CHAPTER X

HEREDITY AND SEX

THE value of a domesticated animal often depends in considerable measure on its sex. Therefore, if a means could be devised for controlling the sex of offspring, it would be of great economic value to the breeder. Endless attempts have been made to do this, and occasionally a claim of success has been made, but none of these claims has withstood the test of critical analysis or experiment. The hypotheses advanced to explain how sex may be controlled have been of the most varied character. In some the determination of sex has been supposed to inhere in the nature of the parents, in others it is referred to conditions of the gametes themselves.

Relative age or vigor of the parents have been supposed to influence sex in various ways. The same idea has been advanced regarding the gametes themselves, it being supposed that early or late fertilization of the egg might influence its sex. Experimental evidence, however, as to these several hypotheses is wholly negative, when one eliminates other possible factors from the experiment. Everything points to the conclusion that sex rests in the last analysis upon gametic differentiation, just as the color of a guinea-pig in a mixed race of blacks and whites depends upon whether the gametes which unite to produce it carry black or white. As the heterozygous black guinea-pig forms black-producing and white-producing gametes in equal numbers, so there is reason to think male-producing and female-producing gametes are formed in equal numbers by the parent, in many cases at least. But is it not possible that there may exist individuals which produce the two sorts of gametes in unequal numbers, and so would have a tendency to produce more offspring of one sex than of the other? Perhaps so, though we have no evidence that such a condition, if it does exist, is transmitted from one generation to another. On this point I made experimental observations upon guinea-pigs extending over a series of years. Oftentimes I found an individual that produced more offspring of one sex than of the other, but this was probably due merely to chance deviations from equality. I could get no evidence that the condition was inherited, though the experiment was continued through as many as seven generations, including several hundred offspring.

The essential difference between a female and a male individual is that one produces eggs, the other sperm. All other differences are secondary and dependent largely upon the differences mentioned. If in the higher animals (birds and mammals) the sex-glands (*i. e.* the egg-producing and sperm-producing tissues) are removed from the body, the superficial differences between the sexes largely disappear. In insects, however, the secondary sex-characters seem to be for the most part uninfluenced by presence or absence of the sex-glands. Their differentiation occurs independently though simultaneously with that of the sex-glands.

The egg or larger gamete (the so-called

macro-gamete) in all animals is non-motile and contains a relatively large amount of reserve-food material for the maintenance of the developing embryo. This reserve-food material it is the function of the mother to supply. In the case of some animals, for example flat-worms and mollusks, the food-supply of the embryo is not stored in the egg-cell itself, but in other cells associated with it, and which break down and supply nourishment to the developing embryo derived from the fertilized egg. Again, as in the mammals, the embryo may derive its nourishment largely from the maternal tissues, the embryo remaining like a parasite within the maternal body during its growth, feeding by absorption. But in all cases alike the mother supplies the larger gamete and the food-material necessary to carry the zygote through its embryonic stages. The father, on the other hand, furnishes the bare hereditary equipment of a gamete, with the motor apparatus necessary to bring it into contact with the egg-cell, but without food for the developing embryo produced by fertilization. The gamete furnished by the father is therefore the smaller gamete, the so-called *micro-gamete.*

From the standpoint of metabolism, the female is the more advanced condition; the female performs the larger function, doing all that the male does in furnishing the material basis of heredity (a gamete), and in addition supplying food for the embryo. As regards the reproductive function, the female is the equivalent of the male organism, plus an additional function, — that of supplying the embryo with food. When we come to consider the structural basis of sex, we find reasons for thinking that here, too, the female individual is the equivalent of the male plus an additional element. The conclusion has very naturally been drawn that if a means could be devised for increasing the nourishment of the egg or embryo, its development into a female should be thereby insured, while the reverse treatment should lead to the production of a male. But in practice this *a priori* expectation is not fulfilled. Better nourishment of the mother may lead to the production of *more eggs,* but not of more *female offspring,* as has been repeatedly demonstrated by experiment. Also poor nutrition of the mother may diminish the number of eggs which she liberates, but will not increase the proportion of males among the offspring produced.

