

V. RELATIONSHIPS IN THE MELANICA SPECIES GROUP

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Among the North American members of the subgenus *Drosophila* the *melanica* group of species is conspicuous because of its wide geographical distribution and its relatively large population size. In these respects the *melanicas* are surpassed by only one other member of the subgenus, the *repleta-hydei* complex. These groups present excellent opportunities for the study of speciation within categories having large and widespread populations in nature. It is the purpose of the present paper to give a preliminary account of the relation between members of the *melanica* group. The data presented here were obtained from genetic and cytological studies of three cross-fertile members. *Drosophila micromelanica* has been omitted because of its complete sterility to other forms and *melanissima* because of its failure to survive in laboratory cultures.

MATERIALS AND METHODS

The following stocks have been used in the initial determination of the relationship and grouping of the members:

Drosophila melanica Sturtevant. Strains from Coffeerville, Kan., and the Ozark Mountains were the source of the test stocks for this form. These strains were kindly sent by Professor A. H. Sturtevant. Other *melanicas*, discussed in a subsequent section, were collected in the southern portion of the United States and in northern Mexico by members of the Texas laboratory.

Drosophila melanica paramelanica Patterson (Article I, this Publication). Five strains of this subspecies were used from collections at Madison, Wis.; Woodstock, Md.; Woodbury, Conn.; Zealand, and Wooster, Ohio. The first four were supplied by Professor Sturtevant and the fifth by Professor W. P. Spencer.

Drosophila nigromelanica Patterson and Wheeler. Three strains were obtained from collections made at Wood's Hole, Mass., and Wooster, Ohio, by Professor Spencer and at Cleveland, Texas, by Professor J. T. Patterson and the writer.

There are several sharp differences between *melanica* and *nigromelanica*, such as the darker body color and the red eyes of the latter as contrasted with the lighter body color and brownish eyes of *melanica*. Moreover, the males of *nigromelanica* have orange-colored testes whereas in *melanica* these organs are a dull yellow. The differences between *melanica* and *paramelanica* are not so marked, the general lighter coloration of *melanica* being the only outstanding quality. This lighter coloration is quite conspicuous in southwestern *melanicas*, most of which have a tan or very light brown coloration that easily permits identification.

The relationships which are presented here are based on cross-fertility between members and strains of the species and upon the gene arrangements as seen in salivary gland chromosomes of hybrids. All breeding tests were carried out on banana food which, though not entirely suitable for *nigromelanica*, has made possible comparisons of fertility under standard conditions; all cultures and matings were grown at 72° F. since this temperature was found to provide optimum conditions for mating, oviposition and development. The test stocks of the several strains were developed from inbred pairs.

CYTOLOGICAL OBSERVATIONS

The metaphase chromosomes of *melanica*, *paramelanica*, and *nigromelanica* all show the same configurations; all stocks thus far examined have one pair of large V's, one pair of small V's, two pairs of rods and a pair of microchromosomes which are generally small and rounded except in *nigromelanica*, where these bodies are somewhat larger and rod-shaped. It is probable that the large V-shaped element arose through the fusion of two rod-shaped chromosomes as has been demonstrated in the virilis complex (Patterson, Stone, and Griffen, 1940); the identity of this V is being determined through segregation tests. The small V is the result of a pericentric inversion which moved the centromere to a submedian position. This element is readily detectable in salivary gland cells and consists of two completely euchromatic arms. A similar case has been reported for *D. montana* (Stone, Griffen, and Patterson, 1941).

