

2—a shaft of one diameter long—the angle of twist at a given radius plotted against  $v = z/a$  is practically a straight line from  $v = 0.5$  to  $v = 1.5$ . That is, the influence of the terminal moments extends only about half a radius from the ends. The total angle of twist comes out to be about 5% more than the value predicted by the simple formula. For a very long shaft the effect of the non-linear distribution of the stresses at the ends disappears at a distance of about one radius. Note that  $B_n = -1$  for large  $k$ ; then for large  $v$ , (15) reduces to its first term.

This discussion has been limited to terminal loads having circular symmetry about the shaft axis  $z$ . It has shown that a non-linear symmetrical stress distribution at the ends does not change the linear relation *derived* by Saint-Venant and *assumed* by engineers. It is reasonable to infer that any type of distribution, symmetrical or not, will also be without appreciable influence.

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### TRANSPLANTATION IN *DROSOPHILA*<sup>1</sup>

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The application of the method of transplantation, which has been so fruitful in the study of many biological problems, to genetically well known material, has advantages which are at once apparent to those who have thought about questions concerning the relation of genes to the developmental process. In this communication we wish to present, in a preliminary way, certain results obtained by the use of a technic which we have developed specifically for the transplantation of organs of *Drosophila*.

In short, this technic consists of the injection of the desired organ into the body cavity of the host by means of a specially designed glass micropipette. This pipette is used in the pipette-holder and with the syringe and metal capillary tube of the Chambers' micro-injection apparatus. The operation is carried out free-hand under a dissecting microscope. In practice, two persons cooperate using two dissecting microscopes, one inclined, arranged so that their fields coincide.

By means of this technic we have successfully transplanted larval ovaries as well as imaginal discs of eyes, antennae, wings and legs. In all cases we have used as hosts, flies in the larval stages. In particular cases, organs taken from pupae have been implanted in larvae. The transplantations can be made rapidly and a sufficient number of individuals

having the implanted organ reach maturity to make the technic efficient for experimental work.

Following Sturtevant's work<sup>2</sup> on the differentiation of vermilion eye color in elimination mosaics of *D. simulans* in which he showed that the gonads play a part, we were led to try transplants of larval ovaries in *D. melanogaster*. It was found, on dissection, that such implanted ovaries grow and differentiate normally. In preliminary breeding tests it was found that functional connections of the implanted ovary with a host oviduct may be established. A series of transplantations of ovaries were then made to determine (1) the frequency with which implanted ovaries differentiate and (2) the frequency with which functional connections are established. The results with regard to the frequency of differentiation, as determined by dissection of adults, are as follows:

NUMBER OF OVARIES IMPLANTED	SEX OF THE HOST	NUMBER OF OVARIES OBSERVED	NUMBER OF INDIVIDUALS
1	Female	1	2
		2	22
		3	57
	Male	0	2
		1	16
2	Female	3	2
		4	4
	Male	1	1
		2	2
3	Female	5	2

Considering only those cases in which one ovary was implanted, it is seen that of 99 adults, 73 had the implanted organ developed and differentiated.

In order to determine the frequency with which functional connections of the implanted ovary were established, ovaries of one genetic constitution were implanted in hosts which differed by at least one gene (homozygous in both cases). By mating to males recessive for this gene, the progeny coming from the implanted ovary were easily distinguished from those coming from a host ovary. Of females with one supernumerary ovary, progeny were obtained from 44. In 20 of these cases part of the progeny came from eggs originating in the implanted ovary. This shows clearly that an implanted ovary can compete with the normal ovaries in becoming attached to the genital ducts. On dissection it was found that two ovaries were attached and the third unattached to the oviducts. Hence it is clear that in the 20 cases in which fertile eggs were obtained from the implant, a normal ovary had been replaced. If the attachment of two of the three ovaries were a simple matter of chance, the implanted ovary would be expected to become attached in 67 per cent of the cases. It is not surprising that this frequency is not realized considering the several factors

which might put the implanted ovary at a disadvantage. In addition to the 20 cases of functional attachment mentioned above, there were 3 cases of functional attachment in which dissection showed only two ovaries. In one of these the dissection was somewhat questionable. In the other two we must assume that a normal ovary was completely replaced by the implanted one, probably because of injury to a normal ovary during the operation.

We have made a small experiment to see if *D. simulans* ovaries are able to differentiate and become attached when implanted in *D. melanogaster* hosts. Four melanogaster females in which simulans ovaries had been implanted were tested by mating to melanogaster males (genetic markers used as above) and all showed simulans-melanogaster hybrids among their progeny.

The possible uses to which this method of transplanting ovaries can be put are obviously several, among them (1) the production of interspecific hybrids where psychological or mechanical difficulties in mating prevent making them in the ordinary way, (2) the study of cases of intra- and inter-specific sterility (the work of Bytinski-Salz<sup>3</sup> on *Celerio* species is a good example of this), (3) the more precise definition of the characteristics of cases of maternal inheritance and (4) the study of the part played by gonads in various physiological processes such as, for example, in the case referred to above, the differentiation of eye colors (Caspari's work<sup>4</sup> on transplantation of testicles in *Ephestia* provides an example of this).

Our most extensive series of studies of transplants have been concerned with eye color differentiation. We have investigated in a preliminary way most of the eye color mutants known in *D. melanogaster*. We have also shown that successful eye transplants can be made between species as different as *D. melanogaster* and *D. funebris*. In this report we can give only examples to illustrate the kind of studies that are being made.

