

PART III

THE PHENOMENA OF HEREDITY RESULTING FROM SEXUAL REPRODUCTION

INTRODUCTORY REMARKS ON THE NATURE OF SEXUAL REPRODUCTION.

THE phenomena of heredity have so far been considered in connection with a purely asexual form of reproduction only: the complications of the germ-plasm arising from the intermingling of the hereditary parts of *two* parents have been left aside, and the composition of the germ-plasm has been assumed to be of such a nature as would result if *monogonic* reproduction were the only form in which the process existed. The advantage of this method of procedure is seen in the fact that it has only been necessary for us to bear the essential part of the processes in mind when analysing the fundamental phenomena of heredity, and this essential part has therefore not been lost sight of in the confusing and ever changing intermixture of individual variations which result from amphigonic reproduction. The course we have followed is justified by the fact that fundamental processes — such as ontogeny, regeneration, and multiplication by fission and gemmation — cannot owe their origin to amphigonic reproduction, but would take place even if this form of multiplication did not exist at all.

Bearing this fact in mind when considering the complications arising from sexual reproduction with which we have to deal in analysing the phenomena of heredity and their material substratum, it will now be profitable to consider the facts concerning this form of reproduction, and to see how they can be explained. I will now therefore give a short account of the processes in

question as far as is necessary in order to render comprehensible the complications in the phenomena of heredity resulting from them.

Until far into the present century 'sexual reproduction' was considered to be the *essential* and *primary* form of the process; and although it gradually became more and more evident that several kinds of 'asexual reproduction' may also occur, these nevertheless only take place in the lower forms of animals and plants. As the details of the phenomena of reproduction were for a long time known almost exclusively with regard to the higher animals, and as in them sexual reproduction alone occurs, the special peculiarities of the latter were naturally considered to be necessary and indispensable in the process. *Fertilisation* was looked upon as an essential part of this process, and it alone was supposed to render life from one generation to another possible at all; in short, fertilisation was regarded as a 'process of rejuvenescence,' and sexual reproduction was considered to form the foundation from which all forms of reproduction have arisen. The existence of different forms of asexual reproduction was explained as an 'after-effect' of the process of fertilisation or rejuvenescence occurring in sexual reproduction.

This view appeared to receive support from the fact that sexual reproduction is of universal occurrence, from the lowest to the highest forms of animals and plants; and also that asexual reproduction never takes place in the higher organic forms, and even in the lower ones it only alternates with the sexual form of the process.

The present state of our knowledge of the process of fertilisation, however, justifies us in considering these earlier views to be totally erroneous. In no case does fertilisation correspond to a rejuvenescence or renewal of life, nor is its occurrence necessary in order that life may endure: it is merely *an arrangement which renders possible the intermingling of two different hereditary tendencies*. We shall deal later on with the question as to why such a mingling has been introduced and so extensively adopted by Nature; at present it is only necessary to prove that this is the case. Fertilisation consists in the union of two hereditary substances, *i.e.*, of the germ-plasms of two individuals: all the complicated and varied phenomena of differentiation — beginning with that of the two different kinds of reproductive cells, usually known as male and female, up to that of the individuals them-

selves into males and females, and including the innumerable other resulting adaptations and phenomena — take place solely for the purpose of rendering possible the union of the primary constituents of two individuals.

This process of the fusion of two germ-plasms, which constitutes the essential part of fertilisation and is as a rule connected with the fusion of two cell-bodies, I have designated as *amphimixis*. It is not always connected with reproduction, for these two processes take place independently of one another in all unicellular organisms. In the Infusoria, for instance, two individuals in the course of their life-history come into contact with one another, and then either fuse completely into one, or else undergo a partial or temporary fusion; in both of which cases half the hereditary substance is transferred from one individual into the other, and thus amphimixis is brought about. The latter process is only invariably connected with reproduction in the case of multicellular forms: this is necessitated by the fact that the union of two different germ-plasms cannot take place by the fusion of entire individuals, as the germ-plasm is enclosed in separate cells, a male and a female, the fusion of which takes place in a similar manner to that which occurs in the process of conjugation in unicellular organisms. This act of amphimixis must then be followed by the multiplication of the fertilised egg-cell, accompanied by the differentiation of its successors, — or, in other words, *by the ontogeny of a new individual*; for did this not result, the process of amphimixis would be useless. *Amphimixis is therefore always connected with reproduction in all multicellular forms*, and these two processes together constitute ‘*sexual reproduction*’ or ‘*amphigony*’ (Haeckel).

