Hereditary characters and their modes of transmissions / by Charles Edward Walker.

Contributors

Walker, Charles Edward, -1953.

Publication/Creation

London : Edward Arnold, 1910.

Persistent URL

https://wellcomecollection.org/works/m39g2xhp

14/4
Back

STARY
ACTERS
D
MODES
ISSION

LKER

OLD

HEREDITARY CHARACTERS

HEREDITARY CHARACTERS

AND THEIR MODES OF TRANSMISSION

BY

CHARLES EDWARD WALKER
M.Sc., M.R.C.S., L.R.C.P.
Director of Research in the Glasgow Cancer Hospital; Formerly
Assist. Director of Cancer Research in the University
of Liverpool; Sometime Demonstrator in Zoology
Royal College of Science, London
Author of "Essentials of Cytology," Etc.

LONDON
EDWARD ARNOLD
1910

TO

MY FRIENDS IN LIVERPOOL

PREFACE

During recent years an enormous advance has been made in the knowledge of cell-phenomena. As cells are the ultimate units of all living matter, the significance of their phenomena in connection with a study of the problems of heredity is obvious. Such information is, however, scattered in a number of scientific journals, and it is difficult for the general biologist to keep up to date. In the present volume I have attempted to apply recent discoveries, as well as experimental work upon cells, to some problems in heredity, and I believe that I have thus arrived at a satisfactory harmonising of the results of the Mendelian experiments with the observations of the Biometricians. This has been done by showing that some parts of the cells involved in fertilisation—that is, in the production of a new individual—are distributed in an alternative manner, while other parts simply divide in bulk. Correns has suggested that the characters that are inherited according to the Mendelian law are not specific. In 1907 I suggested that there were two classes of characters, which behaved in different manners with regard to inheritance, but I believe that a complete theory, dividing characters into individual and racial, and attributing to each a different mode of transmission, is put forward here for the first time.

To this theory I suggest as a corollary, a fresh hypothesis regarding the problem of sex.

In every case I have tried to deal impartially with the evidence at my disposal, and have accepted the facts demonstrated by all parties, while often disagreeing with particular interpretations. A few experimental results of my own are given, but only where the observations on which they are based are already published and available for reference.

It will be seen that I have assumed in the following pages a certain continuity of individuality with regard to the chromosomes. In some insects, during the pupal stage, the cells appear to pass into a condition of hopeless confusion. It is not possible to distinguish the various organs of the animal's body; yet it would seem probable, unless evidence be forthcoming to the contrary, that the cells or the protoplasm derived from the cells forming the various organs in the larva, go to form the corresponding organs in the imago. We know that this is what happens in other insects where the apparent disintegration referred to above does not occur. In some organisms the chromosomes visibly retain their identity from generation to generation of cells, though in many organisms they appear only in connection with the process of division. In the fear that it may be held that I have assumed too much for the chromosomes, I would point out that as a matter of fact I have not assumed more for them than is assumed for the protoplasm forming the cells of the organs of the insects referred to in the example quoted above.

Cytology is unfortunately almost a foreign subject to some biologists, and I therefore attempted to make the beginning of my book sufficiently untechnical to be understood by the ordinary cultured reader. Having begun in this way, I have tried so to continue throughout the volume, in the hope of interesting a wider audience. This plan has, of course, involved, for the sake of completeness, the covering of much ground which is quite familiar to the general biologist. Hence the inclusion of much that might otherwise be considered as out of place in a book which professes to present fresh aspects or interpretations of problems that are of great current interest.

I have many to thank for help and advice. Professor

Oliver Elton has read the whole of the MSS. from the point of view of the man who is not a biologist, and has suggested many alterations in order to render the meaning clearer. He owed this infliction largely to the fact that Sir Francis Galton, who had kindly read several chapters, suggested that I should get some non-biological friend to read my MSS. Professor Poulton has also read several chapters and given me valuable advice. Professor E. B. Wilson suggested several alterations in my chapter on the determination of sex. Professor Harvey Gibson suggested several excellent examples of adaptation in plants, and Mr. George Arnold several in animals, particularly with regard to Hymenoptera. I have also to thank him for the drawings of *Typhlopone*.

CHARLES WALKER.

CONTENTS

CHAPTER I

PAGE

The structure of living matter—Unicellular and multicellular animals and plants—Life cycles of unicellular animals—Reproduction in multicellular animals and plants—The life cycles of multicellular organisms—Theories of emboîtement, pangenesis, and idioplasm—Experiments bearing upon these theories 1

CHAPTER II

Structure of a cell—Phenomenon of cell division—Selective division of certain parts—Theory identifying Nägeli's idioplasm with chromatin—Objections—The maturation of the gametes—The meiotic phase—The impossibility of particular characters common to the race being borne by particular chromosomes—Fertilisation—Parthenogenesis—Fertilisation in unicellular animals—Experiments in artificial fertilisation and their bearing upon the existence of an hereditary substance—Conclusions 13

CHAPTER III

Differentiation of cells—Inborn and acquired characters—Mental characters in man—Physical characters—Instinct—Lamarck's theory—The Darwin-Wallace theory—Weismann's theory—Oscar Hertwig's theory 45

CHAPTER IV

Variation—De Vries' mutation theory—The case of Œnothera—The disappearance of characters—Variation in grafts—The cell layers in the embryo—Variations in wild and domesticated races—Arguments against the origin of species *per saltum*—Fertility of hybrids . . 59

CHAPTER V

Adaptation—Difficulty of explaining by the mutation theory—Examples of adaptation—Protective coloration—Seasonal changes—Imitative adaptation—Pitcher-plants—Drosera—The Yucca and the moth Pronuba—Parasitic adaptation—The material provided by variation for natural selection to work upon—The biometrical principle—Conclusions 77

CHAPTER VI

Racial and individual inborn characters—Immunity to diseases—Malaria—Measles—Tuberculosis—Conclusions 102

CHAPTER VII

PAGE

Progressive and regressive variations—Recapitulation—Reappearance of the characters of remote ancestors—Regression in domesticated animals—Crosses between natural races—Galton's theory of heredity—The bulk of characters inherited from remote ancestors—The village-sheik—Prehistoric human remains—Conclusions 109

CHAPTER VIII

Causes of variation—Amphimixis—Not compatible with facts of maturation and fertilisation—Elimination of useless variations by bi-parental reproduction—Conclusions 124

CHAPTER IX

Environment as the cause of acquired characters but not of inborn variations—Discussion of so-called inherited diseases—Cases claimed as proving the transmission of acquired characters—Acquired immunity and inborn immunity—Brown-Séquard's experiments—The inheritance of instincts—Social bees and ants—Effect of illness upon growth—Favourable conditions cause degeneration—Stringent selection causes improvement—The case for the transmission of acquired characters—Environment causes selection—Lamarckian explanation of immunity—Natural selection of inborn variations is a question of adaptation to the environment—Lamarckian explanation of the production of physical characters—Inborn variations arise in the germplasm—Conclusions 134

CHAPTER X

Mendel's discovery—Segregation of gametes—The extent of the Mendelian experiments—Comparison between the results of the Mendelian experiments and the distribution of the chromosomes in fertilisation—A suggestion that Mendelian characters are represented by chromosomes—Blended inheritance—Exclusive inheritance—Particulate inheritance—Mendelian phenomena most perfect in self-fertilising plants—A suggestion that Mendelian characters are individual variations and that characters which blend are racial—Evidence in support of this theory 166

CHAPTER XI

The function, production, and determination of sex—Sex alternating in the same individual—Experiments on the determination of sex—Wilson's theory of the determination of sex—The Mendelian interpretation of the determination of sex—Archdall Reid's theory that Mendelian characters are non-sexual traits reproduced in the sexual mode—A suggested explanation—Potentiality of producing secondary sexual characters present in both sexes—Sex is a character which is probably transmitted alternatively like individual variations—Conclusions 190

CHAPTER XII

Some general considerations 212

BIBLIOGRAPHY 222

INDEX 231

HEREDITARY CHARACTERS

AND THEIR MODES OF TRANSMISSION

CHAPTER I

The structure of living matter—Unicellular and multicellular animals and plants—Life cycles of unicellular animals—Reproduction in multicellular animals and plants—The life cycles of multicellular organisms—Theories of emboîtement, pangenesis, and idioplasm—Experiments bearing upon these theories.

THE phenomenon of heredity, or the transmission of characters from parents to offspring, is exhibited by all living organisms, both animals and plants. But before dealing with heredity directly, it is necessary to examine some other properties which are also common to all living organisms.

As far as our knowledge goes, living matter, whether it be animal or vegetable, exists in only one form, that is, as minute masses of a complex jelly-like substance known as *protoplasm*. The minute masses are called *cells*, and are composed of certain definite parts. Cells when not pressed upon by surrounding cells or specially modified, are roughly spherical in shape. Within each cell is an area, generally surrounded by a membrane, which is denser than and differs in some other ways from the rest of the cell. This is the *nucleus*. The rest of the protoplasm forming the cell is known as the *cytoplasm*. There are other organs usually found in cells, but for the present we shall confine ourselves to the nucleus and cytoplasm.

Every part that is alive of an animal or plant consists of cells and of nothing else. There are parts of the bodies of animals and plants that are not composed of cells, but these are not alive. The hard parts of the bones in man are an example of lifeless substance within the body. Such dead material, however, has been produced by cells which form part of the animal or plant during its life.

Living matter, then, as far as we know, exists only in the form of cells. There is no evidence at present available to show that cells are, or can be, derived from anything but pre-existing cells. Many attempts have been made to show that living matter exists in a more primitive form, but when carefully investigated they have all broken down. Theories, of course, exist, but they are quite unsupported by any direct evidence, and even that which is indirect suggests no more than the possibility that living matter may have at some time existed in a more simple form than it does at present.

We may, for the sake of clearness, divide the whole of the living organisms into two great groups: the unicellular—those in which an individual contains but a single cell; and the multicellular—those in which the individual contains more than one cell. The vast majority of the unicellular organisms are invisible to the naked eye, but nevertheless they perform the same functions of digestion, secretion, excretion, and so on, as the whole body of the multicellular organism, which may be built up of many millions of cells.

In some unicellular forms of whose life-cycles we have an intimate knowledge, many generations of new individuals are produced from pre-existing individuals by a simple process of division. Thus in *Stylonychia,* one of the Infusoria, simple division goes on for over a hundred generations. Sooner or later, however, the individuals in the swarm begin to conjugate. Two individuals adhere to each other, and exchange portions of their nuclei in a somewhat complicated manner. The individuals are all similar, there is no sex. After conjugation has occurred, the animals separate, and another period of simple division intervenes, during which an enormous number of new individuals is produced from the individual that conjugated. After a time, however, some or all of a new generation of individuals again conjugate. We thus have a regular series of events. Comparatively long periods pass during which generations of individuals are produced merely by simple division. But at recurring intervals the individuals composing the swarm at the moment, pair off and conjugate. Each individual pairs only once. Maupas, who first observed these facts, also showed that if conjugation was prevented by artificial means, the race degenerated very rapidly.[1] The nuclei first showed signs of degeneration, and eventually all the animals died. When conjugation was allowed to take place, however, a fresh period of simple divisions occurred. Though it has been shown that conjugation may be delayed, apparently almost indefinitely, by artificial conditions of temperature and food, still it is certain that under natural conditions conjugation is necessary for the perpetuation of the race in the case of many of the unicellular forms, though in some, particularly among unicellular plants, it seems certain that it never occurs.

Although among the unicellular organisms it appears that there are some which can continue to propagate indefinitely by the simple division of pre-existing individuals, in the higher forms of animals two individuals are necessary for the production of a new individual. Indeed, in the higher animals we may say that bi-parental reproduction is universal, for the only exceptions have apparently been modified by selection from forms which have been bi-parental.[2]

Among the higher animals the universality of bi-parental reproduction is very obvious. Among the higher plants, however, the matter is a little more complicated. The body of the plant itself is formed of an asexual generation of cells which has no counterpart in the life-history of the higher animals. The sexual elements are produced by

---

[1] Maupas, *Arch. Zool.*, Exp. 2, Série VI., 1888; *Ibid.*, Série VII., 1889; *Comptes Rendus*, Paris, 1891.

[2] The apparent exception of parthenogenesis is really only a modification, more or less easily explained, of the usual form of bi-parental reproduction. For the sake of clearness it is necessary to leave the detailed explanation until later.

"gametophytes," which are in reality separate individuals growing upon the plant. Strictly speaking, it is not the plant itself which must be regarded as corresponding to the body of the animal, but the gametophyte. In the higher plants, therefore, as in the higher animals, two individuals may be said to be usually necessary to the production of a new individual.

All multicellular organisms commence their existence as single cells. This single cell divides into two cells. Each of the two thus produced divides again, and this process continues until the whole body of the multicellular animal or plant is built up. Among the cells of the earlier generations there is a great similarity in appearance; in fact, until a great number of cells have been produced, it is impossible to see any differences between them. As more and more are produced, however, they become divided into groups, and the individuals forming each of these groups are often very different indeed from those forming others. This differentiation appears very gradually, and it is only when the organism is well advanced in its development that the complete differentiation between various kinds of cells is reached. It is due to the fact that the cells produced from the original one develop along different lines, that the tissues of the body differ from each other. The final stage of differentiation in the enormous number of cells produced from the single original cell forms the complete body of the multicellular organism. One group of cells, however, does not, in the case of many organisms at any rate, act in this manner. The cells composing it do not become modified in shape and function as do those belonging to other groups. Instead of serving some purpose necessary to the well-being of the organism, as is the case with all the rest of the cells, those belonging to this group are destined to be thrown off from the body, and to go to the formation of new individuals. Two of these cells thrown off from different individuals (in the case of the higher animals and plants usually from individuals of opposite sex) meet and fuse to form a single cell, the *fertilised ovum*. This new individual then undergoes a series of divisions, becoming multicellular, and in its turn throwing off cells which become parents in due course.

It will now have become evident, that as the single cell from which all the cells forming the body of the multicellular individual are produced is formed from the fusion of two cells, one derived from each parent, every cell entering into the formation of the various tissues of the body probably contains matter originally derived from each parent. As we shall see later, this is actually the case.

Every multicellular organism begins its existence as a single cell. It is evident, therefore, that until the first division occurs, this single cell itself performs all the functions necessary to its own well-being. Indeed for the time this single cell is to all intents and purposes a unicellular individual, and particularly in the case of some plants it leads a comparatively prolonged existence as such. In many of the higher animals, the cells that are eventually going to be thrown off to form new individuals—the sexual cells or *gametes*—are differentiated at a very early period, frequently long before birth. These cells live a parasitic existence in the body which has produced them, and in a certain sense can hardly be regarded as forming an integral part of it. They are certainly not necessary to the individual, but they are necessary for the production of new individuals, and are thus essential to the race.

A very interesting comparison has been drawn with regard to these facts by Bütschli and Minot, between the life-cycle in a swarm of unicellular animals, and the successive production of new multicellular individuals.

According to this theory, the numerous generations of unicellular individuals produced by simple division correspond to the cells forming the body or *soma* of the multicellular individual. The number of generations without fertilisation (conjugation) in the unicellular form is, under ordinary circumstances, limited. Upon the occurrence of fertilisation, however, a fresh series of simple divisions is started. In the multicellular organism, all the tissues of the body are built up by cells produced by a process of division from a single cell, without any further fertilisation. Among the cells that form the body of an individual is a particular group, the members of which group are thrown off, as described above, from the body. When they are thrown off, these cells are capable of fusing with another cell thrown off from a similar individual in a similar manner. This fusion inaugurates a fresh cycle of simple divisions, which results in the production of a new and independent body. According to this theory, the body of the multicellular organism is practically a colony of unicellular organisms living together and dependent upon each other; and with certain limitations this idea is sufficiently near the truth to be very helpful in obtaining a proper idea of the nature of a multicellular organism and of the transmission of characters from parents to offspring.

As all the cells forming the multicellular body are derived from a single cell, this single cell produces all the different kinds of cells that go to the formation of the animal or vegetable body.

In the case of unicellular organisms, any given kind of organism produces organisms that are like itself. We find in fact that cells, when in the form of unicellular organisms, produce other cells like themselves. On the other hand in the case of the multicellular organism, the single cell—the fertilised ovum—produces at first cells that are like itself, but later on, though still within a comparatively few generations, it produces a great variety of cells, including individuals that are quite as unlike each other as different species of unicellular organisms. These different kinds of cells are always produced in the same order; that is to say, the same series of different kinds of cells are always produced at the same periods in the building up of the organism from the fertilised ovum. Thus the fertilised ovum of one species of animal produces similar groups of cells to the groups composing the bodies from which it was derived, hence the offspring is like its parents and not like any other kind of animal. Further, when once differentiation has taken place, and the cells derived from the fertilised ovum have formed the different tissues that go to make up the body of the organism, the cells forming these tissues will, under ordinary conditions, produce cells similar to themselves and not another kind of cell. The cells forming the skin will, when they divide, produce skin cells, cells forming the liver will produce liver cells, and so on.[1] We are thus forced to the conclusion that cells produce similar cells or groups of cells to the cells or groups of cells from which they are derived.

The knowledge that the fertilised ovum produces an organism similar to the two organisms from which it is derived, has given rise to several theories.

The earliest fully formed theory that professed to explain how it is that the fertilised ovum produces a complete organism like the parents from which it is derived, was the theory of *emboîtement*. This theory was worked up in the greatest detail by Bonnet. It assumed that the egg contained a fully formed animal in miniature. Every part of it was there, although very small, all the parts being packed very closely together. The development simply consisted in the growth and unfolding of these already existing parts. When this theory of *emboîtement* was pushed to its logical conclusion, even its upholders were bound to admit that in the case of a hen, for instance, the egg contained not only a miniature chicken, but that that miniature chicken must contain all the miniature eggs for the next generation; that these miniature eggs must in turn contain still more minute chickens, that these minute chickens again contain still more minute eggs, which again contain chickens, and so on for all generations down to infinity. It is only fair to say that Bonnet himself eventually renounced this theory.

Darwin's theory of pangenesis assumes that the germ

---

[1] See pp. 45, 68, 69.

cells (*i.e.* the ovum and sperm) contain innumerable very minute entities which he called "gemmules." Each of these gemmules is supposed to represent a portion of matter which develops eventually into a cell. Some of these gemmules arise from the cells forming the body of the parent, and their nature depends upon the various effects of the environment upon the parent. Thus anything that produces a considerable change in any part of the body of the parent, will cause the cells of that part to produce a particular kind of gemmule which has the potentiality of producing cells like those in the parent after they have been modified by the environment. Such gemmules are supposed to travel from the various parts of the body to the germ cells. According to this theory, fresh gemmules are produced in every generation, their character being dependent upon the modifications that have been produced in the body of the parent by the environment. It is quite evident that only a few characters can be represented by gemmules produced in this way. There must be a great many that owe their origin to other gemmules that existed in more or less remote ancestors. We are faced by the difficulty that some of the gemmules which are destined to give rise to germ cells in the body of the new individual, must be again divided into a sufficient number of entities smaller than gemmules, which will give rise to other gemmules in their turn.[1]

The theory of germinal localisation, first formulated by Wilhelm His, assumes that the egg contains definite areas, or definite substances, destined to produce the various parts of the body.[2] According to this theory, when worked out in its logical conclusion, development consists simply in the dividing up of pre-existing entities or areas that represent the various parts of the body. Much the same criticism as

---

[1] This represents only part of the theory of pangenesis. The remainder is dealt with on p. 58.

[2] His, W., *Unsere Körperform und das physiologische Problem ihrer Entstehung*, Leipzig, 1874.

has been applied to the *emboîtement* theory and to the pangenesis theory, can also be applied here.

A theory of quite a different kind is Nägeli's "idioplasm theory."[1] It assumes the existence of a particular substance —the *idioplasm*—and it is through this substance that the hereditary characters are transmitted from parent to offspring. The idioplasm is of course different in every different kind of animal and plant, and it is to this intrinsic difference in substances that the different characters of different organisms are due; it is, in fact, supposed to regulate the process of development, and the lines along which development will go. The idioplasm itself is supposed to alter in its organisation, and this alteration is supposed to precede the differentiation which occurs among the cells that go to form the body of the multicellular organism. This theory has been developed along different lines, and in some cases by advocates of the hypothesis of pangenesis and of the localisation theory. Thus Weismann and Roux believed that the idioplasm was not a particular compound with particular properties and characters, but was a complicated mixture of many different substances, each particular substance representing a particular character.[2] Here we again see the *emboîtement* theory looming up. Instead of holding that all the characters developed in a multicellular individual were due to the presence of one particular kind of substance in all the cells of the organism, this development of the idioplasm theory necessitates the assumption of innumerable different kinds of substance, which, as succeeding generations of cells are produced from the fertilised ovum in the building up of the various tissues, are divided in a qualitative manner, each group of cells in the later cell generations receiving portions of the idioplasm which was present in the ovum, different from those portions received

---

[1] Nägeli, C., *Mechanisch-physiologische Theorie der Abstammungslehre*, München und Leipzig, 1884.

[2] Weismann, A., *The Germ Plasm*, New York, 1893; Roux, W., *Über die Betendung der Kernteilungsfiguren*, Leipzig, 1883.

by the other cells in the body. This theory appears to claim, in fact, that each collection of idioplasm present in a fertilised ovum contains a sufficient number of different substances to provide for all the different tissues building up the body. The only difference in the end between this and the germinal localisation theory appears to be that instead of particular areas we have particular substances.

In spite, however, of the inherent improbability of *every* character being usually represented by a particular entity, whether of area or substance, there can be but little doubt that under normal conditions a particular area of a fertilised ovum does generally produce a particular part of the body in certain animals. An experiment performed by Roux on the frog's egg is a very good illustration of this.[1] He took the fertilised ova of the frog which had reached the two-cell stage, that is, the original cell of the fertilised ovum had divided into two cells. In each case he killed one of these cells with a hot needle, and in some cases the remaining cell developed into a half-embryo possessing only the right or left side, according to which of the two sides had been destroyed. On the other hand, Roux also found that in his experiments, when carried on further, the existing half-embryo restored more or less completely the missing half. Later experiments by other observers were made with the eggs of several other animals, which appear to show that, in the earlier stages of development at any rate, all the cells into which the fertilised ovum divides retain the power of producing all the tissues that would under ordinary circumstances be produced by the fertilised ovum itself. Driesch, Morgan, Wilson, Zoja, and others have separated the cells produced by the division of the fertilised ovum, when development had gone as far, in some cases, as the sixteen-cell stage.[2] The cells thus shaken apart have developed into

[1] Roux, W., "Über das künstliche Hervorbringen halber Embryonen durch Zerstörung einer der beiden ersten Furchungskugeln," &c., *Virchow's Archives*, 114, 1888.

[2] Driesch, H., *Analytische Theorie der Organischen Entwicklung*, Leipzig, 1894; Morgan, T. H., "Experimental Studies on Teleost Eggs," *Anat. Anz.*,

complete embryos, and even larvæ in some cases. Although these embryos contained all the ordinary tissues and parts found in embryos produced from the ordinary fertilised ovum, they were smaller in size. Thus embryos produced by shaking the cells apart in the two-cell stage produced embryos half the normal size. Those shaken apart when in the four-cell stage gave rise to embryos a quarter of the normal size; and so on up to the sixteen-cell stage, which is the latest period at which this experiment has hitherto been successful with any animal, where the embryos, although perfect, were only one-sixteenth of the normal size. These experiments seem to prove that the characters cannot be represented by entities that are distributed in a selective manner among different cells during the process of development, as is assumed by the Roux-Weismann theory. If it were so, this selection of different entities must begin at the first cell division; but it has been proved by experiment, that even when the sixteen-cell stage has been reached, each of the sixteen cells possesses within itself the power of producing, not only the tissues which it would produce under normal conditions were the ovum left to itself to develop, but, when separated from its fellows, also all those tissues that would have been produced under normal conditions by the other fifteen cells.

Against the idioplasm theory in its original form there is no evidence whatever. With such facts as are known to us, it is quite reasonable to assume the existence of a substance somewhere in the fertilised ovum which has the property or characteristic of developing along particular lines, and of producing particular kinds of cells. Such a substance must differ in different kinds of organisms, and

---

x. 19, 1895; Wilson. E. B., "On Cleavage and Mosaic Work," *Arch. f. Entwick.*, iii. 1, 1896; Zoja, R., "Sullo sviluppodei blastomeri isolati dalle uova di alcune Meduse," *Arch. f. Entwick.*, i. 4, ii. 1 and 4, 1895; Herlitzka, A., "Contribuzione allo studio della capacità evolutiva dei due primi blastomeri nell' uove di Tritone," *Arch. f. Entwick.*, ii. 3, 1895; Crampton, H. E., "The Ovarian History of the Egg of Molgula," *Journal of Morphology*, XL. Supplement, 1899.

can only produce and regulate the production of the cells that go to build up its own particular kind of animal or plant. Moreover, it can only produce the different kinds of cells in a particular order. Such an assumption is in exact accordance with such facts as are known to us. We are so used to seeing like produce like in the case of animals and plants, that we should be just as surprised if a cat produced a puppy, as if the sun were to rise in the west; one event is indeed as likely to happen as the other.

All these theories have been evolved with the object of explaining how it is that the fertilised ovum of any particular kind of animal or plant produces an organism similar to those from which it was derived, no matter how complicated that organism may be. As all multicellular organisms arise from a single cell, and are produced by the division of this single cell into two more, each of these two dividing again, and so on until the organism is completed, it appears certain that something must be present in the fertilised ovum which is handed on from it throughout the succeeding generations of cells, which regulates and limits the lines along which development takes place. The questions remain as to whether the ovum itself consists entirely of this substance and of nothing else; whether this substance is distributed throughout the ovum, with the main part of the ovum as a medium in which it lies; or whether it is limited to some particular part of the ovum, and of the cells subsequently produced from the ovum. As in any case this substance must be handed on from the fertilised ovum to the two cells into which the ovum divides, and from them on to the subsequent generations of cells produced from them, it seems desirable to consider such facts as are known about the way in which cells divide, in order to see whether in this process there is any suggestion as to the existence and history of such a substance.

CHAPTER II

Structure of a cell—Phenomenon of cell division—Selective division of certain parts—Theory identifying Nägeli's idioplasm with chromatin—Objections—The maturation of the gametes—The meiotic phase—The impossibility of particular characters common to the race being borne by particular chromosomes—Fertilisation—Parthenogenesis—Fertilisation in unicellular animals—Experiments in artificial fertilisation and their bearing upon the existence of an hereditary substance—Conclusions.

We have already seen that a cell consists of a minute mass of protoplasm. Within this mass is a denser area surrounded by a membrane—the nucleus. The rest of the cell surrounding the nucleus is called the cytoplasm (Fig. 1). In the cytoplasm, generally near the nucleus, two minute bodies may frequently be observed. These are known as the *centrosomes* (Fig. 1).[1] When a cell is in the vegetative condition, that is, when it is not preparing to divide, or in process of division, the nucleus is seen to contain numerous small masses of a substance which is denser than the rest of the contents of the nucleus. These small masses are joined together by a fine meshwork, which frequently contains still smaller particles of this same substance. When cells are stained in order to make them more easy to study under the microscope, this dense substance, joined together by the fine meshwork, stains more darkly than any of the other parts of the cell. For this reason it has been called *chromatin*. The chromatin is contained in an envelope of clear slightly staining material, which is known as *linin*. The fine meshwork joining the masses of chromatin is also formed of linin, and granules of chromatin are distributed in the strands.

When a cell is going to divide into two daughter cells,

---

[1] Centrosomes are not present in the cells of the higher plants. (See note at end of chapter.)

the chromatin is seen to arrange itself in a long coiled-up thread within the nucleus (Fig. 2). This coiled-up thread is known as the *spireme*.[1] At the same time that the spireme is in process of formation, the two centrosomes are seen to send out radiations into the surrounding cytoplasm. These radiations are collectively known as "*Asters*," having been given this name on account of the appearance they present. Some of these radiations extend between the two centrosomes, thus forming a figure shaped like a spindle, made up of a number of minute threads. As these radiations are formed, the centrosomes begin to separate from each other, gradually getting further and further apart (Fig. 2). Soon

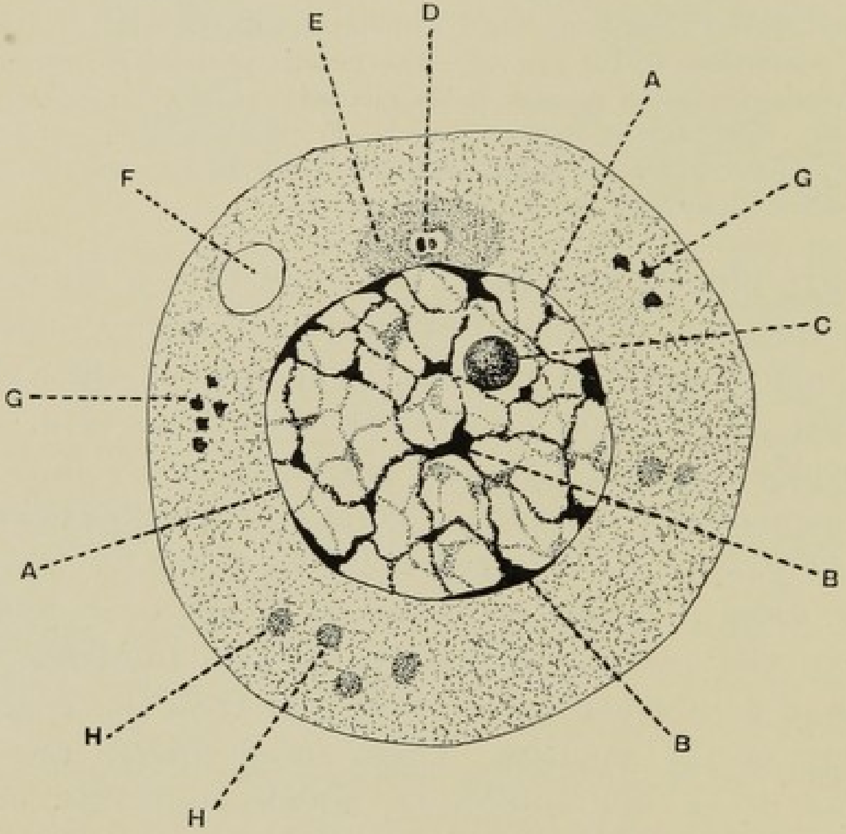


FIG. 1.—A. Nuclear membrane. B. Masses of chromatin, joined by threads of linin containing chromatin. C. Nucleolus. D. Centrosomes, contained in E, the archoplasm. F. Contractile vacuole. G. Food particles. H. Plastids.

---

[1] The formation of the spireme does not necessarily precede division in all cells. It is, however, usual.

after the spireme has been completely formed, it breaks up into a number of lengths, which retain the curves and bends that existed in the spireme, generally appearing in the form of U's or V's (Fig. 3). These separate lengths of the spireme are known as the *chromosomes.* The number of chromosomes appearing in a cell during the process of division is different in different species of animals and plants, but is constant in the cells of the same species. Thus, in man 32 chromosomes appear in a dividing cell; in a mouse, 24; in a newt, 24; in *Artemia,* a crustacean, 168; in *Ascaris megalocephala univalens,* 2; and so on.

While this is happening within the nucleus, the centrosomes are travelling further and further apart, the threads between them which form the spindle lengthening out considerably, so that eventually the centrosomes with their radiations and the spindle, between them occupy a large area of the cytoplasm (Fig. 3). At this stage the nuclear membrane disappears, so that there is nothing dividing the ground substance of the nucleus from that of the cytoplasm (Fig. 4). They are in fact left to mingle freely. We now have the two centrosomes, with the spindle between them, and the chromosomes, free inside the cell, the nuclear membrane no longer separating the chromosomes from the spindle. At this stage each of the chromosomes attaches itself to a fibre of the spindle, the two centrosomes generally

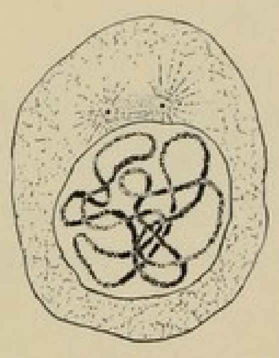


Fig. 2.—Spireme. Radiations from centrosomes.

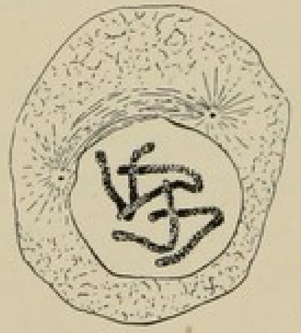


Fig. 3.—Spireme broken into short lengths, the chromosomes. Spindle is being formed.

being at opposite poles of the cell, and the chromosomes being attached to the spindle on the equatorial plane (Figs. 5 and 6). The chromosomes still retain the shape of U's and V's in the majority of cases, and they lie flat upon the equatorial plane at right angles to the axis of the spindle. Very soon after they get into this position, it is seen that each of the chromosomes is split lengthwise. This splitting becomes more and more evident, until each chromosome is completely divided into two longitudinal halves (Fig. 7). Each of these halves is gradually drawn away from its fellow towards opposite poles of the spindle, until two groups of half-chromosomes are collected round each centrosome (Fig. 8). In each of

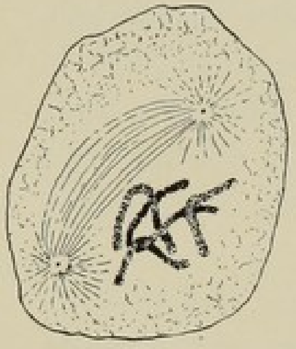


Fig. 4.—Disappearance of nuclear membrane.

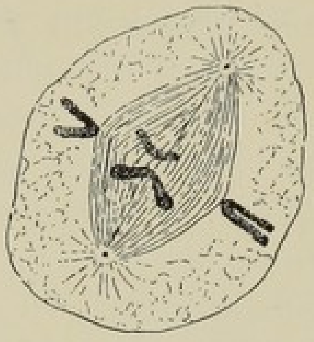


Fig. 5.—Chromosomes attached to spindle fibres (lateral view).

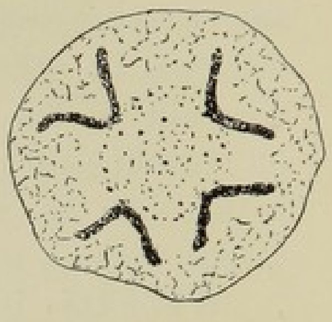


Fig. 6.—Same (polar view).

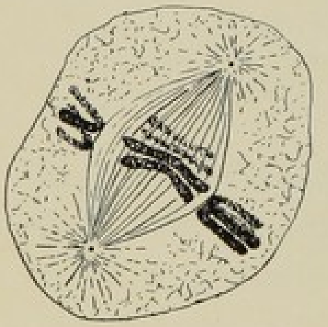


Fig. 7.—Splitting of the chromosomes.

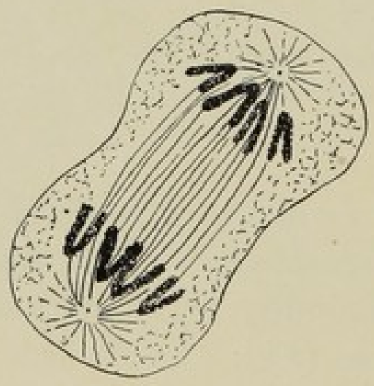


Fig. 8.—Longitudinal halves of chromosomes drawn towards opposite poles of spindle.

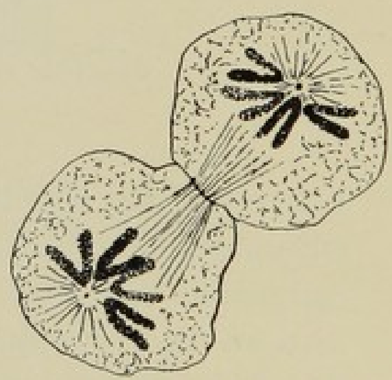


Fig. 9.—The cytoplasm dividing.

these groups there is a longitudinal half of each of the chromosomes that originally appeared. While the chromosomes are thus separating, the whole cell gradually assumes an hour-glass shape (Fig. 8), and this becomes more and more accentuated until the original mass of protoplasm, that is, the cell, is divided into two at the narrow point in the centre (Fig. 9). We thus have two masses of protoplasm produced from the original single mass, and each of these two masses contains an exact longitudinal half of every chromosome that appeared during the preparation for division in the mother cell. Each chromosome in the group surrounding the centrosome in the daughter cell now proceeds to throw out small processes which join the chromosomes to each other, and a new nuclear membrane is formed (Figs. 10 and 11). The shapes of the chromosomes are gradually lost, and as the processes of linin form a network within the new nucleus, the chromatin is gradually distributed through this network, and the nucleus of the daughter cell assumes the appearance that was described in the case of the mother cell. The single centrosome which has been received into the daughter cell divides into two, as a rule, very soon after the nuclear membrane has been formed, but unless another division is imminent these two centrosomes remain quiescent for a time.

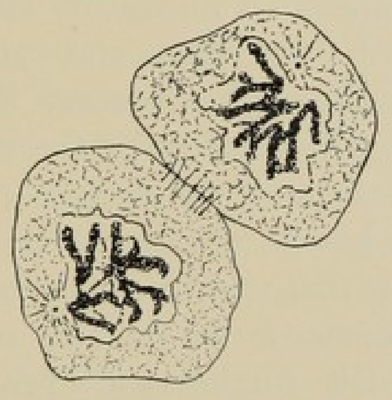


Fig. 10.—Commencement of reconstruction of daughter nuclei.

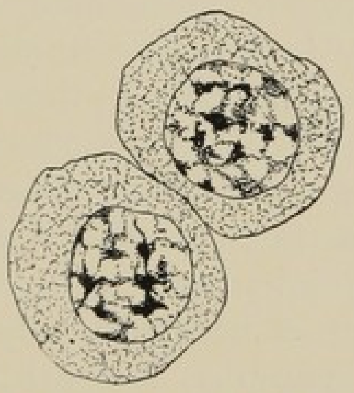


Fig. 11.—The two daughter cells complete.

The whole of this process of division is very rapid, and from the first signs of preparation for division until the two daughter cells are completely separated from each other, probably but a few minutes elapse in the case of some organisms. The process is particularly rapid in the higher animals. Divisions succeed each other with the greatest possible rapidity in the earlier stages in the development of the embryo, that is, from the time the ovum divides into two cells until the formation of the organism has reached a comparatively advanced stage.

A consideration of the mode of division seems to show that the only parts of the cell that divide in a selective manner are the chromosomes; all the rest of the cell, excepting the centrosomes, seems to divide simply according to bulk, the ground substance of the nucleus and cytoplasm being mingled at the time division takes place. This fact has led very many observers to believe that in the chromosomes and chromatin are contained all the hereditary characters of the race. Chromatin has in fact been identified as Nägeli's idioplasm. The fact that the chromatin in its envelope of linin generally seems to be in the form of minute granules, has led to the further conception that each of these granules represents a character, more particularly as when these granules are observable in the chromosome, each granule is sometimes seen to split individually, half of each granule being contained in each daughter chromosome.

This theory is at first sight an extremely fascinating one. An exact representative half of every chromosome in the fertilised ovum is handed on to each daughter cell. The same happens again in the daughter cells, and subsequently in every division that takes place in the building up of the body of the organism. Thus in the adult organism every cell contains a similar number of chromosomes to that contained in the fertilised ovum, and moreover each of these chromosomes is derived from a similar individual chromosome that was present in the ovum. The mode of division in the chromosomes seems to ensure that half of every individual portion of every individual chromosome will be handed on throughout the succeeding generations of cells, for the division of the chromosome does not appear to be merely a non-selective division of the bulk of substance forming it.

Unfortunately for the theory which identifies the chromatin with the idioplasm of Nägeli, several facts have been observed recently which seem to show that the chromatin is not the permanent substance that it was formerly believed to be. During certain stages preparatory to the divisions which precede fertilisation the amount of chromatin contained in the spireme, waxes and wanes in the most remarkable manner, in the case of several animals at any rate. To such an extent does this happen, that in some cases the spireme seems to consist almost entirely of linin, containing little or no chromatin within it.[1] This seems to suggest that the chromatin is rather a secretion or excretion of the linin than a permanent constituent of the cell. In our search for a permanent constituent in the cell, which divides in a selective manner, we are thus thrown back on the linin. As has already been stated, the chromatin is surrounded by an envelope of linin. The spireme sometimes consists of a tube, sometimes of a ribbon or thread of linin, in which are contained granules of chromatin. The framework of the chromosomes is also formed of linin containing chromatin, so that were the chromatin washed out of the spireme and the chromosomes, we should still have the same coiled thread or ribbon, and the same U or V shaped bodies formed entirely of linin. If, therefore, there is a permanent constituent of the cells which is handed on individually from generation to generation, it would appear to be rather the linin than the chromatin. What has been said with regard to the selective mode of division which ensures that an exact representative half of each chromosome is handed on at each division, applies to the linin even more forcibly than to the chromatin.

---

[1] Walker, C. E., *Essentials of Cytology*, Constable, London, 1907.

There thus appears to be a mechanism which ensures the presence in every cell in the body of exact representative derivatives of certain bodies—the chromosomes—that are present in the fertilised ovum, and were there no other complications to be faced, it would appear extremely probable that these bodies, and perhaps even particular portions of each of these bodies, represented particular characters. There are, however, other complications which prevent one from accepting this theory. These complications occur in connection with fertilisation, that is, with the production of a new individual.

We have already seen that at some stage in the life of a multicellular organism a certain group of cells is differentiated and destined to be cast off from the body as gametes or sexual elements. As soon as they enter upon this course of differentiation, which is sometimes at quite an early stage in the development of the embryo, these cells live practically as parasites upon the organism in which they occur, and cease to form an integral part of it. Like the cells in the *soma* or body these cells multiply. In the higher animals, however, the ova do not multiply after a very early period in the development of the organism. In sexual cells produced in both the male and female organisms, at a certain stage preceding the production of the mature gametes, a mode of division occurs that is quite different from that described as occurring in the cells that go to build up the body of the animal or plant, and this mode of division introduces that complication to which reference has just been made. In this division the chromosomes appear in half the number that is observed in the cells forming the tissues of the body. The researches of many investigators indicate that this is due to the fact that, during the stage preparatory to division, instead of a spireme being formed, a definite number of separate loops of linin and chromatin appear in the nucleus (Fig. 12). The number of these loops is half that of the chromosomes in the *somatic* or body cells. Observations also show that these loops are made up of two chromosomes joined end to end.[1] When these pairs of chromosomes are differentiated they become attached to the spindle fibres just as happened in the case of the somatic chromosomes. Instead of splitting lengthways, however, the two chromosomes forming each pair are pulled apart, one whole chromosome going to one pole of the cell, and the other whole chromosome going to the other pole (Fig. 13). This form of division results in the production of two daughter cells, each having half the number of whole chromosomes that were present in the mother cell. It has been called the meiotic division. Thus, if we imagine an organism with four chromosomes, and call these chromosomes A, B, C, and D, in this reducing division two daughter cells will be produced, one possessing the chromosome A and B, the other C and D, or of course any other combination of A, B, C, and D in pairs (see Fig. 15). Taking the same organism to illustrate the division in the somatic or body cell, each of the daughter cells produced would of course contain an accurate longitudinal half of each of the four chromosomes A, B, C, and D (see Fig. 14).

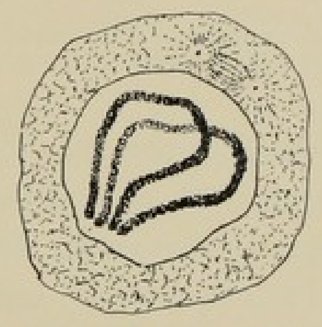


FIG. 12.—Early stage in the meiotic division.

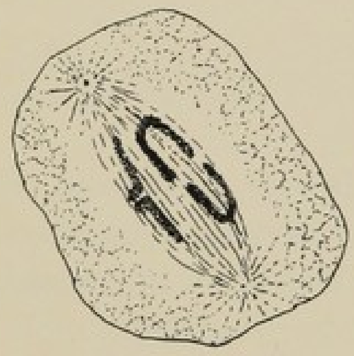


FIG. 13.—The pairs of chromosomes separating in the meiotic division.

We have seen that the number of chromosomes in the cells of any given organism remains the same from generation to generation of new individuals. We have also seen

---

[1] See note on meiotic phase at end of chapter.

that a new individual is formed by the fusion of two cells, one thrown off from each parent. Now, if each of the gametes which fuse to form the fertilised ovum contained the full number of chromosomes, it is obvious that the number of chromosomes would be doubled every time a new individual was produced. The reducing mode of division which has just been described prevents this from happening, and ensures the number of chromosomes remaining the same in organisms of the same kind from generation to generation.

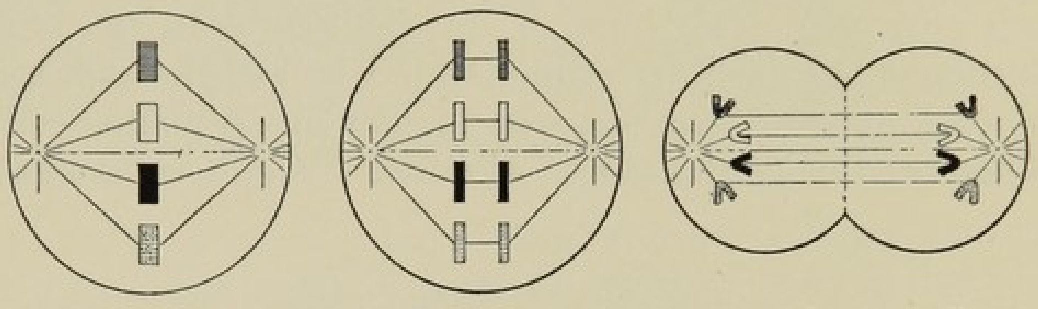


FIG. 14.—Diagram showing distribution of chromosomes to daughter cells in the ordinary or somatic form of division.

But this reduction presents a very considerable difficulty with regard to accepting the chromosomes as being the portions of the cell, the individual entities in fact, by which hereditary characters are generally transmitted. To go back to the example of the organism whose cells contain four chromosomes A, B, C, and D. It is quite obvious that when reduction takes place some of the *sperms* (the sexual cells

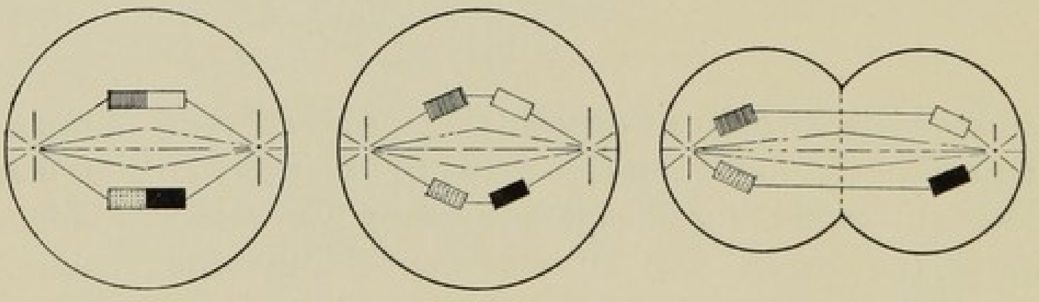
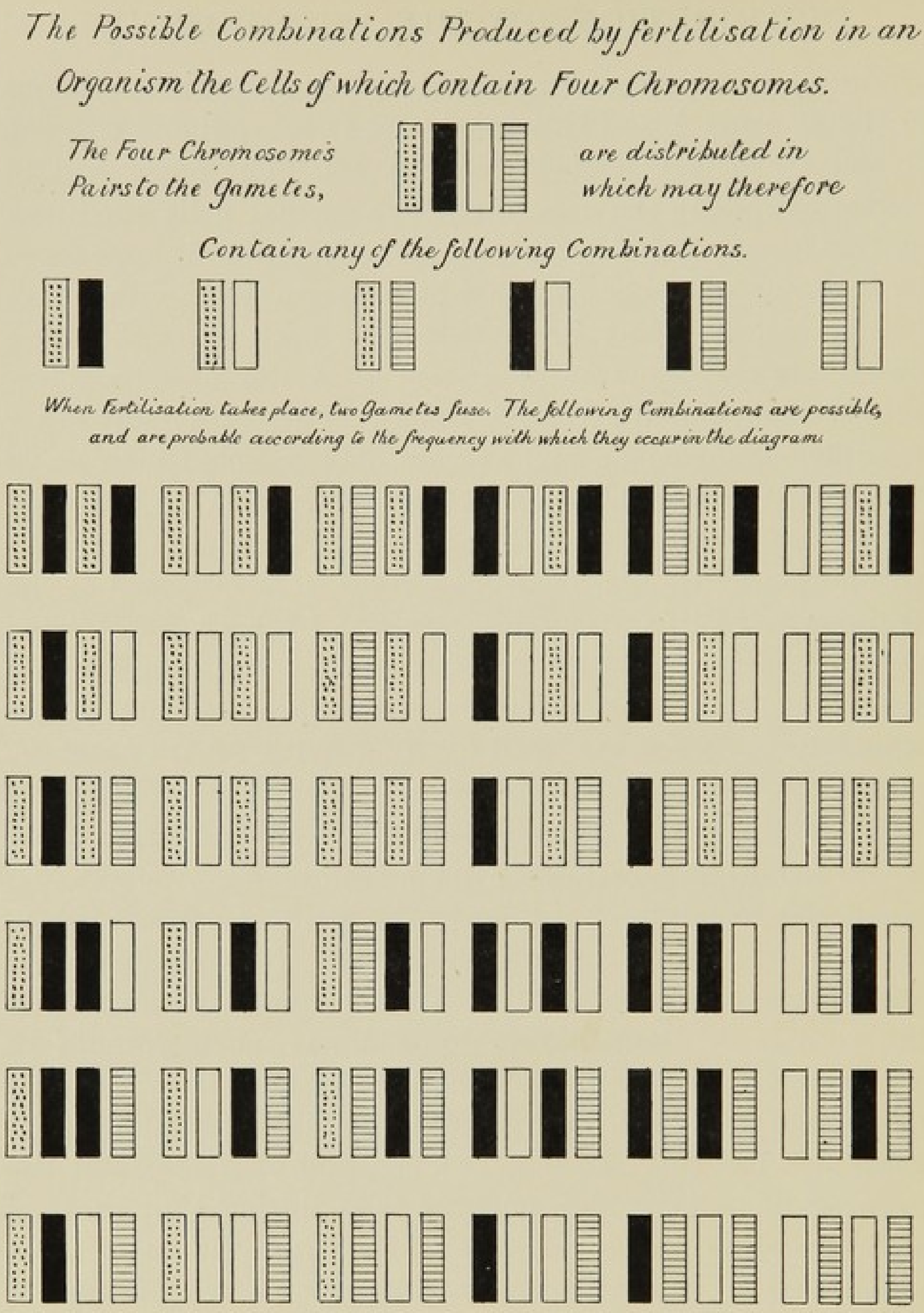


FIG. 15.—Diagram showing distribution of chromosomes to the daughter cells in the meiotic or reducing form of division.

produced in the male organism) will contain chromosomes A and B, some A and C, some A and D, some B and C, some B and D, some C and D (see Fig. 16). The same will of course happen in the case of the ova (sexual cells produced in the female individual). As far as we know, it appears to be a matter of chance as to which sperm joins with which ovum, and it seems impossible that such a combination would always occur as to ensure that the new organism should again contain A, B, C, and D. There are many other possible combinations, and there is only one chance in six of this particular combination occurring again in an organism with four chromosomes. In man, where there are thirty-two chromosomes, there is only one chance in 601,080,390 of the same combination occurring again. In both cases even these chances involve the assumption that the chromosomes are the same in both parents. If they are not, the chances would be more remote (see Fig. 16). With regard to those characters, therefore, which always occur in every individual of a species, it appears quite impossible that different characters should be contained in different chromosomes. Taking a concrete example—hairiness of the scalp—a constant character in the case of the human animal. Now suppose that this character is contained in chromosome A, the number of individuals in whom chromosome A was missing would be 25 per cent. according to the laws of chance in the first generation produced from parents who all possessed chromosome A. But this character is a constant character, and the number of individuals occurring who, during the whole of their lives, fail to develop any hair upon the scalp is so small that it is not worth considering. It would appear, therefore, that if a character common to the race is present at all in the chromosomes, it must be present in each of them individually; otherwise it must be present in some other part of the cell, or is a common potentiality of the whole substance of the cell.

But this leaves two complicated phenomena without any ostensible function. If the common racial characters are



The Possible Combinations Produced by fertilisation in an Organism the Cells of which Contain Four Chromosomes.

The Four Chromosomes are distributed in Pairs to the Gametes, which may therefore Contain any of the following Combinations.

When Fertilisation takes place, two Gametes fuse. The following Combinations are possible, and are probable according to the frequency with which they occur in the diagram.

FIG. 16.—The diagram shows that in an organism the cells of which contain four chromosomes, six different combinations of two chromosomes are equally probable in the gametes. It also shows that in fertilisation these pairs contained in the gametes may be combined in thirty-six different ways. In six of these the chromosomes are the same as in the parent organism. Thus in an organism, the cells of which contain four chromosomes, there is one chance in six that the original combination will be reproduced in the offspring, and this only when it is assumed that the chromosomes in both parents are the same. In man, where there are thirty-two chromosomes in a cell, the number of different sets of sixteen is enormously large, and the chance of the original combination being reproduced in fertilisation is only one in over six hundred million.

all represented in every chromosome, nothing particular is accomplished by the complex process of cell division in which an exact representative half of every chromosome present in the fertilised ovum is handed on to every cell produced in the building up of the organism. Again, there would seem to be no point in the still more complicated process of reduction which always precedes fertilisation, and which ensures an *alternative* distribution of whole chromosomes to the germ cells. Both these phenomena are universal among multicellular plants and animals, and are found in many unicellular forms. It is inconceivable that they can be without any significance. Were every character represented in every chromosome there would be no useful function performed, in so far as these characters are concerned, by the complex processes that ensure that a derivative of every part of every chromosome present in the fertilised ovum shall be distributed to every cell forming the body of the individual arising from it, while they equally ensure that whole chromosomes shall be distributed in an alternative manner to every new individual produced.

