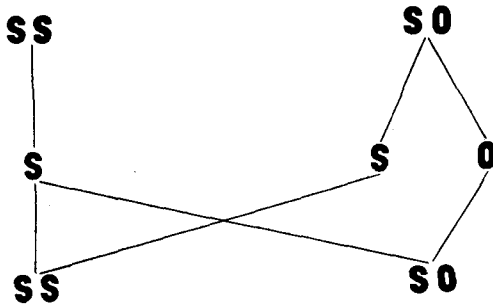


CHAPTER IV

SEX INHERITANCE

There are two types of sex inheritance known in those species in which separated sexes exist. In one type, which may be called the *Drosophila* type (XX-XY type, or, for short, the XY type), the female is homozygous for a sex factor, the male heterozygous; in the other, the *Abraxas* type (the WZ-ZZ type, or, for short, the WZ type) the female is heterozygous for a sex factor, the male homozygous. Since in both cases the heterozygous individuals must always mate with the homozygous ones there should result in each succeeding generation equal numbers of heterozygous and homozygous individuals, and so the bisexual condition is perpetuated as follows:



The genetic evidence so far gained has placed in the *Drosophila* type the following animal forms: Dro-

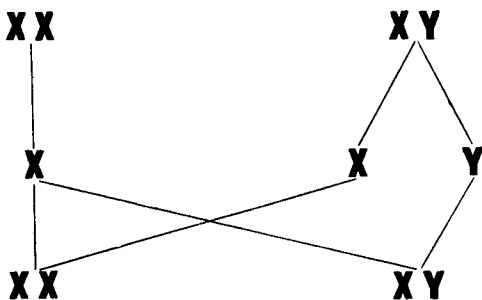
sophila, man, cat; and the plants, *Lychnis* and *Bryonia*. The cytological evidence refers to the same type the insect groups of bugs, flies, beetles, grasshoppers; the spiders, certain worms (*Ascaris*), echinoderms, amphibia and mammals (including man). The genetic evidence has placed in the *Abraxas* type several moths and butterflies, and several birds; viz., chickens, ducks, and canaries.¹ Favorable cytological evidence has been found only in the case of a few moths.

In many cases of the *Drosophila* type, in which the history of the sex chromosomes has been worked out cytologically, it has been found that in the male there is a pair of chromosomes, the two members of which are different in size or shape. These are the "sex chromosomes" and are designated as X and Y. In many species of the *Drosophila* type the Y is slightly smaller than the X, and in the various other species of this type all gradations in the relative size of the Y are found, between this condition and the condition where Y is completely absent. In some related species, on the other hand, the chromosomes which obviously correspond to X and Y are alike in appearance. It is not, after all, the size difference usually visible in the male, between X and Y, which gives these two chromosomes their significance in sex determination, but rather a difference in the factors they contain. The size difference is an incidental concomitant, or, as it were, a token or label that is

¹ Richardson's work on strawberries suggests that this plant may come under the *Abraxas* type

not present in all species. In all these cases the female contains two X chromosomes, the Y chromosome being confined to the male line.

This type of sex determination represents all eggs as alike—each containing one X (after the polar bodies have been extruded), but the sperm is of two kinds, one containing the X and the other Y, or merely no X. The scheme is as follows:



It will be seen that all the spermatozoa carrying X produce females, while all those carrying Y or no X produce males.

The Y chromosome, when present, descends from father to son. It might seem, therefore, that if the Y carried a sex factor for maleness the scheme would work out as well as if a sex factor were carried by the X chromosome. But in several cases there is no Y in the male, and in certain cases to be described later, due to non-disjunction, there are females that have a formula XXY and yet their sex is not affected in any way on account of the presence of the supernumerary Y. It follows that sex is not determined by the presence or absence of the Y chromosome but by the

number of the X chromosomes that are present. In the cases that follow, where sex determination of the *Drosophila* type was discovered by a study of sex linked inheritance, as well as in the above cases, where the mechanism was discovered through cytological observations, proof that the male is heterozygous for a *Mendelian factor* for sex is derived from the fact that he gives rise to two kinds of spermatozoa—male producing and female producing—in equal numbers. We know this in the cases worked out cytologically because here the spermatozoa carrying X must all produce females, while the other half must produce males; and we know it, in the cases worked out genetically, because here only half the spermatozoa from a male with a dominant sex linked character carry the dominant factor, and these all produce females, while the rest produce males. The female must contain the same Mendelian sex factor as is present in the female-producing spermatozoa of the male; but the female must be homozygous for this factor, since any egg, if fertilized by a male-producing spermatozoon, contributes this factor to the resulting male.

Although the only way in which the results of sex linked inheritance of the *Drosophila* type differ from non-sex linked cases is the one above stated, namely, that a dominant male transmits his dominant sex linked factor only to his *daughters*, nevertheless it may be well at this point to recall specifically what ratios are produced in consequence, in the various types of crosses.

Examples of sex linked inheritance in *Drosophila*

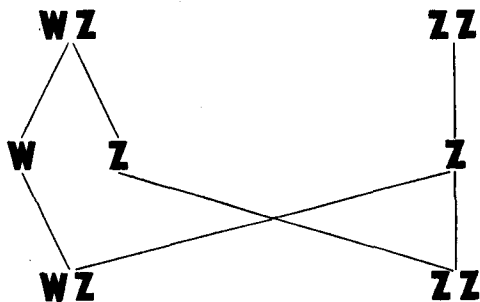
have already been given; that of white eyes is typical of all the rest. The main facts may be restated here. If a white eyed male is bred to a red eyed female the offspring are red eyed (Fig. 9). If these are inbred all of the F_2 daughters are red eyed, but half of the sons are white eyed and half red eyed. In a word, the grandfather transmits his characters visibly to half of his grandsons but to none of his granddaughters.

