THE INHERITANCE OF A FLUCTUATING CHARACTER.

By T H. MORGAN and CALVIN B. BRIDGES.

(From the Department of Zoology, Columbia University, New York, and the Carnegie Institution of Washington.)

(Received for publication, May 23, 1919.)

In the fall of 1909 Morgan observed that the trident-pattern on the thorax of flies of some of the wild stocks of *Drosophila melanogaster* varied both in the intensity of the pigmentation and in the extent to which the pattern was spread over the thorax. The degree of pigmentation and the extent of the pattern seemed to vary together. A scale of grades was devised (Fig. 1) by means of which it was possible to describe rather accurately the different populations dealt with. Thus, Table I and Curve *a* give the distribution of individuals in "Falmouth" wild stock (October, 1911).

Morgan selected throughout the fall and winter of 1909–10 for increased trident-pattern, with no certain progress until January, 1910, when a few flies were found that were considerably darker than any hitherto observed. By breeding from these darker flies a race was quickly obtained which showed no individuals as low in grade as those in Classes I and II and very few in Class III. This stock was called "with" and mass selection in it was continued for about a year (thirty generations) with no apparent result further than possibly to decrease the numbers in the lower grades. It seems clear that the various grades observed in the stock prior to January, 1910 were merely the normal fluctuations of the wild type pattern, and that a definite mutation had then occurred which gave rise to higher grades and a characteristic new distribution. A census taken of this new "with" mutant population (October, 1911) revealed the condition shown in Table I, and by Curve *b*, Fig. 2. The most numerous class in the "with" stock was VII, which was not represented at all among the wild flies.

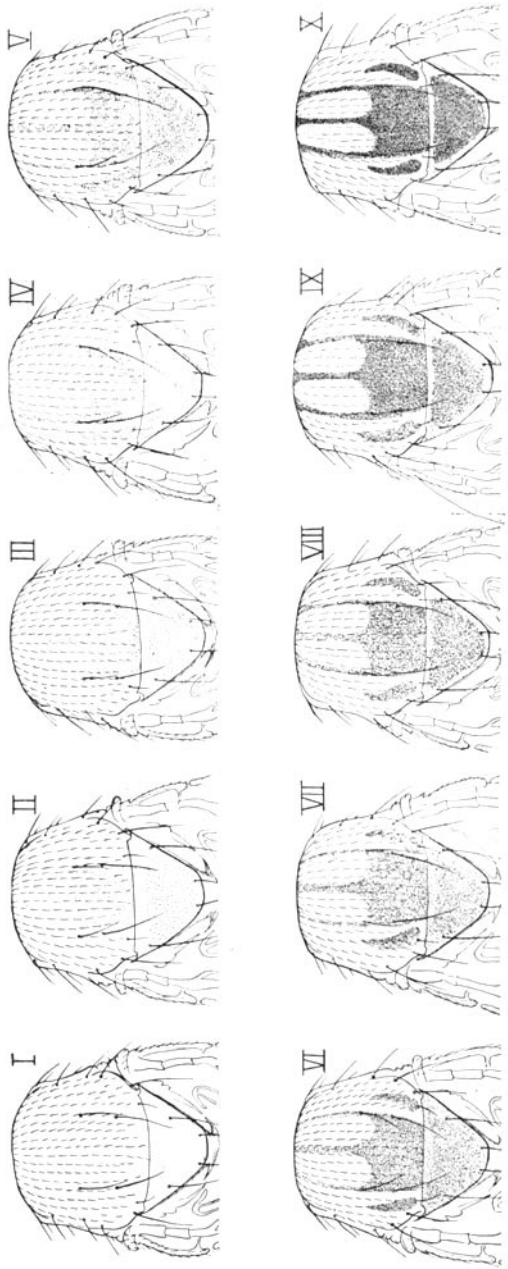

FIG. 1. The scale of grades of the trident-pattern "with."

TABLE I.

Grades of the Trident-Pattern "With" in Various Stocks and Experiments.

Stock or experiment.		"Falmouth" wild stock.		"With" stock.		F_1 "Falmouth" × "with."		F_2 "Falmouth" × "with."		F_2 expectation.	"Super-with" stock.	
		No. of flies.	Per cent.	No. of flies.	Per cent.	No. of flies.	Per cent.	No. of flies.	Per cent.	Per cent.	No. of flies.	Per cent.
Grades of "with" trident-pattern.	I	180	11.1	—	—	32	1.2	118	3.8	3.4	—	—
	II	585	36.3	—	—	393	15.2	621	20.0	16.7	—	—
	III	442	27.4	—	—	697	26.9	773	24.9	20.3	—	—
	IV	275	17.0	365	13.3	700	27.1	578	18.7	21.1	—	—
	V	106	6.6	398	21.8	519	20.1	432	14.0	17.2	—	—
	VI	26	1.6	729	26.6	218	8.4	313	10.1	11.2	—	—
	VII	—	—	773	28.3	28	1.1	233	7.5	7.6	53	18.1
	VIII	—	—	273	10.0	—	—	32	1.0	2.5	65	22.3
	IX	—	—	—	—	—	—	—	—	—	70	24.0
	X	—	—	—	—	—	—	—	—	—	104	35.6
Total.....		1,614		2,538		2,587		3,100			292	

