CHAPTER XIII

HEREDITY AND SEX

"Sex lies deeper than culture."—MAUDSLEY

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§ 1. *The Problem of the Determination of Sex*

The Problem.—Much interest has always been excited by the question: *What determines the sex of the offspring?* The fertilised ovum will develop into a cock or a hen, into a bull or a cow, into a horse or a mare, into a man or a woman, and it is obviously of practical as well as theoretical interest to inquire what determines the sex of the offspring. What are called "true twins" in the human race, which appear to result from the division of an ovum into two, are always of the same sex; but ordinary twins, which result from two ova developing simultaneously, are often of different sexes. What determines this? In one household all the children are boys, next door they are all girls, in most cases there are both boys and girls: what determines this? The eggs of a bird's clutch develop into males and females in varying proportions, but in one case at least it has

been noticed that males and females were produced in regular alternation following the order of laying: what determines this? The unfertilised eggs of a queen-bee always develop into drones, the fertilised eggs develop into workers (usually sterile females) and queens (fertile females): what does this mean? Throughout the summer the green-flies or aphides produce parthenogenetic eggs which all become females, but at the end of the season males are produced (also, of course, from parthenogenetic eggs), and then the normal bisexual reproduction occurs: what does this mean?

Can we discover *when* the sex of the offspring is determined, and *how* it is determined? It must be confessed that in many cases we have no secure data as to the earliest moment at which it is possible to say of a developing embryo that it is going to be a male or a female. More precise information on this point would probably eliminate at once a number of the factors alleged to have a determining influence.

Various Kinds of Answers.—To the question, What determines whether an organism shall develop into a male or into a female, many and varied answers have been given. Some of these answers are bound up with theories as to the nature of sex, which are legion. In fact, the number of speculations as to the nature of sex has been well-nigh doubled since Drelincourt, in the eighteenth century, brought together two hundred and sixty-two "groundless hypotheses," and since Blumenbach caustically remarked that nothing was more certain than that Drelincourt's own theory formed the two hundred and sixty-third. Subsequent investigators have long ago added Blumenbach's theory of "Bildungstrieb" or formative impulse to the list.

"As in so many other cases, the problem of the determination of sex has been looked at in three different ways. For the theologian, it was enough to say that 'God made male and female.' In the period of academic metaphysics, still so far from ended, it was natural to refer to 'inherent properties of male-

ness and femaleness'; and it is still a popular 'explanation' to invoke undefined 'natural tendencies' to account for the production of males or females. Thirdly, it has been recognised that the problem is one for scientific analysis" (Geddes and Thomson, *Evolution of Sex*, 1889, revised edition 1901, p. 35).

But even after the problem was recognised as one which could be tackled scientifically, non-scientific solutions have been attempted in scores of pamphlets and booklets—non-scientific in the sense that they lay stress on unverifiable factors, such as the desire of the parent; that they base a generalisation on a few cases, as in Schenk's theory; that they universalise particular instances; that they allege the operation of factors which are physiologically absurd, in a manner which can only be called superstitious; and that they confuse statistical generalisations with physiological interpretations.

Classification of Scientific Answers.—

A. Statistical. Some generalisations as to the sex of the offspring have been based on statistics, which show how the relative numbers of male and female offspring vary in different localities, at different times (*e.g.* in times of war or famine), according to the relative ages of the parents, and so on. These statistics are very valuable, and the more of them the better. But, as we have already seen, great care is necessary in giving a physiological interpretation of statistical results.

B. Observational. Some generalisations as to the sex of the offspring have been based on the observation of particular cases. Thus, it has been shown that ova fertilised by spermatozoa with "an accessory chromosome" (in the case of some insects) develop into females; that the unfertilised ova of the bee always develop into drones; that the parthenogenetic ova of aphides always develop into females as long as summer conditions persist; that some animals have two sizes of eggs, the larger developing into females; and so on.

C. Experimental. Some generalisations as to the sex of the offspring have been based on experiment. Thus, in one of the best-known experiments, made by Prof. Emil Yung on tadpoles, it was found that the percentage of females could be raised from a normal of about 57 to 78, 81, and even 92, according as the brood was fed with beef, fish, or flesh of frogs.

Physiological View of the Problem.—As we have already seen, it seems necessary to assume that the germ-cells liberated from a male or a female organism have a complete equipment of hereditary qualities—a complete potential equipment *for both sexes*. An ovum without the aid of a spermatozoon may give rise to a male animal, as in the case of drone-bees. A non-nucleated fragment of ovum may be fertilised by a spermatozoon and develop into a perfect young organism. There is nothing peculiarly female in the egg, there is nothing peculiarly male in the spermatozoon, though the contrast between the two kinds of cells, considered as cells, does express in all typical cases the fundamental antithesis between femaleness and maleness. But the idea of feminine characters having their basis in the ovum and of masculine characters having their basis in the spermatozoon, is, of course, quite absurd. Every gamete has a complete bisexual equipment. Many of the lower animals, *e.g.* earthworm, leech, and snail, are hermaphrodite. A parthenogenetic ovum may give rise to males or females.

It may be said that in all ordinary cases the ovum and the spermatozoon are equally the vehicle of all the characteristics of either sex, and, *a fortiori*, that the fertilised ovum has always inherent in it the potentiality of both sexes. Eventually the cells derived from it by continuous cell-division will give rise, some to male, some to female offspring, or in many cases (in lower animals) to hermaphrodite offspring.

It is strange that even expert writers, who should have known better, have persisted in speaking of the ovum as a female gamete

and the spermatozoon as a male gamete. Each is a *complete gamete*—a vehicle of the potentialities of both sexes; neither has any bias towards masculinity or femininity, though *as cells* they are expressions of the fundamental contrast of the sexes.

