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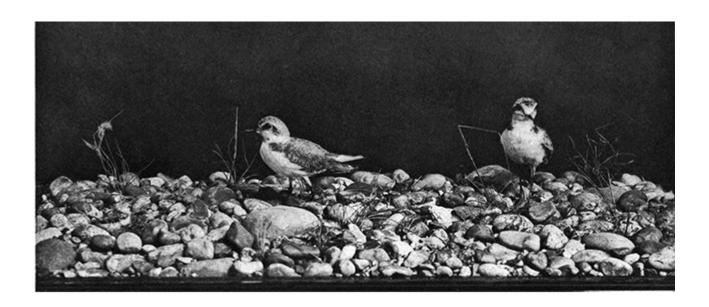
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Kentish Plover with Eggs and Young. From the Exhibit in the British Natural History Museum.

ANIMAL LIFE AND INTELLIGENCE.

BY

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1891.

TO MY FATHER.

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PREFACE.

There are many books in our language which deal with Animal Intelligence in an anecdotal and conventionally popular manner. There are a few, notably those by Mr. Romanes and Mr. Mivart, which bring adequate knowledge and training to bear on a subject of unusual difficulty. In the following pages I have endeavoured to contribute something (imperfect, as I know full well, but the result of several years' study and thought) to our deeper knowledge of those mental processes which we may fairly infer from the activities of dumb animals.

The consideration of Animal Intelligence, from the scientific and philosophical standpoint, has been my primary aim. But so inextricably intertwined is the subject of Intelligence with the subject of Life, the subject of organic evolution with the subject of mental evolution, so closely are questions of Heredity and Natural Selection interwoven with questions of Habit and Instinct, that I have devoted the first part of this volume to a consideration of Organic Evolution. The great importance and value of Professor Weismann's recent contributions to biological science, and their direct bearing on questions of Instinct, rendered such treatment of my subject, not only advisable, but necessary. Moreover, it seemed to me, and to those whom I consulted in the matter, that a general work on Animal Life and Intelligence, if adequately knit into a connected whole, and based on sound principles of science and of philosophy, would not be unwelcomed by biological students, and by that large and increasing class of readers who, though not professed students, follow with eager interest the development of the doctrine of Evolution.

Incidentally, but only incidentally, matters concerning man, as compared with the dumb animals, have been introduced. It is contended that in man alone, and in no dumb animal, is the rational faculty, as defined in these pages, developed; and it is contended that among human-folk that process of natural selection, which is so potent a factor in the lower reaches of organic life, sinks into comparative insignificance. Man is a creature of ideas and ideals. For him the moral factor becomes one of the very highest importance. He conceives an ideal self which he strives to realize; he conceives an ideal humanity towards which he would raise his fellow-man. He becomes a conscious participator in the

But while we must not be blind to the effects of new and higher factors of progress thus introduced as we rise in the scale of phenomena, we must at the same time remember that biological laws still hold true, though moral considerations and the law of duty may profoundly modify them. The eagle soars aloft apparently in defiance of gravitation; but the law of gravitation still holds good; and no treatment of the mechanism of flight which neglected it would be satisfactory. Moral restraint, a higher standard of comfort, and a perception of the folly and misery of early and improvident marriage may tend to check the rate of growth of population: but the "law of increase" still holds good, as a law of the factors of phenomena; and Malthus did good service to the cause of science when he insisted on its importance. We may guide or lighten the incidence of natural selection through competition; we may in our pity provide an asylum for the unfortunates who are suffering elimination; but we cannot alter a law

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evolution of man, in the progress of humanity.

which, as that of one of the factors of organic phenomena, still obtains, notwithstanding the introduction of other factors.

However profoundly the laws of phenomena may be modified by such introduction of new and higher factors, the older and lower factors are still at work beneath the surface. And he who would adequately grasp the social problems of our time should bring to them a mind prepared by a study of the laws of organic life: for human beings, rational and moral though they may be, are still organisms; and man can in no wise alter or annul those deep-lying facts which nature has throughout the ages been weaving into the tissue of life.

Some parts of this work are necessarily more technical, and therefore more abstruse, than others. This is especially the case with Chapters III., V., and VI.; while, for those unacquainted with philosophical thought, perhaps the last chapter may present difficulties of a different order. With these exceptions, the book will not be beyond the ready comprehension of the general reader of average intelligence.

I have to thank many kind friends for incidental help. Thanks are also due to Professor Flower, who courteously gave permission that some of the exhibits in our great national collection in Cromwell Road might be photographed and reproduced; and to Messrs. Longmans for the use of two or three illustrations from my text-book of "Animal Biology."

C. LLOYD MORGAN.

University College, Bristol, *October*, 1890.

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ANIMAL LIFE AND INTELLIGENCE.

CHAPTER I. THE NATURE OF ANIMAL LIFE.

I once asked a class of school-boys to write down for me in a few words what they considered the chief characteristics of animals. Here are some of the answers—

- 1. Animals move about, eat, and grow.
- 2. Animals eat, grow, breathe, feel (at least, most of them do), and sleep.
- 3. Take a cat, for example. It begins as a kitten; it eats, drinks, plays about, and grows up into a cat, which does much the same, only it is more lazy, and stops growing. At last it grows old and dies. But it may have kittens first.
- 4. An animal has a head and tail, four legs, and a body. It is a living creature, and not a vegetable.
- 5. Animals are living creatures, made of flesh and blood.

Combining these statements, we have the following characteristics of animals:—

- 1. Each has a proper and definite form, at present described as "a head and tail, four legs, and a body."
- 2. They breathe.
- 3. They eat and drink.
- 4. They grow.
- 5. They also "grow up." The kitten grows up into a cat, which is somewhat different from the kitten.
- 6. They move about and sleep.
- 7. They feel—"at least some of them do."
- 8. They are made of "flesh and blood."
- 9. They grow old and die.
- 10. They reproduce their kind. The cat may have kittens.
- 11. They are living organisms, but "not vegetables."

Now, let us look carefully at these characteristics, all of which were contained in the five answers, and were probably familiar in some such form as this to all the boys, and see if we cannot make them more general and more accurate.

1. An animal has a definite form. My school-boy friend described it as a head and tail, four legs, and a body. But it is clear that this description applies only to a very limited number of animals. It will not apply to the butterfly, with its great wings and six legs; nor to the lobster, with its eight legs and large pincer-claws; to the limbless snake and worm, the finned fish, the thousand-legs, the oyster or the snail, the star-fish or the sea-anemone. The animals to which my young friend's description applies form, indeed, but a numerically insignificant proportion of the multitudes which throng the waters and

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the air, and not by any means a large proportion of those that walk upon the surface of the earth. The description applies only to the backboned vertebrates, and not to nearly all of them.

It is impossible to summarize in a sentence the form-characteristics of animals. The diversities of form are endless. Perhaps the distinguishing feature is the prevalence of curved and rounded contours, which are in striking contrast to the definite crystalline forms of the inorganic kingdom, characterized as these are by plane surfaces and solid angles. We may say, however, that all but the very lowliest animals have each and all a proper and characteristic form of their own, which they have inherited from their immediate ancestors, and which they hand on to their descendants. But this form does not remain constant throughout life. Sometimes the change is slight; in many cases, however, the form alters very markedly during the successive stages of the life of the individual, as is seen in the frog, which begins life as a tadpole, and perhaps even more conspicuously in the butterfly, which passes through a caterpillar and a chrysalis stage. Still, these changes are always the same for the same kind of animal. So that we may say, each animal has a definite form and shape or series of shapes.

2. Animals breathe. The essential thing here is that oxygen is taken in by the organism, and carbonic acid gas is produced by the organism. No animal can carry on its life-processes unless certain chemical changes take place in the substance of which it is composed. And for these chemical changes oxygen is essential. The products of these changes, the most familiar of which are carbonic acid gas and urea, must be got rid of by the process of excretion. Respiration and excretion are therefore essential and characteristic life-processes of all animals.

In us, and in all air-breathing vertebrates, there are special organs set apart for respiration and excretion of carbonic acid gas. These are the lungs. A great number of insects also breathe air, but in a different way. They have no lungs, but they respire by means of a number of apertures in their sides, and these open into a system of delicate branching tubes which ramify throughout the body. Many organisms, however, such as fish and lobsters and molluscs, breathe the air dissolved in the water in which they live. The special organs developed for this purpose are the gills. They are freely exposed to the water from which they abstract the air dissolved therein. When the air dissolved in the water is used up, they sicken and die. There can be nothing more cruel than to keep aquatic animals in a tank or aquarium in which there is no means of supplying fresh oxygen, either by the action of green vegetation, or by a jet of water carrying down air-bubbles, or in some other way. The skin, etc., of the back has been removed, And then there are a number of animals which have no special and the crop (cr.) and alimentary canal (al.c.) organs set apart for breathing. In them respiration is carried on by the general surface of the body. The common earthworm is one of these; and most microscopic organisms are in the same condition. Still, even if there be no special organs for breathing, the process of respiration must be

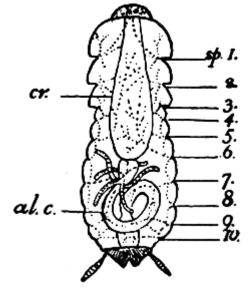


Fig. 1.—Diagram of spiracles and air-tubes (tracheæ) of an insect (cockroach).

displayed. The air-tubes are represented by dotted lines. The ten spiracles are numbered to the right of the figure.

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carried on by all animals.

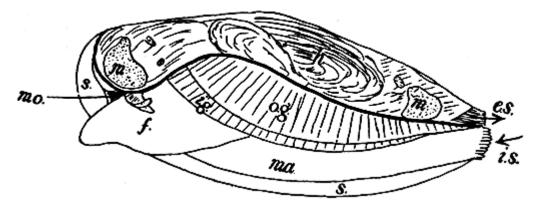


Fig. 2.—Gills of mussel.

o.g., outer gill; i.g., inner gill; mo., mouth; m., muscles for closing shell; ma., mantle; s., shell; f., foot; h., position of heart; e.s., exhalent siphon, whence the water passes out from the gill-chamber; i.s., inhalent siphon, where the water enters. The left valve of the shell has been removed, and the mantle cut away along the dark line.

- 3. They eat and drink. The living substance of an animal's body is consumed during the progress of those chemical changes which are consequent upon respiration; and this substance must, therefore, be made good by taking in the materials out of which fresh life-stuff can be formed. This process is called, in popular language, feeding. But the food taken in is not identical with the life-stuff formed. It has to undergo a number of chemical changes before it can be built into the substance of the organism. In us, and in all the higher animals, there is a complex system of organs set aside for the preparation, digestion, and absorption of the food. But there are certain lowly organisms which can take in food at any portion of their surface, and digest it in any part of their substance. One of these is the amœba, a minute speck of jelly-like life-stuff, which lives in water, and tucks in a bit of food-material just as it comes. And there are certain degenerate organisms which have taken to a parasitic life, and live within the bodies of other animals. Many of these can absorb the material prepared by their host through the general surface of their simple bodies. But here, again, though there may be no special organs set apart for the preparation, absorption, and digestion of food, the process of feeding is essential to the life of all animals. Stop that process for a sufficient length of time, and they inevitably die.
- 4. They grow. Food, as we have just seen, has to be taken in, digested, and absorbed, in order that the loss of substance due to the chemical changes consequent on respiration may be made good. But where the digestion and absorption are in excess of that requisite for this purpose, we have the phenomenon of growth.

What are the characteristics of this growth? We cannot, perhaps, describe it better than by saying (1) that it is organic, that is to say, a growth of the various organs of the animal in due proportion; (2) that it takes place, not merely by the addition of new material (for a crystal grows by the addition of new material, layer upon layer), but by the incorporation of that new material into the very substance of the old; and (3) that the material incorporated during growth differs from the material absorbed from without, which has undergone a preparatory chemical transformation within the animal during digestion. The growth of an animal is thus dependent upon the continued absorption of new material from without, and its transformation into the substance of the body.

The animal is, in fact, a centre of continual waste and repair, of nicely balanced constructive and destructive processes. These are the invariable concomitants of life. Only so long as the constructive processes outbalance the destructive processes does growth continue. During the greater part of a

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healthy man's life, for example, the two processes, waste and repair, are in equilibrium. In old age, waste slowly but surely gains the mastery; and at death the balanced process ceases, decomposition sets in, and the elements of the body are scattered to the winds or returned to mother earth.

There are generally limits of growth which are not exceeded by any individuals of each particular kind of animal. But these limits are somewhat variable among the individuals of each kind. There are big men and little men, cart-horses and ponies, bloodhounds and lap-dogs. Wild animals, however, when fully grown, do not vary so much in size. The period of growth is also variable. Many of the lower backboned animals probably grow during the whole of life, but those which suckle their young generally cease growing after a fraction (in us from one-fourth to one-fifth) of the allotted span of life is past.

5. But animals not only grow—they also "grow up." The kitten grows up into a cat, which is somewhat different from the kitten. We speak of this growing up of an animal as its development. The proportion of the various parts and organs progressively alter. The relative lengths of the arms and legs, and the relative size of the head, are not the same in the infant as in the man or woman. Or, take a more marked case. In early spring there is plenty of frog-spawn in the ponds. A number of blackish specks of the size of mustard seeds are embedded in a jelly-like mass. They are frogs' eggs. They seem unorganized. But watch them, and the organization will gradually appear. The egg will be hatched, and give rise to a little fish-like organism. This will by degrees grow into a tadpole, with a powerful swimming tail and rounded head and body, but with no obvious neck between them. Legs will appear. The tail will shrink in size and be gradually drawn into the body. The tadpole will have developed into a minute frog.

There are many of the lower animals which go through a not less wonderful, if not more wonderful, metamorphosis. The butterfly or the silkworm moth, beginning life as a caterpillar and changing into a chrysalis, from which the perfect insect emerges, is a familiar instance. And hosts of the marine invertebrates have larval forms which have but little resemblance to their adult parents.

Such a series of changes as is undergone by the frog is called *metamorphosis*, which essentially consists in the temporary development of certain provisional embryonic organs (such as gills and a powerful swimming tail) and the appearance of adult organs (such as lungs and legs) to take their place. In metamorphosis these changes occur during the free life of the organism. But beneath the eggshell of birds and within the womb of mammals scarcely less wonderful changes are slowly but surely effected, though they are hidden from our view. There is no metamorphosis during the free life of the organism, but there is a prenatal *transformation*. The little embryo of a bird or mammal has no gills like the tadpole (though it has for a while gill-slits, pointing unmistakably to its fishy ancestry), but it has a temporary provisional breathing organ, called the allantois, pending the full development and functional use of its lungs.

All the higher animals, in fact—the dog, the chick, the serpent, the frog, the fish, the lobster, the butterfly, the worm, the star-fish, the mollusc, it matters not which we select—take their origin from an apparently unorganized egg. They all, therefore, pass during their growth from a comparatively simple condition to a comparatively complex condition by a process of change which is called development.

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But there are certain lowly forms, consisting throughout life of little more than specks of jelly-like life-stuff, in which such development, if it occurs at all, is not conspicuous.

6. They move about and sleep. This is true of our familiar domestic pets. The dog and the cat, after periods of restless activity, curl themselves up and sleep. The canary that has all day been hopping about its cage, or perhaps been allowed the freedom of the dining-room, tucks its head under its wing and goes to sleep. The cattle in the meadows, the sheep in the pastures, the horses in the stables, the birds in the groves, all show alternating periods of activity and repose. But is this true of all animals? Do all animals "move about and sleep"? The sedentary oyster does not move about from place to place; the barnacle and the coral polyp are fixed for the greater part of life; and whether these animals sleep or not it is very difficult to say. We must make our statement more comprehensive and more accurate.

If we throw it into the following form, it will be more satisfactory: Animals exhibit certain activities; and periods of activity alternate with periods of repose.

I shall have more to say hereafter concerning the activities of animals. Here I shall only say a few words concerning the alternating periods of repose. No organism can continue in ceaseless activity unbroken by any intervening periods of rest. Nor can the organs within an organism, however continuous their activity may appear, work on indefinitely and unrestfully. The heart is apparently restless in its activity. But in every five minutes of the continued action of the great force-pump (ventricle) of the heart, two only are occupied in the efforts of contraction and work, while three are devoted to relaxation and repose. What we call sleep may be regarded as the repose of the higher braincentres after the activity of the day's work—a repose in which the voluntary muscles share.

The necessity for rest and repose will be readily understood. We have seen that the organism is a centre of waste and repair, of nicely balanced destructive and reconstructive processes. Now, activity is accompanied by waste and destruction. But it is clear that these processes, by which the substance of the body and its organs is used up, cannot go on for an indefinite period. There must intervene periods of reconstruction and recuperation. Hence the necessity of rest and repose alternating with the periods of more or less prolonged activity.

7. They feel—"at least some of them do." The qualification was a wise one, for in truth, as we shall hereafter see, we know very little about the feelings of the lower organisms. The one animal of whose feelings I know anything definite and at first hand, is myself. Of course, I believe in the feelings of others; but when we come to very lowly organisms, we really do not know whether they have feelings or not, or, if they do, to what extent they feel.

Shall we leave this altogether out of account? Or can we throw it into some form which is more general and less hypothetical? This, at any rate, we know—that all animals, even the lowest, are sensitive to touches, sights, or sounds. It is a matter of common observation that their activities are generally set agoing under the influence of such suggestions from without. Perhaps it will be objected that there is no difference between feeling and being sensitive. But I am using the word "sensitive" in a general sense—in that sense in which the photographer uses it when he speaks of a sensitive plate, or the chemist when he speaks of a sensitive test. When I say that animals are sensitive, I mean that they answer to touches, or sounds, or other impressions (what are called stimuli) coming from without. They may feel or not; many of them undoubtedly do. But that is another aspect of the sensitiveness. Using

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the term, then, with this meaning, we may say, without qualification, that all animals are more or less sensitive to external influences.

8. They are made of "flesh and blood." Here we have allusion to the materials of which the animal body is composed. It is obviously a loose and unsatisfactory statement as it stands. An American is said to have described the difference between vertebrates and insects by saying that the former are composed of flesh and bone, and the latter of skin and squash. But even if we amend the statement that animals are made of "flesh and blood" by the addition of the words, "or of skin and squash," we shall hardly have a sufficiently satisfactory statement of the composition of the animal body.

The essential constituent of animal (as indeed also of vegetable) tissues is protoplasm. This is a nearly colourless, jelly-like substance, composed of carbon, hydrogen, nitrogen, and oxygen, with some sulphur and phosphorus, and often, if not always, some iron; and it is permeated by water. Protoplasm, together with certain substances, such as bony and horny matter, which it has the power of producing, constitutes the entire structure of simple organisms, and is built up into the organs of the bodies of higher animals. Moreover, in these organs it is not arranged as a continuous mass of substance, but is distributed in minute separate fragments, or corpuscles, only visible under the microscope, called cells. These cells are of very various shapes—spherical, discoidal, polyhedral, columnar, cubical, flattened, spindle-shaped, elongated, and stellate.

A great deal of attention has been devoted of late years to the minute structure of cells, and the great improvements in microscopical powers and appliances have enabled investigators to ascertain a number of exceedingly interesting and important facts. The external surface of a cell is sometimes, but not always in the case of animals, bounded by a film or membrane. Within this membrane the substance of the cell is made up of a network of very delicate fibres (the *plasmogen*), enclosing a more fluid material (the *plasm*); and this network seems to be the essential living substance. In the midst of the cell is a small round or oval body, called the nucleus, which is surrounded by a very delicate membrane. In this nucleus there is also a network of delicate plasmogen fibres, enclosing a more fluid plasm material. At certain times the network takes the form of a coiled filament or set of filaments, and these arrange themselves in the form of rosettes and stars. In the meshwork of the net or in the coils of the filament there may be one or more small bodies (nucleoli), which probably have some special significance in the life of the cell. These cells multiply or give birth to new cells by dividing into two, and this process is often accompanied by special changes in the nucleus (which also divides) and by the arrangement of its network or filaments into the rosettes and stars before alluded to.

Instead, therefore, of the somewhat vague statement that animals are made of flesh and blood, we may now say that the living substance of which animals are composed is a complex material called protoplasm; that organisms are formed either of single cells or of a number of related cells, together with certain life-products of these cells; and that each cell, small as it is, has a definite and wonderful minute structure revealed by the microscope.

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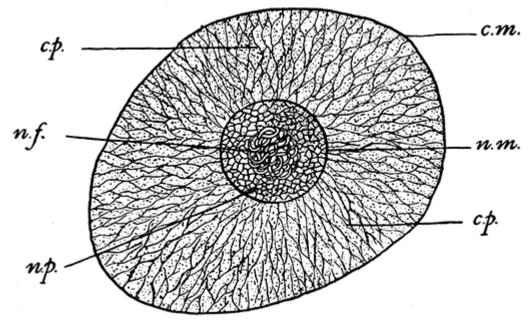


Fig. 3.—A cell, greatly magnified.

c.m., cell-membrane; c.p., cell-protoplasm; n.m., nuclear membrane; n.p., nuclear protoplasm; n.f., coiled nuclear filament.

9. Animals grow old and die. This is a familiar observation. Apart from the fact that they are often killed by accident, by the teeth or claws of an enemy, or by disease, animals, like human beings, in course of time become less active and less vigorous; the vital forces gradually fail, and eventually the flame of life, which has for some time been burning dimmer and dimmer, flickers out and dies. But is this true of all animals? Can we say that death—as distinct from being killed—is the natural heritage of every creature that lives?

One of the simplest living creatures is the amœba. It consists of a speck of nucleated protoplasm, no larger than a small pin's head. Simple as it is, all the essential life-processes are duly performed. It is a centre of waste and repair; it is sensitive and responsive to a stimulus; respiration and nutrition are effected in a simple and primitive fashion. It is, moreover, reproductive. First the nucleus and then the protoplasm of the cell divide, and in place of one amœba there are two. And these two are, so far as we can tell, exactly alike. There is no saying which is mother and which is daughter; and, so far as we can see at present, there is no reason why either should die. It is conceivable that amæbæ never die, though they may be killed in immense numbers. Hence it has been plausibly maintained that the primitive living cell is by nature deathless; that death is not the heritage of all living things; that death is indeed an acquisition, painful indeed to the individual, but, since it leaves the stage free for the younger and more vigorous individuals, conducive to the general good.

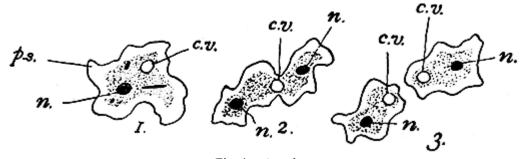


Fig. 4.—Amœba.

1. An amœba, showing the inner and outer substance (endosarc and ectosarc); a pseudopodium, p.s.; the nucleus, n.; and the contractile vesicle, c.v. 2. An amæba dividing into two. 3. The division just effected.

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In face of this opinion, therefore, we cannot say that all animals grow old and die; but we may still say that all animals, with the possible exception of some of the lowest and simplest, exhibit, after a longer or a shorter time, a waning of the vital energies which sooner or later ends in death.

10. Animals reproduce their kind. We have just seen the nature of reproduction in the simple unicellular amæba. The reproduction of the constituent cells in the complex multicellular organism, during its natural growth or to make good the inevitable loss consequent on the wear and tear of life, is of the same character.

When we come to the higher organisms, reproduction is effected by the separation of special cells called egg-cells, or ova, from a special organ called the ovary; and these, in a great number of cases, will not develop into a new organism unless they be fertilized by the union with them in each case of another cell—the sperm-cell—produced by a different individual. The separate parents are called male and female, and reproduction of this kind is said to be sexual.

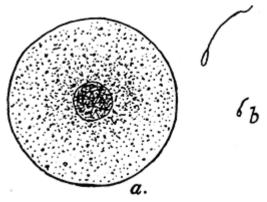


Fig. 5.—Egg-cell and sperm-cell. *a*, ovum or egg; *b*, spermatozoon or sperm.

The wonderful thing about this process is the power of the fertilized ovum, produced by the union of two minute cells from different parents, to develop into the likeness of these parents. This likeness, however, though it extends to minute particulars, is not absolute. The offspring is not exactly like either parent, nor does it present a precise mean between the characters of the two parents. There is always some amount of individual variability, the effects of which, as we shall hereafter see, are of wide importance. We are wont to say that these phenomena, the transmission of parental characteristics, together with a margin of difference, are due to heredity with variation. But this merely names the facts. How the special reproductive cells have acquired the secret of developing along special lines, and reproducing, with a margin of variability, the likeness of the organisms which produced them, is a matter concerning which we can at present only make more or less plausible guesses.

Scarcely less wonderful is the power which separated bits of certain organisms, such as the green freshwater hydra of our ponds, possess of growing up into the complete organism. Cut a hydra into half a dozen fragments, and each fragment will become a perfect hydra. Reproduction of this kind is said to be asexual.

We shall have, in later chapters, to discuss more fully some of the phenomena of reproduction and heredity. For the present, it is sufficient to say that animals reproduce their kind by the detachment of a portion of the substance of their own bodies, which portion, in the case of the higher animals, undergoes a series of successive developmental changes constituting its life-history, the special nature

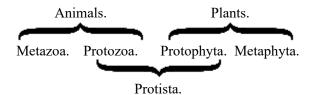
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of which is determined by inheritance, and the result of which is a new organism in all essential respects similar to the parent or parents.

11. Animals are living organisms, and "not vegetables." The first part of this final statement merely sums up the characteristics of living animals which have gone before. But the latter part introduces us to the fact that there are other living organisms than those we call animals, namely, those which belong to the vegetable kingdom.

It might, at first sight, be thought a very easy matter to distinguish between animals and plants. There is no chance, for example, of mistaking to which kingdom an oak tree or a lion, a cabbage or a butterfly, belongs. But when we come down to the simpler organisms, those whose bodies are constituted by a single cell, the matter is by no means so easy. There are, indeed, lowly creatures which are hovering on the boundary-line between the two kingdoms. We need not discuss the nature of these boundary forms. It is sufficient to state that unicellular plants are spoken of as *protophyta*, and unicellular animals as *protozoa*, the whole group of unicellular organisms being classed together as *protista*. The animals whose bodies are formed of many cells in which there is a differentiation of structure and a specialization of function, are called *metazoa*, and the multicellular plants *metaphyta*. The relations of these groups may be thus expressed—



There are three matters with regard to the life-process of animals and plants concerning which a few words must be said. These are (1) their relation to food-stuffs; (2) their relation to the atmosphere; (3) their relation to energy, or the power of doing work.

With regard to the first matter, that of food-relation, the essential fact seems to be the dependence of animals on plants. Plants can manufacture protoplasm out of its constituents if presented to them in suitable inorganic form scattered through earth and air and water. Hence the peculiar features of their form, the branching and spreading nature of those parts which are exposed to the air, and the far-reaching ramifications of those parts which are implanted in the earth. Hence, too, the flattened leaves, with their large available surface. Animals are unable to manufacture protoplasm in this way. They are, sooner or later, dependent for food on plant-products. It is true that the carnivora eat animal food, but the animals they eat are directly or indirectly consumers of vegetable products. Plants are nature's primary producers of organic material. Animals utilize these products and carry them to higher developments.

In relation to the atmosphere, animals require a very much larger quantity of oxygen than do plants. This, during the respiratory process, combines with carbon so as to form carbonic acid gas; and the atmosphere would be gradually drained of its oxygen and flooded with carbonic acid gas were it not that plants, through their green colouring matter (chlorophyll), under the influence of light, have the power of decomposing the carbonic acid gas, seizing on the carbon and building it into their tissues, and setting free the oxygen. Thus are animals and green plants complementary elements in the scheme

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of nature. [A] The animal eats the carbon elaborated by the plant into organic products (starch and others), and breathes the oxygen which the plant sets free after it has abstracted the carbon. In the animal's body the carbon and oxygen recombine; its varied activities are thus kept going; and the resultant carbonic acid gas is breathed forth, to be again separated by green, growing plants into carbonaceous food-stuff and vitalizing oxygen. It must be remembered, however, that vegetable protoplasm, like animal protoplasm, respires by the absorption of oxygen and the formation of carbonic acid gas. But in green plants this process is outbalanced by the characteristic action of the chlorophyll, by which carbonic acid gas is decomposed.

Lastly, we have to consider the relations of animals and plants to energy. Energy is defined as the power of doing work, and it is classified by physicists under two modes—potential energy, or energy of position; and kinetic energy, or energy of motion. The muscles of my arm contain a store of potential energy. Suppose I pull up the weight of an old-fashioned eight-day clock. Some of the potential energy of my arm is converted into the potential energy of the weight; that is, the raised weight is now in a position of advantage, and capable of doing work. It has energy of position, or potential energy. If the chain breaks, down falls the weight, and exhibits the energy of motion. But, under ordinary circumstances, this potential energy is utilized in giving a succession of little pushes to the pendulum to keep up its swing, and in overcoming the friction of the works. Again, the energy of an electric current may be utilized in decomposing water, and tearing as under the oxygen and hydrogen of which it is composed. The oxygen and hydrogen now have potential energy, and, if they be allowed to combine, this will manifest itself as the light and heat of the explosion. These examples will serve to illustrate the nature of the changes which energy undergoes. These are of the nature of transferences of energy from one body to another, and of transformations from one mode or manifestation to another. The most important point that has been established during this century with regard to energy is that, throughout all its transferences and transformations, it can be neither created nor destroyed. But there is another point of great importance. Transformations of energy take place more readily in certain directions than in others. And there is always a tendency for energy to pass from the higher or more readily transformable to the lower or less readily transformable forms. When, for example, energy has passed to the low kinetic form of the uniformly distributed molecular motion of heat, it is exceedingly difficult, or practically impossible, to transform it into a higher and more available form.

Now, both animals and plants are centres of the transformation of energy; and in them energy, notwithstanding that it is being raised to a high position of potentiality, is constantly tending to be degraded to lower forms. Hence the necessity of some source from which fresh stores of available energy may be constantly supplied. Such a source is solar radiance. This it is which gives the succession of little pushes which keeps the pendulum of life a-swinging. And it is the green plants which, through their chlorophyll, are in the best position to utilize the solar energy. They utilize it in building up, from the necessary constituents diffused through the atmosphere and the soil, complex forms of organic material, of which the first visible product seems to be starch; and these not only contain large stores of potential energy, but are capable, when combined with oxygen, of containing yet larger stores. The animal, taking into its body these complex materials, and elaborating them together with oxygen into yet more complex and more unstable compounds, then, during its vital activity, makes organized use of the transformation of the potential energy thus stored into lower forms of energy. Thus there go on side by side, in both animals and plants, a building up or synthesis of complex and unstable

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chemical compounds, accompanied by a storage of potential energy, and a breaking down or analysis of these compounds into lower and simpler forms, accompanied by a setting free of kinetic energy. But in the plant, synthetic changes and storage of energy are in excess, while in the animal, analytic changes and the setting free of kinetic energy are more marked. Hence the variety and volume of animal activities.

The building up of complex organic substances with abundance of stored energy may be roughly likened to the building up, by the child with his wooden bricks, of houses and towers and pyramids. The more complex they become the more unstable they are, until a touch will shatter the edifice and liberate the stored-up energy of position acquired by the bricks. Thus, under the influence of solar energy, do plants build up their bricks of hydrogen, carbon, and oxygen into complex molecular edifices. Animals take advantage of the structures so elaborated, modify them, add to them, and build yet more complex molecular edifices. These, at the touch of the appropriate stimulus, topple over and break down—not, indeed, into the elemental bricks, but into simpler molecular forms, and these again in later stages into yet simpler forms, which are then got rid of or excreted from the body. Meanwhile the destructive fall of the molecular edifice is accompanied by the liberation of energy—as heat, maintaining the warmth of the body; as visible or hidden movements, in locomotion, for example, and the heart-beat; and sometimes as electrical energy (in electric fishes); as light (in phosphorescent animals and the glow-worm), or as sound. It is this abundant liberation of energy, giving rise to many and complex activities, which is one of the distinguishing features of animals as compared with plants.

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We have now, I trust, extended somewhat and rendered somewhat more exact our common and familiar knowledge of the nature of animal life. In the next chapter we will endeavour to extend it still further by a consideration of the process of life.

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CHAPTER II. THE PROCESS OF LIFE.

In the foregoing chapter, on "The Nature of Animal Life," we have seen that animals breathe, feed, grow, are sensitive, exhibit various activities, and reproduce their kind. These may be regarded as primary life-processes, in virtue of which the animal characterized by them is a living creature. We have now to consider some of these life-processes—the sum of which we may term the process of life—a little more fully and closely.

The substance that exhibits these life-processes is protoplasm, which exists in minute separate masses termed cells. It seems probable, however, that these cells, separate as they seem, are in some cases united to each other by minute protoplasmic filaments. In the higher animals the cells in different parts of the body take on different forms and perform different functions. Like cells with like functions are also aggregated together into tissues. Thus the surfaces of the body, external and internal, are bounded by or lined with epithelial tissue; the bones and framework of the body are composed of skeletal tissue; nervous tissue goes to form the brain and nerves; contractile tissue is found in the muscles; while the blood and lymph form a peculiar nutritive tissue. The organs of the body are distinct parts performing definite functions, such as the heart, stomach, or liver. An organ may be composed of several tissues. Thus the heart has contractile tissue in its muscular walls, epithelial tissue lining its cavities, and skeletal tissue forming its framework. Still, notwithstanding their aggregation into tissues and organs, it remains true that the body of one of the higher animals is composed of cells, together with certain cell-products, horny, calcareous, or other. The simplest animals, called protozoa, are, however, unicellular, each organism being constituted by a single cell.

We must notice that, even during periods of apparent inactivity—for example, during sleep—many life-processes are still in activity, though the vigour of action may be somewhat reduced. When we are fast asleep, respiration, the heart-beat, [B] and the onward propulsion of food through the alimentary canal, are still going on. Even at rest, the living animal is a *going* machine. In some cases, however, as during the hibernating sleep of the dormouse or the bear, the vital activities fall to the lowest possible ebb. Moreover, in some cases, the life-processes may be temporarily arrested, but again taken up when the special conditions giving rise to the temporary arrest are removed. Frogs, for example, have been frozen, but have resumed their life-activities when subsequently thawed.

Let us take the function of respiration as a starting-point in further exemplification of the nature of the life-processes of animals.

The organs of respiration, in ourselves and all the mammalia, are the lungs, which lie in the thoracic cavity of the chest, the walls of which are bounded by the ribs and breast-bone, its floor being formed of a muscular and movable partition, the diaphragm, which separates it from the stomach and other alimentary viscera in the abdominal region. The lungs fit closely, on either side of the heart, in this thoracic cavity; and when the size of this cavity is altered by movements of the ribs and diaphragm,

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air is either sucked into or expelled from the lungs through the windpipe, which communicates with the exterior through the mouth or nostrils. It is unnecessary to describe the minute structure of the lungs; suffice it to say that, in the mammal, they contain a vast number of tubes, all communicating eventually with the windpipe, and terminating in little expanded sacs or bags. Around these little sacs courses the blood in a network of minute capillary vessels, the walls of which are so thin and delicate that the fluid they contain is only separated from the gas within the sacs by a film of organic tissue.

The blood is a colourless fluid, containing a great number of round red blood-discs, which, from their minute size and vast numbers, seem to stain it red. They may be likened to a fleet of little boats, each capable of being laden with a freight of oxygen gas, while the stream in which they float is saturated with carbonic acid gas. This latter escapes into the air-sacs as the fluid courses through the delicate capillary tubes.

Whither goes the oxygen? Whence comes the carbonic acid gas? The answer to these questions is found by following the course of the blood-circulation. The propulsion of the blood throughout the body is effected by the heart, an organ consisting, in mammals, of two receivers (auricles) into which blood is poured, and two powerful force-pumps (ventricles), supplied with blood from the receivers and driving it through great arteries to various parts of the body. There are valves between the receivers and the force-pumps and at the commencement of the great arterial vessels, which ensure the passage of the blood in the right direction. The two receivers lie side by side; the two force-pumps form a single muscular mass; and all four are bound up into one organ; but there is, during adult life, no direct communication between the right and left receivers or the right and left force-pumps.

Let us now follow the purified stream, with its oxygen-laden blood-discs, as it leaves the capillary tubes of the lungs. It generally collects, augmented by blood from other similar vessels, into large veins, which pour their contents into the left receiver. Thence it passes on into the left force-pump, by which it is propelled, through a great arterial vessel and the numerous branches it gives off, to the head and brain, to the body and limbs, to the abdominal viscera; in short, to all parts of the body except the lungs. In all the parts thus supplied, the vessels at length break up into a delicate capillary network, so that the blood-fluid is separated from the tissue-cells only by the delicate organic film of the capillary walls. Then the blood begins to re-collect into larger and larger veins. But a change has taken place; the blood-discs have delivered up to the tissues their freight of oxygen; the stream in which they float has been charged with carbonic acid gas. The veins leading from various parts of the body converge upon the heart and pour their contents into the right receiver; thence the blood passes into the right forcepump, by which it is propelled, by arteries, to the lungs. There the blood-discs are again laden with oxygen, the stream is again head; B., capillary plexus of the body; purified of its carbonic acid gas, and the blood proceeds on its A.C., alimentary canal; Lr., liver; R.A., course, to renew the cycle of its circulation.

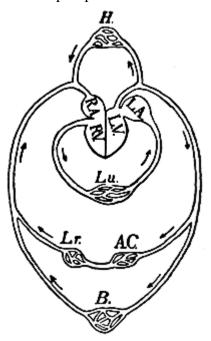


Fig. 6.—Diagram of circulation.

L.A., left auricle of the heart; L.V., left ventricle; H., capillary plexus of the right auricle of the heart; R.V., right ventricle; Lu., lungs.

