

## **An introduction to the study of heredity / by E.W. Macbride.**

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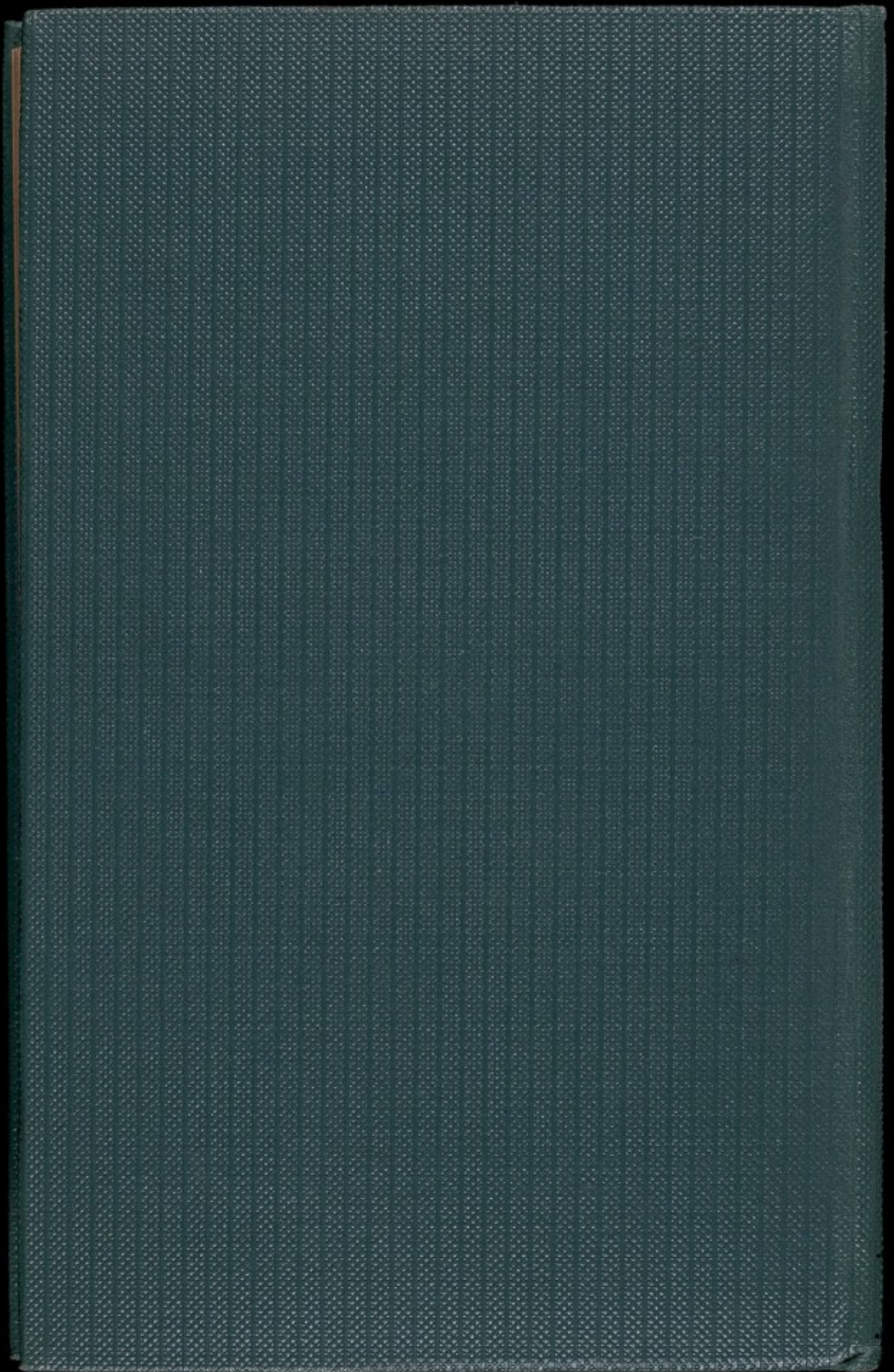
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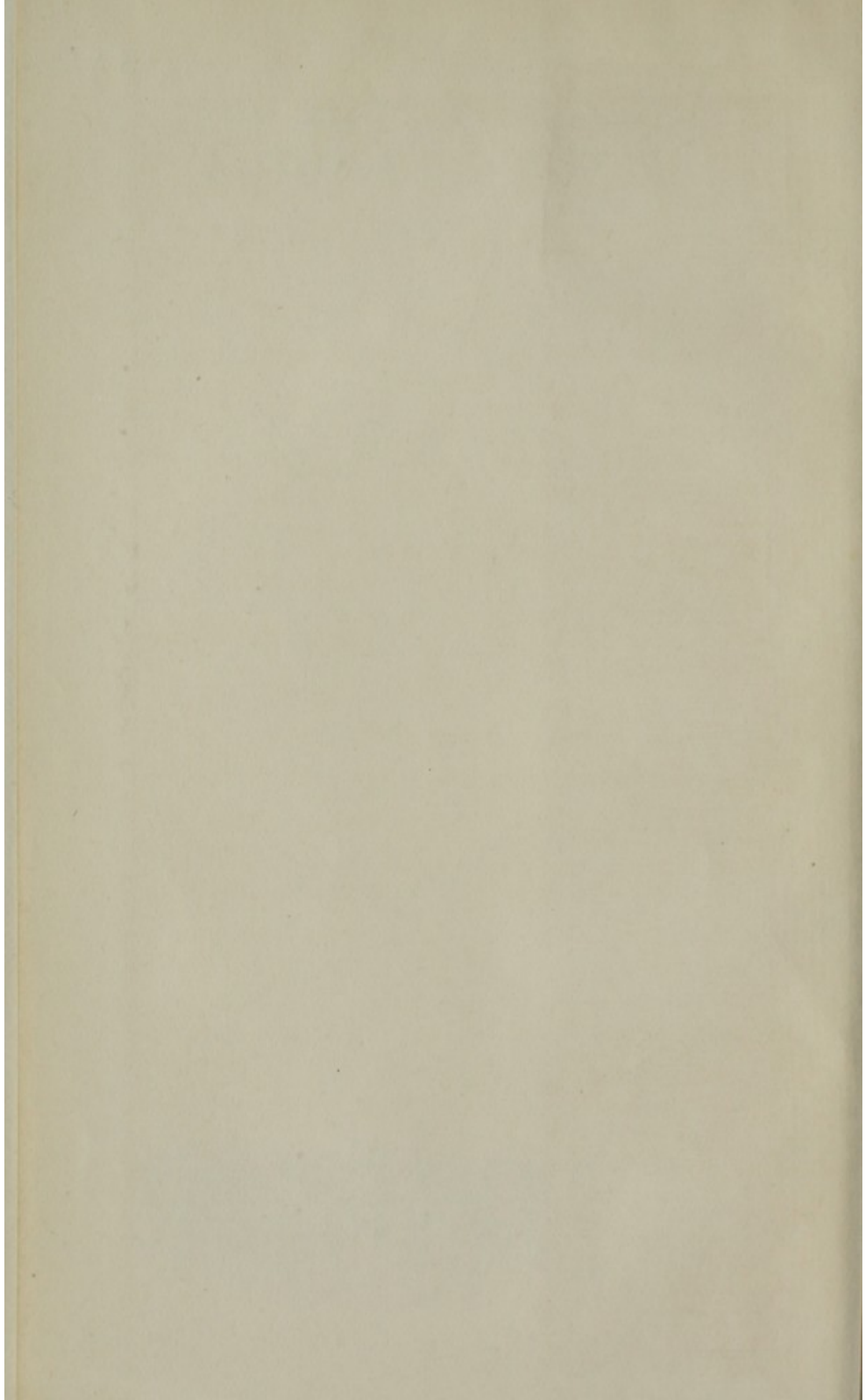


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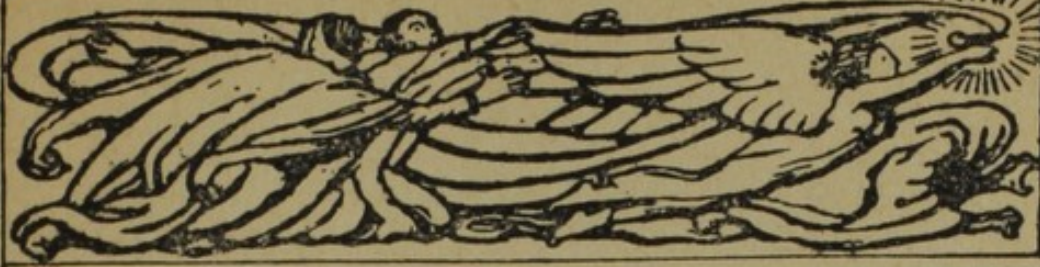
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AN  
INTRODUCTION  
TO THE STUDY  
OF HEREDITY

BY

E. W. MACBRIDE, M.A.,

D.SC., LL.D., F.R.S.

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## PREFACE

IN offering this little primer to those interested in learning something about the present state of our knowledge of the laws which govern heredity, it is hardly necessary to say that space only allows the briefest outline of the subject. The principle which has been followed is to give as far as possible one sample of each type of research bearing on the subject, and in selecting that sample to be guided by considerations of clearness and simplicity. So in dealing with statistical researches we have confined ourselves to the exposition of the normal curve of error and have omitted all references to those "skew curves" to which Professor Pearson has devoted so much research, since the mathematical treatment of these is too complex for an elementary text-book. In dealing with experiments on Mendelian inheritance those were selected which exemplify in the clearest way the principles involved, and exceptional and irregular phenomena were left out of account. The purpose for which this book

has been written will have failed of achievement if its readers are content with the account of heredity which it gives and are not spurred on to undertake further and more advanced reading on the subject.

E. W. M.



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# AN INTRODUCTION TO THE STUDY OF HEREDITY

## CHAPTER I

### INTRODUCTION

THE word "heredity" is derived from a Latin word "hereditas," which meant originally a piece of property belonging to a man which passed to his son when he died. Now everyone knows that it is from their parents that children derive their bodily and mental qualities; and this handing on of the parents' very essence to their children has come metaphorically to be called "heredity." Since in the human race a child has two parents, its nature tends to exhibit the features of a compromise between the qualities of father and mother. But the child's nature is not an exact mean between the natures of its two parents. If it were so, all children of the same family would be alike save for

differences depending on age and sex. The science of heredity consists in an investigation of the causes which bring it about that one child often resembles one parent in a certain feature and another parent in another, and differs from its brothers and sisters in this respect; why, further, a child occasionally reproduces the characters of a grandparent or of an aunt or uncle even when none of these characters is obvious in either parent. Our science then starts, like every other science, from the basis of common everyday knowledge; physics, for instance, began with the knowledge gained from handling of heavy objects, etc., through thousands of years, whilst chemistry commenced with observations on the effect of fire on stones, and the experience of the value of the various "simples" which could be extracted from herbs. Science, after all, consists in looking closely and consistently at the same things which the ordinary man regards carelessly and superficially.

The first and most fundamental problem which presents itself in the science of heredity is the manner in which the bodies of children are derived from those of their parents. In the lowest and simplest organisms, the parent

divides in two, thus yielding up its own existence in giving rise to two children. This phenomenon is known as reproduction by **fission**. When we ascend somewhat higher in the scale, we find that the offspring is often produced as an excrescence or **bud** on the body of the parent, from which it later becomes separated. In the animal kingdom when the bud grows and begins to exhibit the characteristic features of the parent, but does not separate from it, the compound system is spoken of as a **colony**. Perhaps one of the most familiar examples of propagation by means of buds is the strawberry plant. As all gardeners know, procumbent horizontal branches are given off from the stem of this plant. These branches are known as runners. At the extremity of each runner there is formed a bud which proceeds to grow up into a new strawberry plant, and the runner connecting this with the parent plant dies away.

But in the human race and in the higher animals most nearly related to it, in which we take most interest, we find that reproduction is effected neither by means of fission nor buds, but only by the formation and expulsion of small fragments of living matter

which are called **germ-cells**. This method is the most widely distributed mode of reproduction in both the animal and vegetable kingdoms. In most cases it coexists with budding and fission wherever these methods of reproduction are found, and it is in every way more interesting than they are. It is indeed apparently absent in only the very lowest plants and animals; we use the word "apparently" advisedly, for in many cases amongst these the equivalents of germ-cells are known to be formed, and he would be a rash man who would assert that in the case of any species of plant or animal germ-cells were never formed. It is therefore of the greatest importance to the scientific student of heredity to obtain a clear conception of the nature and origin of the germ-cell, and for this purpose a short digression on the fundamental nature of the structure of the bodies of animals and plants will be necessary.

All who have the slightest acquaintance with natural history are aware that it is an accepted doctrine amongst naturalists that both animals and plants are composed of cells, but few have any but the vaguest ideas as to what cells are like. It is therefore necessary to clarify our ideas on the subject

of cells, and to do this, let us reflect for a few moments on the historical origin of the word **cell**. This word was originally used to designate the chamber which housed the image of the god in a temple, but had long been employed as a name for one of the chambers in a honeycomb in which the bee stores honey, which was supposed to resemble in shape the "cella" of a temple. In the seventeenth century, Hooke, one of the pioneer English naturalists, whilst examining thin slices of cork by means of the primitive microscopes then available, discovered that these slices, viewed by transmitted light, showed a structure which he compared to that of a honeycomb, and to the cavities which he saw in them he gave the name of cells. A short time afterwards, it was discovered—chiefly by the English naturalist Grew, and the Italian naturalist Malpighi—that all living plants possessed the same structure, and the conception of a plant as a spongework of hollow cells filled with watery fluids obtained wide recognition. As investigation advanced it was pointed out that all young and active cells exhibited a layer of clear jelly-like material lining the cell-wall, and that inside this layer was the watery fluid which consti-

tuted a drop called the **vacuole**. In order to distinguish it from this, the layer of jelly was termed the **primordial utricle**. Further observation showed that when this primordial utricle disappeared, the cell exhibited no further changes and could rightly be described as dead, although it might continue to serve a useful purpose in the plant owing to the mechanical strength of its cell-wall. Attention was thus focussed on the primordial utricle, and the name **protoplasm** was invented by Von Mohl in 1846 for the material of which it was composed. When various staining fluids were employed to colour this protoplasm, and thus render it more conspicuous, it was discovered that in the protoplasm of each cell there was embedded a body, usually of oval shape, which absorbed the stain more strongly than the rest, and held it more tenaciously. On this body the name **nucleus** was bestowed. It was discovered further that in young and actively growing parts of the plant the cells increased in number by a process of division, and that this division of the cell was in all cases preceded by a division of the nucleus. Meanwhile investigators had been endeavouring to discover whether the bodies of animals showed any analogous

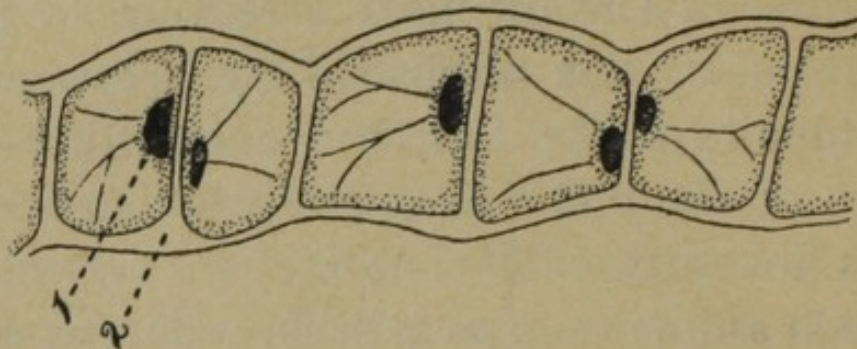


structure to that exhibited by plants; and it was soon found that these bodies were made up of a repetition of units, each of which might be described as a mass of protoplasm, with a nucleus embedded in it, and to these units the name cell was extended. The cell-theory, as an hypothesis of the fundamental similarity of the ultimate structure of plants and animals, was published by Schwann and Schleiden in 1837; but their conception of the nature of the cell was entirely erroneous, and it was not until 1853 that the real relationship between animal and vegetable cells was clearly and correctly stated by Cohn.

It is a familiar truism, that when the application of a concept is widened its content is diminished; and to this rule the word "cell" is no exception. If we take a broad survey of the matter, we find that whereas the majority of vegetable cells might fairly be described as hollow cases with thick, tough walls filled with watery fluid, the majority of animal cells, on the contrary, have cell-walls of excessive tenuity and consist of compact masses of protoplasm without any large central inclusions of water; further, that many of the larger cells of animals, such as muscle-fibres, may contain many nuclei. Indeed,

if the study of the structure of living beings had commenced with animals, the conception of the unit would not have been that of a cell, but something more analogous to a brick; and one would have compared the

A



B

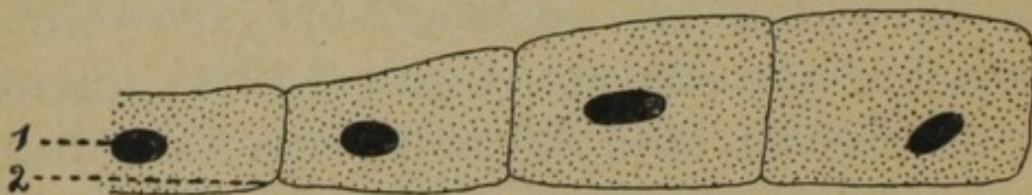


FIG. 1.

Illustrating the differences between vegetable and animal cells. A. Cells from the vine. B. Cells from the larva of the star-fish. 1. Nucleus. 2. Cell-wall.

body to a wall composed of bricks united by mortar rather than to a honeycomb (Fig. 1, A and B).

Different from one another as are the great masses of adult animal and vegetable cells, very young animal and vegetable cells resemble one another more closely, for in

the young cells of plants the cell-wall is thin and the central vacuole has not as yet appeared.

The simplest animals and plants do not exhibit cell structure and have been supposed to be equivalent to single cells, but this is not a just way of looking at the matter. The smallest may, perhaps, be regarded as equivalent to single cells of the higher animals, but the larger, which have many nuclei, cannot be regarded in this light. They must be rather described as destitute of cellular structure. Such simple animals and plants are known collectively as **Protista**, because in regard to many of them it is very difficult to say whether they are plants or animals, and the whole class may perhaps be regarded as the seed-ground out of which the higher animals and plants have developed.

If we confine our attention for the present to the higher animals and plants, we may define germ-cells as cells which, when separated from the parent, can grow into new organisms, and these cells exhibit a considerable uniformity of structure. In the vast majority of cases they are of two kinds, termed **male** and **female** respectively, and in order that a young organism should be produced, it is

necessary that a male cell should unite with a female cell, and so produce a compound cell which is termed a **zygote**. This union is termed the **sexual process**, and in it the nuclei of the two cells unite to form a single nucleus. The zygote begins, either at once or after a period of rest, to develop into the young animal or plant, as the case may be, and the first step in this development is the division of the zygote into a mass consisting of numerous cells. The distinction between a member of the class Protista and one of the higher organisms is that in the Protista all these cells separate from one another, and each one grows into a new adult Protist, whereas in the case of a higher plant or animal, the mass of cells continues to cohere and becomes moulded into the tissues of the new individual.

In the group of plants to which the Fungi or Moulds belong, great numbers of simple germ-cells are produced which can give rise to young organisms without the sexual process, as well as germ-cells which must unite with one another before development can take place. Such simple germ-cells are termed **conidia** (Fig. 2, A), whilst to germ-cells which unite with one another in pairs the term **gametes**

is applied, from the Greek word signifying marriage.

“Conidia” or their equivalent are not found among the higher animals, but it occurs exceptionally amongst animals that gametes acquire the power of developing without union. This phenomenon is known as **parthenogenesis**. We distinguish such perverted gametes from true conidia by the fact that in shape, size and origin they resemble the normal gametes in closely allied genera, and we know that they are perverted and not original from the fact that parthenogenesis is the exception and not the rule, and appears sporadically in different cycles of animal affinity, and is by no means characteristic of primitive forms. Lastly, gametes which should undergo the sexual process may be induced to develop without it by applying artificial stimuli to them.

Returning now to the consideration of gametes which undergo the sexual process, we find that in a few cases in the lowest plants and animals they are all alike in appearance, so that male and female varieties cannot be distinguished; but, as we have already mentioned, in the overwhelming majority of cases they are divided into two categories, male and

female. The male germ is exceedingly small, and it is motile; in almost all animals, and in the lower plants, it is provided with one

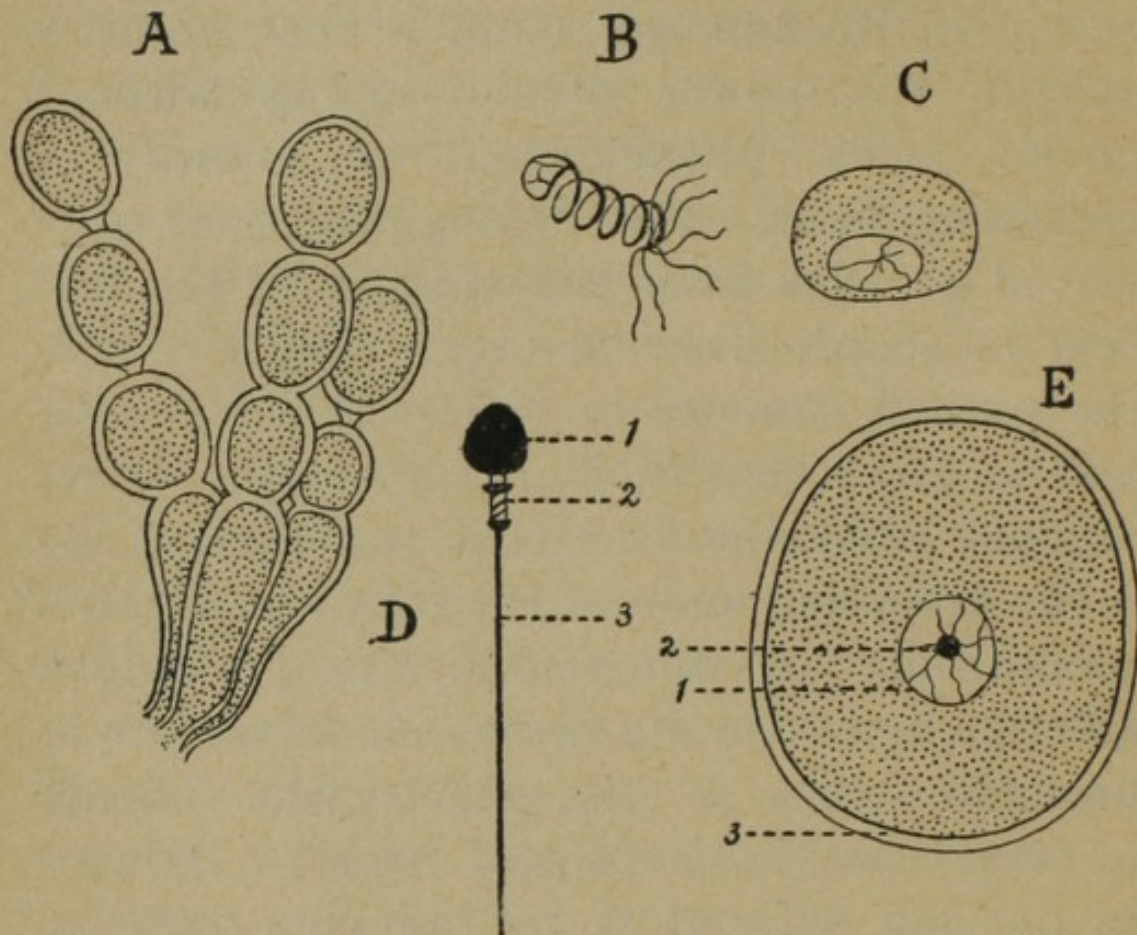


FIG. 2.

Illustrating the different types of germ-cells. A. The conidia of a mould. B. The spermatozoid of a fern. C. The oosphere of a fern. D. The spermatozoon of a man. E. The egg of a woman. 1. The head (in D), the nucleus (in E). 2. The middle-piece (in D), the nucleolus (in E). 3. The tail (in D), the vitelline membrane (in E).

or more hair-like filaments capable of rapid vibration, which propel it from place to place. In plants it is termed an **antherozoid** or

**spermatozoid** (Fig. 2, B) and it is provided with several of these hairs, and there is sometimes a small cell-body in which a nucleus is embedded. In animals the male germ-cell is provided with a single vibratile hair which is termed the tail, and it consists, besides this, of a rod-like nucleus without any discoverable cell-body at all. The nucleus is termed the head, and the whole germ-cell is termed the **spermatozoon** (Fig. 2, D). The structure of spermatozoids and spermatozoa indicates that they are adapted to swim in fluids, and union with female gametes, or **fertilization**, usually does not take place in a fluid medium. But in the higher plants this is not the case, and here the male cell consists of a small naked drop of protoplasm, with a nucleus which becomes pressed against the female cell. Again, certain animals, such as crabs, lobsters, and threadworms, are constitutionally incapable of producing typical spermatozoa owing to the tendency of their protoplasm to produce horny matter. In these animals the male germ-cells are either simple naked cells (threadworms) or cells consisting of a nucleus, having attached to it a complex horny disk which absorbs water and swells and thus pushes the

nucleus into the female gamete (crabs and lobsters).

The mass of developing male gametes surrounded by a wall of protecting cells is known as an **antheridium** in plants, and as a **testis** in animals.

The female germ-cell in all the higher plants and animals is a motionless cell, and it is always considerably larger than the male germ-cell. In plants it is called the **egg-cell**, **oosperm** or **oosphere** (Fig. 2, C), in animals the **egg** or **ovum** (Fig. 2, E). The mass of developing female germ-cells surrounded by a protective wall is known in plants as an **archegonium**, and in animals as an **ovary**. The female germ-cell contains embedded in its substance a certain amount of unworked-up food material, which serves as capital on which the zygote lives until it can feed itself. The size of the egg-cell depends chiefly on the quantity of this reserve material contained in it, which in the animal kingdom is known as **yolk**. In birds the true egg is popularly termed the "yolk," and this in the case of the ostrich reaches the size of a cricket-ball and is the largest cell known. On the other hand, the egg of a woman when it is discharged into the womb is about  $\frac{1}{250}$  inch in diameter, and



the egg-cell or oosphere in one of the higher plants is not of any greater size. The reason for the disparity in size in these cases is the difference in the source from which the young organism derives the greater part of its nourishment. In the egg of the ostrich nearly the whole of this nourishment consists of the yolk embedded in the protoplasm of the egg, and hence the large size of the latter. The "white" of the egg constitutes a somewhat unimportant addition to this store. But in the case of the higher plant and of the woman the nourishment contained in the protoplasm of the egg only suffices for the first few steps in the development of the young organism. In the woman additional nourishment is supplied to the egg from the walls of the womb, and it is at the expense of this nourishment that the baby is enabled to reach its full size. In the plant the additional nourishment is supplied by a series of cells surrounding the egg-cell which are termed **endosperm**, and which are absorbed as the seed develops.

Now common experience, to which we referred as the starting-point of the science of heredity, teaches unequivocally that the father is just as potent in transmitting his

qualities as the mother. The essential hereditary element in the female germ-cell cannot, therefore, consist of the yolk or of the protoplasm in which the yolk is embedded, but must consist of the nucleus, since in the spermatozoa of animals both yolk and protoplasm are absent. This comes out quite clearly when the sexual process is studied in detail. This can be easily done in the case of creatures like star-fish and sea-urchins, which produce quantities of minute transparent eggs and shed them into the sea, where they are fertilized by the spermatozoa of the male. If a sea-urchin egg be placed in a drop of sea-water and some spermatozoa added, it is not difficult to watch the process of fertilization through a microscope. The spermatozoa propel themselves in a spiral course through the water by lashing their tails. One at last strikes the surface of the egg and proceeds to bore into it by a continuance of the same spiral motion. As soon as the "head" becomes embedded, the superficial layer of the protoplasm of the egg undergoes a change and becomes converted into a skin called the **vitelline membrane** or primary egg-shell. This skin cuts off the "tail" of the spermatozoon and prevents any other

spermatozoon from entering. Then the head pursues its way through the protoplasm of the egg, swelling up as it does so, and taking on the appearance of a nucleus. It gradually approaches the nucleus of the egg and the two join to form the nucleus of the zygote (Fig. 9, p. 49).

Since the father is just as potent as the mother, we arrive at the remarkable conclusion that the nuclei of the germ-cell are the transmitters of the hereditary qualities and constitute the bridge between parent and offspring.

When we look closely at a spermatozoon, we can see that between head and tail there intervenes a short neck, which is termed the **middle-piece**. The middle-piece follows the head into the protoplasm of the egg and there acts on this protoplasm so that it becomes the centre of a clear sphere with radiating streaks. This sphere is known as the "aster," from its resemblance to the conventional figure of a star; it comes to lie at the side of the compound nucleus of the zygote, and it plays an important part in the division of that nucleus, as we shall see later. The middle-piece of the spermatozoon only gives rise to a minute particle called the **centrosome**,

which lies in the centre of the aster, but it is the action of the centrosome on the maternal protoplasm which produces the aster (Fig. 9, B, C). We have termed the protoplasm a jelly-like substance; in life it is constantly altering from this condition, in which it is termed a "gel," to the condition of a thick syrup, in which we call it a "sol," and vice versa. The action of the centrosome consists in liquefying some of the protoplasm round it, which becomes a sphere of thick sol, into which radial currents of fluid ("clear streaks") flow from the rest of the egg. These clear streaks are separated by semi-rigid bars of "gel." The centrosome is normally produced from the middle-piece of the spermatozoon; but if the egg just after the spermatozoon has entered it be subjected to violent centrifugal force it is possible to tear away the middle-piece; the head of the spermatozoon—that is, the male nucleus—then gives rise to another centrosome. In eggs which have not been fertilized at all it is sometimes possible to start the formation of one or of several asters by subjecting them for a short time to the action of over-concentrated sea-water, and in this way an unfertilized egg may be caused to develop. This phenomenon is known as

**artificial parthenogenesis**; and its possibility shows clearly that the centrosome must be a comparatively simple substance readily produced in different ways, and cannot have any part in transmitting the peculiar qualities of the parents. The division of the nucleus is preceded by the division of the centrosome, and one half goes to each daughter nucleus.

The course of events leading up to the union of the germ-cells of plants differs in many important respects from that of animals, and as the higher plants have been the subjects of most important researches on the laws of heredity, a short account of the origin of the germ-cells in these plants must be given. In order to make this as clear as possible, we must commence by the consideration of the case of the common fern. The ordinary gardener is well aware that on the back of the graceful fronds of this plant there are to be found at certain seasons multitudes of very small dark kidney-shaped patches. Each patch is termed a **sorus**, and is covered by a brown scale called the **indusium**. Underneath this scale are to be found multitudes of minute bodies of microscopic dimensions which are termed **sporangia**. Each sporangium is a tiny box having the shape of two watch-

glasses pressed together, mounted on a slender stalk. Inside the box are multitudes of excessively minute rounded bodies termed **spores** (Fig. 3). Each spore is in fact a non-sexual germ-cell or conidium, and consists of a small mass of protoplasm, with a nucleus

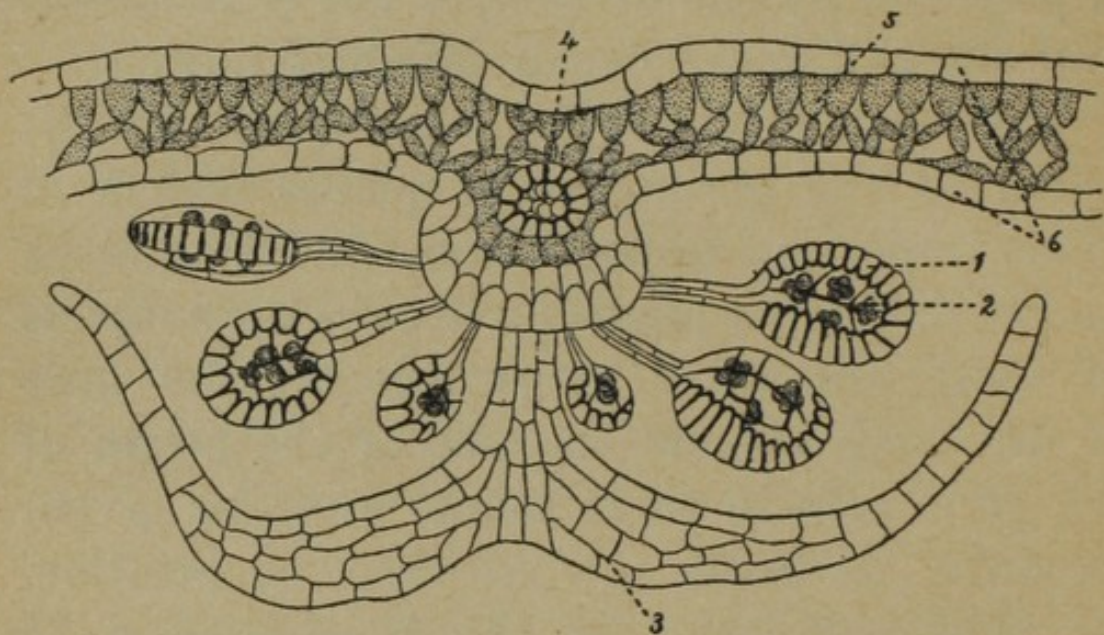


FIG. 3.

Transverse section through the sorus of a fern leaf. 1. Sporangium. 2. Spores inside the sporangium. 3. Indusium. 4. Bundle of sap-conveying cells in the leaf (fibro-vascular bundle). 5. Green cells of the leaf. 6. Skin cells of the leaf.

and a thick brown cell-wall. If these spores be sown on a damp brick and exposed to moderate light they will germinate after a somewhat prolonged period of rest, and give rise to, not new ferns, but minute plants termed **prothallia**, which resemble

little pieces of duckweed (Fig. 4). If we examine the structure of these prothallia, we shall find that they show on the under surface numerous minute cavities, and that these cavities are of two kinds: one sort are hemispherical and the other sort are flask-shaped. The outer walls of both kinds pro-

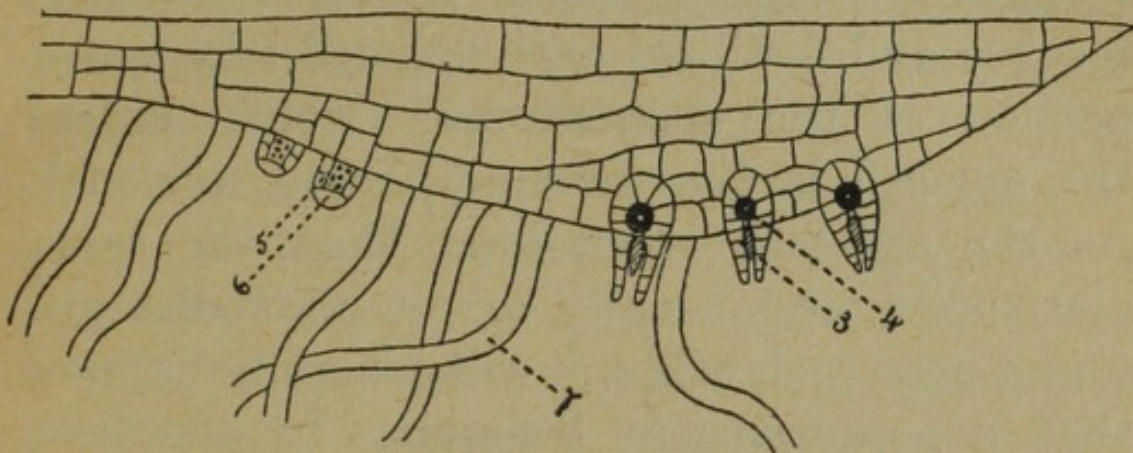


FIG. 4.

Section through the prothallium or "oophore" generation of the fern. 3. Archegonium. 4. Oosphere, or egg-cell in the archegonium. 5. Antheridium. 6. Spermatozoids, or male cells, in the antheridium. 7. Root-hairs of the prothallium.

ject very slightly above the ground level of the surface of the plant. The hemispherical cavities are antheridia, and contain the male germ-cells, which in the case of the fern are spermatozoids, differing from spermatozoa in possessing several whip-like tails instead of one. The flask-shaped cavities are archegonia, each of which contains one female germ-cell

or oosphere surmounted by several cells situated in the neck of the flask, which break up into a kind of slime. When the male cells are ripe, the lid of their case breaks, they swarm forth and, swimming in the film of moisture underneath the prothallium, are attracted by the substances contained in the slime above the egg-cells. One spermatozoid reaches and fertilizes each egg-cell (the spiral portion of the spermatozoid which enters the egg-cell is the metamorphosed nucleus). As the egg-cells ripen later than the spermatozoids, and usually many prothallia are found near each other, it will generally happen that a spermatozoid belonging to one prothallium will fertilize the egg-cell belonging to another prothallium. The fertilized egg-cell then begins to divide and develops into a young fern plant, and as this grows the prothallium withers away. It follows that one prothallium can give rise to several fern plants.