Though it would seem that we must dismiss the chromosome as the bearers of those characters that are common to all the individuals of the race, there is good reason to suppose that they may be the bearers of some characters. We shall see later that there are characters that are transmitted in an alternative manner. After we have considered the nature of these characters and the manner in which they pass from parents to offspring, the possible relationship between these phenomena and the manner in which the chromosomes are distributed in the building up of the organism from the fertilised ovum and in the process of reduction and fertilisation, will be dealt with. At present we must see what evidence there is for an hereditary substance being contained in any particular part of the cell, or whether the transmission of the racial characters is not possibly a potentiality of the whole cell.

Very many observations upon the phenomenon of fertilisation have been made, particularly during recent years. We have already seen that for the production of a new multicellular individual, two cells derived from two individuals of the same species generally fuse, forming a single cell—the fertilised ovum. In both animals and plants, the cells that fuse to form the fertilised ovum are the cell produced by the male parent—the sperm, and the cell produced by the female parent — the ovum. We have already considered the phenomena which bring about the reduction in the number of chromosomes in the reproductive cells. This process is identical in both the sperms and the ova. In other respects, however, there are some differences between the processes undergone by these two kinds of reproductive cells before they are ready to fuse and form the fertilised ovum. In the male a certain group of cells is differentiated at some period during the life of the organism, and is destined to produce sperms. These cells contain the full number of chromosomes, and they multiply throughout the active sexual life of the organism. The process of reduction begins to occur when the organism approaches maturity, and thenceforward takes place continuously, those cells containing half the number of chromosomes being sooner or later separated from the body. All the reduced cells form sperms, and all of these sperms are capable of fertilising an ovum. Generally a vastly greater number of sperms are produced than can possibly be utilised in fertilising ova, but nevertheless all of them are capable of doing so.

The case of the ova is somewhat different. In the higher animals they are differentiated at a very early period in the life of the organism. In plants and in some animals they may be differentiated at varying times, sometimes quite late in the life of the organism. In every case, however, the ova at first contain the full number of chromosomes. Before the ovum is ready for fertilisation its nucleus divides meiotically and reduction takes place. One of these nuclei remains in the bulk of the cytoplasm of the ovum; the other is extruded, carrying with it a very small portion of cytoplasm. This division is in every sense a division of the one cell—the immature ovum—into two; but the two cells are very different in bulk, one of them being many hundred times larger than the other. This small cell is called the "*first polar body*"; the large one is the ovum. The first polar body, when it is outside the ovum, divides into two small cells, which then degenerate. The nucleus remaining in the ovum divides again, and a second small cell is thrown off from the ovum—the "*second polar body*"—which also degenerates without any further division. The large cell (the ovum) is now ready for fertilisation, and remains passive until this phenomenon takes place.[1] Sperm cells are generally motile, possessing flagella which enable them to swim in fluids rapidly. As a rule they are several hundred or even thousand times smaller than the ovum. The great difference in the mode of production of the sperms and the preparation of the ovum for fertilisation is, that in the case of the former all the cells produced are potential sex cells, while in the latter all the cells resulting from the divisions included in the process of reduction, excepting one, are destined to degeneration and cannot be used in the production of new individuals.

Fertilisation takes place through a sperm cell reaching the ovum and penetrating into its substance, generally leaving behind it its flagellum. A very important point in fertilisation is, that the centrosomes of the first division appear to be usually derived from the sperm. The centrosomes belonging to the ova degenerate at the time of fertilisation, and so play no part in the cell divisions that subsequently take place. The fertilised ovum thus contains two nuclei, its own and the sperm nucleus. When division takes place in the fertilised ovum the chromosomes appearing are derived, half from the ovum and half from the sperm cell. The two daughter cells of the first division of the

---

[1] The sperm enters the ovum before the extrusion of the polar body in the case of some organisms.

fertilised ovum receive half their chromosomes from each parent.

There are some cases, however, among multicellular plants and animals, where new individuals are produced from a single cell derived from one individual without fertilisation taking place. Such individuals have one parent only, which produces them without the intervention of a second parent as is usually necessary. This phenomenon is known as "parthenogenesis." In parthenogenesis both among animals and plants, no fertilisation takes place. For instance the female Aphis (common green-fly) produces other females without any intervention of the male. These females again produce females, and so on for many generations throughout the summer, without any fertilisation taking place. The same thing happens in the case of bees. The queen-bee lays a number of eggs, some of which are fertilised, and some of which are not. Those which are unfertilised develop into drones; those which are fertilised develop into queens or workers, according to the manner in which the larvæ are fed. There are many other cases of parthenogenesis among animals and plants, and in some of them it has been demonstrated that one of the polar bodies, after having been thrown off, re-enters the ovum, and acting as a sperm cell, brings back the number of chromosomes to that normal to the species. In other cases, reduction apparently does not take place.

In many of these parthenogenetic organisms, although a number of generations of females are produced without fertilisation taking place, males appear at different periods and a generation is produced from fertilised eggs. Thus in the case of Aphis, towards the end of the summer some males are produced, and the ova are fertilised in the next generation, producing the so-called "winter eggs." In this case the phenomenon of fertilisation recurs regularly at the end of every summer. There are many other similar cases, but there are others again among animals, and more still among plants, where fertilisation is extremely rare or never takes place at all.

It is evident, however, that this phenomenon has been produced in the course of evolution as a modification of bi-parental reproduction. Sex is present, but has ceased to be functional. The evidence at our disposal makes it clear that in these multicellular organisms bi-parental reproduction existed at some time in their previous history, but that it has been wholly or partially eliminated in some cases, and that here only one sex is necessary.

This is the general course of events with regard to fertilisation among the multicellular animals and plants. Something similar, however, has been shown to occur among unicellular organisms, both animals and plants. This phenomenon was first described by Maupas in Paramecium and other unicellular animals.[1] What happened in the animals he examined may be briefly summarised as follows:—For a large number of generations the unicellular animals multiplied by a process of simple division ("fissiferous bi-partition"). When many generations, hundreds in some cases, had been produced in this way, the individuals of the swarm were seen to approach each other and come into contact, remaining attached to each other for some time. During this period of conjugation the nuclei divided, and a daughter nucleus from each of the individuals left the organism in which it arose and migrated into the body of the other partner in the conjugation. There the migrated nucleus fused with the other daughter nucleus, which had remained in the body of each animal. We see, therefore, that one of these nuclei acted as a sperm cell, the other as an egg cell. When this fusion had taken place, the two unicellular organisms separated and a fresh period of simple division took place, which again lasted for a great many generations. Maupas also found that when he artificially prevented these unicellular organisms from conjugating they all degenerated, and that when conjugation did not take place the race died out. It is true that the experiments of subsequent observers have shown that the period

---

[1] Maupas, *op. cit.*, p. 3

of conjugation may be retarded, apparently indefinitely, by suitable conditions of nourishment and temperature, but nevertheless it appears certain that under ordinary conditions conjugation is necessary to the well-being of the race in the case of many unicellular organisms.

There are, however, many unicellular forms in which no process of fertilisation has been discovered, and this fact suggests very strongly that fertilisation, that is, bi-parental reproduction, is an early product of evolution.

It has been shown by experiment that in the case of some animals, segmentation of the ovum and the production of an embryo may take place without any fertilisation. Loeb subjected the unfertilised eggs of a sea-urchin to the action of a magnesium salt.[1] The eggs proceeded to segment and produced larvæ, and these larvæ continued to develop to the pluteus stage, existing for some time as free swimming, independent, and well-developed organisms. This experiment shows that fertilisation is not absolutely necessary, even in an organism where parthenogenesis does not occur normally, for the production of a new individual, in this case, at any rate.

Morgan showed that in embryos produced from one nucleus, only half the number of chromosomes were present and not the full somatic number.[2] This suggests that the full number of chromosomes is not necessary for an organism to develop and to exhibit all its normal racial characters.

In all cases where fertilisation takes place the main part of the contribution of the sperm is its nucleus. We have already seen that the ovum is generally many hundred, even many thousand times larger than the sperm. At the time of the entry of the sperm into the ovum, the nucleus of the former is, as a rule, very much smaller than that of the latter. A much greater difference in size, however, exists

---

[1] Loeb, J., "On the Nature of the Process of Fertilisation and the Artificial Production of Normal Larvæ," *American Journal of Physiology*, iii. 3, 1899.

[2] Morgan, T. H., "The Fertilisation of Non-nucleated Fragments of Echinoderm Eggs," *Archiv für Entwicklungsmechanik*, ii. 2, 1895.

with regard to the cytoplasm. The bulk of the sperm consists of nucleus in most cases, and there is very little cytoplasm. Under normal conditions the centrosomes in the fertilised ovum are derived from the sperm. Besides the centrosomes a small amount of cytoplasm is brought into the ovum by the sperm. Several observers have declared that the cytoplasm thus brought in degenerates shortly after fertilisation has taken place. It would appear that the centrosomes cannot be the probable bearers of hereditary characters generally, as otherwise the offspring would inherit the characters of the male parent only, and not those of the female. These observations taken alone suggest strongly that the nucleus is the only part of the sperm that continues to exist in the fertilised ovum as a probable bearer of hereditary characters. There is, however, a great deal more evidence that suggests that the hereditary characters are determined by the nucleus. Oscar and Richard Hertwig broke the unfertilised eggs of a sea-urchin by shaking them. They took some portions of the egg which did not contain any part of the nucleus and fertilised them with sperms. These portions of the egg proceeded to segment, and developed up to a certain point. In these cases the cells formed contained nuclei derived entirely from the sperm, while the bulk of the cytoplasm was derived from the ovum.[1]

Morgan subsequently repeated this experiment, and showed that in the cells of such an embryo only half the number of chromosomes appeared.[2]

Boveri carried these experiments still further. He showed that such enucleated portions of the ovum as were used by the Hertwigs in their experiments and fertilised by a sperm, developed into larvæ perfect in every way except in size. An even more interesting and suggestive experiment was subsequently carried out by Boveri. He fertilised the enucleated portions of the ovum of one species of sea-urchin

---

[1] Hertwig, O. and R., *Über den Befruchtungs- und Teilungsvorgang des tierischen Eies unter dem Einfluss aüsserer Agentien*, Jena, 1887.

[2] Morgan, T. H., *op. cit.*, p. 30.

(*Sphærechinus granularis*) with a sperm of another species (*Echinus microtuberculatus*). Some of these fertilised fragments developed into dwarf larvæ, and these larvæ exhibited nothing but the paternal characters.[1]

There is also a good deal of evidence suggesting that the nucleus controls all the functions performed by a cell, and this is interpreted by some as meaning that the lines along which the cells will develop depend upon the nucleus or upon something contained within it. It has been shown in the case of many unicellular animals, that if they be divided into small pieces, those which contain even a minute portion of the nucleus will regenerate into a perfect animal with all its parts and organs. The rate at which this regeneration takes place depends upon the size of the portion of nucleus contained. On the other hand, fragments of cytoplasm which are devoid of any portion of nucleus die in a comparatively short time. For a certain period they are able to move about, and even to engulf food particles, but they are unable to digest, and regeneration never takes place.[2] There is evidence also of the supreme importance of the nucleus in the case of the cells forming the bodies of multicellular animals. As an instance of this we may take what happens when a nerve fibre in an animal is divided. The peripheral portion, that is, the part which is separated from the nucleus, proceeds to degenerate; the proximal portion, that is, the part which is still connected with the nucleus, sends out a new fibre which takes the place of the degenerated portion.

In addition to these observations, we must remember that it has been clearly demonstrated in many organisms that not only do half the chromosomes appearing in the first division of the fertilised ovum come from the male and half from the female parent, but that these groups of chromo-

---

[1] Boveri, Th., "Über die Befruchtungs- und Entwickelungsfähigkeit kernloser Seeigel-Eier," *Archiv für Entwicklungsmechanik*, ii. 3, 1895.

[2] Gruber, A , "Mikroskopische Vivisektion," *Berichte der Naturforschender Gesellschaft*, Freiburg, vii., 1893.

somes remain distinct, the paternal from the maternal, for at least several generations of cells.[1]

We must also remember that while an accurate division of the nuclear contents takes place, the cytoplasm seems to divide in bulk without anything very marked in the way of selective division.

There are many biologists who accept the theory that the chromatin is the substance in the cell that conveys the hereditary character from generation to generation of cells. The waxing and waning of the chromatin, and its occasional disappearance,[2] seems to suggest, as has already been stated, that linin should be taken rather than chromatin, if a particular part of the nucleus is really the vehicle of hereditary characters, but this is perhaps a minor point, and we will take the theory in the sense of dealing with the chromosomes and that part of the nucleus which goes to form them. Granting this, it seems eminently probable that such a substance is handed on from cell generation to cell generation in a selective manner.

The wide consideration given to this theory may be adequately estimated by the following quotation:—Professor E. B. Wilson, referring to the observations just cited, says: "It was in the main these considerations that led Hertwig, Strasburger, Kölliker, and Weismann, independently and almost simultaneously, to the conclusion that *the nucleus contains the physical basis of inheritance, and that chromatin, its essential constituent, is the idioplasm postulated in Nägeli's theory*. This conclusion is now widely accepted and rests upon a basis so firm that it must be regarded as a working hypothesis of high value."[3] We

---

[1] Rückert, J., "Über das Selbständigbleiben der väterlichen und mütterlichen Kernsubstanz während der ersten Entwicklung des befruchteten Cyclops-Eies," *Archiv für mikroscopische Anatomie*, xlv. 3, 1895; Herla, V., "Étude des Variations de la mitose chez l'ascaride mégalocéphale," *Archives de Biologie*, xiii., 1893; Zoja, R., "Sulla independenza della chromatina paterna e materna nel nucleo delle cellule embrionali, *Anatomischer Anzeiger*, xi. 10, 1905.

[2] See p. 19.

[3] *The Cell in Development and Inheritance*, p. 403, 1904.

have seen, however, that the alternative manner in which the chromosomes are distributed before fertilisation takes place, precludes the possibility of the characters common to a race of individuals being represented in separate chromosomes, and as has already been said, there is not any good reason to suppose that all characters are represented in every chromosome and in no other part of the cell.

On the evidence we have considered so far, however, there is no reason to suppose that the nucleus as a whole does not convey the hereditary characters, and all the observations already quoted in favour of particular parts of the nucleus may be used with equal justice in favour of the nucleus as a whole. This theory has been, and still is, held by many biologists. Professor J. A. Thomson says: "The view has gained ground and general acceptance that the nucleus is the chief or exclusive bearer of hereditary qualities."[1]

There is, however, a great deal more evidence that must be taken into account, and this suggests that another opinion may reasonably be held.

Recent experimental work shows that there is much to be said for those biologists who claim that the cytoplasm bears an important part in conveying hereditary characters, and some of those who supported the view that the chromatin was the only physical basis of inheritance at the time that Wilson wrote the passage quoted above, have ceased to adhere to the opinion expressed in it. Even the broader view that the nucleus is the chief or exclusive bearer of hereditary qualities is questioned by several biologists of the highest standing, and there is some reason to doubt the accuracy of the statement just quoted from Professor Thomson as to its general acceptance.

Meves has collected a great deal of evidence supporting the view that the cytoplasm plays a very important part in the transmission of hereditary characters. He points out that a large number of observers have insisted upon the

---

[1] *Heredity*, p. 58, London, John Murray, 1908.

fact that not only nucleus but also cytoplasm is contributed by both the male and female cells in fertilisation. He suggests that certain cytoplasmic structures, "*chondriosomes*," divide with the cell, and are handed on individually from generation to generation.[1] Although he seems to have demonstrated the presence of chondriosomes in the cells of different animals and one plant,[2] such structures are not, as far as we know at present, demonstrable in the case of a great many, perhaps not in the majority. The chondriosomes demonstrated by Meves occur mainly in animals, but cytoplasmic structures, which like the nucleus and centrosome divide and grow and are handed on from one cell generation to another, have long been known in plants. They are known as "chromatophores," and although characteristic of plants, have also been demonstrated in a few animals. These, in the fully developed organism, are differentiated into bodies which produce starch, chlorophyll, and other pigments, and they seem at all stages to retain the power of division. They appear, however, to be of a different nature to Meves's chondriosomes.

With regard to the experiments in the fertilisation of enucleated portions of ova which are cited above, it must be pointed out that these have since been to some extent counterbalanced, or their interpretation modified, by other similar experiments which have given different results.

Godlewski fertilised enucleated eggs of sea-urchins with the sperms of Crinoids.[3] These developed into embryos (gastrulæ[4]) which possessed pure maternal characters only.

---

[1] Meves, F., "Die Chondriosomen als Träger erblicher Anlagen, Cytologische Studien am Hühnerembryo," *Archiv für mikroskopische Anatomie und Entwicklungsgeschichte*, Bd. 72, 1908.

[2] "Über das Vorkommen von Mitochondrien bezw. Chondromiten in Pflanzenzellen," *Sonderabdruck aus den Berichten der Deutschen Botanischen Gesellschaft*, Bd. 12, Heft 5, 1904.

[3] Godlewski, E., "Untersuchungen über die Bastardierung der Echiniden und Crinoidenfamilie," *Archiv für Entwicklungsmechanik*, Bd. 20, 1906.

[4] *Gastrula.* This is a stage in the development of the embryo from the fertilised ovum. At first the cells produced by the series of divisions that follow upon fertilisation are arranged in a single spherical layer. It is as though

Recent experiments in hybridisation also seemed to throw quite a different light upon the influence of the nuclei in fertilisation.

Experiments performed by Driesch[1] and Boveri[2] (1903) showed that in rapidity of segmentation and general appearance, hybrid embryos possessed pure maternal characters.[3]

Loeb fertilised sea-urchins' eggs with the sperm of the star-fish, and the resulting larvæ exhibited pure maternal characters.

Many interesting experiments have been made in the way of extirpating various parts of the eggs of different animals, which seem to throw a good deal more upon the cytoplasm than was generally admitted only a few years ago.

Fischer removed from unsegmented Ctenophore eggs a certain portion of the yolk, and showed that in the resulting larvæ one or more of the ctenidia are not developed.[4] He also found that when certain parts of the ovum were removed, other parts of the larvæ failed to develop. Similar experiments with similar results were made by Wilson with the eggs of *Patella* and *Dentalium*.[5]

there were a layer of cells upon a ball. The next stage is that the surface of the ball is pushed in at one point. This goes on until quite a large hollow is produced, lined inside by cells derived from the outer layer, just as though the surface of an indiarubber ball had been pushed in at one point with the finger. At first the mouth of the hollow is large. It gradually narrows, the space inside is completely cut off, and eventually gives rise, among other structures, to the alimentary canal. From the time that the outer surface of the ball is depressed at one point, until the hollow space is cut off from the outer surface, is the gastrula stage.

[1] Driesch, H., "Über Seeigelbastarde," *Archiv für Entwicklungsmechanik*, Bd. 16, 1903.

[2] Boveri, Th., "Über den Einfluss der Samenzelle auf die Larvencharaktere der Echiniden," *Archiv für Entwicklungsmechanik*, Bd. 16, 1903.

[3] Loeb, J., "Über die Befruchtung von Seeigeleiern durch Seesternsamen," *Archiv für der gesammte Physiologie*, Bd. 99, 1903.

[4] Fischer, A., "Entwicklung und Organdifferenzierung," *Archiv für Entwicklungsmechanik*, Bd. 15, 1903.

[5] Wilson, E. B., "Experimental Studies on Germinal Localisation—(1) The Germ-Regions in the Eggs of Dentalium; (2) Experiments on the Cleavage-Mosaic in Patella and Dentalium," *Journal of Experimental Zoology*, vol. i., 1904.

Godlewski sums up his results as follows: "So, however cautiously these experimental results are considered, we arrive at least at this: up to the gastrula stage maternal characters may occur without the presence of the maternal nucleus."[1]

Meves in criticising these experiments comes to the conclusion that the results are sufficient to controvert the theory that the nucleus is the sole bearer of those entities which ensure the transmission of hereditary characters.[2]

Boveri's later views seem also to tend somewhat towards a similar conclusion.[3] He points out that it is obvious that those factors which so work together in the egg as to give rise to an individual of the same species as the parents, must lie partly, at any rate, in the cytoplasm. There is, however, a great difficulty in the enormous preponderance of cytoplasmic material in the egg as compared with that in the sperm, and in the fact that nevertheless the new individual is as much like the father as the mother. Here, according to Boveri, the cytoplasm of the egg is not concerned. The transmission of specific characters from the parents to the offspring depends exclusively upon the chromosomes supplied by the egg and the sperm. Boveri comes to the conclusion that in development there are two distinct periods. In the first, the cytoplasm of the egg is directive, and only certain properties of the chromosomes come into action. In the second period, the chromosomes begin to exercise their full influence. According to this, the first developmental period is decided by the constitution of the cytoplasm, and Meves considers this the more probable because in some hybridisation experiments the characters appearing during this period are purely maternal. Boveri considers that his theory is brought into line with the experiments of Godlewski, because in the enucleated fragments of the Echinus eggs fertilised with

---

[1] Godlewski, 1906, *op. cit.*, p. 35.

[2] Meves, 1908, *op. cit.*, p. 35.

[3] Boveri, Th., *Zellen-Studien*, Heft 6, 1907.

the sperm of a Crinoid, development only reached the gastrula stage. According to Boveri's theory, this stage is the utmost which could be reached in these experiments. They certainly have been carried no further up to the present.

Oscar Hertwig has expressed very similar views.[1]

Meves's idea is that "the unfertilised egg builds up plasma substances during the long maturation periods, which, even if they are not 'organ-bildende,' are yet certainly necessary to the formation of the particular organs later on. These different forms of plasma (cytoplasm) are localised in a definite manner in the contents of the egg."[2] Godlewski says: "But at any rate these experiments show that the organ-forming substances (Anlagesubstanzen), or whatever else they may be called, cannot be regarded, as they generally are, as being derived entirely from the nucleus. The cytoplasm which the sperm brings into the egg, small as it is, cannot be disregarded."[3]

Morgan showed that enucleated fragments of Echinoderm eggs fertilised with sperms, developed, but that the cells of the embryos only exhibited half the normal number of chromosomes. This suggests that all the nuclear contents are not necessary.[4]

These experiments and observations upon fertilisation and development have led some biologists to regard the cytoplasm as a bearer of hereditary qualities conjointly with the nucleus. There is another and a somewhat different view put forward by Verworn, which also attributed a share in the transmission of the hereditary qualities to the cytoplasm.[5] Verworn, by cutting certain unicellular animals into small pieces, showed that neither nucleus nor cytoplasm

---

[1] Hertwig, O., "Allgemeine Biologie, Zweite Auflage des Lehrbuchs," *Die Zelle und die Gewebe*, 1906.

[2] Meves, *op. cit.*, p. 35.

[3] Godlewski, *op. cit.*, p. 35.

[4] Morgan, *op. cit.*, p. 30.

[5] Verworn, M., "Die physiologische Bedeutung des Zellkerns," *Archiv für die gesammte Physiologie*, ii., 1891.

is able to live for any length of time by itself. Unless portions of both nucleus and cytoplasm are present, the piece separated from the organism dies. Both the nucleus and the cytoplasm take part in the metabolism of the cell, and both are indispensable. If metabolism (Stoffwechsel) be taken in its most generalised sense as the expression of the sum of the phenomena of life, the inherited characters must, in a similar sense, be held as the expression of metabolism. According to Verworn, then, each organism inherits the individual or characteristic form of metabolism. Cytoplasm and nucleus are both bearers of hereditary substance, and inheritance can only occur when both are transmitted to the offspring.

When the available evidence is considered, we are forced to the conclusion that nothing like a demonstration as to the nature or situation in the cell of the substance that carries the common hereditary qualities has yet been made. There are many opinions, several worthy of consideration, and many of them forcibly expressed. It is necessary to realise very definitely, however, that we are dealing with personal opinions, and that all of them are not only open to question, but are disputed by one group or other of reputable biologists.

The only generalisation it is safe to make, is to go a very little further than Huxley did more than thirty years ago. Instead of saying with him it is "probable," we can say it is practically certain that every part of the adult contains molecules derived from the male and from the female parent.

The more detailed conclusions to be derived from the evidence we have considered may be summarised as follows:—

1. The only origin of cells known to us is from pre-existing cells.

2. A new multicellular individual is usually produced from the fusion of two cells derived from two similar multicellular individuals.[1]

3. The potentiality of producing all the characters of the

---

[1] The exceptions to this rule are dealt with on pp. 28, 29, 30.

adult individual is present in the single cell produced by this fusion (the fertilised ovum). There is no conclusive evidence as to the nature or situation in the cell of hereditary substances representing racial characters.

4. Certain parts of the cell divide in a selective manner which is not a mere division in bulk. These are:—

(*a*) The chromosomes appear to be handed on individually from the fertilised ovum to all the cells building up the body of the organism. They are, however, distributed in an alternative manner to the cells that are destined to be thrown off as sperms or ova. Also it has been shown that embryos produced from one nucleus only and possessing only half the normal number of chromosomes exhibit all the racial characters. Apparently, therefore, if individual chromosomes represent hereditary characters, such characters cannot be common to all the individuals of the race, but must be characters that are transmitted in an alternative manner from parent to offspring.

(*b*) The centrosomes, when present, are handed on individually from one cell generation to another, according to some observers. Others, however, dispute this, and say that in many organisms they are formed *de novo* prior to each cell division. In any case, centrosomes are absent in the higher plants.

(*c*) Certain cytoplasmic structures may divide individually and be handed on from one cell generation to another. This is common in the case of certain cytoplasmic structures in many plants and in a few animals. Wider claims have recently been made in this direction for cytoplasmic structures by at least one very eminent biologist.

Note on Centrosomes.—Besides being absent in the higher plants, centrosomes are said by some observers to pass out of existence at the end of one cell division, to be reformed at the onset of the next. It has been shown by Loeb[1] that the eggs of the sea-urchin may be stimulated to develop by an artificial chemical stimulus. Unfertilised eggs may also be induced to develop asters (the radiations surrounding the centrosomes when present) by various stimuli; particularly by chemical stimuli.[2] In the centre of these artificially produced asters, central granules may appear that are indistinguishable from normal centrosomes. On the other hand, these central granules may be absent. These facts suggest that not only may cell division be stimulated by a chemical action, but that the real centre of force may be where some chemical substance is present, and that the appearance of a definitely visible body, the centrosome, is not a matter of primary importance. This view is held by many competent observers, and is compatible with what we know of cell division. In any case, the fact remains that in the cells of the higher plants no centrosome appears in the midst of the radiations of the asters at the poles of the division figures. There is simply a space there filled with a fine reticulum, and apparently structureless. These spaces take the place of the centrosomes during the process of cell division.

The Meiotic Phase.—The meiotic division produces two daughter cells with half the number of chromosomes present in the somatic cells. In animals these two cells divide again, and the resulting cells are converted into mature gametes without any further division. In plants a number of divisions may occur, all the cells retaining the reduced number of chromosomes. In the division following the meiotic, the chromosomes divide longitudinally, exactly as they did in the somatic divisions.

There are two interpretations as to the manner in which

---

[1] Loeb, J., "On the Nature of the Process of Fertilisation and the Artificial Production of Normal Larvæ," *American Journal of Physiology*, iii. 3, 1899.

[2] Morgan, T. H., "The Action of Salt-Solutions on the Fertilised and Unfertilised Eggs of Arbacia and other Animals," *Archiv für Entwicklungsmechanik* viii. 3, 1898.

the reduction in the number of the chromosomes takes place in animals and plants. The larger number of observers state that the loops which appear in the prophase of the reduction division are formed by the union of two chromosomes end-to-end. Shortly after the formation of the loops the threads forming them split, but join up again into a single thread before the nuclear membrane is disintegrated. This splitting of the thread is supposed to foreshadow the longitudinal splitting of the chromosomes in the next division. The observers who maintain this view seem to offer the best and most detailed evidence; the researches of some of them are the most recently published, and have been made with full knowledge of the other interpretation.[1] A smaller number of cytologists, mainly belonging to the school of Louvain, state that what is interpreted by other observers as a splitting of one thread, is actually an approximation of two threads, and that these two threads, which join in a parallel manner, represent two chromosomes. They maintain, therefore, that the loops are not formed of two chromosomes joined end-to-end, but of two chromosomes joined side by side.[2] A careful investigation of the pub-

---

[1] Arnold, G., "Ovigenesis and Spermatogenesis of Planaria lactea," *Archiv für Zellforschung*, iii., 1909; Farmer, J. B., and Moore, J. E. S., "On the Meiotic Phase in Animals and Plants," *Quarterly Journal of Microscopical Science*, xlviii., 1905; Fick, R., "Betrachtungen über die Chromosomen, ihre Individualität, Reduction, und Vererbung," *Archiv für Anatomie und Physiologie*, Anat. Abt. Suppl. 1905; Goldschmidt, R., "Über das Verhalten des Chromatins bei der Ei-reifung und Befruchtung des Dicro coelium lanceatum," *Archiv für Zellforschüng*, i., 1908; Meves, F., "Spermatocytenteilungen bei der Honigbiene," *Archiv für mikroskopische Anatomie*, lxx., 1907; "Es gibt keine-parallele Konjugation der Chromosomen," *Archiv für Zellforschung*, i. 4, 1908; Montgomery, T. H., "The Heterotypic Maturation Mitosis in Amphibia," *Biological Bulletin*, iv., 1903; Moore, J. E. S., and Walker, C. E., "The Meiotic Process in Mammalia," *Thomson-Yates Reports*, University of Liverpool, 1905; Otte, H., "Samenreifung und Samenbildung bei Locusta Viridissima," *Zoologische Jahrbücher*, xxiv., 1907; Popoff, M., "Eibildung bei Paludina vivipara, &c.," *Archiv. für Mikroskopische Anatomie*, lxx., 1907; Schockaert, R., "L'ovigénèse chez le Thysanozoon brocchi," *La Cellule*, xviii., xx., 1900, 1901; Tannreuther, G. W., "History of the Germ Cells and Early Embryology of certain Aphids," *Zoologische Jahrbücher*, xxiv., 1907.

[2] Grégoire, V., "La formation des gemini hétérotypiques dans les végétaux," *La Cellule*, xxiv., 1907; Jannsens, F. A., "Évolution des Auxocytes

lished observations of the latter band of workers suggests very strongly that they have missed a stage which has been described by the others. Besides this, a much wider field has been covered by the adherents of the first interpretation. It therefore seems probable, that in the majority of animals and plants two chromosomes are joined end-to-end to form the loops, and that whole chromosomes are distributed to the daughter cells. Supposing the other interpretation to be correct in some cases, there would still appear to be an alternative distribution of morphological entities to the gametes. According to this interpretation the two chromosomes are joined together side by side, as shown in Fig. 17, *a*. Some of the upholders of this theory state that at the meiotic division the two chromosomes are drawn apart and distributed whole to the daughter cells. Here we have the

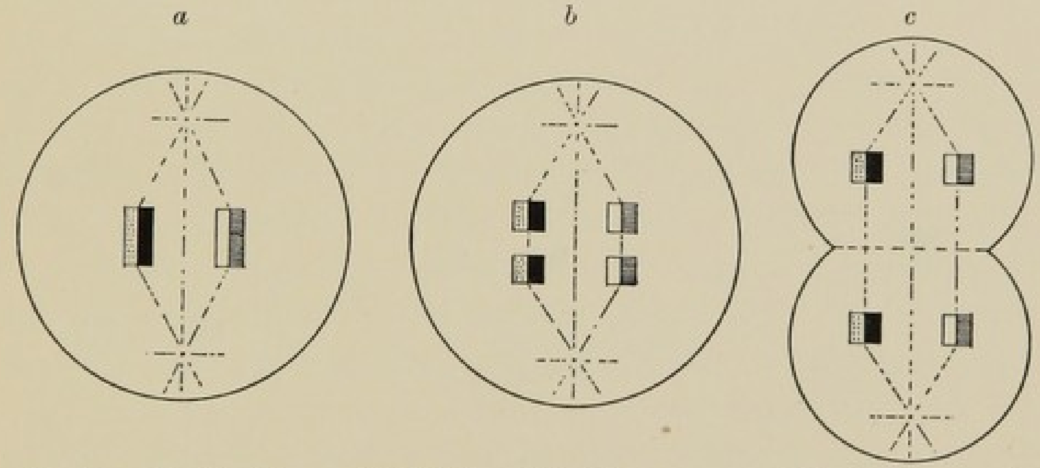


FIG. 17.—Showing the parallel joining of the chromosomes and their subsequent distribution to the daughter cells in the meiotic (reducing) division, according to the Louvain School.

mâles dans Batrocoseps attenuatus," *La Cellule*, xxii., 1905; Van Mollé, J., "Les Spermatocytes dans l'Écureuil," *La Cellule*, xxiv., 1907; Schreiner, A. and K. E., "Über die Entwicklung der männlichen Geschlechtszellen von Myxine glutinosa (L.)," *Archives de Biologie*, xxi., 1905; "Neue Studien über die Chromatinreifung der Geschlechtszellen": (1) "Die Reifung der männlichen Geschlechtszellen von Tomopteris onisciformis (Eschscholtz)," *Arch. de Biologie*, xxii., 1906; (2) "Die Reifung der männlichen Geschlechtszellen von Salamandra maculosa (Laur.), Spinax niger (Bonap.) und Myxine glutinosa (L.)," *Arch. de Biologie*, xxii., 1906; (3) "Die Reifung der Geschlechtszellen von Ophyotrocha puerilis (Clprd-Merz.)," *Anatomische Anzeiger*, xxix., 1906.

same alternative distribution of chromosomes to the gametes as is supposed to occur by the other school of observers, so in so far as the argument in Chapter II. is concerned, it is of no importance which interpretation is correct. Some of the upholders of the approximation theory, however, appear to believe that the pairs of chromosomes joined side by side divide transversely *en bloc,* as shown in Fig. 17, *b* and *c*. But the division in which reduction takes place is not the last division; in both animals and plants there is always another division before the production of the mature gametes. Now all biologists are agreed that in the division following that in which reduction takes place, the chromosomes split longitudinally, so that even if the pairs of chromosomes in the meiotic division are joined lengthways and not end-to-end, the alternative distribution is brought about in the next division just as certainly as it would be in the meiotic division were the chromosomes joined end-to-end (Fig. 18). Thus, whichever interpretation is accepted, we still have the alternative distribution of the chromosomes.

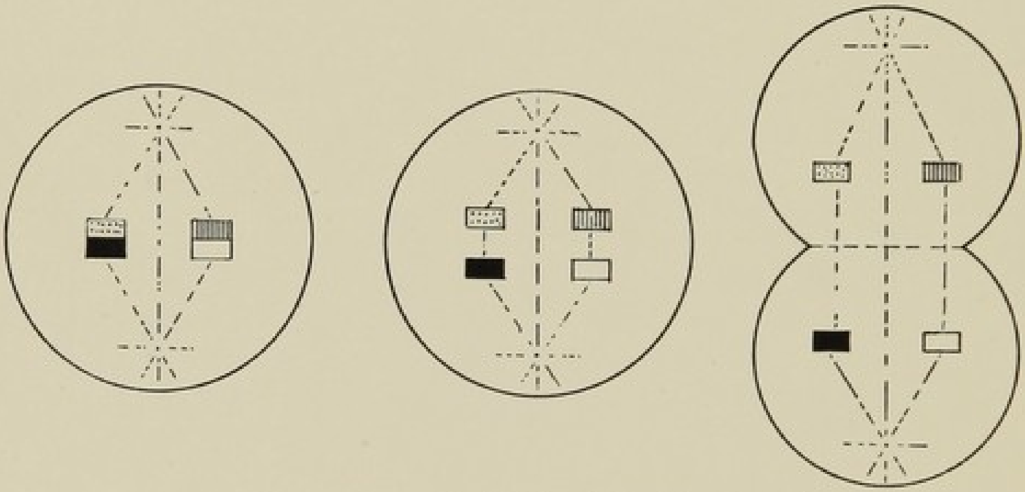


FIG. 18.—Showing the result of the division following the meiotic with regard to the distribution of the chromosomes to the gametes, if the chromosomes behave as described by the Louvain School.

CHAPTER III

Differentiation of cells—Inborn and acquired characters—Mental characters in man — Physical characters — Instinct — Lamarck's theory — The Darwin-Wallace theory—Weismann's theory—Oscar Hertwig's theory.

THE following inquiry into evolution, variation, and bi-parental reproduction may appear to travel wide of our main object—heredity. It must be remembered, however, that man is essentially a wild and not a domesticated species. All the various conditions under which he lives have been produced by himself and not for him by some other species which has interfered with natural selection. It is therefore most necessary that in studying heredity we should study the action of natural selection and the material it works upon, and at the same time inquire with the greatest care into the extent to which a comparison between the phenomenon of heredity in domesticated races, and in races under natural conditions, may be made with safety.

Heredity, according to Herbert Spencer, is "the capacity of every plant and animal to produce other individuals of a like kind." We have seen how it is that substance derived from both parents is conveyed to every cell included in the multicellular organism. The cells included in the body of an organism differ among themselves, but the varying groups are arranged in a similar manner in organisms of the same kind. In different organisms, however, the cells and groups of cells differ in their arrangement and form, in their function, and in the phenomena they exhibit. The fertilised ovum of a dog will produce similar cells arranged in similar groups, and performing the same functions as those forming the bodies that produced the sperm and ovum. The characters of the new individual will in fact be similar to the characters of the parents.

The characters of the adult are not, however, all of the same kind, at any rate among the higher animals. Some of them are inborn, and under normal conditions of nourishment will develop without any other stimulus. Others depend upon various kinds of stimuli to produce them. We will take a concrete case as an example—the possession of two arms with the normal complement of bones and muscles is an inborn character in man. By exercise he is able to increase the size of the muscles in one or in both arms, and even the size of the bones if the exercise is begun early and continued long enough. These are not inborn but acquired characters, often called modifications. They are due to stimuli acting upon the cells derived from the fertilised ovum. The potentiality of producing them is present, but only comes into action in the presence of suitable stimuli. Such characters will not be produced without the stimulus, as we see from the converse case. A man might not use one of his arms at all through disease or accident, and in this case the muscles and bones will not be developed to anything approaching the normal extent. If he uses his arms less than is usual with men, his muscles will be less developed than is normally the case.

The failure to produce acquired characters does not mean that the potentiality of producing them is absent. Given similar stimuli the offspring will produce the acquired characters of the parent, very often with a greater degree of accuracy than the inborn characters. Leaving this question for the moment, we shall consider the nature of inborn and acquired characters a little further.

Inborn characters are those due to the potentiality of the ovum to develop along certain lines under normal conditions of nourishment and when protected from injury. They are the characters that are developed merely by nourishment irrespective of any other stimulus. It must be clearly understood that the inborn characters do not necessarily include all the characters that are present when the individual is born, for environment may have acted upon the embryo and fœtus before actual birth. Thus the condition of a child at birth may have been influenced by the condition under which the mother has lived during pregnancy.

The offspring always varies from its parent, often in many ways. It may vary in size under similar conditions of nourishment and environment; it may vary in colour, hairiness, shape of features, and in a hundred other points. These differences are inborn and are known as variations. Variation is a common property of living matter, and will be dealt with more fully later.[1] At present it is sufficient to refer to it thus briefly. The new individual then inherits the bulk of its inborn characters from its parents, but possesses some new inborn characters of its own in the form of variations.

Acquired characters are, as has already been said, those characters that are due to the action of various stimuli upon the organism from the time it commences its existence as a fertilised ovum. But these characters could not appear unless the potentiality of producing them were present in the fertilised ovum and in the cells derived from it. The potentiality of producing a character—of reacting in a particular manner to a particular stimulus—is itself an inborn character; therefore acquired characters must be regarded as modifications of inborn characters produced by external stimuli. This does not mean that acquired characters are inborn in themselves, but simply that the potentiality of making an acquirement is inborn. We will take the classical example of a scar. The father may have a particular shaped scar on his nose, which has been produced by an injury during some period of his life. His nose may be of a characteristic shape. It is quite likely that the child may inherit the peculiar shape of his nose, but it is certain that the child will not inherit the scar. The child will, however, inherit the potentiality of reacting to injury in the same way as his parent reacted; thus when a certain portion of tissue is destroyed or distorted by injury, the cells will react to the

---

[1] See p. 59.

injury in a particular manner, and, going through a process of inflammation and repair, will produce scar tissue. This reaction to injury is an inborn character, and the tissues of the offspring react in a similar manner to the tissues of the parent. Thus if a child receives a similar injury to his nose to that which was received by the father, he will reproduce a similar scar. He will do this, moreover, whether he has inherited the characteristic shape of his father's nose or not.

A consideration of this case makes it clear that the shape of the nose inherited from the father was an inborn character, that is, it was present in the germ cell and develops without any other stimulus than that of nourishment. The scar, however, will never develop unless a particular stimulus is applied, in this case the stimulus of injury. Furthermore, unless the injury to the child's nose is exactly similar to that inflicted on the father's nose, the scar will not be the same.

In considering the mental characters of man we are forced to the conclusion that almost all are acquirements, and that very little besides consciousness, memory, capacities for making various acquirements, and a few instincts is inborn. All the other characters are acquirements dependent upon the existence of consciousness and memory in the individual. It must be clearly understood that here memory is used as meaning the power of mentally recording impressions upon the consciousness, that is, the storing up of the past experiences. The records themselves are of course acquirements. The power of thought is entirely dependent upon consciousness and memory, and is therefore an acquirement. Besides consciousness and memory, certain mental aptitudes are also undoubtedly inborn characters; thus a child of a great calculator may be born with a great aptitude for figures. Under ordinary conditions of environment the necessary stimulus will be applied, and the child's capacity in calculating will be developed in proportion to his inherited aptitude to a very large extent. His calculating powers are acquired, his aptitude for acquiring them is inborn. It is very necessary to keep this difference clearly before the mind in considering inborn and acquired characters.

It is impossible here to deal with the instincts of man in any detail. It is certain that man possesses but few unmodified instincts, but inquiry into this matter is still in a state of considerable confusion. Undoubtedly the child possesses the instinct to suck.

There can be little doubt as to the sexual instinct. Psychologists are not agreed as to how the play of young animals ought to be regarded. Play has been attributed to a surplus of nervous energy in the young animal, which, being tended by its parents, is not obliged to seek its own livelihood. This theory was first propounded by the poet Schiller, and was elaborated by Herbert Spencer. Another theory[1] supposes that the play of young animals renders them skilful in various ways that will be useful in later life. The kitten plays with various dead objects and thus trains itself in rapid movements of a kind that will be useful when it is obliged to seek its own prey. According to this theory, play is not exactly an instinct, but is due to a premature ripening of other instincts that will subsequently be useful to the individual. A more recent theory[2] suggests that play is "a peculiarly modified form of the combative instinct." This theory assumes pugnacity as the true instinct, and play as a modification due to an innate tendency to rivalry.

It is exceedingly difficult for the biologist and student of heredity to fall in with any of these views. That play is the result of superfluous energy is directly contrary to the well-recognised parsimony of nature, and it is inconceivable that

---

[1] Groos, Karl, *Die Spiele der Thiere*, Jena, 1898, translation E. L. Baldwin, New York, 1906; *Die Spiele der Menschen*, Jena, 1899, translation E. L. Baldwin, New York, 1901.

[2] M'Dougall, William, *An Introduction to Social Psychology*, Methuen, London, 1908.

superfluous energy should have been produced with such uniformity in the latest stages of evolution. If we consider in what kinds of animals the play of the young individuals is most marked and lasts for the longest time, we find that the more acquirements the animal makes in the ordinary course of nature, the more it will play and the longer the period during which it plays will be. Young mammals play incomparably more than the young of any other animals. The development of their muscles, bones, and some of their internal organs is largely dependent upon use. It is therefore most important to the well-being of the individual that it should use its limbs and take as much exercise as possible during the period of growth. If it does not, it will not be fitted for the struggle of life when it has to care for itself and its offspring. It seems probable that play is an instinct produced by the action of natural selection, and is primarily no more than an inborn impulse to move about quickly and exercise the body, limited only by temporary exhaustion. Of course, particularly in the case of man, subsequent mental acquirements will direct this instinct into various channels, so that the play of children becomes more complicated as they grow older and more mental acquirements are made. There seems, however, no reason to regard play as anything but a pure instinct, one of the few left to us, and one without which no individual would reach anything approaching what we regard as normal bodily development. It will be readily realised, then, that almost all mental characters are acquirements which do not begin until after birth.

Of the physical characters of an individual, a certain number are inborn, such as the possession of a head and limbs, nails, teeth, internal organs. Some of them are modified to a certain extent by acquirements. Thus, although human beings all possess a heart, the muscles of that organ may be considerably modified by the strain thrown upon it by exercise. The same kind of thing may happen in other internal organs. Of the external characters, the ears, nose, teeth, nails, hair, and some other appendages, seem to depend almost entirely with regard to their shape and development upon nourishment, and are therefore inborn characters. Almost everything else, however, is modified by acquirement. The development of the muscles, the growth of the bones, and the general form of the whole organism in the higher animals, are modified by acquirements. Some of these acquirements are as constant in the race as the inborn characters. This is because all individuals are subjected to similar stimuli during their period of growth. All children, unless prevented by disease or accident, learn to walk and gratify the instinct to play, thus producing similar acquirements in all normal individuals.

The comparison between the higher and lower animals makes this difference between inborn and acquired characters clearer. In the vast majority of insects, for instance, there are practically no acquired characters; almost all of them are inborn. Take the life-history of a moth or butterfly as an example. The caterpillar hatches out of the egg complete in all its parts, and capable of looking after itself; directly it hatches out it simply grows in response to the stimulus of nourishment. It does not acquire any knowledge with regard to the kind of food which is necessary for its well-being; it is born with this knowledge. When the next stage in its life-history arrives, it spins itself a cocoon, and that without ever having seen a cocoon. This knowledge and skill is an inborn character, and the caterpillar is prompted to spin a cocoon at the proper time purely by instinct. When in the cocoon, the caterpillar is metamorphosed into a chrysalis, and in the chrysalis all the parts of the perfect butterfly or moth are developed simply by growth. When the butterfly or moth hatches out in due course, all its muscles and organs are developed, and it is not dependent upon the stimulus of use, that is, of exercise in the case of the muscles, for development. Here we see nothing but inborn characters, and no acquired characters. As we go up the scale of animal life, we find fewer inborn characters, fewer instincts, and an infinitely greater inborn capacity for making acquirements.

Let us for a moment consider a comparison between the building of a dwelling by civilised men and the making of a cocoon by a caterpillar. All the skill and powers brought into use in the series of actions involved in the building of a house are acquirements. First there is the planning of the house, which requires a special set of acquirements. Following this, in the actual building, many different kinds of special skill are required, and very probably a dozen different classes of skilled workmen will be employed, each possessing a different set of acquirements, which are necessary in order that he may possess a particular kind of skill. To meet certain contingencies among civilised men, different individuals acquire certain kinds of skill and knowledge. Thus many of their acquired characters differ, although in the main they are very similar. No man could carry out any of the operations involved in the building of a house by the aid of his inborn characters; he is entirely dependent upon acquired characters. The caterpillar, however, carries out the operation of spinning its cocoon—to do which it is quite probable no man could ever acquire the requisite skill—without ever having had any experience in spinning cocoons before, without any practice, and without ever having made any acquirements in that direction. Moreover, it performs this operation once only in its life. It is enabled to do it entirely through its inborn characters. It would be easy to produce any number of similar illustrations, but the one already given is probably sufficient.

These facts are rendered very evident by considering the condition under which the young of various animals are born into the world. Young insects are born, in the great majority of cases, with just as great a capacity for looking after themselves as they have at any time during their life. When we come to mammals, we find that the young are largely dependent upon their parents for protection. The higher we go the longer this necessary period of protection becomes. Thus in man the new-born infant is absolutely helpless; it relies almost entirely upon acquired, and hardly at all upon inborn characters, excepting of course the greatest of all inborn characters, the capacity for making acquirements.

When we speak of higher animals, we do not necessarily mean that a more complicated structure exists among them, or a higher differentiation of tissues than in the lower animals, but that there is a greater capacity for making acquirements. What we call intelligence is in direct proportion to, and dependent upon, the capacity for making acquirements. It is because of this that we say that a dog is more intelligent than a fly, and that man is more intelligent than a dog.

The various kinds of characters may be classified as follows:—

Inborn.

(1) Those inherited from a parent or parents.
(2) Those which are due to individual variations.

Acquired.

(3) Those acquired before birth. (Pre-natal acquired.)
(4) Those acquired after birth. (Post-natal acquired.)

It must be born in mind also that (4) and even (3) may be dependent upon a potentiality of making certain acquirements, inherited as an inborn character from the parents.

Perhaps the most important question connected with heredity is whether acquirements can or cannot be transmitted from parent to offspring. There is no question as to whether inborn characters are so transmitted—all biologists are agreed on this point; and no one who has studied the matter at all doubts that inborn characters are transmitted. With regard to acquired characters, however, although probably the majority of biologists are convinced that these characters cannot be transmitted, quite a large number are equally convinced that acquired characters may be and are transmitted. The theories supported by these two different sections of biologists involve the whole question of evolution, that is, the question as to how complicated organisms have been produced in the course of long ages from pre-existing and simpler forms. Before considering the evidence for and against the transmission of acquired characters, it is necessary, therefore, to deal briefly with the existing theories that bear upon this point. There are many subdivisions and modifications of the more generally known theories, and it will only be possible to deal here with the most important and most generally known in their simplest form.

The theory of Lamarck was generally accepted by biologists before the time of Darwin and Wallace, and is still, in a modified form, accepted by a great many. Lamarck assumed that characters due to environment that were acquired by parents were by them transmitted to their offspring. He would explain that the antlers of a stag were developed somewhat in the following manner. The bucks fought with each other for the does, and they fought by butting at each other's heads. This produced callosities on the forehead. These callosities were transmitted to the male offspring, which went on butting and made the callosity larger. This went on for many generations, until the antlers reached their present size and form. Again, the deer generally developed their speed also through the transmission of acquired characters. The individual deer, being chased by animals of prey, acquired considerable speed in its efforts to escape. This speed was transmitted to its offspring. The offspring were also chased by beasts of prey, and developed speed in addition to what they had inherited from their parents, and so on from generation to generation.

The theory that evolution is due to the action of natural selection upon inborn variations was published by Darwin and Wallace simultaneously. Darwin, while admitting the possibility of the transmission of acquired characters sometimes, held that natural selection played the greatest part in the development of new characters. The speed of the deer will serve again in order to explain the working of natural selection. In this case the explanation is, that those deer which possessed the greatest inborn capacity for developing speed were those that escaped from the animals that hunted them. Thus deer possessing this inborn character would survive and produce offspring in greater numbers than those that lacked it. The offspring would vary from the parents and from each other, some towards a greater capacity for developing the speed, some remaining about the same and varying perhaps in other characters, and others again would vary towards less speed. With the offspring the same thing would happen again; those with the greatest speed would have the best chance of escaping from their enemies, and would thus survive and produce offspring. At every generation, in fact, those individuals which varied toward less speed would be eliminated; while those which varied toward greater speed would possess even greater advantages than their parents. As long, therefore, as the selection was kept up, that is, as long as other animals continued to hunt the deer, the deer would go on developing greater speed until they reached a point where the race had attained a considerable amount of safety by this means. And even then, the high standard of speed would be maintained by the elimination of individuals which varied toward less speed, as long as beasts of prey continued to hunt the deer.

The theory that evolution is due to natural selection acting upon inborn characters, and upon inborn characters only, is due to Weismann. Weismann formulated his idea in his theory of the continuity of the germ-plasm. His theory is that the hereditary substance (the germ-plasm) always remains distinct in the body of the multicellular organism. When the single cell—the fertilised ovum—divides into two, one of these daughter cells is destined to produce the reproductive cells (the sperms or ova), the other is destined to produce the soma or body.[1] Some of the progeny of the one cell remain comparatively undifferentiated until the time when the mature sexual elements are to be produced. The progeny of the other cell become highly differentiated, and form the different tissues of the body. The germ-cells, from the earliest stages of development, contribute nothing to the support of the body, and live upon it in a parasitic manner. The *soma*, or body, on the other hand, serves as a support and protection to the germ-cells. The line of cell generations passing throughout any number of generations of individuals is absolutely direct as far as the germ-cells are concerned; they, or rather their contained germ-plasm, being handed on from generation to generation of new individuals. The cells forming the soma are, however, destined to certain death within a measurable space of time. On this hypothesis Weismann concluded that modifications produced by environment in the body of a multicellular organism could not produce any change in the germ-plasm itself, that natural selection acted upon variations occurring in the germ-plasm, that all new inborn characters were due to such changes, and none of them to changes produced in the body by stimuli, or any other external influence.

Oscar Hertwig has put forward the theory that the germ-plasm, or the power of producing germ-cells under certain conditions, is retained by all the cells of the body.[2] Apparently something of this kind must exist in the case of many plants, for in them even a small portion of a leaf in some cases will, when separated, grow into a whole new plant and produce germ-cells. It is obvious, therefore, that the cells in the portion of leaf separated from the original plant must have possessed the potentiality of producing

---

[1] Weismann's theory does not necessarily assume that one of the two cells produced from the fertilised ovum produces nothing but germ-cells, but that all are produced from among the progeny of one, none from the other.