An excellent summary of evidence on this point was made by Cuénot in 1900. Attempts to influence the sex of an embryo or larva by altered nutrition of the embryo or larva itself have proved equally futile. Practically the only experimental evidence of value in favor of this idea has been derived from the study of insects, and this is capable of explanation on quite different grounds from those which first suggest themselves. It has sometimes been observed, as by Mary Treat for example, that a lot of insects poorly fed produce an excess of males. In such lots, however, the mortality is commonly high, and more females die than males, because the female is usually larger and requires more food to complete its development. The fallacy in concluding from such evidence that scanty nutrition causes individuals which would otherwise become females to develop into males was indicated years ago by Riley.

Nevertheless an argument for the artificial control of sex based on such evidence is from time to time brought forward, as, for example, a few years since by Schenk. The latest advocate of sex-control by artificial means is an Italian, Russo (1909). He claims in the case of rabbits that by feeding the mother on lecithin or by injections of lecithin, the proportion of female births may be increased. His evidence in support of this claim is, however, wholly inadequate, and two independent repetitions of his experiments, made by Basile in Italy and by Punnett in England, have given entirely negative results.

An alternative hypothesis concerning the determination of sex has been steadily gaining ground during the last ten years, that sex has its beginning in gametic differentiation and is finally determined beyond recall in the fertilized egg by the nature of the uniting gametes. Instructive in this connection is a study of parthenogenesis, — reproduction by unfertilized eggs. But before entering upon this, it may be well to review briefly the changes which regularly take place in the egg which is to be fertilized, and compare with this the changes which occur in eggs not to be fertilized.

In each cell of the ordinary animal there occurs a characteristic number of bodies called chromosomes. We do not know that they are any more important than other cell constituents, but we know their history better. These are contained in the nucleus of the cell, and at the time of nuclear division they are found at the equator of the division spindle. For example, in the egg of the mouse (Fig. 4, *A*), the nucleus is seen to be in the spindle stage, and its chromosomes are gathered together at the equator of the spindle. There each of them regularly splits in two, and one derivative goes to either end of the spindle, and so into one of the daughter-nuclei. Thus each new nucleus has, as a rule, the same chromosome composition as the nucleus from which it was derived.

But the egg which is to be fertilized undergoes two nuclear divisions in succession, in only one of which do the chromosomes split (see Fig. 4, *A–D*). In the other division the chromosomes separate into two groups without splitting, and each group goes into a different cell product. Consequently, in each of these products the number of chromosomes is reduced to half what it is in the cells of the parental body. Thus in the egg of the mouse, by maturation, the number of chromosomes becomes reduced from about twenty-four to about twelve.

Similar changes occur in the developing sperm-cell (see Fig. 5). Starting with the double or 2 N chromosome number, there are formed by two nuclear divisions, with only one splitting of chromosomes, four cells, each with the reduced or simplex number of chromosomes, N. Consequently, when the sperm enters the egg at fertilization it brings in a group of N chromosomes (in the mouse apparently twelve), which, added to the egg-contribution of N chromosomes, brings the number in the new organism again up to 2 N (in the mouse twenty-four).

Now, as regards the maturation of parthenogenetic eggs, those which are to develop without having been fertilized, three categories of cases deserve separate discussion. The simplest of these in many respects is found among the social hymenoptera (ants, bees, and wasps).

See Fig. 49, left column. The eggs are, so far as we can discover, all of a single type. They

