Chapter I

THE MECHANISM OF SEX-DETERMINATION

1. INTRODUCTORY.

Sex is the term used to define that differentiation of different parts of an individual, or of the same individual at different times, or of different individuals, which is associated with the elaboration of physiologically and often morphologically dissimilar gametes in the union of which the next generation of individuals has its origin. Maleness is the state or quality associated with the elaboration of spermatozoa (or of their physiological equivalents); femaleness is the state or quality associated with the elaboration of ova (or of their physiological equivalents). Sexuality is the state or quality of being distinguished by sex. A male is an individual that exhibits the state or quality of maleness, one that is efficiently equipped for the elaboration of functional spermatozoa and for the conveyance of these towards the site of fertilisation; a female, one that exhibits the state or quality of femaleness, one efficiently organised for the elaboration of functional ova, for the conveyance of these to the site of fertilisation, and often for the prenatal accommodation of the zygote, the fertilised egg, for the transit to the exterior of this new individual at some stage of its development and for the nurture of it thereafter. If in a group (e.g. a species) it is customary for maleness and femaleness to be exhibited by one and the same individual, coincidently or in succession, the group and the individuals comprising it are monoeious, hermaphroditic, though it follows that in certain cases an individual can at one time be a male and at another a female. If in a group it is not customary for maleness and femaleness to characterise one and the same individual the group is dioecious, bisexual; the sexes are separate, and every individual within the group is throughout its sexual life either a male or else a female.

Sexuality is an attribute of the function of reproduction; it is concerned with the capacity of living things to multiply. Sexual
reproduction (amphigony), distinguished by the preliminary process of fertilisation (syngamy), requires that two physiologically and in many instances morphologically dissimilar gametes derived, in most cases, from physiologically dissimilar areas of one and the same individual or from two separate and sexually distinct individuals, shall unite to form a zygote in which the new individual shall have its beginning.

Sexual reproduction has been demonstrated in all groups of the non-cellular Protozoa. When the different modes of such sexual reproduction are compared with that which obtains in the case of the Metazoa, it is found that certain essential features are common to both. There is in both cases reduction of nuclear material and, following this, a fusion of nuclear material derived from different sources.

Sexual reproduction is practised by all forms of animal life and it is reasonable to assume that it is beneficial to the race. It would appear that the reproductive elements of the individual body are not involved in the general bodily functioning, in the processes of individuation, but lie dormant and protected within the body, specially reserved for their own particular destiny. They constitute the material chain that binds the generations and are in a sense immortal. It can be shown in favourable instances that this segregation of the reproductive elements is a fact, and it is probable that it is so in all groups of organisms. In *Ascaris meglclocephala* it has been possible to demonstrate that the first division of the fertilised egg results in two cells which can be recognised from the beginning as being different in their organisation; one of these cells gives rise to the somatic tissues and the other to the germ-cells. In the case of the former the nuclear material undergoes a marked diminution in quantity whereas in the other no such reduction takes place. The lineage of the sex-cells from embryo to adult is demonstrable and these can be shown to form the material link between the generations.

Bisexuality can be regarded as the basis of evolutionary plasticity since through it mutations that have occurred remotely in space and independently in time can meet to reinforce each other, offering among the number of their random combinations characterisations which, when tested by the selective agencies within their
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environment, are judged on their merits, the harmful leading to
the elimination of their exhibitors. The possible benefits of bi-
sexuality seem to be foreshadowed in some degree in the case of
the conjugation of Paramoecium. Jennings (1913), in the course of
extended and critical experimentation, has demonstrated perfectly
clearly that conjugation is not in itself necessarily beneficial and
that its value lies in the opportunity it provides for the attainment
of the state of heterozygosis. For an explanation of this reference
must be made to the Chromosome Theory of Heredity. If it is
true, as this hypothesis postulates, that for all the characters,
anatomical and physiological, there are antecedent determiners,
factors, or genes, in the gerplasm, the chromosomes themselves;
if new characterisations are but reflections of specific regional
alterations in the organisation of the chromatin material, of muta-
tions, and if new characters, having arisen, persist in virtue of the
integrity of the hereditary mechanism, then it follows that in
allogamy—cross-fertilisation—there exists the mechanism for the
spread of a new characterisation through the race to which the
individual belongs, since it can be brought into association with
other genetic variations, other genetic deviations from the usual
characterisation, that have occurred independently in time and
remotely in space. This mingling of different hereditary constitu-
tions, of different genotypes, leads to different factorial recombi-
inations, and thence to new character combinations, new phenotypes,
these being the raw material upon which selective agencies may
work. Thus if \( N \) mutations occur in the gerplasm of an asexually
reproducing organism, only \( N \) phenotypes can arise, whereas if
\( N \) mutations occur in the gerplasm of a sexually reproducing
organism, \( 2^N \) phenotypes can be formed. Ten mutations mean
10 phenotypes in the first case, 1024 in the second. If for every
heritable character there is an antecedent determinant or gene, then
this gene may be present in the gerplasm in the duplex state,
having been contributed by both parents, or it may be present in
the simplex state, having been contributed by one. All characters
are not advantageous; the harmful can, however, be balanced by
the helpful. The end-result of a gene in the simplex state may not
be so disadvantageous as that of the same gene in the duplex state.
A heterozygous individual, possessing the gene (or genes) for a
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character (or characters) in the simplex state may thus be better fitted to accommodate itself to the variations of an inconstant environment than the homozygote, which, because of the purity of its factorial constitution, is not so plastic. By means of conjugation and of allogamy generally advantageous genetic acquisitions can be pooled. Equally truly, disadvantageous genetic acquisitions can be pooled also, but if it is permissible to speak of advantage at all, it is to the advantage of the race and not of the individual that reference is made.

