

CHAPTER XIV

SEX AND GENES

OUR present understanding of the mechanism of sex-determination has come from two sources. Students of the cell have discovered the rôle played by certain chromosomes and students of genetics have gone further and have discovered important facts as to the rôle of the genes.

Two principal types of mechanism for sex-determination are known. They both involve the same principle, although they may seem, at first, to be the converse of each other.

The first type may be called the insect type, because in insects we have the best cytological and genetic evidence for this kind of sex-determining mechanism. The second type may be called the avian type, because in birds we now have both cytological and genetic evidence for this alternative mechanism. It is also present in moths.

The Insect Type (XX-XY).

In the insect type the female has two sex-chromosomes that are called X-chromosomes (Fig. 109). When the eggs of the female ripen (that is, after each has given off its two polar bodies), the number of the chromosomes is reduced to one-half. Each ripe egg, then, contains one X and, in addition, one set of ordinary chromosomes. The male has one X-chromosome only (Fig. 112). In some species this X has no mate; but in other species it has a mate that is called the Y-chromosome (Fig. 113). At one of the maturation divisions the X and the Y pass to oppo-

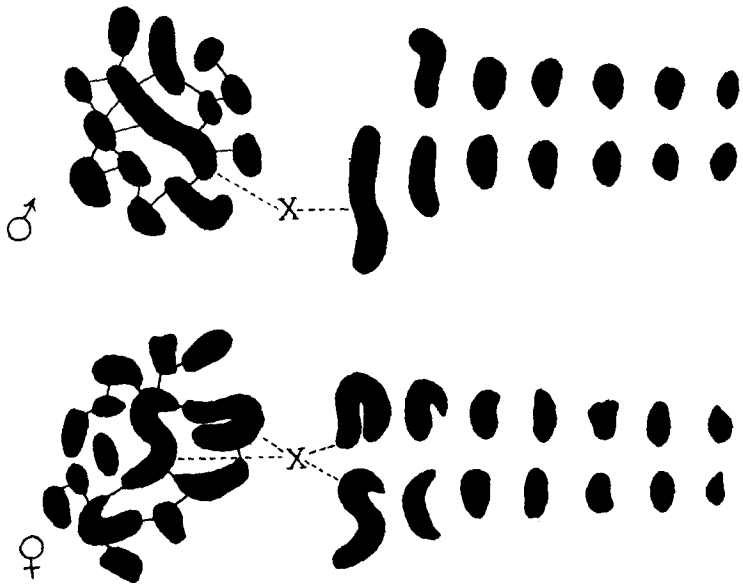


FIG. 112.

Chromosome group of male and of female *Protenor*, the former having one X-chromosome and no Y-chromosome; the latter having two X-chromosomes. (After Wilson.)

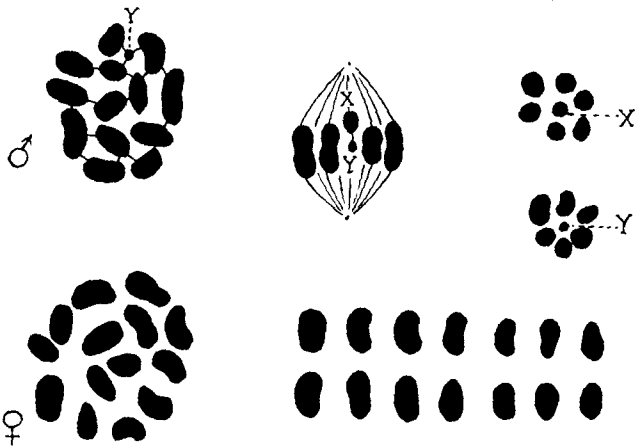


FIG. 113.

The male and female type of chromosome groups of *Lygaeus*, the former with X and Y; the latter with two X-chromosomes. (After Wilson.)