In connection with the theory that the fertilised egg has in it the complete potentiality of both sexes, there are several facts to be noted. Many of the lower animals, such as earthworm, leech, snail, and sea-squirt, are normally and intimately hermaphrodite; in many cases and in very varied degrees casual hermaphroditism is common at almost every level up to and including birds and mammals; there are quaint cases, especially in ants, bees, and butterflies, of gynandromorphism, where one part of the body has distinctively masculine characters while another part is as distinctively feminine; in a number of cases, such as tadpoles, it seems certain that the developing organism passes through an embryonic or even a larval phase of hermaphroditism.

Now, so much being clear, that every germ-cell is the vehicle of the potentialities of both sexes, the problem is what factors determine which set of potentialities will find expression. It is plain that a decision as to these possible determining factors will depend a good deal on the time when sex is defined. Thus, if the embryo lingers for a while with evident expressions of both male and female gonads and associated structures, it is evidently of use to look for factors operative during this period. This is a question for embryologists.

In the higher animals (mammals and birds) it is possible at a very early date in embryonic life to tell whether the developing organism will turn into a male or into a female, though in the very earliest stages it seems quite impossible to determine whether the primordium, or rudiment of the reproductive organs which has been laid down, is going to become a testis or an ovary.

But in lower vertebrates, such as frogs, the period of embryonic indifference seems to be greatly prolonged, and it seems as if

even the larvæ (tadpoles) remained for a time undecided. In this connection, it should be remembered that there is strong evidence showing that the hagfish (*Myxine glutinosa*) is for a time distinctively male, producing spermatozoa, and that it afterwards becomes as distinctively female, producing only ova (Cunningham, Nansen).

Among Invertebrates, the sexual organs are often late in acquiring definiteness in favour of either sex—that is, the period of sexual neutrality or indifference is prolonged.

It seems as if, the higher the organism is in the series, the earlier is its sexual destiny sealed.

What Sex primarily means.—In the simplest cases, which should be considered first, the ovum developing into a female differs from an ovum developing into a male only in this—that the one contains the dominant potentiality of an ovary, while the other contains the dominant potentiality of a testis. This appears to us to be a purely physiological difference, a slight difference in the equation of metabolism, a slight difference in protoplasmic gearing, quite comparable to that between an active and a sluggish cell. In more complex cases, where there is marked difference between the sexes as regards the gonads themselves, the genital ducts, the external genital organs, and secondary sexual characters, we suppose that there are definite determinants gradually established and elaborated to correspond to these organs, that these are equally present for both sexes in all ova and in all sperms, and that their liberation or latency depends on the bias towards egg-production or sperm-production, by hypothesis a difference in physiological gearing.

When we consider the very marked and detailed contrasts between the sexes which are familiar in many birds and mammals, insects and crustaceans, and so on, it may seem idle to refer this to a primary difference in "physiological gearing." But our familiarity with these secondary sexual characters is apt to lead us away from the main problem, which is better studied in

simple creatures like starfish and sea-urchins, where it often requires a microscopic examination before we can be sure whether

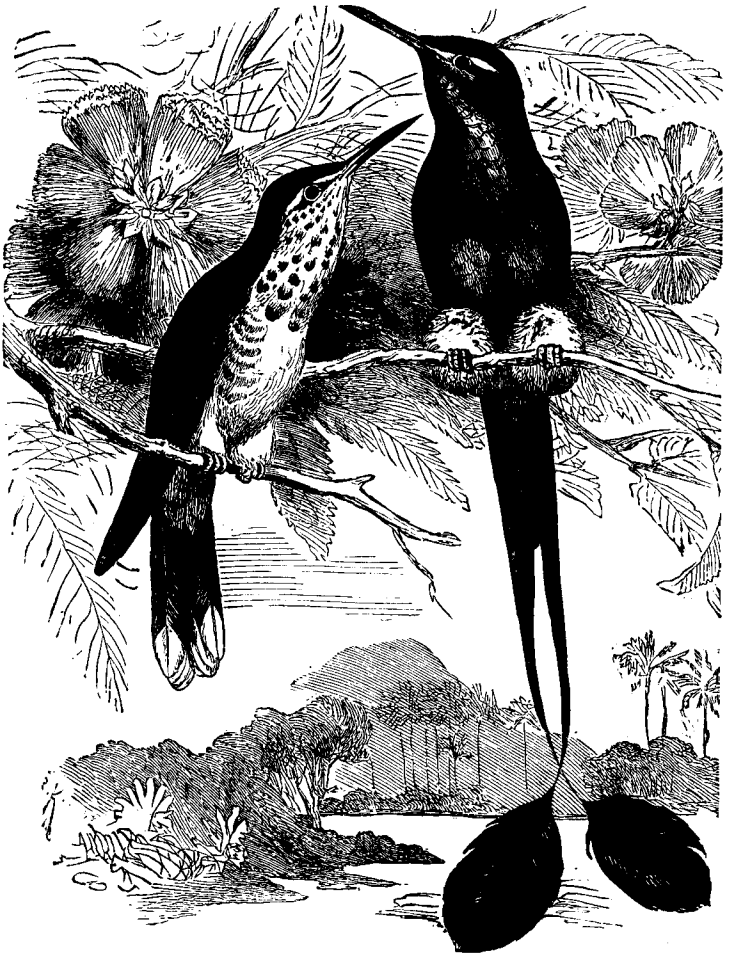

FIG. 45.—Decorative male and less adorned female of Spathura—a genus of Humming-birds. (From Darwin, after Brehm.)

we are dealing with a male or a female organism. The primary difference between the sexes is that between egg-production

and sperm-production, and this, we think, may be expressed as a difference in "physiological gearing."

Embryological View of the Problem.—It does not seem necessary or useful to suppose that there are in the germ-cells any constituent particles or determinants corresponding to maleness or femaleness. The germ-cell is physiologically determined to produce an egg-bearing or a sperm-bearing organism—according to its degree of anabolic preponderance it will become a producer of eggs or of sperms. The ratio of anabolism to katabolism in the female $(\frac{a}{\kappa})$ is assumed to be always greater than the corresponding ratio in the male $(\frac{a}{\kappa})$. It is not unlikely that this physiological bias towards different metabolic ratios is due rather to the cytoplasm of the nucleus than to the chromosomes, and it must be remembered that in its physiological relations every cell is a co-operative organisation with continual interactions between nucleoplasm and cytoplasm—a "cell-firm" in short.

