For more than a month subsequent to the birth of her dilute young, the mutant was so feeble that all hope was given up for her recovery. After this, however, she rallied sufficiently to produce a second litter of three. These all developed intense pigmentation, proving the mutation to have been germinal and to have involved probably one only of the two gametes from which she was derived.

TRISOMIC INHERITANCE OF DOUBLENESS, COMPLICATED BY LETHALS, IN *MATTHIOLA INCANA*¹

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It is a matter of peculiar interest to find evidence of trisomic inheritance of doubleness in *Matthiola*, a character whose exceptional behavior in disomic inheritance was held by Bateson to be evidence against the general occurrence of genetic segregation at meiosis.² Doubleness is recessive and doubles are completely sterile. In a "double-thrower" (or "ever-sporting") race, as Miss Saunders has shown,³ all singles are heterozygous for double; their functional sperms transmit double only, and their eggs, both single and double, but their double progeny from selfing slightly exceed the 50 per cent expected from a simple back cross; in F_2 from crosses of double-thrower with pure single, diploid F_1 plants which carry doubleness usually give about 25 per cent of doubles (that is, these F_1 's are ordinary heterozygotes, not double-throwers).

The genic formulation for doubleness developed by Haldane and Waddington⁴ will be mainly employed, although the dihybrid ($XYxy$) scheme of Miss Saunders,³ as completed by Muller with two pollen lethals,⁵ gives similar expectations in large part. In view of the fact that the symbols Ll had previously been used for other genes,⁶ Waddington suggests in correspondence the substitution of l_s and l_w for his published v and l . On this basis the normal or "wild-type" constitution is $\frac{L_sSL_wW}{L_sSL_wW}$ (homozygous for single flowers, colorless petal plastids, and absence of lethals); and the ordinary diploid double-thrower single of a sulfur-white race is $\frac{l_sSl_wW}{L_sL_ww}$, the recessive mutant genes being: l_s , pollen lethal,⁴ and also egg lethal unless l_w is present; l_w , pollen lethal; s , double (sterile) flowers; w , cream plastids. The dominants will hereafter be omitted in

the zygotic formulas; those just given may then be written $+/+$ and $l_s l_w / s_w$. Crossing-over is assumed to occur within this group only in the $s - l_w$ region. As the data to be reported here do not involve cream flower color, the genes Ww will be omitted in the following discussion.

The Crenate trisomic occurs frequently among the progeny of normal (diploid) parents of the long-chromosome variety "Snowflake," while Slender seems much rarer.^{6,7}

Crenate ($7_{II} + Cr$) has a large extra chromosome, presumably complete;

FIGURE 1

Chromosomes in pollen mother cells of one hybrid $CrSl$ plant; iron-acetocarmine; camera lucida, Zeiss 70X water-immersion objective, 25X ocular; about 3050 diameters, reduced one-third in reproduction. All at first metaphase, except C and D slightly earlier. A : $7_{II} + 1_{II}$ (Cr and Sl , apparently joined), chromosomes on two levels displaced in drawing as indicated. B : $7_{II} + 1_I Cr + 1_I Sl$. $C-G$: behavior of the extra chromosomes of five pollen mother cells; C, D : $1_{II} CrSl$; E : $1_{III} CrCrSl + 1_I Cr$; F, G : $1_I Cr + 1_I Sl$; in E, F and G , the separate chromosomes shown relatively about half as far apart, horizontally, as in the original drawings.

trivalents frequently occur at the first metaphase, although, as in the other *Matthiola* trisomics examined, the extra chromosome is unconjugated in a very large part of the pollen mother cells. Slender ($7_{II} + Sl$) has a much smaller extra chromosome, evidently a fragment, and trivalents seem to be much less common than with Crenate.⁸ An unconjugated extra chromosome in *Matthiola* may either divide in the first division and assort in the second, or vice versa.⁹

In the plants of the incompletely tetrasomic form, Crenate Slender ($7_{II} + Cr + Sl$), the two extra chromosomes are readily distinguished

by their relative size (Fig. 1); that they are homologous is indicated by the fact that in one of the two *CrSl* plants examined they often constituted an eighth pair at the first metaphase in the pollen mother cells. Of 52 counted groups from this plant, 18 showed only eight chromosomes, all clearly or probably bivalent; in 5 of these 18, one bivalent was visibly composed of two elements very unequal in size (Fig. 1, A, C, D).