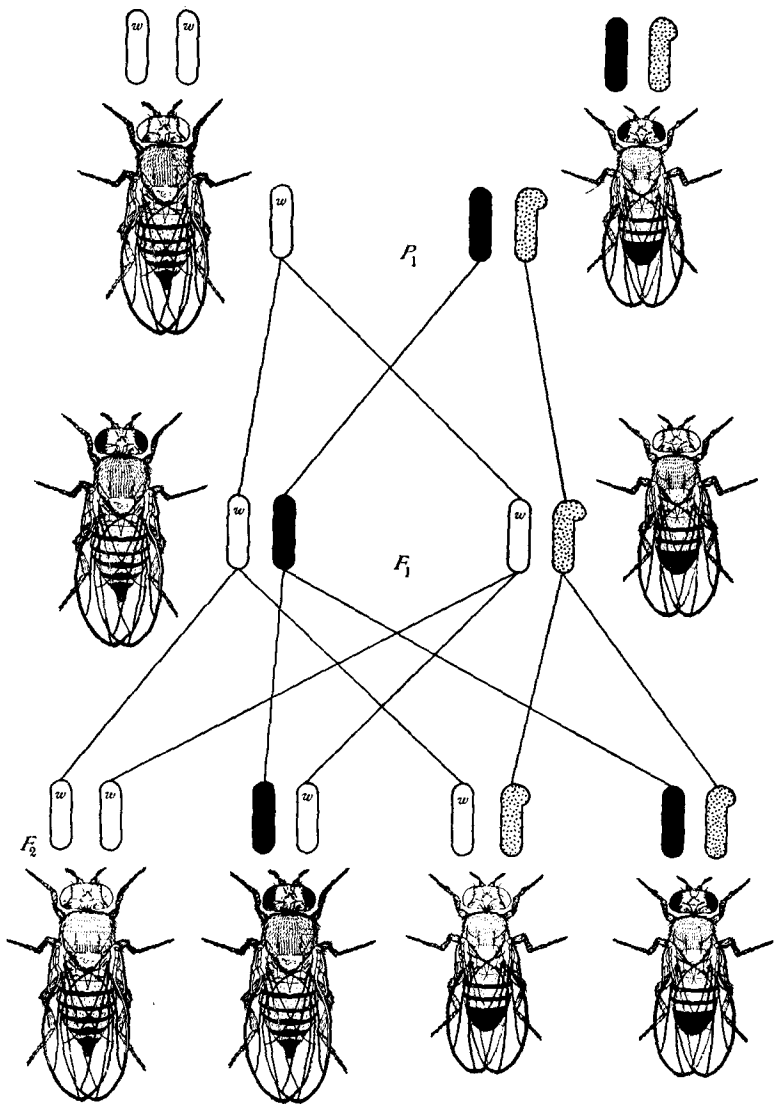


FIG. 115.

Inheritance of the white-eyed character in *Drosophila*. The gene for white eye is carried by the X-chromosome represented here by an open rod (w). The normal allelomorph to the "white-eyed gene," namely, the "red-eyed gene" is carried here by the black rod. The Y-chromosome is stippled.

explanation is obvious, if the X-chromosomes carry the differential genes involved, namely, the red- and white-producing genes. The son gets his single X from his white-eyed mother; and the daughter gets also such an X, but also one from her red-eyed father. The latter being dominant, the daughter has red eyes.

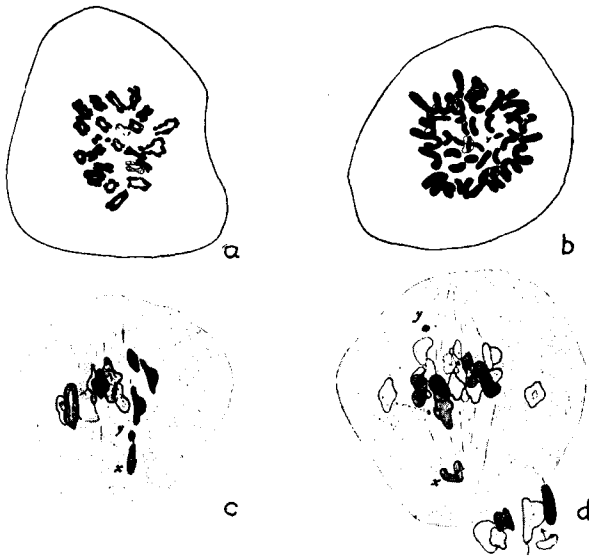


FIG. 116.

a, The reduced group of chromosomes in man, according to de Winiwarter; b, chromosome group in man, according to Painter; c and d, side view of first maturation division showing the separation of the X- and Y-chromosomes, according to Painter.

If these two individuals are inbred there will appear in the next generation white-eyed and red-eyed offspring in the ratio of 1 : 1 : 1 : 1. This ratio is due to the distribution of the X-chromosomes, as shown in the middle of the diagram (Fig. 115).