But when we come to consider all the appanages of the primary sexual characters of egg-producing and sperm-producing—the differences in the gonads, in their ducts, in the external genital organs, and in the secondary sexual characters—then it becomes, as it seems to us, both necessary and useful to people the chromosomes with definite representative particles or determinants corresponding to these varied structures.

We believe that these are ultimately traceable to germinal variations or mutations, appearing now in the sperms and again in the eggs, or it may be in the combination of the two. We suppose that these have, like other variations and mutations, run the gauntlet of selection in one or more of its various modes, and have sooner or later come to form part of the normal inheritance, just like any other peculiarities unconnected with sex. We suppose that they are represented in all gametes, whether ova or spermatozoa, and that their expression or latency depends on the physiological determination of the gamete towards

either of the fundamental alternatives of maleness or femaleness in the simple sense already defined.

It is not inconsistent with this view to suppose that some of the distinctions which eventually become obvious between males and females in any given case are simply physiological reactions due for instance to the stimulus of secretions from the gonads which saturate through the body. It also seems to us that in certain cases the so-called contrasted peculiarities of the two sexes are due to internal physiological conditions which give the

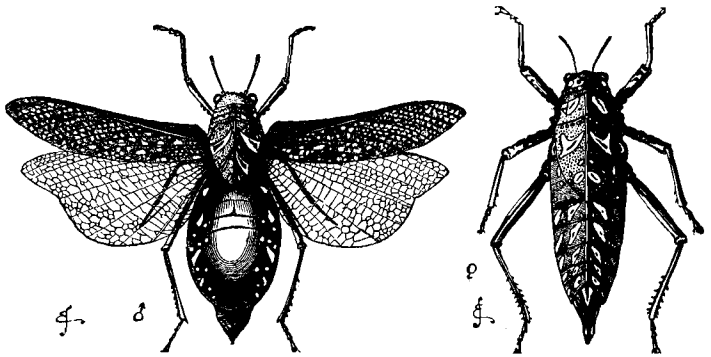

FIG. 46.—Winged male and wingless female of Pneumora, a kind of grasshopper. (From Darwin.)

same primordium two different expressions—much less different than they seem. We may conceive of a sort of internal physiological "poecilomorphy."

§ 2. *Variety of Possible Factors in Sex Determination*

Variety of Organisms probably implies a Variety of Sex-determining Factors.—As the variety of organisms is very great and their modes of development very diverse, it seems unlikely that there is any one answer to the question, What determines the sex of the offspring? In some cases we know that a certain kind of egg, *e.g.* the larger eggs of the Rotifer *Hydatina*, will develop

into females only; in other cases, *e.g.* tadpoles, it seems as if the young offspring pass through a sexually neutral or potentially hermaphrodite stage, during which environmental conditions may give them a bias towards maleness or femaleness. In some cases we know that an unfertilised egg will certainly give rise to a male, as in the eggs which develop into drone bees; in other cases we know that an unfertilised egg will as certainly give rise to a female, as in the aphides throughout the summer months. Although recent work points more and more clearly to the conclusion that in a large number of cases the sex is absolutely fixed in the fertilised ovum or even earlier, yet the variety of organisms is so great that it seems at present rash to exclude the possibility that nurtural conditions before and after birth have an influence on the sex of the developing organism.

Among the considerations which suggest that the future sex of the organism is often determined in the fertilised egg, we may mention the alleged fact that the sex of "identical" twins is always the same. The interest of this is that identical twins appear to be produced from one ovum which becomes separated—at an early stage—into two independently developing halves. The material being identical to start with, the results are identical. In the case of ordinary twins, which arise from two distinct ova, the sex may be the same in the two, or one may be male and the other female. It must be admitted, however, that this sharp distinction between identical twins and ordinary or fraternal twins is not unanimously accepted. (See Thorndike, cited by T. H. Morgan [1907] p. 412.)

In one of the armadillos (*Praopus* or *Tatusia hybrida*), Jhering found in two cases eight embryos in a common chorion which were all males. Arguing from the inclosure of identical human twins in a common chorion, Jhering concluded that these eight embryos were all derived from one ovum, and that this was the explanation of their sameness of sex.

In some remarkable cases of "poly-embryony" recorded by

Marchal and others in certain parasitic Hymenoptera, it seems that one fertilised egg may give rise to a chain of embryos, and these are of the same sex. This again corroborates the view that the sex may be absolutely determined in the egg.

Classification of Possible Factors.—Ingenuity has almost exhausted itself in discovering possible factors in the determination of sex, and though *the majority* of the suggestions offered cannot be taken seriously (and need not even be mentioned) there remain a number of factors which may be reasonably considered.

We may arrange these possible factors in three sets :—

A. *External Influences,* such as nutrition and temperature, operative on the parents, or on the liberated germ-cells, or on the embryos, or even on the larval stages if there are such.

B. *Parental Influences,* other than those directly traceable to peculiarities of diet and the like : *e.g.* whether the parent is young or old, strong or weakly ; whether the birth is a first or a last ; whether one parent is much older than the other ; and so on.

C. *Internal Conditions* in the germ-cells themselves : *e.g.* the size of the ovum, the age of the ovum, the relative freshness or staleness of the spermatozoa, the equality or inequality of the number of chromosomes in the ovum and the sperm, the chances of maturation divisions, the conditions of amphimixis itself.

It may be useful also to classify the factors according to the time at which the sex may be thought of as fixed.

(*a*) It may be that a young and immature ovum has already a constitutional predisposition towards becoming a male or a female—that is (from our point of view) towards becoming a sperm-producer or an egg-producer. It may be that this early predisposition, which will apply also to the spermatozoa, is dependent on nutritive conditions, directly affecting the cytoplasm of the germ-cell, or the nucleoplasm, or both. Or it may be that the young germ-cells fluctuate as regards the ratio of anabolism and katabolism, and that they may be swayed by slight

somatic stimuli now to one side and now to the other. We believe that this quantitative fluctuation is a primary characteristic of living units ; a summation of quantitative fluctuations may eventually result in a qualitative bias towards maleness or femaleness in development.

