**Evolution and heredity : theories and problems / by Charles Edward Walker.**

**Contributors**

Walker, Charles Edward, -1953.

**Publication/Creation**

London : A. & C. Black, Ltd., 1936.

**Persistent URL**

https://wellcomecollection.org/works/ej9nywt4

TION

in

ITY

s and

ms

EBB

# EVOLUTION AND HEREDITY

# EVOLUTION AND HEREDITY

## THEORIES AND PROBLEMS

BY
CHARLES EDWARD WALKER
D.SC., M.R.C.S., L.R.C.P.
ASSOCIATE PROFESSOR OF CYTOLOGY
IN THE UNIVERSITY OF LIVERPOOL
AUTHOR OF 'ESSENTIALS OF CYTOLOGY', 'HEREDITARY CHARACTERS', 'THEORIES AND PROBLEMS OF CANCER', ETC.

With twenty figures
in the text

A. & C. BLACK LTD
4, 5 & 6 SOHO SQUARE, LONDON, W.1
1936

MADE IN GREAT BRITAIN
PRINTED BY R. & R. CLARK LTD. EDINBURGH

*The United States*
THE MACMILLAN COMPANY, NEW YORK
*Australia and New Zealand*
THE OXFORD UNIVERSITY PRESS, MELBOURNE
*Canada*
THE MACMILLAN COMPANY OF CANADA, TORONTO
*South Africa*
THE OXFORD UNIVERSITY PRESS, CAPE TOWN
*India and Burma*
MACMILLAN AND COMPANY, LIMITED
BOMBAY CALCUTTA MADRAS

'In the course of the historical development of any branch of science, what is universally observed is this: that the men who make epochs, and are the real architects of the fabric of exact knowledge, are those who introduce fruitful ideas or methods. As a rule, the man who does this pushes his idea, or his method, too far; or, if he does not, his school is sure to do so; and those who follow have to reduce his work to its proper value, and assign it its place in the whole. Not unfrequently, they, in their turn, overdo the critical process, and in trying to eliminate error, throw away truth.'

T. H. HUXLEY: AGNOSTICISM AND CHRISTIANITY, 1889.

# PREFACE

Much of the contents of the earlier chapters in this book have been included in the hope of making the whole clear to the general reader.

An attempt is made to correlate and harmonise many of the observations recorded during the past thirty years that appear to contradict each other. One example will be sufficient to show that confusion of thought may be caused by what has been written about the transmission of characters from parent to offspring.

Johannsen originated the genotype theory and defined a 'gene' as a unit-factor or element representing a character, demonstrated by modern Mendelian researches. But Johannsen has said more recently:

> 'The talk of genes for any particular character ought to be abandoned.' 'There are no unit characters at all.' 'Personally, I believe in a great central "something" as yet not divisible into separate factors.'

Yet, within a few lines he says:

> 'Disregarding this (perhaps only provisional ?) central something, we should consider the numerous genes, which have been segregated, combined or linked in our modern genetic work.'

If we abandon some of the current interpretations of recorded observations, the genes will fit in quite comfortably with the 'great central something', and much the same may be said of some other apparent contradictions.

I have to thank Professor H. E. Armstrong, Sir John Bretland Farmer and Mr Clifford Dobell for kindly criticisms. I have followed much of their advice.

# CONTENTS

# EVOLUTION AND HEREDITY

## CHAPTER I

The interdependence of evolution and heredity
The definition of characters

THE problems of Evolution and Heredity are so closely related and interdependent as far as any reasonable interpretations of them are concerned, that it is impossible to deal with the one subject without the other.

The theories of the evolution of living organisms attempt to explain how the more complicated have arisen from the simple.

Theories of heredity attempt to explain the continuance through the parents to the offspring of various points of similarity and also the occurrence of differences between the offspring and their parents and between each other.

It seems clear that the production of the more complicated organisms from the simple, which are assumed to be the more primitive, must, if it has occurred at all, have been through the preservation of the similarities and the accumulation and transmission of the differences between parents and offspring during succeeding generations. It is of course possible, as has been done by the Government of one of the States in America, to deny the existence of evolution altogether and forbid the teaching of any such theory in school and university; but such an attitude is, in our present state of knowledge, unusual and to be deprecated.

It thus appears that the probable truth of any theory of evolution must depend upon its agreement with the known facts of heredity; and conversely, the probable truth of theories relating to the details of how points of similarity between parents and offspring are continued through generations and how differences between them arise, must depend upon their compatibility with what we know of the order in which different animals and plants appeared upon this earth during the succeeding periods of its existence.

The current opinions upon matters vital to the correct interpretations of the phenomena involved in the continuance through parents to offspring of various points of similarity, are often directly contradictory, more strikingly so perhaps than in the case of any other scientific problems of immediate interest and practical importance.

That correct interpretations are practically important becomes evident when it is realised that upon what views are generally accepted will depend the nature, direction and efficacy of any attempts to control the multiplication of the feeble-minded, of the insane and of habitual criminals, and to check a decline in the general efficiency of the race.

Different schools contradict each other flatly upon such important points as whether or not characters acquired by parents can influence their appearance in the offspring, and whether characters may or may not be completely eliminated from inheritance in one or two generations.

The desirability of coming to a definite conclusion as to what is implied by the term 'character' when used by the biologist in relation to living organisms is then obvious, but a definition is by no means easy or simple.

Most people, whether biologists or not, will agree that the possession of a peculiarly shaped nose or other feature in man should be included, and that such characters frequently continue to appear in successive generations.

The colour of a flower or of parts of an animal would also be generally accepted as characters. The number of scales in the lateral line of a fish is accepted as a character by zoologists, and may be among those which determine the species. There would probably be no question raised by anyone as to these being called characters. But there is much to be said for claiming the presence of two arms, two legs, or a head, as characters in man, though there are possibly some who would disagree. Yet the difference is only one of degree or size.

Is it possible to place a limit of degree, or size, or nature, beyond which the term 'character' should not be applied? Any property, peculiarity or quality of a living organism, whether of structure, of shape, of parts or arrangement and interrelation of parts, of colour, of texture, of function or of size, is rightly called a character; and as the gradation between the extremes is frequently by very minute steps, there seems no justification in applying the term only to comparatively small differences in certain features between more or less similar individuals.

In order to render what follows more intelligible, such characters as colour, structure, shape, texture and arrangement in interrelation of parts will be called 'morphological'. It is common knowledge that such characters may be inherited.

Another group of characters is called 'mental'.

By a mental character is meant some distinctive capacity to perform or acquire skill in the performance of certain actions or series of actions, intellectual or mechanical, which are not obviously due to direct physical or chemical stimuli. What are commonly referred to as instinct, intelligence and educability are included.

We know that some of these at any rate, if not all, may be inherited. One example will suffice. It is easy to teach a pointer puppy to point at game. It might be possible in some cases, though in all very difficult, to teach a bulldog to point. The only possible interpretation of this is that the pointer pup has inherited the capacity to acquire this accomplishment easily from its parents.

A still further group of characters may be called 'functional'. Among these are included such characters as the production of secretions and excretions, various forms of metabolism and other physiological processes; the production of enzymes and hormones as in the digestive processes and metabolism; the production of highly poisonous substances as in the case of some snakes and insects; the various reactions, nervous and others, to stimuli; and the power of resisting unfavourable factors in the environment, such as the comparative immunity to the tubercle bacillus enjoyed by the races of Northern Europe and the immunity of cows to atropine (deadly nightshade), are examples of what are included under the term 'functional' character.

While it would not be true to say that any writer has definitely limited the term 'character' to comparatively small differences between more or less similar individuals, still it is true that some such limitation is implicit in many, if not most, of the writings on the transmission of characters from parents to offspring, more particularly during the past thirty years, that is, since Mendel's discoveries were made generally known.

Taking, then, the term 'character' in its widest sense, we know that all, great and small, *may* be handed on from parent to offspring. The larger, such as the presence of limbs in a mammal, may include within themselves a number of smaller characters. The larger characters are more constant than the smaller, so much so that their absence might leave little or no chance of survival for the individual. For instance, a mammal, including man, may be born with practically no head. An anencephalic monster, that is, an individual with only the vestiges of a head, can survive birth for only a few seconds, but there are many gradations in the deficiency, and according to the amount of brain present, so the possible survival of such an individual will vary. Such gross failures to reproduce a large character are rare. On the other hand, the failure to reproduce peculiarities in small features is not uncommon and may involve no disadvantage to the individual.

It will probably be generally accepted that large characters which are common to all the individuals of a group are almost invariably transmitted, and that the larger the group or collection of groups of individuals to which the character is common, the more rarely will the offspring fail to reproduce it.

Thus, while human parents would regard the occurrence of a tail in their child with astonishment, the fact that its features did or did not resemble those of the father or mother might give rise to satisfaction or disgust, but certainly not to any surprise; so generally is the fact recognised that to differ from the parents in the larger is unusual, but common in the smaller characters. Headless human children (anencephalic monsters) are of very rare occurrence, while children born with tails are not so rare. The possession of a head is common to all vertebrates, a very large group; while tails are common to the larger part of a group to which man belongs, usually being absent in him and a few other of the most closely allied forms.

There is, however, a great variety within any of these larger characters. Though there is no doubt as to a head being present in vertebrates, these heads vary greatly from each other, these differences forming smaller characters which are superimposed on the larger.

Continuing the process of analysis we come down to quite small characters. From the difference between the heads of amphibia, fishes, birds and mammals, we come to the differences between orders, genera and species; to such characters as are peculiar to the race; to the family (using the word in its most restricted sense) and finally to those peculiar to the individual.

The differences in the larger characters, as, for instance, between the heads of various kinds of vertebrates, would then seem to depend upon smaller characters superimposed upon the larger. If this be true, the larger characters, those common to the greatest range of groups of organisms, are the most ancient.

The practical application of the study of heredity would at first sight appear to be concerned chiefly with the smaller characters, that is, those which are found to differ only within the smaller groups of organisms. In man, for instance, we are interested mainly with those characters which are peculiar to him alone, and more particularly perhaps to those of small groups of men or even of an individual. The same might be said with regard to domesticated animals and plants which man breeds and improves for his own use and pleasure. Though the larger characters common to whole groups of organisms are so constant that their consideration does not appear to be of practical importance, they must be taken into account in any theory that includes all the phenomena involved in the transmission of hereditary characters.

To put the matter crudely and briefly: the presence of a head, arms and legs, is not less certainly due to heredity than are the shape of the nose or the colour of the eyes or hair.

Any enquiry into how characters are transmitted from parents to offspring should aim at ascertaining whether there is any differences in the modes of transmission; whether, in fact, the reappearance of characters in successive generations is brought about in the same way in all; what mechanism exists capable of producing the observed phenomena; and how far the recorded observations relating to the manner in which characters reappear in succeeding generations are explicable by what we know of the physical and mechanical means available.

# CHAPTER II

Structure of living organisms · Cell multiplication
Fertilisation and reproduction in plants and animals

So much of a popular or semi-popular nature has been said and written in lectures, books and articles about heredity, that for the sake of completeness and in the hope of appealing to those who are interested in the subject but do not possess the special biological knowledge involved, a short sketch of some of the essential points relating to the structure of living matter and the process of fertilisation is given.

Living organisms, vegetable and animal, are composed of cells, and of material that has been manufactured by cells while the organism was developing or growing. A cell is a minute mass of a complex jelly-like substance called protoplasm. Within each cell is an area, generally surrounded by a membrane, which is apparently denser than the rest of the cell and differs from it in some other ways. This is the *nucleus*. The rest of the cell is known as the *cytoplasm*.

The individual begins its existence as a single cell. This cell divides into two daughter cells, each of them into two more, and so the process goes on until the whole body of the organism is built up. It is during this process of multiplication that the cells become divided into groups; are differentiated from each other in function, shape, structure and size.

Cells multiply in two different ways. In *Amitosis* or direct cell division the cell divides just as a drop of viscous fluid divides into two drops. The nucleus within the cell divides in the same way. It is fairly generally accepted that amitosis occurs in the higher organism only among the cells which form tissues of a transitory nature or as a prelude to degeneration. It may serve a useful purpose in increasing the nuclear surface, so facilitating metabolism in some cases; and may possibly play a part in the multiplication of cells of a highly differentiated type; but it seems very improbable that in the higher organisms it comes into sequence with any continuous line of reproduction and multiplication of cells. It seems probable, on the other hand, that amitosis plays an important part in the multiplication of some of the lower organisms.

*Mitosis* or indirect cell division is a complicated process. We have already seen that a cell consists of a minute mass of protoplasm, within which mass is the nucleus. The rest of the cell surrounding the nucleus is called the cytoplasm (Fig. 1). In the cytoplasm, generally near the nucleus, a minute body may frequently be observed. This is known as the centrosome (Fig. 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

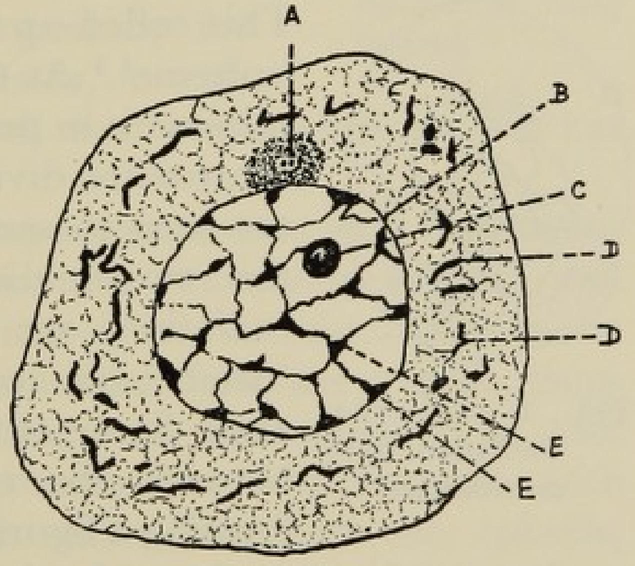


FIG. 1.—A. Centrosomes. B. Nuclear membrane. C. Nucleolus. D. Chondriosomes or Mitochondria. E. Masses of chromatin joined by threads of linin.

the nucleus. These small masses are joined together by a fine mesh-work which frequently contains still smaller particles of the 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 mesh-work, 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 mesh-work 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, the chromatin is seen to arrange itself in a long coiled-up thread within the nucleus (Fig. 2).[1] This coiled-up thread is known as the 'spireme'.[2] At the same time that the spireme is in process of formation, the centrosome divides into two and these are seen to send out radiations into the surrounding cytoplasm. These radiations are collectively known as 'Asters', on account of their appearance. 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 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

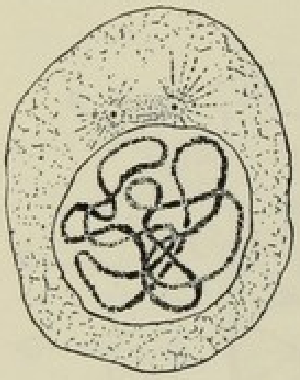


FIG. 2.—Spireme. Radiations from centrosomes.

---

[1] This figure, and figs. 2–8, 10, 12–18, are reproduced from the author's *Hereditary Characters* (Edward Arnold).

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

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 a cockroach 32 chromosomes appear in a dividing cell; in a mouse, 24; in a newt, 24; in *Artemia*, a crustacean, 168; in *Ascaris megalocephala* var. *univalens*, 2; and so on. The number of the chromosomes does not appear to have any relation to the size or complexity of the organism, for the Radiolarian *aulacantha*, a unicellular animal, has well over 1000, while the pig has only 40.

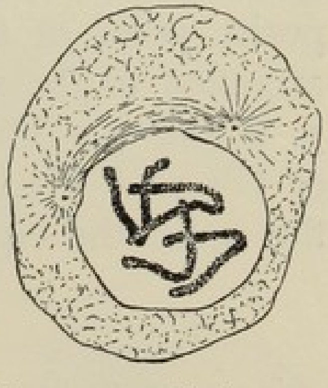


FIG. 3.—Spireme broken into short lengths, the chromosomes. Spindle is being formed.

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

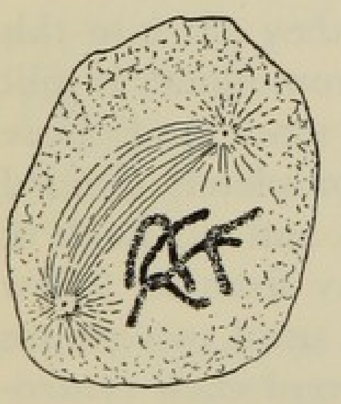


FIG. 4.—Disappearance of nuclear membrane.

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 being at opposite poles of the cell, and the chromosomes being attached to the spindle on the equatorial plane (Figs. 5, 6 and 7). 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 (Figs. 8 and 9). 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. 10). In each of 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 (Figs. 10 and 11), and this becomes more and more accentuated until the original mass of protoplasm, that

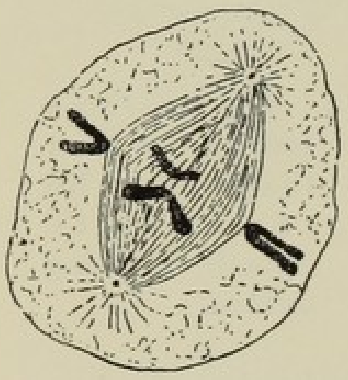


Fig. 5.—Chromosomes attached to spindle fibres (lateral view).

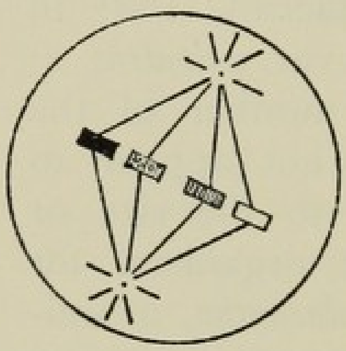


Fig. 6.—Diagram of same.

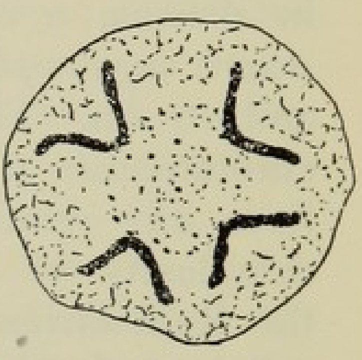


Fig. 7.—Same (polar view).

is, the cell, is divided into two at the narrow point in the centre (Fig. 12). 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

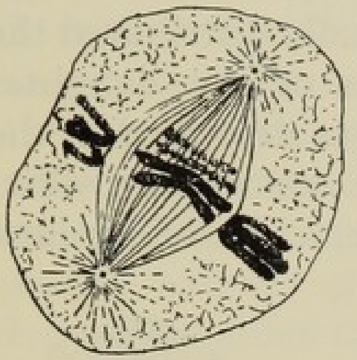


FIG. 8.—Splitting of the chromosomes.

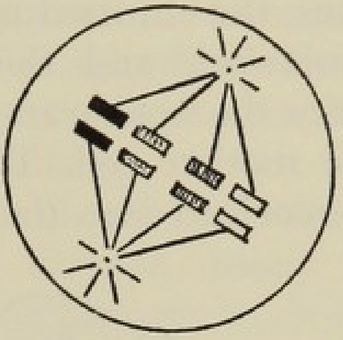


FIG. 9.—Diagram of same.

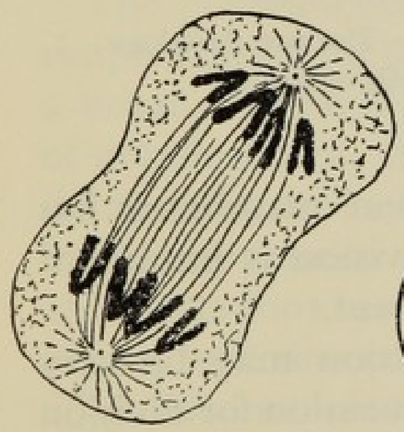


FIG. 10.—Longitudinal halves of chromosomes drawn towards opposite poles of spindle.

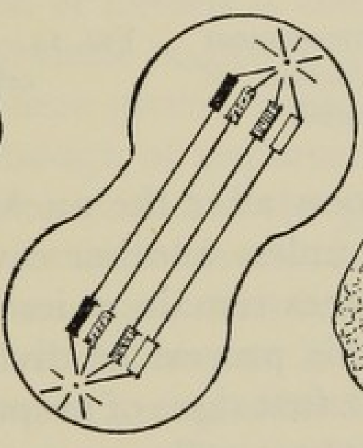


FIG. 11.—Diagram of same.

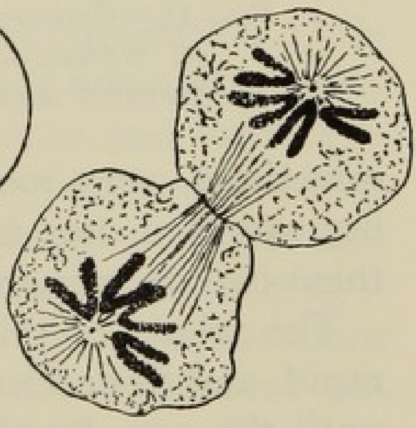


FIG. 12.—The cytoplasm dividing.

nuclear membrane is formed (Figs. 13 and 14). 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, sometimes, very soon after the nuclear membrane has been formed, but unless another division is imminent these two centrosomes remain quiescent.

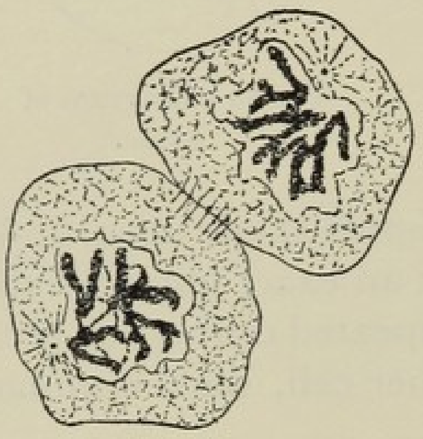


FIG. 13.—Commencement of reconstruction of daughter nuclei.

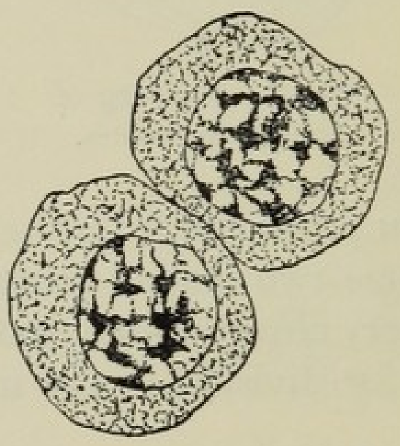


FIG. 14.—The two daughter cells complete.

The whole of this process of division may be 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 often 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.

The important point in this phenomenon is that each daughter cell receives an exact longitudinal half of each of the chromosomes present in the mother cell; consequently each chromosome of every cell in the organism has been derived by a series of longitudinal divisions from the corresponding chromosome in the single cell from which that organism was built up.

There are, of course, many modifications in detail of this general scheme of mitotic division, many more recorded observations than here described; but it is safe to say that, as far as our present knowledge goes, none of these modifications or additions as a rule alter the final result of mitotic division in so far as it concerns the chromosome content of the cells of those organisms with which we have to deal, or with any possible connection between the presence of the chromosomes and the development of the characters of an organism.

The phenomenon of mitosis is complicated, but it is simple compared to those involved in fertilisation. Only a broad outline is here given, missing out a great bulk of details which, though of importance and interest in themselves, are not essential to the proper understanding of the general result achieved. In spite of considerable variations in the ways in which this result is brought about, and the great differences in the interpretations of particular phenomena advanced by different observers, nearly all are agreed as to the final result.

At some period during the life of those organisms in which bi-parental reproduction occurs, certain groups of cells become differentiated. These are the gametogenic cells, and after a varying number of cell generations these produce sexual cells or gametes, which are thrown off from the body of the organism. These groups of gametogenic cells live a parasitic existence in the body that has produced them, and in a certain sense can hardly be regarded as forming an integral part of it. They are not necessary to the individual, but they are necessary for the production of new individuals in the case of the higher animals, and do so when occasion arises in the case of plants. Two of these gametes, one derived from each parent, fuse to form the fertilised ovum, which gives rise to the new individual.

In animals the sperm, that is, the sexual cell produced by the male, is usually motile and generally may be described as seeking and penetrating into the substance of the ovum—the sexual cell produced by the female. Both sperms and ova reach full maturity in the body of the animal before they are separated from it.

Among the higher plants, however, the process is a little more complicated. The actual body of the plant is formed of an asexual generation of cells which has no counterpart in the life history of the higher animals. The sexual cells are produced by 'gametophytes', which are in reality separate individuals growing upon the plant. Strictly speaking, it is not the plant itself which corresponds to the body of the animal, but the gametophyte. Cells derived from different gametophytes on the same plant are therefore to be regarded as being derived from separate individuals.

In the higher forms, both of plants and animals, a peculiar type of cell division is interpolated between two of the ordinary mitotic divisions before the mature sexual cells, known as gametes, are produced. The effect of this division is to distribute whole chromosomes to the daughter cells and consequently to reduce their number to one half of that found in the cells of the body.

The preliminary stages of this particular division are far more complicated than in the case of the ordinary mitotic division, and have been the subject of much controversy; but it is fairly generally agreed that, no matter which of the several interpretations is accepted, the final result is the same—whole chromosomes are distributed to the gametes, and a mature gamete, whether sperm or ovum, contains only half the number found in the body cell of the plant or animal. There are particular exceptions, as in the case of the 'sex'-chromosomes, but this does not affect the general significance of the phenomenon. In the case of the higher animals, only one cell generation follows that in which reduction in the number of chromosomes takes place. In plants a practically unlimited number may occur, producing a separate individual, in some cases another plant in fact, with different characters (*e.g.* the prothallium of a fern). These divisions following that in which the number of chromosomes is reduced, are similar in every way to the ordinary mitotic division, except, of course, that only half the full number of chromosomes are present.

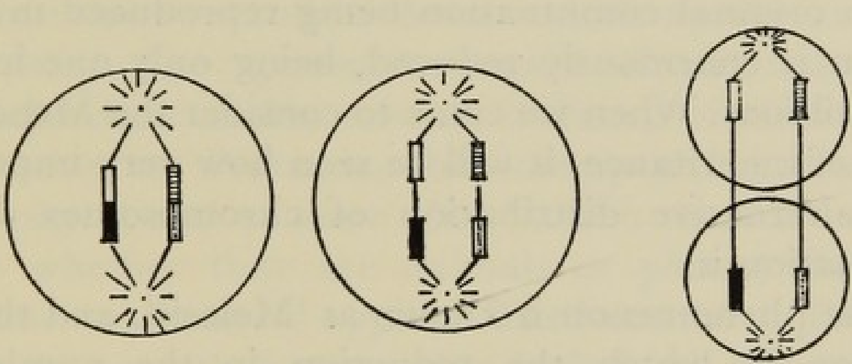


Fig. 15.—Distribution of the chromosomes before fertilisation.

It is most important to realise exactly what the result of this phenomenon is. Suppose an animal, the body cells of which contain four chromosomes which we will call A, B, C and D. The gametes (sexual cells) thrown off by this animal will each contain only two of these chromosomes which may of course be any pair—AB, AC, AD, BC, BD or CD. (See Fig. 15.) One of these gametes fuses with a gamete from another individual which has gone through a similar process, and so the usual body number of chromosomes is restored in the new individual which arises from this fusion. But even assuming that the chromosomes of the other parent were similar to those of the first, there is only one chance in six that, in an organism, the cells of which contain four chromosomes, the original combination A, B, C, D, would be restored in the offspring. Where the number of chromosomes is larger, thirty-two, for instance, as in the cockroach and several other organisms, the chance of the original combination being reproduced in fertilisation is enormously reduced, being only one in over 600 millions. When we come to consider the Mendelian form of inheritance, it will be seen how very important this alternative distribution of chromosomes during fertilisation is.

This phenomenon is known as 'Meiosis', and the cell division in which the reduction in the number of chromosomes takes place is called the first Meiotic division.

Such is the usual course of events in bi-parental reproduction among the higher animals and plants. Two cells fuse to form what is called the *zygote*, and this proceeds to divide into two cells, each of these into two more, and so on until the whole organism is built up.

In some animals, however, the female may produce eggs which develop into new individuals without any fertilisation, and this may go on for many generations; indeed, in some forms no male has been discovered though it probably existed at some period in the past. This process is known as parthenogenesis.

A complete plant may be produced from a small portion of an existing plant, sometimes even from a portion of a leaf; and there are cases where a portion of a plant has developed new characters which have been preserved by propagating this without any fertilisation. Such is the nectarine, derived from the peach tree. Again in plants we have an exaggerated form of budding which produces new individuals without any process of fertilisation. A good example of this is the production of new plants by the strawberry through 'runners'.

In order to appreciate the nature of the problems by which we are faced in heredity and evolution, it is necessary to have a clear idea of the great difference between those organisms that are made up of many cells and those that appear to consist of one only. The animals whose bodies are not built up of several cells are known as Protozoa, the corresponding plants as Protophyta, and to those about which there is a doubt as to whether they are animals or plants, the term Protista was formerly applied. The latter term, Protista, has more recently been used to include all three groups (Schaudinn, 1902; Dobell, 1911, and others).

In some cases many generations of individuals may be produced by a simple process of fission or budding. More primitive forms of fertilisation than that described as occurring in cellular organisms are found among the Protista. In some cases two individuals coalesce, their nuclei divide and daughter nuclei are exchanged between them. They then separate and a varying number of generations of new individuals are produced before pairing and fertilisation again occurs. In other cases a complicated life-cycle occurs in which two types of individual are produced which fuse in a similar manner to the sperm and ovum of the higher organisms.

All the functions performed by the many groups of cells forming the cellular individual are performed by the Protist individual. In some of the Protozoa particularly, there is a considerable amount of differentiation in the various parts of the body; but in others, beyond that between the nucleus and cytoplasm, little or none is apparent. Many have more than one nucleus. It is, however, evident that the Protist is just as much a whole individual as is a cellular organism. The majority of biologists have in the past considered the Protist as analogous to one of the cells in a cellular organism and conversely a cellular organism as analogous to a colony of Protista. This has led on to the further conception that the succession of generations between two periods of conjugation in Protozoa should be regarded as analogous to the body of the cellular animal. The obvious difficulties in the way of accepting such interpretations have given rise to many protests (Huxley, 1853; Whitman, 1888–93; Sedgwick, 1894–5, and others). The problem has been dealt with more fully by Dobell (1911). He points out that the word 'cell' is used to represent:

(1) A whole organism (*e.g.* a protist individual).
(2) A part of an organism (*e.g.* a liver cell).
(3) A potential whole organism (a fertilised egg).

All living organisms are composed of protoplasm, and, to quote Dobell:

> 'The investigation of an immense number of organisms has brought to light a most important fact, namely, that the protoplasm of a living organism always consists of two elements, a nucleus (or nuclei) and cytoplasm.'

Most biologists will agree that this statement is generally true, but there are possible exceptions. Among these many people will be inclined to include those Protista in which the nucleus, if present, is diffused. In these it does not consist of a circumscribed area of different structure to the rest of the protoplasm. That diffused granules of chromatin may be analogous to the more usual, well-defined form, is probably true, but it will appear to the reader later that the fact that a definite circumscribed nucleus is not always present, is of great importance.

In the Metazoa and Metaphyta (cellular animals and plants) there are very many nuclei, and during the process of development, as the nuclei multiply, so the cytoplasm becomes divided into a corresponding number of compartments. These, everyone is agreed, are rightly called cells, and the organisms which they form are 'cellular'. To quote again:

> 'Very many organisms, however, are uninucleate, binucleate or multinucleate, but show no subdivision of the cytoplasm into compartments containing the nuclei. These organisms may therefore justly be called—when compared with the former group—non-cellular. It is obviously incorrect to call them uni-cellular, for the cells of cellular animals and plants are sub-divisions of whole organisms. . . . It is quite clear that the correct antithesis, in the present case, is between cells and not-cells, and not between many cells and one cell—as has hitherto been universally assumed' (Dobell, 1911).

With regard to the fertilised egg, Dobell says:

> 'The fertilised egg, before it undergoes cleavage, is not a cell any more than a Protist individual is a cell. It shows no cellular differentiation, but is a (potentially) complete organism. The blastomeres,[1] on the other hand, are properly named cells. They are parts of a whole. After the first cleavage, the organism as a whole has acquired a cellular structure. It matters not whether there are two blastomeres constituting the whole organism, or two thousand. They are cells in just the same sense that liver-cells and brain-cells are cells.'

In defining a cell Dobell says that to the usually

---

[1] The cells produced by the earlier divisions of the ovum.

accepted definition—a mass of protoplasm containing a nucleus—we must add:

> 'That the cell is part of an organism and not a whole organism . . . the cell is bounded by a membrane or cell wall of some sort . . . the cell must be defined in terms of the organism, and not the organism in terms of the cell.'

As there is much to be said against the conception that a Protist individual is analogous to a cell forming part of a Metazoan or Metaphyte, so there is much against accepting the converse—that a Metazoan may be interpreted as a colony of Protista.

Many observations and experiments indicate that the cellular structures of Metazoa and Metaphyta is secondary and subordinate to the dominance of the organism as a whole. Morgan's (1898) experiments with Planaria showed that when parts were cut from the animal, it was able to regenerate its body, but only to a small extent by the multiplication of cells; most of the regeneration was due to the remoulding of the existing cells to the original form.

The observations of Hofmeister (1867), de Bary (1862) and Sachs (1892) suggest that the mode of growth and form of plants are the cause and not the result of the multiplication of the cells. Hofmeister says:

> 'The growth of the individual cells of a growing point is controlled and conditioned by the growth of the entire vegetative point, whether it be striving towards increased size alone or towards the developments of a particular shape.'

De Bary says:

> 'The cells do not form the plant: the plant forms the cells.'

There is a great deal of evidence of a similar nature, some of which will be cited later when dealing with particular points, which is against the conception of the cellular organism as a kind of colony, and shows that each Metazoan and Metaphyte must be regarded as a separate individual, though each is built up of many cells. It is the organism as a whole that constitutes the individual, and not each of the cells of which it is formed.

But this is not the whole story. Though there is this great and striking difference between the Protista and individuals built up of many cells, there are some stepping-stones that suggest a way across the gap. In some Protozoa the individuals are joined together by a branching stem, the end of which is attached to some solid substance in the water (e.g. *Epistilis. Zoothamnium arbuscula*). The stem is common to all the individuals and sometimes when one is touched, the whole colony will react and the stem and branches contract. Others again form colonies in which the individuals are embedded and held together in a common gelatinous matrix (e.g. *Uroglena americana*). Other colonies are formed by the union of two or more individuals end to end or side by side.

There are some simple plants (e.g. *Hydrodictyon, pediastrum*) of which new colonies are formed by division within the mother cells. The cells thus produced are motile, swimming about freely within the mother cell, but soon coalesce to build up new colonies, each having the characteristics of the original colonies. (Harper, 1918.) If certain sponges are separated into their component cells by being rubbed through fine cloth, the cells will subsequently reassemble in small groups, each group producing a perfect sponge. (Wilson, H. V., 1908–10.) Some of the dissociated cells may lose their specialised characters, but most retain them and reassemble already differentiated for their special functions to form another sponge. (Galtsoff, 1923–4.)

There are organisms in which at some period of their lives the cells become de-differentiated and form an indiscriminate mass. The structure of the different parts is lost. At a later stage the cells are sorted out and become differentiated.

A consideration of these and many other similar cases suggest that the gulf between the Protista and the cellular organisms is not so sharply defined as would appear at first sight, but that the latter arose from the former.

There is another property of living matter that has been known for many years. Living cells removed from the bodies of the higher animals can be kept alive and caused to multiply for an indefinite number of generations. (Carrel, 1911, 1913, 1924; Fischer, 1925.) It is difficult to determine how to regard such a colony of living cells, which will apparently continue to grow and multiply indefinitely and even arrive at certain stages of differentiation and produce fresh colonies without apparent limit under suitable conditions, after the cells have been removed from the individual by which they were produced. They have ceased to be part of that individual and yet are not new individuals themselves.

