

CHAPTER XVII

SEX REVERSALS

IN the older literature dealing with sex-determination the idea is often expressed that the sex of the embryo is determined by the environmental condition under which the embryo develops. In other words, the young embryo has no sex, or is indifferent, and its fate is determined by its environment. It is unnecessary to go over again the evidence from which this idea originated, since practically all of it has been shown to be defective in one way or another.

In recent years there has been some discussion concerning the reversal of sex, which means, by implication, that a male, already determined as such, can become changed into a female, and vice versa. It has even been suggested that, if this can be shown to occur, the genetic interpretation of sex is discredited or even overthrown. It is scarcely necessary to point out that there is nothing in the theory of sex as determined by sex-chromosomes or genes contradictory to the idea that other influences may so affect the development of the individual as to change or even reverse the balance normally determined by the genes. To fail to appreciate this is to fail entirely in grasping the ideas that underlie the theory of the gene; for this theory postulates no more than that in a given environment such and such effects are expected as a result of the genes present.

It is no more surprising that a genetic male might, in an abnormal environment, turn into a female, or vice versa, than that an individual might at one stage of its

development function as a male and at a later stage as a female. It remains, then, entirely a question of fact whether evidence can be produced proving that an individual having the genetic make-up of a male may, under a

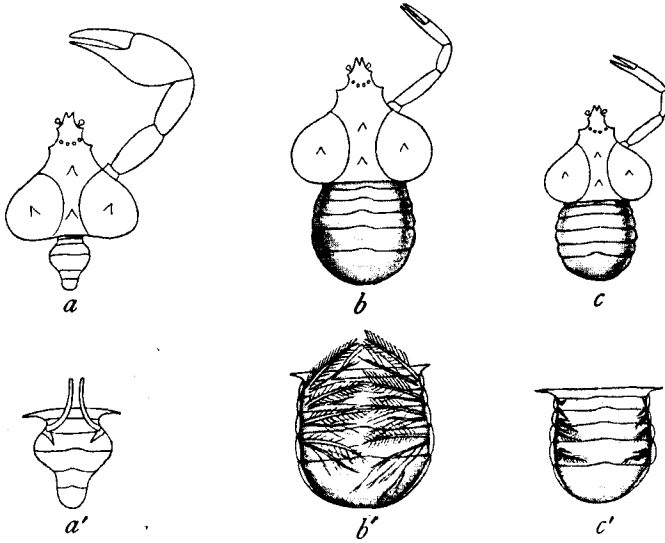


FIG. 142.

Spider crab, *a*, normal male; *a'*, abdomen of normal male from below; *b*, normal female; *b'*, abdomen of normal female from below; *c*, parasitized male; *c'*, abdomen of parasitized male from below. (After Geoffrey Smith.)

different set of conditions, become a functional female, or the reverse. Several such cases have been reported in recent years which call for a careful and unprejudiced scrutiny.

Environmental Changes.

It was shown by Giard in 1886 that when the males of crabs are parasitized by other crustaceans, such as *Pelto-*

gaster or *Sacculina*, they then develop external characters like those of a female. In Fig. 142a, an adult male crab is shown, with its large claws, and in a' the under side of its abdomen with the copulatory appendages, and in b an adult female is shown, with her small claws, and in b' the under side of her abdomen with the setose bifurcated egg-carrying appendages. In c is shown a male that has been infected at an early stage; the claws are small, resembling those of the female, and the abdomen is broad and female-like; in c' the under side of the abdomen of the infected male is shown. It has small bifurcated appendages like those of the female.

The parasite sends long root-like processes into the body of the crab, on which the parasite lives by absorbing the juices, and may, in turn, set up physiological processes in the crab itself. The testes of the crab may not at first be affected, but later may degenerate. In one case, at least, where the parasite had fallen off, Geoffrey Smith found large germ-cells developing in the regenerating testis, which he interpreted as eggs.

Giard left open the possibility as to whether the change in the crab was due to the absorption of the testis, or whether the action was more direct on the host. Geoffrey Smith has brought forward some evidence relating to fat in the blood, and certain arguments in favor of the view that the change in the crab is due to the physiological effects on the host. There is no evidence in crustacea that the destruction of the gonads affects the secondary sexual characters.

In insects, where there is evidence from castration, it has been shown that the removal of the testes or ovary does not alter the secondary sexual characters. It is all the more significant, therefore, that in one case described by Kornhauser (1919), in a bug (*Thelia*) that is parasitized by a hymenopter (*Aphelopus*), the male shows

the secondary characters of the female or at least fails to develop those of the male.

While most of the decapod crustacea have male and female sexes there are a few cases where both ovaries and testes are present in one or in both sexes, and there are a few cases where the young males may have large egg-like cells in the testes. Several crayfish have also been described that are sex intergrades, but no complete reversals are known.¹

In Daphnians, and related forms, intersexual individuals have been described by several observers (Kuttner, Agar, Banta, etc.), but no complete reversals are known. Sexton and Huxley have recently described some individuals of *Gammarus* that are called female intersexes, which, "on reaching maturity, more or less closely resemble females but gradually come to resemble males more and more nearly."

Most of the barnacles are hermaphroditic. In some genera there are, in addition to the large sessile hermaphrodites, minute complemental males, and there are a few other species with sessile female individuals and complemental males. The sessile individuals are generally supposed to be true females, but Geoffrey Smith has suggested that if a free-swimming larva becomes fixed it grows to full size, passing through the male stage to become a female, but if a free-swimming larva attaches itself to a female it develops no further than the male stage. This seems to mean no more than that the environment determines whether a potential individual develops into a female or being arrested in its development becomes a male.