A first metaphase of Slender, in which both whole *Cr* chromosomes go to the same pole and the *Sl* chromosome to the other pole, would give one Crenate-producing second-metaphase group ($7_I + Cr$), while the other second-metaphase group ($6_I + Sl$) would presumably produce non-functional pollen. The fact that Crenate mutants are only occasional among the progeny of Slender parents, indicates that in Slender the two whole chromosomes of the trisome usually disjoin (segregate) at meiosis.

Therefore, if the extra chromosome of Crenate carries the *Ss* locus, it may be anticipated that Crenate parents will give doubleness ratios corresponding more or less closely to random segregation in the trisome, but that with Slender the ratios will diverge markedly from the random trisomic expectation.

The selfing ratios given by Crenate and Slender double-throwers indicate that these singles are always *Sss*, never *SSs*.^{7,10} Since there is evidence¹⁰ that within a double-thrower race functional pollen may carry an *S* chromosome, provided an *s* chromosome is also present, it may be assumed that at least the constitution $s/l_sl_w/l_sl_w$ is zygotically lethal. It will be tentatively assumed that any trisomic constitution including either $L_sl_sl_s$ or $L_wl_wl_w$ is zygotically lethal, although the latter combination may be viable.

When double-thrower Crenate ($2n + Cr$) or Slender ($2n + Sl$) is crossed with a pure single (*SS*) normal ($2n$), therefore, all F_1 plants receiving the extra chromosome are expected to be either *Sss* or *SSs*. If we assume that the Crenate double-thrower parent had the constitution $s/s/l_sl_w$, the most probable *Sss* constitution among the F_1 hybrids will be $+/s/s$; the expected F_2 ratios will then be: normals, 5 single: 4 double; trisomics 7 single: 2 double. Three F_1 Crenate parents (table 1, parents *Cr* 1 to *Cr* 3) gave ratios corresponding well with this expectation.

The calculations for both Crenate and Slender assume, primarily, equal transmission of the extra chromosome by eggs and sperms. Actually the male transmission appears to be only about one-fifth of the female in Crenate, and one-half in Slender. In cases where unequal transmission would modify the ratio, therefore, the expectation for transmission through the eggs alone is added in parenthesis.

On the assumptions stated above, the only possible crossover *Sss* constitution in F_1 is $+/s/sl_w$. The F_2 expectation here, assuming that crossing-over between L_sSL_w and L_sl_w chromosomes cannot occur,⁴

and ignoring the possibility of differential viability, is: normals, 2 single:1 double; trisomics, 11 single:2 double (for egg transmission, 5:1). The F_2 Crenate parent Cr 4 (table 1) gave practically 2:1 among the normals; among the trisomics there was a small excess of doubles.

TABLE 1

SINGLE AND DOUBLE PROGENY OF CRENATE TRISOMICS ($2n + Cr$) AND OF RELATED NORMALS ($2n$); PARENTS SNOWFLAKE (DOUBLE-THROWER) OR F_1 HYBRIDS BETWEEN SNOWFLAKE AND PURE SINGLE RACES (NUMBERS IN PARENTHESIS CALCULATED FROM PROBABLE CONSTITUTION)