Certain structures found in the cytoplasm of the cell must be taken into consideration. These are the Chondriosomes, also known as Mitochondria and by various other names. They are constantly found in the cells of animals and plants, and are similar in structure. They appear as small granules, rods or filaments outside the nucleus. They are stated to play an important part in the formation of the germ-cells, and are distributed with approximate equality to the daughter cells. (Meves, F., 1904, 1907, 1908. Many other authors since.) The sperm is said to bring chondriosomes with it into the ovum which mingle with those already there, divide individually, and are thus distributed to the daughter cells. (Meves, 1911, 1912, 1914.) They are supposed also to give rise to special differentiated structures of the cells such as the fibrils of muscle. (Duesberg, 1907, 1909, 1919, and others.) They are also supposed to be related to secretion and other chemical processes in the cell. (Heidenhain, 1911, and others.) Observations on the living cells in tissue-cultures show that generally they are in constant movement, changing their shape from moment to moment (Lewis, 1915).

# CHAPTER III

## Variation and variability

There is a property of all living matter which must be fully realised before the significance of the evidence bearing upon the problems of heredity can be made clear. This is variability, the property of constantly varying from generation to generation, whether of cells, or of groups of cells, or of whole organisms. This property seems to be universal throughout the animal and vegetable kingdoms, in Protista and cellular forms, from Amoeba to man, from Algae and the like to the most highly differentiated plants. On the other hand, cells produce other cells similar to themselves, animals and plants produce other organisms similar to themselves; but always with differences. Sometimes the differences are slight, sometimes they are large, but no cell ever produces other cells exactly like itself, and consequently, no cellular organism can do so.

The fact that the progeny are similar to the parents has so impressed some observers, that they have apparently been led to ignore or deny the differences, claiming that the progeny are sometimes identical with each other and the parents; and they find it necessary to explain how this imaginary identity is brought about. Here is an example:

'In some cases, as we have said, it is impossible to distinguish offspring from parent, or brother from brother, or cousin from cousin. On what does this completeness of heredity resemblance (*i.e.* the absence of variation) depend? It means, in the case of unicellular organisms, that the separated parts are identical in substance and carry on the complete organisation of the parent cell in absolute integrity. In the case of multicellular organisms it depends on the same thing. The cell which in the embryo begins the germ-cell lineage may be identical with the fertilised ovum, and the complete heritage may be continued intact through successive cell-divisions until the next generation is started, and the process begins anew. The completeness of hereditary resemblances depends, in Bateson's phrase, on "that qualitative symmetry characteristic of all non-differentiating cell-divisions!"' (Thomson, J. A., 1912).

This purports to be a statement of fact, supported by two well-known biologists, and so deserves careful consideration. The first point in this statement that attracts the notice of the critic is that it claims that in cellular organism, not only may every cell in the 'germ-cell lineage' be identical, but by implication that the two gametes, derived from two different individuals, may have been identical; that the gametes given off by individuals in subsequent generations may have been identical with the two original gametes, and with all the gametes of all the individuals of the different generations involved.

No actual evidence is produced as to this identity, either of the cells, the gametes, the fertilised ova or the organisms, so we must turn elsewhere for it.

To begin with, it is obvious that when organisms with which the observer is not very familiar are examined, small differences are likely to escape his notice. To the white man all negroes at first appear much alike, but when he has lived among them for some years he will probably see as much difference between them as between his fellow white men. The leaves of an oak tree are, in a sense, alike, but when they are examined individually, it is found that they differ from each other, even if only slightly, in shape, size, arrangement of veins and other points. In the case of microscopic animals and plants, small differences are even more likely to escape notice. When we come to individual cells, we find that the similarity between them is often marked. The cells of the liver in mammals, for instance, are so much alike that the trained observer will always be able to recognise one as a liver cell, whether it be from a man, a dog, a mouse or a pig. But the trained observer will also be able to point out the differences, small no doubt but present nevertheless, between adjacent liver cells in the same liver. After more than thirty years' experience of high-power microscopic work, I can say with confidence that I have never seen two cells from any organ or tissue, no two germ-cells, no two Protist organisms that were identical, and all who have had a like experience will probably agree with me in this sweeping statement. The variations involve even smaller items than the cells. Where a particular chromosome among those occurring in an organism can be recognised from generation to generation, it may vary within considerable limits as to shape and size. While there is never any doubt as to the chromosome being the same, no two are ever identical. (Walker, 1911.)

It is necessary to produce independent evidence. This is available in overwhelming abundance. Accurate portraits of cells, more particularly of those included in the processes involved in the production of gametes, are available in numbers that it would be difficult or even impossible to estimate. Many scientific journals have been publishing such portraits for many years past, and anyone who doubts the truth of this statement may search in vain for two cells that are identical among these portraits. He might begin with a few volumes of

*The Quarterly Journal of Microscopical Science; La Cellule;* and the *Archiv für Zellforschung.*

But this evidence deals only with the morphological or structural differences between cells. That other differences also exist may be demonstrated easily.

If a number of similar living cells be placed under the microscope and poison of a suitable kind be applied to them, it will be seen that some die at once, while others survive for varying periods. This experiment may be modified in different ways and demonstrates that the power of resistance to the poison varies considerably between individuals when a large number of similar cells are involved. Other variations can be demonstrated by similar methods.

While it would be foolish to state that it is inconceivable that two identical cells have ever existed or will be produced in the future, the chance seems as remote as that the finger-prints of two men have been or ever will be identical; this matter of finger-prints being, by the way, further evidence to the universal occurrence of the phenomenon of variability in living organisms, for they are different even in the case of so-called 'identical twins'. But, if it be highly improbable that even two cells can be or ever have been or will be identical, it is even more improbable that this should happen in the case of two cellular organisms, and further discussion of the point is a waste of time. Unfortunately, there are various complications that must be considered.

Much has been written on the causes of variation, but at the moment this need be dealt with but briefly.

Several authorities, including Weismann, attribute a stimulation, at any rate, of variability in organisms, to the mingling of the germ-plasm of two individuals in fertilisation. Weismann called this 'amphimixis'. It has been argued against this view, that while the process of fertilisation produces a mixture of the potentialities derived from each parent, new variations cannot thus be produced. If the two parents differ from each other considerably, the offspring are likely to be very different from each other and from either parent, as in the case of crossing the zebra with the horse, but that this does not suggest that any new variation has been produced, but only a mixture of already existing characters, or rather of potentialities for producing characters. Indeed, it has been argued that bi-parental reproduction assists the elimination of useless variations rather than producing them. (Archdall Reid, 1905.) This is of course going further than denying that variability is increased by bi-parental reproduction, which is done by many (*e.g.* Karl Pearson, 1900.)

On the other hand, there is a great deal of evidence which proves that a considerable degree of variability is common among parthenogenetic organisms. Speaking of the great variability of the Polyzoa, aquatic animals which are without exception characterised by increasing in an asexual manner, Harmer (1908) said:

> '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.'

There are many more instances of similar observations by others, including Weismann.

More recent work on what have been called 'pure line' researches suggests that occasional fertilisation in colonies of protozoa may have a definite effect upon variability, but the discussion of this must be put off to a later stage.

A group of biologists claim that variation is caused by the action of the environment upon the soma, and here the evidence is of such a complicated nature that it requires very careful sifting. The soma of an animal is the whole body excluding the germ-cells. Biologists believe that a change of environment extended over a long period produces changes in the characters of races of living organisms. The converse, that a change in the characters of a race is preceded by or concomitant with a change in the environment, is also widely, though perhaps not so generally accepted. Whether we believe that this is in favour of the environment having caused the variations in the individuals, depends on whether we believe in the inheritance of acquired characters; otherwise, we must believe that variations in the germ-cells themselves, selected by the change in the environment in succeeding generations, are sufficient to account for the changed characters of the race. This question is discussed in a later chapter, but the consideration of some evidence relating to the results of a change of environment will show with what caution the modification in characters thus produced must be received, quite apart from which of these two theories is accepted.

C. von Nägeli (1884) took some Alpine plants from their ordinary surroundings and placed them in rich soil, under the usual conditions of cultivation in the Botanical Gardens at Munich. The plants thus removed from their normal environment changed in their characters so much that they would not have been recognised by anyone who had not seen the transformation. The seed of these grown in the Botanical Gardens under the same conditions, reproduced the characters that their parents had developed under cultivation, and this went on for about thirteen years. But when, at the end of this period, some of the plants were removed to poor and stony soil they reverted to the characters of their Alpine ancestors of thirteen generations before. Moreover, the seeds of the plants in the Botanical Gardens, grown under Alpine conditions, showed the characters of their comparatively remote ancestors, and not of their immediate parents. It is most important always to bear in mind that, in some organisms at any rate, a power exists of producing one set of characters in one environment, and another set in a different one; and that this dual capacity may remain latent through many generations. It is a quite different phenomenon from a new variation.

This is a very simple example of the kind of thing that may happen in breeding experiments, whether with plants or animals, and had not the late generations of these plants been returned to their original environment, very erroneous conclusions might have been arrived at. It would be tedious to the reader to labour this point, and show how easily one may be misled by incomplete observations, particularly as the sources of error are often not at all obvious, and usually far more complicated and subtle than in the simple cases quoted.

A reasonable view is that variability is an intrinsic property of all living matter, and that the problem of its origin is at present in the same category as the origin of life. It seems probable, however, that the variability of a race may be increased or diminished under certain circumstances.

There are some organisms still existing whose characters have not changed materially from those of their ancestors who lived in remote geological times. *Lingula* and *Discina*, two existing genera of Brachiopoda living in the sea, are found in the lower Cambrian rocks. They have gone on from generation to generation, without any material change of characters, through the vast period involving the formation of the whole of the fossiliferous rocks, which at a conservative estimate must be 400 million years.

On the other hand, many of the higher animals have changed very greatly and separated into many divergent branches, differing widely in their characters from each other and from a common ancestor, which itself was recent when compared to the ancient *Lingula*. The most primitive mammals did not appear until the Tertiary period, between 100 and 200 million years ago.

It has been suggested that such facts as these might be supposed to indicate that some groups of organisms may be more variable intrinsically than others. But against this it is argued that a constant environment in the one case and a changing one in the other gives a more satisfactory explanation. This question will arise again at a later stage.

It is claimed that there are two different kinds of variation, one of which is inherited, the other not. At the moment, however, it is sufficient to point out that variations occur in all directions, round the mean of a character. It has been shown that Gauss's Law of Frequency in Error is applicable to variations in living organisms. (Galton; Quetelet, 1816.)

Sir John Herschel's illustration of this law makes its application to variations very clear.

If a large number of shots are fired at a target, the shots aggregate most thickly round a particular spot, and become fewer in proportion to the distance from this spot. The area of 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 shots are found. Precisely the same thing happens in the case of variations. With regard to some characters and in some races, the vast majority of variations are small. In other races and under certain conditions, more considerable variations may be comparatively common.

The smaller variations have been called 'fluctuating', the larger 'mutations', and it is stated that only the latter are inherited. Some of the smaller variations are claimed as mutations; indeed, it is now stated that the only way in which a fluctuating variation can be distinguished from a small mutation is by breeding experiments. It is also claimed that all variations, great and small, may be inherited. This will be discussed later.

Apart from the possibility of there being more than one kind of variation, there can be no doubt that some races are more variable than others. In other words, while in some races marked differences between individuals are rare, in other races, such variations are common. The latter is the case very noticeably in many domesticated races.

It is difficult to follow the argument frequently advanced, that because variations are 'chance', 'random', 'contingent', they cannot be used in scientific explanations of Evolution or Heredity, unless we know the causes of variations. It has been proved in every case that has been carefully investigated that variations do occur round every character according to Gauss's Law of Frequency in Error, and whether we know the cause or not, it does not seem unscientific to make use of an established fact. Variability appears to be an intrinsic property of living matter. To refuse to accept variations as an explanation of a phenomenon unless we know their cause (MacBride, 1931), seems just as unreasonable as to refuse the use of any recorded observations of living organisms because we do not know the cause of life.

# CHAPTER IV

Facts upon which theories of evolution are based
Theories of evolution

THAT some geological formations are older than others and that the sequence in time of these formations is known with considerable accuracy, will hardly be questioned except by the captious critic who, refusing any circumstantial evidence however convincing, insists that we cannot be sure unless we have actually seen the process of formation in each individual case. In these geological layers the remains and traces of animals and plants appear in regular sequences which, in spite of gaps, have influenced the formulation of the current views of evolution.

As the earliest of these remains resemble what appear to be the simpler among the organisms living today, the idea arose that the complex animals and plants had gradually, in the course of ages, evolved from simpler and more primitive forms that existed in the past. There is no necessity to weary the reader by repeating the order in which the various groups of animals and plants have appeared in successive geological periods. The evidence has been so frequently described in detail that it may be treated almost as common knowledge. But one example is taken as an illustration. The case of fishes and mammals will serve admirably to make the point clear.

Remains of fishes are found in geological formations millions of years older than those in which the first traces or remains of mammals are found. True it may be that all the existing fishes differ from these ancient forms, some very greatly, some to a less degree. In time the existing fishes are as widely separated from the early fossil forms as are the mammals, but both fossils and modern fishes are very definitely fishes and not amphibia, reptiles, birds or mammals; still less do they belong to any invertebrate group.

*Lingula* and *Discina* have already been cited as having continued almost unchanged for some 400 millions of years. Scorpions, but little different from scorpions now living, existed at the time when coal was formed from forests of long-extinct trees. The continuance of any particular form of living organism with little or no change throughout several geological epochs is apparently of rare occurrence, but the continuance of a large group with particular characters is usual. According to the available evidence, animals that lived partly in the water and partly on land appeared later than the earlier fishes, and so on through successive geological steps to the earliest remains of birds and mammals in order of time. Every variation that tended to adapt the organism in which it occurred more closely to the existing environment or to some change in environment, would help its own survival, but it would at the same time in all probability change the environment of other living organisms, and this would tend to accentuate the divergence of different strains. While some strains taking to deep water became more definitely 'fishy', others in different localities became adapted to a gradually changing environment, and ended by living on land. At any rate, the fact remains that fishes existed long before mammals, and though fishes living at present have many new characters that differ greatly from any fossil fishes, the difference is not so great that there can be the slightest doubt that the most ancient and most modern belong to the same group of animals with easily recognisable common characters separating them from other equally definite groups that appeared before or after the first fishes of which we have any records.

Palaeontology indicates that certain groups of animals appeared successively, and apparently some became the dominant type for a period.

One of the most remarkable arguments in favour of the generally accepted view of the lines along which the evolution of living organisms has travelled, can be drawn from a paper read by Huxley to the Zoological Society in 1880. In this he stated that, if this law of evolution was true, then a zoologist who knew a certain part of the course along which evolution had travelled in any particular case ought to be able to reason backwards through earlier and unknown stages. He put this theory into practice, and described certain unknown organisms which, according to this view, must have existed. The fossil remains of many, if not most, of the organisms thus postulated by him have since been discovered. (Woodward, 1931.) It is unnecessary to make any further comment upon these facts than to point out that but few theories have received such remarkable confirmation.

When the general practice of calling one organism 'higher' than another is followed here, it is meant that the group to which the animal or plant belongs (for the same is true of both) appeared later in the course of evolution than the groups to which the term 'lower' is applied. No existing organism is earlier or later than another. It is not correct to apply the term 'higher' to an organism because it is more highly differentiated, because the 'higher' in the sense used here might well be less highly differentiated in many ways than the 'lower'. 'Higher' in the sense of being most nearly related to man may be, and generally is, only used with regard to the very restricted group of apes, near relations of man, and this because so far the highest and latest point reached by evolution in brain development, intelligence and educability is in man, and has given him the dominance over all other animals, just as the great reptiles were dominant at an earlier period. 'Higher' in this case does not mean more highly differentiated, for in some points (*e.g.* the great bony ridge on the skull of the male gorilla) differentiation is greater in some apes than in man. All the existing anthropoid apes must be separated from the common ancestor by the same period of time as man.

Clearly it is too much to hope that we may find remains of simple Protista in early geological formations, but the skeletons of highly differentiated Protista, similar to those still existing, are found in limestone and chalk. Palaeontology has provided us with examples of organisms showing the main lines along which evolution has travelled and where and how the main groups have separated off from each other; the only assumptions that have been made have been on the lines of known evolutionary changes, and in the case of organisms that from their character and structure could hardly have left any traces.

Further evidence is provided for the generally accepted view, by the way in which organisms belonging to the groups that appeared in later geological times develop from the ovum. In the development of a mammal, for instance, the embryo passes through stages that correspond roughly and broadly to the lines along which palaeontology suggests that evolution has followed. At one stage the embryo has some of the characters of an aquatic animal. Even at a comparatively late stage it is impossible to discriminate between the embryo of a dog, a man, or other mammal. That at no stage, particularly in the earlier, the embryo ever resembles very closely some remote ancestor, is to be expected, for variation must have occurred at every stage in the development of the individual, just as it has in the evolution of the successive groups. Some stages have been shortened, some missed altogether, all must have been greatly modified. Sufficient remains, however, to provide a remarkable parallel between the development of the individual and the history of the evolution of the group as suggested by palaeontology.

Objection to this view of development—known as 'recapitulation'—has been made on the ground that the division of the fertilised ovum into two cells is not analogous to a Protist individual dividing into two. In Chapter II, examples of links between the Protozoa and Metazoa were given.

The fertilised ovum of the Metazoan divides into two daughter cells, each of these again divides, and so the process goes on, at any rate in the earlier stages of development. These cells are known as blastomeres. Now if, at an early stage, these blastomeres are separated, each will grow up into an embryo complete in all its parts. (Driesch, 1892, 1900, and many others.) We will take the four blastomere stages for the purpose of illustrating what really happens, and we will call the four blastomeres A, B, C and D. If the ovum had been left to develop in the usual way, it is evident that the later generations of cells produced by A, B, C and D would have had very different destinies. A would have produced different tissues with different functions from what would have been produced by B, C and D. The same is true, of course, of all four blastomeres. Yet A, when it is separated from B, C and D, produces all the tissues that would, in the usual course of events, have been produced by the other three blastomeres. There is, then, some interaction between A, B, C and D which, when they are together, limits what each of them will produce in the body of the animal, though each is able by itself to produce the whole body. The term 'Somatic co-ordination' has been applied to this interaction or common influence that limits the line of differentiation of the blastomeres when they form parts of an individual animal. (Walker, 1907.)

It seems that the fact that a separated portion of some of the lower animals is capable of reproducing the whole, is a manifestation of the same phenomenon, and that the regeneration of parts that have been removed is this also. But this power of regeneration decreases as the later stages of evolution are reached in the higher animals. While in a newt such a highly differentiated structure as the lens of the eye is reproduced if removed, in man many of the differentiated tissue cells can never be replaced if once destroyed, and the power of regeneration, even of those groups of cells which continue to multiply throughout life, is very limited. For example, in the cells forming the skin, any considerable injury results, not in regeneration, but a process of rather inefficient repair by the wandering connective tissue cells in the production of a scar. This seems to indicate that the general capacity of the cells is gradually lost as a higher and higher degree of differentiation among them is reached in the later stages of the evolution of Vertebrates. But it is probable that even in man, in the earlier stages of the segmentation of the ovum, at any rate, this general capacity of the cells is not lost altogether, for there is every reason to suppose that the occurrence of similar twins is often, if not generally, due to the separation of the two first blastomeres.

Great though the change from non-cellular to cellular structures may be, any other interpretation than that it occurred is difficult in view of the evidence at present available. We have some indications of the manner in which it was brought about. There may be other lines along which evolution might have gone. The Protista might have increased in size without separating into compartments—cells—but the semi-fluid consistency of the protoplasm of which they are formed would have placed a very definite limit to any advantage gained by any considerable increase in size over smaller organisms; nor could it have added to their own well-being, without some structural differentiation to support their bodies. Some of them have developed a kind of skeleton by secreting a hard framework; but this again could give but little advantage to the individual if it increased in size beyond a very limited extent. It is also difficult to conceive how such processes as excretion could have occurred in one large continuous mass of protoplasm.

On the other hand, the separation of the mass of jelly forming the individual into separate compartments, in the manner suggested by the transitional forms of which we know, offers a plausible explanation of the evolution of the cellular organism, giving it great advantages by the great increase in size; differentiation of its compartments to fulfil various functions; stability through being built up of separate units; greater facility in secretion and excretion; and the greater capacity for adaptation to the concomitant changes in the environment which we find in the higher organisms. It must be realised that the evolution of living organisms along divergent lines must have played a very important part in changing the environment, as great in many cases as the changes in physical conditions.

The evidence of palaeontology indicates that evolution has proceeded on the whole from the simple to the more complex, up to a certain point at any rate. It has diverged at certain stages, and at the present time no one would argue that any point reached by one of these various branches is in itself more remote from the starting-point than another. Take one example, the vertebrates, culminating in the fishes, amphibia, reptiles, birds and mammals; and also in the arthropods, culminating in spiders, crustacea, insects, etc. In the former, the framework which supports the body and gives the points of leverage to the muscles is an internal skeleton. In the latter, it is an external casing, an exo-skeleton. In the former, evolution has tended to an elimination of instinct with an increasing dependence upon intelligence or educability. In the latter, it has culminated in a development of instinct to a degree inconceivable to anyone who is not familiar with these creatures, and that without the development of intelligence or educability. No one would claim that many of the arthropods are not as remotely separated from the primitive forms of life and from the common ancestor as are the mammals. They are referred to as 'higher' animals and palaeontology suggests that they arose from more primitive forms at about the same period as the vertebrates.

Such are the broad outlines of the evidence which forms the basis of the theories of evolution. This evidence has been presented in a somewhat unusual form, but this has been done with the object of meeting certain criticisms of the terms universally adopted when speaking of different plants and animals in relation to evolution. No doubt these criticisms (*e.g.* Dobell, 1911; Franz, 1911) are justifiable, in that many words have been used very loosely. For instance, in applying the terms 'higher' or 'lower' to an animal or a plant, it should be made clear that in using these terms—used for so long that it is practically impossible to abandon them—no more is implied than that they belong to groups that appeared later or earlier in the process of evolution. One example will suffice to show how misleading these terms used in any other sense would be.

There are parasitic animals, belonging to groups that existed long before any vertebrates appeared, that live upon vertebrates, and cannot exist without the particular vertebrate upon which they live. Yet these branches from the original group must have evolved after the vertebrates appeared. Moreover, these parasitic 'lower' animals are often less complex than their non-parasitic ancestors almost certainly must have been, and certainly less complex than their contemporary non-parasitic, free living relations. Lamarck (1802) in referring to evolution said:

> 'The series which constitutes the animal scale resides in the distribution of the groups, and not that of the individuals and species.'

Apart from beliefs postulating Special Creation, Lamarck was the first to formulate an hypothesis that covered the known facts. Before him Buffon, who died in 1778, believed that all animals might have arisen from a single type. Erasmus Darwin, who died in 1802, held that all animals arose from a single 'filament'. Buffon believed that Nature advances by insensible gradations from one species to another. Both he and Erasmus Darwin laid great stress upon the influence of environment, but neither had a complete hypothesis.

Lamarck's hypothesis was that evolution depended upon two factors. The first, and in his view the more important, was that living organisms possessed an innate tendency to evolve towards increasing complexity of structure. The second factor was the inheritance of acquired characters. What does not seem to be realised by the modern supporters of Lamarck's second factor is that he himself regarded it as less important than his first.

The second factor according to Lamarck modified the first, which ensured only that each animal in each fresh generation would be slightly more complex. The inheritance of acquired characters ensured many additions to this simple process, particularly in the way of adaptation to the environment, and so provided a more satisfactory explanation of evolution. Acquired modifications of an organism may be produced by the action of the environment in two ways. Directly, by such modifications as change in colour and other characters of the superficial layers of the body through the action of light or heat, and by mutilation. Indirectly, by inducing the greater or less use by the individual of any part or organ. Lamarck himself believed that only the latter kind of modifications were inherited, though his modern followers appear to claim instances of inheritance of the former. The latter are referred to as 'functional modifications' and their inheritance as 'use inheritance'. They are sometimes described as 'habits', though the use of the word habit in this sense is apt to mislead. What is meant is that any change in the environment that lasts for a long time necessitates new activities in the animal, not only with regard to movement of parts but also of the various functions, secretions, and so on. Thus, the development of certain parts and functions, and even the production of new ones, is brought about, and new 'habits' are formed, not only as regards movement but also functions. In the same way, a structure or function that was not used would tend to disappear.

A few examples taken from Lamarck's own writings will illustrate how he explained the evolution of new characters:

> 'The bird which necessity drives to the water to find there the prey needed for its subsistence separates the toes of its feet when it wishes to push (frapper) the water and move on its surface. The skin which joins these toes at their base, contracts thus the habit of extending itself. Thus in time the broad membranes which connect the toes of ducks, geese, etc., are formed in the way indicated' (Lamarck, 1801).

The immediately preceding passage gives the 'way indicated'. This is that the influence of the environment causes changes of habits, movements, action, mode of multiplying themselves and so on, upon individual living organisms. By slow degrees these changes are preserved and propagated by heredity.

Giraffes have developed their long necks through the constant stretching to reach the leaves of trees, continued through many generations of ancestors. Snakes have lost their legs through having acquired the habit of gliding along the ground, where legs impeded them.

Charles Darwin, on the other hand, believed that evolution depended upon the selection by the environment of intrinsic changes in the organism, variations that occurred continually round a character in every direction on the production of new individuals. While admitting that the acquirements of the individual might be transmitted to the offspring sometimes, he held that evolution was mainly, if not entirely, dependent upon the selection during succeeding generations of those intrinsic, not acquired, variations that were advantageous to the animal or plant in relation to its environment.

Weismann (1893 and 1904) went much further. He postulated the continuity of the germ-plasm. He claimed that the germ-plasm, the material from which the gametes (sperms and ova) are produced, is completely cut off from the rest of the body or 'soma'. No modifications of the soma can possibly affect the germ-plasm; hence there can be no inheritance of acquirements, only of variations occurring in the germ-plasm itself.

These theories have, of necessity, been modified by more recent discoveries. Each of them is denied by one or other group of biologists.

There remain the vitalistic interpretations of evolution. The authors of these, dissatisfied with all current theories, postulate some metaphysical force, generally in the form of a directing influence which determines the lines of development and evolution.

The following chapters deal with these various theories, the evidence and arguments for and against, and suggest conclusions.

# CHAPTER V

The inheritance of acquired characters
Evidence and arguments for and against
Immunity to disease · Sufficiency of variations

THE fertilised ovum—produced by the fusion of two gametes each derived from one of the parents—divides into two and multiplies until the whole body is built up. The cells during this process of multiplication are gradually divided into various groups which differ widely from each other in shape, structure and function. As the development of the new individual proceeds, the different characters, morphological, functional and mental, appear. It is quite clear that all these characters must be derived from the fertilised ovum, with the assistance of the environment, whether by the absorption of material from without or through other external influences. That the form which this collection of groups of cells takes is due to something inherent in the fertilised ovum is clear, for no change of environment will cause a human ovum to develop into anything but a human being, if it develops at all; and the same is of course true of the ovum of any other animal or any plant.

On the other hand it is also clear that modifications of characters are produced by the action of the environment. It seems, however, that such modifications in the individual must be definitely limited. Any factor or factors in the environment which are unfavourable beyond certain limits, would cause the death of the individual, and so stop any further development. A less unfavourable factor in the environment might cause a definite deformity or the failure of some character to develop. And so through insensible gradations we arrive at the other extreme, a completely favourable environment in which all the characters are developed to their fullest capacity, a state of affairs which, though conceivable, can rarely if ever be realised. These influences of the environment may begin before birth. We must drop the old idea of preformation, described in great detail by Bonnet in his theory of 'emboîtement'. Every part was supposed to be present, practically as in the adult animal, in the egg. The egg in fact was supposed to contain what was practically a little hen, which in its turn contained more little eggs, and so on. Modern observations show that this is not the case.

A consideration of these facts leads to the conclusion that all characters are dependent upon the action of the environment upon some intrinsic properties of the cells, which properties are derived from the fertilised ovum. This would appear to apply to every kind of character. If we take a particular shape of feature, it may be true that given a favourable environment this shape will appear, but the action of the environment may be such as to prevent, not only the shape appearing, but may destroy the feature itself. By exercise a man may increase the size and power of his muscles, but if his environment be such as to prevent his taking exercise, his muscles will never develop even to average size. No one could develop skill with a musical instrument or in mathematics, unless his environment were such as to enable him to exercise and develop the particular capacity.

The old controversy regarding inborn and acquired characters still continues, but in view of the fact that every character must of necessity be partly an acquirement, this controversy must be, in some cases at any rate, quite meaningless. As von Nägeli's Alpine plants showed, one group of characters does not appear at all in a new environment during an apparently indefinite number of generations; but the fresh group of characters that has replaced the old will again disappear and the old group reappear when the plants or seeds are returned to the original one. Only when it is realised that every character in an organism is a mixture of some intrinsic potentiality or capacity for development in the ovum, with acquirements dependent upon the environment, is it possible to formulate the problem accurately.

The real question then is, whether the effects of environment upon the soma, that is the body excluding the germ-cells and their ancestors, can so influence the germ-cells or gametes as to alter the nature of their potentialities for development? This effect would not be a general but a particular change. For instance, a general effect would be that of a poison which injures the soma and which may obviously at the same time injure the germ-cells. A particular effect would be if the children of a parent whose brain had been injured by accident or disease in such a manner as to produce epileptic fits, also suffered from epileptic fits without their having received a similar injury to the brain. Again, callosities produced by constant use of a limb in the parent, would appear in the offspring without the stimulus that had produced them in preceding generations.

The earliest expression of opinion as to the non-inheritance of acquired characters was given by the great surgeon, John Hunter, in 1781. This was before the time of Lamarck, and of course long before Darwin and Weismann, and therefore before any controversy had arisen. The occasion was the trial of Captain John Donellan (30th March 1781) for the murder of Sir Theodosius Boughton, at Warwick Assizes. Captain Donellan was convicted and hanged on 2nd April. The quotation is taken from the shorthand report of Hunter's evidence given at the trial and published in *Hunter's Works,* edited by Palmer, vol. i. p. 195, 1837.

> 'There is no disease whatever that becomes *constitutional* but what can be given to a child. There is no disease which is *acquired* that can be given to a child; but whatever is constitutional in the father, the father has a power of giving that to the children; by which means it becomes what is called hereditary. There is no such thing as an hereditary disease, but there is an hereditary disposition for a disease.'[1]

There are two kinds of evidence that are pertinent:

I. Evidence that shows what happens when a new factor comes into the environment of a race.

II. Direct evidence that a recognisable modification in the development of a potentiality produced by a temporary and isolated factor in the environment of the individual, reappears in the subsequent generations of individuals when that factor has been removed from the environment.

I. The available evidence seems to show that when an unfavourable factor appears in the environment of a race, one of two things happens. Either the race is exterminated, or it develops characters that enable it to withstand the effects of this unfavourable factor. Supposing the race survives, how is this change brought about? To take a concrete example. We will suppose that a micro-organism causing a disease comes into the environment of a race, and that the race develops a degree of immunity which is sufficient to ensure its survival. This has happened in several cases of which we have a considerable amount of evidence.

The races of Northern Europe have attained a com-

---

[1] I am indebted to Mr Clifford Dobell for this reference.

paratively high power of resistance to the ravages of the tubercle bacillus. Practically every individual is infected to such an extent that at some time during life the bacillus has been well established in the body; but in all but a small proportion the power of resistance has been sufficient to overcome the infection. The evidence for this general infection is very convincing.

> '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' (Osler, 1904).

Ribbert's inspection was of 5000 consecutive cases dying from all causes in general hospitals. Referring to the traces of tubercular infection found in series of post-mortem examinations, Brouardel says:

> 'These lesions in the majority of cases are not phthisis in early stages manifested by small disseminated foci; they are cicatrices of large foci; sometimes of wide completely cicatrised cavities' (Brouardel, 1902).

As variability ensures that individuals differ from each other, so some will be more susceptible to the tubercle bacillus than others, and thus the still numerous cases that are very ill or die of the disease among us are to be accounted for. But even these are frequently cured when placed under favourable conditions, or if they die in the end, generally take a long time in doing so.

We have, on the other hand, much evidence as to what happens to races when they are first brought into contact with the tubercle bacillus. There are certain parts of the world where the more susceptible Europeans who have contracted the disease at home, may expect to be cured in the majority of cases, owing to the conditions being less favourable to the bacillus. Among such are New Zealand, the Pacific Islands, Australia, South Africa and parts of America. What has happened to the natives in these countries?

> 'Consumption is prevalent to a most disastrous extent among the races of the Southern Pacific. We have more particular accounts for Fiji and Tonga, Samoa, Tahiti, the Marquesas and Hawaii (Honolulu). In New Caledonia the death-rate from consumption among the Kanakas is estimated at two-fifths of the mortality from all diseases. Almost all the authorities are of the opinion that the great prevalence of the malady in these islands dates from the time when the natives began to come into more intimate relations with European immigrants. . . . In the Hawaian Islands, where phthisis at the present time creates great ravages among the natives, it was of rare occurrence forty or fifty years ago' (Hirsch, 1883a).
>
> 'In New Zealand phthisis has made frightful ravages among the natives, and has been one of the chief causes of the gradual extinction of that race' (Hirsch, 1883b).

There is also evidence that tuberculosis when occurring in such races is very frequently of the acute rapid form known as 'Galloping Consumption' which is rare in this country.

In Northern Europe we have had tuberculosis with us for several thousand years.

> 'Consumption of the lungs may be traced with certainty in the writings of every period as far back as the earliest attempts of the ancient world to deal with medicine according to a method' (Hirsch, 1883c).

But we can go further back than this. Tuberculosis existed in Egypt about 5000 years ago, and Egypt had then communication with countries further North.

(Elliot Smith and Jones, 1910.) The climate there is unfavourable to the tubercle bacillus, which does not thrive in the bright sunlight. It seems probable then, that, as there is evidence for the visits of travellers and a limited migration from the North at this early date, tuberculosis occurred in the countries to the north of the Mediterranean, where conditions would be more favourable to the successful propagation of the bacillus.

A consideration of this small part of the available evidence makes it clear that we as a race are immune to the tubercle bacillus as compared with the races of the Southern Pacific, and also that we have been subjected to the attacks of the bacillus for hundreds of generations, while the natives of the Southern Pacific for instance have had it introduced among them recently. There is similar evidence available with regard to other races.

Those who hold that the individual acquirements of the parents are handed on to the offspring would interpret this racial immunity somewhat as follows: When the parents suffer from the disease and survive long enough to produce children, they have acquired a certain degree of immunity, which is inherited by the children. The same happens in the next generation, with an increased immunity in the case of individuals who, in their turn, have suffered from the disease. A modification of this interpretation is, that a degree of immunity is acquired by the germ-cells in something like the way immunity to certain diseases is produced by suitable vaccines. This modification is not, of course, quite the same thing as the actual inheritance of the acquired immunity of the parents, for the acquirement has also been made by the germ-cells, which are really the potential individuals of the next generation; but the same consequence must follow whether we accept the original proposition or the modification.

It is so probable as to be almost certain that the body of the individual must suffer some injury from the disease, even if that injury be but slight (Galton). It has been shown that growth and development are temporarily inhibited in children by even slight illnesses, and that this arrest is not made up for by aftergrowths. (Galton.) Even if the injuries be slight, these must be cumulative from generation to generation if we accept the inheritance of acquirements, and must therefore result in the physical degeneration of the race if not in its eventual extinction. But the races that have been long subject to infection by the tubercle bacillus do not show any marked degree of general physical degeneracy.

It is stated that no character is beneficial, favourable, injurious or unfavourable, and that the same statement is made with regard to the factors of the environment. These statements are in the nature of quibbles, calculated to obscure the issue and not at all helpful in arriving at the truth. It is clear that an acquirement is beneficial or favourable to an individual if it enables it to escape or resist a factor in the environment which threatens its destruction or injury. The acquirement of additional speed is favourable, beneficial, advantageous or useful to a deer when it is living under conditions that render it liable to be hunted by tigers or leopards. The presence of the tiger or leopard in its environment is disadvantageous, unfavourable or injurious to the deer. To the tiger or the leopard, the presence of plenty of deer in the environment is advantageous or favourable, and an increase in the speed of the deer is disadvantageous or unfavourable. In this sense the speed of the deer may be either advantageous or disadvantageous.

But that these statements have been made with apparent authority in a way likely to mislead, the reader would not have been inflicted with these platitudes.

