ISOGENICITY IN PARTHENOGENETIC STRAINS OF *DROSOPHILA MERCATORUM*

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IN 1961, several strains of the normally bisexual species *Drosophila mercatorum* were found to display a small amount of parthenogenesis. In the highest unselected strain, about one unfertilized egg per thousand developed into a normal, fertile, diploid female. By intercrossing and selecting from recombinants, the senior author (1967) was able to increase the rate of parthenogenesis about 60-fold, to around six percent. No polyploidy has been found.

Despite the success in selection, however, the mode of inheritance and of diploidization in the parthenogenetic eggs of this species has remained unknown. The present paper addresses itself to this problem. It will be shown that more than 90% of the females produced parthenogenetically are isogenic; they apparently arise from post-meiotic doubling of a haploid nucleus. The remainder of the impaternate offspring show some heterozygosity; these apparently arise through fusion of two haploid meiotic products.

MATERIALS AND METHODS

This work was done exclusively with *Drosophila mercatorum mercatorum* (for details see WASSERMAN 1962). The strains used are listed in CARSON (1967) and in Table 1 of the present paper. This species is highly vigorous; high-ranking thelytokous strains are almost as easy to maintain in the laboratory as bisexual ones. A number of new mutants were obtained by X irradiation. Each mutant used will be described later. All flies were reared at 25 ± 0.5°C.

TABLE 1

Presence or absence of orbital spot in various strains of* Drosophila mercatorum

Strains with spot (=wild type)	*Strains without spot* (=spotless, *sl/sl*)
Man-11 Manizales, Columbia	R Rochester, New York
Med-1 Medellin, Columbia	S La Palma, El Salvador
L Lima, Peru	RS-3-Im
O Oahu, State of Hawaii	RSB-7-Im
O-2-Bridge	RSS-17-Im
O-2-Im	RSS-17-Bridge
OB-2-Im (+)	OB-2-Im (*sl/sl*)
	OB-2-Bridge

* Im = impaternate.

TABLE 2

Bisexual reproduction: sex-linked inheritance of orbital spot in Drosophila mercatorum

Cross No.	Source and phenotype of: ♀ parent	♂ parent	Phenotype of F_1 progeny ♀♀ spot	♀♀ spotless	♂♂ spot	♂♂ spotless
1	RS-3-Im spotless	wild-type strains spot	359	7	3	259
2	wild-type strains spot	F_1 ♂ from Cross No. 1 spotless	390	0	404	0
3	F_1 from Cross No. 1 spot	F_1 from Cross No. 1 spotless	436	427	447	445
4	F_1 from Cross No. 1 spot	wild-type strains spot	570	0	299	291

RESULTS

Bisexual Inheritance: Some strains of *D. mercatorum* show the presence of a dark spot surrounding the base of the posterior reclinate orbital bristle. Others lack such a spot (Table 1; for details of the origin of these wild and laboratory strains, see CARSON 1967).

Table 2 gives the results of matings involving this character. The results are wholly consistent with monofactorial, sex-linked inheritance, with the spotless condition recessive to the presence of the spot in females. Accordingly, the symbols *sl* (spotless) and sl^+ (wild type, with spot) have been used. Although both alleles are present in natural populations, it appears that sl^+ is the original one and is thus more logically considered as the wild type. This is not only because this allele is dominant but also because none of a series of related repleta-group species lacks this spot. The species which have been examined for this feature include not only a very close sibling species of *D. mercatorum*, *D. paranaensis*, but also *D. repleta* Wollaston (*sensu stricto*), *D. hydei*, *D. bifurca*, *D. buzzatii*, *D. meridiana*, *D. stalkeri* and *D. mulleri*.

In cross No. 1 (Table 2), the seven exceptional females are apparently impaternate offspring from the RS-3-Im parent. This latter is a wholly thelytokous stock reproducing by parthenogenesis. The three wild-type (spot) males in this cross were evidently patroclinous and X0; they were tested and proved to be sterile.

In the summer of 1966, a number of additional mutants were obtained by irradiation of *D. mercatorum* with X rays. The details of these experiments will be reported elsewhere. One of the mutants, white eye color (*w*), is recessive to wild-type red (w^+) and sex-linked; accordingly, it is linked to spotless. White females (*w*/*w*) crossed to spotless males (*sl*) in five replicated pair matings gave 823 wild-type females and 825 white males. In addition, four white females and one spotless male were obtained. The females were apparently impaternate offspring of the white female and the single male was apparently a patroclinous X0 male; on testing, it proved to be sterile.