In the reciprocal cross (Fig. 10), a white eyed female bred to a red eyed male produces the criss-cross result of red eyed daughters and white eyed sons. These give white and red eyed males and females in equal numbers. On the assumption that the factor for white eyes is carried by the sex chromosomes the inheritance of white eyes can be readily understood. It will be observed that a female transmits to each of her sons one of her X chromosomes with all the factors contained in it. Her sons will show all of these sex linked characters whether they be dominant or recessive since they receive no other X to dominate those characters and the Y contains no dominant factor. For example, if a stock be made up pure for yellow body color, white eyes, abnormal abdomen, bifid wings, sable body color, forked spines and bar eyes, and if a female of this stock be bred to a wild male, all of her sons will be yellow, white, abnormal, bifid, sable, forked and bar. The daughters, however, will receive not only this chromosome from their mother, but will also receive a chromosome from the wild male (their father) con-

taining the normal allelomorphs of all these factors. In the case of all the factor-pairs, except abnormal and bar, the normal allelomorph dominates. Therefore, the females will appear normal for all characters except abnormal and bar, which are dominant.

In the cat, Doncaster has discovered a sex linked factor affecting the coat color. In man several characters, such as color blindness, hæmophilia, and others less certainly identified have been found to follow the same scheme.

A comparison of sex linkage in *Abraxas* with that in *Drosophila* shows that the mode of inheritance of sex linked characters is identical in these two cases, but the sex relations are exactly reversed. In the *Abraxas* type sex linked inheritance takes place in accord with the plan that the female is heterozygous in sex production. If the chromosome that carries this sex differentiator is called Z, and its mate in the female W, the formula for the male would be ZZ and that for the female WZ. The scheme follows:



Inheritance in *Abraxas* is illustrated in the following diagrams (Figs. 30 and 31), in which the common

wild type *A. grossulariata* is crossed to the rare mutant type *A. lacticolor*.

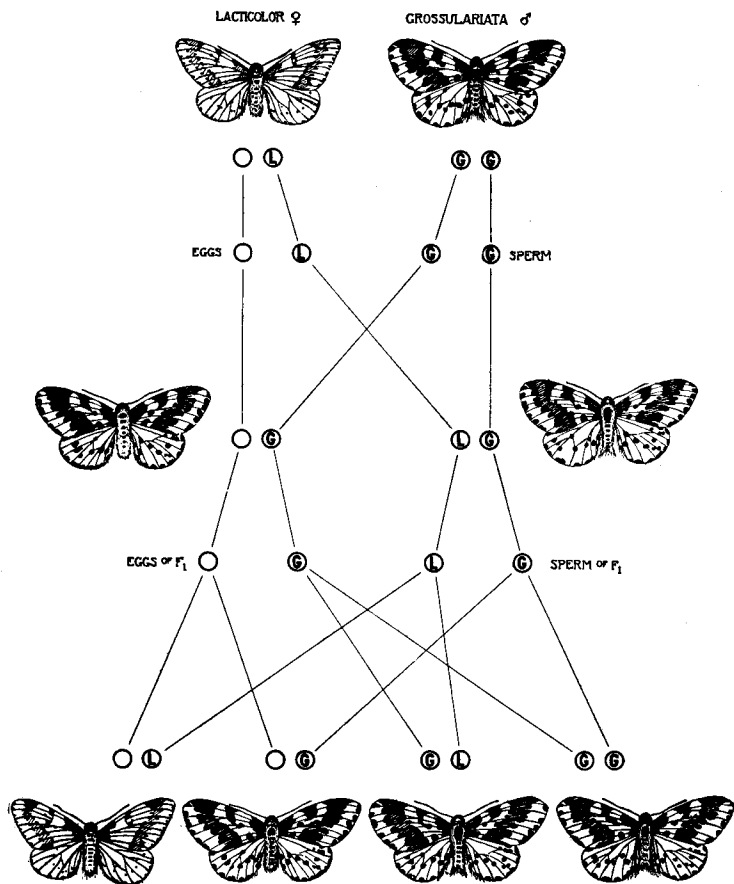


FIG. 30.—*Abraxas lacticolor* female by *A. grossulariata* male. The sex chromosomes are represented by the circles in the center of the diagram, and the letters contained in them stand for the factors that each carries. The W chromosome, confined to the female line, is represented without either G or L; for it, like the Y chromosome in *Drosophila*, carries no sex linked factors.

In the first cross (Fig. 30), where the lacticolor female is mated to the grossulariata male, the off-