Unfortunately when silly and confusing quibbles of this kind are advanced with authority there is no other way of meeting them. Suffice it to say, that when an acquirement or character or a factor in the environment is referred to as being beneficial, advantageous, favourable or the opposite, all that is meant is that it is so to the individual or race under immediate consideration. With the race as with the individual, these terms indicate the tendency of the effect of their presence towards survival or elimination.

The Darwinian point of view is, that the acquirements of the parents produce no change in the potentialities of the germ-cells. The interpretation of the gradual acquirement of immunity by the race according to this theory is roughly as follows:

When the tubercle bacillus was first brought into its environment, the mean power of resistance in the race was 0. But as all individuals differ from each other, some possessed greater resistance, some less than the mean. We may therefore arbitrarily represent this first generation as being made up of −1, 0 and +1 individuals, neglecting the intermediate differences which of course existed. It is quite clear that the +1 individuals would on the average have a far better chance of surviving and producing offspring than the 0's and the −1's, therefore the new generation would tend to start from a new mean which would be approximately +1. But variation still continued, and this new generation must be represented as 0, +1 and +2. The tubercle bacillus was still in the environment, infecting all the individuals, and in this new generation the +2 individuals again survived in greater numbers, establishing a new mean of resistance in the next generation. And so the process went on, until a degree of immunity was reached by the race which made its survival certain.

The presence of the tubercle bacillus in the environment has kept up this standard of immunity, by eliminating those individuals in which unfavourable variations occurred, and still occur in each succeeding generation.

It will be seen that according to this theory neither the favourable nor unfavourable effects of the environment produce any effect upon the potentialities of the germ-cells of the individual. The whole phenomenon is dependent upon the action of environment at each succeeding generation in selecting the favourable and eliminating the unfavourable variations that occur in the potentialities of the germ-cells, but not at all upon the acquirements, injurious or beneficial, made by the body of the individual. The injuries caused to the body of the individual would produce no effect upon the potentialities of the germ-cells, and so there would be no progressive degeneration of the physical characters of the race.

One more example will suffice, that of immunity to malaria. Here again we find some parts of the world where, at any rate until quite recently, the disease was so prevalent that no one could hope to escape infection. The native races in these places have reached a degree of immunity which is in some ways even more striking than our comparative immunity to tuberculosis. It was stated, before we possessed any exact knowledge of the cause and means of preventing infection, that Europeans going to West Africa might be divided into four classes; those who were apparently quite immune, but that among all the Europeans in West Africa these might be 'counted upon the fingers of one hand'; another class who escaped fever for twelve months at a time, 'these you want the fingers of your two hands to count, but no more'; the third and much the largest class consists of those who have a dose of fever once a fortnight and eventually die of it; and the fourth, 'a very considerable class' who die within a month or a fortnight of landing. It is also stated that 85 per cent of those going to the West Coast 'die of fever, or return home with their health permanently wrecked'. (Mary Kingsley.)

Conditions have altered considerably with the advance of knowledge, but this illustrates very well the state of the race suggested in the previous example as having a mean of resistance of 0, with $-1$ and $+1$ variants. Among the natives there is still a high infant mortality from malaria, but not among the adults, who are comparatively immune. That the immunity is not due primarily to acquirements of the individual, but to potentialities of germ-cells, is suggested strongly by some evidence with regard to negro soldiers descended from slaves transported to the West Indies, mainly Jamaica, many generations before. A letter from an officer of a regiment of West Indian negroes, who died from malaria after three seasons, states that on their first arrival in West Africa both officers and men suffered greatly; but that after a single season the men acquired immunity, whereas the white officers continued to suffer as much as ever. (Archdall Reid, 1905.) The suggested explanation of this is that the race had acquired a considerable immunity to malaria before the slaves were transported from West Africa to the West Indies, and the comparatively few generations of absence of selection had not been sufficient to allow it to die out. The two theories may be applied to the case of malaria in the same way as they were applied to tuberculosis. There is apparently the same evidence as to the continual appearance of new individuals who have not inherited the average immunity of the race.

It will be noticed that the evidence upon tuberculosis and malaria is not recent. If the evidence is to be of any value it must of necessity be derived from data collected before the practical application of our comparatively recent knowledge had materially interfered with the natural course of events. This natural course of events must have been very considerably modified in the case of tuberculosis by recent legislation and by methods of treatment and prevention adopted.

From the naturalist's point of view the position is even worse with regard to malaria, for by the exercise of proper care the European can, to a great extent, escape the risk of infection, while the native does not trouble to use these precautions. A comparison therefore, under modern conditions, would be misleading.

II. One of the most acrimonious scientific controversies of recent times still continues round the validity of the direct evidence for the transmission to the offspring of acquirements made in response to the action of the environment by the soma or body of the parent organism; nor does the animosity of this controversy appear to show any signs of abatement. It led recently to a lamentable tragedy in the case of Kammerer, when he found that some unknown person had been tampering with his specimens in such a manner as to bring discredit upon some of his results.

Before dealing with this evidence, it is necessary to stress the fact that every character of an organism is of a composite nature. It is in part dependent upon the inherent potentiality of the germ-cell to develop along certain lines, and in part dependent upon the action of the environment. The relative importance of these two factors may vary in different characters, but both are essential. Without the inherent potentiality, the environment has nothing to act upon. Without the action of the environment, the potentiality cannot become manifest. Potentialities to develop certain characters may be present in germ-cells for an apparently indefinite number of generations, but unless a particular environment be present they cannot appear.

It is necessary to deal with this matter in such detail even to the point of tediousness, because characters are so often treated as though they were concrete objects, 'things' in Bishop Berkeley's sense, whereas they are really phenomena due to a sequence of events, though the nature of the final result—the character—may be modified by a variation occurring at any part of this sequence. The potentialities upon which the appearance of a character are dependent are inherited. If acquirements are inherited it means that the process of making that acquirement has so affected the potentialities of the germ-cells as to alter their nature.

The most convinced follower of Lamarck would laugh at the idea that a race of tailless dogs might be produced by cutting off the tails of the parents in consecutive generations. We have at any rate evidence that the cutting off of tails has produced no such result in the case of terriers, though the practice has existed for a very long time. Mutilations then may safely be placed among acquirements that are not transmitted.

The earliest experiments claiming to demonstrate the transmission of acquirements that attracted any general attention were those of Brown-Séquard. He produced epilepsy in guinea-pigs by operations upon the spinal cord and various nerves, and in a few cases the offspring were stated to have epileptic fits. In some other guinea-pigs in which a large nerve in the hind limb had been cut, the animals gnawed off two or three toes which had been rendered insensitive by the operation. In some of the offspring of these, two or three toes were absent. (Brown-Séquard, 1869-93.) Other independent investigators have failed to confirm these results, and it has been claimed that the attacks were not epileptic. The validity of Brown-Séquard's interpretation is not generally accepted to-day, even among the followers of Lamarck, and so we will pass on to cases that are accepted as good evidence by some biologists.

Kammerer's experiments with Alytes are accepted by some as a definite proof that changes in the characters of the soma of the parent brought about by the environment may be reproduced in the offspring, and that this provides a definite case of transmission of acquired characters.

Alytes is a toad which lives and breeds on land. The eggs are adherent to each other in strings, and the male, when he has fertilised them after they are discharged by the female, carries these strings wound round his legs until they hatch out. Other toads and frogs mate in the water, and the eggs at the moment they are emitted by the female are fertilised by the male, who has nothing further to do with them. When first hatched out, the larvae possess gills, but these are gradually covered by a fold of skin which grows over them, and the tadpole stage, familiar to most children, is reached. In Alytes, this larval stage is passed through before hatching, and the young do not possess any gills. This is a phenomenon observed also in other embryos, including man; for at one period of its development the human embroy possess rudimentary gills, a relic of its pre-human ancestors. Another difference between Alytes and other toads and frogs is, that it lacks what is known as the nuptial pad, a hard excrescence on the inner side of the hand which enables the male to clutch the female securely when mating. This pad would be useless to Alytes as the skin of the female is not soft and slippery as is the case with other toads and frogs that breed in the water.

What Kammerer did was to keep a number of Alytes warm and give them free access to water in sufficient quantity to allow them to immerse themselves in it. They paired in the water instead of on land; the eggs, after fertilisation, were deposited there as are those of allied species and genera, instead of being carried about by the male; the larvae from these eggs hatched out in the water, and had gills; the males, it is stated, developed nuptial pads similar to those of other male toads and frogs, though they were imperfect, and these pads continued to appear in succeeding generations. The development of the pads has been disputed by many biologists who saw Kammerer's specimens, but has been supported by others.

The presence or absence of the pads, imperfect or not, is not an important point. The real question is whether Kammerer's results are not the same nature as von Nägeli's with Alpine plants? (see Chapter III). All Kammerer's Alytes were given free access to water. Indeed, had they not been allowed this, several of the changes of character must have proved fatal to the offspring, unless the parents reverted to their previous methods of reproduction.

It seems probable that, had these subsequent generations of Alytes been deprived of access to water, they would have reverted to the characters of their ancestors, including the disappearance of the nuptial pads. Apparently nothing of this kind has been tried, and until it is, these new characters appear to mean no more than did the new characters in von Nägeli's Alpine plants. What happened in both cases may be explained most simply by the presence in the germ-cells of a potentiality to respond in a definite manner to changes in the environment, and the simplest explanation appears most likely to be true; any other would require quite unnecessary assumptions.

Until, therefore, some enterprising biologist who has the facilities, completes the experiment as suggested, the question must remain open. It is quite probable that the answer will be that Alytes will behave much as did the Alpine plants.

Kammerer carried out some experiments in breeding two species of Salamander, and produced results which were in many ways similar to those which he obtained with Alytes, excluding the development of the nuptial pad, but here the same criticism obtains as in the case of Alytes.

Some other experiments he carried out with regard to the colour changes in two species of Salamander may be regarded as coming under a different category. Very briefly, the following results were described. It was found that when *Salamandra maculosa,* which is black-spotted with yellow, was kept in a yellow environment, the yellow was increased; while if kept in a black environment, the black increased at the expense of the yellow. The young of those chosen for their blackness which had been kept in a yellow environment were reared in a neutral environment until their metamorphosis. Some were then kept in a yellow, some in a black environment. Those in the yellow environment became more yellow than their parents. Those kept in a black environment lost nearly all their yellow.

Breeding from individuals chosen for their large share of yellow and kept in a black environment the yellow practically disappeared in the offspring kept in a black environment, while in those kept in a yellow environment, the distribution of yellow was not like that of the parents. It is claimed that the behaviour of the colour in the offspring was due to the effects of the environment upon the bodies of the parents. There are many more details than those given here.

Kammerer also carried out further experiments in transplanting the black and yellow skin from one individual to another, but the case for the inheritance of acquirements would not be furthered by describing them, more particularly in view of some experiments described below. Kammerer's experiments have not been repeated. (Kammerer, 1907–26.) Incidentally, it may be pointed out that Lamarck himself denied the inheritance of modification produced by light upon the body of the parent.

More convincing because less complicated, though still against the teaching of Lamarck, are the results obtained by J. W. H. Harrison (1928). He exposed the larvae of a butterfly to lights of different colours. The pupae of the butterflies produced from these larvae varied in colour according to the colour of the light to which the original larvae had been exposed. Of the progeny of those exposed to an orange light, 93·4 per cent were green; of those exposed to any other coloured light, about 20 per cent were green. He eliminated all but the green from those that had been bred in orange light, and continued the same exposure. In the next generation 95·2 per cent of the pupae were green. He bred another generation, having eliminated all but the green. These were bred in ordinary daylight. Only thirty-one pupae were produced, all being green. The captious critic might suggest the possibility of selection having some influence upon the results. Düiken and Brecher (1923) described very similar results with other lepidoptera.

r/

Less definite results were obtained by Stockard (1923) in his experiments on the effects of alcohol upon successive generations of guinea-pigs. These experiments extended over thirteen years, and 5000 animals were used. The guinea-pigs were intoxicated by alcohol vapour for various periods, the longest being six years, which is a long life for a guinea-pig. They were intoxicated six days in the week. The offspring were obviously injured, but eventually a superior group of individuals was produced. Stockard sums up his results as follows:

> 'When we consider the welfare of the race or stock rather than that of the individual it is found that the descendants of those groups of animals which suffered the highest mortalities and thus withstood the most rigorous elimination are superior in quality to the descendants from the groups less severely affected. This individual selection furnishes a great advantage to the later generation, as is shown by the superior quality of the F4 group (4th generation of guinea-pigs). . . .
>
> 'From the standpoint of genetics, just how are such results to be interpreted? They certainly show that the germ cells of the treated guinea-pigs were injured or changed. And this change in the germ cell gave rise to generations of individuals inferior in quality to the control. But also after several generations the individuals of these treated lines actually became superior to the control. This can only mean one of two things. Either, in the first place, the treatment only injured a portion of the germ cell population and was not severe enough to injure the most resistant germ cells, so that each generation of progeny are derived from a mixture of injured and uninjured cells. The uninjured ones were actually the best or most resistant germ cells of the original group. The second possibility is that the less resistant members of the germ cell population are injured and give rise to the inferior individuals of subsequent generations, while other germ cells are actually stimulated or benefited by the treatment, and these give rise to superior individuals. In any case the injured individuals are eliminated after several generations and the superior uninjured group remains.'

Evidently the injuries to the parents reappeared in the offspring as a general effect and not as a change in any particular character or even several characters, and it might reasonably be held that the result was due to a general injury of the germ-cells and soma together. It is evident that an alcohol-immune race was produced. The results of the experiments might well be claimed as an example of the successful selection of variations against the effects of alcohol.

Another set of experiments with regard to the effect of alcoholism on rats, showed that the weight of the young at birth and for twenty days after was not affected in the tenth generation. (Hanson, Blair, Scholes and Keys, 1928.)

A similar criticism has been advanced against interpreting the results of long-continued rotation of rats as demonstrating the transmission of somatic acquirements. These rats were kept in cages on large rotating-tables. They frequently developed disease of the ears and the death-rate was high. Disease of the ear was claimed to be commoner than usual in the next generation. (Detlefsen, 1923; Griffins.)

While what is given above does not include all the evidence available for the inheritance by the offspring of the direct effect of the environment upon the bodies of the parents, it includes the most important items of it.

One of the strongest arguments against the inheritance of acquired characters being a usual occurrence and having played an important part in evolution is provided by what happens in the Hymenoptera (bees, wasps and ants). In the social bees and ants only some of the eggs are fertilised. The fertilised produce females, the unfertilised males. Among the larvae 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 larvae 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, and who have never developed the habit. These facts make it perfectly apparent that the instincts must be due to inherent potentialities, and not at all to acquired habits or characters, for the individuals through which they are invariably transmitted never possess them, and so certainly have made no acquirements in that direction.

Nor are instincts the only characters transmitted through individuals that do not possess them. The same thing happens with regard to very striking morphological 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 and from the other workers that the untrained observer would class them as belonging to a different genus. 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 workers 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. 16).

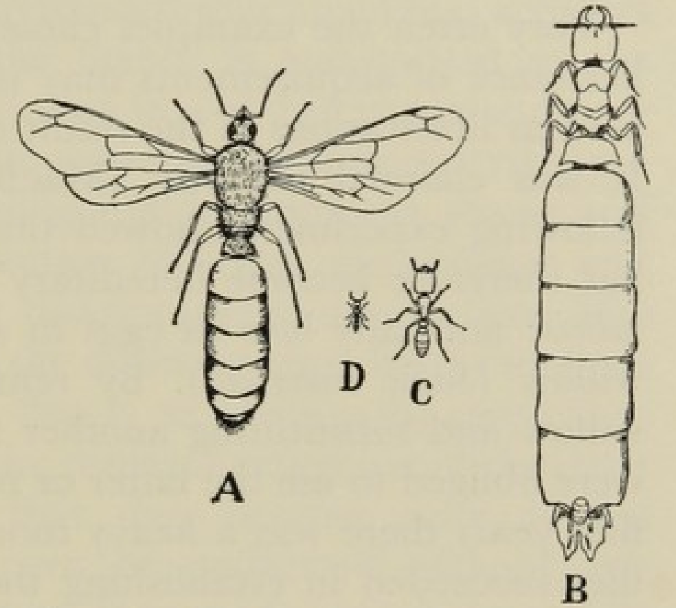


FIG. 16.—A. Male of *Typhlopone*, formerly classed in a separate genus (*Dorylus*). B. Female, formerly classed in a separate genus (*Dicthadia*). C. Neuter soldier (worker). D. Neuter minor (worker). [Actual size.]

The polymorphism among social ants and bees has been the subject of much argument, and has produced a great deal of speculation. 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.

Very often the examples chosen to illustrate the inheritance of acquirements may be just as satisfactorily used as illustrations of the result of selecting variations. It was claimed recently (MacBride, 1931) that the following experiment showed that 'the acquired habit has therefore become hereditary'. A gall-fly (*Pontiania salicis*) normally lays its eggs in a particular species of willow (*Salix andersoni*). By removing this species of willow and substituting another (*S. rubri*) the gall-flies were obliged to use the latter or none at all. During the first years there was a heavy mortality and only a few flies succeeded in establishing themselves, but as time went on more were produced. After five years *S. andersoni* was brought back, but the then existing gall-flies continued to use *S. rubri*. It is more likely that as only a few gall-flies were capable of using the strange willow, this was due to the fact that variations in this direction were not very common. Those that possessed it produced young, and these young, varying from a new mean, produced some offspring that were even better adapted to *S. rubri* than their parents, and so on until at the end of five years of selection the race was no longer adapted to *S. andersoni*. It might indeed be taken as an excellent example of how natural selection works.

In considering the evidence for and against the transmission of the effects produced upon the soma of the parent to the offspring, several points become evident. In the case of the indirect evidence, that for and against compete on more or less equal terms. As to the direct evidence, it is quite clear that it must be impossible to prove that the effect of the environment upon the soma of the parent *cannot* be inherited by the offspring, while observations of its occurrence would definitely prove that it does happen.

The issue has been frequently confused by the manner of presentation. It is contended that an animal acquires a 'habit' and that the 'habit' is transmitted to the offspring. This word is used in a rather vague and very comprehensive sense. It appears to include everything—colour, modes of breeding and development, shape, and the increase or diminution of limbs, appendages and organs, even to their disappearance or creation. The word is rarely used in the ordinary sense by the modern followers of Lamarck, that is, to indicate the result that so frequently follows the constant repetition of the same series of actions, so that they become more or less automatic and may even be performed without any deliberate act of volition. It seems to include any effect of the environment upon the individual, even that of light. The effect of the environment upon the *race* is frequently confused with its effect upon the *individual*.

If we analyse carefully, however, every case must come down to the simple question, whether or not the changes in the soma of the parent brought about by the environment produce changes in the potentialities of the germ-cells of such a nature that similar changes appear in the offspring, those particular factors that produced the changes in the parent being absent from their environment.

One example of 'habit' will suffice, that already described—von Nägeli's Alpine plants. These experiments have been extended and amplified since. (Clements, 1925, 1929 and 1930.) They certainly show that the 'habit' of the plants is profoundly affected by the environment, but they provide no evidence at all that the potentialities of the plant have been affected by a change of 'habits' acquired and continued for many generations as a result of a change of environment. Indeed they prove exactly the opposite in the case of these plants.

Taking the direct evidence first, it seems to show that the transmission of the acquirements of the body of the parents to the offspring must be of rare occurrence. Instances have been diligently sought and described for more than sixty years. Many have been discredited; many are more satisfactorily explained by the selection of variations; few have escaped cogent criticism; and those for which claims of confirmation are made are complicated, obscure, or of little importance, might be counted on one's fingers, and seem to be against Lamarck's own theory.

The indirect evidence seems to point even more strongly in the same direction. We find everywhere races of plants and animals adapted to their environments, and, as we have seen with regard to some diseases, there are records indicating the lines along which adaptation has travelled. Many characters in individuals counteract factors in the environment which threaten the destruction of the race, and others again enable the individual to derive advantages from the environment which it could not do in the absence of these characters. Fundamentally the two come to much the same thing. For instance, sight is of great value to the individual in the case of many animals in procuring food and escaping from enemies. The environment remaining the same, such an animal would run a great risk of starving or being destroyed if its sight became weak.

The most probable explanation of an increase of immunity in a race seems to be the accumulation of variations towards an increase in this capacity through selection.

The chance of survival of a race would appear to be proportional to the chance of survival of the average individual, as the race cannot continue without the production of offspring, so we may rightly speak of a character being advantageous to both the individual and the race.

A factor in the environment which is injurious to the individual should thus be generally injurious to the race, but where we find a race existing with an injurious factor in its environment we also find that the majority, or at least a sufficient proportion of the individuals to ensure survival, possess characters which are adequate to counteract the injurious factor. But injurious factors must produce injurious effects upon the individuals which survive to produce offspring, and as we have seen in the case of the tubercle bacillus, there is no evidence at all that these injuries are handed on to the offspring, otherwise we in Northern Europe, where most, if not all, suffer from the disease at some period during life, must have accumulated a vast stock of injuries, which we have not done.

The only way out, if changes produced by the environment on the body of the individual are generally, or even in a comparatively few cases, transmitted to the offspring through the germ-cells, is to assume that these cells have a selective capacity, and reject those changes which are injurious to the individual. Were no other explanation available, there might be some excuse for accepting it as a temporary working hypothesis, but as the theory of selection offers a plausible solution without any such assumption, it seems preferable. Even if the few cases of the inheritance of acquirements for which there is evidence that will bear criticism be accepted, the case for the appearance and modification of racial characters by the selection of variations in the potentialities of the germ-cells by the environment seems to be strengthened, for it emphasises the view that variations take place in all directions, even towards producing a potentiality to transmit somatic modifications in the germ-cells, and explains why, being injurious to the race, this tendency is eliminated.

Those who believe that the selection of chance variations round a mean is inadequate to explain evolution, and that it is necessary to assume the inheritance of characters acquired by the soma or some metaphysical power of direction, do not seem to realise that the selection of variations by the environment itself automatically alters the mean from which variation occurs at each generation, as is evident in the illustration used with regard to the manner in which immunity to tubercle might be acquired by a race. This illustration was first used twenty-five years ago (Walker, 1910), and it makes the cumulative, hastening effect of selection clear. The idea has been formulated in a rather different way. (Morgan, 1919.)

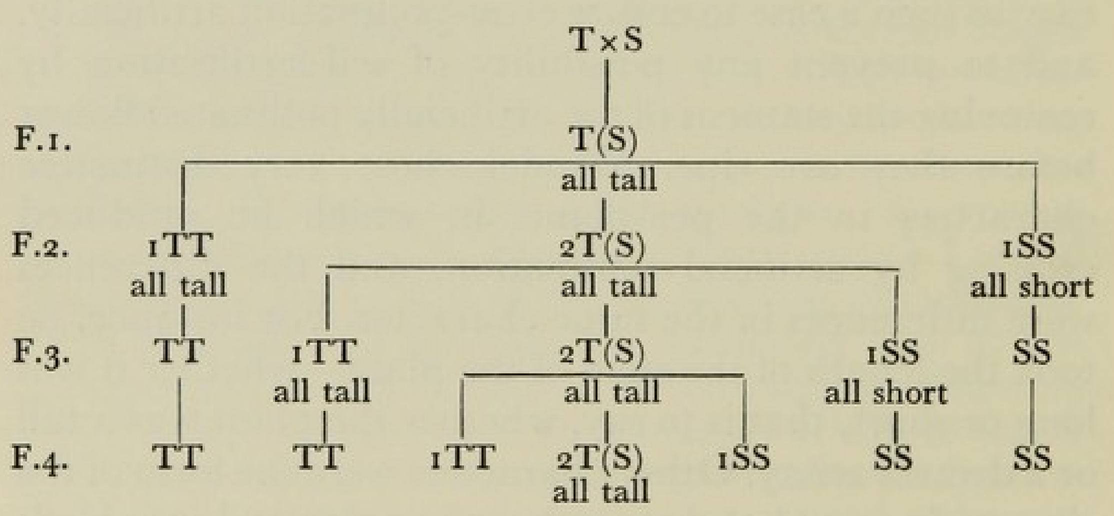
> 'Starting at any stage, the degree of development of any character increases the probability of further stages in the development. The relation can better be illustrated by specific cases. The familiar example of tossing pennies will serve. If I have thrown heads five times in succession, the chance that at the next toss of a penny, I may make a run of six heads is greater than if I tossed six pennies at once. Not, of course, because five separate tosses of heads will increase the likelihood that at the next toss a head rather than a tail will turn up, but only that the chances are equal for a head or a tail, so that I have equal chances of increasing the run to six by that throw, while if I tossed six pennies at once the chances of getting six heads in one throw are only one in sixty-four times.'

# CHAPTER VI

## Mendelian experiments and interpretations

THE most important discovery connected with heredity that has been made in comparatively recent years is that of Gregor Johann Mendel, Abbot of Brünn in Austria (now Brno in Czecho-Slovakia). He published the results of his experiments in an obscure journal in 1865 and it escaped notice until 1900, when it was 'rediscovered' by Correns, Tschermak, de Vries and Bateson, all in the same year.

Mendel's experiments dealt with the manner in which certain definite characters in edible 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 on 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 drawfs, 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.



It is customary to call the first generation which is composed entirely of hybrids, the first Filial, written for the sake of brevity F.1. The second generation is F.2, and so on.

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, the tall, appeared in the first generation, to the apparent exclusion of the other. Mendel called the character that appeared the 'dominant', that which 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 factors in the gametes. Each of the pure-bred parents from which the first generation of hybrids was produced, would contain only one kind of unit. In the first generation of hybrids, however, both units representing the characters must be present. He supposed that in the production of the gametes of the hybrids, these units representing two opposing characters, separated from each other, so that half the gametes contained units representing one character, and half contained units 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 is known as 'segregation' and it is assumed that offspring with the perfectly pure characters of the two

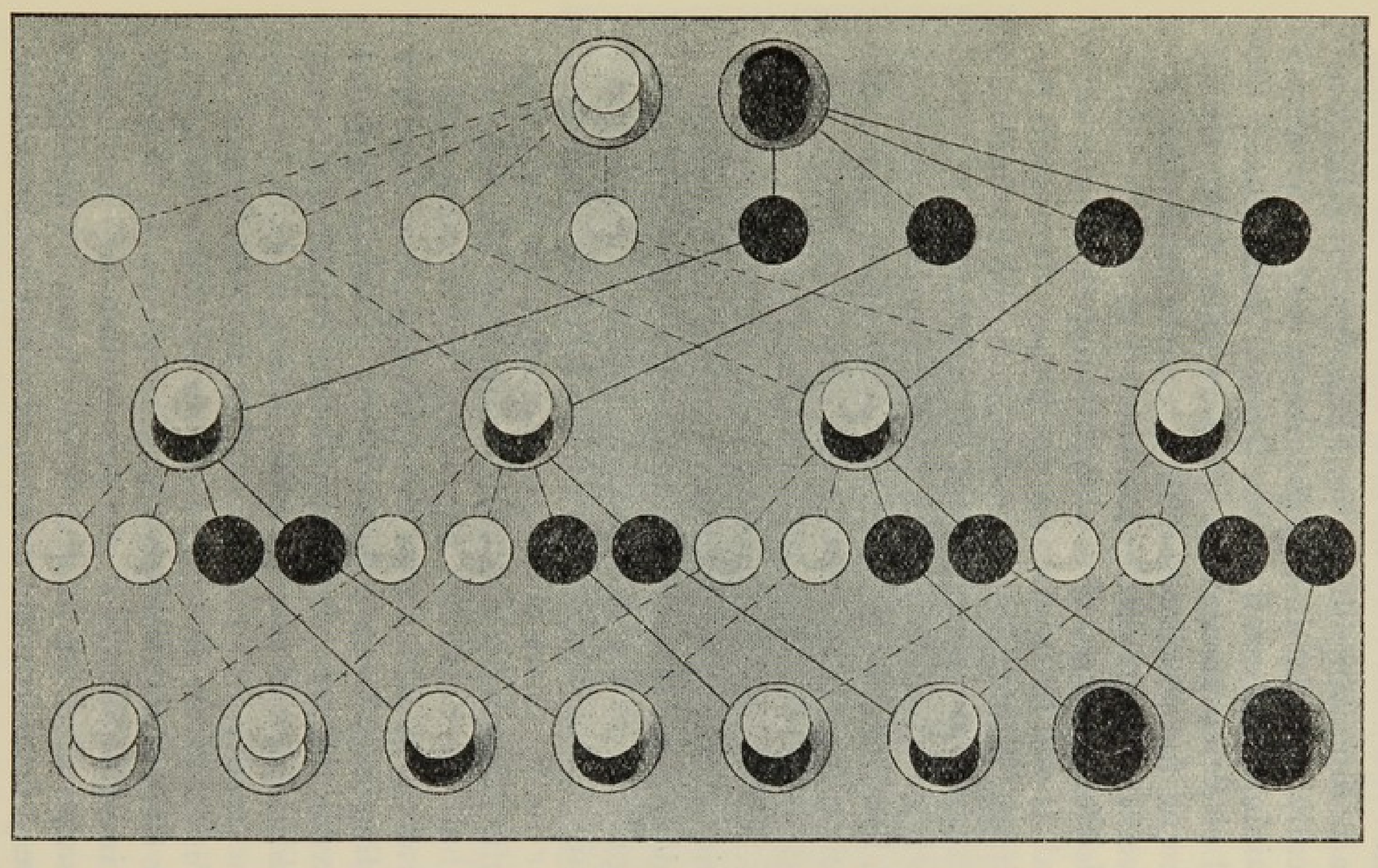


FIG. 17.—The large circles represent individuals, the small gametes. White represents the dominant, black the recessive. In the individuals containing both kinds of gamete, only the dominant character appears. The recessive character appears only when both gametes are recessive as indicated by shading.

parent organisms may be bred out from the hybrids. The accompanying illustration (Fig. 17) shows diagrammatically how this is brought about. 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.

The validity of Mendel's principle, this 'law of segregation', has been tested by crossing one of the 'extracted recessives', that is, an individual of F.2 or later generation which shows the recessive character, with the hybrid (F.1). If Mendel's assumption is correct, then as the F.1 individual will produce gametes half of which will bear the 'dominant' factor and half the 'recessive', and as all the gametes of the extracted 'recessive' will carry the recessive factor, and as in the presence of the 'dominant' factor the dominant character appears in the individual, half the offspring of this cross should show the recessive and half the dominant character. The accompanying diagram (Fig. 18) shows how this happens. Mendel's breeding experiments showed that the characters did behave in this way; the proportions of offspring showing the different characters was according to expectation.

The reader will remember that the cell formed by the fusion of the two gametes, one from the male, the other from the female parent, is known as the 'zygote'. The individuals whose gametes contain two factors of the same kind are called 'homozygous', while those whose gametes contain a factor of each kind are said to be 'heterozygous'. All the hybrids are 'heterozygous'. The pairs of characters are called 'allelomorphs'.

Since the rediscovery of Mendel's principles, a vast number of breeding experiments with animals and plants have been carried out, and the results show that they are true of many characters in a wide range of organisms.

It was soon discovered, when a number of breeding experiments were conducted after the year 1900, that while dominance of one character was as complete as those described by Mendel in some cases, in a great many plants and animals the hybrids were intermediate in the characters crossed, or that the particular character might be different from that in either parent, though the two characters could be bred out from the cross, that is to say they segregated.

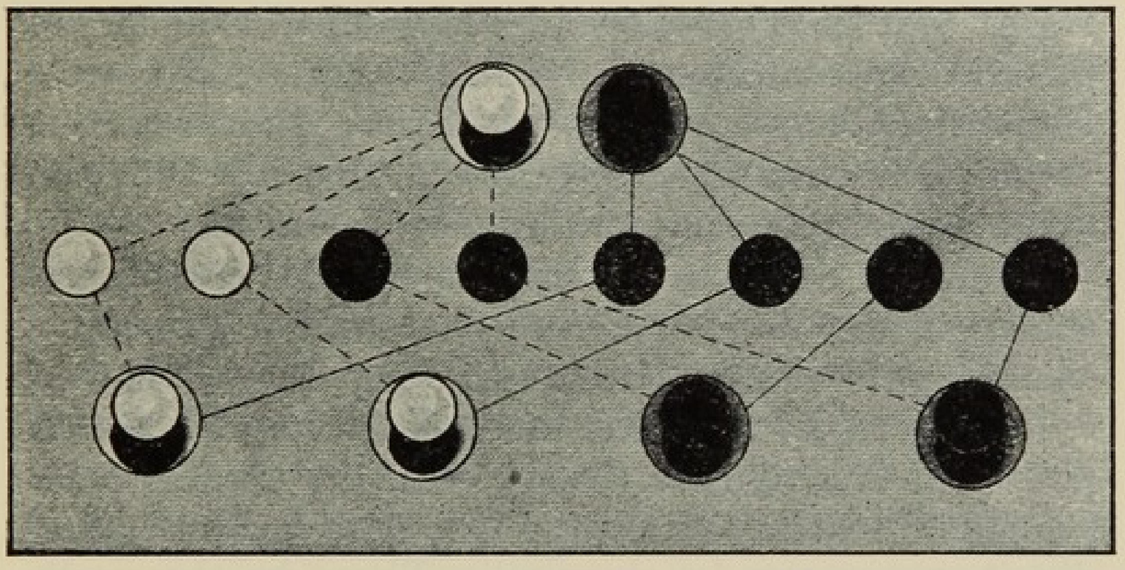


Fig. 18.—Illustrating a cross between an impure dominant and a recessive. A pure dominant cannot be produced from this cross.

Thus if the red-flowered variety of the Marvel of Peru (*Mirabilis jalapa*) be crossed with the white-flowered variety, all the first generation have pink flowers. If the next generation is self-fertilised, the offspring will give the proportions 1 red-, 2 pink- and 1 white-flowered. In this case the hybrids can be distinguished from the extracted red and white. The hybrids go on producing red-, pink- and white-flowered plants in succeeding generations in the same proportion.

When Japanese waltzing mice are crossed with albinos, the first generation of hybrids are all coloured like the wild house-mouse (Darbishire, 1902), and this is the case with all the heterozygotes.

If the reader will recall the facts described in Chapter II relating to the manner in which cells multiply and to the cell phenomena that precede fertilisation, he will realise that if, as is believed by Mendelians, the factors or units representing the characters that behave in the Mendelian manner are conveyed by the chromosomes, a mechanism exists which provides all that is required to explain the Mendelian results so far described.

It will be remembered that during the preliminary stages of the division before the mature gametes—sperms and ova—are produced, when the number of chromosomes is reduced to one half the number that is present in the somatic (body) cells, the chromosomes are joined together in pairs, whole chromosomes being distributed to the daughter cells. These daughter cells with half the number of chromosomes divide again in the usual (somatic) manner, their daughter cells thus retaining the reduced number. When these cells in due course produce mature gametes, it is clear that each gamete contains only half the full number. Now, if the factors representing or controlling the appearance of particular characters are conveyed by individual chromosomes, we have here a mechanism for their alternative distribution; but more than this is required to account for the Mendelian results. In the cells produced from the fertilised ovum—the fusion of the two gametes into a single cell—all must contain representatives of those chromosomes that were derived from each parent. For instance, in an organism whose chromosome number was four, each gamete would contribute two. Two of these in each cell going to build up the new individual must be derived from the male, two from the female parent. There is evidence to show that probably, at the time the division in which reduction in the number of chromosomes occurs and the chromosomes join in pairs, this pairing is between corresponding chromosomes derived from the male and female parent respectively. In the bug *Protentor* two of the chromosomes are conspicuously larger than any of the others. When reduction takes place, the sizes of the fused pairs show that these two large chromosomes must always join together. (Morgan, 1919.) In several species of the vinegar-fly *Drosophila* the sizes of the pairs show that two very minute chromosomes must have joined together to form the smallest pair in the reduction division. (Morgan, 1919.) There are individual chromosomes that appear regularly in the ordinary somatic divisions of the cells of some organisms that are easily recognisable through being much longer, more bulky, or much smaller than their fellows, but this is true usually of only one or two among many. On the other hand, the pairs of chromosomes in the reduction division often assume shapes that are unmistakable, and constant in the number of pairs of chromosomes that assume each particular shape. (Baumgartner, 1902; Moore and Arnold, 1906; Walker, 1911 and 1925.) These shapes are most obvious when the cells of the organism are large. In the newt, for instance, the cells are on the average about ten times the bulk of those of mammals, including man, and in the reduction division in the cells of the newt, the shapes of the chromosome pairs whose sizes are proportionate to that of the cell are particularly striking. As is to be expected, in the case of smaller chromosomes the shapes are less obvious, and they have not so far been described in very many organisms.