[2] Hertwig, O., *The Biological Problem of To-day*, English translation, Heinmann, London, 1896.

germ-cells. In some of the lower animals the same power of producing gametes seems to exist in most of the cells of the body, but when we come to the higher animals the germ-plasm is generally separated from the rest of the body at a comparatively early stage in the development of the individual.[1] The fact that if the cells be shaken apart when the ovum has divided into two or more, even into as many as sixteen, each of them is capable of producing an embryo complete in all its parts, also suggest the existence of germ-plasm in all the cells of the body, in some organisms at any rate.[2]

It is quite possible that in some cases the germ-plasm is separated off at an early stage in the development of the organism. It seems quite certain that in other cases this does not happen. The period at which the germ-plasm emerges is not of vital importance, nor is it essential to assume that it is always limited to a particular group of cells in all organisms. Weismann's main points are not seriously affected. It still remains quite possible, or even probable, that the germ-plasm continues independently, that inborn variations arise only in the germ-plasm itself, that there is no transmission of any characters from parent to offspring except those existing germ-plasm, and there is no necessity to believe that acquired characters may be transmitted because Weismann's original theory is thus modified with regard to some details.

---

[1] It is interesting to note, in relation to Hertwig's theory, that the cells of cancer in man and other vertebrates have been described as presenting very many important points of resemblance to germ-cells. For instance, reduction is said to take place among them, and several other phenomena generally only found in such cells as are about to produce mature gametes. Farmer, Moore, and Walker, "On the Resemblances exhibited between the Cells of Malignant Growths in Man and those of Normal Reproductive Tissues," *Proc. Roy. Soc.*, vol. lxxii., 1903; "On the Resemblances existing between the Plimmer's Bodies of Malignant Growths and certain Normal Constituents of Reproductive Cells in Animals," *Proc. Roy. Soc.*, B. vol. lxxvi., 1905; "On the Cytology of Malignant Growths," *Proc. Roy. Soc.*, B. vol. lxxvii., 1906.

[2] Identical twins developed from one ovum and polyembryony in plants, also suggest that the separation of the germ-plasm does not occur at the first segmentation of the ovum.

For a theory which allows of the transmission of acquired characters from parent to offspring we must turn again to Darwin's theory of pangenesis. We have seen that this theory assumes the presence in the germ-cell of innumerable gemmules, each of which represents or determines the development of a cell similar to a pre-existing cell in the bodies of the parents. This theory assumes further that gemmules are produced in the cells forming the various tissues and organs of the body, and migrate thence into the germ-cells that are contained in the organism. Thus any changes brought about by environment, or in fact by any external influence, might, according to this theory, be represented in the germ-cells, and acquired characters might thus be transmitted to the offspring.

There are of course many modifications of this theory. For instance, de Vries assumes that what he called "pangens" (which seem to correspond more or less to Darwin's gemmules) are contained in the nucleus. He does not believe, however, that the pangens are cell-germs as Darwin assumed for his gemmules, but that they are the ultimate units containing potentialities of particular hereditary characters, and that from these units the cells forming the body are built up during the process of development. This theory of de Vries, which has been accepted by many biologists, partakes both of the idioplasm theory of Nägeli, and of Darwin's theory of pangenesis. It assumes of course that the idioplasm is made up of pangens which migrate from the nucleus, and in growing and multiplying build up the cytoplasm.

We are faced then with two opposing theories; one the theory of Weismann—that no acquired characters can be transmitted from parent to offspring; the other, the theory of Lamarck—that acquired characters may be and are transmitted, and that the transmission of these acquired characters has played an important part in the process of evolution. The value of these opposing theories will be discussed later.

CHAPTER IV

Variation—De Vries' mutation theory—The case of Œnothera—The disappearance of characters—Variation in grafts—The cell layers in the embryo—Variations in wild and domesticated races—Arguments against the origin of species *per saltum*—Fertility of hybrids.

THE similarity of offspring to their parents is very marked in the case of both animals and vegetables, and extends to all the characters of the race. It is, however, a matter of common knowledge that among the higher animals at any rate, offspring differ both from their parents and from each other to some extent. Variability appears to be a property common to all living organisms in spite of the fact that individual animals and plants produce new individuals that are generally similar to themselves. For instance, if a collie dog be mated with another collie, the pups produced will grow to about the same size as their parents; they will have similarly shaped heads, and be similar generally. Every individual, however, in the litter of pups, will differ in some way from its brothers and sisters, and also from its parents. But though these differences are very evident, upon careful examination they are in the overwhelming majority of instances comparatively small differences; the pups will, in fact, though differing from their parents, still resemble them beyond all comparison more nearly than they will resemble a fox-terrier or any other breed of dog. Although among the lower animals and plants this appearance of difference between parent and offspring, and between different offspring of the same parents, is not nearly so noticeable, owing to our scanty powers of observation due to lack of familiarity with the organisms concerned, still this variation is of universal occurrence throughout the animal and vegetable kingdoms. Before considering the theories that have been put forward as explanations of the occurrence of variation, it is necessary to consider in some detail the nature of the phenomenon itself.

In the great majority of cases the differences between parent and offspring, and between the offspring of the same parents, are small, often being limited in the case of the higher animals, as far as superficial examination goes, to colour or to differences in size generally or in some particular part. The differences most familiar to us are of course those occurring among other human beings, where, for instance, besides frequently observing a resemblance between father and son, we are also able to see considerable differences. This is due to the fact that we are trained to observe differences between individuals of our own kind with an accuracy that is impossible in the case of other animals or of plants. The evidence of trained observers shows us that variations occur even among microscopic organisms. Besides occurring in microscopic organisms, variations also occur in new individuals that have been produced parthenogenetically. Dr. E. Warren observed several generations of one of the Entomostraca—*Daphnia magna*—a minute crustacean which produces many generations without any fertilisation taking place.[1] He found "considerable variability" even among the children of the same brood. Weismann also found variations among the parthenogenetic offspring of *Cypris reptans*. Warren's recorded differences were obtained by measurements; Weismann's differences were in colour.[2]

Another very good example of variation occurring in parthenogenetic organisms is afforded by the Polyzoa.

"The Polyzoa are a class of aquatic organisms of world-wide distribution and including a large number of species. They occur both in fresh water and in the sea, and the

---

[1] Warren, E., "An Observation on Inheritance in Parthenogenesis," *Proc. Roy. Soc.*, vol. lxv., 1899.

[2] Weismann, A., *The Germ Plasm: a Theory of Heredity*, translation, 1893 German edition, 1892.

marine forms are found from between tide-marks to the deepest abysses of the ocean. Some of the species are among the commonest objects of the seashore, and others may be obtained in numbers by the use of the dredge or trawl. They often occur as delicate encrustations, usually calcareous, on plants, stones, or shells; or they may assume the appearance of seaweeds, corals, or hydroids. Although most of them are of comparatively small size, they are usually large enough to be recognised by the naked eye, while the largest of them reach a diameter of a foot or two."

"The statement has often been made, as the result of a theoretical conception of the physical basis of heredity, that the asexual method of reproduction gives rise to little or no variability. Although there are many reasons for doubting the validity of this conclusion, it may be well to state at the outset that the Polyzoa, which are without exception characterised by increasing in an asexual manner, show a high degree of variability in the individuals thus produced. So much is this the case, that the want of fixity of type which results from the tendency to vary, renders the definition of species particularly difficult in this group of animals."[1]

As an illustration of how easily considerable differences between individuals may escape the observation of the untrained eye, the case of the white man living among negroes may be considered. At first all the negroes appear alike to the white stranger; he sees little or no difference between them, and is unable to distinguish between the features of individuals belonging to different tribes. The first step in his training will be, that he will be able to distinguish with ease differences between members of different tribes. If he live long enough among them, he will see just as much difference between negro brothers and other near relations as he does between white men.[2] The observation of differences

---

[1] Harmer, Sidney F., Presidential Address to the Zoological Section, British Association Meeting, 1908.

[2] This was the personal experience of my brother, Major H. A. Walker, after seven years' service with the King's African Rifles.

between individuals is, in fact, a matter of training where small differences are in question. Though in the very great majority of instances these variations are comparatively small, occasionally we come across cases where the individual varies in some very striking manner from its parent. In the case of the higher animals, for example, an individual is occasionally born with a greater number of digits than usual, a human child with six fingers or six toes. Such considerable differences between parent and offspring are, however, comparatively rare. It is also generally known that monstrosities appear occasionally, such as a calf with two heads. We may dismiss monstrosities, however, as there is no evidence that they are ever perpetuated, and so need not be considered in dealing with heredity.

There are then two kinds of variations which we have to consider. Innumerable small differences between parents and offspring and between the offspring of the same parents, which are found to occur always and continuously; and more considerable differences appearing in new individuals, which are of comparatively rare occurrence. *It is necessary, however, to point out that there seems to be a regular gradation without any definite line of demarcation between these small and universal variations and the large and comparatively rare variations.* Biologists are divided with regard to the question as to whether evolution is brought about by the selection of the small universal variations, or whether it is entirely due to selection acting upon the larger variation. Darwin himself expressed it very definitely as his opinion that evolution depended entirely upon the selection of small differences, but more recently de Vries has propounded the theory that the production of new species depends entirely upon the selection of large differences. He and his followers claim most emphatically that they are the true exponents of the Darwinian theory carried a little further than it was carried by Darwin himself, and that all their teachings are perfectly compatible with all that was written in the earlier editions of the *Origin of*

Species. On the other hand, Wallace, who advocated the theory of evolution by natural selection at the same time as Darwin, maintains, as Darwin did also most emphatically, that large differences do not play the important part claimed for them by de Vries and his followers.

De Vries's "mutation theory" may be briefly stated as follows:[1] Two kinds of variations occur normally among living organisms; innumerable small variations occur constantly; they fluctuate round a specific mean much as the shot-holes cluster round the bull's-eye of a target. Variation occurs in every direction, but the differences are small. These are "*fluctuating variations,*" and though they may be selected up to a certain point, and a particular character may be exaggerated in this way, such a character cannot be permanently established, but will disappear as soon as the selection ceases. On the other hand, large variations of quite a different kind occur sometimes. Compared with the "fluctuating variations" they are rare, and may not occur in any given race for a long period of time. They may, however, appear in considerable numbers in a particular race at a particular period during its history. These are "*mutations,*" and de Vries holds that they are the only kind of variation which is permanent. If the individual in which a mutation has occurred produces young, and they in their turn breed and perpetuate the race, this race will form what he calls an elementary species. It will remain permanently different from the stock in which the mutation originally occurred. The way a new species is established is by the selection, not of the fittest individual, but of the fittest species. Mutations, that is, elementary species, which are unfavourable are eliminated; those which are favourable survive.

The first difficulty met with in de Vries's hypothesis is the impossibility of distinguishing between a large fluctuating variation and a small mutation. Apparently the only way

---

[1] De Vries, Hugo, *Die Mutations-theorie,* 2 vols., Leipzig; vol. i., 1901; vol. ii., 1903.

of finding out whether a difference belongs to the one or the other category, is by a process of experimental breeding. If the new character remains permanent, it is a mutation; if it disappears, it is a fluctuating variation.

The particular case upon which de Vries first built his hypothesis was that of *Œnothera lamarckiana*—the evening primrose. The European history of this species is obscure. Some species of *Œnothera* was probably introduced from America into France in the eighteenth century. Apparently it does not exist in a wild state in America, but several closely allied species do. De Vries, having searched in vain in the neighbourhood of Amsterdam for a plant in which large and permanent variations occurred, found *Œ. lamarckiana* in a deserted potato-field, whither it had probably escaped from some garden. On breeding these plants he found that several large variations occurred, two of which he called *Œ. brevistylis* and *Œ. lævifolia.* He found that they bred true when self-fertilised. He was also able in later generations to establish several other new varieties which apparently bred true. These he regarded as mutations, and considered that *Œ. lamarckiana* was passing through a stage when it produced a large number of mutations which were likely, if favourable, to produce new species; if unfavourable, to die out.

There are several other cases which seem to show that among domesticated plants under artificial conditions, these large differences, sports, or mutations, may be perpetuated, and may produce a race with permanent new characters. A well-known example of this is the Shirley poppy, which occurred as a sport and now breeds true.

When we come to inquire, however, in more detail into these mutations, we find that they become established as new races only among plants that have been domesticated, that is, which have been subjected to artificial selection. There is no evidence at all that *Œ. lamarckiana* is a wild species, and there is a strong suggestion that it is artificially produced by a cross. G. A. Boulanger's experiments, which gave very different results to those of de Vries, suggest that it was produced by crossing various forms of *Œ. biennis*,—which is polymorphic,—and is known to have been previously introduced into Europe.[1] In any case *Œ. lamarckiana* is an organism that has been domesticated for a very considerable time, and is an exotic imported from another continent.

De Vries was unable to find a single instance of a permanent mutation among the wild plants that he investigated. The other probable cases of perpetuation of mutations are among domesticated plants that have been subjected to artificial selection for a considerable period of time, and possibly also to artificial hybridisation. Until we find some well-authenticated cases of mutations being perpetuated among wild species, the theory that evolution of any species has been brought about by mutations and not by constant fluctuating variations, cannot be held as probable.

There appears to be no evidence at all with regard to mutations being perpetuated among animals, even among the lower forms. If, for instance, we take *Aurelia aurita*—a common jelly-fish—in which sports or mutations are very frequent, we find considerable evidence that these sports are not perpetuated, but are eliminated. The sports in this animal were recorded by Ehrenberg in 1835. His facts have been confirmed by several observers, and Browne in 1895, by examining large numbers of the young and adult animals, showed that the abnormal forms, that is, those in which mutations had occurred, seemed to survive just as well as the normal individuals.[2] In spite of this, the race, that is, the bulk of the individuals in the species *A. aurita*, remains the same, and no new race appears to be established although mutations are extremely common.

It is argued by de Vries and his followers that an accumulation of small fluctuating variations produced by selection, although transmitted from parent to offspring,

---

[1] Boulanger, G. A., *Journal of Botany*, October 1907.

[2] Browne, E. T., "On the Variation of the Tentaculocysts of Aurelia aurita," *Quart. Journ. Microscopical Science*, xxxvii., 1895.

always disappears when the selection which has produced it ceases. The example of the sugar produced from beetroot is cited. The percentage of sugar in beetroot has been raised by artificial selection from 7 per cent. or 8 per cent. to 15 per cent., but directly selection ceases the percentage of sugar returns to what it was originally.

This fact, although of great interest, may not, and very likely does not, mean anything more than that characters rapidly produced by selection will disappear with equal or greater rapidity when the selection ceases; particularly in the case of characters produced by the selection of small variations. In this case of the beetroot, selection can at most have been in action for but a few years, and the probability is that such a character is stable more or less in proportion to the length of time for which selection has been acting upon it.[1] We should therefore naturally expect it to disappear with extreme rapidity upon the cessation of the selection.

We know that the disappearance of characters no longer acted upon by selection is almost as common as the production of new characters by the same process. In organisms that have not been subject to domestication, characters are, however, much more stable and take a very long time to disappear. An example of a structure in process of disappearing is the vermiform appendix in man. Extreme examples of the disappearance of characters due to the cessation of selection may be found among parasitic animals. We may take as an instance some of the parasitic crustacea which have relations who, not having taken to a parasitic life, have retained those characters useful to them in leading an independent existence. *Cyclops* is one of the free-swimming Eucopepoda found everywhere in fresh and brackish water.

---

[1] I have been unable to ascertain whether or not the environment was maintained in the case of the rapid fall in the percentage of sugar yielded by the beetroot. If it was not, there is of course nothing in the change of percentage of sugar, which may not have been a modification due to change of environment. See description of Nägeli's experiments with alpine plants, p. 136.

It is very small, but is easily recognised by its elongated form, its rapid jerky movements, and by the egg-sacs of the female. It has numerous complicated appendages which are used for locomotion, eating, catching prey, and various other purposes. We may take *Cyclops* as a good example of the free-swimming Eucopepoda, not the most complicated, but not more highly differentiated in the way of appendages than its fellows. In parasitic Eucopepoda, however, we find forms such as *Lesteira*, where almost all appendages, organs, and the general form are lost, excepting those connected with digestion and reproduction. The beautiful antennules, the legs, and other complicated appendages have disappeared, or are present only as mere vestiges of the original structures.

It is very advisable in considering whether or not mutations are the groundwork on which new species have been produced, that is, through which evolution has taken place, to keep in mind the great differences existing between animals and plants with regard to certain very important points, bearing in mind also that de Vries has built his theory upon observations in domesticated plants. In animals, that is, in all animals excepting the lowest forms, variations can apparently only take place upon the production of a new individual. Plants may be propagated by grafts, cuttings, and runners, without any throwing off or fusing of sexual elements. In some cases even a portion of a leaf of the plant when placed under suitable conditions will grow up into a complete plant with all its organs and structures. Now it appears quite legitimate to regard plants thus produced as being in a sense all parts of the same individual. We will take one example, the Lombardy poplar. Only one sex of this tree exists, at any rate in Northern Europe. For several hundred years all the Lombardy poplars have been produced by cuttings; they are therefore possibly actual portions of the same individual.

Variations, such as those that can only occur upon the production of a new individual (using the term in the strictest sense) among animals, may occur among plants, not only in a graft or cutting, but even in a part of the same plant. A very good example of this is the nectarine, which is a variation appearing on a peach-tree. The variation occurs somewhat as follows:—On a peach-tree which has hitherto always produced rough-skinned fruit, a branch appears which bears the smooth-skinned fruit that has been called the nectarine. This branch will go on bearing nectarines and not peaches, and trees produced from cuttings from it will also produce nectarines, although of course a further variation may take place back to the original rough-skinned fruit. It is thus evident that inborn variations may occur in a part of a plant in a manner that is inconceivable in the case of the higher animals.

This property exhibited by plants, of reproducing all the tissues and organs necessary to form a new individual from a small portion cut off from an existing individual, is exhibited among some of the lower animals. Among unicellular forms it is usual, if the animal be cut into several pieces, for all those which contain a portion of the nucleus to form a new animal complete in all its parts. Among the lower multicellular forms, such as *Hydra*, this also happens, but the complete phenomenon is not present in the higher animals. Thus in many plants, and among some of the lowest multicellular animals, we find that all the cells of the body, even those which are most differentiated, retain the potentiality of producing all the other cells forming the various tissues of the body, including the reproductive cells. As we go higher up the animal scale, however, we find this potentiality is more and more limited. It still exists to a certain extent even among vertebrates, some of which will grow new limbs or organs containing all the various tissues involved, upon the destruction by accident of the original limb. One of the most remarkable instances of this kind is the way in which the lens in the eye of the salamander is reproduced after removal.[1]

---

[1] Wolff, Gustav, " Die Regeneration de Urodelenlinse," *Archiv für Entwicklungsmechanik*, i. 3, 1895 ; Muller, E.. " Über die Regeneration der Augenlinse nach Exstirpation derselben bei Triton," *Archiv für mikroscopische Anatomie*, xlvii. 1, 1896.

During the series of cell-divisions, following the fertilisation of the ovum, which go to build up the embryo, the cells produced are arranged in layers. The outer layer is called the *epiblast,* the inner layer the *hypoblast.* At a later period another layer—the *mesoblast*—appears between the epiblast and the hypoblast. Different organs and different tissues are produced from different embryonic layers, and the older embryologists believed that epiblastic cells could only become differentiated into tissues usually produced from the epiblast. They believed the same with regard to the mesoblast and the hypoblast. The crystalline lens of the eye is produced from epiblast, but when it is removed in the salamander, the new lens grows from cells that were produced from the mesoblast. Under normal conditions mesoblast cells in the salamander would never become modified into anything at all like the crystalline lens. Here the mesoblastic cells have still retained the general potentiality of the fertilised ovum in a very high degree, and are able to reproduce such a specialised structure as the lens, in spite of the fact that under normal conditions this is only produced from epiblastic cells. When we come to mammals, however, we find only very limited traces of the retention of common potentialities among the differentiated cells forming the soma.

The phenomena exhibited by the cells of the higher animals is very different from what happens in plants. In the latter we find the whole organism reproduced from a few differentiated cells cut off from an existing individual. There is no counterpart to this phenomenon among animals except among the lowest.

Very frequently we find this potentiality of growing from grafts, cuttings, or runners, coexistent in the same plant with bi-parental reproduction. Thus a strawberry may be grown from seeds, but also from runners. Whether the plant produced from a runner ought to be regarded as a new individual, or as an actual part of the parent, is not a material point to us at the present moment. It is evident that it can hardly be considered as a new individual in the same sense as a plant produced from seed. The practical result is that we have a strawberry plant produced in which the complicated process of fertilisation has been passed over, and that in spite of this absence of the reproductive cycle, variations may occur in the separated parts of the same individual in plants.[1] Neither need we consider at present whether this skipping of the reproductive cycle is due to the retention of an ancient character, or a new character produced after the evolution of bi-parental reproduction in any particular kind of plant.

The essential point at which we arrive is, that while among all but the lowest multicellular animals variation does not occur except upon the production of a new individual, in plants variation may occur in parts of the same individual, and that when a part of a plant is separated from an existing individual it may, under suitable conditions, lead an entirely independent existence, and may exhibit variation. This difference in potentiality as regards variation between animals and plants depends upon the fact that in plants a separated portion, in many cases *any* portion, of an individual, is capable of reproducing all the tissues, including the reproductive cells, that were contained in the original individual. It has already been suggested[2] that the germ-plasm in the higher animals is probably separated at a very early stage in the development of the individual, while in plants and in the lower animals it is distributed throughout the organism. This would account for this difference. Any comparison, therefore, between variations occurring in plants and variations occurring in animals must be made with these facts in view, and they must to some extent modify our ideas in this relation.

The comparison between variations occurring in wild and in domesticated races of animals and plants should be made

---

[1] *e.g.* nectarines on peach-trees. See p. 68.

[2] See p. 57.

with the greatest caution. Reference has already been made to the difficulty of observing small differences between individuals of the same race among animals and plants. It is quite obvious that all the special characters of the domesticated races have been produced by the intervention of man. Man, however, has generally been capable of selecting only considerable differences, that is, differences which are larger than usual. He has always selected animals or plants which vary from the mean of the race more than did their fellows. *Whatever else he has selected, then, he has always selected variability, which is just as much a character as anything else.* We should therefore naturally expect the larger variations to be much more frequent among domesticated animals and plants than among wild races. This coincides exactly with the experience of de Vries, although not with his conclusions. Among about a hundred wild indigenous plants in Holland, he found that no considerable variations occurred. When, however, he dealt with *Œnothera lamarckiana*, he found many large variations. It has already been shown that *Œ. lamarckiana* is not known as a wild species, that it is not indigenous to Holland, that it has been subjected to artificial selection for considerably over a hundred years, and is probably a hybrid. We have seen also, in the cases where large variations are common among wild animals, that these are not perpetuated as a rule.[1]

G. A. Boulanger, after describing his breeding experiments with *Œ. lamarckiana,* writes as follows: "To sum up, I would suggest the possibility of the mutations-theorie being based on false premises. De Vries has assumed, without any justification, that *Œnothera lamarckiana* is a natural species. The fact that it was originally described from a garden flower, grown in the Paris Jardin des Plantes, and that, in spite of diligent search, it has not been discovered wild anywhere in America, favours the probability that it was produced by crossing various forms of the poly-

---

[1] See p. 65.

morphic *Œ. biennis*, which had previously been introduced into Europe."[1]

Sir W. T. Thiselton-Dyer, contrasting the variability of plants under cultivation with their variability when under natural conditions, says: "In all these cases I think we may safely infer, from the persistent specific stability at the commencement of cultivation, that the changes which subsequently occur would not have occurred in nature. . . . The evidence, on the other hand, that such changes follow cultural conditions as a result is simply overwhelming."[2]

Darwin, writing to Wallace on February 2, 1869, says: "I always thought individual differences more important; but I was blind and thought that single variations might be preserved much oftener than I now see is possible or probable. . . . I believe I was mainly deceived by single variations offering such simple illustrations, as when man selects." "Single variations" here are what de Vries now calls "mutations," "individual differences" what he calls "fluctuating variations."

The demonstration of de Vries' mutation theory, in so far as experimental evidence goes, must then be regarded as highly unsatisfactory. It rests entirely upon domesticated plants, and mainly upon *Œnothera lamarckiana*, which is possibly, even probably, an artificially produced hybrid. The theory is, however, accepted by a number of biologists of high standing, and must be considered here on general as well as upon experimental evidence. De Vries claims that new species arise by mutations, and that the small fluctuating variations have nothing to do with evolution; as though transmissible from parents to offspring, they are not stable. He says: "The current belief assumes that species are slowly changed into new types. In contradiction to this conception the theory of mutation assumes that new

---

[1] "On the Variations of the Evening Primrose," *Journal of Botany*, October 1907.

[2] "Specific Stability and Mutation," *Nature*, November 28, 1907, pp. 77–79.

species and varieties are produced from existing forms by sudden leaps."[1]

This statement seems to assume that "species" are individual groups of animals or plants always distinct and rarely or never merging into each other. This assumption appears to be very generally made by the followers of Bateson. Thus R. H. Lock writes: "The species riddle presents itself definitely as the problem of the existence of a series of discontinuous groups of creatures, sharply marked off the one from the other." And again: "Species arise by mutation, by a sudden step in which either a single character or a whole set of characters together become changed."[2] Bateson writes: "We see all organised nature arranged in a discontinuous series of groups differing from each other by differences which are specific."[3] J. A. Thomson writes: "But to think of new species arising by slow changes of this sort is in many ways difficult, apart altogether from the fact that definite demonstration of the operation of selection has rarely been attempted."[4] "Now there is no need to hamper the evolution theory by restricting selection to minute variations. We know that sports, mutations, or discontinuous variations are frequent, and that they are remarkably stable in their hereditary transmission."[5] (This may be, but we know of the stability of variations, large and small, only under artificial conditions.)

Now, those biologists who have been largely occupied in the study of species and varieties find that their work of classification is often rendered almost hopeless by the way that the so-called species merge into each other. The following quotation expresses this feeling very strongly: "It is the discontinuity which strikes Bateson and those who

---

[1] De Vries, H., *Species and Varieties, their Origin by Mutation*, Chicago and London, 1905.

[2] *Recent Progress in the Study of Variation, Heredity, and Evolution*, pp. 11 and 144, London, John Murray, 1906.

[3] *Materials for the Study of Variation*, p. 17, London, 1894.

[4] *Heredity*, p. 80, London, 1908.

[5] *Op. cit.*, p. 81.

follow him; but it is the continuity which rather aggressively impresses the great majority of those whose lives are devoted to the study of species. The work of the systematist would be immensely facilitated by that very discontinuity which is always eluding him but obtrudes itself upon Bateson. The letters of Darwin . . . are almost pathetic in their statement of difficulties due to continuity in Cirrhipedes."[1] Rothschild and Jordan write: "Whoever studies the distinctions of geographical varieties closely and extensively, will smile at the conception of the origin of species *per saltum*."[2]

It is quite clear, then, that many varieties and so-called species do merge into each other, or at any rate that they are not sharply marked off from each other. It is apparent, however, that different writers mean different things by the term "species," or at any rate have different ideas as to what constitutes a species. It is impossible to deal here with the question, "What is a species?" It is necessary, however, to deal with some points very briefly, in order to arrive at a proper conception of what is claimed for the mutation theory. It seems fairly obvious that the property of breeding true does not constitute a species or even a variety, even when there are considerable differences between several races. Local groups of individuals differ considerably from other similar groups in other places, but no one would claim for them the rank of a variety, let alone a species. Such groups generally breed true. Yet breeding true has been classed very recently as "one of the crucial tests of specific or sub-specific rank."[3] Neither can it be admitted that fertility between two divergent forms necessarily proves that they belong to the same species. Hybrids between individuals of obviously different species and even different genera have frequently been produced.[4] Neither does the fertility

---

[1] E. B. Poulton, *Essays on Evolution*, pp. xiv, xv, Oxford, 1908.

[2] *Novitates Zoologicæ*, vol. x. p. 492, 1903.

[3] Thomson, 1908, *op. cit.*, p. 92.

[4] See pp. 75, 117, 118.

of hybrids necessarily indicate that their parents belonged to the same species, for here again the progeny of parents belonging to obviously different species have been shown to be perfectly fertile in some cases.[1] On the other hand, considerable difference in characters between two races does not necessarily constitute a species.[2] Sir E. Ray Lankester is inclined to think that the word species should be abolished altogether.[3] As, however, we are still obliged to use the term, it is desirable to arrive at some definite idea. It is not likely that any definition would be accepted by all biologists. Probably it is not possible, without risk of contradiction, to go farther than to say that forms which exhibit "free interbreeding under natural conditions" and "have been shown by human observation to be descended from common ancestors or from a common parthenogenetic or self-fertilising ancestor,"[4] belong to the same species. Admitting this, we should imply that forms that do not interbreed freely under natural conditions and cannot be shown by human observation to be descended from common ancestors, should be classed as separate species. If we add to these points of difference certain morphological differences, the majority would admit that two forms were rightly so classed. According to this there is no evidence for the mutation theory, for there is nothing to show that mutants will not interbreed freely with forms that exhibit only fluctuating variations under natural conditions, and the mutants have been shown to have the same ancestors as

---

[1] The hybrids between the common and the Chinese goose are fertile (*Life and Letters of Darwin*, vol. iii. p. 240). These geese are "so distinct that they have been placed by some authorities in distinct genera or sub-genera" (Darwin). The hybrids from the ring-dove and domestic pigeon are also fertile (P. St. M. Podmore, *The Zoologist*, November 1903, p. 401). See also p. 118, for cases among fishes, and p. 117.

[2] *e.g.* the case of the polymorphic butterfly *Limnas chrysippus* (Poulton, *Essays on Evolution*, pp. 70–71).

[3] Stated by Poulton, *op. cit.*, p. 62.

[4] Poulton, *op. cit.*, pp. 60 and 61. (Presidential Address to the Entomological Society of London, January 20, 1904.)

the non-mutants. Yet mutants, according to de Vries, are "elementary species."

Whatever view we take of what constitutes a species, we have to face the fact that there are some considerably divergent forms, related to each other but having no connecting links, and we have to judge whether it is more probable that such cases are due to the intermediate links having died out; or whether in cases where so-called species merge into each other, the intermediate links have been "formed *after* the species to which they are theoretically supposed to give rise."[1]

---

[1] J. A. Thomson, *op. cit.*, p. 82.

CHAPTER V

Adaptation—Difficulty of explaining by the mutation theory—Examples of adaptation—Protective coloration—Seasonal changes—Imitative adaptation—Pitcher-plants—Drosera—The Yucca and the moth Pronuba—Parasitic adaptation—The material provided by variation for natural selection to work upon—The biometrical principle—Conclusions.

THERE is a phenomenon in nature, so striking and so general, that no theory of evolution can be accepted as plausible, or even possible, which fails to explain it. This is the extraordinary adaptation of living organisms to their surroundings. Not only are they adapted to their physical conditions, but above all, to each other. The mutation hypothesis not only fails to explain this,[1] but a careful consideration of its postulates shows, that the co-adaptation of living organisms to each other and to their environment, and the origin of species by mutations, are incompatible. The only means of escaping from this conclusion would be by assuming (1) that a mutation takes place first, and the adaptation afterwards, through the accumulation of fluctuating variations, the organism surviving during this process, although it is out of harmony with its environment; or (2) that adaptation has been arrived at by just as great a number of minute mutations as Darwin and Wallace assumed of fluctuating variations for the same process.

There is no living organism which would not serve as an example of the phenomenon of adaptation. We must, however, consider a few individual cases in order to realise its full significance.

Sitaris humeralis, a beetle belonging to the family

---

[1] This has been admitted by the mutationists themselves, *e.g.* Bateson, W.: "Nor have we any definite light on the problem of adaptation . . ." (*Report of British Association, Cambridge Meeting*, p. 587, 1904).

Cantharidæ, is a parasite upon the solitary bee *Anthophora*. The female *Sitaris* lays over 2000 eggs, burying them in the earth near the entrance to the nests of the bee. These eggs hatch, producing larvæ which possess six legs, as is usual in the larvæ of beetles. The larvæ are triungulins, that is, they possess three claws at the extremity of each leg. This is exceptional among beetle larvæ. The larvæ hibernate until the following spring, when they become active. They do not, however, try to enter the nests of the bees, but attach themselves to any hairy object that happens to approach them. No discrimination is shown in the choice of an object beyond the fact that it must be hairy. The majority of the larvæ are doomed to extermination, for they attach themselves to any hairy object with which they come in contact, and there is a vastly greater number of chances that they will fix upon the wrong than upon the right insect. They have been found upon hairy beetles, flies, and bees of the wrong kind. Those, however, which are fortunate enough to chance upon *Anthophora*, are carried to the nest. Now the male *Anthophora* appears about a month earlier than the females, therefore most *Sitaris* that arrive at their proper destination are attached to the males. They transfer themselves, however, to the female. When the female *Anthophora* lays her eggs in the cells of the nest, the triungulin larva slips off her body on to the egg she has just deposited upon the honey. Here the larva remains, balanced carefully upon the egg, for if it left it for the honey, it would be drowned. The bee then seals up the cell, and the larva proceeds to eat the egg, living upon its contents for about eight days. It remains in the shell of the egg during this time, for it would be suffocated if it came into contact with the honey. At this period the larva moults, and appears in a form specially adapted to floating upon the honey which is to be its food for the next six weeks. The legs of the triungulin stage have disappeared together with the other appendages, and the larva now seems but little more than a vesicle. It is shaped, however, in such a way that one surface must float uppermost in the honey, and round this surface are the openings of the spiracles, so that the animal is adapted to breathe while it floats passively upon the surface of the honey which is its food. When it has finished the honey, it is metamorphosed into a pseudo-pupa. Individual *Sitaris* may vary in their subsequent life-history before reaching the stage of the perfect insect, but we will leave these stages and deal with those described.[1] The main adaptations here are: the numerous eggs laid by the female, which meets the high mortality among the larvæ; the three claws upon the legs, which enable the larva to cling to the bee; its emergence from hibernation at the same time that *Anthophora* appears; the instinct to leave the male bee and go to the female, and to leave the female and float upon the egg; the equally remarkable instinct through which it rigidly keeps within the egg; the metamorphosis into a shape, unknown among other beetles, which is perfectly adapted to a passive existence floating upon the honey in the cell of the bee.

Now some of the morphological adaptations might conceivably have been brought about by mutations, though in all of them it seems probable that ancestors of *Sitaris* that first took to parasitism upon *Anthophora*, or the ancestor of *Anthophora*, would have perished while waiting for the mutation to occur, but the metamorphosis of the larva from the triungulin to the vesicular form involves too much to be conceivable as the result of a mutation. This form of larva is unknown among even allied forms, and therefore it is necessary on the mutation theory to assume that it simultaneously got rid of all its appendages, assumed a shape such that one surface must always float uppermost in a fluid of the density of honey, and that the orifices through which it obtained air were so placed that they would be above the surface of the fluid upon which it floated. The instincts without which the race would certainly be exterminated, seem also inexplicable by mutations. An allied form, *Epicauta*, lives upon the eggs of

---

[1] Fabre, *Souvenirs Entomologiques*.

a genus of locusts. The triungulins of this beetle, unlike that of *Sitaris*, run about actively, and hunt for the egg-pods of the locust in cracks and holes in the ground. Did the larvæ of *Sitaris* act in this manner, they could not arrive at the egg of the bee, for they are incapable of living in the honey where it is deposited, until the first metamorphosis has taken place. There appears to be no way in which they could reach the egg except by slipping from the body of the female *Anthophora* as she deposits it upon the surface of the honey.

The females of a genus of flies (*Empis*) live upon the juices which they suck from the bodies of other insects. The males of some species of this genus probably feed in a like manner, but in no case are their habits so pronounced in this direction as are those of the females, and in some species the male is probably quite innocent. So voracious are the females, that, did the males make amorous advances without due precaution, it is quite probable their overtures would end in a manner not at all conducive to the perpetuation of the race. The instincts of the male *Empis* prompt him to capture some insect, tempting to the female, and to transfer it, generally living, to her clutches. While she is occupied in dealing with the prey thus provided, the male proceeds to the consummation of his courtship.[1]

Another instinct which is conceivable as having been evolved by the selection of minute variations is the spinning of a cocoon by a caterpillar. It seems inconceivable that this can have been achieved by "a sudden leap." It seems explicable only as the outcome of a long series of minute progressive changes, but not of one or even several large mutations.

A mite, *Antennophorus uhlmanni*, is parasitic upon an ant (*Lasius*). The mite is of such a size that it would hamper the movements of the ant if it were attached on

---

[1] Howlett, M., "Note on the Coupling of Empis Borealis," *Entomologist's Monthly Magazine*, vol. xliii. p. 229, 1907 ; Hamm, A. H., "Observation on Empis livida," *Entomologist's Monthly Magazine*, vol. xliv. p. 181, 1908.

one side or the other. It attaches itself under the middle of the ant's head. The mite eats the food of the ant, but does not injure it individually; for anything that prevented the ant seeking its food would directly injure the parasite. When the ant feeds, the mite moves forward slightly, and takes its share of food from the ant's tongue. Should a second mite attach itself to an ant, the first moves over to one side and the second takes up a position upon the opposite side, thus keeping the ant well balanced and hampering its movements as little as possible. Should one of the mites drop off, the other moves to the middle. When three mites attach themselves to one ant they arrange themselves one on either side and one in the middle, and if one drops off the remaining two arrange themselves accordingly.[1] Are these instinctive actions conceivable as the outcome of a mutation? Hardly, unless of a long series of minute mutations indistinguishable from fluctuating variations.

Among the ants we find, besides species that live in colonies in an independent manner, species that make slaves of other species of ants. Among these slave-owners we find gradations between those which are often without any slaves and perfectly able to look after themselves and their young, and those which are not able to feed themselves or even to fight. *Formica sanguinea* is the only slave-making ant in Great Britain. Regular expeditions are made in which the nests of other ants are attacked, and the pupæ are carried off by the conquerors. When the pupæ hatch out they do most of the house-work for their owners, who are very lazy. There are workers, however, who do the household duties in the absence of slaves. *Polyergus rufescens* has gone further in the slave-owning direction than *F. sanguinea*. It is admirably adapted to its part. While *F. sanguinea* is not really a great warrior, and fights only in numbers, *P. rufescens* does not mind any odds, and fights single-handed most splendidly. When in an attacking force,

---

[1] Janet, Ch., *Études sur les fourmis, les guêpes et les abeilles*, note 13; *Sur le Lasius mixtus et l'Antennophorus uhlmanni*, &c., Limoges, 1897.

however, these ants act in concert in the most remarkable manner, the fierceness of the individual being subordinated to the various necessary tactical movements, even when these involve retreat. Their mandibles are so modified from the usual form, that they are practically useless to the owner except for fighting. The ant is thus not only unable to perform the delicate actions involved in feeding its own larvæ, but it is quite unable to feed itself, and will starve in the midst of plenty unless its slaves are there to feed it. *P. rufescens* attacks the nests of other ants, killing many of them, and carries off some of the larger pupæ. When these hatch out, they serve their masters willingly and faithfully, even fighting in defence of the nest. In an allied American species, the slaves even carry their masters and mistresses when the colony migrates, as the latter do nothing for themselves. The extreme of dependence is exhibited by *Anergates*, which is unable to feed itself or its larvæ, and would be quite unable to cope with the other ants that live with and tend it did the latter decline to serve. How *Anergates* obtains the slaves, and why they serve it, is at present an unsolved problem.

A common "winter moth," *Hybernia leucophæaria*, which frequents the bark of oak-trees, has dark and light horizontal lines upon its wings, matching the colours of the oak-bark. When this moth settles upon the bark it nearly always assumes a horizontal position, "thus bringing the lines of the wings into parallelism with the dark shadows in the vertical cracks of the oak-bark." In this position the moth escapes the notice of its enemies.[1] A moment's thought must show that this instinct is kept up because those individuals that vary away from it run enormous risks of being killed by insectivorous animals, and so only those which have it in full have a good chance of producing offspring. To these they transmit their own characters,

---

[1] Hamm, A. H., *Trans. Entomological Society of London*, pp. 321-23, 1885, and pp. 483-85, January 1907. (In the latter paper several other similar instances are described.)

with variations, and the offspring will inherit the instinct unless some vary away from it, in which case they will be eliminated. The origin of the instinct is explicable in the same way.

The coloration of animals which serves the purpose of rendering them inconspicuous in their usual surroundings, is so well known that it is not necessary to deal with the phenomenon here except in the most general manner. The way in which shadow is eliminated in the bodies of animals, particularly in mammals and birds, has been admirably demonstrated by models.[1] The colour of the back is similar to that of the surroundings, often with markings resembling the usual environment, while the belly shades off into white, thus doing away with the solid appearance which would otherwise make the animal very obvious.

Insects frequently resemble their surroundings with an accuracy that must be seen to be thoroughly appreciated.

A remarkable example ot protective coloration is that of the butterfly *Kallima,* the under surfaces of whose wings resemble dead leaves. One of the most interesting points of resemblance is that on the fore-wing is an oval and transparent patch. Through this the light passes, producing the effect of a hole in what is apparently a dead leaf. On another part of the same wing is a representation of a hole brought about by means of white body-colour, which, though an admirable imitation, is not so exact as the transparent patch. If we examine the transparent patch microscopically, we find that there are numerous opaque white scales scattered upon its surface. The suggestion is very strong that the hole now represented by the transparent patch was formerly represented by an opaque white patch, and that, as we still find some white scales, the process is not quite complete. The process has not yet been started on the other white patch, so probably this patch arose later than that which is now transparent.[2] At any rate it seems almost

---

[1] By A. H. Thayer, in the Natural History Museum, South Kensington.

[2] Poulton, *Essays on Evolution,* p. 203.

certain that the change has, or rather is, taking place by very gradual steps, and there is no suggestion of a sudden mutation.

Some butterflies vary greatly in their appearance at different times of the year, so that they are protected by their similarity to their surroundings in both the wet and dry seasons, when conditions vary enormously. The difference is so great in some cases, that the wet and dry season phases have been classed as different species. "Naturalists were fairly astounded when, in 1898, Mr. Guy K. Marshall first bred the black and blue dry season *Precis sesamus* from the black and red *P. natalensis*. The two butterflies differ in size, form, pattern, colours, relation of upper to under surface, and habits."[1] This is not by any means a solitary case among butterflies; there are large numbers of similar ones already described, and doubtless many that have so far escaped observation. This is particularly the case in tropical countries, where the wet and dry seasons produce such differences in the surroundings, that what would be a protective coloration in one season would be the reverse in the other. Now a change in coloration might well take place as a mutation, and it might be a favourable one towards concealment. It does not seem probable that mutations would take place in size, form, pattern, relation of upper to under surface, and habits in the same individual simultaneously. Moreover, these changes take place with the utmost regularity every year, and are always the same changes, except for the constant fluctuating variations in individuals. Sports or mutations are comparatively rare, and vary from each other just as much as fluctuating variations. According to the mutation theory, it is difficult to conceive of this alteration of forms being produced. By the accumulation of small variations it seems explicable enough.

Protective seasonal changes of colour also occur among mammals and birds in countries where the snow lies for a

---

[1] Poulton, *op. cit.*, p. 208.

long period during the year. Here the individuals turn white in the winter.

In insects, again, we find that large groups of butterflies, distasteful to insectivorous birds, though not related to each other, resemble each other nearly in coloration. "The central types in these groups belong to sub-families which are more abundant and even more unpalatable than the generality of their orders."[1] Insects possessing stings and other means of defence are closely resembled by quite different orders of insects that are quite defenceless. Among the commonest forms imitated are wasps and ants (Hymenoptera). These stinging or biting insects are frequently imitated by flies (Diptera), bugs (Hemiptera), moths (Lepidoptera), spiders (Arachnida), and beetles (Coleoptera). The most striking feature in these resemblances is that they are arrived at in quite different ways by insects that are related to each other. Thus, for instance, in Lepidoptera the transparency of the wings, necessary to resemble the wings of a wasp or the transparent wings of other distasteful butterflies, may be gained by the "loose attachment of the scales, so that they easily and rapidly fall off, and leave the wings bare, except for a marginal line and along the veins." In others the scales remain, but become transparent. They may also be set upon edge, so allowing the light to pass freely between them.[2] In beetles the wing-cases may be coloured so as to represent the coloration and shape of the body of the wasp or ant imitated. The narrow waist may be represented by white marks which tend to conceal the real shape of the outline and make it appear like that of the model. In other beetles the wing-cases are so reduced as to show the under-wings which closely resemble those of a wasp. "Furthermore, the elytra (wing-cases) are reduced in two different ways—in some genera to linear rudiments more or less broadened at their bases; in others to small subquadrate or oval structures representing the bases alone."[3]

---

[1] Poulton, *op. cit.*, p. 233.

[2] Ibid., pp. 251 and 266.

[3] Ibid., p. 252.

Remarkable adaptive changes in appearance may be found among marine forms. The young stages of many fishes and other animals which live near the surface are frequently transparent, thus escaping the observation of their enemies. The young of flat-fishes (soles, plaice, dabs, flounders, &c.) are all hatched out at first with bodies shaped like those of ordinary round fishes, and swim upright. Gradually they become flattened from side to side, and the eye on one side travels to the same side as the other, so that both eyes are on that side of the fish destined to be the upper. A study of the gradual changes which bring about this adaptation in each individual fish, suggests most strongly that the characters of the race have been acquired by the selection of small variations, and not by large mutations. We find no gap in any part of the process of change: all is gradual and regular.

Among the Holothurians (sea-cucumbers) only one is known that lives in the open sea.[1] Its anterior extremity is expanded like a parachute, and the whole organism is semi-transparent. It lives at the surface of the sea and has lost the characteristic spicules. All the other Holothurians live at the bottom and are not transparent, many of them being most brilliantly coloured and conspicuous. Among them there is a regular gradation between allied forms with a full complement of spicules and those having none. *Chirodota* has two kinds of spicules, *Sigmodota* has but one kind, while *Rabdomolga* has none. There are connecting links, which in some cases make classification difficult.[2]

The adaptation in the pelagic form is obvious, the change to transparency being the most striking in the direction of concealment.

When we turn to plants, we find adaptation just as prominent and striking as among animals.

---

[1] Dendy and Hindle, *Linn, Soc. Journ.* (Zoology), vol. xxx., October 1907.

[2] Ludwig, H., "Holothurians of the Albatross Expedition," *Bull. Mus. Comp. Zoo.*, Harvard, vol. xxiv., 1893; *Mem. Mus. Comp. Zoo.*, vol. xvii., No. 3, 1894, p. 183.

In the "pitcher-plants" the leaves take the form of upright pitchers. The upper part secretes honey, which attracts numerous insects. Below this zone is a slippery surface, the slide-zone, which causes the insects to fall into the next—the zone of hairs. These hairs are inclined downward, so that they catch and prevent the insects from climbing out, and they are drowned in the water at the bottom of the pitcher where they decompose and provide food for the plant.

It has been said that a further adaptation takes place in one species of pitcher-plant (*Nepenthe bicalcarata*). The species occurs in Borneo, where a little lemur (*Tarsius spectrum*) has learned that it can get a number of insects from a pitcher-plant without the trouble of catching them for itself. This particular pitcher-plant has got the better of the lemur, however, for it grows two long strong prickles from the lower side of the base of the lid. These project downwards into the opening of the pitcher, so that the would-be robber is seriously scratched.[1]

The manner in which some other carnivorous plants catch their prey is equally remarkable. The leaves of *Drosera* are provided with numerous tentacles, at the ends of which are glandular enlargements. The tentacles round the margin of the leaf are long, those in the middle are short. The glands secrete a quantity of a glistening and very sticky substance, which insects mistake for dew or honey and are attracted. Now if the short central tentacles are stimulated, *all* the long peripheral tentacles bend over so that their enlarged ends cover the middle of the leaf. If an individual long tentacle is stimulated, only that particular tentacle moves. Let us see what happens when an insect touches any of the tentacles of a leaf. If it touches the central tentacles, it is held by the sticky substance, and all the long peripheral tentacles bend over and enclose it. If it touches one of the long peripheral tentacles, it is also

---

[1] Quoted by P. Geddes in *Chapters in Modern Botany*, p. 26, Murray, London, 1893.

held fast by the sticky secretion, and the tentacle bends over and deposits it on the centre of the leaf. But this stimulates the short central tentacles, and so all the other large tentacles bend over and enclose the victim. When the prey is thus secured, the glands proceed to secrete a ferment that digests the insect, and the products are absorbed by the leaf.[1]

In *Scorpiurus* the pod containing the seeds in some species closely resembles a caterpillar, with the result that insectivorous birds are tempted to seize it. They probably carry it some distance before discovering the mistake, and thus distribute the seeds.

In *Acanthorhiza* adventitious roots provide a thorny palisade above the ground at some distance from the tree, thus preventing the approach of animals.

There are also remarkable co-adaptations between plants and animals, particularly in relation to the pollination of the former. In flowers that depend upon insect pollination we have every gradation from forms where the honey, which serves to attract insects, is freely exposed, to those where the honey is so protected that only insects with very long tongues can reach it. It is impossible to deal with many examples here, but the co-adaptation between the Yucca and a moth (*Pronuba*) is particularly striking. The Yucca has a large white flower, which emits a strong perfume, particularly at night when it is visited by the moths. The female at first collects the pollen. This she rolls into a pellet, using for this purpose maxillary appendages specially modified and found only in this genus. She continues doing this until she has made a pellet about three times as large as her head. She then proceeds to lay her eggs inside the ovary of *another* flower. She does this by means of an ovipositor, which is sufficiently sharp to penetrate the tissues of the ovary and sufficiently long to reach the inside.[2]

---

[1] Darwin, *Insectivorous Plants;* Pfeffer, *Unters. bot. Inst. Tübingen*, i. 483, 1883; Rosenberg, *Phys.-Cytolog. Unters. über Drosera rotundifolia*, Upsala, 1899.

[2] The possession of a long and sharp ovipositor by a moth is very remarkable.

Having deposited her eggs, she climbs up to the stigma, the natural entrance to the interior of the ovary, into which she presses the ball of pollen, thus sealing it up. Of course this also fertilises the ovules, and, moreover, as she always lays her eggs in a different flower to that from which she collected the pollen, cross-fertilisation is secured. The moth only lays a few eggs in each ovary, which hatch out into larvæ, which feed upon the fertilised ovules of the Yucca. As, however, the ovules of the plant are very numerous, there are plenty, both to provide food for the larvæ of the moth and also for the reproduction of the plant.[1]

It has been recorded that, during recent years, many species of moths found in Lancashire and Yorkshire, and thence over a gradually extending area, have been growing much darker. This is probably due to the darkening of their environment, brought about by smoke and the dying off of the lichen. The process has been gradual, and in every case except one intermediate gradations between the dark and light forms are found, the lighter becoming rarer, the darker commoner. The one exception is *Amphidasys betularia*. A dark variety, *doubledayaria*, was known to exist before the present darkening of the environment, but was rare. At the present time the dark variety has supplanted the light in these districts.[2] This might be claimed as a mutation, but it is explicable in another way. The dark variety already existed, and there is nothing to show that it was not produced locally in a very gradual manner. When the general environment over a large area changed, the dark variety had a great advantage over the light, and it would most likely happen that the already existing dark race would multiply more rapidly than the selection of small variations would modify the light race. On the other hand, we have, in some cases, an obviously gradual change produced by the selection of small variations. It

---

[1] Riley, *Third Ann. Rep. Missouri Bot. Gdn.*, 1892.

[2] Porritt, G. T., *British Association Report*, p. 316, 1906; Tutt, J. W., *Entomologist's Record*, vol. i., 1890–91; Poulton, *op. cit.*, pp. 308–10.

seems more reasonable to explain the one exceptional case in the light of what usually happens, than to seek a special explanation, contrary to what is usual, for the one exception, particularly when there is a simple explanation perfectly compatible with what occurs in all.

My friend Professor Harvey Gibson has described to me a case of gradual adaptation which came under his own observation. When he was a student of the late Professor Dixon in Edinburgh, it was observed that the flowers in a bed of Campanulas failed to set seed. He was deputed to find out the cause. He found that the humble bees had taken to piercing the calyx of the flower, and extracting the honey thus instead of in the usual way, which would have ensured pollination. A few plants, however, set seed, and from these new plants were grown. In the next generation more flowers set seed, and still more in the third. Upon microscopical examination it was found that a layer of sclerotic tissue was generally developed in the calyces of the flowers in this generation, so that it was more difficult or impossible for the bees to pierce them. The bees were therefore forced to pollinate the flowers which had developed the most sclerosis if they wished to get at the honey. This appears easily explicable upon the selection of small variations. There is no evidence whatever of a mutation.