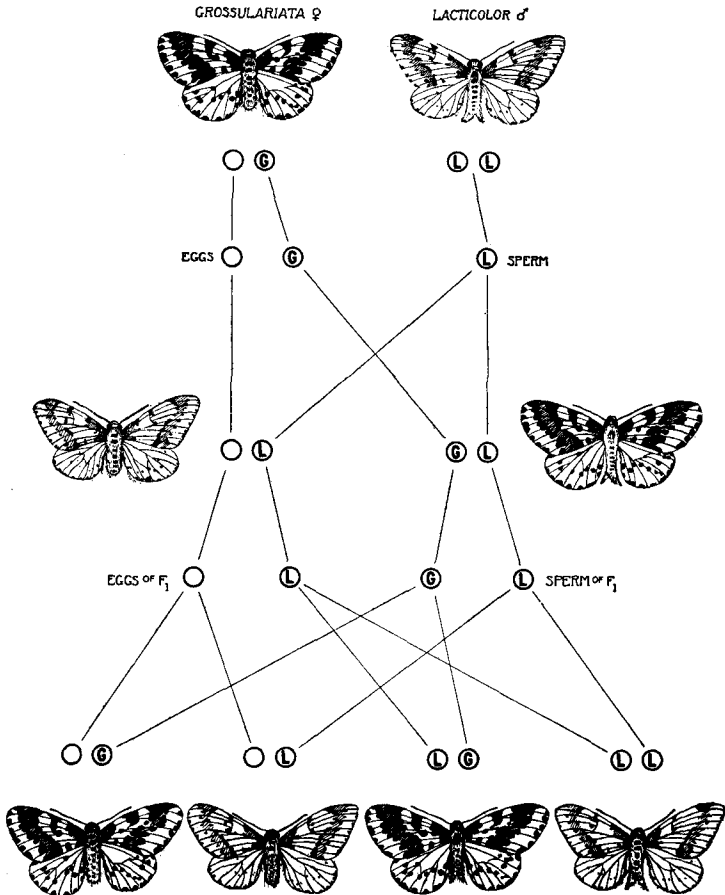


FIG. 31.—*Abraxas grossulariata* female by *A. lacticolor* male. The reciprocal cross of the one shown in Fig. 30.

spring are all of the grossulariata type. When these are inbred they give (F₂) three grossulariata to one

lacticolor, but the lacticolors are females only. The lacticolor grandmother has transmitted her peculiarity *visibly* to half of her granddaughters, but to none of her grandsons.

In the reciprocal cross (Fig. 31) of lacticolor male by grossulariata female, the daughters are like their father (lacticolor), and the sons are like their mother (grossulariata). This is so-called criss-cross inheritance. When the hybrids (F_1) are inbred, they give lacticolor males and females and grossulariata males and females in equal numbers.

Sex linked inheritance, as shown by the foregoing results, becomes intelligible if the factor for lacticolor is carried by the chromosome Z. Its occurrence in Z is indicated here by writing an L inside the circle which represents that chromosome, while the allelomorph character carried by the Z of the grossulariata individual is indicated by writing G in the circle. The W chromosome is indicated by the blank circle. The two cases then work out as shown in the diagrams.

The preceding analysis shows that the genetic evidence calls for a mechanism in which the female is heterozygous for sex, since those of her eggs which carry the factor for grossulariata all develop into females, the others into males. In the case of Abraxas there was for some years no positive cytological evidence in support of this view. Fortunately, the cytological side is now in a much better position owing to the work of Doncaster and Seiler.

Doncaster examined Abraxas cytologically, and

found that both the female and the male have 56 chromosomes, with no obviously unequal pair.

Normally in *Abraxas* the sex ratio is about 1 to 1. In one exceptional line this equality of sexes was not the rule. In this strain Doncaster found many females which gave only daughters, and not a single son. Other females of this line gave many daughters but also a few sons, while still others gave practically a normal 1 to 1 ratio.

When Doncaster examined this line cytologically, he found that although the males were normal, with 56 chromosomes, the females were aberrant, having only 55 chromosomes.

In the maturation of the eggs of such a 55 chromosome female, the odd chromosome went to one pole, so that one polar plate had 27 and the other 28 chromosomes. Doncaster found further that the odd chromosome went more often to the polar body than to the egg. The many eggs that eliminate the odd chromosome become after fertilization individuals with 55 chromosomes, that is, females—while the few that retain it become 56 chromosome individuals—that is, males. The preponderance of the females is thus accounted for. Such females having 55 chromosomes would belong to the OZ type.

In normal strains there is a W chromosome present, but since this W chromosome may be absent without effect upon the sex of the individual, as shown above, it must be regarded as functionless in determining sex, and in this sense it corresponds to the Y of *Drosophila*. This evidence proves that there is

present in *Abraxas* that cytological basis which the evidence from sex linkage demands, namely, a condition the converse of that known in other groups of insects.

The evidence that Seiler has obtained relates to the wild strains of the moth *Phragmatobia fuliginosa*. The reduced number of chromosomes in the polar plate of the egg is 28 (Fig. 32, *a*). The large dyad formed by synapsis of the sex chromosomes *Z* and *W* is shown in the middle of the group. At the first polar division all the chromosomes separate from their mates, the ordinary chromosomes (autosomes) as well as the sex chromosomes. But as *W* separates from *Z*, it breaks into two parts which we may call large *W* and small *w* (Fig. 32, *b, c*). As a result there are 29 chromosomes at one pole (the pole that contains *W* and *w*) and 28 chromosomes at the other pole (the pole containing *Z*). It is a matter of chance which group goes into the polar body and which remains in the egg. Consequently there are two kinds of eggs, *Ww* and *Z*.

In the male there are 56 chromosomes, which give the reduced number 28. The two large *Z*'s can be made out in Fig. 32, *d*. These meet, when the reduced number 28 is formed, and then separate, one going to each pole (Fig. 32, *h*). Each spermatozoon contains, therefore, one *Z* chromosome.

FIG. 32.—*Phragmatobia fuliginosa*. *a*, equatorial plate of first polar body of egg; *b* and *c*, daughter plates of the first polar spindle; *d*, equatorial plate of spermatogonium; *e*, equatorial plate of first spermatocyte; *f* and *g*, equatorial plates of second spermatocyte; *h*, anaphase stage of first maturation; *i* and *j*, equatorial plates of somatic cells with 56 (in *i*), and 61 chromosomes (in *j*). (After Seiler.)

