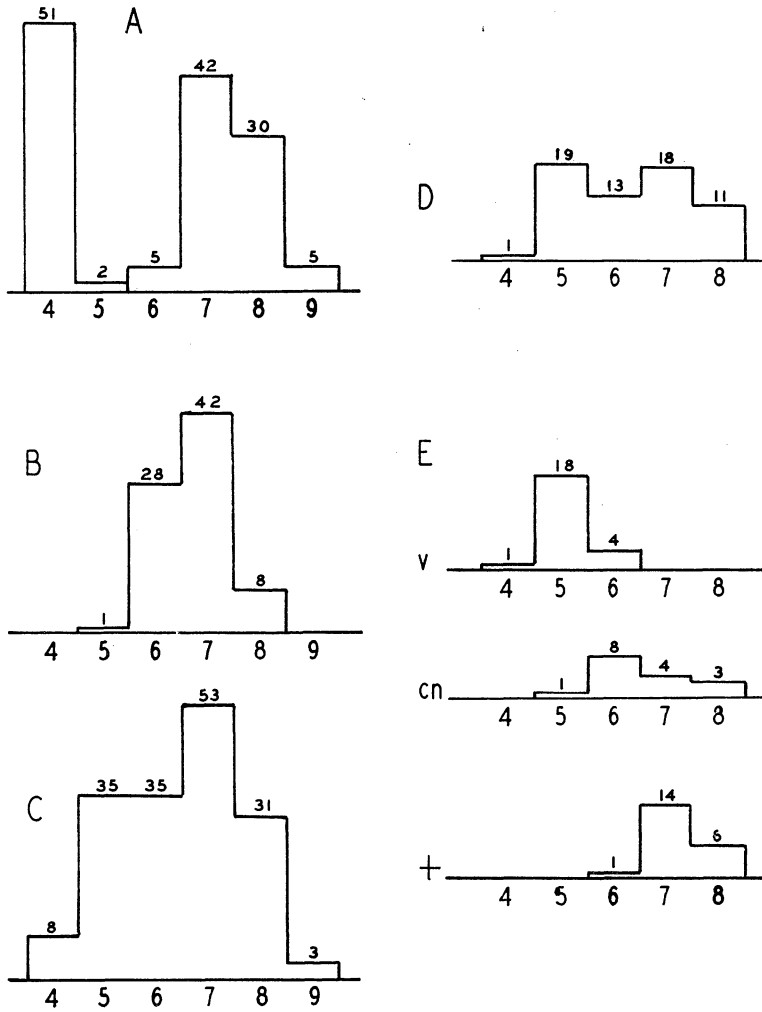


FIG. 1. Histograms representing sex comb teeth counts in *D. algonquin*, *D. athabasca*, hybrids between these species, and males of the backcross of hybrid females to *D. algonquin*. The abscissa classes represent numbers of teeth in the sex comb on the right prothoracic leg. The number at the top of each column is the number of individuals in the class. A. The histogram at the left is based on *athabasca* vermilion males, the one on the right on *algonquin* cinnabar males. B. Hybrids involving the *algonquin* cinnabar strain. C. Backcross males, the *algonquin* strain being cinnabar. D. Part of the males of "C" derived from hybrids containing *athabasca* vermilion. E. The types constituting the backcross males of "D."



deviation not significant by Chi-square test). Consequently, it appears that the presence of vermilion is most probably responsible for the low frequency of males with bright red eyes in the backcrosses involving vermilion and cinnabar. The possibility exists that males carrying *athabasca* vermilion and homozygous for *algonquin* cinnabar die early and were not observed. If this were the case, the backcross ratio of wild to vermilion to cinnabar males should be 1:1:1, and that, in fact, was the ratio closely approximated by the observations (deviation not significant by Chi-square test). However, since the possibility still exists that vermilion is epistatic to cinnabar and has a semi-lethal effect

TABLE 2

PROGENIES OF BACKCROSSES TO *algonquin* MALES OF *algonquin-athabasca* FEMALE HYBRIDS

A. Offspring of backcrosses of *algonquin-athabasca* females heterozygous for *athabasca* vermilion and *algonquin* cinnabar to *algonquin* males homozygous for cinnabar (totals of three pair matings).

" wild "	Males		Females		Total
	" bright red eyes " " v "	" cn "	" wild "	" cn "	
27	24	25	47	47	170

B. Progeny of backcrosses of *algonquin-athabasca* females heterozygous for *algonquin* cinnabar (and no other mutant genes) to *algonquin* males homozygous for cinnabar (totals of 24 pair matings).