In all the examples cited there is a strong suggestion, in some of them there is a great deal of direct evidence, that the changes have been brought about in a gradual manner—by the accumulation of small variations. We must apparently admit, then, that adaptation is generally produced by a series of very small variations, but there must also be some means by which the adaptations are kept up to the required standard and become even more accurately suited to varying and to more stringent conditions. Any theory which professes to explain how new characters arise, must explain this also. As small variations are always occurring round the mean of every character of a race, the action of the surrounding conditions must be, that those individuals best adapted will have the best chance of surviving and producing the most numerous offspring. Thus those individuals that vary away from the most favourable characters will be gradually or suddenly eliminated, while those that vary towards more accurately adapted characters will survive and transmit their characters. The subsequent offspring will therefore start from a new racial mean, round which they will again vary. Selection will keep up this mean to a definite standard so long as the same conditions prevail. The mutation theory assumes rigid types to be departed from only *per saltum*, and this necessarily assumes also an inflexibility in races of living organisms which we know does not generally exist. On the contrary, we see everywhere that races are influenced by changes in the environment, in the most marked and yet in the most delicate and gradual manner. The frequency of the "fluctuating variations" is enormously in favour of their being the ground upon which new characters are built. They occur *always* and in all directions. Mutations, on the other hand, are comparatively rare, and also occur in all directions, so the chance of their being in the direction of adaptation is proportionately a small one. In favour of the action of the fluctuating variations is their very smallness, for a great number of them may occur at the same time without throwing the organism completely out of harmony with its environment, which would certainly end in its death. Even single mutations are comparatively rare, and yet if adaptation is brought about by mutations, we must imagine several mutations occurring in various parts of the organism simultaneously in a favourable direction. The argument that small differences are of two kinds, mutations and fluctuating variations, seems to involve a quite unnecessary assumption. It is admitted that the two kinds cannot be distinguished from each other except by breeding. So many possibilities of error must exist in applying such a test, that even were some such assumption necessary to the plausible explanation of evolution, it would hardly meet with general acceptance. As a matter of fact such an assumption seems quite unnecessary. On the other hand, fluctuating variations constantly appear in every character.

The following metaphor puts the situation in a very lucid manner:—

"Darwin's view, that Selection is the paramount power in the production of species, is made very clear by his metaphor of an architect constructing a beautiful building out of the fragments of broken stone at the foot of a precipice.[1] For the purpose of the controversy of the hour, a more appropriate metaphor is that of the artist. Pictorial effects could no doubt be obtained from time to time by the simple method of throwing colours at a screen; occasionally, perhaps, such 'Mutations' would be superior to anything which an artist could achieve by adding here a little and there a little to the developing picture. It would hardly be reasonable to infer from a few such successes that the proper function of the artist is merely to wait for the appropriate Mutation, and to cease producing effects by the accumulation of minute increments—in fact, 'to select not to create.' The essential difficulty about the chance method is that it could never yield representations of particular objects. Now there is an important section of the organic world where the metaphor passes into reality. I refer to the countless thousands of cases in which there has been evolved on the surface of an animal a picture of some portion of its environment—the unending instances of Protective Resemblance and the still more striking examples of Mimicry. Is is as unlikely that a key could be made to fit a complicated lock by a number of chance blows upon a blank piece of metal, as that the elaborate pattern on the wings of a butterfly should have been reproduced on those of its mimic by Mutation."[2]

It might of course be claimed that adaptation is brought about by a number of small mutations. Apart from the fact that this seems to be against the writings of de Vries and his supporters,[3] such an interpretation would throw an even

---

[1] *Variation under Domestication*, London, 1875, vol. ii. pp. 426–27.

[2] Poulton, *op. cit.*, p. xxiii of Introduction.

[3] See pp. 72, 73.

more heavy weight upon the theory of evolution than that which is already considered by some as too great even when *all* small variations are held to be capable of operating in the production of new characters.[1] The following extract from a criticism by F. A. Dixey of the writings of an upholder of the mutation theory puts this admirably: "A point, however, on which we should like to be satisfied is this: the author asserts that 'no one questions the validity of natural selection as a means of exterminating types which are unfitted for their environment'; further, he thinks it is at least probable that certain types have survived in consequence of their 'fitness.' But, since these latter types arose, as he would say, suddenly or discontinuously, how did it happen that they sprang into being in such exact harmony with their surroundings? Would Mr. Lock have us fall back upon the theory of 'directed variation,' or, what comes to the same thing, Paley's view of 'contrivance' by special creation? If it be replied that a well-adapted type must have arisen, not by one or more large mutations, but by a series of mutations both numerous and minute, we should wish to know how such mutations are to be distinguished from continuous variations. To say, with de Vries, that selection of individual differences is powerless to raise permanently the mean of a species, seems perilously like begging the question. As soon as the mean has been permanently raised, the result would be claimed as a mutation."[2]

The difficulty of reconciling adaptation with evolution by mutations is perhaps rendered more evident in the cases of certain parasites than in any others. In animals that are not parasitic, it might be conceivable that a certain amount of adaptation would be arrived at by large mutations, although it requires a considerable exercise of the imagina-

---

[1] See p. 73, quotation from J. A. Thomson's *Heredity*.

[2] F. A. Dixey, "The New Evolution," *Nature*, vol. lxxv., April 18, 1907; A Review of *Recent Progress in the Study of Variation, Heredity, and Evolution*, by R. H. Lock, London, John Murray, 1906.

tion to conceive of this being the regular way by which adaptation has occurred. When, however, we come to consider the case of a host and its parasite where new characters have been recently developed in response to the presence of the parasite, and the parasite has developed new characters to meet the new characters of its host, large mutations are obviously out of the question. If the new character appeared in the host suddenly by a mutation, the parasite would be hopelessly out of harmony with its environment and must certainly perish, unless a mutation occurred in it *immediately*. The strongest upholders of the mutation theory do not claim that mutations are frequent enough to account for such a case as this. They say that periodically in the life-history of a race mutations appear fairly frequently. Between-whiles, however, mutations are said to be very rare, or entirely absent. Even during the mutating period, mutations are not frequent enough or diverse enough to account for the delicate adaptation of the parasite to its host. While such adaptation is inconceivable by means of mutations, it is readily explicable by the selection of small variations. Natural selection acts first upon small variations occurring in the host. When these small variations affect the parasite, natural selection acts in turn upon the small variations of the latter, and it becomes gradually adapted to a gradually changing environment. There is a parasitic mollusc (*Stilifer linckiæ*) that lives upon star-fish. It is found in an outgrowth on one of the arms. This outgrowth is produced as the result of the reaction of the tissues of the host to the presence of the parasite, which it encloses and protects, only a small opening being left as a communication with the exterior. Now the parasite obtains its nourishment from the body cavity of the star-fish. It grows a long process which penetrates into the body of its host, so the parasite is always in direct communication with the source whence it draws its nourishment.[1]

---

[1] Sarasin, Paul, and Fritz, "Über zwei parasitische Schnecken," *Ergebnisse Naturwissenschaftlicher Forschung auf Ceylon*, 1884–86.

There are other cases which can hardly be considered as instances of true parasitism, for the two organisms involved mutually benefit each other. Organisms thus living together in a mutually dependent manner are termed "symbiotic." One of the most remarkable and best known of these examples is afforded by Lichens. Lichens are composed of Fungi and Algæ living together. Some of the Algæ involved are unicellular plants, others are multicellular or groups of cells united together in colonies. The cells of the fungus grow round the Algæ. The Algæ multiply and follow this growth, enclosed by the fungus. The bodies thus composed of fungus and Algæ combined are known by the name of Lichens. "The two processes of vegetation mutually support and supplement each other. The Alga can live alone as a plant containing chlorophyll, though it may be open to question whether it can do so in all cases, but its vegetation is not hindered by the fungus; it can often be shown to be permanently promoted by it. The fungus as a strictly obligate parasite is dependent for its growth upon the Alga, without which it cannot attain to its full development, and in most cases, cannot get beyond the first stages of germination."[1] In many Lichens small brood-buds are formed which separate spontaneously. These contain both fungus and Alga, and under favourable conditions may develop into another Lichen similar to the parent structure. We thus have a widely distributed form, well known to every one, which consists of two entirely different organisms living symbiotically, which in many cases is capable of continuing its existence and becoming distributed by brood-buds containing both organisms.

A still more remarkable case is afforded by a very low form of worm (*Convoluta roscoffensis*) which lives symbiotically with green Algæ.[2] The Algæ appear to form a special assimilation tissue within the worm, enabling it to live like a

---

[1] De Bary, A., *Comparative Morphology and Biology of the Fungi*, English translation, Oxford, 1887.

[2] Haberlandt, quoted by Von Graff in *Die Acoela*, Leipzig, 1892.

green plant. The worms are elongated and coloured green, and at Roscoff live in the sandy tide-pools, fully exposed to the sun's rays, looking like a mass of floating weed upon the surface of the water. Now the stomach, and indeed the whole of the alimentary apparatus, has disappeared in the worm, and it lives exclusively upon carbohydrates formed within its body by the Algæ. The Alga has undergone most profound changes. It has lost its membrane, thus allowing its secretions and excretions to pass freely among the cells of the worm, and it cannot live independently. If the worm dies, the Algæ contained in it die. All the allied forms of this worm seek the dark, and live concealed under stones and vegetation, and they are carnivorous. *Convoluta*, however, being dependent upon the well-being of the Alga for its nourishment, seeks the sunlight and the surface of the water. The sunlight is necessary to the growth and metabolism in the Alga, which in its turn supplies food to the worm which has ceased to be carnivorous. The two forms are thus absolutely dependent upon each other and incapable of living apart.

All these cases involve changes in two different organisms, and it is inconceivable that they can have been brought about by the action of large mutations. The small variations must have been selected by means of very gradual and very small changes of environment. As far as the available evidence goes at the present time, it would seem that a sudden and great change in the environment tends to exterminate the race subjected to it. Thus English dogs taken to India do not thrive, and their offspring generally die out in one or two generations. On the other hand, the dogs that have been long subjected to the environment of India, thrive just as well there as the English dog does at home. It is the same with the human race. English children can be reared in India only with difficulty, and in spite of our having occupied the country to a considerable extent for many years, the English race has never become established there. Although the adult is capable of resisting environment, children are not resistant. It would therefore seem that adaptation to the environment is a very gradual process.

The converse of this also holds good. We find that all the available evidence goes to show that the change of environment has always been very gradual. Formerly it was believed that catastrophes occurred during various geological periods. Now, however, geologists appear to be agreed that there is no evidence suggesting that changes took place more rapidly in former times than they are taking place at present.[1] We are in fact obliged to believe that a sudden change of environment can have rarely been produced in relation to any organisms in the past, except by some such artificial means as occurs in the case of transporting an English dog to India.

The argument brought forward most frequently against small variations is, that they are insufficient to account for the production of new species owing to their smallness, and to the enormous amount of time that would be involved. It is argued that these "chance variations" are very unlikely to be in a favourable direction sufficiently often. Let us consider for a moment what kind of chance we have to deal with. We know that the number of individuals of any given species remains about the same during very long periods of time. When we do get a large increase in the number of individuals, the reasons for the increase can generally be accounted for more or less easily, and it is due to some such causes as the removal of an enemy, or an increase of food supply. These cases are, however, exceptional. As a rule, the number of individuals remains about the same. We may take it that the number of offspring surviving is generally about the same as the number of parents that have produced all the offspring. Now, the house-fly lays five or six batches of eggs with about 120 to 150 in each. In hot weather a generation occupies about three weeks; that is to say, that from the time the egg is

---

[1] Geikie, Sir Archibald, Presidential Address to the British Association, 1892; Poulton, *op. cit.*, pp. 1–45; and many other authorities.

laid to the time the fly produced from that egg is laying eggs itself, is about three weeks. On these facts it has been calculated, that if the progeny of one pair of flies survived, producing offspring which in their turn survived, and so on, a quarter of a million cubic feet of flies tightly pressed together into a solid mass would be produced from the single original pair in one summer. This is allowing 200,000 flies to the cubic foot, and assuming that an equal number of males and females are produced.[1] But this is not what happens. We find that the number of house-flies does not vary to any great extent from year to year, so that we must assume that all excepting one pair has been eliminated. Every individual varies in some way from all the other individuals; it is extremely improbable that any two are exactly alike. From the enormous masses of potential individuals, natural selection has allowed only two survivals. It has acted upon every stage from the egg to the adult fly, and the survivors must have been among those most accurately adapted to the condition under which they have to live. The number from which this selection has been made is so great, that except by some such illustration as that given above, it is impossible to conceive it. There has been then no lack of variations for selection to act upon.

The female cod-fish lays from three to five million eggs each year. She begins to lay eggs when about four years old, and goes on laying for at least five or six years. What would the numbers produced by one female cod and her progeny be if any considerable proportion of them survived? We know that the number of cod is not increasing. The numbers that natural selection has to act upon here are just as inconceivable as in the case of the fly, and offer ample material for the selection of minute favourable variations. The number of instances of this kind which might be cited would fill many volumes.

In the case of organisms that do not produce numerous eggs or young, there is still amply sufficient material to

---

[1] "Biological Problems of To-day," *Edinburgh Review*, January 1909.

allow of variations. Such organisms are generally far more long-lived, and although they do not produce such a number of young at a time, still, as they go on producing young for a greater number of years, a simple calculation will show that if all the offspring survived and bred in their turn, the world would, in a very few years, be overwhelmed by the organism in question.

Small variations occur in every direction round the mean of every character. It has been shown that Gauss's law of frequency of error applies to variations.[1] Sir John Herschel's illustrations of this law makes its application very clear.[2] He pointed out that if a large number of shots were fired by a rifleman at a target, the shots aggregated most thickly round a particular point, and became fewer in proportion to the distance from this point. The area of the closely collected shot-marks varies according to the skill of the marksman. The greater the skill, the smaller will the area be in which the greater number of the shots are found. Precisely the same thing happens in the case of variations. With regard to some characters, the vast majority of variations are generally very small, while with regard to others, more considerable variations may be comparatively common. The probability is that those characters upon which selection has acted most stringently for the longest period of time, will be those which show the smallest variations. When, however, we go to the opposite extreme, and consider characters that have been rapidly produced by artificial selection, we find more considerable variations exceedingly common.

We have, then, apparently ample material in the way of variations to account for the production of new characters under the action of natural selection.

Formerly a comparatively limited time was allowed for

[1] Quetelet, *Lettres à S.A.R. le Duc regnant de Saxe-Cobourg et Gotha sur la Theorie des Probabilités appliquée aux Sciences Morals et Politiques*, Brussels, 1846; Galton, *Inquiries into Human Faculty* (Everyman's Library Edition), pp. 33 *et seq.*

[2] *Edinburgh Review*, 1850.

the age of the earth, and the argument that the available time was insufficient to allow for evolution by natural selection was upheld by many. Lord Kelvin and Sir George Darwin were considered liberal in allowing five hundred million years as the age of the sun. Other arguments, limiting the available time, were based upon the heat conductivity of the earth. The discovery of radium has, however, modified the time allowance to such an extent that " we are now in a position to say that the physicist can make no calculation either as to the probable or possible age of life on the earth."[1]

We are then driven to the conclusion that whatever the results of mutations may be, they are not usually the groundwork of evolution. It is quite possible that occasionally a favourable mutation may be preserved, but according to the whole evidence at present available, it seems probable that under natural conditions this could happen but rarely, and that the usual course of events is that mutations are eliminated and adaptation depends upon the selection of small and continual variations. But adaptation is, in a sense, evolution; so it seems equally certain, according to our present state of knowledge, that evolution has also depended upon small variations, mutations having played little or no part in the phenomenon. It also appears that the way in which new characters are produced and preserved in domesticated races is very different from what happens in races living under natural conditions. Man is able to select large variations (mutations, sports), and to preserve them. He is able to do away with the necessity for accurate adaptation in the organisms under his protection. *As he frequently if not generally, selects large variations (mutations), it is certain that he has unknowingly selected the character of "sporting" or "mutating" in most domesticated races.* The property of variation is an hereditary character just as subject to selection as any other. Under natural conditions

---

[1] Professor Perry writing to Professor E. B. Poulton, quoted by the latter in *Essays on Evolution*.

the tendency to large variations is a variation away from the mean of the race. It tends to be eliminated by bi-parental reproduction.[1] As large variations are comparatively rare, it must be very unusual that they should occur in the direction of more accurate adaptations. It must also be remembered that domesticated races live under artificial conditions. Natural selection, therefore, must generally also tend to eliminate large variations. The property of exhibiting large variations must at any rate be rigidly limited by natural selection and bi-parental reproduction in the vast majority of organisms living under natural conditions. In domesticated races, however, man has eliminated the effects of both bi-parental reproduction and natural selection in this direction, and it is therefore not surprising that they commonly exhibit large variations, and that these large variations or mutations are preserved when man so wishes.

---

[1] See p. 124 *sqq.*, where the effect of bi-parental reproduction is fully discussed.

CHAPTER VI

Racial and individual inborn characters—Immunity to diseases—Malaria—Measles—Tuberculosis—Conclusions.

We have seen that the offspring, though resembling its parents in characters common to the race, and often in certain characters not common to the race, such as the shape of a feature or the colour of the hair, also varies from them. The new individual thus commences existence with inborn characters, the bulk of which are inherited through or from its parents, but some of which are additions, which we call variations. These individual differences may or may not be transmitted from parent to offspring, together with those characters that are common to the race. Hence it seems necessary to divide inborn characters into two classes—Racial and Individual.

It must be obvious to the most casual observer that individuals of the same race exhibit similar characters. These common characters are far more striking and obvious than the differences between the individuals. Thus a negro has a dark skin, thick lips, a prognathous jaw, a receding forehead, and woolly hair. Chinamen and other Mongolian races are distinguished among other characters by oblique eyes and high cheek-bones. The resemblances between individuals are so much greater than and so overbalance the differences, that to the stranger all individuals at first appear alike. According to the observer's familiarity with the individuals of a particulur race, however, the individual differences seem more and more obvious. The same thing applies to all the various races and species of animals and plants. There are characters common to the individuals of every race which are striking and obvious, yet every individual of a race possesses certain characters peculiar to itself.

These individual differences are the immediate outcome of variation. Variations may be transmitted from parent to offspring; therefore in races we may find subdivisions in which all the individuals possess certain peculiarities which are not generally found in the other members of the race. The subdivisions may include only the members of one family for two or three generations; they may include the members of a large number of families all descended from a common ancestor. Though it is quite usual for these individual characters to be preserved for several generations, in the great majority of cases they seem to disappear very rapidly. The racial characters are incomparably more permanent than these smaller individual differences.

It appears certain, however, as evolution has been brought about by the selection of variations, that the comparatively stable racial characters must have been derived from the comparatively unstable individual characters. The former are the more remote, the latter the immediate results of variations. We may in fact say that the *individual characters are the variations of the individual perhaps transmitted through a few generations of the offspring, while the racial characters are the variations of the race.*

Most racial characters in man are of such long standing, that if we were confined to such differences as colour, features, or shape of skull, it would be difficult to cite an example of the probable transition of a character from individual to racial. Immunity to particular disease, however, gives us what we want.[1] We will take malaria as an example. It is well known that strangers going to a malarial country vary in their susceptibility to the disease. A few—very few—appear to be quite immune. Others have attacks,

---

[1] The application to the study of heredity and evolution of the available evidence with regard to immunity to disease is due to Archdall Reid, who has formulated the following theory in a most able manner in *The Principles of Heredity*, Chapman & Hall, London, 1905.

but survive perhaps for many years. Others again succumb to the first attack.[1] Here we have evidence of individual variation with regard to immunity to malaria. What now happens in the case of the inhabitants of the country? We find that there is a very high rate of mortality from malaria among negro children on the West Coast of Africa. The mortality among adult natives is comparatively very small. We have seen that some English people are able to resist malaria, temporarily at any rate, on the West Coast of Africa, but it has been found impossible to rear English children there. Thus apparently there is a greater power of resistance in the adult than in the child both in the English and in the negro inhabitants. There is no reason to suppose that the negroes were more resistant to malaria to begin with than white men are now. When first attacked by the disease, individuals varied in their powers of resistance, and the most resistant survived and produced offspring. The offspring inherited the characters of their parents with variations. Some varied towards more, some towards less resistance; the more resistant survived in their turn; and so on from generation to generation. The process of selection is still going on, and immunity has not been attained by the race. Large numbers of children die; these have varied in the wrong direction. The mean of the race has been raised, however, with regard to resistance to malaria, for we find that after several generations have lived in another country, the negro still resists malaria better than the white man on the West Coast of Africa. Archdall Reid quotes a letter from an officer, who died of malaria on the West Coast, in which it is stated that when his regiment (West Indian) arrived on the Coast, both the white officers and men suffered greatly from malaria. After a single season, however, the men, West Indian negroes, acquired immunity, whereas the white officers continued to suffer as much as ever. Now as the West Indian negroes originally came largely if not entirely from the West Coast, the con-

---

[1] Kingsley, Mary, *Travels in West Africa*, Macmillan.

nection between their easily acquired immunity and an hereditary character secured by stringent selection acting upon many generations of ancestors seems evident. Here, however, even the negroes that have continued to live in the malarial country from generation to generation without interruption have not attained complete immunity. The negro is still subject to an attack of the disease, particularly during childhood. Ought it not to happen that complete immunity should be attained by the race if the selection is sufficiently stringent and lasts long enough? According to the theory here advanced, the answer is, that complete immunity may never be attained, but the race may develop the hereditary capacity of acquiring immunity to the disease in so high a degree that the mortality caused through individuals succumbing in the process of acquiring immunity will be so small that it does not materially affect the race. Indeed, as individuals must always vary, some must inherit less capacity for acquiring immunity, and so there must remain some mortality as long as the selection, that is, so long as the disease, continues, in order to eliminate unfavourable variations.

Examples of hereditary power of acquiring immunity exist in this country. Almost every child has measles, but it is comparatively rare that the same individual has more than one attack of the disease. Neither is the disease usually a serious one in the case of English children. There are of course some serious and even fatal cases, but these again are comparatively rare. We, as a race, have been subject to selection with regard to measles for a very long period. What happens when measles attacks a race which has never been subjected to any selection with regard to it? In the Polynesian Islands, and in several other cases where measles was an unknown disease, the result of its introduction by Europeans has been very fatal indeed. Large numbers, not only of the native children, but of the native adults, died of it, and to them it was just as serious and fatal as the old gaol fever (typhus) was to the English a couple of centuries ago.

Now it is quite evident that we, as a race, have not acquired immunity to measles. What we have acquired is a high-resisting power to the disease, and the capacity of acquiring immunity individually very readily. With us measles is as a rule a very trivial matter, only the few individuals who have varied away from this inborn capacity succumbing to it. We see that to a race that has not been subjected to any selection with regard to measles, it is very fatal, and has helped in some cases seriously to diminish or even exterminate the native population. It must be borne in mind, that we cannot regard these cases of imported disease in quite the same light as the malaria among the West African negroes or measles among the European races. In the case of the imported disease, a race ready to supplant the existing population is necessarily present, and so, before the original race has time to acquire immunity or resistance, the race which has imported the disease takes its place. These are two cases amongst many where races have partially acquired a new character. Whether, if selection went on long enough, complete immunity to such diseases might be obtained, is doubtful. In both these cases, however, the immunity seems to have reached a condition where the disease is no longer a danger to the race.

A comparison between the immunity to tuberculosis in Northern European races, and in races where the disease has only recently been introduced, is also highly instructive. The Northern European races still suffer considerably from the ravages of the tubercle bacillus, but have acquired a considerable degree of resisting power. In towns, almost every one must be infected at some time or other, and very frequently the bacilli live and multiply for some time in the body, being eventually eliminated. Post-mortem examination reveals the presence of tubercular infection in a great proportion of the cases where its traces are sought. "The statement is made by Bouchard that of the post-mortems at the Paris Morgue—generally upon persons dying suddenly — the percentage found with some evidence of tuberculous lesion, active or obsolete, is as high as 75. . . . If, as has been done in Ribbert's laboratory, a systematic inspection is made for the purpose, tuberculous lesions are found in practically 100 per cent. of the bodies of adults."[1] Nägeli laid down the principle that "every adult is tuberculous," and Bertzke, discussing this, states that of the adults that have died in hospital some 70 per cent. show evidence of tuberculous changes.[2] Moreover, when a person suffering from tuberculosis leaves Northern Europe and goes to South Africa or some other suitable climate, he generally recovers. Even without leaving the country in which the disease has been acquired, recovery must be very frequent, even in comparatively advanced stages. "These lesions in the majority of cases are not phthisis in an early stage manifested by small disseminated foci; they are cicatrices of large foci; sometimes of wide completely cicatrised cavities. Phthisis, therefore, is curable even in its most advanced stages."[3] In races where there has been no selection, however, individuals form a suitable soil in which the bacilli can flourish and multiply under conditions where the most susceptible of individuals in Northern Europe would be able either to resist the infection,[4] or would eliminate the bacillus after it had established itself.

---

[1] Osler, W., *The Principles and Practice of Medicine*, 5th edition, London, Appleton & Co., 1904.

[2] Bertzke, "Über Haüfigkeit und Infectionswege der Tuberculöse," *Tuberculosis*, April 1906, vol. v., No. 4, Berlin.

[3] Brouardel, *Trans. British Congress on Tuberculosis*, vol. i., W. Clowes, London, 1902.

[4] Dr. Cleasby Taylor, who has practised for many years in Las Palmas, informs me that when a native of the Canary Islands is stricken with tuberculosis, many members of his family also die of it in a short time. This is so marked, that he has known of whole households practically exterminated. The Spaniards colonised the islands more than four hundred years ago, and cannot then as a race have been subjected to anything like the selection with regard to tubercle that has been the lot of more northern races. They intermarried to some extent with the natives, so that the present race is a mixed one. This race has not been subject to selection since that time, and the tubercle bacillus has been carried there since the islands have been used as a health resort by tubercular patients. The cases of the aborigines in North America, Australia, and New Zealand are still more striking. They become infected easily and always die.

In some other diseases, however, the tendency seems to be towards complete immunity.[1]

Apparently, then, in the case of immunity to different diseases, we have examples of the process by which new characters may be produced in a race. The selection in the case of contagious disease must necessarily be very stringent, and probably acts more rapidly than in the case of most other characters. The consideration of the production of immunity to disease in a race is also very useful in making clear that, as regards the race, such characters grow up gradually, and are transmitted from generation to generation, being increased by the slow accumulation of favourable inborn variations occurring in individuals. The change produced by the environment on individual characters, as we shall see later, is not a permanent change. The change produced in the race by the selection of inborn variations is, comparatively speaking, a permanent one. The production of characters in the race is, then, the result of natural selection acting upon the inborn variations occurring in individuals. Individuals varying in a favourable direction have advantage over those that do not, while those varying in an unfavourable direction are eliminated. It is probable that the new racial characters are derived from individual characters; individual characters being in their turn the result of individual variations.

[1] This seems to be the case in some zymotic diseases that are generally more serious than measles, *e.g.* scarlet fever. Complete immunity appears to exist in some families. My father, although at different times much exposed to contagion, never had scarlet fever, neither had any of my uncles. When I was Assistant Medical Registrar at St. George's Hospital, I was exposed to contagion by scarlet fever several times a day for many weeks during a very bad epidemic. I took no special precaution to prevent contagion, but I never had scarlet fever, neither have any of my five brothers or sisters. I have come across several similar instances in other families.

CHAPTER VII

Progressive and regressive variations—Recapitulation — Reappearance of the characters of remote ancestors—Regression in domesticated animals—Crosses between natural races—Galton's theory of heredity—The bulk of characters inherited from remote ancestors—The village-sheik—Prehistoric human remains—Conclusions.

HITHERTO we have considered only those variations which are additions to the already existing characters in living organisms. These are known as "progressive" variations. As variations occur in all directions, it is evident that only a few of them can be of use to the organism, while a large number of them must be either disadvantageous or useless. It is easy to understand that disadvantageous variations will be eliminated by natural selection, as the organism in which they occur will have no chance of surviving in the struggle for existence against the more fortunate individuals which possess advantageous variations. All variations which are additions to the stock of characters are progressive, and some of them, although not disadvantageous, are not advantageous. Though these indifferent variations are not harmful to the organism, according to the evidence which we have considered up to the present there is no apparent reason why they should not be preserved in the offspring as well as the advantageous characters. Moreover, it is also evident that characters at one time advantageous to a race may cease to be so if the environment changes, and may become either indifferent or actually disadvantageous. We have seen that characters no longer useful tend to disappear. This disappearance of characters also depends upon variations, but these variations are "regressive" and not "progressive." Thus we have two kinds of variation, "progressive" and "regressive." The regressive variation may be briefly described as the failure of some character present in the parents to appear in the offspring. In the disappearance of racial characters such as we have seen in organisms which take to a parasitic mode of life, we have an example of the disappearance of well-established characters.[1] Variations, however, occur constantly, and the great majority of them do not tend to produce new racial characters, although they are capable of being transmitted from parent to offspring. The majority of variations occurring in an individual are, as we shall see later, generally eliminated in two or three generations unless they are the subjects of selection. Thus, regressive variations—the disappearance in the offspring of variations occurring in the parent — must be quite as frequent as progressive variations. It is necessary, in order to obtain a clear conception of this phenomenon, to consider very briefly some facts connected with the development of the individual.

We know that in the case of man, as in all multicellular organisms, every individual commences existence as a single cell—the fertilised ovum. This cell divides, the daughter cells again divide, and so the organism is built up.[2] In the complicated process of development the cells produced are at first arranged in two layers, then a third layer grows between the first two, and by gradual and complicated but orderly stages all the parts of a man are developed. The same series of changes takes place in the development of every normal human individual, so it is quite certain that in man the same processes are gone through in the development of the offspring that were gone through in the development of the parent. The same thing happened in the case of the parents, for they in their turn went through the same series of changes in the process of development that their parents went through before them. Thus, the

---

[1] See p. 66.

[2] The following theory of recapitulation has been formulated in detail by Archdall Reid, *The Principles of Heredity*, 1905, p. 52 *sqq*.

offspring recapitulates the life-history of its immediate parents from the time it is a single cell until it reaches adult life, but the recapitulation is always associated with variations in detail. These variations are very small in comparison to the points of similarity, but still the recapitulation is of the life-history of the parents *with variations*.

In plants growing from buds, cuttings, and runners, recapitulation is avoided, but otherwise it is a phenomenon common to all multicellular organisms. Going back to man, it is evident that, as the new individual has always recapitulated the orderly succession of steps in development that were passed through by its parents, the ancestors of man must have also recapitulated the development of their parents, so that in different stages in the production of a man, the life-history of the development of the race from more primitive forms should theoretically be reproduced in every individual. This is true to some extent, but there is another point which must be borne in mind. Variations occur in every stage of the development.

As evolution of the race proceeds, the environment of the individual during its development must change at every progressive step. The remote ancestors of man were apparently at one time aquatic animals. The human embryo passes through a stage where the arrangement of the large blood vessels is similar to that which supplies the blood to the gills of fishes. But at a very remote period the power of absorbing free oxygen from water must have become useless. The embryo within the uterus could gain no advantage from the possession of gills, and this stage has been so far eliminated that there is but a shadowy representation of it. The same is true with regard to a great many other stages in the development of the human embryo.

Now many of these variations are regressive, and it will be readily realised that unless these regressive variations had occurred, not only during the later stages but at every step in the development of the individual, the production by evolution of the more highly differentiated animals would have been impossible. If between the single cell stage—the fertilised ovum—and the adult, the human organism had to recapitulate exactly the life-history of all its ancestors, the period of time would be impossibly long. Organs and characters which were useful to the remote ancestors, would be not only useless but actually injurious to the human individual when passing through the various stages of its life-history. The gills, useful to the free-swimming aquatic animal in enabling it to breathe, would be useless to the human fœtus which derives its oxygen from the maternal blood. Regressive variation has therefore eliminated or abbreviated many stages in the life-history. Besides elimination, however, additions have also been made. Progressive as well as regressive variations have occurred at every stage. Thus the mechanism for supplying oxygen to the human embryo has been developed, by progressive variations, concurrently with the elimination of the functional gills of the remote ancestor. The placenta —the temporary organ, partly maternal, party fœtal—in which the exchange of oxygen and nutrient substances takes place between the maternal and the fœtal circulations, and which would have been not only useless but injurious to a free-swimming animal, has been developed since the ancestor of man carried its young for gradually lengthening periods within its own body.

As one would expect, the earlier stages are those where the representation of the development of the race is most inexact, for they have been longer subjected to selection than the other periods. We must realise that different characters have probably been subjected to different forms of selection at different times, according to variations in the environment. It is also very improbable that continuous progressive variations can have occurred with regard to one particular character or organ. Besides progressive variations occurring in one part of the body and regressive ones in another at the same time, progressive and regressive variations must have occurred in different parts of the same organ at the same time. Regressive variations, then, are the failure on the part of the offspring to recapitulate some particular step in the life-history of the parents with regard to some particular character.

Unless we believe that evolution has *not* taken place by gradual forward steps, it is difficult to avoid the conclusion that the development of the individual is a recapitulation with abbreviations and alterations of the life-history of the race. If we do not admit this, it seems necessary to assume that at some period or other there was a break, and that the ancestors of any given species produced individuals that were very different from themselves; that an individual, or rather a whole generation of individuals, gave origin to monstrous and even miraculous offspring. "The parent did not reproduce his like; the child did not follow in the developmental footsteps of the parent; but an individual of one species reproduced an individual of quite another species."[1] Even mutation will not explain an event of this kind, for an individual that exhibits a mutation follows in the main the developmental footsteps of its parents and simply shows a progressive variation, or perhaps several variations in one or more individual characters. Besides this, if such a break in development had ever taken place, it would be necessary to assume that the individual that had broken away from the usual order of things still remained adapted to its environment. Had not this happened it could not have survived and produced offspring.

Among domesticated races cases are very common in which the offspring of particular parents exhibit characters of remote ancestors rather than those of their immediate parents. Such cases are particularly common when different breeds of the same species are crossed. Thus, if two different kinds of domesticated pigeons are crossed there is a great tendency to produce the colours of the wild blue-rock. Even without the crossing of two breeds the markings of the wild

---

[1] Archdall Reid, *op. cit.*, p. 54.

ancestor occasionally appear among domesticated pigeons. These individuals continue to produce offspring with the markings of the wild bird. "When a blue or a blue and checkered bird having black wing bars once reappears in any race and is allowed to breed, these characters are so strongly transmitted that it is extremely difficult to eradicate them."[1]

If a Japanese waltzing mouse is crossed with an albino, the offspring are coloured in just the same way as the wild house-mouse.[2] Not only this, but although the ancestors have been bred in captivity for many hundred generations and have been tame, the offspring of this cross are just as wild and timid as the wild mouse taken direct from its natural conditions. The same tendency to revert to ancestors is found in a great many other animals, and is extremely common among plants.

Most of the theories of inheritance explain these reappearances of ancestral characters by assuming the existence of individual entities representing them.[3] These entities are supposed to be passed on from generation to generation, some of them remaining dormant. A change of some kind in the environment or in the egg itself stimulates the dormant entity, and the ancient character it represents reappears after having been in abeyance for perhaps many hundreds of generations. The theory of recapitulation, on the other hand, assumes no entities representing characters. It assumes no more than was assumed for Nägeli's idioplasm.[4] The substance of the fertilised ovum is such that it is capable of developing along particular lines only, and of producing only certain characters. We know that the development of the offspring is a repetition of the development of the parents, so that this theory really assumes nothing that cannot be demonstrated in the case of any normal

---

[1] Darwin, *Animals and Plants under Domestication*, vol. i. p. 210.

[2] Darbishire, *Biometrica*, vol. ii. pp. 101–165 and 282, 1902.

[3] Darwin, *gemmules;* Haeckel, *plastidules;* Weismann, *biophors;* Nägeli *micella;* Galton, *stirps;* de Vries, *pangens.*

[4] See p. 9.

individual, at least in so far as the characters common to the race are concerned. On these lines the explanation of the many cases of reversion to an ancestral character is not that an entity representing those characters has lain dormant in the individuals of many generations, but that the individual in which they appear has stopped short, at a certain point in the recapitulation of the life-history of its parents and ancestry, and exhibits characters of a more or less remote progenitor. Instead of recapitulation going on as far as it did in the parents, it has ceased at a definite point, and the later stages are simply missed altogether. The individual therefore exhibits the characters of a more or less remote ancestor in whom the recently developed characters had not been superimposed upon the older ones.

The cases quoted of the reappearance in domesticated races of the characters of the wild ancestor involve only the reappearance of a character that has been absent for a comparatively few generations and which is comparatively recent. There are other cases in which the characters of much more remote ancestors reappear in the offspring. The ancestor of the modern horse (the Hipparion) possessed three fully formed toes. The modern horse possesses only one. In the embryo of the horse, we find a stage in which there are three toes on each limb, just as well developed as in the ancient Hipparion. As development goes on the two outer toes disappear and only one remains functional. Thus, when a foal is born it possesses only the one functional toe of the modern horse. Occasionally, however, a foal appears with two toes, and more rarely with three. Now, the disappearance of the two outer toes is obviously a late addition to the life-history of the modern horse, and the simplest explanation of the occurrence of a foal with more than one toe upon each limb, seems to be that the later stages have been dropped in the case of such an individual. It is, in fact, easier to interpret this phenomenon by supposing that the toes which are normally developed in the embryo, continue in a few rare cases owing to failure of complete recapitulation, than to attempt to explain it in any other way.

"Progression implies a divergence from the ancestral type, the complete recapitulation plus an addition; whereas regression always implies reversion towards the ancestral type and incomplete recapitulation."[1]

Most of the cases of regression in domesticated animals and plants are comparatively simple. The parent form is still with us, and we are able to make a direct comparison. The various breeds of domesticated pigeons have been derived from the blue-rock, and we know that by stringent artificial selection we are able to modify the characters of the parent form to a very considerable extent in a few generations. The recapitulation then, in the individual that returns to the characters of the blue-rock, is very nearly a complete recapitulation, and only a few recently added characters are omitted. But sometimes the reversion to older and the disappearance of later characters must be due to some further cause than a failure to recapitulate completely. To return to the modern horse, the embryo recapitulates the development of the three toes of its remote ancestor, but as development goes on two of these toes disappear. Here we have an addition to the recapitulation, not a failure to recapitulate completely, involving the disappearance of an already established character. This is "reversed selection," and it is necessary to distinguish such cases from simple regression. The three toes of the Hipparion must have been produced by natural selection. The continued action of natural selection upon the descendants eliminated the two outer toes in the adult animal, but this was arrived at without the elimination of the stage in the embryo where the three toes existed. When a foal is born with two or three toes the reversion is a failure to recapitulate the later stages which have been produced under the influence of natural selection acting in a reversed direction, but the disappearance of the two outer toes in the adult

---

[1] Archdall Reid, *op. cit.*, p. 61.

horse is an addition to the recapitulation and not a regression. Reversed selection then is a prolongation of the life-history, while reversion is a shortening of it.

The results of crosses between different natural races and species are very interesting when considered in connection with the theory of recapitulation. Sometimes the progeny are fertile, but often they are sterile. Thus the mules produced from a cross between a donkey and a pony are almost always sterile. Crosses between domestic European cattle and bison have been found fertile. Among plants, crosses between different species are frequently fertile. An attempt has been made to explain these facts by supposing that the number of chromosomes is different in the two races which when crossed produce sterile offspring, while it is the same in those cases where the progeny are fertile. We have seen that the chromosomes cannot possibly be the bearers of racial characters, so this interpretation does not seem probable. There is some evidence which suggests that difference in the number of chromosomes in the two parents does not necessarily render the progeny sterile,[1] although the evidence is not direct or conclusive.

One of the most interesting points about the crosses of natural races is, that generally a blend between the characters of the two parents is found in the offspring, whereas in a cross between different artificially produced races the offspring generally stop short, and do not develop the recently produced characters. For instance a cross between the common English trout (*Salmo fario*) and American brook trout (*Salvelinus fontinalis*) blends the characters of the parents. Sometimes a character resembles that of one parent more than that of the other. For instance the shape may be more like *fontinalis* than *fario*, but the reverse also occurs. The progeny of the cross are sterile.[2]

---

[1] Rosenberg, O., "Das Verhalten der Chromosomen in einer hybriden Pflanze," *Berichte der Deutschen Botanischen Gesellschaft*, 1903.

[2] Information with regard to this cross was kindly given to me by Mr. F. G. Richmond, The Surrey Trout Farm, Shottermill, Haslemere; Mr. J. B. Fielding,

An interesting fact in connection with this cross is that a large proportion of the progeny are deformed.[1] This may be due to the fact that the characters of the two parents are so different that a very slight individual variation in one of the gametes prevents a recapitulation of the blended characters.

Crosses between the common trout (*Salmo fario*) and the British char (*Salvelinus alpinus*) produce sterile offspring with blended characters.[2]

Crosses between the salmon (*Salmo salar*) and the sea trout (*S. trutta*), between the salmon and common trout (*S. fario*), and between the sea-trout and common trout, all produce fertile offspring with blended characters.[3]

A cross betweeu the salmon (*S. salar*) and the Loch Leven trout (*S. fario var levenensis*) gave very interesting results. The progeny of the first cross were markedly less fertile than either of the parents. Apparently only some of the ova could be fertilised. When, however, the ova produced by the hybrid females were fertilised by pure-bred trout, the progeny were perfectly fertile.[4]

Hybrids between trout, sea-trout, and salmon occur under natural conditions, and the characters are sometimes so intimately blended that it is very difficult or impossible to classify a particular specimen.[5]

Crosses between the roach and bream-flat, the roach and rudd, the chubb and bleak, the common bream and rudd, are not uncommon under natural conditions.[6] Other crosses

---

22 St. James's Street, London, S.W. ; Mr. A. W. Armistead, The Solway Fishery, Dumfries; and the Manager of the Howietoun Fishery, Stirling. All have had personal experience of the cross.

[1] Mr. J. B. Fielding says about 75 per cent.

[2] Howietoun Fishery.

[3] Day, F., *British and Irish Salmonidæ.*

[4] The Manager of the Howietoun Fishery, Stirling, N.B.

[5] I have examined young specimens, with a view to identification, where such important characters as the number of the vertebræ were intermediate between two species.

[6] Cuvier and Val., Säckel, Bloch, and Siebold. Quoted by F. Day, *British Fishes*, London, Williams & Norgate, 1884.

are constantly being recorded between species and genera of fishes.

Galton's theory of heredity[1] supposes that the individual derives half of its total heritage of characters from its immediate parents, one-quarter from its grandparents, one-eighth from its great-grandparents, and so on in a lessening degree from its more remote ancestors. In a comparatively few generations, according to this theory, we find that the amount derived by an individual from its remote ancestors almost vanishes. This has been put in a slightly different way, taking into account the individual variations of the offspring. "Suppose, for the sake merely of a very simple numerical example, that a child acquired one-tenth of his nature from individual variation, and inherited the remaining nine-tenths from his parents. It follows that his two parents would have handed down only nine-tenths of nine-tenths, or $\frac{81}{100}$ from his grandparents, $\frac{729}{1000}$ from his great-grandparents, and so on; the numerator of the fraction increasing in each successive step less rapidly than the denominator, until we arrive at a vanishing value of the fraction. The part inherited by this child in an unchanged form from all his ancestors above the fiftieth degree, would be only one five-thousandth of his whole nature."[2]

This interpretation appears to be directly contrary to the theory of recapitulation "which supposes that the ancestors (*i.e.* mid-ancestors) are represented not *en masse* but in orderly succession beginning with the first and ending with the last."[3]

Now according to what we actually observe, it would

---

[1] Galton, *Proc. Roy. Soc.*, vol. lxi. p. 402.

[2] Galton, writing on Darwin's theory of Pangenesis, in *Hereditary Genius*.

[3] Archdall Reid, *op. cit.*, p. 63.

"The word 'mid-parent' . . . expresses an ideal person of composite sex whose stature is half-way between the stature of the father and the transmuted stature of the mother" (Galton, *Natural Inheritance*, p. 87).

"Similarly a mid-grandparent is a conception obtained by striking an average between the characters of the four grandparents, and a mid-ancestor of any generation by striking an average between all the ancestors of that generation" (Archdall Reid, *op. cit.*, p. 48).

appear that the great bulk of the characters of the individual, in the case of practically all organisms excepting perhaps in some domesticated races, are those which have been possessed by its ancestor for thousands of generations. In man we have very good evidence that practically no change has occurred for several thousand years even in the external appearance of different races. In ancient Egyptian paintings and figures, the negro was as he is now, and the native of Egypt was exactly similar. That the race inhabiting Egypt has not changed in characters for several thousand years was illustrated in a very simple manner upon the discovery of a figure by Mariette at Sakkarah. This figure was the portrait-statue of an unknown man of the Fourth Dynasty. Mariette's workmen mistook it for a statue of the present Sheik-el-Beled (Mayor) of Sakkarah, and the figure has in consequence since been known as the "Village Sheik" or the "Sheik-el-Beled." Now the man of whom this figure is a portrait cannot have lived less than 4400 years ago, and probably not less than 5000.[1] Other statues and paintings tell the same story. "Even to the present day the peasants or *fellahs* have almost everywhere preserved the physiognomy of their ancestors, although the upper classes have lost it by repeated intermarriage with strangers."[2]

Although we have no evidence with regard to the outward appearance of the human race in the geological periods antecedent to our own, the skeletons that have been discovered from time to time make it extremely probable that no great change has taken place since the reindeer period in Northern Europe. The skeletons at Cro-Magnon in the valley of the Vezère are older than the reindeer age. The men were apparently about 5 feet 10 inches, the women 5 feet 6 inches. They were dolicho-cephalic (long-headed),

---

[1] Adolf Erman, *Life in Ancient Egypt*, English translation, Macmillan, 1894; Perrot and Chipiez, *A History of the Art of Ancient Egypt*, English translation, Chapman & Hall, 1883.

[2] Maspero, *Histoire Ancienne*, p. 16.

but not more so than occurs in the best European skulls, and the average capacity of the skull exceeded most modern races. There was no prognathous jaw or prominent ridge over the eyes, and it is practically certain that the features were of no lower type than the most civilised European races. These facts are entirely in accord with the theory of recapitulation. The racial characters appear to be very little susceptible to change, and it seems that but little of the inheritance of the offspring can be derived from the individual variations of the immediate ancestors. Any theory which involves the assumption of morphological units as representing characters must bring us to an *impasse* in a very few generations, as is demonstrated by the working out of such a theory to comparatively few degrees upward from offspring to parents, grandparents, and so on.

It is quite obvious that the resemblances between individuals of the same race are enormously greater than the differences. Every individual, however, differs from its fellows in small points. The bulk of the characters are similar, but nevertheless there are small differences. These small differences may be due to variations in the particular individual, or to small variations inherited from the immediate ancestors. It would seem then that from the parents, grandparents, and more immediate ancestors there is a great probability that the offspring will inherit some of these comparatively small individual variations, but that as the bulk of the characters are similar in all the individuals of the race they must have been inherited from a much more remote ancestry. It is true that the bulk of the characters must necessarily have been inherited through the parents and immediate ancestors, but regression has been constantly at work upon the variations of the individual, and only a few of them have been preserved. The individual variations even of the parents frequently do not appear in the offspring, and this happens at every generation. It is only the common racial characters that go through many generations, either unchanged or so little changed that the difference escapes our observation.

Bearing all these facts in mind, we have an explanation for the transmission of the bulk of the characters of the race in Nägeli's idioplasm theory in its simplest form, in conjunction with recapitulation and regression. This involves but little in the way of assumption. Recapitulation is in the individual a demonstrable fact, and the idioplasm theory and regression assume hardly anything—certainly no more than is absolutely necessary in view of the facts at our disposal. The assumption of morphological units for the transmission of racial characters does not therefore seem necessary. Indeed, it seems unjustifiable in view of some of the evidence which we have already considered.

If every racial character were represented by a morphological unit, all the gametes, from both male and female parents, must contain every unit; otherwise, it would be impossible to account for the constant appearance of the racial characters in every individual. But this would double the units in every new individual, which seems unnecessary waste, incompatible with the parsimony of nature. On the theory here advocated, the only assumption is that the gametes are formed of a particular kind of protoplasm which has a potentiality of developing only along particular lines in a particular manner, and this we know practically always happens. If it does not, that individual collection of protoplasm perishes and does not reproduce its kind. With regard to the individual variations, however, there are, as we shall see later, some reasons to suppose that they may possibly be represented by morphological units or entities. Some of them are transmitted alternatively, and it would be difficult to explain this without some such assumption.

Apparently then the bulk of the characters are inherited by the individual from comparatively remote ancestors. The greater part of the variations occurring in the individual are destined to be eliminated either at once or in a few generations, through the failure of the offspring to recapitulate the individual variations of the parents.

It is necessary now to consider the evidence at our disposal as to the possible causes of variations, both progressive and regressive.

CHAPTER VIII

Causes of variation—Amphimixis—Not compatible with facts of maturation and fertilisation—Elimination of useless variations by bi-parental reproduction —Conclusions.

MUCH has been written in explanation of the probable causes of variation. A very favourite theory is that variations are stimulated by the mingling of the germplasm of two individuals, which always takes place in those organisms where bi-parental reproduction is the rule. This mingling of the germplasm, and the complicated distribution of the chromosomes in fertilisation, has been called "amphimixis," and it has been put forward by many as the immediate cause of variations in the offspring. Weismann was the first to advocate this theory, and it has been supported since by many others.[1] Now we have seen that individual chromosomes cannot possibly be the bearers of different racial characters, but there seems nothing against their being the bearers of individual characters. We shall consider later whether it is probable that they are so; at present it is necessary to consider only what would be the effect of the mode of distribution and recombination of the chromosomes involved in fertilisation. We have seen that in the case of man, where the cells contain thirty-two chromosomes, there is only one chance in over six hundred millions of the same combination occurring as was present in the parents, and this is after making the assumption that the chromosomes in the two parents are similar. At first sight this suggests a possibility of innumerable variations, but when we come to

---

[1] Thomson, *Heredity*, p. 102 *et seq.*, 1908; Ziegler, H. E., "Die Chromosomen-Theorie der Vererbung in ihrer Anwendung auf den Menschen," *Archiv Rassen-gesellschaftliche Biologie* vol. iii. pp. 797–812.

look more closely into the problem it presents a very different aspect. Take one of the thirty-two chromosomes and assume that it represents an individual character.[1] Assume also that it is present in both parents. It will be present in half the sperms, and the chances that it will be retained in the ovum or thrown out with the first polar body are equal. In the fusion that takes place upon fertilisation the mathematical chances of its occurrence in the fertilised ovum are: one in four that it will be duplicated, one being brought by the sperm, the other being present in the ovum; an even chance that it will be present singly; and one chance in four that it will not be present at all. Now the same argument applies to all the thirty-two chromosomes, and supposing that they are the vehicles of individual characters, we have in the process of fertilisation a mechanism of mixing them up in an enormous number of different combinations, so that unless a character were represented in several chromosomes there would be little chance of its being handed on through several generations from parent to offspring. There is, however, no suggestion in the phenomenon of fertilisation, in so far as we know it, of the production of new characters, and variations are new characters and not the mixing up of old ones. Indeed, on this hypothesis we should have in fertilisation not a means by which new characters were produced, but a very obvious means by which they might be eliminated. The tendency of bi-parental reproduction would be, not to produce variations, but to eliminate those that had been inherited from the parents and to bring the offspring back to the mean characters of the race. But we have seen that individual variations are the source from which new racial characters are drawn. Thus unless there be some means of explaining how individual variations may be preserved in spite of the eliminating influence of bi-parental reproduction, the hypothesis

---

[1] It may possibly represent several or only part of a character, but for the sake of clearness it is necessary to deal with only one. This does not affect the soundness of the argument.

that individual variations may be represented in individual chromosomes must be wrong. Not only can this preservation be explained, but the explanation provides for that elimination of variations which is so obvious in evolution and is but inadequately provided for by natural selection alone. Natural selection explains the elimination of individuals that vary in unfavourable directions. We know, however, that variations occur constantly in all directions, and some though not unfavourable are not definitely favourable. We ought therefore, under the action of natural selection alone, to find races overloaded with useless variations and even greater and more sharply defined differences within species and races than we do, for a very few generations would tend to produce individuals with new and very divergent but useless characters. As a matter of fact, however, we find that, under natural conditions in spite of individual variations, the mean of the race remains the same, that individual characters are few in comparison with racial characters, and that the acquisition of new racial characters is a very lengthy process indeed. How then does the hypothesis of individual chromosomes being the bearers of individual variations work out with the theory of natural selection? In formulating the proposition it was allowed in the case of man that the cells of the two parents might possibly contain thirty-two similar chromosomes. Though possible, this is extraordinarily improbable, for the parental cells in turn derived their chromosomes in a manner similar to those of the offspring, and a similar process of mixing was gone through. It is therefore very probable that the same character might be represented in several, even in many chromosomes. If the character gave the possessor an advantage, it would come under the influence of natural selection, and he would have a proportionately better chance of rearing offspring. His offspring would stand a better chance of possessing the character than those of other parents that had it not.

If a character is represented by chromosomes or any other entities perhaps smaller than chromosomes, then it is necessary to assume not only that the character which appears is represented, but also some latent characters. For instance, a child may be exceedingly like some ancestor several generations removed, although the likeness has not appeared between whiles. Again, in the disease hæmophilia (bleeding) a generation is generally skipped, for this disease very rarely appears in females, although it is transmitted through the females.[1] A man who is a "bleeder" may have sons and daughters none of whom have his disease. It will, however, very probably appear in his grandchildren by his daughters, but not in his grandchildren by his sons. Thus the disease is latent in the females, patent in the males, although transmitted almost always through the females and not through the males.