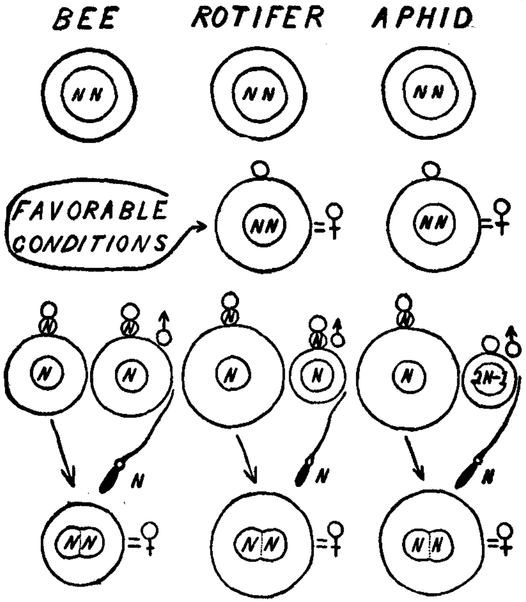

FIG. 49. — Diagram of sex-determination in parthenogenesis. First row, nuclear condition of the parthenogenetic mother; second row, of her eggs when they develop without reduction, after forming a single polar cell; third row, condition of the eggs after complete maturation — the fertilized egg in each case produces a male; fourth row, nuclear condition of the fertilized egg, always a female.

undergo maturation in the manner already described, the chromosomes being reduced to the

N or simplex number. The eggs of most animals, after they have undergone reduction, are incapable of development unless fertilized, but those of the hymenoptera may develop either fertilized or unfertilized. In the former case a female is produced, in the latter a male. The simplex, or N condition is in this case the male, the duplex or 2 N condition is the female, naturally the one of higher metabolic activity, the one which forms the macro-gametes.

In an earlier chapter I explained how the development of the sperm-cells in a male having the reduced or simplex number of chromosomes differs from that in the ordinary male. Reference to Fig. 8 may help to recall this. The cells of the male are in this case already in the reduced or simplex condition, N. In the production of the sperms the reducing division is omitted so far as nuclear components are concerned, so that each sperm formed contains the full simplex chromosome number, N. If it were less, the gamete formed would perhaps not be capable of transmitting all the hereditary characteristics of an individual.

A second category of cases (Fig. 49, middle column) is represented by such simple aquatic organisms as rotifers and small crustacea, like Daphnia. In these parthenogenesis occurs exclusively, when the food supply is very abundant and conditions otherwise favorable, whereas reproduction by fertilized eggs occurs only when external conditions, including food-supply, are not good. Under favorable conditions only female offspring are produced. The conclusion has naturally but erroneously been drawn that good nutrition in itself favors the production of females in animals generally, which is not true. The egg produced by Daphnia, or by a rotifer, under optimum conditions *does not undergo reduction* (see Fig. 49, second row). It remains in the 2 N condition, forming but a single polar cell. It is therefore unprepared for fertilization, and in fact it is not fertilized. Its sex is like that of the animal which formed it, female. Under unfavorable conditions, however, the eggs of the rotifer and of Daphnia do not begin development until they have undergone maturation. They are also of two sizes (Fig. 49, third row), — small eggs, which develop without fertilization and which form males, and large eggs, which require fertilization, and which form females. In this category of cases, as in that of the hymenoptera, the egg which develops in the 2 N condition, either from failure of reduction to occur in maturation or from fertilization following reduction, forms a female; whereas the egg which develops in the N condition forms a male.

In a third category of cases there is a quantitative difference in chromatin between male and female, just as in the foregoing cases, but this does not amount to a whole set of chromosomes, N, but to only a partial set, one or two chromosomes (see Fig. 49, right column). This category of cases occurs in plant-lice (aphids and phylloxerans); evidence of its existence rests chiefly on recent observations made by von Baehr and Morgan. Females are formed by parthenogenesis without reduction, occurring under favorable conditions, just as in the case of rotifers. Females are also formed by fertilization following reduction under unfavorable conditions, just as in rotifers. In both cases the female is 2 N. Males arise only by parthenogenesis under unfavorable conditions, just as in rotifers, but the reduction which occurs before development begins is partial only. A whole set, N, of chromosomes is not eliminated in maturation, but only 1 or 2 chromosomes. Hence the male condition here is 2 N — 1 or — 2. The condition of the gametes formed, however, is N in both sexes. In spermatogenesis, division of the germ-cells takes place into N and N — 1 daughter cells, but the latter degenerate (like the non-nucleated cells of the bee and wasp), and only the former produce spermatozoa. *Hence in fertilization* only 2 N zygotes are produced, which are invariably female.