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Now, if we study the process of respiration and that of circulation, with which it is so closely associated, in other forms of life, we shall find many differences in detail. In the bird, for example, the mechanism of respiration is different. There is no diaphragm, and the lungs are scarcely distensible. There are, however, large air-sacs in the abdomen, in the thoracic region, in the fork of the merrythought, and elsewhere. These are distensible, and to reach them the air has to pass through the lungs, and as it thus passes through the delicate tubes of the lungs, it supplies the blood with oxygen and takes away carbonic acid gas. In the frog there is no diaphragm, and there are no ribs. The lungs are hollow sacs with honey-combed sides, and they are inflated from the mouth, which is used as a force-pump for this purpose. In the fish there are no lungs, respiration being effected by means of gills. In these organs the blood is separated from the water which passes over them (being gulped in by the mouth and forced out between the gill-covers) by only a thin organic film, so that it can take up the oxygen dissolved in the water, and give up to the water the carbonic acid it contains. In fishes, too, we have only one receiver and one force-pump, the blood passing through the gills on its way to the various parts of the body. In the lobster, again, there are gills, but the mechanism by which the water is drawn over them is quite different, and the blood passes through them on its way to the heart, after passing through the various organs of the body, not on its way from the heart, as in vertebrate fishes. The blood, too, has no red blood-discs. In the air-breathing insects the mechanism is, again, altogether different. The air, which obtains access to the body by spiracles in the sides (see Fig. 1, p. 3), is distributed by delicate and beautiful tubes to all parts of the organs; so that the oxygen is supplied to the tissues directly, and not through the intervention of a blood-stream. In the earthworm, on the other hand, there is a distributing blood-stream, but there is no mechanism for introducing the air within the body; while in some of the lowliest forms of life there is neither any introduction of air within the body nor any distribution by means of a circulating fluid. Beginning, therefore, with the surface of the body simply absorbent of oxygen, we have the concentration of the absorbent parts in special regions, and an increase in the absorbent surface, either (1) by the pushing out of processes into the surrounding medium, as in gills; or (2) by the formation of internal cavities, tubes, or branching passages, as in lungs and the tracheal air-system of insects.

What, then, is the essential nature of the respiratory process thus so differently manifested? Clearly the supply of oxygen to the cellular tissue-elements, and, generally closely associated with this, the getting rid of carbonic acid gas.

Let us now glance at the life-processes which minister to nutrition, beginning, as before, with the mode in which these processes are effected in ourselves.

The alimentary canal is a long tube running through the body from the mouth to the vent. In the abdominal region it is coiled upon itself, so that its great length may be conveniently packed away. Opening into this tube are the ducts of certain glands, which secrete fluids which aid in the digestion of the food. Into the mouth there open the ducts of the salivary glands, which secrete the saliva; in the stomach there are a vast number of minute gastric glands; in the intestine, besides some minute tubular glands, there are the ducts of the large liver (which secretes the bile) and the pancreas, or sweetbread. Since, with the exception of the openings of these ducts, the alimentary canal is a closed tube, its contents, though lying within the body, are in a sense outside it, just as the fuel in a tubular boiler, though within the boiler, is really outside it. The organic problem, therefore, is how to get the nutritive materials through the walls of the tube and thus into the body.

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At an ordinary meal we are in the habit of consuming a certain amount of meat, with some fat, together with bread and potatoes, and perhaps some peas or beans and a little salt. This is followed by, say, milky rice-pudding, with which we take some sugar; and a cheese course may, perhaps, be added. The whole is washed down with water more or less medicated with other fluid materials. Grouping these substances, there are (1) water and salts, including calcium phosphate in the milk; (2) meat, peas, milk, and cheese, all of which contain albuminous or allied materials; (3) bread, potatoes, and rice, which contain starchy matters; and here we may place the sugar; (4) fat, associated with the meat or contained in the cream of the milk. Now, of all the materials thus consumed, only the water, salts, and sugar are capable, in their unaltered condition, of passing through the lining membrane of the alimentary canal, and thus of entering the body. The albuminous materials, the starchy matter, and the fat—that is to say, the main elements of the food—are, in their raw state, absolutely useless for nutritive purposes.

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The preparation of the food begins in the mouth. The saliva here acts upon some of the starchy matter, and converts it into a kind of sugar, which *can* pass through the lining membrane of the alimentary canal, and thus enter the body. The fats and albuminous matters here remain unaltered, though they are torn to pieces by the mastication effected by the teeth. In the stomach the albuminous constituents of the meat are attacked by the gastric juice and converted into peptones; and in this new condition they, too, can soak through the lining membrane of the alimentary canal, and thus can enter the body. In the stomach all action on starch is arrested; but in the intestine, through the effect of a ferment contained in the pancreatic juice, this action is resumed, and the rest of the starch is converted into absorbable sugar. Another principle contained in pancreatic juice takes effect on the albuminous matters, and converts them into absorbable peptones. The pancreatic juice also acts on the fats, converting them into an emulsion, that is to say, causing them to break up into exceedingly minute globules, like the butter globules in milk. It furthermore contains a ferment which splits up the fats into fatty acids and glycerine; and these fatty acids, with an alkaline carbonate contained in small quantities in pancreatic juice, form soluble soaps, which further aid in emulsifying fats. The bile also aids in emulsifying fats.

The effect, then, of the various digestive fluids upon the food is to convert the starch, albuminous material, and fat into sugar, peptones, glycerine, and soap, and thus render them capable of passing through the lining membrane of the canal into the body.

The materials thus absorbed are either taken up into the blood-stream or pass into a separate system of vessels called lacteals. All the blood which comes away from the alimentary canal passes into the liver, and there undergoes a good deal of elaboration in that great chemical laboratory of the body. The fluid in the lacteals passes through lymphatic glands, in which it too undergoes some elaboration before it passes into the blood-stream by a large vessel or duct.

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Thus the blood, which we have seen to be enriched with oxygen in the lungs, is also enriched with prepared nutritive material through the processes of digestion and absorption in the alimentary organs and elaboration in the liver and lymphatic glands.

Here let us again notice that the details of the process of nutrition vary very much in different forms of life. In some mammals the organs of digestion are specially fitted to deal with a flesh diet; in others they are suited for a diet of herbs. In the graminivorous birds the grain is swallowed whole, and pounded up in the gizzard. The leech swallows nothing but blood. The earthworm pours out a secretion on the leaves, by which they are partially digested before they enter the body. Many parasitic organisms have no digestive canal, the nutritive juices of their host being absorbed by the general external surface of the body. But the essential life-process is in all cases the same—the absorption of nutritive matter to be supplied to the cell or cells of which the organism is built up.

Thus in the mammal the blood, enriched with oxygen in the lungs, and enriched also with nutritive fluids, is brought, in the course of its circulation, into direct or indirect contact with all the myriads of living cells in the body.

In the first place, the material thus supplied is utilized for and ministers to the growth of the organs and tissues. This growth is effected by the multiplication of the constituent cells. The cells themselves have a very limited power of growth. But, especially in the early stages of the life of the organism, when well supplied with nutriment, the cells multiply rapidly, by a process of fission, or the division of each cell into two daughter cells. The first part of the cell to divide is the nucleus, the protoplasmic network of which shows, during the process, curious and interesting arrangements and groupings of the fibres. When the nucleus has divided, the surrounding protoplasm is constricted, and separates into two portions, each of which contains a daughter nucleus.

In addition to the multiplication of cells, there is the formation, especially during periods of growth, of certain products of cell-life and cell-activity. Bone, for example, is a more or less permanent product of the activity of certain specialized cells.

There is, perhaps, no more wonderful instance of rapid and vigorous growth than the formation of the antlers of deer. These splendid weapons and adornments are shed and renewed every year. In the spring, when they are growing, they are covered over with a dark skin provided with short, fine, closeset hair, and technically termed "the velvet." If you lay your hand on the growing antler, you will feel that it is hot with the nutrient blood that is coursing beneath it. It is, too, exceedingly sensitive and tender. An army of tens of thousands of busy living cells is at work beneath that velvet surface, building the bony antlers, preparing for the battles of autumn. Each minute cell knows its work, and does it for the general good—so perfectly is the body knit into an organic whole. It takes up from the nutrient blood the special materials it requires; out of them it elaborates the crude bone-stuff, at first soft as wax, but ere long to become as hard as stone; and then, having done its work, having added its special morsel to the fabric of the antler, it remains embedded and immured, buried beneath the bone-products of its successors or descendants. No hive of bees is busier or more replete with active life than the antler of a stag as it grows beneath the soft, warm velvet. And thus are built up in the course of a few weeks those splendid "beams," with their "tynes" and "snags," which, in the case of the wapiti, even in the confinement of our Zoological Gardens, may reach a weight of thirty-two pounds, and which, in the freedom of the Rocky Mountains, may reach such a size that a man may walk, without stooping, beneath the archway made by setting up upon their points the shed antlers. When the antler has reached its full size, a circular ridge makes its appearance at a short distance from the base. This is the "burr," which divides the antler into a short "pedicel" next the skull, and the "beam" with its branches above. The circulation in the blood-vessels of the beam now begins to languish, and the velvet dies and peels off, leaving the hard, dead, bony substance exposed. Then is the time for fighting, when the stags

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challenge each other to single combat, while the hinds stand timidly by. But when the period of battle is over, and the wars and loves of the year are past, the bone beneath the burr begins to be eaten away and absorbed, through the activity of certain large bone-eating cells, and, the base of attachment being thus weakened, the beautiful antlers are shed; the scarred surface skins over and heals, and only the hair-covered pedicel of the antler is left. [C]

Not only are there these more or less permanent products of cell-activity which are built up into the framework of the body; there are other products of a less enduring, but, in the case of some of them, not less useful character. The secretions, for example, which, as we have seen, minister in such an important manner to nutrition, are of this class. The salivary fluids, the gastric juice, the pancreatic products, and the bile,—all of these are products of cell-life and cell-activity. And then there are certain products of cell-life which must be cast out from the body as soon as possible. These are got rid of in the excretions, of which the carbonic acid gas expelled in the lungs and the waste-products eliminated through the kidneys are examples. They are the ultimate organic products of the combustion that takes place in the muscular, nervous, and other tissues.

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The animal organism has sometimes been likened to a steam-engine, in which the food is the fuel which enters into combustion with the oxygen taken in through the lungs. It may be worth while to modify and modernize this analogy—always remembering, however, that it is an analogy, and that it must not be pushed too far.

In the ordinary steam-engine the fuel is placed in the fire-box, to which the oxygen of the air gains access; the heat produced by the combustion converts the water in the boiler into steam, which is made to act upon the piston, and thus set the machinery in motion. But there is another kind of engine, now extensively used, which works on a different principle. In the gas-engine the fuel is gaseous, and it can thus be introduced in a state of intimate mixture with the oxygen with which it is to unite in combustion. This is a great advantage. The two can unite rapidly and explosively. In gunpowder the same end is effected by mixing the carbon and sulphur with nitre, which contains the oxygen necessary for their explosive combustion. And this is carried still further in dynamite and gun-cotton, where the elements necessary for explosive combustion are not merely mechanically mixed, but are chemically combined in a highly unstable compound.

But in the gas-engine, not only is the fuel and the oxygen thus intimately mixed, but the controlled explosions and the resulting condensation are caused to act directly on the piston, and not through the intervention of water in a boiler. Whereas, therefore, in the steam-engine the combustion is to some extent external to the working of the machine, in the gas-engine it is to a large extent internal and direct.

Now, instead of likening the organism as a whole to a steam-engine, it is more satisfactory to liken each cell to a gas-engine. We have seen that the cell-substance around the nucleus is composed of a network of protoplasm, the plasmogen, enclosing within its meshes a more fluid material, the plasm. It is probable that this more fluid material is an explosive, elaborated through the vital activity of the protoplasmic network. During the period of repose which intervenes between periods of activity, the protoplasmic network is busy in construction, taking from the blood-discs oxygen, and from the blood-fluid carbonaceous and nitrogenous materials, and knitting these together into relatively unstable

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explosive compounds. These explosive compounds are like the mixed air and gas of the gas-engine. A rested muscle may be likened to a complex and well-organized battery of gas-engines. On the stimulus supplied through a nerve-channel a series of co-ordinated explosions takes place: the gas-engines are set to work; the muscular fibres contract; the products of the explosions (one of which is carbonic acid gas) are taken up and hurried away by the blood-stream; and the protoplasm sets to work to form a fresh supply of explosive material. Long before the invention of the gas-engine, long before gun-cotton or dynamite were dreamt of, long before some Chinese or other inventor first mixed the ingredients of gunpowder, organic nature had utilized the principle of controlled explosions in the protoplasmic cell.

Certain cells are, however, more delicately explosive than others. Those, for example, on or near the external surface of the body—those, that is to say, which constitute the end organs of the special senses—contain explosive material which may be fired by a touch, a sound, an odour, the contact with a sapid fluid or a ray of light. The effects of the explosions in these delicate cells, reinforced in certain neighbouring nerve-knots (ganglionic cells), are transmitted down the nerves as along a fired train of gunpowder, and thus reach that wonderful aggregation of organized and co-ordinated explosive cells, the brain. Here it is again reinforced and directed (who, at present, can say how?) along fresh nerve-channels to muscles, or glands, or other organized groups of explosives. And in the brain, somehow associated with the explosion of its cells, consciousness and the mind-element emerges; of which we need only notice here that it belongs to a *wholly different order of being* from the physical activities and products with which we are at present concerned.

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No analogies between mechanical contrivances and organic processes can be pushed very far. To liken the organic cell to a gas-engine is better than to liken the organism to a steam-engine, because it serves to indicate the fact that the fuel does not simply combine with the oxygen in combustion, but that an unstable or explosive combination of "fuel" and oxygen is first formed; and again, because the effect of this is direct, and not through the intervention of any substance to which the combustion merely supplies the necessary heat. But beyond the fact that a kind of explosive is formed which, like a fulminating compound, can be fired by a touch, there is no very close analogy to be drawn. Nor must we press the explosion analogy too far. The essential thing would seem to be this—which, perhaps, the analogy may have served to lead up to—that the vital protoplasmic network of the cell has the power of building up complex and unstable chemical compounds, which are probably stored in the plasm within the spaces between the threads of the network; and that these unstable compounds, under the influence of a stimulus (or, possibly, sometimes spontaneously) break down into simpler and more stable compounds. [D] In the case of muscle-cells, this latter change is accompanied by an alteration in length of the fibres and consequent movements in the organism, the products of the disruptive change being useless or harmful, and being, therefore, got rid of as soon as possible. But very frequently the products of explosive activity are made use of. In the case of bone-cells, one of the products of disruption is of permanent use to the organism, and constitutes the solid framework of the skeleton. In the case of the secreting cells of the salivary and other digestive glands, one of the disruptive products is of temporary value for the preparation of the food. It is exceedingly probable that these useful products of disruption, permanent or temporary, took their origin in waste products for which natural selection has found a use, and which have been, through natural selection, rendered more and more efficacious. This, however, is a question we are not at present in a position to discuss.

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In the busy hive of cells which constitutes what we call the animal body, there is thus ceaseless activity. During periods of apparent rest the protogen filaments of the cell-net are engaged in constructive work, building up fresh supplies of complex and unstable materials, which, during periods of apparent activity, break up into simpler and more stable substances, some of which are useful to the organism while others must be got rid of as soon as possible. From another point of view, the cells during apparent rest are storing up energy which is utilized by the organism during its periods of activity. The storing up of available energy may be likened to the winding up of a watch or clock; it is during apparent rest that the cell is winding itself up; and thus we have the apparent paradox that the cell is most active and doing most work when it is at rest. During the repose of an organ, in fact, the cells are busily working in preparation for the manifestation of energetic action that is to follow. Just as the brilliant display of intellectual activity in a great orator is the result of the silent work of a lifetime, so is the physical manifestation of muscular power the result of the silent preparatory work of the muscle-cells. [E]

One point to be specially noted is the varied activity of the cells. While they are all working for the general good of the organism, they are divided into companies, each with a distinct and definite kind of work. This is known as the physiological division of labour. It is accompanied by a morphological differentiation of structure. By the form of a cell, therefore, we can generally recognize the kind of work it has to perform. The unstable compounds produced by the various cells must also be different, though not much is known at present on this subject. The unstable compound which forms bone and that which forms the salivary ferment, the unstable matter elaborated by nerve-cells and that built up by muscle-cells, are in all probability different in their chemical nature. Whether the formative plasmogen from which these different substances originate is in all cases the same or in different cases different, we do not know.

It may, perhaps, seem strange that the products of cellular life should be reached by the roundabout process of first producing a very complex substance out of which is then formed a less complex substance, useful for permanent purposes, as in bone, or temporary purposes, as in the digestive fluids. It seems a waste of power to build up substances unnecessarily complex and stored with an unnecessarily abundant supply of energy. Still, though we do not know that this course is adopted in all cases, there is no doubt that it is adopted in a great number of instances. And the reason probably is that by this method the organs are enabled to act under the influence of stimuli. They are thus like charged batteries ready to discharge under the influence of the slightest organic touch. In this way, too, is afforded a means by which the organ is not dependent only upon the products of the immediate activity of the protoplasm at the time of action, but can utilize the store laid up during a considerable preceding period.

Sufficient has now been said to illustrate the nature of the process of life. The fact that I wish to stand out clearly is that the animal body is stored with large quantities of available energy resident in highly complex and unstable chemical compounds, elaborated by the constructive energy of the formative protoplasm of its constituent cells. These unstable compounds, eminently explosive according to our analogy, are built up of materials derived from two different sources—from the nutritive matter (containing carbon, hydrogen, and nitrogen) absorbed in the digestive organs, and from oxygen taken up from the air in the lungs. The cells thus become charged with energy that can be set

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free on the application of the appropriate stimulus, which may be likened to the spark that fires the explosive.

Let us note, in conclusion, that it is through the blood-system, ramifying to all parts of the body, and the nerve-system, the ramifications of which are not less perfect, that the larger and higher organisms are knit together into an organic whole. The former carries to the cell the raw materials for the elaboration of its explosive products, and, after the explosions, carries off the waste products which result therefrom. The nerve-fibres carry the stimuli by which the explosive is fired, while the central nervous system organizes, co-ordinates, and controls the explosions, and directs the process of reconstruction of the explosive compounds.

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CHAPTER III. REPRODUCTION AND DEVELOPMENT.

We have now to turn to a fresh aspect of animal life, that of reproduction; and it will be well to connect this process as closely as possible with the process of life in general, of which it is a direct outcome.

It will be remembered that, in the last chapter, it was shown that the essential feature in the process of life is the absorption by living protoplasm of oxygen on the one hand and nutritive matter on the other hand, and the kneading of these together, in subtle metabolism, into unstable compounds, which we likened to explosives. This is the first, or constructive, stage of the life-process. Thereupon follows the second, or disruptive, stage. The unstable compounds break down into more stable products,—they explode, according to our analogy; and accompanying the explosions are manifestations of motor activity—of heat, sometimes of light and electrical phenomena. But in the economy of nature the products of explosion are often utilized, and in the division of labour among cells the explosions of some of them are directed specially to the production of substances which shall be of permanent or temporary use—for digestion, as in the products of the salivary, gastric, and intestinal glands; for support, as in bone, cartilage, and skeletal tissue generally; or as a store of nutriment, in fat or yolk. The constructive products of protoplasmic activity seem for the most part to be lodged in the spaces between the network of formative protoplasm. The disruptive products—those of them, that is to say, which are of temporary or permanent value to the organism—accumulate either within the cell, sometimes at one pole, sometimes at the centre, as in the case of the yolk of eggs, or around the cell, as in the case of cartilage or bone.

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Apart from and either preceding or accompanying these phenomena, is the growth or increase of the formative protoplasm itself; concerning which the point to be here observed is that it is not indefinite, but limited. This was first clearly enunciated by Herbert Spencer, and may be called Spencer's law. In simplest expression it may thus be stated: *Volume tends to outrun surface*. Take a cube measuring one inch in the side; its volume is one cubic inch, its surface six square inches. Eight such cubes will have a surface of (6×8) forty-eight square inches. But let these eight be built into a larger cube, two inches in the side, and it will be found that the surface exposed is now only twenty-four square inches. While the volume has been increased eight times, the surface has been increased only four times. With increase of size, volume tends to outrun surface. But in the organic cell the nutritive material and oxygen are absorbed at the surface, while the explosive changes occur throughout its mass. Increase of size, therefore, cannot be carried beyond certain limits, for the relatively diminished surface is unable to supply the relatively augmented mass with material for elaboration into unstable compounds. Hence the cell divides to afford the same mass increased surface. This process of cell-division is called fission, and in some cases cleavage.

We will now proceed to pass in review the phenomena of reproduction and development in animals.

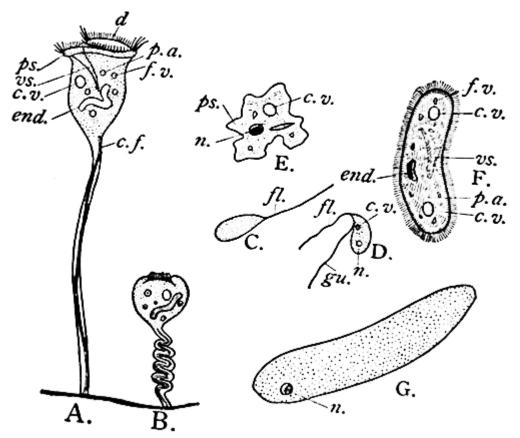


Fig. 7.—Protozoa.

A, vorticella extended. B, the same contracted. C, D, monads. E, amœba. F, *Paramœcium*. G, *Gregarina*. *c.f.*, contractile fibre; *c.v.*, contractile vesicle; *d.*, disc; *end.*, endoplast; *f.v.*, food-vacuole; *fl.*, flagellum; *gu.*, gubernaculum; *n.*, nucleus; *p.a.*, potential anus; *ps.*, (in A) peristome, (in E) pseudopodium; *vs.*, vestibule.]

Attention has already been drawn to the difference between those lowly organisms, each of which is composed of a single cell—the protozoa, as they are termed—and those higher organisms, called metazoa, in which there are many cells with varied functions. Confining our attention at first to the former group of unicellular animals, we find considerable diversities of form and habit, from the relatively large, sluggish, parasitic *Gregarina*, to the active slipper-animalcule, or *Paramæcium*, or the beautiful, stalked bell-animalcule, or *Vorticella*; and from the small, slow-moving amæba to the minute, intensely active monad. In many cases reproduction is by simple fission, as in the amæba, where the nucleus first undergoes division; and then the whole organism splits into two parts, each with its own nucleus. In other cases, also numerous, the organism passes into a quiescent state, and becomes surrounded with a more or less toughened cyst. The nucleus then disappears, and the contents of the cyst break up into a number of small bodies or spores. Eventually the cyst bursts, and the spores swarm forth. In the case of some active protozoa the minute creatures that swarm forth are more or less like the parent; but in the more sluggish kinds the minute forms are more active than the parent. Thus in the case of the gregarina, the minute spore-products are like small amæbæ; while in other instances the embryos, if so we may call them, have a whip-like cilium like the monads.

Very frequently, however, there is, in the protozoa, a further process, which would seem to be intimately associated with fission or the formation of spores, as the case may be. This is known as conjugation. Among monads, for example, two individuals may meet together, conjugate, and completely fuse the one into the other. A triangular cyst results. After a while, the cyst bursts, and an apparently homogeneous fluid escapes. The highest powers of the microscope fail to disclose in it any

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germ of life; and there, at first sight, would seem to be an end of the matter. But wait and watch; and there will appear in the field of the microscope, suddenly and as if by magic, countless minute points, which prolonged watching shows to be growing. And when they have further grown, each distinct point is seen to be a monad.

In the slipper-animalcule, conjugation is temporary. But during the temporary fusion of the two individuals important changes are said to occur. In these infusorians there is, beside the nucleus, a smaller body, the paranucleus. This, in the case of conjugating paramecia, appears to divide into two portions, of which one is mutually exchanged. Thus when two slipper-animalcules are in conjugation, the paranucleus of each breaks into two parts, a and b, of which a is retained and b handed over in exchange. The old a and the new b then unite, and each paramecium goes on its separate way. M. Maupas, who has lately reinvestigated this matter, considers, as the result of his observations on another infusorian (Stylonichia), that without conjugation these organisms become exhausted, and multiplication by fission comes to a standstill. If this be so, conjugation is, in these organisms, necessary for the continuance of the race. But Richard Hertwig has recently shown that this is, at any rate, not universally true.

In the bell-animalcule, fission takes place in such a manner as to divide the bell into two equal portions. Thus there are two bells to one stalk. But the fate of the two is not the same. One remains attached to the stalk, and expands into a complete vorticella. The other remains pear-shaped, and develops round the posterior region of the body a girdle of powerful vibratile cilia, by the lashing of which the animalcule tears itself away from the parent stem, and swims off through the water. After a short active existence, it settles down in a convenient spot, adhering by its posterior extremity. The hinder girdle of cilia is lost or absorbed, a stalk is rapidly developed, and the organism expands into a perfect vorticella.

In some cases, however, the fission is of a different character, with different results. It may be very unequal, so that a minute, free-swimming animalcule is disengaged; or minute animalcules may result by repetition of division. In either case the minute form conjugates with an ordinary vorticella, its smaller mass being completely merged in the larger volume of its mate.

There are, of course, many variations in detail in the modes of protozoan reproduction; but we may say that, omitting such details, reproduction is either by simple fission or by spore-formation; and that these processes are in some cases associated with, and perhaps dependent on, the temporary or permanent union of two individuals in conjugation.

It is essential to notice that the results of fission or of spore-formation separate, each going on its own way. Hence such development as we find in the protozoa results from differentiations within the limits of the single cell. Thus the bell-animalcule has a well-defined and constant form; a definite arrangement of cilia round the rim and in the vestibule by which food finds entrance to the body. The outer layer of the body forms a transparent cuticle, beneath which is a so-called "myophan" layer, continuous with a contractile thread in the stalk. Within the substance of the body is a pulsating cavity, or contractile vesicle, and a nucleus. Such is the nature of the differentiation which may go on within the protozoan cell.

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When we pass to the metazoa, we find that the method of differentiation is different. These organisms are composed of many cells; and instead of the parts of the cell differentiating in several directions, the several cells differentiate each in its own special direction. This is known as the physiological division of labour. The cells merge their individuality in the general good of the organism. Each, so to speak, cultivates some special protoplasmic activity, and neglects everything else in the attainment of this end. The adult metazoan, therefore, consists of a number of cells which have diverged in several, sometimes many, directions.

In some of the lower metazoans, reproduction may be effected by fission. Thus the fresh-water hydra is said to divide into two parts, each of which grows up into a perfect hydra. It is very doubtful, however, whether this takes place normally in natural life. But there is no doubt that if a hydra be artificially divided into a number of special pieces, each will grow up into a perfect organism, so long as each piece has fair samples of the different cells which constitute the body-wall. Sponges and seannemones may also be divided and subdivided, each part having the power of reproducing the parts that are thus cut away. When a worm is cut in half by the gardener's spade, the head end grows a new tail; and it is even stated that a worm not only survived the removal of the first five rings, including the brain, mouth, and pharynx, but within fifty-eight days had completely regenerated these parts.

Higher up in the scale of metazoan life, animals have the power of regenerating lost limbs. The lobster that has lost a claw reproduces a new one in its stead. A snail will reproduce an amputated "horn," or tentacle, many times in succession, reproducing in each case the eye, with its lens and retina. Even a lizard will regenerate a lost tail or a portion of a leg. In higher forms, regeneration is restricted to the healing of wounds and the mending of broken bones.

Closely connected with this process of regeneration of lost parts is the widely prevalent process of reproduction by budding. The cut stump of the amputated tentacle of the hydra or the snail buds forth a new organ. But in the hydra, during the summer months, under normal circumstances, a bud may make its appearance and give rise to a new individual, which will become detached from the parent, to lead a separate existence. In other organisms allied to the hydra the buds may remain in attachment, and a colony will result. This, too, is the result of budding in many of the sponges. In some worms, too, budding may occur. In the fresh-water worm (*Chætogaster limnæi*) the animal, as we ordinarily see it, is a train of individuals, one budded off behind the other—the first fully developed, those behind it in various stages of development. The individuals finally separate by transverse division. Another more lowly worm (*Microstomum lineare*, a Turbellarian) may bud off in similar fashion a chain of ten or fifteen individuals. In these cases budding is not far removed from fission.

Now, in the case of reproduction by budding, as in the hydra, a new individual is produced from some group of cells in the parent organism. From this it is but a step—a step, however, of the utmost importance—to the production of a new individual from a single cell from the tissues of the parental organism. Such a reproductive cell is called an egg-cell, or ovum. In the great majority of cases, to enable the ovum to develop into a new individual, it is necessary that the egg-cell should conjugate or fuse with a minute, active sperm-cell, generally derived from a different parent. This process of fusion of germinal cells is called fertilization (see Fig. 5, p. 13).

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In sponges, the cells which become ova or sperms lie scattered in the mid-layer between the ciliated layers which line the cavities and spaces of the organism. Sometimes the individual sponge produces only ova; sometimes only sperms; sometimes both, but at different periods. The cells which become ova increase in size, are passive, and rich in reserve material elaborated by their protoplasm. The cells which become sperms divide again and again, and thus produce minute active bodies, adance with restless motion. These opposite tendencies are repeated and emphasized throughout the animal kingdom—ova relatively large, passive, and accumulative of reserve material; sperms minute, active, and the result of repeated fission. The active sperm, when it unites with the ovum, imports into it a tendency to fission, or cleavage; but the resulting cells do not part and scatter—they remain associated together, and in mutual union give rise to a new sponge.

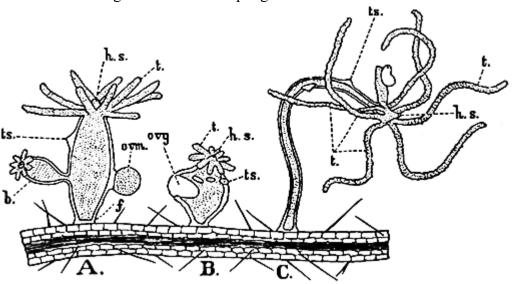


Fig. 8.—Hydra viridis.

A, hydra half retracted, with a bud and an ovum attached to the shrunken ovary; B, a small hydra firmly retracted; C, a hydra fully extended. b., bud; f., foot; h.s., hypostome; ovm., ovum; ovy., ovary; t., tentacles; ts., testis.]

In the hydra, generally near the foot or base of attachment, a rounded swelling often makes its appearance in autumn. Within this swelling one central cell increases enormously at the expense of the others. It becomes an ovum. Eventually it bursts through the swelling, but remains attached for a time. Rarely in the same hydra, more frequently in another, one or two swellings may be seen higher up, beneath the circle of tentacles. Within these, instead of the single ovum may be seen a swarm of sperms, minute and highly active. When these are discharged, one may fuse with and fertilize an ovum, occasionally in the same, but more frequently in another individual, with the result that it develops into a new hydra. Here there are definite organs—an ovary and a testis—producing the ova or the sperms. But they are indefinite and not permanent in position.

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In higher forms of life the organs which are set apart for the production of ova or sperms become definite in position and definite in structure. Occasionally, as in the snail, the same organ produces both sperms and ova, but then generally in separate parts of its structure. The two products also ripen at different times. Not infrequently, as in the earthworm, each individual has both testes and ovaries, and thus produces both ova and sperms, but from different organs. The ova of one animal are, however, fertilized by sperms from another. But in the higher invertebrates and vertebrates there is a sex-differentiation among the individuals, the adult males being possessed of testes only and producing sperms, the adult females possessed of ovaries only and producing ova. There are also, in many cases,

accessory structures for ensuring that the ova shall be fertilized by sperms, while sexual appetences are developed to further the same end. But however the matter may thus be complicated, the essential feature is the same—the union of a sluggish, passive cell, more or less laden with nutritive matter, with a minute active cell with an hereditary tendency to fission.^[F]

It is not, however, necessary in all cases that fertilization of the ovum should take place. The plant-lice, or *Aphides* of our rose trees, may produce generation after generation, and their offspring in turn reproduce in like manner, without any union or fusion of ovum or sperm. The same is true of the little water-fleas, or *Daphnids*; while in some kinds of rotifers fertilization is said never to occur. It is a curious and interesting fact, which seems now to be established beyond question, that drone bees are developed from unfertilized ova, the fertilized ova producing either queens or workers, according to the nature of the food with which the grubs are supplied. Where, as in the case of aphids and daphnids, fertilization occasionally takes place, it would seem that lowered temperature and diminished food-supply are the determining conditions. Fertilization, therefore, generally takes place in the autumn; the fertilized ovum living on in a quiescent state during the winter, and developing with the warmth of the succeeding spring. In the artificial summer of a greenhouse, reproduction may continue for three or four years without the occurrence of any fertilization.

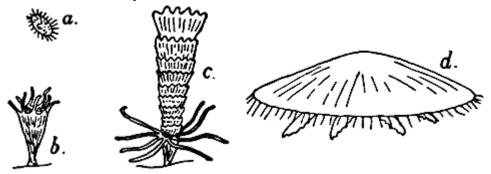


Fig. 9.—Aurelia: Life-cycle.

a, embryo; b, Hydra tuba; c, Hydra tuba, with medusoid segments; d, medusa separated to lead free existence.]

Mention may here be made of some peculiarly modified modes of reproduction among the metazoa. The aurelia is a well-known and tolerably common jelly-fish. These produce ova, which are duly fertilized by sperms from a different individual. A minute, free-swimming embryo develops from the ovum, which settles down and becomes a little polyp-like organism, the *Hydra tuba*. As growth proceeds, this divides or segments into a number of separable, but at first connected, parts. As these attain their full development, first one and then another is detached from the free end, floats off, and becomes a medusoid aurelia. Thus the fertilized ovum of aurelia develops, not into one, but into a number of medusæ, [G] passing through the *Hydra tuba* condition as an intermediate stage.

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Many of the hydroid zoophytes, forming colonies of hydra-like organisms, give rise in the warm months to medusoid jelly-fish, capable of producing ova and sperms. Fertilization takes place; and the fertilized ova develop into little hydras, which produce, by budding, new colonies. In these new colonies, again, the parts which are to become ovaries or testes float off, and ripen their products in free-swimming, medusoid organisms. Such a rhythm between development from ova and development by budding is spoken of as an alternation of generations.

The fresh-water sponge (Spongilla) exhibits an analogous rhythm. The ova are fertilized by sperms from a different short-lived individual. They develop into sponges which have no power of

producing ova or sperms. But on the approach of winter in Europe, and of the dry season in India, a number of cells collect and group themselves into a so-called gemmule. Round this is formed a sort of crust beset with spicules, which, in some cases, have the form of two toothed discs united by an axial shaft. When these gemmules have thus been formed, the sponge dies; but the gemmules live on in a quiescent state during the winter or the dry season, and with the advent of spring develop into sponges, male or female. These have the power of producing sperms or ova, but no power of producing gemmules. The power of producing ova, and that of producing gemmules, thus alternates in rhythmic fashion.

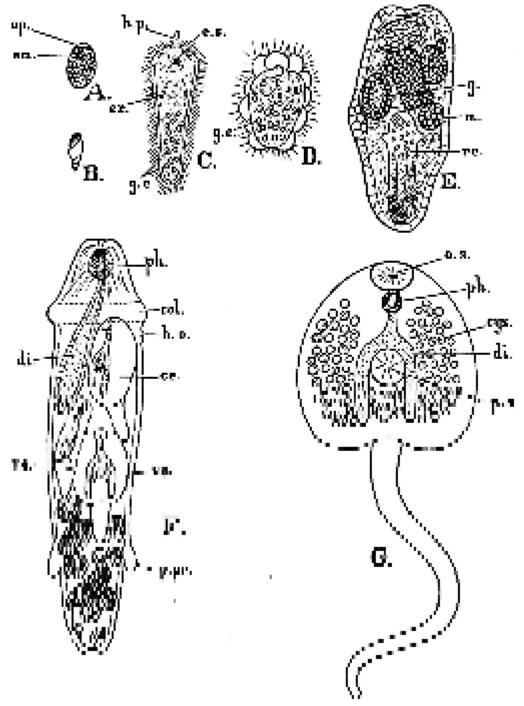


Fig. 10.—Liver-fluke: Embryonic stages. (After A. P. Thomas.)

A. ovum: *em.*, embryo; *op.*, operculum. B. *Limnœus truncatulus* (natural size). C. Free embryo: *e.s.*, eye-spot; *ex.*, excretory vessel; *g.c.*, germinal cells; *h.p.*, head-papilla. D. Embryo preparing to become a sporocyst: *g.c.*, germinal cells. E. Sporocyst: *g.*, gastrula; *m.*, morula; *re.*, redia. F. Redia: *b.o.*, birth-opening; *ce.*, cercaria; *col.*, collar; *di.*, digestive sac; *ph.*,

pharynx; *p.pr.*, posterior processes; *re.*, daughter redia. G. Cercaria: *cys.*, cystogenous organ; *di.*, digestive sac; *o.s.*, oral sucker; *p.s.*, posterior sucker; *ph.*, pharynx.