RACE AND TRISOMIC TYPE	PARENTAGE		NORMAL PROGENY		TRISOMIC CRENATE PROGENY	
	PROBABLE CONSTITUTION	INDIVIDUALS TESTED*	SINGLE	DOUBLE	SINGLE	DOUBLE
Snowflake, Crenate, selfed	$s/s/l_w l_w$	Many	92	413	150	57
Snowflake, Crenate	Crenate X					
X normal (diploid)	$s/l_w l_w$	Several	4	37	5	4
Snowflake, normal	$s/l_w l_w X$					
X Crenate	Crenate	Several	143	172	10	7
	$+s/s$	Cr 1	69	58	41	10
	Same	Cr 2	46	47	36	8
	Same	Cr 3	105	78	43	16
Hybrid, F_1 , Crenate, selfed	Same	Cr 1 to	220	183	120	34
		Cr 3	(224)	(179)	(120)	(34)
	$+s/sl_w$	Cr 4	99	52	82	24
			(101)	(50)	(90)**	(16)**
	$+s/l_w l_w$	Cr 5	147	33	42	1
			(150)	(30)	(43)	(0)
	Same ?	Cr 6	45	4	10	0
		N 1	69	15	0	0
		N 2	59	18	0	0
		N 3	108	31	0	0
Hybrid, F_1 , normal, selfed	$+s$	N 4	104	26	1	0
		N 5	93	31	0	0
		N 6	126	43	0	0
		N 1 to	559	164	1	0
		N 6	(542)	(181)	(0)	(0)

* "Cr" indicates Crenate trisomics; "N" indicates normals. Parents Cr 1, N 1 and N 2 came from one varietal cross, Cr 2, Cr 4, N 3 and N 4 from a second and the other hybrid parents from a third; except that Cr 6 came from a fourth cross. All hybrid Crenate parents except Cr 2 and Cr 4 were new chromosome mutants in F_1 , but probably received the extra chromosome from the Snowflake (long-chromosome) parent.⁶

** With egg transmission only, 88:18.

From the parentage assumed, the most probable SSs constitution in F_1 is $+s/l_w l_w$, corresponding to an expectation (without crossing-over) of: normals, 5 single:1 double; trisomics, all single. Crossing-over between $L_s L_w$ and $l_s l_w$ would slightly increase the proportion of normal singles. The progeny of Cr 5 approximate 5:1 and 1:0 very closely;

the one exceptional trisomic can be explained either by crossing-over in the four-strand stage or by double non-disjunction in the second division without crossing-over. Parent Cr 6 was inadequately tested, from poor seed; its constitution may have been $+s/l_s l_w$, or possibly $+s l_w/l_s$.

The six comparable normal F_1 hybrids tested have given ordinary disomic ratios. Altogether, the results agree well with expectation on the assumption that the Ss locus was present in triplicate in the hybrid Crenates, with random reduction in the trisome.

For double-thrower Crenate, which might be either $s/s/l_s l_w$, $s/s l_w/l_s$ or $s/s/l_s$, the available data are summarized in table 1. Without crossing-over, the ratios expected from selfing of $s/s/l_s l_w$ are: normals, 1 single:2 double; trisomics, 2.25 single:1 double (egg transmission, 2:1). If the $l_s S l_w$ chromosome crosses over in the $s-l_w$ region with each $L_s s L_w$ chromosome in 6 per cent of the sporocytes (about the rate indicated for disomic crossing-over by Miss Saunders' results), the ratios become 1:2.27 and 2.15:1 (2:1). A lower rate of crossing-over than in the one pairing of the disomic would be expected. Selfing of $s/s l_w/l_s$ similarly gives 0:1 and 2.5:1 (2:1), changed by crossing-over to 1:33.33 and 2.36:1 (2:1). And $s/s/l_s$ (lacking the lethal l_w) would give only 0:1 and 2:1, single normals being entirely absent.

Obviously, both here and with the hybrid Crenates, there is much elimination of the extra chromosome, which (table 1) occurs very largely in the pollen mother cells or in the pollen. Extended consideration of these ratios has suggested no plausible complete explanation (aside from the improbable one of sampling error) that does not also involve both non-random segregation (widening both ratios) and selective elimination of singleness among the Crenates—the two complications suggested by Waddington for Slender. Probably the two similar (s) chromosomes conjugate more readily with each other than with the lethal-bearing S chromosome. The selective elimination of single may not be entirely confined to the Crenates, or to the haploid stage, however; there is evidence suggesting a slightly lower viability of single, probably in part zygotic, in ordinary double-thrower races.^{3a,11,12} Such an effect may well be much more marked in the weak and relatively infertile Crenate parents, and among the Crenate haplonts and embryos.