In passing, it is not without interest to note that the cytological evidence and the genetic evidence, especially

the latter, show that man belongs to the XX-XO or to the XX-XY type. The number of chromosomes in the human race has only recently been determined with any degree of accuracy. The earlier observations giving fewer have

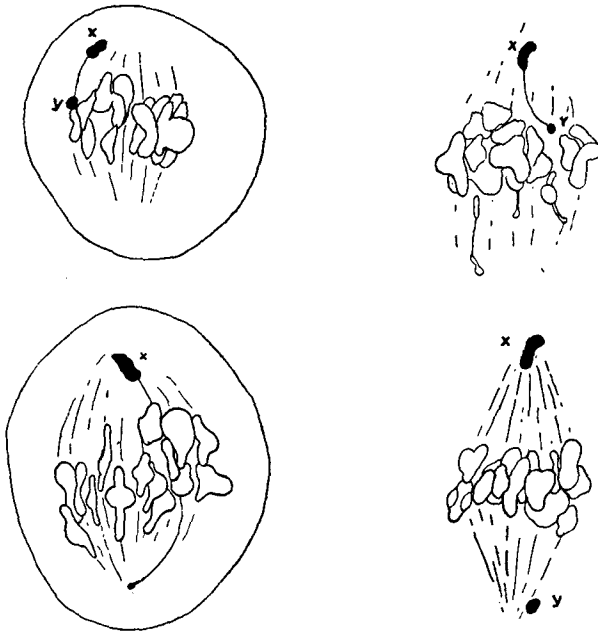


FIG. 117.

Maturation division of the germ-cells of man, illustrating the separation of the X- and the Y-chromosome. (After Painter.)

been shown to be faulty, owing to the tendency of the chromosomes to stick together in groups when the cells are preserved. De Winiwarter gives the number as 48 in the female ($n=24$) and 47 in the male (Fig. 116a), and this count is practically confirmed by Painter, who recently has shown that there is also present in the male a small chromosome that acts as the mate of a much

larger X (Fig. 117). He interprets these two as an XY pair. If so, there are 48 chromosomes in each sex, but in the male those of one pair, the sex-chromosomes, are unequal in size.

More recently still Oguma, who confirms de Winiwarter's numbers, finds no Y-chromosome in the male.

The genetic evidence for man is quite clear. The inheritance of haemophilia (or bleeding), of color blind-

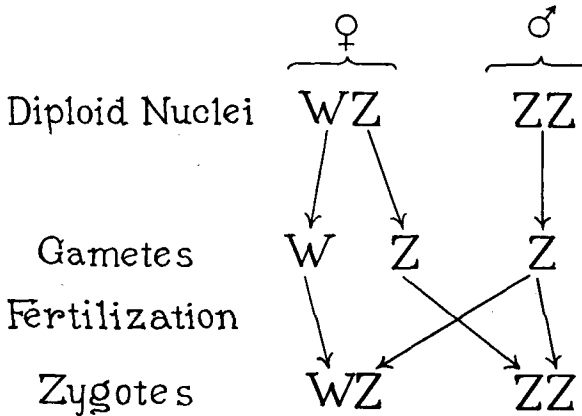


FIG. 118.

Diagram illustrating the WZ-ZZ type of mechanism in sex determination.

ness, and of two or three other human characters, follow in their inheritance the same method of transmission seen in the white-eyed flies.

The following groups of animals belong to the XX-XY type or to a modification of this type, *viz.*, the XX-XO type, in which O means the absence of Y or no X. Several mammals in addition to man have been reported to have this mechanism—the horse and the opossum, and possibly the guinea pig. It is probable that the Amphibia also belong here, as well as teleostean fish. Most of the

insects belong to this group, with the exception of the Lepidoptera (moths and butterflies). In the Hymenoptera, however, another mechanism determines sex (see below). The roundworms (Nematodes) and sea urchins belong also to the XX-XO type.

The Avian Type (WZ-ZZ).

The other type of sex mechanism, the avian-moth type, is shown in the diagram (Fig. 118). The male has two like sex-chromosomes that may be called ZZ. These sepa-

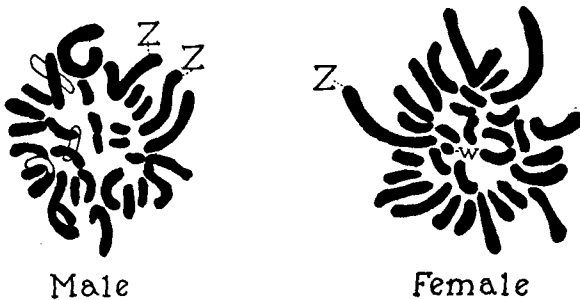


FIG. 119.

Male and female chromosome groups of the fowl. (After Shiwago.)

rate at one of the two maturation divisions and each ripe sperm-cell comes to contain one Z. The female has one Z-chromosome and a W-chromosome. When the eggs mature, each egg is left with one or the other of these chromosomes. Half the eggs contain a Z- and half contain a W-chromosome. Any W-egg fertilized by a Z-sperm produces a female (WZ). Any Z-egg fertilized by a Z-sperm produces a male (ZZ).

Here again we find a mechanism that automatically produces two kinds of individuals, females and males, in equal numbers. As before, a 1 to 1 sex-ratio results from the combination of chromosomes that takes place

at fertilization. The evidence for this mechanism in birds comes both from cytology and from genetics, although the former is as yet not entirely satisfactory.