But one more example of these modified forms of reproduction can here be cited (from the author's text-book on "Animal Biology"). The liver-fluke is a parasitic organism, found in the liver of sheep. Here it reaches sexual maturity, each individual producing many thousands of eggs, which pass with the bile into the alimentary canal of the *host*, and are distributed over the fields with the excreta. Here, in damp places, pools, and ditches, free and active embryos are hatched out of the eggs. Each embryo (<u>Fig. 10</u>, C., much enlarged) is covered with cilia, except at the anterior end, which is provided with a head-papilla (h.p.). When the embryo comes in contact with any object, it, as a rule, pauses for a moment, and then darts off again. But if that object be the minute water-snail, Limnœus truncatulus (Fig. 10, B., natural size), instead of darting off, the embryo bores its way into the tissues until it reaches the pulmonary chamber, or more rarely the body-cavity. Here its activity ceases. It passes into a quiescent state, and is now known as a sporocyst (Fig. 10, E.). The active embryo has degenerated into a mere brood-sac, in which the next generation is to be produced. For within the sporocyst special cells undergo division, and become converted into embryos of a new type, which are known as rediæ (F.), and which, so soon as they are sufficiently developed, break through the wall of the sporocyst. They then increase rapidly in size, and browse on the digestive gland of the water-snail (known as the intermediate host), to which congenial spot they have in the mean time migrated. The series of developmental changes is even yet not complete. For within the rediæ (besides, at times, daughter rediæ) embryos of yet another type are produced by a process of cell-division. These are known as cercariæ (Fig. 10, G.). Each has a long tail, by means of which it can swim freely in water. It leaves the intermediate host, and, after leading a short, active life, becomes encysted on blades of grass. The cyst is formed by a special larval organ, and is glistening snowy white. Within the cyst lies the transparent embryonic liver-fluke, which has lost its tail in the process of encystment.

The last chapter in this life-history is that in which the sheep crops the blade of grass on which the parasite lies encysted; whereupon the cyst is dissolved in the stomach of the host, the little liver-fluke becomes active, passes through the bile-duct into the liver of the sheep, and there, growing rapidly, reaches sexual maturity, and lays its thousands of eggs, from each of which a fresh cycle may take its origin. The sequence of phenomena is characterized by discontinuity of development. Instead of the embryo growing up continuously into the adult, with only the atrophy of provisional organs (e.g. the gills and tail of the tadpole, or embryo frog), it produces germs from which the adult is developed. Not merely provisional organs, but provisional organisms, undergo atrophy. In the case of the liver-fluke there are two such provisional organisms, the embryo sporocyst and the redia.

We may summarize the life-cycle thus—

- 1. Ovum laid in liver of sheep, passes with bile into intestine, and thence out with the excreta.
- 2. Free ciliated embryo, in water or on damp earth, passes into pulmonary cavity of Limnæus truncatulus, and develops into
- 3. *Sporocyst*, in which secondary embryos are developed, known as
- 4. *Rediæ*, which pass into the digestive glands of *Limnæus*, and within which, besides daughter rediæ, there are developed tertiary embryos, or
- 5. Cercariæ, which pass out of the intermediate host and become

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- 6. *Encysted* on blades of grass, which are eaten by sheep. The cyst dissolves, and the young flukes pass into the liver of their host, each developing into
- 7. A liver-fluke, sexual, but hermaphrodite.

Here, again, we notice that one fertilized ovum gives rise to not one, but a number of liver-flukes.

We must now pass on to consider the growth and development of organisms. Simple growth results from the multiplication of similar cells. As the child, for example, grows, the framework of the body and the several organs increase in size by continuous cell-multiplication. Development is differential growth; and this may be seen either in the organs or parts of an organism or in the cells themselves. As the child grows up into a man, there is a progressive change in his relative proportions. The head becomes relatively smaller, the hind limbs relatively longer, and there are changes in the proportional size of other organs.

In the development of the embryo from the ovum, the differentiation is of a deeper and more fundamental character. Cells at first similar become progressively dissimilar, and out of a primitively homogeneous mass of cells is developed a heterogeneous system of different but mutually related tissues.

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This view of development is, however, the outcome of comparatively modern investigation and perfected microscopical appliances. The older view was that development in all cases is nothing more than differential growth, that there is no differentiation of primitively similar into ultimately different parts. Within the fertilized ovum of the horse or bird lay, it was supposed, in all perfection of structure, a miniature racer or chick, the parts all there, but too minute to be visible. All that was required was that each part should grow in due proportion. Those who held this view, however, divided into two schools. The one believed that the miniature organism was contained within the ovum, the function of the sperm being merely to stimulate its subsequent developmental growth. The other held that the sperm was the miniature organism, the ovum merely affording the food-material necessary for its developmental growth. In either case, this unfolding of the invisible organic bud was the *evolution* of the older writers on organic life. More than this. As Messrs. Geddes and Thomson remind us, [H] "the germ was more than a marvellous bud-like miniature of the adult. It necessarily included, in its turn, the next generation, and this the next—in short, all future generations. Germ within germ, in ever smaller miniature, after the fashion of an infinite juggler's box, was the corollary logically appended to this theory of preformation and unfolding."

Modern embryology has completely negatived any such view as that of preformation, and as completely established that the evolution is not the unfolding of a miniature germ, but the growth and differentiation of primitively similar cell-elements. In different animals, as might be expected, the manner and course of development are different. We may here illustrate it by a very generalized and so to speak diagrammatic description of the development of a primitive vertebrate.



Fig. 11.—Diagram of development. See text. The fine line across *G*. indicates the plane of section shown in *H*.

The ovum before fertilization is a simple spherical cell, without any large amount of nutritive material in the form of food-yolk (A.). It contains a nucleus. Previous to fertilization, however, in many forms of life, portions of the nucleus, amounting to three parts of its mass, are got rid of in little "polar cells" budded off from the ovum. The import of this process we shall have to consider in connection with the subject of heredity. The sperm is also a nucleated cell; and on its entrance into the ovum there are for a short time two nuclei—the female nucleus proper to the ovum, and the male nucleus introduced by the sperm. These two unite and fuse to form a joint nucleus. Thus the fertilized ovum starts with a perfect blending of the nuclear elements from two cells produced by different parents.

Then sets in what is known as the segmentation or cleavage of the ovum. First the nucleus and then the cell itself divides into two equal halves (B), each of these shortly afterwards again dividing into two. We may call the points of intersection of these two planes of division the "poles," and the planes "vertical planes." We thus have four cells produced by two vertical planes (C). The next plane of division is equatorial, midway between the poles. By this plane the four cells are subdivided into eight (D). Then follow two more vertical planes intermediate between the first two. By them the eight cells are divided into sixteen. These are succeeded by two more horizontal planes midway between the

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equator and the poles. Thus we get thirty-two cells. So the process continues until, by fresh vertical and horizontal planes of division, the ovum is divided into a great number of cells.

But meanwhile a cavity has formed in the midst of the ovum. This makes its appearance at about the eight-cell stage, the eight cells not quite meeting in the centre of the ovum. The central cavity so formed is thus surrounded by a single layer of cells, and it remains as a single layer throughout the process of segmentation, so that there results a hollow vesicle composed of a membrane constituted by a single layer of cells (E.).

The cells on one side of the vesicle are rather larger than the others, and the next step in the process is the apparent pushing in of this part of the hollow sphere; just as one might take a hollow squash indiarubber ball, and push in one side so as to form a hollow, two-layered cup (F). The vesicle, then, is converted into a cup, the mouth of which gradually closes in and becomes smaller, while the cup itself elongates (G.).[1] Thus a hollow, two-layered, stumpy, worm-like embryo is produced, the outer layer of which may be ciliated, so that by the lashing of these cilia it is enabled to swim freely in the water. The inner cavity is the primitive digestive cavity.

A cross-section through the middle of the embryo at this stage will show this central cavity

surrounded by a two-layered body-wall (H.). A little later the following changes take place (J. K.): Along a definite line on the surface of the embryo, marking the region of the back, the outer layer becomes thickened; the edges of the thickened band so produced rise up on either side, so as to give rise to a median groove between them; and then, overarching and closing over the groove, convert it into a tube. This tube is called the neural tube, because it gives rise to the central nervous system. In the region of the head it expands; and from its walls, by the growth and differentiation of the cells, there is formed—in the region of the head, the brain, and along the back, the spinal cord. Immediately beneath it there is formed a rod of cells, derived from the inner layer. This rod, which is called the notochord, is the primitive axial support of the body. Around it eventually is formed the vertebral column, the arches of the vertebræ embracing and protecting the spinal cord.

Meanwhile there has appeared between the two primitive body-layers a third or middle layer. [J] The cells of which it is composed arise from the inner layer, or from the lips of the primitive cup when the outer and inner layer pass the one into the other. This middle layer at first forms a more or less continuous sheet of cells between the inner and the outer layers. But ere long it splits into two sheets, of which one remains adherent to the inner layer and one to the outer layer. The former becomes the muscular part of the intestinal or digestive tube, the latter the lining of the body-wall. The space between the two is known as the body-cavity. Beneath the throat the heart is fashioned out of this middle layer.

Very frequently—that is to say, in many animals—the opening by which the primitive digestive tube communicated with the exterior has during these changes closed up, so that the digestive cavity does not any longer communicate in any way with the exterior. This is remedied by the formation of a special depression or pit at the front end for the mouth, and a similar pit at the hinder end. [K] These pits then open into the canal, and communications with the exterior are thus established. The lungs and liver are formed as special outgrowths from the digestive tube. The ovaries or testes make their appearance at a very early period as ridges of the middle layer projecting into the body-cavity. For some time it is [54]

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impossible to say whether they will produce sperms or ova; and it is said that in many cases they pass through a stage in which one portion has the special sperm-producing, and another the special ovum-producing, structure. But eventually one or other prevails, and the organs become either ovaries or testes.

Thus from the outer layer of the primitive embryo is produced the outer skin, together with the hairs, scales, or feathers which it carries; from it also is produced the nervous system, and the endorgans of the special senses. From the inner layer is formed the digestive lining of the alimentary tube and the glands connected therewith; from it also the primitive axial support of the body. But this primitive support gives place to the vertebral column formed round the notochord; and this is of midlayer origin. Out of the middle layer are fashioned the muscles and framework of the body; out of it, too, the heart and reproductive organs. The tissues of many of the organs are cunningly woven out of cells from all three layers. The lens of the eye, for example, is a little piece of the outer layer pinched off and rendered transparent. The retina of that organ is an outgrowth from the brain, which, as we have seen, was itself developed from the outer layer. But round the retina and the lens there is woven from the middle layer the tough capsule of the eye and the circular curtain or iris. The lining cells of the digestive tube are cells of the inner layer, but the muscular and elastic coats are of middle-layer origin. The lining cells of the salivary glands arise from the outer layer where it is pushed in to form the mouth-pit; but the supporting framework of the glands is derived from the cells of the middle layer.

Enough has now been said to give some idea of the manner in which the different tissues and organs of the organism are elaborated by the gradual differentiation of the initially homogeneous ovum. The cells into which the fertilized egg segments are at first all alike; then comes the divergence between those which are pushed in to line the hollow of the cup, and those which form its outer layer. Thereafter follows the differentiation of a special band of outer cells to form the nervous system, and a special rod, derived from the inner cells, to form the primitive axial support. And when the middle layer has come into existence, its cells group themselves and differentiate along special lines to form gristle or bone, blood or muscle.

The description above given is a very generalized and diagrammatic description. There are various ways in which complexity is introduced into the developmental process. The store of nutritive material present in the egg, for example, profoundly modifies the segmentation so that where, as in the case of birds' eggs, there is a large amount of food-yolk, not all the ovum, but only a little patch on its surface, undergoes segmentation. In this little patch the embryo is formed. Break open an egg upon which a hen has been sitting for five or six days, and you will see the little embryo chick lying on the surface of the yolk. The large mass of yolk to which it is attached is simply a store of food-material from which the growing chick may draw its supplies.

For it is clear that the growing and developing embryo must obtain, in some way and from some source, the food-stuff for its nutrition. And this is effected, among different animals, in one of three ways. Either the embryo becomes at a very early stage a little, active, voracious, free-swimming larva, obtaining for itself in these early days of life its own living; as is the case, for example, with the oyster or the star-fish. Or the egg from which it is developed contains a large store of food-yolk, on which it can draw without stint; as is the case with birds. Or else the embryo becomes attached to the maternal

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organism in such a way that it can draw on her for all the nutriment which it may require; as is the case with the higher mammals.

In both these latter cases the food-material is drawn from the maternal organism, and is the result of parental sacrifice; but in different ways. In the case of the bird, the protoplasm of the ovum has acquired the power of storing up the by-products of its vital activity. The ovum of such an animal seems at first sight a standing contradiction to the statement, made some pages back, that the cell cannot grow to any great extent without undergoing division or fission; and this because volume tends to outrun surface. For the yolk of a bird's egg is a single cell, and is often of large size. But when we come to examine carefully these exceptional cases of very large cells—for what we call the yolk of an egg is, I repeat, composed of a single cell—we find that the formative protoplasm is arranged as a thin patch on one side of the yolk in the case of the bird's egg, or as a thin pellicle surrounding the yolk in the case of that of the lobster or the insect. All the rest is a product of protoplasmic life stowed away beneath the patch or within the pellicle. And this stored material is relatively stable and inert, not undergoing those vital disruptive changes which are characteristic of living formative protoplasm. The mass of formative protoplasm, even in the large eggs of birds, is not very great, and is so arranged as to offer a relatively extensive surface. All the rest, the main mass of the visible egg-yolk, is the stored product of a specialized activity of the formative protoplasm. But all this material is of parental origin—is elaborated from the nutriment absorbed and digested by the mother.

Thus we see, in the higher types of life, parental sacrifice, fosterage, and protection. For in the case of mammals and many birds, especially those which are born in a callow, half-fledged condition, even when the connection of mother and offspring is severed, or the supplies of food-yolk are exhausted, and the young are born or hatched, there is still a more or less prolonged period during which the weakly offspring are nourished by milk, by a secretion from the crop ("pigeon's milk"), or by food-stuff brought with assiduous care by the parents. There is a longer or shorter period of fosterage and protection—longer in the case of man than in that of any of the lower animals—ere the offspring are fitted to fend for themselves in life's struggle.

And accompanying this parental sacrifice, first in supplying food for embryonic development, and then in affording fosterage and protection during the early stages of growth, there is, as might well be supposed, a reduction in the number of ova produced and of young brought forth or hatched. Many of the lower organisms lay hundreds of thousands of eggs, each of which produces a living active embryo. The condor has but two downy fledglings in a year; the gannet lays annually but a single egg; while the elephant, in the hundred years of its life, brings forth but half a dozen young.

We shall have to consider by what means these opposite tendencies (a tendency to produce enormous numbers of tender, ill-equipped embryos, and a tendency to produce few well-equipped offspring) have been emphasized. The point now to be noted is that every organism, even the slowest breeder that exists, produces more young than are sufficient to keep up the numbers of the species. If every pair of organisms gave birth to a similar pair, and if this pair survived to do likewise, the number of individuals in the species would have no tendency either to increase or to diminish. But, as a matter of fact, animals actually do produce from three or four times to hundreds or even thousands of times as many new individuals as are necessary in this way to keep the numbers constant. This is the *law of increase*. It may be thus stated: *The number of individuals in every race or species of animals is tending*

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to increase. Practically this is only a tendency. By war, by struggle, by competition, by the preying of animals upon each other, by the stress of external circumstances, the numbers are thinned down, so that, though the births are many, the deaths are many also, and the survivals few. In the case of those species the numbers of which are remaining constant, out of the total number born only two survive to procreate their kind. We may judge, then, of the amount of extermination that goes on among those animals which produce embryos by the thousand or even the hundred thousand. The effects of this enormous death-rate on the progress of the race or species we shall have to consider in the next chapter, when the question of the differentiation of species is before us.

There is one form of differentiation, however, which we may glance at before closing this chapter—the differentiation of sex. We are not in a position to discuss the ultimate causes of sex-differentiation, but we may here note the proximate causes as they seem to be indicated in certain cases.

Among honey-bees there are males (drones), fertile females (queens), and imperfect or infertile females (workers). It has now been shown, beyond question, that the eggs from which drones develop are not fertilized. The presence or absence of fertilization in this case determines the sex. During the nuptial flight, a special reservoir, possessed by the queen bee, is stored with sperms in sufficient number to last her egg-laying life. It is in her power either to fertilize the eggs as they are laid or to withhold fertilization. If the nuptial flight is prevented, and the reservoir is never stored with sperms, she is incapable of laying anything but drone eggs. The cells in which drones are developed are somewhat smaller than those for ordinary workers; but what may be the nature of the stimulus that prompts the queen to withhold fertilization we at present do not know. The difference between the fertile queen and the unfertile worker seems to be entirely a matter of nutrition. If all the queenembryos should die, the workers will tear down the partitions so as to throw three ordinary worker-cells into one; they will destroy two of the embryos, and will feed the third on highly nutritious and stimulating diet; with the result that the ovaries and accessory parts are fully developed, and the grub that would have become an infertile worker becomes a fertile queen. And one of the most interesting points about this change, thus wrought by a stimulating diet, is that not only are the reproductive powers thus stimulated, but the whole organism is modified. Size, general structure, sense-organs, habits, instincts, and character are all changed with the development of the power of laying eggs. The organism is a connected whole, and you cannot modify one part without deeply influencing all parts. This is the *law of correlated variation*.

Herr Yung has made some interesting experiments on tadpoles. Under normal circumstances, the relation of females to males is about 57 to 43. But when the tadpoles were well fed on beef, the proportion of females to males rose so as to become 78 to 32; and on the highly nutritious flesh of frogs the proportion became 92 to 8. A highly nutritious diet and plenty of it caused a very large preponderance of females.

Mrs. Treat, in America, found that if caterpillars were half-starved before entering upon the chrysalis state, the proportion of males was much increased; while, if they were supplied with abundant nutritious food, the proportion of female insects was thereby largely increased. The same law is said to hold good for mammals. Favourable vital conditions are associated with the birth of females; unfavourable, with that of males. Herr Ploss attempts to show that, among human folk, in hard times there are more boys born; in good times, more girls.

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On the whole, we may say that there is some evidence to show that in certain cases favourable [60] conditions of temperature, and especially nutrition, tend to increase the number of females. We have seen that many animals pass through a stage where the reproductive organs are not yet differentiated into male and female, while in some there is a temporary stage where the outer parts of the organ produce ova and the inner parts sperms. We have also seen that the ova are cells where storage is in excess; the sperms are cells in which fission is in excess. Favourable nutritive conditions may, therefore, not incomprehensibly lead to the formation of well-stored ova; unfavourable nutritive conditions, on the other hand, to the formation of highly subdivided sperms. By correlated variation,[L] the ova-bearing or sperm-bearing individuals then develop into the often widely different males and females.

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CHAPTER IV. VARIATION AND NATURAL SELECTION.

Everything, so far as in it lies, said Benedict Spinoza, tends to persist in its own being. This is the law of persistence. It forms the basis of Newton's First Law of Motion, which enunciates that, if a body be at rest, it will remain so unless acted on by some external force; or, if it be in motion, it will continue to move in the same straight line and at a uniform velocity unless it is acted on by some external force. Practically every known body is thus affected by external forces; but the law of persistence is not thereby disproved. It only states what would happen under certain exceptional or perhaps impossible circumstances. To those ignorant of scientific procedure, it seems unsatisfactory, if not ridiculous, to formulate laws of things, not as they are, but as they might be. Many well-meaning but not very wellinformed people thus wholly misunderstand and mistake the value of certain laws of political economy, because in those laws (which are generalized statements of fact under narrowed and rigid conditions, and do not pretend to be inculcated as rules of conduct) benevolence, sentiment, even moral and religious duty, are intentionally excluded. These laws state that men, under motives arising out of the pursuit of wealth, will act in such and such a way, unless benevolence, sentiment, duty, or some other motive, lead them to act otherwise. Such laws, which hold good, not for phenomena in their entirety, but for certain isolated groups of facts under narrowed conditions, are called laws of the factors of phenomena. And since the complexity of phenomena is such that it is difficult for the human mind to grasp all the interlacing threads of causation at a single glance, men of science have endeavoured to isolate their several strands, and, applying the principle of analysis, without which reasoning is impossible, to separate out the factors and determine their laws. In this chapter we have to consider some of the factors of organic progress, and endeavour to determine their laws.

The law of heredity may be regarded as that of persistence exemplified in a series of organic generations. When, as in the amæba and some other protozoa, reproduction is by simple fission, two quite similar organisms being thus produced, there would seem to be no reason why (modifications by surrounding circumstances being disregarded) hereditary persistence should not continue indefinitely. Where, however, reproduction is effected by the detachment of a single cell from a many-celled organism, hereditary persistence^[M] will be complete only on the condition that this reproductive cell is in some way in direct continuity with the cells of the parent organism or the cell from which that parent organism itself developed. And where, in the higher animals, two cells from two somewhat different parents coalesce to give origin to a new individual, the phenomena of hereditary persistence are still further complicated by the blending of characters handed on in the ovum and the sperm; still further complication being, perhaps, produced by the emergence in the offspring of characters latent in the parent, but derived from an earlier ancestor. And if characters acquired by the parents in the course of their individual life be handed on to the offspring, yet further complication will be thus introduced.

It is no matter for surprise, therefore, that, notwithstanding the law of hereditary persistence, variations should occur in the offspring of animals. At the same time, it must be remembered that the occurrence of variations is not and cannot be the result of mere chance; but that all such variations are

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determined by some internal or external influences, and are thus legitimate and important subjects of biological investigation. In the next chapter we shall consider at some length the phenomena of heredity and the origin of variations. Here we will accept them without further discussion, and consider some of their consequences. But even here, without discussing their origin, we must establish the fact that variations do actually occur.

Variations may be of many kinds and in different directions. In colour, in size, in the relative development of different parts, in complexity, in habits, and in mental endowments, organisms or their organs may vary. Observers of mammals, of birds, and of insects are well aware that colour is a variable characteristic. But these colour-variations are not readily described and tabulated. In the matter of size the case is different. In Mr. Wallace's recent work on "Darwinism" a number of observations on size-variations are collected and tabulated. As this is a point of great importance, I propose to illustrate it somewhat fully from some observations I have recently made of the wing-bones of bats. In carrying out these observations and making the necessary measurements, I have had the advantage of the kind co-operation of my friend Mr. Henry Charbonnier, of Clifton, an able and enthusiastic naturalist. [N]

The nature of the bat's wing will be understood by the aid of the accompanying figure (Fig. 12). In the fore limb the arm-bone, or humerus, is followed by an elongated bone composed of the radius and ulna. At the outer end of the radius is a small, freely projecting digit, which carries a claw. This answers to the thumb. Then follow four long, slender bones, which answer to the bones in the palm of our hand. They are the metacarpals, and are numbered II., III., IV., and V. in the tabulated figures in which the observations are recorded. The metacarpals of the second and third digits run tolerably close together, and form the firm support of the anterior margin of the wing. Those of the third and fourth make a considerable angle with these and with each other, and form the stays of the mid part of the wing. Beyond the metacarpals are the smaller joints or phalanges of the digits, two or three to each digit. The third digit forms the anterior point or apex of the wing. The fourth and fifth digits form secondary points behind this. Between these points the wing is scalloped into bays.

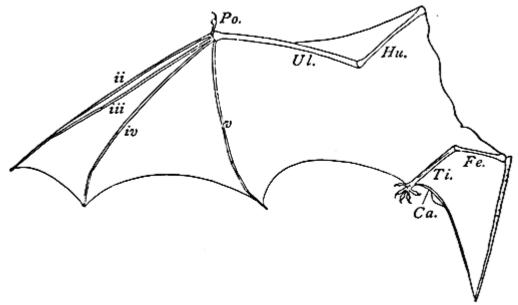


Fig. 12.—"Wing" of bat (Pipistrelle).

Hu., humerus, or arm-bone; *Ul.*, conjoined radius and ulna, a bone in the forearm; *Po.*, pollex, answering to our thumb; II., III., IV., V., second, third, fourth, and fifth digits of the manus, or hand. The figures are placed near the metacarpals, or palm-

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bones. These are followed by the phalanges. Fe., femur or thigh-bone; Ti., tibia, the chief bone of the shank. The digits of the pes, or foot, are short and bear claws. Ca., calcar.

From the point of the fifth or last digit the leathery wing membrane sweeps back to the ankle. The bones of the hind limb are the femur, or thigh-bone, and the tibia (with a slender, imperfectly developed fibula). There are five toes, which bear long claws. From the ankle there runs backward a long, bony and gristly spur, which serves to support the membrane which stretches from the ankle to the tip (or near the tip) of the tail.

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Thus the wing of the bat consists of a membrane stretched on the expanded or spread fingers of the hand, and sweeping from the point of the little finger to the ankle. Behind the ankle there is a membrane reaching to the tip of the tail. This forms a sort of net in which some bats, at any rate, as I have myself observed, can catch insects.

I have selected the wing of the bat to exemplify variation, (1) because the bones are readily measured even in dried specimens; (2) because they form the mutually related parts of a single organ; and (3) because they offer facilities for the comparison of variations, not only among the individuals of a single species, but also among several distinct species.

The method employed has been as follows: The several bones have been carefully measured in millimetres, [O] and all the bones tabulated for each species. Such tables of figures are here given in a condensed form for three species of bats.

			2nd Digit.	Third Digit.			Fourth Digit.			Fifth Digit.				
	R&U	Po	M.	M.	P1.	P23.	M.	P1.	P23.	M.	P1.	P23.	Tibia.	
Hairy-armed bat (Vesperugo leisleri).	41	6.5	38	40	16	19	38	14	7	32	8	7	16	8
	41	6	38	40	16	19	39	15.5	7	33	8	6.5	16	8
	41	6	39	40	16	18	39	16	6.5	33	8	7	16	8
	41.5	5	39	40.5	17	20	39	16	7	33	8	7	15	8
	40	6	39	37	15.5	18	37	14.5	7	32	8	6.5	15	9
	41	5.5	38.5	39	16.5	20	39	15	7.5	33	8	7.5	17	9
	41	6	39	40	15.5	20.5	39	15.5	7	33	8	7	16	9
Horseshoe bat (Rhinolophus ferri-equinum).	51	5	39	36	19	29	40	11	18	40	13	15	22	8
	54	5	40	36	18	32	40	11	19	40	14	16	28	9
	52	5	39	36	18	31	39	10	19	40	13	14	23	9
	54	5	39	36	18	32	40	11	17	40	13	13	25	9
	46	5	36	34	16	29	36	10	19	36	13	17	22	?
Lesser horseshoe bat (Rhinolophus hipposideros).	34	4	25	23	12	17	26	6.5	12	26	9	13	17	8
	37	3	26	24	13	20	28	8	13	28	9	14	17	8
	35	3	26	24.5	13	17	27	7	12	26	10	12	15	8

Bat-Measurements (in Millimetres).

Transcriber's note: In the preceding table some headings have been shortened to save space. The key is as follows:

• R&U: Radius and Ulna.

- Po: Pollex.
- M.: Metacarpal.
- P1.: Phalange 1.
- P23.: Phalange 2, 3.

If the mouse is held over the abbreviation, the full text appears.

It would be troublesome to the reader to pick out the meaning from these figures. I have, therefore, plotted in the measurements for four other species of bats in tabular form (Figs. 13, 14, 15, 16).

Fig. 13, for example, deals with the common large noctule bat, which may often be seen flying high up on summer evenings. Now, the mean length of the radius and ulna in eleven individuals was 51.5 millimetres. Suppose all the eleven bats had this bone (for the two bones form practically one piece) of exactly the same length. There would then be no variation. We may express this supposed uniformity by the straight horizontal line running across the part of the figure dealing with the radius and ulna. Practically the eleven bats measured did not have this bone of the same length; in some of them it was longer, in others it was shorter than the mean. Let us run through the eleven bats (which are represented by the numbers at the head of the table) with regard to this bone. The first fell below the average by a millimetre and a half, the length being fifty millimetres. This is expressed in the table by placing a dot or point three quarters of a division below the mean line. Each division on the table represents two millimetres, or, in other words, the distance between any two horizontal lines stands for two millimetres measured. Half a division, therefore, is equivalent to one measured millimetre; a quarter of a division to half a millimetre. The measurements are all made to the nearest half-millimetre. The second bat fell short of the mean by one millimetre. The bone measured 50.5 millimetres. The third exceeded the mean by a millimetre and a half; the fourth, by three millimetres and a half. The fifth was a millimetre and a half above the mean; and the sixth and seventh were both half a millimetre over the mean. The eighth fell short by half a millimetre; the ninth and tenth by a millimetre and a half; and the eleventh by two millimetres and a half. The points have been connected together by lines, so as to give a curve of variation for this bone.

> Fig 13.—The noctule (*Vesperugo noctula*). [68] Fig. 14.—The long-eared bat (*Plecotus auritus*). [69] Fig. 15.—The pipistrelle (Vesperugo pipistrellus). [70] Fig. 16.—The whiskered bat (Vespertilio mystacinus).

The other curves in these four tables are drawn in exactly the same way. The mean length is stated; and the amount by which a bone in any bat exceeds or falls short of the mean can be seen and readily estimated by means of the horizontal lines of the table. Any one can reconvert the tables into figures representing our actual measurements.

Now, it may be said that, since some bats run larger than others, such variation is only to be expected. That is true. But if the bones of the wing all varied equally, all the curves would be similar. That is clearly not the case. The second metacarpal is the same length in 5 and 6. But the third metacarpal is two millimetres shorter in 6 than in 5. In 10 the radius and ulna are *longer* than in 11; but [67]

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the second metacarpal is *shorter* in 10 than in 11. A simple inspection of the table as a whole will show that there is a good deal of *independent* variation among the bones.

The amount of variation is itself variable, and in some cases is not inconsiderable. In the long-eared bats 4 and 5 in <u>Fig. 14</u>, the phalanges of the third digit measured 26.5 millimetres in 4, and 34 millimetres in 5—a difference of more than 28 per cent. This is unusually large, and it is possible that there may have been some slight error in the measurements. [P] A difference of 10 or 12 per cent. is, however, not uncommon.

In any case, the observations here tabulated show (1) that variations of not inconsiderable amount occur among the related bones of the bat's wing; and (2) that these variations are to a considerable extent independent of each other.

So far we have compared a series of individuals of the same species of bat, each table in Figs. 13-16 dealing with a distinct species. Let us now compare the different species with each other. To effect such a comparison, we must take some one bone as our standard, and we must level up our bats for the purposes of tabulation. I have selected the radius and ulna as the standard. In both the noctule and the greater horseshoe bats the mean length of this bone is 51.5 millimetres. The bones of each of the other bats have been multiplied by such a number as will bring them up to the level of size in these two species. Mr. Galton, in his investigations on the variations of human stature, had to take into consideration the fact that men are normally taller than women. He found, however, that the relation of man to woman, so far as height is concerned, is represented by the proportion 108 to 100. By multiplying female measurements by 1.08, they were brought up to the male standard, and could be used for purposes of comparison. In the same way, by multiplying in each case by the appropriate number, I have brought all the species in the table (Fig. 17) up to the standard of the noctule. When so multiplied, the radius and ulna (selected as the standard of comparison) has the same length in all the species, and is hence represented by the horizontal line in the table.

Fig. 17.—Variations adjusted to the standard of the noctule.

Compared with this as a standard, the mean length of the second metacarpal in the seven species is forty-three millimetres; that of the third metacarpal, forty-four millimetres; and so on. The amount by which each species exceeds or falls short of the mean is shown on the table, and the points are joined up as before. Here, again, the table gives the actual measurements in each case. For example, if the mean length of the third metacarpal of the greater horseshoe bat be required, it is seen by the table to fall short of the mean by four horizontal divisions and a quarter, that is to say, by eight millimetres and a half. The length is therefore (44 - 8-1/2) 35.5 millimetres.

Now, it will be seen from the table that the variation in the mean length of the bones in different species is much greater than the individual variations in the members of the same species. The table also brings out in an interesting way the variation in the general character of the wing. The noctule, for example, is especially strong in the development of the second and third metacarpals, the phalanges of the third digit being also a little above the average. Reference to the figure of the bat's wing on p. 64 will show that these excellences give length to the wing. It fails, however, in the metacarpal and phalanges of the fifth digit, and in the length of the hind leg as represented by the tibia. On consulting

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the figure of the wing, it is seen that these are the bones which give breadth to the wing. Here the noctule fails. Its wing is, therefore, long and narrow. It is a swallow among bats.

On the other hand, the horseshoe bats fail conspicuously in the second and third metacarpals, though they make up somewhat in the corresponding digits. On the whole, the wing is deficient in length. But the phalanges of the fourth and fifth digits, and the length of the hind limb represented by the tibia, give a corresponding increase of breadth. The wing is, therefore, relatively short and broad. The long-eared bat, again, has the third metacarpal and its digits somewhat above the mean, and therefore a somewhat more than average length. But it has the fifth metacarpal with its digit and also the tibia decidedly above the mean, and therefore more than average breadth. Without possessing the great length of the noctule's wing, or the great breadth of that of the horseshoe, it still has a more than average length and breadth.

The total wing-areas are very variable, the females having generally an advantage over the males. I do not feel that our measurements are sufficiently accurate to justify tabulation. Taking, however, the radius and ulna as the standard for bringing the various species up to the same level, the greater horseshoe seems to have decidedly the largest wing-area; the noctule stands next; then come the lesser horseshoe and the long-eared bat; somewhat lower stands the hairy-armed bat; while the pipistrelle and the whiskered bat (both small species) stand lowest. [Q]

Sufficient has now been said in illustration of the fact that variations in the lengths of the bones in the bat's wing do actually occur in the various individuals of one species; that the variations are independent; and that the different species and genera have the character of the wing determined by emphasizing, so to speak, variations in special directions. I make no apology for having treated the matter at some length. Those who do not care for details will judiciously exercise their right of skipping.

As before mentioned, Mr. Wallace has collected and tabulated other observations on size and length variations. And in addition to such variations, there are the numerous colour-variations that do not admit of being so readily tabulated. Mr. Cockerell tells us that among snail-shells, taking variations of banding alone, he knows of 252 varieties of *Helix nemoralis* and 128 of *H. hortensis*.^[R]

That variations do occur under nature is thus unquestionable. And it is clear that all variations necessarily fall under one of three categories. Either they are of advantage to the organism in which they occur; or they are disadvantageous; or they are neutral, neither advantageous nor disadvantageous to the animal in its course through life.

We must next revert to the fact to which attention was drawn in the last chapter, that every species is tending, through natural generation, to increase in numbers. Even in the case of the slow-breeding elephant, the numbers tend to increase threefold in each generation; for a single pair of elephants give birth to three pairs of young. In many animals the tendency is to increase ten, twenty, or thirtyfold in every generation; while among fishes, amphibians, and great numbers of the lower organisms, the tendency is to multiply by a hundredfold, a thousandfold, or even in some cases ten thousandfold. But, as before noticed, this is only a tendency. The law of increase is a law of one factor in life's phenomena, the reproductive factor. In any area, the conditions of which are not undergoing change, the numbers of

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the species which constitute its fauna remain tolerably constant. They are not actually increasing in geometrical progression. There is literally no room for such increase. The large birth-rate of the constituent species is accompanied by a proportionate death-rate, or else the tendency is kept in check by the prevention of certain individuals from mating and bearing young.^[S]

Now, the high death-rate is, to a large extent among the lower organisms and in a less degree among higher animals, the result of indiscriminate destruction. When the ant-bear swallows a tongueload of ants, when the Greenland whale engulfs some hundreds of thousands of fry at a gulp, when the bear or the badger destroys whole nests of bees,—in such cases there is wholesale and indiscriminate destruction. Those which are thus destroyed are nowise either better or worse than those which escape. At the edge of a coral reef minute, active, free-swimming coral embryos are set free in immense numbers. Presently they settle down for life. Some settle on a muddy bottom, others in too great a depth of water. These are destroyed. The few which take up a favourable position survive. But they are no better than their less fortunate neighbours. The destruction is indiscriminate. So, too, among fishes and the many marine forms which produce a great number of fertilized eggs giving rise to embryos that are from an early period free-swimming and self-supporting. Such embryos are decimated by a destruction which is quite indiscriminate. And again, to take but one more example, the liver-fluke, whose lifehistory was sketched in the last chapter, produces its tens or hundreds of thousands of ova. But the chances are enormously against their completing their life-cycle. If the conditions of temperature and moisture are not favourable, the embryo is not hatched or soon dies; even if it emerges, no further development takes place unless it chances to come in contact with a particular and not very common kind of water-snail. When it emerges from the intermediate host and settles on a blade of grass, it must still await the chance of that blade being eaten by a sheep or goat. It is said that the chances are eight millions to one against it, and for the most part its preservation is due to no special excellence of its own. The destruction is to a large extent, though not entirely, indiscriminate.

Even making all due allowance, however, for this indiscriminate destruction—which is to a large extent avoided by those higher creatures which foster their young—there remain more individuals than suffice to keep up the normal numbers of the species. Among these there arises a struggle for existence, and hence what Darwin named *natural selection*.