From each of the five P_1 pair matings, five replicated F_2 progenies were reared,

TABLE 3

Bisexual reproduction: recombination frequencies between the sex-linked recessives spotless (sl) *and white* (w)

Repulsion phase	Experiment No.	Phenotypes of F_2 progeny (males only) Parental classes: Spotless	White	Recombinant classes: Wild-type	Spotless, white	Total flies counted	Recombination frequency (percent)
$\frac{sl\ +}{+\ w}$	I.	2014	2011	1212	1184	6421	37.3
	II.	890	848	540	470	2748	36.7
	Total	2904	2859	1752	1654	9169	37.1
Coupling phase		Recombinant classes		Parental classes			
$\frac{+\ +}{sl\ w}$	III.	208	208	469	477	1362	30.5

Coupling *vs.* repulsion: $\chi^2_{(1)} = 22.37$; $P = < .0001$

using 10 F_1 females and 10 F_1 males from each P_1. The results of counts of males, given in Experiment I, Table 3, provide data on linkage between *sl* and *w* in the repulsion phase. The replicates gave homogenous data: $\chi^2_{(4)} = 6.76$; $P = .10–.20$. This experiment was repeated at approximately the same time by another investigator (Experiment II, Table 3) and gave essentially the same result, despite the fact that the larvae were more crowded. A smaller experiment was performed in which crossing over in the coupling phase was studied. The distance between *sl* and *w*, as measured in this manner, was significantly less than in the repulsion phase. The reason for this difference is not clear; it may be related, however, to the fact that Experiment III was done six months after I and II, using a different wild-type strain.

Two recessives induced by X rays, droopy wings (*d*) and ebony body color (*e*) show autosomal inheritance. Thus, when either droopy or ebony females are crossed to males lacking the gene, the F_1 are all wild type. When droopy was recovered in the F_2, it was close to the expected frequency for an autosomal recessive, although when crowding occurs, droopy individuals are fewer than expected on this hypothesis (Table 4, Experiments I and II). Droopy homozygotes apparently suffer some loss of viability under these conditions.

Table 4 also gives data on the inheritance of ebony (*e*). Although its viability is high when a simple cross is made (Experiment III), *e/e* homozygotes suffer considerable inviability when crosses are made with other mutants (see Experiments IV and V, Table 4). In such experiments, and under some circumstances in simple crosses, it was noted that ebony individuals are frequently unable to eclose from the puparium. Because the latter is black in color, contrasting with the yellow of wild type, such individuals may be easily identified. Droopy and ebony probably are on different autosomes, although further tests would be necesssary to establish this point. So far, males combining the two genes have proved to be sterile.

Inheritance in parthenogenesis: Spotless females (*sl/sl*) from the high-par-

TABLE 4

Bisexual reproduction: mode of inheritance of droopy (d) *and ebony* (e)

	Experiment No.	Phenotypes observed in F_2 generation (males and females) Wild-type	Droopy	Ebony	Droopy, ebony	Total	χ^2	df	P value
I.	F_1 $d^+/d \times d^+/d$								
	Observed number	1017	318	...	...	1335			
	Expected number*	1001	334	...	...	1335	1.03	1	.70–.80
II.	F_1 $d^+/d \times d^+/d$ (crowded conditions)								
	Observed number	1199	273	...	...	1472			
	Expected number*	1104	368	...	...	1472	32.69	1	<.0001
III.	F_1 $e^+/e \times e^+/e$								
	Observed number	741	...	270	...	1011			
	Expected number*	758.3	...	252.7	...	1011	1.57	1	.20–.30
IV.	F_1 d^+/d; $e^+/e \times$ d^+/d; e^+/e								
A.									
	Observed number	761	274	197	23	1255			
	Expected number†	705.9	235.3	235.3	78.4	1255	55.67	3	<.0001
B.									
	Observed number	685	240	115	10	1050			
	Expected number†	590.6	196.8	196.8	65.7	1050	106.03	3	<.0001

* Based on 3:1 phenotypic ratio.
† Based on 9:3:3:1 phenotypic ratio.

thenogenesis stock OB-2-Im were crossed to wild-type males from 0-2-Bridge[18]. Eighty-six F_1 virgin wild-type females (+/*sl*) were isolated. Impaternate offspring of these females were: wild-type females, 581; spotless females, 541. This does not differ significantly from a 1:1 ratio ($\chi^2_{(1)} = 1.36$; P = .20–.30). In addition to the female progeny, there were four wild-type and six spotless males. Seven of these males were tested by crossing to virgin R stock females and all proved to be sterile, indicating that they had an *X*0 genotype.