If, as seems probable, the paternal and maternal chromosomes do join in corresponding pairs, then the mechanism provided by their distribution accounts for the appearance of pairs of characters in succeeding generations in the Mendelian breeding experiments.

To complete the argument there remains only the question as to whether or not the chromosomes retain their individuality through succeeding cell-generations.

We have, to begin with, the fact of the persistent number of chromosomes that appears in the cells of a given organism when the cells divide, in spite of their disappearance between whiles. Moreover, when the process of reduction has taken place, half the somatic number appears. This half number continues through many generations, in the case of some plants even giving rise to a separate plant, as in the prothallium of a fern, the full number being restored when fertilisation takes place, that is, when the two cells showing the reduced number of chromosomes fuse. There are many cases which show that whatever number of chromosomes goes into a cell, that number will appear persistently in its progeny, unless of course a reduction division intervenes.

In the eggs of *Ascaris megalocephala* var. *bivalens*, a parasitic worm, whose normal chromosome number is 4, one or both of the chromosomes that would be separated off in the reduction division are sometimes, accidentally, retained in the egg. When the sperm enters and the first division takes place, these additional chromosomes join with the normal ones derived from the nuclei of the sperm and egg, and the succeeding generation of cells show this increased number of chromosomes when they divide. (Boveri, 1909; zur Strassen, 1898.) Instead of the normal 4 chromosomes, there are 5 or 6 in each cell of the worm that develops. What has already been said with regard to the sizes and shapes of individual chromosomes or pairs of chromosomes as being in favour of the idea that they join in corresponding pairs, is also in favour of their continued individuality.

In some plants of the evening primrose, *Œnothea lamarckiana*, the cells have 15 instead of the usual 14 chromosomes. This is probably brought about by some accidental irregularity when a gametogenic cell was dividing. Half the gametes of such a plant would contain 8 and the other half 7 chromosomes. When a gamete with 8 chromosomes fused with one containing 7, the cells of the resulting individual would contain 15 chromosomes. This is found to occur.

In a cross between two kinds of moths which differed as to the size and number of their chromosomes, it was found that the number of chromosomes in the cells of the hybrids was the sum of the halves of that found in each parent, and that the sizes of the chromosomes corresponded, as there were the expected number of large and of small chromosomes. (Harrison and Doncaster, 1919.)

Such is the evidence which suggests that, though in the vast majority of cases the chromosomes become diffused in the nucleus and can no longer be recognised individually during the vegetative stage, they may probably retain their identity from generation to generation of cells. The point, however, is not actually proved from the cytological point of view.

The second of Mendel's principles is, that when two varieties of plants or animals are crossed that differ from each other in two or more pairs of characters, the inheritance of each pair is independent.

Taking one example from among a large number. Red Hereford cattle have white faces. If they are crossed with black Welsh with black faces, two pairs of characters are involved. The red coat is recessive to the black, but the white face is dominant to the coloured face. In the first generation (F.1) all the offspring are black with white faces, showing the two dominant characters. The distribution and combination of the two pairs of characters in the next, F.2, generation are complicated, but show clearly that the two pairs are appearing independently. We will take 16 as a convenient number for calculation and explanation of details of the F.2 generation. Of the 16 offspring, 9 will be black with white faces, 3 black with black faces, 3 red with white faces and 1 red with a red face. Of course it is improbable that these proportions would actually be achieved unless a much larger number than 16 were involved, but they represent what happens with large numbers. To make clear what has happened it is desirable to adopt letters for the different characters. The two dominant characters, black coat and white face, are represented by the capital letters 'B' and 'W'. The two recessive, red coat and coloured face, by the small letters 'r' and 'c'. It is clear from the results of the experiment, that the pairs of characters are behaving independently. If a table is made of the possible combinations of postulated factors it will be seen whether this works out with the results. On this assumption the cells of the hybrid, F.1, generation will all contain all the factors, BrWc. When the gametes are produced, these factors are distributed in corresponding pairs, there being four possible combinations from each parent, BW, Bc, rW, and rc. In the table on page 85 it is shown how these pairs will be combined on fertilisation.

It must be remembered that the dominant characters, those represented by capital letters, will always appear to the exclusion of the corresponding recessive. There is only one combination of four recessive factors, which

| | | Gametes from Female Parent | | | |
|---|---|---|---|---|---|
| | | BW | Bc | rW | rc |
| Gametes from Male Parent | BW | BW BW | Bc BW | rW BW | rc BW |
| | Bc | BW Bc | Bc Bc | rW Bc | rc Bc |
| | rW | BW rW | Bc rW | rW rW | rc rW |
| | rc | BW rc | Bc rc | rW rc | rc rc |

corresponds with the experimental results, as do the rest of the other combinations.

It would seem, then, that the results of experimental breeding confirm Mendel's second principle, the independent assortment of the unit factors; but it remains to be seen how far the chromosome mechanism provides for this phenomenon. The evidence already considered indicates that probably the chromosomes from the male and female parent join in corresponding pairs during the reduction division. If the single chromosomes from the pairs are distributed indiscriminately, to the daughter cells from which gametes are derived, the Mendelian requirements are satisfied; if all the maternal chromosomes go to one daughter cell and all the paternal to the other, they are not.

The general impression given by the appearance of microscopical preparations is, that the distribution of the chromosomes is haphazard, but now that this question has arisen more definite evidence is necessary.

In a genus of grasshoppers, there is a pair of chromosomes that differ so much in size and shape that they can easily be distinguished from each other. There is also in the male a single sex-chromosome, which, when the cell divides, goes to one pole or the other, so that one daughter cell has this sex-chromosome and the other has not. (Sex chromosomes are dealt with later in this chapter.) Among a large number of cells observed it was found that the smaller of this pair of easily recognisable chromosomes went to the same pole as the sex chromosome, in about half the cases, to the other pole in the other half. (Carothers, 1913.) Similar cases have been described in other organisms. (Robertson, 1916; Voinov, 1914–16.) There is some further evidence with regard to the random assortment of pairs of chromosomes based on the way in which they are attached to the spindle fibres. (Carothers, 1917.)

Though there is no direct evidence that the distribution of the members of the pairs of chromosomes is according to mathematical chance in all organisms, the fact that it is so in those cases where demonstration has been found possible, suggests that it is the usual way. Indeed one of the leading living cytologists states definitely that he considers this evidence conclusive. He says:

> 'It has thus been possible to set aside every doubt concerning the independent segregation or assortment of the synaptic mates.' (Chromosome pairs in the reduction division.) (Wilson, 1925.)

This free and independent assortment of factors would be possible only with regard to pairs that were carried by separate chromosomes, according to the evidence we have considered so far, for considering the large number of Mendelian characters that have been studied in individual organisms, it is clear that if the factors representing them are carried by the chromosomes, one chromosome must carry many.

The results of the enormous number of breeding experiments that have been carried out since 1900 show that many characters keep together in groups. These are said to be linked. In one case, the vinegar fly, *Drosophila melanogaster*, about 300 Mendelian characters have been studied, and they are found to fall into four linkage groups. Each pair of characters is linked to one group, but shows free assortment with the pairs of the other three groups. (Morgan, 1924.) These groups of characters agree with the number of chromosomes, of which there are four pairs. The linkage of characters varies in degree, however, in different cases. In some cases their cohesion seems to be absolute, that is to say, they always go together. In others there seems to be but little more tendency for them to hold together than to assort freely. All degrees of linkage between these two extremes may exist.

Linkage was first observed by Bateson and Punnett in 1906. Since then a number of cases have been found in animals and plants. Taking as an example two characters in *Drosophila melanogaster*, that are linked, yellow wings and white eyes. A female with yellow wings and white eyes is mated with a male with grey wings and red eyes. All the daughters have grey wings and red eyes and all the sons yellow wings and white eyes. If this F.1 generation is inbred, 98·5 per cent of the F.3 generation have either yellow wings and white eyes, or grey wings and red eyes. In 1·5 per cent there has been a change, and these are in an equal number of flies with yellow wings and red eyes or grey wings and white eyes. (Morgan, 1924.)

In some cases the percentage of pairs of characters that change thus may be much higher than 1·5 per cent, in others less, possibly only one in several thousand. The phenomenon has been called crossing-over, and the relative proportions of crossing-over to remaining linked, that is, in other words, the tightness or looseness of the linkage of characters as shown by the frequency of crossing-over, is known as their cross-over value.

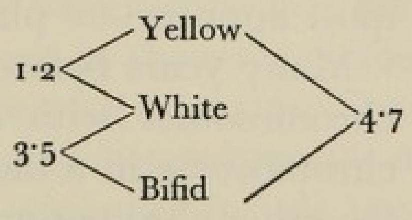
The mechanism of cell division provides opportunities for the transfer of unit factors. As pointed out in Chapter II, there are two schools of cytologists who differ in opinion as to how the pairs of chromosomes join together in the reducing division. Some Mendelians are disturbed by the possibility that those who believe that the chromosome pairs are joined end to end may be right. They fear that this would preclude the possibility of an interchange of unit-factors between the pairs of chromosomes. The opportunity for such an exchange is of course obvious if the chromosomes are joined side by side. There are no real difficulties, due to lack of opportunity for an exchange of unit-factors among the chromosomes, quite apart from the relative position of the members of pairs in the actual division. As pointed out in Chapter II, the preliminary stages of the reduction division are far more complicated than is the case in the ordinary somatic cells. Instead of a simple coiled-up thread appearing in the nucleus, a complicated process is gone through in which threads containing small masses of chromatin, which will eventually contract to form the chromosomes, split, coalesce and split again in an order and with a frequency which vary with the accounts of different observers. In all of these different accounts there are opportunities for the exchange of factors, if the factors are contained in the precursors of the chromosomes, and the opportunities are most easy and numerous in some of the latest accounts of the complicated processes that take place in the cell immediately before the reduction division. (Digby, 1919; Sarbadhikari, 1924; Walker, 1925 and 1926.) Besides this a set of elaborate and ingenious experiments were made, the results of which are claimed to establish the fact that crossing-over must take place before the gametes are mature. (Plough, 1917.)

It is claimed that the genes (unit-factors) are arranged in a linear order. The arguments for this view are dependent upon linkage. (Morgan, 1919 and 1924.) It is found that this view is consistent with the results of breeding experiments, and moreover that on this assumption it is possible to predict the behaviour of any new factor in a series in relation to all the other members of the series, provided its cross-over value and that of any other two of them is known.

Here is a simple case from Morgan's *Physical Basis of Heredity*:

> 'If *a*, *b*, and *c* stand for three genes, and if the linkage relations of *a* to *b* and of *b* to *c* are known, the relation of *a* to *c* is a function of *a b* and *b c* or of the difference of *a b* and *b c*. For example, if the cross-over value *a b* is expressed as 5, and that of *b c* as 10, then *a c* is a function of the sum (15) or the difference (5) of *ab* and *bc*.'

The experiments illustrating this is as follows. Three characters in *Drosophila* were all used together in a single experiment, yellow wing, white eye and bifid wing. There were 1160 non-cross-overs, 15 flies represented cross-overs between yellow and white, and 43 cross-overs between white and bifid. This makes the yellow-white cross-over value 1·2 and the white-bifid 3·5. The same data gave the yellow-bifid cross-over 4·7, which is just right.



To quote again from the same source:

> 'The simplest way in which such a relation can be thought of is that the three genes stand in a line. Suppose a fourth linked gene, *d*, is added to the series. It is then found that *bd* is a function of the sum or of the difference

of *b* to *c* and *c* to *d*. Four points arranged in a straight line still fulfil the relations here found. I know of no other geometrical configuration that covers all these results—perhaps there is none. When we add more and more linked genes to the series, and find the same predictable relations continue to hold, the theory of the linear arrangement becomes firmly established.'

There are many complications and elaborations beyond the simple case quoted, but large numbers of breeding experiments with *Drosophila* support the theory in its various details.

Certainly this assumption of linear arrangement makes the interpretation of some of the results of the crossing-over in breeding experiments feasible on mechanical grounds, for the chromosomes of the reduction division, before they are fully formed, are represented by very considerable lengths of attenuated threads which split and approximate; these approximated pairs of threads also approximate, and then separate again, during the period immediately preceding the actual division.

The sex-chromosomes are so intimately associated with the Mendelian investigations that this seems the most appropriate place in which to deal with them.

Many years before there was any idea of connecting chromosomes with sex, Henking (1891) described a chromosome in a bug, *Pyrrhocoris*, which lagged behind the other chromosomes in the division immediately preceding the production of the gametes, and eventually went to one pole without dividing like the other chromosomes. Thus two kinds of gametes were produced, one with 5, the other with 6 chromosomes. This additional chromosome was called X, but Henking had no idea of its nature or functions.

The presence of an additional chromosome was described in many other organisms by other observers later. This 'additional' chromosome was observed in the production of the male germ-cell only and this led to the suggestion (McClung, 1901–2) that as two kinds of gametes were produced, one with and one without the X chromosome, the X chromosome was probably what determined sex. This hypothesis was satisfactory up to a point, but was found quite incompatible with some further discoveries as to the chromosomes. Finally, all these troubles were settled by the discovery that it was the female that had one additional chromosome. The female was found to possess two X or sex-chromosomes, the male only one. All the female gametes must possess an X chromosome, while only half the male gametes will do so. Therefore half the fertilised ova will possess two X chromosomes and half only one. Those with two will develop into females, those with only one into males.

It was found later (Wilson, 1905–6) that in some forms the single X chromosome in the male had a 'mate'. The 'mate', which commonly differs from the X chromosome in size, form and structure, is known as the Y chromosome. This condition is probably more primitive than that first described where the male has only one sex-chromosome. In this case there will be an equal number of X and Y bearing gametes produced by the male, while the female will produce only X bearing gametes. One parent, in this case the male, was heterozygous—a hybrid as far as sex is concerned, while the female was homozygous. As all the female gametes contain X and half the male gametes contain X, half Y, there is an equal chance of a male or female being produced.

Correns (1907) crossed some monoecious with dioecious species of the plant *Bryonia*. He found that in the dioecious species the sex is determined by the pollen grains which were made up of two classes, male and female producing, while the eggs were all of one type.

The experiment of course is exactly comparable to crossing an extracted recessive character with a hybrid from the F.1 generation. (See pp. 78, 79.)

In the majority of cases it appears that the male is heterozygous as described above; that is, the sperms, being of two kinds, determine the sex. In other cases, however, the female is heterozygous, and the sex is determined by the egg. In mammals, reptiles, most insects, spiders, echinoderms, nematodes, and some other organisms the female is said to be homozygous, while she is heterozygous in butterflies. In birds the females are heterozygous as far as breeding experiments go, but it is claimed that in the common fowl and in the guinea-hen there are two kinds of sperms, one with and one without an unpaired chromosome. (Guyer, 1909a, 1909b, 1912.) In birds, therefore, the breeding experiments and microscopical observations at present do not agree.

As characters are many, and chromosomes are few, it is not surprising to find that other characters besides sex are carried by the sex-chromosomes. The result is that these sex-linked characters are inherited in a different way to those carried by the other chromosomes.

The type that has X and Y chromosomes in the male and XX in the female may be taken as an example. Y differs from X in a way that no other chromosomes differ from each other, and only the male ever possesses Y, which is presumed to determine the sex.

In *Drosophila* the gene for white eye is recessive, and is carried by the X chromosome. The gene for red eye is dominant and is also carried by the X chromosome.

If a male with white eyes is crossed with a female with red eyes, the following gametes are produced by the parents and fuse according to mathematical chances.

The letter 'w' is attached to the X in those gametes that carry the white-eye character, R to those that carry the red-eye character. The male will produce equal numbers of Xw and Y gametes, the female all XR gametes. The result of the cross is that all the F.1 generation will have red eyes. The gametes produced by the F.1 generation will be in the proportions, two XR to one Xw and one Y. The female cannot carry the Y chromosome. The results in the breeding experiment are that all the daughters (50 per cent of the whole number) have red eyes, half the sons (25 per cent) have white eyes and half red eyes.

The converse of this cross confirms the linkage of these characters in the sex-chromosome. If a white-eyed female is crossed with a red-eyed male, all the daughters are red-eyed and all the sons are white-eyed. In this case the male produces an equal number of gametes containing XR and Y, while the female are all Xw. Therefore Y, the male-producing gamete, can join only with an Xw gamete, and all the males are white-eyed. On the other hand, the gametes produced by the female can contain only Xw and females can be produced only by joining with an XR gamete from the male. As R is dominant, all the daughters have red eyes. In the F.2 generation, when the numbers of the F.1 are bred together, half the females are red- and half white-eyed, and the same is the case with the males. As all the females of F.1 generation are hybrids (heterozygous), they should, if crossed with white-eyed males, give 50 per cent red- and 50 per cent white-eyed offspring. This they have been found to do. (Morgan, 1919.)

There have been many Mendelian experiments in which the crosses have been unsuccessful, in that the progeny have failed to survive. This has been explained by the assumption of 'lethal genes'. These are supposed to be units, the presence of which prevent the healthy and complete development of the offspring. The only justification for this assumption seems to be that no other explanation of the phenomenon occurred to the observers.

Several other types of sex-linked inheritance are assumed, but it is sufficient here to give these leading examples.

# CHAPTER VII

## Mutations and pure line investigations

The phenomenon of variability has proved to be far more complicated than it appeared to Darwin and his contemporaries. The really serious complications started with de Vries' 'Mutation Theory' (1901 and 1903). Briefly, the theory as originally stated is as follows. 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. Variations occur 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 '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 held 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 called 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 thus by the selection, not of the fittest individual, but of the fittest elementary species.

The original theory has been modified. It is now held that the only way to distinguish between a large fluctuating variation and a small mutation is by experimental breeding; a mutation, indeed, need be no larger than a fluctuating variation. Recent writers are inclined to regard mutations as of more frequent and regular occurrence among animals and plants than was originally suggested. The claim remains, however, that only mutations are permanent. It is admitted that an accumulation of fluctuating variations may be produced by selective breeding and may continue to reappear in the offspring, but that this accumulation always disappears when the selection which has produced it ceases. The example of sugar produced from beetroot has been cited. The percentage of sugar in beetroot was raised by artificial selection from 7 or 8 to 15, but directly selection ceased, the percentage of sugar returned to what it was originally.

In the absence of selection, characters in a race tend to disappear, even in the case of those that are very well-established, such as the eyes in *Proteus*. *Proteus* is a kind of newt which is found in subterranean waters in Dalmatia. A very large number of generations have lived in the dark, and the power of sight is useless to existing individuals in their present environment. They are quite blind, and all that remains of their eyes are rudimentary sacs covered by the skin.

There is evidence to show that characters that have appeared recently under selection, as for instance in domesticated animals, disappear with a corresponding rapidity when selection ceases. In fact, the evidence that a character disappears in the absence of selection seems to be a rather weak argument in favour of mutations being the only form of variation that is stable. There is, however, other evidence in favour of the 'Mutation Theory'. A number of experiments have been carried out in breeding and observing offspring derived from a single parent. Among the higher animals two parents are necessary to produce offspring. New individuals can be produced only by the fusion of two cells, one derived from the male, the other from the female parent. In many of the higher plants and some animals, however, the individuals are hermaphrodite, and in some cases self-fertilisation may and does occur. Again in some animals, what is known as parthenogenesis occurs; that is the female is able to produce eggs that develop without any fertilisation by the male, and this may go on for many generations. In some cases fertilisation only occurs in the eggs produced just before the winter, when the adults die off. In a few species the male seems to have disappeared altogether, and fertilisation never takes place. Lastly, there are many Protista which divide bodily into two, and thus large numbers of generations are produced from a single individual. Fertilisation may take place at intervals through individuals conjugating, but this may be delayed by suitable manipulation of the environment, and an almost unlimited number of generations produced without.

Now it is clear that it is possible for a large number of generations to be produced from a single individual in the case of organisms that are self-fertilised, parthenogenetic or from Protista, and it is from such as these that what are called 'pure lines' have been bred, and the phenomena of variation and inheritance in them studied.

The results claimed for these 'pure line' investigations are roughly as follows. The succeeding generations of individuals bred in this way show that there may be several strains in the make-up of an individual, as well as in that of an apparently homogeneous species or race. By selective breeding these strains can be separated from each other. These are the 'pure lines'. When these 'pure lines' were bred, it was found that the mean of a character chosen for measurement did not vary, though there might be considerable difference between the individuals. Let us take an example, which will make what happened clearer. We will suppose that a particular Protozoan is chosen for experiment. The succeeding generations produced from a single individual may vary much in length, but it is claimed that after a certain number of generations separate strains may be established in each of which the mean or average length of the individuals remains the same. Within the strain or line, the length may vary much as between individuals of the same generation, but the *average* length of all the individuals of any one generation will be the same as that of any previous or subsequent generation. No selection will alter this average size. For instance, if the lengths of the various individuals of a generation be classified as 1, 2, 3, 4 and 5, 3 is the mean length. If we breed from the dwarf 1, the mean length of its progeny will be 3. The same will happen if we breed from the giant 5, the mean length of its progeny will still be 3. These results prove, it is claimed, that the usual variations within a 'pure line' are not inherited. Thus unless some other kind of variation—a mutation in fact—occurs, the 'pure line' must remain for ever stationary within narrow limits with regard to its characters.

The first of these 'pure line' breeding experiments was carried out with a bean (Johannsen, 1908), followed by Roemer (1910) with peas; Jennings (1910–11) with a Protozoan, *Paramecium*; and Agar (1914) with a small parthenogenetic water-flea, *Simocephalus*. They all obtained similar results.

The Mendelians also claim that their results prove that there are two kinds of variations in living organisms, and that the mutations only are stable. No one can dispute the fact that some characters reappear in succeeding generations in the Mendelian manner, while others do not. Also it is true that the way in which these characters will reappear in succeeding generations—their proportionate distribution among the individuals subsequently produced—can be foretold with considerable accuracy. On the other hand, this cannot be claimed for many variations which are said to be fluctuating.

If two kinds of variations be granted, a somewhat obvious interpretation of the facts at our disposal seems to offer itself. The mutations may be variations in the chromosomes, while the 'fluctuating variations' may be those in some other part of the cells, partly due to the influence of the environment, partly to the intrinsic variability of living matter. Many more facts must, however, be considered before this interpretation can be accepted.

To deal with some of the criticisms of the 'pure line' investigations. As already pointed out, the variations within the 'pure line' may be considerable, so much so that the extremes of two 'pure lines' may overlap. Now it is obvious that the larger the numbers of measurements available and the more accurately they are classified in any series of 'pure line' investigations, the more nearly will the conclusions made from them approach the truth. The converse is also obvious: with insufficient data the results may be misleading.

Before quoting the criticisms, it is necessary to define some of the words used. Of 'genes' and 'genotypes' we shall hear much more later. Johannsen (1911) who invented the word 'gene', defines it as meaning a unit-factor, element or allelomorph in the gametes representing a character and 'demonstrated by modern Mendelian researches'. A 'genotype' is the sum of all the genes in a gamete or zygote. This definition of genotype really requires amplification, for it is understood by the specialists in 'pure lines' to mean the genes contained in the gametes of a 'pure line' only. The way in which a change in a 'pure line' can be effected is by a mutation, which would produce a new genotype.

Criticising the 'pure line' investigations, Harris (1911) made careful analyses of Roemer's data. He says:

> 'Roemer's data for "pure lines" in peas are the only passably satisfactory published series available.
>
> 'Roemer's data and conclusions have been accepted as perfectly valid by genotype specialists.
>
> 'He is, so far as I am aware, the only one who has put on record sufficient data for a critical test of his conclusions.'

With regard to the variations within the 'pure lines' of Roemer's peas, Harris goes on to say:

> 'The remarkable thing about these standard deviations is that in most cases the variability within the individual "pure lines" in 1909 is greater than that of a mixture of all the lines in 1908. The excess is very striking in some cases.
>
> 'Truly this is an anomalous state of affairs! Analysed by the best available statistical methods, Roemer's data certainly indicate that the lines studied are significantly differentiated. Pure line specialists dispense with any statistical analysis at all and accept the data as "a confirmation . . . of Johannsen's epoch-making investigations on beans." Yet if the differentiation in these lines be due to anything other than faulty experimental conditions, the observations described destroy entirely the value of Johannsen's theory by showing that herit-

able variations may occur in great numbers in the pure line.

'The differences observed within these lines and considered by him and other pure linists to be of genotypical value and a confirmation of Johannsen's results with beans are probably the result of faulty experimental conditions. If they are not, they go squarely against Johannsen's theory.'

These quotations are from the various conclusions derived from detailed analyses of Roemer's figures which are given in Harris's paper. Of course the heritable variations that occurred in great numbers in the 'pure lines' may have been mutations; but this interpretation of the observations, while clearing up one difficulty, adds one in another direction; for while a large number of individuals is required to provide data for accurate conclusions, the larger the number of individuals produced the greater will be the chance of mutations, which will complicate the results hopelessly, and must throw doubt upon the validity of the interpretation.

Another line of criticism is afforded by the results obtained by selective breeding.

Four strains of wheat have been selected for protein and oil content. (Winter, F., 1929.) The strains selected for high contents have increased 50·01 and 109·7 per cent respectively. Those selected for low content have decreased 23·26 and 67·87 per cent. All the increases and decreases have been very gradual without sudden changes. The low protein strain has varied but little in twenty years. And now comes the most interesting fact about this experiment. While the strains selected for high protein and oil contents show no signs of having reached their limit of increase, that selected for low oil content appears to have reached a physiological limit, for it produces a very large and increasing proportion of germless seeds, which of course means the extinction of the strain.

Wheat offers a peculiarly suitable subject for experiment on the 'pure line' genotype theory. In wheat, which is self-fertilising, it would seem that within a limited number of generations, each of these strains must have become a 'pure line', if it were not so when the experiment was begun. If any strain consisted of a mixture of more than one 'pure line', some of the offspring must be produced by the fusion of two gametes of the same genotype; they will in fact be 'pure line' or homozygous. (See p. 78.) Other offspring will be produced by the fusion of gametes that differ in their genotypical constitution. These will be heterozygous. Only some of the seeds were allowed to develop in these selection experiments, which must hasten the process of producing pure lines, for while the homozygous plants will produce nothing but homozygous seeds, that is a 'pure line', the heterozygous will go on producing homozygous and heterozygous. The process must end by all being homozygous, that is 'pure line'.

Unless we assume a series of mutations in the same direction, these results are not compatible with the conception of limited non-inherited variations within a 'pure line'. The differences are too great.

Another difficulty also arises. As these wheat experiments indicate, it seems probable that there is a physiological limit to which any character can possibly be developed in relation to the organism as a whole. It is highly improbable by any means of selection, including the Mendelian selection of mutations, that a race of poultry could be produced of which the hens would lay six eggs a day all the year round. We have no data to go upon at present that indicate anything with regard to the physiological limit of development of particular characters beyond a few suggestions such as that provided by Winter's results from wheat.

A series of experiments carried out some years ago (Walker, 1912 and 1923) seem to have some bearing upon this subject.

Certain cancers in mice when grafted into other mice will grow in the new host as definitely circumscribed tumours. Other mice may be grafted from these transplanted tumours, and the process may be carried on indefinitely through an unlimited series of new hosts. There are existing strains of tumours that have been carried on through successive batches of mice, for more than twenty years, though the life of a mouse is only about three. If a number of mice be grafted with minute portions of a tumour, the cells of the tumours developed from the grafts are derived from the cells composing the graft—they are direct descendants of the cells forming the graft. It was desirable to find out whether variations in the rate of growth in these grafted tumours might be influenced by selection, so 20 mice were grafted from the same part of a tumour making the grafts as nearly as possible the same size. At the end of two weeks 20 more mice were grafted from that mouse in which the original graft had grown largest. This is batch B. At the end of another four weeks that tumour which had grown largest among batch B was grafted into 20 more mice and so the experiment continued the series up to five, selecting the most quickly growing tumour from each fresh batch of mice. From the original batch after twelve weeks, the smallest tumour was selected, 20 mice were grafted from that, and the process was repeated as had been done with the other batches, but after an interval of six weeks, choosing the slowest growing tumour. The result is shown on the accompanying

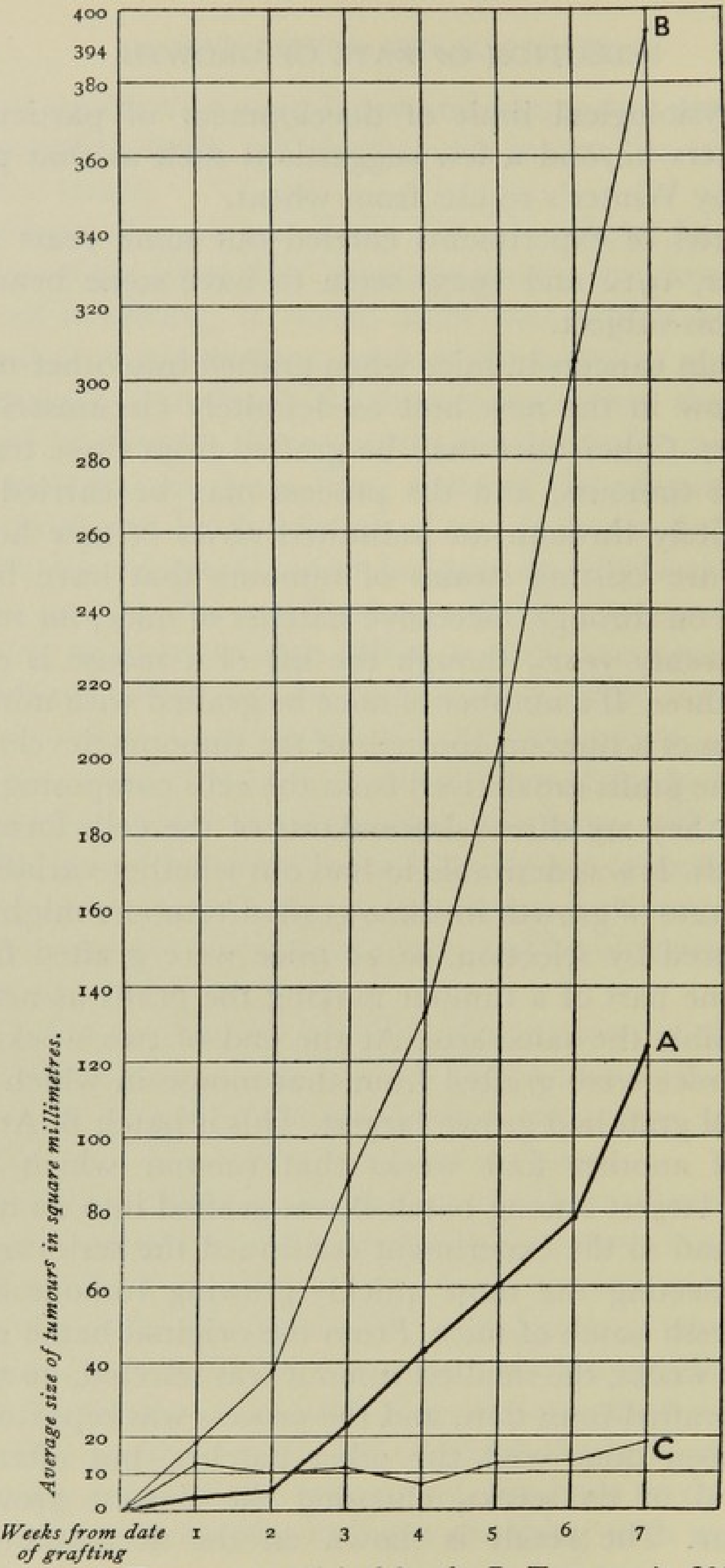


FIG. 19.—A. Tumours in original batch; B. Tumours in fifth batch selected successively from A; C. Tumours in second batch selected successively from A.

graph. The mean size of the tumours in 3 batches is shown. It must be realised that these figures do not represent anything like the real bulk of the tumours, for it was possible to measure them only in two dimensions. Actually the bulk must have been something more nearly the square of the figures than the figures themselves. Only the original, the quickest and the slowest growing batches are shown here though the curves for all the 7 batches were given in the original paper and these were intermediate. Now although there are obvious possibilities of error in these results, the huge difference between the rates of growth attained by the two final strains is sufficient to justify the conclusion that selection had produced a very large change indeed in this character. There can be no question of crossing, for the growth was due to the multiplication of pre-existing cells without any fertilisation. It does not seem likely that there can have been genotypes among the cells of the original graft that differed so widely in the character selected as to account for the results attained in so short a time. The only alternative is to assume a number of very large and rapidly succeeding mutations in the same direction, and this does not seem probable. Moreover, these experiments were undertaken to test the accuracy of another series of experiments which were interpreted as showing that there was a rhythm in the rate of growth of these grafted mouse tumours in succeeding batches. (Bashford, 1911.) If the usual course of events was a periodic gentle increase and decrease in the rate of growth, it seems obvious that the results were due to selection, and a rapid series of large mutations does not seem very probable. The graph shows no sign of anything of the kind.

While importance must be attached to the 'pure line' investigations, the results do not appear to justify the very dogmatic statements that are made about them. Only sufficient of the evidence against the unqualified acceptance of the theories that have been founded upon them is given to suggest that, when we have a larger number of data at our disposal, these theories may require some modification.

The obvious certainty of there being a physiological limit to the development of any character by itself, apart from the rest of the characters of the organism, in view of the available evidence, is very significant. It seems probable that the accumulation of fluctuating variations by selection, may develop a character up to its physiological limit. Mutations can do no more. Thus the same result may be produced, though more quickly, by a few steps, instead of by many.

Unless other characters change concomitantly the limit of development of any given character must be strictly defined. It seems possible, then, that *the fluctuating variation* may have played an important part in evolution.

# CHAPTER VIII

## The genotype hypothesis

REFERENCE was made in a previous chapter to the Genotype Hypothesis. It was impossible to deal with it in detail at that earlier stage, as it involves, is indeed the outcome of Mendelism and the pure line investigations. The hypothesis was originated by Johannsen, who invented the terms 'gene' and 'genotype'. He explained his views fully in a paper from which the following quotations are made. (Johannsen, 1911.)

Protesting against what he calls 'the transmission conception' of heredity, he says that:

> 'The students of this science have again and again tried to conceive or explain the presumed transmission of general or peculiar characters and qualities inherited from parents or remote ancestors.
>
> 'The *personal qualities* of any individual organism do not at all cause the qualities of its offspring; but the qualities of both ancestor and descendant are quite in the same manner determined by the nature of the "sexual substances"—*i.e.* the gametes—from which they have developed. Personal qualities are then the *reactions of the gametes* to form a zygote; but the nature of the gametes is not determined by the personal qualities of the parents or ancestors in question . . . the transmission conception of heredity represents exactly the reverse of the real facts.
>
> 'Weismann has furthermore built up an elaborate hypothesis of heredity, suggesting that discrete particles of the chromosomes are "bearers" of special organising functions in the mechanism of autogenesis, a chromatin particle in the nucleus of a gamete being in some way

the representative of an organ or a group of tissues.

'These two ideas: that "elements" in the zygote correspond to *special organs* and that *discrete particles of the chromosomes* are "bearers" of special parts of the whole inheritance in question are neither corollaries of, nor premises for, the stirp—(Galton) or genotype conception. Those special ideas may have some interest as expressions of the searching mind, but they have no support in experience; the first of them is evidently erroneous, the second a purely speculative morphological view of heredity without any suggestive value.'

Believing that new words to express ideas similar to, but differing in some ways from those previously held, would help to dissociate the mind from the 'transmission' conception, Johannsen proposed and defined, among others, the following:

' "The Genes" are the "unit-factors", "elements" or "allelomorphs" in the gametes, demonstrated by modern Mendelian researches.

'A genotype is the sum total of all the "genes" in a gamete or zygote.'

Johannsen is quite familiar with the Mendelian hypotheses, but nevertheless he goes on:

'Hence the talk of "genes" for any particular character ought to be omitted, even in cases where no danger of confusion seems to exist. So, as to the classical cases of peas, it is not correct to speak of the gene—or genes—for "yellow" in the cotyledons or for their "wrinkles",—yellow colour and wrinkled shape being only reactions of factors that may have many other effects in the pea-plants. It should be a principle of Mendelian workers to minimise the number of different genes as much as possible.'