If a character were represented in one chromosome only, it would very likely be eliminated in one or two generations. We find, however, that individual characters often continue for several generations. It is probable, therefore, if characters are represented by entities, that there will be several entities representing differences in the same character. We will take ten as a convenient hypothetical number, and assume a group of these divergences in the same character which are favourable to the organism and so are subject to selection. We will represent these favourable divergences as A, and suppose that two entities A are present in one parent, and one in the other. All the other entities we will represent as X. In one parent the entities will be $2A+8X$, in the other parent the entities will be $A+9X$. In the gametes these entities are halved, and in those of one parent there may be $2A+3X$, $A+4X$, or $5X$. In the gametes of the other parent there may be $A+4X$, or $5X$. In the offspring of these parents there may be $3A+7X$, or $10X$, or anything between the two. If the A's give the individual an advantage, those offspring with 3A will succeed

---

[1] Osler, W., *The Principles and Practice of Medicine*, 1904.

best, and so will have the best chances of producing offspring in their turn. In the next generation we might conceivably get individuals with 6A+4X. In any case, if selection went on in favour of A for a large number of generations, it would seem that we ought theoretically to end with 10A. Without selection, however, the chances of A being preserved are exceedingly small. Even supposing a large proportion of the entities were represented by the variation A, and some other favourable variation B were the subject of selection while A ceased to be the subject of selection, A would certainly be eliminated in favour of B.

Thus, there does not appear to be any material objection to the assumption that individual chromosomes or parts of chromosomes represent individual variations, and on this hypothesis *the effect of bi-parental reproduction must be to eliminate all those variations which are not the subject of selection.*

This problem—the effect of bi-parental reproduction—has been approached in quite a different way, and similar conclusions have been arrived at by Archdall Reid.[1] He begins by citing examples which must have come within the experience of every one. He points out that the offspring of parents differing from each other materially, are generally more like the average of the race than like either of the parents. "The exceptional peculiarities of the parents tend to disappear." If two people both possessing the same peculiarity mate, however, "the children tend to inherit the progressive variations which the parents possess in common." If varieties or species are crossed, instead of new variations being produced, there is generally a great tendency towards reversion, that is, to the non-appearance of some of the characters of one or both parents. If a Burchell zebra is mated with a horse, "some of the hybrids in make and disposition strongly suggest their zebra sire, others their respective dams, but even the most zebra-like in form are entirely unlike their sire in their markings. It is not a matter of taking after the

---

[1] *Principles of Heredity.*

grandparent, but after an ancestor thousands of generations removed, an ancestor probably far more like the Somali than any of the Burchell zebras."[1] This is only one among many examples which all tend to show that the effect of bi-parental reproduction is generally markedly the reverse of the production of new variations. Usually any great variations would interfere with the adaptation of the organism to its environment. Natural selection, therefore, must tend to eliminate great variations as a rule. Bi-parental reproduction tends to plane away all those variations which are not the subject of selection, or which are not present in both parents. The tendency to large variations being itself a variation—for it is not probable that all individuals will tend to vary to the same extent—this character must be just as much the subject of selection as are other characters, and as the environment does not generally change rapidly, natural selection usually chooses those individuals which exhibit only small variations. It would appear then that "under conditions of Natural Selection, bi-parental reproduction insures that all evolution shall be on lines of small variations, not on lines of great abnormalities."[2]

The conclusion arrived at is, that bi-parental reproduction "is an exceedingly effective device to assist and direct the retrogression which is the necessary result of development by recapitulation; for unlike the latter, it is selective in action. It eliminates as a rule only useless variations. . . . Bi-parental reproduction, indeed, is only another name for bi-parental selection."[3]

Other writers have arrived at the conclusion that bi-parental reproduction does not cause variations. "Variability is not a product of bi-parental inheritance. . . . Whatever be the physiological function of sex in evolution, it is not the production of greater variability."[4]

---

[1] *Penicuik Experiments*, p. xii.

[2] Archdall Reid, *op. cit.*

[3] *Ibid.*

[4] Pearson, Karl, *Grammar of Science*, 1900.

Considering the matter in its general aspect, we are obliged to fall in with the suggestion conveyed by the distribution of the chromosomes in fertilisation. Under natural conditions, that is, where there is no artificial intervention with regard to the selection of the parents, the most numerous offspring will tend to be produced by the best generally equipped males and the most attractive and best-equipped females. The result, therefore, will be the tendency to perpetuate in the race those characters possessed by individuals varying in these directions. Besides the variations in these directions, variations in other directions will certainly occur. Some of these variations will be advantageous to the individuals possessing them. They will be transmitted to the offspring in a greater or less degree. Those which inherit the advantageous character with a variation towards an increase, will have an advantage over those offspring which inherit with a variation in the opposite direction, and a still greater advantage over other individuals in the race which do not possess the character at all. Thus natural selection will perpetuate the advantageous characters, and will increase each of them according to the stringency of the selection. Some other variations will not be advantageous, and therefore will not be subject to selection, but will tend to be eliminated in a comparatively short time. It is improbable that a variation which is not the subject of natural selection will be present in both parents. It is still less likely that such a variation will be present, both in the offspring of these parents, and in the individuals with which these offspring pair in their turn. Thus, all characters not the subject of selection must tend to be eliminated by bi-parental reproduction through a process of swamping. Bi-parental reproduction, in fact, tends to eliminate individual variations whatever they may be ; while natural selection tends to preserve such individual variations as give their possessors an advantage over their fellows. In a sense, bi-parental reproduction and natural selection are working against each other, bi-parental reproduction tending to eliminate individual variations, natural selection tending to preserve those that are favourable. What we should expect according to this theory is, that only such characters would be perpetuated as are the subject of natural selection, and that as soon as they cease to be subjects of selection they would tend to disappear. This we find is actually the case.[1] To take a very crude example: a child is born with six digits on the hand instead of five. There is very little chance that this child will mate with another individual also possessing six digits. If it does not, this character will be diluted in the offspring. Some of the offspring may again possess six digits, but there is just as little chance that they will marry other individuals with six digits, so that this variation is certain to be eliminated sooner or later, as it is not an advantage to the individual or a subject of natural selection.

According to this theory, the mean characters of the race should be more uniform where the individuals travel long distances and spread over large areas of country; where, in fact, there is less chance of mating between near relations, and a better chance of a general mixing of the individuals of the race. On the other hand, where individuals remain in the place where they are born and do not travel, marked differences should appear between races that obviously have had a common and comparatively recent origin. This we find to be the case. The snails in Madeira, for instance, vary in almost every different valley. They are hermaphrodites, and moving very slowly and for short distances only, probably do not travel out of their own valley. Every individual is capable of fertilising every other individual, and so inbreeding must occur to a very considerable degree. The result is, that in comparatively few generations, the snails in one valley have become differentiated from those in the next valley. On the other hand, among mammals ranging over considerable areas the characters are more uniform, and in order to find varieties in the same species, we

---

[1] See p. 66.

generally have to go to entirely different districts where different conditions prevail, and often to districts which have been cut off from each other geographically for a very long period of time.

We have also very good evidence to show that as soon as a structure or character ceases to be useful to the race it tends to disappear.[1] This means that when a character ceases to be the subject of selection it will be eliminated, the time during which it will be retained apparently being proportionate to the period during which it has existed among the ancestors of the organisms.

We meet with statements that races of domestic animals reproduce themselves with great uniformity if inbred, but that "the moment one mixed up two different races, strains, or breeds, one did something that was difficult to put in words, but the result was what has been best described as an 'epidemic' of variations."[2] To begin with, variations occur so frequently in inbred races of domestic animals, that it is difficult for the standard to be kept up in many cases. It is only maintained by rigid selection. Of course when two different breeds are crossed, the offspring vary from each other and from their parents enormously. This is what one would expect, for the newly acquired characters of the two parents are peculiarly liable to regression, and when two different sets of newly acquired characters are mixed, it is likely that many will disappear, and any characters between those of the common ancestor of the two parents and those of the two parents themselves may appear in the offspring. There is, however, nothing to suggest the appearance of an unusual number of *new* variations.

Lastly, we have the fact that variations occur in parthenogenetic and in unicellular forms, where bi-parental reproduction does not occur.[3]

---

[1] See p. 66.

[2] Cossar Ewart, "Discussion on Heredity in Disease," in *Scottish Medical and Surgical Journal*, 1900, iv. p. 308.

[3] See p. 60.

The light thrown by these considerations upon the difference in the histories of inherited characters in natural and in domesticated races is of the utmost importance. It is quite evident that in domesticated races the influence of bi-parental reproduction is partly eliminated. Man generally selects animals and plants to breed from which possess, in a marked degree, the characters which he desires to perpetuate. The characters selected by man need not be of any advantage to the individual, and the normal action of bi-parental reproduction is done away with. Thus in domesticated races we find that natural selection, the necessity for adaptation, and the normal action of bi-parental reproduction are all interfered with, while in natural races these are the factors that have influenced the variations always occurring in all kinds of organisms, and that have brought about evolution. In bi-parental reproduction, then, instead of a cause of progressive variations, we find an explanation of regressive variations. It is by this means that all useless variations are eliminated. The bulk of the characters of a new individual must, under the influence of bi-parental reproduction, be limited to those that are common to the race. Even these tend to be eliminated unless they are preserved by the continuous action of natural selection. All progressive variations occurring in an individual tend to be eliminated rapidly unless they are advantageous, in which case they are preserved by natural selection. Hence it would seem that very few characters are inherited from the parents and immediate ancestors; on the contrary the overwhelming bulk of characters appearing in any individual are the heritage of the race, and are derived from comparatively remote ancestors.

CHAPTER IX

Environment as the cause of acquired characters but not of inborn variations—Discussion of so-called inherited diseases—Cases claimed as proving the transmission of acquired characters—Acquired immunity and inborn immunity — Brown-Séquard's experiments — The inheritance of instincts — Social bees and ants—Effect of illness upon growth—Favourable conditions cause degeneration—Stringent selection causes improvement—The case for the transmission of acquired characters—Environment causes selection—Lamarckian explanation of immunity—Natural selection of inborn variations is a question of adaptation to the environment—Lamarckian explanation of the production of physical characters—Inborn variations arise in the germplasm—Conclusions.

THE action of the environment upon an organism has been claimed by some writers as the cause of variation in its offspring. In considering this question it is necessary to have a very clear idea of what it means. We have seen that the environment may produce very great modifications in the individual. These modifications are acquired characters, and appear in the individual at different periods of its life, in response to stimuli from without. They are not inborn characters, and unless the necessary stimulus is applied, they will not appear. Variations, however, are inborn, that is, they are present in the germ cells, and appear independently of any stimulus. In other words, the inborn characters of the individual are not dependent on the environment, unless indeed the environment is such as to kill the organism. All the environment can do is to modify the inborn characters. Some stimuli may add to the inborn characters. Use will develop the muscles and other tissues in man and other mammals. Long exposure to a tropical sun will bronze a European, and this may be carried to such a length that the skin may not lose its pigmentation even after many years subsequently spent in a temperate climate. Other stimuli may take away from the inborn characters. Apart from the mutilations due to accident or design, the development of the organism may be interfered with in some way. Many deformities are due to this cause. The case of a child born with several fingers missing, may be just as much the result of an accident as the case of a man having several fingers crushed in a machine. These are all acquired characters.

The environment, then, is certainly the direct cause of acquired characters in the individual. How is it possible for the environment to cause inborn variations, that is, changes in the germ cells? In only one way — through the parent. The changes produced in the parent by the environment must react upon the germ cells and produce modifications in them. Unless this occurs, the environment can have nothing to do with the production of inborn variations. It is quite evident that the germ cells are dependent upon the organism in which they exist for sustenance, so that if the organism dies the germ cells contained in it will also die very shortly, but beyond this it would appear that the production of changes in the germ cells through changes in the organism containing them involves the transmission of modifications in the parent to the offspring. We are thus brought to the consideration of a controversial question; for if inborn variations are due to the action of the environment upon the parents, then acquired characters are transmitted to the offspring. Moreover, they are transmitted, not as acquired characters, but as inborn characters. The acquired characters of the parent must, in fact, be transmuted into inborn characters in the offspring.

There are cases of chronic alcoholism where the effect of partial poisoning may be produced on the germ cells through the parent. Here, however, if any effect from the poisoning is produced in the offspring, it does not involve the transmission of special modifications produced in the parents, but it is due to the direct action of the poison upon the germ cells themselves. We must seek for evidence of quite another kind for the transmission of parental acquirements.

In considering the evidence available with regard to the effect of the environment upon the characters of the individual, we find at once that very marked changes are often produced. Nägeli took some Alpine plants and placed them in rich soil, under the usual conditions of cultivation, in the Botanical Gardens at Munich.[1] The plants thus removed from their normal environment changed in their characters so enormously that they would not have been recognised. The seeds of these plants grown in the Botanical Gardens reproduced the acquired characters of their parents, and this went on for about thirteen years. When, however, the plants were removed to poor and stony soil, the acquired characters disappeared, and the seeds of the plants in the Botanic Garden grown in a poor and stony soil exhibited none of the acquired characters of the parents but only those of the original Alpine ancestors. There was no question of the acquired characters disappearing gradually in succeeding generations under the normal conditions of Alpine plants ; only the inborn characters appeared, and the characters produced by the environment left no trace whatever even for one generation. Here we obviously have a very good illustration of the effect of the environment upon the characters of the individual, but no evidence whatever that the modifications acquired by a change in the parental environment produce any effect upon the germ cells. If the offspring were grown in the environment that had produced the acquired characters in the parents, the same result was produced, that is, the offspring acquired similar characters to those acquired by the parents under similar stimuli. All that was proved was that the offspring inherited the inborn capacity possessed by their parents for making certain acquirements.

Some diseases are often spoken of as being inherited. The only evidence available on this point shows very

---

[1] Nägeli, C. von, *Mechanisch-physiologische Theorie der Abstammungslehre* Munich and Leipzig, 1884.

definitely that the ovum or sperm may be infected with a parasitic micro-organism; that the ovum may be infected after fertilisation; and that the embryo may be infected before birth. Thus with syphilis the micro-organism of the disease (a spirochete) may have found its way into the sperm cells of the male parent, or into the ova of the female parent. That this is the case, is shown very clearly by the fact that a woman may bear a syphilitic child without exhibiting any of the symptoms of the disease herself. In any case, there is not a shadow of evidence to support the view that the disease acquired by the parents is transmitted to the offspring. What the evidence shows is, that the ovum, or sperm, or embryo, is directly infected by the spirochete.

The cells of *Hydra viridis,* a very simple multicellular animal living in fresh water, contain a large number of minute green bodies. These are *Algæ,* unicellular plants. Now these *Algæ* are present in the eggs of *Hydra* before the organism begins to develop, but they are not present in the earliest stages of the maturation of the egg. As the cells of *Hydra* multiply, so the *Algæ* multiply and live within them. This case affords an excellent illustration of the way in which ova or sperms may be infected with the parasites of disease, although the presence of the *Algæ* in the cells of *Hydra* cannot be regarded as a disease, as they do no harm to the animal.[1]

A case which seems to suggest a definite influence of the environment upon the germ cells has been recorded in some experiments upon a species of *Daphnia,* a minute crustacean living in fresh water. Salt was gradually introduced into the water in which the *Daphniæ* were living. In forty-five days the water contained 1·5 per cent. of salt, and at this time all the adults died. Some of the eggs, however, continued to live, hatched out, and the offspring did well.[2] At first sight it would appear that the probable explanation of

---

[1] Zeigler, H. E., *Die Vererbungslehre in der Biologie,* Fischer, Jena, 1905.

[2] Packard, A. S., "On the Inheritance of Acquired Characters in Animals with a Complete Metamorphosis," *Proceedings of the American Academy of Science,* xxix., 1894.

this result is, that the eggs became gradually accustomed to the salt, and that the capacity to live in this new environment was due to a direct action upon the germ cells while in the parent. Upon considering the matter more carefully, it becomes evident that as the eggs were capable of development as soon as maturation had occurred, that is, before the death of the parent, the acquirements may have been made entirely by the new generation, and certainly were not made by parents, as they all died.[1] Again, there is apparently no record in the experiment as to what proportion of eggs survived, and so the result was most likely due entirely to the selection of an inborn variation occurring in a certain percentage of the eggs, which variation was towards tolerating a certain amount of salinity. It may be in this case that some of the ova, which of course were new individuals capable of making acquirements on their own account, acquired the capacity for living in a salt solution. The selection of the inborn variation towards adaptation to the new environment seems a more probable explanation. As the parents were killed by the new environment, there is not the slightest evidence that an acquired character was transmitted, or that the effect of the environment upon the parents produced any modification in the germ cells.

It has been claimed that the results of certain experiments with unicellular forms afford evidence for the transmission of acquired characters. Certain pigment-producing bacteria, when subjected to a temperature a little less than that sufficient to kill them, lose the character of producing pigment, and the immediately succeeding generations are perfectly colourless. After a varying number of generations the power of pigment production is regained. The number of generations that do not produce pigment seems to be proportionate to the severity of the treatment.[2]

---

[1] As the great majority of *Daphniæ* are reproduced parthenogenetically (see p. 28), it is probable that the eggs must be regarded as separate individuals at a very early stage.

[2] Adami, J. G., "An Address on Theories of Inheritance with Special Reference to an Inheritance of Acquired Conditions in Man," *Brit. Med. Journ.*, June 1, 1901.

It is doubtful whether an effect of this kind in unicellular forms can be compared to the inheritance of characters in multicellular forms. In no bacilli is there any differentiation between somatic and germinal tissue, nor do we know anything with regard to their multiplication beyond the fact that they reproduce by simple division and budding. According to Bütschli and Minot's theory[1] a swarm of unicellular forms between the periods of conjugation may be regarded as corresponding to the soma of a multicellular organism. Looked at in this light, the continuation of an acquired character during several generations of bacilli in which no conjugation has been demonstrated affords no evidence one way or the other that any effect has been produced upon the germplasm. On the other hand, with regard to some unicellular animals, certain cases which are cited as examples of the inheritance of acquired characters seem to afford evidence of quite a contrary kind.

Several tropical diseases, among them sleeping sickness, are caused by minute unicellular animals called trypanosomes. An arsenic compound, atoxyl, has been found to destroy these parasites when injected into the animal in which they are living, and to cause their disappearance, temporarily at any rate, from the blood. It has been found that strains of trypanosomes obtained from animals that have been treated with atoxyl and have subsequently relapsed, are highly resistant to it. In fact, in some cases, a strain of trypanosomes entirely resistant to atoxyl has been produced. The explanation has been offered that this resistance to atoxyl is due to the transmission of an acquired character. The trypanosomes have gradually become used to the atoxyl and have developed resistance to it, which they have handed on to succeeding generations.

Some animals are much more resistant than others to trypanosomes, and if a strain be taken from an animal which is comparatively resistant, it is found to have in-

---

[1] See p. 5.

creased in virulence. The ordinary course of the disease is as follows. First there is a certain incubation period, that is, a period between the inoculation with the trypanosomes and their appearance in the blood. Then a short period during which the trypanosomes are more or less numerous. They then disappear again, and after a period they reappear. These relapses continue at varying periods until the animal dies. For instance, in rats inoculated with *Trypanosoma gambiense*, the ordinary course of the disease without treatment is from two and a half to four and a half weeks, often with three relapses and terminating in death. The probable explanation of these relapses is that they form the crises in a struggle between the trypanosomes and the animal in which they are living. At one time the reaction of the organism is sufficient to almost exterminate the trypanosomes. The few trypanosomes that survive, however, are the most resistant, and these give rise to a fresh generation with a higher mean of resistance than the preceding. Some individuals will vary towards a greater, some towards less resistance than their parents. Those that vary towards less will be killed by the environment. A further reaction takes place, and the same thing happens again. The trypanosomes almost invariably win in the end. If this explanation is correct, we ought to find that the strain of trypanosomes successfully inoculated into highly resistant animals is subsequently virulent to animals that are less resistant. The baboon is highly resistant to *T. gambiense*, and the following experiment shows how the strain of trypanosomes passed through it gained in virulence.[1] The baboon was inoculated on 21st August. Parasites were first seen on 1st October, disappeared, and reappeared on 4th October; death occurred on 10th October. At death no trypanosomes were found in the blood, but a rabbit was inoculated with it. Twenty-three days afterwards parasites were found in the rabbit, and other animals were inoculated from it. The ordinary period of

---

[1] Thomas and Breinl, *Liverpool School of Tropical Medicine*, Memoir XVI. October 1905.

incubation in rabbits is from five to fifteen days, so that in this first inoculation from the baboon the incubation period was greatly lengthened. This would suggest that though, as was subsequently shown, the strain of parasites introduced was far more virulent than usual, very few can have been introduced into the first rabbit, and so a longer time was taken for them to multiply sufficiently to be apparent in the blood. The animals subsequently inoculated from this rabbit very often showed parasites in their blood in two days, and death frequently occurred as early as the fifth day; whereas the average period at which death occurs in rabbits inoculated with *T. gambiense* is from four to sixteen weeks after the first appearance of the parasites in considerable numbers.

Some other monkeys (*Cercopithecus callitrichus*) were inoculated with *T. gambiense* on 5th October 1908.[1] This kind of monkey is resistant to the disease and sometimes recovers. From 21st October to 24th October trypanosomes were present in scanty numbers in the circulation. They disappeared and reappeared on the 31st, and continued until the 8th November. From this date no more appeared until 18th December, when they were present in scanty numbers in one of the monkeys. Two rats were inoculated from this monkey on this date (18th December), and died with numerous trypanosomes on the 24th. Three rats inoculated from one of these on the 24th, showed numerous trypanosomes on the 28th, and were then treated with atoxyl. Four rats inoculated from one of the latter on the 28th showed numerous trypanosomes on the 30th; that is, two days after inoculation. Another of the monkeys in this experiment showed a relapse much later than the first one, and rats inoculated from it died in three days. The rat from which the monkeys were originally inoculated lived from 10th September, when it was first inoculated, until

---

[1] The details of these experiments performed in the Runcorn Research Laboratory, Liverpool School of Tropical Medicine, were kindly given to me by Mr. E. Hindle. They are not as yet published.

8th October. It had three relapses, and only on 6th October were the parasites at all numerous.

Now, were the increased resistance of the trypanosomes due to immunity acquired by the individuals and transmitted by them to their offspring, there should be a steady increase in the numbers of trypanosomes present in the blood of the infected animal, due to the gradual increase in immunity of the individuals, which is never lost but is handed on to the offspring. This is not what happens. If, however, we accept the explanation offered by the transmission of inborn variations in the presence of a stringent selection, the case is met perfectly. The individual trypanosomes must vary among themselves as to their resisting power to the new environment when transferred from the rat to the monkey. Only those most resistant will survive, and according to the results of the experiment but few were able to survive. These multiplied, and the offspring varied, some towards greater, some towards less resistance. Only the former survived, and the same thing went on from generation to generation, until the trypanosomes were sufficiently numerous to cause a reaction in the monkey. Selection then became more severe, and hardly any trypanosomes were able to survive. The same thing happened again at intervals, the culminating points in the struggle being marked by the relapses in the monkey. When eventually this highly resistant strain was again transferred to the more favourable environment in the rat, they flourished in an extraordinary manner, and were fatal to the rats in a far less time than was the strain of trypanosomes that had not been subjected to this selection. The most virulent strain of trypanosomes was obtained from the monkey that showed the greatest power of resistance.

This explanation may be applied with equal or greater success to the case of trypanosomes that have become resistant to atoxyl. The effect of atoxyl is at first to lengthen the period between the relapses, and to cause the trypanosomes to be less numerous at these periods. At each relapse, however, the atoxyl produces less and less effect, until it makes no difference. When this strain of trypanosomes is inoculated into another animal, it is insusceptible to the action of atoxyl from the first. The only difference between this and the results of inoculating a highly resistant animal is, that the selection is for resistance to atoxyl. There is no evidence that the individual trypanosomes ever acquire resistance to atoxyl. What the temporary disappearance of the parasites from the blood suggests is that all those that are not naturally resistant are killed, and the production of an immune race is due to the selection of inborn variations towards immunity.

Some experiments performed by Brown-Séquard provide evidence of quite a different kind.[1] Sir E. Ray Lankester says: "The one fact which the Lamarckians can produce in their favour is the account of experiments by Brown-Séquard, in which he produced epilepsy in guinea-pigs by section of the large nerves or spinal cord, and in the course of which he was led to believe that in a few rare instances the artificially produced epilepsy was transmitted."[2]

It is impossible here to go into the details of these experiments and of the results obtained. The following brief account may give a general idea of what happened. In a few cases the offspring of guinea-pigs that had been rendered epileptic by operations upon the spinal cord and

---

[1] Brown-Séquard, "Nouvelles Recherches sur l'Épilepsie due à certaines Lésions de la Moelle Épinière et des Nerfs Rachidiens," *Arch. Physiol. Norm. Path.*, ii., 1869; "Faits nouveaux concernant la Physiologie de l'Épilepsie," *Arch. Physiol. Norm. Path.*, iii., 1870–71; "Remarque sur l'Épilepsie causée par la Section du Nerf Sciatique chez les Cobayes," *Arch. Physiol. Norm. Path.*, iii., 1870–71; "Quelques Faits nouveaux relatifs à l'Épilepsie qu'on observe à la Suite de diverses Lésions du Système Nerveux chez les Cobayes," *Arch. Physiol. Norm. Path.*, iv., 1872; "Transmission par Hérédité de certaines Altérations des Yeux chez les Cobayes," *Gaz. Médicale de Paris*, 1880; "Faits nouveaux établissant l'extrême Fréquence d'États Morbides produits accidentellement chez des Ascendants," *Comptes Rendus Acad. Sci.*, Paris, vol. xciv., 1882; "Hérédité d'une Affection due à une cause accidentelle, Faits et Arguments contre les Explications et les Critiques de Weismann," *Arch. Physiol.*, xxiv., 1892; "Transmission Héréditaire de Caractères acquis," *Arch. Physiol.*, 1893.

[2] *The Advancement of Science*, 1890.

various nerves, also suffered from epileptic fits. In some other guinea-pigs, in which a large nerve in the hind limb (sciatic) had been divided, the animals gnawed off two or three toes, which had been rendered insensitive by the operation. In some of the offspring of these guinea-pigs two or three toes were absent. The results obtained by Brown-Séquard himself were partially confirmed by some of the assistants in his laboratory during the same period. When, however, Sommer repeated several of these experiments he obtained quite different results.[1] He did similar operations upon similar nerves, and produced epileptic fits in the animals he operated upon, but in no case did epilepsy or any other defect such as those described by Brown-Séquard and his assistants, appear in the offspring of these guinea-pigs. Certain remarks made by Professor T. H. Morgan are very suggestive with regard to some of the results in these experiments.[2] "While carrying out some experiments in telegony with mice, I found in one litter of mice that when the young came out of the nest they were tail-less. The same thing happened again when the second litter was produced, but this time I made my observations sooner, and examined the young mice immediately after birth. I found that the mother had bitten off, and presumably eaten, the tails of her offspring at the time of birth. Had I been carrying on a series of experiments to see if, when the tails of the parents were cut off, the young inherited the defect, I might have been led into the error of supposing that I had found such a case in these mice. If this idiosyncrasy of the mother had reappeared in any of her descendants, the tails might have disappeared in succeeding generations. This perversion of the maternal instincts is not difficult to understand, when we recall that the female mouse bites off the navel-string of each of her

---

[1] Sommer, Max, "Die Brown-Séquard'sche Meerschweinschenepilepsie und ihre erbliche Uebertragung auf die Nachkommen," *Aus der psychiatrischen Klinik der Universität Jena*, 1900.

[2] Morgan, T. H., *Evolution and Adaptation*, New York, Macmillan Co., 1903.

young as they are born, and at the same time eats the after-birth. Her instinct was carried further in this case, and the projecting tail was also removed. Is it not possible that something of this sort took place in Brown-Séquard's experiment? The fact that the adults had eaten off their own feet might be brought forward to indicate the possibility of a perverted instinct in this case also."

Again, there is some evidence which indicates that in epilepsy a poison is produced in the body of the diseased animal which, when injected into healthy animals, causes convulsions.[1] It is thus possible that the embryos of the guinea-pigs, in which epileptic fits had been produced by operations upon various parts of the nervous system, absorbed toxins from the maternal circulation. It is also possible that such a poison may have acted directly upon the germ cells before fertilisation. This is the more probable because "the conditions exhibited by the offspring were very diverse—general feebleness, motor paralysis of the limbs, trophic paralysis resulting in loss of toes, cornea, &c., other nervous and sensory disorders, and in some cases the particular 'epileptic' state. In a number of cases the condition of the offspring was so different from that of the parent, that the only common feature was that in both cases there were abnormal neuroses."[2]

The extraordinary instincts observed among insects have been brought forward in support of the theory that acquired characters are transmitted.[3] The instincts of *Ammophila* and *Sphex*, two genera of fossorial wasps, have been given as particular cases. The larvæ of *Ammophila* feed upon caterpillars, those of *Sphex* upon crickets and grasshoppers which are supplied by the female. In both cases the female

---

[1] Voisin and Peron, *Archives de Neurologie*, xxiv., 1892, and xxv., 1893; Voisin, *L'Épilepsie*, Paris, 1897.

[2] Thomson, J. Arthur, *Heredity*, 1908. The excellent description and criticism of Brown-Séquard's experiments in this work have been freely drawn upon in the account given here.

[3] Lord Avebury, *On the Senses, Instincts, and Intelligence of Animals, with Special Reference to Insects*, London, 1888.

wasp first makes a nest, then drags the prey into it and lays her egg or eggs upon the animals which are destined to provide food for the larvæ when they hatch out. The female then seals up the nest and does not visit it again. Now, in providing the food supply for the future larvæ, several extraordinary instincts come into play. It is necessary that the caterpillars, crickets, and grasshoppers should be paralysed when they are caught, otherwise the wasp would have tremendous difficulty in conveying them to her nest, for frequently the prey is much larger than the wasp. Again, when the larvæ are hatched out, they are very delicate in structure, and if these comparatively large animals were able to move about freely they would probably kill the larvæ instead of providing them with food. On the other hand, if the prey were killed outright by the wasp when caught, decomposition would set in in a few hours, and thus the provision made by the female wasp would be useless to the larvæ. This difficulty is, however, overcome by the wasp. When *Ammophila* catches a caterpillar she stings it in each of the segments of the body. In the caterpillar there is a separate nervous centre (ganglion) in each segment, and if only one or two were stung, the other segments would still be able to move quite freely. In the prey of *Sphex*, however—grasshoppers and crickets — there are three separate nervous centres (ganglia) which control the movements of the animal. These are situated in the thorax, and when the *Sphex* catches her prey she stings it in these three separate ganglia. The result of this is that the prey is rendered unable to move, but is not killed. Fabre, who first described these phenomena,[1] was at first unable to understand how it was that the prey he found in the nests of these fossorial wasps did not decay, but he subsequently showed exactly what happened by some very ingenious experiments.

---

[1] Fabre, J. H., *Souvenirs Entomologiques*, Paris. English translation of first series *Insect Life* (Macmillan, London, 1901) contains account of Ammophila and Sphex.

He took some of the crickets and introduced poison into their bodies with a needle. When this was done indiscriminately, that is, in no particular part of the animal's body, it either killed the animal or produced very temporary results, according to the amount of poison introduced. When, however, he introduced the needle into the three nervous centres (thoracic ganglia) which control the movements of the insect, he found that complete paralysis ensued. More than this the metabolism was checked, and the paralysed insect continued to live without food for several weeks, which it certainly could not have done under normal conditions. An interesting point about this instinct of *Sphex* is that the prey is stung at one particular point where the tissues are soft and the nerve centres are easily reached from the surface. Much the same thing happens in the case of *Ammophila* and its prey the caterpillars, only here the wasp has to apply its sting many times, so that all the middle segments at least of the animal's body are paralysed.

Now the supporters of the theory that acquired characters are transmitted say that it is impossible to account for the origin of these instincts in any other way than that the ancestors of the existing wasps first exercised a certain amount of intelligence. A wasp found that when it stung a grasshopper in a particular place, that grasshopper was paralysed and was much more easily carried to the nest. It remembered this, and led by past experience, always stung its prey in the same place. This habit produced an effect on the germplasm, and the offspring tended to sting their prey in the same manner until the instinct became established, and so no longer depended upon the intelligent action of the wasp. This interpretation, however, appears to break down when carefully considered. To begin with, it assumes that intelligent action preceded instincts. We find that the higher we go in the animal kingdom, the fewer the instincts and the greater the intelligence. We only find intelligent action as a very late product in evolution. To place intelligent action before an instinct, in fact to derive instincts from intelligent actions, seems to be placing the cart before the horse. Another very important point is that the capture of the grasshoppers, crickets, and caterpillars, paralysing them without killing them, and storing them in the nest, is not of the slightest use to the individual wasp. It simply provides food for the larvæ which the wasp will never see, and of whose needs it can have no experience. This interpretation, in fact, attributes to the wasp a prophetic knowledge with regard to subsequent events, of which neither it nor any of its ancestors have had any experience.

Other investigators since Fabre have provided us with a great many more details with regard to these wasps. Apparently they are not by any means uniform in the skill which they exhibit in paralysing their prey. Very often they kill the prey outright, so that it decomposes in the nest. At other times, the paralysis is not at all complete, and the prey exhibits active movements.[1] Thus, it is evident that the larvæ of those individuals in which the instinct is most perfect will probably supply the bulk of the individuals in the next generation, and they will have a greater chance than any other individuals of inheriting the instinct in its fully developed form. There is thus a stringent selection with regard to this instinct, which explains how it is maintained at a high standard by the action of the selection upon inborn variations. Individuals that do not inherit the instinct in its fullest form will stand a very poor chance of producing offspring in a manner likely to ensure their survival in comparison with those that inherit it fully or vary towards greater perfection. The origin of the instinct is equally satisfactorily explained by the action of natural selection upon inborn variations.

Many of the instincts of insects do not benefit the indi-

---

[1] Peckham, G. W. and E. G., "On the Instincts and Habits of the Solitary Wasps," *Wisconsin Geological and Natural History Survey*, Madison, Wis., U.S.A., 1898; *Wasps Social and Solitary*, Boston and New York, 1905.

vidual in any way. Indeed the insect can have no experience of the results produced, for the results of the instinct frequently occur after the death of the individual which has performed the instinctive action. The benefits are confined entirely to the offspring; the general result is to ensure the preservation of the race, not in any way to benefit the individual, and it is inconceivable that they can have originated in individual acquirements.

Perhaps the strongest argument that can be brought against the inheritance of acquired characters is that of social bees and ants. In bees and ants some of the eggs are destined to produce males and some females. Among the larvæ hatching out from the eggs destined to produce females, two or three in each colony are specially fed by the workers. These individuals develop into functional females which have been called "Queens," and which lay the eggs that produce the future generation. The other eggs produce larvæ that are potentially females, but are not thus specially fed, and become workers. The workers do not usually lay eggs, and in them sex normally never becomes functional. They have on this account been called neuters. In quite exceptional cases, where the queen or queens have been destroyed by some accident, a few workers may lay eggs which produce only males. Such a nest always dies out eventually, and this laying of eggs on the part of the workers must be regarded as an abortive attempt to continue the life of the colony. Now, all the complicated instincts exhibited in the social life of bees and ants, which have, by the perfect organisation resulting from them, excited the admiration of naturalists for several generations, are possessed in the great majority of social bees and ants only by these neuter individuals. Neither the queens nor the males show them, yet it is only the queens and the males that contribute towards the production of the next generation. Whatever inheritance of instinct there may be, must be through the queens and the males; that is, therefore, through those individuals of the colony which do not exhibit these instincts at all. These facts make it perfectly apparent that the instincts must be due to inborn variations entirely, and not at all to acquired characters, for the individuals through which they are invariably transmitted do not possess them, and so certainly have made no acquirements in that direction.[1]

Nor are instincts the only characters transmitted through individuals that do not possess them. The same thing happens with regard to very striking physical characters. The soldier ant in the case of true ants is an example. The soldier ants are neuters, and in them the head is greatly enlarged, as also are the mandibles. Various parts of the body coverings are modified, and serve the purpose of defence. In fact the soldiers of the colony are so different from their parents, the males and queens, that the untrained observer would class them as belonging to a different family.

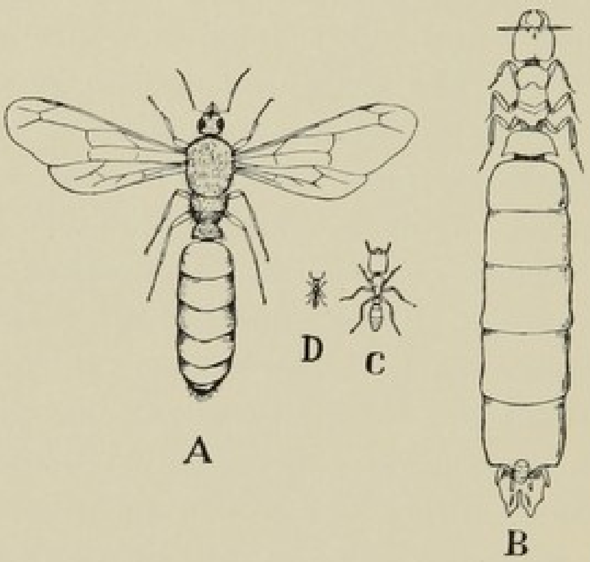


FIG. 19.—A. Male of *Typhlopone*, formerly classed in a separate genus (*Dorylus*). B. Female, formerly classed in a separate genus (*Dicthadia*). C. Neuter soldier (worker). D. Neuter minor (worker). [Actual size.]

---

[1] The bearing of the cases of neuter insects upon the theory of Lamarck was briefly referred to by Darwin in the first edition of the *Origin of Species*, 1859. Attention was drawn to this suggestion of Darwin's by Professor Poulton in *Essays on Evolution*, p. 165, where he expressed surprise that after advancing so forcible an argument Darwin had apparently admitted the transmission of acquired characters. These are the only two cases I have been able to find in which this argument has been brought forward.

In some ants, such as the driver ants of Africa (*Typhlopone*), the physical differences between the queens and neuters is so great, that even trained entomologists have been misled, and have classed them as entirely different insects. Thus the queen, the male, and the worker of *Typhlopone* are now known, but until comparatively recently the queen was put in one genus (*Dicthadia*), the male in another (*Dorylus*), and the worker in yet another (*Typhlopone*), and this mistake was made by skilled entomologists, who were misled by the enormous difference in the structure of the three kinds of individual. The male has well-developed eyes, while the worker has none (Fig. 19).

The polymorphism among social ants and bees has been the subject of much argument, and has produced a great deal of speculation.[1] We are not here concerned with such questions as how polymorphism has arisen. It is sufficient to emphasise the fact that the potentiality of producing the various morphological characters peculiar to the different forms of workers, to the males, and to the queens, must be present in the eggs of the queen, though neither she herself nor any direct ancestor has possessed those that appear regularly in the workers.

Among the honey ants (*Myrmecocystus*) some workers are used by the others as reservoirs for honey. These individuals remain in the nest, clinging to the roughened ceilings of certain galleries. In the other galleries the ceilings are smooth. They remain in this position for the rest of their lives. Beforehand, they feed on honey for some time, and when they have eaten as much as they can, take up their positions in the nest. Here the other ants feed

---

[1] Wheeler, W. M., *Ants: Their Structure, Development, and Behaviour*, New York, Columbia University Press, 1910; Escherich, K., *Die Ameise. Schilderung ihrer Lebensweise*, Braunschweig, Fr. Vieweg und Sohn, 1906; Ihering, H. von, "Zur Frage nach dem Ursprung der Staatenbildung bei den sozialen Hymenopteren," *Zool. Anz.*, xxvii., 4, 1903; Herbst, C., *Formative Reize in der Tierischen Ontogenese*, Leipzig, Arthur Georgi, 1901; Silvestri, F., "Contribuzioni alla conoscenza dei Mirmecofili, *Ann. Mus. Zool. Univ. Napoli*, i. 13, 1903.

them with honey, until they are distended to many times their normal size. Honey is not procurable at certain seasons of the year, and the stored honey is regurgitated by these individuals as it is required to feed the larvæ and workers. It is obvious that nothing of this kind can ever happen to the queen.

Considered from a general point of view, the effect of the inheritance of acquired characters would be to cause improvement in those races which live under favourable conditions; degeneration in those which live under unfavourable conditions. If the struggle amongst individuals of the same species is very slight and there is an ample supply of food for all, if there are no enemies that must be escaped and no hard physical conditions, such as cold, to contend against, the individual organism would develop much better than organisms that did not enjoy these favourable conditions. If the environment of the parents has any effect on the germ cells, conditions which favour the higher development in the parents should react on the germplasm and improve the race. On the other hand, unfavourable environments where the struggle for existence is hard should cause the race to deteriorate in succeeding generations. Such an influence as an infectious disease should react upon the germ cells. Even if the parents survive, the germ cells must be injured in some way by the poison in the parent's body. It is inconceivable that they could be benefited by it. It may be argued that, as the parent acquires a certain amount of immunity, possibly through the production of "anti-bodies" to the poison of the disease, the germ cells may share in acquiring immunity to the poison, and the anti-bodies in the parent organism may act upon them also and render them more immune. Even supposing this happened, it is difficult to see how the whole effect upon the germ cells can be otherwise than injurious. Even a partial poisoning with subsequent recovery cannot do any good, and must also certainly injure the individual. It has been shown that growth and development are temporarily inhibited in children by even slight illnesses.[1] Periodic measurements of the circumference of children's heads have shown that growth may be represented by a curve with a regular sweep, which curve, however, shows checks in the growth exactly corresponding to periods of infantile illness. It is important to note that the arrest "was not made up for by aftergrowths." There is every reason to suppose that as the growth of the skull was checked during these periods of illness, growth in the rest of the body was checked also. In any case an inborn character was modified. This must have been going on ever since man appeared, for hardly any children escape brief periods of illness. We do not find, however, that there is any evidence that this constant and long-continued acquirement has diminished the stature of man, for the most ancient prehistoric remains show that the then existing races were much the same in size as the races existing at the present time.

If the inheritance of acquired characters is usual, we ought then to find improvement in races subject to the most favourable conditions and degeneration in races subjected to unfavourable conditions, for if an unfavourable environment injures the individual from childhood, and the germ cells are influenced by the action of the environment upon the individual, the unfavourable environment must injure the germ cells.

Observed facts seem to contradict this suggestion in the strongest manner possible. In parasites which live inside other animals, the conditions of living are extremely favourable. The parasite has its food supplied to it, and has no enemies from which it is obliged to escape. It would be difficult to imagine conditions more favourable to the wellbeing of the individual. We find, however, that in parasites the tendency to degenerate from the parent forms is universal. While closely allied free living species have complicated

---

[1] Galton, *Inquiries into Human Faculty*, Everyman's Library Edition, pp. 168–69.

appendages useful to them in the pursuit of their prey, and in escaping their enemies, the parasite frequently consists of very little more than a digestive and a generative apparatus. Every other part of its body has degenerated. On the other hand, races subjected to stringent selection show no signs of degeneration. On the contrary they improve from generation to generation in so far at least as to become more resistant to the unfavourable factors in their environment. If they do not, they disappear.

It has been claimed that races of men living in slums degenerate. The slum environment is supposed to react unfavourably upon the parents, and this injures their germ cells, so that the offspring are weakly and degenerate. This is supposed to go on from generation to generation, the race subjected to slum environment deteriorating. In this case it must be realised first of all, that just as with Nägeli's Alpine plants, the children are subjected to the same external influences during their period of growth, and indeed for their whole lives, as were the parents. Therefore it is obvious that they must tend to make the same acquirements as their parents. With regard to the effect upon the race, a recent Royal Commision has collected and considered the available evidence upon this point. One of the conclusions of the Commision is as follows: "Many races have been exposed to one or other of all the ill conditions which have been alleged as causes of filial deterioration. In every case the only apparent effect has been to render these races capable of dwelling comparatively unharmed under such conditions. It is not to be conceived that a race which deteriorates in every generation can emerge from the struggle not weakened but strengthened. Moreover, almost complete disproof of this hypothesis is furnished by the facts submitted to us by the medical investigators."[1] Of all the existing races in

---

[1] *Report of the Royal Commission on the Care and Control of the Feeble-minded*, p. 184. It was subsequently stated in print that the Royal Commission had found evidence to show that degeneration was produced by slum environment. In answer to this, Dr. H. B. Donkin, one of the members of the Commission, wrote as follows to the *Westminster Gazette*, August 22, 1908:

Northern Europe that have been subjected to a slum environment, none have probably suffered more or for a longer time than the Jews. They were kept in slums throughout the Middle Ages until almost modern times. Yet the Jews show no signs of physical deterioration as a race. Jew children are at least as healthy as the children of other races in the north of Europe.

One of the most curious points about the controversy as to whether or not acquired characters are transmissible is, that the majority of the upholders of the view that the acquired characters of the parent are transmitted, either do not take the trouble or are unable to understand the theory advocated by those who disagree with them. The simplest way of making this clear, is to quote from and criticise the very recently expressed arguments and opinions of a well-known upholder of the Lamarckian theory. He quotes the case of certain fishes living in caves where light never penetrates. In these fishes the eyes have disappeared as functional organs, though traces of them remain, showing that their ancestors possessed functional eyes. The writer in question, having said that the followers of Weismann *will not allow that the environment has any share in the production of new characters,* gives the following satirical interpretation of what he believes to be the Neo-Darwinian explanation of the degeneration of the eyes of these fish: "But in this retrogression the circumstance of darkness has no share. It exercises no influence. The retrogression and atrophy of the eyes is a 'spontaneous' variation, or rather it is the consequence of a long series of 'spontaneous' variations all in the same direction, with which the circumstance of darkness has nothing to do. The variation just happens to occur. Natural selection exterminates the individuals with efficient eyes, and by a happy accident 'spontaneous'

"The evidence before us as to the causation of feeble-mindedness gave, as a whole, no support to the popular view of bad hygiene, alcoholism, &c., being in any sense productive of racial or filial degeneration, however harmful such agencies are to the individuals who are subject to them."

variation in the direction of eyes that are less and less efficient happens to take place, until a race of blind animals is 'selected,' that is to say, is allowed to survive."[1] There is no sentence in this with which a Neo-Darwinian would agree. Besides, the whole phenomenon is not a case of natural selection at all, but simply the disappearance of a character which is no longer the subject of selection. As we have already seen, characters disappear sooner or later when they cease to be the subjects of selection.[2] The theory of natural selection does not assume that variations occur all in the same direction. The variations occur in all directions, and it is the environment that determines which of many variations shall be preserved. With the case of the disappearance of the eyes of these fishes natural selection has nothing to do, as there is no evidence that this is a case of reversed selection. The eyes were not injurious, they were merely useless. Within a few lines, however, we have another travesty of the theory that characters are produced by the action of natural selection acting upon inborn variations: "Similarly, the ear happened to be evolved without any reference to, or influence exerted by, the sound waves in the air. Some bones and other structures in the head and neck happened to vary 'spontaneously' in such a way as fitted them to receive the sonorous waves; but in the production of this 'spontaneous' variation the action of the sonorous waves had no share. The same variation would have taken place if there had been no sound waves."[3]

But the real interpretation of those who uphold the theory that acquired characters are never transmitted is somewhat as follows. Some low form of animal, in an early period of evolution, happened to vary in such a way that some part of its body was sensitive to sound waves. This gave it an advantage over its fellows, and it had a longer

---

[1] Mercier, Charles, "The Transmission of Acquired Characters," *The Contemporary Review*, December 1908.

[2] See pp. 66, 131.

[3] Mercier, Charles, *loc. cit.*

time and better chances of producing offspring. The offspring tended to inherit this character, some in an increased, some in a decreased degree. Those that varied towards an increase had still greater advantages over their fellows, and so selection preserved and increased the character until the ear of the mammal was produced. Now according to this view the production of new characters, through the selection of inborn variation, is due entirely to the action of the environment. Variations are always occurring, but by themselves they could do nothing towards evolution. Instead of believing that the environment does nothing towards the production of new characters, the followers of Darwin and Weismann believe that it does everything. *It is the environment that selects the inborn variations, and so the new characters depend upon the environment. Change the environment, and some existing characters must necessarily disappear and some new ones be produced, otherwise the race must be exterminated.*

The most complete misunderstanding of the theory of natural selection is shown in the following passage: "How is it that the immunity to the influence of malaria arises in races that have been long exposed to malaria? *Ex hypothesi,* the influence of malaria in the environment—of Leishman's organism and the mosquito which carries it—has nothing whatever to do with producing immunity. It happens by blind chance that, among the fortuitous variations occurring in the germplasm, there happens to occur a variation that renders the blood in some way antagonistic to this organism. Not only this, but it happens by the same blind chance that, in succeeding generations, many individuals are born with an intensification of this curious variation. The same thing does not occur in other districts, where there is no malaria. . . . Produced sporadically everywhere, it must, on the doctrine of chances, be frequently intensified in the offspring in non-malarial districts, by its accidental presence in both parents; and thus in every place, malarial or non-malarial, there will occur, by the operation of the blindest chance, persons who are partially or wholly immune to the malarial parasite. But this is not what happens. . . . The heritable immunity against these diseases occurs nowhere except among races that have been exposed to their ravages; and yet if acquired qualities are not inherited, the existence of the disease in their environment has no effect whatever in producing this immunity. Such reasoning would not be admitted in any other science."[1]

To those who understand the theory of natural selection, nothing could be more grotesque than this interpretation of it. Variations towards immunity to malaria certainly do occur among races that are never subjected to it, as is shown by the varying susceptibility of Englishmen living in a country where the disease is prevalent, but no race could acquire immunity without selection. The immunity of the race is entirely due to the presence of the disease in the environment. In so far as the development of the new racial character—immunity to malaria—is concerned, there is no "chance," blind or otherwise, about it. With regard to the individual the question is whether he has varied in the right or in the wrong direction. The man who has varied towards immunity transmits his variation with new variations. Some of his children will vary towards greater immunity, and so on in each generation. The individuals that vary in the wrong direction, that is, *towards being out of harmony with their environment*, are eliminated. *Natural selection of inborn variations is a question of adaptation to environment.* The conclusion that follows the extracts quoted above is this: "When I am confronted with these difficulties in the way of accepting the non-transmission of acquired qualities, I find it as easy to believe that gloves were made without reference to hands; that carts were made without reference to horses; that keys were made without taking locks into consideration; that, when we find a seal and its impression in wax side by side, we must suppose that the impression came into

---

[1] Mercier, Charles, *op. cit.*

being spontaneously, fortuitously, and without any assistance from the seal of which it is the complement."[1]

This simply accentuates the importance of adaptation to the environment; which is after all the main feature of the theory that natural selection acting upon inborn variations, and inborn variations only, produces all new characters, and that they cannot be produced in any other manner. The case should be stated thus:—The believers in the inheritance of acquired characters say that the new characters of a race are acquired through the action of the environment upon the individual, while the Neo-Darwinians say that the new characters of a race are acquired through the action of the environment upon the inborn variations occurring in all the individuals of a race.[2]

The production of definite structures in the animal body through the transmission of parental acquirements has been explained somewhat as follows:—Teeth have been supposed to grow in response to the stimulus of biting. The continuous pressure on the jaw has caused bony protuberances in the parent. These have been transmitted to the offspring, and in them have been increased by continual use, growing harder and larger from generation to generation. The obvious objection to this particular interpretation is;—that the continued use of the teeth in masticating the food does not cause them to grow but wears them out. The only acquirement made by man with regard to his teeth is, that the longer he lives and the more he uses them the more they will be worn. The same is the case with a great many mammals, particularly those which chew their food a great deal. In some cases the teeth have the character of con-

---

[1] Mercier, Charles, *op. cit.*

[2] To any one who understands the theory of natural selection this detailed explanation may appear superfluous. That it is really necessary is rendered evident by the quotations from the recent writings of a Lamarckian just quoted. In considering the relative merits of two theories, where one theory has been misrepresented by the upholders of the other, it is most important that the ground should be cleared of these misrepresentations, and a fair field given to both parties.

tinuous growth throughout the life of the animal. In rats, for instance, in whom the capacity for gnawing hard substances is very necessary, the teeth appear to grow throughout the animal's life. If one of the upper eye teeth be lost through accident, the corresponding lower tooth grows to such an extent that it prevents the animal feeding properly, and sometimes even grows into its skull and causes death. The two opposing teeth wear each other away under normal conditions, so that when this check is removed in one jaw, the tooth in the other grows until it kills its possessor, either through preventing its feeding or by penetrating some vital part. Now the capacity for indefinite growth in this case actually meets and renders ineffective the acquirement made by the individual. The acquirement is the wearing out of the teeth, the inborn character is the capacity to grow indefinitely. The power to gnaw though hard substances and the possession of sharp teeth is a necessary adaptation to the environment in the case of the rat. If the teeth did not grow throughout the animal's life they would soon be worn out, and the evolution of this character is explained very simply by natural selection acting upon inborn variations. If it is explained by the transmission of acquired characters, we must suppose that the wearing out of the teeth in the parent has been transmuted into an inborn capacity for indefinite growth in the offspring.

The origin of joints has been explained in a somewhat similar manner. By continual friction, the end of one bone is supposed to have become rounded, the end of the other to have become hollowed out. At first this shaping of the end of one bone by the other was very slight, but was increased at each generation as an acquirement made by the individuals. This explanation fails to show us why it is that this process of reciprocal wear, which means destruction of a certain amount of bone, does not continue indefinitely. If this interpretation were true, joints should be getting deeper and deeper and the long bones should be becoming shorter as they are worn out in each generation. Observation shows us that the continuous use of the joint has no effect whatever in the way of wearing out the surfaces of the bones in the absence of disease.

