ness nor even as being involved in any way in the mechanism of sex determination.

[1] Sturtevant, A. H., *Genetics*, **6**, 179–207 (1921).
[2] Lebedeff, G. A., *Proc. Nat. Acad. Sci.*, **20**, 613–616 (1934).
[3] Lebedeff, G. A., *Ibid.*, **24**, 165–172 (1938).
[4] Lebedeff, G. A., *Genetics*, **24**, 553–586 (1939).
[5] Sturtevant, A. H., and Dobzhansky, Th., *Ibid.*, **21**, 473–490 (1936).
[6] Dobzhansky, Th., *Bull. Bureau Genetics*, Leningrad, **8**, 91–158 (1930).
[7] Dobzhansky, Th., *Arch. Entw. Mech.*, **123**, 719–746 (1931).
[8] Stern, C., and Hadorn, E., *Genetics*, **24**, 162–179 (1939).
[9] Dobzhansky, Th., and Schultz, J., *Jour. Genetics*, **28**, 349–386 (1934).
[10] Goldschmidt, R., *Jour. Genetics*, **31**, 145–153 (1935).
[11] Bedichek Pipkin, S., *Univ. Texas Publ.*, **4032**, 126–156 (1940).
[12] Goldschmidt, R., *The Material Basis of Evolution*, New Haven (1940).

THE ORIGIN OF JERKER, A NEW GENE MUTATION OF THE HOUSE MOUSE, AND LINKAGE STUDIES MADE WITH IT

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In June, 1938, a woman who raises mice for her own amusement brought to one of us (Grüneberg) a dancing adult female mouse which had been given to her by a schoolboy. The mouse was of the *Mus musculus* type and not appropriate to keep with her waltzers which were *Mus bactrianus*. It was, however, pregnant, she claimed, by one of her genuine Japanese waltzers, yet the litter consisted of three perfectly normal animals, thereby indicating that the mutation was distinct from waltzing.

Such a genetic test was apparently the only way to distinguish waltzers and jerkers, as the new mutation was named. The age of onset of the jerker characteristics is about 11 or 12 days. At this age signs of poor balance, shaking the head and traveling in a circle become visible, but not until the animal's eyes are open and they become more active at 14 days can the jerker animals be distinguished from the normals with certainty. One good way to tell is to hold the animal by the tail just off the table. The jerkers twist and turn their whole bodies while normals stretch out and try to reach the surface beneath. So far as we could tell, jerkers also are stone-deaf as they show no reaction to a sharp metallic click as do normals—a fact which suggests that the inner ear is abnormal in some way. The jerkers whirl in both directions, shake their heads and back up instead of running ahead. Often the adults when aroused leap and twist about in

somersaults much as waltzers do. The animals breed poorly chiefly because the mothers do not nurse well. In all these respects the new mutation resembles waltzing and the shaker mutations. Accordingly crosses were carried out to test the individuality of the mutation and also its linkage relations. These crosses are described below and the actual data are given in table 1.

In the first place, in order to distinguish the new mutation from other similar ones, a homozygous jerker animal was crossed with waltzers again and with shaker-2 animals. No offspring exhibiting any kind of dancing abnormalities resulted from these crosses. Three different waltzing (*vv*)

TABLE 1

TABLE OF LINKAGE DATA AND CROSSOVER PERCENTAGES OF JERKER GENE

GENE	MATING	*Xje*	*xJe*	*Xje*	*xje*	NO. MICE	CROSSOVER PERCENTAGE
a	F_2 repulsion	37	21	16	6	80	44.2 ± 8.8
	MC repulsion	58	60	17	16	151	48.5 ± 8.7
b	F_2 repulsion	55	17	15	2	89	38.3 ± 7.8
	F_2 coupling	29	12	10	5	56	47.3 ± 9.6
c	F_2 coupling	12	9	5	3	29	24.4 ± 9.4
Ca	*BC* to *jejecaca* coupling	31	33	36	21	121	57.0 ± 4.6
d se	F_2 repulsion	146	46	45	9	246	43.6 ± 5.1
f	*BC* to *JeJeff* repulsion	17	4	14	5	40	55.0 ± 7.9
ln	*BC* to *JeJelnln* repulsion	9	9	17	10	45	42.2 ± 7.9
p	F_2 repulsion	149	42	39	12	242	51.2 ± 4.8
Re	*BC* coupling	18	20	15	15	68	51.5 ± 6.1
s	*BC* to *JeJess* repulsion	9	9	21	6	45	33.3 ± 7.5
	F_2 coupling	132	40	43	14	229	49.0 ± 4.9
sh-2	*BC* to *JeJesh-2sh-2*	15	6	13	6	40	47.5 ± 7.9
T^1	*BC* to *jejett* coupling	2	47	2	51	102	
v	*BC* to *JeJevv* repulsion	12	6	18	9	45	46.7 ± 7.5
W	*BC* to *jejeww* coupling	20	41	26	34	121	55.4 ± 7.5
wa-1	*BC* to *JeJewa-1wa-1* repulsion	7	11	14	13	45	44.4 ± 7.5
wa-2	*BC* to *JeJewa-2wa-2* repulsion	13	8	11	8	40	52.5 ± 7.9

mothers produced 12 normal young; 4 different shaker-2 mothers (*sh-2 sh-2*) produced 18 normal young, thus definitely establishing the jerker mutation as distinct from *v* and *sh-2*. In a cross with pink-eye (*p*) and albinism (*c*) in later tests, the jerker gene showed no linkage with these two characters, and hence cannot be identical with shaker-1 which is linked with both of these.

