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SEX BALANCE IN DROSOPHILA MELANOGASTER: ANEUPLOIDY OF LONG REGIONS OF CHROMOSOME 3, USING THE TRIPLOID METHOD[1]

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IN contrast with X chromosome triploid aneuploid studies (DOBZHANSKY and SCHULTZ 1934; PIPKIN 1940), alterations of dosage of any one short region of chromosome 2 (PIPKIN 1947) or of chromosome 3 (PIPKIN 1959) have revealed no pronounced sex shift in hyperintersexes or hypointersexes. Although the mean sex types of hyperintersexes bearing in excess of 2X3A a short right-hand end fragment of three different 3;4 translocations were slightly but significantly more male-like than the mean sex types of their control intersexes; hypointersexes for each of two components of this region showed no corresponding shift in the female direction (PIPKIN 1959). The purpose of the present investigation has been to study sex balance of long-region aneuploids in a further attempt to locate the autosomal chromosomal region responsible for the shift toward maleness in ordinary 2X3A triploid intersexes caused by the addition of an extra set of autosomes to the 2X2A female chromosome complement.

MATERIALS AND METHODS

Certain of the same 3;4 translocations used in the short-region aneuploid study (PIPKIN 1959) have been used in the present investigation of long regions. These include the following: T(3;4)c (DOBZHANSKY 1929a; LEWIS 1951), broken at 86C; T(3;4)A13, broken at 67E; T(3;4)A12, broken at 73C; T(3;4)A2, broken at 94A3-4; T(3;4)A28, broken at 94D3-4 (LEWIS, personal communication); T(3;4)A30, broken at 96E; all T(3;4)A translocations being studied by PATTERSON, STONE, BEDICHEK and SUCHE (1934) and PATTERSON, BROWN and STONE (1940); T(3;4)85C (LEWIS, personal communication), broken at 85C; T(3;4)89E (LEWIS, personal communication), broken at 89E; T(3;4)H1 and T(3;4)H3, each broken in the chromocenter; and T(3;4)H5, broken at 96E. The *y*^{2}; *ru ca* triploid stock used has been described previously (PIPKIN 1959). All of the experimental crosses were placed in a B.O.D. incubator to develop at 22 ± 0.5°C.

To study aneuploidy of long end regions, males heterozygous for a given 3;4 translocation carrying normal alleles and an intact third chromosome carrying the recessive markers *ru* (roughoid) and *ca* (claret) were crossed with homozygous *y*^{2}; *ru ca* triploid females according to Figure 1 (y^2 = yellow). The possible surviving long-region aneuploid progeny, hypertriploid females and hyperinter-

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sexes, are shown in Figure 2. Hypertriploid females carrying a long left-end fragment appear simply *ca*. Hyperintersexes may be either *ca* or y^2; *ca*, depending on the parental source of the X chromosomes. Similarly, hypertriploid females carrying a long right-hand end fragment appear *ru;* such hyperintersexes, appear either *ru* or y^2; *ru*. To demonstrate that the surviving long fragment aneuploids are hypertriploids and hyperintersexes rather than hypotriploids and hypointersexes, a control cross was made as follows: Males with the given 3;4 translocation carrying normal alleles and an intact *Dcx* third chromosome (carrying the dominant marker *D*, Dichaete, associated with an inversion) were crossed with y^2; *ru ca* triploid females. Any triploid aneuploid progeny (distinguished by coarse wing texture and large eye facets) showing either *ru* or *ca* from this cross must be either hypotriploid females or hypointersexes since only two third chromosomes with recessive markers are derived from the y^2; *ru ca* triploid parents. Since no *ru* or *ca* aneuploid progeny appeared from any of these control crosses, the aneuploids appearing from the cross shown in Figure 1 must be hypertriploid females and hyperintersexes.