The last case is similar to another in the gephyrean worm, *Bonellia*, described by Baltzer. If a free-swimming

¹ See Faxon, Hay, Ortman, Andrews, Turner.

larva attaches itself to the proboscis of a female it remains extremely small and develops testes, but if it settles down by itself it becomes a large female individual. The evidence does not positively rule out the possibility that there are two kinds of individuals that behave in one or the other way, but Baltzer's interpretation seems very probable.

If the correct interpretation for the barnacles and for *Bonellia* is that suggested above, it means that sex is determined in these forms by environmental conditions, which means, in terms of genes, that all the individuals are alike.²

Changes of Sex Associated with Age.

Biologists are familiar with several cases both in animals and in plants where an individual may first function as a male and later as a female, or vice versa. But the special cases in which sex reversal takes place are those whose sex is known to be *determined* in the first place by their chromosomal make-up, yet which are said, in rare cases, to turn into the opposite sex without changing their chromosome complex.

The hagfish, *Myxine*, according to Nansen and Cunningham, is male when young, and later becomes female; but the subsequent observations of the Schreiners indicate that while the young *Myxine* is hermaphroditic—the anterior end of the gonad being a testis, the posterior an ovary—it is not so functionally. Later each individual becomes definitively male or female.

Breeders of the aquarium fish, *Xiphophorus helleri*, have reported at various times that females change into males, but, unfortunately, as yet there is no account of

² According to Gould, if a young individual of *Crepidula plana* settles down near a female it becomes at first a male and remains so permanently; but if it settles down away from large individuals it fails to develop testes and passes later into a female.

the sex of the offspring produced by these transformed females, although ripe sperm has been found in one case at least. Recently Essenberg has studied the development of the gonads in the young of this fish. At birth the fish measures 8 mm. and the gonads are in an "indifferent stage," containing two kinds of cells of peritoneal origin. At 10 mm. the sexes are distinct; in the females the primordial germ-cells gradually change into young eggs; in the male the definitive germ-cells (sperm-cells) come from the peritoneal cells. In the immature condition, between 10 and 26 mm. in length, Essenberg records 74 females and 36 males, counting amongst the females the retrogressive types, *i.e.*, those in process of transformation from "females" to "males." The sex ratio of adult fish, taken from Bellamy's records, is given as 75 ♂ to 25 ♀. The change does not appear to be due to differential viability, but to "sex inversion." This occurs most commonly in fishes from 16 to 27 mm., but may occur in later stages also. The data indicate, then, that approximately half of the "females" become males. This statement does not mean, however, that functional females have changed into males, but that half of the young "females" are identified as such by the presence of an ovary, which later changes into a testis. Recently Harms (1926) records in *Xiphophorus* the change of old females, that have become sterile, into functional males. These transformed females when bred as males produced only female offspring which means if this fish is homogametic that all the functional sperms of the secondary male are X-bearing.

A curious case has recently been described by Junker in the stonefly, *Perla marginata*. The young males (Fig. 143) pass through a stage in which an ovary is present that contains rudimentary eggs (Fig. 143). The male has an X- and a Y-chromosome and the female two X's (Fig.

144). The ovary in the male disappears when the insect becomes adult, and the testes produce normal spermatozoa. In this instance, then, we must infer that, in the young stages of the male, the absence of one X does not

Perla marginata

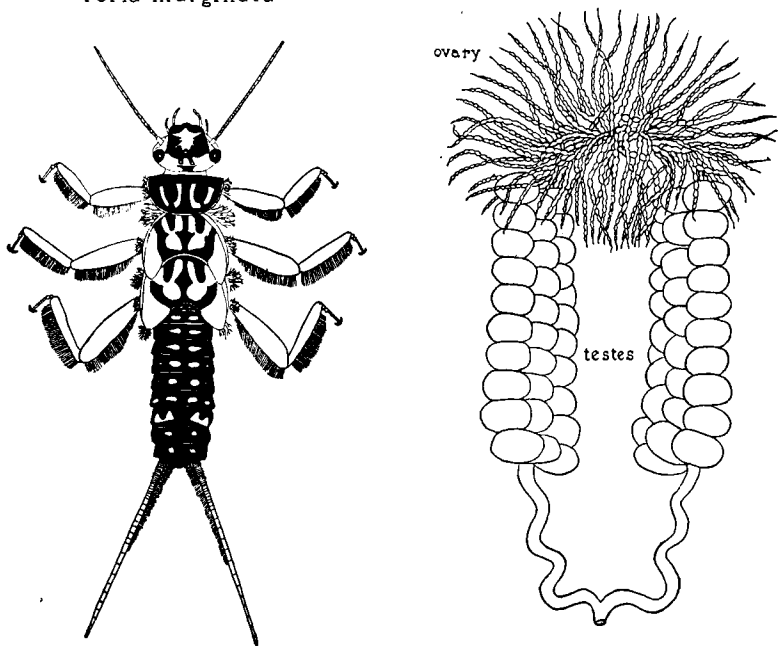


FIG. 143.

Perla marginata to the left. The ovotestis of a young male to the right. (After Junker.)

suffice to suppress the development of an ovary, but when the individual becomes adult its chromosome composition asserts itself.

Sex and Sex Reversal in Frogs.

It has been known ever since the work of Pflüger in 1881-1882 that sex ratios in young frogs are peculiar, and that, at the time of metamorphosis of the tadpole into

the frog, the gonads often appear to be intermediate. The classification of individuals of this sort as male or female has led to much dispute. In recent years it has been shown that these intermediate forms often become males, and it has even been claimed that in many races all males pass through this stage.