"How will the struggle for existence"—I quote, with some omissions, the words of Darwin—"act in regard to variation? Can the principle of selection, which is so potent in the hands of man, apply under nature? I think that we shall see that it can act most efficiently. Let the endless number of slight variations and individual differences be borne in mind; as well as the strength of the hereditary tendency. Let it also be borne in mind how infinitely complex and close-fitting are the mutual relations of all organic beings to each other and to their physical conditions of life; and consequently what infinitely varied diversities of structure might be of use to each being under changing conditions of life. Can it, then, be thought improbable, seeing that variations useful to man have undoubtedly occurred, that other variations, useful in some way to each being in the great and complex battle of life, should occur in the course of many successive generations? If such do occur, can we doubt (remembering that many more individuals are born than can possibly survive) that individuals having any advantage, however slight, over others, would have the best chance of surviving and of procreating their kind? On the other hand, we may feel sure that any variation in the least degree injurious would be rigidly destroyed. This preservation of favourable individual differences and variations, and the destruction of

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those which are injurious, I have called Natural Selection, or the Survival of the Fittest. Variations neither useful nor injurious would not be affected by natural selection, and would be left either a fluctuating element, or would ultimately become fixed, owing to the nature of the organism and the nature of the conditions."[T]

"The principle of selection," says Darwin, elsewhere, "may conveniently be divided into three kinds. *Methodical selection* is that which guides a man who systematically endeavours to modify a breed according to some predetermined standard. *Unconscious selection* is that which follows from men naturally preserving the most valued and destroying the less valued individuals, without any thought of altering the breed. Lastly, we have *Natural selection*, which implies that the individuals which are best fitted for the complex and in the course of ages changing conditions to which they are exposed, generally survive and procreate their kind."[U]

I venture to think that there is a more logical division than this. A man who is dealing with animals or plants under domestication may proceed by one of two well-contrasted methods. He may either select the most satisfactory individuals or he may reject the most unsatisfactory. We may term the former process *selection*, the latter *elimination*. Suppose that a gardener is dealing with a bed of geraniums. He may either pick out first the best, then the second best, then the third, and so on, until he has selected as many as he wishes to preserve. Or, on the other hand, he may weed out first the worst, then in succession other unsatisfactory stocks, until, by eliminating the failures, he has a residue of sufficiently satisfactory flowers. Now, I think it is clear that, even if the ultimate result is the same (if, that is to say, he selects the twenty best, or eliminates all but the twenty best), the method of procedure is in the two cases different. Selection is applied at one end of the scale, elimination at the other. There is a difference in method in picking out the wheat-grains (like a sparrow) and scattering the chaff by the wind.

Under nature both methods are operative, but in very different degrees. Although the insect may select the brightest flowers, or the hen-bird the gaudiest or most tuneful mate, the survival of the fittest under nature is in the main the net result of the slow and gradual process of the elimination of the unfit.

[V] The best-adapted are not, save in exceptional cases, selected; but the ill-adapted are weeded out and eliminated. And this distinction seems to me of sufficient importance to justify my suggestion that natural selection be subdivided under two heads—natural elimination, of widespread occurrence throughout the animal world; and selection proper, involving the element of individual or special choice.

The term "natural elimination" for the major factor serves definitely to connect the natural process with that struggle for existence out of which it arises. The struggle for existence is indeed the reaction of the organic world called forth by the action of natural elimination. Organisms are tending to increase in geometrical ratio. There is not room or subsistence for the many born. The tendency is therefore held in check by elimination, involving the struggle for existence. And the factors of elimination are three: first, elimination through the action of surrounding physical or climatic conditions, under which head we may take such forms of disease as are not due to living agency; secondly, elimination by enemies, including parasites and zymotic diseases; and thirdly, elimination by competition. It will be convenient to give some illustrative examples of each of these.

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Elimination through the action of surrounding physical conditions, taken generally, deals with the very groundwork or basis of animal life. There are certain elementary mechanical conditions which must be fulfilled by every organism however situated. Any animal which fails to fulfil these conditions will be speedily eliminated. There are also local conditions which must be adequately met. Certain tropical animals, if transferred to temperate or sub-Arctic regions, are unable to meet the requirements of the new climatic conditions, and rapidly or gradually die. Fishes which live under the great pressure of the deep sea are killed by the expansion of the gases in their tissues when they are brought to the surface. Many fresh-water animals are killed if the lake in which they live be invaded by the waters of the sea. If the water in which corals live be too muddy, too cold, or too fresh—near the mouth of a great river on the Australian coast, for example—they will die off. During the changes of climate which preceded and followed the oncoming of the glacial epoch, there must have been much elimination of this order. Even under less abnormal conditions, the principle is operative. Darwin tells us that in the winter of 1854-5 four-fifths of the birds in his grounds perished from the severity of the weather, and we cannot but suppose that those who were thus eliminated were less able than others to cope with or stand the effects of the inclement climatic conditions. My colleague, Mr. G. Munro Smith, informs me that, in cultivating microbes, certain forms, such as Bacillus violaceus and Micrococcus prodigiosus, remain in the field during cold weather when other less hardy microbes have perished. The insects of Madeira may fairly be regarded as affording another instance. The ground-loving forms allied to insects of normally slow and heavy flight have in Madeira become wingless or lost all power of flight. Those which attempted to fly have been swept out to sea by the winds, and have thus perished; those which varied in the direction of diminished powers of flight have survived this eliminating process. On the other hand, among flower-frequenting forms and those whose habits of life necessitate flight, the Madeira insects have stronger wings than their mainland allies. Here, since flight could not be abandoned without a complete change of life-habit, since all must fly, those with weaker powers on the wing have been eliminated, leaving those with stronger flight to survive and procreate their kind. [W] In Kerguelen Island Mr. Eaton has found that all the insects are incapable of flight, and most of them in a more or less wingless condition. [X] Mr. Wallace regards the reduction in the size of the wing in the Isle of Man variety of the small tortoiseshell butterfly as due to the gradual elimination of larger-winged individuals.[Y] These are cases of elimination through the direct action of surrounding physical conditions. Even among civilized human folk, this form of elimination is still occasionally operative in military campaigns, for example (where the mortality from hardships is often as great as the mortality from shot or steel), in Arctic expeditions, and in arduous travels. But in early times and among savages it must be a more important factor.

Elimination by enemies needs somewhat fuller exemplification. Battle within battle must, throughout nature, as Darwin says, be continually recurring with varying success. The stronger devour the weaker, and wage war with each other over the prey. In the battle among co-ordinates the weaker are eliminated, the stronger prevail. When the weaker are preyed upon by the stronger and a fair fight is out of the question, the slow and heavy succumb, the agile and swift escape; stupidity means elimination, cunning, survival; to be conspicuous, unless it be for some nasty or deleterious quality, is inevitably to court death: the sober-hued stand at an advantage. In these cases, if there be true selection at work, it is the selection of certain individuals, the plumpest and most toothsome to wit, for destruction, not for survival.

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This mode of elimination has been a factor in the development of protective resemblance and so-called mimicry, and we may conveniently illustrate it by reference to these qualities. If the hue of a creature varies in the direction of resemblance to the normal surroundings, it will render the animal less conspicuous, and therefore less liable to be eliminated by enemies. This is well seen in the larvæ or caterpillars of many of our butterflies and moths. It is not easy to distinguish the caterpillar of the clouded yellow, so closely does its colour assimilate to the clover leaves on which it feeds, nor that of the Lulworth skipper on blades of grass. I would beg every visitor to the Natural History Museum at South Kensington to look through the drawers containing our British butterflies and moths and their larvæ, in the further room on the basement, behind the inspiring statue of Charles Darwin. Half an hour's inspection will serve to bring home the fact of protective resemblance better than many words.

It may, however, be remarked that not all the caterpillars exhibit protective resemblance; and it may be asked—How have some of these conspicuous larvæ, that of the magpie moth, for example, escaped elimination? What is sauce for the Lulworth goose should be sauce for the magpie gander. How is it that these gaudy and variable caterpillars, cream-coloured with orange and black markings, have escaped speedy destruction? Because they are so nasty. No bird, or lizard, or frog, or spider would touch them. They can therefore afford to be bright-coloured. Nay, their very gaudiness is an advantage, and saves them from being the subject of unpleasant experiments in the matter. Other caterpillars, like the palmer-worms, are protected by barbed hairs that are intensely irritating. They, too, can afford to be conspicuous. But a sweet and edible caterpillar, if conspicuous, is eaten, and thus by the elimination of the conspicuous the numerous dull green or brown larvæ have survived.

A walk through the Bird Gallery in the National collection will afford examples of protective resemblance among birds. Look, for example, at the Kentish plover with its eggs and young—faithfully reproduced in our frontispiece—and the way in which the creature is thus protected in early stages of its life will be evident. The stone-curlew, the ptarmigan, and other birds illustrate the same fact, which is also seen with equal clearness in many mammals, the hare being a familiar example.

Many oceanic organisms are protected through general resemblance. Some, like certain medusæ, are transparent. The pellucid or transparent sole of the Pacific (Achirus pellucidus), a little fish about three inches long, is so transparent that sand and seaweed can be seen distinctly through its tissues. The salpa is transparent save for the intestine and digestive gland, which are brown, and look like shreds of seaweed. Other forms, like the physalia, are cærulean blue. The exposed parts of flat-fish are brown and sandy coloured or speckled like the sea-bottom; and in some the sand-grains seem to adhere to the skin. So, too, with other fish. "Looking down on the dark back of a fish," says Mr. A. R. Wallace, "it is almost invisible, while to an enemy looking up from below, the light under surface would be equally invisible against the light of clouds and sky." Even some of the most brilliant and gaudiest fish, such as the coral-fish (Chætodon, Platyglossus, and others), are brightly coloured in accordance with the beautiful tints of the coral-reefs which form their habitat; the bright-green tints of some tropical forest birds being of like import. No conception of the range of protective resemblance can be formed when the creatures are seen or figured isolated from their surroundings. The zebra is a sufficiently conspicuous animal in a menagerie or a museum; and yet Mr. Galton assures us that, in the bright starlight of an African night, you may hear one breathing close by you, and be positively unable to see the animal. A black animal would be visible; a white animal would be visible; but the zebra's black and white so blend in the dusk as to render him inconspicuous.

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To cite but one more example, this time from the invertebrates. Professor Herdman found in a rock-pool on the west coast of Scotland "a peculiarly coloured specimen of the common sea-slug (*Doris tuberculata*). It was lying on a mass of volcanic rock of a dull-green colour, partially covered with rounded spreading patches of a purplish pink nullipore, and having numerous whitish yellow *Spirorbis* shells scattered over it—the general effect being a mottled surface of dull green and pink peppered over with little cream-coloured spots. The upper surface of the Doris was of precisely the same colours arranged in the same way.... We picked up the Doris, and remarked the brightness and the unusual character of its markings, and then replaced it upon the rock, when it once more became inconspicuous."[Z]

Then, too, there are some animals with variable protective resemblance—the resemblance changing with a changing environment. This is especially seen in some Northern forms, like the Arctic hare and fox, which change their colour according to the season of the year, being brown in summer, white and snowy in winter. The chamæleon varies in colour according to the hue of its surroundings through the expansion and contraction of certain pigment-cells; while frogs and cuttle-fish have similar but less striking powers. Mr. E. B. Poulton's[AA] striking and beautiful experiments show that the colours of caterpillars and chrysalids reared from the same brood will vary according to the colour of their surroundings.

Fig. 18.—Caterpillar of a moth (*Ennomos tiliaria*) on an oak-spray. (From an exhibit in the British Natural History Museum.)]

If this process of protective resemblance be carried far, the general resemblance in hue may pass into special resemblance to particular objects. The stick-insect and the leaf-insect are familiar illustrations, though no one who has not seen them in nature can realize the extent of the resemblance. Most of us have, at any rate, seen the stick-caterpillars, or loopers (Fig. 18), though, perhaps, few have noticed how wonderful is the protective resemblance to a twig when the larva is still and motionless, for the very reason that the resemblance is so marked that the organism at that time escapes, not only casual observation, but even careful search. Fig. 19 gives a representation of a locust with special protective resemblance to a leaf—not a perfect leaf, but a leaf with fungoid blotches. This insect and the stick-caterpillar may be seen in the insect exhibits on the basement at South Kensington, having been figured from them by the kind permission of Professor Flower.

Fig. 19.—A locust (*Cycloptera speculata*) which closely resembles a leaf. (From an exhibit in the British Natural History Museum.)]

Perhaps one of the most striking instances of special protective resemblance is that of the Malayan leaf-butterfly (*Kallima paralecta*). So completely, when the wings are closed, does this insect resemble a leaf that it requires a sharp eye to distinguish it. These butterflies have, moreover, the habit of alighting very suddenly. As a recent observer (Mr. S. B. T. Skertchly) remarks, they "fly rapidly along, as if late for an appointment, suddenly pitch, close their wings, and become leaves. It is generally done so rapidly that the insect seems to vanish." [AB] Instances might be multiplied indefinitely. Mr. Guppy thus describes a species of crab in the Solomon Islands: "The light purple colour of its carapace corresponds with the hue of the coral at the base of the branches, where it lives; whilst the light red colour of the big claws, as they are held up in their usual attitude, similarly imitates the colour of the

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branches. To make the guise more complete, both carapace and claws possess rude hexagonal markings which correspond exactly in size and appearance with the polyp-cells of the coral."[AC]

When the special protective resemblance is not to an inanimate object, but to another organism, it is termed mimicry. It arises in the following way:—

Many forms, especially among the invertebrates, escape elimination by enemies through the development of offensive weapons (stings of wasps and bees), a bitter taste (the Heliconidæ among butterflies), or a hard external covering (the weevils among beetles). The animals which prey upon these forms learn to avoid these dangerous, nasty, or indigestible creatures; and the avoidance is often instinctive. It thus becomes an advantage to other forms, not thus protected, to resemble the animals that have these characteristics. Such resemblance is termed mimicry, concerning which it must be remembered that the mimicry is unconscious, and is reached by the elimination of those forms which do not possess this resemblance. Thus the *Leptalis*, a perfectly sweet insect, closely resembles the *Methona*, a butterfly producing an ill-smelling yellow fluid. The quite harmless *Clytus arietis*, a beetle, resembles, not only in general appearance, but in its fussy walk, a wasp. The soft-skinned *Doliops*, a longicorn, resembles the strongly encased *Pachyrhyncus orbifex*, a weevil. The not uncommon fly *Eristalis tenax* (Fig. 20), is not unlike a bee, and buzzes in an unpleasantly suggestive manner. [AD]

Mimicry is not confined to the invertebrates. A harmless snake, the eiger-eter of Dutch colonists at the Cape, subsists mainly or entirely on eggs. The mouth is almost or quite toothless; but in the throat hard-tipped spines project into the gullet from the vertebræ of the column in this region. Here the egg is broken, and there is no fear of losing the contents. Now, there is one species of this snake that closely resembles the berg-adder. The head has naturally the elongated form characteristic of the harmless snakes. But when irritated, this egg-eater flattens it out till it has the usual viperine shape of the "club" on a playing-card. It coils as if for a spring, erects its head with every appearance of anger, hisses, and darts forward as if to strike its fangs into its foe, in every way imitating an enraged berg-adder. The snake is, however, quite harmless and inoffensive.[AE]

Here we have mimicry both in form and habit. Another case of imperfect but no doubt effectual mimicry is given by Mr. W. Larden, in some notes from South America. [AF] Speaking of the rhea, or South American ostrich, he says, "One day I came across an old cock in a nest that it had made in the dry weeds and grass. Its wings and feathers were loosely arranged, and looked not unlike a heap of dried grass; at any rate, the bird did not attract my attention until I was close on him. The long neck was stretched out close along the ground, the crest feathers were flattened, and an appalling hiss greeted my approach. It was a pardonable mistake if for a moment I thought I had come across a huge snake, and sprang back hastily under this impression."

Protective resemblance and mimicry have been considered at some length because, on the hypothesis of natural selection, they admirably illustrate the results which may be reached through long-continued elimination by enemies.

Sufficient has now been said to show that this form of elimination is an important factor. We are not at present considering the question how variations arise, or why they should take any particular direction. But granting the fact that variations may and do occur in all parts of the organism, it is clear

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that, in a group of organisms surrounded by enemies, those individuals which varied in the direction of swiftness, cunning, inconspicuousness, [AG] or resemblance to protected forms, would, other things being equal, stand a better chance of escaping elimination.

Elimination by competition is, as Darwin well points out, keenest between members of the same group and among individuals of the same species, or between different groups or different species which have, so to speak, similar aims in life. While enemies of various kinds are preying upon weaker animals, and thus causing elimination among them, they are also competing one with another for the prey. While the slower and stupider organisms are succumbing to their captors, and thus leaving more active and cunning animals in possession of the field, the slower and stupider captors, failing to catch their cunning and active prey, are being eliminated by competition. While protective resemblance aids the prey to escape elimination by enemies, a correlative resemblance, called by Mr. Poulton aggressive resemblance, in the captors aids them in stealing upon their prey, and so gives advantage in competition. Thus the hunting spider closely resembles the flies upon which he pounces, even rubbing his head with his fore legs after their innocent fashion.

As in the case of protective resemblance, so, too, in its aggressive correlative, the resemblance may be general or special, or may reach the climax of mimicry. And since the same organism is not only a would-be captor, but sometimes an unwilling prey, the same resemblance may serve to protect it from its enemies and to enable it to steal upon its prey. The mantis, for example, gains doubly by its resemblance to the vegetation among which it lives. Certain spiders, described by Mr. H. O. Forbes, in Java, closely resemble birds'-droppings. This may serve to protect them from elimination by birds; but it also enables them to capture without difficulty unwary butterflies, which are often attracted by such excreta. A parasitic fly (*Volucella bombylans*) closely resembles (Fig. 20) a bumble-bee (*Bombus muscorum*), and is thus enabled to enter the nest of the bee without molestation. Its larvæ feed upon the larvæ of the bee. The cuckoo bee *Psithyrus rupestris*, an idle quean, who collects no pollen, and has no pollen-baskets, steals into the nest of the bumble-bee *Bombus lapidarius*, and lays her eggs there. The resemblance between the two is very great, and it not only enables the mother bee to enter unmolested, but the young bees, when they are hatched, to escape. Another bee (*Nomada solidaginis*), which plays the cuckoo on *Halictus cylindricus*, does not resemble this bee, but is wasp-like, and thus escapes molestation, not because it escapes notice, but because it looks more dangerous than it really is. [AH]

Many are the arts by which, in keen competition, organisms steal a march upon their congeners—not, be it remembered, through any conscious adaptation, but through natural selection by elimination. Mr. Poulton describes an Asiatic lizard (*Phrynocephalus mystaceus*) in which the "general surface resembles the sand on which it is found, while the fold of their skin at each angle of the mouth is of a red colour, and is produced into a flower-like shape exactly resembling a little red flower which grows in the sand. Insects, attracted by what they believe to be flowers, approach the mouth of the lizard, and are, of course, captured." [AI] The fishing frog, or angler-fish, is possessed of filaments which allure small fry, who think them worms, into the neighbourhood of the great mouth in which they are speedily engulfed; and certain deep-sea forms discovered during the *Challenger* expedition have the lure illumined by phosphorescent light.

Fig. 20.—Mimicry of bees by flies.

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a, b, Bombus muscorum; c, d, Volucella bombylans; e, Eristalis tenax; f, Apis mellifica. The underwings of the hive bee (f) were invisible in the photograph from which the figure was drawn. (From an exhibit in the British Natural History Museum.)]

We need say no more in illustration of the resemblances which have enabled certain organisms to escape elimination by competition. Once more, be it understood that we are not at present considering *how* any of these resemblances have been brought about; we are merely indicating that, given certain resemblances, advantageous either for captor or prey, those organisms which possess them not will have to suffer elimination—elimination by enemies, or else elimination by competition.

The interaction between these two kinds of elimination is of great importance. Hunters and hunted are both, so to speak, playing the game of life to the best of their ability. Those who fail on either side are weeded out; and elimination is carried so far that those who are only as good as their ancestors are placed at a disadvantage as compared with their improving congeners. The standard of efficiency is thus improving on each side; and every improvement on the one side entails a corresponding advance on the other. Nor is there only thus a competition for subsistence, and arising thereout a gradual sharpening of all the bodily and mental powers which could aid in seeking or obtaining food; there is also in some cases a competition for mates, reaching occasionally the climax of elimination by battle. There is, indeed, competition for everything which can be an object of appetence to the brute intelligence; and, owing to the geometrical tendency in multiplication—the law of increase—the competition is keen and unceasing.

Such, then, in brief, are the three main modes of elimination: elimination by physical and climatic conditions; elimination by enemies; elimination by competition. Observe that it is a differentiating process. Unlike the indiscriminate destruction before alluded to, the incidence of which is on all alike, good, bad, and indifferent, it separates the well-adapted from the ill-adapted, dooming the latter to death, and allowing the former to survive and procreate their kind. The destruction is not indiscriminate, but differential.

Let us now turn to cases of selection, properly so called, where Nature is in some way working at the other end of the scale; where her method is not the elimination of the unfit, but the selection of the fit. Such a case may be found on Darwin's principles in brightly coloured flowers and fruits. "Flowers," he says, "rank amongst the most beautiful productions of nature; but they have been rendered conspicuous in contrast with the green leaves, and, in consequence, at the same time beautiful, so that they may be easily observed by insects. I have come to this conclusion from finding it an invariable rule that, when a flower is fertilized by the wind, it never has a gaily coloured corolla. Several plants habitually produce two kinds of flowers—one kind open and coloured, so as to attract insects; the other closed, not coloured, destitute of nectar, and never visited by insects. Hence we may conclude that, if insects had not been developed on the face of the earth, our plants would not have been decked with beautiful flowers, but would have produced only such poor flowers as we see on our fir, oak, nut, and ash trees, on grasses, spinach, docks, and nettles, which are all fertilized through the agency of the wind. A similar line of argument holds good with fruits; that a ripe strawberry or cherry is as pleasing to the eye as to the palate; that the gaily coloured fruit of the spindle-wood tree, and the scarlet berries of the holly, are beautiful objects,—will be admitted by every one. But this beauty serves merely as a guide to birds and beasts, in order that the fruit may be devoured and manured seeds disseminated: I infer that this is the case from having as yet found no exception to the rule that seeds are always thus

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disseminated when embedded within a fruit of any kind (that is, within a fleshy or pulpy envelope), if it be coloured of any brilliant tint, or rendered conspicuous by being white or black."[AJ]

Here we have a case of the converse of elimination—a case of genuine selection under nature. But even here the process of elimination also comes into play, for the visitations of flowers by insects involve cross-fertilization. The flowers of two distinct individuals of the same species of plants in this manner fertilize each other; and the act of crossing, as Darwin firmly believed, though it is doubted by some observers nowadays, gives rise to vigorous seedlings, which consequently would have the best chance of flourishing and surviving—would best resist elimination by competition. So that we here have the double process at work; the fairest flowers being selected by insects, and those plants which failed to produce such flowers being eliminated as the relatively unfit.

If we turn to the phenomena of what Darwin termed sexual selection, we find both selection and elimination brought into play. By the law of battle, the weaker and less courageous males are eliminated so far as the continuation of their kind is concerned. By the individual choice of the females (on Darwin's view, by no means universally accepted), the finer, bolder, handsomer, and more tuneful wooers are selected.

Let us again hear the voice of Darwin himself. "Most male birds," he says, "are highly pugnacious during the breeding season, and some possess weapons especially adapted for fighting with their rivals. But the most pugnacious and the best-armed males rarely or never depend for success solely on their power to drive away or kill their rivals, but have special means for charming the female. With some it is the power of song, or of emitting strange cries, or of producing instrumental music; and the males in consequence differ from the females in their vocal organs or in the structure of certain feathers. From the curiously diversified means for producing various sounds, we gain a high idea of the importance of this means of courtship. Many birds endeavour to charm the females by love-dances or antics, performed on the ground or in the air, and sometimes at prepared places. But ornaments of many kinds, the most brilliant tints, combs and wattles, beautiful plumes, elongated feathers, top-knots, and so forth, are by far the commonest means. In some cases, mere novelty appears to have acted as a charm. The ornaments of the males must be highly important to them, for they have been acquired in not a few cases at the cost of increased danger from enemies, and even at some loss of power in fighting with their rivals[AK].... What, then, are we to conclude from these facts and considerations? Does the male parade his charms with so much pomp and rivalry for no purpose? Are we not justified in believing that the female exerts a choice, and that she receives the addresses of the male who pleases her most?"[AL]

Here again, then, we have the combined action of elimination and selection. And now we may note that selection involves intelligence—involves the play of appetence and choice. Hence it is that, when we come to consider the evolution of human-folk, the principle of elimination is so profoundly modified by the principle of selection. Not only are the weaker eliminated by the inexorable pressure of competition, but we select the more fortunate individuals and heap upon them our favours. This enables us also to soften the rigour of the blinder law; to let the full stress of competitive elimination fall upon the worthless, the idle, the profligate, and the vicious; but to lighten its incidence on the deserving but unfortunate.

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Both selection and elimination occurring under nature, but elimination having by far the wider scope, we may now inquire what will be their effect as regards the three modes of variationadvantageous, disadvantageous, and neutral. It must be remembered that these modes are relative and dependent upon circumstances, so that variations, neutral under certain conditions, may become relatively disadvantageous under other conditions. Selection clearly leads to the preservation of advantageous variations alone, and these variations are advantageous in so far as they meet the taste of the selecting organism. For selection depends upon individual choice; and uniformity of selection is entirely dependent upon uniformity in the standard of taste. If, as Darwin contends, the splendid plumage and tuneful notes of male birds are the result of a selection of mates by the hens, there must be a remarkable uniformity of taste among the hens of each particular species, since there is a uniformity of coloration among the cock-birds. It may be said that in all their mental endowments there is greater uniformity among animals than among men; and it is true that individuation has not been carried so far in them as in human-folk. Still, careful observers of animals see in them many signs of individual character; and this uniformity in the standard of taste in each species of birds seems to many naturalists a real difficulty in the way of the acceptance of sexual selection. We shall, however, return to this point. For the present it is clear that selection chooses out advantageous variations, that the advantage is determined by the taste of the selector, and that uniform selection implies uniformity of taste.

Turning to elimination, it is clear that it begins by weeding out, first the more disadvantageous, then the less disadvantageous variations. It leaves both the advantageous and the neutral in possession of the field. I imagine that many, perhaps most, of the variations tabulated by Mr. Wallace and other observers belong to the neutral category. Their fluctuating character seems to indicate that this is so. In any case, they are variations which have so far escaped elimination. And I think they are of great and insufficiently recognized importance. They permit, through interbreeding, of endless experiments in the combination of variations, some of which cannot fail to give favourable results.

It is just possible that it may be asked—If in natural elimination there is nothing more than the weeding out of the unfit and the suppression of disadvantageous variations, where is the possibility of advance? The standard may thus be maintained, but where is the possibility of progress? Such an objection would, however, imply forgetfulness of the fact that all the favourable variations remain to leaven the residual lump. Given a mean, with plus and minus variations: if in any generations the minus variations are got rid of, the mixture of the mean with the plus variations will give a new mean nearer the plus or advantageous end of the scale than the old mean. By how much the favourable variations tend to raise the mean standard, by so much will the race tend to advance. But in this process I see no reason why the neutral variations should be eliminated, except in so far as, in the keen struggle for existence, they become relatively unfavourable.

It is clear, however, that the intercrossing and interbreeding which occurs between average individuals on the one hand, and those possessing favourable variations on the other, while it tends gradually to raise the mean standard, tends also at the same time to reduce the advantageous variations towards the mean. It must tend to check advance by leaps and bounds, and to justify the adage, *Natura nil facit per saltum*. At the same time, it will probably have a greater tendency to reduce to a mean level neutral variations indefinite in direction than advantageous variations definite in direction. Still, it is a most important factor, and one not to be neglected. It tends to uniformity in the species, and checks individualism. It may act as a salutary brake on what we may figuratively term hasty and ill-advised

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attempts at progress. And at the same time, it favours repeated new experiments in the combination of variations, occasionally, we may suppose, with happy results.

But it does more than this. It tends to check, and, if the offspring always possessed the blended character of both parents, would be absolutely fatal to, divergence of character within the interbreeding members of a species. And yet no fact is more striking than this divergence of character. It is seen in the diversified products of human selection; for example, among pigeons. It is seen in the freedom of nature. Mr. Wallace gives many examples. "Among our native species," he says, "we see it well marked in the different species of titmice, pipits, and chats. The great titmouse, by its larger size and stronger bill, is adapted to feed on larger insects, and is even said sometimes to kill small and weak birds. The smaller and weaker coal-titmouse has adopted a more vegetarian diet, eating seeds as well as insects, and feeding on the ground as well as among trees. The delicate little blue titmouse, with its very small bill, feeds on the minutest insects and grubs, which it extracts from crevices of bark and from the buds of fruit trees. The marsh-titmouse, again, has received its name from the low and marshy localities it frequents; while the crested titmouse is a Northern bird, frequenting especially pine forests, on the seeds of which trees it partially feeds. Then, again, our three common pipits—the tree-pipit, the meadow-pipit, and the rock-pipit, or sea-lark—have each occupied a distinct place in nature, to which they have become specially adapted, as indicated by the different form and size of the hind toe and claw in each species. So the stone-chat, the whin-chat, and the wheat-ear are all slightly divergent forms of one type, with modifications in the shape of the wing, feet, and bill adapting them to slightly different modes of life." [AM] There is scarcely a genus that does not afford examples of divergent species. The question then naturally occurs—How have these divergent forms escaped the swamping effects of intercrossing?

That perfectly free intercrossing, between any or all of the individuals of a given group of animals, is, so long as the characters of the parents are blended in the offspring, fatal to divergence of character, is undeniable. Through the elimination of less favourable variations, the swiftness, strength, and cunning of a race may be gradually improved. But no form of elimination can possibly differentiate the group into swift, strong, and cunning varieties, distinct from each other, so long as all three varieties freely interbreed, and the characters of the parents blend in the offspring. Elimination may and does give rise to progress in any given group as a group; it does not and cannot give rise to differentiation and divergence, so long as interbreeding with consequent interblending of characters be freely permitted. Whence it inevitably follows, as a matter of simple logic, that where divergence has occurred, intercrossing and interblending must in some way have been lessened or prevented.

Thus a new factor is introduced, that of *isolation*, or *segregation*. And there is no questioning the fact that it is of great importance.^[AN] Its importance can, indeed, only be denied by denying the swamping effects of intercrossing, and such denial implies the tacit assumption that interbreeding and interblending are held in check by some form of segregation. The isolation explicitly denied is implicitly assumed.

There are several ways in which isolation, or segregation, may be effected. Isolation by geographical barriers is the most obvious. A stretch of water, a mountain ridge, a strip of desert land, may completely, or to a large extent, prevent any intercrossing between members of a species on either side of the barrier. The animals which inhabit the several islands of the Galapagos Archipelago are

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closely allied, but each island has its particular species or well-marked varieties. Intercrossing between the several varieties on the different islands is prevented, and divergence is thus rendered possible and proceeds unchecked. It is said that in the Zuyder Zee a new variety of herrings, the fry of which are very small compared with open-sea herrings, is being developed. And the salmon introduced into Tasmania seem to be developing a fresh variety with spots on the dorsal fin and a tinge of yellow on the adipose fin. In the wooded valleys of the Sandwich Islands there are allied but distinct species of landshells. The valleys that are nearest each other furnish the most nearly related forms, and the degree of divergence is roughly measured by the number of miles by which they are separated. Here there is little or no intercrossing between the slow-moving molluscs in adjoining valleys; none at all between those at any distance apart.

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But even if there are no well-marked physical barriers, the members of a species on a continent or large island tend to fall into local groups, between which, unless the animal be of a widely ranging habit, there will be little intercrossing. Hence local varieties are apt to occur, and varieties show the first beginnings of that divergence which, if carried further and more deeply ingrained, results in the differentiation of species. Geographically, therefore, we may have either complete isolation or local segregation, and in both cases the possibility of divergence.

Another mode of segregation arises also out of geographical conditions. If variations of habits occur (and structure is closely correlated with habit) such that certain individuals take to the mountains, others to the plains or valleys; or that certain individuals take to the forests, others to the open country; the probabilities are that the forest forms will interbreed frequently with each other, but seldom with those in the open, and so with the other varieties. The conditions of forest life or mountain life being thus similar throughout a large area, and life being through elimination slowly but surely adapted to its environment, there might thus arise two distinct varieties scattered throughout the length and breadth of the area, the one inhabiting the mountains, the other the forests. In illustration of this mode of segregation, we may take the case of two species of rats which have recently been found by Mr. C. M. Woodford on one of the Solomon Islands. These two quite distinct species are regarded by Mr. Oldfield Thomas as slightly modified descendants of one parent species, the modifications resulting from the fact that of this original species some individuals have adopted a terrestrial, others an arboreal life, and their respective descendants have been modified accordingly. Thus Mus rex lives in trees, has broad foot-pads, and a long rasp-like, probably semi-prehensile, tail; while Mus imperator lives on the ground, has smaller pads, and a short, smooth tail. The segregation of these two species has probably been effected by the difference of their mode of life, and each has been adapted to its special environment through the elimination of those individuals which were not in harmony with the condition of their life. It is probable that this mode of segregation has been an important one. And it is clear that in many cases competition would be a co-operating factor in this process, weaker organisms being forced into otherwise uncongenial habitats through the stress of competitive elimination, the weaker forms not perishing, but being eliminated from more favoured areas.

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Protective coloration may also be a means of segregation. A species of insects having no protective resemblance might vary in two directions—in the direction of green tints, assimilating their hue to that of vegetation; and in the direction of sandy or dull earthy colours, assimilating them to the colour of the soil. In the one variety elimination would weed out all but the green forms, and these would be left to intercross. In the other variety, green forms would be eliminated, dull-brown forms

being left to interbreed. Stragglers from one group into the other would stand a chance of elimination before interbreeding was effected. [AO]

In the case of birds whose freedom of flight gives them a wide range, sometimes almost a world-wide range, it would seem at first sight that their facilities for interbreeding and intercrossing are so great that divergence is well-nigh impossible. And yet the examples of divergence I cited from Mr. Wallace were taken from birds, and it is well known that divergence is particularly well shown in this class. But when the habits of birds are studied attentively, it is found that, wide as is their range, their breeding area is often markedly restricted. The sanderling and knot range freely during the winter throughout the Northern hemisphere; but their breeding area is restricted to the north polar region. The interbreeding within this area keeps the species one and homogeneous, notwithstanding its wide range, and, at the same time, prevents intercrossing with allied species with different breeding-grounds.

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Another most important mode of segregation among animals arises out of habitual or instinctive preferences. Where varieties are formed there is a tendency for like to breed with like. In the Falkland Islands the differently coloured herds of cattle, all descended from the same stock, keep separate, and interbreed with each other, but not with individuals outside their own colour-caste. If two flocks of merino sheep and heath sheep be mixed together, they do not interbreed. In the Forest of Dean and in the New Forest, the dark and pale coloured herds of fallow deer have never been known to intermingle. [AP] Here we have a case of selective *segregation through preferential mating*, and may find therein the basis of sexual selection in its higher ranges as advocated by Darwin.

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The question of sexual selection will, however, be briefly considered in the chapter on "Organic Evolution." At present what we have to notice is that, through preferential mating, segregation is effected. The forms that interbreed have a distinguishing colour. From this it is but a step to the possession, not merely of a distinguishing colour, but of distinguishing colour-markings. Hence, through preferential mating, may arise those special markings which so frequently distinguish allied species. They not only enable us to recognize species as distinct, but enable the species which possess them to recognize the members of their own kind. Mr. Wallace calls these diacritical marks recognitionmarks, and gives many illustrative examples. [AQ] They are especially noticeable in gregarious animals and in birds which congregate in flocks or which migrate together. Mr. Wallace considers that they "have in all probability been acquired in the process of differentiation for the purpose of checking the intercrossing of allied forms;" for "one of the first needs of a new species would be to keep separate from its nearest allies, and this could be more readily done by some easily seen external mark of difference." This language seems, however, to savour of teleology (that pitfall of the evolutionist). The cart is placed before the horse. The recognition-marks were, I believe, not produced to prevent intercrossing, but intercrossing has been prevented because of preferential mating between individuals possessing special recognition-marks. To miss this point is to miss an important segregation-factor. Undoubtedly, other tendencies co-operate in maintaining the standard of the recognition-marks. Stragglers who failed in the matter of recognition would get separated from their fellows, and stand a greater chance of elimination by enemies; young who failed in this respect would be in like condemnation. Still, I cannot doubt that the foundations of recognition-marks were laid in preferential mating, and that in this we have an important factor in segregation.

We may here note, in passing, as also arising out of preference, how the selection of flowers by insects may lead to segregation; for insects seem often to have habitual or instinctive colour-preferences. Flowers of similar colour would be thus cross-fertilized, but would not intercross with those of different colour, whence colour-varieties might arise. It is important to note that in these cases there is a psychological factor in evolution.

We have so far assumed that intercrossing of parents and interblending of their characters in the offspring always go together. This, we must now notice, is not always the fact. If a blue-eyed Saxon marry a dark-eyed Italian, the children will have blue eyes or dark eyes, not eyes of an intermediate tint. The characters do not interblend. The *ancon*, or otter-sheep, a breed with a long body and short, bandy legs, appeared in Massachusetts as a chance sport in a single lamb. The offspring of this ram were either ancons or ordinary sheep. The ancon characters did not blend. Hence for a time a definite breed was maintained. We may call this mode of isolation *isolation by exclusive inheritance*.

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A further mode of isolation or segregation, for which Mr. Romanes^[AR] claims a foremost, indeed, the foremost, place, is *physiological isolation* as due to differential fertility. One among the many variations to which organisms are subject is a variation in fertility, which may reach the climax of absolute sterility. But it is clear that a sterile variation carries with it its own death-warrant, since the sterile individual leaves no descendants to inherit its peculiarity. Relative infertility, too, unless it chances to be correlated with some unusual excellence, would be no advantage, would be transmitted to few descendants, and would tend to be extinguished. The same is not true, however, of differential fertility. "It is by no means rare," said Darwin, [AS] "to find certain males and females which will not breed together, though both are known to be perfectly fertile with other males and females." Mr. Romanes assumes, as a starting-point, the converse of this, namely, that certain males and females will breed together, though they are infertile with all other members of the species.

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Suppose, then, a variety to arise which is perfectly fertile within the limits of the varietal form, but imperfectly fertile or infertile with the parent species. Such a variety would have to run the risks of those ill effects which, as Darwin showed, [AT] are attendant upon close interbreeding. But Mr. Wallace points out [AU] that these ill effects may not be so marked under nature as they are under domestication. Suppose, then, that it escapes these ill effects. In this case, Mr. Romanes urges, it would neither be swamped by intercrossing nor die out on account of sterility. But although it could not be swamped by intercrossing, still, if it arose sporadically, here a case, there a case, and so on, the chances would be enormously against the perpetuation of the variety, unless some co-operating mode of segregation aided in bringing together the varying individuals. If, for example, there were a segregation of these variants in a particular habitat—all the variants meeting in some definite locality for breeding purposes; or if there were a further segregation through mutual preferences; or if, again, there were a further segregation in time the variety might obtain a firm footing. But without these co-operating factors it is clear that if one male and one female in a hundred individuals varied in this particular way, the chances would be at least forty-nine to one against their happening to mate together.