Waddington's hypothesis will be applied to the ratios from selfing of Crenate double-thrower, assuming the constitution $s/s/l_s l_w$. If the ratio of the pairing between the two s chromosomes, to that between the S and s chromosomes (assuming in each case, for simplicity, that the third chromosome assorts independently), is represented by $m:2$ (in random assortment, $m = 1$), and if p gametes of the constitution $L_s s L_w/l_s S l_w$ survive for every one $L_s s L_w/L_s s L_w$ gamete, the progeny ratios of singles to doubles (assuming equal transmission and no crossing-over) will be:

diploid, $1:m+1$; trisomic, $p(m+1) + \frac{1}{2(m+1)}:1$. The two observed doubleness ratios are precisely fitted if we take $m = 3.49$ and $p = 0.56$. With egg transmission only, the expected trisomic ratio is $p(m+1):1$ and $p = 0.59$.

The data (mainly published⁷) might represent the constitution $s/s/l_s l_w$, and perhaps occasionally $s/sl_w/l_s$.

The two constitutions that are possible for double-thrower Crenate

TABLE 2

SINGLE AND DOUBLE PROGENY OF SLENDER TRISOMICS ($2n + Sl$); PARENTS SNOWFLAKE (DOUBLE-THROWER) OR HYBRIDS BETWEEN SNOWFLAKE AND PURE SINGLE RACES, ALL SELFED EXCEPT AS INDICATED (THESE ARE SELECTED TYPICAL CASES)

RACE AND TRISOMIC TYPE	PARENTAGE POSSIBLE CONSTITUTION OF SLENDER	INDIVIDUAL TESTED*	TRISOMIC SLENDER PROGENY			
			NORMAL SINGLE	PROGENY DOUBLE	SINGLE	DOUBLE
Snowflake, Slender	$s/s/(l_s l_w)$	Sl 1	6	98	34	8
	Same	Sl 2	1	53	26	2
	Same	Sl 2 X Crenate**	5	65	26	3
	(X s pollen)					
	Same	Sl 3	5	122	36	12
	Same	Sl 1 to Sl 3, selfed†	12	273	96	22
Hybrid, F_1 , Slender	$s/l_s l_w/(s)$	Sl 4 to Sl 7†	35	94	80	27
	$+s/(s)$	Sl 8	73	20	43	16
	Same	Sl 9	70	24	51	17
	$+s/(l_s l_w)$	Sl 10	75	30	37	0
	$+sl_w/(s)$ or					
	$+l_s l_w/(s)$	Sl 11	136	2	132	1

* "Sl" indicates Slender trisomics. Hybrid parents Sl 8 and Sl 10 came from the same varietal cross as Cr 3 and Cr 5 of table 1; parents Sl 9 and Sl 11, from the same varietal cross as Cr 2 and Cr 4 of table 1. The pollen parent of Sl 8 and Sl 10, and the seed parent of Sl 9, was Sl 2; the pollen parent of Sl 11 was another Snowflake Slender.

** The functional pollen of Crenate, except for a small percentage producing Crenate progeny, must be $L_s SL_w$. The expectation is very nearly the same as with selfing for this constitution of Slender (see text).

† The observed percentages of double Slender cited by Waddington⁴ are exaggerated by an arithmetical slip in his calculations. The value for selfing should be 28.6 (not 40) per cent.

on the $XYxy$ scheme, under the corresponding assumptions as to lethals, give (with crossing-over) either similar or less promising expected ratios, as follows: (1) normals, 1:2.41, and trisomics, 1.78:1 (egg transmission, 1.68:1); (2) 1:49 and 1:1.05 (1:1.83).

Slender is much more vigorous and fertile than Crenate, and consequently the genetic tests have been much more extensive; selected typical results are reported in table 2. The main features of the cytology and transmission of the Slender type, as previously described, preclude the

application of the hypothesis of selective segregation, *in the simple form stated by Waddington*, to these ratios.

That parent Sl 1 of table 2 had the constitution $ss(S)$ (that is, with the one S carried in the Sl fragment) is shown by the fact that it produced a variant branch with some fully double flowers and normal-appearing leaves; loss of the Sl chromosome obviously removed the only S gene carried by this plant.¹³ Cytological examination of several similar cases of somatic "mutation" (not involving doubleness) has confirmed this interpretation of the nature of the change. The ratios indicate that all other Snowflake Slenders adequately tested (for example, Sl 2 and Sl 3 of table 2) carried only one S .