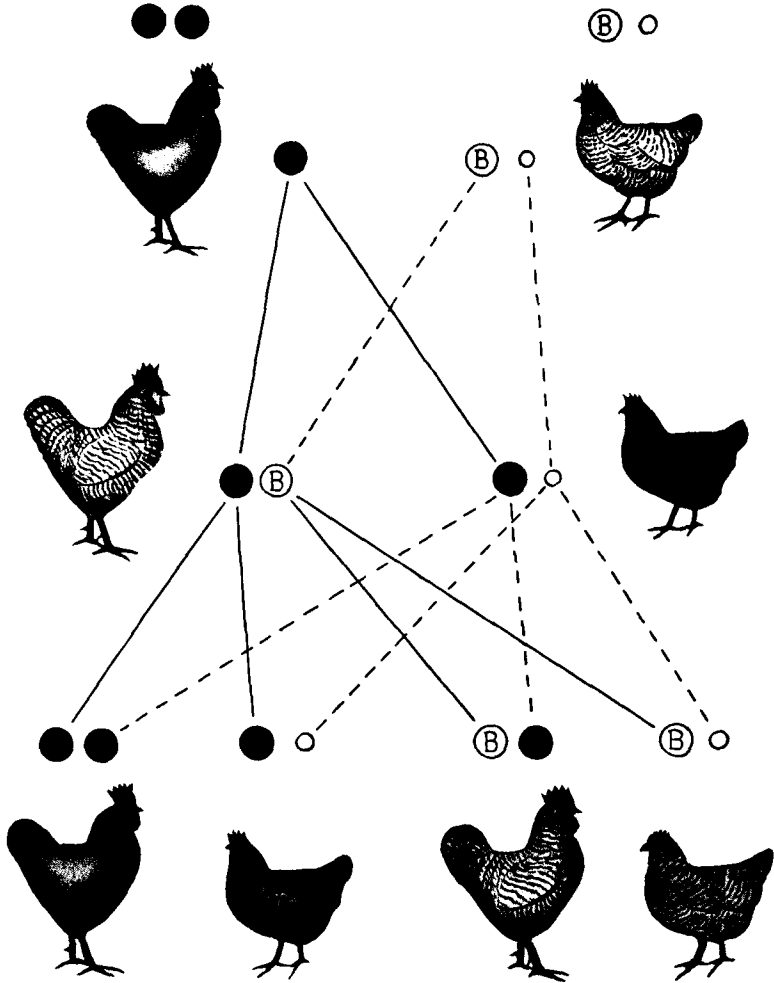


FIG. 120.

Diagram of cross between black and barred poultry, showing sex-linked inheritance.

According to Stevens, in the chick the male appears to have two large chromosomes equal in size (Fig. 119), presumably X's; the female has only one of these. Shiwago and Hance confirm these relations.

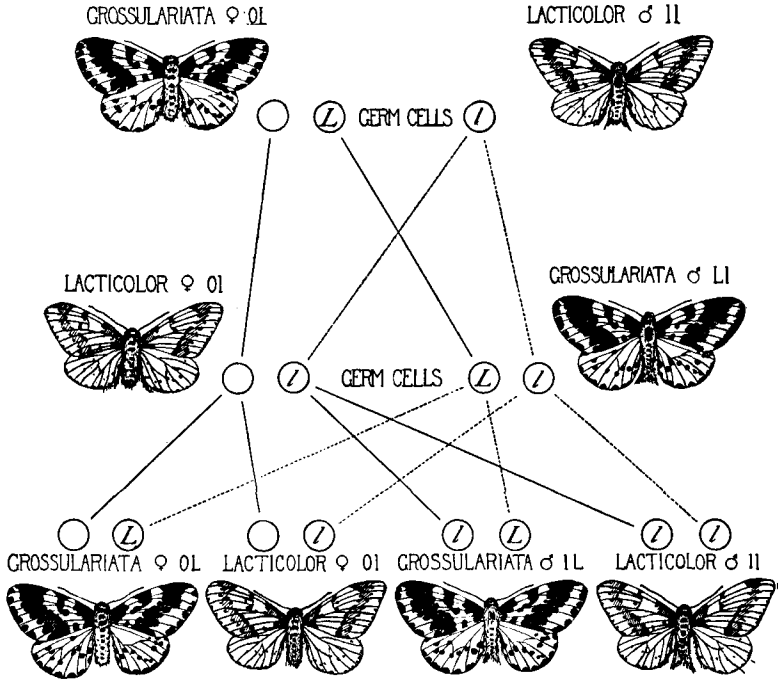


Fig. 121.

Sex-linked inheritance in the currant moth, *Abraxas*.