CROSS FERTILITY AND GENE ORDER

For the determination of cross-fertility in the *melanica* group, crosses of the test stocks were prepared as follows: All the possible combinations were set up as mass matings of ten pairs in each of ten vials. In cases showing no fertility the number of cultures was increased to a total of 150 ten-pair matings and the cultures were kept for eight weeks with several changes to new food. At the end of this period the crosses were counted fertile or sterile; cases of sterility have been indicated by the letter *S* in the table. Any crosses which produced offspring were then tested for degree of fertility through pair matings. Vials which had both members of the cross alive at the end of eight weeks, but which showed no indication of larvae, were counted as sterile. For each cross a minimum of one hundred living pairs was used, and in those cases where a cross-fertility of less than 1 per cent is indicated, a minimum of 150 pairs. The gene orders were determined in salivary gland cells of F_1 larvae.

On the basis of their cross-fertility the test stocks can be arranged as shown in the table. The *nigromelanicas*, *melanicas*, and *paramelanicas* form three distinct mating groups. There is considerable fertility within

the groups, but very low fertility between them; *melanica* and *nigromelanica* are slightly cross-fertile to *paramelanica*, but sterile to each other. All hybrids which have been obtained thus far are fertile, and the sexes appear in equal numbers.

As a preliminary step in the comparisons of gene orders each test stock was examined cytologically for the presence of rearrangements. In two cases, Madison and Wooster, of the *paramelanica* group, inversions were present in the longest autosome in approximately half of the preparations; other strains have shown no such heterozygosity thus far. Within the *paramelanicas*, aside from the inherent Madison and Wooster rearrangements, the following differences were noted in comparisons with Madison as a standard: In Woodstock a small proximal inversion in the longest autosome; no rearrangements in Zealand and Woodbury; in Wooster, three small inversions in the X, two small, proximal, overlapping inversions in the longest autosome and two small inversions in a third autosome. In the *melanicas* the two test strains showed identical arrangement; each in comparison with *paramelanica*, represented by Madison, shows a large central inversion in the X and in the longest autosome a proximal rearrangement which has not been sharply delimited at present, but which is apparently different from any of those mentioned above. From these observations it is apparent that, with the exception of Wooster, the *paramelanica* strains have common gene orders in all of the chromosomes except the longest autosomal element. Similarly the *paramelanicas* and the *melanicas* have the same order in all but the X and the long autosome. In the *nigromelanicas* Wood's Hole and Wooster show the same gene order, while Texas shows two conspicuous inversions in relation to either; the details of differences between this group and *paramelanica* are at present obscure because of the low degree of synapsis found in salivaries of the scarce hybrid larvae.

With the initial grouping on the basis of fertility and gene order as the basis for further study, survey tests have been begun upon strains derived from population samples collected by Dr. G. B. Mainland, Mr. M. R. Wheeler, and Mr. R. B. Wagner, and by Dr. J. T. Patterson and the writer. Thus far it has been found that all samples are highly fertile to the *melanicas* and slightly fertile, often in only one direction, to the *paramelanicas*; no fertility to the *nigromelanicas* has been observed. The gene order is predominantly that of *melanica* with several variations indicating the geographical extent of common genomes. For example, a group of Southwestern forms from Arizona, New Mexico, Utah, and northern Mexico (Sonora) seem to differ from Ozark and Coffeeville only in two small distal inversions in the long autosome. Strains from a group of populations extending northward through central Texas and into Oklahoma show a striking gene order difference in the form of a series of overlapping inversions in one of the autosomes; and finally a group of strains from Louisiana, Mississippi, and Florida show no gene order differences.

DISCUSSION

Between the three members of the *melanica* group examined in this study there is a rather strong degree of isolation. In view of the fact that hybrids, when produced, are viable and fertile, the mechanism which can best be indicated is that of sexual isolation in P_1 crosses between the groups. Geographical isolation enters to an extent which can only be surmised; yet the distribution of the *paramelanicas* across the northern and the *melanicas* across the more southern regions gives evidence of a temperature barrier of some effectiveness. Ecological isolation can best be seen in *nigromelanica*. The Texas populations of this species are primarily forest dwellers (Patterson and Wheeler, 1942) and can be found feeding on fungi on the ground and in the cavities of stumps and logs. In Texas and other southern collecting points this species is found only in small numbers in traps; hence it may be classed as a fungus-feeder, although it is not completely dependent upon this type of food. This food preference and the marked sexual isolation of *nigromelanica* readily account for its identity as a species in spite of the geographical coincidence of its populations with those of both *melanica* and *paramelanica*. There is no apparent thermal barrier between this form and its relatives.