If the chromosomes have their usual diploid constitution, and there is no crossing-over involving the fragment, an $ss(S)$ double-thrower Slender parent should produce only double normals and single Slenders. On the same conditions, and in the absence of selective segregation or elimination, an $sS(s)$ Slender should give the ordinary ratio of 1 single:1+ double among the normal progeny, and 3 single:2+ double (by egg transmission, 1:1+) among the trisomic progeny. Neither of these results has been secured, but most of the observed ratios suggest the former constitution with considerable crossing-over (table 2). This constitution may be represented by the formula $s/s/(l_w l_w)$. As will be shown below, the expectation is nearly the same if l_w changes places with an L_w in this constitution.

With the constitution $s/s/(l_w l_w)$, if the deficiency of the Sl -chromosome lies to the right of the l_w locus, crossing-over in the $s-l_w$ region, involving the fragment, would produce Slender doubles, but normal singles would be absent because of the egg-lethal effect of $l_w l_w$. Crossing-over to the right of l_w (that is, beyond the completely linked W_w locus) would give both cross-over classes. With the constitution $s/sl_w/(l_s)$, on the other hand, normal singles could be produced only by crossing-over in the former region.

The ratios given by the selfing totals for parents Sl 1 to Sl 3 could be produced, with the first constitution, by crossing-over alone (14 per cent in the former region and 4 per cent in the latter, in each pairing, giving: normals, 13 single:272 double; trisomics, 97:21). So high a rate in the former region is improbable, however, and it seems more likely that selective elimination of trisomic single has a marked effect on this ratio. The elimination of the extra chromosome has been somewhat similar to that with Crenate, although considerably less severe in the pollen.¹⁰

The assumption of 6 per cent of crossing-over in each pairing in the $s-l_w$ region, with 4 per cent in the other region, gives the ratios: normals, 1:22.5; trisomics, 9.01:1 (egg transmission, 9:1), the ratio among the trisomics requiring extensive selective elimination of trisomic single in

order to correspond to the observed ratios. Unless otherwise stated, these rates of crossing-over are to be understood whenever crossing-over is mentioned below.

Most of the progeny tests agree with the sample cases reported in table 2 in suggesting the parental constitution $ss(S)$. Such ratios are fitted about equally well whether the lethal l_w is in the fragment or in a whole chromosome; the constitution $s/sl_w/(l_s)$ gives, with crossing-over, doubleness ratios (normals, 1:30; trisomics, 9.79:1; with egg transmission only, trisomics, 9:1) not readily to be distinguished from those given by the first constitution above. One $sS(s)$ constitution, $sl_w/l_s/(s)$, gives somewhat similar ratios, 1:18.33 and 3.03:1 (egg transmission, 1.22:1), with crossing-over; without crossing-over, normals would be entirely absent (and with egg transmission only, trisomics also absent).

If the deficiency of the Sl fragment is to the *left* of l_s , the ratios with crossing-over are: normals, 1:24; trisomics, 23.30:1 (24:1), for the first constitution discussed, 0:1 and 28.96:1 (24:1) for the second, and nearly as above for the third (egg transmission, 1.08:1). Therefore it seems more probable that the missing region is located to the right of l_w (and hence to the right of w), and that location is generally assumed in this discussion. This inference agrees with the assumption that l_s is the deficiency which Philp and Huskins have demonstrated cytologically.⁴

The disagreement of the earlier data for selfed Slender double-thrower¹⁰ with those just considered is due mainly to small-scale data from four parents (Sl 4 to Sl 7), which gave closely accordant results totaling: normals, 35:94; trisomic Slenders, 80:27; the remaining parents gave 7:195 and 60:29. This suggests for the former parents the constitution $s/l_sl_w/(s)$, which without crossing-over would give 1:1 and 1.5:1 (1:1), and with crossing-over would give 1:1.31 and 1.54:1 (1.22:1). No other constitution that is possible under the present assumptions gives an expectation even remotely approaching the observed narrow ratio for normals that is here in question. *This* constitution, however, might give such a ratio as a result of selective segregation such as Waddington has suggested; if (L_sl_w) separates from L_sl_w much more often than from l_sl_w , the ratios would be much widened. The expected ratio for the trisomics, however, does not leave room for the marked selective elimination of single which would be anticipated.