The genetic evidence for birds is beyond dispute. It comes from sex-linked inheritance. If a Black Langshan male is mated to a Barred Plymouth Rock female, the sons are barred, the daughters are black (Fig. 120). This is expected if the differential genes are carried by the Z-chromosomes, because the daughter gets her single Z-chromosome from her father. If the F₁ offspring are bred

together, they produce barred and black males and females as 1:1:1:1.

A similar mechanism is found in moths, where the cytological evidence is more certain. When a female of the darker wild type variety of the currant moth (*Abraxas*) is mated to a lighter mutant type, the daughters have a

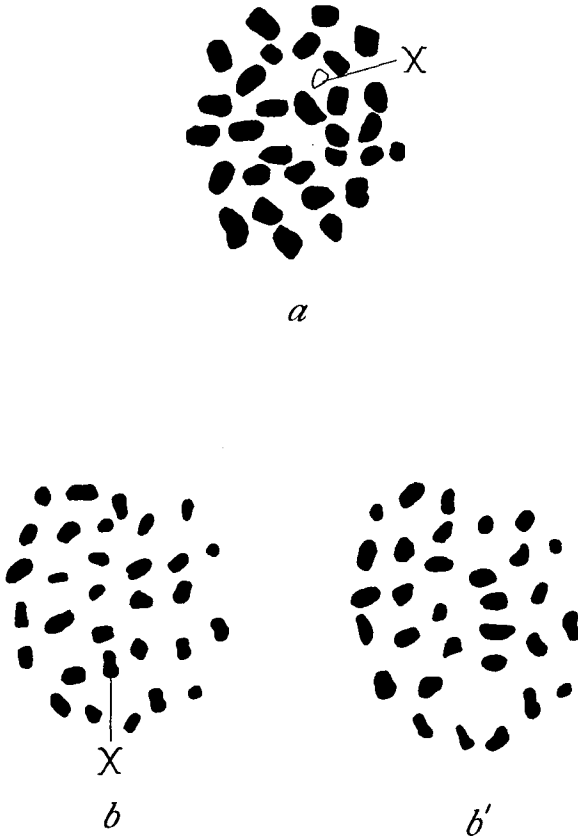


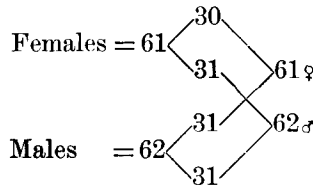
FIG. 122.

a, Reduced group of chromosomes of the egg of *Fumea casta*; *b* and *b'* outer and inner pole of the first maturation division of the egg; the single X-chromosome is present only at one pole. (After Seiler.)

lighter color, like the father; the sons a darker color, like the mother (Fig. 121). The daughter gets a single Z from her father; the son also gets this Z from his father, but another from his mother. This maternal Z carries the gene for darker color that is dominant, hence the darker color of her sons.

In the silkworm moth, Tanaka has found a sex-linked character, translucent skin of the larva, that is inherited as though carried in the Z-chromosomes.

In the moth *Fumea casta* there are 61 chromosomes in the female and 62 in the male. After conjugation of the chromosomes in the egg there are 31 chromosomes present (Fig. 122a). At the first polar division, when the first polar body is given off, 30 of the chromosomes (bivalents) divide and pass to opposite poles; the thirty-first single chromosome passes undivided to one or the other pole (Fig. 119b and b'). Half of the eggs will come to contain 31, half 30 chromosomes. At the next polar division all the chromosomes present divide, leaving each egg with the number it had before this division (*i.e.*, 31 or 30). In the ripening of the sperm of this moth, 31 bivalent chromosomes are present after conjugation of the chromosomes. At the first division the members of each pair separate and at the second each divides. Each spermatozoön carries 31 chromosomes. Fertilization of the eggs gives the following combinations:



In another moth, *Talaeporia tubulosa*, Seiler finds 59 chromosomes in the female and 60 in the male. In *Solen-*

bia pineti an unpaired chromosome is not visible in the female or in the male, nor is an unpaired chromosome visible in several other moths. On the other hand, in *Phragmatobia fuliginosa* there is a compound chromosome containing the sex-chromosome. In the male there are two of these present; in the female only one is compound like those of the male. It seems not improbable that this relation may also exist in other moths where the W-element and the Z-elements do not appear as separate chromosomes.

Another demonstration of sex-linked inheritance in moths has been given by Federley in a cross between two species of moths (*Pygaera anachoreta* and *P. curtula*). This case is interesting because within each species the male and female caterpillars are alike. They show specific differences, however, when the caterpillars in the two species are compared. This specific difference, that is not dimorphic within the species, becomes the basis for a sexual dimorphism in the F_1 caterpillars (when the cross is made "one way"), because, as the results show, the main genetic difference between the caterpillars in the two races lies in the Z-chromosomes. When *anachoreta* is the mother and *curtula* the father, the hybrid caterpillars, after the first molt, are markedly different. The hybrid male caterpillars are closely similar to those of the maternal race (*anachoreta*), while the hybrid female caterpillars resemble those of the paternal race (*curtula*).