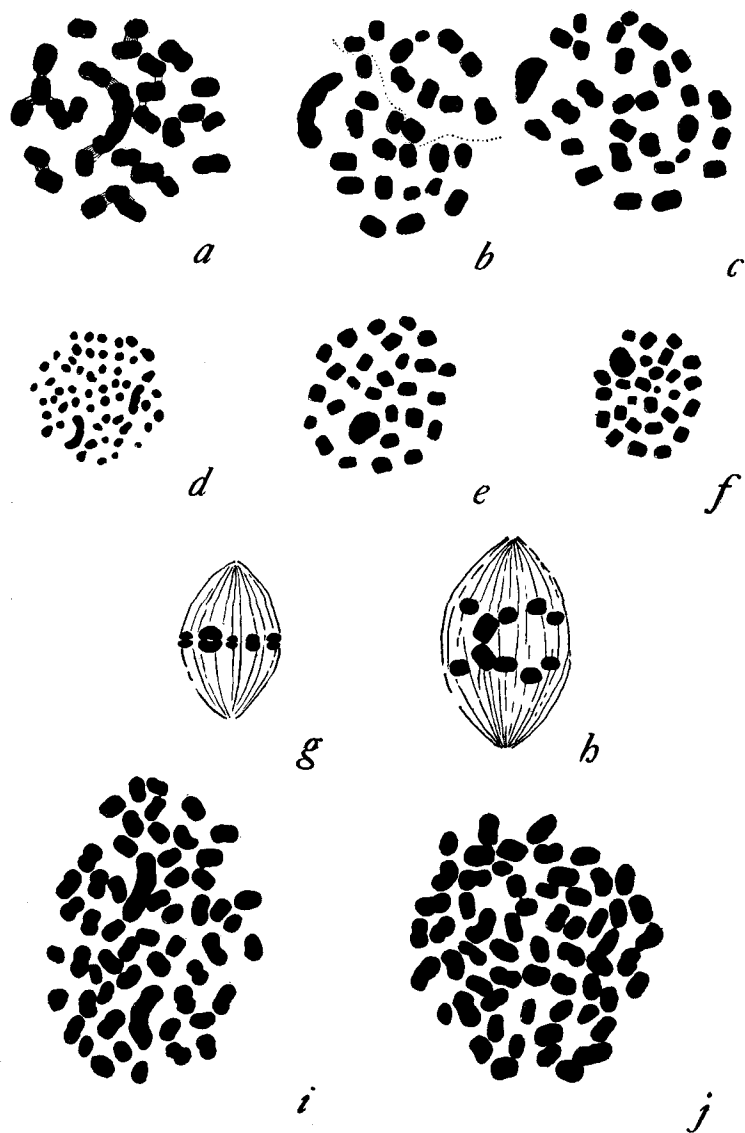


FIG. 32.

Any sperm fertilizing an egg containing Ww produces a female. The male embryos should contain therefore 56 chromosomes, the female 57. Counts of chromosomes in embryos show that while some contain 56, others contain 58, 61 and 62. Seiler suggests that the Z element is also compound and sometimes separates into four components in the somatic cells. Aside from this peculiarity his results indicate that the male is monogametic and the female digametic in accordance with the WZ-ZZ scheme.

In other Lepidoptera, examined by Stevens, by Doncaster, by Dederer and by Seiler, the males and females have the same chromosome configuration. In other words, if a WZ pair is present in the female the members are of the same size, or so nearly of the same size that they cannot be distinguished. It will be recalled that in a few other insects, believed for other reasons to belong to the *Drosophila* type, the X and the Y chromosomes are of the same size. The failure to find two sizes of sex chromosomes in moths is, therefore, not an argument against the view that the female is heterozygous for a sex factor. On the contrary, it is to be considered only a fortunate circumstance that this difference in a sex factor is sometimes associated with a size difference in no way directly depending on the sex factor itself.

WHAT ARE SEX FACTORS

The inheritance of sex is explained by the assumption that one difference distinguishes the male from

the female; the difference is a single or a double amount of the so-called sex factor. The chromosomes are the carriers of these sex factors. The symbols used here, viz., XX-XY and WZ-ZZ, are intended primarily for the chromosomes, but also for the sex factors.

These formulæ for the *Drosophila* type and for the *Abraxas* type raise the question as to whether the postulated sex *factors* are identical in the two cases. The employment of different letters for the two types suggests, of course, that the sex factors may be different. And it is true that the two sets of letters are used to avoid an apparent paradox that appears if we use only X and Y in both cases. If this is done, XY on one scheme represents the male and on the other scheme the female. Nevertheless, for the present the employment of different letters need not necessarily mean that different factors for sex are present in the two great classes, for these reverse results may be due to the action of the same factor-difference in a different setting. For example, acid may be the color differentiator in a setting of a certain solution containing it and litmus (with one drop of acid the color being blue, with two drops red), but in a setting containing Congo red the same differentiator may produce just the opposite effects (one drop red, two drops blue). On the other hand, it is conceivable that the setting (litmus and acid) may remain the same and yet a reverse result be produced by having a different differentiator—alkali instead of acid.

Since genetics has at present nothing to offer that will decide the question as to whether another set of sex differentiators is present, or whether the same differentiators with a different setting are involved in these two cases, discussion is quite certain to be futile.