Summarizing the three categories described, we may say that in all known cases of parthenogenesis, the female is in the duplex, 2 N condition, the male in the simplex (N) or partially duplex condition (2 N — 1, or 2 N — 2). *The female in all cases has the greater chromatin content.*

In a great many insects and other arthropods, which are not parthenogenetic, it is known that, although the male, like the female, develops only from a fertilized egg, nevertheless the male possesses fewer chromosomes than

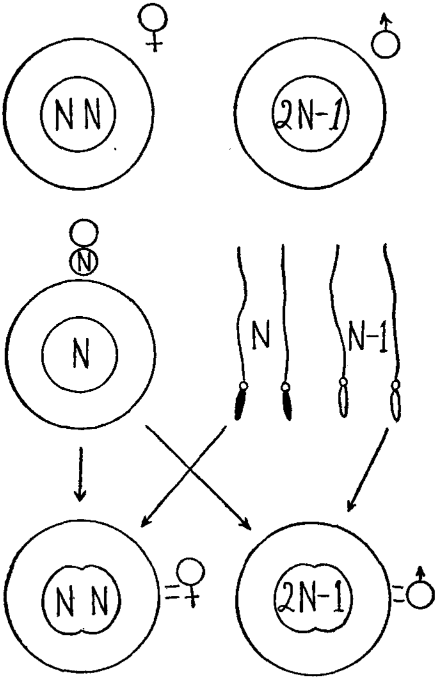

FIG. 50. — Diagram of sex-determination when the female is homozygous, the male heterozygous.

the female. In such cases the female forms, as in cases of parthenogenesis, only N gametes, but the male forms gametes of two sorts, N and

N — 1 or N — 2 (see Fig. 50). In consequence zygotes of two sorts result, — those which are 2 N, female, and those which are 2 N — 1 or 2 N — 2, male. Thus in the squash-bug, Anasa tristis, according to Wilson, the mature egg contains 11 chromosomes, the spermatozoa either 10 or 11 chromosomes, the two sorts being equally numerous.

Egg 11 + sperm 11 produces a zygote 22 (2N), a female;
Egg 11 + “ 10 “ “ “ 21 (2N–1), a male.

N in this species = 11; 2 N = 22, the female; 2 N — 1 = 21, the male. Males and females are therefore approximately equal in number, as in most animals where the two sexes are not subject to unequal mortality. In the Mendelian sense the female is in such cases a homozygote, the male a heterozygote. The sex of an individual in such cases depends upon which sort of a sperm chances to enter the egg.

But the experimental evidence indicates that both as regards sex and as regards heritable characters correlated with sex, these relations may in some cases be reversed, the female being heterozygous, the male homozygous. In such cases there is reason to think that structurally the male is 2 N but the female 2 N +. That is, the female is still the equivalent of the male *plus* some additional element and function. A structural basis in the chromosomes for such a condition has been described by Baltzer in the case of the sea-urchin. He found the regular duplex number of chromosomes in the male; but in the female, while the number was the same, one of the chromosomes was larger than its mate, having an extra or odd element attached to it. In such a case the gametes formed by the male would all be N, but those formed by the female would be of two sorts equally numerous, viz. N and N + (see Fig. 51). Egg N fertilized by sperm N would produce a zygote 2 N, a male; egg N + fertilized by sperm N would produce a zygote 2 N +, a female. Hence here, as in other animals, the sexes would be approximately equal, but the sex of a particular individual would depend upon which sort of egg gave rise to it.

Upon the existence, as in the foregoing cases, of an unpaired or odd structural element in the egg, may perhaps depend the explanation of a curious sort of heredity known as sex-limited heredity.

