MODERN
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A Review of the Principal Phenomena of Animal Life in Relation to Modern Concepts and Theories

BY

J. T. CUNNINGHAM

M.A. (Oxon.), A.L.S., Sometime Fellow of University College, Oxford ; Formerly Lecturer in Zoology at East London College, University of London

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PREFACE

Various definitions of science have been proposed; it has been stated that science is measurement, or that it is experiment, or that it is description. Doubtless all these operations are necessary in scientific investigation, but neither is by itself sufficient. In the discovery of the transformation of work into heat it was necessary to measure the quantities of work and heat involved, and to devise experiments by which the transformation could be effected in such a way as to allow of measurement. It is sometimes stated that there are no such things as cause and effect, that we can only describe the changes in the position of matter and the transformations of energy. It has also been maintained that the relation of cause and effect has only been completely understood when the two are shown to be identical. For example, if we hammer a piece of iron, the iron becomes hotter, and the hammering is said to be the cause of the rise in temperature. But it is now known that the movement of the hammer or the energy of this movement is transformed into vibratory movement of the molecules of the iron: the cause and the effect are the same energy in different phases. In Biology, in consequence of the complexity of organic structure and the great variety of detail, an enormous amount of simple observation and description are required; but no one supposes that this is the whole or the most important part of the science of life. On the other hand, with regard to experiment, especially in Biology, a great many experiments are made merely because they can be called experiments without sufficient knowledge of the structures and functions subjected to experiment, or of the relation of the experiments to the problems to be solved.

I venture to suggest that a fourth proposition is as worthy of consideration as the three above mentioned, namely that science is reason. Logic is sometimes taught in the Universities as a substitute for mathematics for the benefit of those who have little mathematical ability, but without logical reasoning sound conclusions cannot be drawn from either measurement, experiment, or observation, even with the aid of mathematical methods. Some of the conclusions drawn from recent biological researches seem to me to be reached by fallacious reasoning, and in this book I have attempted to show in certain cases what the fallacies are.

At the present time the general public is being supplied in books and journals with views on heredity and evolution which are derived chiefly from the school of Mr. T. H. Morgan of Columbia College, New York. Briefly the doctrine is that hereditary characters in animals and plants are conveyed by certain particles in the nuclei of the reproductive cells, male and female, and these particles are called genes. The combinations and separations of characters correspond to the unions and separations of the genes in fertilization. Occasionally new characters appear, and these are called mutations, and are attributed to changes that have occurred in the genes. Prof. Morgan's researches on these matters have been made chiefly on a little fly called Drosophila, bred for many successive generations in bottles and fed with pieces of banana. It is an essential article in the doctrine that mutations do not correspond to any external influence acting upon the body and directly tending to adaptation, although we are now told that Mr Muller of Texas has shown that by the application of X-rays mutations can be artificially produced. The mutations themselves are not adaptive, but adaptation is due to the natural selection of mutations in the course of many successive generations.

I have attempted in this volume to test the validity of such views by applying them to the fundamental questions of Biology in order to ascertain whether they give a satisfactory answer to such questions—in other words, whether they afford a reasonable explanation of the facts. There is no suggestion of doubt concerning the facts of heredity and mutation observed in the fly Drosophila and in many other organisms. The question is whether these facts are of the same kind as the facts of adaptation and development. My own conviction is that the theory founded on the facts of Mendelian heredity and mutation is applied to the explanation of phenomena of quite a different kind. For example, it has not been proved, or even made probable, that the gradual development after birth of man's adaptation to the erect position, or the gradual changes by which an aquatic tadpole becomes a terrestrial, air-breathing frog, in any way correspond to the difference between a fly with normal wings and one with vestigial wings, or between a grey wild mouse and a white mouse.

It is curious to notice how little connexion can be recognized in the expositions of some of the younger and more talented biologists between the views of heredity and evolution which they teach, and some of the phenomena on which they have themselves carried out important researches. At the meeting of the British Association in Leeds in 1927, Dr F. A. E. Crew gave one of the evening lectures to the general public. It consisted of a detailed description of the architecture of the germ-plasm as conceived by the followers of Prof. T. H. Morgan, the chromosomes of the nuclei of the reproductive cells being regarded as consisting of linear series of genes, each of which carried and determined independently in development some unit character. But no attempt was made to show how this conception could be reconciled with the reversal of sex in the adult bird or the relation of sex characters to internal secretions on which Dr Crew himself has obtained such surprising results. Similarly, Mr Julian Huxley omits to explain how the doctrine of genes, unit characters, and mutations is related to the influence of the thyroid and other internal secretions on development and metamorphosis, although he has carried out experimental researches on such influence. In fact, Mr Huxley has admitted that we know extremely little of how the genes exercise their control of development.

The best criterion of the validity of the mutation theory is afforded by the phenomena of secondary sexual characters. It is a somewhat recent discovery that the difference between the male and female in these characters is chiefly due to the influence of internal secretions of the reproductive organs. The mutation theory affords no explanation of this, one of the most extraordinary facts in physiology. To say that the evolution of the antlers of stags, with their dependence on the internal secretion of the testes, was the result of one or many mutations, is a mere formula of empty words. We have to explain why the growth of the bone of the antler is so profoundly affected by a chemical secretion from the testes, while the rest of the skeleton is not affected at all in the same way. There is a Lamarckian theory which fits the facts, but no other theory fits them. Prof. Morgan and Mr Julian Huxley give two quite different versions of the origin of secondary sexual characters according to the mutation theory. The former believes that the influence of the internal secretion from the testis in producing increased strength and vigour in the stag is due to natural selection, and the antlers are a mere by-product of this influence. To me this suggestion seems entirely without meaning. Mr Huxley thinks that the facts are explained by sexual selection, although it is obvious, as Darwin himself pointed out, that selection of male variations would not prevent them from being inherited by the females, and thus the variation or mutation must have been controlled by the sexual internal secretion or 'hormone' before the selection took place. The question, therefore, of the origin of this extraordinary control remains where it was before.

And yet the Bishop of Birmingham, who is also a Fellow of the Royal Society, gives the support of his enormous public influence in a recent publication[1] to the views of Morgan on heredity and evolution. It seems to me that he is unconsciously encouraging dogmatism in biology while he repudiates it in theology.

I have had the privilege of discussing the difficult question of entropy in reference to Dr James Johnstone's opinion concerning the essential peculiarity of life with Prof. Partington, Head of the Chemical Department of East London College, and the question of colour vision and other subjects with Prof. Roaf and Dr Smart of the Physiology Department of London

[1] The Rt. Rev. E. W. Barnes, *Should this Faith Offend?* London, Hodder & Stoughton, 1927.

Hospital Medical College. I am glad to take this opportunity of thanking these friends for the assistance I have received from them, although they are not responsible for any of my conclusions, nor for any errors I may have made.

I hope that none of the distinguished biologists whose published conclusions I have criticized will be offended. I have tried to express my arguments in quite scientific and impersonal terms. I may be wrong in some or all of my criticisms, but they have been made with the object of reaching what appeared to my own mind to be the logical truth, and in the interests of what I believe to be sound Biology.

J. T. CUNNINGHAM.

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CHAPTER I

MECHANISTIC BIOLOGY AND NEO-VITALISM

There are changes of fashion in biology as in costume, especially feminine costume. From about fifty years ago for a considerable period one of the greatest effects of Darwin's *Origin of Species* upon zoological science was the earnest endeavour, especially by embryological research, to trace out the pedigrees of existing animals and to discover the primitive ancestors of the dominant types such as Vertebrates. We heard much of recapitulation. Haeckel formulated the 'biogenetic law' or the repetition of phylogeny, the evolution of the race, in ontogeny, the development of the individual. Milnes Marchall, the brilliant young Cambridge zoologist, cut off in his prime, like his contemporary Frank Balfour, by a mountaineering accident, spoke of each animal being compelled to climb its own genealogical tree. Anton Dohrn, the founder and Director of the Zoological Station of Naples, devoted a great deal of time and work to elaborating a detailed scheme of the evolution of Vertebrates from segmented worms or Annelids; while Bateson, from his investigations of the development of the extraordinary worm-like form, Balanoglossus, obtained evidence that the primitive ancestor of the Vertebrates probably possessed affinities with the ancestor of the star-fishes and sea-urchins, since the larva of Balanoglossus in important points of structure resembled the larvæ of those animals, in their adult condition so dissimilar in all respects from the Vertebrate type. In fact, in spite of the fact that Darwin's problem and the title of his famous book was the *Origin of Species*, previously regarded as immutable, zoologists were for a time chiefly interested in the historical course of evolution as indicated by embryology and morphology, and the study of species was very much neglected except by the specialists, who, whether amateur or professional, went on their traditional way little disturbed by the excitement caused by the theory of natural selection. Many, if not all, of the systematists accepted the theory, but little attention was given to the question whether specific characters were really adaptive or advantageous, or to the facts of variation.

At a later date we have had the vogue of Mendelism and of Biometrics, between the disciples of which there has been controversy as keen as that between the supporters of epigenesis and of preformation in earlier times. And now we have the commencement at least of the vogue of biochemistry, which seems to be regarded by some of its devotees as the only branch of experimental biology worth attention. Mr Joseph Needham, in the volume of essays published in 1925 under the title *Science, Religion and Reality*, contributes a paper on *Mechanistic Biology and the Religious Consciousness*.[1] In this paper he states that in the change of outlook between the Victorian era and to-day one of the most interesting passages is that from zoology to biochemistry, in their influence

[1] *Science, Religion and Reality.* Edited by Joseph Needham. The Sheldon Press London, 1925.

upon philosophy and religion. It is the general habit among the younger people of the present day to refer to the Victoran era as benighted and obsolete. The self-confidence and enthusiasm of the young are splendid gifts, and in every generation are the fruitful sources of progress, of knowledge, and discovery, but these gifts are often accompanied by some narrowness of vision and a tendency to forget or ignore the truths established by their predecessors. It is necessary to consider new methods and new knowledge in relation to the science of biology in general, and I propose to discuss Mr Needham's essay as one of the most important and interesting examples of the attitude of the younger physiologists.

Before considering what Mr Needham has to say of the influence of biochemistry on philosophy, we have to give our attention to his statements concerning biochemistry itself. In his opinion the progress of biochemistry tends to establish, if it has not already done so, the mechanistic theory of life, and a considerable part of his essay is an argument in favour of this mechanistic theory against what is called vitalism. Vitalism, apart from special theories, may be described as the belief that there is something more in life than chemical and physical processes.

Mr Needham reviews the historical progress of mechanistic biology from the time of Democritus, born about 440 B.C., to the present day, which shows that although he is somewhat contemptuous of the Victorians he does not ignore the ancient Greeks. Without following the story through earlier centuries we may begin with the statement that in the nineteenth century the tide of mechanistic interpretations went steadily forward. In 1828 Wöhler carried out at Giessen the synthesis of urea in the laboratory.

Before that time it was generally held that though the chemical elements inside and outside the body might be the same, yet the compounds found in the body could only be manufactured by the body. This whole conception was shattered by Wöhler's synthesis of urea, all the constituents of the body must be one day capable of synthesis in the laboratory. No vital force was necessary. The vitalists had to retire from that position.

In reply to this it may be pointed out that it was known long before 1828 that carbon dioxide, a somewhat simpler compound than urea, was produced in the living bodies of both animals and plants, and also produced by every coal-fire, every gas-jet, and every candle. What is remarkable about the synthesis of urea in comparison with the synthesis of carbon dioxide? Urea itself is not synthetized in the body, but is a decomposition product of protein and itself oxidizes to carbonate of ammonia, which is not usually considered an organic compound. It would be more important if it could be said that chemists had been able to produce protein artificially, or an enzyme. Compounds which resemble in their properties some of the simpler proteins have been synthetized, and it is possible that the more complex members of the group will ultimately be produced artificially, but the synthesis of an enzyme has not yet been accomplished. But, as we shall see later, it would not affect the question of mechanistic biology if this feat had been performed.

In 1897 Atwater and Rosa showed that the amount of energy taken in by an animal or a man was exactly balanced by the amount of energy given out, and therefore the law of the conservation of energy held as rigidly within the animal body as it did for inorganic nature. It would have been a miracle if it had not, and the law of the conservation of energy would have had to be considerably modified. Here again it seems to me that Mr Needham fails to appreciate the real objection to the mechanistic or physico-chemical explanation of life.

Mr Needham proceeds to consider and reply to the arguments of Driesch and J. B. S. Haldane, two of the principal supporters of neo-vitalism. But I am not concerned to defend the particular views of these biologists, but rather to analyze Mr Needham's arguments.

I will, however, briefly consider one of the peculiarities which Haldane attributes to the living organism, namely the tendency to keep its environment, both exterior and interior, constant, to maintain the conditions which are optimum for its own existence. He cannot conceive of a machine being able to do that. I have heard the same doctrine stated by another physiologist in other words, namely that the ideal environment is the constant environment. There may be much truth in this with regard to the internal environment of mammals, and the minute knowledge of the blood of mammals by physiologists goes farther than that of most other subjects. But only mammals and birds have a constant temperature of blood and body, and it is obvious that the condition of the blood of cold-blooded vertebrates is very far from being constant with regard to temperature. The amount of sugar in the blood of the portal-vein of a mammal is very different during digestion and after digestion. The percentage of fat in the blood must be different when the thoracic duct is pouring in fat from the intestines, and when it is not. But it is when we consider the external environment that it seems most difficult to justify the statement that the animal tends to keep it constant. It is true that birds migrate south to avoid the winter of the north temperate region, that many mammals keep themselves warm in burrows, or hibernate like bats, marmots and squirrels, but here again the cold-blooded vertebrates are exposed to enormous differences of temperature which they cannot avoid entirely. Eels migrate when young from the region of the Sargasso Sea in the Atlantic Ocean to the uppermost streams of the river systems of Europe, and even overland to isolated ponds, and when sexual maturity approaches accomplish the reverse migration from these inland shallow fresh waters to the abyssal depths of the Atlantic. They pass, therefore, from one extreme to the other of salinity, pressure, and temperature. Similar journeys in opposite directions are made by the salmon of the North Pacific, the species of Oncorhynchus. These fish travel from the ocean up the great rivers of North-western America and North-eastern Asia more than a thousand miles from the coast, and the young descend from the upper streams, where they are hatched, to the sea.

The idea of the constancy of external environment seems to be based on the tropisms of the Protozoa and other lower organisms, in which experiment shows that they move towards a region in the water where there is a certain proportion of oxygen, or of acidity, or of light, or of temperature, and away from the opposite condition. But when we consider the notion of the constant environment as the ideal, we may ask, ideal for what? Is any evolution possible in a constant environment? Is the ideal man developed when he spends his days in the same room at the same temperature, performing always the same task, with the same diet? Are the oyster, or the sea-squirt or the barnacle the highest forms of the groups to which they respectively belong? A sessile animal with a constant current of water bringing to its interior a constant supply of oxygen and food in a sea with little variation of temperature realizes a near approximation to a constant environment, but sessile animals are generally regarded as degenerate or primitive forms.

The meaning of environment is sometimes restricted to the general chemico-physical conditions of the surrounding medium, the air or water in which the animal lives, and I have already referred to cases in which the animal seems to seek the extreme in inconstancy rather than constancy in these. But if we consider all the external conditions of life, we have to include the organic environment, the relation to other organisms, and the habits and actions, that is, the effects of external stimuli on the activities of the organism. Then we see the relation of evolution in animals to the inconstancy of the supply of food and the attacks of enemies.

Animals are forced by necessity into adaptation to new modes of activity and of existence. Optimum conditions in water would not lead to the evolution of animals or plants adapted to terrestrial life ; optimum conditions on the ground would not lead to the evolution of flight in pterodactyls, bats, or birds. It seems to me that the characteristic tendency of the animal organism at least is not to maintain its external environment constant, but to obtain the material and conditions necessary to its existence in competition with other organisms, the essential conditions being oxygen, warmth, moisture, food and protection or escape from enemies. The ideal and optimum from the point of view of evolution is not constancy of the environment, but the struggle for existence.

The animal can modify its environment in a given situation only to a very limited degree. When the environment in which it is living changes, either in consequence of seasonal or other physical changes, or from the multiplication of other organisms, it is driven to change its position or its mode of life in order to obtain the essential conditions and requirements of its existence. The change in the environment acts as a stimulus which calls forth a response in the animal, the response consisting of changes, in function and structure. The essential peculiarity, therefore, of the animal, it seems to me, is not to keep its environment constant, but to adapt itself, or rather to be adapted, to an inconstant environment. And the same is true of plants.

Mr Needham admits that the mechanistic view is not completely proved, that it is possible for the biologist to believe that in time physico-chemical explanations will be capable of describing all the phenomena of bodily life, or to believe the opposite. But I am impressed with the mental myopia which Mr Needham shows in some of the cases he brings forward in support of his arguments. He states that in biochemistry key-discoveries are frequently made which bring in their train the explanation of a hundred other facts. He instances his own discovery, that in the developing chick inorganic phosphorus is produced from organic phosphorus ; hence calcium is taken from the shell to form the bones, hence the shell becomes more brittle ; hence carbon dioxide which is produced in proportionally larger quantities in the later stages of development can escape more easily, and so on. But why are the bones formed the bones of a chick, and not the bones of a duckling ? The removal of the calcium from the shell to combine with phosphorus does not explain this. In the eggs of many reptiles there is little or no calcium in the shell ; how are the bones formed, then ? Similarly, with the discovery to which Needham refers, of an enzyme in calcifying bone which transmutes phosphorus in combination with sugar into phosphorus in combination with calcium. The future, according to Needham, will see first of all the conditions of the enzyme's working thoroughly understood, next the isolation of the enzyme in a pure state, next its synthesis, etc. But no organic enzyme has yet been synthetized ; in no case is the molecular formula known.

It seems to me that Mr Needham and other biochemists have no true conception of the problem of life at all, because they have approached the subject from the chemical point of view and have not studied living organisms from any other point of view. It is very probable, if not absolutely certain, that life is a phenomenon which is altogether different from the chemico-physical processes which take place both inside and outside the organism. Biochemistry and physiology in the ordinary medical sense treat the organism as an engine in action at a given moment without regard to the past or future of the organism.

