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APPARENT CYTOPLASMIC STERILITY IN DROSOPHILA PAULISTORUM

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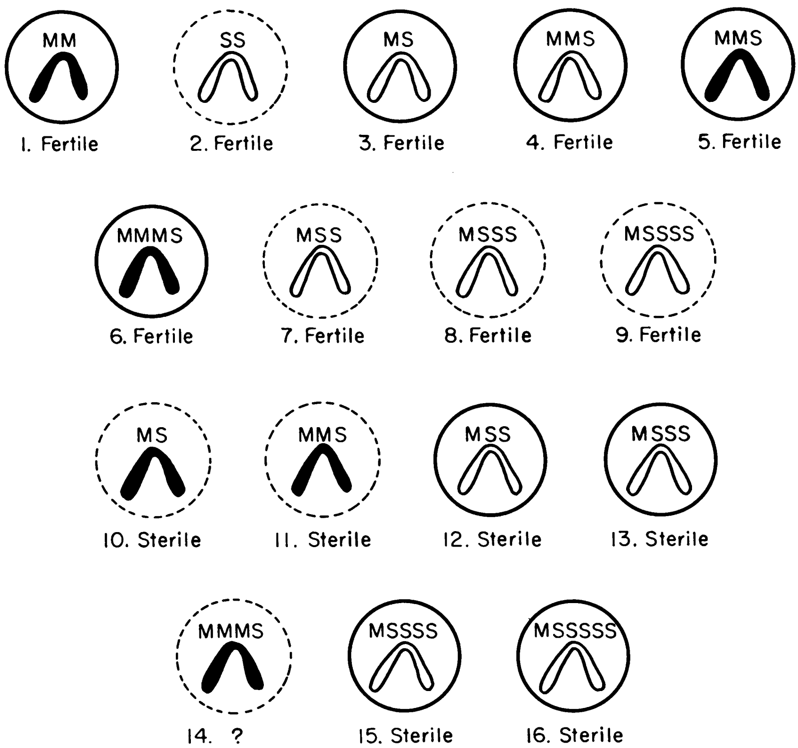
A hybrid inherits its chromosomes from both parents, but its cytoplasm mainly or exclusively from the mother. This may be expected to result in differences in the outcomes of the reciprocal crosses between a given pair of species or races. Differences between reciprocal crosses are indeed not uncommon,[1] but, at least in animals, most of them cannot be ascribed to influences emanating from the cytoplasm autonomously from the nuclear genes. In the first place, in organisms with separate sexes, the heterogametic sex is chromosomally not identical in the progenies of reciprocal crosses. Furthermore, certain characteristics of a progeny may be due to "maternal effects," i.e., to predetermination of the qualities of the egg cell by the chromosomal complement present in that cell before meiosis.[2] Laven[3] has, however, reported a thoroughly authentic case of hybrid sterility due to cytoplasmic differences in mosquitoes of the *Culex pipiens* species complex. A possible, but not certain, case of cytoplasmic sterility has been described in *Drosophila virilis* × *D. littoralis* hybrids by Patterson.[4] The purpose of the present communication is to report an apparently valid case of cytoplasmic hybrid sterility in *Drosophila paulistorum.*

D. paulistorum is a complex of at least six races or incipient species.[5, 6] Five of the races are difficult to intercross because of sexual isolation; when hybrid progenies are obtained they consist of fertile daughters and sterile sons. The sixth, Transitional race, produces fertile hybrids when crossed to at least one strain of every other race. Hybrids between different strains of the Transitional race are as a rule also fertile, but the case described below is an exception. The strains involved are Santa Marta (referred to below as "S") and Mesitas (referred to as "M"), both from Colombia, South America. The S strain is derived from flies collected in the Sierra Nevada de Santa Marta by Professors H. L. Carson and M. Wasserman; the M strain was collected at Mesitas, west of Bogotá, by Professor Alice Hunter of the Universidad de los Andes, Bogotá, Colombia. The S strain produces fertile hybrids with strains of Centro-American, Transitional, and Orinocan races.[5] The M strain yields fertile hybrids with the Bucaramanga, Buenaventura, and Palmira strains of the Transitional race, and the Angra and Tarapoto strains of the Andean-South Brazilian race (data of B. Spassky and the author).