In the fern plant we are thus confronted with an alternation of generations. A generation which produces spores, or a spore-bearer (**sporophore**), is succeeded by a generation which produces egg-cells (**oophore**). A similar alternation of generations can be traced in all



the higher plants, although modified and obscured, and we can trace a series of stages in this modification. Thus in certain water-ferns (Salviniaceae) there are two kinds of spores produced, viz. small spores, termed **microspores**, and large spores, termed **macrospores**. The sporangia containing these two varieties of spores are termed **microsporangia** and **macrosporangia** respectively. The microspores on germination give rise to prothallia which bear only spermatozoids, whereas the macrospores give rise to prothallia which produce only egg-cells. These may be termed the male and female prothallia respectively. The male prothallium sometimes consists of a single filament at the end of which two cells with granular contents are cut off. These cells constitute the antheridium, and in them the spermatozoids are developed (Fig. 5, A).

The female prothallium (Fig. 5, B) consists of a mass of tissue projecting only a little way beyond the burst wall of the spore. In this mass are formed one or more archegonia, in each of which an egg-cell is developed. The macrospores, which produce female prothallia, are larger than the microspores, which produce male prothallia. Both macrospores and microspores are produced in fours by two

successive divisions of a mother cell, but whereas in the formation of microspores all

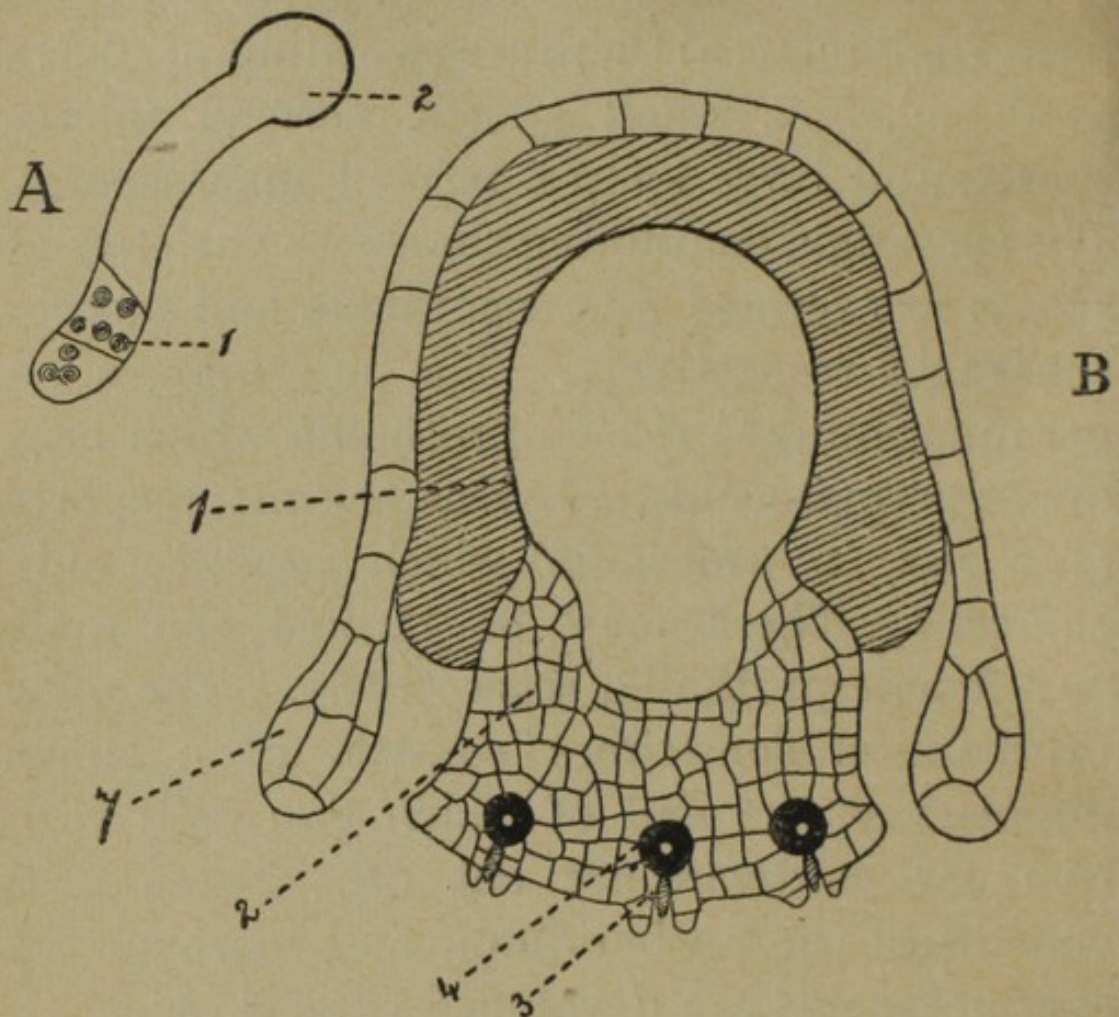


FIG. 5.

Illustrating the germination of the two kinds of spores of the water-fern (*Salvinia*). A. The germination of the microspore. 1. The spermatozoids in the vestigial antheridium. 2. The burst microspore. B. The germination of the macrospore. 1. The burst macrospore. 2. The vestigial prothallium. 3. The archegonium. 4. The egg-cell in the archegonium. 7. The wall of the burst macrosporangium.

four sisters become spores, in the case of the macrospores only one of the four becomes a

spore, whilst the other three cells remain small and remind us of the polar bodies in animal eggs.

In that strange tropical plant the cycad there is essentially the same arrangement, but the female prothallium (termed the **endosperm**) remains entirely within the macrospore, only one of which is produced in each macrosporangium. The macrospore is now termed the **embryo-sac**. We find the further modification that the filamentous male prothallium is produced only when the microspore, or, as it is now termed, the **pollen-grain**, is wafted by the wind so as to alight on the macrosporangium, or, as it is now termed, the **ovule**. This male prothallium consists of a filament termed the pollen-tube, at the apex of which the male germ-cells are formed, which, as in ferns, are spermatozoids, each provided with several flagella. In the pines and their allies the male cells are no longer typical spermatozoids, but small rounded naked nuclei, which when they escape, fall directly on the slime cells in the necks of the archegonia in the female prothallium. They easily traverse the slime and fertilize the egg-cells. Several young pine plants are thus formed in each embryo-

sac, but only one survives; the rest perish in consequence of the withdrawal of nourishment from them by the successful one (Fig. 6, A).

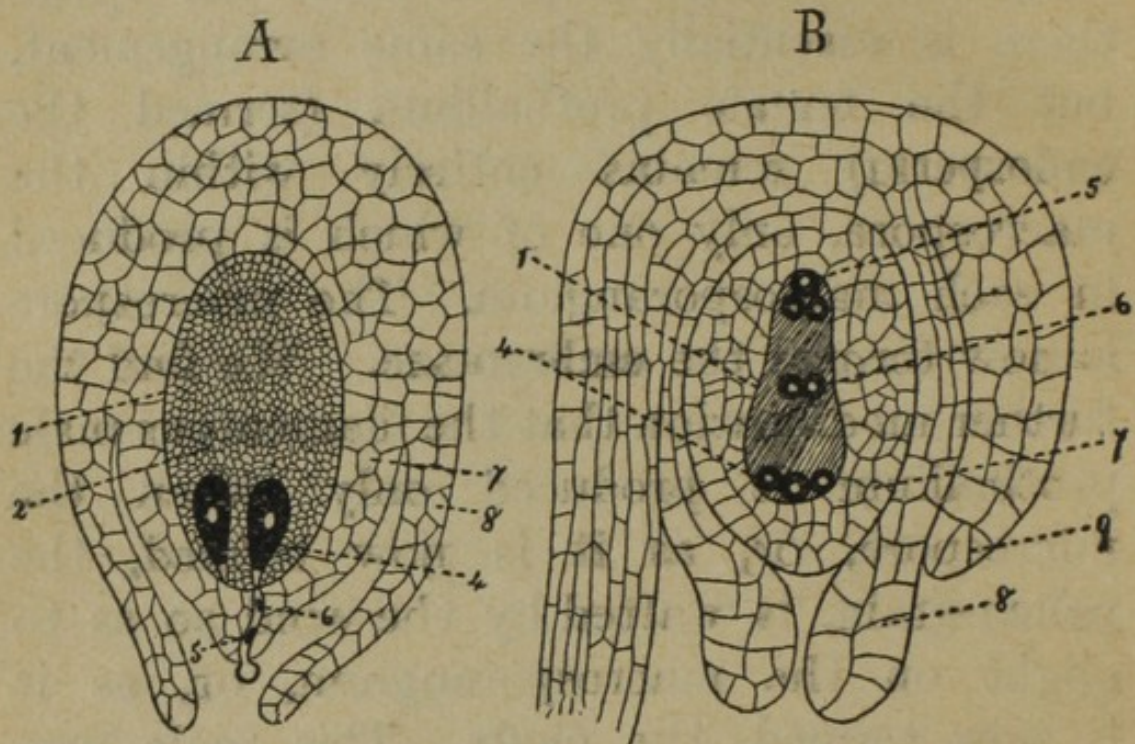


FIG. 6.

Longitudinal section through the "ovules" or macrosporangia of the seed-plants. A. Section through the ovule of a pine. 1. Macrospore or embryo-sac. 2. Endosperm or prothallium inside embryo-sac. 4. Archegonium. 5. Pollen-tube in male prothallium. 6. Male nucleus in pollen tube. 7. Macrosporangial wall. 8. Envelope surrounding macrosporangial wall. B. Section through the ovule of a flowering plant. 1. Embryo-sac. 4. Egg-cell and its two sister cells. 5. Antipodal cells. 6. Endosperm-forming cells. 7. Macrosporangial wall. 8. Inner envelope of macrosporangium. 9. Outer envelope of macrosporangium.

Finally, in ordinary flowering plants matters are very much as they are in the pines, but the macrosporangia or ovules are enclosed in a box or case formed by conjoined leaves

called the **ovary** (not to be confounded with the ovary of an animal). The tips of these leaves form the sticky surface or **stigma** on which the microspores or pollen-grains fall, and where they germinate and produce the male prothallia or pollen-tubes. Each pollen-tube produces only one male cell, which is to all intents and purposes a naked nucleus. The female prothallium is represented only by eight cells, devoid of cell-walls, embedded in the protoplasm of the macrospore or embryo-sac; these are produced by three successive divisions of the macrospore nucleus. Of these, three are situated in the upper part of the macrospore where the contact with the pollen-tube takes place, three, termed "antipodal" cells, at the lower end, and two in the middle. These last two coalesce to form a single cell, termed the mother-cell of the endosperm. The endosperm is a nutritive tissue formed by the division of this mother-cell after fertilization, which fills up the cavity of the macrospore, and very possibly does not correspond to the endosperm of cycads and pines. Of the six remaining cells only one is a ripe egg-cell, and is fertilized by the male cell; the remainder are to be regarded as vestigial egg-cells and disappear (Fig. 6, B).

In the case, therefore, of the flowering plant,

only one young plant is formed in each prothallium, that is to say, in each macrospore; and as one macrospore is formed in each macrosporangium, we can further assert that only one baby plant is formed inside each macrosporangium. The macrosporangium grows rapidly and forms the **seed**, and the seed when fully formed drops off the plant and falls to the ground. By the time that this has occurred the baby plant has also grown enormously, and in many plants, such as peas and beans, it has completely absorbed the endosperm; but in other plants, such as wheat, maize and the cereals generally, it lies embedded in an unconsumed mass of endosperm. The wall of the macrosporangium and that of the macrospore crushed together form the seed-coat or **testa**. It follows, therefore, that what we call a seed consists of parts belonging to two different generations; the seed-coat or testa is part of the tissues of the mother plant, whilst the baby plant or embryo within represents the next generation. When endosperm is present we may assert that three generations are represented, for the endosperm represents the prothallium or oophore, which is produced by an asexual spore from the mother plant or sporophore.

## CHAPTER II

### THE NUCLEUS AS THE BEARER OF THE HEREDITARY QUALITIES

IN Chapter I we saw ourselves driven to the conclusion that the nucleus of the male germ-cell was the sole channel through which the qualities of the father were transmitted to the child. Since father and mother are equally potent in transmitting their qualities to their offspring, it is practically certain that it is through the nucleus of the egg that the mother also perpetuates her individual peculiarities. As soon as these conclusions were seen to be inevitable, the minute structure of the nucleus assumed an enormous importance in the eyes of all students of Biology, and a corresponding amount of study was devoted to its elucidation.

In some Protista, and in some cells in the higher animals, the nucleus can be seen during life; it then appears as a vesicle surrounded by a thin wall and containing a clear fluid,

which is known as the **nuclear sap**. In small transparent eggs the nucleus can be easily seen and it is relatively very large; it was called by the older authors the **germinal vesicle**, and it contains a conspicuous solid inclusion which they called the **germinal spot**, but which is now known as the **nucleolus**.

It is only, however, when the cell is preserved and stained that the full particulars of the structure of the nucleus can be observed. It is then seen to stand out from the rest of the cell by reason of its greater power of absorbing colouring matter, and when this colouring matter is removed from the rest of the cell by dilute acid, the nucleus still holds on tenaciously to it. The nuclear wall and the nuclear sap are not coloured, but the coloured portion consists of the nucleolus (when this is present) and of a series of grains of peculiar substance called **chromatin**. This substance is sometimes arranged in streaks along the nuclear wall and sometimes in lines on what appear to be cords traversing the nuclear sap. These cords have been termed **linin**. In some large nuclei they can be seen in the living condition, and they can be investigated by means of a long, excessively fine needle of glass. It



then transpires that they are not cords but sheets of denser material traversing the fluid sap. When a nucleus divides into two the lines of chromatin contract, and become arranged in a number of bands called **chromosomes**. It is a most wonderful thing that whenever they can be counted these chromosomes appear in the same number in all the cells of the body when the nucleus divides. This number is typically the same for all members of the same species of animal, but varies from species to species. For reasons which will soon transpire it is termed the **diploid** number, and is denoted by the symbol  $2x$ . The chromosomes continue to contract, and as they grow shorter and thicker the nucleolus, if there is any, becomes dissolved in the cell sap and totally disappears, and a little later the nuclear wall is also dissolved and the nuclear sap mingles with the protoplasm. It has been proved in several cases that the material of the nucleolus is ejected from the nucleus into the protoplasm. Whilst these changes have been going on the centrosome, which lies outside the nuclear wall, has divided into two and the daughter centrosomes have moved away from each other, each of them producing round itself an "aster" with out-

streaming rays. Then each of the chromosomes is seen to be split longitudinally, and soon to each half of each chromosome a ray from one of the two asters is seen to be

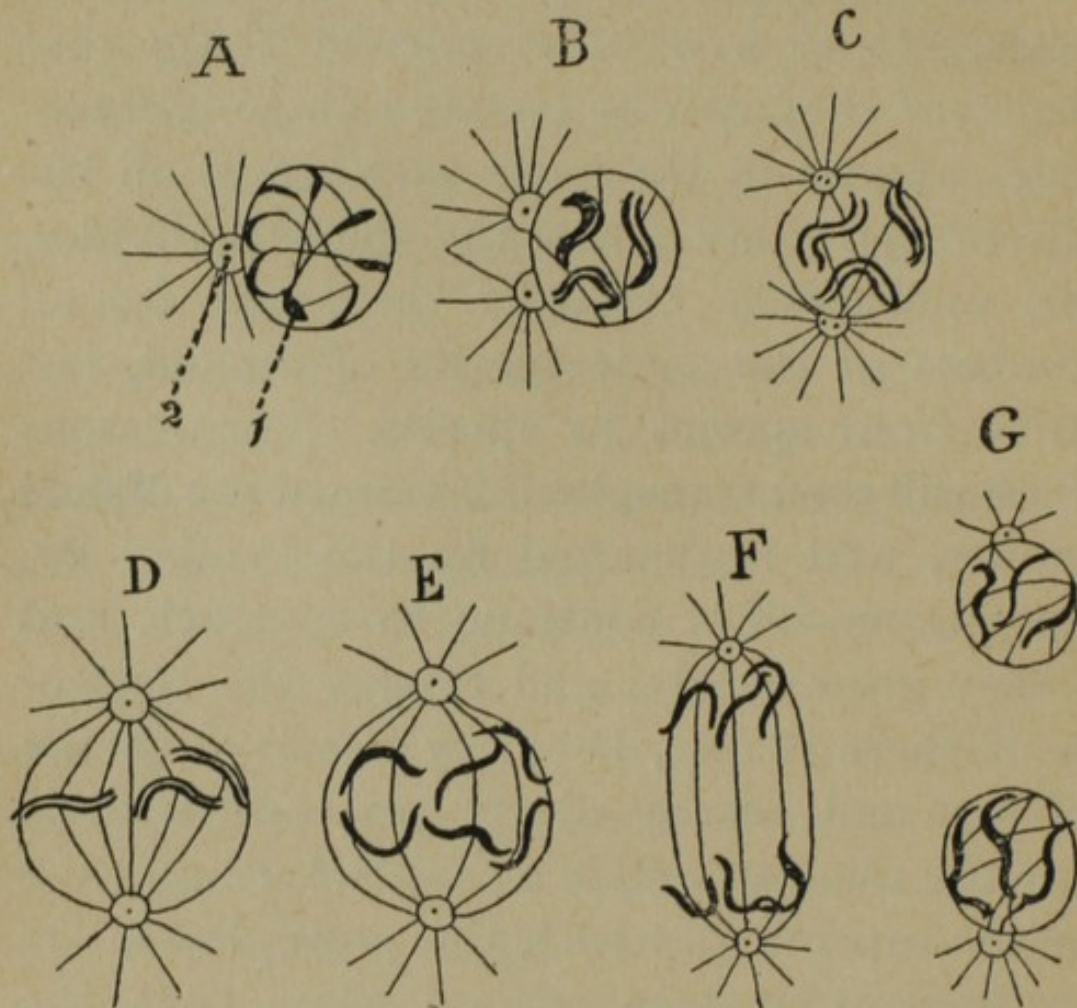


FIG. 7.

Illustrating the process of karyokinesis (mitosis). A, B, C. Prophase. D. Metaphase. E, F. Anaphase. G. Telophase. 1. Chromosome. 2. Centrosome.

attached. As the daughter centrosomes continue to move apart, these rays *seem* to pull on the halves of each chromosome. The first effect of this pull is to cause

all the chromosomes to be arranged in a plane at right angles to the line joining the two centrosomes. In this way a disk of chromosomes is formed which is known as the **equatorial plate**, and it is in this phase of division that the chromosomes are most easily counted. The fibres converging from each side of the plate to an aster constitute a biconical figure known as the "**spindle.**"

As the process of nuclear division proceeds the halves of each chromosome move apart as if each was being pulled towards one of the two asters. As they separate longitudinal fibres of linin are seen to connect them. Eventually a group of chromosome-halves becomes aggregated in the neighbourhood of each aster. Then a nuclear wall is formed round each group, and so two daughter nuclei are constituted. It only remains for the chromosomes in each daughter nucleus to lengthen and gradually to lose their distinctness in order that the division should be completed and each nucleus should pass back into the resting condition.

This method of nuclear division is known as **mitosis** or **karyokinesis**. It is much the most frequent method, but occasionally when multiplication takes place in a group of

specialized cells, which have no power of developing into anything unlike themselves, the nucleus divides directly by simple constriction into two parts without any rearrangement of its chromatin. In contrast to karyokinesis this method is sometimes known as "**direct division.**"

Mitosis is divided into phases. The gradual differentiation of the chromosomes out of the resting nucleus from the time of the separation of the centrosomes up till the dissolution of the nuclear wall is known as the **prophase**; the formation of the equatorial plate and of the spindle is known as the **metaphase**; the separation of the halves of the chromosomes is known as the **anaphase**; and the passing of the daughter chromosomes back into the resting daughter nucleus is known as the **telophase**.

We may now turn to consider the features of special interest which are to be observed in the growth and development of the germ-cells. The germ-cells, both male and female, when they first make their appearance are small and rounded, and consist of somewhat denser and more deeply staining protoplasm than their neighbours. In this condition they are known as **primitive germ-cells**, or,

when sex can be distinguished, as **spermatogonia** and **oogonia** respectively. They divide

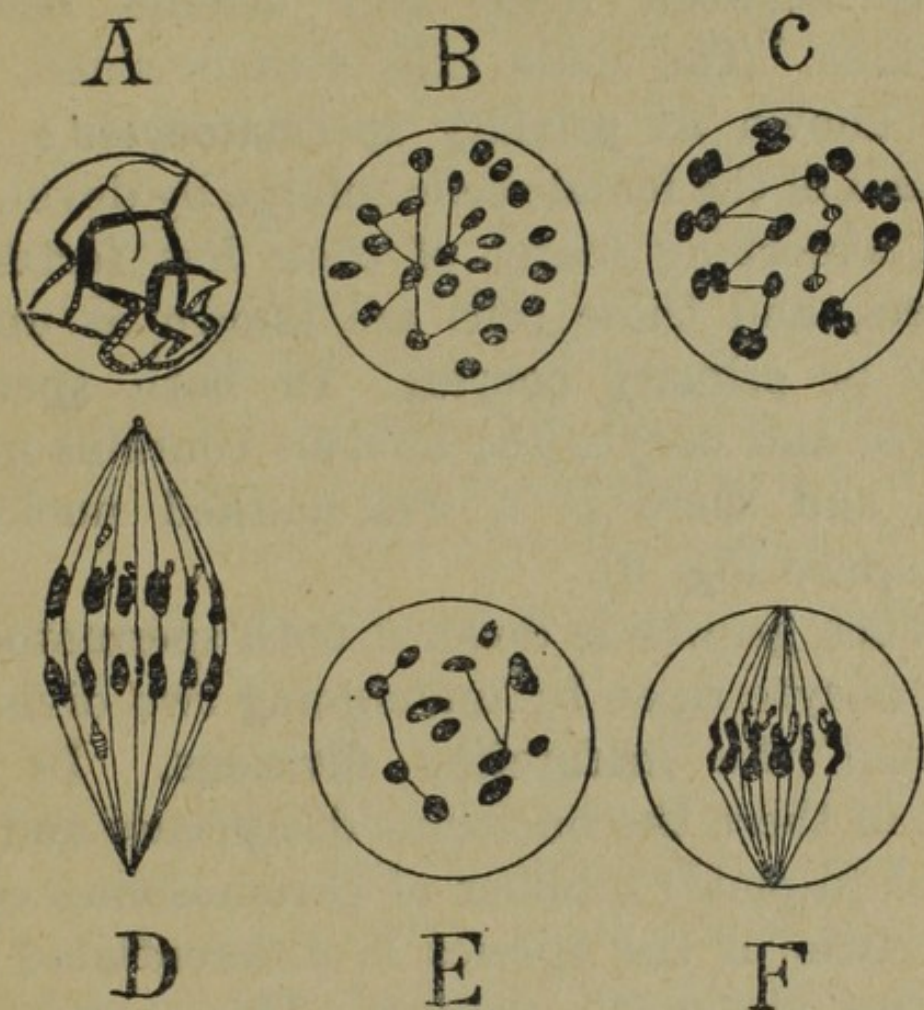


FIG. 8.

Illustrating the stages in the ripening of the nucleus of the male germ-cell. A. Prophase of the first maturation division. B. Metaphase (*i. e.* the equatorial plate) of the first maturation division seen from above. C. The same a little later, showing the beginning of "pairing" or "meiosis." Eight "paired" and six as yet unpaired chromosomes are shown. D. The first maturation division seen from the side. E. The equatorial plate of the second maturation division seen from above. F. The second maturation division seen from the side.

repeatedly and multiply rapidly in number by ordinary mitosis. After a time these

divisions cease and the cells enter on a period of growth and rest, during which the distinctions between male and female become obvious. The male cells remain small, and are known as **primary spermatocytes**; but certain of the female cells enlarge by devouring and absorbing many of their less fortunate sisters, and these cells are known as unripe eggs or **primary oocytes**. In both spermatocyte and oocyte the nucleus contains much sap, and there is a well-marked nucleolus (compare Fig. 9).

When growth is finished both spermatocyte and oocyte ripen by undergoing two divisions termed the **maturation divisions**. In the first of these the nucleolus disappears and the usual (diploid) number of chromosomes characteristic of the species is differentiated out of the chromatin grains. This number is in the vast majority of cases an even one. Then the chromosomes join together in pairs, so that the number is halved (Fig. 8, C). The half number is known as the reduced or **haploid** number, and is designated by the symbol  $x$ . In the best attested cases the junction takes place in such a way that the two chromosomes lie alongside one another and fuse into one. Sometimes it is true that

the members of a pair join end to end, but this is only the beginning of a side-by-side union, since the two attached chromosomes subsequently swing round so as to be parallel with one another. Later a split appears in the centre of the region where the junction took place, and as the two halves of the compound chromosome still adhere at the ends, it takes the form of a ring. When the equatorial plate and the spindle are formed, the two halves of the ring are dragged apart, and one half-ring, which corresponds to one of the original diploid chromosomes, is incorporated in each daughter nucleus. This nuclear division, therefore, differs from every other nuclear division in this, that instead of one half of each diploid chromosome passing into each daughter nucleus, some whole chromosomes go to one daughter nucleus, and some to the other. This division constitutes, therefore, an exception to the rule that there is an equal distribution of material to each daughter nucleus; it is called the **reducing** or **meiotic division**, and the process of the union and subsequent separation of two chromosomes is known as **meiosis**. Meiosis of perfectly typical character is found in the Protista, in the higher animals and the higher

plants; it must, therefore, be of enormous antiquity, and must have originated at a time when the ancestors of existing animals, plants and Protista formed one uniform stock of lowly organisms.

In the male cell the meiotic division results in the production of two precisely equal cells which are known as the **secondary spermatocytes**, but in the case of the female cell the division is unequal, and results in the formation of one large daughter cell, which is known as the **secondary oocyte**, and a very small daughter cell, which is termed the **first polar body**.

The second maturation division now takes place. So far as the nuclei are concerned this is a quite ordinary case of mitosis in which each chromosome is halved longitudinally in the usual manner. In order to mark its contrast with the reducing or meiotic division it is sometimes known as the **equational division**, but this name is unnecessary. In the case of the male cell each secondary spermatocyte divides into two precisely equal cells called **spermatids**; in the case of the female cell the secondary oocyte divides unequally, giving rise to one large daughter, which is the **ripe ovum**, and one small daughter,



which is the **second polar body**. The first polar body usually divides at the same time into two equal daughters, but sometimes this division fails to take place (Fig. 9). It is obvious from this description that the three polar bodies are reduced and starved sister-cells of the egg, and correspond to the three vestigial spores which are formed along with the macrospore in the macrosporangium of the water-fern (Chap. I). This was pointed out by Hertwig in 1890; previous to this time, mysterious powers had been attributed to the polar bodies by various authors, especially Weismann.

When an egg has given off the second polar body, it is ready to receive the spermatozoon; the nucleus, which is termed the **female pronucleus**, does not return to the resting condition until it has united with that of the spermatozoon, and indeed in many eggs the second maturation division does not take place until after the spermatozoon has entered the protoplasm of the egg. In the case of the male cell, however, the spermatid has to undergo considerable modification before it becomes the spermatozoon. The nucleus shrinks and expels fluid and becomes converted into an apparently solid dense

mass of chromatin; the centrosome which had occupied one side of the spindle in the last maturation division gives rise to the tail filament, which appears as a tiny thread growing out from it and piercing the protoplasm. Then the nucleus, dragging the tail with it, emerges from the protoplasm, which forms for a time a mantle round the tail; but this mantle eventually disintegrates and is cast off, and so the perfect spermatozoon is formed.

As already mentioned, when the spermatozoon head penetrates the egg it swells up, owing to the absorption of fluid from the protoplasm of the egg, and forms the **male pronucleus**, which possesses a definite nuclear wall, nuclear sap and has its chromatin arranged in chromosomes. Now Boveri showed that in the case of some eggs after fertilization it was perfectly possible to demonstrate in the zygote nucleus two groups of chromosomes, one derived from the female pronucleus and one from the male pronucleus, each group consisting, of course, of the haploid number. These two groups taken together therefore represent the diploid number characteristic of the species.

When the fertilized egg divides for the first time so as to give rise to the first two

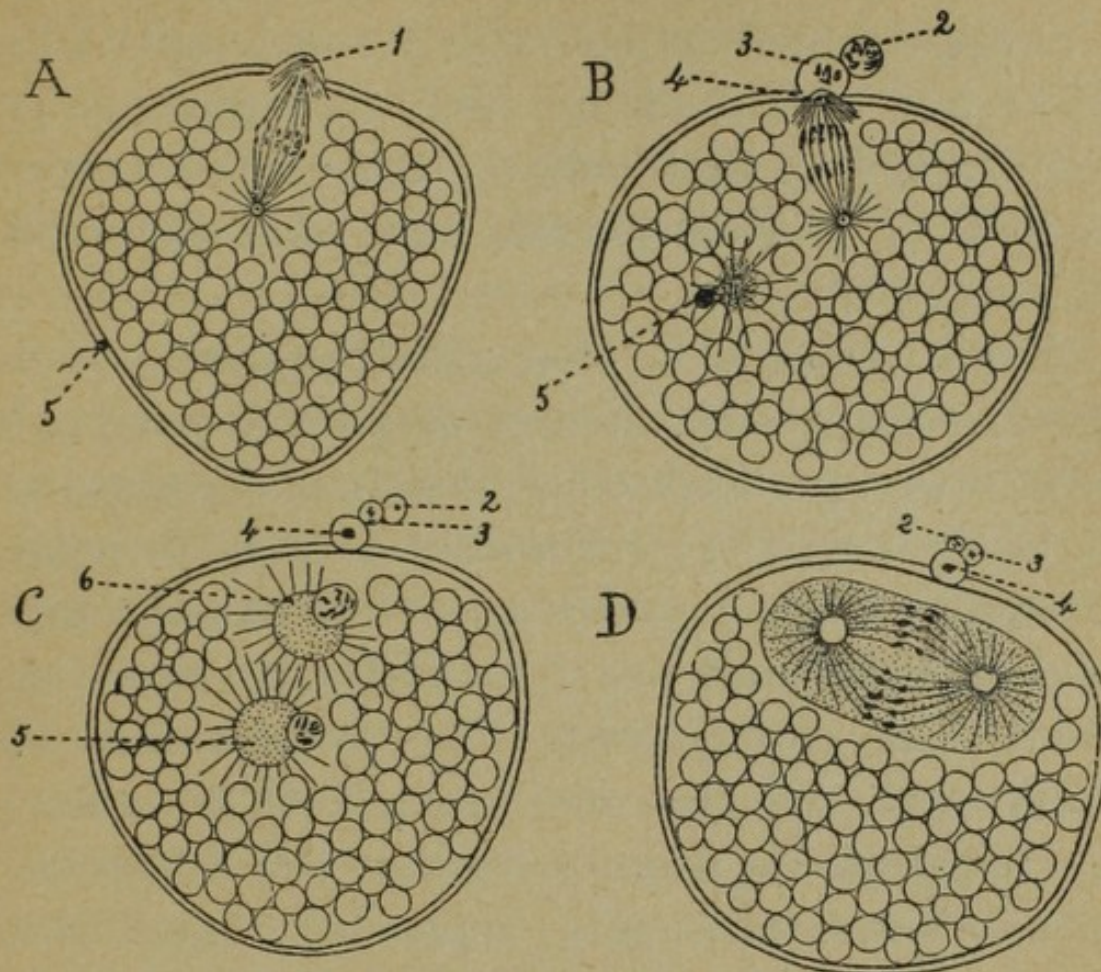


FIG. 9.

Illustrating the ripening and fertilization of the egg of a sea-snail (*Crepidula*). A. First maturation division, which gives rise to the first polar body. The spermatozoon is just entering the egg. B. Second maturation division, which gives rise to the second polar body. The first polar body has divided into two cells. The head of the spermatozoon has become the male pronucleus. C. Male and female pronuclei approaching one another, each accompanied by a large aster. D. The first division of the zygote nucleus. The male and female chromosomes form two separate groups. 1. The first polar body. 2, 3. The two cells into which it divides. 4. The second polar body. 5. (in A) the head of the spermatozoon; (in B) the male pronucleus; (in C) the aster at the side of the male pronucleus. 6. The aster at the side of the female pronucleus.

cells of the embryo, each chromosome of the zygote nucleus splits as usual longitudinally, and one half of each chromosome is distributed to each cell, so that each receives a half of each maternal and each paternal chromosome.

From the fact that the spermatozoon head, which is the bearer of all the paternal hereditary qualities, consists only of chromatin, it is obvious that chromatin is the essential element in the nucleus and that nuclear sap and nuclear wall are formed by its reaction with the protoplasm. This conclusion is confirmed by the observation that when, as happens in some irregular cell-divisions, one chromosome gets separated from the rest and does not become included in either of the two daughter nuclei, this errant chromosome is able to gather round itself nuclear sap and a nuclear wall of its own, and so constitute itself into a miniature nucleus.

The diploid number of chromosomes in the fertilized egg is, as we have seen, composed of two sets of chromosomes equal in number, one set being paternal and one maternal. As this diploid number reappears in all subsequent cell-divisions of the embryo, the question arises whether the chromosomes persist as individuals through the resting

stages of the nucleus when all that we can detect are lines of chromatin granules apparently irregularly arranged. There is strong reason for believing that this is indeed so. When the chromosomes disappear after one cell-division they present a peculiar bunched arrangement (the so-called **synaptic knot**), and when they reappear in the prophase of the next division they present the same appearance. The growth in size of the primitive oogonium which is converted into the oocyte or unripe egg begins after the prophase of the first maturation division. During this period the chromosomes become invisible owing to the loss of their staining powers, but they reappear when growth is completed. The chromosomes which can expand and contract and change their composition without losing their individuality, and which reproduce themselves, are really elementary living organisms.

In a later chapter we shall discuss the evidence for and against the idea that individual chromosomes contain distinct substances destined to serve different ends in the building up of the embryo.

The development of the germ-cells in those of the higher plants in which it has been thoroughly investigated follows a different

course from that which has been observed in animals. We have already learned that in all the higher plants there is a constant alternation of two kinds of individual, viz. a small oophore which produces egg-cells and spermatozoids, and a large leafy sporophore which produces spores. Now Farmer has shown clearly that in all these higher plants the all-important meiotic or reducing division does not occur during the formation of the sexual germ-cells, but during the formation of the spores. The nuclei of all the cells of the prothallia (oophores) produced by the germination of the spores have therefore the reduced number of chromosomes, and this is equally true of the comparatively large prothallia of ferns, and of the vestigial prothallia of the pines. The germ-cells produced by these prothallia have likewise the reduced number, and, as in animals, the diploid number is restored by the act of fertilization.

The endosperm of the flowering plants, although it represents the prothallium, has, however, the diploid number of chromosomes in its nuclei. This is due to the fact that the mother cell from which its formation starts is formed by the fusion of two of the nuclei formed in the embryo-sac or oophore.

## CHAPTER III

### THE DEVELOPMENT OF THE GERM INTO THE ADULT

WHEN the germ-cells have united with one another, and the zygote has been formed, it has, of course, a long period of development to undergo before it attains the adult form. From this development some important facts can be gleaned about the nature and mechanism of heredity. This is especially true of animal development, and we may now indicate a few general points in the nature of this.

The egg of one of the higher animals begins its development by dividing into a number of cells, which are termed **blastomeres**; this process is known as **segmentation**. Then these cells are moulded, by folding, into the **primary organs** or **germinal layers**. Of these there are three, viz. the **ectoderm** or primary skin, the **endoderm** or primary gut-wall, and the **mesoderm** or primary lining of the body-cavity. This process is known as the **formation of the layers**. Finally, these primary organs, by further processes of growth and

folding, give rise to the secondary organs; thus, for example, the ectoderm gives rise to the outer layer of the skin, the nervous system and the sense organs; the endoderm to the liver, the pancreas and the lungs, as well as to the lining of the alimentary canal, whilst the mesoderm forms the bones and muscles. This process is known as **organogeny**.

The growing organism during the first part of its existence is sheltered from outside influences either by an egg-shell, or by being retained within the mother's body, or in rare cases by being taken into cavities in the father's body. During this period it is called an **embryo**. When it finally escapes into the outer world it is still in many cases very unlike the parent, and has to undergo a series of changes or **metamorphoses** before it attains the adult form; during this period it is known as a **larva**.