Another difficulty with regard to the inheritance of acquired characters is, that acquirements are not made in the case of all characters. It is known that the nerve cells do not multiply after birth, at any rate in the case of mammals. The young individual is born with its full complement of nerve cells, and the number is never increased in after life. Now it is obvious that evolution in the higher animals, culminating in man, has worked through the increase of the intelligence—particularly through the increase of the nervous tissue of the brain in proportion to the size of the animal. The differences between man and the higher apes are most marked in the case of the brain. Man's brain is very large in proportion to that of the highest ape, and the surface area of the human brain—that is, the most important part of it—is in proportion larger still. But this means an increase in substance—in the number of nerve cells in the brain at any rate—and we have no jot of evidence to show that any acquirement of the individual can add a single cell to the brain. On the contrary, we know that if a nerve cell is destroyed by accident or disease, it is gone for ever. It is never replaced by the multiplication of other similar cells as may happen in other tissues in the body. Therefore the only acquirements that can be made, in so far as the substance of the brain is concerned, by man and the higher vertebrates, are losses.

Many other characters that are inherited do not depend upon use for their appearance, and yet have very obviously appeared or been increased in the later stages of evolution.[1] These cannot be dependent upon the transmission of the acquirements of the parent to its offspring, for they are not modified by use or disuse on the part of the organism in which they occur. If, then, the transmission of acquired characters has played an important part in evolution, there

---

[1] Such characters are the plumage of the peacock and cock pheasant.

are two ways in which adaptation has occurred—in which new characters have appeared. One is by the selection of inborn variations, the other by the transmission to the offspring of the acquired characters of the parents. But apparently the selection of inborn variations is sufficient to account for all characters, whether they are or are not of such a nature that the transmission of acquirements would have influenced them. The transmission of acquired characters, on the other hand, could at best account for only a part of the process of evolution. It is always dangerous to assume more than is absolutely necessary in explaining any phenomenon, and therefore, even were there no other reason, very strong evidence would be necessary before the inheritance of acquired characters could be accepted as a usual occurrence in nature. As a matter of fact there is very little evidence that suggests that they ever are inherited, and this evidence may be interpreted in an equally plausible manner without making any assumptions beyond the occurrence of variations in all directions, the transmission of such variations, the extermination of individuals with unfavourable variations, and the elimination of all variations that are not in the direction of adaptation to the environment. As much as this must be assumed in either case.

It must also be borne in mind that the assumption that acquired characters are transmitted implies some extremely complicated and almost inconceivable mechanism by which the acquirements of the individual produce a definite effect upon the germ cells. This effect is not a general effect, but a particular effect. That the germ cells as a whole might be generally injured or generally benefited by some acquirement of the organism in which they are contained, is readily conceivable. But it is hard to conceive that some small difference appearing in adult life can so influence the germ cells as to appear in the organisms produced from them, without the germ cells being affected in other ways as well. Such a theory assumes too much, without need, practically without evidence.

An enormously greater number of individuals of every kind of animal and plant is produced than can possibly survive. This holds true of the most slowly breeding animals, and is one of the main factors in the Darwin-Wallace theory of evolution. It is evident that those individuals will survive which are best adapted to their environment, and that whatever the other factors in evolution may have been, the obvious fact remains that organisms are adapted more or less perfectly to their environment. Now, if the acquired characters of the parent were transmitted to the offspring, all the acquirements good and bad would seem to have an equal chance, and therefore races in a very bad environment must degenerate, those in a very good environment improve. A bad environment must necessarily injure even those individuals that survive. The chief acquirements of the individuals will therefore be towards degeneration, not towards improvement. The individuals of each fresh generation would inherit all the injuries the environment caused in their parents, and would in their turn suffer fresh injuries and transmit them to their offspring. Under such conditions a race must be rapidly exterminated. The opposite would happen in the case of a race in a favourable environment.

No one disputes either the existence or the transmission of inborn variations. This being admitted, natural selection —that is, the influence of the environment—must have tended always, for so long as variation has occurred and been transmitted, to preserve those organisms which possess variations adapting them more closely to their environment, and to eliminate those that varied in the other direction. The more stringent the selection, particularly in the way of disease, the more injurious the transmission of acquired characters must be to the race. But variation occurs in every direction, and it is more than probable that the germplasm may sometimes vary towards being influenced by the action of the environment upon the parents. If it varies thus, the effect upon the race must be injurious.

The case of malaria again serves as an example. If the poison produced by the malarial parasite affected the germ cells as well as the body of the parent, it is not conceivable that the effect could be anything but injurious, it could do the germ cells no good. In the same way, anything injurious to the individual must injure the germ cells also, unless they are highly resistant to the environment. Favourable variations in the germplasm can only be preserved and permanent improvement in the race take place if the germplasm and germ cells are highly resistant to any external influences.

The evidence bearing upon the subject shows that we have no undoubted example of the transmission of an acquired character. This, however, does not make it legitimate to say that acquired characters can never be transmitted. A general consideration of the case seems to show that it is safe to conclude that acquired characters can be transmitted but very rarely, if ever, and that natural selection must tend to eliminate variation in this direction if it happens to occur in any organism.

There does not appear, then, to be any evidence showing that the environment has any effect in the production of progressive variations in the germ cells. In fact, the evidence seems to show that natural selection must have tended towards making the germ cells or germplasm highly resistant to the environment.

It has been suggested [1] that, when life was near its origin, there arose among the simple organisms then existing some that varied from the parent organism. This result may have been brought about by the action of the environment being different upon different portions of the organism. This is of course speculation pure and simple, but as we have no evidence with regard to the subject, nothing more than speculation is possible.

The conclusion arrived at with regard to variations may be summarised as follows:—We have the simple fact that

---

[1] Reid, Archdall, *Principles of Heredity*, 1905, p. 95.

organisms do vary continuously and in all directions from the characters of the parent organisms, and further than this it is impossible to go with regard to the ultimate cause of variation. Given, however, the smallest variation in the simplest organism, the remainder of the process of evolution is conceivable. Natural selection would increase variability up to the point where it ceased to be useful in adapting a race to its environment, and then would check it. It would appear probable also, that as the modifications produced by the environment in the parent organism would frequently be injurious to the germ cells and to the offspring arising from them, natural selection would eliminate variations in the germ cells that tended to be thus influenced. On the other hand, variations among the germ cells themselves, as they would tend to give an advantage to the race, would be increased. All other cells vary among themselves, and evidently germ cells do the same. Variations in the germ cells involve variations in the organisms produced from them. There is no evidence that bi-parental reproduction—the mixing of the germplasm—has any effect in producing fresh variations. On the contrary, it eliminates useless variations, and is thus a cause, probably the cause of regressive variations. It does not appear to be legitimate to go further than this with regard to the cause of progressive variations.

CHAPTER X

Mendel's discovery—Segregation of gametes—The extent of the Mendelian experiments—Comparison between the results of the Mendelian experiments and the distribution of the chromosomes in fertilisation—A suggestion that Mendelian characters are represented by chromosomes—Blended inheritance—Exclusive inheritance — Particulate inheritance — Mendelian phenomena most perfect in self-fertilising plants—A suggestion that Mendelian characters are individual variations and that characters which blend are racial—Evidence in support of this theory.

Of all the recent discoveries relating to heredity and evolution, probably none has aroused more interest and more controversy in this country than that of Gregor Johann Mendel, Abbot of Brönn in Austria. One school of biologists would have us believe that the discoveries of Mendel combined with the theory of mutations have not so much extended the Darwin-Wallace theory of natural selection as replaced it.[1] With regard to Mendel's work, a number, perhaps the majority of biologists, regard it as interesting and important, but do not take it in so serious a manner as the others. Mendel's observations were first published in 1865 in a comparatively obscure journal, and escaped observation for many years,[2] but several botanists "rediscovered" Mendel's discoveries many years later.[3]

Mendel's experiments dealt with the manner in which

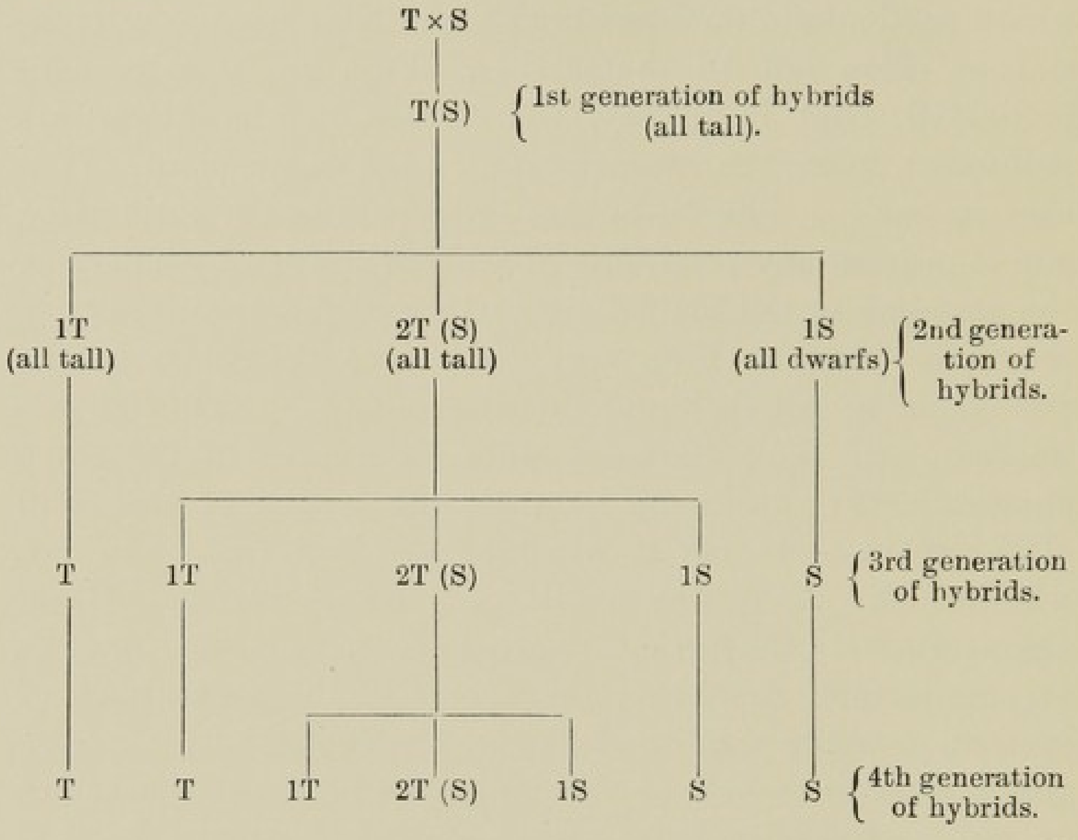
---

[1] Bateson, *Report British Association*, 1904, p. 574.

[2] Mendel, G. J., "Versuche über Pflanzen Hybriden," *Verhandlungen des Naturforschaftlichen Verein in Brünn*, Band IV., 1865.

[3] Correns, C , "G. Mendel's Regeln über das Verhalten der Nachkommenschaft der Rassenbastarde," *Ber. Deutsch. Bot. Ges.*, xviii., 1900 ; Tschermak, E., "Über künstliche Kreuzung bei Pisum sativum," *Zeitschr. Landwirthschaft. Versuchswesen in Oesterreich.*, iii., 1900 ; Vries, H. de, "Sur la loi de disjonction des Hybrides," *Comptes Rendus Acad. des Sciences Paris*, cxxx., 1900.

certain definite characters in domesticated peas were transmitted when varieties were crossed. He chose plants in which particular characters bred true under normal circumstances when left to themselves. Peas are usually self-pollinated, that is to say, the ovules in the flower are pollinated from the same flower or the same plant. It is easy in such a case to ensure cross-pollination artificially, and to prevent any possibility of self-fertilisation by removing the stamens of the artificially pollinated flower before they are ripe. Mendel chose very distinctive characters in the pea-plants in which he produced crossing by artificial pollination, and the differences were differences in the same character. For instance, he took the length of the stem of the plant—whether it was long or short, that is to say, whether the plant was a tall or a dwarf variety. Other characters were the form of the ripe seeds, round and smooth, or angular and wrinkled; the colour of the seeds, plain or spotted, green or yellow. To make the results of his experiments clear, it is best to take only one of these characters, or rather one pair of characters—tallness and dwarfness of the plant. All the plants produced from the seeds of the first cross between a tall and a dwarf plant were tall. These hybrids were self-fertilised, and the plants grown from these differed from each other in that some were tall and some were dwarf. Out of over a thousand plants the average proportion of tall to short plants was as three to one. These plants were again self-fertilised. The dwarfs produced nothing but dwarfs, and this apparently went on for many generations, the tall character never reappearing in them. Of the progeny of the tall plants, however, one-third produced tall plants only in succeeding generations. The other two-thirds produced again one-quarter dwarf plants and three-quarters tall plants. The dwarf plants continued to produce dwarf plants indefinitely, while the tall plants broke up again into the same proportions of plants that produced only tall plants, and others that produced the same proportion of tall and dwarf plants. The following diagram illustrates what happens. The T stands for the tall character, S for the dwarf.



When two individuals, one with the tall and the other with the short character, were crossed, though both characters were really present in the offspring, only one of them was visible to the apparent exclusion of the other. Mendel called the character that appeared the "dominant" character, and the character that was concealed the "recessive" character. Of other pairs of characters, roundness and smoothness of the seeds was dominant over the wrinkled character; colour in the seeds was dominant over whiteness; purple flowers were dominant over white flowers.

A consideration of the diagram shows that in the second generation from the cross, that is, in the offspring of the hybrids, 75 per cent. showed the dominant character—tallness; 25 per cent. the recessive character—dwarfness. The 25 per cent. recessive bred true when self-fertilised. Of the 75 per cent. showing the dominant character only one-third bred true; the remaining two-thirds again gave the same percentage of dominants and recessives as the preceding generation. From this it may be concluded that from the hybrids when self-fertilised are obtained 25 per cent. pure dominants; 50 per cent. impure dominants—that is, plants exhibiting the dominant character but containing the recessives; and 25 per cent. pure recessives. In succeeding generations, the same proportions of pure dominants, impure dominants, and pure recessives are always obtained from the impure dominants.

Mendel assumed that these characters, with which he experimented, were represented by units or entities in the gametes. In each of the pure-bred parents from which the first generation of hybrids was produced, there would be only one kind of entity. In the first generation of hybrids, however, both entities representing the characters must be present. He supposed that in the production of the gametes of the hybrids, these entities representing two opposing characters separated from each other, so that half the gametes contained entities representing one character, and half contained entities representing the other. In the production of the next generation, according to the laws of chance, as the number of each kind of gamete would be equal, 50 per cent. would fuse with other gametes like themselves, 50 per cent. with the opposite kind of gamete. Of the gametes that fused with others like themselves, half would be dominants, and half would be recessives. The results in the second generation then would be 25 per cent. of individuals produced from two gametes both containing the dominant character, 25 per cent. produced by the fusion of two gametes both containing the recessive character, and 50 per cent. by the fusion of two gametes, one containing the dominant, the other the recessive character. A very simple illustration of this phenomenon may be shown experimentally by putting 100 white beans and 100 black beans into a bag. These are supposed to represent the two different kinds of gametes whose fusion is to produce the second generation of hybrids. Now, if these beans be withdrawn from the bag haphazard in pairs, it will be found that about 25 pairs are composed of two white beans, 25 composed of two black beans, and 50 composed of one black and one white. The greater the number of beans used in the experiment, the more nearly will it come to these proportions, or the greater number of times these 200 beans are mixed together and drawn in pairs the more nearly will the average of the draws come to 25, 50, and 25 per cent.

This theory of Mendel's is known as the segregation of the gametes, and it is assumed that, in so far as the characters behaving in this manner are concerned, offspring with the perfectly pure characters of the two parent organisms may be bred out from the hybrids. The accompanying illustration shows diagrammatically how this is supposed to be brought about (Fig. 20). The large circles containing two small ones represent individuals; the small circles represent the gametes. The white circles represent the dominant character, the black the recessive. The large circles are shaded to show whether the dominant or recessive character appears in the individual. It will be seen that in the impure dominants the dominant character only appears, although the recessive gametes are also contained in the individual.

Experiments have since been carried out with a number of other domesticated plants and animals, and dominance and recessiveness have been determined with regard to certain pairs of characters. Thus in sweet peas and stocks, coloured flowers are dominant, white recessive. In mice a coloured coat is dominant, an albino coat recessive. In rabbits a coloured coat is dominant, an albino coat recessive; and angora fur is dominant, short fur recessive. In poultry a rose comb is dominant, a serrated single comb recessive, and so on with a number of other pairs of characters. There are very frequently several pairs of characters involved in the crossing of two pure-bred individuals. In these cases each different pair of characters seems to act independently of the rest. For instance, if two characters,

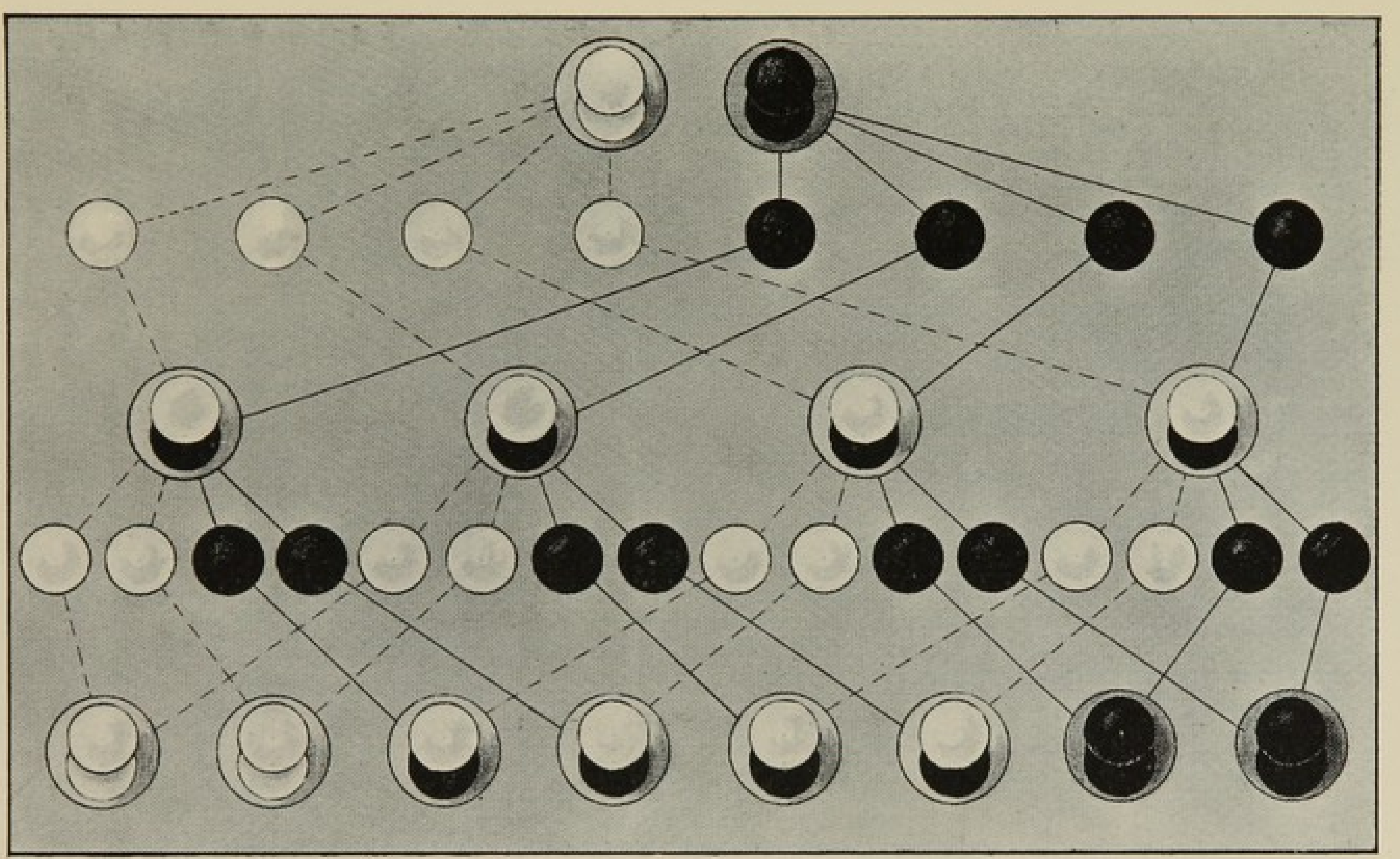


FIG. 20.—Diagram illustrating Mendel's theory of gametic segregation. The large circles represent individuals, the small represent gametes. White represents the dominant character, black the recessive. In the individuals containing both kinds of gametes, only the dominant (white) character appears. In the individuals containing only recessive (black) gametes, the recessive character appears. This is indicated by the shading of the large circles.

both dominants, are present in one parent, and two recessives in another parent, among the descendants individuals with the two dominant characters pure and other individuals with the two recessive characters pure will appear in Mendelian proportions. If, however, each parent possess a dominant and a recessive character, the two dominants and two recessives may be segregated together. Again, a particular character exhibited by one of the parent individuals may not be a pure character, the individual being an impure dominant. Thus, if the impure dominant tall pea be crossed with a pure dwarf recessive, while the pure dominant has equal numbers of gametes containing the dominant and the recessive character respectively, the pure recessive produces only gametes containing the recessive character. In this case an equal number of tall and dwarf plants will be produced. All the tall plants, however, will have a recessive character, because they could only be fertilised by gametes derived from the pure recessive parent; whereas there was only a possibility of half the gametes of the recessive parent fusing with gametes

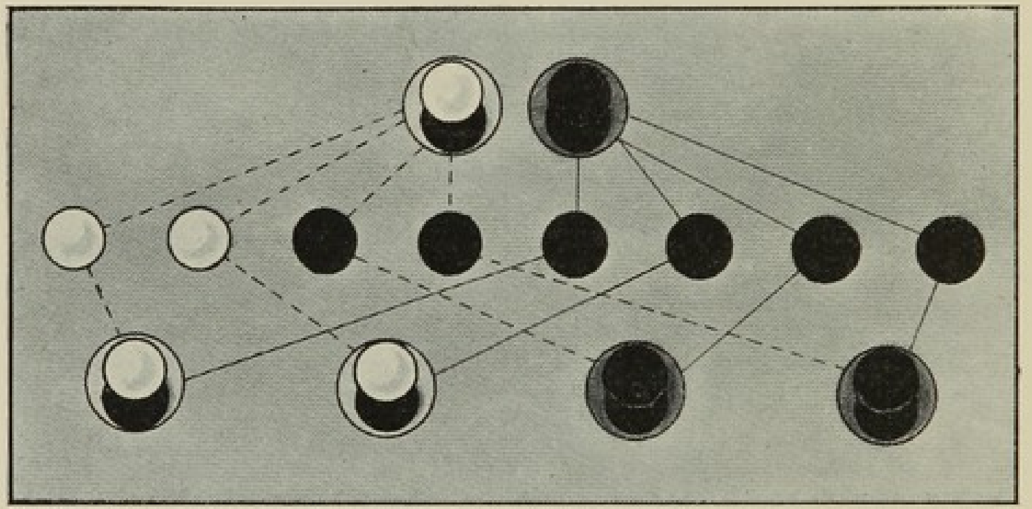


FIG. 21.—Diagram illustrating a cross between an impure dominant and a recessive. The small circles represent the gametes, white dominant, black recessive. The large circles represent individuals, and are tinted to show whether the dominant or recessive character is apparent. It will be seen that a pure dominant cannot result from this cross, and from it are produced individuals of which 50 per cent. exhibit the dominant, 50 per cent. the recessive.

containing the dominant character derived from the impure dominant parent.

There is not the slightest doubt that some characters do behave in this manner, for Mendelian inheritance is established by an enormous number of experimental results, but it is also a fact that many characters are most definitely not transmitted according to "Mendel's law." Instead of separating out in successive generations of individuals, they blend and remain blended. There are also some characters that are intermediate, that is to say, they only follow Mendel's law to a limited extent and not entirely.

Taking the Mendelian characters first, we find that the degree of segregation varies a great deal. In some cases, as with the tallness and dwarfness, the colour of the flowers and of the unripe pods in peas, segregation appears almost, if not quite complete. If all Mendelian characters behaved in this way, it would be conceivable that one character might be represented by one entity or unit. For instance, the tallness would be represented by one entity, dwarfness by another, and these would be distributed singly to the gametes. Such cases are, however, rare, and there are few experiments which give such simple results. The suggestion is very strong, that besides the two characters which appear in the offspring in an alternative manner, other characters of the same order may also be represented. In animals the first generation often differs from both parents with regard to a particular character, and this character of the hybrids in subsequent generations apparently splits up again into the two parent characters, dominant and recessive. Take for the sake of simplicity one character only, colour. When two different-coloured animals are crossed, the first generation is generally different from either of the parents, although the two original colours may be extracted in a more or less pure form in subsequent generations. Sometimes the mixture of colour characters is still more obvious. For instance, Correns crossed the white and yellow varieties of the Marvel of Peru (*Mirabilis jalapa*), both of which, under ordinary circumstances, breed true. The first generation had rose-coloured flowers with red streaks. The hybrids, however, produced many different varieties, some white, some red, some rose, some yellow, and some yellowish. All these colours occurred pure or with various streaks.[1] Similar results have been obtained by crossing varieties of sweet peas.

If the colour characters are represented by entities, as is suggested so strongly by the alternative distribution, it seems obvious that there must be a good many entities all representing colour, but which need not necessarily represent the same colour. Where a particular colour has been the object of man's selection in a domesticated race, it would seem probable that although his selection may have reached a point where the majority of the colour entities represent the desired colour, it can but rarely happen that the selection has been so stringent and so long continued, that all the colour entities are the same. Take the case of a cross between a grey and an albino rabbit, the albino being derived from a black variety. From this cross, black, white, and grey rabbits can be bred out. This appears to show that the black in the albino remained discrete, although the albino character concealed it. In the first cross the progeny are grey, but the albino and black characters are also present. Assume 20 as a convenient hypothetical number of entities representing individual variations in colour; A representing albinism, and B black. Now even if the albino character is represented by only one of these entities, if it be subjected to selection it will in time completely oust all the other 19 entities which are not selected. But it is very unlikely that in an artificial breed of rabbits the colour entities can have been so selected that they are all of one kind. In this particular case the black character is present. Suppose that in this rabbit the colour entities are 10A+5B +5X; X representing all the other colour entities, which

---

[1] Correns, C., "Über Bastardierungsversuche mit Mirabilis sippen," *Ber. Deutsch. Bot. Ges.*, xx., 1902.

may all differ from each other. The wild grey rabbit must be treated somewhat differently if this conception is correct. The grey is a racial character representing a general potentiality of the race. The 20 entities will therefore represent individual variations away from the common racial characters, the mean being kept to by the unchecked influence of bi-parental reproduction and natural selection. Its 20 entities may therefore represent different kinds of greyness, some darker and some lighter than the mean. A few may even be departures from grey, arising *de novo* as individual variations, or being derived from some ancestor. They should therefore all be represented as X. It is obvious that where alternative transmission takes place the sexual elements can individually contain only half the entities representing the alternative characters that are contained in the cells forming the body of the parent. The number of entities contained in the sexual elements of the albino rabbit cannot be more than 10, and may vary from 10A to 5B+5X. These are the two extremes, but of course any 10 entities that can be derived from 10A+5B+5X may be contained in the gametes. The X's in the wild rabbit may each represent a different kind of grey, or any number of them up to 20 may represent the same kind of grey. It is extraordinarily improbable that any of the gametes of the albino rabbit would contain nothing but the character A. They would almost certainly contain one or two B's or X's. In the first generation the obvious chances are that greys would predominate. Even did a gamete containing 10A fuse with one containing 10X, albinism is generally a recessive character, and the individual produced would be grey. In the succeeding generations produced by inbreeding from the hybrids, the chances of individuals being produced with a predominating number of A's would be roughly Mendelian, but none of them would be quite pure. The same explanation would apply to the black, although of course fewer black individuals would be produced. A similar explanation applies equally in the case of the flowers. It also accounts for the many cases where dominance is imperfect, and where traces of the cross remain in extracted dominants and recessives. Such cases are common.

Although dominance appears to be perfect in the case of some plants, we find that in animals the first generation of hybrids usually differs from both parents. Instead of only the dominant character appearing in the impure dominant, reversion to the character of a more or less remote ancestor frequently occurs. Thus when waltzing mice are crossed with albinos, the first generation of hybrids are coloured like the wild house-mouse.[1] In some cases the first generation of hybrids are something in the nature of a blend between the two parents. Thus when black and white fowls are crossed, a blue Andalusian is sometimes produced, with a minute patchwork of black and white. Again, the dominant character may show to a great extent, but the recessive also, though much less. When white Leghorn poultry are crossed with brown Leghorn, most of the offspring have some ticks of colour.[2] Very often the extracted dominants and recessives, that is, those individuals in the second and third generation, which in the case of peas appear to have segregated completely and possess only the dominant or recessive character, show traces of the cross. " Very frequently, if not always, the character that has once been crossed has been affected by its opposite with which it was mated and whose place it has taken in the hybrid. It may be extracted therefrom to use in a new combination, but it will be found altered. This we have seen to be true for almost every character sufficiently studied. . . . Everywhere unit characters are changed by hybridism."[3]

With regard to the characters that follow Mendel's law, the assumption that discrete entities representing these characters exist in the individual and are transmitted to

---

[1] Darbishire, "On the Results of Crossing Japanese Waltzing Mice with European Albino Races," *Biometrika*, ii. pp. 101–65 and 282, 1902.

[2] Punnet, R. C., *Mendelism*, Cambridge, 1905.

[3] Davenport, *Inheritance in Poultry*, p. 80.

the gametes in an alternative manner, seems not only justifiable but necessary. Characters that have been, so to speak, put into a hybrid, may not appear for several generations, but the fact that they may be subsequently extracted in the descendants, seems to imply that they have remained throughout as discrete entities. If the characters are not so represented, then it is necessary to assume other entities which are distributed in an alternative manner, and control their appearance. It is immaterial which assumption is made, but the less assumed the better. In any case, whether the entities represent the characters themselves or merely influences controlling the appearance of the characters, they must be transmitted in an alternative manner.

Now the alternative manner in which the Mendelian characters appear in the succeeding generations produced from hybrids, corresponds in a most extraordinary way with the distribution of the chromosomes to the gametes and their recombination when fertilisation takes place. No other constituents of the cells are thus distributed, and the suggestion is very strong that the two processes are intimately connected. It has already been shown[1] that racial characters cannot be represented by chromosomes, because the latter are distributed alternatively to the gametes. Mendelian characters *are* distributed alternatively.

Of course there is no suggestion that there is a chromosome for each character, but there is a suggestion that each entity representing a potential character is represented in some part of a particular chromosome.

For the purpose of illustration, imagine a species of animal, the cells of which contain two chromosomes. In two breeds of this species, however, the chromosomes are different in character. Two individuals, A and B, one from each breed, are crossed. Now the gametes of these individuals will contain only one chromosome each, so that the result of the fertilisation of the one by the other will be that the cells

---

[1] See pp. 22-3.

of the hybrids produced will contain two chromosomes, one of each different kind, A and B. When reduction takes place the chromosomes are so distributed to the gametes of this hybrid that each will contain only one chromosome. Half of them will contain chromosome A, and half of them chromosome B. Now if these hybrids are inbred, the mathematical chances of the combination of chromosomes in the succeeding generation will be as follows:—In 25 per cent. of the offspring the cells will contain chromosomes A and A, in 50 per cent. the cells will contain chromosomes A and B, and in 25 per cent. the cells will contain chromosomes B and B. This is very obviously comparable with the results of the Mendelian experiments, and if A contained one and B the other of a pair of Mendelian characters, we should have a Mendelian result in a perfect form. As it is probable, however, that there are several entities representing each character, the distribution of chromosomes would explain some of the discrepancies which are so apparent in the results of the Mendelian experiments.

In a great many cases characters are transmitted in a manner that does not coincide in the least with the Mendelian results. The offspring of a cross between two different races may show a blending of particular parental characters, and this blending continues for an indefinite number of generations. It does not appear that such characters can ever be bred out pure again in subsequent generations derived from the original hybrids. They are inextricably mixed, and cannot be unmixed or segregated. The two opposing characters seem to be mixed when crossed, just as the colour is mixed when a pint of water is poured into a pint of claret. These characters in subsequent generations will behave in the same way as the colour of such a mixture will behave, according to whether water or claret is subsequently added to an equal quantity of the half-and-half mixture. The only way of arriving back at either of the original characters in an approximately pure form would be by a process of swamping. At every subsequent generation pure-bred parents of one kind only would have to enter into the cross, and then in time it is conceivable that the other character might be *apparently* eliminated, just as the colour of a portion of the mixture of equal parts of water and claret would be lost by taking half of the mixture and adding to it an equal quantity of water, then taking this mixture and doing the same thing, and so on for an indefinite number of times.

Before Mendel's interesting discovery became generally known the different modes of inheritance were described as blended, exclusive, and particulate.[1]

In *blended inheritance* of a particular character, the offspring exhibits an intimate mingling of the characters of both parents. The character, in fact, is intermediate between the corresponding characters appearing in the two parents. Thus the child of a white man and a black woman is generally brown. If a narrow-leafed willow be crossed with a broad-leafed willow, the shape of the leaf in the offspring is intermediate between the two. In several plants the hybrids show an accurate mean in many characters between those of the two parents.[2] It may be, however, that though the character of both parents are recognisable, the one preponderates over the other. Thus mules are sometimes more like donkeys than like ponies, but at other times this resemblance may be reversed. The characters which preponderate are called " prepotent."

---

[1] Galton, *Natural Inheritance*, p. 7.

[2] Macfarlane, J. M., "A Comparison of the Minute Structure of Plant Hybrids with that of their Parents," &c., *Trans. Roy. Soc. Edinburgh*, xxxvii., 1891.

In 1902 I investigated a cross between the bream-flat (*Abramis blicca*) and the rudd (*Leuciscus erythrothalmus*). The characters of the cross appeared to be a definite mixture between the two parent forms. The shape, body measurements, and head measurements were intermediate between the two parent forms, as were apparently all the other characters. For instance, in the anal fin of the bream-flat there are from 22 to 27 rays; in the rudd there are from 13 to 15. In the cross the number of anal fin rays was 17, and the number was apparently much more constant in the cross than in either of the parent forms, for in the numerous specimens examined the same number of anal fin rays was always found. Other cases of blending are given on pp. 117–9.

In *exclusive inheritance* the offspring appears to take entirely after the male or the female parent. Many characters are often involved, and the offspring appears to take after one parent only, in so far as there are any differences between the parents. In these cases one parent is said to be "absolutely prepotent."

In *particulate inheritance* the characters of the parents do not blend, but both are expressed. In some cases it appears as though certain parts of the organism inherited the male parent's peculiarity, other parts of the female parent's with regard to the character. Probably the best-known instance of this kind is a piebald horse, where the different patches represent the two different colours inherited from the parents, both being present though not blended. Another less common example is the colour of the eyes. A child generally inherits its eye colour from one parent only, but in one or two cases in a thousand in man the two eyes differ in colour, or one eye shows different patches of colour.[1]

In domesticated races those which are longest established tend to be prepotent over newer races. A race which has never been domesticated tends to be prepotent over a domesticated race. It is generally supposed that very inbred races are prepotent over races that have been less inbred. When natural varieties or species are crossed, however, it is quite usual for the characters to be blended.

There is no more doubt with regard to the fact that some characters blend in inheritance, than there is that some tend to segregate. Some extreme Mendelians would have us believe that all inheritance is Mendelian, and where blended inheritance seems to be the rule, they bring forward what are apparently exceptions, and claim that when we know more, the Mendelian phenomena will be found universal. For instance, in the crossing of a black and white race of men, a few obscure cases are brought forward, and it is claimed that these show that the black and the white colours in the two races segregate. It is quite

---

[1] Pearson, *Grammar of Science*, 2nd edition, London, 1900.

unnecessary to discuss the authenticity of these cases; if they exist, they are obviously rare exceptions. If they rarely exist, an explanation of these rare exceptions must be found which is in accordance with what generally happens, and what generally happens is that the colours of the two races blend. Francis Galton, writing of the blending of the black and white colours in man, says: "If the whiteness refuse to blend with the blackness, some of the offspring of the white man would be wholly white and the rest wholly black. The same event would occur in the grandchildren mostly, but not exclusively in the children of the white offspring, and so on in subsequent generations. Therefore, unless the white stock became wholly extinct, some undiluted specimens of it would make their appearance during an indefinite time, giving it repeated chances of holding its own in the struggle for existence."[1] Whether the exceptions that are claimed are valid or not, it is quite evident that segregation is not what generally happens. When there is a trace of black blood in a white family it does not manifest itself by the appearance of apparently pure-bred negroes. What we see is a mixture of the characters proportionate to the nearness of the negro ancestry. Of course there are variations, and a child may show negro characters more strongly marked than they were in the immediate parent through whom the negro blood came, but nevertheless the child is never as black as the pure-bred negro, and it takes a very long time of mating with the pure white race for a negro strain to be swamped. It is the same with a great many characters in other crosses. Frequently the hybrids when inbred preserve the blended characters, and the offspring do not tend to revert to the characters of either parent. Even Mendel's experiments showed that characters did not always segregate in the same way as did the characters in the case of the peas, and there are many other cases, some of which have been described already.[2]

---

[1] Galton, *Natural Inheritance.*

[2] See pp. 176–7.

It appears that we have two opposite modes of transmission. One in which certain characters are definitely segregated, and for which it is necessary to assume entities which are distributed in an alternative manner to the gametes when new individuals are produced. Another in which characters apparently blend when crossed.

Having thus apparently two very different ways in which characters may be transmitted from parent to offspring, it becomes necessary to inquire whether any difference can be distinguished between the characters that are transmitted in one way, and those that are transmitted in the other.

The most striking point about the Mendelian characters is that almost all that have been subjects of experiment, have been in domesticated races of animals or plants. On the other hand, when natural races are crossed, we find differences in characters are generally blended. Between these two extremes, the Mendelian and the blending characters, we have many gradations. It is very suggestive that the cases which show the most perfect segregation are those in self-fertilising plants, while departures from the Mendelian law become more and more frequent when we come to organisms where the gametes must necessarily be derived from two separate individuals. It is necessary only to refer to the difference in the results obtained from crossing characters in peas and poultry to realise this.[1] Many of the gradations between segregation and blending have already been dealt with in the explanation that was offered with regard to the cases of incomplete segregation. It is obvious that the segregation of entities must be most perfect in self-fertilisation. Even in self-fertilising plants which have been domesticated for a long period of time, some of the characters do not behave as did the characters in Mendel's original experiments with peas. For instance, two peas were crossed in one of which the starch grains were "potato-shaped" and large and single,

---

[1] See pp. 173, 176.

while in the other they were compound, consisting of from two to eight parts. In the first generation of hybrids, the starch grains were intermediate in size and form between the characters in the parents. Other characters were also found to be intermediate.[1]

Another very striking thing about the Mendelian results, suggesting that segregation is often by no means perfect even in the most favourable cases, is, that when the accounts of Mendelian results are examined, many individual exceptions appear, although the average may show the expected figures with considerable accuracy. For instance, in the account of some carefully conducted experiments with peas, we find the following remark: "When a discrepancy occurs in Tables II., III., and IV. between the totals for cotyledon colour and totals for shape in a given plant, it signifies that in the case of some of the seeds of that plant the shape was determinable whilst the colour was dubious, or *vice versa*." These tables refer to peas of the fifth inbred generation from the cross,[2] so segregation should theoretically have been perfect. This is only one example, but Mendelian results are full of such cases of individuals in which segregation has not occurred.

In considering the differences between racial and individual characters, considerable stress was laid upon the fact that man had probably always selected large variations.[3] By eliminating the usual effect of bi-parental reproduction and the necessity for accurate adaptation to the environment, and by constantly selecting considerable variations, man has produced races of animals and plants which, within certain limits, breed true with regard to the particular characters he has selected, for as long as he keeps on selecting. These characters have generally been produced in an extraordinarily short space of time in comparison

---

[1] Darbishire, A. D., "On the Result of Crossing Round with Wrinkled Peas, with Especial Reference to their Starch Grains," *Proc. Roy. Soc.*, B., vol. lxxx., 1908.

[2] Darbishire, A. D., *op. cit.*

[3] See p. 71.

with the production of characters under normal conditions. It seems reasonable in fact to regard many of these characters as exaggerated individual variations. If this conception be correct, it would seem probable that individual variations are transmitted according to the law of Mendel.

Individual characters are either individual variations, or characters inherited from a parent which are not common to the race, but are confined to individuals that have inherited a variation from a near ancestor. It is probable, then, that individual characters are transmitted in an alternative or Mendelian manner, and that racial characters tend to blend.

The alternative distribution of individual characters or variations, would make two results quite certain under natural conditions. (1) That useless variations would be eliminated in a very short time by the action of bi-parental reproduction. (2) That individual variations that are the subjects of selection would be much more readily preserved and characters be more quickly produced from them, than if the variations blended.

It is necessary to examine this hypothesis in some detail in order to realise the extent to which it coincides with the known facts of hereditary transmission.

If the characters in domesticated races that are transmitted in the Mendelian manner are really individual variations exaggerated by man's interference, we ought to find that only some characters in domesticated races are alternative, while others are not, and do not tend to segregate in succeeding generations. This is probable, because man can hardly have applied his selection to many characters at the same time. The other characters of which he took no notice would be subjected to the influence of bi-parental reproduction, and also to a limited extent to natural selection. With regard to the particular characters which he had selected, the greatest purity ought theoretically to be met with in the case of self-fertilising organisms, and the least purity in those where most crossing is necessary. It is a matter of common knowledge that mammals, when closely inbred for many generations, tend to become sterile and lose in vigour. Breeders, therefore, have to bring in new blood, that is, they are obliged occasionally to cross with a race which is not very nearly related to the particular strain they are developing. Thus in mammals, we should expect many cases where no segregation of characters occurred, and this is exactly what we find. For instance half-bred sheep derived from Border Leicester rams and Cheviot ewes, when inbred, continue to exhibit blended characters and show no signs of segregation. The same thing has happened in many cases in crosses in cattle.[1] The case of a particular calf is worth quoting. The sire was a cross between a pure Hereford and a shorthorn-cross bull. The dam was a pure black polled Aberdeen Angus cow. The calf was a creamy white heifer with a black muzzle and black hair on insides and tips of ears. As well as in its colour, the calf showed other points of resemblance to the Chillingham white cattle, a very ancient breed.[2] Even in domesticated plants many characters are found which do not appear to follow the Mendelian law.[3] Mendel himself with *Hieracium*[4] did not obtain Mendelian results, and the same has happened in other cases. It is thus evident that all characters even in domesticated races do not follow the Mendelian law.

When we come to consider natural races, we find that such characters as frequently follow the Mendelian law in domesticated races, rarely do anything but blend when crossed. There are some that apparently do segregate, but this is the exception rather than the rule. In fact, but a very few instances of the segregation of parental char-

---

[1] Thomson, J. A., *Heredity*, pp. 336, 377, 378, 384, 1908.

[2] Thomson, *loc. cit.*, p. 378.

[3] Report of Lecture by Professor Weldon, *Lancet*, March 25, 1905. Reference to Tschermak's experiments.

[4] Mendel, G. J., "Über einige aus künstlicher Befruchtung gewonnene Hieracium-Bastarde," *Verhandlung des Naturforschaftlichen Verein in Brünn*, 1869.

acters in the progeny of the hybrids, have been recorded. There are two series of breeding experiments with silk-worm moths. In the first series, two races of Siamese silk-moths were crossed, in one of which the caterpillar spun yellow, and in the other white cocoons. The result was segregation on Mendelian lines.[1] Another series of experiments with silk-moths gave entirely opposite results. The hybrids were sometimes blends and differed from both parents, sometimes some in the same brood were like one parent and some like the other, and in other cases the individuals of a brood were all like one parent or all like the other.[2] To begin with, it is of course very doubtful whether these silk-moths ought to be taken as natural races. They have been under domesticated conditions for hundreds of years in some cases, but the illustration is nevertheless very interesting. It seems probable that in the one case two comparatively newly-established characters were crossed, and that the ancestry of the two races was not at all remote, while in the other the two races had been separated for a much longer period, or even had been derived from two naturally distinct species.

There are, however, some direct experiments upon undoubtedly natural races. Individuals of a geometric moth, *Acidalia virgularia*, from two different races were crossed. The one race, found near London, was dark. The other, from Hyères in the South of France, was white. Ten generations from this cross were produced, giving between five and six thousand specimens. The results as regards segregation were negative. There was great variability and an enormous number of intermediate forms, with apparently a very indefinite tendency to revert. The intergrades between the two parent forms were so gentle that attempts to sort out the specimens into light and dark groups were

---

[1] Toyama, quoted by J. A. Thomson, *Heredity*, p. 361.

[2] Coutange, G., "Recherches Expérimentales sur l'Hérédité chez les Vers à Soie," *Bull. Scientifique de la France et de la Belgique*, xxxvii., 1902.

impracticable.[1] Other experiments with *Lepidoptera* have shown segregation.[2] The results he obtained from breeding *Lepidoptera* led Mr. A. Bacot to express the opinion that the characters blend when geographically separated races are crossed. In order to obtain segregation of the parental forms from hybrids, aberrations occurring in a race occupying the same geographical area must be crossed; and he believes that all recorded instances of Mendelian inheritance among *Lepidoptera* are of the latter class.[3] The same opinion is repeated in the joint paper with Mr. Prout describing the experiments referred to above.

Now this conclusion exactly coincides with the hypothesis that individual characters are transmissible in an alternative manner, while racial characters tend to blend. Various theoretical interpretations of the blending of characters have been put forward in order to make them compatible with the obvious Mendelian results. It has been stated, for instance, that when an intermediate colour between the parents appears in the offspring, the two colours really remain distinct, and are present as a very fine mosaic. Many such characters have, however, shown no tendency to segregate in the offspring, and this interpretation seems therefore too far fetched to be probable.

With regard to the classification of inheritance as blended, exclusive, and particulate, it would seem that the blended characters are generally racial. In cases of exclusive inheritance, some may be impure dominants, and it may be the same with regard to particulate inheritance.

It seems quite probable that the so-called aberrations in the breeding experiments with *Lepidoptera* referred to above, correspond to what have been very generally called

---

[1] Prout, L. B., and Bacot, A., "On the Cross-breeding of the moth Acidalia virgularia," *Proc. Roy. Soc.*, B. vol. lxxxi., 1909.

[2] Bacot, A., *Entomologist's Record*, xiii. pp. 114–17 and 142–44.

[3] Similar results have been obtained by Prout and Bacot with *Triphæna comes* and its dark aberration, *Entomologist's Record*, xv. and xvi.; *Xanthorhoë ferrugata* and its black aberration, *Trans. Entomological Society*, London, 1906, and *Proc.*, 1907.

mutations. Mutations, according to de Vries himself, are far more limited than would be gathered from the utterances of his followers. His conception apparently is, that mutations form that particular class of variations from which new species or sub-species are suddenly produced. On his hypothesis evolution has proceeded entirely through the selection of this particular class of variation, and he holds that characters due to mutations would blend when crossed, and would not be transmitted in the Mendelian manner. There seems to be no material evidence for this theory. It would of course be possible to say that when two characters blended they had arisen as mutations, and that when they segregated they had arisen as fluctuating variations. There is more reason to suppose that individual variations give rise to individual characters, and that these in turn give rise to racial characters. Individual characters tend to segregate, racial characters tend to blend when crossed. There is not the slightest necessity to assume two kinds of variations, though they may be large or small. Were any obvious difficulty overcome by such an assumption, there might be some excuse for making it. No such difficulty exists.

The new characters in a large variation are of course individual characters, just as much as they are in a small variation, so it is to be expected that the aberrations would behave in a Mendelian manner. It has been shown experimentally that this happens. It must be remembered that when an aberration is crossed with an individual possessing the mean characters of the race, natural conditions are interfered with, and artificial conditions are at once produced. As has already been pointed out, large variations must under natural conditions generally throw the individual out of harmony with its environment, and therefore such an individual would tend to be eliminated. Also, as the character is apparently transmitted in an alternative manner, if offspring were produced those that inherited it in a pure form would also be under a disadvantage and tend to be eliminated. If the improbable happened, however, as it may do sometimes, and the mutation or large individual variation in a character gave the individual an advantage, the fact that it is transmitted in an alternative manner would prevent that disappearance or diminution of the character that would be produced by blending. Conditions in an environment are conceivable where such a thing might happen. A race of moths, for instance, might occupy a large area of country in which the environment differed abruptly in a particular locality. Suppose that for some reason the physical surroundings became darker rapidly in this restricted locality than in the rest of the area, if a sudden large variation towards a darker colour occurred in an individual moth it might give it a considerable advantage. This changed locality might have harboured but few dark variants previously, because they were too conspicuous. The dark variation would survive its lighter fellows, in its descendants the dark character would segregate, and so a dark race would be established in this dark area much more rapidly than could happen if only small variations were available. Such an occurrence, however, must be extremely rare, and would generally be due to artificial conditions, such as the interference of man. He might not have intentionally changed the environment, but he might nevertheless have brought this result very effectually.

Apparently then we have characters that are transmitted alternatively from parent to offspring, and there seems to be evidence that such transmission occurs only in the case of individual characters. We also have characters that blend in the offspring. Racial characters behave in this manner. There is a mechanism in cell division by which certain parts of the cell are distributed in an alternative manner to the gametes, and while the bulk of the cell-substance mingles when two gametes fuse, these particular parts are distributed to the cells subsequently produced in such a manner as to suggest very strongly that they are intimately connected with the phenomenon of alternative inheritance of characters.

CHAPTER XI

The function, production, and determination of sex—Sex alternating in the same individual—Experiments on the determination of sex—Wilson's theory of the determination of sex—The Mendelian interpretation of the determination of sex—Archdall Reid's theory that Mendelian characters are non-sexual traits reproduced in the sexual mode—A suggested explanation—Potentiality of producing secondary sexual characters present in both sexes—Sex is a character which is probably transmitted alternatively like individual variations—Conclusions.

THE function, production, and determination of sex are problems so intimately connected with heredity that they must necessarily occupy an important place in any work upon this subject. The word sex is generally used to denote certain morphological differences found uniformly in individuals of the same species, but we find that it is only in the later stages of evolution that such differences exist. Where the production of a new individual necessitates the fusion of cells derived from two pre-existing individuals, it is obvious that a mingling of the germplasms must occur. We have seen that in some unicellular forms, periods of conjugation occur at intervals in the life-history of the race,[1] but in these organisms there is no sex. Any individual is capable of fertilising any other individual. We find that something of a similar nature happens in much more highly differentiated organisms. In some snails, for instance, the individuals are hermaphrodites, and every individual produces both ova and sperms. The effect of this mingling of the germplasm was considered in detail in Chapter VIII., and it is not necessary to do more here than point out that the conclusion arrived at was that the elimination of useless variations is thus ensured.

---

[1] See pp. 2, 3, 29.

The differentiation of the individuals of a species into males and females, that is, into individuals producing only sperms or only ova, is, as has already been said, a comparatively late product of evolution, and one evident result of this must be that inbreeding is rendered less close than it is in those races where every individual can play the part either of fertilising or being fertilised. Though the gametes produced by the two sexes vary much in size, structure, and appearance, it is a mistake to consider them, or speak of them, as male or female gametes, in the sense that one represents maleness and the other femaleness. As far as sex is concerned, there is no suggestion, in the great majority of cases, that a sperm represents maleness or an ovum femaleness. Indeed, in some cases the ovum may be destined to produce a male individual quite apart from any subsequent fertilisation by a sperm. Thus the unfertilised ova of a queen-bee produce males only, while the fertilised ova produce females, which may be either functional females or neuters according to the way in which the larvæ are fed. We must generally regard both sperms and ova as being potentially of both sexes, that is to say, under certain conditions either may produce males or females.

Passing from those organisms in which the individual is capable of performing both the paternal and maternal functions in reproduction, we find that there is evidence that sex, where it exists, sometimes remains undetermined much longer in the lower than in the higher organisms. In the hag-fish[1] (*Myxine glutinosa*), the sex of the individual appears to change. The fish is apparently at first a male and produces sperms, but later in life it produces ova and is functionally a female. In mammals, on the other hand, it is possible to distinguish between male and female at a very early stage in development.

Some direct experiments suggest that, in the case of

---

[1] Cunningham, J. T., *Sexual Dimorphism in the Animal Kingdom*, London, 1900.

some organisms at any rate, external conditions may play an important part in determining the sex of the individual long after fertilisation has taken place.[1] Yung found that tadpoles when kept under ordinary conditions produced about 57 per cent. female frogs. Tadpoles fed upon beef produced female frogs to the extent of 78 per cent., while those fed upon the flesh of frogs produced 92 per cent. females. The results of these observations have been disputed, and similar experiments with mammals have given negative results.[2] Nussbaum claimed that in the case of *Hydatina*—one of the Rotifers (wheel animalcules)—the amount of food determines whether the newly-hatched female will produce eggs giving rise to male or female individuals.[3] In other organisms it has also been claimed that an abundance of food and a low temperature result in the production of a large number of females in proportion to males.[4] It is possible that in the case of some organisms the proportions of the sexes depends to a considerable extent upon the action of the environment, though the results of some experiments made more recently do not agree with those mentioned.[5]

A plausible explanation in such cases is not far to seek, and might well be the result of natural selection. Taking the case of *Daphnia* (water-flea), if there were a very abundant food supply, it is evident that the race would benefit by the production of a large number of females.

---

[1] Yung, E., "De l'influence des variations de milieu physico-chimique sur le développement des animaux," *Arch. Sci. Phys. Nat.*, xiv., 1885; Born, G., "Experimentelle Untersuchungen über die Entstehung der Geschlechtsunterschiede," *Breslauer Aerztliche Zeitschrift*, 1881.