In order to determine the genotype of the impaternate wild-type females (i.e. whether they are +/+ or +/*sl*), individuals were chosen at random and mated singly in vials to two spotless R stock males each. At least 40 offspring (20 males and 20 females) were counted from each cross which gave bisexual progeny. Of 184 crosses from which bisexual offspring were obtained, 183 (99.5%) gave wild-type females and males in a 1:1 ratio. In five of the crosses, a small number of spotless males (from one to six in each cross) were produced. Each male was tested and found to be sterile; they are interpreted as patroclinous *X*0 males. Accordingly, each of these 183 wild-type females was judged to be a homozygote of the genotype sl^+/sl^+. The impaternate offspring, although normal diploids, occur in the gametic ratio of 1:1. The single exceptional cross gave 51 wild-type females, 46 *sl*/*sl* females, 45 wild-type males, 41 *sl* males. There is no reason to believe that this case is due to contamination and it appears to have been a bona fide heterozygote (+/*sl*).

TABLE 5

Unisexual reproduction: recombination frequencies between the sex-linked recessives spotless (sl) *and white* (w). *All progeny are impaternate female offspring of heterozygous F_1 females*

Cross No.	Genotype of F_1 females	Phenotypes observed among impaternate offspring: Parental classes Spotless	Parental classes White	Recombinant classes Wild-type	Recombinant classes Spotless, white	Total	Recombination frequency (percent)
I.	$+sl/w+$	384	343	193	161	1081	32.7
II.	$+sl/w+$	117	124	66	64	371	35.0
III.	$+sl/w+$	623	611	285	241	1760	29.9
		Recombinant classes		Parental classes			
IV.	$++/sl\ w; e+/e$	161	163	329	272	925	35.0
V.	$++/sl\ w$	102	159	261	222	744	35.1
VI.	$++/sl\ w;$ $e+/; d+/d$	263	211	584	515	1573	30.0
Total recombination (I, II, IV, V)*						3121	34.3
Total recombination (III, VI)†						3333	30.0

III *vs.* I–II: $\chi^2_{(1)} = 9.74$; P = .005–.002
* $\chi^2_{(3)} = 1.66$; P = .70–.80.
† $\chi^2_{(1)} = 0.02$; P > .90.

In addition to the above test crosses, 57 *sl/sl* impaternate female sibs of the above females were also tested by crossing to *sl* males. Only spotless offspring were produced. As a further double-check on the genetics of this system, 43 of the F_1 females, known to be $+/sl$ were also crossed individually to R stock *sl* males and about 40 flies counted in each case. The expected 1:1:1:1 ratio was obtained. The totals are: +♀ ♀555, *sl/sl*♀ ♀528, +♂ ♂518, *sl*♂ ♂548: $\chi^2_{(3)} = 1.65$; P = .70–.80.

Accordingly, it appears from these data that almost all of the impaternate offspring of heterozygous females are homozygous. Further tests involving spotless as well as other markers will be presented below.

Crosses were made to produce females heterozygous for both of the sex-linked recessives *sl* and *w*. In some cases, the autosomal genes *e* and *d* or both were also present; autosomal results will be presented in later paragraphs.

Three experiments were made in unisexual inheritance with *sl* and *w* in the repulsion phase (Experiments I-III, Table 5) and three in the coupling phase (Experiments IV-VI, Table 5). The resulting diploid female zygotes appear to occur in frequencies close to the gametic frequencies observed in males in bisexual crosses (cf. Table 3). The data obtained in 1966, for both coupling and repulsion experiments, are homogenous, giving a recombination frequency of 34.3%. Data obtained in 1967 are also homogenous but different from 1966: $\chi^2_{(1)} = 13.36$; P < .005. It will be recalled that this same kind of difference between the 1966 and 1967 data was observed in the bisexual experiments. The recombination frequency in the pooled 1966 bisexual data (37.1%, Table 3) is significantly greater than that observed in the unisexual data (34.3%) from the same year: $\chi^2_{(1)} =$

8.43; P = .005. In 1967, data from both unisexual and bisexual experiments are homogenous: $\chi^2_{(2)} = 0.16$; P > .90.