Of the seven constitutions permitted to double-thrower Slender by our hypothesis, another that might be expected to be common is $s/l_s/(sl_w)$; without crossing-over this gives: normals, 0:1; trisomics, 1:1; and with crossing-over: 0:1 and 1.23:1 (1.22:1)—ratios not suggested by any results. There are two possible constitutions carrying only one lethal (l_s); the ratios with crossing-over are 0:1 and 9:1 from $s/s/(l_s)$ and 0:1 and 1.22:1 from $s/l_s/(s)$.

Under the limitations imposed above, the $XYxy$ scheme permits five constitutions of double-thrower Slender parents, corresponding respectively to the first five Ss constitutions above; the expectations with crossing-over are very similar in the first, fourth and fifth cases, and somewhat similar in the third (1:32.33 and 1.94:1; egg transmission, trisomics 1:9); in the second case, the ratio among the trisomics is only 1.30:1 (1.08:1). On account of the second case, the $XYxy$ scheme seems to correspond to the results somewhat less well than the Ss scheme.

Most if not all of the F_1 hybrid Slenders tested seem to fall into three classes. Often the F_2 progeny ratios approach 3 single:1double for both normal and trisomic progeny (table 2, parents Sl 8 and Sl 9). This suggests the F_1 constitution $+s/(s)$, which indicates an $s/(s)$ gamete from the P_1 Snowflake Slender. Another F_2 result (Sl 10) approaches: normals, 3:1; trisomics, 1:0. This suggests $+s/(l_s l_w)$, the constitution which we should expect to find much the most often if the P_1 Slender was $s/s/(l_s l_w)$. The third result (Sl 11) approaches entire absence of doubles; this is common, and has been obtained both when the double-thrower Slender was seed parent and when it was pollen parent in the cross. This suggests the presence of one or both lethals in the whole chromosome derived from the P_1 Slender, as is indicated in table 2.

The suggestion is obvious that Miss Saunders' cases of marked deficiency of doubles, in F_2 from crosses with pure single,^{3a} may be due to a lethal in the s chromosome in F_1 —apparently a lethal other than l_w , since $L_s SL_w/L_s s l_w (= XY/Xy)$ seems to give no recombination for plastid color.^{3b} Evidence for this interpretation is furnished by one case in my cultures. Of two F_1 sibs, belonging to a trisomic type (Smooth) that is disomic for the Cr (doubleness) chromosomes, one gave in F_2 about 3 single:1 double, while the other gave only about 3 per cent of doubles. A gene for recessive intense sap color (p)¹⁴ had entered the cross in the s chromosome, and the deficiency of double was accompanied by a similar deficiency of intense.

A thorough analysis of the genetic behavior of doubleness in these trisomic forms, which would necessarily include a study of the linked gene pairs Ww and Pp , would obviously require many times as many plants as the few thousands grown in the work here discussed. The correspondence of result with theory has been sufficiently extensive and varied, however, to encourage the hope that the main features of an adequate explanation have been indicated by the evidence at hand.

A point of especial theoretical interest is the clear indication, from crosses in which Slender was pollen parent,¹⁰ that in a double-thrower race functional pollen can carry a singleness chromosome, or at least a portion of it which includes the singleness locus, *provided* it also carries a doubleness chromosome. This fact tends to confirm the gamete-lethal

hypothesis for the explanation of the absence of singleness from ordinary double-thrower pollen, as also does the indicated non-occurrence of *SSs* double-thrower Slenders in spite of the abundance of *S* eggs and *Ss* sperms.

The frequent occurrence of crossing-over involving a chromosome fragment (*Sl*) seems unquestionable.

¹ Paper No. 253, University of California, Graduate School of Tropical Agriculture and Citrus Experiment Station, Riverside, California.

² Bateson, W., *Science*, n. s., **40**, 287-302, 1914.