The best known example of a larva is the tadpole of the frog. Now every animal begins its existence by being an embryo, and it may be fairly said that every animal later becomes a larva, for none leaves the egg-shell or the body of the parent with the proportions and powers of the adult. The small boy can be justly characterized as a human larva,



for in body, but still more in mind, he is different from the adult. The relative importance, however, of the embryonic and larval stages varies greatly. Sometimes the development is mainly of the embryonic type and sometimes of the larval type.

Now the startling thing about some larvæ is that they are unquestionably reproductions of a former state of the race to which the parents belong. This will become clear when some examples are given. Thus, as everyone knows, the vast majority of fish are bilaterally symmetrical animals, that is to say, that in them the right and left sides resemble one another as an object resembles its image in a mirror. But in a small but very important group of fish (the flat-fish) this is not so. These fish swim lying on one side. On the side directed upwards are both eyes, and the mouth is often unevenly placed, the greater part being directed downwards. The larvæ of these fish are, however, symmetrical, for in them each side has its eye and the mouth is straight in front. Again, the overwhelming majority of bivalve molluscs (*i. e.* cockles, mussels, scallops, clams, etc.), burrow in the mud, and possess for this purpose a muscular tongue-like appendage termed

the foot, which they protrude from between the valves of the shell. The oyster, however, is an exception to the rule, for it lies throughout life on one side and possesses no foot. But the American oyster, when young, creeps about and possesses a tongue-like foot. Still one more example of this phenomenon may be given. The majority of those exquisite marine animals, the feather-stars or "lily-encrinites" (Crinoidea), are extinct, but we learn from their fossilized remains that nearly all of them during life were rooted to the bottom by long stalks. Some of the living species show the same structure. The commonest form, however (*Antedon rosacea*), has no stalk when adult and possesses the power of swimming from place to place, but when it is young it is rooted to the bottom by a stalk exactly like its fossil relatives. When it approaches maturity it breaks loose from its stalk and swims free. In the case of these larvæ we may say that the life history "recapitulates" the history of the race.

The discovery of cases like these fired the imagination of zoologists thirty years ago, and for some considerable time one main preoccupation of zoological research was the attempt to reconstruct ancestral history from

a study of the life history. Unfortunately, the recapitulatory element, as we may call it, is not the only influence which moulds the life history; other influences which modify and obscure the ancestral element are at work, and the disentanglement of the parts played by the various influences is no easy matter. The attempt to do so led to much wild speculation and mutually contradictory hypothesis, and the apparent impossibility of arriving at certainty in the matter resulted in the disparagement of the whole idea.

But if there be any truth in the idea that there is a recapitulatory element in development, we simply cannot afford to ignore it if we are attempting to elucidate the laws of heredity. For the recognition of this element implies this: that when an animal changed its mode of life and sought a new environment and new ways of acquiring food, this usually happened at adolescence, and the new structures which were at first acquired as a reaction to the environment became, in course of time, so fixed in the animal's constitution that they appeared at progressively earlier periods in the growth of the animal, and eventually independently of the environment altogether,

as in the case where the young animal completes the greater part of its development within the mother's womb.

But we must remember that when the young organism passes its early life in the open as a larva its circumstances may change, so as to produce modifications in its structure which were utterly unknown to the adult animal when the race was in the stage now represented by the larva, and such modifications can be compared to falsifications of an old record. Only when we base our conclusion on a comparison of the life histories of many allied forms can the true record be discriminated from the secondary falsifications, just as an historian bases his views as to what actually happened in the past more on the points on which old documents agree than on those on which they differ.

Of course a critic might maintain that we have no proof that the ancestors of the flat-fish ever were like ordinary fish, or that the ancestors of the oyster ever burrowed, or, finally, that those of the feather-star were ever permanently fixed. The only conclusive proof would be furnished if some angelic recorder had watched the transformation slowly proceeding, and had left a duly attested

account of the whole thing. As Huxley has said: "If a man chooses to assert that a fossil shell is a mineral concretion it is impossible to drive him from his position by logic." But the fact that in the three cases mentioned no naturalist, however much he might inveigh against recapitulatory interpretations in general, would question the ancestral significance of the larva is proof enough for most sensible people. Exactly the same kind of proof convinced people that Fraunhofer's lines in the solar spectrum and similar lines seen in the spectra of heated metals were due to the same cause. But if we once admit that in the life histories of *some* animals there are reminiscences of a former condition of the race, it becomes almost certain that there is a recapitulatory element in *all* life histories, however obscured and falsified. It is in the highest degree unlikely that the development from egg to adult in different species of animals is a phenomenon of a totally different nature in different cases.

Once it is understood that the larval phase is often a partial reproduction of some bygone condition of the race, the relation of the embryonic phase to it becomes plain. The embryonic phase is a modification of the

larval phase. Taking the tadpole as a typical larva, we find that all its organs are adapted for life in water. Now there is in the island of Martinique a toad (*Hylodes*) which is hatched from the egg as a toad. If we examine what goes on within the egg-shell we find that the egg develops into a tadpole, some of whose organs are useless under embryonic conditions and only comprehensible if we allow that in a former condition of the race the tadpole escaped from the egg and lived in the water. A still more striking instance of the same thing is shown by the salamanders of Europe. There are two of these, a yellow and black *Salamandra maculosa*, which lives in the valleys, and a black one, *Salamandra atra*, which lives high up on the mountains. In both cases the eggs are fertilized before they are laid and development begins whilst they are still inside the mother. The young of *Salamandra maculosa* when born possess feathery gills, a flattened tail, and they immediately take to the water; those of *Salamandra atra*, on the other hand, resemble their parents from the first. But if a pregnant *Salamandra atra* be laid open there will be found inside her embryos provided with beautiful feathery gills, and these embryos if

taken from the mother and placed in water will occasionally survive and take up their life there as creatures breathing by means of gills. Who can entertain any doubt that the ancestors of *Salamandra atra* once produced tadpole-like larvæ like those which its gaily-coloured cousin bears, but has been forced by the unfavourable circumstances under which it lives to nourish them in its body instead of casting them forth to seek their fortunes in the water?

It is often asked, if the development of animals be a partial recapitulation of the history of the race, why the ancestral history of plants should not be revealed by their life history. The answer to this is twofold: first, sharply-marked larval phases are found where an animal changes its environment and lives during the earlier part of its life under one set of conditions, and the later part under another set, and the earlier set of conditions then represents what was the environment of the adult in the ancestral state of the race. A plant cannot move from one environment to another during its growth, and so when the surrounding conditions change they generally leave their impress on the plant from its first appearance above

ground, and leave little or no room for a larval stage. Secondly, in some few cases plants have a larval stage, or, as botanists term it, a "youth-form." The common gorse, in which green thorns replace leaves, has, when young, leaves like other plants, but these drop off as it grows older, and the Australian acacia, in which flat green leaf-stems take the place of leaves, has likewise leaves like those of other acacias when young.

If we then accept the view that in its broad outlines the life history of an animal is an epitome of the past history of the race, it becomes a matter of interest to investigate how this development is brought about in the individual. In a few cases we might plausibly accept the view that the development was caused by the reaction to new conditions. If the tadpole of a frog be kept cool and in the dark and prevented from rising to the surface of the water, it will, if well fed, grow very much in size, but it will never change into a frog. In order that it may metamorphose, it must have sunlight and be allowed to come up to the top of the water and swallow air; but when an embryo undergoes a parallel development to this inside the egg-shell or its mother's womb no



such explanation is available. The endeavour to analyse the causes of development in the individual, whether these be external stimuli or internal causes, forms the object of the science of experimental embryology. The principal objects which have been experimented with are the eggs of frogs, sea-squirts (*Tunicata* or *Ascidians*), molluscs, thread-worms (*Nematoda*), star-fish, and sea-urchins (*Echinodermata*), and comb-bearers (*Ctenophora*).

The eggs of the sea-urchin have formed the *corpus vile* for such experiments more often than those of any other form. The reason for this will readily be understood when the fact is grasped that our large British sea-urchin will produce in one season about 20,000,000 eggs, which can be easily got to develop into a characteristic larval form termed the *Echinopluteus*, although to rear them into the adult condition is a very difficult matter.

Amongst those who have investigated the causes of the development of the sea-urchin's egg no one has done more brilliant work than the German zoologist Driesch. Driesch has shown that when a sea-urchin's egg divides into two cells, if these cells be separated by violent

shaking, each will develop into a perfect larva of reduced size. The same result is obtained if one of the first four cells be separated from the

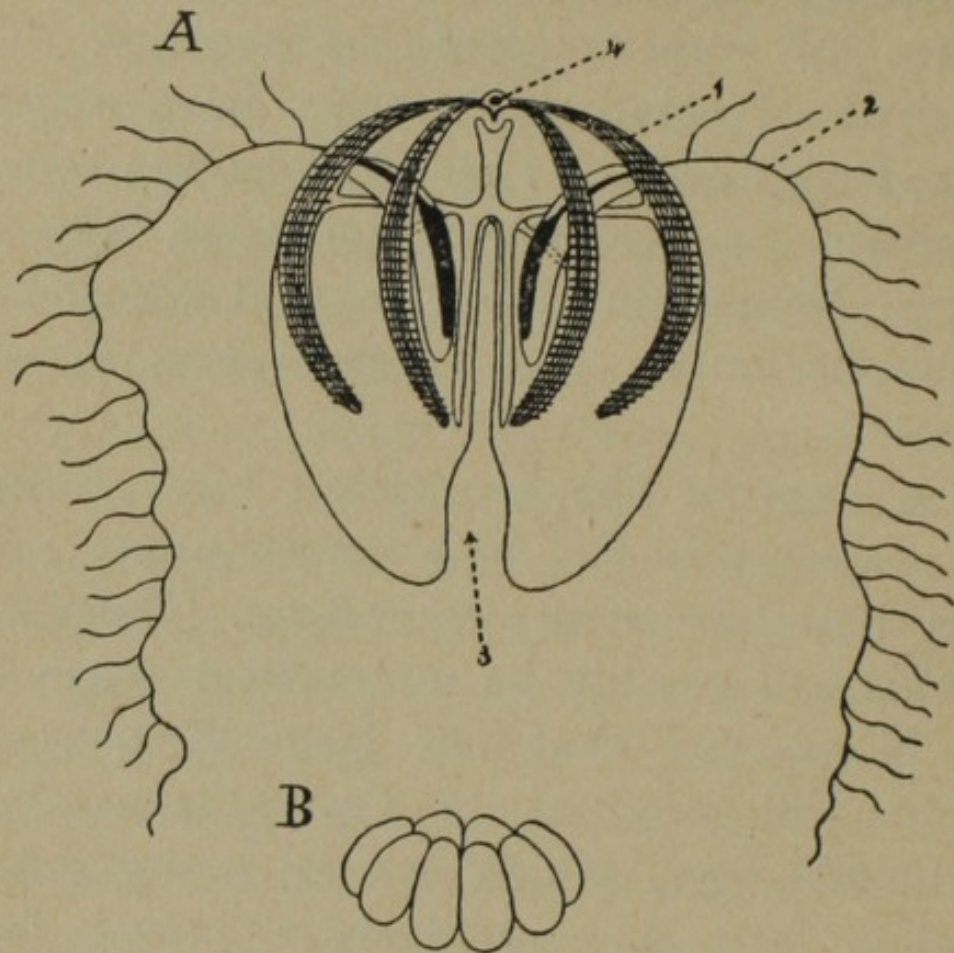


FIG. 10.

Illustrating the structure and development of a comb-bearer (Ctenophore). A. Adult form. 1. "Rib." 2. Tentacle. 3. Mouth. 4. Apical sense organ. B. The eight-cell stage in the development of the embryo.

rest, and even occasionally if one of the first eight cells be separated from the rest. But, on the other hand, if we take the eggs of the comb-bearers (Ctenophora) (Fig. 10) we get

a different result. These animals are shaped like elongated grapes. They pass their lives swimming in the sea; they are perfectly transparent, and they move by the aid of eight meridians of delicate comb-like structures which converge to meet at the upper pole, where there is situated a delicate brain and sense organ. Each "comb" consists of a short transverse row of cilia or vibratile hairs united at the base but free at the tips. Each row of combs is known as a rib. As the Ctenophora come to the surface in a calm sunlit sea, these combs glisten with the most lovely iridescent colours, and the whole creature presents a spectacle of great beauty. The first stage in the development of these animals is that the egg divides into eight cells ranged in a circle (Fig. 10, B). From each cell one-eighth of the animal, including one rib, is developed. If we remove one of the eight cells the remaining seven give rise to a creature with seven ribs; if we remove two a creature with six ribs is produced, and so on.

How are these differences in the constitution of the two eggs to be accounted for? The most plausible explanation which has been put forward is that there exist **organ-forming**

**substances**, and that in each cell of the Ctenophore there is a substance which contains the materials necessary for the formation of a particular rib. In each of the first eight cells of the segmenting sea-urchin egg, on the contrary, there is the same kind of substance, so that any one of them contains the necessary materials for constructing the whole body.

The question then arises, in what part of the cell are these materials to be found, in the protoplasm or the nucleus? Now Driesch has shown that if a fertilized egg of a sea-urchin be allowed to develop under such pressure as is produced by being squeezed between two glass slides, the first eight cells, instead of forming two tiers of four each, as they do in the normal egg, are all spread out in one plane. If now the pressure be removed the eight cells divide into two tiers and thus the sixteen-cell stage is reached, and this mass of cells is capable of developing into a perfectly normal animal, although the nuclei which should have been situated at its lower pole are now placed at its sides. The nuclei can therefore be juggled about like a handful of marbles without altering the course of development, and therefore the

peculiar organ-forming substances must be in the protoplasm and not in them. This result is confirmed by some experiments which Driesch made on the Ctenophore egg. He cut pieces from these eggs before they had divided into cells at all, and he showed that when these mutilated eggs survived they gave rise to imperfect animals, in which the full number of ribs was not produced. The specific organ-forming materials for the ribs must be in the protoplasm, for there was as yet only one nucleus and it was not touched by the operation.

These quite unexpected results were seized on by those who opposed the view that the nucleus was the sole bearer of the hereditary qualities as confirmatory of their objections. Of course, even if we were forced to admit that the bases for the qualities which the young animal inherits from its mother were situated in the protoplasm and not in the nucleus, we should still have to face the difficulty that the evidence compels us to believe that all qualities inherited from the father are carried in the head of the spermatozoon, which is a nucleus.

Fortunately, further experiments enable us to get over this apparent contradiction in

the constitution of the two kinds of germ-cells. The egg of the threadworm is a very specialized object. At its first division it gives rise to two cells, one of which is clear and the other granular. The clear cell gives rise to a part of the skin and to the nervous system; whilst the granular cell produces the internal organs. If the fertilized egg, however, be fixed to the rim of a horizontal wheel so that its axis of symmetry points towards the centre, and be allowed to develop whilst the wheel is kept in rapid rotation, it will divide into two granular cells which will develop into a double monster with two sets of internal organs, which cannot survive. It is obvious that the centrifugal force has caused the equal distribution of the organ-forming materials between the two cells, so that each in developing must give rise to the same result.

But if the same treatment be applied to the unfertilized egg we find that it can lose large portions of its protoplasm and become much reduced in size, but that nevertheless if it be afterwards fertilized it will develop into a normal embryo. Its protoplasm at this period of its development is, therefore, homogeneous, and we can only attribute its

subsequent heterogeneity to its infiltration by materials given off from the nucleus, and we have already learnt that the material of the nucleolus is ejected into the protoplasm; these materials obviously give rise to the different organ-forming substances.

This hypothesis is completely borne out when we examine the egg of the sea-squirt *Cynthia*. Here also we find strongly localized organ-forming substances. Indeed, in one species they are distinguishable in the living egg by their different colours. If we examine the ripening egg we find that streams of minute granules of chromatin are pouring into the protoplasm from the nucleus. Further, in the development of the species (*Cynthia partita*) in which the different organ-forming substances are distinguished by different colours it has been shown by an American zoologist (Conklin) that the ectoderm of the embryo is formed from the fluid contents or sap of the nucleus of the egg. When the egg ripens and the nuclear membrane is dissolved the escaping sap forms a cap of clear material at one side of the egg, and when its development is followed it is found to be changed into the ectoderm or primitive skin of the young animal.

We therefore arrive at two conclusions : first, that the nucleus of the female germ-cell is just as much the bearer of the hereditary qualities as is the nucleus of the male cell ; and, secondly, that the protoplasm of the growing egg becomes, in many cases, organized into substances which are the rudiments of the organs of the future animal by the emission of materials into it from the nucleus.

Once the protoplasm has been organized in this way, the nucleus ceases for a time to have any further influence, but after the first-formed organ-forming substances are used up the nuclei at a later period of development resume their active rôle.

If we now turn to examine the development of the sea-urchin we find that when the egg has divided into about 1000 cells these form a little hollow balloon or vesicle known as the **blastula** (Fig. 11). Then one side of the blastula becomes flattened and cells termed **mesenchyme** cells are budded from the flattened area and pass into the interior. Immediately afterwards the rudiment of the future gut is produced by the pushing in of one side of the blastula as if by an invisible finger. The in-turned portion forms the lining of the gut, and the embryo is now termed a



**gastrula.** Now Driesch has shown that the blastula may be cut in pieces with a fine pair of scissors, and each piece if above a certain minimal size will develop into a perfect larva. But if the operation be repeated after the mesenchyme has been produced, this is no

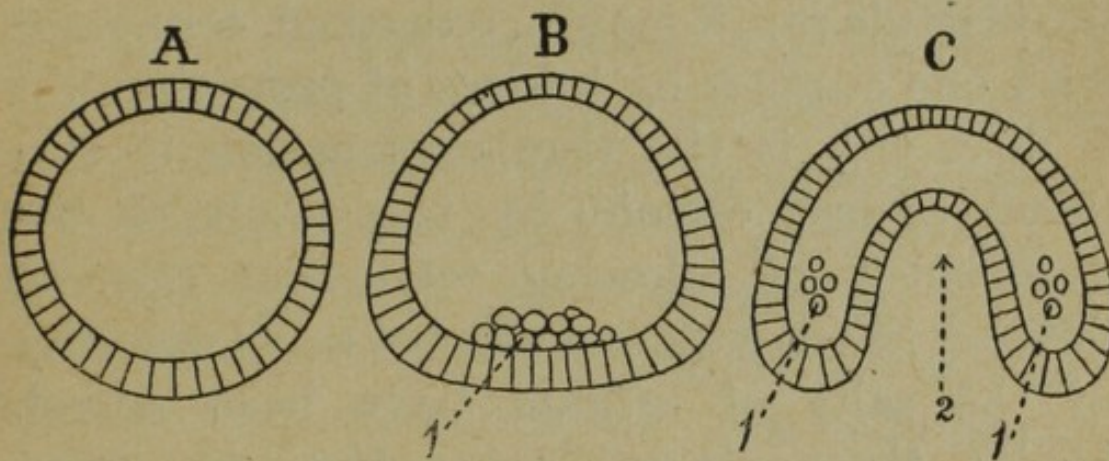


FIG. 11.

Three stages in the development of the egg of a sea-urchin. A. The blastula stage. B. The formation of mesenchyme cells. C. The gastrula. 1. The mesenchyme cells. 2. The gut.

longer the case; then fragments of the blastula will, indeed, heal up and produce smaller blastulæ, but these are incapable of further development—only the piece taken from the region where the mesenchyme has been produced can form a gut. The wall of the blastula, which was at first homogeneous, has now become heterogeneous, and one possible explanation of this is the assumption

that both skin-forming and gut-forming substances are at first found in every cell of the blastula, but gradually the gut-forming substances flow down, as it were, towards one end and become concentrated there, and the skin-forming substances remain in a pure state at the other end. The cells forming the blastula are, it may be remarked, connected with one another by bridges of protoplasm.

That this is the true explanation is rendered almost certain by the result of the experiment of allowing sea-urchin eggs to develop in sea-water to which a small quantity of the salts of lithium have been added. Under these circumstances the gut grows outwards instead of inwards, and a very large portion of the blastular wall is used up in forming the gut, so that the skin-forming portion is reduced to a mere button. This result is only obtained if the eggs are placed in the lithium solution soon after fertilization and kept there till the blastula stage has been reached. It is obvious, then, that it is during this stage that these substances are formed and that the absorption of lithium compounds causes a great deal more gut-forming substance to be made than is usually the case.

These organ-forming substances are, indeed, amongst the most striking discoveries of biological science, and we are as yet only on the threshold of our knowledge of them. Whether a certain mass of such a substance will give rise to one organ or two of the same kind seems to depend on its shape. If, for instance, we take the egg of a frog and allow it to divide into two cells, and then clamp it between two slides and reverse it, we may get a double-headed or a double-tailed tadpole. If we do the same with the egg of the newt we may get a complete double embryo. What is the explanation of this phenomenon? We have added nothing and removed nothing, we have, in fact, only turned the embryo upside down. The answer to this conundrum is that in the frog's egg there are two organ-forming substances which stand in a fixed spatial relation to one another, because of their different specific gravities, so that if the egg be turned upside down they sort themselves out under the influence of gravity. But if the egg be turned upside down when it has divided into two cells, then, since the contents of these cells are to a certain extent cut off from one another, the materials in each tend to sort themselves in the same way as if each cell

were a separate egg, and hence the tendency to produce two embryos. We can attain the same end by constricting not the egg, but the blastula of the newt, by a fine hair. If this be done in such a way as to constrict the front end longitudinally a two-headed monster is produced. In this case there can be no possible doubt that shape is the determining factor in deciding whether a normal or a two-headed embryo is to be produced.

Another instance of the same thing can be seen in the tail of the lizard. When this is broken off a little bud is formed on the surface of the stump by which a new tail is produced. If the surface of this bud be slightly indented by the prick of a knife it will produce two tails.

When once the primary organs have been formed, they seem to emit substances which act on each other and produce further modifications by which the secondary organs are formed.

One instance of this must suffice. All students of animal biology are aware that the type of eye found in man and the higher vertebrates is a complex organ consisting of two main portions, one formed as an outgrowth from the brain and constituting the

**retina**, and one formed as an ingrowth from the skin and constituting the **lens**. The retinal portion appears first in development, and if this portion be cut off in a young unhatched tadpole and planted under the skin in another part of the body, it will cause the skin above it to form a lens. We are, therefore, driven to the conclusion that the formation of a lens in the normal development of the tadpole is not due to a special quality of the skin in the region of the head, but is the result of the modification of the skin in this place under the influence of the growing retina beneath it.

These influences are known as **formative stimuli**. Even less is known about them than about organ-forming substances, but their further investigation would be a most fascinating study. Their existence, however, shows quite clearly that Weismann's conception of the growth of the body as the development of a mosaic pavement-like arrangement of rudiments, each predestined to form a distinct organ, is fundamentally wrong. Just as the sea-urchin blastula in its earlier stages is a mass of relatively homogeneous material, any part of which can form the whole animal, so the primary tissues are

relatively homogeneous, and what organs they will give rise to depends to a large extent on the influences to which they are subject.

To sum up, we conclude that the bearers of hereditary influence are the chromosomes of the nuclei of the male and female germ-cells. These chromosomes are brought together in fertilization, and cause the development of the offspring by the emission of substances into the protoplasm which change its character and confer on it the power to develop into the primary organs. These primary organs in turn emit materials into the fluids of the body which affect parts of other primary organs so as to give them the power of developing into the secondary organs, and so the adult form is attained. Therefore we must always remember that in looking for the reappearance of parental characters in the offspring, we must not only compare with one another corresponding stages of development, but also the offspring must be exposed to the same conditions during its development as the parent. Adverse conditions by interfering with the complex mechanism of development may altogether prevent the appearance of parental characters.

## CHAPTER IV

### THE INHERITANCE OF HABITS AND OF THEIR EFFECTS

IN the three preceding chapters we have studied the material bridge between parents and offspring. We have seen ourselves driven to the conclusion that the bearers of the hereditary qualities are to be found in the nuclei of the germ-cells, and that the essential parts of the nucleus are constituted by the chromosomes, which undergo great changes during the growth and division of the cell, but which retain their individuality throughout them all. If, as we have already said, like always produced like, the problem of heredity would be a simple one, but children do not completely resemble their parents, and the task of the science of heredity is to find out the causes of this divergence.

Now one of the oldest ideas on this subject was that the experience which the parent underwent, especially during the time shortly before the birth of the child, affected the nature of the child. Thus a pregnant mother

who had constantly seen a cripple passing and repassing her house gave birth to a deformed child, and this pre-natal impression was given as the reason. In its extreme form this doctrine finds few defenders to-day, but the question whether the habits and activities of the parents have any effect on those of the child is at present one of the most hotly debated questions in zoology and it is one of fundamental importance. The doctrine that habits and their effects are inherited was first clearly stated by the French naturalist Lamarck in 1810, and this theory is usually called Lamarckism. Lamarck stated his views as follows :

(1) Every fairly considerable and permanent alteration in the environment of a race of animals works a real alteration in the needs of that race.

(2) Every change in the needs of animals necessitates new activities on their part for the satisfaction of those needs and so new habits are formed.

(3) Every new need which necessitates new activities for its satisfaction requires the animal either to make more frequent use of some of its parts which it previously used less, and thus greatly to develop or enlarge



them, or else to make use of entirely new parts to which the new needs have imperceptibly given rise by inner feeling.

(4) All the acquisitions or losses wrought by nature on individuals through the influence of the environment in which their race has *long* been placed,—all these are preserved by reproduction to the new individuals which arise.

If Lamarck's views were to be accepted a great part, if not all, of the evolution of animals and plants from simple ancestors could be explained, for the principal differences between allied organisms consist in their different habits and the structures associated with those habits, and the more closely animals are examined in their natural surroundings, the more clearly does this fact come out. But Lamarck's theory has been vehemently denied; and other alternative explanations of evolution have been put forward. Of these there are two which may be termed the Darwinian and the Mendelian, although Darwin accepted the truth of Lamarck's theory and Mendel did not deal with evolution at all, but only with the laws governing the characters of hybrids produced when two races of the same species were crossed.

Darwin pointed out that if members of the same litter, all of which are produced at the same time, be closely examined it will be seen that no two are exactly alike, but that each one differs slightly from its fellows in its shape or colour. He assumed that these differences were inheritable and that some characters would better suit the environment to which the young animal was to be exposed than others; those fortunate members of the litter which chanced to possess these characters would survive and propagate the race, whereas the others would perish prematurely. Thus the "fittest" would survive, and this process was likened by Darwin to the selection which a breeder practises when he chooses the individuals of his stock which he wishes to mate together in order to obtain progeny, and so he termed it "natural selection." To this selection he attributed the major part of evolution, the inheritance of the effects of use and disuse (Lamarck's principle) occupying only a subordinate place in his idea of the causes of evolution.

Mendel, as we have seen, dealt only with the qualities of hybrids, but when that considerable school of modern biologists who are usually termed Mendelian began to repeat

Mendel's experiments, they soon discovered that amongst any large collection of domesticated animals or of cultivated plants individuals showing marked divergences from the type "crop up" occasionally, and that when these individuals are mated with typical ones, the offspring obey the Mendelian rules governing hybrids. No reason has been assigned for the appearance of these abnormal individuals by Mendelians other than "chance" or "accident." Nevertheless to the occurrence of such "accidents" they do not hesitate to attribute the whole process of evolution.

We must postpone to a later chapter the critical examination of the efficiency of natural selection and of Mendelian "accidents" or "mutations," as they are called, as agents in evolution, and return to the question of the inheritance of habits—or, as they are usually termed, "acquired characters."

The early exponents of evolution, such as Darwin and Haeckel, accepted Lamarck's principle. It was first explicitly denied by Weismann, and that on two grounds: viz. (1) Weismann could imagine no mechanism by means of which changes in the structure of the body resulting from changed habits could be transformed into representative

changes in the germ-cells; (2) the experiments which Weismann instituted seemed to prove that acquired characters were not inheritable.

We shall deal with (2) first. Weismann cut the tails off young white mice, reared them to maturity and bred several generations of offspring from them. None of these offspring showed the slightest sign of any deficiency in the tail. But it may be at once objected that to lose a tail by mutilation is not to acquire a habit; and the experiment is therefore entirely irrelevant. As to (1), we may say that it is likewise irrelevant, for no one has any clear idea as to the mechanism by means of which the chromosomes of the paternal and maternal nuclei in the fertilized egg give rise to the bodily organs of the adult; this undoubtedly occurs, and yet it is as incomprehensible as the transference of the qualities of the parent to the egg.

Inconclusive as was Weismann's reasoning it was widely accepted, and it became for a time almost a biological dogma that under no circumstances could the effects of habits be handed on to posterity. It is therefore not to be wondered at that when new evidence was offered to the effect that, after all,

acquired characters *are* passed on to posterity, this evidence aroused the most violent opposition; for scientific men dislike as much as religious men to be awakened from a dogmatic sleep. The researcher who first questioned the accepted belief was openly charged with fraud; and this facile way of dealing with the subject, adopted by a leading English biologist, was at once copied by a large number of his less original followers. During the recent war the question could not be probed further, as Kammerer, the author of the new researches alluded to, is a native of Vienna and all his work has been done in the Institute of Experimental Biology in that city. But quite recently Kammerer has visited England, bringing his critical specimens with him, and has demonstrated these to English scientific men, and all who have discussed the matter with him are convinced that he is an upright and skilled investigator. It is still more important to observe that precisely similar results to those obtained by Kammerer have been reached by two other investigators who dealt with widely different animals, one of them working in Moscow and one in Breslau. In neither of these two latter cases would it

occur to anyone to bring forward the hypothesis of fraud to account for the results, the more so as the Russian scientist before taking up the question of inheritance at all had acquired world-wide fame as one of the leading physiologists of the day. The reader will thus observe that a great mass of careful scientific experiment has been accumulated which demonstrates the inheritability of the effects of habit. When this mass of evidence has had time to penetrate the scientific world and be appreciated at its proper value it will revolutionize many of the current ideas on heredity.

We shall now give an account of some of Kammerer's experiments which demonstrate Lamarck's principle in the clearest way. We have already mentioned (see Chap. III) that there are two species of salamander commonly found in Europe, viz. *Salamandra maculosa* and *Salamandra atra*. The former is of a black colour spotted with patches of yellow, but the relative quantities of these two pigments varies very much; some specimens are nearly black with a few minute dots of yellow, whereas in others the yellow predominates so much that the black is nearly suppressed. A fairly common variety has received the name *taeniata*, because in it the

yellow forms two conspicuous longitudinal stripes on the back separated by a median black stripe, but this variety is not found wild in the neighbourhood of Vienna, for it only occurs in the Jura mountains and westward of them, and when Kammerer began his researches he had never seen it. The adult animal lives on land in damp nooks, under moss or among stones; it is often difficult to find, but sometimes after a heavy thunder shower hundreds will be found where not one could be seen before. It is an inhabitant of the warmer regions near the sea-level in Austria, Italy and Southern Europe generally. The animal is born as a larva which lives in the water. This is of the same general shape as the adult, but is distinguished by the possession of three feathery gills on each side of the neck between which are slits leading into the throat, and by having a flattened tail suitable for swimming. The larva is of a yellowish colour owing to a plentiful development of yellowish-white pigment, but this pigment is quite distinct from the adult pigment, which only becomes conspicuous after the creature leaves the water and the metamorphosis has been accomplished, although traces of it can be seen in the larva. Traces

also of the adult black can be detected in the larva, but it, like the yellow, increases in quantity only after the metamorphosis.

*Salamandra atra* is an inhabitant of the colder upland regions among the Alpine meadows. It is of a uniformly black colour, and, as already mentioned, brings forth its young in a shape completely resembling the adult, without gills and with a rounded tail.

Preliminary experiments showed that young, just metamorphosed specimens of *Salamandra maculosa* slowly altered their coloration as they grew older, if they were kept living on black or yellow backgrounds strongly illuminated from above. In those kept on black backgrounds the black increased in quantity and overshadowed the yellow, whilst in those kept on yellow backgrounds the reverse change took place. But if the background were of any other colour, or even of black and yellow patches in even proportion, or, lastly, if it were not brightly illuminated, no change whatever took place; so that when an experiment was being carried out it was only necessary to enclose a similarly coloured salamander in a neighbouring cage from which bright light was excluded in order to establish a perfectly satisfactory "control" experiment.



Long experience and many unfortunate failures were required before the best way of keeping the beasts healthy was discovered. The larvæ were always kept under neutral conditions, *i. e.* they were kept in diffused light and were not exposed to the influence of black or yellow backgrounds. They were fed with blood-worms (*Tubifex*), which could be procured in large quantities. The adults, on the contrary, were kept in boxes of considerable size, lit from above. These were kept damp by basins of water, one of which was placed in each of them, and in this the salamander could bathe itself; in each there was also a "den" of moss and stones in which the animal could hide. The food given consisted of meal-worms (the grub of a beetle which infests flour mills); these were placed in a little dish at some considerable distance from the "den," so that the salamander had to make frequent journeys across the open to get them.

The whole series of experimental cages were placed in a sunny gallery in the laboratory of the Institute of Experimental Biology at Vienna. It is therefore clear that for the successful performance of an experiment of this kind a very considerable "plant" is

necessary, and it will demand practically the whole of the experimenter's time. Indeed, Kammerer says expressly that anyone who desires to repeat his experiments and test their validity must be prepared to devote a large part of his life-time to the work.

The nature of the experiments performed was as follows :

The floors of some of the cages were covered with yellow loam and the sides were painted yellow. The animals confined in them were thus exposed from the beginning to adult life to the influence of a yellow background. The floors of other cages were strewn with black garden earth and their sides were painted black, so that the salamanders in them lived on a dark background.

When individuals chosen for their predominantly black colour, which had been reared on a background of yellow loam, gave rise to young—which only happened when the parents were four years old—these young were reared as larvæ on neutral backgrounds. When they had undergone metamorphosis they were divided into two lots, one lot being reared further on a background of yellow loam, and the other on a background of black garden earth. Those which were reared on yellow

earth became increasingly yellow. The yellow pigment, which in the parents had increased till it formed two longitudinal rows of large



FIG. 12.

Illustrating the effect of a background of yellow loam on a comparatively black salamander. A. Young form just after metamorphosis. B. Fully-grown form.

spots (Fig. 12, B), grew in the children to such an extent that the rows of spots became amalgamated so as to form longitudinal streaks, and

finally the streaks became connected by transverse ridges until the whole dorsal surface was predominantly yellow (Fig. 13, B). In those



FIG. 13.

Illustrating the effect of a background of yellow loam on the offspring of salamanders born from those represented in Fig. 12. A. Young form just after metamorphosis. B. Adult form.

young which were reared on black garden earth, the yellow pigment made its appearance as two longitudinal lines of spots, and these

spots for some considerable time increased in size owing to the persistence of the influence



FIG. 14.

Illustrating the effect of a background of black garden mould on the offspring of salamanders which had been reared on a background of yellow loam. A. Young salamander five months after metamorphosis, showing influence of the yellow background to which its parents were exposed. B. Adult salamander, showing influence of the black background.

of the yellow background on which their parents had lived (Fig. 14, A); but as the young

generation grew older the spots began to diminish in size, and finally, when maturity was attained, the yellow pigment was reduced



FIG. 15.

Illustrating the effect of exposing the offspring of salamanders reared on black earth to the same influences as those to which their parents were exposed. A. Just metamorphosed form. B. Adult form.

to two longitudinal rows of small spots (Fig. 14, B).

If, on the contrary, salamanders were

chosen which had comparatively large yellow spots, and these were reared on a background of black garden earth, the yellow spots diminished in size till by the time that maturity was attained many of them had entirely disappeared, and those which remained had become very small. The offspring of such salamanders, just before and at the time of metamorphosis, were distinguished by the possession of a single median row of small yellow spots (Fig. 15, A). If these young were allowed to grow up on a background of garden earth the yellow spots became smaller and finally almost disappeared—indeed, on the ventral surface they totally disappeared, and an almost perfectly black salamander was produced, in appearance closely resembling *Salamandra atra* (Fig. 15, B). If, on the contrary, the offspring of salamanders reared on black earth were transferred to yellow loam, the median row of spots slowly enlarged and finally fused to form a single longitudinal stripe of yellow, but it will be noticed that this distribution of yellow and black was totally different from that observable in the parent with which the experiment started. As in the case of the experiment which began by placing salamanders on yellow earth, the

influence of the environment made itself felt in the constitution of the young, although these might be born and pass the first part of their life under neutral conditions.