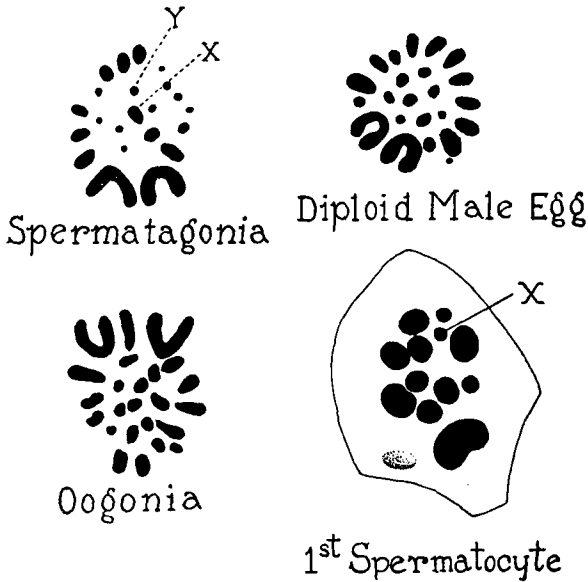


FIG. 144.

Chromosome groups, spermatogonia and oögonia, and diploid male egg of *Perla*. (After Junker.)

The experiments of Richard Hertwig have shown that by delaying the fertilization of the frog's egg, the proportion of males is greatly increased, and, in extreme cases, all individuals become males. The attempts to correlate these cases of retarded fertilization with chromosomal alterations have not been successful.

Further study has shown that the earlier results were obscured by failure to realize that different races of frogs show remarkable differences in the development of the testes and ovaries. Witschi has shown that in general there are two kinds or races of the European grass frog, *Rana temporaria*. In one of these the testes and ovaries differentiate directly from the early gonad. Such races are found in the mountains and in the far North. In the other races, living in the valleys and in the middle of Europe, the gonad in those individuals that will become males passes through an intermediate stage in which large cells are present in its interior which he regards as immature eggs. These are replaced later by a new set of germ-cells that become the definitive sperm. These races are called undifferentiated races.

Swingle also finds in the American bullfrog two types or races, speaking broadly, in one of which the testes and the ovaries differentiate early from the progonad. In the other races the differentiation is delayed: In the female of these races the larger cells of the progonad become later the definitive eggs, but in the male the progonad persists for some time after the female has differentiated. Its large cells may differentiate into spermatozoa. These are, however, later absorbed for the most part, but some of those that remain undifferentiated become the definitive sperm-cells. Swingle does not interpret the large cells in the male progonad as eggs, but as male spermatocytes. He shows that these cells pass through an abortive maturation division and then, for the most part, break down. In other words, the male does not pass through a female stage, but makes, as it were, an abortive attempt to form sperm before its second and later differentiation takes place.

Whatever interpretation is placed on these large cells in the progonad, the important point for present con-

sideration is whether external or internal conditions may affect the progonad of the prospective female in such a way that it produces later functional sperm-cells. Witschi's evidence is in favor of such a transformation in those races that are indifferent.

In the following table (Table III) Witschi has brought together the sex ratios reported by different observers from different parts of Germany and Switzerland. In the right-hand column the per cent of females is given; 50 per cent means a 1 to 1 ratio. It will be seen that in the first two groups (Group I and II) the sex ratio is approximately 1 to 1, while in the last three groups (III, IV, V) the proportion of females is higher, culminating in those regions where all the individuals from a pair may be females (100 per cent). These belong to the indifferent races.

The most important facts discovered by Witschi relate to the inheritance of these differences shown by the differentiated and undifferentiated races. Hertwig made crosses between females and males of the different races.

(1) ♀ undif. by ♂ differ. = 69 undif. ♀ + 54 ♂

(2) ♀ dif. by ♂ undif. = 34 ♀ + 52 ♂

In (1) the daughters were all undifferentiated; in (2) the daughters differentiated early. Witschi draws the conclusion that eggs of a differentiated race are more strongly female-determining than the eggs of an undifferentiated race.

In another experiment Hertwig crossed undifferentiated races whose "female determining power" (Kraft) was greater or less. Witschi concluded that weak eggs by strong sperm give the same result as strong eggs by weak sperm. "Eggs and female determining sperm of the same type have the same genetic constitution."

TABLE III

SEX RATIOS IN DIFFERENT LOCAL RACES OF THE GRASS FROG SHORTLY
AFTER METAMORPHOSIS (AT MOST TWO MONTHS)

Those with asterisk were caught in the open.

Group	Locality	Author	Number of Animals Examined	Per cent of Females
I	Ursprungtal (Bayr. Alpen) . . .	Witschi (1914 b) . .	490	50
	Sertigtal, Davos (Rätische Alpen) .	Witschi (1923 b) . .	814	50
	Spitalboden (Grim- sel, Berneralpen) .	Witschi	46*	52
	Riga	Witschi	272	44.5
	Königsberg	Pflüger (1882) . .	370 500*	51.5 53
II	Elsass (Mm)	Witschi	424	51
	Berlin	Witschi	471	52
	Bonn	Witschi	290	43
	Bonn	v. Griesheim und Pflüger (1881-82) }	806 668*	64 64
	Wesel	v. Griesheim (1881)	245*	62.5
	Rostock	Witschi	405	59
III	Glarus	Pflüger (1882) . .	58	78
IV	Lochhausen (München)	Witschi (1914 b) . .	221	83
	Dorfen (München) .	Schmitt (1908) . .	925*	85
	Utrecht	Pflüger (1882) . .	780 459*	87 87
V	Freiburg (in Baden)	Witschi (1923 a) . .	276	83
	Breslau	Born (1881)	1,272	95
	Breslau	Witschi	213	99
	Elsass (r)	Witschi	237	100
	Irschenhausen (Isar- tal südl. München)	Witschi (1914) . .	241	100
		Total	10,483	

