Aida, T., "On the Inheritance of Color in a Fresh-Water Fish, *Aplocheilus latipes* Temmick and Schlegel, with Special Reference to Sex-Linked Inheritance," *Genetics*, **6**, 554–573 (1921).

"Further Genetical Studies of *Aplocheilus latipes*," *Genetics*, **15**, 1–16 (1930).

"Sex Reversal in *Aplocheilus latipes* and a New Explanation of Sex Differentiation," *Genetics*, **21**, 136–153 (1936).

Bellamy, A. W., "Sex-Linked Inheritance in the Teleost *Platypoecilus maculatus* Günth.," *Anat. Rec.*, **24**, 419–420 (1922).

"Bionomic Studies on Certain Teleosts (Poeciliinae). I," *Genetics*, **9**, 513–529 (1924).

"Bionomic Studies, etc. II. Color Pattern Inheritance and Sex in *Platypoecilus maculatus* Günth.," *Genetics*, **13**, 226–232 (1928).

Fraser and Gordon, "The Genetics of Platypoecilus. II. The Linkage of Two Sex-Linked Characters," *Genetics*, **14**, 160–179 (1929).

Friedman and Gordon, "Chromosome Numbers in Xiphophorin Fishes," *Amer. Nat.*, **68**, 446–455 (1934).

Friess, Else, "Untersuchungen über die Geschlechtsumkehr bei *Xiphophorus helleri* Heckel," *Arch. Entw.-mech.*, **129** 255–355 (1933).

Kosswig, Curt, "Genotypische und Phänotypische Geschlechtsbestimmung bei Zahnkarpfen. V. Ein X (Z)-Chromosom als Y-Chromosom in fremdem Erbgut," *Arch. Entw.-mech.*, **133**, 118–139 (1935).

Winge, O., "On the Occurrence of *XX* Males in Lebistes with Some Remarks on Aida's So-Called 'Non-Disjunctional' Males in Aplocheilus," *Jour. Gen.*, **23**, 69–76 (1930).

"The Experimental Alteration of Sex Chromosomes into Autosomes and Vice Versa as Illustrated by Lebistes, C. R. du Lab. Carlsberg," *Serie Physiol.*, **21**, 1–49 (1934).

[1] The distinction between sex determination and sex differentiation is emphasized here for the reason that it is, as yet, not at all clear to what extent an explanation of the erratic sex ratios appearing in the several species of these fishes is to be sought in connection with determination as such, or with differentiation.

DEVELOPMENT OF EYE COLORS IN DROSOPHILA: TRANSPLANTATION EXPERIMENTS WITH SUPPRESSOR OF VERMILION

BY G. W. BEADLE AND BORIS EPHRUSSI[1]

WILLIAM G. KERCKHOFF LABORATORIES, CALIFORNIA INSTITUTE OF TECHNOLOGY, AND INSTITUT DE BIOLOGIE PHYSICO-CHIMIQUE, PARIS

Communicated August 5, 1936

The vermilion eye color character in *Drosophila melanogaster* has been shown, by studies of mosaics (Sturtevant[2]) and by transplantation experiments (Beadle and Ephrussi[3]), to be dependent on the genetic constitution of parts of the body other than eye tissue. Thus if a vermilion (*v*) eye disc is transplanted to a wild type host, an eye develops which has the pigmentation characteristic of a genetically wild type eye. The recessive mutant suppressor of vermilion (*su-v*, 1–0.0; known not to be a duplication of the *v* locus, Schultz and Bridges[4]) is of such a nature that a fly homozygous for *su-v* and for *v* is but slightly different from wild type in eye color. Since it is clear that a genetically *v* eye can become phenotypically wild type if a diffusible substance which has been called v^+ substance,[3] acts on it, it is of particular interest to determine the characteristics of a suppressed vermilion fly. For example, is the v^+ substance present in such a fly?

By means of the transplantation technique (Ephrussi and Beadle[5]), a series of experiments were made, designed to answer the above and similar questions and to supplement the information obtained by Schultz[6] in studies of mosaics involving *su-v*. Transplantation operations were made on flies in the late larval stage, generally within 12 hours of pupation.[7] In all determinations control transplants were made, e.g., *v* in *v* and *su-v v* in *su-v v* served as controls for *su-v v* in *v* experiments.