2. SEX-DIMORPHISM.

In the great majority of animals every individual is either a male or else a female. Male is commonly to be distinguished from female by differences in the sexual phenotype, the sexual characterisation consisting of (1) the gonads or sex glands, (2) the accessory sexual apparatus of ducts and associated glands concerned with the transference of the products of the gonads and in the female of many forms of the zygote itself, (3) the external organs of reproduction, and (4) certain skeletal and cutaneous and other less definite physiological and psychological characters, often loosely referred to as the secondary and tertiary sexual characters, some of which are employed not directly in sexual congress but in some cases in courtship, combat, concealment, and in the case of the female, in the care and nourishment of the young. Gräfenberg (1922), Manoilov (1922–3), Satina and Demerec (1925), and Edlbacher and Röthler (1925), amongst others, have recently described certain pieces of experimentation that bear directly upon this question of sex-dimorphism for they confirm the impression that the sexes are biochemically distinct.

The relegation of the function of reproduction to a specialised system of the individual’s body has been attended by the provision of an efficient equipment for sexual congress. In the simpler forms the products of the gonads are merely liberated at the body surface and the prospects of the fertilisation of the ovum by the sperm are relatively remote; fertilisation is entirely a matter of the chance

1 Geddes and Thompson, 1899; Cunningham, 1900; J. S. Huxley, 1923; Havelock Ellis, 1914; Morgan, 1914; Meisenheimer, 1922; and Goldschmidt, 1923; treat this question of sex-dimorphism fully.
meeting of dissimilar gametes. The development of the accessory sexual apparatus and external genitalia provided the means for the direct transference of spermatozoa to the genital passages of the female and so rendered fertilisation far more certain. Highly elaborated sexual tropisms, when developed, further increase the certainty of profitable sexual congress, whilst amazingly perfect contraptions, such as the phosphorescent organ of the firefly, _Photinus pyralis_, have been utilised to bring the sexes together for this purpose. Care of the young is exhibited by those species in which the production of gametes, particularly by the female, is restricted, and in those cases in which the offspring themselves possess but a limited supply of nutritive material. As a general rule, it seems that the earlier an embryo is forced by its organisation actively to provide for its own subsistence, the more care it needs. The mother in some cases merely protects her offspring, in others she also nurses them. In some cases the young actively seek parental protection, in others the father and not the mother cares for the embryonic young, _e.g._ _Alytes obstetricans_. The parents in some cases carry the developing zygotes in different parts of the body which often take the form of specialised sacs, _e.g._ the marsupial pouch and the uterus. Oviparity is replaced by viviparity with associated changes in the maternal organism, since it demands internal fertilisation and the anatomical, physiological, and psychological equipment for coitus. Such are the evidences of _storge_, the postulated hereditary instinct which tends to preserve a species.