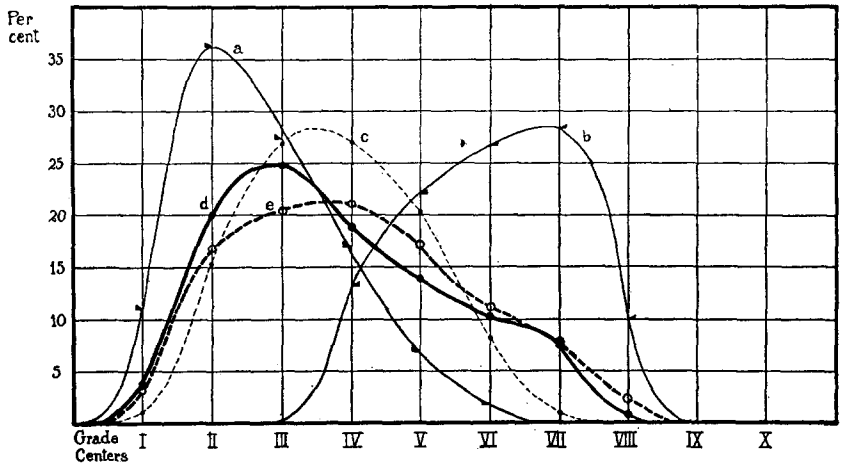

FIG. 2. Curves representing the distribution of grades of the trident-pattern "with" in various stocks and experiments. Curve *a* = "Falmouth" wild stock, *b* = "with" stock, *c* = F_1 from "Falmouth" × "with," *d* = F_2 from "Falmouth" × "with," *e* = expected F_2 as calculated from the observed distributions in the parental stocks and F_1. The curves were drawn free-hand to conform to the plotted points.

The F_1 Result of the Cross between "With" and the Wild Stock.

The above classifications were made preparatory to a cross between these two lines. The F_1 flies from the cross of "without" wild flies to "with" flies of the mutant stock were in the main intermediate in grade between the two parental types (Table I, and Curve *c*, Fig. 2). The mode of the F_1 was at Grade IV. There were very few flies that did not show a faint pattern (Grade I = 1.2 per cent). At the other extreme there were no flies that were as dark as Grade VIII and only a very few (1.1 per cent) as dark as Grade VII. A comparison of the F_1 distribution with that of each parent (Fig. 2) shows that, as judged by the means, modes, and extent of overlap, the F_1 population resembles the wild parent more closely than the "with" parent. "With" is classified as a "partial" dominant since it is known to be the mutant type and the F_1 flies show considerable effect of the "with" gene.

The F_2 from the Cross of "With" to Wild.

The F_2 results (Table I, Curve *d*, Fig. 2) gave a range of grades that included the faintest "withouts" of the wild grandparent and the darkest "with" of the other grandparent. In shape the F_2 curve presented its main mode at Grade III and an indication of another mode at Grade VII. If our assumption is correct that the "with" stock differed from the wild because of a single mutant difference, the F_2 population should be composite, one quarter being like the wild parent, one quarter like the "with" parent, and two quarters like the F_1 type. On this basis an expectation for the F_2 that should result from the given P_1 stocks and the known F_1 distribution, can be readily calculated (Table I).

The curves of Fig. 2 show that the observed F_2 result (Curve *d*) is in good accord with the expectation (Curve *e*). The observed F_2 differed from that calculated in that there was slightly too great a proportion in Grade VII (which corresponds to the mode of the "with" stock) and also a similar excess in Grades II and III (which corresponds to the bulk of the wild stock).

It should be noted that had "contamination of genes" been acting, the F_2 should have deviated from the calculated F_2 in the direction

of the F_1 result, so that the curve of the observed F_2 should have lain between the calculated F_2 curve and the F_1 curve. Instead of this the actual deviations were mainly in the opposite direction.

Chromosome Carrying "With."

That the gene for "with" is situated in the third chromosome was determined by means of the F_2 of the cross of pink by "with," which produced no pinks that were surely "with" (higher grades) or, conversely, no sure "withs" that were pink. The higher grades of "with" are the homozygates and the ratio was thus comparable with the 2:1:1:0 ratio ordinarily observed in "repulsion," crosses between two recessives whose genes are carried by the same chromosome.

"Super-With."

The "with" stock used in the preceding experiments had just undergone somewhat over a year of mass selection with little or no observable progress. However, after a few months of selections, decided progress had been obtained in a sister line. A certain culture (E, November, 1910) was seen to contain individuals of still darker grades (IX and X) and selection soon established a "super-with" population. This E line then proved as immovable as before, although selection was practiced continually. At the end of twenty-three more generations a census of this line (September, 1911) showed the condition in Table I. This stock was lost before tests were carried out, but we can judge from its sudden manner of origin and subsequent stability that a second mutation had occurred. Whether this second mutation ("super-with") was a modifier of "with" or an allelomorph of "with" was not determined.