It occurred to Kammerer that some part of the influence of the yellow and black backgrounds might be due to the amounts of water they contained—in a word, to their comparative dampness. He determined experimentally that the yellow loam was much more hygroscopic, and therefore damper than the black earth. In order to get rid of this factor he replaced in some of his experiments the yellow and black earth with yellow and black paper. For the experiment in which yellow paper was to be the background salamanders were chosen in which black predominated; the result of the experiment was that the yellow increased in amount—but solely by the increase in size of spots which were already in existence—practically no new yellow spots made their appearance. The offspring of these parents reared also on yellow paper showed the same phenomenon; the large spots amalgamated into broad yellow stripes, but the yellow was of a dusky appearance, showing that it was mixed with the black pigment; in a word, as no new yellow pigment spots had



been generated, the existing pigment had been spread out in a very thin layer. When the young of parents reared on yellow paper were reared on a background of black paper, very much the same effect was produced as when they were reared on a background of black earth, but there was this difference, that the yellow spots diminished in size, not by a gathering together of the yellow pigment and a drawing in of the root-like outgrowths of the yellow spots, which is what happens over a background of black earth, but by a darkening of the borders of the spots due to an invasion of them by the black pigment (melanin). It was thus obvious that some other factor in the background besides that of mere colour played a part in bringing about the result; and it appeared probable that this was the moisture of the environment. In order to test this a background was chosen which produced no colour reaction in salamanders which were raised on it. A very suitable one was found in grey river sand, which could, of course, vary very much in the quantity of moisture which it contained without sensibly altering in colour. When young salamanders, chosen for the small number of yellow spots which they possessed,

were placed on sand so wet that the air in the cage had a humidity of from 80 to 90 per cent. of saturation, then the yellow spots did not increase in size, but a great number of small new spots made their appearance, especially on the under surface, where ordinarily few yellow spots are to be found. The offspring of these salamanders, just after metamorphosis, were distinguished from all other salamanders by the great number of minute yellow spots peppered over them. When these salamanders were transferred to a background either of yellow earth or yellow paper all the existing spots began to increase rapidly in size. On the other hand, when salamanders characterized by having numerous yellow spots were reared on a background of relatively dry river sand in an atmosphere the humidity of which did not reach more than 50 per cent. of that required for saturation, these spots all diminished in size, not, as on black earth, by contraction, but by the invasion of their borders by black pigment, so that the yellow colour became fainter and eventually disappeared.

It appears, therefore, that the presence of a yellow background causes the yellow spots to increase in area, to throw out roots and

eventually to join with one another, whilst the presence of a damp atmosphere causes the production of new yellow spots, and that both these changes are to a considerable extent inherited, insomuch that the offspring start their career at a phase nearly, but not quite, as advanced as that at which their parents left off.

The question now arises as to the channel through which the environment acts on the animal. Does it take place through a direct action on the skin, or is it indirect through the influence of the environment on the eyes of the animal? That such influence can take place through the eyes is known from the behaviour of the plaice and other flat-fish. These fish are able to alter the coloration of the upper surface according to the colour of the ground on which they lie. Now it is well known that when a flat-fish is blinded it remains pale and does not take on the colour of its surroundings. The answer to the question so far as the salamander was concerned was found by Kammerer by a series of the most ingenious experiments.

He first found out what occurred when a piece of skin was removed and the wound became covered with new skin. If a piece of

yellow skin which had been originally black and had been turned yellow by the environment was removed and the animal continued to live on a yellow background, then the new skin when first formed was of an olive-green colour, due to the presence of both yellow and black pigments in equal quantities, the black pigment being situated in a more superficial layer and the yellow pigment showing through it, but soon the new skin became bright yellow under the continuous influence of the yellow background. If a piece of black skin which was formerly yellow were removed, the new skin began by being yellow and remained so if the animal was placed on a yellow background. If a piece of yellow skin which was formerly black were removed and the animal were placed on a black background the new skin began by being black and remained black. If, however, the skin removed were black, but had been yellow, then, if the animal continued to live on a black background, the new skin when first formed was flecked with dusky yellow spots, but soon became totally black. Kammerer concludes that the regenerated skin tends to repeat the history of that which it replaces, but that this history is shortened and may be even entirely suppressed.

Then the experiment was made of transplanting a black piece of skin from a black salamander living on a black background to a bare place on a yellow salamander living on a yellow background. The foreign skin thrived in its new situation and the wound healed. If the animals were transferred to neutral backgrounds no change at all took place in the colours of the transplanted skin; but if the animal carrying the black skin were removed to a background of yellow loam, then quickly numerous small yellow spots began to appear, but they did not grow any bigger. After a period of fourteen or fifteen months of living on this background the spots suddenly began to enlarge and eventually the whole patch of skin became yellow. Kammerer interprets this remarkable result as follows: The appearance of yellow spots on black skin was due to the effect of the humidity of the loam acting directly on the skin, but in order that the yellowness of the loam should produce its effect on the black skin, new nervous connections must be formed, and this was a process which required time. He concludes, therefore, that the background, so far as it is yellow, produces its effect through the eye of the animal. The correctness of this conclusion was confirmed by keeping yellow

animals, on to each of which a piece of black skin had been transplanted, on backgrounds of wet sand and yellow paper respectively. On the first background the black skin began at once to develop small yellow spots, due to the direct influence of the humidity of the background on the skin; on the second no change took place for a year, but then, if there had been small yellow spots on the black skin when it was removed from its former host, these began suddenly to increase in size, owing to the influence of the yellow colour of the background indirectly on the skin through the eye.

But Kammerer's experiments were by no means limited to the investigation of the inheritance of colour. He succeeded in altering the whole of the breeding habits of both *Salamandra maculosa* and *Salamandra atra*. When *Salamandra atra* was kept in warm and moist surroundings, instead of producing only two youngsters at a birth, one from each side of the body, it began to produce more, first three, and then at subsequent seasons four or five or even six young. This change is rendered possible by the mode of embryonic development. At each breeding period about six eggs pass from each ovary into the egg-

tube beneath it, but of these six only the lowest on each side develops into an embryo, the remainder degenerate into a kind of yolky soup, which serves as food for this embryo. When, however, the parent was kept warm and moist, more of the eggs developed and the young which developed from them were born whilst they were still provided with gills; these young took to the water and lived in it like the young of *Salamandra maculosa*. When these young were reared to adults under the same conditions and allowed in turn to produce young, they gave birth to still larger broods than did their parents, and these young of the second filial generation were born at as early a stage as those of *Salamandra maculosa*. Conversely, if *Salamandra maculosa* was kept in comparatively cool dry surroundings, it produced at each breeding season fewer young, and these were born at a later stage of development. These young when reared under similar conditions to those to which their parents were exposed produced still smaller broods, and eventually gave rise at each birth to only two or three fully-developed young in which the gills were almost completely absorbed—only small stumps of them remained, just as is the case with *Salamandra atra*. It is still more

interesting to find that if *Salamandra maculosa* be kept in semi-tropical conditions in which the warmth and moisture are both greater than those to which it is accustomed, its young become more numerous and are born at still earlier periods of development, and these young, reared to adults and allowed to pair, give rise to eggs from which issue larvæ with only the forearms developed. Such is normally the case in the allied genus Triton (Molge), to which our English newts belong.

The so-called midwife toad *Alytes* was also the subject of another of Kammerer's experiments. Ordinary frogs and toads pair in the water, the male clasping the female round the waist, and remaining in this position sometimes for weeks, till the female emits the eggs, when he fertilizes them by a simultaneous emission of sperm. The young are hatched from the eggs as very small larvæ, which at first carry on each side of the neck three feathery gills like those of the salamander larva, but these gills soon become covered up by a fold of skin growing back from the side of the head, and the larvæ then assume the rounded plump form so familiar to all as the tadpole. *Alytes*, however, pairs on the land, and when the eggs are emitted, as they are in the case of all



kinds of toads, in long strings, the male winds these strings round his legs after he has fertilized them, and he carries these strings about with him till the young hatch. These hatch as tadpoles which have passed through the stage with feathery gills whilst still embryos within the egg membrane, *but whilst in this stage the embryo only develops one large feathery gill on one side.* If, now, *Alytes* be kept in a warm place, however dry it be, it will thrive provided it is given access to a pool in which it can occasionally bathe itself. Under these circumstances it breeds in the water and the egg-strings slip off the legs of the male and lie in the water. Most of the eggs perish, but by transferring them to sterilized water some may be reared. *Alytes* in Vienna breeds twice a year, and it is soon noticed that at each successive breeding period more eggs are produced than usual, and these are of a smaller size than those normal to the species. From these smaller eggs tadpoles emerge in the stage in which each carries one large feathery gill on each side. If these young be reared to adults they at once resort to the water to pair and produce eggs from which young are hatched with *three* feathery gills on each side of the neck, as occurs in

other forms of toad. In this generation also the males develop a horny pad on the inner side of the palm of the hand and of the fingers. This pad enables the male to retain his hold on the female during the nuptial embrace. A similar pad is developed by the males of all other species of frogs and toads which pair in water; but the normal *Alytes* male does not develop it because, since he pairs on land, the skin of his partner remains dry and horny, and he does not need it for the purpose of maintaining his embrace. An indication of this pad is seen in males of the second generation reared from eggs lying in water, but only becomes marked in the third generation of such males. Kammerer exhibited a male with such a pad in London in 1923.

It has been suggested that Kammerer's results on *Salamandra maculosa* may have been due to the influence of yellow light reflected from the yellow background penetrating the body of the animal and acting directly on the germ-cells. In order to test this a pupil of Kammerer, Secerov, dissected out the ovaries of female salamanders and inserted in their place sealed glass tubes containing each a roll of photographic paper.

After remaining exposed to yellow light for a period of months the salamanders were killed and the tubes extracted and examined. The photographic paper showed a very faint indication of darkening. It is thus seen that the light which reaches the ovaries through the tissues is of minimal amount and utterly unlikely to have any effect on the egg-cells. Kammerer himself brought further proof that the egg-cells are affected through the medium of the body in a series of most painstaking and difficult experiments. He transplanted ovaries from females which were striped to females which were spotted, and vice versa, and he crossed these females with males similar to them in colour. The transplantation of ovaries rather than testes was undertaken, because the testis of the salamander is an elongated, lobed organ, and it was difficult to make certain that it was completely removed. When the young produced by these crossings were examined it was found that they were sometimes influenced by what we may term the foster-mother and sometimes not. Upon examining the matter more closely it was found that if the foster-mother were the natural striped variety, and if she were supplied with the ovary of the spotted variety,

then she had no influence on the offspring whatever, which turned out exactly as if the eggs had still been carried by the female which produced them. If, however, the female were the artificially produced striped variety which was supplied with the eggs of the spotted variety, then the young turned out striped like the foster-mother. This result was produced even though the foster-mother during the time of the experiment was kept in dim light, so that all direct action of the environment was excluded. In the results of these experiments then we have a proof of the direct action of the body on the germ-cells, which is, after all, the crucial point in the question of the inheritance of acquired qualities. It will be observed that in Kammerer's experiments the newly-acquired qualities are those which are most potent in influencing the germ-cells.

Kammerer's experiments are unique in their extent and in the length of time (eleven to twelve years) which has been devoted to their execution, but other workers have obtained confirmatory results in the case of other animals.

Thus Durkhem showed that pupæ of the common white butterfly are usually greyish

in colour owing to the deposition of a quantity of black and opaque white pigments in the pupal integument. But when these pupæ are exposed during the latest caterpillar stage to the influence of orange light, then the deposition of these pigments is prevented and the pupæ appear green owing to the green blood of the insect shining through. Not all the pupæ show this reaction; ordinarily only about 65-70 per cent. of them turn green. When, however, these pupæ give rise to butterflies and these lay eggs, and the pupæ reared from these eggs are exposed to orange light, about 95 per cent. turn green. If, on the other hand, these pupæ of the second generation are allowed to grow in ordinary white light, then about 40 per cent. turn green, whereas in control pupæ, the parents of which were never exposed to orange light, the number of green caterpillars did not exceed 4 per cent.

Pavlov experimented with white mice, to which he endeavoured to teach an association of ideas. They were fed once a day, and each time food was put into their cages an electric bell was rung. It required 300 lessons to impress on these mice the meaning of the ringing of the bell. When, however, a first "filial" generation of mice was bred from

them, 100 lessons sufficed to teach these younger mice to seek their food when the bell was sounded. In the second filial generation this result was accomplished in 30 lessons, and in the third filial generation in 5 lessons.

Kammerer's, Durkhem's and Pavlov's experiments thus all give the same result, viz. that the exercise of a habit on the part of an animal renders the formation of the same habit easier in the offspring. The pigmentary reaction to light and the association of food with sound are both habits. Of course the newly-inherited habit does not persist in its full strength if the young are not exposed to the same conditions as their parents, because the transference of the young to new conditions sets up an opposing reaction and begins the formation of a new habit. But nevertheless, Durkhem's and Kammerer's experiments show that traces of the effect of parental habit still persist, especially in young animals, and this persistence is the basis of that "*recapitulation of ancestral history*" which is such a prominent feature in animal development.

The question as to *how* the tendency to form a habit is transferred from the body of an animal to its germ-cells is one on which

we can only speculate. Rignano has suggested that every reaction of an animal tends to deposit in the tissues, and incidentally in the germ-cells, a substance which acts as a stimulus towards the performance of the same reaction in the young which develop from the germ-cells. We have already seen that in the formation of the bodies of animals a stage is arrived at where the primary organs act on each other and determine each other's future development. We can only picture such an action as the emission of substances from these organs into the body fluids. Some such substances have been detected and they are known as **hormones**. Thus if the thyroid gland which lies beneath the throat be removed from a tadpole, it will not metamorphose into a frog, and if this gland is diseased in a human being the mental powers do not develop and he or she becomes an idiot. If we assume that all the tissues are continually throwing off hormones into the blood, and that these hormones are stored in the germ-cells, then when a new habit is learned we may imagine that an altered product is given off into the blood and stored in the germ-cells; and so when the germ-cell develops into a young animal this is rendered

more sensitive to the change that calls forth the original formation of the habit. The tendency of the young to repeat the parental habits may be likened to memory. In Kammerer's experiments with *Alytes* the formation of a pad on the hand of the male *Alytes* in the third generation after the animals had repaired to the water to mate could be regarded as the revival of a half-forgotten memory, for undoubtedly the ancestors of *Alytes* resembled other toads in possessing this pad. It has been suggested, and it is perhaps true, that the revival of an old habit is an easier matter than the formation of a new one, but the principle that the experience of the parents affects the children is the same in both cases. Another good example of the revival of an old memory is afforded by another experiment of Kammerer. In the caves of Carniola in Austria there lives a blind, pale, flesh-coloured newt called *Proteus*, which retains its external gills throughout life. The eye in this species is represented by a minute sac of pigmented cells buried beneath the skin. If young *Proteus* are brought out into the light the skin acquires pigment but the eye does not develop; but by exposing the young animal only to red light the formation of skin



pigment is prevented and the eye develops into a large normal eye, capable of sight. This experiment may be compared to the revival of a forgotten childish memory by some special stimulus.

## CHAPTER V

### THE INHERITANCE OF FLUCTUATING VARIATIONS

WE have already mentioned the fact that Darwin in constructing the famous theory of evolution, although he accepted Lamarck's principle, yet laid far greater stress on the small differences of size, shape and colour which distinguish members of the same brood of nestlings and of the same litter of mammals from one another. These differences are usually known as **fluctuating variations**, and Darwin assumed that they were inheritable, and in this assumption he was followed by Alfred Russel Wallace, who shares with Darwin the glory of having first clearly enunciated the principle of natural selection.

But Darwin and Wallace, without perhaps clearly realizing it, assumed more than this. It is not enough to suppose that, for instance, the differences in length of beak amongst the same brood of nestlings are inheritable. If natural selection favours the survival of the

bird with the longest beak, unless amongst the offspring of this bird there appear some nestlings with still longer beaks, evolution will not proceed. Therefore we must suppose that the characters of the offspring of the survivor will fluctuate around the characters of their immediate parent, just as did the characters of that parent and his brothers and sisters around those of the grandparent.

Wallace tried to show that if this assumption were granted the action of natural selection would account for every kind of change of which we have evidence in the animal and vegetable kingdoms, including those which Darwin was inclined to attribute to the effects of use and disuse.

If these individual differences had the tremendous significance which Darwin and Wallace attributed to them, it was clearly of the first importance that they should be measured; and this step was taken by Sir Francis Galton, Darwin's cousin, who devised a scheme for the measurement of the inheritance of individual peculiarities among the human population. A short account of how this scheme was applied to the question of the inheritance of stature will exemplify its character. Galton offered a considerable sum

of money as prizes for good family records of stature, and in this way he secured a large supply of data. When he came to analyze these he found that on the whole adult women were shorter than adult men, and that the ratio of the average male stature to the average female stature was as 13 to 12. For this reason he felt justified in multiplying all his figures for female stature by 1.08, thereby implying that each woman if she had been a man would have been taller in that proportion. In this way he got rid of the disturbing factor of sex. He next sorted his records into groups, in which no individual differed from another in height by more than half an inch. Then a distance (abscissa) was measured from one fixed point along a horizontal line, proportional to the mean stature of each of these groups, these ranging from 62 to 76 inches. At every point on this line corresponding to the stature of each group, a perpendicular (ordinate) was erected, proportional in length to the number of individuals comprised in that group, and through the summits of these upright lines a curve was then drawn. The more numerous the measurements upon which the curve was based the smoother it became, and as the number of measurements was

increased the curve continually approached a geometrical form well known to mathematicians, called the **curve of error**. If  $x$  represent the length of the abscissa and  $y$  the length of the corresponding ordinate, then the relation between these two for all points lying on the curve of error is defined by the equation  $y = ke^{-h^2x^2}$ , where  $h$  and  $k$  are constants which define the slope of the curve, and  $e$  is the logarithmic base.

To those unversed in mathematics it may be explained that the shape of this curve is that of a summit having a slope of the same steepness on both sides, the inclination of which diminishes as it approaches the horizontal axis with which it tends to coincide, but never quite succeeds in reaching. Translated into ordinary language this curve indicates that in a sufficiently large sample of the population taken at random, a considerable proportion may be described as being of medium stature (this is generally indicated by the height of the ordinate at the summit of the curve), that the number of those who are taller and of those who are shorter than the mean stature by a given amount is approximately equal, and that the number of giants and of dwarfs is extremely small. The extent

to which the mean stature of any of the classes into which the population has been divided differs from the mean stature of the whole population is known as the **deviation**

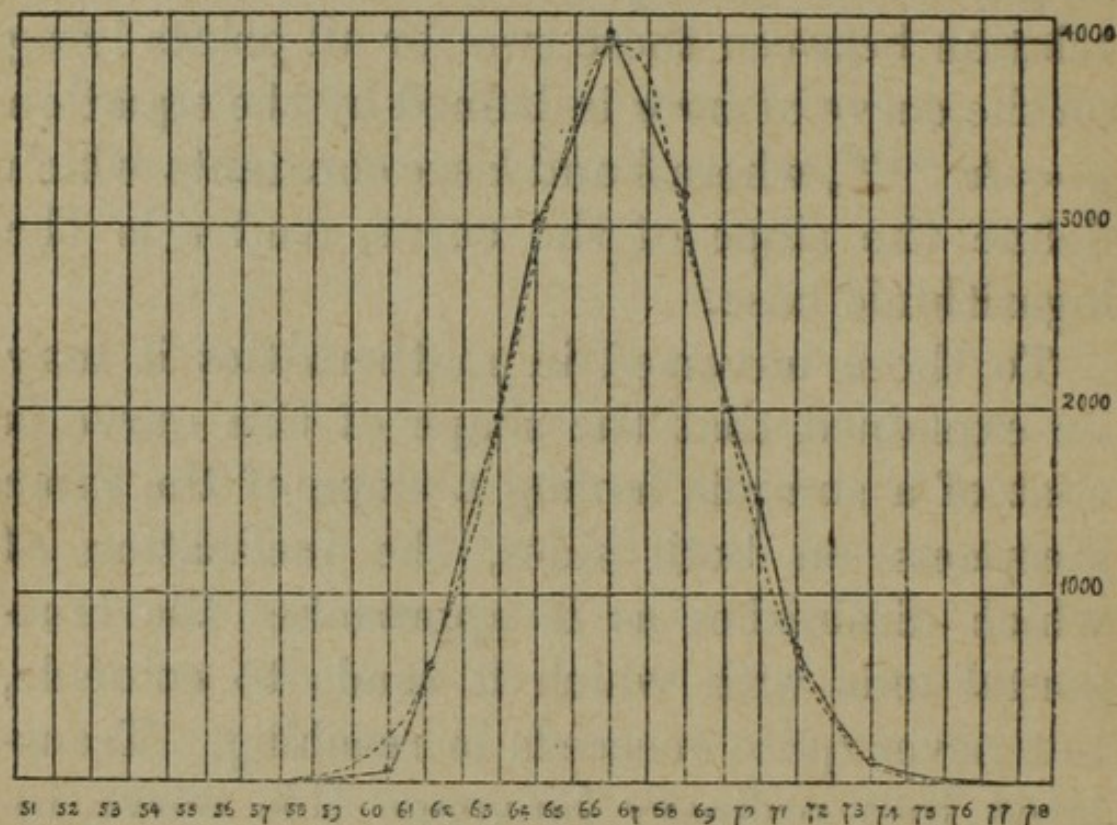


FIG. 16.

Diagram to show the distribution of stature amongst 20,000 recruits of the American army. The figures on the base line indicate height in inches. The dotted line indicates the continuous curve to which the records approximate.

of that class. If we now select two individuals from the population, one of whom is taller than one-quarter of the population and shorter than the remaining three-quarters, and the other of whom is taller than three-quarters

of the population and shorter than one-quarter, then the deviations of the statures of these individuals from the mean are known as the **quartiles**, and are designated by the symbols  $Q$  and  $Q^1$ . If the curve were perfectly symmetrical  $Q$  would be equal to  $Q^1$ , but in practice the smoothness and perfect proportions of the ideal curve are never attained, and so Galton used the mean of the quartiles  $\frac{Q + Q^1}{2}$  as a measure of the variability. The

deviation of this mean from the mean of the whole population is known by the extremely unfortunate name of **probable error**—a name against which Galton emphatically protests. For mathematical reasons, however, workers on heredity who use Galton's method now employ another measure of the variability, which is termed **standard variation**.

It is arrived at in this way. We take the deviation of each group, square it and multiply it by the number of individuals in the group. We add together all the values so obtained, divide the sum by the total number of individuals measured, and take the square root of the whole. Suppose the letters  $e_1, e_2, e_3$ , etc. represent the values of the deviations corresponding to the different groups,  $n_1,$

$n_2, n_3$ , etc. the numbers of individuals in those groups, and  $n$  the total number of individuals measured, then the formula for the "standard deviation" is

$$\sqrt{\frac{n_1e_1^2 + n_2e_2^2 + n_3e_3^2 + \dots}{n}}$$

or more briefly

$$\sqrt{\frac{\sum ne^2}{n}}.$$

Having discovered a method of expressing at the same time the value and frequency of a variation, the next step was to investigate how far it was inherited. By adding together the statures of the father and of the mother (reduced to the male standard) and dividing the sum by two, a value is arrived at which Galton denominates the stature of the **mid-parent**. First we take the statures of the children of the group of mid-parents having the same stature and determine their mean. Then the statures of each parental group are plotted out along a vertical line, and the means of the statures of the children belonging to each mid-parental group are indicated by distances measured along a horizontal line. If lines perpendicular to the vertical and horizontal lines respectively are drawn at the points



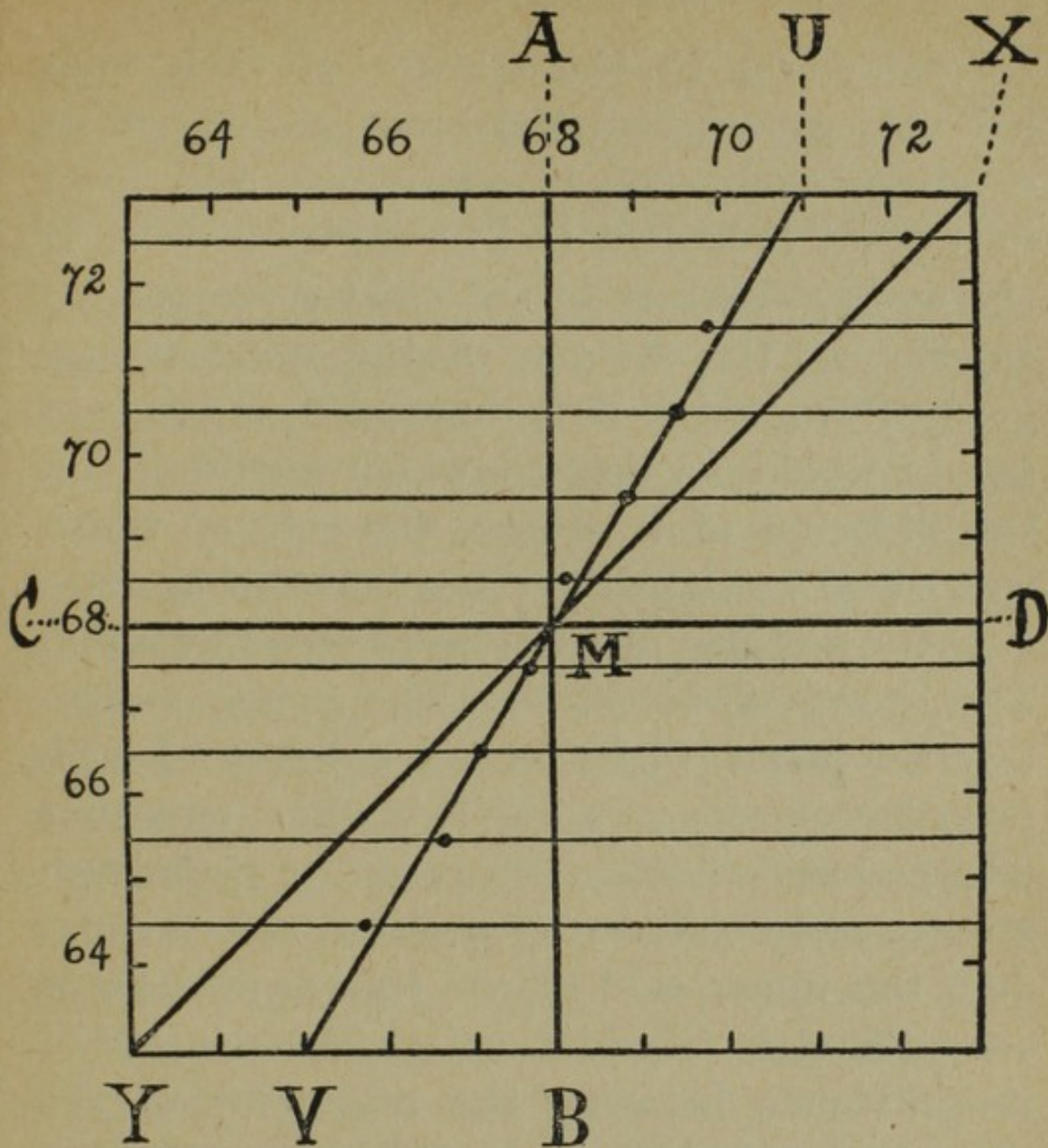


FIG. 17.

Diagram illustrating the correlation of the height of children with their mid-parents. The figures along the vertical line indicate the heights of various mid-parental groups in inches, those along the upper horizontal line the mean heights of the corresponding groups of children. A B is a vertical line drawn through the point indicating the height of the group of children of medium stature. C D is a horizontal line drawn through the point indicating the height of the mid-parental group of medium stature. These two lines meet at the point M in the mathematical centre of the square, since the heights of the medium groups of parents and of children are identical. U V is the line along which the points indicating the mean heights of the children of each parental group lie. X Y, the diagonal of the square, is the line on which the points indicating the heights of the children would lie if they corresponded exactly to those of the parents.

corresponding to the stature of each mid-parental group, and the mean stature of its children, each pair of such lines will meet in a point indicated in Fig. 17 by a dot. If the average stature of the child corresponded exactly to the stature of the mid-parental group from which it is descended, a series of points would be defined which would lie on the diagonal of a square, the side of which was equal to the differences between the two extreme statures of parental groups measured. This, however, is not so. The points indicating the mean heights of the children of each parent group lie on a line  $UV$  which cuts that diagonal at its centre, since parents of medium stature have children of medium stature, and cuts the upper side of the square at a point some distance from its end. The relation of the distance between the mid-point of the upper side of the square (which corresponds to the mean stature of the children of the parental group of medium height) and the point where this line cuts it (which corresponds to the mean height of the children of the tallest parents), and of the distance from the mid-point to the end of the side of the square, is what Galton called the **coefficient of regression** of filial stature on mid-parental stature,

and its value in this instance is about two-thirds; this ratio may be expressed by the symbol  $\frac{AU}{AX}$ . Translated into ordinary

language it means this : that people of average stature have children also of average stature, that tall people on the whole have tall children, but not so tall as the stature of the parents would lead one to expect, and similarly that the children of short people are not proportionately as short as their parents.

The relation between the deviations of two related variables is now usually computed by a different method, which may be termed algebraical as contrasted with the geometrical method of arriving at the coefficient of regression which has just been outlined.

Suppose we desire to know how far the variability of any one organ in an animal is dependent on that of another organ, let us term the deviations of the sizes of these organs in the various members of the population from their respective means  $x_1, x_2, x_3$ , etc., and  $y_1, y_2, y_3$ , etc. respectively. Then let us note that the sum of each of these sets of terms, *i. e.* both  $\Sigma x$  and  $\Sigma y$ , is equal to zero, because a deviation in size above the mean is reckoned as positive, and one below the mean

as negative, and the sum of the positive deviations cancels the sum of the negative deviations. But of course in each case the sum of the squares of the deviations will be positive owing to the well-known algebraical rule that the square of a minus quantity is positive. (Incidentally this is one reason for adopting the standard deviation as a measure of the variability.) If we now multiply together the deviations in the two organs of each individual of the population we get a series of products the sum of which is represented by the symbol  $\Sigma(xy)$ . The mean of these products will be  $\frac{\Sigma xy}{n}$  if  $n$  be the number

of the population. Let  $m_1$  and  $m_2$  represent the standard deviations of the two organs, then the ratio of the mean of the products of the two deviations determined for each individual to the product of the two standard deviations is termed the **coefficient of correlation**, and is used as a measure of the variability. A couple of examples will serve to show how this ratio measures the correlation of the two variabilities. It is represented by the formula  $\frac{\Sigma(xy)}{nm_1m_2}$ . Let us first suppose that the variabilities of the two organs are

*perfectly independent* of one another; then a large size in one of the organs is just as likely to be associated with a small size in the other as with a large size. But a large size is a positive deviation from the mean and a small size a negative deviation, and the product of two such deviations gives a minus quantity. Therefore, of the terms included in the formula  $\Sigma(xy)$ , half will be positive, and half negative quantities, and the sum of the whole will be practically zero, for the negative terms will cancel the positive ones. Therefore the value of the coefficient of correlation will be zero, as it should be.

Now let us make the opposite assumption, viz. that the deviations of the one organ are strictly proportional to those of the other. In this case every value of  $x$  will bear the same ratio to the corresponding value of  $y$ . Let us represent this ratio by the symbol  $\delta$ ; then  $y = \delta x$  and our formula becomes  $\frac{\Sigma \delta x x}{nm_1 m_2}$ , that is  $\frac{\delta \Sigma(x^2)}{nm_1 m_2}$ .

Now the standard deviation  $m_1$  is, of course,

$\sqrt{\frac{\Sigma(x^2)}{n}}$ , and the standard deviation  $m_2$  is

$\sqrt{\frac{\Sigma y^2}{n}}$ , that is  $\sqrt{\frac{\Sigma \delta^2 x^2}{n}}$ , or  $\delta \sqrt{\frac{\Sigma x^2}{n}}$ , and our

formula for the coefficient of correlation becomes  $\frac{\delta \Sigma x^2}{n} \div \delta \sqrt{\frac{\Sigma x^2}{n}} \sqrt{\frac{\Sigma x^2}{n}}$ , i. e.  $\frac{\delta \Sigma x^2}{n} \div \frac{\delta \Sigma x^2}{n}$ ,

or unity which expresses the complete correlation of the two organs. When the deviation of one organ is only partly dependent on that of the other, the coefficient of correlation has a value situated somewhere between unity and zero. When it approaches unity it is said to be high and the two organs are said to exhibit a high degree of correlation; when the coefficient is represented by a small fraction, the two organs are said to exhibit a low degree of correlation.

The methods of Galton were applied by Weldon to the measurement of the variations of animals, but few cases present such simple conditions as those of the human stature. We may take, for instance, the common shore-crab, *Carcinus mænas*. This little green crustacean, familiar to all visitors to our sea-coast, occurs between tidemarks, hiding in pools and under seaweed left bare by the receding tide. It varies considerably in shape, some specimens being comparatively broad and others rather slim-waisted. But if we wish to determine the curve of error for this

variation, it is of no use plotting out absolute measurements of the breadth of the carapace along our abscissa line, for the crabs vary so much in size that a given value might correspond to the breadth of the carapace of a small broad crab or that of a larger slim one. If, however, we divide each absolute value of the breadth of the carapace by its length, then we obtain a fraction which indicates the broadness or slimness of the crab, and which is independent of its size. This is the procedure which was adopted by Professor Weldon in dealing with this case, and the fractional values which he obtained by measuring the carapaces of 500 crabs when plotted out constituted a curve of error as perfect as that yielded by the records of human stature. It is not a practicable thing to rear shore-crabs in the laboratory under experimental conditions, so that Weldon could not directly determine how far variations in the breadth of carapace were inherited, but he was able to show that variations in the size of other organs, such as that of the great claw, were correlated with the breadth of the carapace, just as is the stature of children with that of their parents; there is a correspondence between changes in sizes of the two organs,

but it is not a complete correspondence. But Professor Weldon was able to discover many other interesting things by measuring the carapaces of crabs of different ages. If the "curve of error" for the carapace of young crabs be compared with the similar curve for

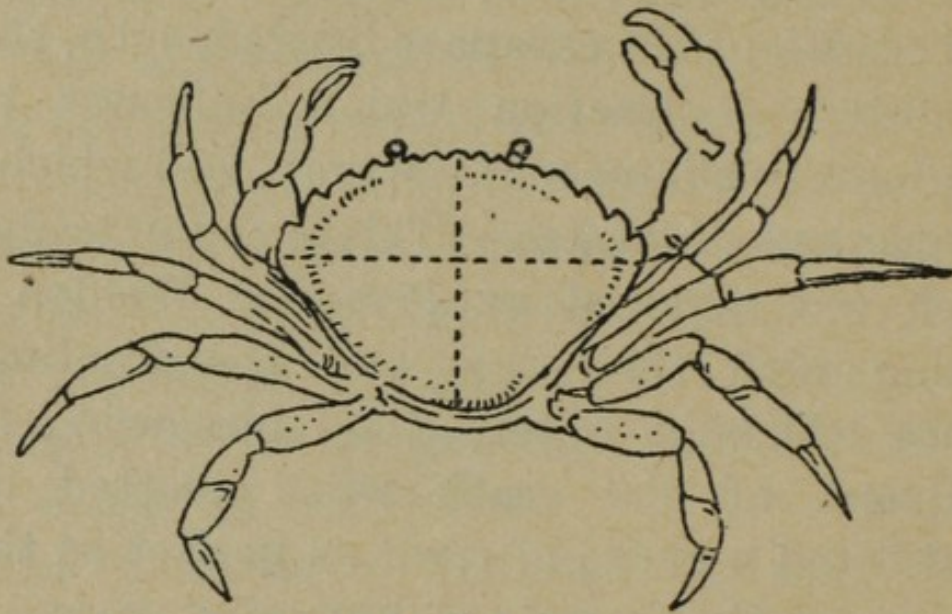


FIG. 18.

The common shore-crab, *Carcinus maenas*. The dotted lines indicate the dimensions which were measured.

older crabs, then it will be seen that the former curve has a more gentle slope than the latter. It is thus seen that there are much more marked deviations from the mean among younger than among older crabs; and the most probable explanation of this is, that the more extreme types become weeded out by natural selection. In confirmation of this idea Professor Weldon tried the experiment



of mixing the water in which the crabs lived with fine china clay. A great many died, but when the carapaces of all were measured it was found that those which survived had narrower carapaces than those which died; that the cause of death was the covering of the gills with silt, and that a broader carapace was associated with a broader ingress into the gill-chamber, and consequently a greater clogging of the gills with silt. It may be explained that in a crab the gills are contained in two chambers roofed over by the lateral parts of the carapace, and the entrances into these chambers are slits between the in-turned edges of the carapace on either side and the bases of the legs.