To study aneuploidy of interior long regions, use was made of the overlapping translocation method, first described by MULLER and STONE (1930), and employed in a number of aneuploid studies since. Homozygous y^2; *ru ca* triploid females were crossed with males heterozygous for two different 3;4 translocations. For long interior region studies, the translocation with breakage point to the left carried *ca* and the normal allele of *ru*, whereas the translocation with the breakage point to the right carried *ru* and the normal allele of *ca*. This procedure insured that possible hypertriploid females, which of all aneuploids are most apt to survive, would be *ru ca*. This method is diagrammed in Figure 3.

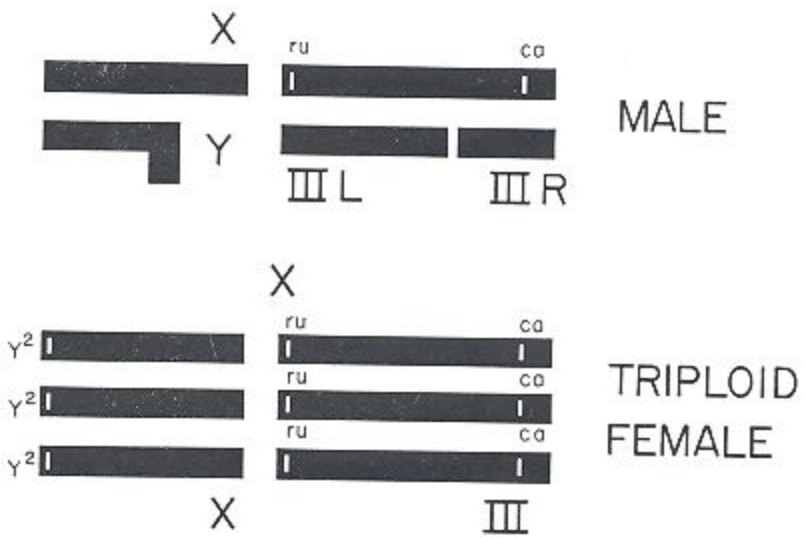

FIGURE 1.—Cross designed to produce hypertriploid and hyperintersex progeny carrying in excess of 3X3A or 2X3A, respectively, a long left-hand end fragment.

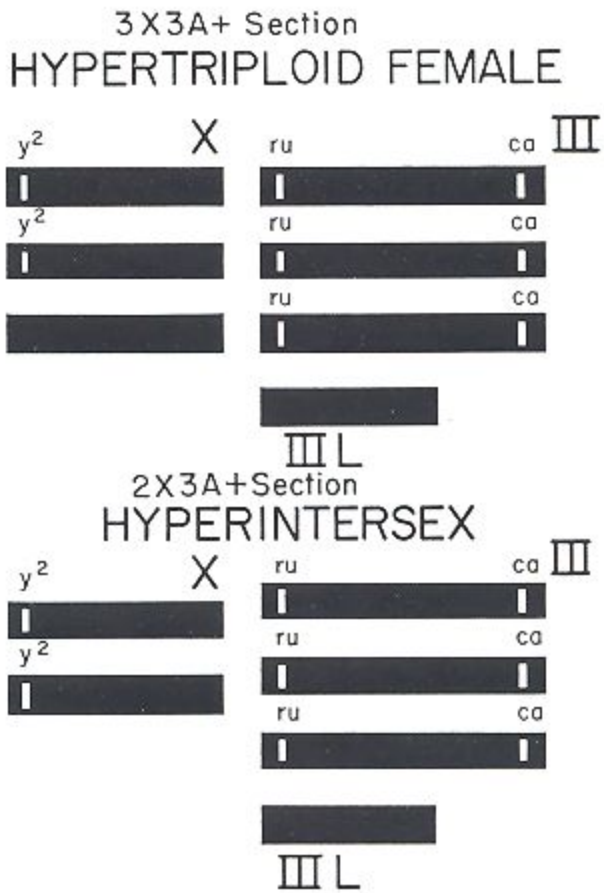

FIGURE 2.—Claret hypertriploid female and y^2; *ca* hyperintersex, each carrying a long left-hand end fragment of chromosome 3.