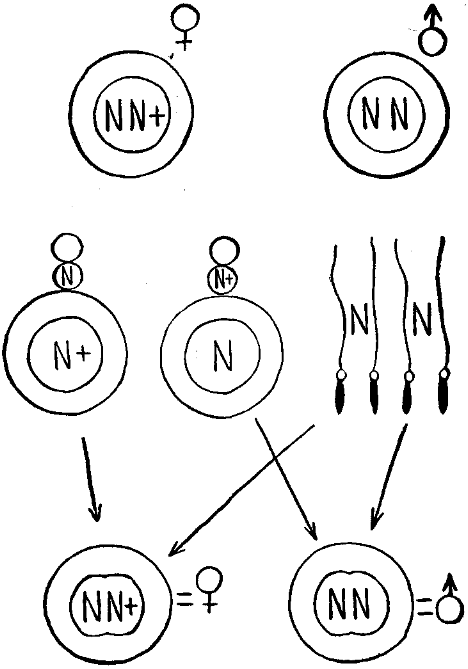

FIG. 51. — Diagram of sex-determination when the female is heterozygous, the male homozygous.

Every one who knows anything about poultry is acquainted with the popular American breed known as the barred Plymouth Rock. In this breed the feathers are marked with alternate bars of darker and lighter black. Pure barred Rocks breed true, but when crossed with other breeds, the male proves to be homozygous, the female, heterozygous in barring. For the male Rock crossed with a non-barred breed produces only barred offspring in both sexes, but the female Rock crossed with the same non-barred breed produces offspring approximately half of which are barred, the other half being non-barred. Further, the barred individuals in this cross are invariably males, the non-barred ones being females. Accordingly, the distribution of barring and non-barring in the cross is sex-limited.

The barred offspring produced by a cross between barred Plymouth Rocks and a non-barred breed, whether those offspring are males or females, prove to be heterozygous in barring, as we should expect, the barring factor having been received only from one parent, the barred one. Further, the *non-barred* offspring produced by a barred Rock female crossed with a non-barred breed, do not transmit barring, hence they are pure recessives as regards barring. Hence, also, we are forced to conclude, as already suggested, the female of the pure barred Rock breed is heterozygous as regards barring, and transmits the character only to her male offspring, her female offspring (if the father is non-barred) neither being themselves barred nor being able to transmit barring.

A pure Plymouth Rock race breeds true to barring merely because all its *males* are pure, for the females are not pure. This is shown by the following experiment. If a heterozygous barred male, produced by a cross between a Rock and a non-barred breed, is crossed with barred females, either those of a pure Rock race or those produced by a cross, the result is the same. The male offspring are all barred; the females, half of them barred, half non-barred. This result shows that all barred females alike are heterozygous in barring.

Sex-limited inheritance such as this finds at the present time its most probable explanation in the existence in the egg of an extra or *plus* element never found in the sperm, this element pairing with the sex-limited character in the reduction division. Thus, in the barred Rock, calling barring B, the male of pure race is plainly B B and every sperm is B. But the female clearly contains only one B and cannot be made to contain two. Perhaps a second B is kept out by some structural element, X, the distinctive structural element of the female individual. Then the eggs will be of two sorts: B and X. Since the sperms are all B, the first type of egg when fertilized will contain B B, a homozygous barred individual and

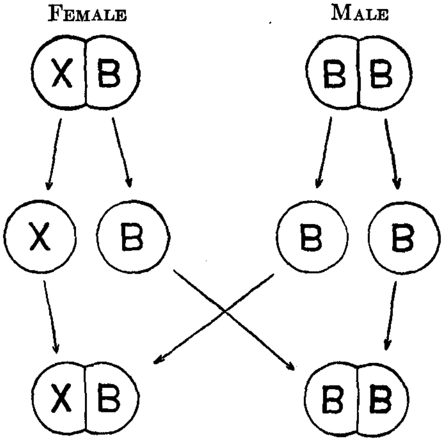

FIG. 52. — Diagram of sex-limited inheritance when the female is a heterozygote, as in barred fowls. X, female sex determiner; B, barring.

a male, since it lacks X; the second type will contain B X, a bird heterozygous in barring, and a female, since it contains X. This agrees with the experimental result (see Fig. 52).