Most of the eye transplants made have been between larvae at a stage of development shortly before pupation. Optic imaginal discs, with or without the antennal discs with which they are attached at this stage, are implanted into the body cavities of host larvae. In this position they grow and differentiate normally except that at maturity the implanted eyes are inverted, i.e., the curvature is reversed, the facets being on the inside, the pigment cells on the convex surface. (Failure of evagination of implanted imaginal discs has been observed in the case of legs and is probably characteristic of implanted wings as well.) That pigment differentiation, which is what we have been most interested in, is normal, is shown by many "control" transplants, i.e., eye discs of a given constitution implanted in hosts of the same constitution.

Our experiments on eye transplants have confirmed the conclusions drawn from studies of spontaneous mosaics<sup>5</sup> in that most eye transplants

are auto-differentiating with respect to pigmentation, i.e., they show the pigmentation characteristic of development in their normal tissue environment. Sturtevant has shown that vermilion eye color is, under certain conditions, not autonomous in its development in mosaics. In transplants it is likewise not autonomous; a vermilion (*v*) eye implanted in a wild type host develops the pigmentation characteristic of wild type.<sup>6</sup> By means of transplantation we have been able to study many combinations not easily obtained in natural mosaics and in this way have found that cinnabar (*cn*), an eye color phenotypically similar to vermilion, is not autonomous in its pigment differentiation. Two other eye color mutants, scarlet (*st*) and cardinal (*cd*) likewise phenotypically similar to vermilion, are, however, completely autonomous in their pigment development in all the combinations in which we have studied them. In the case of *v* or *cn* eyes implanted in a wild type host, there is obviously some kind of "host-implant influence" leading to a change in the reactions concerned in pigment formation. In a previous communication<sup>7</sup> we have considered the question of the relation of the *v* and *cn* host-implant influences. Briefly, we have shown that a *v* disc in a *cn* host gives a wild type eye, but that a *cn* disc in a *v* host gives a *cn* eye. From this it is clear that the host-implant influences in the two cases are not the same. But at the same time it is evident that we are not dealing with two independent influences, one controlled by the *v* gene, the other by the *cn* gene, for, if such were the case, the reciprocal transplants should give similar results, wild type in each case.

Given the behavior of *v* and *cn* implants in a wild type host, we have available a means of testing other mutants for the presence or absence of the two host-implant influences mentioned above. Thus by implanting a *v* eye disc in a host homozygous for another eye color mutant, we can determine whether or not this mutant is characterized by the presence or absence of the *v* host-implant influence. In a similar way, a test for the *cn* host-implant influence can be made. In this way we have been able to show that when a *v* eye is implanted in certain hosts (eye color mutants), *v* is autonomous in development. In all such cases studied so far, *v* and *cn* implants behave in the same way, for example, in a claret (*ca*) host, both *v* and *cn* implants are autonomous, in *st* or *cd* hosts they are both modified to wild type. This corroborates the conclusion drawn from reciprocal transplants between *v* and *cn* in indicating that the *v* and *cn* host-implant influences are genetically—and presumably chemically—closely related. At the same time these studies lead one to the conclusion, *a priori* probable, that the autonomous or non-autonomous nature of a given character in transplants is not necessarily an inherent property of the gene differentiating that character but may be determined by the genetic nature of the tissue environment. Other experiments show that

the genetic constitution of the implant itself as well as the relative stages of development of implant and host may also influence this property of autonomy or non-autonomy of the implant.

As a concluding example, we shall mention briefly, experiments made to establish the time in development at which vermilion pigmentation is irreversibly determined, i.e., after which a vermilion eye disc implanted in a wild type host will no longer give wild type pigmentation. By implanting eye discs from *v* pupae of successively older stages in wild type larvae almost ready to pupate (this procedure was used because of technical difficulties in implanting eye discs in pupae), it was shown that the characteristic host-implant influence operates, under these conditions, until very late stages, until about 48 hours after the formation of a puparium (at 25°C.). Shortly after this time, actual pigment can be seen in the eye.

Details of the above-mentioned experiments, as well as a description of the technic, will be published elsewhere.

<sup>1</sup> The work on which this report is based was done at the Institut de Biologie physico-chimique, Paris.

<sup>2</sup> Sturtevant, A. H., *Proc. VI Int. Cong. Genet.*, 1, 304 (1932).

<sup>3</sup> Bytinski-Salz, H., *Arch. f. Entw.-mech.*, 129, 356 (1933).

<sup>4</sup> Caspari, E., *Ibid.*, 130, 353 (1933).

<sup>5</sup> Morgan, T. H., Bridges, C. B., and Sturtevant, A. H., *Bibliog. Genet.*, 2, 1 (1925).

<sup>6</sup> Ephrussi, Boris, and Beadle, G. W., *Comptes rendus acad. sci.*, 201, 98 (1935).

<sup>7</sup> Beadle, G. W., and Ephrussi, Boris, *Ibid.*, 201, 620 (1935).

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## THE TEMPERATURE-EFFECTIVE PERIOD OF THE SCUTE-1 PHENOTYPE

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*Introduction.*—The recently published papers of Child<sup>1</sup> have shown that for temperatures ranging from 14 to 31°C. there exists a temperature-effective period for the scute-1 phenotype which lies entirely within the latter half of the third larval instar period, when a mass of flies is concerned. For all bristles of the scute pattern, and at all temperatures tested, the effective period occupies the same relative position in the developmental period; and it is apparently restricted to the period between 89.3 and 96.8% of egg-larval development for any individual fly.

The study reported here is likewise on the temperature-effective period