It is interesting to note that almost the only particular example given by Mr. Romanes in illustration of his theory is one that involves the co-operation of one of these further segregation-factors. Suppose, he says, the variation in the reproductive system is such that the season of flowering or of pairing becomes either advanced or retarded. This particular variation being inherited, the variety

breeding, let us say, in May, the parent species in July, there would arise two races, each perfectly fertile within its own limits, but incapable of crossing with the other. Thus is constituted "a barrier to intercrossing quite as effectual as a thousand miles of ocean." Yes! a time-barrier instead of a space-barrier. The illustration is faulty, inasmuch as it introduces a mode of segregation other than that in question. I think it very improbable that differential fertility alone, without the co-operation of other segregation-factors, would give rise to separate varieties capable of maintaining themselves as distinct species.

That distinct species are generally mutually infertile, or more frequently still, that their male offspring are sterile, is, however, an undoubted fact. But there are, exceptions. Fertile hybrids between the sheep and the goat seem to be well authenticated. Of rats Darwin says that "in some parts of London, especially near the docks, where fresh rats are frequently imported, an endless variety of intermediate forms may be found between the brown, black, and snake rat, which are all three usually ranked as distinct species."[AV] Fertile hybrids have been produced between the green-tinted Japanese and the long-tailed Chinese pheasants. Mr. Thomas Moore, of Fareham, in Hants, has been particularly successful in producing a hybrid breed between the golden pheasant (*Thaumalia picta*), whose habitat is Southern and South-eastern China, and the Amherst pheasant (*Thaumalia amherstiæ*), which is found in the mountains of Yunnan and Thibet. In answer to my inquiries, Mr. Moore kindly informs me that he "has bred the half-bred gold and Amherst pheasant, crossed them again with gold, and recrossed them with half-bred Amherst, and kept on crossing until only a strain of the gold pheasant remained. The result is that the birds so produced are far handsomer than either breed, since the feathers composing their tiplets as well as those under the chin are of so beautiful a colour that they beggar description. They all breed most freely, and are much more vigorous than the pure gold or Amherst, and their tails reach a length of over three feet. They are also exceedingly prolific. Out of a batch of fortytwo eggs, forty chickens were hatched out, of which thirty-seven were reared to perfection."

Still, though there are exceptions, the general infertility of allied species when crossed is a fact in strong contrast with the marked fertility of varieties under domestication; concerning which, however, it should be noted that our domesticated animals have been selected to a very large extent on account of the freedom with which they breed in confinement, and that domestication has probably a tendency to increase fertility. The question, therefore, arises—Is the infertility between species, and the general sterility of their male offspring, a secondary effect of their segregation? or is their segregation the direct effect of their differential fertility? The former is the general opinion; the latter is held by Mr. Romanes. He contends that sterility is the primary distinction of species, other specific characters being secondary, and regards it as a pure assumption to say that the secondary differences between species have been historically prior to the primary difference. I do not propose to discuss this question. While it seems to me in the highest degree improbable that differential fertility, apart from other co-operating factors, has been or could be a practical mode of segregation, it has probably been a not unimportant factor in association with other modes of segregation or isolation. Suppose, for example, two divergent local varieties were to arise in adjacent areas, and were subsequently (by stress of competition or by geographical changes) driven together into a single area: we are justified in believing, from the analogy of the Falkland Island cattle, the Forest of Dean deer, and other similar observed habits, that preferential breeding, kind with kind, would tend to keep them apart. But, setting this on one side, let us say they interbreed. If, then, their unions are fertile, the isolation will be annulled by intercrossing—the

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two varieties will form one mean or average variety. But if the unions be infertile, the isolation will be preserved, and the two varieties will continue separate. Suppose now, and the supposition is by no means an improbable one, that this has taken place again and again in the evolution of species: then it is clear that those varietal forms which had continued to be fertile together would be swamped by intercrossing; while those varietal forms which had become infertile would remain isolated. Hence, in the long run, isolated forms occupying a common area would be infertile. Or suppose, once more, that, instead of the unions between the two varietal forms being infertile, they are fertile, but give rise to sterile (mule) or degenerate offspring, as is said to be the case in the unions of Japanese and Ainos: then it is clear that the sterile or degenerate offspring of such unions would be eliminated, and intercrossing, even though it occurred, would be inoperative while breeding within the limits of the variety continued unchecked.

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Sufficient has now been said concerning the modes of isolation and segregation, geographical, preferential, and physiological. We must now consider their effects. Where the isolated varieties are under different conditions of life, there will be, through the elimination of the ill-adapted in each case, differential adoption to these different conditions. But suppose the conditions are similar: can there be divergence in this case? The supposition is a highly hypothetical one, because it postulates that all the conditions, climatal, environmental, and competitive, are alike, which would seldom, if ever, be likely to occur. Let us, however, make the supposition. Let us suppose that an island is divided into two equal halves by the submersion of a stretch of lowland running across it. Then the only possible causes of divergence would lie in the organisms themselves [AW] thus divided into two equal groups. We have seen that variations may be advantageous, disadvantageous, or neutral. The neutral form a fluctuating, unfixed, indefinite body. But they afford the material with which nature may make, through intercrossing, endless experiments in new combinations, some of which may be profitable. Such profitable variations would escape elimination, and, if not bred out by intercrossing, would be preserved. In any case, the variety would tend to advance through elimination as previously indicated. But in the two equal groups we are supposing to have become geographically isolated, the chances are many to one against the same successful experiments in combination occurring in each of the two groups. Hence it follows that the progress or advance in the two groups, though analogous, would not be identical, and divergence would thus be possible under practically similar conditions of life.

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In his observations on the terrestrial molluscs of the Sandwich Islands, Mr. Gulick notes that different forms are found in districts which present essentially the same environment, and that there is no greater divergence when the climatic conditions are dissimilar than there is when those conditions are similar. As before noticed, the degree of divergence is, roughly speaking, directly as the distance the varietal forms are apart. Again, Darwin notes that the climate and environment in the several islands of the Galapagos group are much the same, though each island has a somewhat divergent fauna and flora. These facts lend countenance to the view that divergence can and does occur under similar conditions of life, if there be isolation. They seem, also, so far as they go, to negative the view that the species is moulded directly by the external conditions. For, if this factor were powerful, it would override the effects of experimental combination of characters when the conditions were similar, and would give rise to well-marked varietal forms when the conditions were diverse.

If we admit preferential breeding as a segregation-factor (and arising out of it sexual selection, in a modified form, as a determining one in the evolution of the plumage of male birds), it is evident that

the standard of recognition-marks can only be maintained by a uniformity of preference or taste. Still, the uniformity is not likely to be absolute. In this matter, as in others, variations will occur, and after the lapse of a thousand generations, in which elimination has been steadily at work, it is hardly probable that the recognition standard would remain absolutely unchanged. For, though there may not be any direct elimination in this particular respect, there might well be colour-eliminations in other (e.g. protective) respects, and the mental nature would not remain quite unchanged. Moreover, we know that secondary sexual characters are remarkably subject to variation, as may be well seen in the case of ruffs (Machetes pugnax) in the British Natural History Museum. In the case of our two islands with isolated faunas, therefore, if they formed separate breeding-areas for birds, the chances would be many to one against the change in the standard of recognition-marks being identical in each area. Hence might arise those minute but definite specific distinctions which are so noteworthy in this class of the animal kingdom. Instance the Old and New World species of teal, the Eastern and Western species of curlew and whimbrel, and other cases numerous. [AX] This, in fact, is probably in many cases the true explanation of the occurrence of representative species, slight specific variations of the same form as it is traced across a continent or through an archipelago of islands.

The question has been raised, and of late a good deal discussed, whether specific characters, those traits by which species are distinguishable, are always of use to the species which possess them. Here it is essential to define what is meant by utility. Characters may be of use in enabling the possessor to resist elimination; or, like the colours of flowers, they may be of use in attracting insects, and thus furthering selection; or, like recognition-marks, they may be of use in effecting segregation. This last form of utility is apt to be overlooked or lost sight of. In speaking of humming-birds, the Duke of Argyll says that "a crest of topaz is no better in the struggle for existence than a crest of sapphire. A frill ending in spangles of the emerald is no better in the battle of life than a frill ending in spangles of the ruby." But if these characters be recognition-marks, they may be of use in segregation. They are a factor in isolation. But it may be further asked—What is the use of the segregation? Wherein lies the utility of the divergence into two forms? This question, however, involves a complete change of view-point. The question before us is whether specific characters are of use to the species which possesses them. To this question it is sufficient to answer that they are useful in effecting or preserving segregation, without which the species, as a distinct species, would cease to exist. We are not at present concerned with the question whether divergence in itself is useful or advantageous. If it be pressed, we must reply that, although divergence is undoubtedly of immense advantage to life in general, enabling, as Darwin said, its varying and divergent forms to become adapted to many and highly diversified places in the economy of nature, still in many individual cases it is neither possible nor in any respect necessary to our conception of evolution to assign any grounds of utility or advantage for the divergence itself.

In any case, we are dealing at present with the utility of specific characters to the species which possess them; and under the head of utility we are including usefulness in effecting or maintaining segregation. Now, we have already seen that variations may be either advantageous (useful), or neutral (useless), or disadvantageous (worse than useless). The latter class we may here disregard; elimination will more or less speedily dispose of them. With regard to neutral (useless) variations, we must also note that they may be correlated with variations of the other two classes. If correlated with disadvantageous variations, they will be eliminated along with them; if correlated with advantageous variations, they will escape elimination (or will be selected) together with them. There remain neutral,

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or useless, variations, not correlated with either of the other two classes. Are these in any cases distinctive of species?

It is characteristic of specific distinctions that they are relatively constant. Elimination, selection, or preferential breeding gives them relative fixity. On the other hand, it is characteristic of neutral variations that they are inconstant. There is nothing to give them fixity. It is, of course, conceivable that all the migrants to a new area were possessed of a useless neutral character, which those in the mother area did not possess; or that such a useless character was in them preponderant, and by intercrossing formed a less fluctuating, useless character than their progenitors exhibited. Still, the extensive occurrence of such neutral, or useless, characteristics would be in the highest degree improbable. Our ignorance often prevents us from saying in what particular way a character is useful. We must neither, on the one hand, demand proof that this, that, or the other specific character is useful, nor, on the other hand, demand negative evidence (obviously impossible to produce) that it is without utilitarian significance; but we may fairly request those who believe in the wide occurrence of useless specific characters to tell us by what means these useless characters have acquired their relative constancy and fixity. A suggestion on this head will be found in the next chapter.

We must now pass on to consider briefly a most important factor in the struggle for existence. Hitherto we have regarded this struggle as uniform in intensity; we must now regard it as variable, with alternations of good times and hard times, and indicate the causes to which such variations are due.

With variations of climate, such as we know to occur from year to year, or from decade to decade, there are variations in the productiveness of the soil; and when we remember how closely interwoven are the web and woof of life, we shall see that the increased or diminished productiveness of any area will affect for good or ill all the life which that area supports. The introduction of new forms of life into an area, or their preponderance at certain periods owing to climatic or other conditions particularly favourable to them as opposed to other forms, may alter the whole balance of life in the district. We are often unable to assign any reason for the sudden increase or diminution of the numbers of a species; we can only presume that it is the result of some favourable or unfavourable change of conditions. Thus Mr. Alexander Becker [AY] has recently drawn attention to the fact that whereas for several years various species of grasshoppers appeared in great numbers in South-east Russia, there came then one year of sudden death for most of them. They were sitting motionless on the grasses and dying. He gives similar cases of butterflies for a while numerous, and then rare, and states that a squirrel common near Sarepta suddenly disappeared in the course of one summer, probably, he adds, succumbing to some contagious disease. Such is the nice balance of life, that the partial disappearance of a single form may produce remarkable and little-expected effects. Darwin amusingly showed how the clover crops might be beneficially affected by the introduction of a family of old maids into a parish. The clover is fertilized by humble-bees, the bees are preyed upon by mice; the relations between cats and mice, and between old maids and cats, are well known and familiar: more old maids, more cats; more cats, less mice; less mice, more humble-bees; more humble-bees, better fertilization. A little thing may modify the balance of life, and increase or diminish the struggle for existence, and the rigour of the process of elimination.

But when we take a more extended view of the matter, and include secular changes of climate, the possible range of variation in the struggle for existence is seen to be enormously increased. It is well known to those who have followed the progress of geology, that in early Kainozoic times a mild

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climate extended to within the Arctic circle, while during the glacial epoch much of the north temperate zone was fast locked in ice, and the climate of the northern hemisphere was profoundly modified. The animals in the north temperate zone were driven southwards. [AZ] Not only was there much elimination from the severe climatic conditions, but the migrants were driven southwards into areas already well stocked with life, and the competition for means of subsistence in these areas must have been rendered extremely severe. Elimination was at a maximum. Then followed the withdrawal of glacial conditions. The increasing geniality of the climate allowed an expansion of life within a given area, and the withdrawal of snow and ice further and further north set free new areas into which this expanding life could migrate and find subsistence. The hard times of the glacial period were succeeded by good times of returning warmth and an expanding area; and if, as some geologists believe, there was an interglacial period (or more than one such period) in the midst of the Great Ice Age, then hard times and good times alternated during the glacial epoch.

Expansion and contraction of life-areas have also been effected again and again in the course of geological history by elevations and subsidences of the land. At the beginning of Mesozoic times much of Europe was dry land. In Triassic and Rhætic times there were lakes in England and in Germany, and a warm Mediterranean Sea to the south. Subsidence of the European area brought with it a lessened land-area and an increased sea-area: bad times and increased competition for land animals; good times and a widening life-area for marine forms of life. This continued, with minor variations, till its culmination in the Cretaceous period. Then came the converse process: the land-areas increased, the sea was driven back. A good time had come for terrestrial life; the marine inhabitants of estuaries and inland seas felt the pressure of increased competition in a lessening area. And so there emerged the continental Europe of the beginning of the Kainozoic era. And it is scarcely necessary to remind those who are in any degree conversant with geology that during tertiary times there have been alternate expansions and contractions of life-areas, marine and terrestrial, the former bringing good times, the latter hard times and a heightened struggle for existence.

Now, what would be the result of this alternation of good times and hard times? During good times varieties, which would be otherwise unable to hold their own, might arise and have time to establish themselves. In an expanding area migration would take place, local segregation in the colonial areas would be rendered possible, differential elimination in the different migration-areas would produce divergence. There would be diminished elimination of neutral variations, thus affording opportunities for experimental combinations. In general, good times would favour variation and divergence.

Intermediate between good times and hard times would come, in logical order, the times in which there is neither an expansion nor a contraction of the life-area. One may suppose that these are times of relatively little change. There is neither the divergence rendered possible by the expansion of life-area, nor the heightened elimination enforced by the contraction of life-area. [BA] Elimination is steadily in progress, for the law of increase must still hold good. Divergence is still taking place, for the law of variation still obtains. But neither is at its maximum. These are the good old-fashioned times of slow and steady conservative progress. They are, perhaps, well exemplified by the fauna of the Carboniferous period, and it is not at all improbable that we are ourselves living in such a quiet, conservative period.

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On the other hand, hard times would mean increased elimination. During the exhibitions at South Kensington there were good times for rats. But when the show was over, there followed times that were cruelly hard. The keenest competition for the scanty food arose, and the poor animals were forced to prey upon each other. "Their cravings for food," we read in *Nature*, "culminated in a fierce onslaught on one another, which was evidenced by the piteous cries of those being devoured. The method of seizing their victims was to suddenly make a raid upon one weaker or smaller than themselves, and, after overpowering it by numbers, to tear it in pieces." Elimination by competition, passing in this way into elimination by battle, would, during hard times, be increased. None but the best organized and best adapted could hope to escape. There would be no room for neutral variations, which, in the keenness of the struggle, would be relatively disadvantageous. Slightly divergent varieties, before kept apart through local segregation, would be brought into competition. The weakest would in some cases be eliminated. In other cases, the best-adapted individuals of each variety might survive. If their experiments in intercrossing, should such occur, gave rise to fertile offspring, more vigorous and better adapted than either parent-race, these would survive, and the parent-forms would be eliminated. But if such experiments in intercrossing gave rise to infertile, weakly offspring, these would be eliminated. Thus sterility between species would become fixed. Wherever, during the preceding good times, divergence had taken place in two different directions of adaptation, and some intermediate forms, fairly good in both directions, had been able to escape elimination, the chances are that these intermediates would be in hard times eliminated, and the divergent forms left in possession of the field. Wherever, during good times, a species had acquired or retained a habit of flexibility, that habit would stand it in good stead in the midst of the changes wrought by hard times; but when it had, on the other hand, acquired rigidity (like the proverbially "inflexible goose"), it would be at a disadvantage in the stress of a heightened elimination.

The alternation of good times and hard times may be illustrated by an example taken from human life. The introduction of ostrich-farming in South Africa brought good times to farmers. Whereupon there followed divergence in two directions. Some devoted increased profits to improvements upon their farms, to irrigation works which could not before be afforded, and so forth. For others increased income meant increased expenditure and an easier, if not more luxurious, mode of life. Then came hard times. Others, in Africa and elsewhere, learnt the secret of ostrich-farming. Competition brought down profits, and elimination set in—of which variety need hardly be stated.

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I believe that the alternation of good times and hard times, during secular changes of climate and alternate expansions and contractions of life-areas through geological upheavals and depression of the land, has been a factor of the very greatest importance in the evolution of varied and divergent forms of life, and in the elimination of intermediate forms between adaptive variations. It now only remains in this chapter to say a few words concerning convergence, adaptation, and progress.

Convergence, which is the converse of divergence, is brought about through the adaptation of different forms of life to similar conditions of existence. The somewhat similar form of the body and fin-like limbs of fishes, of ancient reptiles (the ichthyosaurus and its allies), of whales, seals, and manatees, is a case in point. Both birds, bats, and pterodactyls have keeled breastbones for the attachment of the large muscles for flight. A whole series of analogous adaptations, as the result of analogous modes of life, are found in the placental mammals of Europe and Asia, on the one hand, and the marsupial forms of Australia on the other hand. The flying squirrel answers to the flying phalanger,

the fox to the vulpine phalanger, the bear to the koala, the badger to the pouched badger, the rabbit to the bandicoot, the wolverine to the Tasmanian devil, the weasel to the pouched weasel, the rats and mice to the kangaroo rats and mice, and so on. A familiar example of convergence is to be seen in our swallows and martins, on the one hand, and the swifts on the other. Notwithstanding their superficial similarity in external form and habits, they are now generally regarded as belonging to distinct orders of birds.

These are examples of convergence.^[BB] Animals of diverse descent and ancestry have, through similarity of surrounding conditions or of habits of life, become, in certain respects, assimilated. But some zoologists go further than this. They maintain that the same genus or species may, through adaptation to similar circumstances, be derived from dissimilar ancestors. Some palæontologists, for example, believe that the horse has been independently evolved along parallel lines in Europe and in America. Professor Cope considers that in the one continent *Protohippus*, and in the other *Hipparion*, was the immediate ancestor of *Equus*. The probabilities are, however, so strongly against such a view, that it cannot be accepted until substantiated by stronger evidence than is yet forthcoming.

A special and particular form of convergence, at any rate in certain obvious, if superficial, characters, has already been noticed in our brief consideration of mimicry. In the first place, among a number of closely related species of inedible butterflies, the tendency to divergence is checked, so far as external markings and coloration are concerned, that all may continue to profit by the resemblance, and that the numbers tasted by young birds in gaining their experience (for the avoidance seems to be at most incompletely instinctive) may be divided amongst all the species, thus lessening the loss to each. Secondly, there may be a convergence of certain genera of distantly related inedible groups (*e.g.* among the Heliconidæ and the Danaidæ), which gain by being apparently one species, since the loss from young birds is shared between them. And lastly, there is the true mimicry of quite distinct families of butterflies, not themselves inedible, but sheltering themselves under the guise and sharing the bad reputation of the mimicked forms. Such forms of convergence are in special adaptation to a very special environment.

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We must remember that in all cases adaptation is a matter of life and environment. And these, we may now note, may be related in one or more of three ways. In the first place, there is the adaptation of life to an unchanging environment; for example, the adaptation of all forms of life to the fixed and unchanging properties of inorganic matter. If we liken life to a statue and the environment to a mould in which it is cast, we have in this case a rigid mould and a plastic statue. Secondly, the adaptation may be mutual, as, for example, when the structures of insects and flowers are fitted each to the other, or when the speed of hunters and hunted is steadily increased through the elimination of the slow in either group. Here the mould and statue are both somewhat plastic, and yield to each other's influence. Thirdly, the environment may be moulded to life. This, again, is only relative, since life never wholly loses its plasticity. The bird that builds a nest, the beaver that constructs a dam, the insect that gives rise to a gall,—these, so far, mould the environment to the needs of their existence. Man in especial has the power, through his developed intelligence, of manufacturing his own environment. Here the statue is relatively rigid, and the mould plastic.

Progress may be defined as continuous adaptation. In modern phrase, this is called evolution. The continuity makes the difference between evolution and revolution. Both are natural. Both occur in the

organic, the social, and the intellectual sphere. Evolution is the orderly progress of the organism or group of organisms, by which it becomes more and more in harmony with surrounding conditions. If the conditions become more and more complex, the organism will progress in complexity; but if the conditions be more and more simple, progress (if such it may still be called) will be towards simplicity of structure, unnecessary complexity being eliminated, or, in any case, disappearing. Hence, in parasites and some forms of life which live under simple conditions, we have the phenomena of degeneration, or a passage from a more complex to a more simple condition.

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Revolution in organic life is the destruction of one organism or group of organisms, and the replacement in its stead of a wholly different organism or group of organisms. During hard times there may be much revolution, or replacement of one set of organic forms by another set of organic forms. It was by revolution that the dominant reptiles of the Mesozoic epoch were replaced by the dominant mammals of Kainozoic times. It was by revolution that pterodactyls were supplanted by birds. Revolution has exterminated many a group in geological ages. On the other hand, it was by evolution that the little-specialized Eocene ungulates gave rise to the horse, the camel, and the deer; by divergent evolution that the bears and dogs were derived from common ancestors. Palæontology testifies both to evolution and revolution. [BC] That history does the same, I need not stay to exemplify. The same laws also apply to systems of thought. Darwinism has revolutionized our conceptions of nature. Darwin placed upon a satisfactory basis a new order of interpretation of the organic world. By it other interpretations have been supplanted. And now this new conception is undergoing evolution, not without some divergence.

In this chapter we have seen how evolution is possible under natural conditions. If the law of increase be true, if more are born than can survive to procreate their kind, natural selection is a logical necessity. We must not blame our forefathers for not seeing this. Until geology had extended our conception of time, no such conclusions could be drawn. If organisms have existed but six or seven thousand years, and if in the last thousand years little or no change in organic life has occurred, the supposition that they could have originated by any such process as natural selection is manifestly absurd. Lyell was the necessary precursor of Darwin. Given, then, increase and elimination throughout geological time, natural selection is a logical necessity. No one who adequately grasps the facts can now deny it. It is an unquestionable factor in organic evolution. Whether it is the sole factor, is quite another matter, and one we will consider in the chapter on "Organic Evolution."

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CHAPTER V. HEREDITY AND THE ORIGIN OF VARIATIONS.

The law of heredity, I have said above, may be regarded as that of persistence exemplified in a series of organic generations. Variation results—it is clear that it must result—from some kind of differentiating influence. Such statements as these, however, though they are true enough, do not help us much in understanding either heredity or variation.

Let us first notice that normal cases of reproduction exemplify both phenomena—heredity with variation; hereditary similarity to the parents in all essential respects, individual variations in minor points. This is seen in man. Brothers and sisters may present family resemblances among each other and to their parents, but each has individual traits of feature and of character. Only in particular cases of so-called "identical twins" are the variations so slight as not to be readily perceptible by even a casual observer.

Now, when we seek an explanation of these well-known facts, we may be tempted to find it in the supposition that the character of the parents does not remain constant, that the character influences the offspring, and that therefore the children born at successive periods will differ from each other, while twins born in the same hour will naturally resemble each other. As Darwin himself says, [BD] "The greater dissimilarity of the successive children of the same family in comparison with twins, which often resemble each other in external appearance, mental disposition, and constitution, in so extraordinary a manner, apparently proves that the state of the parents at the exact period of conception, or the nature of the subsequent embryonic development, has a direct and powerful influence on the character of the offspring." But a little consideration will show that, though this might, in the absence of a better explanation, account for variation in character, it could not account for variation in form and feature, unless we regard these as in some way determined by the character. Moreover, as we shall see presently, it is open to question whether acquired modifications of structure or character in the parent can in any way influence the offspring. Again, in the litter of puppies born of the same bitch by the same dog there are individual variations, often as well marked as those in successive births.

The facts, then, to be accounted for are—first, the close hereditary resemblance in all essential points of offspring to parent; and, secondly, the individual differences in minor points among the offspring produced simultaneously or successively by the same parents. These are the facts as they occur in the higher animals. It will be well to lead up to our consideration of them by a preliminary survey of the facts as they are exemplified by some of the lower organisms.

In the simpler protozoa, where fission occurs, and where the organism is composed of a single cell, where also there is a single nucleus which apparently undergoes division into two equal and similar parts, it is easy to understand that the two organisms thus resulting from the halving of a single organism partake completely of its nature. If the fission of an amœba is such as to divide it into two similar parts, there is no reason why these two similar parts should not be in all respects alike, and

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should not, by the assimilation of new material, acquire the size and all the characteristics of the parent form. In the higher and more differentiated protozoa, the case is not quite so simple; for the two halves are not each like the whole parent, but have to be remodelled into a similar organism. But if we suppose, as we seem to have every right to suppose, that it is the nucleus that controls the formative processes in the cell, there is not much difficulty in understanding how, when the nucleus divides into two similar portions, each directs, so to speak, the similar refashioning of its own separated protoplasmic territory.

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From the protozoa we may pass to such a comparatively simple metazoon as the hydra. Here the organism is composed, not of a single cell, but of a number of cells. These cells are, moreover, not all alike, but have undergone differentiation with physiological division of labour. There is an inner layer of large nutritive cells, and an outer layer of protective cells, some of which are conical with fine processes proceeding from the point of the cone; others are smaller, and fill in the interstices between the apices of the cones, while others have developed into thread-cells, each with a fine stinging filament. Between the two layers there is a thin supporting lamella. The essential point we have here to notice is that there are two distinct layers with cells of different form and function.

Now, it has again and again been experimentally proved that if a hydra be divided into a number of fragments, each will grow up into a complete and perfect hydra. All that is essential is that, in the separated fragment, there shall be samples of the cells of both layers. Under these conditions, the separated cells of the outer layer regenerate a complete external wall, and the separated cells of the inner layer similarly regenerate a complete internal lining. From these facts, it would appear that such a small adequately sampled fragment has the power, when isolated, of assimilating nutriment and growing by the multiplication of the constituent cells, and that the growth takes such lines that the original form of the hydra is reproduced.

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Here we may note, by way of analogy, what takes place in the case of inorganic crystals. If a fragment of an alum crystal be suspended in a strong solution of alum, the crystal will be recompleted by the growth of new parts along the broken edges. We say that this is effected under the influence of molecular polarity. Similarly, we may say that the fragment of the hydra rebuilds the complete form under the influence of an hereditary morphological tendency residing in the nuclei of the several cells. The case, though still comparatively simple, is more complex than that of the higher protozoa. There the divided nucleus in two separated cells directs each of these in hereditary lines of morphological growth. Here not only do the cells and their nuclei divide, but they are animated by a common morphological principle, and in their multiplication combine to form an organism possessing the ancestral symmetry. If, however, we call this an hereditary morphological tendency or a principle of symmetry; or, with the older physiologists, a nisus formativus; or, with Darwin, "the co-ordinating power of the organization" (all of these expressions being somewhat unsatisfactory);—we must remember that these terms merely imply a play of molecular forces analogous to that which causes the broken crystal of alum to become recompleted in suitable solution. The inherent molecular processes in the nuclei[BE] in the one case enable the cells to regenerate the hydra; the inherent molecular stresses in the crystalline fragment in the other case lead to the reproduction of the complete crystal. In either case there is no true explanation, but merely a restatement of the facts under a convenient name or phrase.

The power of regeneration of lost parts, which is thus seen in the hydra, is also seen, in a less degree so far as amount is concerned, but in a higher degree so far as complexity goes, in animals far above the hydra in the scale of life. The lobster that has lost a claw, the snail whose tentacle has been removed, the newt which has been docked of a portion of its tail or a limb, are able more or less completely to regenerate these lost parts. And the regeneration may involve complex structures. With the tentacle of the snail the eye may be removed, and this, not once only, but a dozen times. After such mutilation, no part of the eye remains, though the stump of its nerve is, of course, left; still the perfect organ is reconstructed again and again, as often as the tentacle is removed. The cells at the cut end of the nerve-stump divide and multiply, as do also those of the surrounding tissues, and the growing nerve terminates in an optic cup, as it did previously under the influences of normal development before the mutilation. Here we have phenomena analogous to, and in some respects more complex than, those which are seen in the regenerative process in hydra. It is well known, however, that, in the case of higher animals, in birds and mammals, this power of regenerating lost parts does not exist. When a bone is broken, osseous union of the broken pieces may indeed take place; and in flesh-wounds, the gash is filled in and heals over, not without permanent signs of its existence, as may often be seen in the faces of German students. But beyond this there is normally no regeneration. The soldier who has lost an arm in battle cannot return home and in quiet seclusion reproduce a new limb. That which seems to be among lower animals a well-established law of organic growth does not here obtain. This is probably due to the fact that the higher histological differentiation of the tissues in the more highly developed forms of life is a bar to regeneration. In their devotion to special and minute details of physiological work, the cells have, so to speak, forgotten their more generalized reproductive faculties. In any case, however the fact is to be explained, the higher organisms have in many cases almost completely lost the power of regenerating lost parts. But this loss of the regenerative power in the more highly differentiated animals does not alter or invalidate the law of organic growth we are considering. The law may be thus stated: Whenever, after mutilation, free growth of the mutilated surface occurs, that growth is directed in such lines as to reproduce the lost part and restore the symmetrical integrity of the organism. This is a matter of heredity. And we may regard the hereditary reconstructive power as residing either (1) in those cells at or adjoining the mutilated surface which are concerned in the regrowth of the lost part; or (2) in the general mass of cells of the mutilated organism.

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There are difficulties in either view. Professor Sollas, supporting the former, says, [BF] "This power [in the snail] of growing afresh so complex and specialized an organ as an eye is certainly, at first sight, not a little astonishing, but it appears to be capable of a very simple explanation. The cells terminating the cut stump of the tentacle are the ancestors of those which are removed; a fresh series of descendants are derived from them, similarly related to the ancestral cells as their predecessors which they replace; the first generation of descendants become in turn ancestors to a second generation, similarly related to them as were the second tier of extirpated cells; and this process of descent being repeated, the completed organ will at length be rebuilt." This explanation is, however, misleading in its simplicity. The cells terminating the cut stump are not the direct ancestors of those which are removed, except in the same sense as gorillas are ancestors of men. They are rather collateral descendants of common ancestors. I think that Professor Sollas would probably agree that, though the lens and "retina" are of epiblastic (outer layer) origin, their relationship with the epiblastic cells at the cut stump is a somewhat distant one. In the reproduction of the lens the cell-heredity is not direct, but markedly indirect. And it is somewhat difficult to understand by what means the ordinary epiblastic cells of the cut stump, which

have had no part in the special and peculiar work of lens-production, should be enabled to produce cell-offspring, some of which, and those in a special relation to other deeper-lying cells, possess this peculiar power.

On the other hand, if we turn to the view that the reproduction is effected, not by the cells of the cut surface alone, but by the general mass of cells in the mutilated organism, we have to face the difficulty of understanding how the influence of cells other than those partaking in the regrowth can be brought to bear on these so as to direct their lines of development. If we say that the organism is pervaded by a principle of symmetry such that both growth and regrowth, whenever they take place, are constrained to follow the lines of ancestral symmetry, we are really doing little more than restating the facts without affording any real organic explanation. That which we want to know is in what organic way this symmetrical growth is effected—how the hereditary tendency is transmitted through the nuclear network which is concerned in cell-division. I do not think that we are at present in a position to give a satisfactory answer to this question.

Let us now return to the hydra, the artificial fission of which has suggested these considerations. Multiplication in this way is probably abnormal. Under suitable conditions, however, if well fed, the hydra normally multiplies by budding. At some spot, generally not far from the "foot," or base of attachment, a little swelling occurs, and the growth of the cells in this region takes such lines that a new hydra is formed. This is at first in direct connection with the parent stem, the two having a common internal cavity; but eventually it separates and lives a free existence as a distinct organism (see Fig. 9, p. 45).

Now, here we may notice, as an implication from these facts, that the size of the organism is limited. When the normal limits of size are reached, any further assimilation of nutriment ministers, not to the further growth of the organism, but to the formation of a new outgrowth, or bud. What determines that the outgrowth, or bud, should originate in this or that group of cells, we do not know. But, like the isolated fragment in the hydra subdivided by fission, the little group in which budding commences contains a fair sample of the various kinds of cells which constitute the hydra. And here, too, we see that their growth and development follow definite lines of hereditary symmetry.

But there is a third method of multiplication in hydra: this is the sexual mode of reproduction, and occurs generally in the autumn. On the body-wall of certain individuals, near the tentacles, conical swellings appear. Within these swellings are great numbers of minute sperms, with small oval heads and active, thread-like tails. They appear to originate from the interstitial cells of the outer layer (see p. 124). Nearer the foot, or base of attachment, and generally, but not quite always, in separate individuals, there are other larger swellings, different in appearance, of which there is generally only one in the same individual at the same time. Each contains a single ovum, or egg-cell, surrounded by a capsule. It, too, and the cells which surround it would appear to be developed from the interstitial cells. It grows rapidly at the expense of the surrounding tissue, but when mature, it bursts through the enveloping capsule, and is freely exposed. A sperm-cell, which seems, in some cases at least, to be produced by the same individual, now unites with it; the egg-cell then begins to undergo division, becomes detached, falls to the bottom, and develops into a young hydra.

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Here, then, we have that sexual mode of reproduction which occurs in all the higher animals. It is, however, in some respects peculiar in hydra. In the first place, the ovum is nearly always in other animals (but occasionally not in hydra) fertilized by the sperm from a separate and distinct individual. In the second place, the germinal cells are generally produced, not from the outer layer, but from the middle layer, which appears between the two primitive layers. In some allies of hydra, however, they take their origin in the inner layer; and it has been suggested that, even in hydra, the true germinal cells may migrate from the inner to the outer layer. But of this there does not seem to be at present sufficient evidence. In any case, however, the essential fact to bear in mind is that a new individual is produced by the union of a single cell produced by one organism and of another cell produced in most cases (but not always in the hydra) from a different individual. In the higher forms of animal life, the organisms are either female (egg-producing) or male (sperm-producing). But there are many hermaphrodite forms which produce both eggs and sperms, as in the common snail and earthworm. Even in these cases, however, there are generally special arrangements by which it is ensured that the sperm from one individual should fertilize the ovum produced by another individual.

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What, we must next inquire, is the relation in the higher forms of life—for we may now leave the special consideration of hydra—of the ovum or sperm to the organism which produces it? This is but one mode of putting a very old question—Does the hen produce the egg, or does the egg produce the hen? Of course, in a sense, both are true; for the hen produces an egg which, if duly fertilized, will develop into a new hen. But the question has of late been asked in a new sense; and many eminent naturalists reply, without hesitation—The egg produces the hen, but under no circumstances does the hen produce the egg. What, then, it may be asked, does produce the egg? To this it is replied—The egg was produced by a previous egg. At first sight, this may seem a mere quibble; for it may be said that, of course, if an egg produces a hen which contains other eggs, these eggs may be said to be produced by the first. But it is really more than a quibble, and we must do our best clearly to grasp what is meant.

We have seen that, in development, the fertilized egg-cell undergoes division into two cells, each of which again divides into two, and so on, again and again, until from one there arises a multitude of cells. Nor is this all. The multitude are organized into a whole. The constituent cells have different forms and structures, and perform diverse functions. Some are skeletal, such as bone and connective tissue; some are protective, such as those which give rise to feathers or scales; some form nerves or nerve-centres; some, muscles; some give rise to glandular tissue; and lastly, some form the essential elements in reproduction. If, now, we express the development of tissues and the sequence of organisms in the following scheme, the continuity of the reproductive cells will be apparent:—

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It is clear that there is a continuity of reproductive cells, which does not obtain with regard to nerve, gland, or skeleton. If, then, we class together as body-cells those tissue-elements which constitute what we ordinarily call the body, *i.e.* the head, trunk, limbs—all, in fact, except the reproductive cells, our scheme becomes—

From this, again, it is clear that the body does not produce the egg, or reproductive cell, but that the reproductive cell does produce the body. Of course, it should be noted that we are here using the term "body" as distinguished from, and not as including, the reproductive cells. But this is convenient,

in that it emphasizes the fact that the muscular, nervous, skeletal, and glandular cells take (on this view) no part whatever in producing those reproductive cells which are concerned in the continuance of the species.

Such, in brief, is the view that the egg produces the hen. We will return to it presently when we have glanced at the alternative view that the hen produces the egg.

