

CHAPTER XVI

INTERSEXES

IN recent years some curious individuals have been found in species with separate sexes, that combine to varying degrees the characters of males and females. At present most of these intersexes, or sex intergrades, may be referred to four sources: (a) to changes in the ratio of the sex-chromosomes to the rest of the chromosomes; (b) to changes in the genes not visibly connected with changes in chromosome number; (c) to changes that result from crossing wild races, and (d) to changes in the environment.

Intersexes from Triploid Drosophila.

To the first class of intersexes belong some of the offspring of triploid females of *Drosophila*. When the eggs of a triploid female mature, the chromosomes are irregularly distributed, and, after the polar bodies have been given off, the eggs are left with different numbers of chromosomes. If such a female is mated to a normal male whose sperm carries one set of chromosomes, the offspring that come through are of several kinds (Fig. 138). There is reason to believe that many eggs do not develop at all, because they lack the right combination to produce a new individual; but amongst the survivors there are some triploids, more diploids (normals), and a few intersexes. These intersexes (Fig. 139) have three sets of autosomes and two X-chromosomes (Fig. 138). The formula is $3a+2X$ (or $3a+2X+Y$). Thus, although the intersex has the same number of X-chromosomes as has

an ordinary female, it has one set more of the ordinary chromosomes. It is clear from this that sex is determined not by the actual number of the X-chromosomes present, but by the ratio of these to the other chromosomes.

Diploid	Triploid	Tetraploid
$2a+2X=\text{♀}$	$3a+3X=\text{♀}$	$4a+4X=\text{♀}$
$2a+X+Y=\text{♂}$	$3a+X+Y=\text{Super♂}$	$4a+2X+Y=\text{♂}$
	$3a+2X=\text{Intersex}$	
	$3a+2X+Y=$ "	

FIG. 138.

Diagram giving the formulae of normal, triploid, tetraploid, and intersexes of *Drosophila melanogaster*. The tetraploid male ($4a+2X+2Y$) is hypothetical. Besides these classes the triploid female gives rise to superfemales ($2a+3X$). (After Bridges.)

From these exceptional relations amongst the chromosomes, described by Bridges, he concluded that sex is determined by a balance between the X's and the other chromosomes. We may think of the X-chromosomes as containing more of the genes that go to produce a female, and the rest of the chromosomes as containing more of the genes that go to produce a male. In the normal female, $2a+2X$, the two X's turn the scale toward femaleness. In the normal male there is only one X, and the balance turns the other way. The triploid, $3a+3X$, and the tetraploid, $4a+4X$, have the same balance as the normal female and are practically identical with her. The expectation for the tetraploid male, $4a+2X+Y$ (that has not yet been obtained), is that he will be like the normal male, since the balance is the same in both.

This evidence from triploids gives no specific information as to the occurrence of genes for sex-determination. If we think of the chromosomes only in terms of genes, it follows that genes are involved, but the evidence does not show what they are like. Even if genes are involved, we

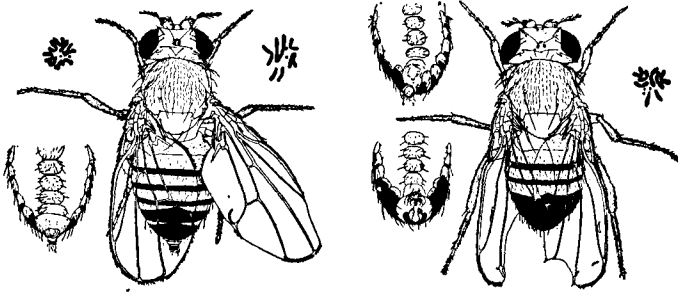


FIG. 139.

To the left the female type of intersex of *Drosophila*, as seen from above and below. The chromosome groups show two X's, three each of the larger autosomes (II and III) and usually (two here) small IV-chromosomes. To the right the male type of intersex, as seen from above and below. The chromosome group has two X's, three each of II and III, and usually only two IV's (here three).

cannot state whether there is one gene in the X that stands for femaleness, or hundreds of such genes. Similarly for the ordinary chromosomes—the evidence does not tell us whether the genes for maleness, if there be such, are in all the chromosomes or in only one pair.

There are, however, two ways in which we may hope, some day, to discover something about the genes that influence sex. The X-chromosome may become fragmented in such a way as to reveal the location of the special genes relating to sex, if there are such. The other hope rests on the occurrence of a gene mutation. If other

genes mutate why not sex-genes, if there are such specific genes?

There is, in fact, one certain case of the occurrence of an intersex that arose by a mutant change in the second chromosome of *Drosophila*. Sturtevant (1920) studied this case, and found it due to a change in genes in the second chromosome. The female is turned into an intersex. Unfortunately, the evidence does not show whether or not a single gene only was affected.