It may seem inconsistent to use the name of the chromosome as the symbol for the sex factor when dealing with the inheritance of sex, while in all other cases a factor representing a point in the chromosome is used to designate the special character under consideration. No doubt with this idea in mind, several writers have followed the practice of indicating the sex factor by a significant letter, such as F for femaleness and M for maleness. As the use of such letters often involves a question of interpretation, a brief consideration may be given to this matter. In the discussion that follows reference is made always to the *Drosophila* type, but exactly the same arguments apply to the *Abraxas* type.

1. It has been suggested, for example, that a factor for the male be added to the formulæ so that maleness may not appear simply as the absence of one factor for femaleness. Thus, in such formulæ as *FMFM* (φ) and *FMM* (δ) the factor for maleness is added to indicate that when a single amount of F is present the male factors produce the male. But since M's are distributed everywhere, the formula is little more than a concession to male vanity, for M is not here a differentiator. Moreover, the use of the letters MM is here unjustifiable because there is no ground

for supposing that maleness is due to one pair of factors. It must be due to a complex of many factors all of which are present in both sexes.

2. Since there is evidence to show in some cases that there is no sex factor in the Y chromosome, the factor or factors carried by X can have no mate in this sex, hence the allelomorph or allelomorphs must be 0. If one chooses to represent this zero by a small letter, by *f* or *m* for instance, there is no inconsistency in doing so, for there is in this instance the cytological observation to justify its use. It is, however, misleading to represent this 0 by *M* as has sometimes been done.

3. There is at present no evidence to show that there is only *one* factor for sex carried by each sex chromosome, however probable this may seem from other relations, for it has not been possible to determine the linkage relation of the sex factor or factors to other factors in the sex chromosome, because crossing over of like factors in the homozygous sex would lead to no visible effect, and in the heterozygous sex no crossing over takes place.

4. If in the formulæ FF (φ) and FO (σ) the letter *F* is interpreted as a factor for femaleness, the formula must not be construed as meaning that *F* may not also be a factor for maleness. For, as a matter of fact, *one* *F* factor may be essential to the production of the male. Therefore, until we get more definite information as to the existence of a single or of several factors for sex, and as to whether they are the same factors in the two types, and what the rela-

tion of F and M may be in hermaphroditic types, it is less inconsistent to use the symbols for the sex chromosomes as the symbols for the sex factors also, if it is at the same time recognized that the whole chromosome is not involved in determining sex.

The same factors that determine whether eggs or sperm develop in an individual must also be responsible for the development of many characters that go along with the male or the female condition, in other words those characters that are different in the two sexes (sex limited). Sex factors of whatever kind, however, must like all factors be supposed to produce their effects in conjunction with the rest of the cell, with other factors, or with anything else there, for it must always be remembered that the sex factor is only one of many factors that are at work. Hence for the realization of any particular character that is associated with a particular sex there are probably many factors that cooperate. If the latter change, the character in question may also change, while the sex factor remains the same. The character may, in this case, be said to be dependent not only on the sex factor, but also on another differentiator that can only realize itself conjointly with the sex factor. Thus while the accessory sexual organs, as well as the secondary sexual characters and all other sex-limited characters, may be modified by special differentiators that are not present in the sex chromosomes, yet the sex factor also produces an effect on their development which is different according to whether the sex factor exists in single or double amount. In

the case of some other characters, however, it is conceivable that the sex factors co-operate in their production, and yet have the same effect whether present in single or double amount. Such characters would not be sex limited.

As in the case of sex limited characters, so in the case of sex itself there must be many factors in the fertilized egg that are as essential to the development of sex as are the sex factors themselves, but as they are distributed to all individuals alike, they are not thought of as differentiators, but as forming the chemical background on which the single or the double amount of the sex factor gives its result. It is quite conceivable that one or more of these other factors might so change that the sex differentiators would become inoperative or even change so that these other factors themselves become the differentiators that determine sex.

The environment—the outer world—is also one of the components that enters into the development of every individual. A specific environment is one of the conditions of development. Why then, it may be asked, may not the environment turn the scale and determine sex? As a general proposition this must be acceded to at once—it is entirely a matter of proof. If there is an internal mechanism to determine sex in a normal environment it is quite conceivable that it might be supplanted in a new world. It is a question of evidence as to how often, if ever, this occurs. It is furthermore quite conceivable that some animals have no internal mechanism to regulate

sex but depend on a difference in their medium. If such an environment can be discovered it would be sex determining in the same sense in which the term is here employed when the sex differentiators are hereditary factors.

Sex determination in the Gephyrean worm *Bonellia* is a case in point. The female is a large oval worm with a long proboscis. The male is very small and degenerate and lives as a parasite on the proboscis of the female. The development has recently been studied by Baltzer. He finds that if the young *Bonellia* embryos are put into an aquarium in which old females are present, they settle down on the proboscis of the female and degenerate into males. If, on the contrary, the young embryos are kept by themselves they pass through an indifferent stage but later differentiate into female worms. Whether a male or a female develops from an egg depends here on whether at a certain stage the embryo comes under the influence of the proboscis of a female or fails to do so. Some secretion from the proboscis may be the differentiator in such a case. It is clear that here it is environment that determines the sex of the individual. The evidence suggests that the male organs develop first in the presence of a certain secretion from the proboscis of the female which also serves to arrest the animals in this stage. If, however, the animal fails to meet with these conditions, it usually ceases for a time to develop and fails to produce the male organs. Later it starts once more to go forward and develops the

female organs which are characteristic of this sex. Baltzer found, however, that only 90 per cent. of these free embryos became females; the remaining 10 per cent. developed into hermaphrodites. He speaks of *Bonellia* as a protandric hermaphrodite in which one or the other sort of reproductive organs may be suppressed by the environment, but this is only another way of describing the results.