I do not mean that there is no physiology of the embryo or of the fœtus before birth, but such processes as are discovered are purely physico-chemical processes ; they have no relation to the question of the determination of the development of the organism, of the meaning of fertilization, of heredity, of sex, of the relation of the organism to its environment, except in a purely physico-chemical sense. In general, it may be said that the physiologist seeks a function ; the biologist seeks a cause ; and the biochemist merely endeavours to show how the function is carried out. If the life of an organism could be explained by purely physico-chemical processes, then it would be possible not merely to synthetize an organic compound, a protein or an enzyme, but to produce a living organism artificially or at least to explain how it could arise from inanimate matter. From time to time men of science have claimed to have very nearly if not quite succeeded in doing this. For example, we may cite the work of the late Prof. Benjamin Moore, whose little book, *The Origin and Nature of Life*,[1] is so full of charm and imaginative vision as to have all the fascination of a fairy story. He explains how the conception of the atom as a solid particle has been changed by modern discoveries into that of a system of electrons in vibration, or in revolution round a central particle, how in some cases atoms are known to disintegrate. He describes the evolution of elements in the sun and in stars much hotter than our sun, and shows how the elements of higher atomic weight and their compounds probably came into existence when in the cooling of the earth and other planets the temperatures at which they could exist were reached. He discusses the special properties of the element carbon and how it forms the classes of compounds, carbohydrates, fats, and proteins, characteristic of living organisms. He explains the combinations of molecules without decomposition, and how such molecular unions give rise to crystals and to colloids, with the properties of which vital phenomena are associated. He suggests the probability that the inorganic continuous evolution of matter and energy ultimately gave rise to living organisms without interruption of the continuity. He points out that the energy of life arises primarily from the radiant energy given off by the sun, and that it is only made available by the action of chlorophyll in green plants in what is called photosynthesis. But

[1] Benjamin Moore, M.A., D.Sc., F.R.S., *The Origin and Nature of Life*, Home University Library. Williams and Norgate, 1912.

chlorophyll is far too complex to arise as a first step from inorganic matter, and therefore it is necessary to seek an inorganic colloid capable of forming under the influence of sunlight some simple organic molecule from which others more complex might evolve. It had been suggested and proved that the first result in ordinary photosynthesis by chlorophyll in plants was the formation of formaldehyde according to the equation $H_2O + CO_2 = CH_2O + O_2$, and Moore states that this simplest carbohydrate had been obtained by Bach by passing carbon dioxide through a solution of a salt of uranium exposed to sunlight.

Subsequently, at Liverpool University, Moore, with his colleague Webster experimented with inorganic colloids containing carbon dioxide and exposed to sunlight, or to a Uviol electric lamp. The description and results of the experiments were published in 1914.[1] One inorganic colloid used was uranium hydroxide, prepared by adding a saturated solution of ammonium carbonate to a 10 p.c. solution of uranium nitrate, and then dialyzing with running water till all the crystalloid uranium compounds were removed. CO_2 was either passed through the residual colloid solution, or the latter was saturated with CO_2 and then hermetically sealed in glass tubes and exposed to direct sunlight for one or two days. Formaldehyde was found to be present after the exposure. Similar positive results were obtained with colloidal ferric oxide.

Photosynthesis of a carbohydrate, however, in the absence of chlorophyll or any living organism only shows the origin of the simplest food compound from which the more complex carbohydrates, and even fats and proteins, might arise. But this does

[1] Moore and Webster, *Synthesis of Formaldehyde, etc.* Proc. Roy. Soc., B, 87, 1914, p. 163.

not bridge the gap between the dead and the living. The next step would be to take mixtures of these food compounds, with required amounts of inorganic salts or ' ions ', and breathe into the mixture the breath of life, to produce something which would automatically continue to oxidize and assimilate and reproduce itself. It has been known since the researches of Pasteur that yeast can live and grow in a solution containing potassium phosphate, calcium phosphate, magnesium sulphate, cane sugar, and ammonium tartrate as the only compound containing nitrogen. In this case without photosynthesis the yeast is able to synthetize fat and proteins when sugar is supplied, and no anmial is able to do this. But even if sugar were formed in the absence of all life we still require a living organism to effect the synthesis above described and to assimilate the resulting food compounds, and the origin of the living organism is still unexplained. Moreover, tartrates are derived from grapes or other vegetable products, and therefore do not take us nearer to the origin of life.

There is much to be said in favour of the hypothesis that life arose naturally and inevitably from inorganic reactions when the cooling earth in the course of its evolution reached the stage at which life was possible. But we have to explain not merely the physico-chemical processes going on in living matter, but the process by which in the course of millions of years the primitive organism evolved into larger and more complicated organisms ; how the primitive fish originated, then became adapted to terrestrial existence and gave rise first to the amphibian, then to the reptile, then to the mammal and lastly to man. Moore suggests that primitive life did not merely originate at one particular remote stage in the history of the earth, but that the process continued, and still continues, although we cannot perceive it. The first living units may be ultra-microscopic in size, to be compared with what are known as filter-passing organisms, and visible ' cells ' may be built up by the union of such particles. In this case the existing higher forms may be of various evolutionary ages, and the highest not necessarily the oldest, since the rate of evolutionary change may vary much. But all this is speculation, and it is at present impossible to reconcile it with the well-known fact which proves that spontaneous generation does not occur in the absence of all living organisms. It is not a question of synthetizing an organic compound such as formaldehyde or sugar. The inorganic colloid uranium hydroxide is not known to occur in bioplasm, and it has not been stated that colloidal ferric oxide occurs. But all the technique of bacteriology and of aseptic surgery is founded on the fact that any mixture of the compounds occurring in animals and plants, provided they have been simply boiled for sufficient time, can be exposed to air and light at any temperature at which life normally continues, and no life originates in it. In the same mixtures, which remain sterile for indefinite time when micro-organisms are excluded, any of the latter when introduced in very small numbers at once multiply and set up chemical changes in the mixture. A flask containing water in which the tissues of animals or plants have been boiled for sufficient time may communicate with the air by a glass tube which is bent down at its outer end like an inverted U, so that microbes in the air cannot fall into it, and the contents will remain sterile and no putrefaction will occur. The tube may be straight at its outer end and bent upwards within the flask above the surface of the contents and left in a room where there are no strong currents of air. Dust containing microbes will fall down the tube and remain at the bend, and no life or putrefaction appears in the contents. If the bend in the tube is merely lowered into the contained liquid so that the dust mingles with the latter, in a few days putrefaction will occur and the liquid will be swarming with micro-organisms and will soon develop moulds and unicellular animals. All attempts to discover conditions in which life spontaneously originates have hitherto failed.

After the war, researches on photosynthesis were continued at Liverpool University by Baly, Heilbron and Barker, but the object of their researches was to discover the exact mode in which chlorophyll acted, and their results do not throw any clearer light on the possible origin of chlorophyll itself. Baly and his colleagues stated in 1921 [1] that formaldehyde was formed by passing a current of CO_2 through water exposed to ultra-violet light in the absence of any inorganic catalyst. But the visible light-rays require a photocatalyst with a vibration of the same frequency as the CO_2. Chlorophyll acts as such a catalyst ; it forms a compound with CO_2 which, under the action of the absorbed rays, combines with H_2O to form formaldehyde. Malachite green, methyl orange, and other dyes which combine with CO_2 act in the same way and produce formaldehyde when exposed to visible light. In another article in *Nature* on the subject in 1922 [2] Baly states that formaldehyde when formed by chlorophyll in the plant is in the activated form, and immediately loses energy by the union of its molecules with one another to form sugar, six molecules of CH_2O becoming one molecule of $C_6H_{12}O_6$. The photosynthetic process from CO_2 to sugar takes place

[1] Article on *Tissue Metabolism*, Nature, vol. 108, Nov. 10, 1921.

[2] E. C. C. Baly, F.R.S., *Photosynthesis*, Nature, vol. 109, Mar. 16, 1922.

in the plant without a break. Simultaneously some of the formaldehyde combines with potassium nitrite KNO_2, forming a compound from which first amino-acids and secondly protein can be derived.

All this deals with the question of the origin of the food compounds on which life depends. But the process of life both in animals and in plants in the absence of chlorophyll depends on the oxidation of these food compounds, or rather of the living substance formed by them. This is the essential point which is often overlooked. Prof. Oliver Lodge, in a recent Address to the Oxford University Psychological Society, made the following statements—

> "Many of the organic compounds found in living organisms, or secreted by them, have now been made in the laboratory, beginning with urea, and continuing up to sugar and starch and numerous other compounds. And it is sometimes said by students of organic chemistry and by the biochemists who study protoplasm, that, if we could contrive in the laboratory to continue the manufacture of these organic compounds until we had made a mass of protoplasm and were able to subject it to suitable treatment, they would expect that artificial protoplasm to exhibit vitality and to manifest one or other of the forms of life."

This is an example of the fashion in which, in popular expositions of science, especially of biological science, the essential problem is concealed under the deceptive veil of a vague phrase which has no distinct meaning at all. Here the vague expression is 'suitable treatment'. The question is, what would be the treatment suitable for such a purpose? It is wrong to assume that the progress of artificial synthesis could produce a mass of protoplasm. This is 'begging the question', for protoplasm means living substance, and a mass of organic compounds is only protoplasm when it is alive. It is curious and surprising that the artificial production of living matter, or the origination of living matter from non-living compounds, should be supposed to depend upon or to have any relation to the artificial synthesis of organic compounds. We have all the required compounds in abundance, proteins, fats, carbohydrates, salts, vitamins, and everything else; they are all contained in our own daily diet. They are constantly being converted from the non-living to the living condition before our eyes, in our own bodies and in those of animals and in the tissues of plants. But hitherto in our experience only life can impart life. We have the fuel in plenty, but the fire can only be kindled from the sacred flame which man has never yet been able to originate artificially.

We can in a sense almost play with life and death. When a person is taken out of the water 'apparently drowned' we know that without 'suitable treatment' that person in most cases would not revive, but would soon become really dead, if not already so. By means of warmth, artificial respiration, and massage the inert unconscious body is often brought back to normal life, though it may be necessary to continue the treatment for an hour or more before it is successful. In such a case the tissues of the body are not yet dead, but the mechanisms of the heart, lungs, and nervous system have almost or quite ceased to function, and by the supply of oxygen and by stimulation they are induced to resume their normal action.

We can enclose a few cockroaches in an atmosphere of nitrogen in a bottle closed by an air-tight rubber stopper, and in a short time they will become quite motionless, and to all appearance dead, and will so remain for days. Take the stopper out, and in a few minutes the animals will be moving actively, as though nothing had happened. This is a case of temporary anaerobic life, in which a small supply of energy is produced by the splitting of carbohydrate without oxidation.

We are brought still closer to the mystery of life in what is called tissue-culture. A fragment of living tissue consisting of only a few cells is taken from a chick embryo or some other living organism, and placed in a small vessel containing a nutritive liquid medium, at a moderate temperature, corresponding to that of the organism from which the tissue was taken. The cells continue to live, grow, and multiply, and even to exhibit in some degree the power of differentiation and development. If we take similar fragments of tissue from a living organism, deprive them of life, and put them into the same medium under the same conditions we cannot make them live again. The dead tissue of a freshly killed animal, placed in a nutritive medium to which the air has access, will remain unchanged indefinitely and undergo no oxidation, provided all micro-organisms are excluded. If the biochemist could discover what it is that causes the living substance to carry on this spontaneous oxidation, whether it is a distinct enzyme, or special relations of the molecules of bioplasm, he would be nearer to the discovery of the secret of life than he is likely ever to get by the artificial synthesis of organic compounds. The tissue culturist can keep cells alive artificially. When the cells die the bioplasm undergoes changes, it coagulates and loses its translucency. It seems certain that the substance of such cells immediately after death is nearer in composition to living matter than any mixture of synthetized compounds can be. All that we need to discover, therefore, is precisely what are the changes that take place when the bioplasm dies and becomes rigid and opaque. If the biochemist could tell us exactly what would be the reversed process by which the dead bioplasm would return to the living state capable of carrying on respiration and assimilation, we should know what the living condition, life, really is, even if we could not produce or restore the condition artificially

CHAPTER II

METABOLISM

One of the signs of animal life most generally recognized is the exhibition of spontaneous movement. We may mistake an inanimate object for a living creature, but if we find that the movement of the object is due to some external force such as the wind we conclude either that it is an inorganic thing or a dead animal. We are referring here to active life, not to any case of suspended animation; and we are considering animals to the exclusion of plants. If we pick up a bird which seems dead, any slight movement which is evidently spontaneous, or originating within the body, convinces us that it is alive. In cases of human death it may require an experienced medical man to decide whether death has taken place or not, but movements of the heart or of respiration are the usual evidence to be sought and trusted.

It is not necessary here to consider plant life in any detail. In vegetable organisms locomotion is usually absent, and movement of any kind is not conspicuous, growth and development being the most obvious characteristics. This growth and development are different from anything that takes place in the inorganic world. Movement, however, is not wanting. Circulation of the bioplasm within the cells occurs and is visible in some cases; cell-division which underlies growth involves movements of nuclear structures; in lower plants locomotive reproductive cells move through water rapidly by means of cilia or flagella.

The first question then, is what is the cause of this power of movement, what is the source of this kinetic energy ? And the answer has been found to be that it is due to the oxidation of part of the substance of which the organism is composed. There are cases in which energy can be obtained from the living substance without the addition of free oxygen, but such cases are rare and need not here be considered. The living substance is composed chiefly of the elements carbon, oxygen, nitrogen and hydrogen with smaller quantities of sulphur and phosphorus. In the process of oxidation the living substance or bioplasm is decomposed, and the elements form simple oxidized compounds, namely carbon dioxide, CO_2, water H_2O, and nitrogenous compounds, of which urea, N_2H_4CO, is one of the most important. In the higher animals such as Vertebrates there is a heart and system of blood-vessels in which the blood circulates, and the oxygen is conveyed to the tissues and organs by the blood, the oxidized products being removed by the same medium. The oxygen is taken in and the CO_2 expelled by the same organs (e.g. lungs), and the exchange of the two gases is called respiration. The nitrogenous waste compounds, together with oxidized sulphur and phosphorus in the form of salts of calcium, magnesium, sodium, etc., which elements are present in small quantities in the body, are excreted in solution by the excretory organs or kidneys. These processes are together called katabolism, the oxidation and decomposition of the bioplasm, e.g. muscle substance, the production of kinetic energy and heat from the potential energy in the bioplasm, and the excretion of the oxidized decomposition products. As these processes go on the bioplasm is continually being oxidized and removed from the body, and if the whole body were bioplasm, and the process went far enough the whole body would disappear and be resolved into carbon dioxide, water urea, etc. But actually death occurs after considerable loss of substance before the whole body has been thus oxidized.

In plant life also we know that kinetic energy is produced by oxidation from the potential energy of the molecules in the bioplasm, and that respiration is as necessary to plant as to animal life. It is a curious fact that the radiant energy absorbed by the chlorophyll is, so far as we know, never directly converted into vital movements or changes in the bioplasm, but is exclusively used to decompose carbon dioxide and water and effect photosynthesis, so that life in plants is essentially similar to that of animals. It depends on the spontaneous oxidation of the compounds formed by photosynthesis, and is a manifestation of kinetic energy arising in this way from the chemical potential energy of these compounds. All life-energy, therefore, arises from the radiant energy of the sun. I do not see any necessity for distinguishing the energy of life by the special term, biotic energy, as proposed by Moore. The energy due to what is called chemical attraction or affinity is already called chemical energy. In vital processes this is transformed into movement, heat, or electricity, and there is no evidence that any other form of energy can be distinguished in the living organism, unless it is mental energy, and this will be considered later.

In normal life, the amount of bioplasm or living tissue is replaced *pari passu* with the destructive oxidation by a series of processes in the opposite direction. Food is taken into the digestive organs by the mouth. Food consists principally of proteins, fats, and carbohydrates, which are converted into soluble and diffusible substances by the action of enzymes in the stomach and intestine. These soluble and diffusible compounds are absorbed by the walls of the stomach and intestine, passed into the blood and lymph, conducted to the tissues and organs and there 'assimilated', which means that they are changed into living bioplasm. They pass from the non-living to the living condition. These functions by which organic compounds from without the body, ultimately derived from plants, are assimilated by the living bioplasm within the body may be called collectively anabolism, though the more important stages of anabolism, the synthesis of the more complex compounds, proteins, fats and carbohydrates from the simple inorganic compounds, carbon dioxide, water and nitrates, takes place in green plants. Attention may be called here to the meaning or definition of the term food, which is not always used with exactly the same meaning by botanists and zoologists. It is sometimes stated as one of the distinctions between animals and plants that the latter absorb and are nourished by inorganic food, that carbon dioxide, water, and nitrates are the food of plants. But this is using the word food in quite a different sense from that which it has when we mention the food of animals. The living tissues of plants depend upon proteins, fats, and carbohydrates for their substance and their energy just as animals do. The word food, therefore, must be defined as those compounds which supply potential energy to the organism, whether plant or animal. Whatever the mode in which other substances such as vitamines, salts, enzymes, etc., may act, they should be called food accessories. Some other term such as food precursors could be used for the oxidized compounds, CO_2, etc., from which food compounds are derived in plants.

Anabolism and katabolism together constitute metabolism. We may write down these chief functions, each of which in a Vertebrate has corresponding special organs, in the following way—

Katabolism { Respiration
Excretion (of nitrogenous waste).

Circulation of blood.

Anabolism { Digestion
Absorption
Assimilation

To the organs which carry on these functions we may add the musculo-skeletal system by which the movements of the organism are effected.

In endeavouring to form a correct conception of the nature of life we may compare the living organism with different kinds of engines artificially constructed by man. An engine is a structure of limited size and definite shape whose function is to convert potential energy into kinetic energy. There are many cases in nature of the conversion of potential energy into kinetic energy or the reverse, such as the descent of water in a waterfall, or its conveyance in the form of water vapour and rain to the high lands, but here we have only to consider artificial engines. And we may confine ourselves to heat engines. A watch or any other contrivance worked by springs or weights is an engine, the potential energy being stored up in the spring or the raised weights, but it is obvious that such an engine is in no way similar to the animal organism. We may then consider first the steam-engine, and we see at once that the movements of the organism are not produced by the expansion of steam derived from water heated by the combustion of fuel. So we come to the internal combustion engine, in which the fuel is used directly in the form of vapour mixed with diluted oxygen undergoing explosive combustion inside the cylinder, and in which the gases produced, chiefly carbon dioxide and water vapour, are expanded by the heat of the combustion so as to move the piston. By means of this kind of engine motor-cars can move about with great rapidity over the surface of the earth, ships on the surface of the sea or below the surface, and aeroplanes show greater power of flight than birds possess. But there are very great differences between the internal combustion engine and the animal organism, although there is some similarity in the fuel in the two cases. The most important differences are two in number—first that in the engine, as in all cases of ordinary combustion, the oxidation takes place only in a dry condition at a high temperature and at a very rapid rate, while in the animal it takes place in water at a low temperature and at a slow rate. For bioplasm contains much water, and every molecule which is oxidized is surrounded by water, the oxygen being conveyed in a state of solution from the blood through the tissues, though it is carried in the blood in combination with hæmoglobin. The second difference is that in the animal there is almost no distinction between the substance of which the engine is made and the fuel which drives it. Every living cell in the body is undergoing oxidation, though many of them are producing heat and very little movement, for example the bone-cells. But the muscles which constitute a great part of the whole body not only contain the fuel which by oxidation supplies the energy, but are also the moving parts. To make an engine similar to the vertebrate animal, we should have to construct the moving parts, or the parts which produce movement, of some kind of coal or carbon compound which would contract as a result of oxidation, and reconstruct itself in proportion as it was destroyed by the oxidation. The engine would also have to repair itself automatically, when not too seriously injured. It is scarcely necessary to mention that the motor-car, boat, or aeroplane rushes straight forward, or in a constant curve, or crashes to the ground and destroys itself, and has no power either to stop or guide itself, but is guided and controlled by the person who drives it.