³ Saunders, E. R., (a) *J. Genetics*, **1**, 303-376, 1911; (b) **20**, 53-77, 1928; (c) *Am. Nat.*, **50**, 486-498, 1916.

⁴ Waddington, C. H., *J. Genetics*, **21**, 193-206, 1929. On the basis of Snow's remark (*Am. Nat.*, **58**, 316-321, 1924) about Haldane's hypothesis, I independently (although later) applied to Miss Saunders' results the same scheme as did Waddington, except for a more inclusive tentative hypothesis for the apparent limitation of crossing-over between the *Ss* and *Lw* loci. I assume that the lethal *lw* (or some condition associated with its presence) inhibits crossing-over of its chromosome with any *LsSLw* ("wild-type") chromosome, but not with *LsLw*. This assumption covers all the cases (matings 1, 2 and 7 of Miss Saunders' tabular analysis)^{3b} where there is some reason for supposing that crossing-over does not occur, while Waddington's assumption covers only mating 7. Miss Saunders' data for the 1:1 ratio from mating 1 (783 white:879 cream; p. 55, 56) give odds of about 3845:1 against sampling deviation from Waddington's 16:15 ratio, but only 52:1 against the 1:1 ratio expected without crossing-over; however, selective elimination of the lethal-bearing white class might account for either deviation. The work of Philp and Huskins indicates that the lethal *ls* consists of the absence of a satellite normally present (Philp, J., and C. L. Huskins, *Anat. Record*, **47**, 379, 1930, Abstract).

⁵ Muller, H. J., *Genetics*, **3**, 422-499, 1918.

⁶ Lesley, M. M., and H. B. Frost, *Genetics*, **12**, 449-460, 1927.

⁷ Frost, H. B., *Univ. Calif. Publ. Agric. Sci.*, **2**, 81-190, 1919.

⁸ Frost, H. B., and M. C. Mann, *Am. Nat.*, **58**, 569-572, 1924. Frost, H. B., *J. Heredity*, **18**, 474-486, 1927. The cytological evidence mentioned in the present paper was mainly obtained by Dr. Margaret Mann Lesley, although the author obtained the evidence here presented relating to the behavior of the two extra chromosomes in a Crenate Slender plant. All general conclusions as to amount of conjunction of extra chromosomes in *Matthiola* are tentative, since as a rule relatively few pollen mother cells permit reliable counts, and doubtless those in which the extra chromosome is separate are more often countable. The chromosomes of the *Ss* pair may in general be designated *A* (instead of *I* as previously;⁷ for simplicity, the trisomic symbol *Cr* has been used throughout the present discussion. Trisomic Crenate might be called Triplo-A.

⁹ Lesley, M. M., and H. B. Frost, *Am. Nat.*, **62**, 22-33, 1927.

¹⁰ Frost, H. B., *J. Heredity*, **19**, 104-111, 1928.

¹¹ Saunders, E. R., *J. Genetics*, **5**, 137-143, 1915.

¹² Frost, H. B., *Am. Nat.*, **49**, 623-636, 1915. Miss Saunders' totals of 1911 for selfing and inter-crossing of double-throwers,^{3a} omitting families indicated as from old seed, 13,631 plants altogether, show, according to my calculations, 56.39 ± 0.29 per cent of doubles, while the percentage expected on her genic scheme, with 6 per cent of crossing-over, is only 53 per cent, and on Waddington's scheme only 51.5 per cent. Snowflake has given 52.90 ± 0.42 per cent.¹⁰ It should be noted that Miss Saunders' scheme requires crossing-over between the *Ww* and single-double loci in the *X-Y* region

alone in double-throwers, and in the *W-X* region alone (when at all) in hybrids with pure single, but the indicated rates for the two regions are identical or similar. Renner's evidence relating to megaspore competition in *Oenothera* indicates that megaspore development should be studied in *Matthiola* (Sturtevant, A. H., *Quart. Rev. Biol.*, 1, 283-288, 1926).

¹³ Frost, H. B., *J. Agric. Research*, 33, 41-46, 1926.

¹⁴ Saunders, E. R., *4e Conf. int. Génétique, Compt. Rend.*, 397-405, 1913.