There are several groups in which a change from parthenogenesis to sexual reproduction takes place in response to changes in the environment. The best known cases are the rotifer (*Hydatina senta*), some of the daphnians (*Moina* and *Simocephalus*) and certain insects (aphids). *Hydatina* gives the clearest evidence (Fig. 33). It has been shown by Whitney and by A. F. Shull that if this rotifer is fed on a colorless flagellate and kept in water from old cultures it can be kept indefinitely reproducing by parthenogenesis, *i.e.*, by eggs that are not fertilized. If taken out of these solutions and put into spring water, a certain percentage of the females will give rise to daughters whose eggs may be fertilized. These daughters behave therefore as sexual females. But if they are not impregnated their eggs remain viable and develop parthenogenetically into males. If in addition to being transferred to spring water the females are fed with a green flagellate, *Dunaliella*, then, as Whitney has shown, almost all of their daughters (80 per cent.) are changed into the sexual form, *i.e.*, a form producing eggs capable of being fertilized (or if not fertilized, developing into males).

An environmental change determines whether parthenogenesis or sexual reproduction takes place. The environment may equally well be said to de-

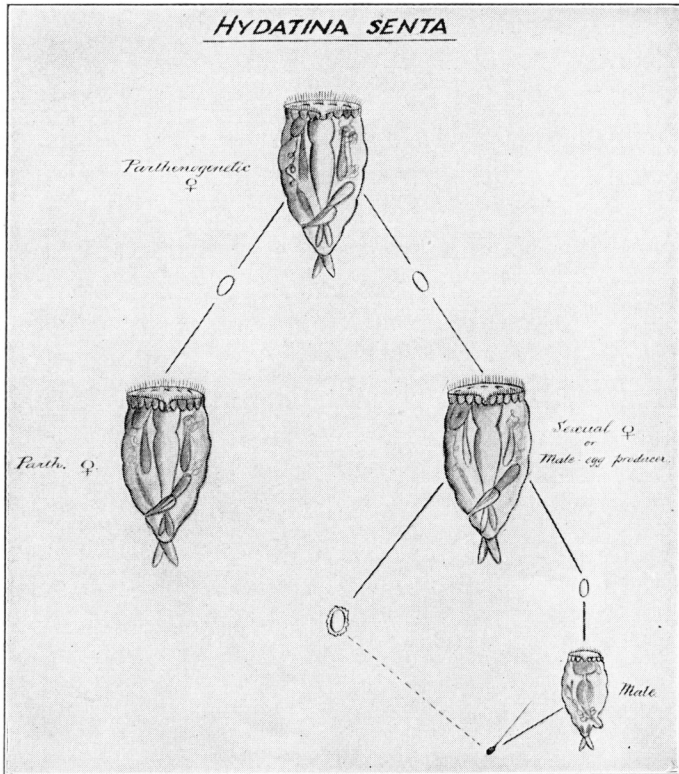


FIG. 33.—Diagram to illustrate the life cycle of *Hydatina senta*. The environment determines whether the parthenogenetic individual (at the top) gives rise to a female like herself, or to one that if fertilized at an early age produces a sexual egg, but if not fertilized produces small eggs from which males develop parthenogenetically.

termine whether an egg becomes a parthenogenetic female-producing female or a male-producing female.

But another difference is necessary to determine whether an egg of the latter individual *develops* into a male or into a female, namely, the entrance of a spermatozoon into the egg before it has completed its growth.

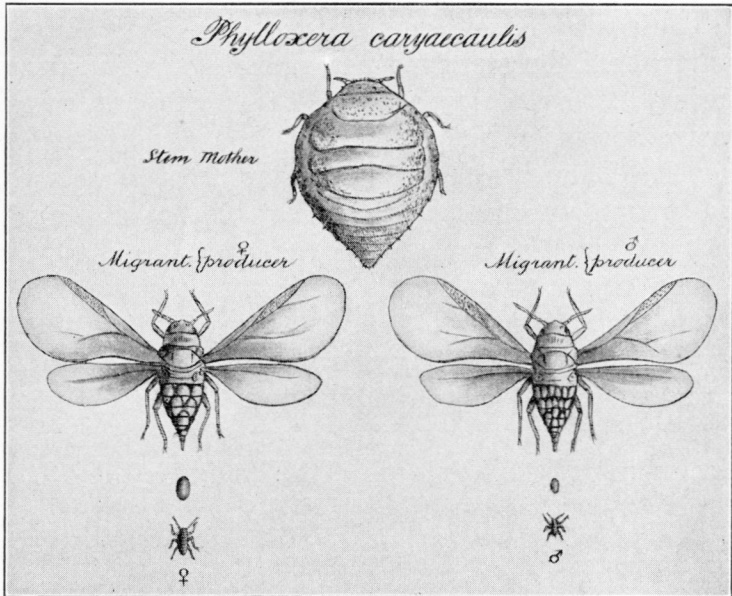


FIG. 34.—Diagram to illustrate the life cycle of *Phylloxera caryæcaulis*.