In the study of mosaics made by Schultz[6] it was found that a *su-v* w^a *v* (w^a — apricot eye color) sector in an eye of a fly otherwise of the genetic constitution *su-v* w^a *v/v Mn* (*Mn* — Minute bristles) shows w^a *v* pigmentation, that is, under these conditions suppressor of vermilion does not suppress the *v* character in the eye tissue. The first series of experiments described here have to do with this same problem, the pigmentation of a *su-v v* eye when grown in a *v* host. From table 1 it can be seen that an eye disc of the constitution *su-v v* transplanted to a *v* host gives an eye with pigmentation of the *su-v v* phenotype. Under these conditions, then, the pigmentation of the eye is not modified by being grown in a host of a different constitution. The question at once arises as to the cause of the difference in behavior of *su-v* in mosaics and in transplantation experiments—dependent development of pigmentation in mosaics and independent or autonomous development of pigmentation in the transplanted eyes. The experiments of Schultz[6] on mosaics were repeated and confirmed, and the transplantation experiments were made several times so that it is quite clear that there is a real difference. Three possibilities may be suggested to account for this difference: (1) a difference in constitution with respect to genes other than *su-v* and *v* in the two types of experiments, (2) a difference in the time during which the two genetic types of tissue are able to interact and finally (3) a difference in behavior between sectors of eyes (mosaic experiments) and whole eyes (transplantation experiments). Data from experiments made to determine whether the presence of w^a in the implant, or whether w^a in heterozygous condition or *Mn* in the host have anything to do with the difference in results are summarized in table 1. They show that these variations in the genotype of implant and host have no influence on the results. It therefore seems improbable that differences in genetic constitution with respect to genes other than *su-v* and *v* are responsible for the observed difference in behavior. Between the second and third possibilities listed above, there is no satisfactory way of distinguishing from the transplantation experiments. However, Schultz (unpublished[8]) has observed a single mosaic individual of the constitution given above for the mosaic experiments in which one entire eye was presumably of the constitution *su-v* w^a *v*. In this case the phenotypic appearance of the eye was light apricot (not w^a *v*). In this fly the apricot eye was somewhat smaller than normal and for this reason there is some question as to whether it was comparable to the sectors which were w^a *v* in appearance. However, this single individual does favor the view that there is a difference in the behavior of whole eyes and sectors of eyes under the conditions of these experiments. Obviously additional experimental evidence is desirable.

TABLE 1

DATA FROM TRANSPLANTATION EXPERIMENTS INVOLVING *su-v*. UNDER THE HEADING "NUMBER OF INDIVIDUALS" ARE GIVEN THE FOUR SEX COMBINATIONS AND THE TOTAL IN THE FOLLOWING ORDER: FEMALE IN FEMALE, FEMALE IN MALE, MALE IN FEMALE, MALE IN MALE AND TOTAL

IMPLANT	HOST	NUMBER OF INDIVIDUALS	PHENOTYPE OF IMPLANT	PHENOTYPE OF HOST
su-v v	*v*	11, 6, 6, 2; 25	*su-v v*	
su-v w^a *v*	*v*	0, 0, 8, 7; 15	*su-v* w^a *v*	
su-v v	*v* (*Mn*/+)	2, 0, 6, 0; 8	*su-v v*	
su-v w^a *v*	*v* (Mn/+)	0, 0, 4, 0; 4	*su-v* w^a *v*	
su-v v	*v* (w^a/*Mn*)	3, 0, 2, 0; 5	*su-v v*	
su-v w^a *v*	*v* (w^a/*Mn*)	0, 0, 11, 0; 11	*su-v* w^a *v*	
su-v v	+	3, 1, 1, 2; 7	+	
su-v v	*cn*	4, 3, 1, 0; 8	+	
v	*su-v v*	5, 4, 4, 6; 19	slightly darker than *v*	
w^a *v*	*su-v v*	1, 2, 1, 3; 7	w^a (lighter ?)	
v	*su-v* w^a *cv t f*	2, 1, 0, 0; 3	+	
v	*su-v cn*	8, 2, 1, 5; 16	+	
cn	*su-v v*	2, 0, 0, 0; 2	*cn*	
w^a *cn*	*su-v v*	1, 0, 1, 0; 2	darker than w^a *cn*	
su-v w^a *cn*	+	0, 0, 5, 4; 9	w^a (light)	
su-v cn (2 discs)	w^a *v*	1, 0, 1, 2; 4	*cn*	w^a (light)
su-v cn (1 disc)	w^a *v*	8, 4, 12, 2; 26	*cn*	w^a (light)

In comparing *su-v v* and wild type control implants, it was observed that *su-v v* implants differ from wild type implants in the direction of *v*. The difference appears to be more marked in the implanted eyes than in the normal eyes of the two types. Transplants of *su-v v* eye discs grown in wild type hosts (table 1) show that, under these conditions, the *su-v v* discs give rise to eyes with pigmentation like that of wild type. Similarly *su-v v* implants grown in cinnabar (*cn*) hosts show wild type pigmentation. It has been shown previously[3] that a *v* implant grown in a *cn* host gives wild type pigmentation.

The development of *su-v v* eye discs transplanted to *v*, to *cn* and to wild type hosts suggests that a fly of the constitution *su-v v* may be intermediate between vermilion and wild type in the amount of v^+ substance formed, that is, some is formed but less than in a wild type fly. This possibility can be tested by implanting *v* discs in *su-v v* hosts. The results of such experiments are summarized in table 1. It is seen that *v* discs grown in *su-v v* hosts do have their pigmentation slightly modified in the direction of wild type. Similar experiments with w^a *v* implants show a clearer modification of the implants, a result in agreement with independent evidence showing that a w^a *v* implant is a more sensitive detector of a small amount of v^+ substance than is a *v* implant (Ephrussi and Beadle[9]).