A heterozygous barred male will form two kinds of sperm, only one of which will contain B. If such a male be mated with a barred female, four sorts of zygotes should result, as follows:

Gametes of heterozygous barred male = B and –,

Gametes of barred female = B and X,

Zygotes = B·B (homozygous barred male); B·– (heterozygous barred male), B·X (barred female), and –·X (non-barred female).

The observed result of this cross accords fully with the foregoing expectation.

The sex-limited inheritance of barring in fowls may be explained, as we have just seen, on the assumption that the female is the heterozygous sex. The same is true of sex-limited inheritance in canary-birds and in the moth, *Abraxas*, according to Bateson and Doncaster. But these relations are exactly reversed in the pomace-fly, *Drosophila ampelophila*, according to Morgan.

In Drosophila the female is apparently homozygous as regards some cell-structure, X, which in the male is never represented more than once. Accordingly the formula of the female is in such cases X X; that of the male, X —. Now the sex-limited characters in Drosophila seem to be bound up with the X structure, not repelled by it, as is barring in fowls. Accordingly, a sex-limited character may be represented *twice* in the female Drosophila, but only *once* in the male; or in other

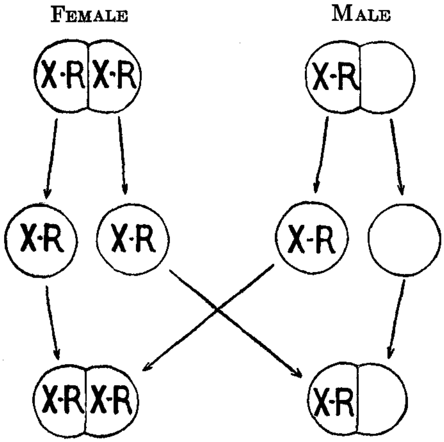

FIG. 53. — Diagram of sex-limited inheritance when the female is a homozygote, as in the red-eyed Drosophila. X, sex-determiner; R, red-eyes.

words, the female may be homozygous as regards a sex-limited character, but the male can only be heterozygous (see Fig. 53).

Drosophila normally has red eyes, but the redness of the eye is a distinct unit-character, sex-limited in heredity. Further males are regularly heterozygous in this character, while females are homozygous. For Morgan has obtained a race in which the eyes are white, owing to the loss of the red character; and reciprocal crosses of this race with ordinary red-eyed animals yield different results. The red-eyed female crossed with a white-eyed male produces only red-eyed offspring, but the red-eyed male crossed with a white-eyed female produces offspring only half of which are red-eyed, viz. the females, whereas the males are white-eyed.

These different results in the two cases apparently come about as follows:

First case.

Gametes of red-eyed female = X-R and X-R,
Gametes of white-eyed male = X and –,
Zygotes = X·X-R (red-eyed female), and = —·X-R (red-eyed male).

Second case.

Gametes of white-eyed female = X and X,
Gametes of red-eyed male = X-R and –,
Zygotes = X·X-R (red-eyed female), and –·X (white-eyed male).

A short condition of the wings in Drosophila, which renders the animal incapable of flight, is likewise sex-limited in heredity, as has been shown by Morgan. By crossing two races of Drosophila, each of which possessed a different sex-limited character, Morgan has been able to combine the two characters in a single race. Thus was obtained a race both white-eyed and short-winged. The synthesis cannot be made originally in a male individual, but only in a female. For only in the female can the two characters be brought together, each associated with a different X, since in the male only one X is present. *Although each sex-limited character seems to be attached to or bound up with an X structure, it evidently has a material basis distinct from X. Otherwise it would not* be possible for the character to leave one X and attach itself to the other, as apparently takes place in the female when the combination of two sex-limited characters in the same gamete is secured through a cross. The combination is apparently secured in this way:

Gametes uniting, X-R and X–L,
Zygote formed, X-R·X-L,
Its gametes, X-R and X-L, or X-R-L and X.