Professor Davenport, who carried on work on the lines begun by Weldon, was able to show how the statistical methods outlined above enable us to find out when a given population consists of two races. For when he measured various dimensions in certain small North American mammals, such as the mole, he found that the resulting curve of error had two summits, showing that there were two values about which the other values tended to group themselves—in a word, that the samples examined consisted of two races

having different median values for the character measured.

The general conclusion which was drawn from Galton's researches was, that the differences between members of the same family were inherited, but that there is **regression towards mediocrity**, that is, that the deviation of the child from the mean was on the average less than that of the parent. This regression would check the gradual modification of a character by natural selection, but would not entirely prevent it, because the number of progeny which survive is only such a small proportion of those which are born, that some few children of an exceptional parent—if only enough children were produced—would be sure to be more exceptional than the parent himself, even though the average of the children was less exceptional than the parent; if these few alone were preserved by natural selection and became the progenitors of the next generation the race would be modified. In a word, the mean value of the character in the survivors would exhibit a greater deviation from the average than the value of the character in the parent, although the mean value of the character in all the children would deviate less.

A great deal of importance was formerly attributed to the "regression to mediocrity" by workers on heredity, but nowadays it is only of historical interest. The reason for this change of attitude is the recognition of the fact that a human population selected at random consists of a mixture of different races with different hereditary potentialities, and that before statistical inquiry can give us any useful help in determining the laws of heredity, the material with which it deals must be selected and purified; in a word, *the conditions of the experiment must be standardized.*

A much better means of investigating the laws of heredity is afforded by what are termed **pure line investigations.** By a pure line is meant a group of children which are the offspring of a single parent. The three cases in which a pure line can be produced are as follows: (1) The vast majority of the higher plants and a certain number of animals belonging to different classes are hermaphrodite, *i. e.* the same individual produces both kinds of germ-cells, and in most cases self-fertilization is possible, so that from one parent a large population can be produced. (2) A certain number of animals exhibit

parthenogenesis—*i. e.* produce ova which will develop without fertilization, and in these cases also a single parent can become the sole progenitor of a large family. (3) The simple organisms termed Protista reproduce by fission, and one specimen by repeated divisions can give rise to an enormous progeny.

The first to study the inheritability of variations within a pure line was the Swedish investigator Johannsen.

Johannsen worked with the common kidney-bean plant (*Phaseolus*). He found that ordinary beans differ from one another in weight, beans of medium weight being the most numerous, whilst unduly light and heavy specimens were comparatively rare. If the heavier beans were sown and plants raised from them, when these plants produced beans the average weight of these was greater than the average weight of the beans produced by the plants raised from the beans of lighter weight, whilst beans of medium weight gave rise to plants bearing beans of medium weight. Nevertheless the same "regression to mediocrity" which was noted in the case of human stature can also be observed here. The average weight of beans produced by sowing the heavier beans, though greater than

the average of the beans produced from sowing the beans of medium weight, was not proportionately greater, and the same was true, *mutatis mutandis*, of the beans produced by sowing the beans of lighter weight. But when the beans produced by self-fertilizing the flowers of a single plant were separated, and heavier, lighter and medium beans were selected from the crop thus produced, and separate "pure lines" produced from single samples of such beans and the resulting progenies weighed, then a totally different result was obtained. It then appeared that curves of error calculated from the weights of the offspring of a heavy bean and of a light bean respectively had the same median values, provided that heavy and light beans were sisters descended from the same plant. In a word, **it appeared that differences in weight between sister beans were not inherited;** that such differences to which Johannsen gave the name **Fluctuations**, were due to differences in nutrition, and did not affect the hereditary mechanism, which was the same for all.

Agar took up for examination the parthenogenetic water-flea, *Simocephalus*. This little crustacean is about  $\frac{1}{13}$  inch long, and is an inhabitant of our ponds and ditches. The

hinder part of its body is enveloped by two flaps of skin stiffened by horny matter, which constitute a bivalve shell or carapace. Its head projects in front, and on it is situated a single compound eye, whilst from it spring

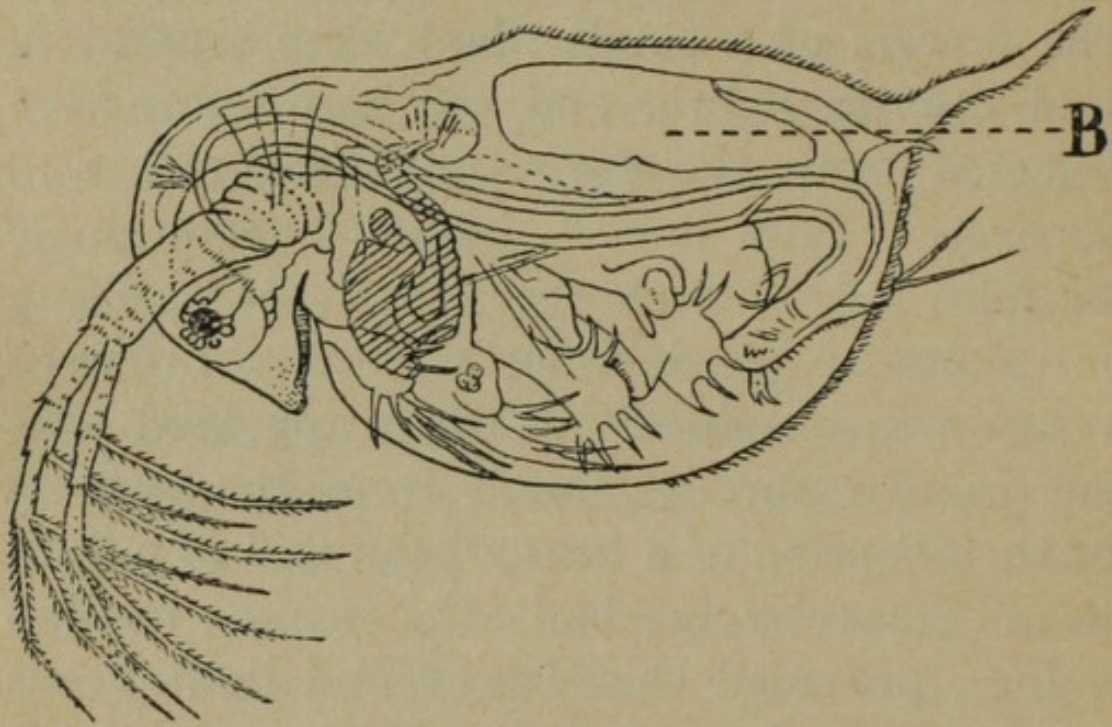


FIG. 19.

Side view of *Daphnia*, a crustacean closely allied to *Simocephalus*. B. The brood-pouch.

two great forked feelers or antennæ, by strokes of which it swims. The two flaps of the carapace are united in the middle line above the back of the animal. The legs behind the mouth are thin, leaf-like and flexible, for which reason *Simocephalus* is classed with the Phyllopoda or Leaf-footed

Crustacea. The animal usually swims lying on its back, and the space between the back and the united valves of the carapace forms a convenient pocket into which the eggs pass as soon as they are laid. In this pocket, or "**brood-pouch**" as it is termed, they develop until they are ready to hatch and take up a free life. The young feed from the beginning, as did their parents, on minute plants found swimming in the water; they moult four times, growing considerably at each moult, and their attainment of the adult condition is marked by their giving birth to living young.

In the autumn some of the eggs develop into males and these males then fertilize the eggs which the females have produced. These fertilized eggs surround themselves with thick egg-shells, and lie dormant during the winter. The skin lining the brood-pouch of the mother becomes thickened by a stiff deposit of horny matter. This deposit is eventually moulted and falls to the bottom, enclosing the fertilized eggs in the brood-pouch. Such a structure is called an **ephippium**. In the spring these eggs develop and hatch out as young *Simocephalus*, but these young *Simocephalus*, so long as the temperature is mild and food abundant, produce eggs which develop into

females directly without any fertilization at all, this being the parthenogenesis.

Agar began by collecting ehippia from a stream near Glasgow University. These were allowed to hatch out in the laboratory, and every young *Simocephalus* was isolated by itself in a corked tube, three-quarters filled with water, containing an abundant supply of microscopic plants. Here it lived, grew, and produced young, two females of which were selected to continue the line and removed to separate tubes. Males were not produced under the conditions of the experiment. The character, whose variation Agar measured, was the length from the anterior apex of the head to the hinder end of the united line of the carapace valves. By selecting those specimens to continue the race which were the largest and smallest respectively of the brood produced by each parent without fertilization, Agar was able to determine whether such differences were or were not inherited. *He arrived at the conclusion that they were not inherited.* The offspring of the shorter specimens were at birth actually rather longer on the average than the offspring of the longer specimens, whilst when they had attained the adult condition they were about the same size.



It must be mentioned that these crustaceans are extremely susceptible to changes in temperature, and in the quality of the water, which may favour or arrest their growth, and Agar had not only to strive to keep the conditions constant, but to make corrections for alterations due to the altering environment.

Finally, we must mention the experiments of Jennings. This observer chose as the subject of his experiments the Protist *Paramecium*, well known to all students of elementary biology as the Slipper Animalcule. This little creature is shaped somewhat like a bedroom slipper without a heel. The part corresponding to the toe is thick, the rest of the animal is like a thin scoop. It is covered all over with short vibratile hairs termed cilia, by means of which it propels itself about. It reproduces by dividing itself into two by a line of fission at right angles to its long diameter. At considerable intervals it undergoes a process known as **conjugation**. In this process two specimens approach one another and adhere together. Then an interchange of nuclear matter takes place between the two and after this they separate, being now known as **ex-conjugates**. This process has been compared with the sexual process amongst higher

animals. Jennings selected from a culture six conjugating pairs and two ex-conjugates—

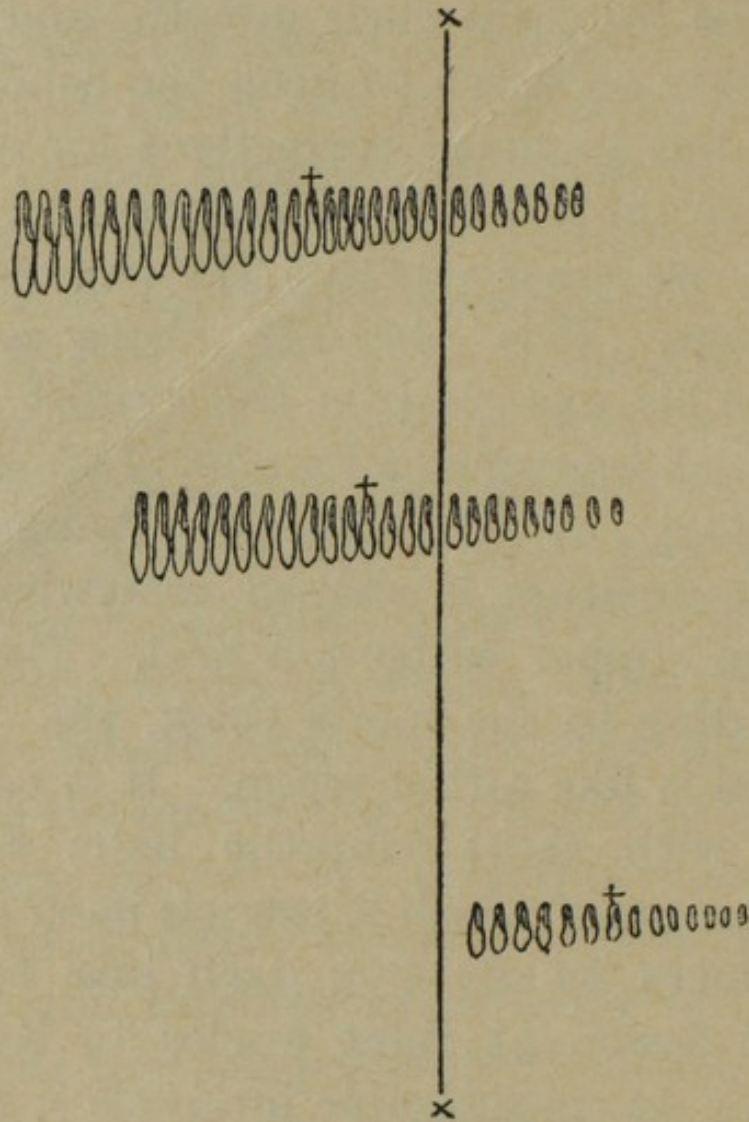


FIG. 20.

Showing three "pure lines" of Paramecium. The sign (+) marks the median value in each strain; the vertical line passes specimens in each of the three strains which are of the same absolute size.

fourteen specimens in all. Each of these was isolated in a separate culture-dish and allowed to reproduce itself by fission. The quality

the variation of which Jennings measured was the length. He found that the offspring of his fourteen selected specimens included six different strains of *Paramecium* differing from one another in length, for if the offspring of each of them was measured so as to give rise to a separate curve of error, it was found that no less than six different median values were to be found. It is true that a giant might be selected from a strain of low median value, which was longer than a dwarf belonging to a strain of high median value, but the offspring of such a giant were no longer on the average than those of a dwarf belonging to the same strain, and were decidedly shorter than those of a dwarf belonging to a strain which had a higher median value. It follows that in the case of *Paramecium*, as in those of *Simoccephalus* and the bean, variations appearing within the pure line are not inheritable. It is to be noted that Jennings, like Agar, had to introduce numerous corrections; for the length attained by a given specimen of *Paramecium* is not only determined by the strain to which it belongs, but also depends on temperature, crowding, and the chemical nature of the solution in which it is situated.

The concordant results obtained in three

sets of experiments in different types of pure line may well give us food for serious reflection. The obvious inference seems to be that in each natural population there exists a large number of strains, each with its fixed unalterable quality of heredity, and that the apparent uniformity in character of the species is due to the constant intercrossing of these strains. The appearance of the possibility of modifying the species by selection would, on this hypothesis, be due to the fact that certain strains would be gradually eliminated, and the population "purified" by being gradually reduced until it consisted solely of individuals belonging to one desired strain.

It is therefore quite clear that the results of carefully conducted experiments carried out under standardized conditions lend no support whatever to the cardinal postulate of Darwin and Wallace that natural selection alone could effect evolution. The question as to how the various strains originated is quite unsolved, but we may surmise, in accordance with what we have learnt in the previous chapters, that they have derived their peculiarities from differences in the environment to which their ancestors have been exposed.

## CHAPTER VI

### THE INHERITANCE OF " MUTATIONS " OR " SPORTS "

IF we survey the animal and plant kingdoms we discover that each is divided into a number of well-marked groups and that the members of each group cross freely with one another and produce fertile offspring. These natural groups are called **species**, and in each kingdom the species show all degrees of difference from one another. In order to express these differences the species most alike are placed together in groups called **genera**, the genera are arranged in **families**, the families in **orders**, the orders in **classes**, and so on. Darwin clearly saw that the first and essential step in any theory of evolution was to show how several species have been developed out of a single species, and for this reason he called his great book *The Origin of Species*.

When members of different species are crossed with one another they are usually but not always sterile, but sometimes they produce

offspring which are termed **hybrids**. The most familiar example of a hybrid is the mule, which is produced by mating a horse and an ass. The mule, however, like the vast majority of hybrids, is sterile; and in the few cases where hybrids between different species are fertile the laws governing the hereditary qualities of their offspring have not been investigated. But when plants are cultivated and when animals are domesticated the original species become divided into a great number of different types which are mutually fertile. These types among plants are known as "**varieties**," amongst animals more usually as "**breeds**" or "**strains**." Darwin thought that these "breeds" or "varieties" had been produced by the conscious or unconscious selection by man of those fluctuating variations which most suited his purpose, and that this action on the part of man showed us how Nature proceeded in producing new species. But the "pure-line" investigations recorded in Chapter V have shown us that this view is no longer tenable, and there is, in fact, no universal agreement on the question as to how domestic breeds were produced. Many think that they owed their origin to the sudden appearance of strongly-marked deviations

from the normal type commonly called “**mutations**” or “**sports**,” which attracted the attention of primitive man and led him to preserve them, and it is noteworthy that when distinct strains are crossed with one another the characters of their offspring obey the same laws as are shown when a recently produced monstrosity is crossed with the type from which it has sprung. These laws were worked out by Gregor Mendel, an Augustinian monk belonging to a monastery in Bronn in Moravia; his experiments have been repeated and confirmed by other workers all over the world, and thus the laws which he discovered are usually termed **Mendelian**. For the reason that we have given, we prefer to call them the laws governing the inheritance of sports.

The cross between two breeds—like the cross between species—is usually termed a hybrid. It is important to remember that Mendel himself in giving an account of his experiments expressly stated that he resolved not to deal with variations of the “more” or “less” description, but to choose for the subjects of his researches varieties distinguished from one another by some sharply-marked character. For this reason he selected the cultivated pea (*Pisum sativum*) because it is easily cultivated

and is obtainable in many clearly-marked varieties. It is usually self-fertilized. We begin our survey of these varieties by taking the case of two which are distinguished from one another by a single differentiating feature. Peas when ripe and dried may be either of a yellowish colour or of a pale green tint. If a plant raised from a yellow pea be crossed with a plant raised from a green pea, a set of hybrid peas will be produced. The crossing is effected by opening the flower buds of the plant which is to provide the ovules (see Chap. I) and removing the stamens before they are ripe so that self-fertilization is prevented, this plant is termed the **seed-parent**. A little later, when the stigma is ripe, it is dusted with pollen procured from the other plant, which is known as the **pollen-parent**. When the hybrid peas ripen it is found that they are all yellow, and this is true no matter whether the ovules have been derived from the plant sprung from the green pea or from the plant sprung from the yellow pea—or, to put it another way, they are yellow whichever kind of plant is employed as the seed-parent. This generation of peas is known as the **first filial generation** and is designated by the symbol  $F^1$ . When these peas are sown and the plants to which they



give rise are self-fertilized, or, as it is termed for the sake of brevity, selfed, a generation of peas is produced which is known as the **second filial generation**, and is indicated by the symbol  $F^2$ .

In this generation—if enough peas are produced—it is found that, as nearly as possible, one-quarter of the peas are green and three-quarters are yellow. Thus the green character, which had been entirely suppressed in the first filial generation, reappears in the second filial generation. Mendel termed the character which is thus temporarily suppressed the **recessive character**, and to the character which alone appears in the first filial generation he gave the name of **dominant character**. When the recessive green peas are sown they give rise to plants which, when “selfed,” bear only green peas, and this is true for however many generations they may be cultivated. When the yellow peas, however, are sown, they give rise to plants which, when “selfed,” yield different results in different cases. One-third of them—that is to say, one-fourth of the total number of plants which were raised from the first filial generation—give rise to yellow peas only, and these yellow peas yield only yellow peas for

however many generations the cultivation may be continued. The remaining two-thirds of the plants raised from the hybrid yellow peas yield both yellow and green peas in the proportion of three yellow to one green; in a word, they behave exactly as did the peas of the first filial generation of hybrids, and the peas of this third filial generation, produced from the hybrids of the second filial generation, behave exactly as did the peas of the second filial generation, that is to say, the green reproduce their like however long they may be cultivated, and one-third of the yellow do the same, but the remaining two-thirds yield yellow and green peas.

In order to account for this strange phenomenon Mendel put forward a theory which has been widely adopted, and which is termed the theory of the **purity of the germ-cells**. According to this theory when two strains are crossed their qualities are, of course, mingled in the body of the hybrid, but when this hybrid in turn forms germ-cells, these germ-cells are of two kinds, each kind carrying the potentiality of developing the qualities of one strain, but not of both. Applying the theory to the case in point, we assume that when the hybrids of the first filial generation come to form germ-

cells, two kinds of pollen-grains and two kinds of ovules are produced, one of these kinds of pollen-grain and one of these kinds of ovule having the potentiality of producing a yellow pea, whilst the other kind, both of pollen-grain and of ovule, has the power of producing a green pea. It is a further assumption of the theory of germ-cell purity that the two kinds of germ-cells are produced in equal numbers. If, for the sake of brevity of expression, we bestow the names of green pollen-grain and green ovule on the type of pollen-grain and ovule respectively which carry the potentialities of becoming a green pea, and corresponding names on those which carry the potentialities of becoming a yellow pea, then the problem we have to solve is this : given equal quantities of green pollen-grains and yellow pollen-grains, mingled together and used to fertilize equal quantities of green ovules and yellow ovules mingled together, what will be the result? On the doctrine of chances it appears probable that once in four times a green pollen-grain will meet a green ovule, for if all the pollen-grains were the same, and there were equal numbers of yellow and green ovules, half the unions would be with each kind of ovule, but as only half the pollen grains are green, it

follows that only a half of a half of the total unions, that is, a fourth, will be between green pollen-grains and green ovules. By a parity of reasoning we deduce that once in four times a yellow pollen-grain will meet a yellow ovule, and that once in four times a yellow pollen-grain will meet a green ovule, and that, finally, once in four times a green pollen-grain will meet a yellow ovule. These last two types of union yield hybrid strains of exactly the same nature, and these hybrid strains appear to the eye like pure yellow peas because of the dominance of yellow; but the union of the yellow pollen-grains and yellow ovules yields pure yellow peas, and these added to the yellow hybrids account for the three-quarters of the second filial generation constituted by yellow peas. Since a green pea can only be produced by the union of a green pollen-grain and a green ovule, it follows that all the green peas produced are "pure" and yield only their like when progeny is raised from them.

It will be observed that in the reasoning which has just been outlined it is assumed that by random mingling of two sorts of pollen-grains and two sorts of ovules a definite numerical result will be obtained. This is only true if very large numbers are considered, for if

smaller numbers were examined we might have accidental "runs" of one kind of pea. To give an idea, however, of the numbers actually required, and of the close approximation between the results obtained by Mendel and those which might be theoretically expected, we may here reproduce one of the sets of figures which he gives. Two hundred and fifty-eight plants raised from the hybrid peas of the first filial generation yielded 8023 seeds, of which 6022 were yellow and 2001 green. The theoretical numbers would be 6018 yellow and 2005 green. The student will do well to regard with the utmost suspicion figures adduced to prove the proportions of strains appearing in the progeny of hybrids if these figures indicate comparatively small numbers.

Besides differences in the colour of the seed, or, to speak more correctly, differences in the colour of the cotyledons or seed-leaves which constitute nearly all the bulk of the ripe pea, Mendel found other strains of peas which differed from one another in a single character. Thus some peas when ripe and dry are rounded, whilst others are shrunken and angular, and some produce plants about six feet high, whilst others give rise to dwarf procumbent plants about one foot high.

Besides selfing the hybrids of the first filial generation or crossing them with one another, the experiment is frequently made of crossing the hybrid with one of the parental strains. If a yellow hybrid pea, for instance, be crossed with the parental recessive strain, *i. e.* with a green pea, equal numbers of yellow and green peas are produced. A moment's reflection will show us why this must be so, for the hybrid produces equal numbers of "yellow" and "green" germ-cells, but the recessive bears only green germ-cells, so that all the germ-cells of the hybrid unite with green germ-cells, and we have already seen that green germ-cell  $\times$  green germ-cell = green pea, and yellow germ-cell  $\times$  green germ-cell = yellow pea.

If **D** denotes the dominant character and **R** the recessive, then the results of crossing two strains may be expressed by the formula  $D \times R = D(R)$  where the brackets indicate that the character enclosed in them is present but not visible; and  $D(R) \times R = D(R) + RR$  indicates the result of crossing the hybrid with the recessive parent. Such matings are regularly employed in experiments on heredity in order to explore the constitution of a suspected hybrid. They are termed "**back-crosses.**"

The question now arises as to what is going to happen when we cross two strains of plants with one another which differ from each other in two differentiating characters. Suppose, to take one instance, we cross plants produced from round yellow peas with plants produced from green angular ones, of what description will the first and second filial generations be? When the experiment is tried we find that the first filial generation consists solely of round yellow peas, since roundness is dominant over angularity and yellowness over greenness. When this generation is selfed we find that in the second filial generation three-quarters of the peas are round and one-quarter angular, and three-quarters are yellow and one-quarter green, and each differentiating quality is inherited as if the others were absent. That is to say, though three-quarters are round and three-quarters are yellow, it is not the same three-quarters which are round which are also yellow, nor is it the same quarter that is angular that is green. It is exactly as if one had a bag of white billiard balls and one were to select three-quarters of them at random and paint them yellow, and then to put the yellow balls back into the bag and jumble the whole lot up together, and then to select again three-

quarters of the whole and paint each of them with a black cross. It is obvious that in a great many cases a ball would receive both the yellow colour and the black cross, but some white balls would receive the black cross and some yellow balls would escape it. Since three-quarters of the whole are yellow and since the black cross is distributed evenly amongst the whole number of these, being attached to three out of every four of them, it is evident that three-quarters of three-quarters will be yellow and have the black cross, that is, nine-sixteenths of the whole. Since one-quarter are white and one-quarter are without the cross, one-quarter of one-quarter, or one-sixteenth of the whole, will be white and unmarked. By a parity of reasoning we deduce that one-quarter of three-quarters, or three-sixteenths, will be yellow and unmarked, and three-quarters of one-quarter, or three-sixteenths, will be white and marked with the cross. So in the second filial generation of the cross between yellow round and green angular peas we find that nine-sixteenths of the peas are yellow and round, three-sixteenths yellow and wrinkled, three-sixteenths green and round, and one-sixteenth green and wrinkled. We have thus obtained two new



varieties of peas, viz. green round and yellow wrinkled, and therein lies one of the most important applications of experimental breeding. We are enabled in this way to combine two valuable qualities belonging to different strains. When we test the qualities of the peas of the second filial generation, by rearing from them by selfing a third filial generation, we find that all the peas which combine the two recessive qualities, viz. greenness and wrinkledness, breed true, and are, therefore, "pure." But of the yellow round peas only one-ninth breed true, *i. e.* one-sixteenth of the whole number of the second filial generation; the remaining eight-sixteenths, or one-half of the whole, exhibit the quality of hybrids with respect to one or both differentiating characters, that is to say, they either yield yellow and green peas, or round and wrinkled, or, finally, peas which may be yellow or green, round or wrinkled. Of the three-sixteenths which are yellow and wrinkled, one-third, *i. e.* one-sixteenth of the whole, breed true, the remaining two-sixteenths, or one-eighth of the whole, behave as hybrids with respect to yellowness; and of the three-sixteenths which are green and round, one-third, *i. e.* one-sixteenth of the whole, breed true, while the remaining two-

sixteenths, or one-eighth of the whole, act like hybrids so far as roundness is concerned.

These facts are explained by an extension of the hypothesis of the purity of germ-cells.

We assume that each hybrid strain produces twice as many types of germ-cells as there are pairs of differentiating characters. Thus yellow round peas of the first filial generation produce (using the abbreviated terminology explained on p. 145) yellow round pollen-grains, yellow wrinkled pollen-grains, green round pollen-grains, and green wrinkled pollen-grains in equal numbers, and ovules of the same four varieties also. When a pollen-grain and ovule of the same kind meet—and this can only happen once in sixteen times—a stable variety is produced. Such a union is called a **homozygous** union, and the organism so produced is termed a **homozygote**. But where a pollen-grain and ovule of different kinds meet, a hybrid variety, or **heterozygote**, is produced, and such a union is termed **heterozygous**. It is clear, however, that a pollen-grain and ovule may be alike with respect to one character and dissimilar with respect to another. When such a pair meet the union is said to be homozygous with

respect to one character and heterozygous with respect to others.

Mendel performed some experiments in crossing strains which were separated by three pairs of differentiating characters. On the principles already explained it is a simple matter to calculate the distributions of these characters in the second filial generation. Let us call the dominant members of these pairs A, B and C, and the recessive members *a*, *b* and *c*. The two pairs of these characters, A, B, *a*, *b*, will, as we have seen, be distributed throughout the offspring in the proportions of 9 AB, 3 Ab, 3aB, 1 *ab*. The third pair of characters is distributed throughout the generation independently of the others in the proportion of the three dominant (C) to one recessive (*c*). We shall, therefore, have 27 ABC, 9 AbC, 9 aBC, 9 AB*c*, 3 abC, 3A*bc*, 3 aB*c* and 1 *abc*; or, in other words, twenty-seven sixty-fourths exhibiting all three dominant characters, three lots of nine sixty-fourths exhibiting two dominant characters accompanied by the one recessive character, and three lots of three-sixty-fourths each exhibiting one dominant character accompanied by two recessive characters, and finally, one sixty-fourth exhibiting all three recessive

characters, and all progeny belonging to this last-named category will breed true. But of the categories some will be heterozygote, with respect to one, two, or all three characters, and further breeding will be necessary to separate out the pure strains.

Since Mendel's time the continuous work of many zoologists and botanists has shown that similar strains, separated by differentiating characters, are to be found in a wide range of animals and plants, and that these strains when crossed behave in the same manner as those investigated by Mendel. Comparatively few new principles have been discovered, but there are one or two extensions of Mendel's principles which have come to light, and we shall now give examples to elucidate these.

The suppression of one character in the first filial generation is known as the principle of **dominance**; the appearance of two types of descendants in the second filial generation is termed the principle of **segregation**. It occasionally happens that in the first filial generation the hybrid can be discriminated from both parental types by its appearance, and even when this is not possible, a microscopic examination will sometimes succeed in distinguishing the hybrid from the pure dominant. Thus in

the cross between round and angular peas the two varieties are distinguished by the size of their starch grains, and the starch grains of the hybrid, which is also a round pea, are intermediate in size between the grains of the two parental varieties. In the second filial generation, in which both parental types reappear, there will in such cases be one-fourth of the offspring reproducing each parental type, and one-half showing the hybrid character. One such case is given by Bateson. The so-called Andalusian fowl is a fancy breed, of a colour described by specialists as blue, but which might be more aptly described as slaty. It is produced as a hybrid by crossing two breeds, one of them of a black colour and the other of a white dotted with black here and there. When one tries to raise a breed of Andalusians one can consequently only obtain half the offspring of the Andalusian type—the other half being made up of black and white birds in equal numbers. For reasons which will be made clear later on, this condition of affairs is termed **imperfect dominance**.

Characters like the yellow or green colour of the cotyledons of the pea, which replace one another, are termed **allelomorphs** of one another. Roundness and angularity are

another such pair of characters, and it is usual to speak of each of them as being a member of an allelomorphic pair. One of the most

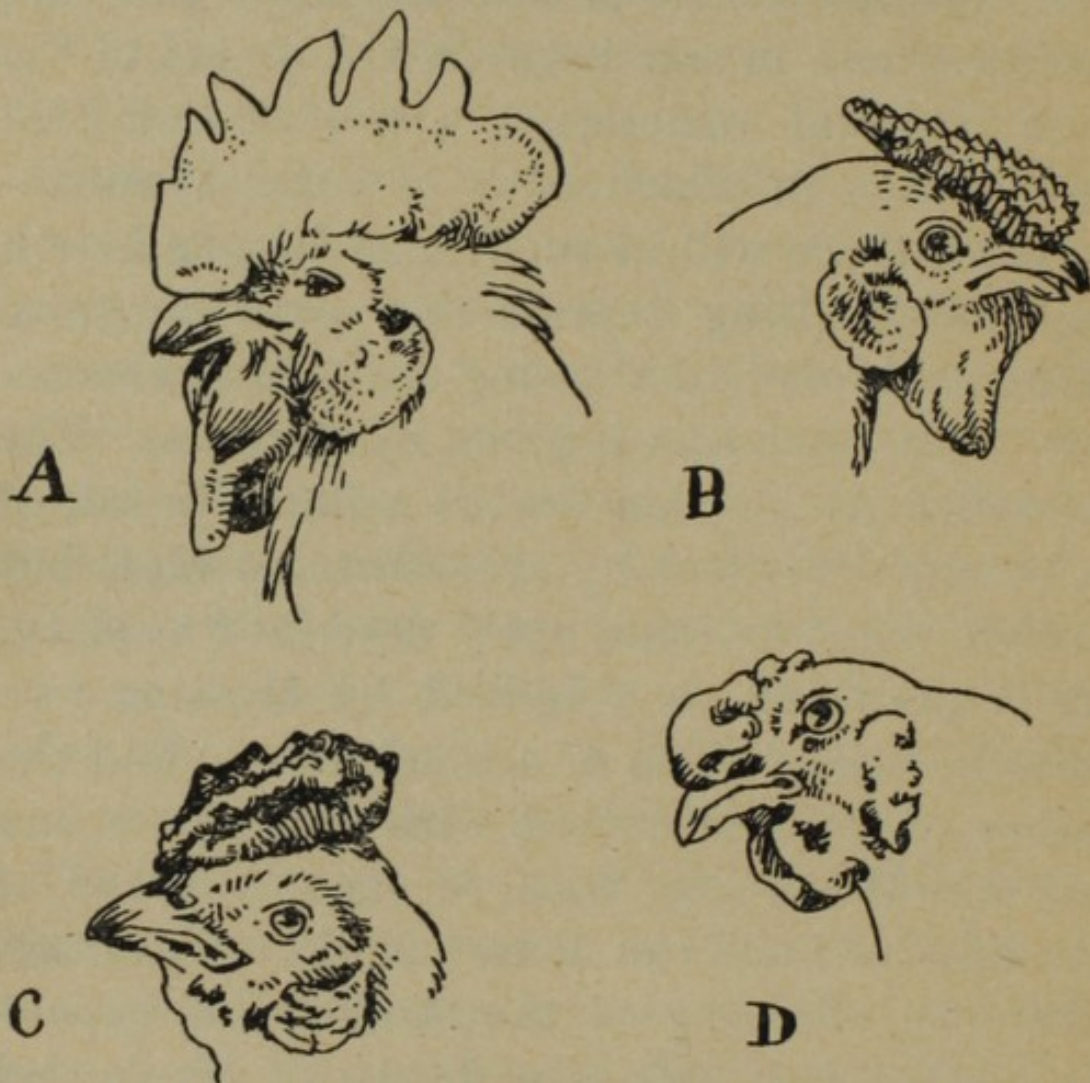


FIG. 21.

Illustrating the types of comb found in different breeds of fowl. A. Single comb. B. Rose comb. C. Pea comb. D. Walnut comb. (After Bateson.)

interesting of the newer results is the discovery by Bateson that the presence in the same embryo of two characters belonging to two different allelomorphic pairs can produce

a new result different from that which would be produced by the presence of either of them alone. Bateson discovered this principle also by crossing fowls. Breeds of fowl differ much in the comb. The original wild type is seen in the Jungle Fowl of India, and also in many domesticated breeds, such as the Leghorn, and is known as a **single comb**, which is blade-like with a serrated edge (Fig. 21, A). Many breeds, such as the Hamburg, have what is called a **rose comb**, which has a triangular horizontal surface covered by small knobs (Fig. 21, B). Then there is a type called a **pea comb**, which is blunter than the single comb and not serrated, but which exhibits laterally a few knobs (Fig. 21, C). Finally we have the **walnut comb**, which is a bulbous, misshapen structure, with here and there a few tufts of vestigial features (Fig. 21, D).

Bateson began by crossing breeds with rose and pea combs, and found, to his great surprise, that the first filial generation all possessed walnut combs. When, however, he bred from these walnut-combed fowls he obtained offspring in the proportion of nine walnut-combed fowls to three rose-combed, three pea-combed and one single-combed fowl, whereas he expected to obtain a generation consisting of two

walnut-combed, one pea-combed and one rose-combed, out of every four, which is what would have occurred had rose comb and pea comb been members of the same allelomorphic pair and walnut comb the hybrid between them. Here, then, the original wild type turned up in the second filial generation in such proportions as one would expect a type bearing two recessive qualities to appear when two strains differing from one another in two differentiating features are crossed (see p. 150). This circumstance at once suggested to Bateson the following explanation of the anomaly. He assumed that a rose comb and a pea comb each owed its peculiarity to the presence of some peculiar **factor** in the germ-cell which altered the typical single comb in a peculiar manner. The allelomorphic fellow of the presence of this peculiar factor was simply its absence, and in its absence the single comb was produced. The factors giving rise to rose and pea combs, respectively, belonged to different allelomorphic pairs, and when both were present at once in the same zygote a walnut comb was produced. When, therefore, we cross rose comb and pea comb bearing strains, we have unwittingly crossed rose, with a strain (pea) characterized by the absence of the rose



factor, and at the same time crossed pea, with a strain (rose) characterized by the absence of the pea factor, and in this way we have produced hybrids possessing two pairs of differentiating factors which segregate in the next generation.