The chromosome composition of frogs has been in dispute for several years, not only as to the number of chromosomes present, but as to whether the male or the female is digametic. The most probable number of chromosomes for several species seems to be 26 ($n=13$). Other num-

bers (24, 25, 28) have, however, been reported. According to the most recent account, that of Witschi, *Rana temporaria* has 26 chromosomes, including a slightly un-

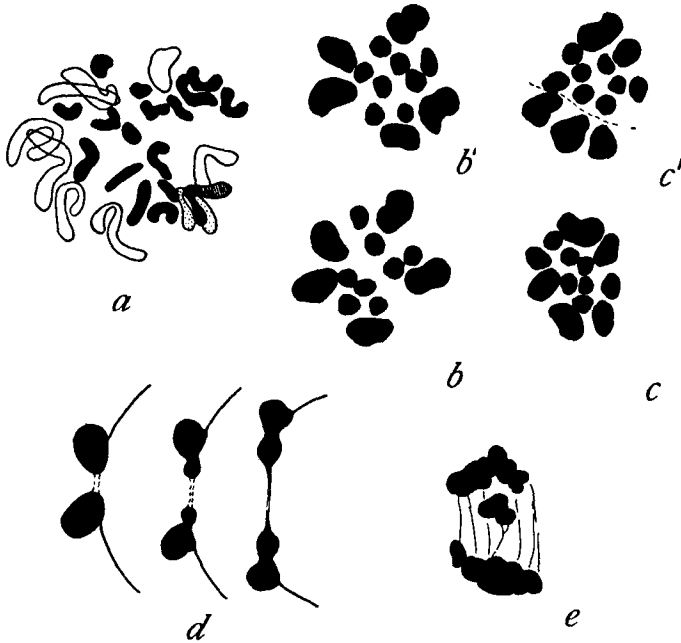


FIG. 145.

Chromosome groups of the frog *Rana temporaria*. *a*, Diploid male group. *b* and *b'* anaphase plates of first spermatocyte division each showing thirteen chromosomes. *c* and *c'* ditto. *d* division of XY-chromosome of first spermatocyte. *e*, separation of X and Y at second spermatocyte division. (After Witschi.)

equal XY pair in the male (Fig. 145). If this is confirmed, the female is XX (homogametic) and the male XY (heterogametic).

Pflüger (1882), Richard Hertwig (1905), and later Kuschakewitsch (1910) have shown that overripe eggs give an increased percentage of males. In so far as these

experiments were not made with the same male for the same sets of eggs, the results are doubtful. Hertwig himself points out there are many resemblances between the effect of cold and that of overripening. Many embryos are deformed. Witschi has confirmed Hertwig's results (with the Irschenhausen race). Eggs estimated to be 80 to 100 hours overripe gave 74 ♂, 21 ♀, 20 indifferent tadpoles.³

Richard Hertwig compared the sex ratio of normal and delayed eggs (67 hours' interval) with the following results. Larvae 49 days old (just before metamorphosis) that came from normal fertilization gave 46 indifferent ♀; those from delayed fertilization, 38 indifferent ♀ and 39 ♂. The normal frogs about 150 days old were differentiated females, indifferent females as to gonads, and males (numbers not given), and from the delayed eggs 45 indifferent ♀ and 313 ♂. Yearling frogs gave 6 ♀ and 1 ♂ (normal fertilization) and 1 ♀ and 7 ♂ (delayed fertilization). The overripeness here would seem to hasten the male differentiation and in the second place transform the indifferent individuals (here ranked undifferentiated females) into males.

The interpretation of the results produced by overripening the eggs is still very obscure. Taken at their face value they seem to show that individuals that would normally become females may become males. As yet no genetic tests have been made of the sex-determining properties of the spermatozoa of individuals obtained in this way. Theoretically, these should be homogametic. It seems improbable that such individuals could live and function under natural conditions, for, although overripeness must not infrequently occur, normal males giving 100 per cent females are practically unknown. Wit-

³ There was 20 per cent mortality in the tadpoles and 35 per cent in the young frogs.

Witschi has pointed out that the overripe eggs undergo an unusual type of cleavage, and that a few embryos that he examined show internal defects, but the relation of these defects to the transformation of females into males is not apparent.

The possibility of transforming individuals having an undifferentiated or juvenile hermaphroditic gonad (or progonad) into females by external agencies is furnished by the following evidence from Witschi's experiments (1914-1915).

Tadpoles of the *Ursprungtal* race, that is, probably a differentiated race, gave, at 10° C., 23 males and 44 females; at 15° C., 131 ♂ and 140 ♀; and at 21° C., 115 ♂ and 104 ♀. The sex of the tadpoles of this race is apparently not affected by temperature.

On the other hand, tadpoles of the *Irschenhausen* race reared at 20° C. gave 241 undifferentiated females, and 6 lots reared at 10° C. gave 25 ♂ and 438 ♀. From this result Witschi concludes that cold is a male determining factor, but it should not be overlooked that many of these so-called females would later develop into male frogs. In a later account of these experiments he states that "cold changes the males into protogynous juvenile hermaphrodites as is in general normal for undifferentiated races."