(*b*) It may be that the sex is not fixed until fertilisation has been accomplished, for it is conceivable that a predisposition in the young ovum towards becoming a female organism might be counteracted or reversed by a more prepotent spermatozoon which had a protoplasmic predisposition towards becoming a male organism.

We think that there is a great deal to be said for the hypothesis that the cytoplasm, as distinguished from the chromosomes, is of great importance in sex-determination, by setting up a particular régime of metabolism which makes for the production of a female or a male, and which liberates or inhibits the determinants of feminine or masculine structures. At the same time it is conceivable that there may be some kind of germinal struggle between analogous feminine and masculine determinants, and that the issue of this struggle decides whether the masculine or the feminine determinants are to find expression in development or are to remain latent.

In the case of the insect *Protenor belfragi*, investigated by Prof. E. B. Wilson, the female insect has in its body-cells one more chromosome than the male has in its body-cells, and some of the spermatozoa have this extra chromosome while others have not. When the egg is fertilised by a spermatozoon with the same number of chromosomes as itself, it develops into a female. When the egg is fertilised by a spermatozoon with one chromosome less than the egg has, it develops into a male. Without in the meantime attaching great importance to this discovery, which we have stated somewhat roughly, we may admit that this inequality of chromosome equipment between the two kinds of spermatozoa may play some rôle in sex-determination.

(*c*) It may be that in some cases, such as tadpoles, the sex is not definitely fixed until a relatively late stage, and it may be that in these cases the conditions of nurture (notably nutrition and temperature) may swing the balance to one side or to the other—may be the deciding moment in determining whether the organism is to become a sperm-producer or an egg-producer, and whether the potentialities of feminine characters or of masculine characters are to find expression in development.

As we have said, there are many reasons for believing that in mammals the sex is determined *ab ovo*, that, once conception has occurred, no influence whatever has any effect on the sex of the offspring. But it does not follow from this that influences brought to bear upon the parents before liberation of ova from the ovary, or of spermatozoa from the testis are of no account. Nor does it follow that because the sex of the offspring is fixed in the fertilised ovum of mammals, it is similarly fixed in the fertilised ova of frogs or much lower animals.

§ 3. *Alleged Determining Influence of External Factors*

Influence of Food.—Various experimenters have been led to conclude that the amount and quality of the food determine whether an embryo or larva becomes a male or female. Thus Landois, Treat, and Gentry believed that this was true of certain caterpillars, but what they seem to have shown is rather that the mortality is greater among the females than among the males when the food is insufficient. The fact is that the sex of the caterpillar is fixed when it leaves the egg, therefore the experiments were irrelevant. Even apart from this fatal objection, it should be noticed that the experiments alluded to have not been confirmed by other experimenters such as Riley. In regard to silkworms it has been shown by Kellogg and Bell that the sex of the offspring is not appreciably affected by the nutrition of the parents or grandparents. Cuénot found that

the nutrition of the parent blowfly had no effect on the sex of the offspring, and that the proportion of sexes in the larvæ was not affected by what they ate. In short, everything points to the conclusion that the sex is fixed in these cases before hatching, that the nutrition of the parents has no influence, and that apparent disturbances of the normal proportions in the larvæ are due to differences in the rate of mortality of the two sexes in unusual conditions.

Experiments by Born, Yung, and others on tadpoles point to the conclusion that the quantity and quality of the food have a determining influence on the sex. It is said that the tadpole remains for a considerable time in a state of what may be called larval hermaphroditism, and the experiments suggest that the development of the gonads and associated structures into male *or* female reproductive organs depends on the nutrition.

Yung found that when the tadpoles were left in natural conditions, the percentage of females was slightly in the majority. In three lots, the percentage proportions of females to males were as follows :—54 : 46 ; 61 : 39 ; and 56 : 44. The average was thus about 57 females in the number. In the first brood, by feeding one set with beef, Yung raised the percentage of females from 54 to 78 ; in the second, with fish flesh, the percentage rose from 61 to 81 ; while in the third set, when the flesh of frogs was supplied, the percentage rose from 56 to 92 !

The experiments of Cuénot on somewhat similar lines did not corroborate Yung's results, but he points out that in his work, as in that of the other's, the sex of those tadpoles that died is not known, which is a fatal objection.

It is desirable that the experiments should be repeated on a large scale, to meet, if possible, the following objections : (1) that the testing of the definitive sex of the tadpoles was inexact ; (2) that the possibly different rate of mortality in the two sexes was not allowed for ; and (3) that even in natural conditions the percentage of females is sometimes very high—*e.g.* 100 females

to 13 males (Pflüger). It should be noted, however, that finding, say, 86·8 per cent. of females in a collection of frogs from a pond does not prove that Yung's results were fallacious. There may have been peculiar nutritive conditions in that locality.

Very interesting results have been published by Nussbaum in reference to the common Rotifer *Hydatina*, in regard to which he finds that the amount of food taken by the newly hatched female determines whether its eggs will give rise to males or females.

Some experiments have been made—*e.g.* by Cuénot and Schultze—on the possible influence of the nutrition of the mammalian parent on the sex of the offspring; but the results are all against the reality of this supposed influence.

On the basis of human statistics some have tried to show that abundant food for the parents favours the production of female offspring, and *vice versâ*; but others have drawn from other statistics the opposite conclusion, that the parental nutrition is of no moment, unless in bringing about a differential death-rate. The fact that 30 per cent. of human twins are of different sexes seems enough to show that the dieting of the parent is not of great importance.

In *The Evolution of Sex* (revised edition, 1901), there will be found a convenient summary of other data—partly experimental and partly statistical—which have been adduced to show that nutrition and temperature may have some sex-determining influence on the developing organism, either directly or through its parents; but it does not seem to us that any one of these is conclusive, though they have a certain cumulative suggestiveness which would warrant further experiment—particularly as regards the lower animals and the indirect influence on offspring through the parents.