And again:

> 'The question of *chromosomes* as the presumed bearers of hereditary qualities seems to be an idle one. I am not able to see any reason for localizing "the factors of heredity" (*i.e.* the genotypical constitution) in the nucleus.'

It is difficult to grasp the meaning of these statements, all in the same paper. His own definition of a 'gene' implies that it is a discrete entity; he calls it a 'unit-factor', and yet in other passages he seems to repudiate this idea with horror.

If the genes are really there, it is difficult to see any legitimate means by which their number could be minimised. There seems to be a suggestion that they are being imagined quite unnecessarily. In any case it is difficult to see how the mere number of the genes can affect the validity of the hypothesis.

Apart from the 'gene' idea, there is nothing in this beyond what has been said about potentialities in the gametes or germ-plasm. The idea of potentialities is old, for von Nägeli (1884) postulated a substance he called 'idioplasm', which is different in every kind of animal and plant, and he attributed to the intrinsic differences in the idioplasm of different kinds of organisms the difference in the characters that appear in them. It is, in fact, supposed to regulate the process of development and the lines along which development will go.

The conception of potentialities as put forward earlier in this book seems a natural evolution of von Nägeli's idioplasm theory and has been developed by many. (*E.g.* Archdall Reid, 1905–10; C. Walker, 1910–13.)

Morgan (1924) in discussing the genotype hypothesis says :

> 'The characters that are inherited must be supposed to be due to the interaction of a large number of

hereditary units. In other words the character is to be considered as a whole rather than as a unit.'

He then discusses the occurrence of a mutation and points out that many parts of the organism may be affected at the same time, but that only a 'visible' difference may be chosen for observation, and goes on:

> 'Since it is manifestly impossible to take account of all the differences between the old and the new types, and since the differences are often more marked in one part of the body than in another, it is customary to use a conspicuous character as the symbol of the change in the germ material, and to baptize the new organism (either in Latin or the vernacular) with the name of this particular character. It is this procedure that is responsible for the much-abused expression unit-character—a term well suited to express the contrast between the old and the new type of character, but entirely misleading if it is taken to imply that the character is the sole product of a single element in the germ material. To what extent there is in addition to the general effects of each gene a more pronounced specific effect is illustrated by those cases in which more than one change has taken place in the same locus. At present there are several cases of this sort known. Thus there are ten different eye colours in *Drosophila*, each due to a change in the white locus. . . . In fact it has been found that when a locus changes it affects the same organ in the same direction.'

A locus, as used here, means one must presume an area or group of genes in a chromosome or a gamete.

To continue the quotation:

> 'Furthermore each organ or character is the end result of the action of many genes. In fact, each part may be said to be the end product of all the genes—each one contributing something to it at one or many states of its development.'

The following quotations are from the same paper:

> 'The occurrence of free assortment makes it necessary to assume that the germ material consists of independent units. This can only mean that those elements in the germ-cells standing for the characters of the individual behave as independent units or elements.'

In the same paper still, it is explained how unit-factors or genes represent characters, including eye-colours, different shaped wings, body markings, and other variations of the same order, and how these genes are in pairs, are linked in groups, are arranged in regular linear order in relation to each other, and at relatively greater or less distances from each other in these lines. Sometimes it seems to be implied that a character can only be represented by a number of genes or the whole of the genes, and then a character is in a locus or is an organ. At other times it is the colour of the eye and represented by a unit-factor. Even the following does not make things clearer:

> 'It may also be well to point out that even if the whole germ-plasm—the sum of all the genes—acts in the formation of every detail of the body, still, evidence from heredity shows that this same material becomes segregated into two parts during the maturation of the egg and the sperm, and that at this time individual elements separate from each other largely independently of the other pairs of elements. It is in this sense, and in this sense only, that we are justified in speaking of the particulate composition of the germ-plasm and of particulate inheritance.' (Morgan, 1919.)

Johannsen made some further statements about the genotype hypothesis in 1923.

> 'It was undoubtedly a step forward to leave the notion

of unit-parts in favour of the notion of unit-characters. Now this notion too is absolutely untenable.

> 'From a physiological or a chemico-biological standpoint we must *a priori* in characters or developed parts of organisms see *Reactions* of the (I should say genotypical) constitution belonging to the zygote in question; and from this point of view *there are no unit characters at all*.'

He goes on later in the same paper to say that we have to deal:

> 'with such genotypical units as are separable, be it independently or in a more or less mutual linkage. Certainly by far the most comprehensive and most decisive part of the whole genotype does not seem to be able to segregate in units; and as yet we are mostly operating with "characters" which are rather superficial in comparison with the fundamental specific or generic nature of the organism.
>
> 'Personally I believe in a great central "something" as yet not divisible into separate factors.'

But before he concluded this paper he felt obliged to return to the Mendelian results and deal with them, thus:

> 'Disregarding this (perhaps only provisional?) central "something" we should consider the numerous genes, which have been segregated, combined or linked in our modern genetic work.
>
> 'From a physiological standpoint we may prefer to regard local conditions (say "chemisms"), in or on the chromosomes as responsible for those units.'

Now it seems, according to the creator of the genotype hypothesis, that from one point of view the germ-plasm must be made up of independent units, factors or genes; but that from another point of view it is not made up of them, but of a substance which is generally capable of producing all the characters. If all the genes are instrumental in causing the appearance of every character, then it seems unnecessary to assume the existence of any at all if we have a substance possessing general potentialities that meet the requirements of the case. If on the other hand individual genes determine the colour of an eye or a flower, or whether a seed is to be wrinkled or smooth, and all other characters of the same order are controlled by individual genes, unit-factors or elements, and it is only in the presence of a particular gene that a particular character will appear, then it seems necessary to assume that the germ-plasm is made up of, or at any rate contains, a number of units with very different properties.

Another supporter of the genotype hypothesis sums up as follows:

> 'The fundamentals of genetics to date are, I take it, the laws of segregation, independent assortment and linkage; the proof that the chromosomes carry the genes and that the genes are arranged in linear order; . . . the individuality of the chromosomes . . . the normal chromosomal determination of sex.' . . . (Huxley, J., 1927.)

The conclusion of another of its supporters is that 'it is nothing but a corollary to that part of Weismannism which was already accepted.' (East, 1911.)

On the one hand is the preformationist theory, which originally postulated that, for all practical purposes, an egg contained a little hen perfect in all its parts, this little hen contained little eggs, each of which in turn contained more little hens with more little eggs inside them, and so on to infinity. More recent and more complicated and obscure modifications of this theory, though not so obviously absurd, come to very much the same thing if followed to their bitter ends.

On the other hand are the results of the Mendelian experiments, which seem to demand the presence of discrete particles of matter in the chromosomes which are capable of producing very definite and independent, often opposing results, and which, though placed in a regular order and at various distances in relation to each other, may and do at times change their positions and relations to each other in ways that can be foretold with considerable accuracy.

However many genes are assumed for each character, if they are to produce Mendelian results, they must act as independent units; it matters not at all whether these units are composed of one or many parts, nor that they may produce other results besides those observed. Even suppose, as a last resort, a non-material, metaphysical power be postulated, this power must be made up of different independent entities that produce different results. But this is clearly preformationism, or something indistinguishable from it, and no suggestion of anything like the preformation theory is to be considered for a moment by the genotypist, as we have seen from the preceding quotations.

Johannsen, in the quotations given from his last summing up of the genotype hypothesis, implies, though he does not actually say so, that he believes there are two kinds of characters. Those forming the larger of the groups are not represented by unit-factors, but appear in all individuals, being dependent upon a 'great central something'. The other group consists of superficial differences, and these alone are represented by unit-factors.

It has been suggested that the Mendelian characters might be represented by 'entities' in the chromosomes, but that the characters common to all the individuals of a race were probably not so represented. (Walker, 1907.) The further development of this view divides the characters appearing in an individual organism into 'racial' and 'individual.' (Walker, 1910.) Correns later suggested that 'specific' characters were not Mendelian in their behaviour. Since then several writers have stated that only 'individual' characters are Mendelian in their behaviour in breeding experiments.

It seems probable that as the chromosomes provide the only mechanism in the cell corresponding with Mendelian inheritance, the Mendelian characters are represented in them. The rest are represented by the rest of the cell (Johannsen's *Great Central Something*).

# CHAPTER IX

Similarities between living organisms
Genes as factors in heredity · Merging of species
Physical objections to genes
Function of the cytoplasm in heredity

In Chapter I the meaning of the term 'Character' was dealt with at some length. It is clear that, if we accept the term as applicable to large differences between considerable groups of organisms, an indefinite number of smaller differences may be superimposed upon the larger. It is also evident that there is an insensible gradation between the largest and smallest observable difference, that is between such characters as the presence of eyes and the colour of the iris in man.

Hitherto it has been necessary to emphasise the fact that all organisms and parts of organisms, even to the single cell, always differ from each other. But there is also a constant similarity, not only between organisms of a like kind, but between those that are related, not even very nearly. Roughly speaking, the points of difference are confined to details, while the similarity is between the general form and arrangement of the parts in relation to each other. This similarity, like the difference, is found to extend to the smallest parts, down to the single cell.

Take the whole of the characters of man, the organism with which we are most familiar. It is not necessary to consider those he possesses in common with other animals lower in the scale than mammals, though they are very numerous. Among the characters common to man and all other mammals, but not to other vertebrates, are the special modifications which provide for the feeding of the young after birth; hairs upon the skin; sweat and sebaceous glands; a peculiar formation of the skull; skeleton generally, and brain; a particular form of red blood corpuscle; and the separation of the body cavity into two large compartments by the diaphragm which provides an addition to the breathing apparatus not found in other animals. The points of similarity extend to very many other characters too numerous to mention even if several volumes of this size were devoted to the subject. The shapes and functions of the various organs are very similar, and the minute structure is often so alike that it would be difficult or impossible to say whether a microscopic preparation was taken from a man, a dog, a monkey, an elephant or a mouse. The similarity extends even to the particular forms of the cells in corresponding organs and tissues. When we come to the animals nearest to man we find that the bulk of the characters are common to both. The arm of a chimpanzee has been used for teaching purposes when human material was not available. It is so much like the human that there is no difficulty in demonstrating even such structures as the small branches of the nerves and blood vessels; indeed, in some points, it can hardly be distinguished from a human arm. It must be remembered that in human anatomy what are comparatively minute structures are described in detail and are well known. Compared with the points of resemblance, the points of difference between man and the existing higher apes are small and few. The differences between the different races of men are smaller and fewer. The conclusion seems inevitable, if we accept any kind of evolution. The overwhelming bulk of man's physical characters come to him, through countless generations, from some pre-human ancestor, and they have remained constant throughout these generations with but comparatively slight modifications.

The individual, in fact, begins its existence with a certain stock of potential characters. The bulk of these are derived from remote ancestors. A smaller proportion come from less remote ancestors, a few from nearer progenitors and a minute proportion from individual variations which are, so to speak, its own personal property.

Mendelians would have us believe that the most usual if not the only form of inheritance is alternative and dependent upon unit-factors.

> 'Alternative inheritance which is the most usual form of heredity.' (Gates, 1929.)
>
> 'The hereditary constitution of at least all higher organisms consists of a number of units (factors or genes), each of which may exist in a number of forms (Allelomorphs); these genes exist in definite proportions, and are arranged in definite order; the whole gene complex is divided up amongst the separate chromosomes.' (Huxley, J., 1927.)

It is possible that in following the behaviour of what are really small more or less individual differences the Mendelian school has so lost sight of the bulk of the characters of the organisms studied that these comparatively slight differences are treated as though they were the only characters of importance. The continual contemplation of these comparatively unimportant differences seems to have monopolised attention to the exclusion of the larger issues.

This similarity and uniform reappearance of the great bulk of characters in large groups of organisms does not seem compatible with alternative inheritance as a universal phenomenon. It does not really matter whether we postulate a large or small group of genes, even a 'chemism' or a 'locus' or a single gene as being the cause of the reappearance of a given character; if *all* characters are represented by units we come to something like preformation.

If alternative inheritance be the rule we ought to find, not occasionally, but generally, races of organisms separated by sharply defined differences, more particularly if the mutation hypothesis be accepted. The realisation of this may have led to the following statements:

> '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 leap in which either a single character or a whole set of characters together become changed.' (Lock, 1906.)
>
> 'The theory of mutation assumes that new species and varieties are produced from existing forms by sudden leaps.' (de Vries, 1905.)
>
> 'We see all organised nature arranged in a discontinuous series of groups differing from each other by differences which are specific.' (Bateson, 1894.)

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 quotations express this feeling very strongly:

> 'It is the discontinuity which strikes Bateson and those who 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.' (Poulton, 1908.)

'Whoever studies the distinctions of geographical varieties closely and extensively will smile at the conception of the origin of species *per saltum.*' (Rothschild and Jordan, 1903.)

The character of size is inherited, and in many cases that have been investigated does not appear to be inherited alternatively. Stock-breeders' experiences have shown that it may be increased by selection. Mendel's own experiments showed that size of the plants, in his peas at any rate, was inherited in an alternative manner, But this is not true apparently with regard to size in all cases. Summing up the results of experiments in breeding, Castle (1922) says:

> 'The genetic agencies affecting size in rabbits are general in their action, influencing in the same general direction all parts of the body.'

Elsewhere Castle (1923) questions whether size is dependent upon genes, as, when crossed, this character blends.

Another set of experiments with the Californian deer-mouse (Summer and Huestis, 1921) were of a more elaborate nature. The differences between the lower jaws, the thighs and the pelvic bones on the right and left sides were measured and it was found that these differences were not inherited.

In criticising Castle's results with rabbits, Gates (1929) interprets them as indicating multiple growth factors influencing the various parts of the body, or, failing this explanation, general growth factors. Un-satisfactory as this interpretation is, for if factors are to be assumed in this unrestrained fashion the Mendelian theory becomes ridiculous, it does not seem applicable to the deer-mice.

There is a physical objection to the supposition that *all* the characters appearing in the organism can be represented by unit-factors which are contained in the chromosomes, and unless they are contained in the chromosomes, alternative inheritance, segregation and independent assortment are difficult or impossible to explain. The maximum number of chromosomes attributed to man by any authority is 48. Probably ·002 of a millimetre is a liberal estimate for the average length of these chromosomes. This allows a total chromosome length of ·096 of a millimetre. No Mendelian would claim that the unit-factor is represented by anything smaller than a molecule of protoplasm. It would be difficult to conceive anything less than a molecule undergoing segregation and free assortment, and being arranged in rows. Indeed it is implied by some authorities that the particles of chromatin visible with the aid of the microscope are these unit-factors, for they are arranged in linear order and at different distances from each other as is required by the most recent Mendelian hypotheses. (*E.g.* McClung, 1924, and others later.) Even if we set aside all question of distances between the unit-factors and disregard the fact that the molecules are almost certainly very irregular in shape, I do not find room for a sufficient number to be packed in linear order in the chromosomes. This is supposing that there is only one pair of genes for each character, and as we have seen, the most authoritative interpretations require a great many for each character. True, the pairs are facing each other, so that we can reckon the length required for each character as only that of the single molecule arranged in a row with others. Probably ·00006 of a millimetre is a conservative estimate for the space required by so complex a molecule as that of protoplasm. This gives room for 16,000 molecules in a row in all the chromosomes of man.

It is probably impossible to obtain anything near a correct estimate of the number of characters in man, but it is possible to show that there must be very many more than 16,000. It is stated definitely (Macalister, 1889) that over 14,800 names are used in the anatomy of the human subject. Of course some of these are probably in a sense duplicated. For instance, femur, the thigh-bone, is one word. But there is a large number of names attached to various parts of the femur and these are all characters. Since this statement was made, many unnamed structures in the body have been found to be of importance, some have been given names, and doubtless more will be added in the future. On the whole it is certain that this number, 16,000, does not exceed the number of characters visible to the naked eye, that had been described in the human body up to 1889. Moreover, many structures that are described in all books of anatomy and are well recognised, have not received special names. For example many branches of arteries and nerves to various structures have no special names. It would appear then, that there is hardly room in chromosomes for enough units to represent only anatomical characters visible to the naked eye. Other units governing such characters as colour of skin, hair, eyes; hairiness or smoothness of various parts of the body, growth, size and so on must be provided for. Even then we have still to include the functional, mental and microscopic characters, the latter being very definite and very numerous. Thus even taking a minimum estimate of the units necessary for entirely alternative inheritance, giving them only molecular size and packing them tightly without any spaces between them, there is not room for them in the chromosomes in the case of the man. Therefore it appears that alternative inheritance for all characters is highly improbable, for unless units representing characters are carried by the chromosomes, it is difficult to see how this could happen.

The physical difficulties do not end here. As already stated, several cytologists claim that the granules of chromatin, being arranged in an appropriate manner, probably represent the actual unit-factors or genes. Unfortunately for this view, the mass of chromatin in the gametogenic cells frequently doubles or even quadruples in volume in a period to be reckoned by minutes rather than hours, during the prophase of the reduction division. There is indeed something to be said for the view that the chromatin is only a secretion of the linin which apparently generally encloses it, and much against any granules having more than a brief individual existence.

It is even doubtful whether the granular structure of the chromatin exists at all in the living cell. All the observations upon which the granular structure of chromatin has been assumed have been made upon material specially prepared for microscopical examination. The first step in this process of preparation is what is known as 'fixation'. A small piece of material is placed in a fluid made up of various chemical reagents which kill and precipitate or coagulate the cells very rapidly, with the object of fixing them in the actual state in which they were when dropped into the fluid, the mixture being such as to produce as little change as possible in the cells.

Now it is impossible, owing to mechanical and optical difficulties which have at present not been overcome, to examine living cells when in the act of dividing, with sufficiently good definition and enough magnification to see any minute structure in the chromosomes or even in the nucleus before division, so we cannot be sure whether the structure of the chromatin is or is not granular in the living cell. But we do know that in fixed material the chromatin in similar cells, fixed in the same way but in different states of activity, is sometimes granular and sometimes not; that we can produce a more or less granular appearance according to our methods; and that we can produce or not just this granular appearance or not in films of artificial mixtures containing egg-white or gelatine and other suitable substances at will, by using exactly the same methods as we use for fixing living cells. Only fixed material can be used for examining the minute details of structures in cells, so it is evident that such structures should be regarded with the greatest caution. It does not seem that any very definite statements with regard to the functions of granules of chromatin are justified.

Godlewski (1906) fertilised the eggs of a sea-urchin, from which the nuclei had been removed, with the sperms of a Crinoid (sea-lily). In this case it is quite clear that the only chromosomes present were those derived from the male parent, yet the earlier stages of the embryo showed maternal character only. Similar results have been recorded by other observers.

It seems to be the general rule that when two different species are crossed, the earlier stages of development are purely maternal in character. (Loeb, 1916, and others.) Moreover, the rapidity of growth, which is so marked a character in some cases as to distinguish one species from the other, is always that of the mother. (Dreisch, 1903; Boveri, 1903.) If portions of the ovum are removed before segmentation begins, definite parts of the body are missing when development takes place, which shows clearly that the groundwork or basis of the characters contained in those parts of the organism were dependent upon that particular part of the ovum. (Fischer, 1903; Wilson, 1904.)

These results have been confirmed by other observers, and are so generally accepted by biologists that it is quite unnecessary to give any further authorities, but it *is* necessary to make quite clear what they mean. The general characters of the individual must depend to a considerable extent upon these early stages of development, and in some cases, at any rate, the characters of the adult organism must depend upon the presence of certain parts, not of the nucleus, but of the cytoplasm of the ovum. It has been shown in many cases that it is not until the later stages of development that the chromosomes begin to exercise a decided influence. The result of the removal of certain parts of the cytoplasm of the ovum before segmentation in those organisms in which the experiment has been performed is that certain parts of the body are missing when development is completed. Yet all the chromosomes, both paternal and maternal, were there. A general view of the evidence seems to suggest that there are some other potentialities of the two cells whose union originates an organism, besides those contained in the chromosomes, determining the characters that it will eventually possess. And it also seems probable that the characters that depend upon the presence of the chromosomes are comparatively lesser differences, superimposed upon more general characters.

There is evidence suggesting that there are some other constituents of the cell that may play a part in heredity.

In the cytoplasm of all cells are found many small bodies known as *mitochondria* or *chondriosomes*. These can only be shown in fixed microscopical specimens when little or no acid is used in the process of preparation. It has been suggested that this fact is against the probability of their presence in the living cell, but recent work with living cells suggests that they may be definite bodies which, when fixed, are soluble in an excess of acid. As seen in the living cell they are described as in constant movement and changing in shape from moment to moment. (Lewis, 1915.) It is of course possible that they are simply collections of lipins (fat-like substances), not soluble in the surrounding aqueous material, but there is some justification for the claims made as to their function. There is considerable evidence that the chondriosomes divide individually and are distributed to the daughter cells equally in the case of some organisms, but in other cases this apparently does not happen. (Benda, 1903; Meves, 1907–8; Duesberg, 1907–19.)

It has been suggested by these authors that the chondriosomes represent a mechanism of cytoplasmic heredity comparable in importance with that represented by the chromosomes.

# CHAPTER X

Units representing Mendelian characters
Selection of variability · Comparison between wild and domesticated races in crossing experiments
Blending of characters

TURNING to the Mendelian characters, the evidence that these must be represented by units or entities of some kind somewhere in the cell seems irresistible. Take one as an example—the white eyes in *Drosophila*. Call it a character, part of a character, an 'end result', what you will; say that it is represented by part of a gene, a gene, a group of genes, all the genes, a 'locus'; or a 'chemism'; you must still assume an individual entity or a specially differentiated part of something, which comes to the same thing; something which acts independently among other entities possessing the same sort of independence. It may be a particle of matter or an individual collection of energy, but it could not segregate or be subject to independent assortment unless it were an entity, discrete and separable from other entities of a like nature which influence other characters. Still less could it be one among a number arranged in a row and having definite spatial relations to each other. No verbal gymnastics or the most subtle of arguments can show that the manner in which these differences in character are inherited is due to a general property or power of the germ-plasm, unless the whole Mendelian position is abandoned.

Loeb (1916) suggested that as the chromosomes in all the cells of the body are identical, a factor for an enzyme (fermen)—

'is contained in every cell throughout the whole body. It is likely, however, that the same factor (which we may conceive to be a definite chemical compound) will find a different chemical substrate to work on in the cells of different organs of the body, since the different organs differ in their chemical composition.'

This seems to shift the 'unit' difference away from the chromosomes. On this hypothesis the chromosomes carry a general factor which acts upon unit differences or factors in the 'substrate' in various parts of the body, these having been derived in an alternative manner, undergoing segregation and assortment during the process, from the germ-cells. The difficulty is even greater, for apart from the chromosomes we have no alternative mechanism of distribution.

The Mendelian characters have certain features in common, besides their behaviour in breeding experiments, that are well worth considering. The majority of those that have come under observation have been in domesticated animals and plants. They are all in a sense unimportant—small—characters. Some may be very striking and noticeable to the eye, but they would not, under conditions of domestication, be in themselves beneficial or the reverse to any considerable extent to the individual in which they occur. An example will make this clear. An albino rabbit might occur under wild conditions, but its chance of survival, owing to its conspicuousness alone, would be poor compared to its normally coloured companions, and so would be that of its descendants if they inherited its albinism. But under domestication, the albinism would become an advantageous variation if man wished to preserve it. All the Mendelian characters seem to be comparatively unimportant individual differences in this sense.

The differences that obey the Mendelian laws are those in closely related organisms. It has been found possible, by altering certain factors in the environment, to fertilise the eggs of a species with the sperms of widely separated species. In these cases, the embryos generally die at an early stage of development. On the other hand, in crossing between closely related species the individuals often survive and the majority reach maturity. (Loeb and others, 1916.) There is just as much reason to suppose that the former result is due to the fact that the chemical or physical properties of the two organisms are so dissimilar that they will not mix as to postulate special Mendelian factors, lethal genes.

The fact that the majority of the Mendelian characters have been observed in domesticated races is of considerable importance. It was pointed out twenty-five years ago (Walker, 1910) that many of the characters of domesticated races must be of comparatively recent origin, and that in the process of domestication man must, quite unintentionally, have selected variability; some would now call it a tendency to produce mutations. A better example could not be found than the long-suffering vinegar-fly, *Drosophila*. Only a fortnight is required for each generation, and as thousands of generations of this fly have been bred, huge numbers been produced and variations selected by many investigators during the past twenty years, it is not surprising that a high degree of mutability has been reached in some of the strains. The evening primrose (*Oenothera lamarckiana*), upon breeding experiments with which de Vries founded the Mutation Hypothesis, is a domesticated plant, and he found that in it mutations were common. He did not find a single instance of a mutation among the wild plants he investigated at about the time he was conducting his experiments with *Oenothera*. Large variations do not seem to be frequent in wild races as a rule, and when they do occur there is little evidence that they are usually perpetuated. The only case recorded of large variations being very frequent in a wild race is *Aurelia aurita*, a common jelly-fish. These 'sports' as they were then called, were first recorded by Ehrenberg in 1835, since when his observations have been confirmed by several writers. Brown (1895) by examining large numbers of the young and adult animals, showed that the unusual forms, that is those in which large variations had occurred, seemed just as capable of surviving when kept under observation as the normal individuals. 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 has been established. *Aurelia* cannot be bred in captivity, and so successive generations cannot be kept under observation. But it seems reasonable to conclude that, as the average characters of the species remain the same in spite of these very frequent mutations, any considerable deviation from the mean is eliminated.

As soon, however, as a strain or race of organism is bred in captivity, man is able to pick out considerable differences when they appear, and to preserve them. He will not be able to select small differences as a rule, for he will not see them. Every time he selects a considerable difference, he is unconsciously selecting the tendency to produce considerable variations, mutations in fact.

Several interpretations have been suggested for the great variability of domesticated races, but this one, which has been suggested already (Walker, 1910 and 1913) seems to be as simple as any, and to be in accord with the evidence. Take even the most inbred stocks that are said to breed quite true. Look at the pedigrees. The same individuals appear constantly as ancestors in the pedigrees of different descendants. This means that only those individuals have been used for breeding purposes who exhibited the desired variation; what is more important, there were comparatively few such individuals produced. Then, if in such a pedigree we look at characters which were not the object of selection, such as colour in racehorses, we find such variations common as are rarely or never found in wild animals. The capacity for producing large variations has been selected as well as the particular characters it was desired to increase.

It does not seem unreasonable to believe that the very considerable differences in characters produced in a comparatively short time by man's intervention in selecting and preserving mutations are different in constitution and quality to similar differences between wild races. A little reflection must force one to realise that the differences cannot have arisen by an exactly similar series of changes in the two cases. In the first case, the larger mutation had every chance of survival, and a very great change in a character may have been produced in a few or even one generation. On the other hand, a wild race is largely dependent for survival on being suitably adapted to its environment. A sudden and large change in any character would in most cases throw the individual out of harmony with its environment, and so lessen its chances of survival. The environment seems usually to change but slowly, so the change in characters in a wild race is probably also slow as a general rule. The differences in the individuals selected by the environment for survival would according to this view be small, and would soon be common to the whole race. These small variations may, when they first appear, be inherited according to the Mendelian laws, and it is probable that larger variations do not as a rule survive in nature, though they may occasionally be noticed by

Mendelian investigators and so preserved. This agrees with what we know about wild races, for though we find species or races merging into each other in many cases, in others there is a very sharp line of demarcation between them, indicating a comparatively remote relationship. The gradation between the two extremes in the former case is often such as to defy classification in groups.

Thus in the organism bred in captivity we have a character that has arisen as a variation within a comparatively few generations and which is inherited alternatively, segregates and is subject to assortment in breeding experiments. In the wild organism a similar character, say colour for example, may be the same in all members of the race, and remain constant throughout countless generations or change slowly with the environment. The Mendelian will agree that when the 'mutation' is crossed with the 'wild' character, it may give Mendelian results. This really means no more than that a variation occurring in a 'wild' animal may be inherited alternatively.

An experiment with two different races of a moth, *Acidalia virgularia* is very suggestive. (Prout and Bacot, 1909.) This moth is very widely distributed. Those found near London are dark. Those found at Hyères in the South of France are white. Individuals from these two strains or races, widely separated in space, probably also in time, were crossed. Ten generations were bred from this cross, giving between five and six thousand specimens. There was no segregation. The gradation in colour from that of one parent form to the other was so gentle that attempts to sort out the specimens into light and dark groups were impracticable. The converse experiments with moths were equally interesting. When local variants, that is single dark individuals appearing in a place where the general character was light, were crossed with the normal colour, the cross gave Mendelian results. (Bacot, 1906; Prout and Bacot, 1906–7.) For the first set of experiments a Mendelian might find an explanation satisfactory to himself, but it would require the assumption of a large number of genes with a number of different properties. In ten generations segregation should have appeared if it was to appear at all. The following words of real wisdom, coming as they do from the chief living exponent of Mendelism, are peculiarly apposite here:

> 'The danger of any appeal to a theory of representative particles obviously lies in the ease with which by its means any phenomenon might be accounted for, if the theoriser is allowed to endow the particles with any and all the attributes he wishes to use in his explanation.' (Morgan, 1924.)

With the second or converse experiments he will probably not quarrel.

Some recent experiments with plants seem to give somewhat similar results to those obtained by Prout and Bacot.

These plants (*Venidium* and *Arctotis*) were crossed, and particular attention was paid to the colour of the flowers. The author states that with the possible exception of the presence or absence of the perilla-purple patches at the base of the rays not one of the characters examined showed segregation. There was wide diversity in the variability of different generations, and the hybrids were less variable than the back crosses or hybrid crossed with hybrid. (Warren, 1931.)

> 'It is not', he says, 'worth while to attempt to force these results into a Mendelian frame by assuming the existence of lethal factors or of intensifying and diluting genes.'

Other experiments by the same author showed that the peloric condition (an abnormality) in foxgloves in the first and second generations shows typical segregation, but in subsequent generations the character becomes 'diluted' and a condition arises where the grouping of the plants is only possible by creating an entirely arbitrary criterion for 'peloric' and 'non-peloric' categories. The same results were obtained by crossing dwarf and straggling nasturtium.

Many believe that observation without experiment may lead to just as great discoveries as experiments, though the procedure is more difficult and tedious. Some recent observations seem of a nature likely, if followed up, to throw some light on the blending that occurred in the experiments just cited.

Two closely allied species of water-beetles, *Deronectes elegans* and *Deronectes depressus* are both found in the British Isles. They are distinguished from each other by size, shape, colour, tarsal claws and width of oedoeagus among other characters. Only *D. elegans* is found in the South of England. Both species with every grade between the two are found in the North of England and the South of Scotland. Only *D. depressus*, with some intermediates, is found in the North of Scotland and Ireland. (Balfour-Browne, 1930.)

The common whirligig beetle, *Gyrinus natator*, was found to include two species which had been confused, though different in size, colour, shape, punctuation and other characters. (Ochs, 1927.) One of these, the true *G. natator*, is found in the N.E. Palearctic region. The second, *G. substriatus*, is found in S.W. Europe. Both are found in Northern Europe. Of the common British form, *G. substriatus*, Omer Cooper (1930) described a variety found in Cambridgeshire, *G. substriatus* var. *fowleri*, which is an almost perfect link connecting *G. natator* and

*G. substriatus*. He has recently received a specimen of the true *G. natator* from Cumberland. His suggestion is that we here have cases of evolution actually in process.

The crosses between some of the *Salmonidae* are interesting. (For full references see Walker, 1910.) Crosses between the Salmon (*Salmo salar*), the Sea-trout (*S. trutta*) and the common trout (*S. fario*) are all fertile and the offspring have blended characters. I have examined many specimens where such characters as the number of vertebrae, the number of scales in the lateral line and the number of gill-rakers were intermediate. It is interesting to note that one of the greatest authorities on *Salmonidae* (Schmidt), does not allow these to be separate species, but only varieties. On the other hand, when more widely separated species are crossed, the progeny are not fertile. The cross between *Salvelinus fontanialis*, the American brook trout, and the common English trout produces sterile offspring, 75 per cent of which are deformed. Unfortunately the breeding of successive generations of these crosses to find out whether segregation occurs does not seem practicable; at best it would be very expensive and difficult.

The available evidence is very much one-sided, for nearly all breeding experiments have been made in order to demonstrate Mendelian inheritance, hardly any to show whether or not blending occurs.

There is, however, some indication in Mendelian literature that the results of the breeding experiments are not always to be accepted as quite so clear cut, so sharply defined, as its general tenor would lead the biassed or careless reader to believe.

There must be a temptation, doubtless not appreciated by the majority of those concerned with Mendelian experiments, to place all the individuals produced into one group or another. As they are not aware of the temptation, it is quite probable that many succumb to it without knowing that they have done so.

Sometimes when a very careful and scrupulous observer publishes his results something like the following may appear. In the account of some experiments with peas, the following note was made to the tables of figures giving the details of the fifth self-fertilised generation from the cross:

> '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*' (Darbishire, 1908).

The segregation of the fifth inbred generation should, theoretically, have been perfect. Here it obviously was not. It is difficult to believe that a man who was peculiarly punctilious as to the accuracy of his observations, and a few others like him, should have happened upon unique exceptions to a general rule. Probably these few cases are not very exceptional, judging by the following remark of a leading Mendelian (Morgan, 1919):

> 'The graded series of forms so often met with in experience and so often ignored or roughly classified by Mendelian workers.'

Writing of crosses between different breeds of poultry, Davenport (1906) says:

> '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.'

Two probabilities seem to be suggested by this evidence. Firstly, that differences in characters which would in nearly-related individuals behave as Mendelian characters do not so behave but blend in some cases when they are found in races widely separated by distance and where the difference must have existed for a long period of time. Secondly, even in domesticated races, the recent Mendelian characters frequently show a tendency to blend.

While it may be that none of the differences between what are apparently separate but related races or strains among domesticated animals have been long enough established to expect blending, something might be done in this direction. Crosses such as between a terrier and a spaniel might produce interesting results. Some of the different characters of these races of dogs, though produced through man's intervention, have been established for a long time, and it seems likely that experiments to ascertain whether any of them blend would advance our knowledge as much as endless experiments with the object of showing that all characters are Mendelian. 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'. Surely this cross offers a promising field for Mendelian investigation. The attempts to demonstrate segregation in crosses between different races of man are very unconvincing, and to them Morgan's remark, quoted above, is particularly applicable.

It is a pity that no experiments have been made with the deliberate object of testing the stability of the characters studied. Had for instance the white-eye and some other variations in eye colour in *Drosophila* been continually inbred and then crossed, it would at least have been possible to say whether, after twenty years and four or five hundred generations, there was any sign of blending. At present it is impossible to say this definitely, though it is open to the captious critic to suggest that some of the ten eye colours that have appeared in this insect may really be cases of partial blending.

Crosses between the water-beetles referred to above should not be difficult to obtain and breed. As there are already intermediate forms between *Deronectes elegans* and *D. depressus* and between *Gyrinus natator* and *G. substriatus*, they offer peculiarly suitable material for such experiments.

With regard to the assumption of 'lethal' genes considerable scepticism is permissible, for it is more probable that a failure to breed is due to an incompatibility of the two kinds of protoplasm.

# CHAPTER XI

Evidence against characters being represented in chromosomes
The chromosomes in some parasitic Protozoa
The connection between chromosomes and sex

So far the chromosomes have been treated as though there was no doubt as to their playing an important part in bringing about the reappearance of the characters of the parents in the offspring. Evidence has been produced suggesting that some other constituents of the cell, particularly of the ovum, may play an important part in heredity, and their function with regard to some characters has been admitted. It is, however, claimed that in case of some organisms the chromosomes have no share in the reappearance of characters from generation to generation.

The reader will remember that in the cycle of events preceding fertilisation the number of chromosomes is reduced to one half the usual number, and that there are, therefore, some generations of cells that possess only half the number of chromosomes peculiar to the particular species of organism. In the higher animals there are only two such generations, but in plants there may be an indefinite number.