It seems questionable, therefore, whether there is anything more here than a retardation of the definitive male condition.

In so far as it is possible to reach a provisional conclusion from the evidence available at present, it appears that in the undifferentiated races the germ-cells, that are present in half the individuals that would normally become females, may be changed over into sperm-cells, or else be replaced by cells from a different source that, in turn, become sperm-cells. In other words, the balance of the

genes that ordinarily suffices in frogs to give males or females may be "overridden" by environmental factors and testes may develop in an individual whose internal chromosomal balance would produce a female. Stated in another way, this may mean that each frog is capable of developing both testes and ovary; that under normal circumstances the XX individual develops only the ovary

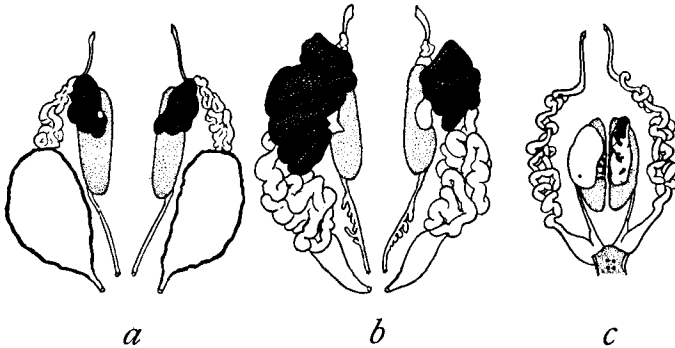


FIG. 146.

Three hermaphroditic frogs. (After Crew and Witschi.)

and the XY individual a testis, but under exceptional conditions a female of the XX type may develop a testis. The possibility of the reciprocal change has not been demonstrated.

There are many records of "hermaphrodite" adult frogs (Fig. 146). Crew has listed 40 recent cases. Whether these hermaphrodites are related in any way to the inversions just described is unknown. It is significant perhaps that a few individual hermaphrodites have also been reported from those experiments. On the other hand, it is possible that some of the hermaphrodites have a different origin. There is not much evidence that they can be explained as gynandromorphs or mosaics due to elimination

of the sex-chromosomes, because only very rarely is there indication of asymmetry of the accessory organs outside the gonads, and the gonad tissue is frequently irregularly distributed. Furthermore, if the evidence that the sperm and eggs of hermaphrodites are both homogametic is valid, the ground of a possible explanation due to chromosome elimination is removed.

From a hermaphrodite (Hh) Witschi was able to obtain ripe sperm and eggs. He tested these with sperm and eggs from a differentiated race with the following results

- (1) Eggs dif. ♀ by sperm from herm. = ♀ ♀
- (2) Eggs herm. by sperm from dif. ♂ = 50% ♀ + 50% ♂

The eggs of the hermaphrodite were also fertilized by sperm of the same individual and gave 45 ♀ and one hermaphrodite, thus

- (3) Eggs herm. by sperm from herm. = 45 ♀ + 1 herm.

These results can be interpreted to mean that the original hermaphroditic female was XX. Each ripe egg carried one X. Likewise each *functional* sperm must also have carried one X. There seems to be no escape from one or the other conclusion, either that every sperm carries an X, or else half carry X, half no X, but the latter die in the female (*i.e.*, never become functional).⁴

⁴ Crew (1921) reports that he has succeeded in fertilizing eggs of a normal female with sperm of an hermaphrodite. In each tadpole the development of the gonad was direct. All the offspring (774) that were sufficiently developed to determine the sex were female. The mother may be regarded as a true XX female that produced eggs and sperm, each with an X-chromosome.

Witschi (1928) has caused the transformation of the ovaries of all the female tadpoles of *Rana sylvatica* into testes (with spermatogonia) by keeping them at 32° C. after the seventh week. The males remained unchanged. [Added 1928.]

*The Transformation of Bidder's Organ of the
Male Toad into an Ovary.*

The anterior part of the testis of the male toad is composed of rounded cells that resemble young egg-cells



FIG. 147.

Bidder's organ at the anterior end of the testis of a half-grown male of a California species of *Bufo*. The lobes of the fat bodies lie at the sides, the kidney beneath. The testes are indicated by the branching blood vessels in their walls, the Bidder's organs lie in front of the testes each consisting of several lobes.

(Fig. 147). It is conspicuous in the young toad even before the germ-cells in the more posterior part or testis proper have differentiated. The anterior part is called Bidder's organ and has for many years excited the inter-

est of zoölogists, who have proposed many views as to its possible functions. The most frequent interpretation is that the Bidder's organ is an ovary and the resemblance of its cells to eggs lends *strong support to this interpretation*; but the presence of a Bidder's organ at the ante-



FIG. 148.

Toad in third year from which the testes have been removed at an early stage. Bidder's organ has developed into an ovary. In the figure (to the right) the ovary is turned to one side in order to show the enlarged oviduct. (After Harms.)

rior end of the true ovary in the young female is difficult to bring into accord with the view that in the male the same organ is an ovary, for, if so, the female has a rudimentary or perhaps ancestral rudimentary ovary in front, and a functional one behind it.