The reciprocal cross gives offspring that are all alike. These results are explicable on the assumption that the *anachoreta* Z-chromosome carries a gene (or genes) dominant to the gene (or genes) in the Z-chromosome of *curtula*. The special interest in this case is due to the genes in one species acting as a dominant to allelomorphic genes in the same chromosome of the other species. The analysis of the result can be carried over consistently

to the next generation, produced by back-crossing the F_1 male to either parent stock, provided, however, the triploid nature of the offspring be taken into account. (See Chap. IX.)

There are no grounds for supposing that the chromosomes involved in the XX-XY and in the WZ-ZZ types are the same. On the contrary, it is difficult to imagine how one type could change over directly into the other. There is no theoretical difficulty, however, in supposing that the change in balance that gives the two sexes may have arisen independently in the two types, even although the actual genes involved are the same or nearly the same in both.

Sex-Chromosomes in Dioecious Flowering Plants.

One of the surprises of the year 1923 was the simultaneous announcement by four independent workers that in some of the flowering plants with separate sexes a mechanism is present that follows the XX-XY type.

Santos found in the male of *Elodea* that 48 somatic chromosomes are present (Fig. 123), consisting of 23 pairs of autosomes and an XY unequal pair. At maturation the X and Y separate. Two kinds of pollen grains result, one with X, the other with Y.

Two other cytologists, Kihara and Ono, found in male plants of *Rumex* 15 somatic chromosomes consisting of 6 pairs of autosomes and 3 heterochromosomes (m_1 , m_2 , and M). These three come together at maturation of the germ-cells to form a group (Fig. 123). The M goes to one pole, the two small m 's to the opposite. Two kinds of pollen grains result, $6a+M$ and $6a+m+m$. The latter are male-determining.

Winge found an XY pair of chromosomes in two species of hops (*Humulus lupulens* and *H. japonica*). Nine

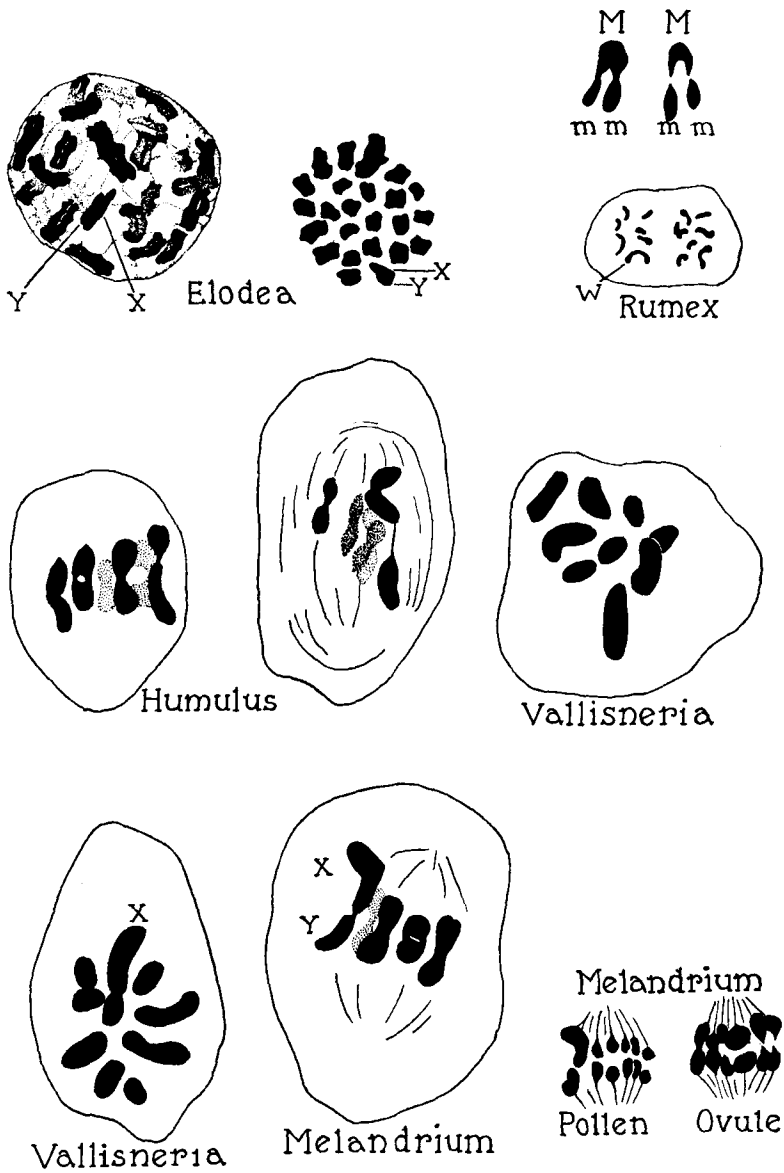


FIG. 123.