EXPERIMENTAL RESULTS

Long end regions: A summary of long end region aneuploid studies is given in Table 1. The first column gives the genetic composition of the translocation-carrying male parent crossed with y^2; *ru ca* triploid females. Numbers of aneuploid progeny and of wild-type control (2X3A) intersexes appear in Table 1. A comparison of the numbers of this one group of control intersexes with those of aneuploids indicates the rarity of the latter in the progeny of a particular experimental cross.

Table 1 shows that no hypertriploid female survived carrying either the left- or right-hand end fragment of either T(3;4)H1 or T(3;4)H3, each broken in the chromocenter. Hypertriploid females and hyperintersexes bearing left-hand end fragments of T(3;4)12, T(3;4)85C, and T(3;4)89E were found when rather high progeny counts were made of the experimental crosses indicated in the first column of Table 1. Aneuploid and control 2X3A sibling intersexes listed in Table

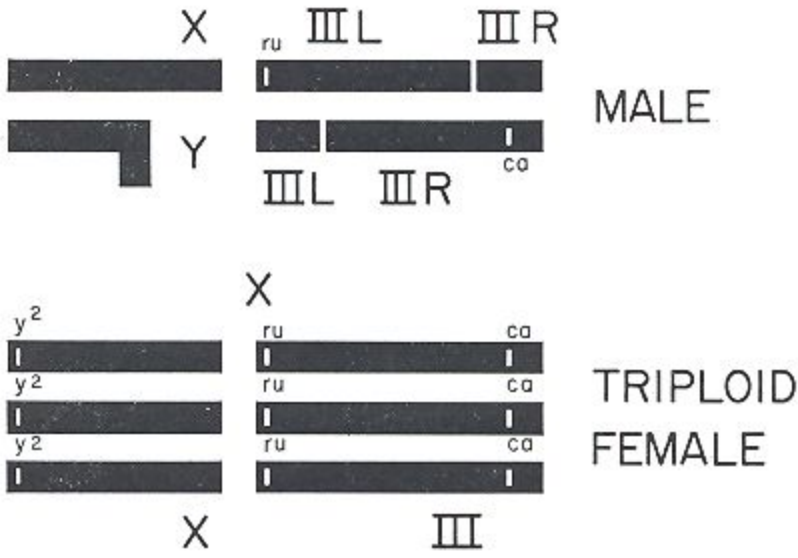

FIGURE 3.—Cross designed to produce hypertriploid or hyperintersex progeny carrying in excess of 3X3A or 2X3A, respectively, a long interior region of chromosome 3.

1 are classified according to the sex types I–V, described by DOBZHANSKY and SCHULTZ (1934). Owing to the low numbers of surviving long region hyperintersexes and to the fact that the control intersexes themselves were predominantly of the male types I and II, little information can be derived from a comparison of the sex types of the two groups. For this reason a detailed study was made of the sex combs of long- and short-region hyperintersexes, their respective control 2X3A sibling intersexes as well as of short region hyperdiploid males, control sibling males (X 2A), and supermales (X 3A) arising from crosses of males heterozygous for one or two 3;4 translocations and y^2; *ru ca* triploid females. The aneuploids, thus studied, occurred in the experimental crosses of the present investigation and also of the previous short-region aneuploid study of chromosome 3 (PIPKIN 1959). A detailed analysis of the sex comb data of these aneuploids will appear in a later paper. In no case did a long-region hyperintersex possess sex combs with a higher number of prongs (i.e., more male-like) than those of its corresponding control 2X3A sibling intersex.

Claret hypertriploid females carrying 12 L in excess of 3X3A are similar to their 3X3A sibling triploids in body size, eyes, wings, bristles, and sexual characters. Hyperintersexes with 12 L + 2X3A differ from their 2X3A control sibs by having thinner bristles, postverticals more often missing, and ocelli partly missing.