In the phylloxerans of the hickories the fertilized egg gives rise to a female called the stem mother (Fig. 34). She emerges from the egg in the early spring and attaches herself by means of her proboscis to a leaf, causing it to produce a gall that envelops her. Within the gall she lays her eggs. These hatch, and produce the winged or migrant generation

(Fig. 34). In one species, *P. caryæcaulis*, all the migrants in one gall are alike in that they produce the same kind of egg, *i.e.*, in some galls all the migrants contain large eggs (that produce sexual females), while in other galls all of the migrants contain smaller eggs (that develop into males).

The sexual female lays one egg, that is fertilized, from which the stem mother emerges the following spring. The males give rise only to female-producing sperm, each spermatozoon containing two sex chromosomes. The other class of sperm degenerates. Hence we can understand why it is that all fertilized eggs produce females only.

The chromosomal cycle undergoes the series of changes shown in Fig. 35. In *P. caryæcaulis* there are eight chromosomes, including four sex chromosomes ($XxXx$). Since the history of the sex chromosomes alone furnishes certain information that makes clear some of the changes in the life cycle, the other chromosomes may be disregarded for the present.

Starting at the bottom of the diagram it will be seen that the sexual egg after extruding the two polar bodies contains two sex chromosomes indicated by X and x . Two kinds of males are indicated in the diagram, one containing Xx the other Xx' , and as a consequence there will be two kinds of female-producing sperm, one kind for each male, namely, Xx and Xx' . If the former fertilizes the sexual egg, the resulting stem mother will be $XxXx$, if the latter, the stem mother will be $XxXx'$. These two kinds of stem mothers are indicated at the top of the diagram.

One of them, $XxXx$, produces eggs which, after extruding one polar body, give rise to the migrants bearing large eggs; from the latter eggs, in turn, come

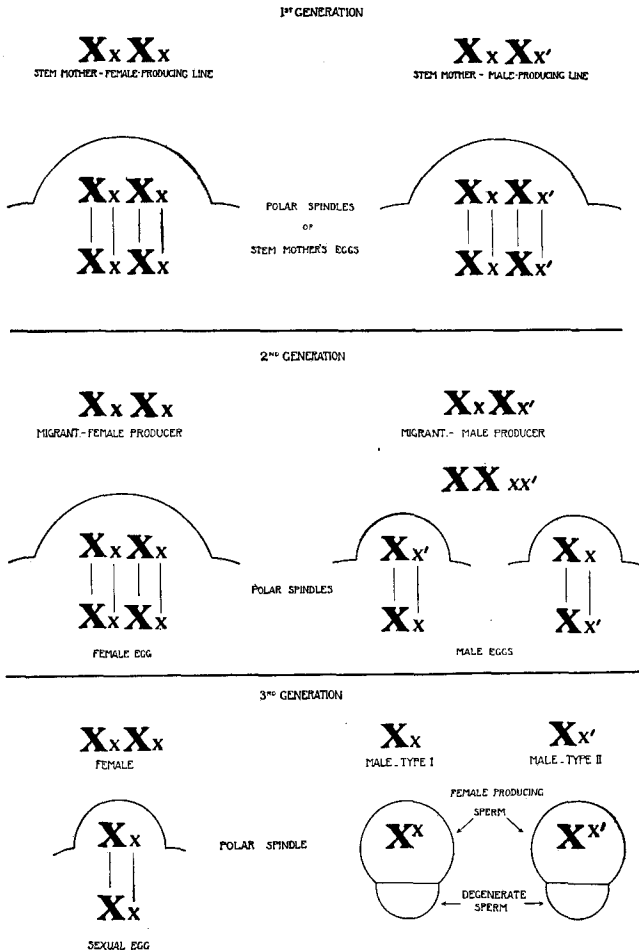


FIG. 35.—Diagram to illustrate the chromosomal cycle of *Phylloxera caryæcaulis*.

the sexual females. The other stem mother $XxXx'$, produces eggs, which, after extruding one polar body, give rise to the migrants bearing small eggs. Prior to the time when these small eggs are about to give off their single polar body, the two large X 's conjugate and the two small x 's conjugate, and when the polar body is given off one large and one small X pass out, and one large and one small X remain in the egg. In other words there is at this time a reduction in the number of sex chromosomes, and, as a consequence, a male is produced. Now as the diagram shows, Xx may remain in the egg and Xx' pass out; or, in other eggs, Xx' may remain in the egg and Xx may pass out. There will be, in consequence, two kinds of males, one Xx , the other Xx' , and as stated, two kinds of female producing sperm Xx and Xx' .

Thus the life cycle is brought back to the starting point. It may be added that so far as the chromosomes other than the X chromosomes are concerned there is no synapsis and no reduction to the haploid number in either line until the maturation divisions of the third or sexual generation occur. The life cycle of this species illustrates three points:

First.—That all of the sperm are female producing, because the male-producing class of sperm degenerates, as has been shown by direct observation.

Second.—That the parthenogenetic females can produce males through the elimination of two chromosomes. The female contains four sex chromosomes and the male two. The elimination of the

two chromosomes in the polar body of the male-producing egg has been directly demonstrated.

Third.—In this species the somewhat unusual relation of one stem mother giving rise to the line that culminates in the sexual eggs, and of another stem mother giving rise to the line that culminates in the males, can be explained on the assumption that one pair of the sex chromosomes is heterozygous in some factor indicated in the diagram by priming one of the x 's. This explanation is in part theoretical, although it is based on the actual observation of two kinds of males that differ in respect to the behavior of one of the smaller x 's.