[2] Cuénot, L., "La détermination du Sexe," *Biblioge. Anat.*, iv., pp. 14–15, 1896; "Sur la détermination du Sexe chez les Animaux," *Bull. Scient. de la France et de la Belgique*, xxxii, pp. 462–535, 1899.

[3] Nussbaum, *Archiv f. mikro. Anat.*, 1897.

[4] Issakowitsch, A., "Geschlechtsbestimmende Ursachen bei den Daphniden," *Biol. Centralbl.*, xxv., 1905; *Arch. mikr. Anat.*, lxix., 1906; Malsen, H. von, "Geschlechtsbestimmende Einflüsse und Einbildung bei Dinophilus apatris," *Arch. mikr. Anat.*, lxix., 1906.

[5] Punnett, R. C., "Sex Determination in Hydatina," *Proc. Roy. Soc.*, B., vol. lxxviii., 1906.

One male is capable of fertilising a large number of females, and so the number of individuals produced in the next generation would be very large indeed. On the other hand, if the food supply were scanty and a large number of males were produced, the fertilisation of the comparatively small number of females would be absolutely ensured without throwing too great a strain on the already scanty food supply. Thus the environment would play an important part in regulating the number of individuals in succeeding generations, and is readily explicable as the result of natural selection.

In some cases the sex of the individual which is to be produced from the fertilised ovum may possibly remain undetermined for some time after development has commenced. In many cases, on the other hand, it appears to be determined from the very beginning. In some organisms we find that the eggs destined to produce females are different, and can be recognised before segmentation has commenced.[1] In other cases, as among bees and ants, the unfertilised eggs produce one sex, the fertilised eggs the other.

A new theory with regard to the determination of sex has been recently advocated. In order to grasp the full meaning of this theory it is necessary to glance back at the sequence of events occurring in the production of the gametes, and upon fertilisation.

The chromosomes are distributed to the gametes in such a manner that each contains only half the number of individual chromosomes contained in the somatic or body cells. In most organisms that have been specially investigated, the number of somatic chromosomes has been found to be an even number. The gametes, therefore, contain exactly half the number contained in the somatic cells. When fertilisation takes place, as each gamete contains half the somatic number, the full number of chromosomes is restored in the fertilised ovum.

---

[1] *e.g.* in Phylloxera Hydatina, and Dinophilus, two kinds of eggs are produced, large and small. The large produce females, the small males.

As long ago as 1891, Henking described two kinds of sperms as occurring in a genus of insects.[1] The same phenomenon has since been stated to occur in several other orders of insects, and in certain centipedes (Myriapoda) and Arachnids.[2] The difference between these two classes of sperms depends upon the presence of one or more additional chromosomes in some of them. This additional chromosome, the "accessory chromosome," is present in the cells of the male organism, and when reduction takes place, as it does not divide, half the sperms receive it, while the other half do not. Thus when fertilisation takes place, the chances that the fertilised ovum will contain this additional chromosome are exactly even.

That this accessory chromosome might be a sex determinant was first suggested by M'Clung.[3]

[1] Henking, H., "Über Spermatogenese und deren Beziehung zur Entwickelung bei Pyrrhocoris apterus," *Zeit. Wiss. Zool.*, li., 1891.

[2] Montgomery, T. H., Jr., "The Spermatogenesis in Pentatoma up to the Formation of the Spermatid," *Zool. Jahrb.*, xii., 1898 ; "The Spermatogenesis of Peripatus (Peripatopsis) Balfouri up to the Formation of the Spermatid," *Ibid.*, vol. xiv., 1900 ; "Further Studies on the Chromosomes of the Hemiptera heteroptera," *Proc. Acad. Nat. Sci.*, Philadelphia, 1901 ; "A Study of the Chromosomes of the Germ Cells of Metazoa," *Trans. Amer. Phil. Soc.*, vol. xx., 1901 ; "Some Observations and Considerations upon the Maturation Phenomena of the Germ Cells," *Biol. Bull.*, vol. vi., 1904 ; "The Spermatogenesis of Syrbula and Lycosa, with General Considerations upon Chromosome Reduction and the Heterochromosomes," *Ibid.*, 1905 ; "Chromosomes in the Spermatogenesis of the Hemiptera heteroptera," *Trans. Amer. Phil. Soc.*, N.S., vol. xxi., Part III., 1906 ; Wilson, E. B., *Science*, N.S., vol. xxix., No. 732, January 1909 ; Paulmier, F. C., "The Spermatogenesis of Anasa tristis," *Journ. of Morph.*, xv., Supplement, 1899 ; Payne, F., "On the Sexual Differences of the Chromosome Groups in Galgulus oculatus," *Biol. Bull.*, xiv. 5, 1908 ; Stevens, N. M., "On the Ovogenesis and Spermatogenesis of Sagitta bipunctata," *Zool. Jahrb. Anat. u. Ontog.*, xviii., 1903 ; "Studies in Spermatogenesis, with Especial Reference to the 'Accessory Chromosome,'" Carnegie Institution, Washington, Pub. No. 36, 1905 ; "Studies in Spermatogenesis : II. A Comparative Study of the Heterochromosomes in Certain Species of Coleoptera, Hemiptera, and Lepidoptera, with Especial Reference to Sex Determination," *Ibid* , Pub. 36, ii., 1906 ; "A Study of the Germ Cells of Certain Diptera, &c.," *Journ. Exp. Zool.*, v. 3, 1908*a* ; "The Chromosomes in Diabrotica, &c.," *Ibid.*, v. 4, 1908*b* ; Lefevre, G., and M'Gill, C., "The Chromosomes of Anasa tristis and Anax. junius," *Am. Journ. Anat.*, viii. 4.

[3] M'Clung, C. E., "The Accessory Chromosome—Sex Determinant?" *Biol. Bulletin*, vol. iii., 1902.

Since this suggestion was made, the theory has been elaborated in detail by Professor E. B. Wilson, and a great deal more evidence has been produced. It has been shown that in several animals the body cells of the female possess at least one more chromosome than those of the male individual. It is claimed that in nearly a hundred species of insects, two classes of sperms have been demonstrated, equal in number, that differ in respect to one or more of the chromosomes that enter into the formation of their nuclei. It is supposed that eggs fertilised by one class of sperm produce males, those fertilised by the other class females.[1] In the simplest cases the course of events is as follows. The cells of the female organism contain two accessory chromosomes, and so all the ova before maturation, that is, before reduction takes place, contain them both. When reduction has taken place, *all* the ova will contain one accessory chromosome. On the other hand, the cells in the male organism only contain one accessory chromosome, including those cells destined to produce sperms. When reduction takes place, half the resulting cells will contain the accessory chromosome, half will not. Only *half* the sperms, therefore, will contain the accessory chromosome. If a sperm containing the accessory chromosome fuses with an ovum, the result will be a cell with two accessory chromosomes, and a female will be produced. If a sperm without an accessory chromosome fertilises an ovum, a male will be produced.

The difference between the sperms are by no means always as simple as this, but the general idea of the theory is adequately conveyed, and it would be out of place to enter into the details in a general work of this nature.

Observations upon bees and certain other animals are

---

[1] Wilson, E. B., "Studies on Chromosomes," I., *Journal of Exper. Zool.*, vol. ii., No. 2, 1905; "Studies on Chromosomes," II., vol. ii., No. 4; "Studies on Chromosomes," III., vol. iii., No. 4, 1906; "Studies on Chromosomes," IV., vol. vi., No. 1, 1909; "Studies on Chromosomes," V., vol. vi., No. 2, 1909; "Recent Researches on the Determination and Heredity of Sex," *Science*, N.S., vol. xxix., No. 732, January 1909.

very suggestive with regard to Wilson's theory. In these particular cases it has been shown that the unfertilised eggs produce males, the fertilised eggs females. But it has also been shown that half the cells destined to be converted into sperms in the males, degenerate and never fertilise the ova.[1] It is also stated that the cells that degenerate are those that lack the supernumerary chromosome. Wilson claims that the functional sperms must therefore all produce females. Tempting as this theory is, it is impossible at present to accept it unreservedly. Among the vertebrates, where the production of sperms has been extensively studied, there is no evidence whatever for two kinds of sperms or for the existence of an accessory chromosome. In some animals it has been shown that there are two kinds of eggs,[2] and it has been suggested that the process in these cases may be reversed, the accessory chromosome being present in some of the eggs but not in the others. Among vertebrates we have no evidence for two kinds of eggs, although the process of ovigenesis has not been so exhaustively studied as that of spermatogenesis.

It is necessary to point out that the existence of the accessory chromosome has been disputed, even in one of the organisms employed by Wilson, and observations upon other insects suggest that there may be a certain amount of misinterpretation on this point.[3] Both parties have repeated their observations and still remain in disagreement. Exhaustive observations upon the maturation of the eggs of an insect closely allied to the subjects of the observations of Wilson and his supporters, upon the eggs of an earthworm (Allolobophora), and upon the spermatogenesis of other insects, suggest very strongly that the interpretation of

---

[1] Meves, F., "Die Spermatocytenteilungen bei der Honigbiene, nebst Bemerkungen über Chromatinreduktion, *Arch. f. mikr. Anat.*, lxx, 1907; Morgan and von Baehr, quoted by Wilson, *Science*, vol. xxix., No. 732, 1909.

[2] *e.g.* Rotifers, see p. 193.

[3] Foot, K., and Strobell, E. C., "The Accessory Chromosome of Anasa tristis," *Biol. Bull.*, xii., 1907; "A Study of the Chromosomes in the Spermatogenesis of Anasa tristis," *Am. Journ. Anat.*, vii. 2, 1907.

the functions of an accessory chromosome cannot be of such general application as is claimed.[1] The existing evidence applies largely to one group of insects. For some members of this group, however, the evidence seems fairly strong that the chromosomes in half the sperms differ from those in the other half, and that in which sex is produced depends upon which class of sperm has fertilised the mature ovum. This theory will be considered again later.

Accepting Wilson's theory, attempts have been made to show that it corresponds to the Mendelian mode of transmission, and that sex is in fact a Mendelian character. Some of these attempts have been controverted by Wilson himself.

"This interpretation has been worked out in three forms, which exhaust the *a priori* possibilities. These are, first, that both sexes are sex-hybrids or heterozygotes[2] (Castle); second, that the male alone is a heterozygote, the female being a homozygote recessive (Correns); third, that the

---

[1] Foot, K., and Strobell, E. C., "The Nucleoli in the Spermatocytes and Germinal Vesicles of Euchistus variolarius," *Biol. Bull.*, vol. xvi., 1909; Arnold, G., "The Nucleolus and Microchromosomes in the Spermatogenesis of Hydrophilus piceus," *Archiv für Zellforschung*, ii. 1, 1908; Farmer and Moore, "The Meiotic Phase (Reduction Division), in Animals and Plants," *Quart. Journ. Micro. Science*, vol. xlviii., Part IV., 1905. Foot and Strobell say (1909), with regard to the work of Lefevre and M'Gill: (1) In her first work on this form (1904), in which she expresses her indebtedness to Professor Lefevre, she found no evidence of a chromatin nucleolus in the resting spermatocyte. She and Lefevre now find, *in the same material*, a chromatin nucleolus persisting through the resting spermatocyte. (2) In her earlier work M'Gill identified the microchromosome as the accessory chromosome. She and Lefevre now identify, *in the same material*, one of the larger spermatogonial chromosomes as the accessory chromosome. (3) In her original count of the spermatogonial chromosomes, M'Gill found an even number, 28. She and Lefevre now find, *in the same material*, an odd number, 27 spermatogonial chromosomes. In view of these contradictions we may justly hesitate to accept as definite the recent conclusions reached by M'Gill and Lefevre in *Anasa tristis*, believing a new point of view may give us still further variations in their very interesting observations.

[2] A "zygote" is the product of the fusion of two gametes. "Heterozygote" is the Mendelian word for a zygote made up of two gametes, each bearing the opposites in a pair of Mendelian characters (one the dominant, the other the recessive). A heterozygote is in fact an impure dominant. A "homozygote" is a zygote in which both gametes contain the same Mendelian character, both dominants or both recessives. Extracted dominants or extracted recessives are called homozygotes.

female is the heterozygote, the male being a homozygote recessive (Bateson). I will very briefly examine each of these hypotheses.

"The earliest of the three was that of Castle, according to which the fertilisation formulæ would be—

[1] Egg ♀ + spermatozoon ♂ = zygote ♀ (♂) (female)
Egg ♂ + spermatozoon ♀ = zygote ♂ (♀) (male)

or

Egg ♀ + spermatozoon ♂ = zygote (♀) ♂ (male)
Egg ♂ + spermatozoon ♀ = zygote (♂) ♀ (female)

according as the dominant character is borne by the egg or the spermatozoon. In either case a selective fertilisation must be assumed, since only gametes bearing opposite tendencies unite.

"This interpretation encounters two principal difficulties. One is the necessity of assuming selective fertilisation, which, though possible, seems *a priori* improbable.

"The other is the case of the bee and some other hymenoptera, which was pointed out by Castle himself, but is now seen to be even more serious than he supposed. In the bee, all the eggs after forming both polar bodies produce males if unfertilised, females if fertilised. Under the hypothesis, therefore, the female tendency must be derived from the spermatozoon. But this is a *reductio ad absurdum;* for the male is derived from an unfertilised egg which has by the hypothesis eliminated the female tendency. Castle offered the very ingenious explanation, based on the results of Petrunkewitsch, that the testis is derived from the polar bodies, which contain the female tendency. But this exit from the difficulty seems to be closed by the work of Sylvestri on certain of the Chalcidæ (*Ageniaspis, Litomastix*) and that of Schleip on the ant (*Formica*), which clearly proves that the products of the

---

[1] ♂ = male character, ♀ = female. The signs in brackets are those which do not appear in the individual containing them.

polar bodies in these forms do not in fact enter into the composition of any part of the body, yet the sexual relations are the same as in the bee. This difficulty seems to me to constitute a formidable obstacle not only to Castle's hypothesis, but to the whole Mendelian interpretation.

"The second hypothesis is that of Correns, which assumes the male to be a sex-hybrid while the female is a homozygous recessive. The fertilisation formulas are accordingly—

Egg ♀ + spermatozoon ♀ = zygote ♀ ♀ (female)
Egg ♀ + spermatozoon ♂ = zygote (♀) ♂ (male).

This conclusion is based on the following beautiful experiments. Crosses between monecious[1] and diecious flowering plants show that the monecious character behaves like a 'unit character' which is recessive to the diecious. If reciprocal crosses be made between the monecious *Bryonia alba* and the diecious *B. dioica*, the results are as follows. Female *dioica* crossed with the male *alba* gives all females. The reverse cross gives half males and half females. From the fact that all the offspring of female *dioica* X male *alba* are females, Correns concludes that all the eggs bear this tendency, which dominates the monecious character of the male parent. In the reverse cross the diecious character again dominates, but in this case is derived from the male parent. The appearance of the two sexes in equal numbers must therefore mean that half the pollen grains bear a dominant male tendency and half a recessive female. A similar result is reached by Boll by experiments of quite a different character on the hemp, but the proof seems to me less cogent.

"Correns's experiments are of admirable ingenuity, and his results seem at first sight to be open to but one conclusion. His interpretation renders the hypothesis of selective fertilisation unnecessary; for the chance fertilisa-

---

[1] A plant (or animal) is said to be *diecious*, when individuals produce only sperms or only ova, that is, when male and female individuals are separate. *Monecious* individuals produce both sperms and ova, the same individual thus performing the functions of both sexes.

tion of any egg by any spermatozoon explains the numerical quality of the sexes in the same way that it explains the equal numbers of the two classes of offspring of an ordinary Mendelian cross between a homozygote recessive and a heterozygote. An obvious difficulty at once appears, however, in the parthenogenetic forms; for here the parthenogenetic females must bear both tendencies, since they, sooner or later, produce males without fertilisation. We need not enter into Correns's suggestions in regard to the aphids and phylloxerans, since they are contradicted by the facts of the spermatogenesis. In the case of the bee, he adopts Beard's supposition that there are two kinds of eggs —sexual female-producing, which require fertilisation, and parthenogenetic male-producing. In the latter the original female tendency is replaced by the activation or setting free of a male tendency previously latent.[1] A similar explanation might be applied to the aphid, phylloxeran, or daphnid. But does not such manipulation of the sexual tendencies greatly weaken the force of the Mendelian interpretation? To me it seems that if the sexual tendencies may thus be shifted back and forth between the active and latent states, the interpretation loses most of its explanatory value.

"Can we then explain the difficulty in question by reversing Correns's hypothesis, assuming the male to be the homozygote, the female the heterozygote? This is the hypothesis of Bateson, who further suggests that different species or groups may differ in respect to the sex that is homozygous. The fertilisation formulas now become—

Egg ♀ + spermatozoon ♂ = zygote ♀ (♂) (female)
Egg ♂ + spermatozoon ♂ = zygote ♂ ♂ (male).

But new and even more serious difficulties now arise. If

---

[1] To understand this it must be borne in mind that Correns regards each "active" sexual tendency (whether dominant or recessive) as accompanied by a "latent" (not to be confused with a recessive) opposite tendency. Such a latent male tendency in the female, upon becoming activated, would dominate the female.

the male be homozygous in the ordinary forms of insects, what sense can be found in the production of two forms of spermatozoa? Still worse is the dilemma presented by the parthenogenesis of the bee or ant. If we here assume that the egg eliminates the female tendency in maturation, fertilisation should produce a homozygous male, which is contrary to fact. If, on the other hand, we assume the male tendency to be eliminated, parthenogenesis should produce females, which is also contrary to fact. The only escape from this seems to lie in the assumption that if unfertilised the egg eliminates the female tendency; if fertilised, the male.[1] But can we regard this as probable?"[2]

Since writing the above Professor Wilson's views have been modified, and he now agrees that, as is pointed out by Castle,[3] his method of quantitative formulation is quite as open to a Mendelian interpretation as the other view. The essence of his present view is, "that one sex is cytologically a 'heterozygote,' the other a 'homozygote,'" the latter being sometimes one sex and sometimes the other, exactly as Bateson assumes from experimental results. Male and female "tendencies" are not conceived (as for instance Correns seems to conceive them) as two distinct and opposing things, but as differing primarily by a quantitative relation—*i.e.* in respect to the X element. This avoids many difficulties, particularly in parthenogenesis, and gets rid of selective fertilisation. This is essentially in agreement with Castle's new view, and wholly different from his early one which involved selective fertilisation.[4]

It will be seen later that the interpretation adopted by Professor Wilson is in many ways similar to that advocated in these pages. Sex being an alternative character, necessarily resembles the Mendelian characters in being alter-

---

[1] This suggestion is due to Professor Morgan.

[2] Wilson, E. B., "Recent Researches on the Determination and Heredity of Sex," *Science*, N.S., vol. xxix., 1909.

[3] *Science*, March 5, 1909.

[4] Letter from E. B. Wilson to Author, April 22, 1910.

native in those organisms where the sexes are separated, but in many ways it differs essentially.

The production of both fertilising and fertilised gametes by the same individual would appear to be a more primitive condition than the production of only one kind of gamete by each individual. The separation of the sexes, that is, the alternative transmission of sex, necessitates our assuming the pre-existence of an alternative mode of transmission for some characters. Also we must remember that the most perfect Mendelian results have been obtained from organisms which are usually self-fertilised, in which sex in the sense implied by the Mendelian experimenters does not exist. It must be admitted then, by those who uphold the purely Mendelian interpretation of the separation of the sexes, that sex may sometimes be a Mendelian character and sometimes may be blended.

If secondary sexual characters are taken as being included in sex, then the case becomes even more difficult, for it is demonstrable in many cases that the secondary sexual characters of both sexes are potentially present in all individuals.[1] This would involve the supposition that all individuals are impure dominants or impure recessives (!), which would hardly be conceivable on Mendelian lines.

Archdall Reid proposes a theory exactly opposite to that put forward by the Mendelians. He believes that "Mendelian characters are non-sexual traits which are reproduced in the sexual mode." "If we examine any of the so-called Mendelian characters, we find that the majority may fairly be described as secondary sexual characters, though not necessarily as sexual differences, for example, colour and form of plumage." "It seems clear, then, that there is no real segregation, no real alternative inheritance, but only an alternative production, alternative patency and latency."[2]

---

[1] See p. 205.

[2] Reid, G. Archdall, Report of paper read to the Linnean Society, December 19, 1907, *Nature*, January 9, 1908.

He states that sexual characters are not alternative, but that while one sex predominates, traces of the other are always evident. The same takes place in the case of the dominant and recessive Mendelian characters, recessive appearing occasionally in lines of pure dominants, and *vice versa.*

This theory appears to agree with the available evidence more nearly in some ways than the purely Mendelian interpretation, but it stops far short of the facts at our disposal. It is quite true that, just as traces of the opposite Mendelian character are found in extracted dominants or recessives, traces of the male are found in the female and *vice versa.* We also find gradations between hermaphroditism and complete functional differentiation of the sexes. To say, however, that there is no real alternative inheritance seems to be playing with words. The alternativeness may not be absolutely complete, but in the case of many organisms the functions of the male and female are confined to separate individuals. It is possible that the potentiality of developing into a male or a female individual may be present in all the fertilised ova. If this be the case, then there must be something controlling the appearance of the characters belonging to one sex, and this something must be transmitted in an alternative manner. The very fact that even in an organism where the sexes are so definitely separated as in man, hermaphrodites occasionally appear, suggests that one set of characters is patent and the other latent. This is also suggested by the fact that one or two male characters appear occasionally in the female and *vice versa.* While therefore it is evident that, as with the Mendelian characters, the alternativeness is generally not complete, still the characters are alternative, and only one set appears fully in one individual.

In the vast majority of cases there seems to be an explanation which is quite compatible with all that is known with regard to the inheritance of sex. In some unicellular organisms where fertilisation has been shown to take place,[1]

---

[1] See p. 205.

every individual is capable of fertilising and being fertilised, and performs both functions. At a later stage in evolution we find that the cells that are to be fertilised—the ova—and the cells that fertilise—the sperms—are differentiated from each other, although both are produced by the same individual. Later still we find that although the same individual produces both ova and sperms, these groups of cells become mature at different periods, the sperms at one time, the ova at another. Thus the fertilisation of the ova by sperms produced in the same individual is prevented, and cross-fertilisation is ensured. Among the higher animals we find that the individual produces only sperms or only ova, that is to say, the sexes are separated.

Now it appears certain these steps in evolution must have been produced by natural selection acting upon variations. It is by the selection of individual characters that racial characters have been produced, and we know of no other material upon which selection could work. Sex, then, must certainly have been produced by the selection of individual characters. We have seen that racial characters when crossed, tend to blend, while individual characters tend to be transmitted in an alternative manner. Variation towards producing sperms and ova at different times, and subsequently variations towards producing only sperms or only ova, would at first be transmitted in an alternative manner. The advantages of sperms and ova being produced in separate individuals are very obvious, for inbreeding is thus limited to a considerable extent. If such variations, however, tended after a long period of selection to produce characters that blended, hermaphrodites would tend to be produced again, that is, the sexes would blend, and the whole advantage of the sexes being in separate individuals would be lost. It is therefore probable that natural selection has so influenced the sexual characters, as to keep them within the category of individual characters, in so far as their mode of transmission is concerned, and has prevented their blending when crossed, as appears to have happened in the case of other ancient characters.

Before proceeding further with this question it is necessary to clear up certain points connected with secondary sexual characters. Secondary sexual characters are those which, though appearing in all individuals of the same sex and not in those of the other sex, are not connected directly with the sexual function, that is, with reproduction. Such characters are the beard and voice of a man and the antlers of a stag. There is a great deal of evidence which suggests that the potentiality of producing these characters is present in the individuals of both sexes. Among mammals and birds we constantly find that the characters of the young male are those of the female, minus of course a few special characters. The plumage of the young cock pheasant is similar to that of the adult female; a boy's voice is similar to that of a woman. If during infancy the sexual glands are removed from a male animal, the male secondary sexual characters do not appear. Not only are the physical characters, such as change in voice and plumage, inhibited, but mental characters, such as pugnacity, do not develop. There are some direct experiments which suggest very strongly that the appearance of the secondary sexual characters is dependent upon the presence in the body of the sexual glands. It has been found that if the fresh sexual gland of a cock be pounded up and injected hypodermically into hens, their combs and wattles grow to a very large size. On the cessation of the injections the combs diminish until they have reached the normal size again.[1] It has also been shown that in the cock, if even a very small portion of the sexual gland is left in the body, the secondary sexual characters become fully developed, and this in spite of the fact that the bird is quite unable to fertilise the eggs of the hen. The same has been shown in the case of sheep.[2] If, however, the

---

[1] Walker, C. E., "The Influence of the Testis upon the Secondary Sexual Characters of Fowls," *Proceedings of the Royal Society of Medicine*, April 1908.

[2] Shattock and Seligmann, *Transactions of the Pathological Society of London*, vol. lvi. p. 57, 1905; vol. lvii. p. 69, 1906.

sexual glands be completely removed in the young male, the secondary sexual characters do not appear. It would seem, therefore, that when the cells forming the male sexual gland are present, the male secondary sexual characters appear whether the individual be male or female. There are other facts which also suggest that the potentiality for producing these characters is present in both sexes. For instance, old hens (*e.g.* pheasants), when they have passed the period of laying eggs, not infrequently develop the plumage of the male bird. The same kind of thing is frequently seen in the human race, where old women grow hair upon their faces. Now this seems to be quite different to what happens in the case of the Mendelian characters. There is no evidence in many of the Mendelian experiments that sex has anything to do with their mode of transmission, In those where segregation appears to be most complete, the individuals are self-fertilised, so in these cases it is obvious that sex is not alternative. The dividing of characters into "individual" and "racial" makes it possible to explain why some characters are transmitted in an alternative manner, while others blend. Apart from this there seems to be no explanation of the Mendelian phenomena. Archdall Reid says that Mendelian characters may be fairly described as secondary sexual characters.[1] By this it must be supposed he means that secondary sexual characters are similar in nature to those which have been found to give more or less complete Mendelian results. But when we come to look into the matter carefully, we find that characters that give Mendelian results in the case of one race, do not do so in another race. Colour has been used in the Mendelian experiments as much as any other character, yet in man colour blends when crossed. Many of the examples of blending previously quoted[2] might just as fairly be described as secondary sexual characters, but there is not the slightest evidence to show that they are, and much which suggests that they are not. Many such characters,

---

[1] See p. 202.

[2] See pp. 118, 186.

which are transmitted in the Mendelian manner, are just as common in one sex as in the other, while others blend, thus behaving in a manner quite different to the secondary sexual characters.

The evidence then seems to suggest that the secondary sexual characters are dependent for their development upon the presence of the sexual glands in the individual, and that the potentiality of producing them is present in all individuals of both sexes. Whatever is alternative in their appearance is dependent upon the fact that sex is alternative.

The fundamental difference between the two sexes is that one produces sperms, the other ova. How far any differences beyond this should be regarded as secondary and not primary sexual characters is immaterial to the question now under consideration. It has already been pointed out that, had sex, like other characters that have become racial, ended in blending when crossed, hermaphrodites would have been produced, and sex would have been eliminated. Natural selection has preserved the alternative transmission of sex, and the race thereby gains material advantages through the limitation of inbreeding. The whole usefulness of sex depends, therefore, upon its inheritance remaining alternative.[1] *Hence natural selection would eliminate all variations towards blending, and sex would continue to be transmitted in the same manner as an individual character. In fact, it seems that sex ought to be regarded as a character*

---

[1] A certain school of biologists holds that the explanation of the appearance of a character on the grounds of its utility is insufficient, and that such an explanation is unscientific and superficial. Apart from the fact that this condemns all our greatest biologists, including particularly Darwin, as unscientific and superficial, it is difficult to see, admitting that evolution is a fact, how the existence of the great majority of racial characters is to be accounted for in any other way. Useful variations have given their possessors an advantage over their fellows, and so they have been preserved. It does not matter in this case whether acquired characters are or are not transmitted. Variations have been preserved and have produced characters because they were advantageous to their possessors—because they were useful. The critics of this explanation fail to distinguish between the meanings of the words why and how. An explanation that is quite satisfactory as to *why* a thing has come about, need not attempt to explain the details of *how* it has done so.

which has been kept in the category of individual characters and has been prevented from becoming a racial character by the action of natural selection, in spite of the fact that it is far more ancient than a great many of the racial characters.

The hypothesis that sex has continued as an individual character in some important respects and is transmitted in a similar manner to individual characters, would rest upon a very insecure basis, were it not that there is a mechanism in cell division which provides for the alternative distribution of certain bodies before fertilisation. All that has been said with regard to the alternative transmission of individual characters applies equally to the alternative transmission of sex. Sex, however, is the only character upon which the action of natural selection has been such as to keep it alternative, and therefore we should expect to find some differences between the way in which it is transmitted and the results of the Mendelian experiments. In the case of every other individual character, the final result must be either elimination or the production of a racial character.

It is of course necessary to assume that there are several entities in every cell representing both sexes. It is quite possible that in the case of the insects observed by Wilson these entities may be collected in one or two chromosomes. It is not necessary, though, to suppose that this has happened in the majority of cases. We constantly find instances of peculiar differentiation with regard to particular characters in living organisms, and it may well be that the cases of the animals where a difference exists between the cells of the male and female, are due to some special differentiation, the exact purport of which we do not as yet understand. Where we have no evidence as to the existence of any particular sex-producing chromosome, it is not at all necessary to assume one. The entities that control the appearance of one sex or the other might be present in one or in several chromosomes. It certainly seems that both sexes are represented in all cells. The alternative distribution of the chromosomes and their recombination upon fertilisation would make it very improbable, but not impossible, that the entities controlling the appearance of the sexes would be equal in any individual. Such an event would happen but seldom. Hermaphrodites do occur among organisms where the sexes are as a rule separate, but they are rare. In the highest animal, man, they are extraordinarily rare. This theory also accounts for those cases where men show female characters and women male characters.

If this view of sex is correct, the secondary sexual characters must be regarded as racial characters, but dependent for their appearance upon the presence of one or other kind of sexual cells, in fact, upon the primary sexual character. We know that a particular reaction to given stimulus may be a true racial character, so there is no reason against supposing that the appearance of the secondary sexual characters depends upon the presence or absence of some stimulus such as an internal secretion of the sexual cells. Indeed, that this is the case is suggested very strongly by the experimental evidence already referred to.[1]

It seems very probable that the Mendelian interpretation of some breeding experiments is due to the fact that the alternative appearance[2] of the secondary sexual characters has been overlooked. In an experimental cross between the moth *Abraxas grossulariata* and its variety *lacticolor*,[3] it was claimed that "sex determinants behave as Mendelian characters," femaleness being dominant. The case may be briefly stated as follows. When a female variant, *lacticolor*, was crossed with a male *grossulariata*, males and females were produced in roughly equal numbers. This continued in subsequent generations, but no males with the *lacticolor* characters were produced. From this it was concluded that all the females were impure dominants (heterozygous) with

---

[1] See p. 205.

[2] Though potentially present the secondary sexual characters under ordinary conditions only appear in the presence of the necessary stimulus, *i.e.* one or other forms of germ cells.

[3] Doncaster, British Association Meeting, 1908.

regard to sex; that all the males were pure recessives (homozygous) and carried only the male character; and that the *grossulariata* character could not be borne by a female bearing gamete. The Mendelian interpretation of the transmission of sex has already been dealt with,[1] but the behaviour of the *lacticolor* character seems readily explicable as a secondary sexual character. This might appear to be a somewhat wild guess, were it not that another variety of *Abraxas grossulariata* is known to be sexually dimorphic.[2] In the variety *varleyata*, the male has white rays upon its wings. These rays are generally present on the hind-wings only, and are usually from two to five in number.[3] They are very noticeable and produce a very pretty effect. They are apparently never present in the female.

The conclusions arrived at may be briefly summed up as follows:—As bi-parental reproduction tends to eliminate all useless variations this effect must be accentuated when the sexes are separate, that is, when any given individual produces only sperms or only ova, for inbreeding cannot then be so close as when every individual produces both sperms and ova. Sex being therefore advantageous to the race, has been produced by the action of natural selection upon individual variations. As the utility of sex depends upon the two characters remaining separate, the effect of natural selection has, while preserving and accentuating them, prevented their tendency to blend, as racial characters generally do. That variations towards blending do occur is shown by the occurrence of hermaphrodites in species where the sexes are generally separate. The fact that sex is transmitted in an alternative manner like individual characters, has led some observers to consider sex as an ordinary individual or Mendelian character. The fact that the secondary sexual

---

[1] See pp. 197, 202.

[2] Porritt, G. T., *Entomologist's Monthly Magazine*, Second Series, vol. xviii. p. 12, 1907.

[3] Mr. Porritt describes one example which has "six rays on each fore-wing and seven and six respectively on the hind-wings," *op. cit.*

characters, although they are really racial characters, only appear in the presence of one or other class of gamete, has led to the assumption that the individual or Mendelian characters are similar to or identical with them. Lastly, the distribution of the chromosomes to the gametes and their recombination at fertilisation, provides a mechanism for the alternative distribution of sex-producing or sex-controlling entities, just as in the case of individual characters.

CHAPTER XII

In the foregoing chapters an attempt has been made to bring together the main points of the available evidence with regard to the transmission of hereditary characters. There are many conflicting theories with regard to the various problems connected with heredity, and no doubt this is in part due to the fact that general theories have been based upon limited groups of phenomena, without taking the evidence afforded by other groups into account. Our knowledge of cell phenomena has advanced with extraordinary rapidity in recent years, and as we have no knowledge of living matter except in the form of cells, it is obvious that the evidence afforded by this branch of biology must be included in all theories of evolution and heredity. Unless such theories are compatible with what we know happens during the processes of cell multiplication, the production of the gametes, and fertilisation, they cannot be true. On the other hand, no interpretation of cell phenomena can be correct unless it harmonises with observed facts with regard to the transmission of characters from parents to offspring.

When apparently contradictory groups of facts are considered separately by different groups of biologists, there is a probability that each party will deny the facts of their opponents. Something dangerously like this has occurred in recent years. The Mendelians have gone very near to denying any mode of hereditary transmission excepting the alternative, while the biometricians have sought to explain the Mendelian experiments in some way that hardly allows alternative transmission as a natural phenomenon. It is really ridiculous to question the observations of either party. Both have provided most valuable evidence. There is no doubt as to alternative transmission, but a failure to consider other evidence in an unbiassed manner seems to have led some of the Mendelians into a narrow interpretation of the results of their experiments which is incompatible with other classes of facts.

The work of the biometricians has proved beyond a doubt that variations occur around a racial mean in so regular a manner that a curve will represent the differences of any given character in the various individuals of a race in any given time.[1] They have also shown that the offspring of parents, which diverge considerably from the racial mean in any character, tend to revert to the mean.

We have seen that there is a provision in the mode of cell division, in the production of gametes, and in the process of fertilisation, for the transmission of characters in an alternative manner; but we have also seen that, according to the evidence at our disposal, only individual characters can be thus transmitted. Racial characters must be transmitted in a different way. It is quite obvious that all characters must be transmitted through the single cell, the fertilised ovum. How this happens in the case of the individual characters is easy to see, for we have individual entities, the chromosomes, that are distributed from cell generation to cell generation, from parents to offspring, in a manner that coincides exactly with the behaviour of the individual characters. The evidence with regard to what part of the cell bears the racial characters is conflicting. It may very likely be that the whole protoplasm of the cell has this power.

Though there are instances of individual characters in process of becoming racial characters, and there is but little doubt as to the broad lines of the process of transformation, we have no evidence as to the cell phenomena connected with this change. It is of course possible to speculate. It is evident that if an individual character is represented in

---

[1] See p. 99.

an individual chromosome, and if this individual character gives the organism an advantage, the entities representing the character must be increased at each subsequent generation through the action of natural selection. Thus in time every chromosome would contain entities representing the character selected. It may be that when all the chromosomes in all the individuals of a race have contained entities representing a particular character for a certain length of time, the potentiality of producing that character is acquired by the general protoplasm of the cell.

Apparently acquired characters can be but rarely if ever transmitted from parents to offspring. Even accepting this view, it is necessary to realise very thoroughly, in considering social and hygienic problems connected with the human race, that most characters in man are acquired characters, or are inborn characters modified beyond recognition by acquirements. The only reason why man has attained his high position in relation to other living organisms is, that he possesses a vastly greater capacity for making acquirements than is the case with any other organism. Most of his instincts have gone, and even most of his physical characters are liable to extreme modifications; indeed, but for use acquirements, the body of man would fail to develop into a form recognisable as that with which we are familiar.

Mental characters are also due very largely to acquirements. Of course individuals differ in their capacities for making various mental acquirements, but these characters must depend to a considerable extent upon environment, that is, upon education in its broadest sense. Any form of education which limits the making of mental acquirements must be fundamentally wrong. That child will have the best chance of complete mental development who is taught to think for itself, and to judge between the true and false, reason and unreason. To bring up children on bald dogma, and to teach them that enquiry in certain directions is wrong, must necessarily limit their mental development.

During the early periods of life, habits of mind are easily formed, and may become almost as strong as instincts. The habit to cultivate is then one of enquiry into the why, wherefore, and how, of everything. Certain forms of religion are opposed to this view on principle. It must not be forgotten that the truth can but become more obvious upon enquiry, if it really be the truth.

On the whole, then, the environment, particularly of children, is most important to the race in civilised communities. So very much depends upon acquirements, and in some ways so little upon the inborn characters, that in spite of acquired characters not being transmitted, too much attention cannot be given to them.

The question of disease is also one upon which the facts connected with heredity have a very direct bearing. There can be no doubt that characters tend to disappear more or less rapidly as soon as they cease to be the subjects of selection. To put the case another way, if the environment of a race changes in such a manner as to render useless certain characters that were previously useful, these characters will disappear. This happens even in the case of anatomical structures, such as limbs;[1] it happens also in the case of immunity to disease. In dealing with diseases occurring among civilised races of men, this point is worthy of consideration. Immunity to a disease can only be obtained by a race in the presence of selection, that is, the disease must exist in the environment. The degree of immunity existing in any given race will be proportionate to the length of time during which selection has acted, and to the extent of the infection. When the disease is such that every individual, or almost every individual, is certain to be infected, a comparatively high degree of immunity will be reached. This is the case with tuberculosis. Practically every one in Northern Europe must be infected with the tubercle bacillus at some time or other, and in towns a large proportion of the population must be infected very

---

[1] See pp. 66–7.

frequently.[1] When tuberculosis is introduced into a race that has not been subjected to selection, a large part of the population is destroyed, or the race may even be exterminated. Of course there will be variations away from the racial standard of immunity, even in the most immune races, and the individuals that vary thus will contract the disease. Anything, then, that diminishes the chance of infection generally in an immune race will tend to lower the racial standard; hence it is doubtful whether it is wise to adopt general measures to lessen the risks of infection in the case of those diseases where it is impossible to hope that *all* risk of infection may be permanently removed. In the case of tuberculosis, it is very doubtful whether anything more than a lessening of the risk of infection could be accomplished. The bacillus is capable of living for considerable periods in a dried state away from the bodies of animals; and it is so widely distributed and is so resistant to heat and cold, that its complete extermination seems an impossible achievement. We have already attained a high degree of immunity, and merely lessening the risks of infection without destroying them altogether, would result in a lowering of the resisting power of the race, and might eventually end in disaster. It all depends, of course, whether the race or the individuals is considered. Here the point of view adopted is what is best for the race.

With some diseases, however, it is quite feasible to prevent all chances of infection. Typhoid fever is an example. The micro-organism is almost always water-borne. The precautions necessary to preclude all possibility of infection are very limited, compared to what would have to be done in the case of tuberculosis, at any rate in civilised communities, and the probability is that the preventive measures will improve in the future. On the other hand, measles, chickenpox, and other similar diseases, to which we as a race have developed a power of acquiring immunity rapidly and easily cannot be dealt with in the same way as typhoid. There

---

[1] See pp. 106-7.

seems but little chance in these cases that selection will cease or even diminish.

The effect of an unhealthy environment upon sections of a race has already been dealt with.[1] Here, though it would seem that the race is not injured by slum conditions, it is not improved except with regard to power of resisting the evils of the particular environment. Hence if slum conditions are removed permanently, good is done to the individual and the race does not lose any useful characters.

If civilised races are deteriorating the cause is not the existence of slums in their towns, but that comparatively unfit individuals who would formerly have died early survive to produce children. Beneficial as the advance of knowledge in medicine, surgery, hygiene, and sanitation is to individuals, it must tend to lower the physical standard of the race, through the preservation of individuals who would not have survived under more stringent conditions of selection.

The increase of lunatics is a most serious problem, and will probably call for very stringent measures in the near future.[2] Lunacy is undoubtedly hereditary,[3] and unfortu-

---

[1] See pp. 154–5.

[2] In 1859 there was one certified lunatic in every 536 individuals of the general population in England and Wales; in 1900 there was one lunatic to every 301 of general population (*Fifty-fourth Report of the Commissioners in Lunacy*). In Scotland the number of lunatics had increased 180 per cent. between 1858 and 1900 (*op. cit.*). In Ireland there was one lunatic or idiot in 657 individuals of the general population in 1851. In 1901 there was one in 178 (*Edinburgh Medical Journal*, May 1903).

[3] "One cannot fail to observe the large number of our patients who are related to one another. We have at the present time in this asylum examples of brothers, sisters, brother and sister, father and daughter, father and sons, mother and daughter, uncle and niece, aunt and nephew, besides many cases of more distant relatives. Out of a total of 1934 persons admitted during the past five years I have discovered evidence of insanity in the family, and often in many members, in 828 instances, or 42·7 per cent. An analysis of these 828 cases brings into prominence three very important facts:—

"1. That the disease makes its appearance early in life.

"2. Should the patients be discharged they are prone to relapse.

'3. Should they remain and die here they usually do so at a good old age.

"The conclusion of the whole matter is this—that our asylum population is constantly recruited from and maintained by persons who have some inherited defect of brain-cell which renders them unfit to meet the ordinary stress of life, nately lunatics seem to be frequently very prolific. Until quite recent times lunatics were treated as criminals. They were kept in chains and under most uncomfortable and insanitary conditions. Such treatment made them worse, and it can but rarely have happened that any lunatic improved sufficiently to be set at liberty. At the present time, we have gone to the opposite extreme. Lunatics are kept under the best possible conditions, and are treated by specialists. Indeed, in comparison with the sane pauper, the mad pauper lives in great luxury. Not only this, but as soon as lunatics improve up to a certain point, they are set at liberty, and frequently have children. Thus the present effect of civilisation is to preserve the mentally unfit who were formerly eliminated.

Lunacy and mental deficiency must be regarded more or less as physical variations from the mean of the race. The brain is so complicated an organ, that a very slight variation would produce the most marked results. These cases must therefore be considered in a different light to other diseases and deformities.

Many misconceptions with regard to the transmission of disease are prevalent. In the case of diseases caused by micro-organisms, the ova or sperms may be infected even before fertilisation takes place. In such cases the micro-organisms enter the gametes from the body or soma of the parent. Infection may also take place after fertilisation, but before birth.[1] These cases are not cases of transmission of a disease at all, they are cases of acquirements.

The very common statement that the tendency to contract a disease that is caused by some species of micro-organism is hereditary, is putting the cart before the horse. For instance, we as a race have gained a new character in relation to the tubercle bacillus. In comparison with races

and until the State is able to devise some suitable means for the permanent care and control of such persons the ranks of the insane will continue to be filled and to burden the ratepayer." (*Annual Report to the County Council*, by H. W. Lewis, Medical Superintendent of the Kent County Asylum, 1910.)

[1] *E.g.* so-called hereditary or congenital syphilis.

that have not been subjected to selection, we possess a very high resisting power. Those individuals who, under the usual conditions in Northern Europe, contract tuberculosis, have varied away from this character, and so their resisting power is below that of the race generally. This variation is hereditary, but it is a mistake to call it a tendency to contract the disease. It is a reversed variation from a racial character, which renders the individual unfit in relation to his environment, and, for so long as the tubercle bacillus continues to exist in the environment, the artificial preservation of these individuals must tend to lower the mean resistance of the race. The same argument applies to many other diseases.

There are two kinds of deformities commonly met with among men ; those due to injuries or disease before or after birth, and those due to faulty development. These are frequently confused by the general public. Fingers, toes, or even a whole limb may be lost by accident while the child is still in its mother's womb. On the other hand, hare-lip, cleft-palate, and similar deformities are due to faulty development. Hare-lip, for instance, is due to the fact that the three parts from which the upper lip is formed in the embryo have failed to join completely. The variation towards incomplete development may be transmitted from parent to offspring. The accidental loss of a part before birth is no more an inborn variation than the absence of the tail of a dog, when the tail has been cut off. Deformities which are due to an addition to a character are always due to inborn variations, and are transmissible. For instance, some of the children of an individual with six instead of five digits are likely to inherit this character, although it will tend to be eliminated.[1]

There can be but little doubt that most of the socialistic theories now in vogue would, if put into practice, end in the decadence and perhaps in the extinction of the race that adopted them. The ultimate object of many of these

---

[1] See p 131.

theories is so to regulate competition, that every one shall live in comfort and comparative ease, irrespective of the relative capacity of individuals. Competition constitutes a very effective mode of selection, and if selection ceases, all the available evidence shows in the clearest manner possible that regression, that is, the disappearance of characters, follows. The race that limits competition so that individuals possessing advantageous characters do not succeed better in the struggle of life than their less gifted fellows, must regress, and will fail in that struggle between races which exists just as really as does the struggle between individuals. Man's greatest and infinitely most important inborn character is the capacity for making acquirements. It is just this character which would suffer most did selection, that is, competition, cease.

The bearing of the fact that some characters are transmitted in an alternative manner has an important bearing upon the breeding of domesticated races. In the case of plants the application of this knowledge is comparatively easy. In animals, however, it must be regarded as more or less problematical, and will certainly be much more difficult. In mammals and birds characters are so complicated and interdependent, that in many, perhaps in most cases, they cannot be dealt with individually. Taking the racehorse as an illustration. Speed and staying powers are the two characters cultivated by the breeder. These are not two separate characters, but the manifestations of a host of other characters, involving bone, muscle, internal organs, and a capacity for making acquirements. It is the same with most desirable qualities in domesticated animals, and time and experiment alone can show how far the application of the knowledge derived from Mendel's experiments will be of service to the breeder. In the case of the larger domesticated animals a long time is necessary to produce a number of generations, and accurate statistics cannot be hoped for in so short a time as in the case of plants or of such short-lived animals as mice.

There seems to be a tendency among biologists of certain schools to disregard every kind of evidence relating to the transmission of hereditary characters, except that provided by experiment. Such was not the method of Darwin, nor does the truly scientific method exclude the use of facts, whether recorded as results obtained under laboratory conditions, or otherwise, so long as the facts are handled in a properly scientific manner. The advantage of the experimental results is that the laboratory conditions exclude sources of error far more effectually than is possible in the case of any other class of observations, and that to a great extent, and very often, the laboratory conditions may be reproduced and the experiment repeated.

It is probable that no branch of knowledge would be more hampered in its growth than the study of heredity by a limitation to that kind of evidence only that can be obtained in the laboratory. Nature is constantly carrying out experiments under conditions the reproduction of which is beyond our powers or knowledge. By observing her results and recording and interpreting as far as possible the conditions under which they are produced, an advance in knowledge is likely to be made, at least as great as by experimental work.

BIBLIOGRAPHY

Adami, J. G., "An Address on Theories of Inheritance with Special Reference to an Inheritance of Acquired Conditions in Man," *Brit. Med. Journal*, June 1, 1901.

Arnold, G., "The Nucleolus and Microchromosomes in the Spermatogenesis of Hydrophilus piceus," *Archiv für Zellforschung*, ii. 1, 1908; "Ovigenesis and Spermatogenesis of Planaria lactea," *Archiv für Zellforschung*, iii., 1909.

Avebury, Lord, *On the Senses, Instincts, and Intelligence of Animals, with Special Reference to Insects*, London, 1888.

Bacot, A., *Entomologist's Record*, xiii. pp. 114–117 and 142–144. See also Prout and Bacot.

Bary, A. de, *Comparative Morphology and Biology of the Fungi*, English translation, Oxford, 1887.

Bateson, W., *Materials for the Study of Variation*, London, 1894; *Report British Association* (Cambridge Meeting), 1904.

Bertzke, "Über Häufigkeit und Infectionswege der Tuberculöse," *Tuberculosis*, April 1906, vol. v., No. 4, Berlin.

Born, G., "Experimentelle Untersuchungen über die Entstehung der Geschlechtsunterschiede," *Breslauer Aerztliche Zeitschrift*, 1881.

Boulanger, G. A., "On the Variations of the Evening Primrose," *Journal of Botany*, October 1907.

Boveri, Th., "Über die Befruchtungs- und Entwickelungsfähigkeit kernloser Seeigel-Eier," *Archiv für Entwicklungsmechanik*, ii. 3, 1895; "Über den Einfluss der Samenzelle auf die Larvencharaktere der Echiniden," *Archiv für Entwicklungsmechanik*, Bd. 16, 1903; *Zellen-Studien* Heft 6, 1907.

Brouardel, *Trans. British Tuberculosis Congress on Tuberculosis*, vol. i., W. Clowes, London, 1902.

Browne, E. T., "On the Variation of the Tentaculocysts of Aurelia aurita," *Quart. Journ. Microscopical Science*, xxxvii., 1895.

Brown-Séquard, "Nouvelles Recherches sur l'Épilepsie due à certaines Lésions de la Moelle Épinière et des Nerfs Rachidiens," *Arch. Physiol. Norm. Path.*, ii., 1869; "Faits nouveaux concernant la Physiologie de l'Épilepsie," *Arch. Physiol. Norm. Path.*, iii., 1870–71; "Remarque sur l'Épilepsie causée par la Section du Nerf Sciatique chez les Cobayes," *Arch. Physiol. Norm. Path.*, iii., 1870–71; "Quelques Faits nouveaux relatifs a l'Épilepsie qu'on observe à la Suite de diverses Lésions du Système Nerveux chez les Cobayes," *Arch. Physiol. Norm. Path.*, iv., 1872; "Transmission par Hérédité de certaines Altérations des Yeux chez les Cobayes," *Gaz. Médicale de Paris*, 1880; "Faits nouveaux établissant l'extrême Fréquence d'États Morbides produits accidentellement chez des Ascendants," *Comptes Rendus Acad. Sci.*, Paris, vol. xciv., 1882; "Hérédité d'une Affection due à une cause accidentelle. Faits et Arguments contre les Explications et les Critiques de Weismann," *Arch. Physiol.*, xxiv., 1892; "Transmission Héréditaire de Caractères acquis," *Arch. Physiol.*, 1893.

CHIPIEZ. See Perrot.

CORRENS, C., "G. Mendel's Regeln über das Verhalten der Nachkommenschaft der Rassenbastarde," *Ber. Deutsch. Bot. Ges.*, xviii., 1900; "Über Bastardierungsversuche mit Mirabilis sippen," *Ber. Deutsch. Bot. Ges.*, xx., 1902.

COUTANGE, G., "Recherches Expérimentales sur l'Hérédité chez les Vers à Soie," *Bull. Scientifique de la France et de la Belgique*, xxxvii., 1902.

CRAMPTON, H. E., "The Ovarian History of the Egg of Molgula," *Journal of Morphology*, xl., Supplement 1899.

CUENOT, L., "La détermination du Sexe," *Bibliogr. Anat.*, iv. pp. 14–15, 1896; "Sur la détermination du Sexe chez les Animaux," *Bull. Scient. de la France et de la Belgique*, xxxii. pp. 462–535, 1899.

CUNNINGHAM, J. T., *Sexual Dimorphism in the Animal Kingdom*, London, 1900.

DARBISHIRE, A. D., "On the Result of Crossing Round with Wrinkled Peas, with Especial Reference to their Starch-grains," *Proc. Roy. Soc.*, B., vol. 80, 1908; "Note on the Results of Crossing Japanese Waltzing Mice with European Albino Races," *Biometrika*, ii. pp. 101–104, 165, and 282, 1902.

DARWIN, C., *The Origin of Species*, Murray, London, 1859; *The Variation of Animals and Plants under Domestication*, Murray, London, 1868; *Insectivorous Plants*, London, 1875.

DAVENPORT, *Inheritance in Poultry*, Carnegie Institution of Washington, 1906.

DAY, F., *British Fishes*, Williams & Norgate, London, 1884; *British and Irish Salmonidæ*.

DENDY and HINDLE, "Some Additions to our Knowledge of the New Zealand Holothurians," *Linn. Soc. Journal* (Zoology), vol. xxx., October 1907.

DIXEY, F. A., "The New Evolution," *Nature*, vol. lxxv., April 18, 1907.

DONCASTER, British Association Meeting, 1908.

DRIESCH, H., *Analytische Theorie der organischen Entwicklung*, Leipzig, 1894; "Über Seeigelbastarde," *Archiv für Entwicklungsmechanik*, Bd. 16, 1903.

ERMAN, ADOLPH, *Life in Ancient Egypt*, English translation, Macmillan, 1894.

Escherich, K., *Die Ameise. Schilderung ihrer Lebensweise*, Braunschweig, Fr. Vieweg und Sohn, 1906.

Ewart, J. Cossar., *The Penicuik Experiments*, A. & C. Black, London, 1899; "Discussion on Heredity in Disease," *Scottish Medical and Surgical Journal*, 1900, iv. p. 308.

Fabre, J. H., *Souvenirs Entomologiques*, Paris, English translation of first series *Insect Life*, Macmillan, London, 1901.