Claret hypertriploids carrying 85C L in addition to 3X3A were about the size of intersexes, had dark trident markings, wings sometimes imperfectly expanded, one posterior scutellar bristle occasionally missing, bristles thin. Wing texture was triploid in appearance, and eye facets were regular and triploid in size. No

TABLE 1

Aneuploidy involving long-end regions of chromosome 3

T(3;4) male parent × y^2; *ru ca* triploids	Hyperdiploid XY2A + L ♂	Hyperdiploid 2X2A + L ♀		Hyper-triploid ♀ 3X3A + L	Hyper-triploid ♀ 3X3A + R	Hyperintersex 2X3A + L	Hyperintersex 2X3A + R	Control intersex wild type				
	y^2; *ca*	*ca*	y^2; *ca*	*ca*	*ru*	*ca* or y^2; *ca*	*ru* or y^2; *ru*	I	II	III	IV	V
12/*ru ca*	1	18	8	19	0	11 I, 4 II(*ca*); 6 I, 2 II, 1 IV(y^2; *ca*)	0	302	106	40	54	2
H1/*ru ca*	0	0	0	0	0	0	1 I (*ru*)	212	69	22	42	2
H3/*ru ca*	0	0	0	0	0	0	0	184	63	25	65	2
85C/*ru ca*	0	0	0	23	1	9 I, 3 II, 1 III, 1 IV (*ca*); 2 I(y^2; *ca*)	2 IV(y^2; *ru*)	346	202	60	160	4
89E/*ru ca*	0	2X2A + R *ru* y^2; *ru* 21 2		12	24	1 III(*ca*)	1 III(*ru*); 1 I, 1 II, 1 IV (y^2; *ru*)	405	175	56	111	3

signs of intersexuality were present, but the hypertriploids were short-lived and none yielded progeny.

Hyperintersexes of the constitution 85C L + 2X3A were either yellow or wild type depending on the source of their X chromosomes. These hyperintersexes regularly lacked both pairs of scutellar bristles, had malformed ocelli, but otherwise were similar to 2X3A sib intersexes in body size, wing texture, and eyes. Dissection of an 85C L + 2X3A hyperintersex revealed a normal male duct system and small coiled testes.

The single 85C R + 3X3A hypertriploid female had wings held erect over the body, wing texture and eye facets triploid in appearance, and body size approximately that of an intersex. All sexual characters were female. Two hyperintersexes carrying the right-hand end of 85C in addition to 2X3A were found.

The 12 claret aneuploid females resulting from the cross of T(3;4)89E/ *ru ca* male with y^2; *ru ca* triploid females were characterized as follows: late hatching, each the size of an intersex, a shrunken abdomen, anterior ocellus missing, slender bristles, eye facets undisturbed but as small as in diploid females, wings deeply clipped medially, and wing texture as fine as that of diploid females. Sexual characters were female. Dissections revealed underdeveloped ovaries with no mature eggs. These 12 aneuploid females are presumed to be 89E + 3X3A hypertriploid females for the following reasons: First, no *ca* aneuploid females were found among the progeny of T(3;4)89E/ *ru ca* males with y^2; *ru ca* diploid females in a testcross designed to demonstrate whether or not hyperdiploid females of the genotype 89E L + 2X2A could survive. Hence, the 12 *ca* aneuploid females from the first cross (of T(3;4)89E/ *ru ca* males with y^2; *ru ca* triploid females) could not have been hyperdiploid females of genotype 89E L + 2X2A even though the wing texture and eye facets of the former were diploid in appearance. Second, since no *ca* aneuploid females resulted from a cross of T(3;4)89E/ *Dcx* males with y^2; *ru ca* triploid females, the *ca* aneuploid females of the first cross could not have been hypotriploid females. Finally, since the 12 *ca* aneuploid females of the first cross possessed eye facets with no irregularities in arrangement, they were not confused with "triple X" females of genotype 3X2A which also have medially clipped wings but, in addition, disturbed eye facets. Triple X (3X2A) females occurring in the progeny of the first cross were expected to be either wild type or *ru ca*. One such triple X (3X2A) *ru ca* female was found among the progeny of the first cross. With profoundly disturbed eye facets, this triple X female could not have been confused with its 12 sibling *ca* aneuploid females possessing undisturbed eye facets. The 12 *ca* aneuploid females are therefore thought to have been 89E + 3X3A hypertriploid females. Their small body size, fine wing texture, slow development, diploid facet size, and medially clipped wings must have been the result of genic imbalance.