In other species of phylloxerans, and in many aphids, one stem mother may produce both lines, *i.e.*, some of her offspring may ultimately give rise to sexual females and others to males. In such cases, as is illustrated in the next diagram (Fig. 36), there is but one kind of stem mother, and the four sex chromosomes (there are only two sex chromosomes in the aphids) are alike. Here some environmental influence must determine that in certain eggs conjugation of two pairs of chromosomes takes place. Such eggs give rise to males. In other eggs where this does not take place the sexual female will be produced.

In both *P. caryæcaulis* and in *P. fallax*, and also in the other forms referred to above, the difference between the behavior of the chromosomes in the stem mother and in the male-producing migrant is dependent on environmental influences. On the

other hand, the difference between the eggs contained in the male-producing and in the female-producing migrants, and between the behavior of the chro-

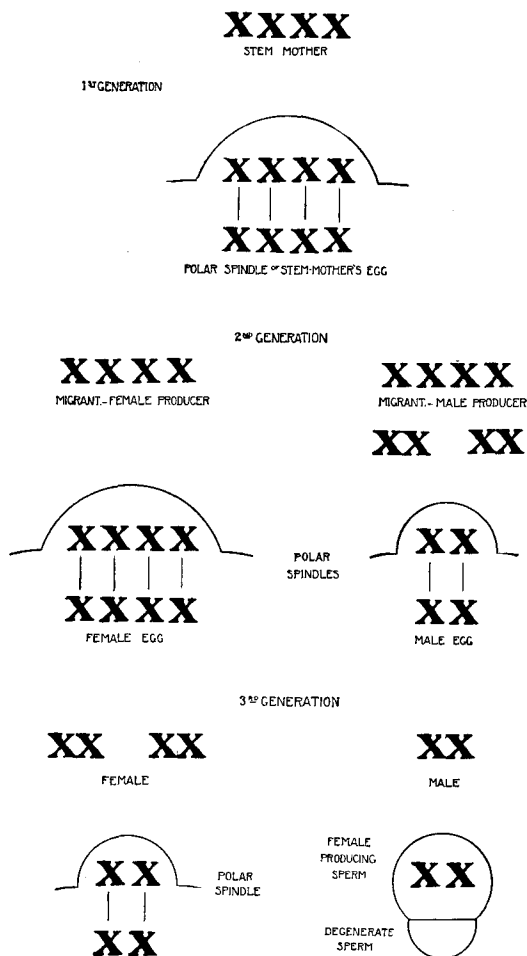


FIG. 36.—Diagram to illustrate the chromosomal cycle of *Phylloxera fallax*.

mosomes in these eggs, depends in *P. caryæcaulis* on an initial chromosomal difference between the types of migrants, but in *P. fallax* on some environmental influence. The difference between the two kinds of sexual individuals, *i.e.*, sex itself, is determined in both cases by the distribution of the chromosomes, however that distribution may itself be conditioned.

It is scarcely necessary to speak of other cases, in which, although an internal mechanism is known to exist for producing equal numbers of males and females, yet more individuals of one or the other sex may actually appear. For instance, it has been shown repeatedly in *Drosophila* that when a sex linked lethal factor is present in the sex chromosome, any male that contains this lethal X chromosome will perish. The females, on the other hand, will live, because they contain in addition another X chromosome, having the dominant normal allelomorph of the lethal factor. These lethal factors may be factors that cause abnormalities in organs essential to the life of the individuals and destroy the individual in this sense. The changed ratios do not at all affect the theory that there exists in *Drosophila* an internal sex-determining mechanism, although were the cases not actually worked out, the abnormal ratios might have seemed to disprove the theory of the sex chromosomes.

We can imagine other ways in which even in the presence of a regulating sex mechanism the actual ratio of males to females might be changed from equality to some other ratio. For instance, since the

female-producing spermatozoa contain one more chromosome and are larger in consequence, as Zeleny and Faust have shown, such sperm might travel up the oviduct with less speed than the male-producing sperm. Hence the sex ratios would be affected in favor of the males. Furthermore, secretions in the oviduct might act differently on the two kinds of sperm, the age of the sperm might affect one kind more than the other, etc. Such effects would be expected to bring about deviations from the normal ratios, but effects of these kinds can not fairly be brought forward to disprove the hypothesis that the X-bearing spermatozoa give rise to females and the no-X-bearing (or Y) spermatozoa give rise to males. It has even been suggested that external conditions might so weaken or strengthen the X chromosome that an X-bearing spermatozoon might produce a male or that a no X-bearing sperm might produce a female. If such effects can be produced they would act, no doubt, in the way postulated. But there is a large amount of evidence showing that factors are not ordinarily altered by environmental influences. Nevertheless there is no conflict here with the sex chromosome mechanism, only another one is imagined to have the power to overthrow it. No adherent of the chromosome theory would deny the theoretical possibility that at times external conditions may at least overcome the usual effect of the sex factor if not the sex factor itself, but the burden of proof for such supposed reversal of the normal result lies with those who maintain it. Proof, if it were forthcom-

ing, that the machinery of sex determination may be upset is not an argument against the sex chromosome theory. It is not a refutation of the factorial hypothesis of sex determination, for in such a case there would only be a substitution of an environmental factor for a genetic one. Opponents and advocates of the chromosome theory of sex determination have often failed to realize that "factor for sex" is not used in an absolute sense, but as the best known or most usual factor-difference among any number of possible theoretical ones; and in consequence the identification of sex as a *character* with the *factor* for sex determination has led to needless confusion. If the factor for sex were identified with sex itself, *i.e.*, if it alone would produce sex, there would be of course only one form of sex determination possible. But, as no one maintains such an interpretation of sex determination, this view can not be properly advanced as an argument against the sex chromosome theory.