Although it seems more and more clear that in the higher animals—such as mammals—the environment of the embryo has no sex-determining influence, it does not follow that this is

true of lower organisms such as Rotifers, Entomostraca, worms and polyps, and some plants.

Issakowitch has recently maintained in regard to the common "water flea," *Cyclops*, and Von Malsen in regard to one of the simple worms, *Dinophilus apatris*, that abundance of food and a low temperature result in the production of a large number of females. This may be due to preponderant production of a particular kind of egg,—that tending to develop into a female. Nussbaum maintains in regard to the Rotifer, *Hydatina senta*, that the nutrition of the female embryo determines whether it will produce large eggs—developing into females, or small eggs developing into both males and females.

We may also refer to the experiments of Klebs (*Die Bedingungen der Fortpflanzung bei einigen Algen und Pilzen*, Jena, 1896), where it is shown that definite environmental conditions of nutrition, temperature, etc., are definitely associated with the occurrence of particular modes of reproduction in Algæ and Fungi. A *Vaucheria* plant, kept sterile for years, can be made to become sexual in a few days. A form normally bisexual can be made unisexual. Asexual spore-formation can be induced with certainty by one set of conditions (*e.g.* in *Hydrodictyon*), and the appearance of sexual gametes by another set of conditions. Only by definite experiments like those of Klebs can we pass from vague interpretations to a precise physiology.

§ 4. *Influence of the Parents*

There seems no satisfactory evidence, as yet, that the sex of the offspring can be influenced by environmental conditions, such as those of nutrition and temperature, operative on the developing organism either directly or indirectly. It may be, however, that the bodily constitution of the parent may have an influence on the germ-cells, giving them a bias towards the production of male or female offspring. Does an aged parent tend to have

offspring of one sex rather than of the other? Is the relative age of the two parents of any importance? Does the health and vigour of the parent matter?

Age of Parents.—Hofacker (1823) and Sadler (1830) independently published statistics referring to about two thousand births, which favoured the conclusion that when the male parent is the older the offspring are preponderatingly male, and *vice versâ*; but this has not been confirmed, far less established, and the experiments of Schultze tell strongly against its validity.

At the same time, if the gametes are for a while indifferent or unbiassed in regard to the sex which they will express, or if there is a selective process which decides whether the gametes determined towards femaleness or those determined towards maleness will survive, it may be that the absolute and relative ages of the parents are not without influence.

Comparative Vigour.—A widespread idea among breeders is that the sex of the offspring tends to be that of the more vigorous parent. But when we try to analyse the concept of comparative vigour, we find ourselves knee-deep in vagueness. Nor do the facts bear out the conclusion. Thus it is usually said that consumptive mothers produce a great excess of daughters, whereas the theory of the influence of comparative vigour, as stated by Girou and others, would lead us to expect the opposite.

According to Starkweather, "sex is determined by the superior parent, and the superior parent produces the opposite sex"; but the concept of "superiority" is even more vague and useless than that of greater vigour. Van Lint has tried to rehabilitate this theory, maintaining that when the spermatozoon is stronger than the ovum, the result is a female, and conversely. There does not seem to be any basis for this view.

An interesting question, which deserves further inquiry, is whether a prepotent sire has, along with his tendency to transmit his somatic qualities, a tendency to bias the offspring towards his own sex, or towards femaleness; or, more generally, whether

prepotency is associated with a tendency towards a preponderance of one sex in the offspring. There do not seem to be any secure data.

So far as parental vigour may depend on what may be called strained reproduction, Schultze's experiments on mice do not in the least confirm the idea that this has any effect on the proportions of the sexes. So far as parental vigour may depend on deterioration supposed to result from close in-breeding, Schultze's experiments are again adverse to the idea that this has any effect on the proportions of the sexes.

§ 5. *Internal Conditions*

It remains to inquire whether, apart from parental conditions, there are any definite peculiarities in the oogenesis and spermatogenesis, in the processes of maturation, or in the fertilisation, which can be associated with the production of male or female offspring. Is any importance to be attached to the size of the ovum, the age of the ovum, the freshness or staleness of the spermatozoon, and so on ?

Age of the Ovum.—It is held by some that if an egg is fertilised soon after its liberation from the ovary, it is more likely to develop into a female, and *vice versâ*. Similarly, it has been held that fresh spermatozoa tend to produce male offspring. But there is no warrant for any such generalisation, though it is possible that the relative age of the gametes may be one of the determining factors in certain cases.

A side-light is thrown on this theory by Vernon's experiments on hybridising sea-urchins, which seem to show that " the characteristics of the hybrid offspring depend directly on the relative degrees of maturity of the sexual products (*Phil. Trans.*, Series B, vol. cxc. (1898) pp. 465–529), and that the degree of staleness of the ova and spermatozoa has an appreciable influence on the development " (*Proc. Roy. Soc.* lxv. [1899], pp. 350–60).

Size of the Egg.—There are some suggestive facts in regard to the size of the ovum. It is well known that some animals normally produce two sizes of egg, and in certain cases (*Phylloxera* among insects, *Hydatina senta* among Rotifers, and *Dinophilus apatris* among worms) the large eggs produce females and the small ones males. In *Dinophilus* the large ova which develop into females are said to be opaque, while the small ova which develop into males are said to be transparent. In the phraseology adopted in *The Evolution of Sex*, the eggs in which the anabolism is relatively high become females, and the eggs in which the anabolism is less high become males. Attempts have been made to extend this generalisation, *e.g.* to the large and small eggs of the silk-moth, but the results are conflicting.

Moreover, as Prof. T. H. Morgan points out (1907, p. 396) "even if large eggs produce fewer males and small eggs more males, it is not clear whether the result is due simply to the size determining the sex, or whether the female eggs tend to become larger than the male eggs. If analogy has any value in this instance [moths], it seems more probable, from the cases of *Phylloxera*, *Dinophilus*, and *Hydatina*, that sex may be sometimes predetermined in the egg and this determines its size."