The theory that members of the same allelomorphic pair are distinguished by the presence in one of something which is absent in the other can be used to explain dominance. If we consider the case of yellow and green peas, we see that all unripe peas are green, but that yellow peas possess a factor absent in green peas, which changes the green into yellow as ripening comes on. When two germ-cells meet, if even only one of them possesses this factor, the hybrid pea will turn yellow and will be distinguishable to the naked eye from the pure yellow pea. But, occasionally, the presence of the factor in only one gamete—or, to use the phrase commonly employed, a single dose of the factor—is not sufficient to confer on the zygote the same outer appearance as two doses, and in these cases the hybrid is distinguishable by the naked eye, and we have a case of imperfect dominance. The blue colour of the Andalusian fowl alluded to above turns out on closer investigation to be

a dilute form of black, due to the zygote receiving only one "dose" of the black colour.

Another principle was discovered by the French zoologist Cuénot; this is, that the presence of a factor belonging to one pair is sometimes necessary in order to allow the influence of a factor belonging to another pair to be visible. Cuénot crossed ordinary grey wild mice with tame white mice, and in the first filial generation, as was to be expected, all the hybrids were grey, since whiteness or albinism is obviously due to the absence of colour. When a second filial generation, however, was raised from these hybrids, a most curious result was obtained. On an average, out of sixteen mice, nine were grey, three were black, and four were white. Here we have to account for the appearance of black, present in neither of the parental strains, and for the ratio 9 : 3 : 4. Cuénot's hypothesis was as follows : colour in the skin of mice is due to the meeting of two factors, one a factor determining the kind of colour (grey, black, chocolate, etc.), and the other a factor which he named **chromogen**, which must be present if the colour factor is to show itself. The albinos in this case were black mice devoid of the chromogen factor, and in the second filial

generation there were produced, according to the rule for the result of crossing two strains, distinguished from one another by two differentiating factors, nine grey with chromogen, three black with chromogen, three grey without chromogen, and one black without chromogen. The grey and black without the chromogen component are, of course, white, and so we see why four ( $3 + 1$ ) mice out of sixteen are white. Greyness is dominant over blackness, the presence of chromogen over its absence. From the reasoning which we have detailed on the nature of dominance we suspect that grey must be a modification of black due to the introduction of another factor. On investigation this proves to be the case, for if the grey hairs be examined under the microscope they are seen to be coloured black at the base, then yellow, and then black, so that they may be described as "barred with yellow." The technical name for grey is **agouti**. The "barring" factor is obviously absent in the purely black mice, but chocolate-coloured mice are also known in which the whole of the hair is suffused with chocolate pigment. When these mice are crossed with black, the first filial generation are black, but when these hybrid blacks are crossed with

another, chocolates reappear in the second filial generation. Black is therefore dominant over chocolate and on investigation it is found that black mice contain chocolate pigment, but that this is overshadowed by the black pigment so as not to be visible when looked at in the mass. When one factor, by its presence, conceals another factor, as in this case, it is said to be **epistatic** to the factor which it conceals, and the concealed factor is said to be **hypostatic** to the one which conceals it. Chocolate indeed appears to be the colour produced when "chromogen" is present alone, without the addition of another factor. When grey is crossed with chocolate it is dominant over it; it is therefore dominant over both black and chocolate; such a relationship is denominated "**multiple allelismorphism.**"

Bateson was able to get one step further than Cuénot, for he discovered a case where two factors were present as members of two different allelomorphic pairs, neither of which could manifest itself without the presence of the other. There exist two races of white sweet-pea (*Lathyrus odorata*) which, when selfed, yield only white flowers, but which when crossed yield purple flowers. The production

of colour in the flower is therefore due to the meeting of two factors, one of which was carried by each white strain, but neither of which taken by itself was able to give rise to colour. When a second filial generation is raised from these purple flowers, then out of sixteen, on an average, nine are coloured and seven are white. If *A* and *B* denote these two factors, and *a*, *b* their absence, then the second filial generation ought to consist of 9 *AB*, 3 *Ab*, 3 *aB*, 1 *ab*. But *Ab*, *aB*, and *ab* will all equally yield only white, and hence we have seven (3 + 3 + 1) white out of sixteen.

We have so far spoken of the different allelomorphic pairs of characters as if each pair in its distribution in the second filial generation was completely independent of every other pair. But this is not always the case. Sometimes two characters belonging to two different pairs show a marked tendency to occur together, and are found together in the fertilized germ-cell or zygote far oftener than is in accordance with the laws of chance. Such an association is known as "**coupling.**" If it were complete, then the two characters would always occur together and would be regarded as two different manifestations of the same "factor." It is, however, of all

degrees of completeness, but the most commonly accepted theory of the cause of its occurrence will be explained in the next chapter, when we deal with the inheritance of sex.

Our survey of what we may term the "Mendelian" laws governing the inheritance of parental qualities by hybrids enables us to come to an important conclusion. It is clearly proved that by the crossing of distinct strains which differ from one another in two or more characters, new strains can be produced, which combine certain qualities derived from both parental strains and which breed perfectly true. If we could conceive of some sudden change in the environment which should sweep away both parental strains, but which a new hybrid strain could successfully resist, then a new species would in this way be produced, and one daring speculator (Lotsy) has asserted that this is the only way in which new species can originate, but in this view he has found few followers. Were we to accept it we should be committed to the position that from the beginnings of life on the earth a large number of independent types of organism had existed, each with definite hereditary characters, and that all progress

had been due to the combination of these factors—such as those for rose comb and pea comb in fowls—as a result of the constant intercrossing of these forms. We must reserve our criticism of such views until a later chapter, in which we shall sum up the general impression produced on us by all the evidence.

In the meantime we may be permitted to point out the great advantage which a knowledge of the laws of Mendelian segregation confers on the practical breeder. He can combine the advantageous qualities of two different strains, and from the numerical proportions in which different varieties appear in the second and third filial generations he can select those which will prove stable and suitable for further propagation. An instance will make the high importance of the matter clear. It is well known to most people that the red, hard wheat grown in Manitoba makes a most desirable bread and commands a high price. The grains of this wheat are rich in gluten, and when dry and broken across exhibit a smooth, glassy surface of fracture. On the other hand, the wheat grown in the east of England makes a heavy, doughy sort of bread, and its grains are surcharged with starch, and when broken across exhibit a

white, granular surface. Now, Professor Biffen, of Cambridge, has shown that when suitable precautions are taken Manitoba wheat can be grown in England. The farmer, however, would find it unprofitable to do so, because the gain from the higher price which this wheat commands is more than offset by the loss due to its much smaller yield per acre as compared with the English wheat. This lessened yield per acre, according to Professor Biffen, is due to the lax system of branching of this plant, which is a racial characteristic; the English plant, on the other hand, produces a thick tuft of close-set branches, which explains its much higher yield per acre.

Professor Biffen, by crossing these two kinds of wheat, secured in the second filial generation a stable hybrid which combined the hard grain of the Manitoba wheat with the thick tufted branching and consequent high yield of the English wheat, and this new strain has proved most successful during a series of years, and has gained high prizes at agricultural shows. It is obvious that whilst the benefits which it confers on English farmers are not to be under-estimated, if it were to be introduced into Canada and were to produce anything like the high yield there which is obtained



from it in England, the profit which it would bring to the Canadian farmer would be colossal. For whereas the English farmer would benefit to the extent of getting three or four shillings more per quarter for his grain, the Canadian farmer would have his harvest increased from 50 to 100 per cent. We confidently expect in the near future great results will be obtained from experiments like this which we have just described.

## CHAPTER VII

### THE INHERITANCE OF SEX

IN the vast majority of the species of the higher animals the individuals are of two different kinds, male and female, which differ from one another even more than do two Mendelian strains of the same species. Indeed, in the case of some insects, male and female might easily be regarded as types of two distinct species if their relationship to one another were not known. The decisive difference between males and females is, of course, that the first carry spermatozoa and the latter eggs, but with this primary difference are associated, as we all know, a number of other differences, as, for instance, the beard and moustache in men or the comb in cocks, which are known as **secondary sexual characters**. The question then arises, whether males and females might not have the same relation to one another as two allelomorphic strains of the same species. Now, of course, when male and female unite and produce

children these are not, like the hybrids of yellow and green peas, all alike, but are of both sexes, since otherwise the race would come to an end, and hence the relation of the two sexes to one another cannot be simply that of dominant and recessive. Since, on the whole, in the human race and in the higher animals, the sexes are produced in approximately equal numbers, the only assumption that is tenable, if the inheritance of sex resembles that of Mendelian characters, is that one of the sexes is hybrid and that the other is a pure recessive; for we have already learnt that when a hybrid and a recessive are mated, equal numbers of hybrids and recessives are produced by the cross. If F denotes femaleness and M maleness, then in a case of sexual union we must either have the cross expressed by the formula  $F(M) \times M = F(M) + MM$ , or by the formula  $M(F) \times F = M(F) + FF$ , the character in brackets being the recessive one. In the first case we assume that the apparent female is a hybrid in which the female quality is dominant over the male quality, but that the male is a pure recessive. In the second case we assume that the apparent male is a hybrid, and that the quality of maleness is dominant over femaleness, but that the female

is a pure recessive. In either case we must assume that the sex which we regard as hybrid produces two kinds of germ-cells in equal numbers, one sort carrying the male and the other sort carrying the female characters. It follows that there must be either two kinds of eggs or two kinds of spermatozoa. Curiously enough, evidence has been produced to show that both these cases can occur. It is the merit of the late Professor Doncaster to have been the first to have almost demonstrated a case where there are two kinds of eggs, and where femaleness is dominant over maleness, and we shall give an account of his work in order to serve as a type of this kind of investigation.

One of the common moths in England is the currant-moth, *Abraxas grossulariata*. It is an undistinguished-looking insect whose wings are mottled with blotches of a dull reddish-brown colour. There exists, however, a rather rare variety, the milky currant-moth, which has the same general type of coloration on its wings, but the splashes of colour are so pale as to be nearly invisible, and have somewhat different outlines. This variety is known as *Abraxas laticolor*, and all the specimens of it which have been caught wild have turned out to be females.

Male specimens of *Abraaxas lacticolor* have, however, been bred in captivity. Now when one of these wild female specimens of *Abraaxas lacticolor* is mated with a male *Abraaxas grossulariata*, all the progeny, males as well as females, are of the *grossulariata* variety. We see from this that the type of coloration denominated *grossulariata* is dominant over the type denominated *lacticolor*, and this latter type, therefore, owes its peculiarities to the loss of some "factor" which confers on the offspring the quality of being *grossulariata* when it is present. When, however, a *grossulariata* female is mated with a *lacticolor* male, a quite different result is produced. In this case all the male offspring bear the *grossulariata* character, and all the females the *lacticolor* character. From this circumstance we are driven to conclude, firstly, that the *grossulariata* female is a hybrid and produces two kinds of eggs, one kind carrying the *grossulariata* factor, and one kind devoid of the factor because all the germ-cells of the recessive *lacticolor* male parent must be devoid of the *grossulariata* factor; and, secondly, that the eggs bearing the *grossulariata* factor always develop into males, and those devoid of this factor into females.

Therefore, in this case at least, there are

male-producing and female-producing eggs, whilst the spermatozoa of the male *grossulariata*, which can carry the paternal character to both male and female offspring, are all alike. But all the eggs, both male-producing and female-producing, of a female *lacticolor* are, of course, of the *lacticolor* variety, and when a male-producing *lacticolor* egg is fertilized by a spermatozoon from a *grossulariata* male, a hybrid male is produced which gives rise to equal numbers of spermatozoa with the *grossulariata* factor and devoid of it. If now we mate this hybrid male with a *lacticolor* female, both male and female eggs will be fertilized with both kinds of spermatozoa, and there will result offspring of the following types, viz. (1) hybrid male *grossulariata* (*grossulariata* spermatozoon  $\times$  *lacticolor* male egg); (2) pure male *lacticolor* (*lacticolor* spermatozoon  $\times$  *lacticolor* male egg); (3) female *grossulariata* (*grossulariata* spermatozoon  $\times$  *lacticolor* female egg); and (4) female *lacticolor* (*lacticolor* spermatozoon  $\times$  *lacticolor* female egg). By this cross, therefore, we are enabled to produce *lacticolor* males. It is a remarkable fact that there is apparently no such thing as a pure *grossulariata* female; every one, whether caught

wild or raised in captivity when tested by being crossed with a *lacticolor* male, reveals its hybrid nature by producing two kinds of offspring.

An instance of the same kind in which the eggs are all alike whilst there are apparently two kinds of spermatozoa is afforded by the little fruit fly, *Drosophila melanogaster*. From the study of the heredity of this insect startling results have been obtained by Professor Morgan of New York and his pupils, who have chosen it as their special subject for investigation. These results have, in fact, formed the basis for a complicated theory of the nature of the "factors" and their relation to the chromosomes. We shall have to examine this theory critically and in detail. *Drosophila* has a very rapid life cycle, since the period which intervenes between the fertilization of the egg and the production of ripe eggs by the female which grows from the egg is only about twelve days. It can be fed on a diet of decaying bananas, and hence it is comparatively easy to raise enormous numbers of the insect and to obtain a considerable number of generations within the period of a year.

The normal colour of the eye in *Drosophila* is red, but Morgan found that when he raised

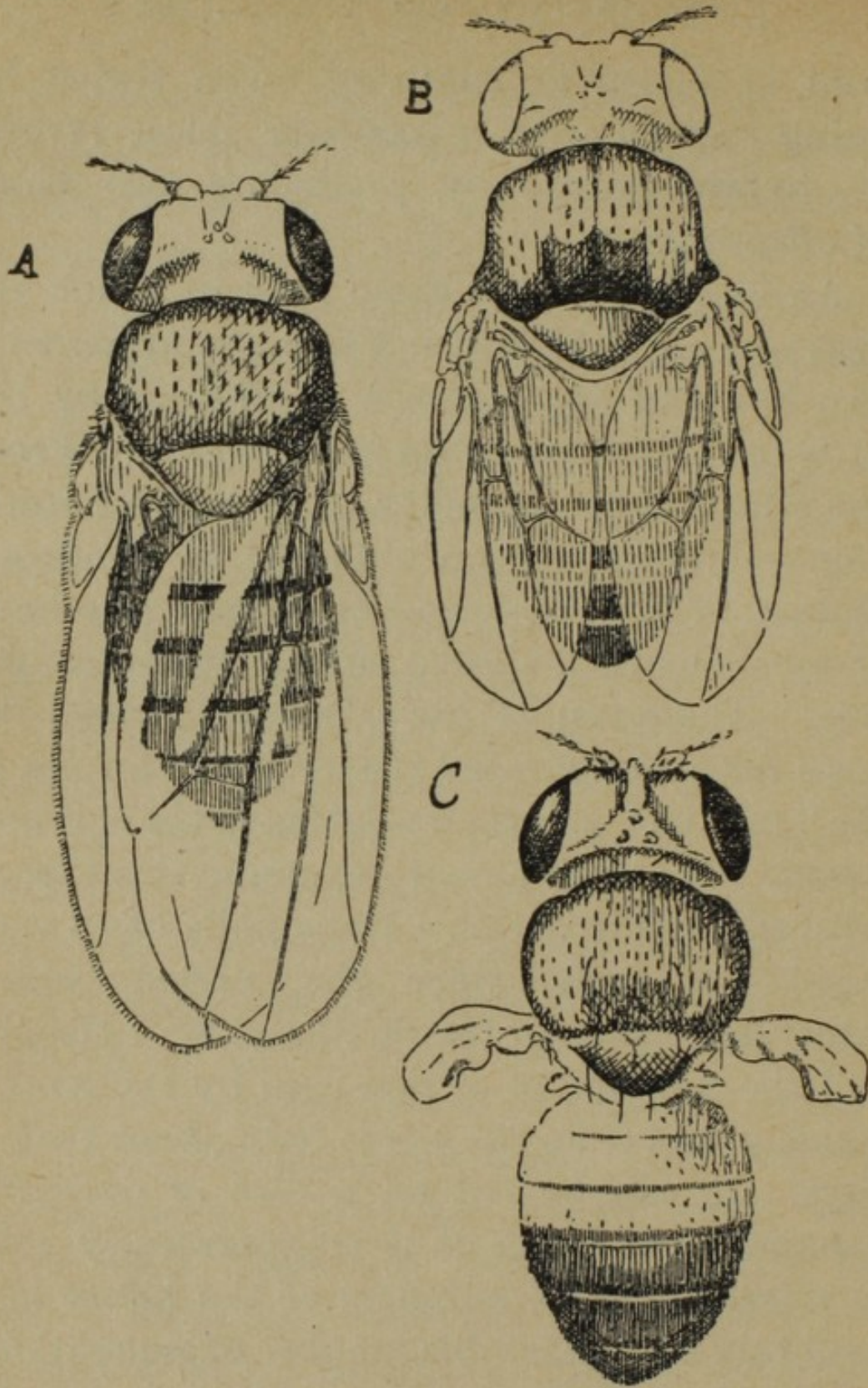


FIG. 22.

*Drosophila melanogaster*, viewed from the dorsal surface. A. Typical specimen. B. White-eyed specimen with abbreviated wings. C. Red-eyed specimen with vestigial wings (after Morgan).



thousands of individuals a few white-eyed males turned up. These "sports" when crossed with the red-eyed type acted like Mendelian recessives. All of the first filial generation had red eyes, and *this was the first case observed where an isolated abnormal individual which turned up in a culture was proved, when mated with the type, to yield offspring following the Mendelian rules.* When these hybrid red-eyed insects were mated with one another, the proportions of red-eyed to white-eyed amongst the offspring in the second filial generation were, as was to be expected, about three to one. All the white-eyed specimens in the second filial ( $F^2$ ) generation were males, as were also one-third of the red-eyed. Since on the average equal numbers of males and females were produced, half the entire population would be males; of these a half—*i. e.* a quarter of the whole population—are provided by the white-eyed members, and therefore another half—*i. e.* a quarter of the whole population—must be red-eyed. As the red-eyed members altogether form three-quarters of the population, it is clear that a third of them must be males. In order to obtain white-eyed females it was necessary to mate the hybrid red-eyed females

with white-eyed males, and in this way both red-eyed and white-eyed males and females were produced. When red-eyed males, *whether obtained in this way or by selection from amongst members of the original strain*, were mated with white-eyed females, they produced red-eyed and white-eyed offspring, amongst which all the females were red-eyed and the males white-eyed. White-eyed males and females mated together gave nothing but white-eyed offspring. Adopting the same kind of reasoning which we made use of in the case of *Abraxas grossulariata*, we conclude: (1) that there are two kinds of spermatozoa, male-producing and female-producing; for we know that a hybrid red-eyed male must produce what we may term "red-eyed" and "white-eyed" germ-cells in equal numbers, and when these are used to fertilize the eggs of a white-eyed female, all of whose eggs must be recessive "white-eyed" germ-cells, all the red-eyed offspring, half of the whole number, are females; (2) that the eggs of the female are all alike with regard to the transmission of sexual characters, for when hybrid red-eyed females, which, of course, produce two kinds of eggs, one bearing the "red-eyed" factor and another devoid of it, were crossed

with white-eyed males, all of whose spermatozoa were devoid of the factor for red eyes, red-eyed males and females were produced as well as white-eyed males and females, showing that both "red-eyed" and "white-eyed" eggs, when fertilized with "white-eyed" spermatozoa, gave rise to males and females in equal numbers. (3) Since in *Drosophila* the male is a hybrid and produces two kinds of germ-cells, yet exhibits male qualities, in this genus maleness must be dominant and femaleness recessive; in *Abraxas*, on the other hand, where the female produces two kinds of germ-cells yet is female in appearance, femaleness must be dominant and maleness recessive.

It is a most interesting thing that there are certain types of human disease, or rather deformity, which seem to be inherited in exactly the same manner as the red eye and the white eye in *Drosophila melanogaster*. One of these is the affliction known as night-blindness, the sufferer from which becomes totally blind in the dusk. This disease is due to the absence from the retina of the eye of certain sense-cells which are adapted to respond to light of low intensity. If a night-blind man marries a normal woman all his

children are normal, and as the affliction is a recessive, due to the absence of something, this is what we would expect. When these children in turn marry, the sons have normal children, but some of the daughters are likely to have night-blind sons. Night-blindness does not seem to affect women, except in very rare cases. We therefore have the paradox that the disease appears in men, but is transmitted by women. Now let us compare night-blindness to the white eye in *Drosophila*, as we may very fairly do, since both are defects of the visual organs. We assume, then, that there are two kinds of spermatozoa, male-determining and female-determining, and *that consequently the sex of a human being is determined by his or her father*. We further assume that the male-producing spermatozoon is devoid of the factor for seeing in the dusk, so that every male is a hybrid who derives his capacity to see in the dusk from his mother, and all his male-producing spermatozoa are devoid of the factor for seeing in the dusk. When a man is afflicted with night-blindness, however, he is a pure recessive, and not only his male-producing, but also his female-producing spermatozoa are devoid of the "dusk-seeing" factor. But still he cannot

transmit his affliction to his children because the defectiveness of his spermatozoa is overcome by the normality of his wife's ova. But their children, both boys and girls, are hybrids, and each produces normal and abnormal germ-cells in equal numbers. When one of these girls marries a normal man who is also *ex hypothesi* a hybrid, then it may happen that one of her imperfect eggs is fertilized by one of his defective male-producing spermatozoa and so a night-blind male baby is produced.

The reader will see, however, that theoretically a night-blind girl baby could be produced if the daughter of a night-blind man were to select another night-blind man as her husband. For all the spermatozoa of her husband, female-producing as well as male-producing, would be defective, and as she can produce defective eggs as well as perfect ones, if such an egg were fertilized by one of her husband's female-producing spermatozoa, she should bear a night-blind daughter; and such cases, though very rare, are not entirely unknown.

So far as investigation has gone, birds agree with moths in producing two kinds of eggs, whilst mammals and bugs and most other insects agree with flies in producing two kinds of spermatozoa.

This type of inheritance, where certain characters appear normally only in one sex but are inherited through the opposite sex, is termed by Morgan "**sex-linked inheritance,**" and it may be defined as a *weakness or defect normally associated with a certain proportion of the eggs or of the spermatozoa which under ordinary circumstances remains entirely concealed, and which can only be rendered manifest when the same defect turns up accidentally in a germ-cell of the opposite sex.* Morgan has brought forward a plausible and ingenious hypothesis to account for this kind of inheritance based on his observations on *Drosophila*. The diploid number of chromosomes in this insect is eight, but in the nuclei of the cells of the female these eight consist of four pairs of similar chromosomes. In the nuclei of the cells of the male, on the other hand, we find three pairs of similar chromosomes and two unlike ones. These aberrant chromosomes are termed the X and the Y chromosomes respectively. The X chromosome is represented by a pair in the female nucleus, but the Y chromosome, distinguished by its hook-like form, is not found in the female. When the reducing division takes place, the X and Y chromosomes undergo longitudinal splitting

as in an ordinary nuclear division, but in the second maturation division of the male nucleus they pair with one another and then separate, an X chromosome being distributed to half the male germ-cells and a Y chromosome to the rest (Fig. 23). The same division in the ripening egg-cells gives rise to ripe eggs and

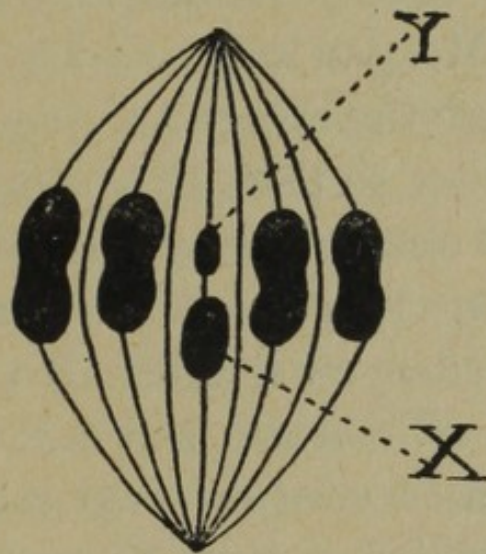


FIG. 23.

The second maturation division of a male germ-cell of *Euschistus variolarius* showing the separation of the X and Y chromosomes.

second polar bodies each with an X chromosome. Since the nuclei of the male body have each an X and a Y chromosome, and since every egg has an X chromosome, the males must have developed from eggs which have been fertilized by spermatozoa each of which had a Y chromosome; and since the nuclei of the female body have two X chromosomes,

the female must arise from an egg fertilized by a spermatozoon with an X chromosome. Now if we assume that the "sex-linked" factor for white eyes is based on something in the X chromosome, then a white-eyed female will possess what we may call white X chromosomes in all her nuclei. We further assume that the Y chromosome "carries no factors," as Morgan says, and is therefore also incapable of giving rise to eye-pigment and may be called white, so that all spermatozoa which possess a Y chromosome will also be white-eyed. When, therefore, an ordinary male fertilizes a red-eyed female all the young are red, because all contain a red X chromosome, but the females contain two red X chromosomes, the males a red X and a white Y. When, however, a normal male fertilizes a white-eyed female all the X-bearing spermatozoa will produce females which have red eyes owing to the red X chromosome, and all the Y-bearing spermatozoa will produce males which are white-eyed owing to their possession, in addition to the maternal white X chromosome, of only a white Y chromosome. The reason, therefore, that the normal male behaves like a hybrid is that it possesses a Y chromosome. It may seem to many a forced



and improbable assumption that Y "carries no factors"; the only justification for it is that in some insects we find in the male nuclei only one X chromosome and no Y at all, whereas the female nuclei possess two X chromosomes; we therefore suppose that the Y chromosome is something that can be present or absent, and hence Morgan assumes that it has no function at all.

On this explanation of these aberrant chromosomes Morgan founds his whole system. If we go back to the simple case of the crossing of two strains of peas, yellow and green, differing from each other only in one character, Morgan assumes that this difference is due to a peculiar factor in one pair of chromosomes of the recessive strain and of a different factor in the corresponding chromosomes of the dominant strain.<sup>1</sup> We shall call the former the weak chromosome pair, the latter the strong chromosome pair. In producing the hybrid a germ-cell with one weak chromosome unites with a germ-cell with a strong chromosome to form a zygote. When the hybrid forms germ-cells in the reducing division, corresponding weak and strong chromosomes come

<sup>1</sup> Morgan does not accept the "presence and absence" theory of Bateson (see p. 158).

together and then separate, the weak chromosome going into one germ-cell and the strong into another, and so we see why the hybrid produces equal numbers of germ-cells bearing the paternal and maternal characters. The formation of four types of germ-cell by hybrids produced by crossing two strains differing from one another in two characters is explained by supposing that each differentiating character is due to an alteration of a different pair of chromosomes. When the hybrid forms germ-cells, corresponding paternal and maternal chromosomes approach one another as before to form diploid pairs, but the paternal ends of different pairs are not all turned in the same direction, *i. e.* towards the same pole of the karyokinetic spindle, whence it follows that when the members of these pairs separate from one another, one germ-cell may receive the paternal member of one pair of chromosomes and the maternal one of another; and so an independent distribution of the two characters amongst the germ-cells of the hybrid results. In theory, therefore, there should be just as many pairs of independent differentiating characters as there are pairs of chromosomes and no more. In practice it is found that there are more, but so far as

*Drosophila* is concerned, Morgan has striven to show that all these characters are "coupled" (see p. 163) into four groups corresponding to the haploid number of chromosomes. (It is always to be remembered, however, that in this computation the Y chromosome is ignored, yet this chromosome in *Drosophila* is at least as large as the X chromosome.) That is to say, that the characters which are "coupled" together are usually found together in one germ-cell when the hybrid produces germ-cells. That this is not always so is explained by means of another daring supposition put forward by Morgan. He assumes that when paternal and maternal chromosomes come together they twist round each other in a spiral line, and that when they separate it often happens that this separation takes place in a different plane from that of the union, so that the paternal chromosome carries away with it a bit of the maternal chromosome and the maternal chromosome a part of the paternal chromosome. This hypothetical occurrence is termed by Morgan "crossing over." From the frequency with which coupled characters accompany one another when the coupled group is broken, Morgan draws deductions as to the nearness to

or distance from one another of the factors which produce them on the chromosome; he assumes indeed that the chromosome consists of a linear group of factors or, as he prefers to call them, "genes." All the characters that normally go with the X chromosome in the female-producing spermatozoon are supposed to have their basis in the "genes" in this chromosome. The smallest group of coupled characters is supposed to be situated in the smallest chromosome, which is a small round dot, and proceeding in this way Morgan has actually constructed chromosome maps. This theory, although it has been readily and uncritically accepted by many "geneticists" both here and on the continent of Europe as well as in America, encounters enormous difficulties when it is followed out in detail. For a full discussion of these difficulties we must wait till the next chapter.

In *Drosophila*, therefore, and in most other insects as well as in mammals, femaleness is supposed to be due to an excess of one particular kind of chromatin (the X chromosome), and maleness to a defect of the same material, whereas in birds, butterflies and moths, maleness is supposed to be the consequence of an excess of the X chromosome

material and femaleness to its defect. But femaleness and maleness are essentially the

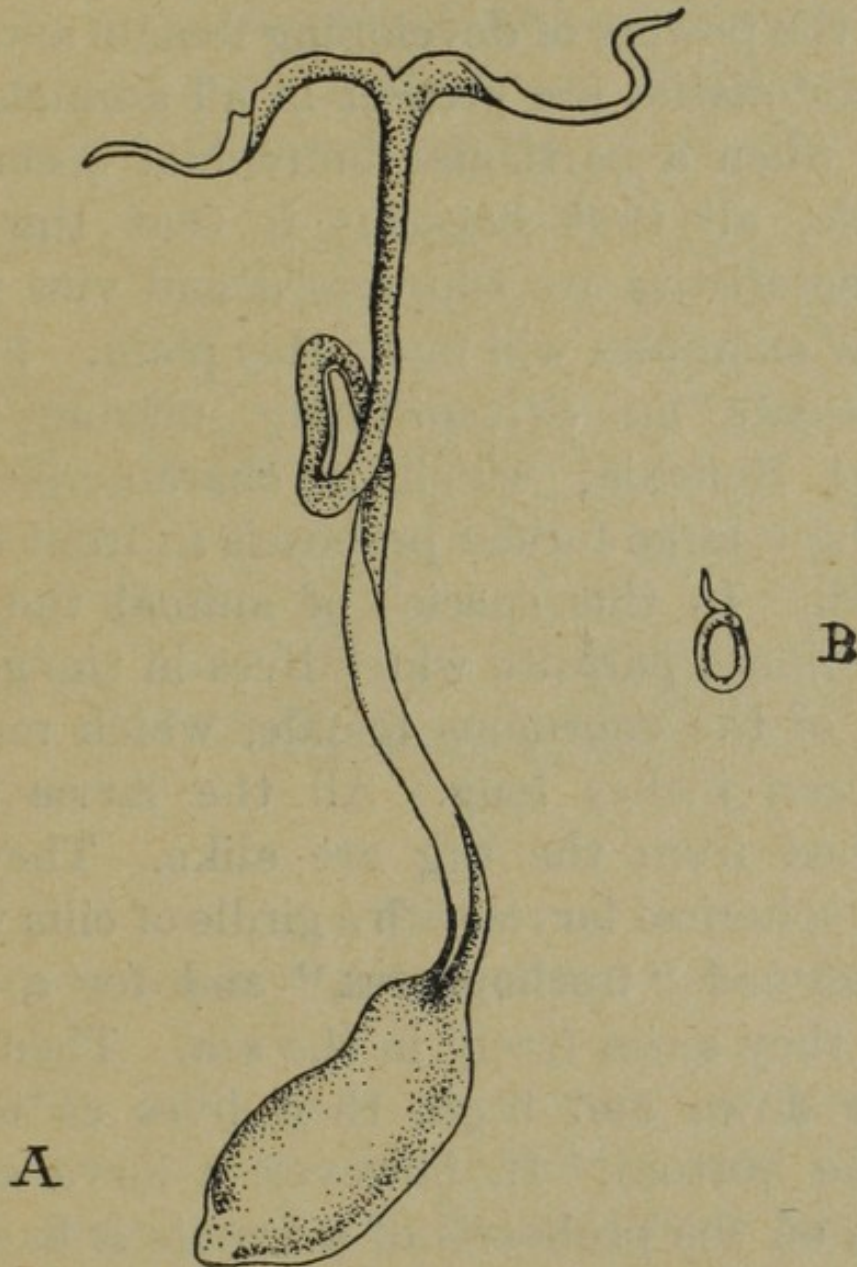


FIG. 24.

Male and female specimens of the worm *Bonellia*.  
A. The female. B. The male.

same kind of quality throughout the animal kingdom, and it is inconceivable that an excess

of a particular kind of substance should cause maleness in one type of animal and femaleness in another. Further, we have strong evidence that the powers of developing female and male characteristics are present in all animals, and that when a particular individual becomes a female, all that happens is that the male characteristics are suppressed and vice versa. A few examples will make this plain. Fig. 24 represents an extraordinary marine worm called *Bonellia*, which is characterized by having a large forked proboscis in front of the mouth. In this species of animal the male is a minute parasite which lives in the genital duct of the enormous female, which may be eighteen inches long. All the larvæ when hatched from the egg are alike. They are little spherical larvæ with a girdle of cilia which are termed "**trochophores,**" and for a short time they swim freely in the sea. Then they settle down and begin their lives as worms on the bottom. If, however, a larva settles down on the proboscis of a female it becomes a male. If a larva be allowed to attach itself to the proboscis of a female and remain there some little time, and be then detached, it develops into a hermaphrodite. Here sex is obviously determined by the environment.

Then, we have the extremely interesting observations of Geoffrey Smith on the effects of certain parasites on their hosts, which, in the case we shall select for special description, consists of a certain species of Mediterranean crab called *Inachus scorio* (Fig. 25). The

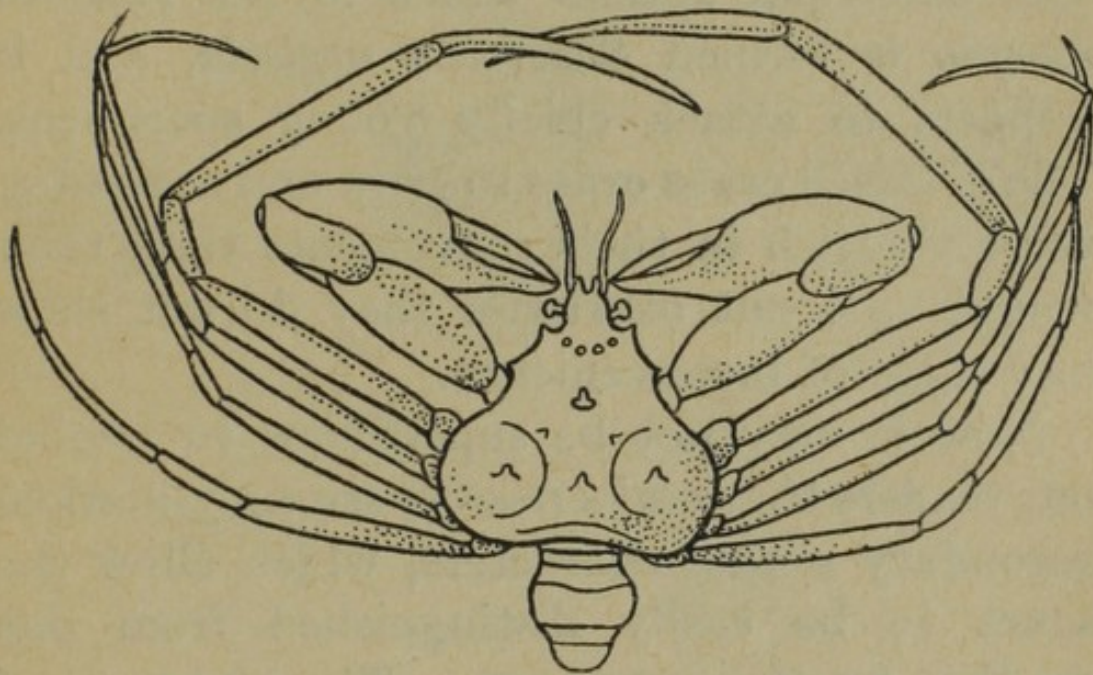


FIG. 25.

Male specimen of the crab *Inachus scorio*, viewed from above.

parasites belong to a race of degenerate barnacles termed Rhizocephala (Gr.  $\rho\acute{\iota}\zeta\omicron\varsigma$  = root), because the stalk by which they are attached to the unfortunate crab grows out into a series of roots which permeate all portions of the crab's body and absorb nourishment from the blood. The alimentary canal and legs of the barnacle, being no longer used,

have disappeared, and its body has become reduced to a shapeless sac containing the generative organs. Like other barnacles, it develops from a small, free-swimming larva provided with antennæ, eyes and swimming feet, all of which it loses when it finds its host. The particular species which infests *Inachus scorpio* is termed *Sacculina neglecta*, and it appears to attack chiefly young specimens. The diseased crabs cease to grow and are rather more sluggish in their movements than their neighbours, but otherwise they do not show any signs of inconvenience.