This is the usual sequence of events, but there are some organisms in which the number of chromosomes peculiar to the somatic cells is the half or single number, while the full or double number is found only at the time fertilisation actually occurs, that is in the fertilised ovum. Reduction takes place at the first division of the fertilised ovum, so all the individuals of all the generations between two fertilisations contain only a single set of chromosomes. Those organisms whose nuclei possess only a single set of chromosomes are called 'haploid'; those with the double set are 'diploid'. In the organisms referred to above the usual condition is haploid, in the higher animals and plants it is diploid. In some plants part of the life history is haploid (prothallium of ferns), part diploid. In some animals (*e.g.* the honey-bee) the male is haploid and the female diploid.

The Sporozoa form a fairly large group of parasitic Protozoa. The following is an account of the life-cycle of one of these:

'*Aggregata eberthi* is a coccidian which has two different hosts and displays a very regular alternation of generations—sexual and asexual. Its sexual cycle—above the dotted line in the figure—occurs in a cuttlefish (*Sepia officinalis*), and its asexual cycle—below the dotted line—in a crab of the genus *Portunus* (several species). The cuttlefish gets infected by eating a crab containing young parasites or *merozoites* (A). These young forms penetrate into the cuttlefish's gut wall, where they develop into sexual parasites—*males* (C) or *females* (B). Each male produces (D) a large number of highly differentiated *microgametes* or spermatozoa (E), while each female gives rise to a single *macrogamete* or ovum (F). Fertilisation then occurs (G), in the usual way, by the fusion of one microgamete with one macrogamete. The resultant zygote (H), which is called a *sporont*, then undergoes division (J, K, L) into a large number of small spherical *spores* (M), in each of which three minute vermiform germs or *sporozoites* are ultimately formed.

'The ripe spores (M), which are incapable of further development in the cuttlefish, pass out of the intestine with the animal's excrement. If they are swallowed by a suitable crab (*Portunus*) they hatch in its gut, and each spore liberates its three contained sporozoites (N). These burrow into the wall of the crab's midgut—just as the merozoites did in the cuttlefish; but here they grow not into sexual individuals—males or females—but into asexual forms, or *schizonts* (O), each of which ultimately produces a large brood of young by a peculiar process

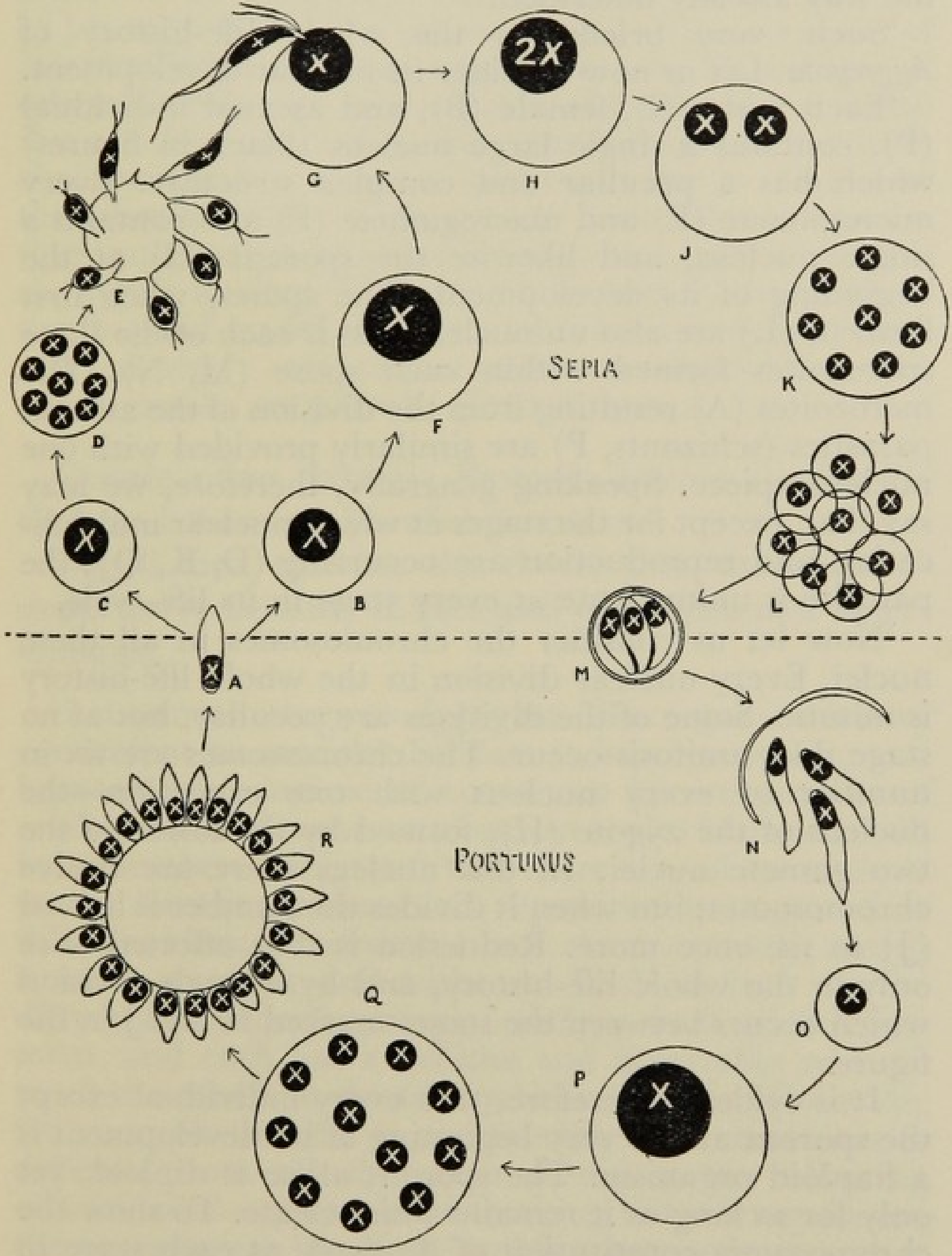


FIG. 20.—*After Dobell.*

of fission (P, Q, R). The young parasites so formed are the merozoites (A) with which our description began.

They can undergo no further development in the crab, but if it is eaten by a *Sepia* they develop in this host in the way already described.

'Such, very briefly, is the whole life-history of *Aggregata*. Let us now consider its nuclear development.

'Each male (C), female (B), and asexual individual (P), contains a single large nucleus (black in figures) which has a peculiar and complex structure. Every microgamete (E) and macrogamete (F) also contains a single nucleus, and likewise the sporant (H) at the beginning of its development. The spores, when first formed, (L) are also uninucleate, as is each of the three sporozoites formed within each spore (M, N). The merozoites (A) resulting from the division of the asexual parasites (schizonts, P) are similarly provided with one nucleus apiece. Speaking generally, therefore, we may say that, except for the stages at which nuclear multiplication and reproduction are occurring (D, K, Q), the parasite is uninucleate at every stage in its life-cycle.

'Now let us consider the chromosomes in all these nuclei. Every nuclear division in the whole life-history is mitotic. Some of the divisions are peculiar, but at no stage does amitosis occur. The chromosomes are six in number in every nucleus with one exception—the nucleus of the zygote (H), formed by the fusion of the two gamete nuclei. In this nucleus there are twelve chromosomes; but when it divides the number is halved (J) to six once more. Reduction is thus effected once only in the whole life-history, and by a single division which occurs between the stages marked H and J in the figure.

'It is evident, therefore, that every individual except the sporont at the very beginning of its development is a haploid organism. The sporont alone is diploid, yet only for so long as it remains uninucleate. To show the chromosomic constitution of *A. eberthi* at each stage in development I have marked all the nuclei in the figure with the conventional symbol X, denoting the haploid number. Stage H alone is 2 X, or diploid (X = 6).

'Now the six chromosomes which form the haploid complex of *A. eberthi* are differentiated among themselves, so that at suitable stages each individual chromosome can be recognised. One (*a*) is very large, and one (*f*) is very small. The others (*b, c, d, e*) form a series of intermediates. At some stages they are filamentar, at others globular, at others again of intermediate forms. But at every stage when they are distinguishable, each chromosome can be recognised by its size in relation to the other members of the group. Every chromosome is thus unpaired—a separate independent individual. But the zygote nucleus (H), which is formed by the fusion of two haploid nuclei, contains two chromosomes of each sort (2a, 2b, . . . 2f); so that at this one diploid stage the chromosomes are paired.' (Dobell, 1924.)

Certain other parasitic Protozoa have a similar life cycle and there are parallels in plants.

Dobell then criticises the theory that the chromosomes carry heredity factors and developmental determinants:

'Let us now return to *Aggregata*. This organism is very convenient to consider because it is polymorphic, and because every individual contains a known number of nuclei, whose chromosome content is also known. It will be remembered (Fig. 20) that there are—if we exclude young forms, gametes, and reproductive stages—four different kinds of individual in *A. eberthi*: namely, males, females, sporonts, and schizonts. Each of these can be distinguished by its structure and its mode of development, and each has a definite and invariable relation to all the others in the life-cycle as a whole. The male, for example, which is structurally and functionally different from all the other forms, is the offspring of a schizont and can beget nothing but microgametes; the sporont can produce nothing but spores; and so on.

'Let us now select a particular character and a particular chromosome, and consider their relations to one another. It is really immaterial which character or which chromosome we take; but for the sake of argument let us take sex[1] as the character to be studied, because this is easy to consider and because it is admittedly heritable, and happens to be the one on which the theory under discussion is largely founded (sex chromosomes of insects); and for our particular chromosome let us select *a*, the largest in the haploid complex of *A. eberthi*.

'Let us begin with the young parasite (sporozoite) just hatched from its spore (N). Every such young organism, which possesses only one *a* chromosome in its whole constitution, grows into an asexual individual (schizont). In this case, therefore, the presence of the chromosome is correlated with complete absence of sex in the organism possessing it.

'The asexual organism, when grown, produces (P, Q, R) a brood of young (merozoites)—each one of which receives a single *a* chromosome directly descended by division from that of its parent. Now these young individuals (A) grow into males or females (C, B), each containing likewise a single *a* chromosome in its nucleus. Consequently, the presence of this chromosome is at this stage completely correlated with the manifestation of sex by the organism possessing it. Furthermore, it is correlated equally with male sex and with female sex; that is to say, it occurs equally, without distinction, in individuals capable of producing microgametes (spermatozoa) or macrogametes (ova).

'When the male and female individuals form their respective gametes, every one of these receives alike a single *a* chromosome. In structure the microgametes differ vastly from the macrogametes; but in respect of their chromosomes all gametes are identical. Gametes have no sex, of course, though they are often miscalled "male" and "female" and consequently, we again reach a stage in the life-cycle at which the presence of an *a*

---

[1] By 'sex' I mean the faculty of producing gametes: by 'male' I mean an organism which produces microgametes (or their equivalent) and by 'female' one which produces macrogametes. I attach a concrete biological—not an abstract or mystical—meaning to these terms. (*Dobell*).

chromosome is correlated with complete absence of sex in its possessor.

'At fertilisation the two gametes fuse (G), and the zygote (H) so formed therefore contains two *a* chromosomes. The zygote becomes a sporont, and the two *a* chromosomes originally present in its nucleus separate at the first nuclear division (the reduction division) which it undergoes. But whether it possess a single nucleus with two *a* chromosomes, or many nuclei each containing one, it is always an asexual individual; and consequently we have again the presence of *a* chromosomes correlated with absence of sex in the organism which possesses them.

'Each spore formed by the sporont receives a single *a* chromosome; and each spore produces, by protoplasmic fission, three sporozoites, each containing also one *a* chromosome. Neither the spore nor the sporozoite is a sexual organism, and therefore in these stages again we have presence of the *a* chromosome correlated with absence of sex.

'It is thus clear that the presence of the chromosome *a* is not correlated with the character *sex* in *A. eberthi*; for it is equally present in males and females and in organisms without sex.

'Moreover it will be evident that we can conduct an exactly parallel argument with any other chromosome (*b*, *c*, *d*, *e* or *f*) and any other known character—structural or functional—of *A. eberthi*. We can, for example, substitute *b* or *c* for *a* in the foregoing paragraphs; or we could take the possession of flagella as our character. In this case, the microgamete alone is so characterised, and in it there is therefore complete correlation between this character and the presence of any selected chromosome—since it possesses all six; while in all other forms the same chromosome is present and the character absent.

'It therefore seems justifiable to conclude that in *Aggregata* there is no correlation whatsoever between the presence of any particular character and the possession of any particular chromosome. Consequently, no particular part or factor included in any chromosome can be said to be specially associated with—still less to "determine" in any legitimate sense of the word—the development or manifestation of any particular character by the organism possessing it. The chromosomes *may* contain such factors, of course; but in the absence of any concrete evidence that they do, speculation on the subject appears idle.

'In *Aggregata* we see great individual diversity associated with apparently complete identity of chromosomic constitution. From generation to generation the forms and functions of the animal change in an orderly sequence, while the chromosomes remain unchanged. They are the constants in a varied series of developmental stages. It is therefore obvious that if any internal "factor" in such a sequence of forms "determines" the manifestation of any particular bodily character at any stage, this factor must be somehow associated not with the chromosomes but with some extra-chromosomic constituent of the organism. The organism models itself and acts not because of its chromosomic components but in spite of them.

'As there is thus no reason whatsoever to suppose that any chromosome—or part of a chromosome—in *Aggregata* is correlated with or determines the manifestation of any character in the individual actually possessing it, it follows that there is no justification for the further supposition that the chromosomes are specially concerned in the hereditary transmission of any character from any individual to its progeny.

'It appears to me impossible, indeed, to make a plausible "chromosome theory of heredity" which will apply to *Aggregata*. We could, of course, make the supplementary stipulation that the factors, though contained in the chromosomes, are somehow activated or inhibited in successive generations. We might suppose, for example, that the factor for sex is contained in the *a* chromosome, but becomes operative in the sexual generations only—being held in abeyance during the rest of the life-cycle. But even if we ignore the difficulty of accounting in this way for opposite sexes, it is evident that sex would then be determined by the extra-chromosomic activating or inhibiting factor—whatever it might be—and not by the factor included in the chromosome; and a hypothesis of this sort would thus be virtually a negation of any "chromosome theory" of sex inheritance.

'Again, we might suppose that the chromosomes and their contained factors have different properties at different stages in the life-history. We might suppose them to have a sort of life-cycle of their own, so that the *a* chromosome—for example—determines sex at one stage in its development and at a successive stage is incapable of doing so. But any such hypothesis would really involve the rejection of the theories of the continuity and individuality of the chromosomes—which form the indispensable basis of *all* chromosome theories of heredity. If the chromosomes change their constitution from generation to generation, no chromosome theory of heredity is tenable.

'It might also be objected that the "chromosomes" of *Aggregata* are not quite the same things as the chromosomes of other organisms, or that the "characters" of such an animal are not equivalent to those of other creatures. "Sex" in *Aggregata*, for example, may be something different from sex, let us say, in an insect. But both of these suppositions are, I believe, unwarranted; and moreover they constitute a double-edged argument which can obviously be turned effectively against anyone who makes use of it.

'It is evident that arguments similar to those advanced above in the case of *Aggregata* can be employed equally well—*mutatis mutandis*—in the case of any other haploid organism. A consideration of *Diplocystis* in the same way, for example, would lead to similar conclusions. The haploid organisms as a whole—of which, as I have already pointed out, there are probably not a few—thus appear to me to furnish considerable evidence against a general chromosome theory of heredity.' (Dobell, 1924.)

But he carries his argument further and holds that there cannot be any possible connection between the chromosomes and the appearance of particular characters in diploid any more than in haploid organisms, and in this opinion he agrees with other distinguished biologists (*e.g.* Fick, 1907; and Della Valle, 1911) though his conclusion is arrived at differently. His argument runs thus.

If we postulate that there is a factor representing a particular character in a particular chromosome, it is clear that this chromosome must be present in the fertilised ovum, and through the process of cell division (postulating the individuality and continuity of the chromosomes) it must be present also in all the cells of the organism. If we take the character of red-eye in *Drosophila* for instance, the chromosome carrying the 'red-eye' factor must be present in the cells that form the wings, legs and all the other organs. It has no effect on the form or function of any cell in which it is present. From this it is argued that it cannot have any particular relation to 'red-eye', for if it had it would be necessary to show that that particular chromosome was present in the eye and nowhere else. It is pointed out that this difficulty obliged Weismann to assume that the chromosomes became qualitatively different in the course of successive cell divisions, and that this assumption involves the abandonment of the individuality and continuity of the chromosomes.

Before discussing this point of view it is necessary to consider some other haploid organisms. In bees, wasps, ants and some other animals, all the eggs that are fertilised produce females, those that are not fertilised produce males. Thus all the males possess only a single set of chromosomes and are haploid; while the females are all diploid. The number of characters common to male and female is of course large, and yet the male and female each have their own peculiar characters. The female has all the chromosomes possessed by the male, and an equal number in addition of her own. Yet the peculiar characters of the male do not appear in her, and the male has all the general characters of the species. The difficulty of correlating the chromosomes with all the characters appearing in individuals is really greater than this difference between male and female in the Hymenoptera (bees, wasps and ants), for very often there are not only the differences between male and female, but also between the various kinds of females such as were described in Chapter V. These differences are sometimes very great indeed and extend to size, structure, shape, appendages, functions and instincts, yet the chromosome complement is the same in all the forms of females, functional and non-functional. It is of course obvious that much of the difference may be due to environment, as for instance the production of the functional female, the queen, by special feeding, but it hardly seems possible that all the differences between three forms of females can be due to this cause.

The influence of the chromosomes upon the determination of sex is another point with regard to which considerable difference of opinion exists, and as this is intimately connected with the theory that chromosomes are the bearers of hereditary factors, it will be most convenient to deal with these three points together.

The thorough-going Mendelian might meet Dobell's argument with regard to the haploid Sporozoa by postulating that there were two different groups of chromosomes involved. These two groups would separate after fertilisation (H) and there would be a random distribution of members of each pair to the two nuclei in J. If we follow one pair of chromosomes, which we will call $a$ and $a_2$, then all we have to do is to duplicate K, L, M, N, O, P, Q and R in Fig. 20, and we start the cycle with two kinds of A, one of which contains chromosome $a$ and the other $a_2$. Of course it is necessary to postulate also that no difference in character is produced by these different chromosomes except between stages A and J, but here it might be said that the different environment caused the character of sex to appear, for it will be seen from Fig. 20 that this happens immediately it enters the new host, the cuttle-fish. Against this are the examples of latent characters appearing upon a change of environment that have already been shown in von Nagëli's Alpine plants. There are other examples available.

This, however, does not evade the difficulty with regard to the haploid males among the Hymenoptera. These same assumptions do not serve both cases and unlimited assumptions will prove anything if they are admitted. It is necessary here to turn to the question: how far is the assumption that sex is determined by the chromosomes justified?

The results of breeding experiments and the corresponding facts observed with regard to the chromosomes, make a most convincing story in so far as the particular organisms dealt with are concerned. The behaviour of the sex-linked characters seems to accentuate and confirm the Mendelian interpretation.

There are, however, many cases in which an interpretation of sex upon a chromosome theory seems quite impossible. Only a few examples can be given here.

*Bonellia* is a marine worm. The body of the female is about the size of a plum and its proboscis may be about a yard long. The male is about half an inch in length and spends the greater part of its life inside the female. All the eggs produced by the female are equally capable of becoming males or females, as also are the young when first hatched. These young forms can swim freely in the water and those that settle down at the bottom of the sea develop into females. Some, however, settle on the proboscis of a fully developed female and these develop into males. If, however, one of the young forms that has settled on the proboscis of a female be removed before differentiation has been completed, it develops into a hermaphrodite which will be more male or female according to the length of time it has been so attached. (Baltzer, 1914.)

In *Taenia*, a parasitic worm, the segments are functionally female when old, male when young.

Hertwig (1912) showed that by interrupting the process of egg-laying by the female frog the proportion of males produced might be modified from about 50 to 100 per cent. Moreover, in normal conditions in some parts of Holland, about 90 per cent of the young frogs that have just left the water are females; though among the adult frogs males and females are about equal in number. Witschi (1914 and 1923) found, on examining half-grown females, that in many of them the ovaries were being transformed into testes. Thus apparently by a mere temporary delay in fertilising the eggs, the sex was changed; and later on in the life of the individual, a change over from female to male is apparently a usual event.

*Rabdonema nigrovenosum* is a parasite in the frog. When in the frog it is hermaphrodite, but outside the frog it separates into males and females, living in the soil. The next generation is again hermaphrodite, and migrates into the frog again. The hermaphrodite has 12 chromosomes, but one chromosome is lost in the production of the sperms of which half have 5 and half 6 chromosomes. The female has 12 chromosomes. In the next generation the male-producing sperms are functionless, so the 12 chromosomes are restored in the hermaphrodite. The female and the hermaphrodite therefore have the same chromosome complement. (Boveri, 1911; Schleip, 1911.)

Moreover, there is abundant evidence that sex tends to blend, even in groups of organisms where the two sexes are apparently most firmly established. Even in mammals hermaphrodites occur, and in the normal males and females rudimentary organs representing those of the opposite sex are present, and under certain conditions the female may assume male characters, the male assume female.

Very many examples might be produced which indicate that whatever influence the chromosomes may have in some cases, the determination of sex is not dependent upon them alone in living organisms generally.

To return to the chromosomes apart from sex. Della Valle (1909) said that:

> 'Not constancy but variability in number of chromosomes is the general rule in all organisms.'

With regard to this statement Wilson (1925), whose general knowledge of the subject commands the greatest consideration, says:

> 'Verbally, perhaps, this is not incorrect, though a palpable exaggeration.'

This is from a strong though cautious supporter of the neo-Mendelian hypotheses, including the genetic continuity of the chromosomes.

What does this variation in the number of chromosomes really amount to?

Variations from the usual number of chromosomes in any organism are more common among the somatic than the germ-cells. In some organisms there is a considerable difference between the number observed in the germ-cells and that in the somatic cells. In the parasitic worm, *Ascaris megalocephala* var. *univalens*, the line producing the germ-cells has two chromosomes, but in the somatic cells 52 have been described in the male and 60 in the female. (Boveri, 1899; Geinitz, 1915; Kautsh, 1912–13.) Doubling of the number of chromosomes and various more or less regular arithmetical progressions have been described in the somatic cells of many and in the germ-cells of a few organisms. (Wilson, 1925.)

Supernumerary chromosomes are stated to have appeared in some organisms, and this phenomenon has been attributed to the failure of a pair of chromosomes to separate at the reduction division or of a somatic chromosome to split. (Wilson, 1909; Bridges, 1913 and 1914, and others.) These supernumerary chromosomes have been found to increase to as many as 5 or 6, and may be of more than one easily recognisable type. (Wilson, 1910.)

The number of somatic chromosomes is said to vary greatly in some cases through their dividing across, though the total chromosome length is said to remain the same. (Hance, 1917–18; Robertson, 1918.) The converse may also happen, and the chromosomes may be joined together and so the whole number apparently reduced. (Robertson, 1916.)

Wilson (1925), in discussing the possible ways in which the chromosome number of any organism might be permanently changed, suggests six that would agree with the facts known to us at present, both as regards an increase or decrease. Some of these ways have already been indicated; there is evidence also suggesting that individual chromosomes may diminish and eventually disappear.

It is, then, certain that the usual number of chromosomes may vary and there is some evidence as to how this happens, but the fact remains that the usual event is for the number to remain constant for many generations in any given organism, particularly in the cells that are destined to produce gametes.

The probability is, that the stability of the chromosomes varies, but is usually constant through many generations in Metazoa and Metaphyta at any rate. Such partial stability was suggested as probable in the case of the Mendelian or individual characters. The distribution of the chromosomes before and during fertilisation and the exactly corresponding reappearance of these characters in breeding experiments seem to indicate the interdependence of the two phenomena.

The characters involved are apparently small and comparatively unimportant. It is more than probable that such variations would escape notice in the case of the parasitic Protozoa dealt with at the beginning of the chapter. The larger differences, including sex, are not really involved in the argument; it would be impossible to subject the behaviour of the smaller differences, even if recognisable, to observation in breeding experiments.

The argument that a chromosome controlling a character must be present in the cells forming the particular part showing that character and not in the cells of any other part of the body does not seem convincing. It is quite certain that characters may be latent for many generations unless the proper stimulus is present. But highly differentiated cells can be modified only to a very limited extent in a limited number of ways. One kind of stimulus applied to the whole body will affect different parts differently or even may affect only one part. The evidence in favour of the chromosomes having a definite influence on particular characters is strong, and there is no other part of the cell that provides any sort of explanation of the undoubted facts.

# CHAPTER XII

## Vitalistic hypotheses

THERE is a curious feature in evolution that must have impressed many people. It is present in the higher groups of animals and plants, but in them is obscured to some extent by the innumerable minor branches into which they have been separated, and by the extraordinary complexity of the environment produced by the great diversity in living organisms which form part of it in relation to each other. Among the Protista it is less confused.

If all the different modes of multiplication and fertilisation among the Protista from the simplest to the most complex are considered, they give the impression of being similar to a series of experiments in a laboratory, made in the attempt to discover the best method of arriving at a certain preconceived objective. Evolution appears to have achieved a certain degree of success in various directions, while what might, in a somewhat distorted sense, be regarded as the most successful, has ended in Man; just such a result as one hopes for in a series of experiments in a laboratory.

This superficial resemblance to a series of events that, within our own experience, is dependent upon an external directing intelligence, has doubtless helped to give rise to the various vitalistic hypotheses when an immediate explanation for a phenomenon in evolution has not been available. They all postulate some metaphysical intelligence, outside our experience or knowledge, that has the power of directing the evolution and development of living organisms, and which is not subject to any natural laws with which we are at present acquainted.

Bergson's (1911 and 1912) vitalistic interpretations of the phenomena of evolution are perhaps the most popular and widely known. He assumes the existence of an 'élan vital'.

It is impossible to give more than the slightest sketch of his philosophy. He regards 'time' as used in science as 'abstract' time, which is a form of space. True time, he says, is something quite different.

> 'Consciousness and life do not occupy space, and true time is applicable only to them.'
>
> 'My mental state as it advances on the road of time, is continually swelling with the duration which it accumulates.'
>
> 'There is, moreover, no stuff more resistant nor more substantial' (*i.e.* time).
>
> 'For a conscious being to exist is to change, to change is to mature, to mature is to go on creating oneself endlessly.'

The following quotations will give some idea of Bergson's conception of the nature of life:

> 'At a certain moment in certain points of space, a visible current has taken rise; this current of life, traversing the bodies it has organised one after another, passing from generation to generation has become divided among species, and distributed among individuals without losing anything of its force, rather intensifying in proportion to its advance.'
>
> 'Life is like a current passing from germ to germ through the medium of a developed organism.'

Bergson appears to conceive 'life', generally and comprehensively, as a huge conscious personality, for he tells us that, as it is 'of a psychical character', it has had a choice of action. It has chosen three lines culminating in *torpor* among the plants, *instinct* among the arthropods and *intelligence* in Man. Instinct corresponds to intuition, which is very different to intelligence in Bergson's view.

'It is to the very inwardness of life that *intuition* leads us,—by intuition I mean instinct that has become disinterested, self conscious, capable of reflecting upon its object and of enlarging it indefinitely.'

'Life, that is to say consciousness, launched into matter, fixed its attention either on its own movement or on the matter it was passing through; and it has thus been turned either in the direction of intuition or in that of intellect.'

'There are things that intelligence alone is able to see, but which by itself it will never find. These things instinct alone could find, but it will never seek them.'

'Of the discontinuous alone does the intellect form a clear idea.'

'The intellect is characterised by a natural inability to comprehend life.'

This somewhat arbitrary and inconsiderate behaviour on the part of 'life' has placed the seeker after knowledge in a very unfortunate position, for the only instrument he can use, his intelligence, is 'characterised by a natural inability to comprehend life', and yet intuition or instinct, which 'alone could find', 'will never seek'. Bergson offers a way out of the difficulty. As far as can be ascertained from his writings, the procedure is to stay the activity of the intellect, if only momentarily, in order to give intuition a chance of working. The seeker after knowledge makes his mind a blank, and then, just as his intellect takes charge again, his intuition is caught for an instant, and he gets a flash of insight to the unknown. We are thus able to 'penetrate the most obscure regions of metaphysics'. This is similar to a much more ancient method for attaining mental enlightenment.

'The fakirs of India, and the monks of the Oriental church, were alike persuaded, that in total abstraction of the faculties of the mind and body, the purer spirit may ascend to the enjoyment and visions of the Deity. The opinion and practice of the monasteries of Mount Athos will be best represented in the words of an abbot, who flourished in the eleventh century. "When thou art alone in thy cell," says the ascetic teacher, "shut thy door, and seat thyself in a corner; raise thy mind above all things vain and transitory; recline thy beard and chin on thy breast; turn thy eyes and thy thought towards the middle of thy belly, the region of the navel; and search the place of the heart, the seat of the soul. At first, all will be dark and comfortless; but if you persevere day and night, you will feel an ineffable joy; and no sooner has the soul discovered the place of the heart, than it is involved in a mystic and etherial light." This light, the production of a distempered fancy, the creature of an empty stomach and an empty brain, was adored by the Quietists as the pure and perfect essence of God himself; and as long as the folly was confined to Mount Athos, the simple solitaries were not inquisitive how the divine essence could be a *material* substance, or how an *immaterial* substance could be perceived by the eyes of the body' (Gibbon, *Decline and Fall of the Roman Empire*, chap. lxiii).

Apparently the only occasion upon which Bergson produces the evidence of recorded observations in favour of a directive force in evolution is with regard to the eye. He compares the eye of *Pecten* (Scallop) with that of the vertebrates. He points out that:

'Molluscs and vertebrates separated from their common stem long before the appearance of an eye so complex as that of the *Pecten*. . . . Yet we find the same essential parts in each.'

He considers it impossible to explain how this similarity can have occurred except by an original impulse towards producing an apparatus, the nature and parts of which were predetermined, presumably by the psychical power of choice inherent in life. He says:

> 'For this reason, no matter how distant two animal species may be from each other, if the progress towards vision has gone equally far in both, there is the same visual organ in each case, for the form of the organ only expresses the degree in which the exercise of the function has been obtained.'

The weak part of this argument is that it is based upon mis-statements of fact. It would be impossible here to go into all the examples available; one will suffice. Evolution has *not* always produced a similar visual organ in each case, even among animals that belong to the same group. The only way in which one can imagine an image of a part of the environment being conveyed to the consciousness of an animal is by its being focussed on to a specialised sensory area. In all cases this has evolved into a screen of specialised nerve endings. There are not many ways by which a detailed image of an area of the environment could be focussed on a small surface. One is by means of a lens, another is by means of a pin-hole in a screen. In the scallop, the object is achieved by means of a lens, in the nautilus, another mollusc, instead of the lens is a pin-hole. Both animals belong to the same group, but while the scallop's eye possesses a lens as do those of the vertebrates, the nautilus has a screen with a small hole.

Ray Lankester (1912) said with regard to this:

> 'By a light-hearted perversion of the facts as to the structure of the eyes of animals and other such things, he endeavours to make them appear as evidence in support of his arbitrary and preposterous fancies. . . . In doing so he ceases to be merely an amusing juggler . . . he becomes a maker of untruth.'

The rest of Bergson's views do not offer any explanation of anything. He has cast a glamour of words over many problems which tends rather to obscure the facts than to advance our knowledge.

Driesch's (1908) view is that no mechanical hypothesis can possibly explain development, and he therefore postulates a directive force which he calls 'entelechy'. He says that the phenomenon described in a previous chapter as somatic co-ordination could be explained only in four ways. Though each blastomere separately is capable of producing all the parts of an organism, when they are together they do not do so, but develop into a harmonious whole. The four ways by which this end might be brought about are (1) by the action of formative stimuli, (2) by chemical means, (3) by a machine in the system and (4) by entelechy. He proceeds to prove to his own satisfaction that (1), (2) and (3) do not offer an explanation, and states definitely that therefore the explanation must be 'entelechy'.

Entelechy is an 'intensive manifoldness', ' a true element of nature'. Because no machine can be divided up many times, as is the ovum, and retain the same potentialities, the machine theory is ruled out, 'Entelechy thus proves to be that which may be said to lie at the very root of inheritance'.

This form of argument is what the old scholiasts called *per exclusionem*, and is unsound. No one can be sure that he has enumerated all possible explanations. In this case there are many more than four. For instance, one can conceive the existence of peculiar forms of very complicated protoplasmic molecules which can be built up in only one way, or in a limited number of ways in each case. This is really only an extension of what happens in some non-living matter. Judging by what happens in certain physical and chemical phenomena, it is possible that the blastomeres, when in contact, or joined together by strands as they sometimes are (Andrews, 1898), react upon each other and behave differently from what they do when separated. There is no reason for limiting the *possible* explanations of the phenomena in question, particularly in our present state of ignorance; at any rate there are more than the four enumerated by Driesch, and as our knowledge of facts increases, doubtless their number will increase. Knowledge is not advanced by such speculations.

Another argument of Driesch's is that reaction to stimuli cannot be explained by mechanical means. He takes the example of the difference in the reaction produced upon a man being told—'Your mother is seriously ill' and 'Your brother is seriously ill'. These two sentences will produce quite different thoughts, entirely different mental images, different emotions, and will stimulate different courses of subsequent action. Yet the difference in the actual stimulus is only that between m and br. Driesch states that all this difference in reaction could not be brought about by a machine. But why not? The auditory apparatus is fairly complicated, but is very simple when compared to the brain. The automatic telephone does something analogous to the reception by the auditory apparatus of the stimuli caused by sound. The whole of the apparatus and wiring of an automatic telephone system supplying the whole country, would be simple when compared with the millions of nerve-cells and their connections in the human brain. Having evidence of the enormously greater complexity of structure, it is not surprising that the complexity of reactions should be greater in the case of the human brain than in that of the automatic telephone.

The difference is one of degree. Moreover, we know that if the brain is deprived of nourishment or is injured it ceases to function or functions incorrectly, just as is the case with the automatic telephone.

A somewhat different attitude with regard to evolution is not unusual, of which the following is an example:

> 'There can, indeed, no longer be any doubt that each group starts its career in geological time with certain innate potentialities which we do not understand, but which compel all its members, however varied may be their respective adaptations and modes of life, to follow the same course to the end' (Woodward, 1931).

This implies that there is some metaphysical power that directs evolution along some predestined lines. Such an assumption seems quite unnecessary. To begin with, it cannot be true. All the members of the group in geological time have not followed the same course to the end. In fact as far as the available evidence goes, only a proportion of the members of any group has ever done so. The original fishes, so far from having inevitably become more 'fishy' as some of them have done, have also given rise to amphibia, reptiles, birds and mammals. And some mammals have become just as 'fishy' in their adaptation to an aquatic mode of life as the primitive fishes. Though it has the structure and physiological functions of a mammal, the whale is as dependent upon an aquatic environment as any fish, and has developed some morphological characters peculiar to fishes as a group. To what end then did this compelling power destine the original fishes and the original mammals? The ends have obviously been just as different as the courses pursued in their attainment.

Geological evidence points to the continual splitting up of the groups according to the increasing complexity of the environment produced by the increasing diversity of living organisms. The only explanation lies in the adaptation of organisms to their environment by means of the selection of variations in succeeding generations.

Actually the sequence of events in the evolution of living organisms proves that if there be a metaphysical intelligence directing it, that 'intelligence' must be either of an inferior or of a very unpleasant kind. It has made its failures go as far as its success if man or any other existing organism was its objective. Otherwise it could not have had a definite objective in view, unless it was to discover, for its own satisfaction, how many different kinds of living organisms it could produce, in how many different ways, and how it could so arrange that these different kinds of organisms should cause the maximum amount of suffering and damage to each other, short of extermination.

Without any control by a directing intelligence, the selection of variations by the changes in the environment must cause an ever-increasing number of divergent lines in evolution, limited only in their extension by these changes of the environment. In the Protista we see that while some lines in the evolution of the processes of multiplication and fertilisation lead to those now existing in the higher plants and animals, others have led to equally complicated but quite different processes in parasitic Protista, while in some cases races of living organisms have remained comparatively unchanged throughout geological time. There is no suggestion of any direction, but the material upon which evolution has had to work, variations, has ensured a great diversity in every direction that has furthered the adaptation of the organism to its environment; and the environment has become increasingly complicated with the increasing variety of living organisms. The attitude of the Vitalists has been summed up thus:

'We cannot conceive how mechanical forces could work such a result: therefore they cannot: therefore vitalism is true' (Elliot, 1913).