" wild "	Males		Females		Total
	" cn "	" wild "	" wild "	" cn "	
73	67	89	75	304	

both with and without cinnabar, and such a relationship might also give the observed results, the lethality of the vermilion-cinnabar combination is not proved. It has been shown by Dobzhansky (1941) that certain mutant genes of *D. pseudoobscura* which do not ordinarily reduce viability appreciably may be quite detrimental in backcross individuals resulting from hybrids between *pseudoobscura* and *persimilis*.

The distribution of sex comb size in the backcross males derived from the cinnabar-vermilion crosses is presented in Fig. 1, D, while in Fig. 1, E, are given the distributions for

the three phenotypic classes separately. It is apparent that the males of the vermilion phenotype, which must have received the *athabasca* X chromosome, tended to have small sex combs (average was  $5.1 \pm 0.094$ ). (Although counts were not made, the impression of a tendency towards small sex combs was not gotten from the other backcross classes.) A possible explanation for this is that the males with the *athabasca* X were in possession of some of the important *athabasca* genes responsible for the difference in sex comb size between *athabasca* and *algonquin*. Although this may be true, there is also the possibility that in these backcross males small sex combs have developed in response to a peculiar combination of *algonquin* and *athabasca* genetic factors, possibly to the influence of the vermilion gene itself.

HYBRIDIZATION BETWEEN *D. affinis* FEMALES  
AND *D. athabasca* MALES

Table 1 also shows insemination frequencies for *D. affinis* and for both reciprocal combinations of *affinis* and *athabasca*. These data were derived in the manner already described for *algonquin* and *athabasca* insemination frequencies. Table 1 shows that the frequency of *affinis* females inseminated by *athabasca* males by the end of the mating period was fairly high (almost two thirds), while the reciprocal combination gave no insemination at all. More recently a few small group matings of *athabasca* vermilion females with *affinis* males of wild-type strains have shown some insemination after ten or eleven days (1/15 for Victoria, Texas; 11/19 for Gatlinburg, Tennessee; and 2/19 for Baltimore, Maryland). Hybrids have been produced by the combination of *affinis* females by *athabasca* males, but to date none of the matings of *athabasca* females to *affinis* males has yielded offspring. It seems likely that more extensive use of wild-type strains of *affinis* will allow for appreciably high frequencies of interspecific insemination of *athabasca* females by *affinis* males and, perhaps, even hybrid production. On the other hand, employment of wild-type *affinis* females and *athabasca* males may well give

reductions in interspecific insemination frequency below those shown in Table 1 (as in series of mass matings reported below).

Some of the crosses made to show insemination frequencies of *affinis* females by *athabasca* males yielded offspring, and these were wild type with respect to eye character, indicating that the normal allele of *affinis* rugose is present in *athabasca*. Other *affinis* recessive mutant genes that have proven to be recessive in hybrids are: cut, pinkish, net, tiny bristle, veinlet, and white (for descriptions, see Sturtevant, 1940).

Although the frequency of inseminated females among *affinis* females that have been kept with *athabasca* males ten or eleven days is fairly high, only very small numbers of hybrids have been obtained. Not only has the frequency of crosses producing offspring been low, but the number of offspring per successful cross has always been very small. The difficulty in obtaining many hybrids from this cross is apparent in the results of a series of mass matings of *affinis* females and *athabasca* males in which the number of flies of each sex (about equal numbers of each) varied from 8 to 15. Here the females were aged 3 to 4 days before mating, and the mating period lasted 10 to 12 days. The *affinis* females were of the following kinds: rugose, Woods Hole (Massachusetts), and strain hybrids of the cross Woods Hole by Austin (Texas). The *athabasca* males were of the following kinds: Sundance (Wyoming), Jackson Hole (Wyoming), Quinault (Washington), Clingman's Dome (North Carolina), and strain hybrids of the cross Jackson Hole by Quinault. Altogether 20 such matings were made. At the ends of the cohabitation periods 201 females were recovered and dissected, and in 51 of these (25.3 per cent.) sperms were found (in 14 out of the 20 crosses at least one inseminated female was found). (Out of 70 *affinis* females kept with *affinis* males under similar conditions 50, or 71.4 per cent., were found to be inseminated.) However, only 6 of the 20 interspecific mass matings yielded hybrids. Moreover, the numbers of hybrids were very low. Alto-

gether there were obtained 13 adult hybrids, 8 females and 5 males. The number of individuals from a successful cross never exceeded 3. The families produced in other crosses of *affinis* females by *athabasca* males have all been of about this size.