It is apparent, from what has been said, that while we can interpret the sex-determining formulae in terms of genes, we have no direct evidence, at present, that there are any specific genes for maleness and femaleness. There may be such genes, or it may be that sex is determined by a quantitative balance between all the genes. But since we have much evidence that the genes differ amongst themselves very greatly as to the kind of effects that they produce, it seems probable, I think, that certain genes may be more influential as sex differentials than are other genes.

Intersexes in the Gypsy Moth.

Goldschmidt has carried out an extensive series of very interesting and important experiments in the production of intersexes in racial crosses of the gypsy moth.

When the female of the common European gypsy moth (Fig. 140a, b) is crossed to a Japanese male, equal numbers of male and female offspring are produced. When the cross is made the other way the sons are normal, but the daughters are intersexes or male-like females (Fig. 140c, d).

Later Goldschmidt carried out an elaborate series of crosses between the European species and several Japanese species and also between different races of Japanese varieties or species. The results may be arranged in two

series. In one series the females are finally all changed over into males; in the other series the males are changed over into females. The former change is spoken of as female intersexuality; the latter, as male intersexuality. Without attempting to review the long series of experiments from which the evidence has come, Goldschmidt's theoretical deductions may be stated as briefly as possible.

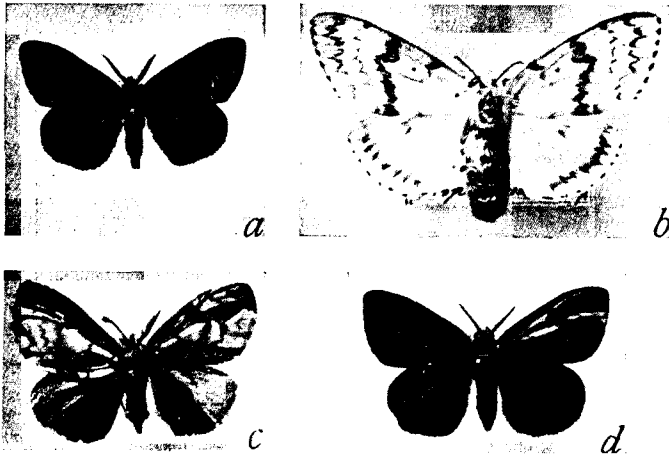


FIG. 140.

a, Male and *b*, female of *Lymantria dispar*; *c* and *d* two intersexes. (After Goldschmidt.)

The formula he uses for the male is MM and for the female Mm; in other words, the WZ-ZZ formula. In addition, however, Goldschmidt adds another set of sex-determining factors that at first he called FF, which stand, in a way, for femaleness. The male factors are supposed to segregate, as do Mendelian factors in general, but the FF factors do not segregate and are transmitted only through the egg. They were supposed to reside in the cytoplasm, although Goldschmidt has later shown an inclination to locate them in the W-chromosome.

By assigning numerical values to the big M's (none to the m) and to FF he has built up a scheme to show how, in the cross first mentioned, equal numbers of males and females result when the cross is made in one direction, and intersexes when it is made in the opposite direction.

In like manner, by assigning suitable values to the letters in each of the other crosses an approximately consistent account can be given of the results.

The unique feature of these formulas of Goldschmidt is not, in my opinion, the numerical values attached to the factors, for these are arbitrary, but the statements that the results can be explained only by the assumption that the factors for femaleness are in the cytoplasm, or else in the W-chromosome. In this respect his view is different from the condition that Bridges has found in *Drosophila* from a study of triploids, where the opposing influences are in the X-chromosomes and in the autosomes.

Goldschmidt has recently (1923) reported a few exceptional cases in which the evidence indicates, he believes, that the female-producing factors lie in the W-chromosome. One such case relates to certain racial crosses, where, through non-disjunction, a female receives a W-chromosome (Y in his formula) from the father and the Z from the mother. This is the reverse of the ordinary transmission of these chromosomes. The results indicate that the female factors follow the W. Logically, the evidence appears satisfactory, but on the other hand both Doncaster and Seiler have reported a few exceptional female moths in which the W-chromosome is at times absent. These moths were normal females in every respect and bred as such.¹ They could not be

¹ There are 56 chromosomes present in the female and in the male of *Abraxas*. That one of those in the female is a W-chromosome is very probable, from Doncaster's discovery of a strain in which the females have only

females, on Goldschmidt's view, if the female factors are in the W-chromosome.

Before leaving Goldschmidt's theories a very interesting suggestion that he has made to account for the mosaic character of the intersexes must be mentioned. The intersex consists of parts that are male and parts that are female—patches of each. Now Goldschmidt suggests that this is brought about by a difference of time at which the male and the female parts are determined in the embryo. Expressed in a different way, one may say that in certain combinations of the sex factors of the racial hybrid-intersexes, the individual starts as a male. The organs of the embryo that are the first to be laid down are therefore male-like. In later stages, the female factors overtake and surpass the male-producing ones, so that the later stages of the embryo are like the female. Hence the mosaic characters for this class of intersexes.