On this view, the reproductive elements are not merely cells, the result of normal cell-division, which have been set aside for the continuance of the species. They are, so to speak, the concentrated extract of the body, and contain minute or infinitesimal elements derived from all the different tissues of the organism which produces them. Darwin^[BG] suggested that all the cells of the various tissues produce minute particles called gemmules, which circulate freely throughout the body, but eventually find a home in the reproductive cells. Just as the organism produces an ovum from which an organism like itself develops, so do the cells of the organism produce gemmules, which find their way to the ovum and become the germs of similar cells in the developing embryo. "The child, strictly speaking," says Darwin, "does not grow into a man, but includes germs which slowly and successively become developed and form the man." "Each animal may be compared with a bed of soil full of seeds, some of which soon germinate, some lie dormant for a period, whilst others perish." Or, to vary the analogy, "an organic being is a microcosm—a little universe formed of a host of self-propagating organisms." This is Darwin's provisional hypothesis of pangenesis, which has recently been accepted in a modified form by Professor W. K. Brooks in America, to some extent by De Vries on the Continent, by Professor Herdman of Liverpool, and by other biologists. The ovum on this view is to be regarded as a composite germ containing the germs of the cellular constituents of the future organism. The scheme representing this view will stand thus-

It is clear that, on this hypothesis, we may frame an apparently simple and, on first sight, satisfactory theory of heredity. Since all the body-cells produce gemmules, which collect in or give rise to the reproductive cells, and since each gemmule is the germ of a similar cell, what can be more natural than that the ovum, thus composed of representative cell-germs, should develop into an organism resembling the parent organism? Modifications of structure acquired during the life of the organism would thus be transmitted from parent to offspring; for the modified cells of the parent would give rise to modified gemmules, which would thus hand on the modification. The inheritance of ancestral traits from grandparent or great-grandparent might be accounted for by supposing that some of the gemmules remained latent to develop in the second or third generation. The regeneration of lost parts receives also a ready explanation. If a part be removed by amputation, regrowth is possible because there are disseminated throughout the body gemmules derived from each part and from every organ. A stock of nascent cells or of partially developed gemmules may even be retained for this special purpose, either locally or throughout the body, ready to combine with the gemmules derived from the cells which come next in due succession. Similarly, in budding, the buds may contain nascent cells or gemmules in a somewhat advanced stage of development, thus obviating the necessity of going through all the early stages in the genesis of tissues. The gemmules derived from each part being, moreover, thoroughly dispersed through the system, a little fragment of such an organism as hydra may contain sufficient to rebuild the complete organism; or, if it contains an insufficient number, we may assume that the gemmules, in their undeveloped state, are capable of multiplying indefinitely by self-

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division. Finally, variations might arise from the superabundance of certain gemmules and the deficiency of others, and from the varying potency of the gemmules contained in the sperm and ovum. Where the maternal and paternal gemmules are of equal potency, the cell resulting from their union will be a true mean between them; where one or other is prepotent, the resulting cell will tend in a corresponding direction. And since the parental cells are subject to modification, transmitted through the gemmules to the reproductive elements, it is clear that there is abundant room and opportunity for varietal combinations.

It is claimed, as one of the chief advantages of some form of pangenetic hypothesis, that it, and it alone, enables us to explain the inheritance of characters or modifications of structure acquired by use (or lost by disuse) during the life of the organism, or imprinted on the tissues by environmental stresses. The evidence for the transmission of such acquired characters we shall have to consider hereafter. We may here notice, however, that at first sight the hypothesis seems to prove too little or too much. For while modifications of tissues, the effects of use and disuse, are said to be inherited, the total removal of tissues by amputation, even if repeated generation after generation, as in the docking of the tails of dogs and horses, formerly so common, does not have the effect of producing offspring similarly modified. Professor Weismann has recently amputated the tails of white mice so soon as they were born, for a number of generations, but there is no curtailment of this organ in the mice born of parents who had not only themselves suffered in this way, but whose parents, grandparents, and greatgrandparents were all rendered tailless. The pangenetic answer to this objection is that gemmules multiply and are transmitted during long series of generations. We have only to suppose that the gemmules of distantly ancestral tails have been passing through the mutilated mice in a dormant condition, awaiting an opportunity to develop, and the constant reappearance of tails is seen to be no real anomaly. In this case the gemmules of the parental and grandparental tail are simply absent. But if the muscles of the parental tail were modified through unwonted use, the modified cells would give rise to modified gemmules, which would unite in generation with ancestral gemmules, and to a greater or less degree modify them. The difference is between the mere absence of gemmules and the presence of modified gemmules. And the fact that it takes some generations for the effects of use or disuse to become marked is (pangenetically) due to the fact that it takes some time for the modified gemmules to accumulate and be transmitted in sufficient numbers to affect seriously the numerous ancestral gemmules.

The direction in which Professor W. K. Brooks has recently sought to modify Darwin's pangenetic hypothesis may here be briefly indicated. He holds that it is under unwonted and abnormal conditions that the cells are stimulated to produce gemmules, and that the sperm is the special centre of their accumulation. Hence it is the paternal influence which makes for variation, the maternal tendency being conservative. The reproductive cell is not merely or chiefly a microcosm of gemmules. It is a cell produced by ordinary cell-division from other reproductive cells. The ovum remains comparatively unaffected by changes in the body; but it receives from the sperm, with which it unites, gemmules from such tissues in the male as were undergoing special modification. The hen does not produce the egg; but the cock does produce the sperm; and the union of the two hits the happy mean between the conservatism of the one view and the progressive possibilities of the other.

Mr. Francis Galton, in 1876, [BH] suggested a modification of Darwin's hypothesis, which included, as does that of Professor Brooks, the idea of germinal continuity which had been suggested by

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Professor (now Sir Richard) Owen, in 1849. He calls the collection of gemmules in the fertilized ovum the "stirp." Of the gemmules which constitute the stirp only a certain number, and they the most dominant, develop into the body-cells of the embryo. The rest are retained unaltered to form the germinal cells and keep up a continuous tradition. Mr. Galton's place in the history of theories of heredity can scarcely be placed too high. Only one further modification of pangenesis can here be mentioned, namely, that proposed in 1883 by Professor Herdman, of Liverpool. He suggested "that the body of the individual is formed, not by the development of gemmules alone and independently into cells, but by the gemmules in the cells causing, by their affinities and repulsions, these cells so to divide as to give rise to new cells, tissues, and organs."

Such are Darwin's provisional hypothesis of pangenesis, and some more recent modifications thereof. Bold and ingenious as was Darwin's speculation, supported as it at first sight seems to be by organic analogies, it finds to-day but few adherents. With all our increased modern microscopical appliances, no one has ever seen the production of gemmules. Although it appears sufficiently logical to say that, just as a large organism produces a small ovum, so does each small cell produce an exceedingly minute gemmule; when closely investigated, the analogy is not altogether satisfactory. It is denied, as we have seen, by many biologists that the organism does produce the ovum. Multiplication is normally by definite, visible cell-division. Nuclear fission can be followed in all its phases. But where is the nuclear fission in the formation of gemmules? It is true that the conjugation of monads is followed by the pouring forth of a fluid which must be crowded with germs from which new monads arise, and that these germs are so minute as to be invisible, even under high powers of the microscope. It might be suggested, then, that in every tissue some typical cell or cells might thus break up into a multitude of invisible gemmules. But there is at present no evidence that they do so. And even if this were the case, it would not bear out Darwin's view, that every cell is constantly throwing off numerous gemmules. It is known, however, or at least generally believed, that there is a constant replacement of tissues during the life of the organism. It is said, for example, that in the course of seven years the whole cellular substance of the human body is entirely renewed. The fact is, I think, open to question. Granting it, however, it might be suggested that the effete cells, ere they vanish, give rise to minute gemmules, which find their way to the ova. But it must be remembered that the new tissue-cells in the supposed successional renewal of the organs are the descendants of the old tissue-cells; that these are, therefore, already reproducing their kind directly; and that the formation of gemmules would thus be a special superadded provision for a future generation. Still, there is no reason why cells should not have this double mode of reproduction, if any definite evidence of its existence could be brought forward. Without such definite evidence, we may well hesitate before we accept it even provisionally.

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The existence of gemmules, then, is unproven, and their supposed mode of origin not in altogether satisfactory accordance with organic analogies. Furthermore, the whole machinery of the scheme of heredity is complicated and hyper-hypothetical. It is difficult to read Darwin's account of reversion, the inheritance of functionally acquired characters, and the non-inheritance of mutilation, or to follow his skilful manipulation of the invisible army of gemmules, without being tempted to exclaim—What cannot be explained, if this be explanation? and to ask whether an honest confession of ignorance, of which we are all so terribly afraid, be not, after all, a more satisfactory position.

That the hen produces the egg, that "gemmules are collected from all parts of the system to constitute the sexual elements, and that their development in the next generation forms a new being," is

further rendered improbable by direct observation upon the mode of origin of the germinal cells, ova, or sperms.

It will be remembered that the view that the egg produces the hen, while the hen does not produce the egg, suggested the question—What, then, does produce the egg? to which the answer was—The egg is the product of a previous egg. On this view, then, the germinal cells, ova, or sperms are the direct and unmodified descendants of an ovum and sperm which have entered into fertile union. Now, in certain cases, notably in the fly *Chironomus*, studied by Professor Balbiani, but also in a less degree in some other invertebrate forms, it is possible to trace the continuity of the germinal cells with the fertilized ovum from which they are derived. In *Chironomus*, for example, "at a very early stage in the embryo, the future reproductive cells are distinguishable and separable from the body-forming cells. The latter develop in manifold variety, into skin and nerve, muscle and blood, gut and gland; they differentiate, and lose almost all protoplasmic likeness to the mother ovum. But the reproductive cells are set apart; they take no share in the differentiation, but remain virtually unchanged, and continue unaltered the protoplasmic tradition of the original ovum." In such a case, then, observation flatly negatives the view that the germinal cells are "constituted" by gemmules collected from the body-cells, though, of course (on a modified pangenetic hypothesis), they might be the recipients of such gemmules.

It is only in a minority of cases, however, that the direct continuity of germinal cells *as such* is actually demonstrable. In the higher vertebrates, for instance, the future reproductive cells can first be recognized only after differentiation of some of the body-cells and the tissues they constitute is relatively advanced. While in cases of alternation of generations, "an entire asexual generation, or more than one, may intervene between one ovum and another." In all such cases the continuity of the chain of recognizably germinal cells cannot be actually demonstrated.

The impracticability of actually demonstrating a continuity of germinal cells in the majority of cases has induced Professor Weismann to abandon the view that there is a continuity of germinal cells, and to substitute for it the view that there is a continuity of germ-plasm (keimplasma). "A continuity of germ-cells," he says, [BJ] "does not now take place, except in very rare instances; but this fact does not prevent us from adopting a theory of the continuity of the germ-plasm, in favour of which much weighty evidence can be brought forward." It might, however, be suggested that, although a continuity of germ-cells cannot be demonstrated, such continuity may, nevertheless, obtain, the future germinal cells remaining undifferentiated, while the cells around them are undergoing differentiation. The comparatively slight differentiation of the body-cells in hydroids renders such a view by no means improbable. But Professor Weismann does not regard such an idea as admissible, at all events, in certain cases. "It is quite impossible," he says, [BK] "to maintain that the germ-cells of hydroids, or of the higher plants, exist from the time of embryonic development, as undifferentiated cells, which cannot be distinguished from others, and which are only differentiated at a later period." The number of daughtercells in a colony of hydroid zoophytes is so great that "all the cells of the embryo must for a long time act as body-cells, and nothing else." Moreover, actual observation (e.g. in Coryne) convinces Dr. Weismann that ordinary body-cells are converted into reproductive cells. After describing the parts of the body-wall in which a sexual bud arises as in no way different from surrounding areas, he says, "Rapid growth, then, takes place at a single spot, and some of the young cells thus produced are transformed into germ-cells which did not previously exist as separate cells."[BL]

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This transformation of body-cells or their daughter-cells into germ-cells seems therefore, if it be admitted, to negative the continuity of germ-cells as such. But this fact, says Weismann, does not prevent us from adopting a theory of the continuity of germ-plasm. "As a result of my investigations on hydroids," he says, [BM] "I concluded that the germ-plasm is present in a very finely divided and therefore invisible state in certain body-cells, from the very beginning of embryonic development, and that it is then transmitted, through innumerable cell-generations, to those remote individuals of the colony in which the sexual products are formed."

This germ-plasm resides in the nucleus of the cell; and it would seem that by a little skilful manipulation it can be made to account for anything that has ever been observed or is ever likely to be observed. It is one of those convenient invisibles that will do anything you desire. The regrowth of a limb shows that the cells contained some of the original germ-plasm. A little sampled fragment of hydra has it in abundance. It lurks in the body-wall of the budding polyp. It is ever ready at call. It conveniently accounts for atavism, or reversion; for [BN] "the germ-plasm of very remote ancestors can occasionally make itself felt. Even a very minute trace of a specific germ-plasm possesses the definite tendency to build up a certain organism, and will develop this tendency as soon as the nutrition is, for some reason, favoured above that of the other kinds of germ-plasm present in the nucleus."

In place, then, of the direct continuity of germ-cells as distinct from body-cells, we have here the direct continuity of germ-plasm as opposed to body-plasm. The germ-plasm can give rise to body-plasm to any extent; the body-plasm can never give rise to germ-plasm. If it seems to do so, this is only because the nuclei of the body-cells contain some germ-plasm in an invisible form. The body-plasm dies; but the life of the germ-plasm is, under appropriate conditions, indefinitely continuous.

So far as heredity is concerned, it matters not whether there be a continuity of germ-cells or of germ-plasma. In either case, the essential feature is that body-cells as such cannot give rise to the germ—that the hen cannot produce the egg. On either view, characters acquired by the body cannot be transmitted to the offspring through the ova or sperms. The annexed diagram illustrates how, on the view that the hen produces the egg, dints hammered into the body by the environment will be handed on; while, on the view that the hen does not produce the egg, the dints of the environment are not transmitted to the offspring. On the hypothesis of continuity, heredity is due to the fact that two similar things under similar conditions will give similar products. The ovum from which the mother is developed, and the ovum from which the daughter is developed, are simply two fragments separated at different times from the same continuous germ-plasm. [BO] Both develop under similar circumstances, and their products cannot, therefore, fail to be similar. How variation is possible under these conditions we shall have to consider presently.

Fig. 21.—Egg and hen.

I. "The egg produces the hen." *II*. "The hen produces the egg." In *I*. the dints produced by the environment are not inherited; in *II*. they are. The letters indicate successive individuals. The small round circles indicate the eggs.]

Now, although I value highly Professor Weismann's luminous researches, and read with interest his ingenious speculations, I cannot but regard his doctrine of the continuity of germ-plasm as a distinctly retrograde step. His germ-plasm is an unknowable, invisible, hypothetical entity. Material though it be, it is of no more practical value than a mysterious and mythical germinal principle. By a little skilful manipulation, it may be made to account for anything and everything. The fundamental

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assumption that whereas germ-plasm can give rise to body-plasm to any extent, body-plasm can under no circumstances give rise to germ-plasm, introduces an unnecessary mystery. Biological science should set its face against such mysteries. The fiction of two protoplasms, distinct and yet commingled, is, in my opinion, little calculated to advance our knowledge and comprehension of organic processes. For myself, I prefer to take my stand on protoplasmic unity and cellular continuity.

The hypothesis of cellular continuity is one that the researches of embryologists tend more and more to justify. The fertilized ovum divides and subdivides, and, by a continuance of such processes of subdivision, gives rise to all the cells of which the adult organism is composed. It is true that in some cases, as in that of peripatus, as interpreted by Mr. Adam Sedgwick, the cells of the embryo run together or remain continuous as a diffused protoplasmic mass with several or many nuclei. But this seemingly occurs only in early stages as a step towards the separation of distinct cells. And even if the process should be proved of far wider occurrence, it would not disprove the essential doctrine of cellular continuity. The nucleus is the essence of the cell. And the doctrine of cellular continuity emphasizes the fact that the nuclei of all the cells of the body are derived by a process of divisional growth from the first segmentation-nucleus which results from the union of the nuclei of the ovum and the sperm. In this sense, then, however late the germinal cells appear as such, they are in direct continuity with the germinal cell from which they, in common with all the cells of the organism, derive their origin. In this sense there is a true continuity of germ-cells.

Now, it has again and again been pointed out that the simple cell of which an amœba is composed is able to perform, in simple fashion, the various protoplasmic functions. It absorbs and assimilates food; it is contractile and responds to stimulation; it respires and exhibits metabolic processes; it undergoes fission and is reproductive. The metazoa are cell-aggregates; and in them the cells exemplify a physiological division of labour. They differentiate, and give rise to muscle and nerve, gut and gland, blood and connective or skeletal tissue, ova and sperms. Are these germinal cells mysteriously different from all the other cells which have undergone differentiation? No. They are the cells which have been differentiated and set apart for the special work of reproduction, as others have been differentiated and set apart for other protoplasmic functions.

Cell-reproduction is, however, in the metazoa of two kinds. There is the direct reproduction of differentiated cells, by which muscle-cells, nerve-cells, or others reproduce their kind in the growth of tissues or organs; and there is the developmental reproduction, by which the germinal cells under appropriate conditions reproduce an organism similar to the parent. The former is in the direct line of descent from the simple reproduction of amœba. The latter is something peculiarly metazoan, and is, if one may be allowed the expression, specialized in its generality.

That the metazoa are derived from the protozoa is generally believed. How they were developed is to a large extent a matter of speculation. But, however originating, their evolution involved the production, from cells of one kind, of cells of two or more kinds, co-operating in the same organism. Whenever and however this occurred, the new phase of developmental reproduction must have had its origin. And if in cell-division there is any continuity of protoplasmic power, the faculty of producing diverse co-operating cells would be transmitted. On any view of the origin of the metazoa, this diverse or developmental reproduction is a new protoplasmic faculty; on any view, it must have been transmitted, for otherwise the metazoa would have ceased to exist. This new faculty of developmental

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reproduction, then, with the inception of the metazoa, takes its place among other protoplasmic faculties, and, with the progress of differentiation and the division of labour, will become the special business of certain cells. On this view, the specialization of the reproductive faculty and of germinal cells takes its place in line with other cell-differentiations with division of labour; and the difficulties of comprehending and following the process of differentiation in this matter are similar to those which attend physiological division of labour in general.

It is probable that, in the lower metazoa, in which differentiation has not become excessively stereotyped, the power of developmental reproduction is retained by a great number of cells, even while it is being specialized in certain cells. Hence the ability to produce lost parts and the reproduction of hydra by fission. But, on the other hand, the special differentiation of a tissue on particular lines has always a tendency to disqualify the cells from performing other protoplasmic faculties, and that of developmental reproduction among the number. I do not know of any definite, well-observed cases on record in the animal kingdom of ova or sperms being derived from cells which are highly differentiated in any other respect. In the vertebrata, the mesoblastic, or mid-layer, cells, from which the germinal epithelium arises, have certainly not been previously differentiated in any other line. And in the case of the hydroid zoophytes, quoted by Professor Weismann, the cells which give rise to the germinal products have never been so highly differentiated as to lose the protoplasmic faculty of developmental reproduction.

Some such view of developmental reproduction, based upon cellular continuity and the division of labour, seems to me more in accord with the general teachings of modern biology than a hypothetical and arbitrary distinction between a supposed germ-plasm and a supposed body-plasm.

To which category, then, does this hypothesis belong? Does it support the view that the hen produces the egg or that the egg produces the hen? Undoubtedly the latter. It is based on cellular continuity, and is summarized by the scheme on p. 131. It adequately accounts for hereditary continuity, for there is a continuity of the germinal cells, the bearers of heredity. But how, it may be asked, on this view, or on any continuity hypothesis, are the origin of variations and their transmission to be accounted for? To this question we have next to turn. But before doing so, it will be well to recapitulate and summarize the positions we have so far considered.

We saw at the outset that the facts we have to account for are those of heredity with variation. To lead up to the facts of sexual heredity, we considered fission, the regeneration of lost parts, and budding in the lower animals. We saw that, if a hydra be divided, each portion reproduces appropriately the absent parts. But we found it difficult to say whether this power resides, in such cases, in the cells along the plane of section or in the general mass of cells which constitute the regenerating portion.

Having led up to the sexual mode of reproduction, we inquired whether the egg produces the hen or the hen produces the egg. We saw that there is a marked difference between a direct continuity of reproductive cells, giving rise to body-cells as by-products, and an indirect continuity of reproductive cells, these cells giving rise to the hen, and then the hen to fresh reproductive cells, which, on this view, are to be regarded as concentrated essence of hen.

Darwin's hypothesis of pangenesis as exemplifying the latter view was considered at some length, and the modifications suggested by Professor Brooks, Mr. Galton, and Professor Herdman were [144]

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indicated. The hypothesis, so far as it is regarded as a theory of the main facts of heredity, was rejected.

It was then pointed out that only in a few cases has a direct continuity of germinal cells *as such* been actually demonstrated. Whence Professor Weismann has been led to elaborate his doctrine of the continuity of germ-plasm. This germ-plasm can give rise to, but cannot originate from, body-plasm. It may lurk in body-cells, which may, by its subsequent development, be transformed into germ-cells. But any external influences which may affect these body-cells produce no change on the germ-plasm which they may contain. We regarded this hypothesis as a retrograde step, much as we admire the genius of its propounder, and considered that the fiction of two protoplasms, distinct and yet commingled, is little calculated to advance our comprehension of organic processes.

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In the known and observed phenomena of cellular continuity and cell-differentiation, we found a sufficiently satisfactory hypothesis of heredity. The reproductive cells are the outcome of normal cell-division, and have been differentiated and set apart for the special work of developmental reproduction, as others have been differentiated and set apart for other protoplasmic functions. Such a view adequately accounts for hereditary continuity, for there is a continuity of the germinal cells, the bearers of heredity. But how, we repeat, on this view or any other hypothesis of direct continuity, are the origin of variations and their transmission to be accounted for?

Every individual organism reacts more or less markedly under the stress of environing conditions. The reaction may take the form of passive resistance, or it may be exemplified in the performance of specially directed motor-activities. The power to react in these ways is inborn; but the degree to which the power is exercised depends upon the conditions of existence, and during the life of the individual the power may be increased or diminished according to whether the conditions of life have led to its exercise or not. The effects of training and exercise on the performance of muscular feats and in the employment of mental faculties are too well known to need special exemplification. By manual labour the skin of the hand is thickened; and by long-continued handling of a rifle a bony growth caused by the weapon in drilling, the so-called *exercierknochen* of the Germans, is developed. Now, it is clear that if these acquired structures or faculties are transmitted from parent to offspring, we have here a most important source and origin of variations—a source from which spring variations just in the particular direction in which they are wanted. The question is—Are they transmitted? and if so, how?

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Let us begin with the protozoa. Dr. Dallinger made some interesting experiments on monads. They extended over seven years, and were directed towards ascertaining whether these minute organisms could be gradually acclimatized to a temperature higher than that which is normal to them. Commencing at 60° Fahr., the first four months were occupied in raising the temperature 10° without altering the life-history. When the temperature of 73° was reached, an adverse influence appeared to be exerted on the vitality and productiveness of the organism. The temperature being left constant for two months, they regained their full vigour, and by gradual stages of increase 78° was reached in five months more. Again, a long pause was necessary, and during the period of adaptation a marked development of vacuoles, or internal watery spaces, was noticed, on the disappearance of which it was possible to raise the temperature higher. Thus by a series of advances, with periods of rest between, a temperature of 158° Fahr. was reached. It was estimated that the research extended over half a million generations. Here, then, these monads became gradually acclimatized to a temperature more than

double that to which their ancestors had been accustomed to—a temperature which brought rapid death to their unmodified relatives.

Now, in such observations it is impossible to exclude elimination. It is probable that there were numbers of monads which were unable to accommodate themselves to the changed conditions, and were therefore eliminated. But in any case, the fact remains that the survivors had, in half a million generations, acquired a power of existing at a temperature to which no individual in its single life could become acclimatized. Here, then, we have the hereditary transmission of a faculty. But the organisms experimented on were protozoa. In them there is no distinction between germ-cell and body-cell. Multiplication is by fission. And if the cell which undergoes fission has been modified, the two separate cell-organisms which result from that fission will retain the special modification. In such cases the transmission of acquired characters is readily comprehensible. We have an hereditary summation of effects.

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With the metazoa the case is different. In the higher forms the germinal cells are internal and sheltered from environing influences by the protecting body-wall. It is the body-cells that react to environmental stresses; it is muscle and nerve in which faculty is strengthened by use and exercise, or allowed to dwindle through neglect. The germ-cells are shielded from external influences. They lead a sheltered and protected life within the body-cavity. It is no part of their business to take part in either passive resistance or responsive activity. During the individual life, then, the body may be modified, may acquire new tissue, may by exercise develop enhanced faculties. But can the body so modified affect the germ-cells which it carries within it?

Biologists are divided on this question. Some say that the body cannot affect the germ; others believe that it can and does do so.

It might seem an easy matter to settle one way or another. But, in truth, it is by no means so easy. Suppose that a man by strenuous exercise brings certain muscles to a high degree of strength or coordination. His son takes early to athletics, and perhaps excels his parent. Is this a case of transmitted fibre and faculty? It may be. But how came it that the father took to athletics, and was enabled to develop so lithe and powerful a frame? It must have been "in him," as we say. In other words, it must have been a product of the germ-cells from which he was developed. And since his son was developed, in part at least, from a germ-cell continuous with these, what more natural than that he too should have an inherent athletic habit? Every faculty that is developed in any individual is potential in the germstuff from which he springs; the tendency to develop any particular faculty is there too; and both faculty and tendency to exercise it are handed on by the continuity of germ-protoplasm or germ-cells. Logically, there is no escape from the argument if put as follows: The body and all its faculties (I use the term "faculties" in the broadest possible sense) are the product of the germ; the acquisition of new characters or the strengthening of old faculties by the body is therefore a germinal product; there is continuity of the germs of parent and child; hence the acquisition by the child of characters acquired by the parent is the result of germinal or cellular continuity. It is not the acquired character which influences the germ, but the germ which develops what appears to be an acquired character. Finally, if an acquired character, so called, is better developed in the child than in the parent, what is this but an example of variation? And if, in a series of generations, the acquired character continuously increases in strength, this must be due to the continued selection of favourable variations. It is clear that the

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organism that best uses its organs has, other things equal, the best chance of survival. It will therefore hand on to its offspring germinal matter with an inherent tendency to make vigorous use of its faculties.

Those who argue thus deny that the body-cells can in any way affect the germ-cells. To account for any continuous increase in faculty, they invoke variation and the selection of favourable varieties. What, then, we may now ask, is, on their view, the mode of origin of variations?

In sexual reproduction, with the union of ovum and sperm, we seem to have a fertile source of variation. The parents are not precisely alike, and their individual differences are, *ex hypothesi*, germinal products. In the union of ovum and sperm, therefore, we see the union of somewhat dissimilar germs. And in sexual reproduction we have a constantly varying series of experiments in germinal combinations, some of which, we may fairly suppose, will be successful in giving rise to new or favourable variations. This view, however, would seem to involve an hypothesis which may be true, but which, in any case, should be indicated. For it is clear that if new or favourable variations arise in this way, the germinal union cannot be a mere mixture, but an organic combination.

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An analogy will serve to indicate the distinction implied in these phrases. It is well known that if oxygen and hydrogen be mixed together, at a temperature over 100°C., there will result a gaseous substance with characters intermediate between those of the two several gases which are thus commingled. But if they are made to combine, there will result a gas, water-vapour, with quite new properties and characters. In like manner, if, in sexual union, there is a mere mixture, a mere commingling of hereditary characters, it is quite impossible that new characters should result, or any intensification of existing characters be produced beyond the mean of those of ovum and sperm. If, for example, it be true, as breeders believe, that when an organ is strongly developed in both parents it is likely to be even more strongly developed in the offspring, and that weakly parts tend to become still weaker, this cannot be the result of germinal mixture. Let us suppose, for the sake of illustration, that a pair of organisms have each an available store of forty units of growth-force, and that these are distributed among five sets of organs, a to e, as in the first two columns. Then the offspring will show the organs as arranged in the third column. [BP]

Parents.		Offspring.
10	10	10
8	10	9
9	5	7
7	9	8
6	6	6
—		
40	40	40
	10 8 9 7 6	10 10 8 10 9 5 7 9 6 6

There is no increase in the set of organs a, which are strongly developed in both parents; and no decrease in the set of organs e, which are weakly developed in both parents. By sexual admixture alone there can be no increase or decrease beyond the mean of the two parental forms. If, then, the union of sperm and ovum be the source of new or more favourable variations other than or stronger than those of either parent, this must be due to the fact that the hereditary tendencies not merely commingle, but under favourable conditions combine, in some way different indeed from, but perhaps analogous to, that exemplified in chemical combination.

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Such organic combination, as opposed to mere commixture, is altogether hypothetical, but it may be worth while to glance at some of its implications. If it be analogous to chemical combination, the products would be of a definite nature; in other words, the variations would be in definite directions. Selection and elimination would not have to deal with variations in any and all directions, but would have presented to them variations specially directed along certain lines determined by the laws of organic combination. As Professor Huxley has said, "It is quite conceivable that every species tends to produce varieties of a limited number and kind, and that the effect of natural selection is to favour the development of some of these, while it opposes the development of others along their predetermined line of modification." Mr. Gulick[BQ] and others have been led to believe in a tendency to divergent evolution residing in organic life-forms. Such a tendency might be due to special modes of organic combination giving rise to particular lines of divergence. Again, we have seen that some naturalists believe that specific characters are not always of utilitarian significance. But, as was before pointed out, on the hypothesis of all-round variation, there is nothing to give these non-useful specific characters fixity and stability, nothing to prevent their being swamped by intercrossing. If, however, on the hypothesis of combination, we have definite organic compounds, instead of, or as well as, mere hereditary mixtures; if, in other words, variations take definite lines determined by the laws of organic combination (as the nature and properties of chemical compounds are determined by the laws of chemical combination), then this difficulty disappears. There is no reason why a neutral divergence one neither useful nor deleterious—should be selected or eliminated. And if its direction is predetermined, there is no reason why it should not persist, though, of course, it will not be kept at a high standard by elimination. It has again and again been pointed out as a difficulty in the path of natural selection that, in their first inception, certain characters or structures cannot yet be of sufficient utility to give the possessor much advantage in the struggle for existence. If, however, these be definite products of organic combination, this difficulty also disappears. So long as they are not harmful, they will not be eliminated, and by fortunate combinations will progress slowly until natural selection gets a hold on them and pushes them forward, developing to the full the inherent tendency. Finally, we must notice that, on this hypothesis, our conception of panmixia, or intercrossing, would have to be modified. As generally held, this doctrine is based upon hereditary mixture, not organic combination. It is a doctrine of means and averages. There is a good deal of evidence that intercrossing does not, at least in all cases, produce mean or average results. And according to the hypothesis of organic combination, it need not always do so. According to this hypothesis, then, divergent modifications might arise and be perpetuated without the necessity of isolation. Sterility might result from the fact that divergence had been carried so far that organic combination was no longer possible; reversion, due to intercrossing, from the fact that combinations long rendered impossible by the isolation of the necessary factors in distinct varieties, are again rendered possible when these varieties interbreed.

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On this hypothesis of organic combination, to which we shall recur in the chapter on "Organic Evolution," the varied forms of animal life are the outcome of definite organic products with definite organic structure, analogous to the definite chemical compounds with definite crystalline and molecular structure; and the analogy between the regeneration of hydra and the reconstruction of a crystal is carried on a step further. I do not say that I am myself at present prepared to adopt the hypothesis, at least in this crude form; but it is, perhaps, worth a passing consideration. Its connection with Mr. Herbert Spencer's doctrine of physiological units is obvious. The analogy there is with crystallization; here it is with chemical combination.

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We must now return to the point which gave rise to this digression, and repeat that mere hereditary commixture in the union of ovum and sperm cannot give rise to new characters or raise existing structures (1) where there is free intercrossing beyond the mean of the species, and (2) where there is rigorous elimination beyond the existing maximum of the species. Variations beyond this existing maximum must be due to some other cause.

Professor Weismann has suggested, as a cause of variation, the extrusion of the polar cells from the ovum. It has before been mentioned that, generally previous to fertilization, the ripe ovum buds off two minute polar bodies. The nucleus of the ovum divides, and one half is extruded in the first polar cell; the nucleus then (except in parthenogenetic [BR] forms, where there is no union of ovum and sperm) again divides, and a second polar cell is extruded. In accordance with his special view of the absolute distinction between the body-plasm and the germ-plasm, the first polar cell is formed to carry off the body-plasm of the ovum-nucleus. For the ovum, besides being a germ-bearer, is a specialized cell, and its special form is determined by the body-plasm it contains. This is got rid of in the first polar cell, and nothing but germ-plasm remains. Now, if nothing further took place, all the ova of this same individual containing similar germ-plasm would be identical, and similarly with all the sperms from the same parent. The union of these similar ova from one parent with similar sperms from another should therefore give rise to similar offspring. But the offspring are not all similar; they vary. Professor Weismann here makes use of the second polar cell. [BS] "A reduction of the germ-plasm," he says, "is brought about by its formation, a reduction not only in quantity, but above all, in the complexity of its constitution. By means of the second nuclear division, the excessive accumulation of different kinds of hereditary tendencies or germ-plasms is prevented. With the nucleus of the second polar body, as many different kinds of plasm are removed from the egg as will be afterwards introduced by the spermnucleus." "If, therefore, every egg expels half the number of its ancestral germ-plasms during maturation, the germ-cells of the same mother cannot contain the same hereditary tendencies, unless we make the supposition that corresponding ancestral germ-plasms chance to be retained by all eggs—a supposition that cannot be sustained."

The two polar cells are therefore, on this view, of totally different character; and the nuclear division in each case of a special kind and *sui generis*. I do not think that the evidence afforded by observation lends much support to this view. But with that we are not here specially concerned. We have to consider how this reduction of the number of ancestral germ-plasms can further the kind of variation required. Now, it is difficult to see, and Professor Weismann does not explain, how the getting rid of certain ancestral tendencies can give rise to new characters or the enhancement of old characters. One can understand how this "reducing division," as Dr. Weismann calls it, can reduce the level of now one and now another character. But how it can raise the level beyond that attained by either parent is not obvious. It is perhaps possible, though Professor Weismann does not, I think, suggest it, that, by a kind of compensation, [BT] the reduction of certain characters may lead to the enhancement of others. Let us revert to the illustration on p. 150, where each individual has an available store of forty units of growth-force; and let us express by the minus sign the units lost in the parents by the extrusion of the polar cell and an analogous process which may occur in the genesis of the sperm. Then the units of growth-force which may thus be lost by a "reducing division" in b, c, and e may be, in the offspring, applied to the further growth of a; thus—

Parents. Offspring.

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a	10	10	14
b	8-1	10-3	7
c	9-1	5-1	6
d	7	9	8
e	6-2	6	5

Here the reduction of the characters b, c, and e has led to the enhancement of a, which thus stands at a higher level than in either parent.

On such an hypothesis we may, perhaps, explain the fact to which breeders of stock testify—that the organ strongly developed in both parents (a) is yet more strongly developed in some of their offspring, and that weakly parts (e) tend to become still weaker. I know not whether this way of putting the matter would commend itself to Professor Weismann or his followers; but some such additional hypothesis of transference of growth-force from one set of organs to another set of organs seems necessary to complete his hypothesis.

Professor Weismann's view, then, assumes (1) that the cell-division which gives rise to the ova in the ovary is so absolutely equal and similar that all ova have precisely the same characters; (2) that the first polar cell leaves the germinal matter unaffected, merely getting rid of formative body-plasm; (3) that the nuclear division giving rise to the second polar cell is unequal and dissimilar, effecting the differential reduction of ancestral germ-plasms. Concerning all of which one can only say that it may be so, but that there is not much evidence that it is so. And, without strong confirmatory evidence, it is questionable whether we are justified in assuming these three quite different modes of nuclear division.

There remains one more question for consideration, on the hypothesis that the germ-cells cannot in any special way be affected by the body-cells. In considering the union of ovum and sperm as a source of variation, we have taken for granted the existence of variations. We have been dealing with the mixture or combination of already existing variations. How were variations started in the first instance?

We have already seen that in the protozoa parent and offspring are still, in a certain sense, one and the same thing; the child is a part, and usually half, of the parent. If, therefore, the individuals of a unicellular species are acted upon by any of the various external influences, it is inevitable that hereditary individual differences will arise in them; and, as a matter of fact, it is indisputable that changes are thus produced in these organisms, and that the resulting characters are transmitted. Hereditary variability cannot, however, arise in the metazoa, in which the germ-plasm and the body-plasm are differentiated and kept distinct. It can only arise in the lowest unicellular organisms. But when once individual difference had been attained by these, it necessarily passed over into the higher organisms when they first appeared. Sexual reproduction coming into existence at the same time, the hereditary differences were increased and multiplied, and arranged in ever-changing combinations. Such is Professor Weismann's solution of the difficulty, told, for the most part, in his own words.

I do not know that Professor Weismann has anywhere distinctly stated what he conceives to be the relation of body-plasm and germ-plasm in the protozoa. Are the two as yet undifferentiated? This can hardly be so, seeing the fundamental distinction he draws between them. Is it the germ-plasm or the body-plasm that is influenced by external stresses? If the former, does it transfer its influence to the body-plasm during the life of the individual? If the latter, then the body-plasm must either directly influence the germ-plasm in unicellular organisms (it would seem that, according to Professor

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Weismann, it cannot do so in the metazoa), or the changed body-plasm, which shares in the fission of the protozoon, must participate in that so-called immortality which is often said to be the special prerogative of germinal matter.