The living animal on the other hand has to obtain the food necessary for the process of anabolism or replacement of lost bioplasm, either by preying upon other animals or by devouring plants. It has in many cases to shelter itself from cold or heat or storm, and to escape from or defend itself against other animals who would prey upon it. It has, therefore, relations to the external world, and if we regard it as an automaton it responds by appropriate movements to stimuli received from its surroundings. The body, therefore, of one of the higher animals, in addition to the organs above mentioned, has sense organs and a nervous system. The sense organs are special parts of the surface of the body affected by light, sound, smell, taste, touch, pressure, and heat, connected by the nerves to the brain and spinal cord, which are again connected to all parts of the muscular system, and also to the organs of metabolism.

If we take the problem of life in stages we may first try to consider the organism so far as the above examination goes, a body of definite form separate and distinct from the non-living materials by which it is surrounded, in which a continuous series of transformations of matter and energy are taking place, and which is in the relation of stimulus and response with external matter and energy. How far can such an organism be explained as a physico-chemical mechanism? Destructive oxidation of the protoplasm supplies all the energy produced in the state of heat or movement. But this discharge or transformation of energy is not a uniform process, nor a process varying directly with mere change of external physico-chemical conditions. If we exclude consciousness or 'mind', to use the term employed by Needham, the movements are regulated by external stimuli. The higher animal responds to the presence of food on the one hand, or an enemy on the other, by movements adapted to secure the one or escape from the other. The response with regard to food depends upon the internal condition of the animal, on the degree of hunger, which may be the relation between destruction and construction of bioplasm, acting upon the central nervous system. The more hungry a wolf is the more dangerous he becomes to other animals. The stimulus acting on the eye is light of different wave-lengths and intensities, but the response is not merely automatic in the physico-chemical sense; it depends on what we call recognition, and that is something mental or psychological, some retained effect of previous stimuli and responses. The living animal has thus a power of self-regulation, of controlling and directing the purely physico-chemical processes that go on within it, although this regulation does not imply any creation or destruction of energy in the physical sense. If we consider the lowest organisms we find according to the researches of Loeb and others that the automatic response is more direct, less apparently dependent on anything which can be called mental or psychological. The unicellular organism moves to or from the light, or vibration, or chemical stimulus. Its actions are due to 'tropisms'. But even so the response to the stimulus is something not found in the inorganic world; it is peculiar to living bioplasm. No combination or treatment of the organic compounds which constitute food has ever yet produced a particle which would act as living organisms act. So far as our knowledge goes, or any indication in that knowledge suggests, nothing can convert food into bioplasm but the contact of living bioplasm.

Bioplasm by mixing them with itself, is able to convert proteins, fats, and carbohydrates in certain proportions, together with other substances in small proportions, such as vitamines and inorganic salts into bioplasm, to change these inanimate chemical compounds into living substance, to make them alive. How can the biochemist produce this change? Given the various constituents of food, proteins, fats and carbohydrates, certain salts with the necessary food accessories, vitamines or whatever they may be, how can the biochemist convert them into living matter or protoplasm, without contact with matter already living? When the chemist, if not actually able to do this, can show how it could be done, under what conditions and by what treatment, then he will be entitled to assert that life is nothing but mechanism. Until then, he does not know what is the mechanism of life. We might even make a more moderate demand, namely, that the biochemist, or biology in general, should be able to explain what goes on in living protoplasm, and what is the process by which it assimilates food to itself and so makes the dead alive. Bioplasm is not a mere chemical compound or a mixture of compounds, its life is like a slow fire in which oxidation is taking place to release kinetic energy in the form of heat and movement, and the fire automatically feeds itself, or takes up fuel. A fire in the ordinary sense is a simple affair, and to kindle it merely requires the fuel to be raised to a certain temperature, a spark of fire may set a house or a whole town or a forest burning. But the life in an organism or in a single protoplasmic cell is a much more complicated process, and biochemists have not yet even discovered how to investigate it. Mr Pantin, of the Marine Biological Association's Laboratory at Plymouth, has devoted himself to the study of movement in a certain kind of Amoeba, and finds that the internal endoplasm is in a fluid state ; it moves forwards and flows out at one end. At the sides it loses fluidity and becomes a gel, while the posterior end is passing from the state of a gel in the fluid state and passing into the endoplasm. But this is all, only a description of what is seen to occur, but no explanation of why it occurs. The question still unanswered is, how does the energy set free by oxidation produce this movement of the endoplasm, what causes the change from fluidity to gel and vice versa.

LIFE IN RELATION TO ENTROPY

Dr James Johnstone, in his very interesting book, *The Mechanism of Life*,[1] reaches the conclusion that the essential peculiarity of living processes is that the increase of entropy is retarded, whereas our inorganic concept is that the entropy of the universe tends to a maximum value. In the course of the book he repeatedly promises to explain what is meant by entropy, but never does so very definitely. He allows the intelligent reader to infer from an example that entropy is the quantity of heat which flows from or to a body in any transformation of energy, divided by the absolute temperature, the zero of which is − 273° C. In other words, 0°C., the freezing-point of water, is 273° C. in absolute temperature. Dr Johnstone's

[1] Johnstone, Dr James, *The Mechanism of Life*. London; Edward Arnold, 1921.

example is as follows: Suppose a vessel whose walls are absolutely impermeable to heat divided by a partition into two equal parts, and that in each half there is the same quantity of gas, but in one half the gas is at 20° and in the other at 10°. Suppose there is a valve between the two divisions. When the valve is opened the gas at higher temperature having a higher pressure will rush through the opening until the pressures and temperatures are equal in the two divisions, when no further change of pressure can occur, although the total energy is the same. The average temperature will be 15°. A certain quantity of heat (the unit quantity being that which can raise 1 cc. of water from 0° C. to 1° C. by the ordinary Centigrade scale) will have flowed from the gas at 20° to the gas at 10°. That is to say, the gas at 20° will have lost Q units of heat and the gas at 10° will have gained the same quantity. The entropy of the Q units at the higher temperature will be $Q/293°$, using absolute temperature, and the entropy of the same quantity at the final average temperature will be $Q/288°$. Obviously the latter fraction is greater than the former, therefore there has been an increase of entropy.

It is better, however, to consider entropy in relation to the reversible cycle of Carnot's imaginary heat engine. This supposes a gas at a certain temperature, T_1, to receive Q_1 units of heat from a body of the same temperature and do a certain amount of work, at the same time giving up a portion of the heat, Q_2, to a body at a lower temperature, T_2. It is shown in the mathematical analysis of this process that $Q_1/T_1 = Q_2/T_2$, which means that the entropy of the energy in the form of heat at the end of the process is the same as at the beginning, supposing that no heat has been lost from the system. This is the condition of the reversibility of the process. By applying work to the system the initial condition can be restored, the amount of heat Q_2 being raised from the lower temperature to the higher. The amount of heat, Q_2, which by the previous equation is equal to Q_1T_2/T_1, is the fraction of the original energy taken up by the gas which cannot be converted into work, and is called the unavailable energy. But under all circumstances which occur in real engines some of the heat escapes from the system into the surroundings, and the amount Q_2 is therefore larger; Q_2/T_2 is therefore larger, and thus both the unavailable energy and the entropy are increased, and the available energy is less than the maximum possible in the reversible cycle. It follows from this that in all energy transformations, whether work is done or not, some energy is converted into heat, which by conduction and radiation is gradually transmitted to the surrounding objects at a lower temperature from which it cannot be raised, and this is called the dissipation of energy. Thus, the laws of thermodynamics state that although the total quantity of energy in the world cannot be either increased or diminished (conservation of energy), all energy at higher potentials is gradually being distributed through the world in the form of heat at a low uniform temperature from which no work can be obtained (dissipation of energy). It appears, therefore, that at some distant future time all energy in the solar system will have been reduced to heat at a uniform temperature, and no further change can take place; life and movement will come to an end.

The work which is done by any source of energy at high potential may either produce other potential energy, for example, pumping water to a high reservoir, or it may produce kinetic energy, such as firing a bullet or shell from a gun or driving a railway train. In the former case the water by reason of its position can fall again and produce kinetic energy, which is merely the movement of matter, or matter in motion. In the latter case the train moves until the supply of energy is cut off and the train brought to rest. Then the whole of its kinetic energy is transformed by friction into heat at a lower temperature distributed in the rails, earth and air in proximity to the train. If there were no friction and no resistance of the air the train would run on for ever at the same speed without any more energy being supplied to it. The permanent result when energy has been dissipated is a change in the relative positions of material objects. The train when it stops is at Edinburgh, for instance, instead of London : so many tons of coal have been burnt, and the energy obtained by the burning is dispersed as heat over the part of the country between the two places, raising the temperature of earth and air by an infinitesimal amount, which rise of temperature is merely temporary because it is soon lowered to that of the surroundings. Suppose we wind up a clock by raising the weights or winding the spring. The clock moves the hands for a certain time until it has run down, and stops. The potential energy produced in weights or spring is converted into kinetic energy, which moves the hands, which may be in the same position when the clock stops as when it started. The kinetic energy has been transformed into heat, which raises the temperature of the parts of the clock and is gradually communicated by radiation to the surroundings. When a rifle bullet is shot vertically from the earth its kinetic energy, acting against the force of gravity, excepting that portion which is transformed into heat by the resistance and friction of the air, is gradually converted into potential energy of height, until the movement finally stops and the bullet begins to fall again. When it reaches the ground again its velocity and kinetic energy have been diminished by the amount converted into heat, which slightly raises the temperature of the air, and when it strikes the ground the whole of the remaining energy is dissipated into heat in the soil. If the surface of the ground were perfectly elastic and there were no air, the bullet would start upwards again with the same velocity, and would continue going up and falling down without cessation, unless the ether offers resistance or friction.

In living green plants, as Dr Johnstone points out, the kinetic energy of the sunlight, or more accurately of the sun's radiation, acting on water and carbon dioxide, produce carbohydrate, and from this is produced fat and, in combination with nitrogen from nitrates, proteins. He then states that protein, fat, and carbohydrate, when aggregated in the form of living protoplasm, do not decompose but increase in quantity by reproduction. According to Dr Johnstone, in these energy transformations entropy decreases and unavailable energy becomes available. Apparently he regards the sun's rays in the absence of living green plants as unavailable energy, whereas in fact they are kinetic energy. It is true that a great deal of the radiant energy from the sun falls upon the earth and becomes unavailable in the form of heat at low temperature, whereas when they act upon green vegetation their energy is converted by photosynthesis into the potential energy of carbohydrates, fats and proteins, which together may be called food compounds. It seems obviously incorrect to state that in the form of living protoplasm these food compounds do not decompose, but increase in quantity by reproduction. In animals they never increase in quantity, but are always decomposing by oxidation. The only increase is by growth, which is the result of additions from outside of food originally synthetized by plants. In plants the increase in quantity is not specially due to reproduction, though certainly the cell-division, growth, and multiplication of the individual plants is a necessary factor. The increase is due to the fact that the products of photosynthesis are increased at a greater rate than they are decomposed, whereas in animals they are not produced at all. In the animal world there is an increase, or there may be, of living individuals, i.e. of protoplasm, but this is merely the conversion of food compounds derived from plants into living protoplasm, and substances formed by it such as bone, feathers, etc. In plants, as there is always a vast supply of radiant energy available, the amount of photosynthesis increases with the amount of green vegetation.

Johnstone states that, in contrast with the world of living organisms, in every inorganic physico-chemical system energy becomes degraded, and entropy increases. But although the ultimate fate of kinetic or potential energy in both cases is to become degraded to unavailable energy in the form of heat at low temperature, some of the kinetic energy in the inorganic world becomes transformed into potential energy, and in the organic world in photosynthesis only a small portion of the radiant energy from the sun is transformed into the potential energy of food compounds. The sun's rays, which cause plants to grow, also raise water in the form of vapour from the surface of the ocean, and precipitate it in the form of rain or snow on the mountains and highlands, where it not only runs down again in the form of rivers, but some of it remains more permanently as lakes or as ice and snow. This is a conversion of the kinetic energy of the sun's radiation into potential energy of position. The winds and thunderstorms are also due to the conversion of potential energy derived from the kinetic energy of the sun's radiation, and so are the ocean currents, excluding those due to the rotation of the earth or the tides.

The fallacy in Dr Johnstone's argument is that he confuses anabolism, or the conversion of kinetic energy into potential, by photosynthesis in plants, resulting in the formation of the essential food-compounds, with vital processes, or metabolism in general. Life energy on the contrary is the result of katabolism, that is, the oxidation of the food compounds in the living protoplasm. Even in plants the activity of the protoplasm in the cells, especially in parts which do not contain chlorophyll, such as roots and the cambium of stems, is due to the oxidation of the protoplasm and is degradation of energy, although in daylight the anabolism or storage of energy is greater than the katabolism or release of energy.

It is impossible to admit Dr Johnstone's proposition that adaptation in general tends to retard the natural degradation of cosmic energy. The general tendency of evolution is rather in the opposite direction. The warm-blooded animal, bird or mammal expends energy at a much greater rate than the cold-blooded reptile or fish, especially the bird. Wings are one of the most striking adaptations for locomotion, and the expenditure of energy in the tireless flight of the swallow or the seagull is very great. The reckless expenditure of energy in animal life in general is much more than sufficient to counterbalance such cases as the accumulation of blubber in a whale to prevent loss of heat, which Dr Johnstone gives as an example of his contention.

Moreover, the blubber of the whale, although it prevents loss of heat by conduction to the water, increases rather than diminishes the transformation and dissipation of the potential energy contained in the whale's muscles, for the rate of oxidation is much higher at a higher temperature than at a lower, and the function of the blubber is to enable the whale to maintain the constant temperature of a warm-blooded mammal. The blubber has not been produced by synthesis in the whale's body, but is derived from the whale's food, and is ultimately due to the photosynthesis carried on in the multitudes of microscopic diatoms in the upper layers of the ocean.

Dr Johnstone mentions that human operations such as war, cutting down of forests, or depletion of coal supplies, may involve expenditure or degradation of energy, but he argues that they may have the opposite tendency as in afforestation, cultivation of land, increase of population, etc. He regards this as another instance of the vital concept, retardation of the increase of entropy. Here again he fails to distinguish correctly between anabolic and katabolic processes.

Increase of population is increase of katabolism, not of anabolism. It is true that cultivation of food-plants such as wheat and other cereals and vegetables and fruits is increase of potential energy derived from sunlight, but all progress in civilized life involves not merely the consumption of plant and animal food of contemporary origin, but an increasing consumption of the stores of potential energy accumulated in former ages, and of forests of recent growth and of petroleum. The vegetable remains of ancient geological periods must have accumulated either in the absence or scarcity of animal life, or consisted of plants which were unfitted for animal food. In the present age all this accumulated energy is being rapidly degraded, and the katabolic effect of life is greatly in excess of the anabolic. We have only to consider the enormous quantities of coal daily burnt in factories, blast furnaces, engines of all kinds, including those that drive our great ships to and fro across the oceans to bring the food supplies from other lands, the petroleum-driven motor vehicles and aeroplanes, to realize that modern civilization depends on increase of entropy, on dissipation of energy. As far as we can see, we are progressing with increasing rapidity towards a time when civilization with its increasing density of population in temperate and northern latitudes will no longer be possible, and when human life will be more dependent on the products of recent and contemporary plant-growth. It is true, therefore, that life is dependent on photosynthesis, but this conversion of the radiant energy of the sun into potential energy is not a general characteristic of vital processes. A great part of life in plants and all animal life consists in a manifestation of kinetic energy derived from the oxidation of the food compounds synthetized in green plants.

From the point of view of thermodynamics then we have two processes which seem to be peculiar to living organisms: (1) photosynthesis by means of chlorophyll, (2) the mode of oxidation by which the potential energy of food compounds is converted into kinetic energy of movement and heat. The two chief peculiarities of oxidation in bioplasm have been mentioned earlier in this book, namely, the low temperature at which it occurs and its occurrence in water. The organic compounds originally formed by photosynthesis may occasionally be oxidized and decomposed by ordinary combustion, but unless raised to the temperature of ignition and sufficiently dry they do not appear to oxidize at all. The oxidation in the living body or cell is probably due to enzymes, and in the dead organism is generally due to the enzymes of other living organisms. Organic matter in water which has been sterilized and protected from minute organisms merely by a plug of cotton-wool remains unchanged for an indefinite time : if the cotton plug is removed so as to admit micro-organisms decomposition soon occurs. A dead animal's body is oxidized and decomposed by bacteria, and vegetable matter such as a haystack or heaps of dead leaves apparently would remain unaltered if they were not acted upon by numerous fungi and micro-organisms. The oxidation thus carried on may sometimes cause such a rise in temperature as to result in ignition and ordinary combustion.

We may conclude that with respect to retardation of increase of entropy there is no essential difference between an animal and the Niagara Falls, but, on the other hand, the transformation in an animal of potential energy in the food compounds by oxidation into kinetic energy of heat and movement occurs in a mode and under conditions which are not found in association with oxidation in the inorganic world. If Johnstone's criterion of life were correct it would follow that animals are not to be considered as living organisms at all.

On the other hand, if we consider green vegetation alone, it is true that anabolism beginning with photosynthesis is in excess of katabolism, and results in a continuous storage of potential energy derived from the kinetic energy of the sunlight, and a continuous accumulation of the compounds containing this potential energy unless they are oxidized by combustion or decomposition. This is one of the phenomena of life, but is not the essential peculiarity of living processes. Katabolism is as essential as anabolism. The two together are included in the term metabolism, which expresses the whole series of transformations of matter and energy taking place in a living organism, but life also includes the various phenomena reviewed in the succeeding chapters.