When the mutation was thus definitely known to be at a new locus, linkage tests were carried out against as many of the known chromosome markers as were available at the Jackson Laboratory. These markers included all the known linkage groups except *r si* and all the known single genes except *dw* and *hy-1*. This meant that out of a possible sixteen markers, thirteen were tested.

The genes used in these crosses are carried at the Jackson Laboratory in four stocks of mice. In the first of these, the *P* stock, inbred for twenty generations, occur five recessive genes *a*, *b*, *p*, *d*, *se*, the last two being very closely linked. The straight F_2 ratio had to be used in this case since the recessive necessary for a backcross of all the genes would be very hard to obtain, and using one gene at a time to backcross would nullify the value of the stock. The plan was simply to cross the *XXjeje* male with the *xxJeJe* females giving the double heterozygote *XxJeje*. This F_1 when interbred would give the normal 9:3:3:1 phenotypic ratio in the F_2 population if no linkage existed. The jerker males used in this cross happened to be heterozygous for *a* and the data had to be separated into two classes, according to the F_1 animals. Some of these would be the double heterozygotes; others would be homozygous for non-agouti. In the latter case the F_2 generation forms the same phenotypes as the straight F_2 but in the ratio of 3:3:1:1 and only the 1:1 classes can be used in determining the crossover genotypes. We have called this a "mixed backcross," abbreviated *MC*. As can be seen from the data in the table, *je* is not linked with any of these genes.

In another stock of mice, three dominant mutations are carried: caracul coat (*Ca*), dominant spotting (*W*) and fused (T^f). To test for these the straight backcross of the multiple heterozygote to the multiple recessive was used, giving a 1:1:1:1 ratio. Unfortunately the fused-tail character showed up in only four animals because of overlapping in this particular stock. This cross should be repeated.

The remainder of the genes *wa-1*, *wa-2*, *s*, *ln*, *f*, *v*, *sh-2* and *w*, all recessives, are carried in two stocks of mice. The same plan was used in each case. It is difficult or impossible to distinguish *v* and *sh-2* phenotypically from jerker. Hence the back-cross animals had to be tested genetically. The plan of the cross:

		JERKER	×	STOCK MICE	
		jejeXX		*JeJexx*	
F_1		*JejeXx*	×	*JeJexx*	
BC	*JeJeXx*	*JeJexx*		*JejeXx*	*Jejexx*

This is essentially the cross described by Castle[1] for testing the linkage between lethal genes.

About 50 back-cross females were outcrossed with jerker animals to determine whether they were homozygous *JeJe* or heterozygous *Jeje*. About one-fifth of these animals failed to nurse their litters due to an overdose of detrimental mutations. In the case of homozygous animals, 7 normal offspring were considered proof of the *JeJe* formula. Here as before no linkage was apparent.

One more character, rex (*Re*), was tested with negative results for linkage with Jerker. The straight backcross of the double heterozygote to the double recessive was used.

From these data we may conclude that no linkage exists with any of the characters tested, except that the data with respect to the *T* locus are inconclusive. Very likely, then, the jerker mutation can be used to mark a different chromosome. *Dw, hy-1* and the linkage group *r si* are the only markers as yet untested. Unless one of these should show linkage with *je*, a new chromosome marker will be established.

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[1] Castle, W. E., *Proc. Nat. Acad. Sci.* **25**, 593–594 (1939).

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*GENIC EFFECTS ON SERUM PROTEINS**

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A previous report[1] from this laboratory has described the segregation of one or more so-called *species-specific* components of the serum proteins of Pearlneck (*Streptopelia chinensis*), following backcrosses to Ring dove (*St. risoria*) of species hybrids and back-cross hybrids from the mating of Pearlneck and Ring dove. Further, two back-cross individuals, obtained by mating to Ring dove hybrids of pigeon and Ring dove, have been shown to possess in their respective sera at least one antigen specific for pigeon, qualitatively different from that in the serum of the other.[2] Complete references to related investigations may be found in the bibliographies of the earlier reports.[1, 2, 6]

These findings are in accordance with the results of investigations of the segregation of cellular antigens in the erythrocytes of several dove and pigeon species and their hybrids and back-cross hybrids, which gave evidence of genic influence on the antigens of the red blood cells.[3–5] However, the genes, affecting the species-specific cellular antigens in the Pearlneck and pigeon, respectively, appear to be independent in action from those affecting the species-specific antigens of the serum.[1, 2]

The present paper submits corroborative evidence of the earlier findings. In this series of tests, the species involved were the Pearlneck and the Sene-