Whatever the cause of the difference between the 1966 and 1967 data, this does not affect the fact that the females produced in unisexual reproduction rather closely conform to gametic ratios. In fact, this conformance is close enough to suggest the hypothesis that meiosis in the eggs of parthenogenetic females is essentially like that in bisexual females and that diploidy, in a very high proportion of offspring, is restored by some sort of post-meiotic doubling of a haploid nucleus.

Data on the unisexual inheritance of the two autosomal genes droopy and ebony provide support for this view. Thus, females heterozygous for either *d* or *e* (Experiments I and II, Table 6) produce mutant and wild-type phenotypes in a 1:1 ratio. In the case of ebony, however, this ratio can be observed only by counting black *vs.* yellow puparia, as mentioned previously. In Experiment II, Table 6, 274 (81%) of the 337 ebony listed failed to eclose. This did not happen in the bisexual cross (see Experiment III, Table 4); the difference may be due to the high degree of isogenicity expected among impaternate offspring on the gamete duplication hypothesis. Such a genetic background would be expected to decrease viability, particularly of individuals homozygous for a somewhat deleterious mutant.

Where females heterozygous for *d* and *e* are allowed to reproduce unisexually, the ratio of the phenotypes produced does not conform to the 1:1:1:1 ratio based on the post-meiotic doubling hypothesis. This is not unexpected in view of the high inviabilities of flies homozygous for one or both of the mutants.

Earlier in this description, data were given which indicate that a female heterozygous for spotless apparently produces homozygous wild-type and spotless daughters in a 1:1 ratio. These and further data on this subject are given in Table 7. Five different genotypes of heterozygous mothers were prepared; these were heterozygous for one, two, three or four markers (Table 7, first column).

TABLE 6

Unisexual reproduction: autosomal inheritance of droopy (d) *and ebony* (e)

	Experiment and genotype of F_1 female	Phenotypes observed among impaternate offspring: Wild-type	Droopy	Ebony	Droopy, ebony	Total	χ^2	df	P value
I.	*d+/d*								
	Observed number	800	748	...	...	1548			
	Expected number*	774	774	...	...	1548	1.68	1	.20–.30
II.	*e+/e*								
	Observed number	331	...	337	...	668			
	Expected number*	334	...	334	...	668	0.06	1	>.90
III.	*d+/d; e+/e*								
	Observed number	727	371	411	64	1573			
	Expected number†	393.25	393.25	393.25	393.25	1573	577.2	3	<.0001

* Based on post-meiotic doubling hypothesis–i.e., mutant:wild-type = 1:1.
† Based on independent assortment and post-meiotic doubling: 1:1:1:1.

TABLE 7

Unisexual reproduction: genotypic tests of impaternate female offspring of mothers heterozygous for one to four markers

Genotype of mother	No.	Phenotype tested	Number of possible heterozygous markers	Impaternate females tested: Genotypes observed	Number of genotypes observed	Percent genotypes heterozygous for at least one marker
+/*sl*	1.	wild-type	1	+/+	183	
				+/*sl*	1	
					184	0.5
+/*w*	2.	wild-type	1	+/+	128	
				+/*w*	1	
					129	0.8
++/*sl w*	3.	wild-type	2	+ +/+ +	48	
				+ +/*sl w**	5	
					53	9.4
	4.	white	1	+ *w*/+ *w*	120	
				+ *w*/*sl w*	2	
					122	1.6
	5.	spotless	1	*sl* +/*sl* +	157	
				sl +/*sl w*	1	
					158	0.6
+ +/*sl w*; +/*e*	6.	wild-type	3	+ +/+ +; +/+	109	
				+ +/*sl w**; +/*e*	5	
				+ +/*sl w**; +/+	1	
				sl +/+ +; +/*e*	1	
					116	6.0
	7.	spotless, white	1	*sl w*/*sl w*; +/+	29	
				sl w/*sl w*; +/*e*	1	
					30	3.3
	8.	spotless	2	*sl* +/*sl* +; +/+	20	0.0
	9.	white	2	+ *w*/+ *w*; +/+	14	0.0
+ +/*sl w*; +/*e*; +/*d*	10.	wild-type	4	+ +/+ +; +/+; +/+	81	
				+ +/*sl w**; +/*e*; +/*d*	2	
				+ +/*sl w**; +/+; +/+	1	
				+ +/+ +; +/+; +/*d*	3	
					87	6.9

* or repulsion phase, *sl* +/+ *w*.