No vitalistic hypothesis is capable of advancing our knowledge. Bergson's 'élan vital' or Driesch's 'entelechy' leave us exactly where we were; not one new fact is established nor is there any encouragement in them to search for new facts. None of these vitalistic views are capable of verification. They are simply dogmatic statements. On the other hand, the various hypotheses based upon known facts, whether they have proved, or will prove in the future, true or false, have always helped to advance biological knowledge. This is true of all, from Lamarck's which is entirely based upon observations, down to the Neo-Mendelian and the genotype hypotheses.

# CHAPTER XIII

## Summaries, Hypotheses and Conclusions[1]

OBSERVERS of living organisms, from the earliest times, began their classification and the elaboration of their theories relating to them with the highest, and worked backward to the lowest. Except for the brief interval provided by Charles Darwin, this method has continued until today. Perhaps this may not be so obvious now as in the case of the earlier writers, but a careful consideration of the current literature shows that it is still with us.

Many modern hypotheses attempt to force the whole of what is known of evolution to fit in with the behaviour of minor characters in highly complicated breeding experiments generally made upon complex organisms; instead of seeking how such results will accommodate themselves most readily to its broad outline; to the order in which organisms appeared on the earth; and to what is known of those organisms that are probably most like the primitive.

The gradual changes that have occurred in the morphological characters of living organisms from forms belonging to the earliest, leading through the various branches of evolution to the latest groups, have been so fully, frequently and admirably described, that it would

---

[1] The terms 'lower' and 'higher', where applied to animals or plants existing at the present time, mean nothing more than that the one belongs to a group that appeared at an earlier period in geological time than the other. (See Chapter IV.)

The terms 'injurious, favourable', etc., as used in relation to variations, characters and factors in the environment refer only to the effect upon a particular race or individual, and does not imply that a particular factor is generally injurious, or a particular variation favourable in itself, apart from the individual or race concerned. (See Chapter V.)

be a work of supererogation to repeat them here. The brief sketch in Chapter IV is sufficient.

But though the fact of the existence of this connecting chain is well established, and the selection by the environment of variations of some kind that occur in living organisms offers a satisfying explanation of a general nature as to the order in which these changes have been produced, essential and large details of the process are still the subject of much controversy, and opinions differ profoundly with regard to the interpretation of recorded observation.

The basis of most of these disagreements lies in the interpretation of the results of breeding experiments and the attempts on the part of the supporters of hypotheses founded upon them to apply them to all living organisms and to evolution generally. The way in which the changes in living organisms have been brought about during evolution must depend to a large extent upon the manner in which the characters of the parent are handed on to the offspring. The processes of multiplication of individuals, of the various methods of reproduction and of fertilisation, differ greatly in different groups, and it is probable, therefore, that a consideration of the order in which these differences appeared, and the lines of evolution they have followed, may show how these contradictory opinions have arisen, and offer a solution to some of the difficulties in the interpretation of the recorded observations relating to the inheritance of characters.

It is obvious that existing organisms must all be equally separated in time, unless it is believed that they are still appearing on the earth independently of pre-existing organisms; for which belief there is no evidence whatever. Thus, any individual, to whatever group it belongs, is as remote from a primitive ancestor as an individual belonging to another group, no matter which group appeared first upon the earth. Any hypothesis as to which of the existing organisms nearly resemble the most primitive forms must therefore be more or less speculative. The acceptability of any such speculation must depend upon the nature and quantity of the evidence upon which it is made.

The earliest organisms of which remains have been found were comparatively complex Protista. They had hard cases or shells capable of resisting the destructive effects of the environment, and these only have been preserved. As these shells resemble those of certain existing organisms, it is assumed that the enclosed bodies were similar. There are other existing organisms belonging to the same group that appear to be far simpler than those that possess these shells, and as bodies like theirs could not have been preserved under the conditions that existed between those remote geological times and the present, it is assumed that these less complex Protista are more like the primitive organisms than those whose remains have been preserved.

Apart from structure, there are other reasons for believing that these apparently simpler forms approach most nearly to the primitive. We know that the modes of growth and reproduction become more complicated in the majority of the species forming a group, according to the period in evolution at which that group first appeared. Probably, then, the simplest of these methods were the most primitive. The organisms in which we find the simplest methods of reproduction existing at present are also among the simplest in structure.

Statements have been made that there is no evidence that evolution has proceeded from the simple to the complex. This disagreement with the usual belief has, no doubt, arisen from the fact that many existing organisms are the recent products of evolution within a group itself. An excellent example is provided by the earliest group to appear, the Protista. The highly complicated processes of reproduction in some of the parasitic Protozoa (e.g. *Aggregata eberthi*, see Chapter XI) are as different from the process of reproduction in the simplest of the free-living Protozoa as they are from those existing in Mammals. From this point of view, then, evolution has produced just as great a differentiation within the lowest group of animals as it has between the lowest and the highest groups, but along different lines, and with very different results.

As all these parasites are dependent for their existence upon animals that belong to much later groups, they must have been evolved after these later groups appeared, so the evidence strengthens the view that the complex arises from the simpler form. The most complex free-living Protozoa do not show the complicated processes of reproduction found in the parasitic, any more than they show the complexity of that in Mammals. Attempts are made to force the facts of breeding experiments with the higher plants and animals to fit in with what has been observed in the parasitic Protozoa. A reasonable co-ordination of facts that are common knowledge to all biologists, should demonstrate the futility of such attempts.

It is sometimes assumed that organisms that were neither plants nor animals were the primordial forms of life, but our knowledge of such forms is very doubtful. It is probable that the first form of life was of the nature of a plant.

The complicated life-history of the Mycetozoa (Slime-fungi) seems to put them out of court as representatives of primitive organisms. They have been claimed as plants by the botanists as Myxomycetes; but during some stages in their life-cycle they have the physiological characters of animals.

While the increased complexity of structure seems to be generally concomitant with increased complexity in the processes of reproduction, it has been claimed that these processes in some organisms of the simplest structure are as complicated as any existing at present. Such statements are, in a measure, again due to that fruitful source of error, evolution along exceptional, and possibly unfamiliar lines, within the group itself. The parasitic Protozoa again offer an example.

It is well known that many characters, whether morphological or functional, that become useless to the individual through changes in the environment, disappear gradually in the course of succeeding generations. Many of the morphological characters—complexities in structure—of a free-living Protozoan must become useless to it when it takes to a parasitic mode of life. But, on the other hand, the developments of new methods of reproduction would become more and more beneficial as it became more and more dependent upon the environment provided by its host. This explanation of the simple structure of many parasites demands but little in the way of assumption; more particularly as some of them at certain periods in their life-cycles that are spent apart from a host, possess the characters of free-living Protozoan ancestors.

The way in which some of the simplest of the existing Protista multiply is, therefore, quite probably the most like the primitive; it is also the simplest way in which any known organisms multiply. In these simple forms, the individual produces new individuals by dividing into two halves; or by budding, that is by a portion smaller than itself separating from its body. There are no indications of chromosomes or of any of the complicated mechanisms of mitosis. In some plants, no nucleus has been demonstrated. In some animals the nucleus is supposed to be represented by a number of granules, known as chromidia or chromioles, which are denser than the surrounding protoplasm.

In existing Protista, it has been suggested that the ancestors of these organisms may have possessed definite nuclei, and that the nucleus has become diffused in the course of evolution. The suggestion that, if this be the case, it may only be an example of the well-known phenomenon of the reappearance of an ancestral character, is equally if not more plausible. But this is not a major objection, for it is obvious that it is extremely improbable that even the simplest forms of Protista now existing can resemble the most primitive forms in detail. All the existing forms exhibit some special differentiation.

There is a partial gap in the evidence for the evolution of Protist plants that does not exist in the case of animals. While bacteria apparently possess no defined nucleus, and divide by fission or budding, mitosis seems to occur in all the others except in the Blue-green Algae.

The evidence provided by the Protozoa has been summarised as follows:

> 'From the multitude of varied phenomena that have here been recorded, two salient facts stand out. First, a few of the Protozoa, including representatives of both the rhizopods and flagellates, exhibit a process of mitosis that appears in all essential respects of the same type as in higher animals. Secondly, this process appears to be connected by successively simpler types with modes of division hardly, if at all, distinguishable from direct or amitotic divisions' (Wilson, *The Cell*, p. 202, 1925).

This general statement must be modified to some extent to meet recent observations. Mitosis, generally similar in so far as the chromosomes are concerned to what occurs in the higher organisms, is much more usual than is suggested, and many of the observations describing amitosis have since been shown to be mistaken. In many cases the chromosomes are described as minute granules, and may be of various shapes and sizes in different Protozoa. It has been claimed that the only Protozoa in which chromosomes do not appear are so small that there is no room for them.

There is a chain of differences with regard to the achromatic structures (spindle, etc.) connected with mitosis, ranging from those forms in which there is no structure at all to those with the complete mitotic figures found in the higher plants and animals. The first suggestion of the achromatic apparatus is a division-centre (Karyosome) which behaves very differently in different Protists.

Finally, two forms of spindle are found in the mitotic figures occurring in Protista. One in which there are numerous radiations extending from the centrosomes at the poles; the other without any centrosomes or radiations. The former is the type found in all mitoses in the cells of the higher animals except the two involved in the maturation of the ovum. The latter is the characteristic mode of all divisions, with but few exceptions, in the higher plants. Of these two types of mitosis then, both common in the Protista (animals and plants), the one has become almost universal in the higher animals, the other in the higher plants.

In the general account of Mitosis (Chapter II) the spindle was described as arising outside the nucleus. Among the Protista it frequently arises within it. This is of rare occurrence in the higher animals and plants.

Terms relating to multiplication and reproduction in animals and plants are sometimes used in a rather vague and loose manner. In attempting to trace the evolution of these processes it is necessary to define the meaning of the words used.

By 'fertilisation' nothing more than the mixing of protoplasm generally is meant.

'Sex' implies the differentiation of individuals into two groups; one producing only the active, the other the passive, gametes.

The term 'gamete' is used only when the two conjugants are dissimilar. Two similar conjugants (*e.g.* Paramecium) are not gametes.

In the simplest forms of fertilisation among the Protista there is no special differentiation between the individuals taking part in the process—there is no suggestion of sex. Among most of the Bacteria and certain other forms of plants and animals, no evidence of any approach to fertilisation exists.

Two individuals may fuse into one, thus providing a mixture of material; or two individuals may come into contact with each other and exchange nuclear material. In these cases, there may be no difference between the individuals—no suggestion whatever of sex. Fertilisation, or what is actually fusion or the exchange of material between two individuals, only occurs at intervals between two periods of multiplication, that may be shortened or prolonged by changes in the environment.

The next step towards more complexity is, that after a number of generations produced without any fertilisation, some differences appear between the individuals that are about to conjugate. This condition also appears in some Protista that, though joined together by stalks, a matrix, or in some other way, must still be regarded as colonies of separate individuals (*e.g.* some species of Spirogyra and of Infusoria).

A striking modification in the phenomenon of fertilisation among the Protista, an important step in differentiation, is that while in some conjugation or fusion may occur between individuals produced by the same parent, in others this cannot occur until the conjugants are many generations apart, which ensures that the mixture of material will not be that of very closely related individuals. This applies to both animals and plants, and is known as exogamous, while that between individuals of the same parentage is endogamous.

In the next stage of differentiation, known as heterogamy, the individuals destined to conjugate may take two widely different forms, both from each other and from those of the main stock. One type is as large or larger than usual, and is generally not mobile, while the other is much smaller, sometimes different in structure, and is mobile. Differences are great between the two in some cases. The mobile conjugant may be proportionately a very small flagellate individual that does not survive unless conjugation takes place. In different organisms numerous other variations in the difference between the characters of the two conjugants exist. This suggests the manner in which the gametes, found in the higher organisms where sex exists, originated.

All of these types of fertilisation merge into each other, and more than one may occur in the same species.

In one of the Protozoa, *Actinophrys*, a process similar in all essentials to the maturation of the gametes in the higher forms, as far as the behaviour of the chromosomes is concerned, has been described. (Bělař, 1921, and 1923.) Other cases have been described which suggest that something of the same kind, forming links with the simpler processes, happens among the Protista, both in plants and animals. The elaborate processes occurring in some parasitic Protista must be excluded at this stage.

They are obviously a late product of evolution, and differ essentially from analogous processes occurring in the groups of animals and plants that appeared late in evolution, as they do also from those in other Protista.

Of course it is possible or even probable that those cases that approach so nearly to mitosis and the maturation of the gametes as observed in the higher animals and plants, may be comparatively recent products of evolution. The probability is supported by the fact that the simpler processes continue in some of the colonial Protista, though these would seem to have appeared later than the solitary forms.

Among the Protista, the earliest of living organisms to appear on earth, we see the beginning of the effects of evolution upon an intrinsic property of living matter, which for want of a better term may be called irritability. This is the capacity to react to stimuli in the environment, often by a release of energy out of all proportion to that provided by the stimulus. It is particularly marked in the case of animals, not only in the form of movement, secretion and the like, but in structural changes in the body. To take only one result produced by the action of the environment upon structure. Its most obvious immediate action is upon the surface of the body of the organisms. Here we find most elaborate coverings and various organs produced. Some of the Protozoa react to light, heat and cold, dryness and moisture, what to us would be sight and smell and touch, in ways that suggest the origin of the senses we ourselves possess. The elaborate nervous system, and the apparatus of the special senses upon which our communication with, and reactions to our environment depend, arise from the outer layer of our bodies.

A consideration of this brief sketch of the phenomena occurring among the Protista suggests certain general conclusions.

Except in a very few instances, which as likely as not are a comparatively recent product of evolution, there is no provision for any such modes of inheritance as those postulated by the Mendelians, the Genotypists, and the supporters of the Pure Line hypotheses. In many cases there is no suggestion of any such mechanism or structure as could be used in the most far-fetched argument, based upon recorded observations, though from them we can trace the beginnings of such mechanism. It seems clear that Mendelian inheritance and the various hypotheses dependent upon it cannot have been true with regard to primitive organisms.

We are faced, however, with the fact that all living organisms and therefore, probably also the most primitive, produce other organisms like themselves with variations.

The molecules of living matter must be of great complexity. Of their actual structure we know little or nothing. Even supposing we knew the differences between the molecules of the dead protoplasm that goes to form the bodies of different races of animals and plants, we should not have solved the problem; for the available methods necessarily involve killing the material examined. There must be differences between living and dead protoplasm as well as between the protoplasm of the different kinds of animals and plants. Recent experiments on the structure of molecules with the assistance of X-rays, suggest that our knowledge in these directions may be increased in the future, but this provides no present help.

The only hypothesis as to why organisms consistently produce others similar to themselves that seems justifiable at the present time, is that it is due to differences in the protoplasmic structure between different species of animals and plants, and that these differences limit the possible combinations of the molecules so that only one particular form can develop.

When the extreme complexity of some organisms is considered this seems at first sight rather far-fetched. We have, however, an analogy in certain inorganic molecules which, when they combine, do so in the form of crystals; sometimes of several different shapes, but all characteristic of that particular substance. Then again, there are certain elements (*e.g.* sulphur and selenium) that possess different physical characters according to the environmental conditions to which they have been subjected. Who can be sure that the difference in complexity between the comparatively simple molecules of these forms of inorganic matter and the molecules of living protoplasm is greater or less than the differences in the number of possible forms in which each may combine? In the inorganic substances there is the limitation of possible combination to a few crystalline shapes or to a few forms with different physical characters; in living protoplasm the large number of forms of combination found within the same organism.

The 'idioplasm' postulated by von Nägeli (see p. 109) is much the same thing as is suggested here.

If something of this kind be admitted as a possible explanation of the production by individual organisms of others like themselves, then the recent admission by the physicists of variability in atoms, offers an explanation that is at least equally plausible for the intrinsic variability of living matter.

Whether this or any other explanation for it be accepted or not, the fact remains that living organisms always do produce others similar to themselves but with variations; and we have no evidence that in the most primitive organisms there was any constituent particularly specialised to control in any way this transmission of the characters of the parent to the offspring. What we know of existing organisms, probably most, like the primitive, suggests that there was not; but it suggests also that the granules, chromidia, or chromioles, were the first manifestation of such differentiation. From them or some of them, if they differed in their properties, we can trace all stages up to mitosis and the maturation of the gametes in the higher animals and plants.

It seems possible or even probable that modification produced by the environment might be transmitted just as frequently as variations in the most primitive organism. Why, then, should instances of this happening among existing races be so rare, and even these generally doubtful? (Chapter V).

The environment would act in two entirely different ways upon such a race of organisms. (1) It would modify the characters of the individual by direct action. (2) It would select those variations that were beneficial to the individuals by destroying those in which such variations did not occur, or those that varied in directions unfavourable to them in relation to it, in a larger proportion than those in which favourable variations had occurred, and the latter would therefore have the best chance of multiplying. But to the individual, the effects of an uncontrolled environment must be more or less equally proportioned between beneficial and injurious, so the transmission of the direct effects of the environment would not tend at all to enable succeeding generations to resist that part of it that is injurious to the individual.

The power to resist unfavourable factors in the environment seems to be one of the most important results of evolution to any race of organisms, always remembering that other organisms form part of its environment, and that any of them may be one of the favourable or unfavourable factors. Indeed, at the present stage of evolution, most of the injurious and many of the beneficial factors in the environment of any race, are provided by other living organisms, more so in the case of animals than of plants. This is due to the fact that, while plants may thrive upon nothing but inorganic material, animals are dependent upon material produced by other living organisms.

To return to the effect of the environment upon the individual organism and its progeny. It is clear that the inheritance of acquirements produced by the effect of the environment could at best be but neutral and might well be injurious on the whole. The accumulation of injurious effects would very likely end in the extinction of the race, as the accumulation of beneficial effects would generally be at least counterbalanced. As, however, at this early stage there would be but few other living organisms forming part of the environment, this mode of inheritance might well continue for long, concomitant with the inheritance of variations, more particularly as the earliest living organisms were probably plants.

A variation toward resisting the transmission of the effects of the environment upon the individual, would do no harm to the succeeding generations, it would leave them just as were their parents, with the advantage of not inheriting the injuries they might have received. On the other hand, the selection by the environment of variations generally must tend to bring the succeeding generations of the race more and more into harmony with it. Being in harmony with the environment at this early stage must have been a far simpler matter than it is at present, for then the innumerable factors, injurious or beneficial to the individual, now provided by other existing organisms, had not appeared.

The beneficial result of transmitting only variations and not the effects of the environment must have been so great to any race, that it is not surprising that, through the selection of variations in this direction, cases of the inheritance of acquired characters at the present stage in evolution are at most very rare and generally doubtful, though they have for long been diligently sought in innumerable breeding experiments. (See Chapter V.) These experiments have usually been made upon the higher animals. It is possible that the inheritance of acquirements may still continue as a usual occurrence among some of the simplest Protista, though to ascertain this would be a matter of very great difficulty. The probability of experimental error would be great. It would, for instance, be extremely difficult, in dealing with minute organisms that generally multiply very rapidly, to be sure that the result was not due to unconscious selection of variations through those very changes in the environment that would be necessary to the experiments.

Evolution, though continually producing changes in races of living organisms as a consequence of changes in the environment, is sometimes extraordinarily conservative in the preservation of characters, even when they have ceased to be necessary or useful to the individual. The more ancient the character, the longer it seems to last after the environment has rendered it useless or undesirable, and thus any case of the inheritance of an acquired character, if it ever does occur among the higher organisms, might be accounted for.

Whether animals and plants arose from some common ancestors or whether, as is most probable, animals arose from plants, the divergence into two different lines of evolution must have been a very early event. The differences between them, both morphological and physiological, are already great among the Protista, but become greater still in the later stages of evolution. There is, however, one striking point of resemblance between the latest groups of both—the similarity between the complicated processes of cell multiplication and of fertilisation.

Among the existing plants there appears to be a gap between what is indistinguishable from simple fission or budding (amitosis) and a form of mitosis closely resembling, if not identical with, that found among the higher groups. In animals this gap does not exist. We can trace the stages between granules in the cell to the fully formed chromosomes. So also the stages in the development of the achromatic apparatus may be traced.

There can be no doubt whatever that the Mendelian experiments show conclusively that some characters are distributed alternatively as units to the offspring and reappear in them in definite proportions, or even disappear altogether, in a manner which can be foretold with considerable accuracy. The distribution of the chromosomes during the process of maturation of the gametes in the higher animals and plants, is exactly similar to the distribution of the Mendelian characters in breeding experiments. Both phenomena are so complicated and agree so well in the results and in the way these are produced, even to the possible disappearance of particular chromosomes or characters in one generation (see pp. 18, 75, 80), that it is impossible not to believe that they are interdependent. We thus have chromosomes definitely connected with certain characters, but not with all.

The only assumption we have to make is that chromosomes generally are connected with certain characters. Whether or not this connection arose gradually or was a primitive feature is not material at the moment.

The evidence provided by the stages found among the Protozoa between granules and complete chromosomes, suggests, *prima facie*, that the granules represent a very early differentiation in the protoplasm that provided for the transmission of variations, and this hypothesis agrees with recorded observations up to a point. But there are difficulties in the way of accepting it as a complete explanation. While the 'idioplasm' of the particular organism may account for the reappearance of the characters in general apart from some recent variations, there are other structures in the cells to which have been attributed some definite connection with the transmission and development of characters, the chondriosomes, mitochondria and other constituents of the cytoplasm. (See Chapters II and IX.) Some of these, in the maturation of the gametes, are, in observed cases, said to divide individually, and all to be distributed to them, but not in that discriminating manner seen in the chromosomes. It may be that the granules that give rise to the chromosomes were only one among several kinds and all may have been differentiated from an original type. There is little to guide us here beyond the facts that all the cells of the higher organisms possess chondriosomes, mitochondria and other bodies; that these are distributed to the daughter cells during mitosis; and that all the apparatus of mitosis, excepting that going to the formation of the chromosomes, is similar in similar cells even when the chromosome content is very different, as it is in the gametes produced from the same gametogenic cell.

The complicated process of mitosis goes on through the colonial Protista to the cellular organisms, Metaphyta and Metozoa, up to the groups that were latest to appear. As far as the chromosomes are concerned, the process is exactly similar in animals and plants down to minute details. The differences outside the chromosomes are minor ones.

Now the fact that the divergence in evolution in plants and animals, while producing such entirely different structural and physiological results, has continued with but little change with regard to the complicated process of multiplication, from the Protista to the cells of which the later organisms are made up, indicates that this phenomenon, unlike most of the physiological phenomena, must be related to something common to both plants and animals. The hypothesis already suggested assumes that this is the transmission of some of the characters to the offspring.

If this hypothesis be correct, then we have in the chromosomes the precursors of something of the nature of Weismann's germ-plasm, but the evolution from this beginning has been along very different lines in animals and plants, though in one detail it has arrived at the same end result.

It is claimed by the Mutationists that only certain variations are inherited in the Mendelian manner and that the others rapidly disappear. The only way, it is said, of ascertaining whether a variation is or is not a mutation is by testing it in breeding experiments, for one may be as small as the other. The evidence for the former claim is convincing. The assumption of two kinds of variations, mutations and fluctuations, was made on these grounds.

When it was admitted that a 'mutation' might be just as small as a 'fluctuating variation', the whole problem assumed a different aspect. The real difference between the two was only that one was inherited in the Mendelian manner, the other was not. Either might be preserved or eliminated by selection. The mutation might be eliminated in one generation, or might be preserved without dilution indefinitely. The fluctuating variation would be diluted. This would account for their behaviour in breeding experiments. The disappearance of a character in the absence of selection applies to all, not only those due to mutations which is really only another name for a Mendelian character.

Having gone to the higher organisms to establish the probability of a definite connection between certain characters and chromosomes, a return to the Protista shows that the occurrence of variations in them must originally have been due to intrinsic changes in the protoplasm, for a certain proportion of them have no chromosomes. It seems therefore probable that the change to some variations arising in and being transmitted by the chromosomes was gradual and concomitant with the evolution of the chromosomes. The question is, whether these two forms of inheritance of variations have continued into the higher groups? Whether variations arising in the molecules or elsewhere in the protoplasm of the cells continue to be transmitted as well as those which can be definitely connected with the chromosomes, and whether both are equally stable?

So far then, the only characters or variations (the terms are interchangeable in the case of a character that has appeared recently) that can be definitely connected with chromosomes are those that behave in the Mendelian manner on breeding. But if we follow the mode of inheritance of characters in plants, we find that new characters may arise in one part of the individual, and if new individuals be produced from cuttings of that part, without the intervention of any gametes or any process of fertilisation, this character will reappear, and will be just as permanent as any of the Mendelian characters in breeding experiments.

The results obtained from crossing the gametes produced by peach-trees with those produced by nectarine-trees would doubtless give some highly interesting and valuable information, and might help us to connect more characters definitely with the chromosomes, apart from those that are involved in the maturation of the gametes, than we are entitled to do up to this point.

It is quite clear, however, that characters arising in the individual may be transmitted and may be just as stable without the intervention of that chromosome mechanism necessary to the interpretation of results of Mendelian experiments, and that it is possible that such characters may be due to variations in the molecular structure of the plant, just as it must be in some of the Protista. If this be the case, then there is no reason whatever for supposing that one kind of variation is more stable than the other, though one may arise in the molecules generally and the other in the chromosomes themselves. On the other hand, variations may have originated in the chromosomes of the cells apart from the production of gametes and so be transmitted to all succeeding generations of individuals produced from cuttings. They would then show Mendelian results, were they involved in the process of maturation.

It seems probable that there would be one great difference in the behaviour of such variations. Those due to molecular differences would blend when crossed, and so would be diluted; while those arising in the chromosomes would go as whole units to a proportion of the offspring. This would obscure the variation in the one and might accentuate it in the other case.

The lines along which the processes of fertilisation and the differentiation of sex have evolved throw more light upon the probable functions of the chromosomes.

Among the Protista the process of fertilisation is essentially similar in animals and plants, and in both we see the beginnings of sex in the production of two different kinds of individuals—the fertilising and the fertilised. This resemblance continues among the lowest of the Metazoa and plants. The capacity of producing a new individual from a separated part or by budding continues throughout evolution in plants up to the latest stages, and coexists in the same individual with the production of gametophytes. In the simplest Metazoa, this may happen also, for an individual may produce offspring by budding or the separation of a part of its body, and may also produce gametes (*e.g.* Hydra).

But from this point plants and animals diverge so widely that it is necessary for a while to deal with them separately.

From what are essentially but little beyond colonies of Protista among the plants, stages may be traced to cellular individuals where the various tissues are fully differentiated, and a whole plant with all its parts is produced, either from a part separated from a pre-existing individual, or from the fusion of two gametes derived perhaps from two separate plants, perhaps from the same individual. The gametogenic cells in plants do not appear until the individual organism has reached maturity, that is until its tissues and parts are fully differentiated. This happens only among the simplest Metazoa, but continues among plants up to and including the latest groups to appear. Nor is there any special line of cell generations between the gametes of the parent individual and those produced by the offspring. Many generations of tissue cells intervene between each occasion when some of them are specialised into gametophytes from which the gametes are produced. These periods may vary greatly in the individuals of the same species, even in the same individual, according to the influence of the environment, and in some cases may be delayed apparently indefinitely. In some cases the production of gametes seems to have ceased altogether, but as the main line up to what is usual in the latest stages of evolution is being followed, these divergences may be neglected for the moment.

In plants apparently there is no differentiation of a germ-plasm in Weismann's sense, for the gametes arise from cells that have indeed shown much in the way of specialised differentiation, but none at all to connect them with this function. The plant in fact goes on its own way, develops to its full capacity in form and differentiation of tissues irrespective of the production of gametophytes. These are separate individuals produced by the tissue cells at certain periods; so much so that in some cases they are thrown off to live as separate plants with quite different characters from those of the individual from which they originated (*e.g.* Prothallium of a fern).

It is indeed probable that the gametophyte may have been the original plant individual, and that the 'sporophyte', the 'plant', familiar to us all, was evolved from it and became the dominant partner in the alternating generations of the vegetable kingdom.

In a way then fertilisation and still more its sequel in evolution, sex, have become rather a convenience than a necessity to plants, for propagation by parts separated from the individual may apparently continue indefinitely in some cases.

If we accept a germ-plasm in Weismann's sense, it seems to be necessary to assume that it is differentiated afresh from the cells of the individual every time that the gametophytes are produced. This is not compatible with the idea of an isolated and specialised germ-plasm passing directly through each generation, controlling all development in the individual and the transmission of characters to the offspring.

If, however, the evolution of sex be regarded as producing a method by which certain characters—but not all—are distributed in a particular manner to the offspring, the recorded observations fit in with the hypothesis; for we have seen that the chromosomes are probably connected definitely with the Mendelian characters. As the chromosomes are passed on in equal longitudinal halves through the succeeding generations of cells that form the individual plant, similar sets of chromosomes are ready to be dealt with by the peculiar form of mitosis that ensures their distribution in a manner corresponding to the appearance of the Mendelian characters in breeding experiments, when gametes are produced. This is true also with regard to the chromosomes of the cells of individuals produced by cuttings, runners or budding; they are the same as those of the individual from which they arose, and should gametophytes be produced, Mendelian inheritance will follow.

Even annuals, which in cold climates suggest a dependence upon sexual reproduction for survival, may be propagated from cuttings under suitable conditions, and the production of new individuals from separated parts is common in tropical and sub-tropical climates. The sexes may be completely separated, so that an individual plant produces only the fertilising or the fertilised gametes; in many of the higher plants the individual produces both male and female gametophytes and in many the same gametophyte produces both fertilising and fertilised gametes. The latter may be self-fertilised or not.

The evolution of sexual reproduction from simple fertilisation has followed a different course and reached a very different end among animals. Most of the Protist animals that have been the subjects of breeding experiments, seem to degenerate and die out unless fertilisation takes place periodically, though it seems probable that no fertilisation takes place in some forms. The periods may be prolonged by changes in the environment, but apparently fertilisation usually takes place sooner or later if the race is to survive. Fertilisation, the mixture of the protoplasm derived from two individuals, seems then to have become necessary to animals at an early stage in evolution. What advantage is gained by fertilisation has been, and doubtless will be, the subject of much speculation. It is clear that in cases where two Protist individuals fuse, an immediate reduction in numbers must result. The advantage then, to the succeeding generations, must be through amalgamating variations that have occurred in different individuals; through a renewal of vigour in the race; or in some other more obscure ways.

In the evolution of animals, sex appeared early, and became essential to the continuation of the race in the later groups. Hermaphroditism is common only among the Metazoa belonging to the earlier groups. Parthenogenesis is generally most reasonably explained as having arisen in forms that at one time required a fusion of two gametes at each generation of new individuals.

Reproduction through the agency of gametes necessarily involves fertilisation, whether the two fusing members are derived from different individuals or from one only. The facts indeed indicate clearly that the function of simple fertilisation, a mixture of the protoplasm of two individuals, is more primitive and possibly more important in some ways than the sorting of the chromosomes brought about by the maturation of the gametes. The function of the latter process is fundamentally different. This is emphasised by the fact that, though fertilisation is probably necessary to all animals and sex or at any rate gametes to all but the earliest groups, neither are necessary to plants. Yet the same complicated process occurs in both animals and plants when gametes are produced, but on no other occasion.

Accompanying these great differences between animals and plants with regard to fertilisation and sex, there are two other differences almost as striking—the early differentiation and isolation of the cells that are destined to produce gametes in animals; and what has been called somatic co-ordination. (Walker, 1907–10.) The latter follows the former, both being most highly developed at the ends of some of the main branches of evolution.

The isolation of the cells destined to produce gametes from the rest of the cells forming the animal, began apparently very shortly after the age of Protozoa. The separation of the two different lines of cell generations, the one going to produce the various tissues of the body, the other destined to produce the gametes, has been traced back in some cases as far as the first segmentation of the fertilised ovum. Here we have something in the nature of the germ-plasm of Weismann. The gametogenic cells form in some ways an independent constituent of the body of the animal. They are dependent upon the body in which they live for their nourishment. The body can exist without them, but the secondary sexual characters are dependent upon their presence. The continuance of the race among the higher animals is dependent entirely upon the continuance of successive generations of gametogenic cells, from which the bodies of the individuals are produced as vehicles for the production of further generations.

This isolation and partial independence of the germ-plasm has led to applying the term 'somatic' to all the cells forming the body of the animal and 'gametogenic' to those destined to produce gametes. The term 'soma' is used to distinguish the body as a whole from the germ-plasm. The facts do not warrant the use of the terms 'soma' and 'somatic' in the case of plants.

The general capacity for producing all or most of the various specialised cells of the soma from cells that have already reached their apparent limit of differentiation, has almost disappeared at the ends of some of the branches of evolution in animals (mammals, birds and some insects). This capacity, so striking in individuals belonging to the early groups, disappears gradually in some of the later. For instance, a newt can reproduce tissues from cells that have already been differentiated to form another kind of tissue. In mammals, however, the latest group of vertebrates to appear, when once differentiation has taken place in the development of the embryo, each cell can reproduce only its own kind. The one exception is a small group of cells, some of the progeny of which remain undifferentiated throughout the life of the individual, and may upon occasion undergo differentiation (*e.g.* the formation of scar-tissue). On the other hand, some of the cells of the body, when once fully differentiated, never multiply at all (*e.g.* nerve-cells). This phenomenon, somatic co-ordination, has been described in a slightly different way as 'Cell Autonomy'. (Ewing, 1908.)

The general conclusion is this. Among the higher animals only the gametogenic cells can continue for an indefinite number of generations, those forming the soma being limited to a comparatively few generations; among the plants, the individual is in a sense potentially immortal, the gametophytes being produced at intervals that may vary greatly, and are not always necessary to the continuance of the race.

Evolution has resulted in fundamental differences, morphological and physiological, between plants and animals with the exception of the processes of mitosis and the maturation of the gametes. Is any explanation of this phenomenon possible?

The only function that can be definitely attributed to the chromosomes up to the point at which we have arrived, is that they are connected with, or actually contain the factors that represent the Mendelian characters.

The Mendelian characters are minor differences superimposed upon already established older characters. They are minor characters because they are never essential to the life of the individual organism. If they were they obviously could not be inherited in the Mendelian manner—they must be common to every individual of the race. Sex is a racial character in many groups. The potentiality to produce either sex is present in all the individuals of such groups, but only one set of characters usually appears. (Chapter XI and p. 196.)

If it be assumed that the chromosomes contain factors controlling only comparatively recent variations, does the assumption agree with all the recorded observations in relation to the inheritance of all characters?

Though each variation must have originated in one, or perhaps more than one individual, it may be transmitted in the Mendelian manner through many generations; so the variations upon which the Mendelian characters depend can be called 'recent' only when compared with those characters, common to all the individuals of the race, upon which they have been superimposed.

Taking the evidence of quite uncompromising

Mendelians, it is clear that the Mendelian characters frequently, if not always, tend to blend—the pairs of 'allomorphs' tend to merge into each other. (See pp. 135 to 137.)

A very large proportion of the Mendelian experiments have been upon domesticated animals and plants. *All* observations upon the inheritance of Mendelian characters necessitate a controlled environment and a controlled crossing of gametes derived from chosen individuals. The only difference between the domesticated races and the wild is that the former have been subjected to these controlled conditions longer and more rigidly than the latter.

Man, in breeding animals and plants, whether with the object of increasing the usefulness or attractiveness of a race as in the case of stock-breeders and horticulturists; or with the object of ascertaining more facts relating to the inheritance of characters, must always unconsciously have selected variability (*e.g.* the breeding experiments with *Drosophila*). Many of the variations are so large that they would have been eliminated at once in an uncontrolled environment. In establishing himself as the most important factor of the environment in preserving and accumulating the particular variations he desires, man has also incidentally preserved many variations that would not have survived but for his intervention, though he may not be interested in them (*e.g.* the colour of race-horses). The greater variability of domesticated races and the greater frequency of *large* variations than in wild races are thus accounted for.