CHAPTER III

REPRODUCTION AND EVOLUTION

So far we have considered the metabolic functions and organs of one of the higher animals, with the addition of the musculo-skeletal system and the sense organs and nervous system. But the condition of the organism is not permanent; its dynamic equilibrium, the power of assimilating food with potential energy to replace the matter and energy given out, does not continue indefinitely; its vigour and activity after a time gradually diminish or cease, and death ensues either from accident, disease, or old age. Thus, if the functions and organs already mentioned were the only functions and organs in the living body, there would soon be no living bodies on the earth; all would sooner or later die and perish. But actually the organism is provided with reproductive organs, which take no part in the maintenance of the life of the body; they are not necessary to the individual, but their function is to produce cells which are liberated from the body and develop into new organisms similar to the parents. Here, then, we arrive in our analysis at those branches of biology which are concerned with reproduction, sex, and development. In the majority of cases two reproductive cells unite into one which develops by cell-division and cell-differentiation into the new organism. Recent progress has brought to light complicated and definite structures and processes in the nuclei of the cells during cell-division, during the preparation for fertilization, and in fertilization itself. These discoveries have been made by observation with the microscope, aided by improving technique. Chemistry is certainly largely concerned in this technique, that is to say in fixing the structure of cell and nucleus, and in making and staining microscopic preparations: but this is not what is meant by biochemistry. The method employed is essentially that of observation, not experiment. We are still very far from understanding why the two reproductive cells or gametes unite in fertilization, although we know much more of the morphological details of the process. Biochemistry has not yet told us what makes the male and female gametes unite, what causes the chromosomes of the two to undergo reduction to half the original number in each gamete and then the half numbers in the two gametes to come together in the fertilized ovum in pairs to restore the original number present in the cell before reduction. We know some of the results, but not the causes. Experimental embryology has shown that an unfertilized ovum which normally does not develop can be made to develop by pricking with a needle in the case of frog's eggs, or by a brief immersion in some chemical solution, some solution of a salt. But we are still ignorant of the real meaning of fertilization. We have evidence of three kinds concerning the process: (1) that fertilization often occurs at the approach of unfavourable conditions for active life, such as summer drought or winter cold, (2) that it maintains or renews the vigour of life, (3) that it produces the union of some of the hereditary characters of the two parents. But we have not learned much, if anything, concerning either of these three effects of fertilization from biochemistry.

Recently, Mr Needham has described experiments on the ova of sea-urchins carried out to ascertain if the 'concentration of hydrogen ions' was greater or less after fertilization than before. The result of these experiments, requiring the most elaborate and delicate technique, great skill and the latest chemical knowledge, was entirely negative: there was no difference in the 'hydrogen ion concentration', which leaves us scarcely any wiser than we were before. In more ordinary language it may be explained that the result was to show that fertilization produced no change in the acidity of the contents of the ovum. It is not suggested that such an experiment was useless. It is necessary to know the chemical aspect of biological processes, as well as the structural and physiological. The case is merely cited to show how little justification there is for Mr Needham's statement that zoology has become comparative biochemistry. Not only has it not yet become so, but I venture to maintain that it never can become so, because the chemistry of the ovum, and of the developing embryo, and of the adult organism would by itself have no significance: it can only be understood in relation to details of structure. How could we discuss the secretion of urine from the chemical point of view alone, without any knowledge of the structure and functions of the kidneys and the liver?

The whole process of reproduction can only be considered in relation not to the functions of the organism at a given moment, but to the whole of its individual history. During growth and differentiation some cells are left unspecialized, and these become at a later stage the gametocytes. In plants we see a more simple and primitive type of growth and reproduction. Growth is more unlimited, and differentiation less complicated. In the whole body of a dicotyledon (one of the higher plants, such as an apple-tree) we find a continuous layer of undifferentiated cells (cambium or meristem), and from these are formed the male and female reproductive cells. There are no specialized reproductive organs before the flowers develop. It may be admitted that cell-growth and cell-division in the last resort are chemical and physical processes, but at present we are unable to follow out these processes in detail, and the important fact is that such a series of chemical and physical processes as results in growth, development, and reproduction occurs only in living organisms, and nothing of the same kind is found in inanimate nature.

In the preceding pages the term reproduction has been used in reference to the higher animals which consist of a multitude of cells differentiated into organs. The concept of reproduction is the development from the fertilized ovum, whether of animal or plant, of a new individual similar to the parent from which the ovum was derived or from which the sperm was derived. The cells of the multicellular organism are differentiated into somatic cells and gametes, and only the latter are capable of union with other gametes in the process of fertilization to form the zygotes which reproduce the original form. In unicellular organisms on the other hand there is no parent and no offspring, the cell divides into two and so multiplies. After division, as in Paramecium, there may be reproduction of parts of the cell, e.g. of the meganucleus, but there is no co-existence of parent and offspring. The parent literally lives in its offspring. Paramecium, however, is not in the strict sense unicellular, it represents two cells with differentiated nuclei. In unicellular organisms there is no differentiation of gametes from somatic cells: all the individuals are capable of conjugation, but there is a difference between the phase of conjugation and the phase of cell-division. Usually conjugation is followed by a number of cell-divisions, and then conjugation takes place again. The evolution of the multicellular organism thus involves the differentiation of the soma, and it was this that 'brought death into the world', for the somatic cells have necessarily lost the power of rejuvenation by conjugation and must therefore ultimately die, and with death came reproduction, for a new soma is developed in each generation. In unicellular organisms there is no soma, and therefore no necessary death nor reproduction.

DIVERSITY OF FORMS. DIAGNOSTIC CHARACTERS AND ADAPTATION

Having hitherto considered an individual organism such as a Vertebrate in a general way we have next to consider the different kinds of organisms, the characters by which they are distinguished and classified. Mr Needham regards these differences as of minor importance: "The forms of the different types of sea-urchins are truly most interesting, but they are only the forms taken by the same chemical elements, and in this case as in others the body is more than the raiment".

But surely the question is, why does, not the same collection of chemical elements, but the same living substance, produce all these different forms? A mechanistic theory of life has to explain not merely the fundamental processes of metabolism, which are the same in an amoeba and a Vertebrate, but all the phenomena of life, including, 'the interesting forms of the different types of sea-urchins'. The form and structure of organisms are not merely raiment. Even the shell of an oyster is secreted by the animal, and the mechanistic theory has to explain why it is secreted, why the Nautilus has a shell and the Octopus has none. The study of form and structure cannot be superseded by biochemistry; on the contrary, if life is a physico-chemical process, the biochemist must be prepared to explain all the facts of morphology and systematic zoology.

We have different forms in inanimate substances. Chemical compounds have their special forms of crystals, their special colours, and other special physical qualities. Different rocks have different physical qualities and different compositions. But it is obvious that the differences of form in animals are not of the same kind as those which occur in inorganic objects. Still less is it correct to regard the structural characters of animals (or plants) as the comparatively unimportant forms assumed by living matter, the 'universal substrate' of organisms. Living matter is not merely moulded or carved into different shapes, as marble into a multitude of statues. We can imagine a chemist looking at a collection of the most exquisite Greek statues and pointing out that they are merely the forms taken by the same chemical compound, calcium carbonate, and that the body is more than the raiment, or more appropriately that the substance is more than the form. In this case the chemist would be merely exhibiting his inability to appreciate artistic beauty. But in living organisms form and structure are the result of processes that have taken place within the living substance. It is necessary to discover what determines the special features in each type, variety, or species. The investigation of the 'physico-chemical attributes of living matter' cannot justify itself until it has explained the forms and structures which living matter develops. Organisms are, as we have seen, engines in a state of activity, and this activity includes not merely the metabolism of a constant or single type, but the development and evolution of a multitude of different types. Growth, development, heredity and evolution are as essentially characteristic of life as metabolism.

Some of the structural features of different types or species are the special organs and characters by which the animal maintains itself in its own particular mode of life. The organs of a fish are different from those of a bird, because the fish lives in the water, the bird chiefly in the air, or partly on land and partly in the air. The fish has fins, the bird has legs and wings. The two most fundamental requirements of animal life are food and oxygen, but there are a vast number of different ways of satisfying these requirements. Animals are adapted not merely to different inorganic conditions such as water, land and air, but to a great variety of different relations to the complex organic world itself. Herbivorous animals live on grass or other plants, and carnivorous animals live on the herbivorous. The study of adaptation may be said in a sense to consist of biophysics and biochemistry, but it is not what the biochemist commonly understands by those terms. The function of flight is a most important problem of biophysics which has been solved by many different kinds of animals, by insects and pterodactyls for instance as well as birds, and yet has only recently been solved by the human intellect, and on somewhat different principles. There are chemical relations to the external world also, but perhaps not in such great variety as the physical relations. Respiration is chemically always essentially the same, and the differences in the mode in which it is carried out are chiefly structural and physical, and evidence is presenting itself that sunlight for instance can cause the formation in the body of the same chemical compounds which are usually obtained from food (vitamines). It seems to me incorrect to state that zoology has become comparative biochemistry except in such cases as the progress of research on the differences between hæmoglobin, hæmocyanin and chlorocruorin, in Vertebrates, Crustacea, and green Annelids. The study of adaptation in feeding and locomotive organs always involves physics or mechanics, but the important question is how the organism evolves mechanisms adapted for special kinds of action. One of Mr Needham's most astounding statements is that whereas evolution was the key-interest of biological philosophy fifty years ago, the mechanistic theory of life is now the important problem. I fail to see how evolution can be divorced from the question of the mechanistic theory of life. If we agree that adaptations are not permanent and immutable, but have been evolved from more primitive conditions, the amphibian from the fish for example, the bird and reptile from the amphibian, that the descendants of fishes have become adapted to terrestrial life by change in their organs of respiration and locomotion, then surely it is necessary for the mechanistic theory to show what is the mechanism of evolution so far as adaptation is concerned.

Here as a Lamarckian I am myself in a sense both a mechanist and a biochemist. Biochemistry and biophysics in the ordinary sense deal chiefly with metabolism and with the relations between the animal and external conditions of a general kind, such as oxygen or temperature. The Lamarckian theory considers the effects of special external stimuli in modifying the growth of the organism, causing one part to grow larger and another to diminish. One large class of such stimuli are of a mechanical kind acting by direct friction or interrupted pressure on the epidermis or bones immediately beneath it. Another class consists of the effect of increased or decreased activity of function on muscles and the parts of the skeleton to which they are attached. We know that such stimuli produce modifications in the individual lifetime, and if such effects were inherited ever so little, there would be a cumulative effect, so that for example the thick external covering of the horns of cattle and antelopes would be of the same nature and origin as corns on the feet caused by friction of the boots, or on the hand from rowing or the handling of tools, etc. But, even, putting evolution aside, although we know that the horny epidermis is thickened by friction, and a muscle increased in size by exercise, it is evident that this is a process of a different kind from the mechanism of an inanimate system, and is not to be explained by physics or chemistry in the ordinary sense. Friction and impact cause dissipation and loss of substance in non-living materials or machines, whereas in the living the same agents cause increased growth. We know little or nothing about the action of mechanical or functional stimuli on the living cells, in increasing the rate of assimilation and cell-division. It is an automatic process, and in that sense due to a mechanism, but it is a mechanism peculiar to life, and in that sense the theory of vitalism is justified. I have attempted to construct a Lamarckian theory of the evolution of adaptations based on the action of hormones or internal secretions. There is good evidence that these secretions are special chemical compounds, or mixtures of such compounds, which are soluble and diffusible, and therefore capable of passing through the tissues, or from the blood and lymph to the tissues. In the case of adrenalin,[1] the specific substance obtained from the medulla of the adrenal gland, the chemical formula has been discovered and the compound has actually been synthetized: the formula is $NC_3H_{10}O_3$.

The chemical compound or compounds which form the essential active constituents of the thyroid secretion have not yet been so completely identified and analyzed. Baumann, in 1895-96, prepared from the gland substance a non-protein nitrogenous material called iodo-thyrin, and this forms a compound with nucleo-protein known as iodo-thyro-globulin. The evidence shows that iodine is an essential constituent of the hormone. The human thyroid was found to contain 0.46 to 0.84 mg. per gram of fresh gland-substance, or less than 0.1 per cent. This organ is the only one in the body which contains iodine in appreciable amount, and when administered by itself, both in children and tadpoles, the element produces to some degree the same effects as the substance of the gland itself. In 1914 Kendall isolated from the gland substance a compound in crystalline form, that is, a single chemical compound in a pure state, which he called thyroxin, and found that it had the formula $C_{11}H_{10}O_3NI_3$. The proportion of iodine by weight in this substance was 65.1 per cent. Kendall believed that this compound was the cause of all the physiological and therapeutic effects produced by the thyroid secretion, but it does not cause increased contraction of the unstriated muscle of a piece of intestine, which is one of the effects of thyroid extract. But although progress has thus been made in investigating

[1] Sir E. Sharpey Schafer, *The Endocrine Organs*, 2nd edit., 1924.

the chemical nature of these hormones, biochemistry has not yet approached the question how they affect the organism in such marvellous ways. This applies specially to the thyroid. Its specific substance is essential to normal development as well as to normal metabolism. Given to cretinous children, their arrested development both of body and mind is resumed. Tadpoles fed with thyroid almost immediately begin to develop legs and undergo precocious metamorphosis. The axolotl, which in normal conditions is not known to metamorphose at all, but breeds in the aquatic phase of development, respiring by gills, and has only been forced to metamorphose with difficulty by exposure to air, can be made to undergo metamorphosis, losing gills and gill-slits and changing its shape and colour, by a single meal of a proper amount of thyroid gland. It cannot be doubted that the metamorphosis of the tadpole, and the absence of metamorphosis in the axolotl, are results of age-long processes of evolution. The administration of thyroid to a fish does not cause it to change into an amphibian, and it has been found by experiment that it has no metamorphic effect on Necturus, an amphibian which, like the axolotl, has gills and gill-slits throughout life, but is not closely related to an air-breathing salamander as is the axolotl. It is therefore obvious that evolution has the closest connexion with the mechanistic theory of life and with biochemistry. Moreover, examination of current biological literature very soon shows that there are a great many earnest biological investigators who are intensely interested in other parts of the science and other methods than biochemistry and its technique. In every civilized country there are societies and publications devoted to experiments on heredity, Mendelism and mutation, and research is carried on concerning such subjects as secondary sexual characters, and the influence of hormones upon them; and the controversy between Lamarckians and anti-Lamarckians is not yet extinct.

THE PROBLEM OF SPECIES AND THE DOCTRINE OF MUTATIONS

Darwin entitled his celebrated volume, first published in 1859, *The Origin of Species by Means of Natural Selection*, but he did not distinguish between the question of species and evolution in general. He had in mind chiefly the view held by the majority of naturalists up to, and at that time, that species were "immutable productions and had been separately created." He did not attempt to explain all the characters of species, but was content to prove that individuals varied, and that those which had new peculiarities, however slight, which gave them an advantage in the conditions of life in which they were produced, or in slightly different conditions to which they had access, would survive in the struggle for existence, and give rise to new species. He seems to have assumed that they might retain other characters, whether useful or not. Logically, however, his theory was an attempt to explain the origin of adaptations, using that word in the sense of characters which are useful in relation to the conditions of life of the organism which possesses them.

At the present time there are some naturalists who hold that all characters, whether specific or otherwise, are adaptive or useful, and that all are sufficiently explained by natural selection, or survival in the struggle for existence. Of these Prof. Poulton is an eminent example, while Mr Tate Regan, Director of the Natural History Museum, concludes from his special study of fishes that specific characters are in many cases the direct effects of habits and conditions of life. On the other hand, we have the Mendelians or geneticists who, either like the late Mr Bateson, pay little attention to adaptation or utility, and devote themselves by crossing experiments to discovering the factors and unit characters which make up the heredity complex of various races; or like Prof. T. H. Morgan, of Columbia College, New York, observe the occurrence of mutations in successive generations of natural species bred in captivity, and trace out the heredity of these mutations and the original characters in relation to the chromosomes of the nuclei in the gametes or reproductive cells.

It seems to me as great a fallacy to conclude that everything is adaptation, as to conclude that everything is mutation. The former view is often supported by the argument that if we knew more we should understand the utility of every character, however minute or unimportant it may seem to be. It follows from this that we can agree at least that there is no evidence hitherto discovered of the utility, or adaptive relation, or survival value, whichever term be preferred, of the majority of specific characters. And not only specific characters are of doubtful utility. It seems certain that many animals survive, not in consequence of their structural characters, but in spite of them. Metameric segmentation, for instance, characterizes all Arthropoda and Annelids, but no zoologist, I think, can prove exactly how this character is related to the conditions of life. Flexibility in other cases is obtained in other ways, and adaptation in the more specialized forms is attained by differentiation of segments or groups of segments primitively all closely similar. Metamerism seems to be the expression of an inner tendency, not something either imposed from without, or related to external conditions. In Echinoderms again, the possession of thousands of tube feet, each having a sucker at the end, seems to be an unnecessarily complicated and singularly ineffective means of locomotion.

On the other hand, consider the allantois, the respiratory membrane which grows out as a bladder from the gut and extends under the part of the shell which is over the dorsal side of the embryo. It is difficult to conceive of a mutation arising by a change in the 'genes' of the gut which should cause this growth of the allantois without any relation to the external oxygen. If it were so, the fact that it was 'adapted' for embryonic respiration would be a pure accident. The allantois occurs in all animals which develop within an eggshell, i.e. all reptiles and birds, or within the mammalian uterus, and does not occur in fishes or Amphibia. It is difficult to avoid the conclusion that the external oxygen was the cause or stimulus which originally caused the ancestral bladder to develop in the embryo into the allantois. There can be little doubt that the growth of the allantois is partly due to factors in the chromosomes, but in all probability it is also partly due in some way to the influence of the oxygen diffusing through the pores of the shell. So far as my knowledge goes, biochemists or other biologists have not yet devised experimental methods of testing this suggestion. Experimental research on development is, however, making great progress. Mr Julian Huxley has recently carried out with a lady colleague experiments on the local effect of temperature on different parts of the embryo of fowl and frog, and Speeman and others have shown that particular parts of an embryo act as 'organizers of development', and when grafted on to other parts cause special development of these parts. It would therefore probably be possible to devise experiments to test the local influence on growth of a local excess or deficit in the supply of oxygen to embryos.