These, however, are matters for Professor Weismann and his followers to settle. I regard the sharp distinction between body-plasm and germ-plasm as an interesting biological myth. For me, it is sufficient that the protoplasm of the protozoon is modified, and the modification handed on in fission. And it is clear that Professor Weismann is correct in saying that the commixture or combination of characters takes its origin among the protozoa. If the unicellular individuals are differently modified, however slightly, then, whenever conjugation occurs between two such individuals, there will be a commingling or combination of the different characters. The transmissible influence of the environment, however, ceases when the metazoon status is reached, and special cells are set apart for reproductive purposes—ceases, that is to say, in so far as the influence on the body is concerned. There may, of course, be still some direct^[BU] influence on the germinal cells themselves. Except for this further influence, the metazoon starts with the stock of variations acquired by that particular group of protozoa—whatever it may be—from which it originated. All future variations in even the highest metazoa arise from these.

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Now, it is obvious that no mere commingling and rearrangement of protozoan characters could conceivably give rise to the indefinitely more complex metazoan characters. But if there be a combination and recombination of these elements in ever-varying groups, the possibilities are no longer limited. Let us suppose that three simple protozoan characters were acquired. The mere commixture of these three could not give much scope for further variation. It would be like mixing carbon, oxygen, and hydrogen in varying proportions. But let them in some way combine, and you have, perhaps, such varied possibilities as are open to chemical combinations of oxygen, hydrogen, and carbon, whose name is legion, but whose character is determined by the laws of chemical combination.

Summing up now the origin of variations, apart from those which are merely individual, on the hypothesis that particular modifications of the body-cells cannot be transmitted to the germ-cells, we have—

- 1. In protozoa, the direct influence of the environment and the induced development of faculty.
- 2. In metazoa—
- (a) Some direct and merely general influence of the environment on the germ, including under the term "environment" the nutrition, etc., furnished by the body.
- (b) The combination and recombination of elementary protoplasmic faculties (specific molecular groupings) acquired by the protozoa.
 - (c) Influences on the germ, the nature of which is at present unknown.

We may now pass on to consider the position of those who give an affirmative answer to the question—Can the body affect the germ? Two things are here required. First, definite evidence of the fact that the body does so affect the germ; *i.e.* that acquired characters are inherited. Secondly, some

answer to the question—How are the body-cells able to transmit their modifications to the germ-cells? We will take the latter first, assuming the former point to be admitted.

Let us clearly understand the question. An individual, in the course of its life, has some part of the epidermis, or skin, thickened by mechanical stresses, or some group of muscles strengthened by use, or the activity of certain brain-cells quickened by exercise: how are the special modifications of these cells, here, there, or elsewhere in the body, communicated to the germ, so that its products are similarly modified in the offspring? The following are some of the hypotheses which have been suggested:—

- (a) Darwin's pangenesis.
- (b) Haeckel's perigenesis; Spencer's physiological units.
- (c) The conversion of germ-plasm into body-plasm, and its return to the condition of germ-plasm (Nägeli).
 - (d) The unity of the organism.
- (a) Concerning pangenesis, nothing need be added to what has already been said. Although, as we have seen, it has been adopted with modifications by Professor Brooks; although Mr. Francis Galton, a thinker of rare ability and a pioneer in these matters, while contending for continuity, admitted a little dose of pangenesis; although De Vries has recently renewed the attempt to combine continuity and a modified pangenesis;—this hypothesis does not now meet with any wide acceptance.
- (b) With the pamphlet in which Professor Haeckel brought forward his hypothesis termed the perigenesis of the plastidule, I cannot claim first-hand acquaintance. According to Professor Ray Lankester, who gave some account of it in Nature, [BV] protoplasm is regarded by Haeckel as consisting of certain organic molecules called plastidules. These plastidules are possessed of special undulatory movements, or vibrations. They are liable to have their undulations affected by every external force, and, once modified, the movement does not return to its pristine condition. By assimilation, they continually increase to a certain size and then divide, and thus perpetuate in the undulatory movement of successive generations the impressions or resultants due to the action of external agencies on the individual plastidules. On this view, then, the form and structure of the organism are due to the special mode of vibration of the constituent plastidules. This vibration is affected by external forces. The modified vibration is transmitted to the plastidules by the germ, which, therefore, produce a similarly modified organism. As Mr. J. A. Thomson says, "In metaphorical language, the molecules remember or persist in the rhythmic dance which they have learned."

Darwin's hypothesis was frankly and simply organic—the gemmules are little germs. This of Professor Haeckel tries to go deeper, and to explain organic phenomena in terms of molecular motion. Mr. Herbert Spencer long ago suggested that, just as molecules are built up, through polarity, into crystals, so physiological units are built up, under the laws of organic growth, into definite and special organic forms. Both views involve special units. With Mr. Herbert Spencer, their "polarity" is the main feature; with Professor Haeckel, their "undulatory movements." According to Mr. Spencer, "if the structure of an organism is modified by modified function, it will impress some corresponding modification on the structures and polarities of its units." [BW] According to Professor Haeckel, the

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vibrations of the plastidules are permanently affected by external forces. In either case, an explanation is sought in terms of molecular science, or rather, perhaps, on molecular analogies. So far good. Such "explanation," if hypothetical, may be suggestive. It may well be that the possibilities of fruitful advance will be found on these lines.

But though, as general theories, these suggestions may be valuable, they do not help us much in the comprehension of our special point. To talk vaguely about "undulatory movements" or "polarities" does not enable us to comprehend with any definiteness how this particular modification of these particular nerve-cells is so conveyed to the germ that it shall produce an organism with analogous nerve-cells modified in this particular way.

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- (c) The hypothesis that the germ-plasm may be converted into body-plasm, which, on its return again to the condition of germ-plasm, may retain some of the modifications it received as body-plasm, seems to be negatived, so far as most animals are concerned, by the facts of embryology and development. The distinction of germ-plasm and body-plasm I hold to be mythical. And there is no evidence that cells specially differentiated along certain lines can become undifferentiated again, and then contribute to the formation of ova or sperms. From the view-point of cell-differentiation, which seems to me the most tenable position, there does not seem any evidence for, or any probability of, the occurrence of any roundabout mode of development of the germinal cells which could enable them to pick up acquired characters en route.
- (d) We come now to the contention that the organism, being one and continuous, if any member suffers, the germ suffers with it. The organs of the body are not isolated or insulated; the blood is a common medium; the nerves ramify everywhere; the various parts are mutually dependent: may we not, therefore, legitimately suppose that long-continued modification of structure or faculty would soak through the organism so completely as eventually to modify the germ? The possibility may fairly be admitted. But how is the influence of the body brought to bear on the germ? The common medium of the blood, protoplasmic continuity, the influence of the products of chemical or organic change,—these are well enough as vague suggestions. But how do they produce their effects? Once more, how is this increased power in that biceps muscle of the oarsman able to impress itself upon the sperms or the ova? No definite answer can be given.

We are obliged to confess, then, that no definite and satisfactory answer can be given to the question—How can the body affect the germ so that this or that particular modification of body-cells may be transmitted to the offspring? We may make plausible guesses, or we may say—I know not how the transmission is effected; but there is the indubitable fact.

This leads us to the evidence of the fact.

It must be remembered that no one questions the modifiability of the individual. That the epidermis of the oarsman's hand is thickened and hardened; that muscles increase by exercise; that the capacity for thinking may be developed by steady application;—these facts nobody doubts. That well-fed fish grow to a larger size than their ill-fed brethren; that if the larger shin-bone (the tibia) of a dog be removed, the smaller shin-bone (the fibula) soon acquires a size equal to or greater than that of the normal tibia; that if the humerus, or arm-bone, be shifted through accident, a new or false joint will be formed, while the old cavity in which the head of the bone normally works, fills up and disappears; that

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canaries fed on cayenne pepper have the colour of the plumage deepened, and bullfinches fed on hemp-seed become black; that the common green Amazonian parrot, if fed with the fat of siluroid fishes, becomes beautifully variegated with red and yellow; that climate affects the hairiness of mammals;—these and many other reactions of the individual organism in response to environing conditions, will be admitted by every one. [BX] That constitutional characters of germinal origin are inherited is also universally admitted. The difficulty is to produce convincing evidence that what is acquired is really inherited, and what is inherited has been really acquired.

Attempts have been made to furnish such evidence by showing that certain mutilations have been inherited. I question whether many of these cases will withstand rigid criticism. Nor do I think that mutilations are likely to afford the right sort of evidence one way or the other. We must look to less abnormal influences. What we require is evidence in favour of or against the supposition that *modifications* of the body-cells are transmitted to the germ-cells. Now, these modifications must clearly be of such a nature as to be receivable by the cells without in any way destroying their integrity. The destruction or removal of cells is something very different from this. If it were proved that mutilations are inherited, this would not necessarily show that normal cell-modifications are transmissible. And if the evidence in favour of inherited mutilations breaks down, as I believe it does, this does not show that more normal modifications such as those with which we are familiar, as occurring in the course of individual life, are not capable of transmission. I repeat, we must not look to mutilations for evidence for or against the supposition that acquired characters are inherited. We must look to less abnormal influences.

These readily divide themselves into two classes. The first includes the direct effects on the organism of the environment—effects, for example, wrought by changes of climate, alteration of the medium in which the organism lives, and so forth. The second comprises the effects of use and disuse—the changes in the organism wrought by the exercise of function.

Taking the former first, we have the remarkable case of Saturnia, which was communicated to Darwin by Moritz Wagner. Mr. Mivart thus summarizes it: "A number of pupæ were brought, in 1870, to Switzerland from Texas of a species of *Saturnia*, widely different from European species. In May, 1871, the moths developed out of the cocoons (which had spent the winter in Switzerland), and resembled entirely the Texan species. Their young were fed on leaves of Juglans regia (the Texan form feeding on Juglans nigra), and they changed into moths so different, not only in colour, but also in form, from their parents, that they were reckoned by entomologists as a distinct species."[BY] Professor Mivart also reminds us that English oysters transported to the Mediterranean are recorded by M. Costa to have become rapidly like the true Mediterranean oyster, altering their manner of growth, and forming prominent diverging rays; that setters bred at Delhi from carefully paired parents had young with nostrils more contracted, noses more pointed, size inferior, and limbs more slender than well-bred setters ought to have; and that cats at Mombas, on the coast of Africa, have short, stiff hair instead of fur, while a cat from Algoa Bay, when left only eight weeks at Mombas, underwent a complete metamorphosis—having parted with its sandy-coloured fur. Very remarkable is the case of the brineshrimp Artemia, as observed and described by Schmankewitsch. One species of this crustacean, Artemia salina, lives in brackish water, while A. milhausenii inhabits water which is much saltier. They have always been regarded as distinct species, differing in the form of the tail-lobes and the character of the spines they bear. And yet, by gradually altering the saltness of the water, either of them was

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transformed into the other in the course of a few generations. So long as the altered conditions remained the same, the change of form was maintained.

Many naturalists believe that climate has a direct and determining effect on colour, and contend or imply that it is hereditary. Mr. J. A. Allen correlates a decrease in the intensity of colour with a decrease in the humidity of the climate. Mr. Charles Dixon, in his "Evolution without Natural Selection," says, "The marsh-tit (*Parus palustris*) and its various forms supply us with similar facts [illustrative of the effects of climate on the colours of birds]. In warm, pluvial regions we find the brown intensified; in dry, sandy districts it is lighter; whilst in Arctic regions it is of variable degrees of paleness, until, in the rigorous climate of Kamschatka, it is almost white." Mr. Dixon does not think that these changes are the result of natural selection. "Depend upon it," he says, with some assurance, [BZ] in considering a different case, "it is the white of the ptarmigan (modified by climatic influence) that has sent the bird to the snowy wastes and bare mountain-tops, and rigorously keeps it there; not the bird that has assumed, by a long process of natural selection, a white dress to conceal itself in such localities." Professor Eimer[CA] contends that in the Nile valley the perfectly gradual transition in the colour of the inhabitants from brownish-yellow to black in passing from the Delta to the Soudan is particularly conclusive for the direct influence of climate, for the reason that various races of originally various colours dwell there.

Mr. A. R. Wallace says^[CB] of the island of Celebes "that it gives to a large number of species and varieties (of Papilionidæ) which inhabit it, (1) an increase of size, and (2) a peculiar modification in the form of the wings, which stamp upon the most dissimilar insects a mark distinctive of their common birthplace." But this similarity may largely, or at least in part, be due to mimicry. Most interesting and valuable are the results of Mr. E. B. Poulton's experiments on caterpillars and chrysalids.^[CC] They show that there is a definite colour-relation between the caterpillar (*e.g.* the eyed hawk-moth, *Smerinthus ocellatus*) and its food-plant, adjustable within the limits of a single life; that the predominant colour of the food-plant is itself the stimulus which calls up a corresponding larval colour; that there is also a direct colour-relation between the chrysalids of the small tortoiseshell butterfly (*Vanessa urticæ*) and the surrounding objects, the pupæ being dark grey, light grey, or golden, according to the nature and colour of the surroundings; and that the larvæ of the emperor moth (*Saturnia carpini*) spin dark cocoons in dark surroundings, but white ones in lighter surroundings. These are but samples of the interesting results Mr. Poulton has obtained.

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What shall we say of such cases? Some of them seem to indicate the very remarkable and interesting fact that changes of salinity of the medium, or changes of food, or the more general influence of a special climate, may modify organisms in *particular* and little-related ways. The larvæ of a Texan *Saturnia* fed on a new food-plant develop into imagos so modified as to appear new species. Changes of salinity of the water modify one species of *Artemia* into another. If these be adaptations, the nature of the adaptation is not obvious. If the new character produced in this way be of utilitarian value, where the utility comes in is not clear. The facts need further confirmation and extension, which may lead to very valuable results. Mr. Poulton's observations, on the other hand, give us evidence of direct adaptation to colour-surroundings. But the effects are, in the main, restricted to the individual. What is hereditary is the power to assume one of two or three tints, that one being determined by the surrounding colour. His experiments neither justify a denial nor involve an assertion of the

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transmissibility of environmental influence. Secondly, some of the cases above cited seem to show clearly that, under changed conditions of life, the changes which have been wrought in one generation may reappear in the next. But are they inherited? Is there sufficient evidence to show conclusively that the body-cells have been modified, and have handed on the modification to the germ? Can we exclude the direct action of the more or less saline water, or the products of the unwonted food on the germinal cells? Can we be sure that there is really a summation of results—that each generation is not affected de novo in a similar manner? No one questions that the individual is modifiable, and that such modification is most readily effected in the early and plastic stages of life. If each plastic embryo is moulded in turn by similar influence, how can we conclusively prove hereditary summation? Take a case that has been quoted in support of hereditary modification. Greyhounds transported from England to the uplands of Mexico are unable to course, owing to the rarity of the atmosphere. Their pups are, however, able to run down the fleetest hares without difficulty. Now, this may be due to the fact that the dogs acquire a certain amount of accommodation to a rare atmosphere, and hand on their acquired power to their offspring, which carry it on towards perfection. But it may also be due to the fact that the pups, subject from the moment of birth to the conditions of a rarified atmosphere, are developed in accordance with these conditions.

Or take another case that has been brought forward. English dogs are known in hot climates, like that of India, to degenerate in a few generations. Let us suppose that these degenerate dogs are removed back to England, and that their pups, born in English air and in our temperate climate, are still degenerate: would not this, it may be asked, show that the influence of climate on the body is inherited? I do not think that such a case would be convincing. For the climate might well influence the germ through the body. The body being unhealthy and degenerate, the germ-cells must, one may suppose, suffer too. The degenerate pup born in England might well owe its degeneracy to effects wrought upon the germinal cells. In other words, such a case would indicate some *general* influence of the environment (including the environing body) on the germ. It does not convince us that *particular* modifications of body-cells as such are transmitted under normal and healthy conditions.

On the whole, it seems to me that the evidence we at present possess on this head is not convincing or conclusive in favour of the effects on the body alone being transmitted to offspring. If cases can be brought forward in which there can be no direct influence on the germ, in which elimination is practically excluded, and in which there is a *gradual and increasing* accommodation of successive generations of organisms to changed conditions *which remain constant*, then such transmission will be rendered probable. I do not know that there are observations of this kind of sufficient accuracy to warrant our accepting this conclusion as *definitely proved*.

Attention may here be drawn to a peculiar and remarkable mode of influence. If a pure-bred mare have foals by an ill-bred sire, they will be ill-bred. This we can readily understand. But if she subsequently have a foal by a perfectly well-bred sire, that foal, too, may in some cases be tainted by the blemish of the previous sire. So, too, with dogs. If a pure-bred bitch once produce a mongrel litter, no matter how carefully she be subsequently matched, she will have a tendency to give birth to pups with a mongrel taint. This subsequent influence of a previous sire is a puzzling fact. It may be that some of the male germ-nuclei are absorbed, and influence the germ-cells of the ovary. But this seems an improbable solution of the problem. It is more likely, perhaps, that in the close relation of mother and fœtus during gestation, each influences the other (how it is difficult to say). On this view the bitch

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retains the influence of the mongrel puppies—is herself, in fact, partially mongrelized—and therefore mongrelizes subsequent litters. It would not be safe, however, to base any far-reaching conclusions on so peculiar a case, the explanation of which is so difficult. At all events, it is impossible to exclude the possibility of direct action on the germ, though the *particular* nature of the results of such influence are noteworthy.

We may pass now to the evidence that has been adduced in favour of a cumulative effect in the exercise of function, or of the inheritance of the results of use or disuse. Here, again, it must be remembered that no one questions the effects of use and disuse in the individual. What we seek is convincing evidence that such effects are inherited.

Physiologically, the effects of use or disuse are, in the main, effects on the relative nutrition, and hence on the differential growth of organs. When an organ is well exercised, there is increased nutrition and increased growth of tissue, muscular, nervous, glandular, or other. When an organ is, so to speak, neglected, there is diminished blood-supply, diminished growth, and diminished functional power. The development of a complex activity would necessitate a complex adjustment of size and efficiency of parts, involving a nice balance of differential growth dependent on delicately regulated nutrition. What is the evidence that adjusted nutrition can be inherited?

With regard to man, there is some evidence which bears upon this subject. Mr. Arbuthnot Lane, in his valuable papers in the *Journal of Anatomy and Physiology*, has shown that certain occupations, such as shoemaking, coal-heaving, etc., produce recognizable effects upon the skeleton, the muscular system, and other parts of the organization. And he believes^[CD] that such effects are inherited, being very much more marked in the third generation than they were in the first. Sir William Turner informed Professor Herdman that, in his opinion, the peculiar habits of a tribe, such as tree-climbing among the Australians, or those natives of the interior of New Guinea whose houses are built in the upper branches of lofty trees, not only affect each generation individually, but have an intensified action through the influence of heredity. [CE]

Mr. Francis Galton's results mainly deal with human faculty; and though faculty has undoubtedly an organic basis, I do not propose to consider the evidence afforded by instinct, intelligence, or intellectual faculties in this chapter. Mention should, however, be made of the interesting results of his study of twins. Twins are either of the same sex, in which case they are remarkably alike, or of different sexes, in which case they are apt to differ even more widely than is usual with brothers and sisters. The former are believed to be developed from one ovum which has divided into two halves, each of which has given rise to a distinct individual; the latter from two different ova. Mr. Galton collected a large mass of statistics concerning twins of both classes. The result of this analysis seems to be that, in the case of "identical twins," the resemblances are not superficial, but extremely intimate; that they are not apt to be modified to any large extent by the circumstances of life; that where marked diversity sets in it is due to some form of illness; and, on the whole, that innate tendencies outmaster acquired modifications. "Nature is far stronger than nurture within the limited range that I have been careful to assign to the latter." On the other hand, speaking of dissimilar twins, Mr. Galton says, "I have not a single case in which my correspondents speak of originally dissimilar characters having become assimilated through identity of nurture." "The impression that all this evidence leaves on the mind is one of some wonder whether nurture can do anything at all, beyond giving instruction and professional [169]

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training." "There is no escape from the conclusion that nature prevails enormously over nurture where the differences of nurture do not exceed what is commonly to be found among persons of the same rank of society and in the same country." [CF]

Combining the results of Messrs. Lane and Galton, we may say that it requires persistent and long-continued influence to modify the individual, and change, even by a little, the structure inherited or given by nature; but that if this structure is thus modified, there may be a tendency for such modification to increase by hereditary summation of effects. We require, however, further and fuller observations to render the evidence of such hereditary summation to any extent convincing.

Turning now from the evidence afforded by man^[CG] to that afforded by animals, we may consider first that presented by domesticated breeds. They might be expected to afford exceptionally good examples. Their modifiability and the readiness with which they interbreed are two of the determining causes of their selection for domestication. They have, moreover, been placed under new conditions of life, and they undoubtedly exhibit changes of structure, many of which Darwin^[CH] regarded as attributable to the effects of use and disuse. In domestic ducks, the relative weight and strength of the wing-bones have been diminished, while conversely the weight and strength of the leg-bones have been increased. The bones of the shoulder-girdle have been decreased in weight and "the prominence of the crest of the sternum, relatively to its length, is also much reduced in all the domestic breeds. These changes," says Darwin, "have evidently been caused by the lessened use of the wings." The shouldergirdle and breast-bone of domestic fowls have been similarly reduced. After a careful consideration of numerous facts concerning the brains of rabbits, Darwin concluded that this "most important and complicated organ in the whole organization is subject to the law of decrease in size from disuse." And Sir J. Crichton Browne has recently shown that, in the wild duck, the brain is nearly twice as heavy in proportion to the body as it is in the comparatively imbecile domestic duck. In pigs, the nature of the food supplied during many generations has apparently affected the length of the intestines; for, according to Cuvier, their length to that of the body in the wild boar is as 9 to 1, in the common domestic boar as 13.5 to 1, and in the Siam breed as 16 to 1. With regard to horses, Darwin tells us that "veterinarians are unanimous that horses are affected with spavins, splints, ring-bones, etc., from being shod and from travelling on hard roads, and they are almost unanimous that a tendency to these malformations is transmitted."

These are samples of the effects of domestication. It has been suggested, however, that, quite apart from any diminution from disuse, the reduction of size in parts or organs may be the result of the absence or cessation of selection. If an organ be subject to selection, the mean size in adult creatures will be that of the selected individuals; but if selection ceases, it will be the mean of those born. Let us suppose that nine individuals are born, and that the size of some organ varies in these from 1, the most efficient, to 9, the least efficient. The birth-mean will therefore be, as shown on the left-hand side of the following table, at the level of number 5, four being more efficient, and four less efficient. But if, of these nine, six be eliminated, then the mean of the survivals will be as shown on the right-hand side of the table:—

1 2 — Survival-mean. 3 4 [171]

The result, then, of the cessation of selection will be to reduce the survival-mean to the birth-mean, and that without any necessary effect of disuse. But unless this be accompanied by a tendency to diminution due to economy of growth or some other cause, this cannot produce any well-marked or considerable amount of reduction. I very much question, for example, whether the cessation of selection, even with the co-operation of the principle of economy of growth, will adequately account for the reduction to nearly one-half its original proportion of the brain of the duck. The subject will be more fully discussed, however, in the next chapter.

There is probably but little tendency for disused parts to be reduced in size through artificial selection. An imbecile duck does not probably taste nicer than one with bigger brains. On the other hand, the increase of size in organs may presumably, in certain cases, be increased by selection. Pigs, for example, have been selected according to their fattening capacity. Those with longer intestines, and therefore increased absorbent surface, may well have an advantage in this respect. Hence, in selecting pigs for fattening, breeders may have been unconsciously selecting those with the longest intestines. Of course, on this view, the longer intestine must be there to be selected, and the increased length must be due to variation. But this may be all-round variation (cause unknown), not variation in one direction, the result of increased function.

Another point that has to be taken into consideration is the amount of *individual* increment or decrement, owing to individual use or disuse, apart from any possible summation of results.

Seeing, then, that it is difficult to estimate the amount of purely individual increment or decrement, and that it is difficult, if not impossible, to exclude the disturbing effects of cessation of selection with economy of growth on the one hand, reducing the size of organs, and artificial selection on the other hand, increasing the size or efficiency of parts, it is clear that such cases cannot afford convincing evidence that the observed variations are the directly inherited results of use and disuse. Indeed, I am not aware of any experiments or direct observations on animals which are individually conclusive in favour of the hereditary summation of functionally produced modifications.

It may, however, be said—Although no absolutely convincing experiments or observations are forthcoming (for, from the nature of the case, it is almost impossible logically to prove that this interpretation of the facts is alone possible), still there are cases which are much more readily explained on the hypothesis that the effects of use and disuse are inherited, than on any other hypothesis. But, so far as Professor Weismann and his followers are concerned, such an argument is wholly beside the question. They are ready to admit that inherited modifications of the body, if they could be proved, would render the explanation of many results of evolution much easier. It would, no doubt, they say, be easier to account for the shifting of the eye of a flat-fish from one side of the head to the other on the supposition that individual efforts were inherited, until, by an hereditary summation of effort, the eye at last came round. The question is—Are we justified in accepting the easier explanation if it be based on a mere assumption, at present unproved, the *modus operandi* of which is inexplicable?

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Let us consider very briefly these two points—first, the "mere assumption;" secondly, "the inexplicable *modus operandi*." Is there any reason why we should not assume the inheritance of effects of use or disuse as a working hypothesis, if it is not in opposition to any known biological law, and if it does enable us to explain certain observed phenomena? I see no such reason. We do not know enough about the causes of variation to be rigidly bound by the law of parcimony. I am not aware of any biological law that would render the acceptance of this view as a provisional hypothesis unjustifiable.

But how, it is asked, can we accept it if its *modus operandi* is inexplicable? I question the validity of this argument. I fear our knowledge of organic nature is not at present so full and exact as to justify us in excluding an hypothesis because we are not able to give an adequate answer to the question—How are these effects produced? Of course, if it can be shown that no *modus operandi* is possible, there is an end of the matter. But who shall dare thus to limit the possibilities of organic nature? And, if possible, then that natural selection in which the neo-Darwinians place their sole trust would certainly develop so advantageous a mode of influence. It is clear that a species sensitive to every shock of the environment on the organism would be unstable, and hence at a disadvantage. But, on the other hand, the ability to answer by adaptation to long-continued and persistent environmental influence or to oft-repeated and consistent performance of function would be so distinct an advantage to the species which possessed it, that, if it lay within the possibilities of organic nature, natural selection, always, as we are told, on the look out for every possible advantage, would assuredly seize upon it and develop it.

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Those who believe in the absolute sway of natural selection have not at present given any adequate answer to the question—How are particular variations (e.g. the twisted skull of flat-fish) produced? They say that constitutional variations, which are alone inheritable, are due to variations in the germs. When asked how these variations are produced, they are forced to reply—We cannot say. But when it is suggested that they may be in some unknown way transmitted to the germ from the body, they are up in arms, and exclaim—You have no right to believe that, or ask us to believe it, unless you can tell us plainly how the effect is produced. Unable themselves to give the modus operandi of the origin of particular variations, they demand the exact modus operandi from those who suggest that variations may arise through this mode of influence of the body on the germ.

We shall have to consider this question from a more general standpoint in the next chapter on "Organic Evolution." We may now very briefly summarize some of the results we have reached in this chapter.

The ova and sperms are specially differentiated cells which have, in the division of labour, retained and emphasized the function of developmental reproduction.

There is a continuity of such cells. The cells which become ova or sperms have never become differentiated into anything else.

Hereditary similarity is due to the fact that parents and offspring are derived eventually from the same germinal cells.

Variation in the existing world is partly due to sexual union. But if there be mere admixture, new characters cannot arise in this way, nor can old characters be strengthened beyond the existing maximum.

Some mode of organic combination (analogous to chemical combination) might afford an explanation of the occurrence of new variations and the increase of existing characters.

In the protozoa there may be a summation of the effects of the environment in succeeding [176] generations.

There is no convincing evidence that in the metazoa special modifications of the body so influence the germ as to become hereditary.

But there is no reason why such influence should not be assumed as a provisional hypothesis.

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CHAPTER VI. ORGANIC EVOLUTION.

It is difficult to realize the wealth, the variety, the diversity, of "animal life." Even if we endeavour to pass in review all that we have seen in woodland and meadow, in pond or pool, in the air, on the earth, in the waters, in temperate or tropical regions; even when we try to remember the results of all anatomical and microscopic investigation displaying new wonders and new diversities hidden from ordinary and unaided vision; even when we call to mind the multifarious contents, recent and fossil, of all the natural history museums we have ever visited, and throw in such mental pictures as we have formed of all the diverse adaptations we have read about or heard described;—even so we cannot but be conscious that not one-tenth, not one-hundredth, part of the diversity and variety of animal life has passed before our mental vision even in sample. It is said that our greatest living poet once, when a young man, left his companions to gaze into the waters of a clear, still pool. "What an imagination God has!" he said, as he rejoined his friends. Fit observation for the poet, whose sensitive nature must be keenly alive to the varied endowments which Nature has lavishly showered upon her animate children.

Certain it is that words, mere words, can never present, though they may aid in recalling, an adequate picture of either the wealth or the beauty of animal life. Fortunately for those who visit London (and who nowadays does not?), we have, in our national collection in South Kensington, the means of getting some insight into the wealth of life. And much is being done there to aid the imagination and to facilitate study for those who are not professed students. Many of the birds are now to be seen set in their natural surroundings, with their life-history illustrated. Our frontispiece is taken from one of these cases. And this admirable system will, no doubt, so far as space permits, be extended; and, perhaps, dramatic incidents may be introduced, like those (notably in the life of heron and hawk) which form so marked a feature in the little museum at Exeter. Anything which leads us to understand the life of animals, and to go forth and study it for ourselves, has an educational value.

In our National Museum, again, much is being wisely done to illustrate the diversity and variety of structure and the principles that underlie them. Observe, as you enter the central hall, the case containing stuffed specimens of ruffs (*Machetes pugnax*). Among the young autumn birds there is not much difference between males and females, the male being distinguished chiefly by its somewhat larger size. Nor do the old birds, male and female, differ much during the winter months. But in pairing-time, May and June, the females are somewhat richer in colour; while the males not only don the ruff to which the bird owes its popular name, but develop striking colour-tints. Among different individuals it will be seen that the colour-variation is tolerably wide; but the same individual keeps strictly, we are told, in successive seasons, to the same summer dress. Note, next, in a bay to the right, the great variety of form, ornamentation, and colouring among the molluscan shells there exhibited. Observe that the rich colours are often hidden during life by the dull epidermis. Half an hour's attentive study of these varied molluscan forms will give a better idea of the beauty and diversity of these life-products than pages of mere description.

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Pass on, too, to note, in a further bay to the right, the extraordinary modifications of the antenna, or feeler, in insects. There is the long, whip-like form in the locust; the clubbed whip in the ant-lion and the butterfly; the feathered form in certain moths and flies; the hooked form characteristic of the sphinx-moths; the many-leaf form in the lamellicorn beetles, like the cockchafer; and the feathered plate of other beetles. Equally wonderful are the diverse developments of the mouth-organs of insects, the spiral tube of the butterfly or moth, the strong jaws of the great beetles, the lancets of the gnat, the sucking-disc of the fly,—all of them special modifications of the same set of structures. Then, in the same bay, note some of the striking differences between the males and females of certain insects. In some there is an extraordinary difference in size (e.g. the locust Xiphocera, and the moth Attacus); in others, like the stag-beetle, it is the size of the jaws that distinguishes the males; in others, again, the most notable differences are in the length, development, or complexity of the antennæ, or feelers; in some beetles the males have great horns on the head or thorax; while in many butterflies it is in richness of colour that the difference chiefly lies—the brilliant green of the Ornithoptera there exhibited contrasting strongly with the sober brown of his larger mate.

The fact that the special characteristics of the male, which we have seen to be variable in the ruff, are also variable among insects, is well exemplified in the case of the stag-beetle, in some males of which the mandibles are far larger than in others. This is shown in <u>Fig. 22</u>, which is copied from the series displayed in the British Museum, by the kind permission of Professor Flower.

Fig. 22.—Variations in the size of, and especially in the head and mandibles of, the male stag-beetle (*Lucanus cervus*). (From an exhibit in the British Natural History Museum.)]

Crossing the hall to where the vertebrate structures are displayed, the development of hair, of feathers, of teeth, the modifications of the skull and of legs, wings, and fins are being exemplified. Note here and elsewhere the special adaptations of structure, of which we may select two examples. The first is that seen in the *Balistes*, or trigger-fish. The anterior dorsal fin is reduced to three spines, of which that which lies in front is a specially modified weapon of defence, while that which follows it is the so-called trigger. These two are so hinged to the underlying interspinous bones and so related to each other that, when once the defensive spine in front is erected, it cannot be forced down until the trigger is lowered. The second example of special adaptation is well displayed in specimens of the mud-tortoise *Trionyx*. Between the last vertebra of the neck and the first fixed vertebra of the dorsal series is a beautiful hinge-joint, enabling the neck to be bent back, S-fashion, when the creature withdraws its head within the carapace. These are only one or two particular instances of what any one who will visit the National Museum may see for himself admirably displayed and illustrated.

No one can, one would suppose, pass through the galleries in Cromwell Road and remain quite insensible to the beauties of animal life. Beauty of form and beauty of colour are conspicuously combined in many species of birds and insects. And much of this colour-beauty and splendid iridescence is known to be due to minute scales, to thin films of air or fluid, and to microscopically fine lines developed upon scales or feathers. But there is one phase of beauty which cannot be exhibited in the museum—the beauty that comes of life as opposed to death. For this we must go out into the free air of nature, where the animals not only have lived, but are still instinct with the glow of life, and where the silence of the museum galleries is replaced by the song of birds and the hum of insect-wings.

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How have this wealth, this diversity, this beauty, this manifold activity, which we summarize under the term "animal life," been produced?

If we answer this question in a word—the word "evolution" [CI]—we must remember that this word merely expresses our belief in a general fact; and we must not forget that many questions remain behind, all centering round that little question, to which an adequate answer is so difficult to give, the question—How? Reduced to its simplest expression, the doctrine of evolution merely states that the animal world as it exists to-day is naturally developed out of the animal world as it existed yesterday, and will in turn develop into the animal world as it shall exist to-morrow. This is the central belief of the evolutionist. No matter what moment in the past history of life you select, the life at that moment was in the act of insensibly passing from the previous towards a future condition. Then at once arises the question—Does life remain the same yesterday, to-day, and to-morrow? A thousand indubitable facts at once make answer—No! Underlying the law of continuity there is a law of change. Life to-day is not what it was yesterday, nor will it be to-morrow the same as to-day. What, then, is the nature of this change? If it be replied that the change must be either for the better or the worse, we shall have to answer the further question—Better or worse in what respects?

Let us narrow our view from the contemplation of life as a whole to the more particular consideration of an organism as one of its constituent units. The individual life of that organism depends on (some would say consists in) its ceaseless adaptation to surrounding circumstances. The circumstances remaining the same, or only varying within constant limits, the adaptation may be *more* or *less* perfect. A change in the direction of more perfect adaptation will be a change for the better, a tendency to less perfect adaptation will be a change for the worse.

But the relation of an organism to its circumstances or environment is itself subject to change. The environment itself may alter, or the organism may be brought into relation with a new environment. We have to consider not only the changes in an organism in the direction of more or less perfect adaptation to its environment, but also changes in the environment. These changes are in the direction of increased simplicity or of increased complexity. So that we may say that the modification of life is in the direction of more or of less complete adaptation to simpler or to more complex conditions. Where the adaptation advances to more complex conditions, we speak of elaboration; where it retrogrades to less complex conditions, we speak of degeneration; but both fall under the head of evolution in its more general sense. Viewed as a whole, there can be little doubt that the general tendency of evolution is towards more complete adaptation to more diverse and complex environment. And this tendency is accompanied by a general increase of differentiation and of integration; of differentiation whereby the constituent elements of life, whether cells, tissues, organs, organisms, or groups of organisms, become progressively more specialized and more different from one another; of integration whereby these elements become progressively more interdependent one on the other. We may conveniently sum up the tendency towards more perfect adaptation to more complex circumstances in the word progress; the tendency to differentiation in the word individuality; and the tendency to integration in the word association.

Nobody now doubts the propositions thus briefly summarized, and it is therefore unnecessary to bring forward evidence in their favour.

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We may pass, then, to the question—How? Evolution being continuity, associated with change, tending in certain directions, and accompanied by certain processes, how has it been effected? What are its methods?

Natural Selection.

Natural selection claims a foremost place. We have already devoted a chapter to its consideration. Animals vary; more are born than can survive to procreate their kind; hence a struggle for existence, in which the weaker and less adapted are eliminated, the stronger and better adapted surviving to continue the race.

It is scarcely possible to over-estimate what Darwin's labour and genius have done for the study of animal life. Through Darwin's informing spirit, biology has become a science. But now we must be on our guard. So long as natural selection was winning its way to acceptance, every application of the theory had to be made with caution, and was subjected to keen, if sometimes ignorant, criticism. Now there is, perhaps, some danger lest it should suffer the Nemesis of triumphant creeds, and be used blindly as a magic formula.

First, we should be careful not to use the phrase, "of advantage to the species," vaguely and indefinitely, but should in all cases endeavour clearly to indicate wherein lies the particular advantage, and how its possession enables the organism to escape elimination; next, we must remember that the advantage must be immediate and present, prospective advantage being, of course, inoperative; then we must endeavour to show that the advantage is really sufficient to decide the question of elimination or non-elimination; lastly, we must distinguish between indiscriminate and differential destruction, between mere numerical reduction by death or otherwise and selective elimination.