We may recall the well-established fact that the so-called "winter" eggs of Aphides and Cladocera, which are fertilised, always develop into females.

Two Kinds of Eggs.—It has often been suggested that there may be two kinds of eggs, one kind predisposed towards developing into females, and the other predisposed towards developing into males. In the same way there may be two kinds of spermatozoa similarly predisposed towards developing into males or developing into females. A fertilisation of an ovum predisposed to female development by a sperm predisposed to female development would naturally result in a female, and *vice versâ*. And the result of the combination of an ovum predisposed to female development with a spermatozoon predisposed to male develop-

ment would depend on the relative prepotency of the two gametes. In the case of hermaphrodite animals, one kind of egg and one kind of sperm would suffice.

This solution savours a little of Columbus and the egg, but it is not to be hastily brushed aside. It is easy to say that it simply shunts the difficulty a little further back, for what are the conditions producing two kinds of eggs ? But *if* the primary difference between male and female, between a sperm-producer and an egg-producer, is merely a slight physiological difference in the gearing of the metabolism, *if* the contrast between male and female is like the contrast between sperm and ovum considered as cells, *if* the antithesis is simply a particular expression of omnipresent fluctuation in the ratio of anabolism to katabolism, then we do not see that the assumption of two kinds of ova and two kinds of spermatozoa is a mere begging of the question.

Where there is complex dimorphism between the sexes, it is necessary to make the further assumption that all the gametes, whether maternal or paternal, and whether disposed towards female-production or towards male-production, have a complete set of the hereditary characters of the two sexes (so far as these require the postulate of germinal representation), and that the physiological difference of protoplasmic "gearing" determines which set is to find expression and which set is to remain latent.

The drawback to the theory is that it remains a hypothesis, except in so far as there are known cases of demonstrable differences between two kinds of ova or between two kinds of spermatozoa.

In his recent theory of sex-determination, Dr. John Beard assumes two kinds of eggs and two kinds of spermatozoa, but he does not credit the spermatozoa with any share in deciding the sex. Indeed, one kind of spermatozoon—the "female" spermatozoon—has not even fertilising power. A "female" egg develops into a female, and a "male" egg into a male. The

determination of these two kinds of egg-cells begins very early in embryonic life, and is completed at maturation.

W. E. Castle has proposed an ingenious hypothesis, which also assumes two kinds of eggs and two kinds of spermatozoa, but is distinctive in the further hypothesis that " male " spermatozoa can only fertilise " female " eggs, and that " female " spermatozoa can only fertilise " male " eggs. Thus the fertilised egg represents a union of " male " and " female " gametes, and the determination of the sex is left undetermined.

Two Kinds of Spermatozoa.—In about thirty different kinds of animals, such as the fresh-water snail *Paludina*, there are two distinct forms of spermatozoa, and it has been suggested that the two kinds are respectively predisposed towards the two sexes. But there is no definite evidence of this.

More interesting is the fact, first noticed by Henking in 1890 in the bug *Pyrrhocoris*, and corroborated in various other insects by a number of American zoologists, that half the spermatozoa differ from their neighbours in having an extra chromosome. McClung has suggested that the presence or absence of this *accessory chromosome* is correlated with the sex of the offspring. Spermatozoa with the accessory chromosome are supposed to tend to produce males. Further inquiry, however, has shown (for some cases) that the female organism has in its body-cells one more chromosome than the male has, and it seems almost certain that the eggs have one more chromosome than half of the spermatozoa have, and the same number of chromosomes as the other half of the spermatozoa have. When a spermatozoon with the same number of chromosomes as the ovum fertilises an ovum, the result is supposed to be a female. When a spermatozoon with one chromosome less than the ovum fertilises an ovum, the result is supposed to be a male. It is possible to conceive that the accessory chromosome is the vehicle of the primary constituents of femaleness, or that the mere quantitative preponderance due to an extra chromosome gives the fertilised

ovum a bias towards the production of a female. On the latter hypothesis we may perhaps find parallel phenomena in ants and bees, where the unfertilised ova produce only males. For an account of E. B. Wilson's exceedingly interesting observations on *Protenor belfragi*, where ova fertilised by a spermatozoon with an accessory chromosome develop into females, while those fertilised by a spermatozoon without the accessory chromosome become males, see Lock (1907), p. 253, where a Mendelian interpretation of the facts is attempted.

On our view, the difference between a gamete which produces a male and another which produces a female is what we can only vaguely call a difference in " physiological gearing," and it may well be that the presence or absence of an extra chromosome is one of the factors determining which " gear " is to find expression.

Maturation.—It has been repeatedly suggested that in the divisions which occur before the ova and the spermatozoa are mature, divisions in which there is a reduction of the number of chromosomes to half the number found in the body-cells, there may be a definition of the sex-tendencies of the germ-cells. But there does not seem to be the slightest warrant for connecting the maturation-divisions with sex-determination—*e.g.* for supposing that the egg becomes more purely female (the phrase is rather an absurdity) or more liable to develop into a female because it gives off two polar bodies. A parthenogenetic ovum of the honey bee forms two polar bodies and yet develops into a drone. We are not aware of a single fact which warrants the suggestion that a maternal gamete becomes, by its maturation divisions, more likely to produce a female organism. But it is conceivable that if there are two kinds of ova and two kinds of spermatozoa, with tendencies in each of the kinds towards female-development or towards male-development, the divisions associated with maturation may sharpen or blunt the point of these tendencies. It is conceivable that a young ovum with a cytoplasmic bias towards female-production may, in the

reduction of its chromosomes in maturation, get rid of hereditary material antithetic to the dominant tendency. It is conceivable that a young ovum with a cytoplasmic tendency towards male-production may similarly get rid of hereditary material antithetic to the dominant tendency. But what really takes place no one knows. In getting rid of some chromatin material and in keeping some a maturing gamete may be dividing its hereditary material in an impartial and random fashion or in a differential fashion. We do not know.