Now it may not be superfluous to remind our readers that crabs possess strongly-marked secondary sexual characters, which allow the sexes to be easily distinguished from one another by the naked eye. The abdomen of the female is broad and hollowed on its under surface, which during life is kept bent upwards against the thorax. It bears four pairs of forked legs fringed with long hairs, and the eggs, after being shed, are attached to these hairs, and so the mother carries the eggs about with her until the young ones hatch out (Fig. 26, B).

The abdomen of the male is much narrower and is not grooved. It bears only two pairs



of appendages, which are not forked, nor much pointed, but are comparatively rigid (Fig. 26, D). These are termed the **copulatory styles**, because they are used to introduce the male

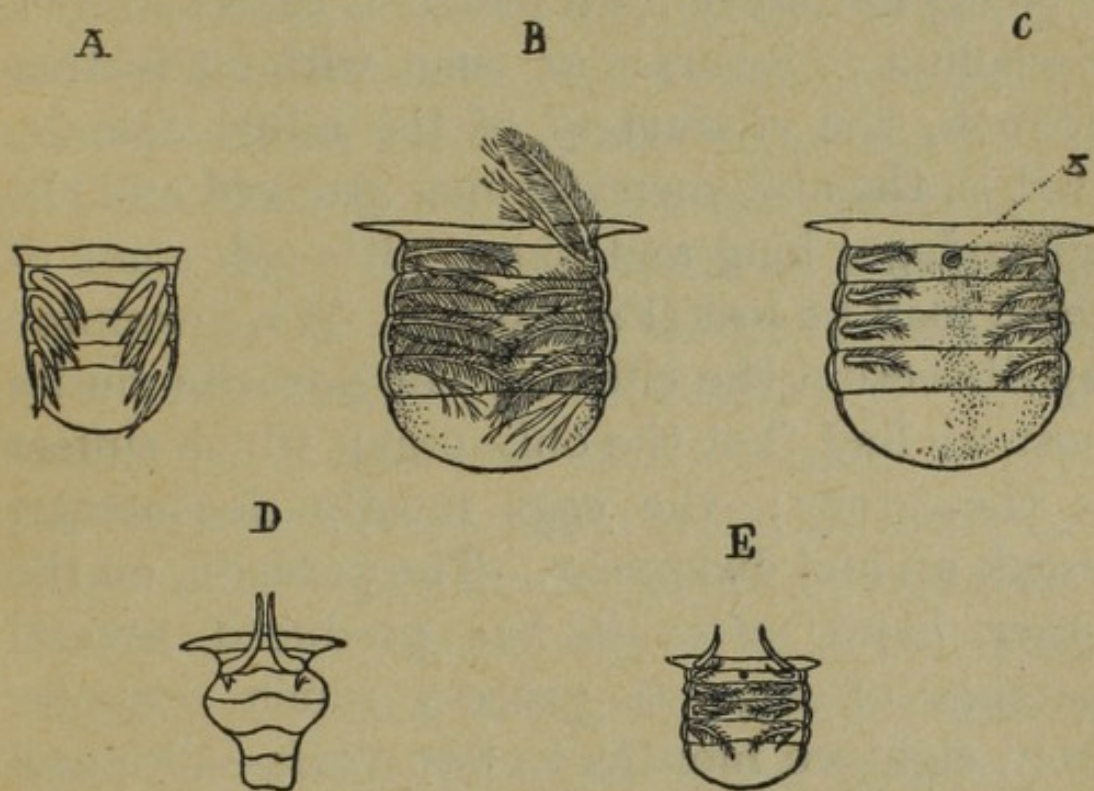


FIG. 26.

Abdomens of normal and diseased specimens of *Inachus scorpio*, viewed from below. A. Abdomen of immature female. B. Abdomen of mature female. C. Abdomen of female which has been infected by *Sacculina neglecta*. D. Abdomen of male. E. Abdomen of male which has been infected by *Sacculina neglecta*. X (in C), the spot where the parasitic *Sacculina* was attached.

germ-cells, which in crabs are motionless (see Chap. I), into the egg-tubes of the female. The male has also much larger claws than the female, which he apparently uses in fights with his male rivals.

In immature females the abdomen is not grooved, and its appendages are not so much jointed nor as richly provided with hairs as in the adult female (Fig. 26, A). Now when a young half-developed female is attacked by a *Sacculina* it assumes at once, without further growth, the characters of the adult female, that is, the abdomen becomes grooved and the appendages long and hairy, although some of them may be lost (Fig. 26, C). If we examine by dissection the effect of the parasite on its host we find that the only organ which suffers is the ovary; the eggs mostly degenerate, break up and disappear. The parasite, on the other hand, after it has produced several batches of eggs—a process which occupies from eighteen months to two years—dies and drops off and its roots become absorbed. The place where it was attached heals up, leaving a noticeable scar (Fig. 26, C), and in some few cases the host still lives on and may resume growth, and in this case a remnant of the ovary may be left and may produce eggs.

On the other hand, when a half-developed male is attacked, a widely different and extremely interesting result is produced. Female secondary sexual characters make their appearance. The abdomen becomes

broad, although not quite as broad as that of a normal female, and additional abdominal appendages appear, which, though smaller than those of the normal female, have the same characteristic form (Fig. 26, E). The claws also remain about the size of those of a female. In the case of the male also dissection reveals the fact that the principal, if not the exclusive, damage done by the parasite is experienced by the genital organ, the lobules of which are seen to be broken up and destroyed. Nevertheless, as in the case of the female, so here, the host sometimes outlives the parasite and then resumes growth and begins to regenerate its generative organs, but these now consist of both ovary and testis, so that the crab has become a hermaphrodite. Here, again, as in the case of *Bonellia*, an accident of the environment has determined sex. How are we to conceive of the action of the parasite? Do its roots emit a corrosive substance which digests and destroys the generative cells of the host, or do these cells dwindle and die simply because the parasite withdraws from the blood of the host the special substance necessary for their maintenance? If the action of the roots of the parasite were a directly digestive one, we could not understand

the introduction of female characters into the male. Geoffrey Smith's brilliant and suggestive hypothesis is as follows : he assumes that every male is a potential hermaphrodite and contains what we may term female substance in his composition, which under normal circumstances is kept under by the superior potency of the male substance ; but the female is supposed to have only female substance. These substances are conceived of by Geoffrey Smith as circulating in the body fluids, and thus producing the secondary sexual characters ; and also, by becoming stored up in certain of the interior cells, producing the primary sexual organs. The roots of the *Sacculina* are supposed to have a special affinity for the male substance, which they absorb in far greater proportion than the female substance ; and, as a result, in a male attacked by a parasite the proportion of female substance increases and is sufficient to produce the female secondary sexual characters, and when the parasite is removed to generate eggs also.

There is, no doubt, a large measure of truth in Geoffrey Smith's hypothesis, but one or two criticisms may be made. He points out that his hypothesis agrees with those cases of sex-

limited inheritance where there are two kinds of spermatozoa, and where the male is represented by the formula  $M(F)$  and is a heterozygote. He asserts that in all cases of hermaphroditism the male elements ripen first, and that hermaphrodites only differ from ordinary males in having more female substance than they. But his hypothesis is in complete contradiction to the case of *Abraaxas grossulariata*, where there are two kinds of eggs and the female is represented by the formula  $F(M)$ , whilst the male is pure  $M$ . Nor is it universally true that in hermaphrodites the male elements ripen first. In compound ascidians like *Salpa*, the eggs ripen before the spermatozoa, and there are numerous indications from other divisions of the animal kingdom that females must contain some male substance.

Thus, in the primitive fish *Amphioxus*, in which the generative organs of both sexes consist of two longitudinal series of sacs, Goodrich has pointed out that in a female, one sac in the series may produce spermatozoa. Again, Crew has recorded the case of a hen which had laid eggs for several years from which chickens had been raised, which turned into a cock in its old age. This animal not

only acquired the comb and the characteristic feathers (hackles) of a cock, but its crow and its attitude towards the hens, and it finally became the father of several chickens by successfully "treading" several hens. When it was killed it was discovered that the ovary had been destroyed by tubercular disease, but that a male-gland or testis had sprouted from the membrane lining the body-cavity. If we assume that in the female there is always some male substance which is inhibited by the preponderance of female substance, we shall be able to understand the effect of the parasite in producing precocious female maturity. For we may reasonably regard the male substance present in a young female as the principal cause of her immaturity, and when this male substance, which normally would be inhibited by the gradually increasing female substance, is suddenly removed by the parasite, maturity at once supervenes.

This modification of Geoffrey Smith's hypothesis which we have adopted is strongly confirmed by the results obtained quite recently by Richard Goldschmidt. Goldschmidt experimented with the moth *Lymantria dispar*, commonly known as the gipsy moth. This species is divided into a good

many local races, and characteristic races inhabit Japan, Europe and North America. When a Japanese female is fertilized by a European male the progeny consists of normal males and females, but when a European female was fertilized by a Japanese male a very different result was obtained. Normal males made up half the filial generation, but the females presented various mixtures of male and female characters. Such abnormal females were termed **intersexes**. Where the male admixture] of characters was slight it concerned only external features, such as the colour of the wings or the shape of the antennæ, but where the male influence was more pronounced, the ovary was partly or completely transformed into a testis, and in extreme cases the female was almost entirely changed into a male. Goldschmidt interprets his results in the following manner. Each individual has in it the potentiality of developing the organs of both sexes, but the development of these organs is dependent on the stimulus of certain ferments set free in the blood during development, which he calls the **sexual hormones**. The intensity of these hormones varies in different races; and when the Japanese spermatozoon penetrates the

European egg it carries into it an exceedingly powerful male hormone. It will be remembered that moths have two kinds of eggs—male-producing and female-producing. Now Goldschmidt assumes that the male hormone is contained in the X chromosome, but that the female hormone is in the protoplasm of the egg. In the male-producing egg the X chromosome which it contains reinforces the action of the X chromosome introduced by the spermatozoon, and a male insect is formed. In the female-producing egg, which is devoid of an X chromosome, the female hormone in the protoplasm is stronger than the male hormone introduced by the X chromosome of its own spermatozoon, but it can be wholly or partly overpowered by the stronger influence of the male hormone introduced by the X chromosome of the spermatozoon of the foreign race.

But if this kind of reasoning is valid it must apply also to *Drosophila*, which has one kind of egg and male-producing and female-producing spermatozoa. Every egg has an X chromosome, and if the action of this chromosome is reinforced by the entry of an X-bearing spermatozoon a female is formed, whereas a spermatozoon without an X leaves the X chromosome in the egg unable to contend



with the male hormone, and so a male is formed. This male hormone must be either in the protoplasm of the egg or in the other chromosomes. Intersexes in *Drosophila* have been actually observed in cases where, owing to irregularities of cell-division, the number of chromosomes has become multiplied. Thus individuals have been noted in whose cells there are twice the number of ordinary chromosomes and three X chromosomes, and these are females with a certain infusion of male characters—in a word, intersexes. In *Drosophila*, then, it would seem that the male hormone is contained in the ordinary chromosomes.

The sexes in frogs show a series of extremely interesting phenomena. The frog mates in spring. Both sexes after waking from their winter sleep go into the water, and there the male mounts on the back of the female, clasping his arms round her waist; he remains in this position for a considerable period, croaking wildly with excitement. At length when the eggs are ripe the female discharges them into the water in which she is sitting, being helped to get rid of them by the pressure which the male exercises on her abdomen. As they pass out the male fertilizes them

by discharging his spermatozoa on to them (see Chapter IV). Now Hertwig showed that whereas both sexes develop in approximately equal numbers from spawn laid under normal circumstances, if a female, after having laid a few eggs, be forcibly separated from her male partner and kept separate from him for two and a half days, and then allowed to rejoin him, she will lay the rest of her eggs, but the proportion of males developing from these eggs will be seven times as great as the females. One of Hertwig's pupils, by keeping male and female apart for four days, succeeded in obtaining a culture from which only males developed. As the rate of mortality in these cultures had been kept quite moderate, it is impossible to resist the conclusion that eggs which would have developed into females under ordinary circumstances had been forced to develop into males by being retained for two or three days too long within the womb of the mother. That the effect was due to a change in the eggs and not in the spermatozoa was proved by allowing males at different periods in the breeding season to fertilize the same female, and in all cases the same proportions of males and females developed from the spawn. The

possibility of performing this experiment was afforded by the wide range of the edible frog (*Rana esculenta*) on the continent of Europe. It is found everywhere from Northern Germany to Central Italy. The breeding season begins very much earlier in the south than in the north, and so when males collected in Central Germany were beginning their breeding season, males collected on the same day in Central Italy were nearly at the conclusion of it. Hertwig procured males from all quarters, which were sent by express train to Munich, where the experiment was performed.

Witschi, a pupil of Hertwig, has made some still more wonderful discoveries. He showed that in certain localities, such as Holland, if one examines young frogs which have just left the water, one finds that nine out of every ten are females; nevertheless amongst the fully-grown frogs from the same locality there are just as many males as females. It follows that four out of every five males must have been produced from females which changed as they grew up. Further observations proved that this is indeed the case. Witschi discovered many half-grown females in which the ovaries were being invaded and destroyed by testis

tubes growing into them from the surface, just as happened in the case of the abnormal hen mentioned above. Further, a review and repetition of Hertwig's experiments showed that in the experiments in which all the eggs were induced to develop into males a large proportion of these when they had reached the stage of young frogs were females, and that their male character only developed as growth proceeded.

We see, therefore, that if the X chromosome exercises an influence in favouring in some cases the production of male characters, and in other cases the appearance of female characters, it is by no means the only cause of the production of these characters, and that the influences of the environment during early growth have also powerful effects in determining some individuals to be males and others to be females.

We must now devote a little attention to the **secondary sexual characters**. By this term is meant not only the outward marks which distinguish the male from the female, but also the ducts or tubes which convey the eggs and spermatozoa to the exterior. Thus a woman is distinguished from a man not only by the absence of a beard and by her large

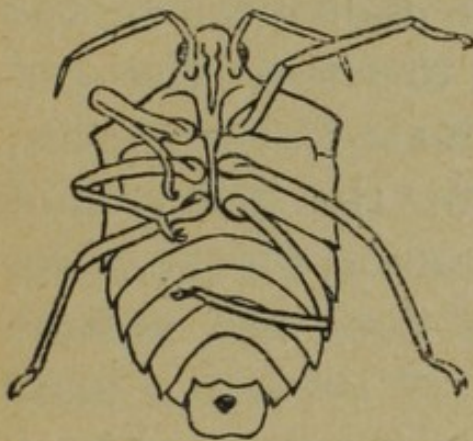
and well-developed breasts, but by the possession of egg-tubes and a womb in which the egg develops. Amongst vertebrates (fishes, amphibia, birds and mammals) the young embryo passes through a stage in which male and female sexes cannot be distinguished from one another, and the development of the external marks of the male or female depends on hormones emitted by the genital cells. If in a young male rat the testis be extracted and replaced by an ovary, the breasts enlarge and secrete milk and the animal takes on the habits and appearance of a female. Therefore in this group the secondary sexual characters are dependent on the primary for their development. But this is not so amongst insects. If the testis be removed from a moth caterpillar and replaced by an ovary, the grub will still metamorphose into an insect with all the external male characters, although its body is full of eggs. The question as to how these secondary characters are inherited in insects has been investigated by Miss Foote and Miss Strobell.

These ladies chose as the subjects of their experiments two species of the genus *Euschistus*. *Euschistus* is a genus of bugs which feed on plants; these insects show

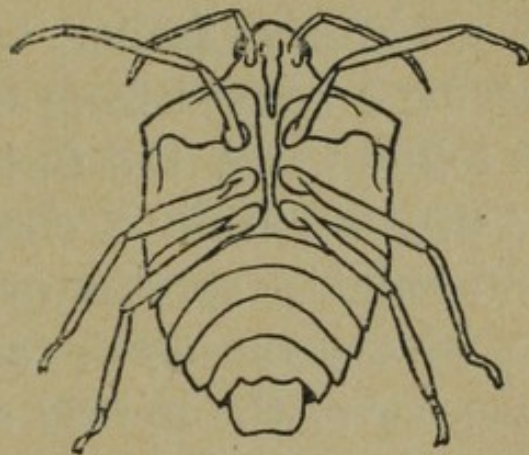
well-marked X and Y chromosomes in their germ-cells (Fig. 23). Like *Drosophila*, the male possesses in its body-cells an X and a Y chromosome, whereas the female has two X chromosomes. One of the species which was experimented with, viz. *Euschistus variolarius*, had in the male sex a well-defined black circular dot on the genital segment, which is the sixth segment of the abdomen (Fig. 27). The other species (*Euschistus servus*) was devoid of this spot, and in neither species did it occur in the female sex. On one occasion, and on one occasion only, a male *E. servus* fertilized a female *E. variolarius*. Fortunately, this union proved so prolific that no less than 120 eggs were produced, but many of these were abnormal and failed to develop. Only twenty-seven of them succeeded in developing to maturity, and of these eleven were males and sixteen females, and these constituted consequently the first filial generation. Seven distinct pairs of this generation were mated with each other and produced an abundant second filial generation. An attempt was made to induce a male *E. variolarius* to mate with a female *E. servus*, but this was unsuccessful. It was possible, however, to induce a male *E. variolarius* to mate with a female hybrid of the first filial

generation, and from this union twenty-six perfect insects were reared.

Now the results of these experiments were somewhat unexpected. It was found that many of the  $F^1$  hybrids exhibited the spot, and, therefore, this essentially male character must have been inherited from the mother,



*E. VARIOLARIUS.*



*E. SERVUS.*

FIG. 27.

The males of the bugs *Euschistus variolarius* and *Euschistus servus*, seen from beneath.

since the male parental strain belonging to the species *E. servus* is devoid of the spot. Consequently the "factor" which produces the spot cannot be situated in the Y chromosome, because there is no Y chromosome in the female. If we evade this difficulty by assuming that the factor for the spot, since it is inherited from the mother, is carried by the X

chromosome, but can only appear in the male sex, then we have to explain the circumstance that in the offspring of the cross between the pure *E. variolarius* male and the F<sup>1</sup> female hybrid the spot appears, and is much more strongly marked than in any of the F<sup>1</sup> male hybrids. This greater strength can only be explained as due to the influence of the *E. variolarius* father, and, therefore, the spot can be inherited from the male *E. variolarius*. It follows that the factor for the spot cannot be situated in the X chromosome, for the male-determining spermatozoon does not possess an X chromosome; and, of course, a male member of the hybrid strain is produced by a male-determining spermatozoon.

In the second filial generation some of the specimens showed the spot as strongly developed as in the original strain, and others were completely devoid of it; but in some cases the offspring of F<sup>1</sup> males, which were devoid of the spot, showed it strongly marked. In other cases the spot was faintly marked. If we are precluded from placing the factor for the spot in either the X or the Y chromosome, our next recourse would be to one of the ordinary chromosomes. But the factors for the spot must be situated in both members



of a pair of ordinary chromosomes, since, if they were in one chromosome only, there would be in the species *E. variolarius* two separate strains, one with and one without the spot, and half the males would be devoid of it, but this cannot be the case, since the spot in the pure species is a constant character. If, however, we make the assumption that the factors for the spot are situated in an ordinary pair of chromosomes, then the sequence of the maturation divisions baffles us entirely. For we must remember that the first maturation division is the reducing division in the case of the ordinary chromosomes, and ordinary longitudinal division occurs in the secondary maturation division, whereas in the case of the X and Y chromosomes ordinary longitudinal division takes place in the first maturation division, but union and final disjunction of the supposedly male and female determining elements occurs in the second maturation division. Any character situated in any ordinary chromosome whatever must therefore inevitably be distributed to both male-determining and female-determining spermatozoa. A diagram will make this clear. Let us call the pairs of ordinary chromosomes A and A<sup>1</sup>, B and B<sup>1</sup>, etc., and the results of

their longitudinal division  $a, a^1, b, b^1$ , etc. Let us suppose that the factors for the spot are contained in the pair of chromosomes  $AA^1$ . Then the maturation divisions will be represented thus :

		female-determining spermatozoon.
	$abcdx$	
$ABCDxy$		
	$abcdy$	male-determining spermatozoon.
$AA'BB'CC'DD'XY$		
		female-determining spermatozoon.
	$a'b'c'd'x$	
$A'B'C'D'xy$		
	$a'b'c'd'y$	male-determining spermatozoon.

We may endeavour to reconcile this conclusion with the facts by supposing that though the factors for the spot are situated in a pair of ordinary chromosomes, and it is therefore inherited by females, yet its appearance in a female is prevented by the presence of an inhibitor. This is a quite reasonable assumption, since in the female the shape of the genital segment is totally different from its shape in the male; it is, in fact, represented by a pair of triangular lobes and there is no room for the spot to appear on it. But we have also to account for the fact that the spot is very feebly developed in most of the  $F^1$  hybrid males and completely absent from

some of them, for all these hybrids have received the factors for the spot with the chromosome which has come to them from their *E. variolarius* mother. Therefore it would seem necessary to assume that *E. servus* males carry an inhibitor for a spot which they do not possess and transmit this inhibitor to the male hybrid offspring, which, to say the least of it, is not a very likely assumption.

We may now sum up our general conclusions as to the inheritance of sex. It seems clear that the development of maleness and femaleness represents two different types of growth which affect in greater or less degree all the organs of the body. The power of starting these two types of growth is inherent in every individual of the species; which type will gain the upper hand depends on a variety of circumstances. Sometimes it is determined by external influences (Bonellia), sometimes by the constitution of the blood as affected by disease (Inachus and Crew's transformed hen), and sometimes—it appears, at any rate, a plausible supposition—by the proportion between two different sets of chromosomes in the same nucleus. But in all cases we are dealing with a wavering balance between two possibilities—it is a question of those varia-

tions of "more" and "less" which Mendel expressly excluded from his consideration, and to talk of sex being determined by a Mendelian "factor" is absurd.

In the human race the knowledge that male potentialities are inherent in the constitution of a woman and that a man has a certain feminine element in his nature helps to explain a number of puzzling facts. We see why in many women when the child-bearing epoch is past and the ovaries diminish in size, the repressed male factors make themselves felt and the grandmother develops a beard and a moustache. Further, the slender and almost girlish build of many growing boys is due to the fact that the feminine element is yet not overcome by the growing male substance. But human beings—whether men or women—are not uniform mixtures of male and female substances. The proportion varies from individual to individual, and so we find that there are womanly women and mannish women, and effeminate men and manly men, or, as the Americans tersely denominate them, "hermen." It has been surmised, and is probably true, that in sexual attraction, which is the great motive power in life, each of the substances in the constitution of an individual

seeks to unite with its opposite, so that the forceful man is attracted by the tender, shrinking woman, and the effeminate man is usually captured by the strong-minded member of the opposite sex.

## CHAPTER VIII

### THE CAUSES OF MUTATIONS

IN Chapter VII we learnt that when Morgan raised large numbers of the fly *Drosophila melanogaster*, "sports" of various kinds turned up, and that these "sports" when crossed with the type behaved in a Mendelian manner—that is to say, they were recessive to the type in the first filial generation, but segregated out in the correct proportions in the second. Morgan's experience in this respect is similar to that of other breeders. In all cases where large stocks of animals or plants are kept, sooner or later "sports" turn up, which breed true when crossed with their like, but which "mendelize" when crossed with the type. It is the fashion to call these sports "**mutations**," in order to emphasize the theory that their appearance is the consequence of a definite change (mutation) in the heredity of the species; they are thus contrasted with the fluctuating variations which we discussed in an earlier chapter, which were supposed to represent the resultant

of the effects on growth and development of varying external circumstance and of a fixed and unchangeable hereditary constitution of the germ-cells. We have already seen that the environment *does* produce an inheritable effect on the constitution of living beings, but the demonstration of this fact belongs to the latest achievements of experimental biology, and many still refuse to accept the evidence offered. These still cling to the belief that the evolution of animals and plants has been brought about by the sudden appearance of mutations which have been preserved by natural selection. Therefore the research into the causes of the mutation assumes the rank of a biological problem of fundamental importance.

Strange to say, most supporters of the evolutionary importance of mutations have only the phrases "chance," "accidents" or "internal causes" to put forward to account for their appearance. De Vries, a Dutch botanist who published a book entitled *The Mutation Theory*, raised this illogical procedure to the dignity of a scientific hypothesis. He experimented with the garden plant *Œnothera lamarckiana*, the so-called evening primrose. Selecting three roots which he discovered in

a potato-field at Hilversum in Holland, he removed them to his botanical gardens at Amsterdam, and from them he raised about 10,000 seedlings a year. Every year a few "mutants" turned up, and these usually—though not always—when fertilized with their own pollen reproduced their like. According to De Vries each of these mutants differed from the type in several characters affecting stem, leaves, flowers and fruit. He at once jumped to the conclusion that he had surprised a species in the act of throwing off fully-developed daughter species, as Minerva was fabled to have been born from the head of Jove complete in all her armour. It was indeed he who invented the term "mutation," and *Oenothera lamarckiana* was regarded by him as a species which was indulging in a "fit of mutation." Gates, who examined the nuclear structure of some of these mutants, was able to show that some of them had a chromosome fewer than the number characteristic of the nuclei of the type, whilst in one of them, *Oenothera gigas* (Fig. 28, B), distinguished by its greater height, stouter stem and larger leaves, the number of chromosomes had been doubled. Gates considered that his discoveries supported De Vries's



theory and showed that the chromosomes have been altered owing to unknown causes—



FIG. 28.

A. *Enothera lamarckiana*. B. *Enothera gigas*—one of its mutants.

possibly “accidents of cell-division”—and that the mutations were the outward and visible result of the chromosomal changes.

Further research has thrown considerable doubt on this easy interpretation of the phenomena exhibited by *Œnothera lamarckiana*. *Œnothera* belongs to the Fuchsia order (Onagracea), and every genus of this order except the willow herb (*Epilobium*) is confined to North America. Yet when we go to North America we fail to find any wild representative of *Œ. lamarckiana*. Therefore we are forced to the conclusion that this species is nothing more than a garden hybrid between two unknown wild species which was produced by some gardener in the eighteenth century, and that the production of "mutants" is a result of the hereditary instability characteristic of such hybrids. Many of them may be mere recombinations of features of the two parental species; for others, such as *Œ. gigas*, this explanation is inadequate, yet other examples of such "tetraploidy" (*i. e.* doubling the ordinary "diploid" number of chromosome) are known to occur amongst the progeny of hybrids between different species. These doubts are reinforced by the results of the experiments carried out by Davies and McClelland, two American botanists. These workers cultivated a wild American species of *Œnothera* for seven or eight years, and no

mutants appeared amongst the offspring of the wild plants. Against this it is urged that "mutants" similar to those of *Æ. lamarckiana* have been found growing near masses of other wild species of *Ænothera* which bear small flowers and are self-fertilizing. But amongst self-fertilizing plants occasional crosses are nevertheless effected both by wind and insects, and these alleged "mutants" have therefore no evidential value. When, however, we come to consider Morgan's cultures of *Drosophila*, there is no evading the conclusion that very numerous mutants have "spontaneously" appeared. Allied species of *Drosophila* are known, but when these are crossed with *D. melanogaster*, either they produce no offspring at all or the offspring that are produced are sterile.

If now we examine the mutants which Morgan has obtained, such, for example, as those shown in Fig. 22, B and C, we are at once struck by their abnormal appearance. They are practically all of them cripples, and the vast majority are recessive to the type. Now we have seen that Bateson and Punnet explain the production of recessive strains by the "dropping of factors," and so if mutations have produced evolution we should

expect that when a "factor" drops out a previous stage in evolution would be reproduced. We know something about the evolution of wings by means of evidence drawn from fossil insects, from the embryonic development of insects, and from the comparative anatomy of living insects, and we are confident that wings at no period of their history ever resembled the shrivelled vestiges represented in Fig. 22, C.

If dropping of "factors" should reveal a previous stage in evolution, the appearance of new "factors" should give us a sample of how evolution progresses. Now the combs of the various breeds of domestic fowl are dominant to the single comb characteristic of the wild Jungle Fowl. We might therefore assume that in the production of these, new factors have appeared. But, again, these factors are abnormal in character. They seem to represent various stages in the loosening of the skin of the head, and they culminate in the Polish fowl, which here has a huge vacuity in the skull. Nothing like them is known in any wild species—only the genus *Gallus* possesses a comb at all, and every species in the genus has a single comb.

Morgan too has discovered a few dominant

“mutations.” These, however, are obviously abnormal; so abnormal indeed that when crossed with their like they are sterile. Only by mating them with the type has it been found possible to propagate them at all.

Now the most eminent palæontologists (students of fossils), embryologists (students of development), and systematic zoologists (naturalists), are all convinced that mutations as found by the breeder and gardener have played no part in evolution; they all seem to be due to pathological—that is, diseased—deviations from the type. The theory of Bateson and Punnet, which accounts for the formation of recessive strains by the “dropping” or “absence” of something, seems an imperfect representation of the truth. A better statement of the matter would seem to be this: a mutation is due to some pathological interference with growth; if it is comparatively slight it does not affect the appearance of the child when inherited from one parent only, and it is then said to be recessive, but if it is severe it makes its effect felt even when it comes in only from one side of the house, and it is then said to be dominant.

Is not there a common type of cause, physiological in its nature, for all these varied

mutations? The only attempt to answer this question has been made by a German zoologist called Tornier, whose work has escaped notice almost as completely as did that of Mendel when he first published his results. It is because we think that Tornier is right in

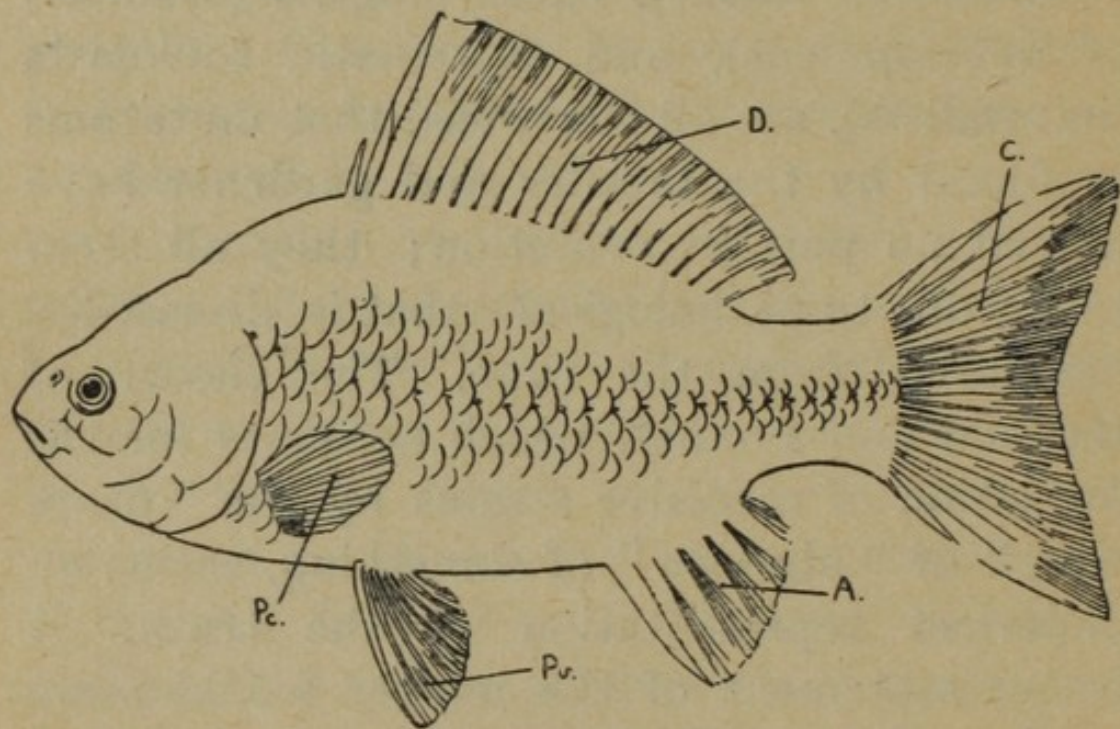


FIG. 29.

*Carassius auratus*, the wild progenitor of the gold-fish, viewed from the side. A., Anal fin. C., caudal fin (*i. e.* tail fin). D., dorsal fin. P.c., pectoral fin. P.v., pelvic fin.

principle, although doubtless his theory will require much modification in detail, that we devote the remainder of this chapter to a short account of his views. Tornier began by studying the various races of gold-fish which are cultivated by purveyors of ornamental fish

both here and in America. All these races have been produced by the domestication of a species of carp, *Carassius auratus*, which is found wild in the rivers of China (Fig. 29). This is a very ordinary fish with well-developed anal, dorsal and caudal (tail) fins, in which, as in many other primitive types of fish, the pelvic fins, which correspond to the legs of land animals, are placed behind the pectoral fins, which correspond to the arms.

All the domesticated races of this fish come from China; for although some have been imported from Japan, the Japanese themselves admit that they have derived all their gold-fish from China. According to Chinese records the gold-fish was "discovered" in 1200, by which is obviously meant that it was then that the characteristic "gold" colour turned up amongst the wild grey *Carassius* that were being kept in tanks. Now the Chinese even to-day keep their gold-fish under the most insanitary conditions; in winter these are kept in earthenware pots ranged in hundreds on shelves in dark, ill-ventilated huts; in summer they are transferred to small, dirty, out-of-door tanks which are overgrown with weed. Under these circumstances much of the spawn that is laid

dies, and amongst the eggs that survive many develop into abnormal forms, and by selection amongst these the various "fancy" races have been produced. These races exhibit the most extraordinary deviations from the normal type of structure; three of them are

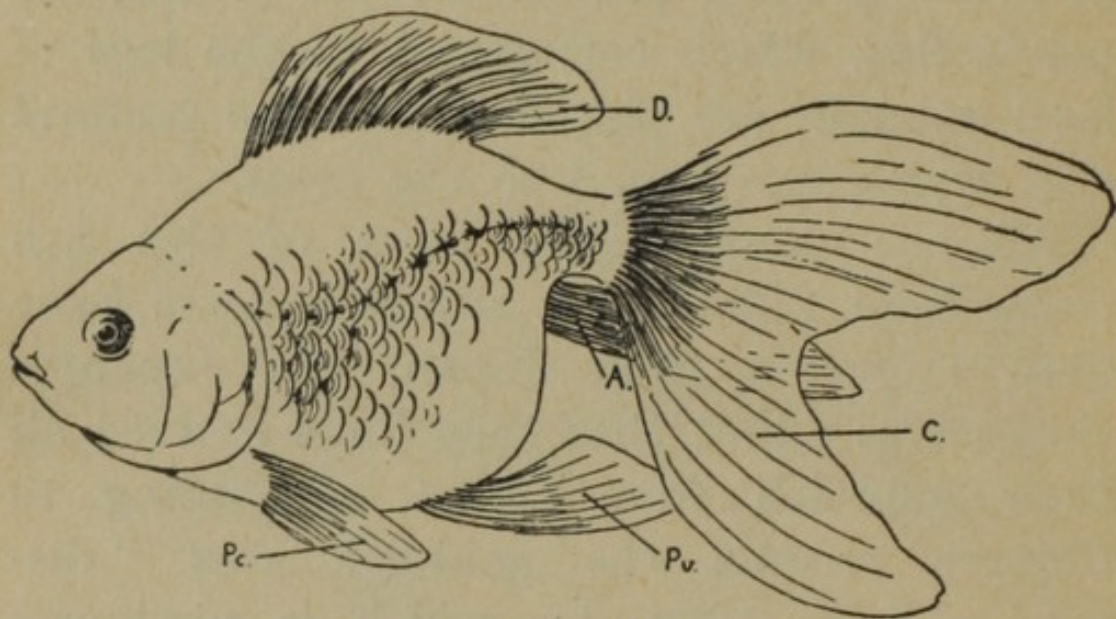


FIG. 30.