All female hybrids between the M and S strains are fertile, but some of the male hybrids are fertile, while others are sterile. The genetic constitution of various male hybrids studied is represented symbolically in Figures 1–16. The cytoplasm derived from M mothers or grandmothers is represented by a continuous black circle, and that from S mothers by a dashed circular line; the Y chromosome of M is



FIGS. 1–16.—Genetic constitution of males of the Mesitas and Santa Marta strains and their hybrids. Black circle—M cytoplasm, dashed circle—S cytoplasm; Y chromosome of M strain shown in black, Y chromosome of S strain shown in white; M and S—genes of the M and S strains respectively.

shown as a black, and that of S as a white Λ-shaped figure. The letters M and S within the circles stand for the chromosomal genes of M and S (other than those in the Y chromosome).

The pure M males (Fig. 1) and pure S males (Fig. 2) are, of course, fertile. The cross M ♀ × S ♂ produces fertile sons (Fig. 3), while the cross S ♀ × M ♂ gives sterile sons (Fig. 10). The fertility or sterility of the males has in every case been diagnosed by repeated subculturing and by dissecting the mature males in physiological saline and checking for the presence of motile spermatozoa.

The M ♀ × S ♂ hybrid females, whose fertile brothers are represented in Figure 3, were backcrossed twice to pure M males; the male progenies of these backcrosses were also fertile (Figs. 5, 6). Similar M ♀ × S♂ hybrid females were backcrossed four times to pure S males; these backcrosses yielded exclusively sterile sons (Figs. 12, 13, 15, 16). Conversely, the S ♀ × M♂ hybrid females, whose sterile brothers are shown in Figure 10, were backcrossed three times to pure S males, and gave quite fertile male progenies (Figs. 7–9). However, when S ♀ × M♂ hybrid females were backcrossed to pure M males, they gave sterile sons (Fig. 11). An attempt to make a second backcross to M was made repeatedly, but without success, apparently because the MMS females with S-derived cytoplasm (sisters of the males in Fig. 11), refused to accept M males. It proved, therefore, impossible to test the fertility of males whose genotype is shown in Figure 14, which should have had a Y chromosome of the M strain, and mostly M genes in an S cytoplasm.

The above data are consistent with the hypothesis that the backcross males whose Y chromosome agrees in its strain origin with their cytoplasm are fertile, while an M cytoplasm with a Y chromosome of the S strain, or an S cytoplasm with a Y of the M strain, make the males sterile. The source of the chromosomes other than the Y seems to have little or no effects. There are, however, two facts which are not consistent with the hypothesis. First, the F_1 hybrid males from the cross M ♀ × S♂ are fertile (Fig. 3), although they carry M cytoplasm and a Y chromosome of the S strain. Secondly, when these F_1 males were backcrossed to pure M females, they produced fertile sons which carried an S Y chromosome in M cytoplasm and a majority of M genes (Fig. 4). By analogy with the males of the constitutions shown in Figures 12, 13, 15, and 16, these males were expected to be sterile; however, males in Figure 4 differ from those in Figure 12 by having a majority of M, rather than of S genes. Therefore, some involvement of chromosomal genes other than those on the Y chromosome cannot be excluded.

However that may be, the sterility of the males in the hybrid progenies of the M and S strains of the Transitional race has a different genetic base from the sterility of the male hybrids between the races. As shown by Ehrman,[7] this hybrid male sterility is genic in origin, with a maternal effect, and with genes fostering this sterility distributed over all the chromosomes of the species karyotype. Thus, the sterility reported in the present article is unique in *D. paulistorum*.

Summary.—When crossed, the Mesitas and Santa Marta strains, both belonging to the Transitional race of *Drosophila paulistorum*, produce fertile female and some sterile male hybrids. A genetic analysis suggests that the sterility in this case is caused, chiefly if not exclusively, by interaction of the Y chromosome of one strain, with the cytoplasm of the other strain. If the Y and the cytoplasm come from the same strain, the male is fertile, while if their sources are different, the male is usually sterile.

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