McClung has suggested that in the maturation of the sperm-cell there *may be* a quantitative division of the tetrads, resulting in two kinds of spermatozoa, comparable to those with and without an accessory chromosome.

As far as facts go, there does not seem to be any warrant at present for correlating maturation-divisions and sex-determination.

Fertilisation.—Let us suppose a fertilised ovum to be in process of developing into a female, and let us leave aside, for the moment, the question why it is becoming a female rather than a male. The fact is that it is becoming a female, and if the constitution *in potentia* has its material basis in the chromosomes of the first cleavage spindle, we may say that these chromosomes are determined in the direction of femaleness—that is, in the direction of an organism producing eggs. Now, on the general theory of germinal continuity, the chromosomes of the germ-cells of this developing female should retain this general tendency and character, *unless there are disturbing nutritive or other influences inducing change.* Thus some have supposed that the chromosomes of an egg have an inherent bias to produce a female, and that the chromosomes of a spermatozoon have an inherent tendency to produce a male. This seems to us entirely illegitimate, since we adhere to the view that the primary difference between maleness and femaleness is simply a slight difference in metabolism, which may quite well be effected in the course

of gametogenesis as the result of nutritive oscillations in the body.

But accepting the idea for the moment, it would appear that, as the fertilised ovum of the next generation has received, let us say, (for man) twelve chromosomes from the mother (by hypothesis tending to the development of female offspring) and twelve chromosomes from the father (by hypothesis tending to the development of male offspring), it will not be biassed towards either direction as far as its complement of chromosomes is concerned. Thus, unless the cytoplasms of the ovum and the sperm, which are also mingled in fertilisation, have some determining influence on the chromosomes, it does not seem as if fertilisation could have anything to do with the determination of sex. (We are here excluding the cases already referred to where there is an accessory or extra chromosome in one of the gametes, and we are supposing that the chromosomes throughout their history within the parents have retained their original tendencies towards production of a male or towards production of a female.)

At this point we encounter the suggestion of Ziegler, that since the parental chromosomes include contributions from the grandfather and grandmother, and since the relative numbers of these depend on the chances of the reduction divisions in maturation, it will be, so to speak, a "toss-up" whether grandfatherly or grandmotherly chromosomes predominate. If the former, the child will be a boy; if the latter, a girl. In fact, it is a matter of chance.

Suppose the potential offspring has twelve chromosomes from the father and twelve from the mother, as in the human species. "If amongst the former there are 8 grandmother chromosomes and amongst the latter 7 grandmother chromosomes, the child will be a girl, for there are at least 15 of the 24 derived from the grandmothers' side" (T. H. Morgan, 1907, p. 419).

Retrospect.—In the *Evolution of Sex* (revised edition,

London, 1901), much importance was attached to the supposed influence of nutritive and other environmental conditions, operative on the parents, on the germ-cells, or even on the early stages of the developing organism where there is evidence of prolonged sexual indifference or neutrality. In some cases it still seems legitimate to believe that external conditions may have a rôle in sex-determination, but in many cases further experiment has invalidated results previously accepted.

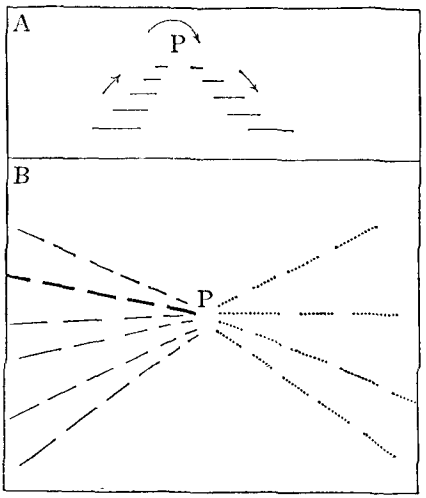

FIG. 47.—Diagram of protoplasmic changes: B, in plan, A, in elevation The anabolic or constructive processes are represented to the left; the katabolic or disruptive processes to the right.

More and more it seems being proved that the sex is fixed in the fertilised ovum or earlier, and it is difficult to verify any hypothesis as to the conditions of determination at this early stage.

In some cases there are demonstrably two kinds of ova, and in some cases the two kinds develop into different sexes. This suggests predetermination of sex on the part of the ovum. But we do not know why there should be two kinds of ova.

It may be that there is a segregation of gametes into two opposed camps, as may perhaps take place in cases of typical Mendelian inheritance. It may be that the two kinds of ova simply express the fundamental alternatives in protoplasmic metabolism—in the continual seesaw between anabolism and katabolism, that the one kind of egg is relatively more anabolic than the other, and that the interrelations between cytoplasm and nucleus are thereby affected in such a way that in one case the potentialities of a female organism find expression, while in another case the potentialities of a male find expression. A physiological variation may serve as the liberating stimulus for the alternative potentialities of the two sexes.

§ 6. *A Statistical Investigation.*

In regard to human offspring many attempts have been made to discover the conditions which determine the sex. The absolute and relative ages of the parents, their constitution and state of health, their diet and conjugal habits, the relation of the time of conception to the periods of menstruation, and so on, have been referred to as possible causes. A certain number of parents have some common characteristic, the ratio of males and females in their offspring is compared with the average ratio, and if the ratio is markedly different the conclusion is drawn that the characteristic in question had some definite influence upon the production of one sex or the other.

Prof. Newcomb (1904) has made a welcome contribution to the discussion by seeking statistically "to discover a criterion by which we may distinguish between inequalities in the division of a family between the two sexes which are simply the result of chance and those which are the result of a unisexual tendency on the part of the parents." He means by a unisexual tendency some constitutional or other characteristic of the parents which tends to the production mainly or wholly of male children, or mainly or wholly of female children.