The blending of Mendelian characters suggests that the dependence of these characters upon particular chromosomes or parts of chromosomes, is gradually transferred to the protoplasm as a whole, or to some other constituents of the cells. Whether this has actually happened already in any of the domesticated races is a matter for enquiry, and is not essential here, as the period of domestication may possibly not be long enough. Experiments to test this could be easily devised in large numbers. Unfortunately most of the breeding experiments have been done with the object of proving that all inheritance is Mendelian. In any case, domesticated animals and plants, when placed in an uncontrolled environment, generally revert to the characters of a wild ancestor.

It is surprising that at the present time species should so frequently merge into each other. The changes produced by the environment seem to be very gradual. There are even cases where a slightly different environment is apparently in process of producing different species. (Chapter X.) Nevertheless, considering the huge period of time involved, a sharp demarcation between species might well have been commoner than it is had all variations been inherited in the Mendelian manner and not tended to blend. Rapid fixation of beneficial, and rapid elimination of injurious or useless variations, would hasten the process of adaptation very materially. The Mendelian inheritance of variations brings about this result in a few generations, while if all variations blended on crossing a vast number of generations would be required to produce it.

The results of selective breeding demonstrate this point. Without Mendelian inheritance it would hardly have been possible for breeders to produce the marked changes in a few generations in response to the requirements of the judges in the case of the poultry described by Darwin.

'The English judges decided that the comb of the Spanish Cock, which had previously hung limply down, should stand erect, and in five years this end was achieved; they ordered that hens should have beards and six years later fifty-seven of the groups of hens exhibited at the Crystal Palace in London were bearded.' (Darwin, 1884.)

These characters were produced in a short time by choosing the birds that showed the required change to breed from.

Yet when two races separated in time and locality are crossed, the characters common to the individuals of each race very definitely blend (p. 132 *et seq.*). It would be interesting and informative if races that are apparently evolving into distinct species were crossed (*e.g.* in *Deronectus* or *Gyrinus*, p. 134).

All this is in favour of the view that the dependence of Mendelian characters upon individual chromosomes is gradually transferred to the protoplasm generally or some constant constituents of the cells, and that the Mendelian inheritance ceases when the character is established. If this be the case, there are characters that are definitely *racial* and blend, and others that may be called *individual* that segregate in breeding. Probably there are stages between the two forms of inheritance, and this might prove an interesting line of investigation.

It has been claimed that the hypotheses built upon Mendel's discoveries have supplanted rather than modified Darwin's Theory of Natural Selection. (Bateson and others.) Actually the effect of Mendel's discoveries is to supplement and strengthen it. Many of the difficulties in explaining the rapid adaptation of organisms to their environment are eliminated by this knowledge gained since Darwin's time.

The experiments described in Chapter IX seem to prove conclusively that some characters, even whole groups of characters, are dependent in some ways upon certain portions of the cytoplasm of the fertilised ovum; for if a portion be destroyed certain parts of the body of the animal developing from it are missing. The absence of a considerable part of the body must involve the absence, not only of the larger racial characters included in it, but of all the smaller characters superimposed upon them. This seems to increase the probability of the chromosomes being connected only with the Mendelian characters—with variations of comparatively recent origin. Without the larger characters, the smaller ones superimposed upon them could not appear.

Apparently we are left with two different kinds of characters in the individual: those controlled by the chromosomes that are inherited in the Mendelian manner; and those controlled by the protoplasm of the rest of the cell. Upon the former evolution has depended mainly since the appearance of the complicated process of maturation of the gametes, particularly in the case of animals; on the latter the earliest stages were entirely dependent, though they now probably play but a small part in the case of animals and but a minor part in the case of most plants.

Mutations are simply Mendelian characters—variations occurring in the chromosomes; more obvious than those that occur in the rest of the protoplasm of the cell because they segregate in breeding experiments instead of blending. The genotype hypothesis depends entirely upon the assumptions made in the interpretation of Mendelian inheritance, in so far as it affects the general interpretation of evolution.

Sex seems in some organisms to be definitely connected with particular chromosomes; in others it seems impossible that it can be related to them in any way. (See Chapter XI, *Bonellia*, Frogs, etc.) It behaves as a Mendelian character in the cases where it can be definitely connected with a particular chromosome.

It is impossible to form any clear idea as to how such a state of affairs has come to exist at the present stage of evolution without a careful consideration of the different stages through which the process of reproduction has passed after that of simple division or budding. There are five stages, at each of which a new process with additional functions is introduced.

The first stage is simple fertilisation, the blending of the protoplasm of two separate individuals. Among its functions is almost certainly a renewal of vigour and fertility in the race.

The second is the appearance of the chromosomes. The evidence already considered suggests strongly that they are definitely connected with the reappearance in succeeding generations of some of the variations occurring in the individual.

The third is the differentiation between the two individuals destined to conjugate. This facilitated the meeting of the conjugants in many ways.

The fourth, and in some ways the most important stage, is the appearance of the process of meiosis, the result of which is that half the number of whole chromosomes is distributed to each gamete instead of a longitudinal half of every chromosome, as occurs in the usual mitotic division. This provides for the rapid fixation or equally rapid elimination of such characters as are connected with the chromosomes. Fertilised and fertilising gametes may be produced by the same individual, so obviously meiosis is not dependent upon sex.

The fifth stage is the differentiation of the individuals of a race into two groups, one producing the fertilising or active gamete, the other the fertilised or passive. These individuals differ from each other in morphological and other characters, sometimes to an enormous extent. Its functions are very numerous. It ensures the mixing of the protoplasm and characters of two individuals. In some cases it ensures that the gametes shall not be derived from nearly related individuals. The ways in which the secondary sexual characters facilitate the union of the gametes in various organisms are too numerous to discuss.

Each of these stages involves all those preceding it. Simple fertilisation, for instance, takes place in all, for some of the protoplasm as well as the chromosomes is always carried by both gametes.

Sex is a character added to those already possessed by an organism, and probably arose through a series of variations. If the male and female characters blended in succeeding generations, any advantage their presence brings to the race would disappear. They must appear alternatively to be of any use. This is not comparable in any way to the disappearance of the Mendelian characters.

The secondary sexual characters are dependent for their appearance upon the presence of the gametogenic cells in the case of all those animals that have been sufficiently investigated. They seem to be due to some internal secretions which are produced as the individual reaches sexual maturity. In many animals the potentiality to produce the secondary characters of the opposite sex is present, as they appear under certain conditions. In mammals, the latest product of evolution, not only are many rudiments of the sexual characters of the opposite sex present in all individuals, but the sexes tend to blend, just as do the Mendelian characters, culminating sometimes in the production of a hermaphrodite.

The effect of the selection of variations would be to eliminate any that tended towards blending as regards sex, though it is evident that variations in this direction still continue to appear.

The probable line of the evolution of modes of reproduction is far more difficult to follow in plants. The continuance of the production of new individuals by parts separated either naturally or artificially from the parent; the production of gametophytes of different sexes by the same individual; the production of gametophytes of one sex only by an individual; and self-fertilising plants in which there is no sex but meiosis occurs all the same: all these conditions are found among plants belonging to recent groups.

The dioecious plants seem to have gone one step towards sex as it exists in the soma of animals. The individuals (sporophytes) that form the asexual generation, give rise to either male or female gametophytes, not to both, and so only one kind of gamete is produced through the individual plant. In this sense there is sexual differentiation in the asexual generation. But here the analogy ends, for while in the animals where sexual reproduction occurs it is a necessity, in plants it is a luxury. The Lombardy Poplar, of which only one sex is known to exist, demonstrates this fact.

In all these cases reproduction involving fertilisation, chromosomes, meiosis and sex, are supplemental to the direct method. These supplements, however, produce just the same results as they do in animals: a mixture of two different protoplasms; the handing on of exact representative halves of chromosomes; the distribution of whole chromosomes; and, where sex exists, the mixing of the protoplasm and chromosomes of two different individuals.

While sex has been definitely connected with particular chromosomes in the case of many insects and some other animals, the case with mammals seems more doubtful. In plants but few cases of sex chromosomes have been described.

On the other hand we have very definite evidence that the sex of the individual animal may change, even in an uncontrolled environment and after the development of all the different tissues including the sexual glands (*e.g.* frogs, Chapter XI).

It would seem then that sex may be determined without the intervention of chromosomes in many cases. Whether it has become definitely connected with particular chromosomes in some cases as a late manifestation of evolution, or, as seems less probable, it was originally so represented and the connection has gradually ceased, does not affect the main issue as to how evolution generally has come about.

The only physiological functions that have followed the same complicated process of evolution down to minute details in animals and plants, are those dependent upon simple fertilisation, the chromosomes, meiosis and sex. No hypothesis pretending to account for the evolution of living organisms can be true unless it fits in with the known facts with regard to these phenomena. The facts, if taken in the proper order, suggest that these processes have followed the same line of evolution in the main in both animals and plants because they thus met the least resistance and the best means of securing the mixing of the protoplasm of different strains, and the rapid fixation of and elimination of variations.

The side lines of evolution in different modes of reproduction, such as that in *Aggregata* (Chapter XI) are not at all incompatible with this general scheme. The process of evolution in this case may have got to the stage involving fertilisation, the differentiation of forms and the appearance of chromosomes, and subsequently as the environment became very different from any experienced by free-living organisms, a very different result was bound to be produced. It shows, however, that though the chromosomes may be connected with the reappearance of variations, they cannot in this case be connected with any large racial character including sex, and that the variations cannot be transmitted in the Mendelian manner, as the distribution of the chromosomes is entirely different to that occurring during the usual form of meiosis. It indicates also that sex was probably not originally connected with individual chromosomes.

The Mendelian experiments have been confined to morphological characters. Breeding experiments with regard to mental characters present very obvious difficulties, and we are dependent upon general observations. The same comment may be made with regard to functional characters such as the immunity enjoyed by cattle and other Herbivora to certain poisons (*e.g.* Belladonna and Aconite.)

We have little or no evidence with regard to the mental and functional characters except that they are frequently inherited.

Galton and others have provided a great deal of evidence with regard to mental ability both general and in particular directions; and also with regard to the inheritance of the capacity to acquire particular skill of different kinds. The criminal taint is also evidently inherited. There are many cases on record. The classical one of the Juke family in the United States will suffice as an example. In the hope of improving the strain, members of the family were taken in babyhood and brought up under circumstances most favourable to the development of any moral and other desirable mental capacities they might possess; some in institutions of different kinds, others in private families; they all turned out as criminally inclined as their ancestors. Their performances appear to have been limited only by their opportunities. (Davenport, 1912.)

That mental capacities may be produced and improved by selection is clear. Pointer dogs are an example. But we have no evidence that there is any segregation of such characters in breeding.

The remarkable condition known as Haemophilia (bleeding to a serious and sometimes fatal extent after a slight injury) is confined to men, but is inherited entirely through the female. The sons of a haemophilic father will not inherit the condition, but his grandsons through his daughters may. The females may show some tendency to bleed a little more freely than usual, but the condition is not marked and is not dangerous.

Here we have a character definitely linked with sex. It has of course been interpreted as a Mendelian sex-linked character in the sex-chromosome. The evidence as to the presence of sex-chromosomes in man is not very satisfactory. It is clear that in some vertebrates sex is not dependent upon the presence or absence of a particular chromosome, so haemophilia may be related to sex without assuming any relation to a chromosome. The question is still open. One assumption is as good as another when the evidence is contradictory.

The experiments upon the inheritance of immunity to 'rust' enjoyed by some kinds of wheat and other cereals, did not show definite segregation, and the later generations were not 'back-crossed'. Moreover the immunity of wheat to 'rust' is not like the immunity of an animal to a disease. The survival is not due to resistance to infection, but to extreme susceptibility. The cells that are attacked die at once and so the infected area is cut off by corky, or apparently corky, dead cells, the rust fungus thus being starved out.

A frequently reiterated objection to Darwin's theory is that 'no one has seen Natural Selection at work'. The previous chapters give several cases of recent observations that can hardly be interpreted in any other sense than that we have seen it at work. Apart from this the distinction between 'Natural' and the miscalled 'Artificial' Selection seems entirely unsubstantial and foolish.

The only difference between the two is that between a controlled and an uncontrolled environment in the selection of variations. Observations upon the inheritance of variations cannot be carried out in an uncontrolled environment. All that Darwin's theory requires is that the environment is capable of selecting variations. Whether the environment is experimentally controlled or not makes not the slightest difference.

Experiment is the most exacting test of any hypothesis, and experiments, unconscious though they may have been, had proved the efficacy of the selection of variations long before Darwin was born. 'Artificial' is used in the same sense as 'Experimental' in relation to Darwin's theory, and the general adoption of such a distinction would invalidate nearly all the results of experimental investigation in most branches of science.

Certain general conclusions seem justifiable from the facts that have been described in this and the preceding chapters.

(1) Evolution has depended upon the occurrence of variations in living organisms.

(2) In primitive forms of living organisms variations were probably due to changes in the general protoplasmic structure of the organism, and were inherited by the offspring.

(3) At some early stage in evolution, chromosomes were gradually differentiated from the protoplasm, and

the transmission to the offspring of some of the variations arising in the individual gradually became connected with them. Variations, however, continued to originate in the protoplasm generally, and were transmitted to the offspring. *Both forms of inheritance still continue in existing organisms.*

(4) The Mendelian forms of inheritance could not have occurred until the appearance of the phenomenon of meiosis, which provided the necessary alternative distribution of the chromosomes to the gametes.

(5) The bulk of the characters that are transmitted from parent to offspring are not connected with the chromosomes, and are not inherited in the Mendelian manner. (Chapters VIII, IX and X.)

(6) The unit potentialities upon which the appearance of the Mendelian characters depend, are of the nature of the genes, postulated by Johannsen. They are definitely connected with the chromosomes and no function apart from the chromosomes can be connected with them.

(7) Mutations and genes are probably manifestations of variations arising in the chromosomes themselves as distinct from any other part of the cell.

(8) Mendelian characters tend to blend and probably give rise eventually to racial characters, common to all the individuals forming large groups—specific and generic characters (pp. 135-7).

(9) The effect of the alternative mode of distribution of the chromosomes in the phenomenon of meiosis and of Mendelian inheritance has been to hasten the fixation and elimination of variations in the later stages of evolution.

The statements made by Huxley in the quotation given at the beginning of this book seem to have been verified in a remarkable manner.

Darwin made an epoch with his Theory of Natural

Selection. Weismann and others carried it too far in certain directions, so that, as they interpreted it, it no longer fitted in with evolution as a whole.

Mendel made an epoch, and some of his followers, in trying to interpret the whole of evolution in terms of his discovery alone, and to discredit the Theory of Natural Selection, have done their best to throw away truth.

The huge superstructure of assumptions built upon Mendel's discovery stands or falls, not with his discovery which remains untouched, but with the fitting in of these assumptions to the structure of evolution as a whole. Darwin's Theory of Natural Selection is affected by Mendel's discovery only to its advantage.

# BIBLIOGRAPHY

AGAR, W. E. 1914. Parthenogenic and Sexual Reproduction in *Simocephalus vetulus* and other *Cladocera*. JOURNAL OF GENETICS, III.

ANDREWS, E. A. 1898. Filose Activity in Metazoan Eggs. ZOOL. BULL. 2, I.

BACOT, A. 1906. ENTOMOLOGIST'S RECORD, XIII. pp. 114-17, 142-4.

BALFOUR-BROWNE, F. 1930. SCOTTISH NATURALIST. November–December.

BALTZER, F. 1914. MITTEIL. D. ZOÖLOG. STATION NEAPEL. XXII.

Die Bestimmung und der Dimorphismus des Geschlechts bei Bonnellia. SITZUNGS BERICHTE DER PHISICK-MED-GESELLSCH. ZU WÜRTZBURG.

BARY, H. A. DE. 1862. Über den Bau und das Wesen der Zelle. FLORA.

BASHFORD. 1911. FOURTH SCIENTIFIC REPORT, IMPERIAL CANCER RESEARCH FUND.

BATESON, W. 1894. Materials for the Study of Variation. LONDON.

BATESON AND PUNNETT. 1905. REPORT, EVOLUT. COM. 2-19-131.

BAUMGARTNER, W. J. 1902. KANSAS UNIV. SCI. BULL. VOL. I. NO. 2. Old Series. VOL. II.

1904. BIOL. BULL.

BĚLAŘ, K. 1921. Untersuchungen über Formwechsel von *Actinophrys*: BIOL. CENTRAL. XLI.

1923. Untersuschungen an *Actinophrys Sol. I.* ARCHIV FÜR ZELLFORSCH. XVI.

BENDA, C. 1903. Die Mitochondria. ERGEBNISSE DER ANATOMIE UND ENTWICKLUNGSGESCHICHTE. WIESBADEN.

BERGSON, HENRI. 1911. Creative Evolution. (English translation. A. Mitchell.)

1912. Matière et mémoire. PARIS.

BOVERI, TH. 1899. Die Entwicklung von *Ascaris megalocephala* mit besonderer Rucksicht auf die Kernverhältnisse. (FESTSCHR. FÜR C. VON KUPFFER.)

1903. Über den Einfluss der Samenzelle auf die Larven-Charactere der Echiniden. ARCHIV FÜR ENTWICKLUNGS-MECHANIK. XVI.

1909. Die Blastomerenkern von *Ascaris megalocephala* und die Theorie der Chromosomen-individualität. ARCHIV FÜR ZELLFORSCHUNG.

1911. VERHAND. D. PHYS. MED. GESELLSCH. WÜRZBURG.

BRIDGES, C. B. 1913. Nondisjunction of the Sex Chromosomes of Drosophila. JOURN. EXPER. ZOOL. XV.

1914. SCIENCE. N.S. XL.

BROUARDEL. 1902. BRITISH CONGRESS ON TUBERCULOSIS. VOL. I.

BROWNE, E. T. 1895. On the Variation of the Tentaculocysts of Aurelia aurita. QUART. JOURN. MICRO. SCI. XXXVII.

BROWN-SÉQUARD. 1869. ARCH. PHYSIOL. NORM. PATH. VOL. II.

1871. VOL. III., 1872. VOL. IV. And many other papers in ARCH. PHYSIOL. up to 1893.

CALKINS. GARY N. 1909. Protozoology. NEW YORK.

CAROTHERS, E. E. 1913. The Mendelian Ratio in relation to certain Orthopteran Chromosomes. JOURN. MORPH. XXIV.

1917. The Segregation and Recombination of Homologous Chromosomes. JOURN. MORPH. XXVIII.

CARREL. A. 1911. Rejuvenation of Cultures of Tissue. JOURN. AMER. MED. ASSN. LVII. 1611.

1913. Artificial Activation of the Growth in Vitro of Connective Tissue. JOURN. EXP. MED. XIV. 17.

1924. Tissue Culture and Cell Physiology. PHYSIOL. REVIEW. 4. I.

CASTLE, W. E. 1922. Genetic Studies of Rabbits and Rats. CARNEGIE INST. PUBL.

1923. CARNEGIE INST. YEAR BOOK. NO. 27.

1929. JOURN. EXP. ZOOL. 53 (3) 421.

CLEMENTS. 1925–29 and 1930. CARNEGIE INST. YEAR BOOK.

(With WEAVER.) 1929. Plant Ecology.

COOPER, J. OMER. 1930. ENT. MON. MAG. VOL. 66.

1931. NATURE, Feb. 14th.

CORRENS, C. 1906. Die Vererbung der Geschlechts formen bei den gynodiöcischen Pflanzen. BERICHTE DER DEUTS. BOT. GESELLSCH. XXIV.

DARBISHIRE. A. D. 1902. Note on the Results of Crossing Japanese Waltzing Mice, etc. BIOMETRIKA. II. pp. 101-4, 165, 282.

1908. On the Result of Crossing Round with Wrinkled Peas, etc. PROC. ROY. SOC. B. VOL. 80.

DARWIN. CHARLES. 1885. The Variations of Animals and Plants under Domestication. *Second Edition.*

DAVENPORT, C. B. 1906. Inheritance in Poultry. CARNEGIE INST. OF WASHINGTON.

1912. Heredity in Relation to Eugenics. LONDON.

DELLA VALLE. P. *See* VALLE, DELLA.

DETLEFSEN. 1923. PROC. AMER. PHILOSOPH. SOC. VOL. LXII. NO. 5.

DIBLE. J. HENRY. 1929. Recent Advances in Bacteriology. CHURCHILL, LONDON.

DIGBY, L. 1919. ANNALS OF BOTANY. VOL. 33. NO. 103.

DOBELL, C. C. 1911. The Principles of Protistology. ARCHIV FÜR PROTISTENKUNDE. VOL. XXIII.

1924. The Chromosome Cycle of the Sporozoa considered in relation to the Chromosome Theory of Heredity. LA CELLULE, t. XXXV. I fascicule.

DRIESCH, H. 1892. Entwicklungsmechanische. ANAT. ANZEIGER. VII.

1900. Die isolierten Blastomeren des Echinoden Klims. ARCHIV FÜR ENTWICKLUNGSMECHANIK. X.

1903. IBID. XVI. 4, XVII. I.

1908. The Science and Philosophy of the Organism. BLACK, LONDON.

DUESBERG, J. 1907. Der Mitochondrialapparat, etc. ARCHIV FÜR MIKROS. ANAT. LXXI.

1909. Les Chondriosomes des cellules embryonnaires du poulet. ARCHIV FÜR ZELLFORSCHUNG. IV.

1919. On the Present State of the Chondrisome Problem. BIOL. BULL. XXXVI.

EAST, E. M. 1911. THE AMERICAN NATURALIST. VOL. XLV. January and November.

ELLIOT, HUGH. 1912. Modern Science and the Illusions of Professor Bergson.

1913. The Spectre of Vitalism. SCIENCE PROGRESS.

1914. Translation with Introduction of Lamarck's 'Philosophie zoologique'.

FICK. R. 1907. Vererbungsfragen, Reduktions-und Chromosomenhypothesen Bastardregeln. ANAT. HEFTE 2. ABT. ERGEBN. D. ANAT. U. ENTWICK. GESCH. XVI. I.

FISCHER, ALBERT. 1903. Entwicklung und Organdifferenzierung. ARCHIV FÜR ENTWICKLUNGSMECHANIK. BD. 15.

1925. Tissue Culture. HEINEMANN, LONDON.

FRANZ, V. 1911. Was ist ein höherer Organismus? BIOL. CENTRALBL. BD. 31.

GALTON, SIR FRANCIS. Inquiries into Human Faculty. EVERYMAN'S LIBRARY, pp. 33 *et seq.*

1892. Hereditary Genius. MACMILLAN. LONDON.

GALTSOFF, P. S. 1923. The Amoeboid Movements of Dissociated Sponge Cells. BIOL. BULL. XLV.

1924. Regeneration after Dissociation. IBID.

GATES, R. RUGGLES. 1929. Heredity in Man.

GEINITZ, B. 1913. ARCHIV FÜR ZELLFORSCH. XII.

GODLEWSKI, E. 1906. Untersuchungen über die Bastardierung der Echiniden und Crinoidenfamilie. ARCH. FÜR ENTWICKLUNGSMECHANIK. BD. 20.

GOLDSCHMIDT, RICHARD. 1923. The Mechanism and Physiology of Sex Determination. (English translation.)

GRIFFINS. SCIENCE. N.S. VOL. 56, p. 676.

GUYER, M. F. 1909. (*a*) The Spermatogenesis of the Domestic Guinea (Fowl). ANAT. ANZ. XXIV; (*b*) The Spermatogenesis of the Domestic Chicken. IBID. XXIV.

1923. PROC. AMER. PHILOSOPH. SOC. VOL. LXII. NO. 5.

HANCE, R. V. 1917. The Diploid Chromosomes of the Pig. JOURN. MORPH. XXX.

1918. Variation in Somatic Chromosomes. BIOL. BULL. XXIV, and Variations in the Number of Somatic Chromosomes. GENETICS. III.

HANSON, BLAIR, SCHOLES and KEYS. 1928. GENETICS. 13, and ZEIT. INDUCKT. ABSTAM. UND VEREB. Supplement b. 2.

HARMER, SIDNEY F. 1908. Presidential Address. Zoological Sect. British Association.

HARPER, R. A. 1918. Organisation, Reproduction and Inheritance in Pediastrum. PROC. AMER. PHIL. SOC. LVII.

Harris, J. Arthur. 1911. AMERICAN NATURALIST. VOL. XLV, p. 686.

Harrison and Doncaster. 1914. On Hybrids between Moths of the Geometrid Sub-family Bistominae. JOURN. OF GENETICS. III.

Harrison, J. W. H. 1928. PROC. ROY. SOC., B, VOL. 102, p. 347.

Heidenhain, M. 1911. Plasma und Zelle. JENA.

Henking, H. 1891. Untersuchungen über die ernsten Entwicklungsvorgänge in den Eiern der Insekten. ZEITS. FÜR WISSEN. ZOOL. LI.

Herschel, Sir John. 1850. EDINBURGH REVIEW.

Hertwig, R. 1912. Über den derzeitigen Stand des Sexualitätsproblems nebst eigenen Untersuchungen. BIOL. CENTRALBL. 32.

Hirsch. 1883. Geographical and Historical Pathology. VOL. III. (*a*) p. 587; (*b*) p. 189; (*c*) p. 167.

Hofmeister, W. 1867. Lehre von der Planzenzelle. LEIPZIG.

Huxley, J. 1927. NATURE, (*a*) December, p. 902; (*b*) March, p. 350.

Huxley, T. H. 1853. The Cell-theory. (Scientific Memoirs of T. H. Huxley. VOL. I.)

Jennings, H. F. 1911. Assortive Mating, Variability, etc., and Pure Breeds in the Study of Genetics. JOURN. EXPER. ZOOL. XI., and Pure Lines in the Study of Genetics. AMERICAN NATURALIST. VOL. XLV.

Jennings and Hargitt. 1910. JOURN. MORPHOL. December.

Johannsen, W. 1908. Über Knospermutation bei Phaseolus. ZEIT. FÜR INDUK. ABST. VERERB. I. LEIPZIG.

1911. The Genotype Conception of Heredity. AMERICAN NATURALIST. (March) XLV.

1923. Some Remarks about Units in Heredity. HEREDITAS. IV.

Kammerer, P. 1907. Die Fortpflanzung des Grottenolmes (*Proteus anguineus*). VERH. ZOOL.-BOT. GES. WIEN. 57, pp. 277-92.

1912. Experimente über Fortpflantzung, Farbe Augen, und Körperreduktion bei *Proteus anguinus*, etc. ARCH. FÜR ENTWICKLUNGSMECHANIK. BERLIN.

1913. Nachweiss normaler Funktion bein herangewachsenen Lichtaugen des *Proteus*. ARCH. GES. PHYSIOL. 153, pp. 430-40.

1914. (With DÄHNE) *Alytes obstetricans* und seine Brutpflage. BL. AQUARIEMK. STUTTGART, pp. 227-9 and 259-61.

1923. Breeding experiments on inheritance of acquired characters. NATURE 111, pp. 637-40; 112, pp. 237-8; 112, pp. 826-27.

1926. (With WETTSTEIN) Der Artenwandel auf Inseln und seine Versachen, etc. LEIPZIG and WIEN. 324 pp. maps, photos and 8 coloured plates of lizards.

KAUTSH, G. 1912. ARCH. FÜR ZELLFORSCHUNG. VIII.

1913. ARCH. FÜR ENTWICKLUNGSMECHANIK. XXXV.

KINGSLEY, MARY. Travels in West Africa. MACMILLAN, LONDON.

LAMARCK. 1801. Système des animaux sans vertèbres.

1802. Recherches sur l'organisation des corps vivants.

1809. Philosophie zoologique. *See also* PACKARD AND ELLIOT.

LANKESTER, SIR RAY. 1912. In Introduction to Hugh Elliot's 'The Illusion of Prof. Bergson'.

LEWIS, M. R. AND W. H. 1915. Mitochondria in Tissue Cultures. AMER. JOURN. OF ANATOMY, XVII.

LILLIE, F. R. 1902. Differentiation without Cleavage. ARCHIV FÜR ENTWICKLUNGSMECHANIK. 14, 477.

LOCK, R. H. 1906. Recent Progress in the Study of Variation, Heredity and Evolution. LONDON AND NEW YORK.

LOEB, JACQUES. 1916. The Organism as a Whole. PUTNAM'S: NEW YORK AND LONDON.

MACALISTER, ALEXANDER. 1889. Human Anatomy.

MACBRIDE, E. W. 1929. An Introduction to the Study of Heredity, pp. 108-10.

1931. Habit: The driving factor in Evolution. NATURE, June 20th, p. 940.

MCCLUNG, P. E. 1901. Notes on the Accessory Chromosome. ANATOM. AUG. XX.

1902. The Accessory Chromosome—Sex Determinant? BIOL. BULL. III.

1924. The Chromosome Theory of Heredity. GENERAL CYTOLOGY.

MEVES, F. 1904. Über das Vorkommen von Mitochondrien bezw. Chondromiten in Pflanzellen. SONDER. AUS DER BERICHTEN DER DEUTSCHEN BOTANISCHEN GESELLSCHAFT. BD. 12. HEFT. 5.

1907. Die Spermatocytenbildung bei der Honingbien. ARCH. FÜR MIKRO. ANAT. LXX.

1908. Die Chondriosomen als Träger erblicher Anlagen. IBID. LXXII.

1911. Über die Beteilung des Plastochondria an der Befruchtung des Eies von Ascaris. IBID. LXXVI.

1914. Was sind die Plastosomen. ANAT. ANZEIGER. LXXXV.

MOORE AND ARNOLD. 1906. PROC. ROY. SOC. B, VOL. 77.

MORGAN, T. H. 1898. Experimental Studies of the regeneration of *Planaria maculata.* ARCHIV FÜR ENTWICKLUNGSMECHANIK. BD. 7.

1901. Regeneration. NEW YORK.

1919. The Physical Basis of Heredity.

1924. Mendelian Heredity and Cytology, in GENERAL CYTOLOGY.

1927. Experimental Embryology. NEW YORK.

NÄGELI, C. VON. 1884. Mechanische-physiologische Theorie der Abstammungslehre. MUNICH AND LEIPZIG.

OCHS, GEORG. 1927. KOLEOPT. RUNDSCHAW. BD. 13.

OSLER, SIR W. 1904. The Principles and Practice of Medicine. *Fifth Edition.*

PACKARD, ALPHEUS S., 1901. Lamarck; His Life and Work; with Translations of his writings on Organic Evolution. LONGMANS GREEN & CO., LONDON.

PEARSON, KARL. 1900. Grammar of Science.

PLOUGH, H. H. 1917. The Effect of Temperature on Crossing Over. JOURN. EXPER. ZOOL. XXIV.

PROUT AND BACOT. 1906. *Xanthorhoë ferrugata* and its Black Aberration. TRANS. ENTOMOL. SOC. LONDON AND PROC., 1907.

1909. On the Cross Breeding of the Moth *Acidalia Virgularia.* PROC. ROY. SOC. B. VOL. LXXXI.

QUETELET. 1846. Lettres à S. A. R. le Duc Régnant de Saxe-Cobourg et Gotha sur la théorie des probabilités appliquée aux sciences morales et politiques. BRUSSELS.

Reid, Sir Archdall. 1905. Principles of Heredity.

1910. The Laws of Heredity. METHUEN, LONDON.

Robertson, W. R. B. 1915. Inequalities and Deficiencies in Homologous Chromosomes. JOURN. MORPH. XXVI.

1916. Taxonomic Relations shown in Chromosomes, etc. KANSAS UNIV. BULL. IV. 13. and JOURN. MORPH. XXVII.

Roemer, T. 1910. ARCH. FÜR RASSEN. W. GESELLSCH. BIOLOGIE. VOL. 7, P. 397.

Sachs, J. 1892. Beiträge zur Zellentheorie. FLORA.

1895. Weitere Betrachtugen über Energiden und Zellen. FLORA.

Sarbadhikari. 1924. ANNALS OF BOTANY. VOL. 38. NO. 149.

Schaudinn, F. 1902. ARCH. FÜR PROTISTENKUNDE. VOL. I.

Schleip, W. 1911. BER. D. NATUR F. GESELLSCH. FREIBURG. I.Bd. XIX.

Sedgwick, A. 1894. On the inadequacy of the Cellular Theory of Development, etc. QUART. JOURN. MICRO. SCI. VOL. 37.

1895. Further Remarks on the Cell-theory. IBID. VOL. 38.

Smith, G. Elliot, and Wood Jones. 1910. Archaeological Survey of Nubia. Report for 1907 and 1908. VOL. II. CAIRO.

Stockard. 1923. PROC. AMER. PHILOSOPH. SOC. VOL. LXII. NO. 5.

Strassen, O. L. zur. 1898. ARCHIV FÜR ENTWICKLUNGSMECHANIK. VII.

Summer and Huestis. 1921. GENETICS. V. 445-85.

Thomson, J. Arthur. 1912. Heredity. JOHN MURRAY, LONDON. *Second Edition.*

Valle, P. Della. 1909. L'organizzazione della chromatina Studiata Mediante il numero dei chromosomi. ARCHIVES ITALIENNES DE BIOLOGIE. 4.

1911. Le analogie fisico-chimiche della formazione e della dissoluzione dei cromosomi. MONITORE ZOOL. ITAL. XX.

Voinov, D. N. 1914. Sur un nouveau mécanisme déterminant la dimorphisme des éléments sexuels. COMPTES RENDUS DE LA SOC. DE BIOL. (PARIS). LXXV.

1916. Recherches sur la spermatogénèse du *Gryllotalpa*. ARCH. DE. ZOOL. EXPER. LIV. PARIS.

VRIES, H. DE. 1900. Die Mutations-Theorie. LEIPZIG. VOL. I. 1903, VOL. II.

1905. Species and Varieties. CHICAGO AND LONDON.

WALKER, C. E. 1907. Essentials of Cytology. CONSTABLE, LONDON.

1910. Hereditary Characters. ARNOLD, LONDON.

1911. On Variations in Chromosomes. ARCHIV FÜR ZELLFORSCHUNG. 6 BAND, 4 HEFT.

1913. The Study of Heredity. SCIENCE PROGRESS. Oct.

1912. JOURN. PATH. AND BACT. VOL. VII.

1923. Theories and Problems of Cancer. LIVERPOOL UNIV. PRESS.

1925. The Meiotic Phase in Triton. PROC. ROY. SOC. B, VOL. 98.

1926. The Meiotic Phase in Certain Mammals. PROC. ROY. SOC. B, VOL. 99.

WARREN, ERNEST. 1931. A Statistical Study of Certain Inter- specific Plant Hybrids and Back-crosses. ANNALS OF THE NATAL MUSEUM. VOL. VI, part 3. February.

WEISMANN, A. 1893. The Germ Plasm. (English translation). The Theory of Evolution (English translation).

WHITMAN, C. O. 1888. The Seat of Formative and Regenerative Energy. JOURN. MORPH. II.

1893. The Inadequacy of the Cell-theory of Development. BIOL. LECTURES, WOODS. VOL. 2, p. 105.

WILSON, E. B. 1904. Experimental Studies on Germinal Localization I and II. JOURN. EXP. ZOOL. I; and Mosaic Development in the Annelid Egg. SCI. XX.

1905. Studies on Chromosomes. SCIENCE.

Chromosomes in Relation to the Determination of Sex in Insects. IBID.

1906. Sexual Differences of the Chromosomes in Hemiptera. IBID.

1909. Studies on Chromosomes V. JOURN. EXPER. ZOOL. VI. 2.

1910. Studies on Chromosomes, VI. IBID. IX. 2.

1925. The Cell in Development and Heredity. *Third Edition.*

WILSON, H. V. 1907. On some phenomena of coalescence and regeneration in Sponges. JOURN. EXPER. ZOOL. 5.

1910. Development of Sponges from Dissociated Tissue Cells. BULL. BUREAU OF FISHERIES. WASHINGTON. XXX.

WINTER, F. L. 1929. The Mean and Variability as affected by Selection in Corn. JOURN. AGRICULT. RESEARCH. 39 (6).

WITSCHI, E., 1914. Die Keimdrüsen von *Rana temporaria*. ARCH. FÜR MIKROS. ANAT. 85.

1915. Studien über Geschlechtsbestimmung bei Fröschen. IBID. 86.

1923. Über die Genetische Konstitution der Froschwitter. BIOL. CENTRALBL.

WOODWARD, SIR ARTHUR SMITH. 1931. Modern Progress in Vertebrate Palæontology. NATURE, May 16th.

# INDEX

THE END

*Printed in Great Britain by* R. & R. Clark, Limited, *Edinburgh*.

✓