(1) In illustration of the first point, we may select a passage from the writings of even so great a biologist as Professor Weismann. As is well known, Professor Weismann believes that senility and death are no part of the natural heritage of animal life, but have been introduced among the metazoa on utilitarian grounds. In his earlier papers, he attributed the introduction of death, and the tissuedegeneration that precedes it, to the direct action of natural selection. [CJ] More lately, he attributes it to the cessation of selection. [CK] Concerning this later view, we shall have somewhat to say presently; we may now consider the former as an example of too indefinite a use of such phrases as "of advantage to the species." "Worn-out individuals," says Professor Weismann, "are not only valueless to the species, but they are even harmful, for they take the places of those which are sound. Hence, by the operation of natural selection, the life of our hypothetically immortal individual would be shortened by the amount which was useless to the species. It would be reduced to a length which would afford the most favourable conditions of existence of as large a number as possible of vigorous individuals at the same time." This may be so, but, as it stands, the *modus operandi* is not given, and is not obvious. We start with a hypothetically immortal metazoon. Barring accidents, it will go on existing indefinitely. But you cannot bar accidents for an indefinite time; hence, the longer the individual lives, the more defective and crippled it becomes. There is neither natural decay nor natural death here. The organism is gradually crippled through accident and injury. But the crippled individuals are harmful to the species, because they take the places of those which are sound. Therefore, says Professor Weismann, natural

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decay and death step in to take them off before they have time to become cripples. Now, the point I wish to notice is that there is no definite statement how or why natural decrepitude should thus be introduced. We must remember that it is not until a late stage in evolution that, through the association of its members, groups of organisms compete with other groups. In the earlier stages, when we must suppose decrepitude and death to arise on Professor Weismann's hypothesis, the law of the struggle for existence is—each for himself against all. The question, therefore, is—What advantage to the individual is there in natural decay and death to enable it, through the possession of these attributes, to escape elimination? Surely none as such. At the same time, it is quite conceivable that natural decay and death may be the penalty the individual has to pay for increased strength and vitality in the early stages of life. This, probably, was Professor Weismann's meaning. But, if so, it would surely have been better to state the matter in such a way as to lay the chief stress on the really important feature, and to say that, through natural selection, those individuals have survived which exhibited predominant strength and vitality for a shortened period, even at the expense of natural decay and death. The increased life-power, not the seeds of decay and death, was that which natural selection picked out for survival, or rather that which elimination allowed to survive.

In such ways—a short life with heightened activity being of advantage to some forms, a more prolonged existence at a lower level of vitality being essential to others—natural selection may have determined in some degree the relative longevity of different organisms. That it caused the introduction of senility as a preparation for death is a less tenable hypothesis.

And here we may note, in passing, that in using the phrase, "of advantage to the race or species," we must steadily bear in mind the fact that it is with *individuals* that the process of elimination deals. In the individual it is that every modification must make good its claim to existence and transmission. Where the principle of association for mutual benefit obtains, as in the case of social insects, it is still the individual that must resist elimination. Self-sacrifice, whether conscious or unconscious, must not be carried so far as to lead to the elimination of the self-sacrificing individual, for in this event it cannot but defeat its own ends. Within these limits, self-sacrifice is of advantage, as in the case of parental self-sacrifice, in that it enables certain other individuals to escape elimination. We should endeavour, then, not to use the phrase, "of advantage to the species," vaguely and indefinitely, but to indicate in what particular ways certain individuals are to be so advantaged as to escape the Nemesis of elimination.

(2) The second point that I mentioned above scarcely needs exemplification. That the advantage which enables an organism to escape elimination must be present and existent, not merely prospective, is obvious. Still, the mistake is sometimes made. I have heard it stated that feathers were evolved for the sake of flight. But clearly, unless the wing sprang into existence already sufficiently developed for flight, this would be impossible. The same is true of the first stages of many structures which could not be of service for the purpose and use to which they were subsequently turned. Not impossibly, the earliest "wings" were for diving, and flight was, so to speak, an after-thought. Undoubtedly, structures which have been fostered under the wing of one form of advantage have been subsequently applied to new purposes, and fostered through new modes of adaptation. Teeth, for example, are probably modified scales, such as are found in the thorn-back skate. But the early development of these scales could have had no reference to their future application to purposes subservient to alimentation.

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Again, such and such a structure is sometimes spoken of as a "prevision against emergencies." In his interesting and valuable work on "The Colours of Animals," for example, Mr. E. B. Poulton says, "Dimorphism [in the larvæ of butterflies and moths] is also valuable in another way: the widening range of a species may carry it into countries in which one of its forms may be especially well concealed, while in other countries the other form may be more protected. Thus a dimorphic form is more fully provided against emergencies than one with only a single form." And after giving, as an example, the fact that the convolvulus hawk-moth has a browner and a greener form of caterpillar, of which the browner is more prevalent under European conditions, and the greener under those which obtain in the Canary Islands, Mr. Poulton adds, "This result appears to have been brought about by the ordinary operation of natural selection, leading to the extermination of the less-protected variety." Now, I do not mean for one moment to imply that so careful and able a naturalist as Mr. Poulton believes that any character has been evolved through natural selection in prevision for future emergencies. But I do think that his statement is open to this criticism.

(3) It is sometimes said, in bold metaphor, that natural selection is constantly on the watch to select any modification, however slight, which is of advantage to the species. And it is true that elimination is ceaselessly operative. But it is equally certain that the advantage must be of sufficient value to decide the question whether its possessor should be eliminated or should escape elimination. If it does not reach this value, Natural Selection, watch she never so carefully, can make no use of it. Elimination need not, however, be to the death; exclusion from any share in continuing the species is sufficient. To breed or not to breed, that is the question. Any advantage affecting this essential life-function will at once catch the eye of a vigilant natural selection. But it must be of sufficient magnitude for the machinery of natural selection to deal with. That machinery is the elimination of a certain proportion of the individuals which are born. Which shall be eliminated, and which shall survive, depends entirely on the way in which the individuals themselves come out in life's competitive examination. The manner in which that examination is conducted is often rude and coarse, too roughand-ready to weigh minute and infinitesimal advantages.

What must be the value of a favourable or advantageous modification to decide the question of elimination, to make it an *available advantage*, must remain a matter of conjecture. It will vary with the nature and the pressure of the eliminative process. And perhaps it is scarcely too much to say that, at present, we have not observational grounds on which to base a reliable estimate in a single instance. We must not let our conviction of its truth and justice blind us to the fact that natural selection is a logical inference rather than a matter of direct observation. A hundred are born, and two survive; the ninety-eight are eliminated in the struggle for existence; we may therefore infer that the two escaped elimination in virtue of their possession of certain advantageous characters. There is no flaw in the logic that has thus convinced the world that natural selection is a factor in evolution. But by what percentage of elimination-marks the second of the two successful candidates beats the senior on the list of failures we do not know. We can only see that, on the hypothesis of natural selection, it must have been sufficiently appreciable to determine success or failure.

(4) And then, to come to our fourth point, we must remember that, apart from the differentiating process of elimination, there is much fortuitous destruction. A hundred are born, and but two survive. But of the ninety-eight which die, and fail to procreate, how many are eliminated, how many are fortuitously destroyed, we do not find it easy to say. And indiscriminate destruction gets rid of good,

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bad, and indifferent alike. It is a mistake to say that of the hundred born the two survivors are necessarily the very best of the lot. It is quite possible that indiscriminate destruction got rid of ninety of all sorts, and left only ten subject to the action of a true elimination. "In the majority of birds," says Professor Weismann, "the egg, as soon as it is laid, becomes exposed to the attacks of enemies; martens and weasels, cats and owls, buzzards and crows, are all on the look out for it. At a later period, the same enemies destroy numbers of the helpless young, and in winter many succumb in the struggle against cold and hunger, or to the numerous dangers which attend migration over land and sea—dangers which decimate the young birds." There is here, first, a certain amount of fortuitous destruction; secondly, some selection applied to the eggs; thirdly, a selection among the very young nestlings; and, fourthly, a selection among the young migratory birds. What may be the proportion of elimination to destruction at each stage it is difficult to say. Among the eggs and fry of fishes fortuitous destruction probably very far outbalances the truly differentiating process.

Panmixia and Disuse.

We may now pass on to consider shortly some of the phenomena of degeneration, and the dwindling or disappearance of structures which are no longer of use.

Many zoologists believe, or until lately have believed, that disuse is itself a factor in the process. Just as the well-exercised muscle is strengthened, so is the neglected muscle rendered weak and flabby. Until recently it was generally held that the effects of such use or disuse are inherited. But now Professor Weismann has taught us, if not to doubt ourselves, at least to admit that doubt is permissible. On the older view, the gradual dwindling of unused parts was readily comprehensible. But now, if Professor Weismann is right, we must seek another explanation of the facts; and, in any case, we may be led to recognize other factors (than that of disuse alone) in the process.

Professor Weismann regards panmixia, or free intercrossing, when the preserving influence of natural selection is suspended, as the efficient cause of a reduction or deterioration in the organ concerned. And Mr. Romanes had, in England, drawn attention to the fact that the "cessation of natural selection" would lead to some dwindling of the organ concerned, since it was no longer kept up to standard. In illustration of his panmixia, Professor Weismann says, "A goose or duck must possess strong powers of flight in the natural state, but such powers are no longer necessary for obtaining food when it is brought into the poultry-yard, so that a rigid selection of individuals with well-developed wings at once ceases among its descendants. Hence, in the course of generations, a deterioration of the organs of flight must necessarily ensue, and the other members and organs of the bird will be sensibly affected."[CL] And, again, "As at each stage of retrogressive transformation individual fluctuations always occur, a continued decline from the original degree of development will inevitably, although very slowly, take place, until the last remnant finally disappears." [CM] Now, I think it can be shown that panmixia, or the cessation of selection, alone cannot affect much reduction. It can only affect a reduction from the "survival-mean" to the "birth-mean." This was referred to in the chapter on "Heredity and the Origin of Variations," but may be again indicated. Suppose the number of births among wild ducks be represented by the number nine, of which six are eliminated through imperfections in the organs of flight. Let us place the nine in order of merit in this respect, as is done in the table on p. 172. The average wing-power of the nine will be found in No. 5, there being four ducks

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with superior wing-power (1-4), and four with inferior wing-power (6-9). The birth-mean will therefore be at the level of No. 5, as indicated to the left of the table. But if six ducks with the poorest wings be eliminated, only three survive. The average wing-power will now be found in No. 2, one duck being superior and one inferior to it in this respect. It is clear that this survival-mean is at a level of higher excellence than the birth-mean. Now, when the ducks are placed in a poultry-yard, selection in the matter of flight ceases, and, since all nine ducks survive, the survival-mean drops to the birth-mean. We may variously estimate this retrogression; but it cannot be a large percentage—I should suppose, in the case under consideration, one or two per cent. at most. But Professor Weismann says, "A continued decline from the original degree of development must inevitably take place." It is not evident why such decline should continue. If variations continue in the same proportion as before, the birth-mean will be preserved, since there are as many positive or favourable variations above the mean as there are negative or unfavourable variations below the mean. A continuous decline must result from a preponderance of negative over positive variations, and for this some other principle, such as atavism, or reversion to ancestral characters, must be called in. But in the case of so long-established and stable an organ as that of flight, fixed and rendered constant through so many generations, it is hardly probable that reversion would be an important factor. Mr. Galton has calculated that among human-folk the offspring inherits one-fourth from each parent, one-sixteenth from each grandparent, leaving onefourth to be contributed by more remote ancestors. There is no doubt, however, that among domesticated animals reversion occurs to characters which have been lost for many generations. But we should probably have to go a very long way back in the ancestry of wild ducks for any marked diminution in wing-power. It must be remembered that, in the case of the artificial selection of domesticated animals, man has been working against and not with the stream of ancestral tendency. Reversion in their case is towards a standard which was long maintained and had become normal before man's interference. Reversion in domesticated ducks should therefore be towards the greater wing-power of their normal ancestry before domestication, not in the direction of lessened wing-power and diminished wing-structure. The whole question of reversion is full of interest, and needs further investigation.

In the dwindling of disused structures, Mr. Romanes has suggested "failure of heredity" as an efficient cause. I find it difficult, however, to distinguish this failure of heredity from the effects of disuse. To what other cause is the failure of heredity due? If natural selection has intervened to hasten this failure, this can only be because the failure is advantageous, since it permits the growth-force to be applied more advantageously elsewhere. And this involves a different principle. Even so it is difficult to exclude the possibility (to put it no stronger) that the diversion of growth-force from a less useful to a more useful organ is in part due to the use of the one and the disuse of the other. But of disuse Mr. Romanes says, "There is the gravest possible doubt lying against the supposition that any really inherited decrease is due to the inherited effects of disuse." We may fairly ask Mr. Romanes, therefore, to explain to what cause the failure of heredity is due. In any case, Professor Weismann and his school are not likely to accept this failure of heredity as an efficient factor in the process. Nor is Professor Weismann likely to fall back upon any innate tendency to degeneration. Unless, therefore, some cause be shown why the negative variations should be prepotent over the positive variations, we must, I think, allow that unaided panmixia cannot affect any great amount of reduction.

In this connection we may notice Professor Weismann's newer view of the introduction of bodily mortality. He says, "The problem is very easily solved if we seek assistance from the principle of [192]

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panmixia. As soon as natural selection ceases to operate upon any character, structural or functional, it begins to disappear. As soon, therefore, as the immortality of somatic [body-] cells became useless, they would begin to lose this attribute." [CN] Even granting that panmixia could continuously reduce the size of ducks' wings, it is not easy to see how it could get rid of immortality. The essence of the idea of panmixia is that, when the natural selection which has raised an organ to a high functional level, and sustains it there, ceases or is suspended, the organ drops back from its high level. But on Professor Weismann's hypothesis, immortality has neither been produced nor is it sustained by natural selection. How, therefore, the cessation of selection can cause the disappearance of immortality—a character with which natural selection has had nothing whatever to do—Professor Weismann does not explain. He seems to be using "panmixia" in the same vague way that, in his previous explanation, he used "natural selection."

If panmixia alone cannot, to any very large extent, reduce an organ no longer sustained by natural selection, to what efficient cause are we to look? Mr. Romanes has drawn attention to the reversal of selection as distinguished from its mere cessation. When an organ is being improved or sustained by selection, elimination weeds out all those which have the organ in an ill-developed form. Under a reversal of selection, elimination will weed out all those which possess the organ well developed. In burrowing animals, the eyes may have been reduced in size, or even buried beneath the skin, through a reversal of selection. The tuco-tuco (*Ctenomys*), a burrowing rodent of South America, is frequently blind. One which Darwin kept alive was in this condition, the immediate cause being inflammation of the nictitating membrane. "As frequent inflammation of the eyes," says Darwin, "must be injurious to any animal, and as eyes are certainly not necessary to animals having subterranean habits, a reduction in their size, with the adhesion of the eyelids and growth of fur over them, might in such cases be an advantage; and, if so, natural selection would aid the effect of disuse." [CO] Granting that the inflammation of the eyes is a sufficient disadvantage to lead to elimination, such cases may be assigned to the effects of a reversal of selection.

Perhaps the best instances of the reversal of selection are to be found in the insects of wind-swept islands, in which, as we have already seen (p. 81), the power of flight has been gradually reduced or even done away with. Such instances are, however, exceptional. And one can hardly suppose that such reversal of selection can be very far-reaching in its effects, at least, through any direct disadvantage from the presence of the organ. One can hardly suppose that the presence of an eye in a cave-dwelling fish^[CP] could be of such direct disadvantage as to lead to the elimination of those members which still possess this structure.

But may it not be of indirect disadvantage? May not this structure be absorbing nutriment which would be more advantageously utilized elsewhere? This is Darwin's principle of economy. Granting its occurrence, is it effective? We may put the matter in this way: The crustacea which have been swept into a dark cave may be divided into three classes so far as fortuitous variations of eyes and antennæ are concerned. First, those which preserve eyes and antennæ in the original absolute and relative proportion and value; secondly, those in which, while the eyes remain the same, the antennæ are longer and more sensitive; thirdly, those in which, while the antennæ are longer and more sensitive, the eyes are reduced in size and elaboration. According to the principle of economy, the third class have sufficient advantage over the first and second to enable them to survive and escape the elimination which removes those

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with fully developed eyes. It may be so. We cannot estimate the available advantage with sufficient accuracy to deny it. But we may fairly suppose that, in general, it is only where the useless organ in question is of relatively large size, and where nutriment is deficient, that economy of growth is an important factor.

We may here note the case of the hermit crab as one which exemplifies degeneration through the reversal of natural selection. This animal, as is well known, adopts an empty whelk-shell or other gasteropod shell as its own. The hinder part of the body which is thus thrust into the shell loses its protective armour, and is quite soft. Professor Weismann seems to regard this loss of the hardened cuticle as due entirely to panmixia. If what has been urged above has weight, this explanation cannot be correct. No amount of promiscuous interbreeding of crabs could reduce the cuticle to a level indefinitely below that of any of the interbreeding individuals. But it is clear that an armour-sheathed "tail" would be exceedingly ill adapted to thrusting into a whelk-shell. Hence there would, by natural selection, be an adaptation to new needs, involving not the higher development of cuticle, but the reverse. So far as the cuticle is concerned, it is a case of reversed selection. Whether this reversal alone will adequately account for the facts is another matter.

Mr. Herbert Spencer has made a number of observations and measurements of the jaws of pet dogs, which lead him to conclude that there has been a reduction in size and muscular power due to disuse. The creatures being fed on sops, have no need to use to any large extent the jaw-muscles. In this case, he argues, the principle of economy is not likely to be operative, since the pampered pet habitually overeats, and has therefore abundant nutriment and to spare to keep up the jaws. It is possible, however, that artificial selection has here been a factor. There may have been a competition among the old ladies who keep such pets to secure the dear little dog that never bites, while the nasty little wretch that does occasionally use his jaws for illegitimate purposes may have been speedily eliminated. Pet dogs are, moreover, a pampered, degenerate, and for the most part unhealthy race, often deteriorated by continued in-breeding, so that we must not build too much on Mr. Spencer's observations, interesting as they undoubtedly are.

There is one feature about the reduction of organs which must not be lost sight of. They are very apt to persist for a long time as remnants or vestiges. The pineal gland is the vestigial remnant of a structure connected with the primitive, median, or pineal eye. The whalebone whales and the duck-bill platypus have teeth which never cut the gum and are of no functional value. With regard to these, it may be asked—If disuse leads to the reduction of unused structures, how comes it that it has not altogether swept away these quite valueless structures? In considering this point, we must notice the unfortunate and misleading way in which disuse is spoken of as if it were a positive determinant, instead of the mere absence of free and full and healthy exercise. Few will question the fact that in the individual, if an organ is to be kept up to its full standard of perfection, it must be healthily and moderately exercised; and that, if not so exercised, it will not only cease to increase in size, but will tend to degenerate. The healthy, functionally valuable tissue passes into the condition of degenerate, comparatively useless tissue. Now, those who hold that the inheritance of functional modifications is still a tenable hypothesis, carry on into the history of the race that which they find to hold good in the history of the individual. They believe that, in the race, the continued functional activity of an organ is necessary for the maintenance of the integrity and perfection of its structure, and that, if not so exercised, the organ will inevitably tend to dwindle to embryonic proportions and to degenerate. The

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healthy, functionally valuable tissue passes at last into the condition of degenerate, comparatively useless tissue. The force of heredity will long lead to the production in the embryo of the structure which, in the ancestral days of healthy exercise, was to be of service to the organism. At this stage of life the conditions have not changed. The degeneration sets in at that period when the ancestral use is persistently denied. There is no reason why "disuse" should in all cases remove all remnants of a structure; but if the presence of the degenerate tissue is a source of danger to the organism which possesses it, that organism will be eliminated, and those (1) which possess it in an inert, harmless form, or (2) in which it is absent, will survive. Thus natural selection (which will fall under Mr. Romanes's reversed selection) will step in—will in some cases reduce the organ to a harmless and degenerate rudiment, and in others remove the last vestiges of the organ.

On the whole, even taking into consideration the effects of panmixia, of reversed selection, and of the principle of economy, the reduction of organs is difficult to explain, unless we call into play "disuse" as a co-operating factor.

Sexual Selection, or Preferential Mating.

It is well known that, in addition to and apart from the primary sexual differences in animals, there are certain secondary characters by which the males, or occasionally the females, are conspicuous. The antlers of stags, the tail of the peacock, the splendid plumes of the male bird of paradise, the horns or pouches of lizards, the brilliant frilled crest of the newt, the gay colours of male sticklebacks, the metallic hues of male butterflies, and the large horns or antennæ of other insects,—these and many other examples which will at once occur to the reader are illustrations of the fact.

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As a contribution towards the explanation of this order of phenomena, Darwin brought forward his hypothesis of sexual selection, of which there are two modes. In the first place, the males struggle together for their mates; in this struggle the weakest are eliminated; those possessed of the most efficient weapons of offence and defence escape elimination. In the second place, the females are represented as exercising individual choice, and selecting (in the true sense of the word) those mates whose bright colours, clear voices, or general strength and vigour render them most pleasing and attractive. For this mode I shall employ the term "preferential mating." Combining these two in his summary, Darwin says, "It has been shown that the largest number of vigorous offspring will be reared from the pairing of the strongest and best-formed males, victorious in contests over other males, with the most vigorous and best-nourished females, which are the first to breed in the spring. If such females select the more attractive and, at the same time, vigorous males, they will rear a larger number of offspring than the retarded females, which must pair with the less vigorous and less attractive males. So it will be if the more vigorous males select the more attractive and, at the same time, healthy and vigorous females; and this will especially hold good if the male defends the female, and aids in providing food for the young. The advantage thus gained by the more vigorous pairs in rearing a larger number of offspring has apparently sufficed to render sexual selection efficient."[CQ]

With regard to the first of the two modes, little need be said. There can be no question that there are both elimination by battle and elimination by competition in the struggle for mates. It is well known that the emperor moth discovers his mate by his keen sense of smell residing probably in the large,

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branching antennæ. There can be little doubt that, if an individual is deficient in this sense, or misinterprets the direction in which the virgin female lies, he will be unsuccessful in the competition for mates; he will be eliminated from procreation. And it is a familiar observation of the poultry-yard that the law of battle soon determines which among the cock birds shall procreate their kind. The law of battle for mates is, indeed, an established fact among many animals, especially those which are polygamous, and the elimination of the unfit in this respect is a logical necessity.

It is when we come to the second of the two modes, that which involves selection proper, that we find differences of opinion among naturalists.

Darwin, as we have seen, suggested that those secondary sexual characters which can be of no value in aiding their possessor to escape elimination by combat result from the preferential choice of the female, the female herself remaining comparatively unaffected. But Mr. Wallace made an exceedingly valuable suggestion with regard to these comparatively dull colours of the female. He pointed out that conspicuousness (unless, as we have seen, accompanied by some protective character, such as a sting or a bitter taste) increased the risk of elimination by enemies. Now, the males, since they are generally the stronger, more active, and more pugnacious, could better afford to run this risk than their mates. They could to some extent take care of themselves. Moreover, when impregnation was once effected, the male's business in procreation was over. Not so the female; she had to bear the young or to lay the eggs, often to foster or nourish her offspring. Not only were her risks greater, but they extended over a far longer period of time. Hence, according to Mr. Wallace, the dull tints of the females, as compared with those of the males, are due to natural selection eliminating the conspicuous females in far greater proportion than the gaudy males.

There is clearly no reason why this view should not be combined with Darwin's; preferential mating being one factor, natural elimination being another factor; both being operative at the same time, and each contributing to that marked differentiation of male and female which we find to prevail in certain classes of the animal kingdom.

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But Mr. Wallace will not accept this compromise. He rejects preferential mating altogether, or, in any case, denies that through its agency secondary sexual characters have been developed. He admits, of course, the striking and beautiful nature of some of these characters; he admits that the male in courtship takes elaborate pains to display all his finery before his would-be mate; he admits that the "female birds may be charmed or excited by the fine display of plumage by the males;" but he concludes that "there is no proof whatever that slight differences in that display have any effect in determining their choice of a partner." [CR]

How, then, does Mr. Wallace himself suppose that these secondary sexual characters have arisen? His answer is that "ornament is the natural outcome and direct product of superabundant health and vigour," and is "due to the general laws of growth and development." [CS] At which one rubs one's eyes and looks to the title-page to see that Mr. Wallace's name is really there, and not that of Professor Mivart or the Duke of Argyll. For, if the plumage of the argus pheasant and the bird of paradise is due to the general laws of growth and development, why not the whole animal? If Darwin's sexual selection is to be thus superseded, why not Messrs. Darwin and Wallace's natural selection?

Must we not confess that Mr. Wallace, for whose genius I have the profoundest admiration, has here allowed himself to confound together the question of origin and the question of guidance or direction? Natural selection by elimination and sexual selection through preferential mating are, supposing them to be *veræ causæ*, guiding or selecting agencies. Given the variations, however caused, these agencies will deal with them, eliminating some, selecting others, with the ultimate result that those specially fitted for their place in nature will survive. Neither the one nor the other deals with the origin of variations. That is a wholly different matter, and constitutes the leading biological problem of our day. Mr. Wallace's suggestion is one which concerns the origin of variations, and as such is worthy of careful consideration. It does not touch the question of their guidance into certain channels or the maintenance of specific standards. Concerning this Mr. Wallace is silent or confesses ignorance. "Why, in allied species," he says, "the development of accessory plumes has taken different forms, we are unable to say, except that it may be due to that individual variability which has served as the starting-point for so much of what seems to us strange in form or fantastic in colour, both in the animal and vegetable world." [CT] It is clear, however, that "individual variability" cannot be regarded as a *vera causa* of the maintenance of a specific standard—a standard maintained *in spite of* variability.

The only directive agency (apart from that of natural selection) to which Mr. Wallace can point is that suggested by Mr. Alfred Tylor, in an interesting, if somewhat fanciful, posthumous work on "Coloration in Animals and Plants," "namely, that diversified coloration follows the chief lines of structure, and changes at points, such as the joints, where function changes." But even if we admit that coloration-bands or spots originate at such points or along such lines—and the physiological rationale is not altogether obvious—even if we admit that in butterflies the spots and bands usually have reference to the form of the wing and the arrangement of the nervures, and that in highly coloured birds the crown of the head, the throat, the ear-coverts, and the eyes have usually distinct tints, still it can hardly be maintained that this affords us any adequate explanation of the specific colour-tints of the humming-birds, or the pheasants, or the Papilionidæ among butterflies. If, as Mr. Wallace argues, the immense tufts of golden plumage in the bird of paradise owe their origin to the fact that they are attached just above the point where the arteries and nerves for the supply of the pectoral muscles leave the interior of the body, are there no other birds in which similar arteries and nerves are found in a similar position? Why have these no similar tufts? And why, in the birds of paradise themselves, does it require four years (for it takes so long for the feathers of the male to come to maturity) ere these nervous and arterial influences take effect upon the plumage? Finally, one would inquire how the colour is determined and held constant in each species. The difficulty of the Tylor-Wallace view, even as a matter of origin, is especially great in those numerous cases in which the colour is determined by delicate lines, thin plates, or thin films of air or fluid. [CU]

Under natural selection, as we have seen, the development of colour is fostered under certain conditions. The colour is either protective, rendering the organism inconspicuous amid its normal surroundings, or it is of warning value, advertising the organism as inedible or dangerous, or, in the form of recognition-marks, it is of service in enabling the members of a species to recognize each other. Now, in the case of both warning colour and recognition-marks, their efficacy depends upon the perceptual powers of animals. Unless there be a rapidly acquired and close association of the quality we call nastiness with the quality we call gaudiness (though, for the animal, there is no such *isolation* of these qualities as is implied in our words [CV]), such that the sight of the gaudy insect suggests that it

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will be unpleasant to eat, the gaudiness will be of no avail. And if there is any truth in the doctrine of mimicry, the association is particular. It is not merely that bright colours are suggestive of a nasty taste. The insect-eating birds associate nastiness especially with certain markings and coloration—"the tawny *Danais*, the barred *Heliconias*, the blue-black *Euplæas*, and the fibrous *Acræas*;" and this is proved by the fact that sweet insects mimicking these particular forms are thereby protected.

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So, too, with recognition-marks. If the bird or the mammal have not sufficient perceptive powers to distinguish between the often not very different recognition-marks, of what service can they be?

Recognition-marks and mimicry seem, therefore, to show that in the former case many animals, and in the latter the insect-eating birds, mammals, lizards, and other animals concerned, have considerable powers of perception and association.

Among other associations are those which are at the base of what I have termed preferential mating. We must remember how deeply ingrained in the animal nature is the mating instinct. We may find it difficult to distinguish closely allied species. But the individuals of that species are led to mate together by an impelling instinct that is so well known as to elicit no surprise. Instinct though it be, however, the mating individuals must recognize each other in some way. The impulse that draws them together must act through perceptual agency. It is not surprising, therefore, to find, when we come to the higher animals, that, built upon this basis, there are well-marked mating preferences. And this, as we have before pointed out, following Wallace, is an efficient factor in segregation. Let us, however, hear Mr. Wallace himself in the matter.

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There is, he says, [CW] "a very powerful cause of isolation in the mental nature—the likes and dislikes—of animals; and to this is probably due the fact of the rarity of hybrids in a state of nature. The differently coloured herds of cattle in the Falkland Islands, each of which keeps separate, have been already mentioned. Similar facts occur, however, among our domestic animals, and are well known to breeders. Professor Low, one of the greatest authorities on our domesticated animals, says, 'The female of the dog, when not under restraint, makes selection of her mate, the mastiff selecting the mastiff, the terrier the terrier, and so on.' And again, 'The merino sheep and the heath sheep of Scotland, if two flocks are mixed together, each will breed with its own variety.' Mr. Darwin has collected many facts illustrating this point. [CX] One of the chief pigeon-fanciers in England informed him that, if free to choose, each breed would prefer pairing with its own kind. Among the wild horses in Paraguay those of the same colour and size associate together; while in Circassia there are three races of horses which have received special names, and which, when living a free life, almost always refuse to mingle and cross, and will even attack one another. In one of the Faröe Islands, not more than half a mile in diameter, the half-wild native black sheep do not readily mix with imported white sheep. In the Forest of Dean and in the New Forest the dark and pale coloured herds of fallow deer have never been known to mingle; and even the curious ancon sheep, of quite modern origin, have been observed to keep together, separating themselves from the rest of the flock when put into enclosures with other sheep. The same rule applies to birds, for Darwin was informed by the Rev. W. D. Fox that his flocks of white and Chinese geese kept distinct. This constant preference of animals for their like, even in the case of slightly different varieties of the same species, is evidently a fact of great importance in considering the origin of species by natural selection, since it shows us that, so soon as a slight differentiation of form

or colour has been effected, isolation will at once arise by the selective association of the animals themselves."

Mr. Wallace thus allows, nay, he lays no little stress on, preferential mating, and his name is associated with the hypothesis of recognition-marks. But he denies that preferential mating, acting on recognition-marks, has had any effect in furthering a differentiation of form or colour. He admits that so soon as a slight differentiation of form or colour has been effected, segregation will arise by the selective association of the animals themselves; but he does not admit that such selective association can carry the differentiation further.

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Now, it is clear that mating preferences must be either fixed or variable. If fixed, how can differentiation occur in the same flock or herd? And how can selective association be a means of isolation? Or, granting that differentiation has occurred, if the mating preferences are then stereotyped, all further differentiation, so far as colour and form are concerned, will be rendered impossible; for divergent modifications, not meeting the stereotyped standard of taste, will for that reason fail to be perpetuated. We must admit, then, that these mating preferences are subject to variation. And now we come to the central question with regard to sexual selection by means of preferential mating. What guides the variation along special lines leading to heightened beauty? This, I take it, is the heart and centre of Mr. Wallace's criticism of Darwin's hypothesis. Sexual selection of preferential mating involves a standard of taste; that standard has advanced from what we consider a lower to what we consider a higher æsthetic level, not along one line, but along many lines. What has guided it along these lines?

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Not as in any sense affording a direct answer to this question, but for illustrative purposes, we may here draw attention to what seems to be a somewhat parallel case, namely, the development of flowers through insect agency. In his "Origin of Species," Darwin contended that flowers had been rendered conspicuous and beautiful in order to attract insects, adding, "Hence we may conclude that, if insects had not been developed on the earth, our plants would not have been decked with beautiful flowers, but would have produced only such poor flowers as we see on our fir, oak, nut, and ash trees, on grasses, docks, and nettles, which are all fertilized through the agency of the wind." "The argument in favour of this view," says Mr. Wallace, [CY] who quotes this passage, "is now much stronger than when Mr. Darwin wrote;" and he cites with approval the following passage from Mr. Grant Allen's "Colour-Sense:" "While man has only tilled a few level plains, a few great river-valleys, a few peninsular mountain slopes, leaving the vast mass of earth untouched by his hand, the insect has spread himself over every land in a thousand shapes, and has made the whole flowering creation subservient to his daily wants. His buttercup, his dandelion, and his meadowsweet grow thick in every English field. His thyme clothes the hillside; his heather purples the bleak grey moorland. High up among the Alpine heights his gentian spreads its lakes of blue; amid the snows of the Himalayas his rhododendrons gleam with crimson light. Even the wayside pond yields him the white crowfoot and the arrowhead, while the broad expanses of Brazilian streams are beautified by his gorgeous water-lilies. The insect has thus turned the whole surface of the earth into a boundless flower-garden, which supplies him from year to year with pollen or honey, and itself in turn gains perpetuation by the baits that it offers to his allurement."[CZ]

Mr. Grant Allen is perfectly correct in stating that the insect has produced all this beauty. It is the result of insect choice, a genuine case of selection as contrasted with elimination. And when we ask in this case, as we asked in the case of the beautiful colours and forms of animals, what has guided their evolution along lines which lead to such rare beauty, we are given by Mr. Wallace himself the answer, "The preferential choice of insects." If these insects have been able to produce through preferential selection all this wealth of floral beauty (not, indeed, for the sake of the beauty, but incidentally in the practical business of their life), there would seem to be no *a priori* reason why the same class and birds and mammals should not have been able to produce, through preferential selection, all the wealth of animal beauty.

It should be noted that the answer to the question is in each case a manifestly incomplete one. For if we say that these forms of beauty, floral and animal, have been selected through animal preferences, there still remains behind the question—How and why have the preferences taken these *æsthetic* lines? To which I do not see my way to a satisfactory answer, though some suggestions in the matter will be made in a future chapter. [DA] At present all we can say is this—to be conspicuous was advantageous, since it furthered the mating of flowers and animals. To be diversely conspicuous was also advantageous. As Mr. Wallace says, "It is probably to assist the insects in keeping to one flower at a time, which is of vital importance to the perpetuation of the species, that the flowers which bloom intermingled at the same season are usually very distinct, both in form and colour." [DB] But conspicuousness is not beauty. And the question still remains—From what source comes this tendency to beauty?

Leaving this question on one side, we may state the argument in favour of sexual selection in the following form: The generally admitted doctrine of mimicry involves the belief that birds and other insect-eating animals have delicate and particular perceptual powers. The generally received doctrine of the origin of flowers involves the belief that their diverse forms and markings result from the selective choice of insects. There are a number of colour and form peculiarities in animals that cannot be explained by natural selection through elimination. There is some evidence in favour of preferential mating or selective association. It is, therefore, permissible to hold, as a provisional hypothesis, that just as the diverse forms of flowers result from the preferential choice of insects, so do the diverse secondary sexual characters of animals result, in part at least, from the preferential choice of animals through selective mating.

If this be admitted, then the elaborate display of their finery by male birds, which Mr. Wallace does admit, may fairly be held to have a value which he does not admit. For if preferential mating is à priori probable, such display may be regarded as the outcome of this mode of selection. At the same time, it may be freely admitted that more observations are required. In a recent paper, "On Sexual Selection in Spiders of the Family Attidæ," [DC] by George W. and Elizabeth G. Peckham, a full, not to say elaborate, description is given of the courtship, as they regard it, of spiders. The "love-dances" and the display of special adornments are described in detail. And the observers, as the result, be it remembered, of long and patient investigation and systematic study, come to the conclusion that female spiders exercise selective choice in their mates. And courtship must be a serious matter for spiders, for if they fail to please, they run a very serious risk of being eaten by the object of their attentions. Some years ago I watched, on the Cape Flats, near Capetown, the courtship of a large spider (I do not know

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the species). In this case the antics were strange, and, to me, amusing; but they seemed to have no effect on the female spider, who merely watched him. Once or twice she darted forward towards him, but he, not liking, perhaps, the gleam in her eyes, retreated hastily. Eventually she seemed to chase him off the field.

We must remember how difficult it is to obtain really satisfactory evidence of mating preferences in animals. In most cases we must watch the animals undisturbed, and very rarely can we have an opportunity of determining whether one particular female selects her mate out of her various suitors. We watch the courtship in this, that, or the other case. In some we see that it is successful; in others that it is unsuccessful. How can we be sure that in the one case it was through fully attaining, in the other through failing to reach, the standard of taste? And yet it is evidence of this sort that Mr. Wallace demands. After noting the rejection by the hen of male birds which had lost their ornamental plumage, he says, "Such cases do not support the idea that males with the tail-feathers a trifle longer, or the colours a trifle brighter, are generally preferred, and that those which are only a little inferior are as generally rejected,—and this is what is absolutely needed to establish the theory of the development of these plumes by means of the choice of the female."[DD] If Mr. Wallace requires direct observational evidence of this kind, I do not suppose he is likely to get any large body of it. But one might fairly ask him what body of direct observational evidence he has of natural selection. The fact is that direct observational evidence is, from the nature of the processes involved, almost impossible to produce in either case. Natural selection is an explanation of organic phenomena reached by a process of logical inference and justified by its results. It is not claimed for the hypothesis of selective mating that it has a higher order of validity.

Use and Disuse.

As we have already seen, biologists a

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