Within the species there is evidence of distinct geographical varieties. In the *melanicas* the division may be made on the basis of gene orders so that distinct southwest, central and southeastern races can be recognized, the Coffeerville and Ozark test-strains belonging, of course, to the southeastern division. There is within these varieties little or no restriction of particular gene orders to small local populations, and the geographical extent of each type is very broad. Incomplete tests of a strain from Beaumont, Texas, have revealed an intermediate condition between the central and southeastern types; Beaumont-Ozark hybrids show a portion of the series of overlapping inversions which, as previously mentioned, are a striking characteristic of hybrids between the two races. The zone of junction between these varieties probably extends northward through eastern Texas and Louisiana into the Ozark region.

In the *paramelanicas* there is as yet no comparable evidence of racial groups; such might be expected, however, in the form of populations north of the Great Lakes and in regions of the northwest. One detail which should receive comment here is the low fertility of the Wooster test stock. It has been demonstrated in the *virilis* group (Patterson, Stone, and Griffen, 1942) that continued inbreeding of progeny from original crosses between some geographical strains of the domestic type eventually resulted in a great reduction of fertility. The continued inbreeding which produced the Wooster test strain likewise has resulted in low fertility, which is expressed in both sexes as shown in out-crosses. The presence of different gene orders is indicative of a heterogeneous local population, which must also have been heterozygous for numerous factors; the continued inbreeding which produced the test strain has

allowed these factors to express themselves to a degree so marked as to indicate that the local population was the result of fairly recent hybridization between adjacent or overlapping groups, each of which had already developed numerous and different sterility factors. This explanation for the heterozygous condition of the Wooster stock is plausible since it is a member of the subspecies which can be called the genetic intermediate of the melanica group.

LITERATURE CITED

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FERTILITY AND AVERAGE NUMBER OF OFFSPRING PER TUBE

		NIGROMELANICA				PARAMELANICA					MELANICA	
♀	♂	Texas	Wood's Hole	Wooster	Madison	Woodstock	Zealand	Woodbury	Wooster	Ozark	Coffeyville	
				86% av. = 24.2	45.2% av. = 46.6	69.2% av. = 34	less than 1%	S	less than 1%	S	S	S
		51.9% av. = 44.5	14.3% av. = 40.6	38.1% av. = 36.4	S	S	S	S	S	S	S	
		52.2% av. = 49.3	22.4% av. = 40.2	36% av. = 38	S	S	S	S	S	S	S	
		S	S	S	82% av. = 43	1.5% av. = 9	4.1% av. = 30.2	22% av. = 35.7	8.0%	less than 1%	0.21%	
		S	S	less than 1%	23.0% av. = 38	75.2% av. = 52	27.3% av. = 32	39.1% av. = 41	15.4% av. = 48.2	less than 1%	S	
		S	S	S	24.2%	32%	42.3% av. = 17	20% av. = 12	incomplete; approx. 10%	S	S	
		S	S	S	13.3% av. = 32.9	3.6%	21.3% av. = 7	52% av. = 21	15% av. = 60.9	S	S	
		S	S	S	34.0% av. = 60	16% av. = 46.8	48% av. = 43	10.5% av. = 15.8	13.5% av. = 51.6	S	less than 1%	
		S	S	S	0.95%	less than 1%	less than 1%	less than 1%	3.2%	67.0% av. = 17	47.7% av. = 23.8	
		S	S	S	S	less than 1%	less than 1%	less than 1%	less than 1%	5.8% av. = 19.12	70.0% av. = 35	