The geneticists in general make their experiments chiefly on varieties of cultivated plants and animals, because it is found that wild species as a rule do not lend themselves so readily to Mendelian methods. My own view is that all these schools are right in their own sphere, and that there are two kinds of characters which in many cases can be definitely distinguished, namely those which, although constant in a very high degree and generally diagnostic of different species, have nothing to do with adaptation or utility, and on the other hand characters which are not merely useful, but more or less essential to the animal's existence, and which have definite relations by their functions to external stimuli. The adaptive characters are not as a rule limited to a single species, but are characteristic of whole divisions, such as orders and classes. The milk glands of Mammals are an example. They may have been originally evolved in a single species, but we have no proof or evidence that they were so. The truth is, in my opinion, that there are two problems or phenomena of evolution, the distinction between which is overlooked by the majority of biologists, namely, divergent evolution which gives rise to the differences between species and varieties, and which is due to the appearance of mutations having no direct relation to stimuli or external conditions, and adaptive evolution which gives rise to adaptations and is the effect of changes in stimuli, habits, and conditions of life.

An interesting example illustrating the relation of adaptive characters to species is the fish *Epibulus* *insidiator* belonging to the family Labridæ, which includes also our common British wrasses. Mr Tate Regan[1] states that Epibulus is closely related to *Cheilinus*, another genus of the Labridæ, with which it agrees in form, fins, scaling, dentition, etc., but from which it differs in the characters of the jaws and their connexion with the skull. The ascending processes of the premaxillaries are very long, the quadrate is a long slender bone movably articulated by its upper end to the lower ends of the symplectic and metapterygoid, and to the lower jaw at its lower end. The quadrate swings the lower jaw forward, and thus a long membranous tube is formed, at the end of which the mouth opens. There can be no doubt, although the actual feeding of *Epibulus* has not been seen, that its protrusible mouth is a special adaptation for the capture of prey, which presumably differs from that of *Cheilinus*. There are several species of *Cheilinus*, distinguished by slight differences of scales, number of fin-rays, etc., and in all probability, but for its peculiar mouth, *Epibulus insidiator* would have been placed in the genus *Cheilinus*. We seldom find a specific character specially adaptive, because, as in this case, when such a character occurs the systematist places its possessor in a separate genus. At the same time the example illustrates in a striking manner the difference between an obviously adaptive character, namely, the protrusible mouth of *Epibulus*, and the specific characters of the species of *Cheilinus*, the adaptive value of which is not evident. To assume that the specific differences and the adaptive structure of the jaws in *Epibulus* all belong to the same category, that all are adaptations, is in my opinion a mistake.

Prof. Morgan's view with regard to adaptation is

[1] *Morphology of a Rare Oceanic Fish, Stylophorus chordatus. Shaw*, Proc. Roy. Soc. B, vol. 96, 1924.

that the condition appeared first as a mutation or a result of successive mutations, and then the animal adopted habits and modes of life which were suited to its structure. In the published results of my own observations and experiments I have stated my conclusions that the asymmetrical structure of flat-fishes was the inherited effect of the modifications produced on the position of the eyes, the extent of the dorsal and ventral fins, and the loss of colour on the lower side by the habit of lying on the ground on one side. The question is whether the change of structure was the cause of the habit, or the habit produced the change of structure. In an article in the number of the *Yale Review* of July, 1924, Prof. Morgan opposed my conclusions, and in my opinion his arguments implied a complete misconception of the problem of what is called the inheritance of acquired characters, a misconception which is shared also by other zoologists. He stated that it was improbable that the asymmetry of structure in flat-fishes should have been caused by their habitual position, because the children of Chinese women whose feet have been artificially distorted for many generations do not appear to have feet different from those of other Chinese people. In reply to this argument there are many points to be mentioned. Firstly, artificial distortion is quite a different thing from a change brought about by muscular action and external stimuli affecting growth, and such distortions are possibly not inherited at all. Then the number of generations, in which the distortion or compression of the feet has been practised in a particular case is not known; classes are not permanent, families of the upper class of Chinese may descend to lower classes and cease the practice, while others may become rich and rise to a higher social level and adopt the practice. Again it would be necessary, not to examine young babies to ascertain whether there was evidence of heredity, but to examine after childhood the feet of Chinese girls whose ancestors had been subjected to the treatment for a great number of generations, and compare them with the feet of other Chinese girls whose ancestors had never followed the practice of binding the feet of their female babies. Such an investigation has never, so far as I know, been carried out by a competent anatomist on a sufficiently extensive scale. If only the evidence of new-born babies or of babies under one year of age were considered it might be maintained that the great length and strength of the human legs in proportion to the arms, and other chief points in the adaptation of the human body to the erect bipedal attitude and locomotion, were not inherited, for these adaptive features are almost absent in the baby and are gradually developed during growth. But even if the evidence in this case was satisfactory it would not be decisive, for the reason that the absence of perceptible hereditary effect of deformation continued during the period of Chinese civilization is no proof that the distortion which is hereditary in flat-fishes was not due to the effects of the change of position repeated in each generation since Eocene times. What is the period of even the whole of human evolution compared with the whole of the Tertiary period?

Prof. Morgan's own theory of the evolution of flat-fishes is that they originally became asymmetrical spontaneously before any change of natural position had occurred, simply by mutation, which means by more or less suddenly appearing changes of structure arising from changes in the reproductive cells or gametes independent of any external influence, and then finding it inconvenient to have two eyes on one side and none on the other they adopted the habit of lying down on one side on the ground so that the two eyes were on the upper side.

The concept of mutation implies in this case that it was a simple accident that pigmentation was absent from the 'blind' or eyeless side, and a fortunate accident that the dorsal and ventral fins were extended along the greater part of the edges of the body, where they are adapted to produce the undulating movement required by the new position of the body.

Another remarkable case which it seems impossible to harmonize with the concept of mutation is that of the males of the oceanic angler-fishes of the sub-order Ceratioidea. In these fishes the only males known are dwarfs in size in comparison with the females, and are not merely parasitic upon the latter, but permanently united with them in most cases by concrescence of the skin at the extremities of the upper and lower jaws in the male, with a projecting papilla of the skin of the female. The digestive organs in the male are vestigial, and, according to Mr Tate Regan,[1] who first showed that the small attached fish were the males, the blood-vessels of the two fish are continuous through the tissue by which they are connected. In *Edriolychnus schmidti*, of which the mature female is only 62 mm. or 2.48 inches, the male, a little over $\frac{1}{2}$ inch long, holds on by toothless jaws to a papilla of the skin of the female on the inner surface of the gill-cover. It is probable therefore that the fusion of dermal tissue between female and parasitic male in the other cases was the direct result of the relations seen in Edriolychnus. It is easy to understand how the evolution of the condition could have taken place gradually as the direct effect of the males holding on to the skin of the females in seeking satisfaction of the sexual

[1] Tate Regan, C., F.R.S., *Dwarfed Males Parasitic on the Females in Oceanic Angler-Fishes.* Proc. Roy. Soc. B., vol. 97, 1925.

instinct. We cannot completely explain how the sexual attraction was evolved in fishes, in which fertilization is external and the sperms simply escape from the body into the water when mature. But we know that the sexual attraction exists in Teleostean fishes. If we are to regard the beginning of the habit of holding on to the skin of the female by the jaws as a mutation, it was evidently a mutation due to sexual attraction, and not an unconditioned change in the chromosomes of the gametes. And it is much more reasonable to believe that the reduction in size of the male, the degeneration of its digestive organs, and the concrescence of blood-vessels, are the direct physiological consequences of the habit of holding on to the female than that they were mutations independent of the habit.

The argument from the non-inheritance of mutilations is still sometimes advanced against the possibility of Lamarckian inheritance, or the inheritance of effects produced by external stimuli. The case of circumcision is mentioned as an example, but here the same reply can be made as in the case of the feet of Chinese women. The case has not been investigated by a competent human anatomist or medical man. It is merely asserted that circumcision is still required in spite of the ages during which the rite has been performed. But to test the question it would be necessary to compare the average development of the prepuce among the offspring of the circumcised, after those offspring had grown up, and compare this average with a corresponding average among offspring of the uncircumcized, say at the age of twenty-one years for both cases. For there is evidence that Lamarckian modification is associated with recapitulation, and shows itself at the later stages of development and not at the beginning, in which respect it differs from mutation, or gameto genic variation. The amputation of tails of lambs and puppies is also cited—it was a favourite argument of Weismann—but here, as in the other case, the best reply is that amputations should be excluded from the discussion, as not being a process of the same kind as the action of external stimuli on growth and development to which the Lamarckian theory refers.

Another argument of Prof. Morgan's is that the Lamarckian theory is contradicted by the fundamental principle of Mendel's law of heredity. He maintains that the segregation of characters in the F_2 generation, for instance the production of pure white mice from hybrid grey mice, themselves the progeny of a cross between grey and white, shows that the factor for white is entirely unaffected by the grey bodies of the hybrids which carry that factor. This argument is in my opinion a fallacy. There is no evidence that the grey colour of wild mice is itself the result of special external stimulus. It may be urged that the grey pigmentation of the skin, although due to the constitution of the chromosomes in the ovum from which the individual was developed, must give off hormones which should on the Lamarckian theory affect the factors for white in the chromosomes of the reproductive cells in the same individual. This is evidently Prof. Morgan's idea. There are two points to be considered on the other side: (1) that we do not suppose any perceptible effect to be produced in one generation; (2) that the factor for white in an albino mouse implies the absence of something which is required for the development of pigment, so that it is impossible for this factor to be made to produce pigment by the influence of the pigment in the hybrid. But is it certain that characters always emerge in the pure state in the second generation from a Mendelian cross? I have published details [1] of a cross between the white Silky fowl and a black-red race, in which the recessive white which emerged was not pure white but had a slight amount of pigment, which increased in subsequent generations when the modified white was repeatedly crossed with the heterozygote form. I do not assert that this was due to the influence of the coloured plumage on the reproductive cells, but it was evidence of incomplete segregation, while, according to Mendelism, segregation is always complete.

[1] *Mendelian Experiments on Fowls.* Proc. Zool. Soc., 1912 and 1922.

CHAPTER IV

RECAPITULATION AND MUTATION

It cannot be maintained that the earlier stages of an animal's development always reproduce the structure of its ancestor, or that the successive stages always repeat the stages of its evolution. Even the Victorian zoologists were aware that there were many exceptions to such a rule. Frank Balfour himself stated the general conclusion from embryology that the repetition of ancestral stages was liable to be abbreviated in embryonic development, and to be obscured by new characters in larval development. He summed up his discussion of the matter [1] thus : "There is a greater chance of the ancestral history being *lost* in forms which develop in the egg ; and of its being *masked* in those which are hatched as larvæ." He believed that variations favourable to the survival of the species were equally likely to be perpetuated at whatever period of life they occurred, prior to the loss of the reproductive powers. In embryonic development abbreviations took place because direct development is simpler and therefore more advantageous, and as the embryo is nourished by food yolk there is nothing to prevent characters which are of functional importance in a free existence from disappearing from the developmental history. In the larva, on the other hand, there is much more scope for favourable variations occurring, favourable that is to new modes of larval existence. Secondary characters

[1] *Comparative Embryology*, 1881, vol. ii, p. 299.

therefore according to Balfour are very numerous in larvæ, and there may be even larvæ with secondary characters only, as, for instance, the larvæ of insects in certain orders.

It is to be noted here that the departures from recapitulation are in Balfour's view new adaptations, for their existence is due to natural selection, to the fact that they are 'favourable to the survival of the species'. On the Lamarckian view, of course, they would be due to the influence of new habits and conditions of life in the embryonic or larval life respectively.

Adam Sedgwick in 1894[1] published a paper in which he maintained the conclusion that the retention of an ancestral condition in the series of embryonic stages indicates that this condition was formerly a larval condition—that is to say, was retained as a necessary adaptive character in a free-living larval stage of the animal after the new adult character had been evolved. Mr Sedgwick was led to this conclusion by considering the contrast between the development of gill-clefts and gill-arches in the embryos of all air-breathing vertebrates, reptiles, birds, and mammals, and, on the other hand, the entire absence of any trace in embryonic life of fore-limbs in snakes. Few if any naturalists would dispute the conclusion that the metamorphosis of Amphibia with respect to gill structures, lungs, and limbs represents the evolution of the terrestrial vertebrate from the aquatic, and it is evident that the development of gill-arches and gill-clefts in the embryo of the terrestrial vertebrate is a repetition of what occurs in the larval amphibian. The embryo of reptile or bird is in fact a tadpole enclosed in an eggshell and supplied with yolk, and there is no apparent reason why the gill structures

[1] *On the Law of Development commonly known as Von Baer's Law.* Quart. Journ. Mic. Science, vol. xxxvi, 1894.

should continue to develop, except the persistent effect of heredity: the structures are not adapted to any requirements of life within the egg, and the adult condition of heart and arteries, etc., could be reached by a much more direct course of development. The absence of recapitulation in such cases as the loss of the fore-limbs in snakes is due, according to Mr Sedgwick's view, to the fact that the character is adapted to habits and conditions which exist throughout the whole life of the animal after hatching, and the change has had a retrospective influence on the embryonic development, so that not even a rudiment of the ancestral limbs appears in the embryo. The Pythonidæ are an exception, having rudimentary hind limbs throughout life.

We have therefore, in studying changes in the course of development from a larval stage to the mature form, to consider not merely change of structure, but change of conditions of life to which the structure is related at each stage. Metamorphosis in such cases as that of the Amphibia is not merely a change of structure, but a change of adaptation. In deciding to what degree the larval stage repeats an ancestral form we have to compare it with the mature form of allied animals. Thus we can see that the branchial organs of the tadpole are essentially similar to and homologous with those of fishes, and we can only conclude that the fish-like ancestors of the Amphibia became air-breathers after they had developed the mature condition of the branchial arches and related structures which originally persisted throughout life. It has been argued [1] that in recapitulation there is no thrusting back of the adult form into a larval or embryonic stage, but merely a repetition of the larval stage of the ancestor. With regard to embryonic development this question has

[1] T. H. Morgan, *Critique of the Theory of Evolution*, 1916.

been sufficiently discussed above, in the case of the branchial arches and clefts of the embryo in the terrestrial vertebrates, but when we consider the origin of air-breathing vertebrates from the fish it seems to me impossible to doubt that the branchial apparatus of the amphibian larva was a permanent adult character in the ancestor. In such cases we are less likely to be misled if we keep in mind the repetition of the probable original evolutionary change, rather than the repetition of ancestral structures. We may consider what evidence there is of the change having gradually become earlier in the individual life ; but however early the stage at which the change occurs, the original character does not cease to be a repetition of an adult character, provided that it is in essentials similar to the adult character of unmodified forms most nearly allied. The Pleuronectidæ, or flat-fishes, afford a typical example. The larvæ are hatched in a symmetrical condition, similar in the most important characters to the larvæ of allied fishes, i.e. Teleosteans. It is true that the metamorphosis takes place very early, before the adult skeleton is fully developed, in fact, during its development, but we do not know whether the first steps in the change originally occurred at so early a stage, or at a later stage. But it is certain that the symmetry of the eyes and of pigment cells which we see in the larval flat-fish occurs not only in the larva of other Teleosteans, but persists throughout their lives. We have therefore not merely the recapitulation of larval characters, but of adult characters.

It is important to consider whether there is any evidence that mutations could give rise to, or have given rise to, changes of character similar to metamorphosis and recapitulation. It is certain that great numbers of the characters of domesticated races of animals and cultivated plants, characters which are investigated in Mendelian experiments, develop directly and not by transformation of the original character which was present in the form from which the variety is derived. I have in previous publications referred to the rose-comb and the single comb of the fowl as an example of this. The chick does not develop a single comb which later becomes a rose-comb. The rumpless fowl does not develop a tail which afterwards disappears. The white rabbit is never at any stage anything other than white. And so on with the characters of countless varieties of animals and plants. There can be little if any doubt that these characters arose as mutations in the course of generations under domestication.

But there may be cases in which characters which have no known relation to habit or conditions of life, and which appear to have no function or utility, are not developed directly in the earliest stages, but appear first in later life by a change from a different character in the young. There is a whole class of cases in birds, fully considered by Darwin,[1] in which the young of both sexes have plumage of one colour, the adults of both sexes plumage of a different colour: e.g. both sexes of the scarlet ibis are alike scarlet, while the young are brown. But in these cases there can be no doubt that the adult plumage is sexual, and therefore is in a sense adaptive, and not to be classed with ordinary mutation.

We have to consider, however, the special researches on successive generations of natural species in captivity, in which mutations have been observed to appear for the first time. In animals the most important of such researches are those of T. H. Morgan on the fruit-fly Drosophila. Now, more recently, a species of the Crustacean Gammarus, *G. chevreuxi*, is becoming under

[1] *Origin of Species*, 2nd Edition, 1885, p. 480.

the long-continued and extremely careful cultivation of Mrs Sexton at the Marine Biological Association's Laboratory at Plymouth, almost as well known and classical in genetics as Drosophila. The first mutation observed in this species was recorded in 1913, but results of a more thorough investigation of its genetic history was published in 1916.[1] The mutation was the appearance of individuals with eyes of red colour instead of black. In the number of *Nature* for February 6, 1926, appeared a letter stating that recently three more mutating stocks had been obtained from different pairs of normal black-eyed individuals obtained directly from the natural state, and bred quite separately from the original stocks in captivity. In one of these stocks a new mutation appeared, namely, individuals without any of the normal body colour, and with white (unpigmented) eyes. These animals with white translucent bodies at the time of hatching were of two kinds, distinguished as the 'permanent white' and the 'changeling white'. The latter are like the permanent whites at the time of hatching, but rapidly develop colour as they grow, till in the adult condition it is impossible to see any difference between the changelings and ordinary red-eyed specimens: the bodies are green, the gonads and eggs dark green, the eyes bright red. The changeling whites arose from a mating of white female and red male. The change in the course of development, therefore, cannot be regarded as an example of a mutation which involves a metamorphosis; it is merely a change of dominance. The final condition, as described, is similar to that of the male parent, while at the time of hatching the young resemble the white mother. It

[1] Sexton and Wing, *Experiments on the Mendelean Inheritance of Eye-colour in the Amphipod, Gammarus chevreuxi.* Journ. Mar. Biol. Assn., vol. xi, no. 1, 1916.

cannot be suggested that the development of a character in the adult which is absent from the young always arose in this way from crossing.

Prof. Walter Garstang, of the University of Leeds, has published an ingenious and interesting criticism of the conception of recapitulation[1] expounded and maintained by Haeckel. His own view is based on the assumption, adapted from T. H. Morgan, that evolution has been due to the natural selection of mutations, and he entirely ignores the possibility of the direct influence of habits and conditions of life in producing structural adaptation. He is impressed with the observations of Morgan on mutations in the fly Drosophila, but has apparently paid little attention to the recent advance in knowledge concerning the action of hormones.