It is known[3] that a *cn* eye disc transplanted to a wild type host gives an eye with pigmentation like that of wild type. It is of interest to determine the effect of a *su-v v* host on a *cn* implant. Data in table 1 show that a *cn* implant gives an eye with *cn* pigmentation but that a w^a *cn* eye implant has its pigmentation modified in the direction of w^a (from w^a *cn* toward w^a cn^+). This indicates that a *su-v v* fly produces a small amount of cn^+ substance, enough to produce a detectable effect on w^a *cn* but not sufficient to appreciably modify a *cn* implant.

A series of tests have been made to determine whether *su-v* flies with the normal allelomorph of *v* show any differences, when used as implants or hosts, from flies carrying the normal allelomorph of the *su-v* gene. The results of such tests (table 1) can be summarized as follows:

1. A *su-v* v^+ host has the same effect on a *v* implant as does a straight wild type host (*v* in *su-v* w^a *cv t f* in table 1); the implant shows wild type pigmentation.

2. A *su-v cn* host has the same effect on a *v* implant as does a *cn* host; the implant shows wild type pigmentation.

3. An implant of the constitution *su-v cn* modifies the normal eyes of a w^a *v* host in the same way as does a *cn* implant.[3]

4. A *su-v wa cn* implant develops *wa* pigmentation when grown in a wild type host in the same way as does a w^a *cn* implant.

It can be concluded that, so far as these experiments go, the *su-v* gene in the presence of the normal allelomorph of *v*, results in no change in the fly, that is, *su-v* v^+ is equivalent to $su\text{-}v^+$ v^+ in all the experiments.

In a previous paper[3] a tentative scheme concerned with the relation to each other of three diffusible substances concerned with eye pigmentation was proposed. This scheme assumes that a chain relation of some kind exists. This may be schematized in the following way:

$$ca^+ \text{ substance} \longrightarrow v^+ \text{ substance} \longrightarrow cn^+ \text{ substance}$$

The experiments with *su-v* have a bearing on only the last two steps of this chain. It is assumed that in a *v* fly the step from ca^+ substance to v^+ substance is interrupted and that a *v* fly therefore lacks both v^+ and cn^+ substances. The evidence presented in this paper is consistent with the assumption that the mutation $su\text{-}v^+ \longrightarrow su\text{-}v$ results in a change such that in a *v* fly the step leading from ca^+ substance to v^+ substance is partially restored, that is, a *su-v v* fly has both v^+ and cn^+ substances (presumably in a fly of such a constitution there is no block to the formation of cn^+ substance once v^+ substance is formed) but in reduced amounts as compared with wild type. This interpretation is consistent with the fact that a *su-v v* fly shows pigmentation intermediate between vermilion and wild type. On the basis of the above considerations one should be able to predict the type of pigmentation resulting from the interaction of *su-v* and *cn*. In a *cn* fly the change leading to the formation of cn^+ substance is in some way prevented. The *su-v* gene in the presence of *v* results in a partial restoration of the reaction or reactions leading to the formation of v^+ substance but has nothing to do with the change v^+ substance $\longrightarrow$ cn^+ substance. It should therefore follow that a fly of the constitution *su-v cn* should lack, as does a $su\text{-}v^+$ *cn* fly, cn^+ substance and should therefore show *cn* pigmentation. In order to determine the relation of *su-v* and *cn*, two stocks were made up, one *su-v cn* in constitution, the other *su-v* w^a *cn*. Phenotypically flies of these constitutions appeared to be identical with straight *cn* and w^a *cn* flies. This result is in agreement with the expectation based on the proposed scheme; *su-v* does not suppress the *cn* character.

[1] Fellow of the ROCKEFELLER FOUNDATION.

[2] Sturtevant, A. H., *Proc. VI Int. Cong. Genet.*, **1**, 304 (1932).

[3] Beadle, G. W., and Ephrussi, Boris, *Genetics*, **21**, 225 (1936).

[4] Schultz, J., and Bridges, C. B., *Amer. Nat.*, **66**, 323 (1932).

[5] Ephrussi, Boris, and Beadle, G. W., *Ibid.*, **70**, 218 (1936).

[6] Schultz, J., *Proc. Nat. Acad. Sci.*, **18**, 485 (1932).

[7] The authors are indebted to Mr. C. W. Clancy for assistance in carrying out the experiments reported in this paper.

[8] Schultz, J., Unpublished. The authors wish to thank Dr. J. Schultz for permission to make use of the unpublished information referred to.

[9] Ephrussi, Boris, and Beadle, G. W., *Bull. Biol. Fr. and Belg.*, in press.