One of the uniting gametes, X-R, is formed by the red-eyed, short-winged parent; the other, X-L, is formed by the long-winged, white-eyed parent. The zygote resulting is a red-eyed individual, since it contains R; it is long-winged, since it contains L; it is a female, since it contains two Xs. Now, its gametes are of four sorts, as indicated. The first two sorts result from simple separation of the two Xs, each with its associated character, R in one case, L in the other. But the third sort could result only from the attachment of R and L to the same X, leaving the other X without either R or L as the fourth kind of gamete. This kind, which transmits neither red eyes nor long wings, would represent the new gametic combination,—white-eyed and with short wings.

The experimental evidence that gametes of these four sorts are formed by females of the origin described is as follows: — When such a female is mated with a long-winged, white-eyed male, there are obtained female offspring, all of which are long-winged, but half of them are red-eyed, half white-eyed. The male offspring, however, are of four sorts, viz. red short, white long, red long, and white short. This result harmonizes with the hypothesis advanced. For if the gametes of the female are X-R, X-L, X-R-L, and X, and those of the male are X-L and —, then the following combinations should result:

X-L· X-R, red long female,
X-L· X-L, white long female
X-L· X-R-L, red long female,
X-L· X , white long female,

——· X-R, red short male,
——· X-L, white long male,
——· X-R-L, red long male,
——· X , white short male.

This expected result accords with that actually obtained by Morgan.

Color-blindness in man is a sex-limited character, the inheritance of which resembles that of white eyes or short wings in Drosophila, rather than of barring in poultry.

Color-blindness is much commoner in men than in women. A color-blind man, however, does not transmit color-blindness to his sons, but only to his daughters, the daughters, however, are themselves normal provided the mother was; yet they transmit color-blindness to half their sons. A color-blind daughter could be produced, apparently, only by the marriage of a color-blind man with a woman who transmitted color-blindness, since the daughter to be color-blind must have received the character from *both* parents, whereas the color-blind son receives the character only from his mother.

Color-blindness is apparently due to a defect in the germ-cell, — absence of something normally associated there with an X-structure, which is represented twice in woman, once in man. Color-blindness follows, therefore, in transmission the scheme shown in Fig 53.

If, as has been suggested, the determination of sex in general depends upon the inheritance of a Mendelian factor differentiating the sexes, it is highly improbable that the breeder will ever be able to control sex. Male and female zygotes should forever continue to be produced in approximate equality, and consistent inequality of male and female births could result only from greater mortality on the part of one sort of zygote than of the other. Only in parthenogenesis can man at will control sex, and until he can produce artificial parthenogenesis in the higher animals, he can scarcely hope to control sex in such animals.

Negative as are the results of our study of sex-control, they are perhaps not wholly without practical value. It is something to know our limitations. We may thus save time from useless attempts at controlling what is uncontrollable and devote it to more profitable employments.

BIBLIOGRAPHY

BATESON, W.
1909. (See Bibliography to Chapter IV.)

CASTLE, W. E.
1909. "A Mendelian View of Sex-heredity." *Science, N. S.*, vol. 29, pp. 395–400.

CUÉNOT, L.
1900. "Sur la détermination du sèxe chez les animaux." *Bull. Sci. de la France et de la Belgique.*

Morgan, T. H.
- 1909. "A Biological and Cytological Study of Sex Determination in Phylloxerans and Aphids." *Journal of Experimental Zoölogy*, 7, pp. 239–352.
- 1910. "Sex-limited Inheritance in Drosophila." *Science, N. S.*, 32, pp. 120–122.
- 1911. "The Application of the Conception of Pure Lines to Sex-limited Inheritance and to Sexual Dimorphism." *The American Naturalist*, 45, pp. 65–78.

Russo, A.
- 1909. "Studien über die Bestimmung des weiblichen Geschlectes." G. Fischer, Jena.

Wilson, E. B.
- 1909. "Recent Researches on the Determination and Heredity of Sex." *Science, N. S.*, 29, pp. 53–70.
- 1910. "The Chromosomes in Relation to the Determination of Sex." *Science Progress*, 5, pp. 570–592.

For references to the earlier literature see Cuénot and Bateson.