Garstang tells us that phylogeny has never been a direct succession of adult forms, but a succession of autogenies or life-cycles. Zygote (fertilized ovum) directly produces zygote in each generation, and each zygote develops by a series of changes either into a similar, or into a 'mutated' adult form. Ontogeny, he states, does not recapitulate phylogeny: it creates it. This is merely going back to Weismann. We all know that the adult body does not give rise to the reproductive cells, but merely contains them. We all agree that the characters of the adult are due to the properties of the fertilized ovum; according to the Morgan school, to particles of the nuclear chromosomes in the zygote. These characters may be the same as in the parents, or they may be different. The question is the origin of the differences.

Garstang, however, admits that the parallelism between ontogeny and phylogeny is undeniable. But he proceeds to state that the former adult structure is

[1] W. Garstang, *Recapitulation Theory*. Linn. Soc. Journal, vol. XXXV, 1922.

not retained and succeeded by the new, but is replaced by the new, and what persists is the larval state of the ancestor. For example, the tadpole lacks dermal skeleton, both scales and fin-rays, paired fins, and biting jaws, which the adult ancestral fish undoubtedly possessed. The tadpole, in fact, is not a modified reproduction of an adult fish ancestor, but a modification of the larva of that fish ancestor. Nearly all Garstang's argument, it seems to me, is directly derived from T. H. Morgan.[1] But the important point is that the gills, gill-slits, and branchial arteries of the tadpole, although modified in smaller details such as the gill processes, are essentially similar to those, not merely of the larval fish, but of the adult fish. When the tadpole becomes a frog the gill-clefts close up, and the gill arches become much reduced. The respiratory organs of the adult fish are recapitulated, not merely those of the fish larva. If one biologist insists that the young stage of the modified animal is not completely similar to any possible adult ancestor, while another insists that in important characters the young stage is similar to the adult ancestor, they will never reach agreement. Both are right. But to me the important point is to consider adaptive characters and the conditions to which they are adapted, not all the other details of structure.

Prof. Garstang takes the flat-fishes as another example. In answer to an article by Prof. MacBride he writes that the latter nowhere shows that the larvæ of flat-fishes resemble the adults of other Teleostei more closely than they resemble the larvæ of those fishes. The important point is that in symmetry of eyes, and of pigmentation, and in the anterior limit of the dorsal fin, the larvæ of flat-fishes are similar to the *adults* of ordinary fishes and different

[1] See T. H. Morgan, *A Critique of the Theory of Evolution*, 1916.

from adult flat-fishes. Here again it is not a question of comparing larvæ and adults as individuals, but their characters, and adaptations. Let us admit that the larval flat-fish resembles in its chief characters, especially in symmetry, the larvæ of other Teleosteans. The fact remains that the adult flat-fish in its asymmetry is different from other adult Teleosteans, and also that the larva and the adult flat-fish are adapted to different orientations in their natural positions, while the adult of the ordinary Teleostean retains the same orientation and the same symmetry as the larva. The fact also remains that in the flat-fish the symmetry of the larva changes into the asymmetry of the adult. The symmetry of structure is therefore recapitulated in the larval flat-fish, and the question is whether the change of symmetry in development is of the nature of a mutation. So far as I know no mutations in any way analogous to the change in position of the eyes in the development of a flat-fish have ever been described.

Another example discussed by Garstang is the down feather of young birds compared with the contour feathers of the adult. The typical down feather is an open hollow tube splayed out at its free extremity into a ring of barbs of equal size, and he asks if this is to be regarded as a phyletic stage in the derivation of feathers from scales. The chick stage, he asserts, throws no light on pre-avian adult ancestry, or the way in which scales were transformed into feathers. I have elsewhere[1] given reasons for concluding that reptilian scales never were converted into feathers, the latter having a quite different structure and mode of development, and therefore there could be no recapitulation. So far I agree with Prof. Garstang that the development of the feather shows no recapitulation of scale-

[1] *Hormones and Heredity*, 1921, p. 228.

like structure, and feathers very possibly originated as a mutation which was not adaptive.

With regard to wingless females in certain species of moths, which Prof. Garstang regards as adaptive to the absence of foliage in the winter season, he does not consider the question why a mutation should arise in the females only, and what prevents the winglessness being transmitted by heredity to the males. He does not consider that there could be no recapitulation in this case in the imago, because the imago undergoes no change. If the wings are more developed at an earlier stage, evidence would have to be sought in the pupa or in the imaginal discs of the caterpillar, and that has not yet been done.

Prof. Garstang cannot so easily explain away the gill-arches and clefts of the embryo of terrestrial vertebrates, but he remarks that a complex double circulation that has been elaborated along channels determined by a branchial circulation cannot readily depart from the phyletic stages of its formation. This is really admitting the doctrine of recapitulation in different words. But this truth applies equally well to the metamorphosis of the tadpole. It seems to me that in the ovum surrounded by the egg-shell or enclosed in the uterus, the adult structure might have been reached by a mutation towards direct development, and that we have here an example showing how the attempt to explain adaptation and recapitulation by mutation completely breaks down. Why should a complex double circulation be influenced by channels determined by a branchial circulation? According to the conception of mutation a single aortic arch on the left side might just as well have developed directly in the mammal instead of being the remnant of a symmetrical system of branchial arteries.

We see here in relation to recapitulation the same defect which seems to me to be present in the treatment in modern biology of other subjects. No attempt, or if any only the most rudimentary, is made to show how the new results harmonize with or explain the old problems. Larval metamorphosis is a change from adaptation to one mode of life to adaptation to another. The frog or newt changes from aquatic respiration and locomotion to atmospheric respiration and terrestrial locomotion. In the larval state it resembles not merely in structure or characters, but in relation to its mode of life, the fishes, and the logical conclusion is that it has been evolved from ancestors which were fishes in adaptation to aquatic conditions. It changes into a form which is adapted to terrestrial existence by a gradual metamorphosis of organs. The barnacle is hatched as a free-swimming form resembling a crustacean, a larval crustacean it is true, but adapted to an active life like the larvæ of other Crustacea. It attaches itself by antennary glands to floating timber, or to rocks or shells, or to a whale, as the case may be, and loses all resemblance to a crustacean, except its segmented appendages. It seems to me impossible to harmonize these facts with the concept of mutation, the essential idea of which is that it arises from a change in a chromosome of the gamete which is independent of external influence. The concept of mutation therefore has no relation at all to the function of a structure, or its adaptation to external conditions. The concept is powerless to explain why a pouch on the œsophagus in the ancestral fish should become filled with air in the frog and carry on the respiratory function. The facts of mutation do not exhibit any resemblance to or analogy with the gradual changes by which the barnacle or the Ascidian after attachment become adapted to the sessile life, gathering nourishment from the minute organisms in the water. Prof. Morgan's view is that the flat-fish, having become asymmetrical by one or many mutations, although the change which takes place in development does not resemble mutation, found it advantageous or necessary to lie on one side on the bottom. Similarly we must suppose, according to his view, that the ancestral fish-like amphibian, having by mutations, quite uninfluenced by conditions, developed lung-pouches for breathing air, its gill-slits having gradually closed up and its gill-processes disappeared, found it advantageous to adopt the terrestrial mode of life, and atmospheric respiration. Of course this involves the assumption that the same mutations might with equal probability have occurred under conditions which offered no possibility for the ancestral mutated fish to leave the water for the land, but there is no evidence that such mutations ever occurred except in the border region between aquatic and terrestrial conditions in fresh water. The assumption of the mutationists is that the adaptation, i.e. the harmony between the structures and their functions, was brought about by selection, which in this case would only occur in the border region mentioned. But the idea of the selection of mutations quite undetermined by conditions is difficult, or impossible to reconcile with the fact of a gradual structural development corresponding with a continuous change of conditions. The idea of mutation is discontinuity, the fact of metamorphosis is continuous change. Moreover, in the case of amphibian metamorphosis, as in other similar cases, there is another argument against the mutation theory, namely, that the metamorphosis can be, and in nature often is, influenced by change of conditions, a low temperature and abundance of oxygen causing a prolongation of the larval life, or, as it is technically termed, neoteny. It might be suggested that the metamorphosis is not in that case hereditary, but the fact is that in many examples of metamorphosis both heredity and influence of conditions influence the process, which is another objection to the mutation theory of adaptation.

The action of hormones, that is, of the soluble chemical compounds in the body, affords a probable explanation of the phenomena of recapitulation and metamorphosis. We know that the air-bladders of bony fishes have been derived from lungs and not vice versa. In some early geological period fishes living in swamps or shallow fresh waters where oxygen was deficient, probably in the tropics, developed pouches from the gullet into which air was gulped to supply the oxygen which the gills were unable to obtain. The tadpoles of common frogs and other Amphibia repeat this change in the course of individual development in each generation. As the lungs develop, the gills diminish, the atmospheric respiration increases as the aquatic respiration decreases, until the animal breathes air only and the gills and gill-slits entirely disappear. Not only does this metamorphosis take place in every individual air-breathing amphibian, but in every terrestrial vertebrate—reptile, bird, or mammal—snake, chick or man; gill structures and their corresponding blood-vessels are developed in the early embryo with an arrangement corresponding to that of an adult fish, and the adult structure of heart and blood-vessels and other organs is developed by a gradual change from the fish-like condition which occurs in the early stage.

On the theory that this change of structure was the direct effect of the change of conditions, that is, of the reaction of the organs and tissues, heart and blood-vessels, to the change from aquatic to atmospheric respiration, we can understand the recapitulation in the hereditary development. The original change at every stage of evolution took place either in adult life, or at a stage subsequent to a period in which the young animal was aquatic and provided with gills. There can be no doubt that in the tadpole the tendency to the change is now inherited, but how can it be inherited in such a way as to take place after the earlier stage, instead of developing directly from the ovum? The reply is that the original modification, due to the breathing of air, took place at a late stage of life when the sum total of the hormones in the body was different from that which was present in the earlier stage. The changed structures gave off hormones which affected the chromosomes in the reproductive cells in such a way that they tended to reproduce these changes of structure in the next generation. But this took place in the presence in the body of a certain hormone complex by which the reproductive cells were bathed and permeated. Therefore not until this same hormone complex was present in the individuals developed from these reproductive cells would the inherited effect appear.

This theory is supported by what has been recently discovered concerning the influence of thyroid secretion on the metamorphosis of tadpoles. We may consider the thyroid secretion as the chief constituent of the hormone complex above mentioned. The modification was first produced when a certain amount of thyroid secretion was being formed, assuming that in the earlier stages less of this secretion was present. The hormones from the modified gills, lungs, etc., would act on the chromosomes of the reproductive cells in the presence of a certain amount of thyroid secretion, and the organs of the individuals developed from these reproductive cells would only exhibit the inherited tendency to change in the presence of the same or a similar amount of thyroid secretion. This theory is strongly supported by the fact that administration of an additional amount of thyroid gland from another animal, e.g. sheep, as food to the tadpoles, causes metamorphosis to begin almost immediately. I have not heard of any suggestion in explanation of this fact on the theory of mutation. In considering the beginning of this evolution we must suppose that, just as in the development of the frog and other Amphibia at the present time, the conditions themselves underwent a seasonal change. If the deficiency of oxygen in the water were a permanent condition the young larvæ with gills would be unable to carry on aquatic respiration, and then either the animals would have become extinct, or some change of development without metamorphosis would have become necessary. But doubtless the original conditions were similar to those in which Amphibia and lung-fishes now live, i.e. either a change from a cooler and more rainy spring to a hotter and drier summer in temperate climates, or from a rainy season to a dry season in the tropics. The development of reptiles, from which birds and mammals are descended, is due to the storage of yolk in the ovum, and the enclosure of the tadpole stage within the egg-shell, together with the evolution of still another method of embryonic respiration ; but the recapitulation still continues, the gill structures are developed in the early stage of the embryo, although now entirely without function. The value of a theory depends on the degree in which it explains the phenomena to which it is to be applied. The mutation theory affords an explanation of diagnostic characters which have no adaptive function or relation to habits and conditions of life. With regard to adaptation and recapitulation, any impartial thinker must come to the conclusion that mutation affords no explanation, and that recent discoveries give increased support to Lamarckian principles.

INDUCED MUTATIONS

The conception of a mutation among geneticists, especially those of the Morgan school, is that it is a change of structure in the individual corresponding and due to a change at one particular portion of a chromosome, a gene. Nothing is known of the cause of such a change, but it is considered certain that it is not the effect of any particular external stimulus or condition. On the other hand, other biologists believe that there is evidence of changes of structure, in some cases hereditary, which are caused by external conditions, not affecting all individuals in the same way in different degrees, but giving rise to abnormalities in some individuals. It has even been maintained that all mutations are really due to some influence, either of a deleterious kind or otherwise, of external conditions especially affecting the reproductive cells or the early stages of development. Changes of this kind, whether real or hypothetical, may be called induced mutations, and are to be carefully distinguished from spontaneous mutations on the one hand, and somatic modifications on the other.

We may consider first the experiments of Dr Heslop Harrison and Mr F. C. Garrett[1] on the origin of melanism in certain moths. Lepidopterists have long noticed an association between melanism in certain species of moths and the conditions prevailing in highly industrialized areas. A dark coloration may occur as an individual variation, or as a distinct variety in various species of moths, but it has been observed both on the Continent and in the British Islands that melanic individuals in certain species have become more and

[1] Harrison and Garrett, *Induction of Melanism in Lepidoptera.* Proc. Roy. Soc., B, vol. 99, 1926.

more common as rural conditions were replaced by manufactures involving factory chimneys and contamination of the air by smoke and other fumes; while in agricultural districts melanic specimens are rare or entirely absent. It seemed probable that the melanism was due to mineral substances taken in by the caterpillars with their food and derived from the impurities thrown into the atmosphere from chimneys or chemical works. Experiments were therefore made (1) by feeding the larvæ of non-melanic strains on food-plants gathered from areas where melanism was prevalent, (2) by feeding similar larvæ on food-plants artificially charged with impurities found to be present in or on the foliage of plants in manufacturing districts. The salts with which the food was charged were lead nitrate and manganese sulphate, separately in different experiments, lead and manganese compounds having been found by direct chemical analysis to occur frequently in factory smoke, and in or on contaminated foliage in manufacturing districts. In the experiments freshly-cut twigs of hawthorn were placed with their cut ends in a solution of one gram per litre of the salt for 24 hours, and then placed in the feeding cages with their ends still immersed in the solution. The larvæ ate the leaves under these conditions readily, and analysis had previously shown that after absorption of the solution for 24 hours all the leaves of the twigs contained some of the salt. The species used were *Selenia bilunaria*, Esp., *Tephrosia bistortata*, Goeze, and in some preliminary experiments *T. crepuscularia*, Bkh. The first species, *S. bilunaria*, called in English the Early Thorn Moth, is quite common, but no melanic form has ever been captured in the wild state. Apparently the species does not occur around Newcastle, South Northumberland and North Durham, where the experiments were carried out. The following is an example of the experiments made. A small batch of eggs was laid by a single female *Selene bilunaria* from Sussex in July, 1921. The larvæ were hatched in August and fed on uncontaminated hawthorn. Nearly 70 pupæ were obtained, and 59 moths (26 ♀♀ and 33 ♂♂) emerged in 1922. Two of these were paired, and the larvæ produced again fed on hawthorn. These became moths in June and July, and there were no melanic forms among them. Pairings were made and two small batches of about 60 ova each were taken and divided, half to serve as control, the other half fed in the one case on hawthorn twigs charged with lead nitrate, in the other on similar twigs charged with manganese sulphate by the method described above.

The results in the lead nitrate experiment were as follows. The controls were inbred for three generations and produced no melanics. The larvæ which had lead in their food became moths in the spring of 1923, and also showed no melanism. But the summer broods derived from these (there are, it will be seen, two broods in the year, the moths emerging in spring and again in June and July) contained melanic specimens for the first time. The first family (AL 1923), L meaning treated with lead, and A the first family to become moths) consisted of 27 moths, of which one male was black. BL 1923 consisted of 31 moths, of which two males were black.

The melanic male of AL 1923 was mated with a light female of BL 1923, and the larvæ obtained fed on untreated hawthorn. The F_1 generation consisted of 26 moths all normal, no melanics, showing that if there was heredity, melanism was a Mendelian recessive. Inbreeding from these moths, 93 F_2 moths were obtained, 70 normal and 23 melanic, a close approximation of the 3 : 1 ratio. These melanic F_2 specimens were necessarily, according to Mendelian principles, homozygous, inheriting melanism from both parents. Therefore if mated together their offspring should be *all* melanic, and this was actually the case with the exception of two males of the normal light colour in one family of 75.

In the case of *Tephrosia crepuscularia*, larvæ imported from Kent, where melanism in this species is not known, were reared on wild plants at Birtley in the Newcastle area, and yielded 23 moths, of which one female was black. This was paired with a normal male from Staffordshire, and *all* the progeny were black, the melanism in this case behaving as a Mendelian dominant instead of a recessive. But the larvæ of this species were difficult to rear, and no later generations were obtained. Many other experiments with the other two species are recorded in the paper, all agreeing with the example above summarized. The next question which arises is whether the dark pigment contains any of the elements in the salts swallowed, though this seems improbable in view of the fact that the melanism is inherited when the administration of the metallic salts is discontinued. The writer has seen Dr Heslop Harrison's specimens showing the pedigrees and the heredity, and they are very remarkable, the contrast between the melanic and the normal specimens being very conspicuous.

EXPERIMENTS ON THE EFFECTS OF INJECTION OF CYTOLYSINS

It has been found by physiologists that as antitoxins can be produced in an animal's blood by the injections of toxins derived from the microbes of infectious diseases, so the injection of the serum from the blood of one animal, e.g. the horse, into, e.g. a rabbit, develops a substance in the rabbit's blood which, when added to some horse serum in a test tube, precipitates part of the proteins in that serum. Similarly, injection of blood corpuscles will produce something in the blood of another animal which will destroy and dissolve the blood corpuscles of the same origin as those injected. Substances having this property are called hæmolysins, or blood-solvents. Similarly, the injection of a particular kind of cells into the body of a living animal is stated to produce a substance in that blood which is able to dissolve the same kind of cells. In this case the substance produced is called a cytolysin, or cell-solvent. There is thus a general principle that the blood of the living animal is able to produce an antidote, not only to the toxins of the microbes of disease, but to other foreign substances derived from the living tissues of other animals, and hence these substances are called anti-bodies.