Impaternate daughters of these mothers which carry one or more wild-type alleles were progeny-tested by crossing each one individually to males carrying the appropriate recessives. The progeny reveal whether the wild-type impaternate females are heterozygous or homozygous for the loci concerned.

The results shown in Table 7 reveal that from 94–99% of the resulting females are homozygous, supporting the view that they result from the doubling of a haploid nucleus. Conversely, the heterozygotes appear to arise as the result of fusion between two of the four pronuclei produced in the egg. When a phenotype is tested which has only one possible heterozygous locus (phenotypes No. 1, 2, 4, 5, 7, Table 7), the frequency of nuclear fusion observed is about 1% (6/623).

On the other hand, when two or more possible heterozygotes are present (phenotypes No. 3, 6, 8, 9, 10, Table 7), recognition of the occurrence of nuclear fusion is apparently more efficient. A value of 6.2% heterozygotes is obtained (18/290). The difference between phenotype 3 (9.4%) and phenotype 10 (6.9%) is not significant: $\chi^2_{(1)} = 0.29$; $P > .50$.

The experiment in which unisexual reproduction of a quadruple heterozygote is studied (Experiment VI, Table 5 and No. 10, Table 7) produced, as expected, ratios which are disturbed by viability differences. Nevertheless, all 16 expected phenotypes were recovered. The results give some idea of the extensive amount of gene recombination which occurs in the meiosis of a heterozygous parthenogenetic female of *D. mercatorum:* + 267, *sl* 110, *w* 90, *sl w* 260, *e* 141, *sl e* 70, *w e* 67, *sl w e* 133, *d* 152, *sl d* 71, *w d* 47, *sl w d* 101, *e d* 24, *sl e d* 12, *w e d* 7, *sl w e d* 21 (total = 1573, see Expt. VI, Table 5).

DISCUSSION

In his definitive work on *D. parthenogenetica*, STALKER (1954) concluded that two normal meiotic divisions occur in the eggs of unmated females of that species, producing four haploid nuclei. Fusion of two of these may occur to form diploid progeny and fusion of three results in triploids, which constitute more than 20% of the impaternate offspring of diploid virgins. Females heterozygous for the sex-linked gene garnet (*g*) gave diploid progeny of which the majority were heterozygotes (62.6%) whereas *g/g* and +/+ homozygotes are estimated at 17.9% and 19.6%, respectively. Based on inheritance in *XXY* females, STALKER concludes that the homozygotes arise from fusion of two meiotic products derived from the same secondary oocyte (fusion of two terminal nuclei in the line of four). Heterozygotes are interpreted as arising from the fusion of meiotic products from different secondary oocytes (central fusion). The two types of fusion appear to occur in approximately the same frequency.

In the obligatory parthenogenetic species *Drosophila mangabeirai*, MURDY and CARSON (1959) observed that the viable progeny are exclusively fixed heterozygotes. They were interpreted as arising always from the fusion of the two central nuclei of the four, a process which was observed cytologically in the egg cytoplasm.

In major outline, inheritance in parthenogenetic *D. mercatorum* is evidently quite different from either of the above cases. In the first place, despite repeated attempts to find them, not a single triploid female has been recognized in *D. mercatorum* (CARSON 1967). On the other hand, the data of Tables 5–7 show that, as in both *D. parthenogenetica* and *D. mangabeirai*, both meiotic divisions occur normally in the eggs of diploid virgin females. Data on the behavior of the sex-linked genes *sl* and *w* during meiosis in *D. mercatorum* indicate that restoration of diploidy must, at least in a very high percentage of cases, be accomplished not by fusion of meiotic products but by post-meiotic doubling of one product. For example, in the repulsion experiment (+ *sl*/*w* +; I–III, Table 5) the double homozygous recessive recombinant, producing the zygotic combination *sl w*/*sl w*, is observed in almost the same frequency as in normal bisexual inheritance. No

type of fusion among any of the four meiotic products could produce such a zygote. Accordingly, it is concluded that diploidy is restored by some sort of post-meiotic doubling which in effect duplicates the genetic constitution of a single haploid gametic nucleus.