His tentative conclusions are :—

(1) The preponderance of male over female births probably varies with the race. Although remarkably uniform in all

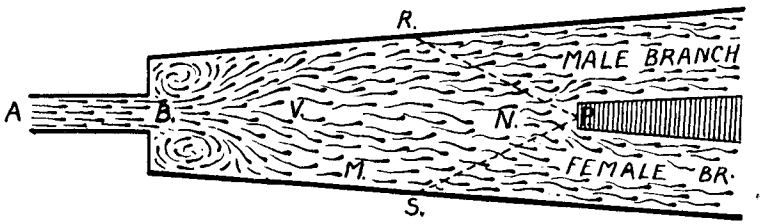

FIG. 48.—Diagram illustrating Determination of Sex. (After Simon Newcomb.)

"Let A be a large pipe or aqueduct, from the mouth (B) of which a stream flows into gradually widening river, V. At a certain distance below the exit B the river is divided into two branches by a promontory, P. On one side of this promontory which we may call the male side, the river is slightly broader than on the other. Between the exit and the promontory, the river flows over a rough bottom with many eddies, but the ultimate result must be that every drop of water which comes from the conduit ultimately passes on one side of the promontory or the other. But the side on which it shall pass is not determined at any one moment. As a drop, or, to give the analogy a more complete form, a small particle suspended in the water, leaves the conduit, it is equally likely to pass into one branch of the river or the other. If it chance to incline to the right after leaving the conduit, there will be a greater probability of its passing into the right branch, but this will be only a probability until a certain point of the course is reached. A particle reaching the point M, for example, will be likely to go into the female branch, but yet may be carried by an eddy across to the opposite side before it reaches it. One at N, although farther down, will still be uncertain; possibly its course may not be decided until it almost reaches P. A particle on one bank or the other will be more and more likely to pass into the corresponding branch the farther down it is found. When the particle once crosses one of the dotted lines PR and PS the branch it will take will be completely determined.

"A case of twins or of triplets has its analogue in the case of two or three particles emerging from the conduit in contiguity. They are more likely to keep together and enter the same eddies than if they were widely separated in the beginning. To speak with numerical exactness, there is a probability of 0·77 that they will pass on the same side of the promontory and of 0·23 that they will separate. In the case of triplets the corresponding probability would be 0·79; but these are only probabilities. At any moment any two particles may widen their distance and be drawn into different parts of the stream, never to reunite.

"We may thus say that the question, which branch of the river a particle, emerging from the conduit, is to flow into, will be determined by a series of accidents tending in one direction or the other; and the most plausible conclusion from the statistics of twins is that sex is determined in an analogous way."

branches of the Semitic race, it seems to be either non-existent or quite small in the Negro race.

There are no important differences as regards capacity for

producing children of one sex rather than the other which are permanent in the individual. All fathers and all mothers are equally likely to have children of either sex, except for the slight variations that may be due to age.

(2) It seems in the highest degree unlikely that there is any way by which a parent can affect the sex of his or her offspring.

(3) The most natural inference from all the statistical data is that the functions of the father in generation are entirely asexual, the sex being determined wholly by the mother. If so, it cannot be said that one father is more likely than another to have children of either sex. This conclusion requires to be tested by making a classification of the sex of third-born and following children according to the age of the father.

(4) The sex is not absolutely determined at any one moment or by any one act, but is the product of a series of accidental causes, some acting in one direction and some in another, until a preponderance in one direction finally determines it. The statistics of twins and triplets seem to show very strongly that these accidents occur after conception.

(5) The first-born child of any mother is more likely to be a male in the proportion of about 8 to 7. There is probably a smaller preponderance in the case of the second child. But there is no conclusive evidence that, after a mother has had two children, there is any change in her tendencies.

(6) The observed preponderance of male births in the Semitic race is due mainly to the unisexual tendency of the mother in the case of a first child.

§ 7. *Inconclusive Conclusions.*

At present, it does not seem safe to go further than Morgan does when he says: "In all species with separate sexes the potentiality of producing both sexes is present in all eggs and

in all sperms; but the development of the one or the other sex is determined by some unknown internal relation. . . . The condition that leads to the development of the alternative characters may exist in the egg alone (as for the male bee), or in the sperm alone (as for certain Hemiptera), or by the combination of egg and sperm, as for the female bee.

"Admitting that all eggs and all sperms carry the material basis that can produce both the male and female, the two conditions being mutually exclusive when development occurs, the immediate problem of sex-determination resolves itself into a study of the conditions that in each species regulate the development of one or the other sex. It seems not improbable that this regulation is different in different species, and that, therefore, it is futile to search for any principle of sex-determination that is universal for all species with separate sexes; for while the fundamental internal change that stands for the male or the female condition may be the same in all unisexual forms, the factor that determines which of the alternative states is realised may be very different in different species." (1907, pp. 422–4.)

Man.—Rauber and others have pointed out that the proportion of male and female births throughout Europe is fairly constant, the mean being 1060 males to 1000 females, and that the relative constancy of this ratio tells against the view that environmental (notably nutritive) conditions have anything to do with the determination. As we have already mentioned, about 30 per cent. of ordinary twins are of different sexes, while identical (monochorial) twins—surrounded by one fœtal membrane or chorion, and almost certainly developed from one ovum —are always of identical sex. Both these facts point to the same conclusion, that the sex is determined in the fertilised ovum. Punnett has investigated the proportions of male and female births in different parts of London, and finds that either no influence on the proportion of the sexes can be attributed to parental nutrition, or, at most, only a very small effect.

If the sex of the offspring is not determined by environmental conditions, on what does it depend? It may depend on a number of minute and variable factors, such as the relative ages of the parents and the relative ages of the sex-cells when they unite in fertilisation, or it may be "hereditary." It seems difficult, at present, to decide which of these views should be adopted, but, in any case, the facts point clearly to the conclusion that, in man at least, the sex is fixed unalterably at or soon after fertilisation.

But what is meant by sex being "hereditary"? It means (*a*) that the particular sex-ratio now general has been long established, and it is known that there has been an excess of male births in England for at least two hundred years; and (*b*) that what results from any individual fertilised ovum—whether a male or a female offspring—is determined by the compromise effected between the ancestral contributions that constitute the inheritance.