It occurred to two American biologists, Messrs M. Guyer and E. Smith, [1] that a cytolysin of this kind might not only destroy cells like those by which it was produced, but might influence specifically the material antecedents of such cells or tissue in the germ. Logically, the right way to test this idea would be to inject the serum containing the anti-body into male and female animals, and then to see if their subsequent progeny showed any deficiency in the organ or tissue containing the cells affected. The method adopted by Guyer and Smith was somewhat different. They selected the lens of the eye as the tissue to be affected, and rabbits and fowls as the animals to be used. Lenses from rabbits taken immediately after death were pounded up in salt solution, and injected into the

[1] Guyer, M., and Smith, E., *Some Prenatal Effects of Lens Antibodies.* Journ. Exp. Zool., vol. xxvi, 1918.

peritoneal cavity of fowls, where they would undergo absorption and thus give rise to an anti-lens substance in the blood. After four or five of such injections the fowl was anæsthetized by ether, and the blood obtained by decapitation, with all antiseptic precautions. The serum was then separated from the corpuscles by centrifuging, mixed with salt solution, and injected into one of the veins of the ear of a pregnant rabbit. The experimenters believed that the lens cytolysin was not likely to affect the lens of the adult rabbit, but might affect the lens of the fœtus. In their first series of experiments an albino female rabbit which had been injected several times with the anti-lens serum gave birth to seven young, in one of which the left eye was much smaller than the normal, and in this eye the lens was opaque. The individual in question was reared to the adult condition, mated with a normal rabbit, and its descendants bred for several generations. Some of these descendants showed eye-defects on one or both sides.

In a second paper[1] published in 1920 a number of other similar experiments are recorded, in which only albino rabbits were used. Many of the experiments failed; the rabbits either died or produced no young. In others, young were produced, but their eyes were normal. A few young were obtained which had defective eyes, and some of these survived. In one case a rabbit with markedly defective eye was son of a female which with the same mate had given a normal litter before being used for a serum experiment, and other females which had produced young with defective eyes were repeatedly bred to the same males after the serum treatment was stopped and never produced any more young with eye defects.

[1] Guyer and Smith, *Transmission of Induced Eye Defects.* Paper II. Journ. Exp. Zool., xxxi, 1920.

These results have not been confirmed by other experimenters. The work is troublesome and difficult, and takes considerable time. In every experiment several fowls must be injected with emulsion of fresh lenses, then the pregnant rabbits must be injected with the prepared serum, and after all the result is often negative, the rabbit either produces a litter with normal eyes or no young at all, because the treatment is very likely to cause abortion. In the course of the years 1923, 1924, and 1925 I carried through six experiments of this kind on female rabbits, some of which produced litters before or after the serum treatment as controls. In all these, complete copulation had occurred before the injections were commenced. Five females were used, one of which was grey, three were perfect albinos, and one was white with a little colour on nose and ears. Two complete experiments were made on this last. The albinos were mated with albino males. In only one experiment were young obtained after the injections of sensitized fowl serum, namely, Albino B ♀, which produced 7 young on April 2, 1925, after six injections. One of the young died; the others, examined on April 18, and subsequently, were found to have perfectly normal eyes. In four of the other experiments no young were produced at the end of the period of gestation, and in one of these obvious evidence of abortion was observed. In the remaining case the female died after an injection.

The number of my experiments is too small to be considered conclusive, but Messrs Julian Huxley and Carr Saunders communicated a paper at the meeting of the British Association at Liverpool in 1923, in which they stated that they had carried out experiments of the same kind on thirty female rabbits, and had obtained no positive results. The question to be considered therefore is whether the eye defects which occurred after the serum treatment in the experiments of Guyer and Smith were the results of that treatment, or were abnormalities arising from gametic defects quite independent of the injections. In support of the latter conclusion we have the small number of individuals in which the eye defect occurred in comparison with the total number born after the serum treatment, and also the fact that, according to the evidence of men experienced in rabbit-breeding, small and imperfectly developed eyes occur occasionally as congenital defects without any experimental treatment. Such spontaneous defects, like other abnormalities, are strongly inherited.

In 1926 I mated one of my albino females which had been injected in an experiment in the previous year, with a male which was one of the litter produced by Albino B ♀ after the serum treatment. The object of this was to see if without further injections any effect of previous injections would appear in the offspring. Six young were born and some of them died while young. In one which died at the age of two months the incisor teeth showed abnormal growth. The upper incisors had grown down to excessive length inside the lower, and so prevented the animal from feeding. The same abnormality had occurred in other cases, but had not been carefully examined. Obviously this defect could not be specifically due to anti-lens serum, and it is possible that the eye-defects which occurred in the experiments of Guyer and Smith were as unconnected with the serum injections as abnormal growth of teeth in my rabbits. This naturally suggests the question whether the evidence in favour of the production of melanism in moths in the experiments of Harrison and Garrett is stronger than that for the production of micro-ophthalmia in rabbits. On the whole we may say that the association of effect and supposed cause in the case of induced melanism in moths is closer than in that of defective eyes in rabbits. With regard to the general principles of the method of Guyer and Smith there are many points to be considered. One of them is the diffusion of substances from the maternal blood to the fœtal through the placenta. In order to pass through the cytolysin must be diffusible, and it is difficult to understand why it should affect only one fœtus in a litter, and still more the eye of one side and not the other. Again, if it affects the eye of the fœtus —because in the early stage of development it is less resistant—why should the injury caused be inherited? It must be supposed that the cytolysin affects the antecedent of eye or lens in the gametes of the fœtus, but there seems no reason why the gametes of the fœtus should be more susceptible than those of the adult. In the course of my experiments I tried injecting the anti-serum into both males and non-pregnant females, but obtained no evidence of effects on the subsequent progeny.

ABNORMALITIES OF JAPANESE GOLDFISHES

A good deal has been heard lately of the views of Gustav Tornier, of Berlin, on the origin of the extraordinary and somewhat grotesque abnormalities of Japanese Goldfish. The most striking of these peculiarities, occurring in various combinations in different specimens, are the shortened body with distended round abdomen, projecting 'telescope eyes', and much enlarged translucent veil-like tail and anal fin, divided into two lateral halves. The geneticist would naturally be inclined to regard these as originally mutations and would expect them to be hereditary. Tornier states that they, like various abnormalities in other animals, are originally due to abnormal external conditions to which the eggs and embryos have been exposed during development.

The literature of this subject is somewhat complicated. Tornier from 1896 to 1908 published a number of papers on the origin of various abnormalities in reptiles, Amphibia, and mammals. In 1908 [1] he published a preliminary paper on the origin of goldfish races. In this paper he states that the goldfish and its races are descended from the common *Carassius vulgaris*, and that the structural and colour characters of these races are not peculiar to them alone, but occur occasionally, at least in an incipient degree, in other species of fish, and have been produced by himself experimentally in embryos of frog and axolotl. Specimens with extreme abnormality have a kind of hood or outgrowth of skin which covers the head from the eyes backward: it may also entirely surround the eye on each side. The tail region may be much shortened and the mouth directed upward. Tornier then proceeds to state that the deformities of the goldfish races are due to the same causes to which he has previously attributed somewhat similar abnormalities, especially, distended abdomen, deformed vertebral column, shortening of face, and even albinism and melanism, supernumerary limbs, digits, and other parts, in frogs, axolotls, mammals and reptiles. The main cause is protoplasmic weakness, which he calls plasmamiosis, which appears in the embryonic development before hatching, for each race in the special part of the body affected. This enfeeblement of the protoplasm produces a tendency to abnormal absorption of water, because the cells are unable to prevent this absorption by the strongly hygroscopic cell products, and especially by the yolk. The swelling of the yolk is

[1] Gustav Tornier, *Vorlaüfiges über das Entstehen der Goldfischrassen.* S. B. d. Gesellsch. naturf. Freunde, Berlin. 1908, pp. 40-45.

called crocoplema. The protoplasmic weakness also causes slowness and feebleness of movement, called kinemargia. The right and left halves of the ventral (or anal) fin, and of the part of the tail below the urostyle, are originally developed separately and afterwards unite. When therefore the part of the yolk which lies between the double rudiments of these fins is much distended, the two halves are so widely separated that they cannot unite. I do not think that there is any basis for this statement in embryology, the rudiments of the tail and ventral fin do not appear until the tail has grown out, whether in frog, or in fish, as a single structure, and the only rudiments which are separated by the yolk are these of the paired fins.

The telescope eyes, according to Tornier, are due to yolk-swelling in the head rudiment, which drives the eyes from their normal relations to other parts of the heads, and thus they grow to gigantic size. In some cases the yolk-swelling behind the anus strongly presses on the rudiment of the ventral (anal) fin, which therefore atrophies. Thus all these abnormalities are attributed to yolk-swelling, though in some cases the abnormalities are in opposite directions, e.g. entire absence or great hypertrophy of the ventral fin. Other abnormalities, however, are attributed to another effect of protoplasmic weakness, namely, feebleness of movement of the embryo. In consequence of this the vitelline membrane is not sufficiently stretched and enlarged to give room to the developing embryo. In the races of highest degree of abnormality this is the cause of the shortened face and round head, the bulldog snout. The protoplasmic weakness which gives rise to the abnormalities was itself caused originally by deficiency of air in the water in which the fish were kept and bred. The goldfish inherits the normal *Carassius* form, but with it protoplasmic weakness of particular degree, and in particular parts of the body. Thus the specific protoplasmic weakness produces its specific yolk-swelling and feebleness of movement, and these determine its special deformities.

Tornier promises a fuller account of the subject at a later time, but so far as I have discovered this intention was never carried out. The only other paper by him which might be regarded as fulfilling his promise is one published in 1911[1] in the Annual Report of the German Zoological Society, but this is only a review of published researches on the influence of external conditions, of which Section II, Chapter 6 deals with Tornier's own work. He describes his first researches on the subject,[2] in which he experimented with eggs and embryos of frog and axolotl on the effects of deficiency of air in the water surrounding the eggs, and of solutions of cane sugar of 5 to 10 per cent. It was on the results of these experiments that he based his theories of protoplasmic weakness, yolk-swelling, etc., which he has applied to the explanation of abnormalities in all classes of Vertebrates. In considering the abnormalities of goldfish he refers to the preliminary paper discussed above, and states that after the publication of this paper he noticed especially that the abnormalities in the body cavity of goldfish, displacements and changes of form in the viscera, distortions and displacements of the swim-bladder, could be produced directly by yolk-swelling, likewise the bending up of the tail peduncle, in the extreme races, as well as their enlarged eyes. He gives, however, a different explanation of the telescopic eyes from that given in the former paper,

[1] Gustav Tornier, *Ueber die Art wie äussere Einflüsse den Aufbau des Thieres abändern*. Verhandl. der deutschen Zoolog. Gesellschaft. Leipzig, 1911.

[2] S. B. Gesellsch. Naturf. Freunde, 1904.

attributing them to the entry of water into the optic cup, and consequent distension of the eye-ball. He does not state that he has himself made any experiments on goldfish.

At the request of Tornier, Krezenberg enquired into the rearing methods employed for goldfish in China, and found that there was no question of selective breeding in that country. In the summer the fish were kept in the open air in ponds of 3 to 5 metres in diameter. They were much crowded, 500 to 1000 in each pond. In winter they were transferred to round earthenware vessels. All kinds and shapes were kept together. When Krezenberg asked the Chinese breeders whether they did not put similar forms together, they looked at him in astonishment and did not know what he meant.

Milewski, a fancier of goldfishes, and a supporter of Tornier's doctrines, in a paper published in 1917 [1] summarizes Tornier's views, and states that according to them the protoplasmic, or plasma-weakness in monstrous goldfishes, once acquired is inherited, but not the typical structural characters, and so arise to-day even under favourable, no longer unnatural, conditions, the well-known monstrous forms. He summarizes the literature, and among other publications cites Dr Doflein, of Freiburg [2], who states that in Japan the abnormal goldfishes abound everywhere in the basins of temples, castles, parks, and gardens. There are three chief types, called wakin, maruko, and ryukin, and innumerable intermediate and allied forms. Doflein describes a visit to a celebrated breeder. The fish were in tanks made of wood, on either side of a

[1] Milewski, A., *Ueber Tornier's Untersuchungen, etc., sowie Weiteres über experiment. Erziehen monströser Goldfischabarten.* Arch. f. Entwicklungsmechanik, Bd. 44, 1917.

[2] *Ostasienfahrt.* Leipzig and Berlin, 1906, p. 384.

yard surrounded by the walls of houses, and lit at night only by the windows of the breeder's house. There were thousands of goldfish of all colours and races; no separation or selection was practised.

Milewski gives important evidence concerning his own experience as a breeder and his own experiments. With regard to the enlarged, veil-like, double posterior fins, which to fanciers are among the most valuable features of the fish, he says that breeding two-veiled specimens (called in German 'schleier') together does not produce only veiled offspring, but in ordinary circumstances, hatching the spawn in the light, only about 10 per cent. of the offspring are worth anything from the fancier's point of view. When, however, he imitated Tornier's experiments by preparing a small glass vessel of water, by putting in aquatic plants such as Elodea, etc., and leaving it for a month in the dark so that the water was full of carbon dioxide, and then putting into it the spawn from a pair of 'schleier' immediately after it was shed, and still keeping it in the dark, he found that there was an absence of fungus on the eggs, a large number hatched, and 60 per cent. were good 'schleier' instead of a mere 10 per cent.

Tornier's statements and theories so far as they refer to the characters of cultivated ornamental goldfishes have been very thoroughly investigated by Dr Wilhelm Berndt,[1] professor at the Zoological Institute of the University of Berlin. He finds, what is generally admitted by breeders, that no distinct definition of varieties is possible, as intermediate conditions are common, and various combinations of the characters

[1] Berndt, Dr Wilhelm, *Vererbungsstudien an Goldfischrassen.* Zeitschr. f. induktiv. Abstammungs- und Verebungslehre, vol. 36, 1925.

occur. The Japanese distinguish three principal types—

Type I.—Ryukin. Body moderately slender, with swollen abdomen, form of head, high fins, and doubling of fins as in Japanese ideal type.

Type II.—Wakin. Body more slender than I; often approximating to the normal Carassius. Fins moderately long, doubling of anal and caudal.

Type III.—Maruko. Body short and stout; more so than I. Abdomen much rounded (the 'egg' of American; 'Eierfisch' of German culture). This type is favoured by breeders in combination with exophthalmia and atrophy of the dorsal fin, but there is no connexion with these characters.

The Americans have distinguished nine race-types, the Germans have three ideal types, normal goldfish, 'Hochflosser-Schleierschwanz', and 'Teleskopfisch'. Berndt then defines the character of colour, squamation, fins, eyes, and unspecific deformities. There are nine types of colour—the wild colour, red, silver, melanotic, and five combinations of these. Squamation ranges from normal to complete absence of both scales and opercular bones. Fins may be simply hypertrophied, i.e. extended, or, in addition, there may be complete doubling either of the caudal alone or of the caudal and anal. The dorsal, or rarely the caudal and anal, may be reduced. The eyes may be exophthalmic with axes directed upwards or forwards or downwards, without association with other characters. Melanophthalmia is a blue-black coloration of the iris. In addition, there are deformities of the vertebral column, and of the head of various degrees.

Berndt finds that there is no question of obtaining a 'pure race' of a certain type because the characters, if inherited at all, are inherited independently. It does not follow from this, however, as Berndt seems to think, that it would be impossible to obtain a strain which was homozygous for a number of well-marked characters, if they were hereditary. How far this is the case we shall see from Berndt's results. Berndt uses the word *preszbauch* for the swollen abdomen after the example of Tornier, although the idea which underlies the expression, namely, yolk-swelling, is not justified. This word *preszbauch* perplexed me considerably for some time, as it would seem to imply an abdomen diminished in size by external pressure, but apparently Tornier's idea was internal pressure from increase of contents, and therefore the word signifies a dilated or distended abdomen. Similarly the word *gedrungen* would seem to suggest compressed or contracted, whereas in reference to the body of the goldfish as used by Berndt it means shortened in length and increased in thickness. One of the first things mentioned by Berndt with regard to heredity is that the short swollen abdomen only begins to develop about twenty days after hatching, the young fish up to this time having the same slender form as the wild Carassius. The yolk-swelling theory of Tornier is therefore not applicable to the distension of the abdomen, the chief racial character of the abnormal goldfishes. Berndt also satisfied himself that the swollen abdomen contained neither water nor watery liquid, nor an enlarged air-bladder, though the latter as well as other organs were more or less displaced by the change in the shape of the abdomen. The three degrees of abnormal distension are not sharply separated, but Berndt reared offspring from seven matings of Ryukin × Ryukin, three of Maruko ×

Ryukin and one of Maruko $\times$ Maruko. In every case he found all three types among the offspring, and these were not distributed in numbers which would suggest any Mendelian interpretation. Whether Ryukin was bred with Ryukin or crossed with Maruko there was a majority of Ryukin in the progeny, but all the matings produced a considerable proportion of Maruko. There is, therefore, heredity, but no evidence of clear-cut segregation.

Berndt found a remarkable linkage (*Allianz* is his own term) between coloration and squamation. There are five types of chequer or tiger-marking, e.g. red marks on white ground or red and black pie-bald. These occurred originally in the true Japanese tiger-fish, which was also a veil-tailed fish, first imported from Japan in 1901. The combination scalelessness + tiger-coloration, apart from the comparatively slight degrees of variation, behaves as a single Mendelian factor, which is dominant over its absence. Berndt indicates the factor by the symbol H*y*, the recessive absence by *hy*. When the heterozygous F_1 ♂ was crossed with the female parent, Carassius colour, fully scaled, double caudal fin, i.e.

$$Hy\ hy \times hy\ hy$$

the offspring were

$$F_2 = 38\ Hy\ hy + 36\ hy\ hy$$

and no intermediates.

FINS.—Berndt finds that there are two hereditary characters in the fins, namely—

1. Hereditary hypertrophy of all the fins.
2. Hereditary tendency to doubling in the caudal and anal.

These two are not linked.

There are also two other characters which are not hereditary, namely—

1. Atrophy or complete absence, especially of the dorsal.

2. Deformities of fins, especially the caudal.

He considers that fin-hypertrophy is due to three pairs of factors represented as AA, AA, AA when present, their absence being represented by *aa, aa, aa*. The character is very rare in other aquarium fishes, but has been observed in the Golden Orfe. Hypertrophy of the dorsal does not occur without that of the other fins, but complete absence of the dorsal may be accompanied by any degree of hypertrophy in other fins.

The maximum height of the dorsal fin in proportion to the total length of the fish is 100 %, the minimum 10 %. Berndt paired two specimens with moderate length of fins, a male with a dorsal of 53.3 %, a female 54.2 %. He obtained 33 offspring of one year old. In these the range in height of dorsal fin was from 84 % down to 10.9 %. He arrived at his conclusion concerning the multiple factors concerned in this heredity by comparing the results in these 33 specimens with the expectation on the assumption of one pair of factors, two pairs, and three pairs. He finds the distribution agrees best with the assumption of three pairs of factors.