*D. athabasca* and *D. affinis* are somewhat more similar morphologically than *athabasca* and *algonquin*. For example, in both these species the males have small sex combs consisting of about 4 teeth. The hybrids are similar to the parent species and apparently quite normal in all external respects. Since the number of *affinis-athabasca* hybrids has been very small, extensive matings to determine fertility have not been possible. Those matings that have been attempted have not been successful. Smear preparations of testes have revealed no sperms. The ovaries of seven females, each aged at least a week, were found to contain no eggs (*affinis* females may lay eggs in 3 or 4 days after hatching), only clusters of small cells. Thus, there is no evidence that either sex is fertile.

Early in the observations of genital tracts of *affinis* females mated to *athabasca* males the impression was gotten that the sperms in the ventral receptacle were fewer and less active than following intraspecific inseminations. In addition, a certain amount of granular material was frequently present in the sperm masses, and it seemed that this was characteristic of the interspecific combination. In order to check on these impressions, an attempt was made to classify cases of insemination with respect to amount of sperms, activity of sperms, and presence or absence of granular material. Classification was applied to part of the cases of insemination found in the females of the 20 interspecific mass matings mentioned above and also to a number of cases of intraspecifically inseminated *affinis* females. Arbitrary separations were made of cases of "many," "medium," and "few" sperms and separations were also made according to whether the sperms were "active" or "quiet." The results of this classification are presented in Table 3. It may be seen from this table that amounts of

sperms were generally greater following intraspecific cohabitation than after interspecific mating. Also, the frequency of definitely active sperms was appreciably higher following the intraspecific combination. However, granular material in the ventral receptacle was found following both kinds of matings, with almost as high a frequency in the intraspecific combination as in the interspecific one.

The appearance of the sperms in the genital tracts of *affinis* females inseminated by *athabasca* males suggests both fewness of sperms and inactivation of sperms as reasons for the low fertility of these interspecifically inseminated females. It is possible that gametic cross-incompati-

TABLE 3  
CLASSIFICATION OF SPERM MASSES OBSERVED IN VENTRAL RECEPTACLES OF  
*D. affinis* FEMALES AT END OF 10-12-DAY MATING PERIOD

A. Classification according to quantity:				
	" Many "	" Medium "	" Few "	Total
<i>aff.</i> ♀ ♀ × <i>aff.</i> ♂ ♂	49 (62.8%)	28 (35.9%)	1 ( 1.3%)	78
<i>aff.</i> ♀ ♀ × <i>ath.</i> ♂ ♂	5 ( 8.9%)	14 (25.0%)	37 (66.1%)	56
B. Classification according to activity of sperms:				
	" Active "	" Quiet "	Total	
<i>aff.</i> ♀ ♀ × <i>aff.</i> ♂ ♂	76 (97.4%)	2 ( 2.6%)	78	
<i>aff.</i> ♀ ♀ × <i>ath.</i> ♂ ♂	38 (67.9%)	18 (32.1%)	56	
C. Presence or absence of granular material:				
	Present	Absent	Total	
<i>aff.</i> ♀ ♀ × <i>aff.</i> ♂ ♂	37 (47.4%)	41 (52.6%)	78	
<i>aff.</i> ♀ ♀ × <i>ath.</i> ♂ ♂	29 (51.8%)	27 (48.2%)	56	

bility, such as has been described for various combinations of *Drosophila* species (see Paterson, 1942, 1947), is responsible for the state of the sperms following insemination of *affinis* females by *athabasca* males. However, additional study will need to be done to establish the nature of the mechanism.

#### ACKNOWLEDGMENTS

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## SUMMARY

*Drosophila athabasca* males will inseminate females of the similar species *D. affinis* and *D. algonquin*, and both these crosses lead to hybrid production. *D. athabasca* females have been inseminated by *D. affinis* males, but hybrids have not been produced.

Female hybrids between *algonquin* and *athabasca* are fertile and have been crossed to *algonquin* males. Sex comb size, which differs between these species (*algonquin* has large sex combs, *athabasca* small ones) has been studied in hybrid and backcross males from some of the crosses.

Although the frequency of *affinis* females inseminated by *athabasca* males is fairly high, the number of hybrids produced by this combination is very low. Neither sex of the hybrids appears to be fertile.

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