The process of amphimixis, as it occurs in amphigonic reproduction, is briefly as follows. The two kinds of germ-cells mutually attract one another, and then fuse together, the smaller male element always entering the larger female one. The nuclei of the two cells then approach each other, and so come to be situated close together, each being accompanied by its ‘centrosome,’ — *i.e.*, that remarkable body, enclosed in a clear sphere, which, as already stated, constitutes the *apparatus for division*. The germ-plasm in both nuclei is at first distributed in the form of fine threads, as is represented in the case of the female nucleus in Fig. 18, I.; it subsequently, however, becomes contracted, so as to give rise to *nuclear rods* or *idants* (Fig. 18, II.). Edouard

van Beneden was the first to prove that the number of these idants is the same in both of the conjugating-cells, and this dis-

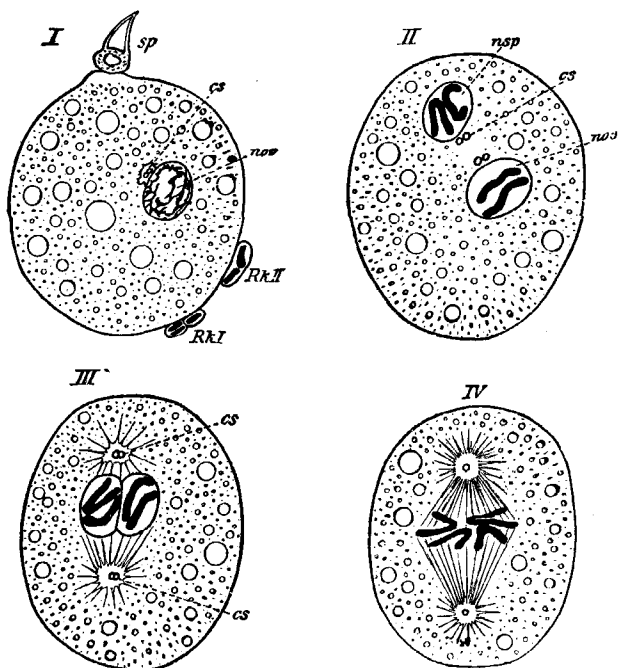


FIG. 18. — Diagram of the fertilisation of the egg in *Ascaris megalocephala*. — (Compounded from the figures and descriptions of Boveri and others.)

- I. — The sperm-cell (*sp*) is about to enter the ovum, which contains a nucleus (*nov*) and centrosome (*cs*). *Rk I* and *Rk II*—the two primary polar-bodies, the first of which has divided into two; each contains two idants.
- II. — The sperm-nucleus (*nsp*) has passed into the egg, near the nucleus of which it is situated. Each of these nuclei contains two idants, and also a centrosome, which has divided into two.
- III. — The two nuclei are now close together: the centrosomes, with their 'spheres of attraction,' are connected together in pairs, and are situated at the poles of the spindle, which is already visible.
- IV. — The nuclear membrane has disappeared, and the first embryonic nuclear division is now taking place.

covery — which has since been confirmed in the case of a large number of species of animals, and has been proved quite recently

by Guignard to apply to plants also — is of decided importance in connection with the conception that idants constitute the hereditary substance. As the two nuclei are approaching one another, their centrosomes become doubled, and the corresponding pairs unite to form the two poles of a nuclear spindle (Fig. 18, III.), which direct the first cell-division leading to the formation of the embryo; this usually only occurs after the nuclear membrane has completely disappeared (Fig. 18, IV.).

The process of fertilisation therefore consists in the union of the nuclei of the two sexual cells within the maternal germ-cell, and also of the bodies of the cells, together with their apparatus for division. One half of the germ-plasm of the 'combination-nucleus' ('Copulationskern') thus formed by the union of the sexual nuclei consists of idants derived from the mother, and the other half of those derived from the father, and the resulting combination of two hereditary substances directs the ontogeny and controls the building-up of the new individual. The entire number of idants nevertheless always remains the same in all the cells of the body: thus, for instance, if eight paternal and eight maternal idants were brought together in the process of amphimixis, there would be sixteen idants in every* cell in the body of the individual arising from the fertilised ovum; and if, again, as represented in Fig. 18, there are only two idants in each germ-cell, each somatic cell will contain four idants.

The nature of sexual reproduction depends therefore on the intermingling of two hereditary tendencies which are individually different from one another; or, to pass from the abstract to the concrete, it depends on the union of *two hereditary substances* in the first rudiment of the individual. We must next investigate the manner in which this combination of hereditary substances affects the composition of the germ-plasm.

* A recent observation renders it doubtful whether 'every' cell contains the same number of idants; but this need not here be taken into consideration, as its importance cannot at present be estimated.