The Ryukin or Veil-fish, seen from the side. A., anal fin. C., caudal fin (*i. e.* tail-fin). D., dorsal fin. P.c., pectoral fin. P.v., pelvic fin.

represented in Figs. 30, 31 and 32. In Fig. 30 a breed is represented which is called by the Japanese the Ryukin, and by the Americans the Veil-fish; the body as compared with the wild *Carassius* is very much shorter and stouter; the anal fin is very long, and the caudal fin is enormously lengthened and flexible, so as to be compared to a lady's



veil. The Lion-head, called by the Japanese the Oranda shishigashira, is depicted in Fig. 31. In this fish the head is covered with loose folds of skin which are puffed out like bubbles. These folds impede the action of the gill-cover

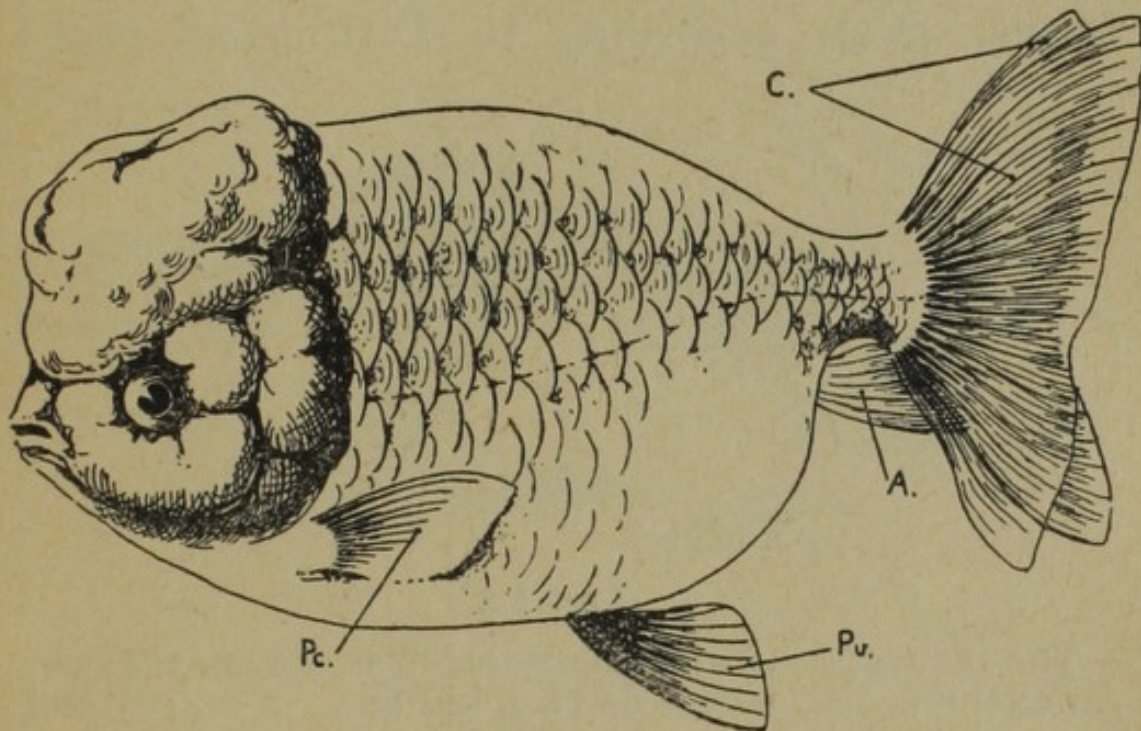


FIG. 31.

The Lion-head or Oranda Shishigashira, seen from the side. A., anal fin. C., caudal fin (*i. e.* tail-fin). P.c., pectoral fin. P.v., pelvic fin.

or operculum and the fish has difficulty in breathing. The body is short and swollen. The dorsal fin is completely absent, but the caudal fin is doubled, there being two tail fins side by side. Finally, in Fig. 32 the extraordinary Telescope-fish or Deme-Ranchu is

shown. In this fish the eyes protrude as hollow tubes from the sides of the head; the caudal fin is doubled and the dorsal fin is absent.

These three breeds are only a selection out of a large number of bizarre abnormal forms. Now according to Tornier all these

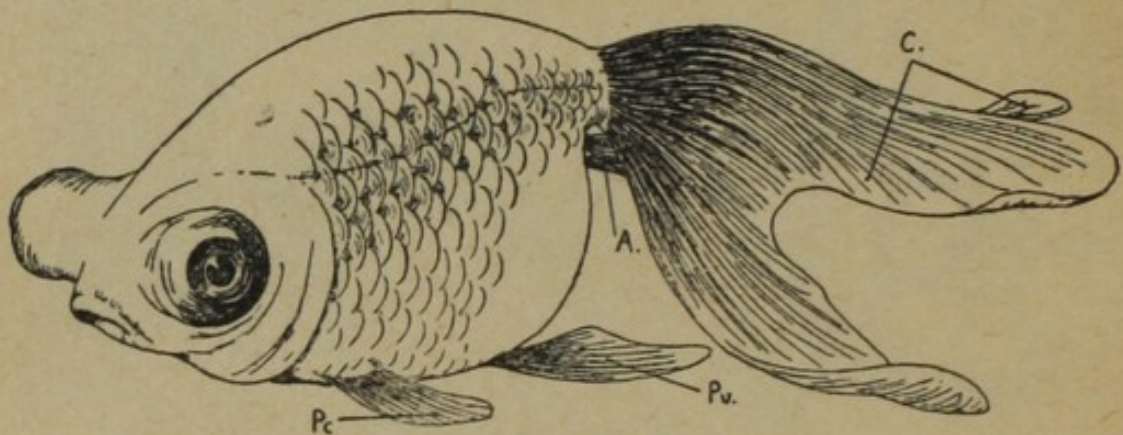


FIG. 32.

The Telescope-fish or Deme-Ranchu, seen from the side. A., anal fin. C., caudal fin (*i. e.* tail-fin). P.c., pectoral fin. P.v., pelvic fin.

mutations are due to the weakening effect on the vigour of the embryo of the abstraction of oxygen from the water during the first few days of its life. He regards each egg as endowed with a certain amount of vital energy (the *élan vital* of Bergson), which shows itself both in vigorous growth and in vigorous movement. One of the first changes which initiates growth is an absorption of water by and

through the protoplasm and a consequent swelling. Davenport and Parker have shown that nearly all the increase in weight which a tadpole acquires during the first period of

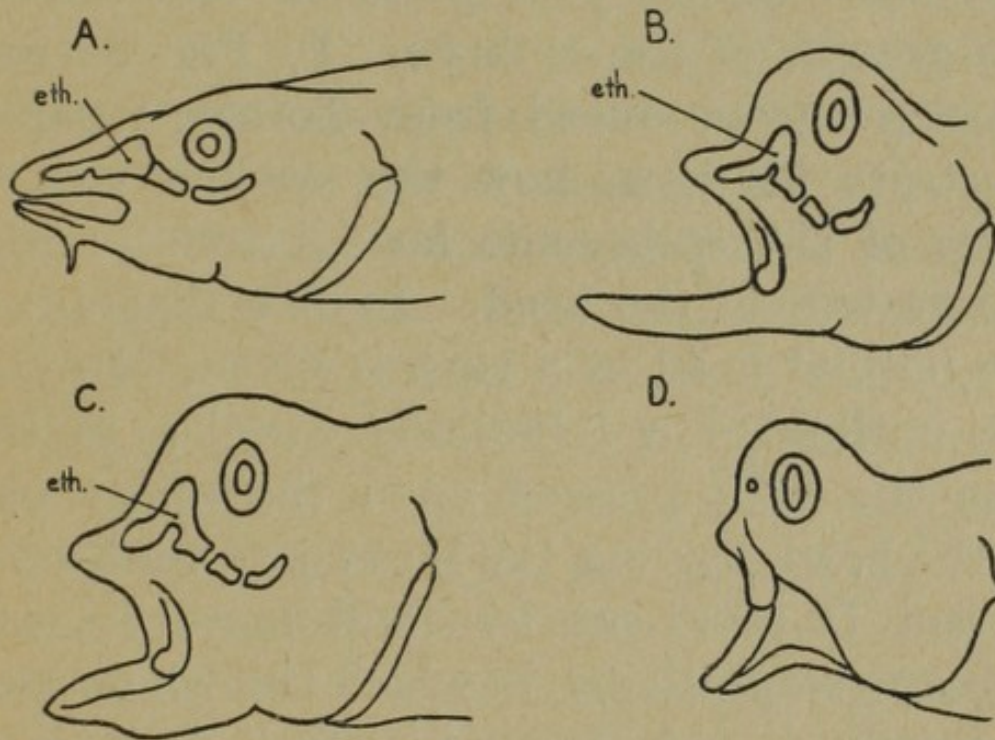


FIG. 33.

A. Head of normal carp B. Head of bull-dog carp. C. Round-head carp. D. Round-head carp. eth., mesethmoid bone; it is this bone which in B, C, and D is buckled up under the longitudinal pressure exercised by the swollen yolk in front of the head.

its growth is accounted for by the imbibed water. But this intake of water is regulated by the activity of the growing cells. When the germ is weakened an excess of water is absorbed. Not only are the more inactive parts of the egg (loosely called the yolk)

unduly swollen, but all the natural cavities of the growing embryo, the mouth-cavity, the gill-cavity and the body-cavity, become distended with water. These swelling cavities and the swelling yolk press on and impede the growth of the embryo. In Fig. 33 four diagrams (reproduced from Tornier's paper) illustrate his idea, how the swollen yolk in front of the embryonic head interferes with the growth of the head. In A a diagram of the normal head of a carp is given. In B is the outline of a "bull-dog carp"; in this case the yolk pressed upon the upper part of the head, leaving the lower jaw unaffected. C and D represent less and more extreme pressure respectively, in which the whole head is involved and "round-heads" have been produced. In the last diagram the enormous distension of the mouth may be noticed. If we apply this principle to the explanation of the three breeds of gold-fish which we have described, we may infer that the longitudinal pressure exerted by the swelling yolk on the backbone has prevented it growing in length and so the whole animal has been shortened. The swollen body-cavity causes a protuberant abdomen. The fins are folds of skin, and when, as in the Veil-fish, the skin area from which

the tail fin arises is stretched, this fin is unduly elongated, for stretching promotes continued growth. At the same time the sluggishness of the weakened embryo causes the tail movements to be feeble. These tail movements in the normal fish tend to stretch the membrane enclosing the embryo and procure more room. In the Veil-fish the elongated tail fin is bent against the unyielding membrane and the drooping veil form produced. On the other hand, when the area of skin from which a fin grows is compressed, the fin remains rudimentary or vanishes altogether, as the dorsal fin does in the Lion-head and in the Telescope-fish. Sometimes the yolk intervenes between paired rudiments which normally coalesce to form a single organ. Thus in the Lion-head and the Telescope-fish swollen yolk separates right and left halves of the developing tail fin, and so two tail fins are produced. In the Lion-head, again, the bones of the head undergo great pressure and are very much shortened, whilst the skin retains its normal length and so great bulbous folds are produced, just like the folds of skin on the face of a bull-pup. Finally, in the Telescope-fish the growing eyeballs absorb a large amount of water and become swollen to preposterous dimensions,

whilst the retina or sensitive layer becomes enormously stretched and thin and is wanting over parts of the internal surface of the eyeball.

Not the least interesting part of Tornier's theory is the way in which he accounts for the change of colour which the gold-fish has undergone from the grey of the wild ancestor to the familiar orange of the cultivated fish. When the "yolk" or food-materials embedded in the protoplasm of the egg imbibe water, they are partly coagulated and rendered indigestible by the growing embryo. This useless material is sooner or later expelled. As a consequence the embryo in its later stages of growth suffers from a deficiency of nourishment and therefore draws on its pigment cells, which act physiologically as reserves of food and so all grades of diminished colour from a normal orange gold-fish to an almost complete albino (silver-fish) are produced.

These abnormalities produced by the weakening of the germ are hereditary. These curious monstrosities selected from the tanks and pots of China have been brought to Europe and to America and used to propagate their like. Moreover, when crossed with other strains they exhibit Mendelian inheritance. Tornier insists that what is transmitted to

posterity is not a "gene" or "factor" for an enormous fin or a doubled tail, a bulbous head or a telescopic eye, but a greater or less degree of **germ-weakening**, and the structural consequences which result from it. He makes the additional hypothesis that this weakening thus hereditarily transmitted may affect different parts of the embryo and that this localization of the weakness is also inherited.

The races of gold-fish when bred yield, as we have seen progeny, like themselves, but this is accompanied by a greater or less amount of reversion towards a more normal type. Thus Veil-fish yield a certain proportion of fish with fairly moderate-sized tail fins. This reversion is interpreted by Tornier as a gradual healing or recovery of the germ, so that as it gains in vigour the abnormal structural consequences of its weakening tend to disappear.

In order to establish his theory Tornier experimented on the eggs of those large newts called axolotls, which ordinarily retain their gills throughout life. When the eggs were fertilized he put them into strong solutions of sugar, which tended to remove the dissolved oxygen from the water. Too long immersion in these solutions would

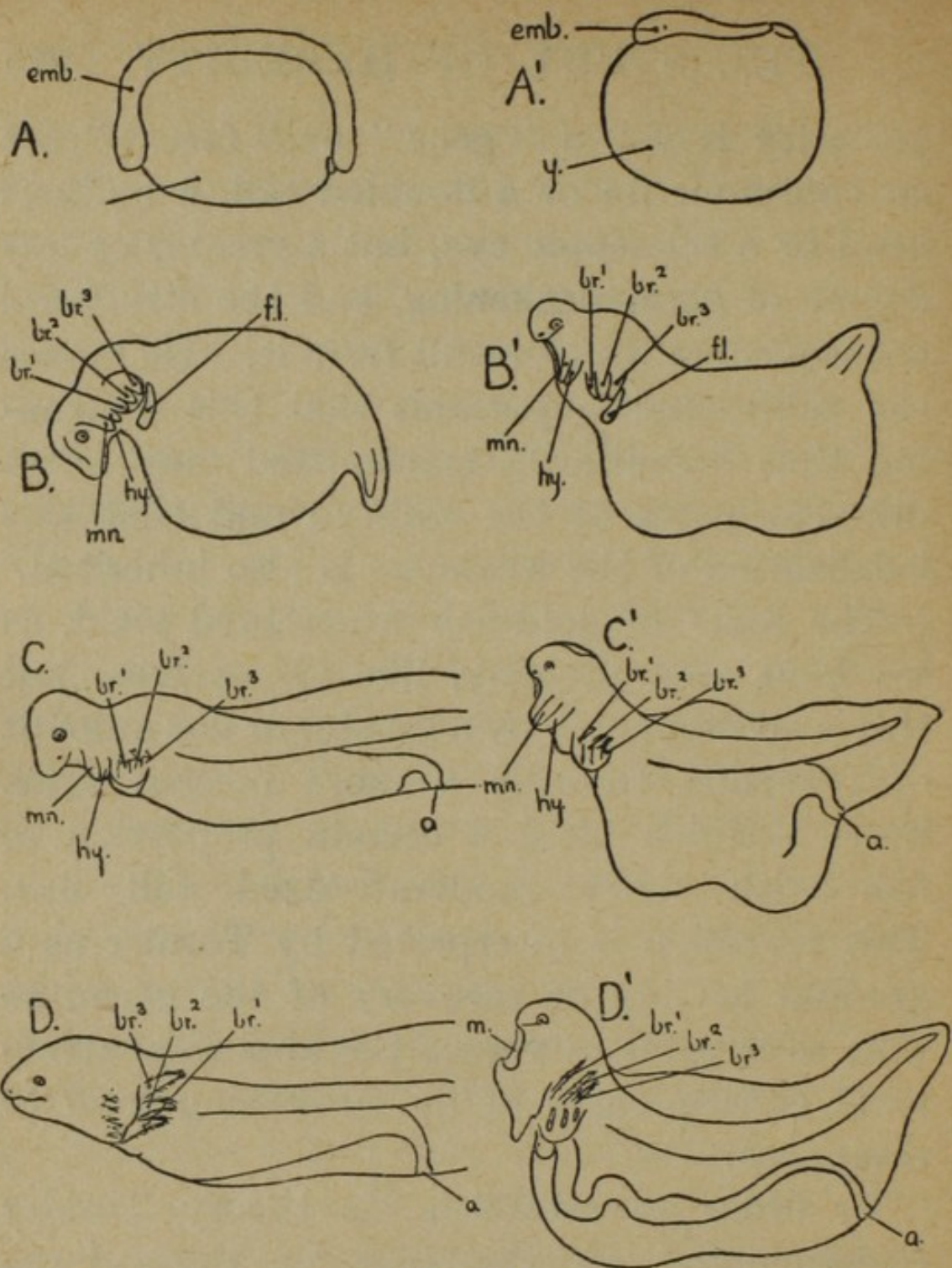


FIG. 34.

Diagrams illustrating the development of a normal and of a weakened axolotl egg. A, B, C, D represent stages in the growth of the normal egg. A', B', C', D' corresponding stages in the growth of the weakened egg. a., anus; br<sup>1</sup>, br<sup>2</sup>, br<sup>3</sup> the rudiments of the three gills; emb., the embryonic rudiment; f.l., rudiment of the fore-limb; hy., the hyoid; m., the mouth; mn., rudiment of the lower jaw; y., the yolk.



have killed the eggs, but when removed in time and brought into clean fresh water they survived and produced weakened embryos. In the axolotl, as in the gold-fish, the embryo grows on the upper surface of a spherical egg, the rest of which is packed with yolk. Fig. 34 consists of a series of diagrams showing side by side the growth of a normal and of a weakened embryo. In the latter we see all the features familiar to us from the study of the races of the gold-fish. The longitudinal axis is shortened and eventually bent, the growth of the tail and of the tail fin is impeded and the mouth cavity is swollen and the mouth gaping (*m*, Fig. 34, D').

Some of the less damaged eggs survived so as to hatch and develop into young axolotls. These had enormously protuberant bellies and were sluggish in their movements. Fig. 35 represents a dissection of one of these abnormal individuals, contrasted with a corresponding dissection of a normal one.

We see at once that the swollen abdomen of the weakened form is produced as a result of the enormous distension of the body-cavity with water. As a consequence nearly all the internal organs, which are contained in this cavity (bladder, lungs, liver, etc.), have been

compressed and impeded in their growth and are mere shadows of their normal selves.

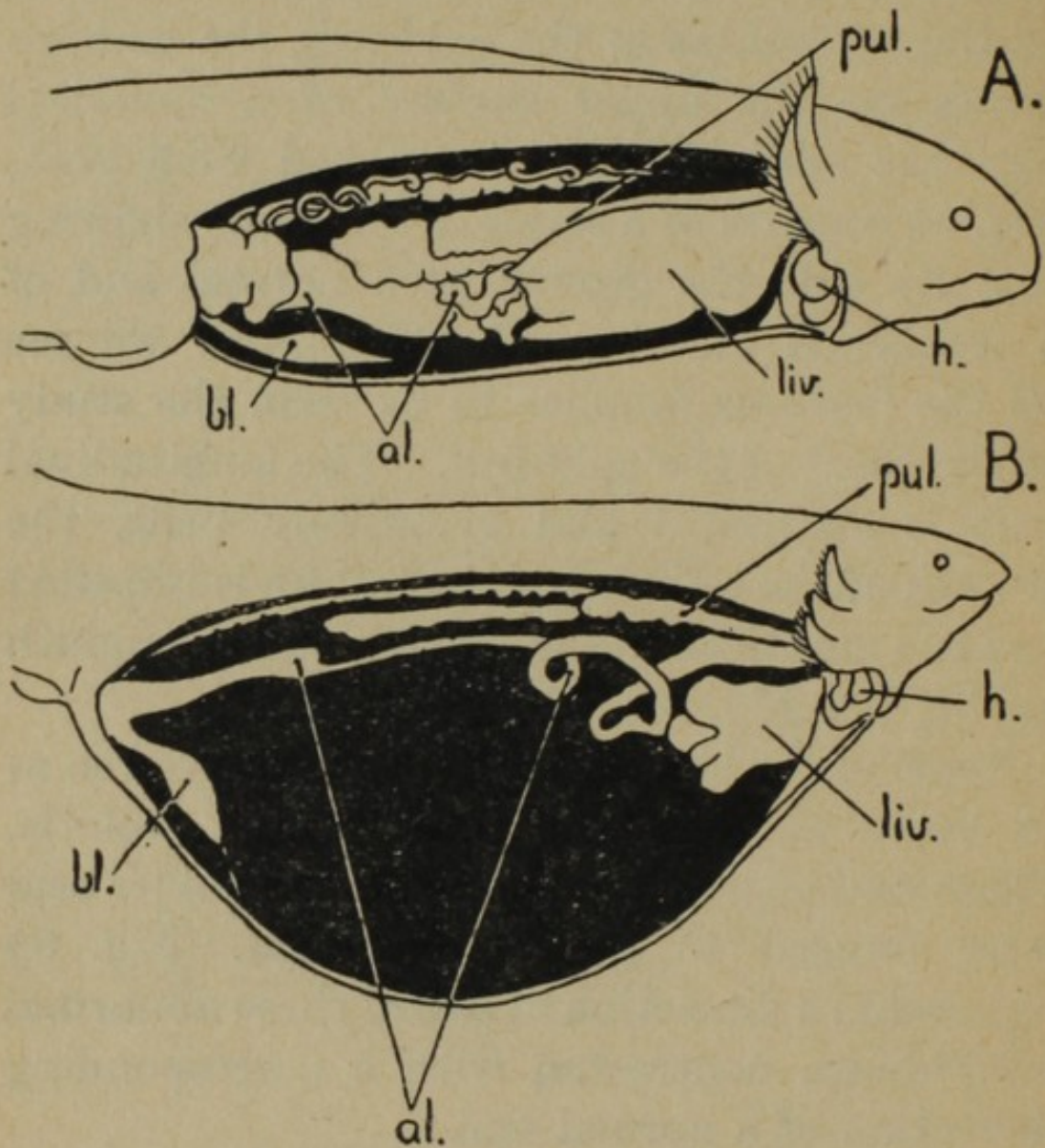


FIG. 35.

A. Side-dissection of a normal axolotl. B. Corresponding dissection of an abnormally weakened axolotl. al., alimentary canal; bl., bladder; h., heart; liv., liver; pul., lung.

Tornier was able to produce varying shades of red and yellow in toad embryos by two

methods, viz. (*a*) by feeding them on innutritious food, (*b*) by stabbing the yolky part of the egg with a fine needle so as to allow part of the yolk to escape. The reduction in pigment was in some cases so great as almost to amount to albinism.

Tornier's theory would have received a complete proof if he had been able to rear these weakened axolotls to maturity, then to have induced them to breed and to have shown that their abnormalities were transmitted to their posterity. But the great extent of time required for this experiment prevented its being carried out; an axolotl requires four or five years to grow to breeding size. Nevertheless, as we have seen, there is a great body of circumstantial evidence in favour of Tornier. The conditions under which the abnormal axolotls were produced were similar to those under which abnormal gold-fish appear, and these last certainly can transmit their abnormalities to their young. A pupil of Tornier, Milewski, has, however, produced further evidence in favour of Tornier's views. He mated together two Veil-fish in which the veil character was but moderately developed. These produced a brood of young, 10 per cent. of which had well-developed

veils, whilst 90 per cent. had moderately developed fins. The same pair were induced to mate again in water which had been rendered poor in oxygen by being filled with water plants and kept in the dark. A second brood was produced; the eggs after two days' sojourn in darkness were transferred to clean, fresh, aerated water. Of this brood 90 per cent. had well-developed veils and only 10 per cent. showed signs of reversion to type! It would, we imagine, puzzle a follower of the "factorial hypothesis" of Morgan to explain why the immersion of an egg in badly aerated water should increase the proportion of the progeny inheriting a "factor" ninefold.

If then the hypothesis of Tornier be accepted—and we think that the cumulative evidence in its favour is irresistible—it throws a brilliant light on the nature and origin of mutations.

As they are all pathological in character, the result of weakened germ energy, they can have played no part in the process of evolution, for in competition with the type they would be inevitably weeded out by natural selection, and to explain evolution we are thus driven back on the inheritance of acquired habits and of the structures that result from these. When we consider how Morgan reared his

flies, confined in glass tubes with bits of rotten banana, we can form a pretty confident guess

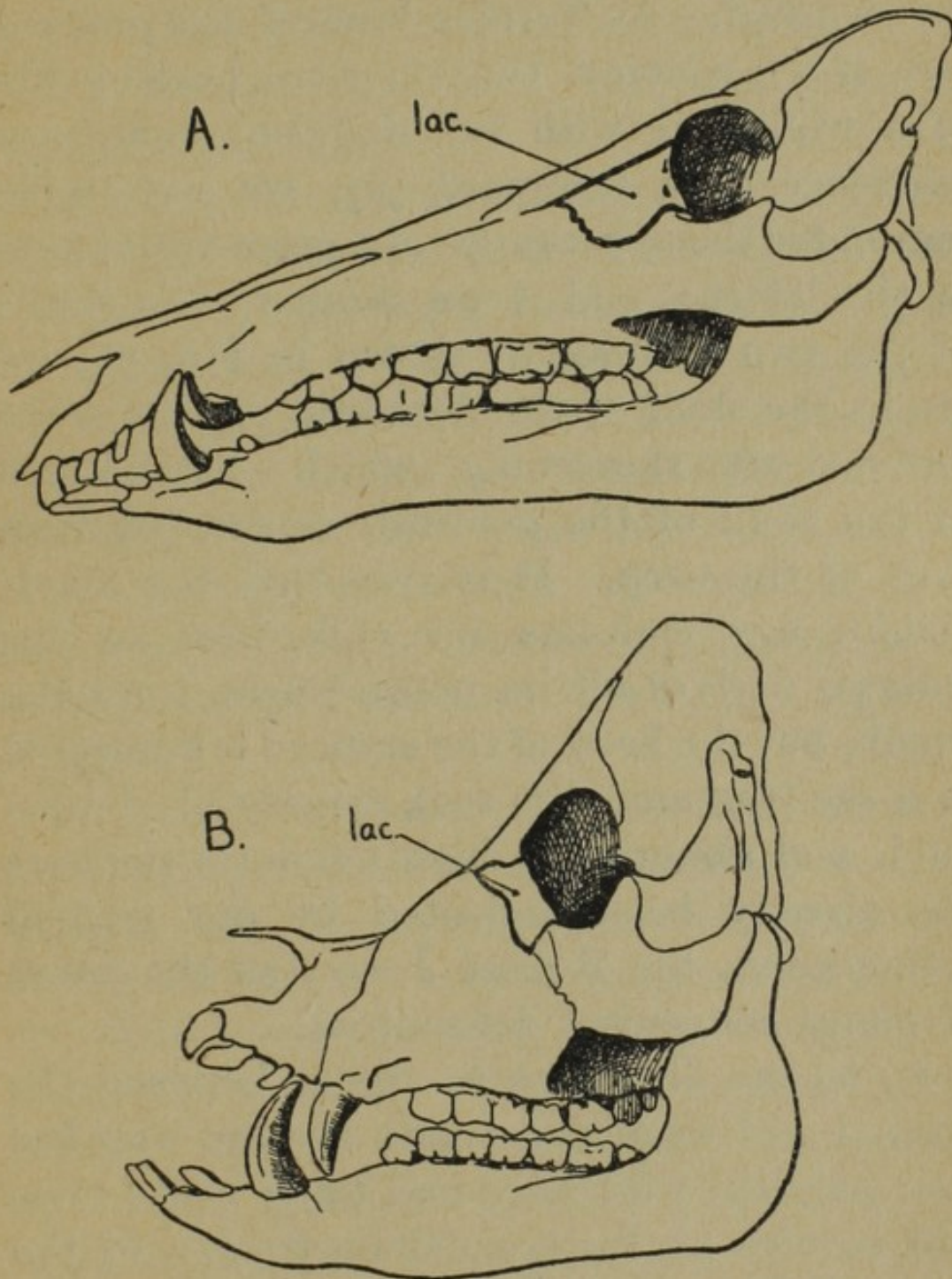


FIG. 36.

A. The skull of the wild boar. B. The skull of a Yorkshire pig. lac., lachrymal bone—note its compression in B.

as to the causes of the production of the wretched pathological mutants with which he has worked. As Tornier himself has pointed out, if we contrast the vigorous, healthy life of a wild boar with the sluggish, insanitary existence of a farmyard pig, we see ample reason for the appearance of a germ-weakening in the latter; and if we compare the skulls of the two animals as shown in Fig. 36, we see in the skull of the domestic pig the same fore-and-aft shortening which we noticed in the skull of the gold-fish contrasted with that of the carp. It is true that the mammalian egg contains no yolk, because the embryo derives all its nourishment from the womb, but the head of the embryo is immersed in a sac (the amniotic sac), tensely filled with fluid, and abnormally high amniotic pressure has already been indicated by our leading orthopædist, Sir Robert Jones, as the cause of many congenital deformities.

As to the difference in vigour between the normal and weakened types, anyone who has ever handled wild mice and tame white mice will require no further demonstration of the truth of Tornier's views in this respect. It was the great mistake of Darwin in that classic book, *The Origin of Species*, that he

imagined that he was discovering in the breeds of domestic animals analogies to the production of the natural races of animals in the field.

It may be asked how Tournier's principle would apply to plants. It is common knowledge that when gardeners want to cultivate a plant they introduce it into rich garden soil, and that after having grown in soil of this kind for some years it "breaks," that is, it begins to "throw" varieties. The life of plants is much slower in its reactions than that of animals, and we may plausibly compare the slow, suffocating effects of over-manured soil on the roots of plants, to the results of scanty oxygen on the developing eggs of animals.

The really curious thing is that when a weakened germ-cell is crossed with a healthy normal one, the hybrid produces germ-cells some of which are normal and some of which are weakened. Further research may possibly show that individual chromosomes behave almost like individual germ-cells, and may undergo weakening in different degrees; that is a question for the future, but the "coupling" which induced Morgan to postulate the existence of separate "factors" for each type of deformity and their arrange-

ment along the chromosome is much more plausibly explained by different degrees of damage exhibited by various organs according to the intensity of the weakening. When this is slight, few organs show the results of it; when it is intense, more organs are affected and then there is marked coupling, but the whole of the phenomena of hybridization will have to be reviewed from the standpoint of Tornier's views when these become widely known and gain general acceptance.

The weakness of the "factorial hypothesis" is its extreme plasticity. When every observed change in the appearance of an animal which can be transmitted to its offspring is ascribed to a new hypothetical factor, and this ascription is regarded as an explanation, then there is no limit to the number of factors which may be postulated, and the explanation, as Goldschmidt has wisely remarked, becomes merely a formal one. Again, the test of Mendelian inheritance has been not dominance in the first filial generation—this under the name of **prepotency** was known long before the days of Mendel—but segregation of the recessive in the second filial generation. If this segregation is complete it is regarded as proof of the Mendelian character



of the mutation; if it is not complete, then a "modifying factor" is assumed which prevents the complete purity of the recessive. In a word, however the facts may turn out, fresh factors are invented to squeeze them into conformity with the factorial hypothesis, and no crucial experiment can be devised, and when a theory reaches this state it has no further interest for the seeker after truth.

## CHAPTER IX

### THE BEARING OF THE LAWS OF HEREDITY ON HUMAN AFFAIRS

WE have now come to the conclusion that the assumption of new habits, that is, the adaptation of the organism to new situations, has been the guiding force which has brought about evolution, and that when animals take on new habits their descendants tend to assume these habits more readily and on slighter stimulation than their parents. To quote Macdougall in the *Outline of Psychology*, "The seal did not take to the water because his legs were flipper-like and his body fish-shaped; he acquired these peculiarities of structure in consequence of his food-seeking instinct having become specialized for the pursuit of fish. The evolution of the animal world may properly be conceived as primarily and essentially the differentiation of instinctive tendencies (that is, habits) from some primordial capacity to strive." In a word,

change of habit preceded change of structure and was the cause of the latter change. The various monstrosities which fill our cattle-pens and adorn our gardens are the result, as we have seen, of germ-weakening with its consequent loosening of the "regulation" whereby in a normal animal one organ is kept in functional relation to another.

Now humanity is divided into a number of natural races, each distinguished from the other by physical and mental characters; they differ indeed as much from one another as do many natural species, and they are only regarded as races because it is assumed that they are all perfectly fertile when crossed with each other, though this assumption—so far at least as the most widely divergent races are concerned—has not been adequately tested.

These races have acquired their characters as reactions to their different environments, and their development out of a common stock of primitive men has occupied a period so long that the entire historical period appears as a brief episode in comparison with it. In the Northern hemisphere at least two glacial ages have passed since the evolution of these races began. It follows that the marks which distinguish one race from another are the

outward and visible signs of differences in habits long established and deeply engrained. Let us, for instance, contrast the Negroes and the Caribs or South American Indians. Both these races inhabit the tropics—the first live in the Equatorial parts of Africa and Malaya, the second in the Amazonian region of South America. The Negro is a thoroughly tropical animal; his dark skin shields him from the deleterious effects of the sun's rays and his wide nostrils permit of a large surge of air into and out of his lungs, and this surge plays an important part in ventilation and the getting rid of superfluous heat. He thrives in heat and in fact luxuriates in it, and competes eagerly for positions in the engine-room of the steamers on the equatorial lakes of Africa. The Carib, although he inhabits the tropical forests of the Amazon, dislikes and shrinks from the heat; according to Bate he perspires profusely in the hottest time of the year and seeks to shelter himself in the deepest recesses of the forest. This is because the Carib is an offshoot of the great yellow Mongolian race which is primarily adapted to life on the cold Northern Steppes of Asia, and has only in the last 3000 years invaded South America, and these people are not yet

thoroughly adapted to their new environment.

The population of the British islands is composed of a mixture of three races: (*a*) the Nordic, tall, long-headed, fair-skinned and blue-eyed, who were evolved round the shores of the North Sea; (*b*) the Alpine or Central Europeans, short, thick-necked, stocky people with broad heads, brown eyes, straight hair and full beards who originated in the steppes of Turkestan and made their way westward over the European plain; and (*c*) the Iberian or Mediterranean race, short, long-headed, rather swarthy people with dark wavy hair and dark eyes; this race, as its name implies, was the aboriginal population inhabiting the shores of the Mediterranean Sea. The blood of the three races is hopelessly intermixed, but the Nordic is found nearly pure in the north-east of Scotland, whilst the Mediterranean exists almost unmixed in the south of Wales and the south-west of Ireland.

Each of these races has its inborn psychic qualities. The Nordic race, who were originally fishermen and mariners, learnt in their struggle with the bleak climate of their old home the virtues of indomitable courage, bold adventure and justice between man and man.

Is not the double meaning of the word "fair" a tribute to their virtue? This race, as Normans and Danes, established and settled the kingdom of England and by their oversea adventures built up the British Empire. They form the bulk of our aristocracy, and are the backbone of the middle-class, the sons of whom still show the racial enterprise in their willingness to seek their fortunes overseas. The Alpine race were the first workers in bronze and they still form a large portion of our artisan class. There is little doubt that the traditional superiority of British workmanship is due to the inherited skill of this type of people. The progress of the Alpine race across England can be traced by their graves, which contain broad skulls and bronze tools. The Mediterranean race form the aboriginal stratum in our population. They are characterized by a mercurial temperament, prone to quarrel and quick to take revenge, with musical and poetical gifts, but without the courage and organizing power of the Nordic race or the plodding industry of the Alpine. Their natural organization, as Irish legends show, is a division into warring and treacherous clans. When they drift into the towns they tend to form the "submerged

population; many thoughtful American citizens view the continuance of this process with grave apprehension.

But in addition to racial differences we have to consider the effects of germ-weakening and the consequent production of "mutations." This germ-weakening seems to arise most readily in large towns under conditions which favour overcrowding and unhealthy conditions during conception. Several so-called "sex-linked" mutations have already been detected in the human race; amongst them are colour-blindness, night-blindness and hæmophilia (inability of the blood to form a clot when it issues from a wound, and hence the tendency of the wounded person to bleed to death); these, however, are not widespread and it cannot be maintained that they do any great amount of social damage; but there is a mutation known as "**mental defect**" which is of colossal social importance. This mutation consists in the inability of the mind to expand and develop its powers as the body grows. It exists in a great variety of grades of intensity, and on being crossed with the type, behaves as a recessive. The various grades are distinguished from one another by the age at which a normal child acquires an

intelligence equal to that of the defective; thus we have defectives of "mental ages" of one, two, three or more years. At fifteen years the normal child develops its full mental powers, though naturally not its complete mental equipment. Now the point to note is that defectives of the mental ages of one, two and three years are unable to dress and feed themselves and must be cared for as babies—these are called **idiots**; those of four, five, six and seven years can be taught to dress and feed themselves and to perform simple tasks under direction—these must be treated as school children, and are termed **imbeciles**. Both these classes are utterly unable to maintain themselves by their own endeavours in competition with their fellows, and so they must be segregated in institutions and maintained at the public expense—but they are prevented from breeding.

Defectives of the mental ages eight, nine, ten, are termed **morons** by American authors, these are just able to support themselves in the lowest paid and least skilled occupations, and so they form a large element in our slum population. For some reason which is still obscure, they are exceedingly prolific, and as they breed recklessly their



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