Though attempts to classify the sex-dimorphic characters for purposes of discussion have been many, it has to be confessed that as yet no satisfactory classification exists\(^1\). That this is so is due to the fact that as yet no exact knowledge exists concerning the genetic nature of many of these characters and of their relation to the sex-glands, and until this has been secured, any attempt to classify them must be premature. For the present, it is enough to hold that the characters which in their combination constitute maleness or femaleness respectively are characters in the genetic sense, being expressions of a genotype that is determined by the nature of the genes brought into the zygote by the conjugating gametes. In the

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\(^1\) See Lipschütz, 1924; Zavadovsky, 1926; Baker, 1926.
fertilised egg there are none of the characters that distinguish race from race, male from female, that make each individual the first and last of its identical kind; these are expressed as ontogeny proceeds and their expression is modelled, encouraged, embarrassed, to a greater or lesser extent, by the impress of the agencies of the external environment, the outer world, and by the changing conditions within the developing zygote itself, the internal environment, established by the whole of the genotype in action and by the functional activity of the characters as these become differentiated. As a working hypothesis, it can be accepted that sexuality is primarily based upon antecedent determiners within the germplasm, upon genes resident in the chromosomes.

3. THE TIME WHEN THE SEX OF THE INDIVIDUAL IS DETERMINED AND THE MECHANISM BY WHICH IT IS DETERMINED.

THE EVIDENCE OF POLYEMBRYONY.

At the beginning of this century, it was generally believed that at the time of fertilisation the egg was completely ambivalent as regards the future sex of the resulting zygote; it was customary to refer the sex of an organism to the conditions incident to development. But certain facts of general biology are now known which are not susceptible to interpretation of this kind. They point to the view that sex in the higher animals is usually predetermined at the time of fertilisation. Identical twins, i.e. twin zygotes derived from a single fertilised ovum, are always of the same sex. Such polyembryony is rare in the human, but in the Texas nine-banded armadillo it is the rule for four young to be produced at a time, all of the same sex and remarkably alike. Newman and Paterson (1909) were able to show that in the case of the armadillo a single fertilised ovum after development to a certain stage budded off four embryos. On the other hand, in those cases in which the different embryos arise from separate ova, it is known that the individuals are not invariably of the same sex. There is no appreciable reason why, if purely environmental factors are at work in determining the sex of the offspring, litters produced from one egg should be of the same sex, while litters produced from separate
EGGS should include both males and females. From such observations as these it would appear that the sex of the individual is determined by the constitution of the fertilised ovum at the time of fertilisation.

**CYTOLOGICAL EVIDENCE.**

In an ever increasing number of instances it can be shown that the phenotypic differences distinguishing male and female are associated with constant differences in the chromosome content of the tissues of the two sexes. This fact is illustrated in the clearest possible manner in the case of *Drosophila melanogaster* which has four pairs of homologous chromosomes. In the somatic cells and immature gametes of the male one of the four pairs is remarkable in that its members are morphologically dissimilar, whereas in these tissues of the female the members of this pair are, as is the case in all the other pairs in both male and female, morphologically alike. Since tissues from male and female differ chromosomally only in this respect, these chromosomes are referred to as the sex-chromosomes, and the members of the sex-chromosome pair in the female and the one sex-chromosome of the male that is morphologically similar to these are known as the X-chromosomes, whilst the unequal mate of the X in the male is known as the Y-chromosome. In respect of the sex-chromosomes the female is XX, the male is XY.

The situation thus arises that in all the cells of the body of the female and in her immature ova there are four pairs of homologous chromosomes, and of these one pair consists of two X-chromosomes, whereas in all the somatic cells and immature gametes of the male there are four pairs and of these one consists of an X-chromosome in association with a Y-chromosome. Into each ripe gamete there passes one or other member of each pair. All eggs are alike in that each contains an X-chromosome but there will be two kinds of sperm, one containing three autosomes and one X-chromosome, the other three autosomes and a Y-chromosome. The female of Drosophila is monogametic; the male is digametic. When egg and sperm unite in fertilisation, into the zygotes will
be received one member of each pair from the father by way of the sperm, and the other member of each pair from the mother by way of the egg, and there will be two forms of zygotes, one that received an X-chromosome by way of the sperm and the other that received a Y-chromosome. The first will have a sex-chromosome constitution that can be symbolised as XX, the chromosome constitution typical of a female, the other a sex-chromosome constitution symbolised as XY, that of a male. This sex-determining chromosome mechanism yields results that are in every way comparable with those that are obtained when a heterozygous dominant (Aa) is mated to a recessive (aa) in a typical Mendelian monohybrid experiment—equal numbers of the two classes that were represented in the mating. In respect of the X-borne genes, the male is constitutionally simplex, the female duplex.

