

parthenogenesis, females from fertilized eggs, has been "the outstanding unsolved puzzle, although before the development of the idea of genic balance it seemed one of the clearest and simplest of cases."<sup>1</sup> Neither genetic nor cytologic work has hitherto been able to solve the problem, although demonstration of the diploid nature of biparental males of *Habrobracon*<sup>2</sup> made it clear that the explanation was not to be sought in chromosome number.

On the basis of study of feminization of genitalia in mosaic males of *Habrobracon*, the suggestion was made that there are two kinds of haploid male tissue (X + A and Y + A) and correspondingly two different types of haploid males differing in sex-determining factors. The X-chromosome contained one or more dominant factors and one or more recessives (F.g), while the Y contained the allelomorphs (f.g). It was postulated that the female was the double dominant (1X + 1Y + 2A) and was digametic, producing from unfertilized eggs the two types of haploid males. Fertilization of eggs would give rise to females or to biparental males, the latter being 2X + 2A or 2Y + 2A, according to the type of sperm entering the egg. Such a hypothesis is consistent with the principle of genic balance.

All fertilized eggs from one mating would be entered by the same type of sperm, X + A, for example, but there would be two kinds of reduced egg nuclei present, X + A and Y + A. It might then be expected that homoeosyngamy, fusion of X + A with X + A, would be as frequent as heterosyngamy, fusion of X + A with Y + A. Extensive studies on ratios of males among biparentals and of biparentals among total offspring, as well as correlated investigations of egg hatchability indicate that selective syngamy takes place: the sperm nucleus uniting with the unlike egg nucleus to produce a female. Heterosyngamy always occurs when parents are unrelated, for all biparentals from such crosses are females. If parents are related, however, a few biparental males appear because of occasional homoeosyngamy. Frequency of males among biparentals, varying according to genetic constitution of stocks and temperatural conditions, is inversely correlated with ratio of total biparental offspring (males and females) and with hatchability of fertilized eggs. Thus it appears that fusion of like gametes has a lethal effect, but that a few combinations are viable, resulting in diploid males.

The theory, which was tentatively advanced a short time ago,<sup>3</sup> needed confirmation such as might be obtained from a sex-linked trait. A number of linkage

groups were therefore tested by back-crossing heterozygous females to their recessive father. Dominant and recessive F<sub>2</sub> males should appear in equal numbers, except for viability differences, but in case of complete sex-linkage there should be no recessive females. If there were crossing-over between the sex-determining region and the gene in question a minority of the recessive females should be found varying according to the strength of the linkage. Another recessive male crossed with the F<sub>1</sub> heterozygous females should, if he were like the father (X + A for example), sire a minority of recessives, but if he were of the opposite type (Y + A) the recessive daughters should be in corresponding majority.

Dominant and recessive females have appeared in approximately equal numbers for several genes tested, but for fused (affecting antennae, tarsi and wings) the recessives were in decided minority among the females resulting from the back-cross, although their fused brothers appeared in expected numbers. Different fused males have been crossed to heterozygous females from the same fraternity. Some males give a marked excess of wild-type daughters while others give a marked excess of fused. No one male produces the two different types of fraternities by different heterozygous females belonging to the same fraternity. Wild-type crossovers average 8.7 per cent., while fused crossovers average 3.8 per cent., a difference expected on account of viability.

It was to be expected that sex-linkage would be incomplete, since all linkage groups thus far found have shown crossing-over. Two other genes have been found loosely linked with fused. These are being tested for sex-linkage.

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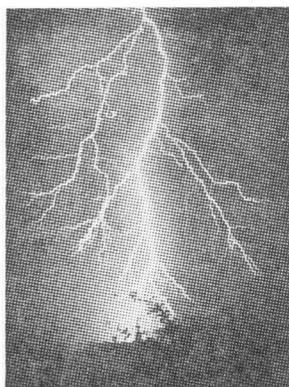
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<sup>1</sup> C. B. Bridges, *Amer. Nat.*, 59: 134, 1925.

<sup>2</sup> Magnhild M. Torvik, *Proc. Penna. Acad. Sci.*, 7: 119, 1933.

<sup>3</sup> P. W. Whiting, *The Collecting Net*, Woods Hole, 8: 11, and *Biol. Bull.*, 65: 357, 1933.



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