VII. UNILATERAL INHERITANCE IN BRUCHUS

J. K. Breitenbecher

From the Zoological Laboratory of the University of Oklahoma. Contribution No. 33, Second Series.

Any person who has observed living things knows that there exists in nearly every animal as well as in man a harmonious relation of functions due to a duplication of structures. Almost every animal manifests symmetry and nearly all are bilaterally symmetrical with the exception of Echinoderms which show a radical type adapted from a bilateral. Bilateral symmetry is found in all vertebrates and nearly all invertebrates. Often, however, one discovers a few organs which are asymmetrical such as the heart, pancreas, etc., i.e., all organs do not manifest symmetry.

In Bruchus, the insect which we use for our studies, bilateral symmetry is manifested by duplication of appendages, wings, and other structure, as well as spots, patterns, and colors. Bruchus has two black spots bilaterally located on each elytrum. From this culture there appeared on October 23, 1922, an abnormal female insect having a right elytrum red spotted, instead of the usual black spots. The first thought was that this unilateral character was a mosaic and due to a somatic mutation. But the offspring from this mosaic proved that the character was inherited, and it is the object of this paper to discuss briefly the problem concerned.

Symmetry has always been a question for scientific debate. Prof. Child whose idol is the "axial gradient theory" maintains that symmetry is determined by differences in metabolic rates. That region of the reproductive cell or part of an organism having the highest rate of metabolism becomes the animal pole. As this rate decreases posteriorly development continues in that direction until polarity is determined. He believes that differences in a metabolic gradient toward the periphery causes bilaterality. In contrast to this idea nearly all embryologists interpret polarity as being pre-shadowed in the cytoplasm of the egg previous to fertilization. This is no doubt true for Bruchus since all insects manifest polarity while the eggs are still in the ovary.

In the frog, as in all animals, bilateral symmetry appears soon after fertilization. Certain animals, especially snails, show a reversion from the normal type of symmetry. In Bruchus we also discover that the asymmetrical trait under our observation may be the reverse from normal due possibly to a different mutation.
In snails the inverse type of symmetry is termed sinistral and the normal dextral. The internal organs of animals, including man, may rarely show a complete reversal such as heart, liver, and the like. Conklin with reference to the question of cytoplasm and chromosomes writes, "There is evidence that the chromosomes of the egg and sperm are the seat of the differential factors or determiners for Mendelian characters, while the general polarity, symmetry, and pattern of the embryo are determined by the cytoplasm of the egg," (Conklin, E. C., Heredity and Environment, 1916, 2nd edition, Princeton Press). Loeb, relative to a similar question writes, "The facts of experimental embryology strongly indicate the possibility that the cytoplasm of the egg is the future embryo (in the rough) and that the Mendelian factors only impress the individual (and variety) characters upon this rough block" (Loeb, J., The Organism as a Whole, 1916, G. P. Putman's Sons.)

The experimental embryologist has maintained, since development of an egg-nucleus plus some of its cytoplasm may be stimulated with the aid of the sperm and, since the sperm alone can not be made to develop by any such manner except with the cytoplasm of the egg, that the cytoplasm of the egg is essential for development. These are in general the evidences against the chromosome mechanism as being the determiners of development. In contrast to this the writer wishes to set his own results with Bruchus, and to list from other sources, evidences in favor of the chromosome mechanism.

The first fact to which I wish to call your attention is that the nucleus plus cytoplasm is necessary for any development. The cytoplasm alone unless it has a male or female nucleus, can not be made to develop. The only conclusion possible from such an argument is that chromosomes and cytoplasm are essential. Cytoplasm may be necessary as a food supply in furnishing possibly, the liberated enzymes given off by the genes, which may be the essential stimulus for development.

Another type of evidence is used by Loeb as leading to the belief that cytoplasm determines polarity, while the Mendelian factors simply shape structures. By puncturing the eggs of frogs with a fine needle, Loeb produced seven parthenogenetic adult male frogs. These males were not unlike the normal males produced by the stimulus of spermatozoon. Bilateral symmetry was evident; this however, is no disproof for the chromosome pair, one chromosome, could carry all genes necessary. Further, the fact that these frogs were all males having only one X-chromosome is also added proof of the determination of symmetry by the chromo-
osome mechanism; likewise the behavior of chromosomes in hymenopteron insects; and again dominant genes are added evidence that one chromosome is all that is essential for development and symmetry. A mono!ome organism instead of one with homologous chromosomes would always breed true for every character.

The usefulness of bilateral symmetry in nature may be also a reason for its inheritance. Radial symmetry is best suited to sessile animals since the similarity of parts enables them to repel enemies and to obtain food from any direction. Bilateral symmetry is one of the most useful adaptations for swimming organisms such as fishes and the like, for flying and for walking, and for running animals. Tropic responses in animals are conditioned by bi'aterality in organisms, such symmetry giving rise to orientation.

The idea of duplicate genes is becoming more common and there is greater evidence in favor of the fact that duplicate genes may exist in every chromosome. The result is that the organism is not a mosaic but an organism as a whole. Symmetry may be inherited in this way due to multiple factors.

Mosaics are also added evidence that asymmetrical characters as caused by the genes. Such mosaics may be due to non-disjunction; chromosome elimination and somatic mutations, and are all accounted for by the chromosome mechanism.

The first matings of this unilateral character gave in the F2 generation approximately 15 normals to one abnormal, which signifies duplicate genes with the character as a recessive. Many of the F2 selfed gave many families normal with no abnormals. But the ratios added together of abnormals gave an approximate 7:1 ratio which agrees with the idea of duplicate genes.

In certain crosses from the F1 progeny black-spotted, red spotted, red-black, unilateral females and black-red unilateral females, but all males are always non-spotted, for each type. This character, as well as all others so far studied, is sex-limited in its inheritance.

When a red-black unilateral mother is mated with a black-red non-spotted male, her offspring will be on the average 2 red-black to 1 black-red, with 3 males non-spotted. The ratio is a 2:1 which is a 1:1 and 3:1 Mendelian ratio added together, since one can not determine whether the males are heterozygous or homozygous; consequently the above ratio results.

The same result is also discovered when a black-red unilateral mother is mated with a non-spotted male from a red-black culture gives approximately ¼ families breeding true for this reverse char-
acter and the others give twice as many females as the red-black females and 3 non-spotted males again: The 2:1 ratio is obtained from the addition of a 1:1 and a 3:1 ratio because as before the males may be either heterozygous or homozygous.

The nearest result is that we have two separate recessive genes for red-black and black-red located in separate chromosome pairs. Different pairs of homologous chromosomes would act as duplicate genes. If these reversals should prove to be a result of crossing over it would be approximately 33 1-3 percent.

Another method is that of incomplete dominance. Here the dextral and sinistral unilateral traits would appear according to 1:1 ratio, instead of 2:1 ratio. Incomplete dominance would of necessity occur only when the organism is heterozygous for red spots and black spots.