TRIPLOID INTERSEXES IN *DROSOPHILA MELANOGASTER*

CALVIN BRIDGES

Bridges, C. 1921. Triploid Intersexes in *Drosophila melanogaster*. *Science*, NS, 54: 252-254.

Electronic Scholarly Publishing Project

Foundations Series — Classical Genetics

Series Editor: Robert J. Robbins

The ESP Foundations of Classical Genetics project has received support from the ELSI component of the United States Department of Energy Human Genome Project. ESP also welcomes help from volunteers and collaborators, who recommend works for publication, provide access to original materials, and assist with technical and production work. If you are interested in volunteering, or are otherwise interested in the project, contact the series editor: *rrobbins@fhcrc.org*.

Bibliographical Note

This ESP edition, first electronically published in 2003, is a newly typeset, unabridged version, based on the 1921 edition published by *Science*. Unless explicitly noted, all footnotes and endnotes are as they appeared in the original work. Some of the graphics have been redone for this electronic version.

Production Credits

Scanning of originals:	ESP staff
OCRing of originals:	ESP staff
Typesetting:	ESP staff
Proofreading/Copyediting:	ESP staff
Graphics work:	ESP staff
Copyfitting/Final production:	ESP staff

Bridges, C. 1921. Triploid Intersexes in *Drosophila melanogaster*. *Science*, NS, 54: 252-254.

TRIPLOID INTERSEXES IN *DROSOPHILA MELANOGASTER*[1]

CALVIN BRIDGES

IN AN EXPERIMENT made to determine the locus of the new second-chromosome recessive mutant "brown" by means of a back-cross with the well-known second-chromosome recessives plexus and speck, one culture was found that produced a total of 96 females, 9 males, and about 80 individuals that were intermediates between males and females.

The "intersexes," which were easily distinguished from males and from females, were large-bodied, coarse-bristled flies with large roughish eyes and scolloped wing-margins. Sex-combs (a male character) were present on the tarsi of the fore-legs. The abdomen was intermediate between male and female in most characteristics. The external genitalia were preponderantly female. The gonads were typically rudimentary ovaries; and spermathecae were present. Not infrequently one gonad was an ovary and the other a testis; or the same gonad might be mainly ovary with a testis budding from its side. The intersexes showed considerable variation, apparently forming a bimodal group — on the one hand a more "female-type," the extreme individuals of which might even lack sex-combs, and, on the other hand, a more "male-type," many of the individuals having large testes and normal male genitalia. All intersexes proved sterile.

Just as striking as the production of intersexes was the fact that the 96 females and 9 males of that same culture showed three, instead of two, large classes representing original combinations, namely, plexus speck, plexus brown, and brown speck. Extensive tests were made of these flies; and each was found to have received from the father a second-chromosome carrying plexus brown and speck, and to have received from the mother one of three different second-chromosomes,

[1] Paper read before the Pacific Division, A.A.A.S., Univ. of Cal., Aug 5, 1921.

namely, a plexus brown, or a plexus speck, or a brown speck chromosome. That is, the mother of the intersexes had carried *three* second-chromosomes, instead of two. For each of the loci plexus, brown and speck she had carried two recessive genes for the mutant character and one wild-type allelomorph, with nearly complete dominance of the wild-type gene in each case.

A condition of triploidy for certain sections of chromosome had been met with in the previous (unpublished) studies on duplications and on translocation; but that this triploidy was far more extensive soon became evident.

The third-chromosome recessive "white-ocelli" had been present in the original culture; and tests of the flies produced by that culture showed that white-ocelli was being distributed in the same abnormal fashion as were plexus brown and speck. Not only were the second- and third-chromosomes involved, but the X-chromosome as well, as was shown by specific tests with sex-linked characters.

The hypothesis that the intersexes were triploid was easily put to test by direct cytological examination. The chromosomes (which were unusually clear and well separated) consisted of two sets of three V's (the two sets differing in the size of the V's), a pair of rods, three or two small round chromosomes, and a J-shaped chromosome or not. That is, all intersexes possessed the second- and the third-chromosomes in triplicate and the X- in duplicate, but they might possess three or two fourth-chromosomes, and have or lack a Y-chromosome, so that four sub-types of intersex constitution were found.

About ten per cent. of the daughters from the original culture, when tested, produced in turn intersexes and further disturbances of the linkage ratios. These females were presumably triploid for all the chromosomes (except the fourth, which might be present in duplicate). It was then discovered that these intersex-producing females could be identified by their somatic characters, which were similar to, but less extreme than, those of the intersexes — namely, large size, coarse bristles, and large roughish eyes. Stocks producing triploids and intersexes were maintained more easily by taking advantage of the fact that triploid females carrying two white and one eosin gene have a pale yellow eye-color lighter than that of their diploid white-eosin sisters, and likewise that the third-chromosome dominant Delta is dominant over two recessive non-Delta genes, but the triploid heterozygote is markedly different from .the diploid heterozygote.

With material from these stocks genetical proof was obtained that the intersex-producing females possess in triplicate the loci for a large variety of first-, second- and third-chromosome genes, and that they might possess fourth-chromosome loci in triplicate or in duplicate. This

genetical finding, checked by cytological examination, extends the direct proof of the chromosome theory of heredity to specific second- and third-group mutant characters and specific V-shaped chromosomes. Such direct proof had already been provided for certain sex-linked mutants and the rod-shaped chromosomes by the phenomena of non-disjunction of the X-chromosomes,[1] and more recently for the small round chromosome and the mutants of the "fourth" group through study of "Diminished" individuals haploid for that chromosome because of non-disjunction.[2]

In the triploid strain individuals triploid for the fourth-chromosome alone have been identified as a distinct somatic type, tested genetically in a variety of ways, and proved to be such by direct cytological examination.

A significant new conclusion proved by the intersexes is that sex in *D. melanogaster* is determined by a balance between the genes contained in the X-chromosome and those contained in the autosomes. It is not the simple possession of two X-chromosomes that makes a female, and of one that makes a male. A preponderance of genes that are in the autosomes tend toward the production of male characters; and the net effect of genes in the X is a tendency to the production of female characters. The ratio of *2X : 2 sets autosomes,* or *3X : 3 sets autosomes* (or 1X : 1 *set autosome?)* produces a female, while *1X : 2 sets autosomes* produces a male. An intermediate ratio, *2X : 3 sets autosomes,* produces an intermediate condition — the intersex. The fourth-chromosome seems to have a disproportionately large share of the total male-producing genes; for there are indications that the triplo-fourth intersexes are preponderantly of the "male-type," while the diplo-fourth intersexes are mainly "female-type."

The condition *3X : 2 sets autosomes* should be "super-females," and *1X : 3 sets autosomes "* super-males." Triploid females produce a small proportion of males that are somatically quite different from males and from intersexes and that are sterile. There is genetical evidence that these males are *1X : 3 sets autosomes* in constitution. Studies of "high non-disjunction" show that triplo-X individuals ordinarily die, but in certain lines they occasionally survive as females that are somatically quite different from diploid or triploid females and that are sterile. Such females occur also in the progeny of triploid females; and, in the case of those produced by non-disjunction, both genetical and cytological proofs of their constitution (*3X : 2 sets autosomes)* are now complete.

---

1 *Genetics*, 1, 1916.

2 In press, Proc. Nat'l Acad.