The experimental work of Guyénot and Ponse (1923) and of Harms (1923, 1926) shows that when the testes are completely removed from a young toad, the organ of Bidder develops after two or three years into an ovary with

eggs (Fig. 148). The eggs have been deposited and fertilized and observed to develop. There can be here no doubt but that a female has arisen after removal of the testes, but whether the individual operated upon is to be called a male or an hermaphrodite is perhaps a question of definition. Personally, I should call the above toad a male, and interpret the result to mean that a male has been transformed into a female by removal of the testes. It seems to me a matter of secondary importance that the male toad carries an organ whose cells are potentially capable of developing into egg-cells, for, in general, even when sex is determined by a chromosomal mechanism, there is no implication that under changed conditions undifferentiated cells situated in that part of the body where the gonads develop might not become egg-cells even with the chromosomal complex that gives rise to a male under other circumstances. In terms of genes, this means that in the toad the balance of the genes is such that under the normal conditions of development one part of the gonad (the anterior end) begins to develop into an ovary, while another part (the posterior end) begins to develop into a testis. The latter overtakes the former as development proceeds and holds its further development in check. If the testicular end is removed, however, this control is lost, and the cells of Bidder's organ proceed to develop into functional eggs. Ponse, using eggs from a transformed male, obtained 9 sons and 3 daughters. Harms reared from a similar male 104 sons and 57 daughters. If it be assumed that the male toad is XY, then it is expected that the eggs of the transformed male will be X and Y in equal numbers. If now, these are fertilized by a normal male, the expected offspring will be $1XX+2XY+1YY$. The YY-individuals probably fail to develop, leaving a ratio of two males to one female, which agrees closely with the actual results.

Champy has described a case of "total sexual inversion" in *Triton alpestris*. A male triton that had functioned as a fertile male was subsequently starved. Under these circumstances the normal renewal of the sperm does not take place, but the animal remains in a sort of "neutral condition," characterized by the presence in the testis of primitive germ-cells. It remains in this condition throughout the winter. Two male tritons that had been treated in this way, underwent, after they had been intensively renourished, a change in color from male to female. One of these examined several months later furnished evidence that Champy interprets as sex inversion. Since this case has been cited recently as furnishing complete evidence of sex inversion, it may be worth while to give a somewhat detailed statement as to what Champy really records. In place of the ovaries he found an elongated organ resembling somewhat a young ovary. When sectioned it was found to contain young egg-like cells ("ovocytes") resembling those of a young triton at the stage of metamorphosis. An oviduct was also apparent, recognizable by its white color and sinuous course. Champy concludes we have here an adult animal with the ovary of a young female. The evidence seems to indicate that the treatment led to the absorption of the spermatocytes and sperm. It does not indicate clearly whether the new cells that come to replace them are enlarged spermatogonia or primitive germ-cells or young ova. In the light of other evidence in the *Amphibia* (Witschi, Harms, Ponse) it may seem not improbable that these cells are in reality young egg-cells and that a partial inversion has taken place.

Sex Reversal in Miastor.

In flies belonging to the genera *Miastor* and *Oligarces* there is a generation consisting of sexual winged males

and females that appear at the end of a long succession of generations of maggots reproducing by parthenogenesis.

The eggs laid by the winged females are supposed to be fertilized by sperm from the winged males and develop as far as the maggot (larval) stage. These maggots, without passing on to the adult stage, produce eggs that develop by parthenogenesis. From these eggs a new generation of maggots arises that repeats the process. This continues throughout the year, the maggots living under the bark of dead trees, and in some species on mushrooms. In the spring or summer, winged males and females appear from eggs laid by the last generation of maggots. The appearance of the winged forms seems to be connected with some change in the environment. Recently Harris has shown that when the cultures become crowded, owing to the presence of many maggots, the adult insects appear if suitable conditions prevail, while if the maggots are reared in isolation, or in small numbers, they continue to reproduce in the larval stages (paedogenesis). The effective factors in crowding are not known. If young from a single individual maggot are reared together, and if their offspring in turn are kept in the same culture, etc., it has been found by Harris that when the adult flies appear they are of one sex in each such culture. This seems to mean that each individual maggot is either male or female in genetic constitution, and reproduces by parthenogenesis the same sex. If this is the correct conclusion, it follows that both the male-determined maggots and the female-determined maggots produce functional eggs. As yet we have no evidence relating to the distribution of the sex-chromosomes in these flies.

There is, here, an example of male-determined individuals producing parthenogenetic eggs at one phase of the life cycle and spermatozoa at another phase.

Sex Reversal in Birds.

It has long been known that old hens, and hens with ovarian tumors, may develop the secondary plumage of the male, and that they sometimes show characteristic male behavior. It was also known (Goodale) that after the complete removal of the single left ovary of a young chick, the bird, when mature, develops the secondary sexual characters of the male sex. Both effects may be interpreted on the hypothesis that the normal ovary of the hen produces some substance that suppresses the full development of the plumage. When the ovary is diseased or removed the hen then develops the full possibilities of her genetic composition as seen ordinarily only in the male.

It is also known that hermaphroditic fowls occur in which both ovaries and testes may be present, although neither, as a rule, is fully developed, and it may or may not be significant that in most of these cases the gonad contains a tumor. There is some doubt here whether the hermaphroditic condition came first, and the tumor later, or, the ovary of a normal hen becoming tumorous, a testis began later to develop. In none of these cases is there evidence of sex reversal in the sense that the bird functioned at one time as a female and later as a male. One case has, however, been recently reported by Crew (1923) in which a hen is said to have laid eggs and reared chicks (from them?) and later to have become a functional male that fertilized two eggs of a normal hen. Concerning the second part of the story there seems to be no question, since the results were obtained under controlled conditions, but the previous history of this hen is not perhaps above suspicion, since it was apparently an unrecorded member of a small flock and no evidence by direct observation or by trap nesting is given that she was known to

lay eggs. When killed the bird was found to have extensive tumor growths in the situation of the ovary. "Incorporated in the dorsal aspect of this mass, there was a structure exactly resembling a testis, while another, similar in appearance, was situated in like position on the other side of the body." Every stage of spermatogenesis was present in the testes. On the left side "a thin straight oviduct could be identified having a diameter of 3 mm. in its widest part near the cloaca."