Twenty-four *ru* hypertriploid females of the genotype 3X3A + 89E R were observed, as Table 1 shows. These late-hatching aneuploids possessed shrunken abdomens, invariably carried wings outstretched and held up over the body. The bristles were thin; eyes were typically roughoid but triploid in facet size. Wing

texture was coarse as in triploids. Sexual characters were female; ovaries, rudimentary.

Wings were widely outstretched in the *ru* hyperintersexes carrying 2X3A + 89E R. Otherwise these hyperintersexes resembled control sibling intersexes. Similarly, wings were widely outstretched in the single *ca* hyperintersex of the genotype 2X3A + 89E L, and wing texture was intermediate between that found in diploids and triploids.

Long interior regions: Using the overlapping translocation method previously described, aneuploidy of a number of long interior regions was studied, as Table 2 shows. Hyperdiploids survived in only two of the experimental crosses, in cases where the portion of the third chromosome carried in excess of 2A was not extremely long. These hyperdiploids, indicated in parenthesis in the body of the table, showed effects of genic imbalance—small eyes and outstretched wings. According to the data in Table 2, hypertriploid females are the most viable long interior region aneuploids. These also often showed signs of aneuploidy—small eyes, misshapen legs, and wings sometimes held apart. Coarse wing texture and large eye facets distinguished these hypertriploids (except in the case of hypertriploids for region 12-89E). Hyperintersexes carrying in excess of 2X3A a long interior region occurred in the progeny of three experimental crosses only. The latter were typically intersexual and showed no shifts toward maleness.

The numerous nondisjunctional forms indicated in Table 2 constitute a surprising feature of the progeny of males heterozygous for two different 3;4 translocations and *y*^{2}; *ru ca* triploids. If nondisjunction of the two third chromosomes, accompanied by normal disjunction of the two second chromosomes, occurred at meiosis in males heterozygous for two 3;4 translocations, then the resulting sperm would be haploid for chromosome 2 and possess either no third chromosome or two of them. Viable nondisjunctional progeny would result from the union of triploid eggs carrying different numbers of chromosome 3 and of chromosome 2, as indicated in Table 3. Possible nondisjunctional sperm types, triploid eggs, and resulting nondisjunctional progeny appear in this table. These nondisjunctional forms, appearing *y*^{2}; *y*^{2}; *ru ca*; and wild type actually occurred in the experimental crosses, as reference to Table 2 will show. Nondisjunction was higher when the breakage points of each of the 3;4 translocations in the male parents were located within a single chromosome arm away from the normal position of the centromere of chromosome 3. More such translocations were available for study in the right arm of chromosome 3. The highest rate of nondisjunction occurred in males heterozygous for T(3;4)85C and T(3;4)A28. To demonstrate that the vigorous, normal appearing *y*^{2} and wild type nondisjunctional forms occurring in the progeny of *ca* T(3;4)85C/ *ru*, T(3;4)A28 males × *y*^{2}; *ru ca* triploid females were not hypoploids, a control cross of the following composition was made: T(3;4)85C/ *ru ca*, T(3;4)A28 males × *y*^{2}; *ru ca* triploids. If the *y*^{2} and wild-type progeny of the first cross had been hypoploids, we should expect to find some *ca* "hypoploids" in the progeny of the second cross. No *ca* offspring was derived from the second cross. Hence, the exceptional *y*^{2}, wild-type and *y*^{2}; *ru ca* progeny of the first cross were assumed to be nondisjunctional forms.