Farmer, J. B., Moore, J. E. S., and Walker, C. E., "On the Resemblances Exhibited between the Cells of Malignant Growths in Man and those of Normal Reproductive Tissues," *Proc. Roy. Soc.*, vol. 72, 1903; "On the Resemblances Existing between the Plimmer's Bodies of Malignant Growths and Certain Normal Constituents of Reproductive Cells in Animals," *Proc. Roy. Soc.*, B., vol. 76, 1905; "On the Cytology of Malignant Growths," *Proc. Roy. Soc.*, B., vol. 77, 1906.

Farmer, J. B., and Moore, J. E. S., "The Meiotic Phase (Reduction Division) in Animals and Plants," *Quart. Journ. Micro. Science*, vol. 48, Part IV., 1905.

Fick, R., "Betrachtungen über die Chromosomen, ihre Individualität Reduction und Vererbung," *Archiv. für Anatomie und Physiologie*, Anat. Abt. Suppl., 1905.

Fischer, A., "Entwicklung und Organdifferenzierung," *Archiv für Entwicklungsmechanik*, Bd. 15, 1903.

Foot, K., and Strobell, E. C., "The 'Accessory Chromosome' of Anasa tristis, *Biological Bulletin*, vol. xii. pp. 119–126, 1907; "The Chromosomes in Anasa tristis," *ibid.*, vol. xii. pp. 279–316, 1907; "A Study of Chromosomes in the Spermatogenesis of Anasa tristis," *Amer. Journ. Anat.*, vii. 2, 1909; "The Nucleoli in the Spermatocytes and Germinal Vesicles of Euchistus variolarius," *Biol. Bull.*, xvi. 5, 1909.

Galton, *Inquiries into Human Faculty* (Everyman's Library Edition); *Proc. Roy. Soc.*, vol. lxi. p. 402; *Hereditary Genius*, Macmillan, London, 1892; *Natural Inheritance*, Macmillan, London, 1889.

Geddes, P., *Chapters in Modern Botany*, Murray, London, 1893.

Geikie, Sir Archibald, Presidential Address to the British Association, 1892.

Godlewski, E., "Untersuchungen über die Bastardierung der Echiniden und Crinoidenfamilie," *Archiv für Entwicklungsmechanik*, Bd. 20, 1906.

Goldschmidt, R., "Über das Verhalten des Chromatins bei der Ei-reifung und Befruchtung des Dicrocœlium lanceatum," *Archiv für Zellforschung*, i., 1908.

Grégoire, V., "La formation des gemini hétérotypiques dans les végétaux, *La Cellule*, xxiv., 1907.

Graff, Von, *Die Acoela*, Leipzig, 1892.

Groos, *Die Spiele der Thiere*, Jena, 1896; Translation, *The Play of Animals*, by E. L. Baldwin, New York, 1898; *Die Spiele der Menschen*, Jena, 1899; Translation, *The Play of Men*, by E. L. Baldwin, New York, 1901.

GRUBER, A., "Mikroskopische Vivisektion," *Berichte der Naturforschender-Gesellschaft*, Freiburg, vii., 1893.

HABERLANDT, quoted by von Graff in *Die Acoela.*

HAMM, A. H., *Trans. Entomological Society of London*, pp. 321–323, 1885; and pp. 483–485, Jan. 1907; "Observations on Empis livida," *Entomologist's Monthly Magazine*, p. 181, vol. xliv., 1908.

HARMER, Sidney F., Presidential Address to the Zoological Section, British Association Meeting, 1908.

HENKING, H., "Über Spermatogenese und deren Beziehung zur Eientwicklung bei Pyrrhocoris apterus," *Zeit. Wiss. Zool.*, li., 1891.

HERBST, C., *Formative Reize in der Tierischen Ontogenese*, Leipzig, Arthur Georgi, 1901.

HERLA, V., "Étude des Variations de la mitose chez l'ascaride mégalocéphale," *Archives de Biologie*, xiii., 1893.

HERLITZKA, A., "Contribuzione allo studio della capacità evolutiva dei due primi blastomeri nell' uove di Tritone, *Arch f. Entwick.*, ii. 3, 1895.

HERSCHEL, SIR JOHN, *Edinburgh Review*, 1850.

HERTWIG, O. and R., *Über den Befruchtungs und Teilungsvorgang des tierischen Eies unter dem Einfluss aüsserer Agentien*, Jena, 1887.

HERTWIG, O., *The Biological Problem of To-day*, English translation, Heinemann, London, 1896; *Die Zelle und die Gewebe*, Jena, 1898; *Allgemeine Biologie*, Fischer, Jena, 1906.

HINDLE. See DENDY and HINDLE.

HIS, W., *Unsere Körperform und das physiologische Problem ihrer Entstehung*, Leipzig, 1874.

HOWLETT, M., "Note on the Coupling of Empis borealis," *Entomologist's Monthly Magazine*, p. 229, vol. xliii., 1907.

IHERING, H. von, "Zur Frage nach dem Ursprung der Staatenbildung bei den sozialen Hymenopteren," *Zool. Anz.*, 27, 4, 1903.

ISSAKOWITSCH, A., "Geschlechtsbestimmende Ursachen bei den Daphniden," *Biol. Centralbl.*, xxv., 1905; *Arch. mikr. Anat.*, lxix.

JANET, CH., *Études sur les fourmis, les guêpes et les abeilles*, Note 13; *Sur le Lasius mixtus et l'Antennophorus uhlmanni, &c.,*" Limoges, 1897.

JANNSENS, F. A., "Évolution des Auxocytes mâles dans Batrocoseps attenuatus," *La Cellule*, xxii., 1905.

JORDAN. See ROTHSCHILD and JORDAN.

KINGSLEY, MARY, *Travels in West Africa*, Macmillan.

LANKESTER, SIR E. RAY, *The Advancement of Science*, London, 1890.

LOCK, R. H., *Recent Progress in the Study of Variation, Heredity and Evolution*, John Murray, London, 1906.

LOEB, J., "On the Nature of the Process of Fertilisation and the Artificial Production of Normal Larvæ," *American Journal of Physiology*, iii. 3, 1899; "Über die Befruchtung von Seeigeleiern durch Seesternsamen," *Archiv für der gesammte Physiologie*, Bd. 99, 1903.

LUDWIG, H., "Holothurians of the Albatross Expedition," *Bull. Mus Comp. Zool.*, Harvard, vol. xxiv., 1893; *Mem. Mus. Comp. Zoo.*, vol. xvii., No. 3, 1894, p. 183.

Macfarlane, J. M., “A Comparison of the Minute Structure of Plant Hybrids with that of their Parents,” &c., *Trans. Roy. Soc. Edinburgh*, xxxvii., 1891.

Malsen, H. von, “Geschlechtsbestimmende Einflüsse und Einbildung bei Dinophilus apatris,” *Arch. mikr. Anat.*, lxix., 1906.

Maspero, *Histoire Ancienne.*

Maupas, *Arch. Zool. Exp.*, Série VI., 1888 ; *ibid.*, Série VII., 1889 ; *Comptes Rendus*, Paris, 1891.

McClung, C. E., “The Accessory Chromosome. Sex Determinant ?’ *Biol. Bulletin*, vol. iii., 1902.

McDougall, William, *An Introduction to Social Pyschology*, Methuen, London, 1908.

Mendel, C. J., “Versuche über Pflanzen Hybriden,” *Verhandlungen des Naturforschaftlichen Verein in Brünn*, Band IV., 1865 ; “Über einige aus künstlicher Befruchtung gerwonnene Hieracium-Bastarde,” *Verhandlungen des Naturforschaftlichen Verein in Brünn*, 1869.

Mercier, Charles, “The Transmission of Acquired Characters,” *The Contemporary Review*, December 1908.

Meves, F., “Über das Vorkommen von Mitochondrien bezw. Chondromiten in Pflanzenzellen,” *Berichten der deutschen botanischen Gesellschaft*, Band XII., Heft 5, 1904 ; “Die Spermatocytenteilungen bei der Honigbiene, nebst Bemerkungen über Chromatinreduktion,” *Arch. f. mikr. Anat.*, lxx., 1907 ; “Es gibt keineparallele Konjugation der Chromosomen!” *Archiv für Zellforschung*, i. 4, 1908 ; “Die Chondriosomen als Träger erblicher Anlagen, Cytologische Studien am Hühnerembryo,” *Archiv für mikroskopische Anatomie und Entwicklungsgeschichte*, Bd. 72, 1908.

Mollé, van J., “Les spermatocytes dans l’Écureuil,” *La Cellule*, xxiv., 1907.

Montgomery, T. H., “The Heterotypic Maturation Mitosis in Amphibia,” *Biological Bulletin*, iv., 1903 ; “The Spermatogenesis in Pentatoma up to the Formation of the Spermatid,” *Zool. Jahrb.*, xii., 1898 ; “The Spermatogenesis of Peripatus (Peripatopsis) balfouri up to the Formation of the Spermatid,” *ibid.*, vol. xiv., 1900 ; “Further Studies on the Chromosomes of the Hemiptera Heteroptera,” *Proc. Acad. Nat. Sci.*, Philadelphia, 1901 ; “A Study of the Chromosomes of the Germ Cells of Metazoa,” *Trans. Amer. Phil. Soc.*, vol. xx., 1901 ; “Some Observations and Considerations upon the Maturation Phenomena of the Germ Cells,” *Biol. Bull.*, vol. vi. 1904 ; “The Development and Structure of the Larva of Paragordius,” *Proc. Acad. Nat. Sci.*, Philadelphia, 1904 ; “The Spermatogenesis of Syrbula and Lycosa, with General Considerations upon Chromosome Reduction and the Heterochromosomes,” *ibid.*, 1905 ; “The Terminology of Aberrant Chromosomes and their Behaviour in certain Hemiptera,” *Science* (N.S.), xxiii., 1906 ; “Chromosomes in the Spermatogenesis of the Hemiptera Heteroptera,” *Trans. American Philosoph. Soc.* (N.S.), vol. xxi., Part III., 1906.

MOORE, J. E. S., and WALKER, C. E., "The Meiotic Process in Mammalia," *Thompson-Yates Reports*, University of Liverpool, 1905. See also FARMER and MOORE, and FARMER, MOORE, and WALKER.

MORGAN, T. H., "The Fertilisation of Non-nucleated Fragments of Echinoderm Eggs," *Archiv für Entwicklungsmechanik*, ii. 2, 1895; "Experimental Studies on Teleost Eggs," *Anat. Anz.*, x. 19, 1895; "The Action of Salt-Solutions on the Fertilised and Unfertilised Eggs of Arbacia and other Animals," *Archiv für Entwicklungsmechanik*, viii. 3, 1898; *Evolution and Adaptation*, New York, Macmillan Co., 1903; "Production of Two Kinds of Spermatozoa in Phylloxerans," *Proc. Soc. Exp. Biol. and Med.*, v. 1908.

MULLER, E., "Über die Regeneration der Augenlinse nach Exstirpation derselben bei Triton," *Archiv für mikroscopische Anatomie*, xlvii. 1, 1896.

NÄGELI, C., *Mechanisch-physiologische Theorie der Abstammungslehre*, München und Leipzig, 1894.

OSLER, W., *The Principles and Practice of Medicine*, 5th edition, London, Appleton & Co., 1904.

OTTE, H., "Samenreifung und Samenbildung bei Locusta viridissima," *Zoologische Jahrbücher*, xxiv. 1907.

PACKARD, A. S., "On the Inheritance of Acquired Characters in Animals with a Complete Metamorphosis," *Proceedings of the Amer. Academy of Science*, xxix., 1894.

PAULMIER, F. C., "The Spermatogenesis of Anasa tristis," *Journ. of Morph.*, XV. Supplement, 1899.

PEARSON, KARL, *Grammar of Science*, 2nd edition, London, 1900.

PECKHAM, G. W. and E. G., "On the Instincts and Habits of the Solitary Wasps," *Wisconsin Geological and Natural History Survey*, Madison, Wis., U.S.A., 1898; *Wasps Social and Solitary*, Boston and New York, 1905.

PERON. See VOISIN and PERON.

PERROT and CHIPIEZ, *A History of the Art of Ancient Egypt*, English translation, Chapman & Hall, 1883.

PFEFFER, *Unters. bot. Inst. Tübingen*, i. p. 483, 1883.

POPOFF, M., "Eibildung bei Paludina vivipara, &c.," *Archiv für mikroskopische Anatomie*, lxx., 1907.

PORRITT, G. T., *British Association Report*, p. 316, 1906; *Entomologist's Monthly Magazine*, Second Series, vol. xviii. p. 12, 1907.

POULTON, E. B., *Essays on Evolution*, Oxford, 1908.

PROUT, L. B., and BACOT, A., "On the Cross-breeding of the Moth Acidalia virgularia," *Proc. Roy. Soc.*, B. vol. lxxxi., 1909; "Triphæna comes and its Dark Aberration," *Entomologist's Record*, xv. and xvi.; "Xanthorhoë ferrugata and its Black Aberration," *Trans. Entomological Society, London*, 1906, and *Proc.*, 1907.

PUNNET, R. C., "*Mendelism*," Cambridge, 1905.

QUETELET, *Lettres à S.A.R. le Duc régnant de Saxe-Cobourg et Gotha sur la Théorie des Probabilités appliquée aux Sciences Morals et Politiques*, Brussels, 1846.

Reid, G. Archdall, *The Principles of Heredity*, 1905; Report of paper read to the Linnean Society, December 19, 1907, *Nature*, January 9, 1908.

Riley, *Third Ann. Rep. Missouri Bot. Gdn.*, 1892.

Rosenberg, O., *Phys-Cytolog. Unters. über Drosera rotundifolia*, Upsala, 1899 ; "Das Verhalten der Chromosomen in einer hybriden Pflanze," *Berichte der deutschen botanischen Gesellschaft*, xxi. 2, 1903.

Rothschild and Jordan, *Novitates Zoologicæ*, vol. x. p. 492, 1903.

Roux, W., *Über die Bedeutung der Kernteilungsfiguren*, Leipzig, 1883; "Über das künstliche Hervorbringen halber Embryonen durch Zerstörung einer der beiden ersten Furchungskugeln," &c., *Virchow's Archives*, 114, 1888.

Rückert, J., "Über das Selbständigbleiben der väterlichen und mütterlichen Kernsubstanz während der ersten Entwicklung des befruchteten Cyclops-Eies," *Archiv für mikroscopische Anatomie*, xlv. 3, 1895.

Sarasin, Paul and Fritz, "Über zwei parasitische Schnecken," *Ergebnisse Naturwissenschaftlicher Forschung auf Ceylon*, 1884–86.

Schockaert, R., "L'ovigénèse chez le Thysanozoon brocchi," *La Cellule*, xviii., xx., 1900, 1901.

Schreiner, A. and K. E., "Über die Entwicklung der männlichen Geschlechtszellen von Myxine glutinosa (L.), *Archives de Biologie*, xxi. 1904; "Neue Studien über die Chromatinreifung der Geschlechtszellen": (1) "Die Reifung der männlichen Geschlechtszellen von Tomopteris onisciformis (Eschscholtz)," *Arch. de Biologie*, xxii., 1906; (2) "Die Reifung der männlichen Geschlechtszellen von Salamandra maculosa (Laur.), Spinax niger (Bonap.) und Myxine glutinosa (L.)," *Arch. de Biologie*, xxii., 1906 ; (3) "Die Reifung der Geschlechtszellen von Ophyotrocha puerilis (Clprd-Merz.)," *Anatomische Anzeiger*, xxix., 1906.

Shattock and Seligmann, *Transactions of the Pathological Society of London*, vol. lvi. p. 57, 1905 ; vol. lvii. p. 69, 1906.

Silvestri, F., "Contribuzione alla conoscenza dei Mirmecofili," *Ann. Mus. Zool. Univ. Napoli.*, I. 13, 1903.

Sommer, Max, "Die Brown - Séquard'sche Meerschweinschenepilepsie und ihre erbliche Uebertragung auf die Nachkommen," *Aus der psychiatrischen Klinik der Universität*, Jena, 1900.

Strobell, E. C. See Foot, K., and Strobell.

Tannreuther, G. W., "History of the Germ Cells and Early Embryology of Certain Aphids," *Zoologische Jahrbücher*, xxiv., 1907.

Thiselton-Dyer, Sir W. T., "Specific Stability and Mutation," *Nature*, pp. 77–79, November 28, 1907.

Thomas and Breinl, *Liverpool School of Tropical Medicine*, Memoir XXI., October 1905.

Thomson, J. A., *Heredity*, John Murray, London, 1908.

Toyama, K., "On Some Silk-worm Crosses with Special Reference to Mendel's Law of Heredity," *Bull. Coll. Agric.*, Tokyo Imp. University, 1906.

TSCHERMAK, E., "Über künstliche Kreuzung bei Pisum sativum," *Zeitschrift Landwirthschaft Versuchswesen in Oesterreich*, iii., 1900.

TUTT, J. W., *Entomologist's Record*, vol. i., 1890–91.

VERNON, H. M., *Variations in Animals and Plants*, Kegan Paul & Co., London, 1903.

VERWORN, M., "Die physiologische Bedeutung des Zellkerns," *Archiv für die gesammte Physiologie*, ii. 1891.

VOISIN and PERON, *Archives de Neurologie*, xxiv., 1892, and xxv., 1893.

VOISIN, "*L'Épilepsie*," Paris, 1897.

VRIES, H. DE, "Sur la loi de disjonction des Hybrides," *Comptes Rendus Acad. des Sciences Paris*, cxxx., 1900 ; *Die Mutations-theorie*, 2 vols., Leipzig, vol. i., 1901, vol. ii., 1903 ; *Species and Varieties: Their Origin by Mutation*, Chicago and London, 1905.

WALKER, C. E., *The Essentials of Cytology*, Constable, London, 1907 ; "The Influence of the Testis upon the Secondary Sexual Characters of Fowls," *Proceedings of the Royal Society of Medicine*, April 1908. See also FARMER, MOORE, and WALKER, and MOORE and WALKER.

WARREN, E., "An Observation on Inheritance in Parthenogenesis," *Proc. Roy. Soc.*, lxv., 1899.

WEISMANN, A., *The Germ Plasm: A Theory of Heredity*, English translation, 1893, German edition, 1892; *The Theory of Evolution*, English translation, Arnold, London, 1904.

WELDON, *The Lancet*, March 25, 1905.

WHEELER, W. M., *Ants: Their Structure, Development and Behaviour*, New York, Columbia University Press, 1910.

WILSON, E. B., "On Cleavage and Mosaic Work," *Arch. f. Entwick.*, iii., 1, 1896; "Experimental Studies on Germinal Localisation—(1) The Germ-Regions in the Eggs of Dentalium; (2) Experiments on the Cleavage-Mosaic in Patella and Dentalium," *Journal of Experimental Zoology*, vol. i., 1904 ; *The Cell in Development and Inheritance*, Macmillan, London and New York, 1904; "Studies on Chromosomes," I., *Journal of Exper. Zool.*, vol. ii., No. 2, 1905 ; "Studies on Chromosomes," II., vol. ii. No. 4; "Studies on Chromosomes," III., vol. iii., No. 4, 1906 ; "Recent Researches on the Determination and Heredity of Sex," *Science*, N.S., vol. xxix., No. 732, January 1909.

WOLFF, GUSTAV, "Die Regeneration der Urodelenlinse," *Archiv für Entwicklungsmechanik*, i. 3, 1895.

YUNG, E., "De l'influence des variations du milieu physico-chimique sur le développement des animaux," *Arch. Sci. Phys. Nat.*, xiv., 1895.

ZIEGLER, H. E., "Die Chromosomen Theorie der Vererbung in ihrer Anwendung auf den Menschen," *Archiv. Rassen-gesellschaftliche Biologie*, vol. iii. pp. 797–812 ; *Die Vererbungslehere in der Biologie* Fischer, Jena, 1905.

ZOJA, R., "Sullo sviluppo dei blastomeri isolati dalle uova di alcune Meduse," *Arch. f. Entwick.*, i. 4, ii. 1 and 4, 1895 ; "Sulla independenza della chromatina paterna e materna nel nucleo delle cellule embrionali, *Anatomischer Anzeiger*, xi., 10, 1905.

INDEX

Abraxas grossulariata, Mendelian experiments with, 209–10
Accessory chromosomes as sex determinants, 193–7
Acidalia virgularia, breeding experiments with, 186–7
Acquired characters—
  Charles Mercier upon transmission of, 155–9
  classification of, 53
  definition of, 46
  man's dependence upon, 52
  potentiality of producing is inborn, 47
  pre-natal, 135
  produced by environment, 134, 136
  transmission of, in bacteria, 138
  transmission of, in *Daphnia*, 137
  transmission of, injurious, 152–4, 163–4
Adaptation, 77–101
  in *Acanthorhiza*, 88
  in *Antenophorus*, 80
  in Campanulas, Harvey Gibson on gradual, 90
  in *Drosera*, 87
  in *Empis*, 80
  in fishes, 86
  gradual in the moth *Amphidasys*, 89
  in Holothurians, 86
  mutations incompatible with, 77, 91
  parasitic, 93
  in plants, 86–9, 90, 95–6
  produced by selection of inborn variations, 158–9
  reasons for supposing always gradual, 90
  in seeds of *Scorpiurus*, 88
  in *Sitaris*, 77
  in the Yucca, to moth (*Pronuba*), 88
Age of the earth, 100
Alcoholism, effect of, upon germ-cells, 135
Algæ symbiotic with *Convoluta*, 95
  symbiotic with fungi (lichens), 95
Alpine plants, Nägeli's experiments with, 136
Alternative transmission of individual characters, 184, 189
Ammophila, transmission of instincts in, 145–8
Amphidasys, gradual adaptation in, 89
Amphimixis as cause of variations, 124
  chromosomes in, 124–8, 177–9
  results of, 125
Ancestral characters, reversion to, 113–118
Antenophorus, adaptation in, 80
Anthophora and its parasite *Sitaris*, 78
Ants, African driver, 150–1
  honey, 151–2
  slave-making, 81
  transmission of instincts in, 149–50
  transmission of physical characters in, 150–2
Aphis, parthenogenetic reproduction in, 28
Aster, definition of, 14
Atoxyl, effect of, upon trypanosomiasis, 139, 142
Aurelia, mutations in, not perpetuated, 65

Baboon inoculated with trypanosomes, 140
Bacot, *see* Prout
Bacteria, supposed transmission of acquired characters in, 138
Bateson on discontinuity between species, 73
Bateson's interpretation of determination of sex, 200–1
Bees, reproduction in, 28, 191

Bees, social, transmission of instincts of, 149–50
Bi-parental reproduction, Archdall Reid on, 128
  chromosomes in, 23, 124–8, 177–9
  effect of, 124–133, 165, 210
  eliminates variations, 125, 129–30, 133, 165
  universality of, 3
Bison crossed with European cattle, 117
Bleak hybrids, 118
Blended characters in half-bred sheep, 185
Blended inheritance, 179
  examples of, 117–8, 179, 185
Blending of characters in crosses between natural races, 117-9, 173, 178–9, 185, 189
Bonnet, theory of emboîtment, 7
Boulenger, G. A., on mutations in *Œnothera*, 64, 71
Boveri, experiments with enucleated ova, 31, 36
  on function of cytoplasm in heredity, 37
Brain of man and the apes, 161
Breamflat hybrids, 118
Brown-Séquard's experiments, 143–5
Bryonia, Correns's experiments with, 199
Bütschli and Minot, comparison between unicellular and multicellular organisms, 5

CAMPANULAS, Harvey Gibson on gradual adaptation in, 90
Cancer. Resemblances to germ-cells (*footnote*), 57
Castle's interpretation of determination of sex, 198–9, 201
Cattle, cross-breeding in, 185
Cell, definition of, 1
Cell division, 14–44
  (somatic), results of, 20
Cells, parts of, dividing in a selective manner, 40
  structure of, 13
Centrosomes, definition of, 13
  details regarding, 40
  in unfertilised ova, 41
Cercopithecus callitrichus, inoculation of, with trypanosomes, 141
Characters, acquired, *see* Acquired characters
  ancestral, Darwin on, in pigeons, 114
  ancestral, reversion to, 113–8
Characters, blending of, in natural races, 117–9, 173, 178–9, 185–7
  bulk of, inherited from remote ancestors, 120, 121, 122
  classification of, 53
  disappearance of, 66, 110
  of domesticated races selected by man, 133
  eliminated when not selected, 132
  inborn, *see* Inborn characters
  individual, *see* Individual characters
  Mendelian, *see* Mendelian characters
  new, not produced by amphimixis (bi-parental reproduction), 125
  physical, of prehistoric man, 120
  physical, transmission of, in ants, 150–2
  prepotent, 179–80
  racial, *see* Racial characters
  represented by entities, 174–6
  theories explaining reappearance of ancestral, 114
Chondriosomes bearers of hereditary characters, 35
Chromatin bearer of hereditary characters, 33
  definition of, 13
  as hereditary substance, 18
  the idioplasm of Nägeli, 18, 33
  not a permanent constituent of nucleus, 19
Chromatophores, 35
Chromosomes, accessory as sex determinants, 193–7
  alternative distribution, 22–5, 41–4, 124–8, 177–9, 189
  combinations of, in fertilisation (amphimixis, bi-parental reproduction), 23, 124–8, 177–9
  definition of, 15
  Mendelian characters contained in, 177–8
  number of, 15
  number of in sterile crosses, 117
  paternal and maternal distinct, 32
  representing individual characters, 128, 189
  not representative of racial characters, 23
  splitting of, 16
  structure of, 19
Chubb, hybrids, 118
Cod-fish, capacity for multiplication, 98
Coloration, protective, 83
Comparison between life-cycle of

unicellular and multicellular organisms, 5

Continuity of germ-plasm, theory of, 55
  between species, 73
  between species, Poulton on, 73
  between species, Darwin on, 74
  between species, Rothschild and Jordan on, 74

Convoluta, symbiotic with *Algæ*, 95

Correns' experiments with *Bryonia*, 199
  experiments with Marvel of Peru (*Mirabilis jalapa*), 173–4
  interpretation of determination of sex, 199–201

Cro-Magon, prehistoric human remains at, 120

Crosses between various *Salmonidæ*, 117, 118

Cytoplasm, function of, in heredity, 34

Daphnia, supposed transmission of acquired characters in, 137

Darwin, Charles, on ancestral characters in pigeons, 114
  on continuity between species, 74
  on large and small variations, 62, 72
  theory of pangenesis, 7, 58

Darwin, George, on age of earth, 100

Darwin and Wallace, theory of evolution, 54

Deformities, transmission of, 219

Degeneration in favourable environment, 153–4, 163
  in parasites, 153–4

Dicthadia (African driver-ant), 150–1

Differentiation in cells of multicellular organisms, 4, 6, 45, 68, 69

Diappearance of characters, 66, 110

Discontinuity between species, R. H. Lock and Bateson, 73

Disease, hereditary susceptibility to, 218–9
  immunity to, 103–8, 147–8, 215–6, 218–9

Diseases, inherited, 136–7, 218–9

Dixey, F. A., upon the mutation hypothesis, 93

Dogs, English, in India, 96

Domesticated races, individual variations exaggerated in, 183–4
  Mendelian characters generally found in, 182

Dominant characters, 168, 170
  often imperfect, 176–7

Dominants, impure, crossed with recessives, 172

Dorylus (African driver-ant) 150–1

Driesch, experiments with enucleated ova, 36

Drosera, mode of catching insects, 87

Egyptians unchanged in appearance for thousands of years, 120

Elimination of useless variations, 126, 130, 165

Emboîtement, theory of, 7

Embryos produced from portions of ovum, 10
  produced from unfertilised ova, 30

Empis, adaptations in, 80

Entomostraca, variations in, 60

Enucleated ova, experiments with, 31, 35

Environment, effect of, upon germ-cells, 135, 136, 152–5, 162–4
  upon inborn variations, 135, 136, 157, 163–5
  upon sex, 191–3
  unhealthy, 154–5, 217
  favourable, produces degeneration, 153–4, 163
  produces acquired characters, 134, 136, 157, 163–5

Epiblast, 69

Epilepsy in guinea-pigs, 143–5

Evolution, theories of, 54–8

Exclusive inheritance, 180

Experiments with enucleated ova, 31, 35

Eyes, inheritance of colour of, 180

Fabre on instincts of fossorial wasps, 145–8

Feeble-minded, Royal Commission upon, 154

Fertilisation in multicellular organisms, 27
  in unicellular organisms, 2, 29

Fertilised ovum, origin of, 4

Fertility of hybrids, 75
  not test of species, 74

Fischer, experiments with *Ctenophore* eggs, 36

Fishes, adaptation in, 86
  blind cave, 155

Fluctuating variations, instability of, 65

Foals with three toes, 115, 116

Fowls, experiments upon secondary sexual characters of, 205–6
  Mendelian characters in, 176

Frequency of error, Gauss's law of, 99

Frogs, determination of sex by environment, 192
Fungi, symbiotic with *Algæ* (lichens), 95

GALTON, Sir Francis, on blending colours in half-castes, 181
  on Darwin's theory of pangenesis, 119
  theory of heredity, 119
Gametes, definition of, 5
  Mendel's theory of segregation of, 169–70
  relation of to Soma, 5
Gastrula, definition of (*footnote*), 35
Gauss's law of frequency of error, 99
Germ-cells, effect of environment upon, 135–6, 152–3, 162–4
  effect of alcoholism upon, 135
  variations in, 164–5
Germinal localisation, theory of, 8
  experiments on, by Roux, Morgan, Wilson, Zoja, 10
Germ-plasm, continuity of, 55
  O. Hertwig's theory of, 56
  de Vries' theory of, 58
Gibson, Harvey, on gradual adaptation in Campanulas, 90
Godlewski, experiments with enucleated ova, 35
  on function of cytoplasm in heredity, 37
Grafts, variations in, 67–8
Growth, effect of sickness upon, 152–3
Gruber, experiments with unicellular animals, 32

HALF-CASTES, blending of characters in, 180–1
Herbert Spencer's definition of heredity, 45
Hereditary characters, chromatin bearer of, 33
  nucleus bearer of, 34.
Hereditary substance, chromatin as, 18
  conclusions with regard to, 39
  general discussion of localisation, 12
  Nägeli's theory of, 9, 11, 114
  Roux-Weismann theory of, 9, 11.
Hereditary disease, 136–7, 218–9
Heredity, Galton's theory of, 119
  Herbert Spencer's definition of, 45
Herschel's illustration of Gauss's law, 99
Hertwig (Oscar), theory of germ-plasm, 56
  O. & R., experiments with enucleated ova, 31
Hieracium, Mendel's experiments with, 185
Higher animals distinguished from lower, 53
Hipparion, 115
His, W., theory of germinal localisation, 8
Holothurians, adaptation in, 86
Honey ants, 151-2
Horse, hybrid with zebra, 128
  piebald, 180
House-fly, capacity for multiplication, 97
Hybernia leucophæria, 82
Hybridism, effect of, upon Mendelian characters, 176-7
Hybrids, 74–5, 117–8, 177–9, 181
  between cattle and bison, 117
  fertility of, 75
  among fishes, 117–8
Hydatina, experimental determination of sex in, 192
Hydra, eggs of, infected with *Algæ*, 137
  regeneration after injury, 68
Hypoblast, 69

IDIOPLASM theory, 9, 11, 114, 122
  and recapitulation, 114, 122
Immunity to atoxyl in trypanosomes, 139, 142
  to disease, 103–8, 215–6, 218–9
  to disease, power of acquiring, 105
  to malaria, 103
  to malaria, Charles Mercier upon, 157–8
  to measles, 105, 216
  to scarlet fever, 108, 216
  to tuberculosis, 106, 215–6
Inborn characters, classification of, 53
  definition of, 46
  modification of, 50
Inborn variations, effect of environment upon, 135–6, 157, 163–5
Individual character, sex an, 210
Individual characters in chromosomes, 128, 189
  definition of, 103
  transition of to racial, 103–8, 213–4
  transmitted alternatively, 184–9, 213
Individual variations, 102
  eliminated in a short time, 121–3

Individual variations eliminated by bi-parental reproduction, 130–3, 165
  exaggerated in domesticated races, 183–4
  represented by chromosomes, 128, 189
Infection of eggs of *Hydr ı* with *Algæ*, 137
Inheritance, blended, 179
  examples of blended, 117–8, 179, 185
  exclusive, 180
  particulate, 180
Inherited diseases, 136–7, 217–9
Injury, reaction to, 47
Insects, mimicry in, 85
Instincts in butterflies, 51
Instincts do not arise from intelligent action, 147–8
  in man, 49
  transmission of in fossorial wasps (*Sphex* and *Ammophila*), 145–8
  transmission of in social bees and ants, 149–50

JAPANESE waltzing mice, crossed with albinos, 114, 176
Jelly-fish, mutations in, not perpetuated, 65
Joints, origin of, 160
Jordan on continuity between species, 74

Kallima, protective coloration in, 83
Kelvin on age of earth, 100
Kingsley, Mary, on malaria, 104

LAMARCK's theory of evolution, 54
Lankester, E. Ray, upon Brown-Séquard's experiments, 143
Lemur, adaptation in pitcher plant against, 87
Lens, regeneration of crystalline, in salamander, 68–9
Lepidoptera, Mendelian experiments upon, 186–7, 209-10
Lichens as examples of symbiosis, 95
Life-cycle of multicellular organisms, 4, 27
Linin, definition of, 13
  a permanent nuclear structure, 19
Living matter, common properties of, 1
Lock, R. H., on discontinuity between species, 73
Loeb, cross fertilisation with echinoderms, 36
Loeb's experiments dealing with centrosomes, 41
Loeb's experiments on unfertilised ova, 30
Lombardy poplar, 67
Lunacy, increase of hereditary, 217–8

MADEIRA, snails in, 131
Malaria, Charles Mercier upon immunity to, 157–8
  immunity to, 103, 157–8
Mariette's village sheikh, 120
Marvel of Peru, Correns' experiments with, 173–4
Maupus on conjugation in unicellular organisms, 3, 29
Measles, immunity to, 105, 216
Meiotic division, 20–44
  results of, 22
  phase, interpretations of, 22, 41–44
Memory, 48
Mendelian characters, 167–189, 197–206
  Archdall Reid on, 202–3
  compound, 173–4
  contained in chromosomes, 177–8
  are exaggerated individual characters, 184
  in fowls, 176
  usually found in domesticated races, 182
  in natural races, 185–7
  as secondary sexual characters (Reid), 202–3
  experiments upon determination of sex, 199, 209–10
  experiments, imperfection of results of, 183
  experiments with *Lepidoptera*, 185–8
  interpretation of sex, 197–202
Mendel's experiments, 166–9
Mental characters mostly due to acquirements, 48, 214
Mercier, Charles, upon immunity to malaria, 157–8
  upon transmission of acquired characters, 155–9
Mesoblast, 69
Meves on chondriosomes, 35
  on function of cytoplasm in heredity, 34, 37, 38
Mice, results of crossing, 114, 176
Mimicry in insects, 85
Mirabilis jalapa, Correns' experiments with, 173–4
Mollusc parasitic upon star-fish, 94
Monkeys inoculated with trypanosomes, 141
Morgan, T. H., upon Brown-Séquard's experiments, 144

Morgan, T. H., embryos from unfertilised ova, 30, 38
  experiments on germinal localisation, 10
Mules, attempted explanation of sterility in, 117
Multicellular organisms, definition of, 2
  differentiation of cells in, 4, 6, 45, 68, 69
  fertilisation in, 3, 27
  life-cycle of, 4, 29
Mutants interbreed freely, 75
Mutating a character selected by man, 100
Mutation hypothesis, De Vries', 62-76
  De Vries' statement of, 72–3
Mutations, 63–101
  absence of in wild plants, 65
  in *Aurelia* (jelly-fish) not perpetuated, 65
  difficulty in distinguishing, 63
  Dixey, F. A., upon, 93
  in domesticated plants, 64
  not groundwork of evolution, 100
  incompatible with adaptation, 77, 91
  in *Œnothera*, 64, 71
  in *Œnothera*, G. A. Boulanger on, 71
  perpetuation of, 189
  Poulton's metaphor upon, 92
  Thiselton-Dyer on, 72
  transmitted on Mendelian lines, 187–9
Myrmecocystus (honey ant), 151–2
Myxine glutinosa, alternation of sex in, 191

Nägeli's experiments with Alpine plants, 136
  idioplasm theory, 9, 11, 114, 122
  idioplasm theory and recapitulation, 114, 122
Natural selection, misrepresented, 155–9
Nerve-cells do not multiply, 161
Nepenthe bicalcarata, adaptation in to a lemur, 87
Nucleus bearer of hereditary characters, 34
  function of in heredity, 30–4, 38–40
Nussbaum's experiments upon *Hydatina*, 192

Œnothera, Boulanger's experiments upon, 64
  mutations in, 64, 71
Ovum, 23
  segmentation of without fertilisation, 30
  maturation of, 26

Pangenesis, Charles Darwin's theory of. 7, 58
  Galton on theory of, 119
Paramecium, conjugation in, 29
Parasitic adaptation, 93
  crustacea, 66
Parasites, degeneration in, 153–4
  Mollusc, upon star-fish, 94
Parthenogenesis, 28
  in *Aphis*, 28
  in bees, 28
  polar bodies in, 28
Pasthenogenetic forms, variations in, 61
Particulate inheritance, 180
Peas, inheritance of starch grains in, 182–3
  Mendel's experiments with, 166–9
Peckham, G. W. and E. G., on instincts in fossorial wasps, 148
Piebald horse, 180
Pigeons, results of crossing domesticated, 113
Pitcher-plants, adaptations in, 87
Placenta, evolution of, 112
Plants, adaptations in, 87
  regeneration of tissue in, 68–9
Play in mammals, 49
Polar bodies, 27
  in parthogenesis, 28
Polydactylism, 131
Polymorphism in ants, 150-2
Polyzoa, Harmer on variations in, 60
Poulton on continuity between species, 73
  metaphor upon mutations, 92
Precis, seasonal changes in, 84
Prehistoric man, physical characters of, 120
Prepotent characters, 179–80
  races, 180
Progressive variations, 109
  at all stages of development, 112
Pronuba, adaptation to Yucca, 88
Protective coloration, 83
Protoplasm, 1
Prout's and Bacot's experiments with *Lepidoptera*, 186–7

Quetelet on Gauss's law, 99

Rabbits, effect of inoculation with trypanosomes, 140

Races, prepotent, 180
Racial characters, blending of, 117–8, 179, 185, 189
  definition of, 103
  mode of transmission of, 184–9, 213
  permanency of, 103
  not represented by chromosomes, 23
  stability of, 121
  transition of individual to, 103–8, 213–4
  variations of race, 103
Rats, effect of inoculation with trypanosomes upon, 140
  growth of teeth in, 160
Reaction to injury, 47
Recapitulation, Archdall Reid on, 113,
  as explanation of reversion, 114, 116
  and Nägeli's idioplasm theory, 114, 122
  reversion implies incomplete, 116
  sometimes absent in plants, 111
  theory of, 110–22
Recessive characters, 168, 170
Reducing division, 20–44
  results of, 22
Reduction in number of chromosomes, 20
Regeneration of crystalline lens in Salamander, 69
  in *Hydra* after injury, 68
  of nerve-cells, 32
  in plants, 68–9
  of tissue in vertebrates, 68
  in unicellular animals after injury, 32
Regressive variations, 109
  at all stages of development, 111
Reid, Archdall, on bi-parental reproduction, 128
  letter to, on malaria among troops, 104
  on Mendelian characters, 202–3
  on recapitulation, 113
  theory of immunity to disease, 103
Reproduction in multicellular organisms, 3, 27
  in unicellular organisms, 2, 29
Reversion to ancestral characters, 113–18
  to ancestral characters in domesticated races, 115
  implies incomplete recapitulation, 116
  recapitulation as explanation of, 114, 116
Roach, hybrids, 118
Rothschild and Jordan on continuity between species, 74
Rotifers, experimental determination of sex in, 192
Roux, experiments on germinal localisation, 10
Roux-Weismann theory of an hereditary substance, 9, 11
Royal Commission on the care and control of the feeble-minded, 154
Rudd, hybrids, 118

Salmo fario hybrids, 117, 118
Salmo salar hybrids, *S. fario*, 118
Salvelinus alpinus hybrid, 118
Salvelinus fontinalis hybrid, 117
Scorpiurus, adaptation in seeds of, 88
Seasonal changes in colours of animals, 84
Secondary sexual characters dependent upon primary, 209, 211
  experiments upon, 205–6
  potentiality of, present in all individuals, 205–7
  are racial, 209–11
Segregration of gametes, theory of, 169–70
  imperfect, 176–7
  most perfect in self-fertilising organisms, 184–5
Selection of variability, 71
Sex alternative in *Myxine glutinosa* (hag-fish) 191
  nature of, 203, 210
Sex, blending of, prevented by natural selection, 207–8, 210
  a comparatively late product of evolution, 190
  definition of, 191
  determination of, Wilson's theory, 195–7, 201–2
  of eggs determined before segmentation, 193
  function, production and determination of, 190–211
  an individual character, 204–5, 207–8, 210
  influenced by environment, 191–3
  Mendelian experiments upon determination of, 199, 209–10
  Mendelian interpretation of, 197–202
  theory of inheritance of, 203–11
Sheep, blended characters in, 185
Sheik-el-Beled, village sheik, 120
Silk-moths, Mendelian experiments with, 186
Sitaris humeralis, adaptations in, 77.

Slave-making ants, 81
Sleeping sickness, 139
Slums, effect of upon inhabitants, 154–5
Snails in Madeira, 131
Sommer's repetition of Brown-Séard's experiments, 144
Species, attempted definition of, 75
  breeding true not a test of, 74
  fertility not a test of, 74
  nature of, 74
  Poulton on, 75
  Ray Lankester on, 75
  Thomson on intermediate links between, 76
Sperm, 22
Sperms, dimorphic, 194
  production of, 26
Sphex, transmission of instincts in, 145–8
Spindle, formation of, 14–17
Spireme, definition of, 14
  structure of, 14–19
Starch grains in peas, inheritance of, 182–3
Stilifer linckiæ parasites upon star-fish, 94
Stylonychia, life-cycle of, 2
Symbiosis, *Convoluta* and *Algæ*, 95
  examples of, 95
  lichens (*Algæ* and fungi), 95
Syphilis, inherited, 137, 218

TADPOLES, Yung's experiments upon, 192
Tarsius spectrum, adaptation against in pitcher-plant, 87
Teeth, growth of, 159–60
Theories of evolution, 54–8
Thiselton-Dyer on mutations, 72
Thomson, J. A., on intermediate links between species, 76
  on nucleus as bearer of hereditary characters, 34
Transmission of characters, two opposite modes of, 182
Trout hybrids, 117–8
Trypanosomes, 139–43
  effect of selection upon, 139–142
Tuberculosis, immunity to, 106, 215–6
  possibility of eliminating infection, 215–6
  traces of infection generally present, 107
Typhoid, possibility of elimination of, 216
Typhlopone (African driver-ant), 150–1

UNFERTILISED ova, experiments upon, 30
Unicellular animals, Gruber's experiments upon, 32
  regeneration in, after injury, 32
Unicellular organisms, definition of, 2
  fertilisation in, 2, 29
  life-cycles of, 2, 3, 29

VARIABILITY a character amenable to selection, 71
Variations—
  in *Cypris*, Weismann on, 60
  in *Daphnia*, E. Warren on, 60
  Darwin on large and small, 62, 72
  different kinds of, 62
  difficulty in observing, 59, 61
  eliminated by bi-parental reproduction, 129, 165
  in *Entomostraca*, 60
  essential differences in, between animals and plants, 67, 70
  fluctuating, 63
  frequency of regressive, 110
  in germ-cells, 164–5
  in grafts, 67–8
  inborn, *see* Inborn variations
  individual, *see* Individual variations
  large, eliminated by natural selection, 101
  large and small, not defined, 62
  in parthenogenetic forms, 60
  in polyzoa, Harmer on, 60
  progressive, 109
  racial, in snails in Madeira, 131
  racial, in wide-ranging species, 131
  regressive, 109
  regressive and progressive, at all stages of development, 111
  said to be increased by crossing races, 132
  small, the material of evolution, 129
  small, sufficiency of, 97
  theory of causation, 124
  universal, 59
  useless, elimination of, 126, 130, 165
  Wallace on large and small, 63
  in wild and domesticated races, comparison between, 70
Verworn on relation between nucleus and cytoplasm in heredity, 38
Village sheik, 120
Vries, H. de, mutation hypothesis, 63–76
  statement of the mutation hypothesis, 72–3
  theory of germ-plasm, 58

WALLACE on large and small variations, 63
Warren, E., on variations in *Daphnia*, 60
Wasps, fossorial, transmission of instincts in (*Sphex* and *Ammophila*), 145–8
Weismann and Roux, theory of hereditary substance, 9, 11
Weismann's theory of evolution, 55
Weismann on variations in *Cypris*, 60
Willows, crosses between varieties of, 179
Wilson on chromatin as bearer of hereditary characters, 33
Wilson, experiments on germinal localisation, 10
  theory of the determination of sex, 195–7, 201–2

Xanthorohë, Mendelian experiments with, 187

YUCCA, adaptation to the moth *Pronuba*, 88
Yung's experiments upon tadpoles, 192

ZEBRA hybrid with horse, 128
Zoja, experiments on germinal localisation, 10

THE END

Printed by BALLANTYNE, HANSON & CO.
Edinburgh & London

MR. EDWARD ARNOLD'S LIST
OF
MEDICAL BOOKS.

Further Advances in Physiology.

EDITED BY LEONARD HILL, M.B., F.R.S.

With Contributions from Professor BENJAMIN MOORE, University of Liverpool; MARTIN FLACK, B.A., M.B. OXON.; LEONARD HILL, M.B., Lecturer on Physiology, London Hospital; Dr. THOMAS LEWIS; Dr. ARTHUR KEITH, Curator of the Hunterian Museum, Royal College of Surgeons; Dr. M. S. PEMBREY, Lecturer on Physiology, Guy's Hospital; Dr. N. ALCOCK, Lecturer on Physiology, St. Mary's Hospital; Dr. JOSEPH SHAW BOLTON; MAJOR GREENWOOD, M.R.C.S., Director of Statistical Department, London Hospital.

448 pages. With Diagrams and Index. Demy 8vo., 15s. net.

Recent Advances in Physiology and Bio-Chemistry.

EDITED BY LEONARD HILL, M.B., F.R.S.

CONTRIBUTORS:

Prof. BENJAMIN MOORE; LEONARD HILL, M.B., F.R.S.; J. J. R. MACLEOD, M.B., Professor of Physiology, Western Reserve University, Cleveland, U.S.A.; late Demonstrator of Physiology, the London Hospital; M. S. PEMBREY, M.A., M.D.; and A. P. BEDDARD, M.A., M.D., Assistant Physician, late Demonstrator of Physiology, Guy's Hospital.

xii+740 pages. With Diagrams. Demy 8vo., cloth, 18s. net.

Practical Physiology.

BY A. P. BEDDARD, M.A., M.D.; J. S. EDKINS, M.A., M.B.; LEONARD HILL, M.B., F.R.S.; J. J. R. MACLEOD, M.B.; and M. S. PEMBREY, M.A., M.D.

SECOND EDITION. xvi+503 pages. With Illustrations. 12s. 6d. net.

Applied Physiology.

BY ROBERT HUTCHISON, M.D. EDIN., F.R.C.P.,
Physician to the London Hospital and to the Hospital for Sick Children, Great Ormond St.

Crown 8vo., 7s. 6d. net.

Physiology of the Special Senses.

BY M. GREENWOOD, JUN., M.R.C.S., L.R.C.P., F.S.S.,
Director of the London Hospital Statistical Department; Senior Demonstrator of Physiology in the London Hospital Medical College; Examiner in Physiology to the University of St. Andrews.

viii+239 pages. 8s. 6d. net.

LONDON: EDWARD ARNOLD, 41 & 43 MADDOX ST., BOND ST., W.

The Physiological Action of Drugs.

An Introduction to Practical Pharmacology.

BY M. S. PEMBREY, M.A., M.D.,
Lecturer on Physiology, Guy's Hospital;
AND C. D. F. PHILLIPS, M.D., LL.D.

With 68 Diagrams and Tracings. Demy 8vo., cloth, 4s. 6d. net.

Human Embryology and Morphology.

BY ARTHUR KEITH, M.D. ABERD., F.R.C.S. ENG.,
Lecturer on Anatomy, London Hospital Medical College; formerly Hunterian Professor, Royal College of Surgeons, England, Examiner in Anatomy, University of Aberdeen, and in the Natural Science Tripos, University of Cambridge.

xii + 402 pages. Second Edition. Demy 8vo., 12s. 6d. net.

Lectures on Diseases of Children.

BY ROBERT HUTCHISON, M.D. EDIN., F.R.C.P.,
Physician to the London Hospital and to the Hospital for Sick Children, Great Ormond St.

NEW AND REVISED EDITION.

440 pages. With Illustrations. Crown 8vo., cloth, 8s. 6d. net.

A System of Clinical Medicine.

Dealing with the Diagnosis, Prognosis, and Treatment of Disease, for Students and Practitioners.

BY THOMAS D. SAVILL, M.D.,
Late Physician to the West End Hospital for Diseases of the Nervous System, and to St. John's Hospital for Diseases of the Skin.

NEW EDITION IN ONE VOL. 8vo. 25s. net.

A Text-Book of Medical Treatment.

ALPHABETICALLY ARRANGED.

BY WILLIAM CALWELL, M.A., M.D.,
Physician, Royal Victoria Hospital, Belfast; University Clinical Lecturer on Medicine, Queen's University, Belfast.

iv + 632 pages. Royal 8vo. 16s. net.

The Diagnosis of Nervous Diseases.

BY PURVES STEWART, M.A., M.D., F.R.C.P.,
Physician to Out-Patients at the Westminster Hospital; Joint-Lecturer on Medicine in the Medical School; Physician to the Royal National Orthopædic Hospital; Assistant Physician to the Italian Hospital.

NEW AND REVISED EDITION.

viii + 450 pages. With many Original Illustrations. 15s. net

A Guide to the Diseases of the Nose and Throat, and their Treatment.

By CHARLES A. PARKER, F.R.C.S. Edin.,
Surgeon to the Throat Hospital, Golden Square, W.

xii + 624 pages. With 254 Illustrations. Demy 8vo., cloth, 18s. net.

Contributions to Abdominal Surgery.

By Harold Leslie Barnard, M.S., F.R.C.S.,
Late Assistant Surgeon, London Hospital.

xix + 391 pages. Illustrated. Price 15s. net.

Movable Kidney: its Pathology, Symptoms, and Treatment.

By H. W. WILSON, M.B., B.S. Lond., F.R.C.S. Eng.,
Demonstrator of Anatomy, St. Bartholomew's Hospital;

And C. M. HINDS HOWELL, M.A., M.B., M.R.C.P. Lond.,
Junior Demonstrator of Physiology, St. Bartholomew's Hospital.

Demy 8vo., 4s. 6d. net.

A Handbook of Skin Diseases and their Treatment.

By ARTHUR WHITFIELD, M.D. Lond., F.R.C.P.,
Professor of Dermatology at King's College; Physician to the Skin Departments, King's College and the Great Northern Central Hospitals.

xii + 320 pages. With Illustrations. Crown 8vo., 8s. 6d. net.

Food and the Principles of Dietetics.

By ROBERT HUTCHISON, M.D. Edin., F.R.C.P.,
Physician to the London Hospital.

xx + 582 pages, with 3 Plates in Colour and 34 Illustrations in the text. Demy 8vo., red buckram, 16s. net.

The Chemical Investigation of Gastric and Intestinal Diseases by the Aid of Test Meals.

By VAUGHAN HARLEY, M.D. Edin., M.R.C.P., F.C.S.,
Professor of Pathological Chemistry, University College, London;

And FRANCIS GOODBODY, M.D. Dubl., M.R.C.P.,
Assistant Professor of Pathological Chemistry, University College, London.

Demy 8vo., 8s. 6d. net.

A Manual of Pharmacology for Students.

By WALTER E. DIXON, M.A. CANTAB., M.D., B.S.,
B.SC. LOND., D.P.H. CAMB.,
Assistant to the Downing Professor of Medicine in the University of Cambridge;
Examiner in Pharmacology in the Universities of Cambridge and Glasgow.

xii+451 pages. With Illustrations. Demy 8vo., cloth, 15s. net.

The Influence of Alcohol and other Drugs on Fatigue.

By W. H. RIVERS, M.D., F.R.C.P., F.R.S.,
Lecturer in Physiological and Experimental Psychology at Cambridge University.

Royal 8vo., 6s. net.

The Sanitary Officer's Handbook of Practical Hygiene.

By MAJOR C. F. WANHILL, R.A.M.C.,
Assistant Professor of Hygiene, Royal Army Medical College;
AND MAJOR W. W. O. BEVERIDGE, D.S.O., R.A.M.C.,
Analyst to the Army Medical Advisory Board.

Interleaved with blank pages for notes. Crown 8vo., 5s. net.

BOOKS FOR NURSES.

Surgical Nursing and the Principles of Surgery for Nurses.

By RUSSELL HOWARD, M.B., M.S., F.R.C.S.,
Lecturer on Surgical Nursing to the Probationers of the London Hospital.

With Illustrations. Crown 8vo., 6s.

Midwifery for Nurses.

By HENRY RUSSELL ANDREWS, M.D., B.SC. LOND.,
M.R.C.P. LOND.,
Examiner to the Central Midwives Board.

New Edition. With Illustrations. Crown 8vo., 4s. 6d. net.

A Text-Book of Nursing.

By C. S. WEEKS-SHAW.

Revised and largely Rewritten by W. RADFORD.

xiv+344 pages. With numerous Illustrations. 3s. 6d.