Maturation groups of several dioecious plants. (After Bělař.)

autosomes and an XY pair are present in the male. He also found in *Vallisneria spirales* that in the male there is an unpaired X-chromosome. The formula is $8a+X$.

In *Melandrium*, Correns has concluded from breeding work that the male is heterogametic. Winge reported that the male formula is $22a+X+Y$, which confirms Correns' deduction.

Miss Blackburn also reported an unequal pair of chromosomes in the male of *Melandrium*. She adds one all-important link to the chain of evidence. The female has two equal sex-chromosomes, one of them corresponding to one of the sex-chromosomes of the male (Fig. 123). At maturation they conjugate and reduce.

From this evidence we may, I think, safely conclude that some at least of the dioecious flowering plants make use of the same kind of mechanism for sex-determination that is present in many animals.

Sex-Determination in Mosses.

Several years before these observations on flowering plants had been made, it had been shown by the Marchals that when the spores are formed in dioecious mosses—mosses that have separate male and female gametophytes¹ (or sexual prothallia)—two of the spores derived from

¹ In mosses, ferns, and liverworts the haploid or gametophyte generation is spoken of as consisting of two sexes, male and female, and the diploid generation (sporophyte) as non-sexual or neutral. In flowering plants, the plant itself corresponds to the sporophyte of the mosses. It carries, as it were, the gametophyte generation within its pistil and stamens. A paradox arises from the use of the same terms male and female in mosses for one generation, that is, the haploid one, and for the alternative generation in flowering plants, that is, the diploid. The paradox is not so much a question of diploid and haploid (this contrast is encountered even within the same generation in some animals—bee, rotifers, etc.), but in using the same terms for contrasted generations, one sexual, the other non-sexual. With this understanding, however, no serious difficulty arises by following conventional usage.

the same sporophyte mother cell produce female gametophytes and the other two male gametophytes.

Somewhat later Allen discovered in the nearly related group of liverworts (Fig. 124) that in the haploid female

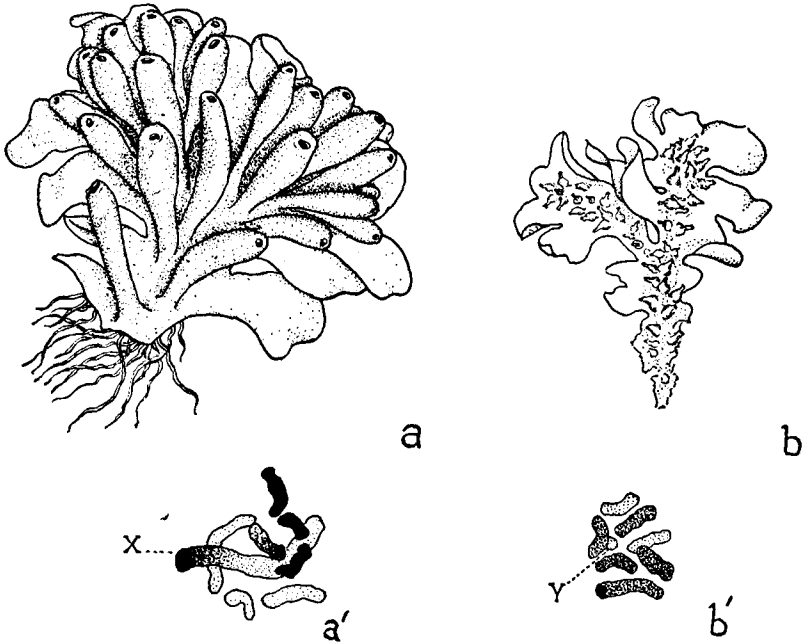


FIG. 124.

a, Female and b, male prothallia of liverwort. The female with one large X-chromosome, a'; the male with one small Y-chromosome, b'. (After Allen.)

prothallium (gametophyte), with eight chromosomes, there is one (X) that is much larger than the other seven chromosomes; and in the haploid male prothallium (gametophyte), with eight chromosomes, one (Y) is much smaller than the other seven (Fig. 121b'). Each egg will

contain an X-, and each sperm a Y-chromosome. After fertilization the sporophyte will have 16 chromosomes (including one X and one Y). When the spores are formed, reduction takes place, the X and the Y separating. Half of the haploid spores so formed will contain an X and give rise to a female prothallium, and half will contain a Y and give rise to a male prothallium.