TABLE 2

Aneuploidy involving interior regions of chromosome 3

T(3;4) male parent × y^2; *ru ca* triploid ♀	Overlap hyper-triploid ♀ *ru ca*	Overlap hyper-intersex *ru ca* or y^2; *ru ca*	Nondisjunctional forms except where noted in parenthesis							Control 2X3A intersex *ca*
			Diploid y^2; *ru ca* ♀	♂	Diploid y^2 or wild type ♀	y^2 ♂	Triploid ♀ wild type	Intersex wild type	Intersex y^2	
ca, 13/*ru*, H1	18	3 y^2; *ru ca* 7 *ru ca*	(3 hyper); 9 n.d.	14	2+	1	4	6	2	256
ca, 13/*ru* 89E	1	0	5	10	3 y^2; 4+	1	20	23	1	135
ca, 13/*ru* 28	1	0	2	3	2+	1	3	0	2	188
ca, 85C/*ru*, 2	42	2 *ru ca*	(4 hyper) 7 n.d.	5	12 y^2; 20+	30	49	10	5	321
ca, 85C/*ru*, 28	3	0	17	10	1 y^2; 4+	1	185	241	152	195
ca, 85C/*ru*, 30	13	0	32	19	14 y^2; 17+	10	11	16	5	309
ca, H1/*ru*, c	42	36 y^2; *ru ca* 60 *ru ca*	1	2	1	0	0	0	0	273
ca, c/*ru*, 30	7	0	(1 hyper)	0	3 y^2; 9+	6	13	12	8	147
ca, 85C/*ru*, H5	1	0	0	0	1+	3	63	68	46	120
ca, 12/*ru*, 89E	2*	0	0	0	0	0	33	14	4	171
ca, H3/*ru*, 89E	0	0	17	6	0	1	2	0	0	100
ca, 12/*ru*, 2	1	0	0	0	11 y^2; 13+	16	42	9	3	65

* May be 89E 1. hyper T.

TABLE 3

Origin of nondisjunctional progeny of wild-type males heterozygous for two 3;4 translocations and y^2; ru ca triploids

N-d sperm	Triploid egg	N-d progeny	
1X 2 III 1 II	2X 1 III 2 II	3X 3 III 3 II	wild-type triploid
1X 2 III 1 II	1X 1 III 2 II	2X 3 III 3 II	wild-type intersex
Y	1X 2 III 2 II	Y 1X 2 III 2 II	y^2; *ru ca* male
Y	2X 2 III 2 II	Y 2X 2 III 2 II	y^2; *ru ca* female
Y 2 III 1 II	2X 1 III 2 II	Y 2X 3 III 3 II	y^2 intersex
Y 2 III 1 II	1X 1 III 2 II	Y 1X 3 III 3 II	y^2 super-male
X	1X 2 III 2 II	2X 2 III 2 II	wild-type female
X	2X 2 III 2 II	3X 2 III 2 II	wild-type triple-X female
Y 2 III 1 II	1X 1 II	Y 1X 2 III 2 II	y^2 male
Y 2 III 1 II	2X 1 II	Y 2X 2 III 2 II	y^2 female

Among the nondisjunctional diploid forms, some haploidy of chromosome 4 occurred. Thus, some y^2 or wild-type individuals had somewhat thinner bristles than normal, and some wild-type individuals exhibited a strong trident marking. The mutant *ru* showed a pronounced expression in haplo-4 y^2; *ru ca* diploids. Haploidy of chromosome 4 occurred because the maternal triploid strain had been carried a long number of years and was probably diplo-4, as RUDKIN and SCHULTZ (1956) found to be true in their triploid strains carried for a long time.