The genotypes observed among wild-type impaternate female progeny of heterozygous females (Table 7) strongly support this conclusion. Thus, well over 90% of all wild-type flies tested are indeed homozygous at all marked loci.

Although previously unknown in Drosophila, a number of cases of post-meiotic doubling has been described cytologically in other organisms. Thus, SEILER and GESSNER (1950) and SEILER (1960) have described such a process for the moth *Solenobia triquetrella.* Similar cases have been described in coccids (NUR 1963; HUGHES-SCHRADER and TREMBLAY 1966). In these cases, diploidy is restored by fusion of haploid cleavage nuclei.

Although more than 90% of the impaternates appear to arise by post-meiotic doubling, there is, nevertheless, a small but consistent number of heterozygotes formed. These probably arise by fusion of two haploid meiotic products. Whether such heterozygotes arise from central or terminal fusion, as previously discussed, is difficult to decide on the basis of the behavior of genetic markers alone. This is because the results can be affected by crossing over between the marker or markers and their centromeres. This matter has been discussed by TUCKER (1968) who has made a study of diploid parthenogenesis in the honey bee using similar methods. The fact that *X*0 males are regularly produced suggests that they are formed by fusion of nullo-*X* and normal *X*-bearing haploid nuclei. As STALKER (1954) has pointed out, such a condition is best explained by fusion between products of different secondary oocytes (i.e., central fusion).

If a few heterozygotes are formed in the first generation after outcrossing, such heterozygosity should be rapidly eliminated in subsequent generations, unless the fitness of the heterozygotes were higher than the homozygotes. WEI (1968) established a unisexual population cage using 100 females of the genotype sl^+/sl as the founders. Wild-type individuals from the cage were tested six times over the period of one year. Heterozygotes amounted to about 17% of the phenotypically wild-type flies at the first two tests. This declined to zero after one year when the "population" came to be composed of the two types of homozygous females only. This rather slow decline suggests that heterosis may play a role in laboratory stocks.

Perhaps the most interesting and important aspect of the *D. mercatorum* mechanism is the fact that a high percentage of the females produced, even by a highly heterozygous mother, becomes individually isogenic. In fact, one such female can serve as the founder of a stock that has a high probability of being composed of genetically identical individuals. Such a stock is isogenic in the same manner as an asexual clone, that is, it is made up of genetically identical individuals.

Because of the high rates of parthenogenesis now existing in laboratory stocks due to laboratory selection procedures, many isogenic stocks are available for further study, Because of the fact that males from "Bridge" stocks (CARSON 1967) can be used for outcrossing without appreciable loss of parthenogenetic

capacity, the genetic system of *D. mercatorum* provides a flexibility not found in other species. The parthenogenetic strains retain the capacity for wide outcrossing; yet, when the parthenogenetic strains are formed, they come about by the most extreme form of inbreeding.

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SUMMARY

Using one natural and three recessive mutants induced by X rays, inheritance in both bisexual and unisexual strains of *D. mercatorum* has been studied. The mutants spotless and white are sex-linked and show about 34% recombination in bisexual crosses. A virgin female heterozygous for these mutants produces impaternate diploid daughters in essentially gametic ratios. The same is true for the autosomal mutants. Wild-type females known to be heterozygous at a locus, therefore, produce wild-type and mutant diploid daughters in essentially a 1:1 ratio. When tested, approximately 94% of the wild-type daughters proved to be homozygous wild type. The remaining 6% are heterozygous at one or more loci.—It is concluded that the two meiotic divisions of virgin females proceed normally, producing, as in other Drosophila, four haploid nuclei in the cytoplasm of the egg. Diploidy appears to be restored in more than 90% of the eggs by post-meiotic nuclear doubling of a single meiotic product producing an isogenic diploid organism. The 6% of the impaternate wild-type offspring which show heterozygosity are judged to have arisen from the fusion of two of the four meiotic products in the manner known to occur in *D. parthenogenetica*. Accordingly, it is concluded that the majority of impaternate stocks of *D. mercatorum* are essentially isogenic. The implications of these findings are briefly discussed.

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