Conversely, in the reciprocal type the embryo starts under the influence of the female factors, and the first parts of the embryo to be laid down are female-like. In later stages the male-producing factors overtake and surpass the female tendencies, and male organs develop.

In general Goldschmidt treats the genes as enzymes, although at times he concedes that the enzymes in question may be the product of the genes, which seems more consistent with what we infer as to the nature of genes. Until we can discover whether all the genes are active all the time, or whether all or some of them are active only when the embryo is passing through certain stages of development, we can do little more than speculate as to what takes place.

55 chromosomes. The absence of one chromosome, presumably the W, produces no visible changes in the character of the female. That the missing chromosome is really a sex-chromosome and not an autosome is highly probable from the fact that individuals lacking it are always females.

The Free Martin.

It has long been known that when twins in cattle are born, one of which is a normal male, the other a "female," the latter is usually sterile. It is known as a free martin. The external genitalia of the free martin are generally female, or much more female-like than male, but it has been demonstrated that the gonads may resem-

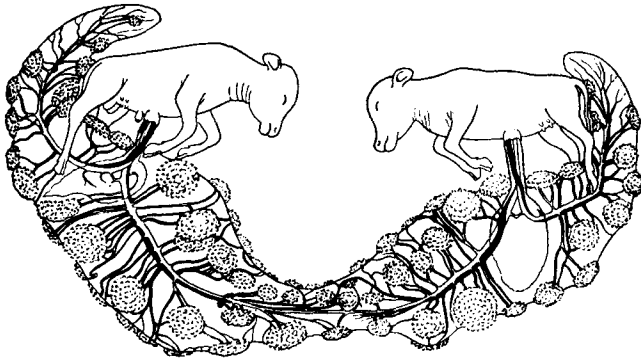


Fig. 141.

Two embryo calves, one of which will become a free martin, whose placentas are united. (After Lillie.)

ble testes. It was shown by Tandler and Keller (1911) that the twins (one of which is a free martin) come from two eggs, and Lillie (1917) has fully confirmed this fact. It was also shown by Tandler and Keller that there is present a vascular connection between the two embryos in utero by means of intra-chorionic connections (Fig. 141). Magnussen (1918) described a considerable number of free martins of various ages, and has shown by histological examination that well-developed testicular-like organs are present in older free martins, *i.e.*, that the characteristic tubular structure of the testes, including rete tubules, sexual cords, and epididymis, is present.

Chapin (1917) and Willier (1921) have confirmed these observations, and the latter especially has given a detailed account of the transformation of the "indifferent stage" of the ovary into a testis-like structure.

Magnussen (who erroneously believed the free martin to be a male) found no spermatozoa in the "testes." Their absence he believed to be due to the retention of the testes within the body cavity (cryptorchidism). It is known that in those mammals in which the testes normally descend into the scrotal sacs, sperm-cells are absent when the testes are retained, but in the early embryo germ-cells appear while the testes are still within the body cavity. In the free martin there are, according to Willier, no primordial germ-cells present in the so-called testis.

Lillie's conclusion that the free martin is a female whose gonads have been transformed into a testis-like organ is so strongly supported by this evidence that it can scarcely be questioned, but whether the effect is to be referred to the composition of the blood of the male, or, as he thinks, to a testicular hormone in the blood is open to question, since there is at present no evidence of any specific substance produced by the gonad of the male embryo that produces such an effect on the development of the young ovary. Since all the tissues of the male embryo have the male chromosomal composition, the blood may likewise have a different chemical constitution from that of the female, and affect, in consequence, the development of the gonad. It is generally recognized that the young gonads have rudiments of both ovary and testes present, or, as Willier puts it, "the primordium of each male structure developed in the free martin gonad is present in the ovary at the time of sex differentiation." The most significant fact in these observations is the absence of male germ-cells in the free martin. The influ-

ence of the blood of the male co-twin does not bring about the transformation of the primordial egg cells into sperm-producing cells.

Individuals with both male and female sexual organs, even including ovaries and testes, have been frequently recorded in mammals, including man. These were formerly called hermaphrodites, but now are sometimes called intersexes or sex intergrades. The conditions that give rise to them are unknown. Crew reports twenty-five cases in goats, seven in pigs.² These, Crew believes, are modified males, since testes were present in all of them. Baker has recently reported that the sex intergrading pigs are surprisingly common on some of the islands [New Hebrides]; "one finds them in nearly every little village." This tendency to sexual abnormality is inherited through the male in some cases reported by him. Baker regards them as probably transformed females.³

² Pick and others had earlier described such individuals, two in horses, one in sheep, one in cattle.

³ Prange has described four hermaphroditic goats with external female genitalia, but with undeveloped mammae. In sex behavior and in coat they were male-like. Internally both male and female ducts were present, but the gonads were testes (cryptorchid).

Miss Harman has described a "gynandromorphous" cat that had a testis on the left side and an ovotestis on the right side. The reproductive system of the left side is like that of a normal male, while that of the right side is like that of the female, except for the size, etc., of the uterine tube.