DISCUSSION

BRIDGE's discovery of 2X3A triploid intersexes in *Drosophila melanogaster* led to his conclusion that male determiners must be present in the large autosomes (BRIDGES 1921, 1922). Succeeding efforts to further locate the autosomal male determiner(s) have proceeded in two directions: (1) by studies of intersex-producing mutants which have occurred in the autosomes of various species of Drosophila, and (2) by diploid and triploid aneuploid studies. GOWEN and FUNG (1957) concluded from the interaction in diploid and triploid combinations of the intersex mutants *Hr*, *tra*, and their normal allele, that the latter is a major sex gene, a view which had been anticipated for this locus by GOLDSCHMIDT (1955). LEBEDEFF (1938) regarded the normal allele of the ix^m mutant he studied in *D. virilis* as a male determining gene, the ix^m mutant being its "stronger allele." SPURWAY and HALDANE (1954) pointed out that if the normal alleles of *ix* mutants are sex genes, then the former must be thought of as hypermorphs rather than hypomorphs according to MULLER's (1932) classification, a conclusion in accordance with that of LEBEDEFF (1938). STONE (1942), working with *D. virilis*, considered the normal allele of Ix^p a sex gene but not necessarily male determining. Earlier authors did not think of the normal alleles of the *ix* mutants as being necessarily sex genes (STURTEVANT 1920; DOBZHANSKY and SPASSKY 1941; WHITE 1948).

Triploid aneuploid studies of both chromosome 2 and 3 in *D. melanogaster* give us no information as to the location of male determining regions within

either of these autosomes (PIPKIN 1947, 1959, and the present work). Hypertriploid females possessing 3X3A plus either the right- or left-hand fragment of two different translocations, T(3;4)85C and T(3;4)89E, showed no intersexual characters. Similarly, no sex shift was found in a number of other different hypertriploid females that in excess of 3X3A carried various long regions, respectively, of chromosome 3 obtained by the overlap method. Long-region hyperintersexes, where these survived, appeared typically intersexual. The normal allele of *Hr* and *tra* is located in the left-hand fragment of T(3;4)85C and of T(3;4)89E. Furthermore, triploid aneuploid studies of chromosome 3 do not confirm the conclusion of KELSTEIN (1938) that a male sex determining region exists between 89A and 94A on the salivary map of chromosome 3, following his study of hypodiploids for this short section.

Since no triploid aneuploids involving any region of chromosome 2 or 3 separately show a sex shift, it is possible that the male determiners responsible for the shift to intersexuality in 2X3A triploid intersexes are located in both the second and third chromosomes. Use of the triploid method to study aneuploidy simultaneously at the locus of L. V. MORGAN's second chromosome intersex mutant and at the locus of the third chromosome *Hr*, *tra* mutants would present the serious technical difficulty of maintaining a sufficiently vigorously triploid strain carrying both second and third chromosome marker mutants. In case such a study is attempted, the sections covering the respective intersex mutant loci should be very short to avoid complications in obtaining aneuploids owing to nondisjunction of one or both pairs of large autosomes in the male parent as well as inviability of the desired aneuploid.

Observations on cell size as determined by facet size and hair spacing in wings (wing texture) in third chromosome triploid aneuploids show that the size of these eye and wing cells is not invariably proportional to the total chromosome content. While most triploid aneuploids show coarse wing texture and large eye facets, the hypertriploid combination 3X3A + 89E L possessed eye facets and wing texture the size of those in diploids. DOBZHANSKY (1929b) also found aneuploid exceptions to the general rule that cell size increases directly with total chromosome content.

SUMMARY

No shift toward intersexuality was observed in hypertriploid females carrying 3X3A + either the right- or left-hand fragments of two different 3;4 translocations, T(3;4)85C and T(3;4)89E. Various other hypertriploid female combinations carrying different long interior regions of chromosome 3, respectively, plus 3X3A showed no intersexual features. Several hyperintersex combinations carrying 2X3A plus a long fragment of chromosome three appeared typically intersexual. Since no sex shift has been observed in triploid aneuploids involving the second chromosome only (PIPKIN 1947) or in triploid aneuploids involving the third chromosome only (PIPKIN 1959 and present study), the suggestion is made that both 2 and 3 chromosome regions may be responsible for the shift toward maleness found in ordinary 2X3A triploid intersexes.

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