More recently still, Wettstein has made some critical experiments with dioecious mosses, experiments that carry the analysis further. By utilizing a discovery of the Marchals, he produced gametophytes that contained both the male and the female groups of chromosomes (Fig. 125 to the left). For example, following the Marchals' method, he cut off pieces of the spore-bearing stalk (whose cells are diploid). From the fragment a gametophyte developed, also diploid. In this way he obtained FM gametophytes.

Then in another way he made diploid male and female moss plants that were double females (FF) and double males (MM). This was accomplished as follows:

By treating the protonema threads with chloral hydrate and other drugs and reagents, he brought about the suppression of a cell division in an individual cell after the chromosomes had already divided. In this way he could produce in these dioecious species, diploid giant cells that were doubled in their female or else in their male elements, chromosomes, for example. From such a diploid cell a protonema or moss plant was produced. By artificial means Wettstein then brought about several new combinations, some triploids, others tetraploids. Some of the most interesting of these combinations are shown in the diagram (Fig. 125, to the right).

A diploid cell from a *female* thread gives a diploid moss plant, FF, that produces diploid egg-cells. Similarly an MM plant is produced from a diploid *male* thread.

When an FF egg and an MM sperm are brought together a tetraploid sporophyte (FFMM) is produced.

When the FF' ovule is fertilized by a normal male

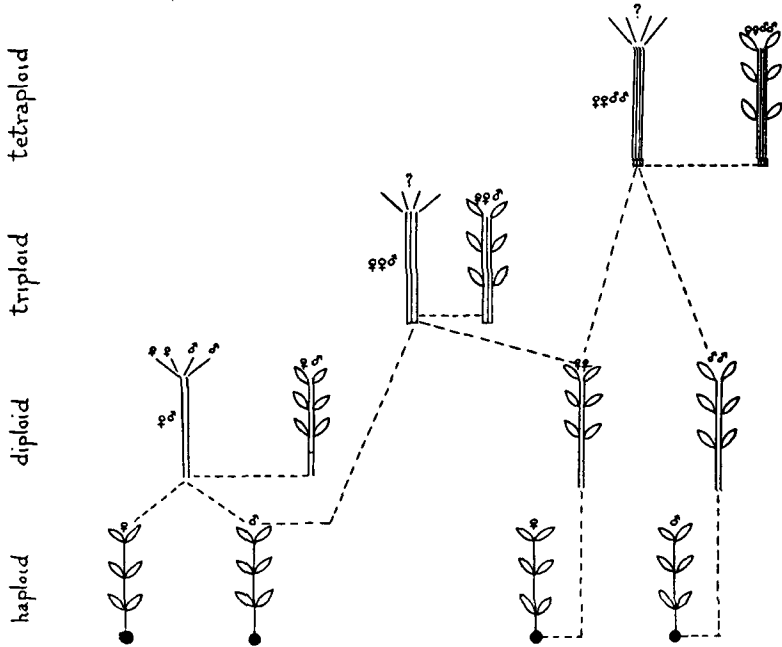
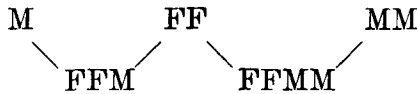


FIG. 125.

Diagram illustrating different combinations of diploids and triploid mosses. (After Wettstein.)

sperm cell M, a triploid sporophyte (FFM) is produced. Thus:



From each sporophyte, FFM and FFMM, a gametophyte can be regenerated. Each of these plants develops both

male and female elements, and both produce eggs and sperm-cells; but the number of female organs (archegonia) and of male organs (antheridia) and their time of appearance show characteristic differences.

The Marchals had obtained, as has been said, the diploid FM gametophyte in the same species used by Wettstein, and had shown that it produces both female and male organs. Wettstein confirms this and reports that the male organs develop before the female.

A comparison of the three types, FM, FFM, FFMM, is interesting. The FM plant is strongly protandric. At first there is a great excess of antheridia or male organs compared with archegonia. The archegonia develop later.

The FFMM plant is, as Wettstein says, twice as strongly protandric as the FM plant. At first only antheridia appear. Very late in the year, when the old antheridia have gone, a few young archegonia appear—some plants never develop them. Still later a vigorous development of female organs may set in.

The triploid plants are protogynic. At least, at the time when the FFMM tetraploid plants have only male organs (in July), the triploids have only female organs. Later (in September) both organs are present.

These experiments are interesting in showing how artificial hermaphroditic individuals may be made from plants that normally have separate sexes by combining the two sets of elements. The results also show that the sequence in which the sexual organs develop is determined by the age of the plant. More important is the actual reversal of this time relation by changing the genetic composition in the opposite direction.