The conclusion that a difference in the gametes of the two sexes is correlated with the sex of the future individual is abundantly supported by the results of other cytological research. As early as 1902, McClung was able to demonstrate that in various Orthoptera (the crickets, cockroaches, and grasshoppers) there is in the male an unpaired chromosome instead of the equal pair in the case of the female. The constitution of the female in these forms is XX, of the male XO, so that while all the female gametes must contain an X element, only half of the spermatocytes will do so. An egg fertilised by an X-bearing sperm must give rise to an XX type of individual, a female. An egg fertilised by a sperm which lacks the X will give rise to an XO type of individual, a male. In other forms it was found by Wilson (1906) and others that the number of chromosomes was identical in both sexes, but that, as in the case of Drosophila, while in one sex the X was equally paired, in the other it was paired with an unequal mate; the female is XX, the male XY in some groups; in others, in Abraxas and birds for example, the female is XY and the male XX.
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In a third type of sex-chromosome constitution the X is represented, not by one chromosome, but by a group of any number from 2 to 8, which during gametogenesis act together as a compound X-element. The group is single in the male, double in the female, and these cases, therefore, conform to the XX = ♀, X = ♂ type. If, as in certain cases there is a Y-chromosome in addition, this is always single. In other forms the X-chromosome is found to be joined to the end of one of the autosomes, remaining constantly associated with the autosome throughout the whole of the chromosome cycle.

(For comprehensive lists showing the sex-chromosome constitution of different species see Harvey 1916, 1920 and Wilson 1925.)

Sperm dimorphism, estimated by measuring the head length of the sperm, has been demonstrated in a considerable number of species (see Wilson 1925). It is found that there are two inter-grading size classes, and it is assumed that the larger consists of the X-bearing, the smaller of the no-X-bearing sperm.

In the case of those forms in which hermaphroditism is customary no satisfactory body of evidence concerning the cytological concomitants of this condition is yet available. In such forms as the oligochaetes, leeches, pulmonates, and ascidians, actual sex-chromosomes have not yet been identified, so that it has been impossible to demonstrate any correlation between chromosomes and sexuality. One instructive and significant case among the normally hermaphroditic nematodes exists, however. Boveri (1911) and Schleip (1911) have studied Angiostomum (Rhabditis) nigrovenosum, a nematode exhibiting an alternation of generations between a free-living dioecious form and a parasitic hermaphroditic form which lives in the lungs of the frog. In the dioecious generation males and females occur in approximately equal numbers and the zygotes produced by these develop into a hermaphroditic form which has the general structure of a female with a gonad that first elaborates oogonia and then later spermatogonia also, the two kinds being produced in irregularly alternating zones. From the spermatogonia spermatocytes arise and these undergo the two usual divisions to form functional sperm. The eggs are fertilised by the sperm elaborated by the same individual with the result that approximately equal numbers of males and females are produced.
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Cytological examination showed that the parasitic hermaphroditic form is diploid containing twelve chromosomes, and that this number is reduced to six in the egg, whereas of the sperm only one half receive six, the other half getting only five, owing to the fact that in the second division one of the X-chromosomes remains near the equator and, failing to enter the daughter nucleus, degenerates. Fertilisation results, therefore, in two kinds of zygotes, one possessing twelve chromosomes, the other eleven. Males of the dioecious generation have eleven chromosomes, so that of the sperm elaborated by these one half carries six, the other only five. All the fertilised eggs, however, produce hermaphrodites with twelve chromosomes. To explain this, Boveri and Schleip suggest that the five-chromosome-containing sperm is non-functional, but, on the other hand, it may be that the eleven-chromosome-containing zygotes are non-viable.

THE EVIDENCE OF PARThENOGENESIS.

Parthenogenesis occurs naturally in many species of plants and animals, e.g. the rotifers, daphnids, and such insects as the aphids, gall-flies, and bees, and in certain instances can be induced artificially by physico-chemical means in the sexual ova of forms in which parthenogenesis is not customary. In the rotifers, daphnids, ostracods, aphids, and phylloerythrines, the parthenogenetic ovum is an agamete incapable of becoming fertilised, and in its mode of maturation and in other ways is markedly different from the sexual ovum although it is commonly held that the agamete is derived from the gametic form of ovum.

Natural parthenogenesis occurs in two forms, (1) that in which the chromosome number in the parthenogenetic egg is diploid, and (2) that in which the number is haploid, though in a few cases the distinction is bridged in that development begins with the haploid number of chromosomes, but ends with the diploid. The two types are to be distinguished by the number of polar bodies formed during the phase of maturation, the diploid egg extruding but one polar body, the haploid producing two. The haploid egg is one that undergoes complete reduction and is capable of fertilisation, but is one that may develop without activation by the sperm. Such an egg, developing parthenogenetically, yields an individual