A second case has been recorded by Riddle. A ring dove functioned first as a female, laying a series of eggs. She ceased later to lay eggs, and frequently acted as a male in courtship and copulation. Many months later she died with very advanced tuberculosis. She was opened and under misapprehension that she was her mate (a male that had died 17½ months earlier) was recorded as a male. Later, when her number and record were determined, it was found that she had been the female, but the "testes" had been thrown away. There is here no record that the bodies identified as testes contained sperm.

The Effect of Ovariectomy in Birds.

The complete removal of the single left ovary of young chicks is a rather difficult operation. In 1916 Goodale carried out several successful operations of this kind. The birds developed the full plumage of the male. Goodale also reported the presence on the right side of a rounded body with tubules which he compared with early nephrogenous tissue. Benoit has also recently described the effect of ovariectomy on young birds. In general, the effect on the plumage, comb, and spurs is the same as in Goodale's birds, but in addition he describes the development of a testis or testis-like organ in the *situs* of the rudimentary right "ovary," and sometimes a similar organ in the place of the left ovary removed. In one case germ-

cells in all stages of ripening and even spermatozoa (pycnotic) were found. This single case calls for careful scrutiny, since it is, so far, the only recorded case of the presence in the testis-like organs of spermatozoa, or even distinctive germ-cells. The left ovary had been removed from a bird twenty-six days after hatching. At six months its comb was red, turgid, stood upright, and was as large as that of a cock. An organ "resembling a testis had developed on the right side." Histologically it was found to contain seminiferous tubules containing all stages of spermatogenesis. The nuclei of the spermatids were pycnotic and the spermatozoa, few in number, appeared abnormal. The efferent canal of the male extended from this body to the cloaca. There was also present at the base of the testis a tubular structure resembling the epididymis of the young cock. The presence of spermatozoa in the testis-like organ is the only record of this kind. In the other birds operated on by Benoit, in which testis-like bodies developed, no germ-cells were found. May it not be possible that in the above case a mistake had been made and that the bird was in reality a male? It should be added that Benoit found, after removing its testis, the comb shrank and the bird came to resemble a capon. In other cases, no such decrease of the comb has been reported. Still, it is just possible that the presence of testis-like organs that were present with sperm in them may be held responsible for the full development of the comb and wattles. Another bird, ovariectomized at four days after hatching, described by Benoit, showed at four months an unusual organ. An examination revealed, on the right side, a testicle-like organ. No report of its contents is made.

Benoit examined the histological structure of the right rudimentary ovary of a young normal female. He describes it as identical with an epididymis of a young male

having efferent ciliated canals and "rete testis." He concluded that the right gonad of birds is not a rudimentary ovary, but a right rudimentary testis that enlarges when the left ovary is removed to become a testis. The evidence does not, I think, necessitate this conclusion, for it is known that in the early stage of development of the reproductive organs in vertebrates, the essential accessory organs of the male and the female are present in both sexes. It is possible, therefore, that upon interference with the normal process of development (removal of the left ovary) these rudimentary organs may begin to develop and produce a testis-like structure, which, in most cases so far reported, does not contain sperm-cells. The occurrence of globular organs (reported by Goodale and by Domm) on the *left side* also seems to support this view, rather than that advanced by Benoit.

A preliminary report of the results of ovariectomy in young birds has recently been given by L. V. Domm (1924). The birds when they become adult not only show secondary male characters in their plumage, comb, wattles, and spurs, but fight with normal cocks, crow, and attempt to tread hens. One bird had a "white testis-like organ" in the position of the normal ovary (removed). Associated with the organ was also a small ovarian follicle. On the right side there was also a testis-like organ. A second bird was similar as to its gonads. In a third bird a testis-like organ was present only on the right side. In none of these cases are germ-cells or spermatozoa reported as present.

Whether these cases are strictly sex reversals cannot be definitely stated, unless Benoit's observation on the presence of sperm is confirmed. Aside from this unique statement, the other results appear to show definitely that, after removal of the ovary, a structure develops resembling in its appearance a testis (except for the pres-

ence of germ-cells). The development of this organ, after castration, can, I think, be provisionally at least accounted for by a secondary growth and enlargement of the fundaments of the male organs that are known to be present in the embryonic stage. The maintenance of a testis, even a functional one, in a female body is not in itself surprising, since it is known that pieces of testis, grafted into the body of a female, may continue to develop, and even to produce sperm.

In general, it appears that the genetic composition of the female bird (present both in the body-cells and in the young ovary) creates a favorable situation for the development of the ovary, rather than a testis. Conversely, in the male the genetic composition is favorable for the development of the testis. In the male, however, the early removal of the testis does not suffice to call forth the development of *structures peculiar to the ovary*.

The Sex of Parabiotic Salamander Twins.

The union of young salamanders by side-to-side fusion has been brought about by several embryologists. The young embryos taken from the egg, just after closure of the medullary folds, have portions of one side of each removed and are then brought in contact by the exposed surface. Their union quickly follows. Burns has studied the sex of the united (parabiotic) twins. He found that members of a pair were always of the same sex; 44 pairs were both males, 36 pairs were both females. Random union would give 1 pair of males to 2 pairs of male-females to 1 pair of females. Since no double-sexed pairs appear, it follows either that pairs of opposite sexes die, or that the sex of one individual changes over that of the other and, since both male and female pairs were found, the influence is sometimes one way, sometimes the other way. Unless some explanation can be found for such a

difference in the reciprocal effects, the results do not convincingly demonstrate the probability of the latter interpretation.

Sex Reversal in Hemp.

Many of the flowering plants develop both pistils containing egg-cells and stamens containing pollen in the same flower, sometimes in different flowers on the same plant. It is not uncommon for the pollen to ripen before the ovules, or, in other cases, the ovules before the pollen. In other plants, the ovules may develop only on one plant, and the pollen on another plant, *i.e.*, the sexes are separate, the species dioecious. In some of these dioecious plants, however, the organs of the opposite sex may occur as rudiments; occasionally they become functional. Correns has studied a few cases of this kind, and has attempted to test the character of the germ-cells of such exceptional cases.

More recently experiments with dioecious hemp (*Cannabis sativa*) by Pritchard, Schaffner, and McPhee have shown that environmental conditions may change a pistil-producing plant (or female) into one in which stamens and even functional pollen are also produced, and, conversely, may change a staminate plant into one producing pistils containing functional eggs.

When hemp seeds are planted at the normal time in early spring they produce male (staminate) and female (carpellate) individuals in about equal numbers (Fig. 149), but Schaffner has found that when planted in rich soil accompanied by a changed light period, the plants show "sex reversal" in both directions. "The amount of reversal is approximately inversely proportional to the length of daylight." That the same environment should change carpellate into staminate, and staminate into carpellate plants is at first sight rather surprising, for

one might anticipate that identical conditions would tend to bring each toward a neutral or intermediate condition or one only toward the other. In fact, something like this seems to take place, for on a carpellate plant stamens



FIG. 149.

Female plant, to left, and male plant, to right, of hemp. (After Pritchard, in *Journal of Heredity*.)

appear; conversely, on a staminate plant, pistils may appear. It is in this sense, in the main, that "sex reversal" occurs, although there are other cases still in which a new branch of a pistillate plant may develop only stamens, and a new branch of a staminate plant develop only pistils. In these extreme cases "sex reversal" may almost be said to take place in those new parts that develop

under changed conditions. McPhee, who has also studied the effect of exposure to light for different lengths of time, has found that male plants may produce branches with pistils, and vice versa; but he points out that many intersexual flowers also appear as well as many abnormal flowers. He states "that the changes produced are in many cases relatively minor ones and a sweeping conclusion that genetic factors are in no way concerned with sex in these species is not warranted at the present time."

The question as to whether there is an internal sex-determining factor system—possibly chromosomal—in hemp, is at present unanswered, and as yet we have only an oral report by McPhee concerning the genetic evidence, but this report is significant. If the normal female hemp plant is homogametic (XX) and the male heterogametic, then we may expect when a female is transformed into a male (or more accurately produces functional pollen) that all the pollen grains will be alike as to their sex-determining properties, *i.e.*, such a male is homogametic. McPhee's oral report⁵ supports this view. Conversely, if the male (XY) is transformed into a female, then two kinds of eggs are expected. This seems to be realized.

Correns had earlier reported somewhat similar results in other plants but the data relating to the kinds of gametes produced are not satisfactory. It is to be hoped that evidence will soon be available that bears on this question. Assuming, in the meantime, that there is an internal mechanism for sex-determination in hemp (possibly of the XX-XY type), there is nothing revolutionary in the discovery that sex reversal may take place through environmental agencies, and there is certainly nothing in these results that is, in principle, in contradiction to

⁵ At the meeting of the Zoölogical Society, 1925.

the presence of a sex-chromosomal mechanism that is sex-determining. Such a mechanism is an agent that tips the scale one way or the other under a given set of environmental conditions. The mechanism has never been understood in any other way. It may be overborne by other agents that turn the scale without thereby losing its power to act in its usual way when the conditions return under which it is accustomed to work. No better example of this relation could we hope to find, if the tentative conclusions stated above are confirmed, namely, the change of a homogametic female into a homogametic male in a species in which the normal male is heterogametic. This, in fact, would furnish another convincing proof of the genetic explanation of sex-determination, and one that would be especially instructive for those who fail to understand the interpretation that geneticists place on this mechanism and on Mendelian phenomena in general.

Another plant, *Mercurialis annua*, has separate sexes but rarely a pistillate flower appears on a male plant, and, conversely, a staminate flower on a female plant. A male plant may have 25,000 male flowers and only from 1 to 47 pistillate flowers, while the staminate flowers on a female may be as 1 to 32.

Yampolsky has reported the sex of offspring produced from both these kinds of plants after self-fertilization. Offspring from selfed female plants are female or predominantly female. Offspring of selfed male plants are male or predominantly male.

It is not possible at present to give a satisfactory explanation of these results on the XX-XY formula unless rather arbitrary assumptions are made. For instance, if the female plant is XX, then all the pollen grains she produces should carry one X, hence all the offspring should be females, as was the case. But if the male plant is XY, half the mature eggs should be X and half Y. Simi-

larly for the pollen. Self-fertilization should then give $1 XX + 2 XY + 1 YY$. If YY dies there should be one female to two male offspring. This, however, was not the result obtained. In order that the selfed male plants should produce only males it must be assumed that the X eggs die as gametes and the Y eggs only are functional. As yet there is no evidence either for or against this hypothesis. Until there is evidence bearing on this question the case must be left open.