Berndt agrees with Tornier in attributing the doubling of ventral (anal) and caudal fins to the failure of the post-anal fin-folds to unite. The inner supports are also doubled, namely the interspinous bones of the ventral, and the hypural bones of the tail, but not the vertebræ. Short-finned comets, i.e. single-tailed fish, are not more frequent than long-finned.

Doubling occurs with both medium and low degrees of extension of fins.

At one time I gave a great deal of attention to the development of fishes, and do not remember any evidence that the ventral and caudal median fins arose in the embryo by the union of paired post-anal fin-folds, although one theory regards the ventral median fins as representing the union of the two lateral folds which give rise to the paired fins.

Tornier's view that the splitting of the post-anal fins is connected with the swollen abdomen is not confirmed by Berndt. The doubling can be recognized in quite young stages before the *preszbauch* is developed. Caudal duplicity shows a tendency to be recessive in relation to the normal. It is distinctly inherited independently of other characters, and may occur as a spontaneous mutation in goldfishes that have neither hypertrophied fins nor swollen abdomen.

In conclusion, Berndt gives the results of his experiments on the influence of conditions and reagents on the developing eggs. He repeated Milewski's experiment with entirely negative results: while the control experiment with part of the same spawn produced from 250 to 300 eggs, 74 young in good condition; the others, kept in the dark with plants for 6 days, were all killed by fungus except three, and these had only moderate development of fins.

Sugar solution killed most of the eggs, and the survivors showed no considerable development of *schleierschwanz* characters. Salt solution gave the same results except that it had a dwarfing effect. The action of alcohol was quite negative. Raising of the temperature had great effect in hastening development and the growth of the young. It had no effect on colour either in wild Carassius or on the cultivated races. The same conditions were tried on normal fishes, and mostly caused death, but two specimens with cane sugar solution developed distinct *preszbauch*, which only appeared after hatching. This last statement is important, for it tends to show that the distended abdomen may be due to solutes in the water, although not in consequence of absorption of water by the yolk, according to Tornier's theory.

Berndt tried crosses with the original Carassius and succeeded three times, obtaining altogether 167 offspring. The results were not essentially different from those of crosses of the artificial races *inter se*. The *preszbauch* was recessive, H*y* absolutely dominant, single tail dominant over double. Hypertrophy of fins crossed with original Carassius produced mostly intermediate sizes of fins. Melanophthalmia is linked with H*y*. Exophthalmia occurred occasionally as a mutation.

It is evident from Berndt's work that Tornier's views cannot be accepted. They are to a great extent speculations based upon insufficient foundation. He regards a weakening of the plasma as the primary cause of abnormalities, producing its effects in two ways: (1) by causing yolk-swelling, because the plasma is unable to prevent the imbibition of water, but of this he gives no satisfactory proof; (2) by causing weakness of movement of the embryo, in consequence of which the vitelline membrane in fish or amphibian or the amnion in mammal, is insufficiently stretched, and therefore there is not enough space for the limbs or other organs of the embryo to grow in. The actual abnormalities are thus, according to Tornier, mechanical results in the individual arising from the effects of the plasma weakness, not themselves inherited. The plasma weakness, however, caused by unfavourable conditions such as want of oxygen and impurities in the surrounding water, is more or less strongly inherited. Although his explanations of particular abnormalities are crude and unsatisfactory, there is, nevertheless, a possibility or even a probability that such abnormalities may be due to some weakening of that control of development or power of regulation which is possessed by the normal healthy ovum, and that this weakening may itself be due to unhealthy condition of life, and to the absence of normal stimuli and activity both in early development and at later stages of life. This is a field in which we have little knowledge.

The defects of Tornier's methods are nowhere more obvious than in his treatment of the subject of supernumerary digits, known technically as polydactyly, and union of digits, known as syndactyly. Starting from a suggestion of Zander that these abnormalities might be due to folds of the amnion which cut into the limb rudiments in mammalian and avian embryos Tornier[1] reasons that amphibian embryos and larvæ have no amnion, and yet Amphibia have sometimes supernumerary limbs or limb parts. Therefore, he thought the latter might be due to mechanical injuries. He accordingly cut in various ways the limbs of *Triton cristatus*, the common newt. In one case he cut off the three inner toes, leaving the first and fifth. Regeneration occurred, and in many cases an excessive number of digits were developed, sometimes from six to eight in place of the three removed. Logically it follows that polydactyly in newts and other Amphibia may be sometimes due to regeneration after accidental loss of digits. But Tornier regards this as proof that polydactyly in mammals is due to

[1]Tornier, Gustav, *Ueber Hyperdactylie, Regeneration und Vererbung mit Experimenten.* Arch. f. Entwicklungsmechanik, vol. iii, 1896.

injury caused by amniotic folds or constriction, although in mammals regeneration is very rare if not entirely absent. He describes cases of supernumerary toes in pigs' feet and entitles his papers *Origin*, or *Causes of Origin of Polydactyly in the Mammalia*,[1] although he knows nothing of the development of these toes, and apparently has never examined mammalian embryos to discover whether folds of the amnion ever do cause injuries to the limbs of the embryo.

[1] Tornier, Gustav, *Entstehungsursachen der Poly- und Syndactyly der Saügethiere*. S. B. Gesellsch. Naturf. Freunde, 1897.

Entstehung eines Schweinehinterfusses mit fünf Zehen, etc. Arch. f. Entwicklungsmechanik, vol. 15, 1903.

CHAPTER V

ACQUIRED CHARACTERS

It has been maintained that every character is in a sense partly acquired, since it is called forth by stimuli, and partly inherited because due to certain peculiarities of the fertilized ovum from which the organism was developed. A character according to this view is the resultant of two influences acting together during development, the germinal factors or genes as they are often called, contained in the chromosomes of the gametes or reproductive cells, two of which usually unite in fertilization, and the external conditions which are the stimuli necessary for development. This proposition has been adopted and defended by Sir Archdall Reid in the columns of *Nature* and elsewhere, by Sir Ray Lankester and by Prof. E. T. Goodrich, in his volume entitled *Living Organisms*.[1]

I think this statement, although verbally true, since an ovum would not develop at all in a vacuum, without light, at the absolute zero of temperature, is apt to mislead many biologists, and a far greater number of people who are not biologists. The distinction between effects of external stimuli, and effects of heredity, that is, characters predetermined in the fertilized ovum, especially in the nuclear chromosomes, is easily made. When a number of animals, or plants in a garden, are developing under

[1] E. T. Goodrich, F.R.S., *Living Organisms: An Account of their Origin and Evolution*. Oxford, Clarendon Press, 1924, p. 52 *et seq.*

the same conditions, obviously their differences are congenital, or gametogenic, i.e. they arise from the constitution of the reproductive cells which united to form the ovum, from which the embryo and the plant developed. In a greenhouse, at the same temperature and moisture, in the same soil, we can grow a large number of different plants. There may be very great differences, such as e.g. ferns and orchids, there may be specific differences such as different species of orchids, and there may be minor differences of varieties, and differences among individuals of the same variety. All these differences are evidently constitutional and not caused by any external differences, if there are none. On the other hand, if we take several individuals of the same variety and develop and keep them under different conditions we shall find that their characters are slightly different. If we take two children who are 'identical twins', arising in all probability by division of a single ovum, we find the greatest resemblance between them, they are of the same sex, their complexion, size, features are all similar, so that it is sometimes difficult even for their mother to distinguish one from the other. But set one to rowing or manual work, and the other to office work and sedentary habits, and corns will form on the hands of the first, not on those of the second. Send one to an open-air life in the tropics, and the other to an indoor life in foggy England, and the first will become sunburnt, the other pale. Let one take hard and regular muscular exercise, or undergo training as a boxer, and the other become an artist, taking only the gentlest exercise, and the muscles of the first will be larger and stronger than those of the other. In this case the difference of external conditions or functional stimulus corresponds to the difference of structure or character: the external condition acts as a stimulus producing a particular modification which would not be produced without it. Those who maintain the view quoted above hold that in these cases the ‘ germ plasm ’, in other words the ova from which the organisms affected arise, must have the power of developing the modifications produced, which is a truism, and therefore the modifications are partly inherited and partly acquired.

There is evidently a fallacy in this argument. Animals (nor plants) cannot live without oxygen, food, and warmth, i.e., some moderate temperature above freezing point, for life is impossible if the protoplasm is frozen. Different characters developed under the same conditions with regard to these requirements are not the resultant of inheritance on the one hand, and the influence of the environment on the other. For example, suppose we have some ducks' eggs, and some hens' eggs in an incubator, or even hens' eggs of which some were fertilized by a cock with a single comb, and some by a cock with a rose-comb, the hen mother having had a single comb. In the first case the ducks' eggs will develop into ducklings, the hen's eggs into chickens. The oxygen, warmth, and the yolk in the eggs were necessary for the development of both kinds of eggs, but they had not an iota of influence in determining that one egg should become a duckling, the other a chick. The special characters were entirely, not partially, due to the gametic factors, the external conditions only enabled them to show themselves in the fully developed young bird. Similarly in the other case all the chicks would develop rose-combs, and this shows that the special character owes no more to the yolk than to the oxygen or temperature, for the rose-comb was determined by the spermatozoon which contributes to the fertilized ovum nothing but nuclear chromosomes.

Part of the fallacy, then, in the statement here considered lies in the application of the term 'stimuli' to the normal conditions of development. If the latter are to be called stimuli at all they are stimuli to the development of the organism, not stimuli to the production of any particular character, as functional exercise is a stimulus to the growth of a muscle, or sunlight to the production of pigment in the human skin. In the case of a bird's egg an increase above the ordinary atmospheric temperature is a necessary stimulus to development both for a sparrow's egg and the egg of an ostrich. But suppose we consider the egg of a frog, it develops without any special increase of temperature, at the same temperature at which the mother is living, and which has nothing at all to do with the fact that the egg develops the characters of a frog and not those of a toad, nor in determining whether the frog developed is a specimen of *Rana temporaria* or of *Rana esculenta*. The *characters* of the frog developed depend entirely, and not partially, on the parentage of the egg—that is, on the factors or genes contained in the egg.

Another part of the fallacy lies in taking the term 'acquired character', which is a special technical term with a special meaning, and using it in an entirely different sense taken from the general meaning of the word 'acquired'. Because characters as such are not present in the fertilized ovum, but only appear as the result of development, therefore it is said they are acquired. The proper term is 'developed', and in biology the word acquired is applied to characters which are different from those due to normal development, and which are determined by special external stimuli, and absent when the stimuli are absent. It has been well said that the ideal in science is to define all terms and prove all propositions. If the same term is used with different definitions by different biologists the science of biology becomes impossible. It is reduced to an interminable dispute about words. Prof. Goodrich writes that we cannot point to this or that bodily or mental structure and say this is acquired, that is not. According to this, the colour of a man's eyes, i.e. of his iris, whether blue or brown, for instance, is as much acquired as blisters or corns on his hands caused by rowing or handling of tools. The fact is that the colour of the iris is determined by the properties of the fertilized ovum and cannot be altered by any external stimulus acting on the individual at any stage of life, while blisters followed by corns can be developed in any individual by a few weeks' rowing practice—at least if the hands had not been hardened by manual work before.

Prof. Goodrich continues : "Characters being of the nature of a response must necessarily be produced anew at every generation. The characters of an organism are but the sum of its past responses". It seems to me that the last sentence is inconsistent with the first, and in itself would admit the whole of the Lamarckian doctrine, which Prof. Goodrich entirely rejects. If the responses are produced anew at every generation, how can they be 'summed'? This could only happen if the response, such as epidermic hypertrophy produced by mechanical friction, were partly inherited, so that the stimulus in subsequent generations produced a greater effect. If the sentence means that each character is one response and the 'sum' is all the characters together, then one must ask what are the several and distinct stimuli in the conditions of development to which the characters of *Rana temporaria* are responses. The same question applies also to the following sentence from Prof.

Goodrich's volume: "For a character to reappear in the offspring it is essential that the germinal factors and the environmental conditions which co-operated in its formation in the ancestor should both be present. Inheritance depends on this condition being fulfilled".

We take again the egg of the frog and that of the toad developing in the same water at the same time under the same conditions. In what way did these *same* conditions co-operate in the formation of the *different* characters of the toad and the frog? Or to avoid the possible complication of the habits of the two animals during metamorphosis we may take the case of the duck's egg and the hen's egg in the same incubator. Here there is no doubt that a duckling hatches from the duck's egg, and a chick from the hen's egg. In what way did the environmental conditions in the incubator here co-operate in the formation in the ancestors of the different characters of the duck and the fowl? If the differences of character were due in any degree to environmental conditions acting on the ancestors during their independent life, it is certain that no such differences are present in the incubator to co-operate in the development of these different characters in the duckling and the chick.

Prof. Goodrich adopts from Sir Archdall Reid the dictum that although there is only one kind of character, there are two kinds of variation. That characters are all of one kind means that they are all partly acquired and partly inherited. This contention has already been examined. The other part of the proposition is explained as follows: The normal structure being due to germinal factors and environmental stimuli, any divergence from this normal structure may be due to a change in the germinal constitution in a constant environment, or to an altered environment acting on an unchanged germinal constitution.

Here Prof. Goodrich is in agreement with the majority of, if not all other biologists, and he adopts the terms generally used for these two kinds of variation, namely mutations for those due to changes in the germinal factors, and modifications for those due to changes in the environment. But he apparently does not see that the attempt to make a constant distinction between variation and character involves him in contradictions, and that the recognition of two kinds of variation is inconsistent with the assertion that there is only one kind of character. He defines a variation as the degree of difference between the characters of two individuals, not a new character, but a difference which can be measured or at least estimated. Variation produces a new character, but is not itself a new character, but a difference. Thus, the white colour of an albino rabbit is a new character, but the difference between a white rabbit and a grey is a variation. This does not seem a very important distinction: it would seem rather that a new character is only recognized by its difference from an old one. Prof. Goodrich states that the new character (due to variation) which is caused by germinal change will always reappear in a constant environment, provided the germinal constitution continues the same. This being the case, what becomes of the contention that every character is partly due to the germinal factors and partly to the stimulus of the environment? Here the germinal factors have changed and the environment has remained constant; therefore, since there has been no change of stimulus the new character is entirely, not partly, due to germinal factors. The constant environment cannot rightly be said to co-operate in the production of a new character due to germinal change. Even if the universal conditions of development are described (incorrectly, in my opinion) as a stimulus, the same stimulus cannot be the cause of a difference of character due to germinal change.

This is, therefore, a subtle fallacy and a dangerous one, since it has already led to much confusion in the discussion of evolutionary questions. The development of an organism is confused with the determination of a character. The development of any organism requires some degree of warmth, some supply of oxygen and moisture, and of nutriment. But these same conditions may cause the development of a fish or a frog. In fact, heat, oxygen, water and food are necessary for the development of all organisms, all animals and all plants. These are the essential conditions of life itself, if we include the fact that oxygen need not be supplied in the free elemental state, but in anaerobic life may be present only in combination in the food compounds. The special characters under normal conditions of development, before an animal enters on its active independent existence, are entirely, not partially, due to the constitution of the ovum; they are predetermined in the ovum and, before that, in the gametes which unite in fertilization. On the other hand, special stimuli which act upon the individual after it enters upon an active existence, stimuli such as light, friction, and muscular exercise, may produce definite effects, or changes in the individual structure. The test is whether the structure or character is present when the stimulus acts and absent when the stimulus is absent. For example, food is not a stimulus corresponding to the development of a character of the brain such as large or small cerebrum, large or small cerebellum, but the mode in which food is obtained may be a stimulus to the development of jaws or limbs. There can be little doubt that in many cases both genetic factors and external stimulus contribute to the development of a character, and there is much evidence to show that this is the case with many adaptive characters. In fact, such characters constitute evidence in favour of the Lamarckian doctrine, for since both causes are producing the same modification it is probable that the genetic factor was originally due to the external stimulus. A good example of such cases is the erect, bipedal attitude of man. As mentioned above, the baby is not at first adapted to the upright position; it has to learn to walk, and at the same time has much less difficulty in so learning than a dog or even an ape. It learns partly by heredity and partly by practice, and this would be intelligible if the degree of heredity were the result of many generations of practice. I am aware of course that experimental embryology has shown many remarkable effects produced in the structure or organs of the embryo by the application of special substances or conditions to its environment; for example, the concrescence of the two eyes in a fish embryo into a single cyclopean eye as the result of the addition of a particular salt to the water in which the embryo is developing. This, however, does not affect the reasoning followed out above. The abnormalities produced are entirely due to the abnormal condition applied, if the genetic factors in the embryos under experiment are the same as in embryos which develop normally. It is agreed that the result shows that these genetic factors possessed the potentiality of producing the abnormal development observed under the experimental condition, but this does not alter the fact that the special abnormality was determined by the experimental condition.

Prof. Goodrich quotes Sir Ray Lankester's argument that Lamarck's first law that a new stimulus alters the characters of an organism, contradicts his second law that the effects of previous stimuli are 'fixed' by inheritance. The advocates of Lamarckism, it is urged, usually begin by taking an organism and submitting it to a new stimulus; if a change is thus induced, this very fact shows that the previous stimulus has not 'fixed' the character in inheritance. "To prove that characters are rendered permanent, evidence is constantly brought forward that they are changeable." This is very ingenious, but it is not really a sound argument. It is no more logical than it would be to assert that the occurrence of mutations proves that no characters are inherited. Modern Lamarckians are not concerned to prove that all Lamarck's statements or laws are correct. They are concerned with the evidence that typical adaptations are often modifications from an ancestral condition which correspond to certain habits involving special stimuli, e.g. the reduction of toes in the horse corresponding to increase of speed and the concentration or intensification of stimulus on the middle toe and disuse of the others. There is nothing illogical nor contrary to the evidence in maintaining that a constantly repeated modification may become hereditary.

Prof. Goodrich, after saying that the popular distinction between characters which have been developed in the individual's lifetime and those which are inborn is misleading and involves a fallacy, only two pages later states that the term mutation may be adopted for new characters (*sic*) due to changes in the factors of inheritance, or alterations in germinal constitution, and the term modifications for those induced by changes in the environment. Thus, 'modifications' are precisely those changes which have been generally known as 'acquired characters', differences due to external stimuli and not to change in the factors of inheritance, that is to the constitution of the reproductive cells or gametes. This leaves the question of Lamarckism just as it was before, namely whether a character, an increase or decrease of the growth or development of a part of the soma, originally due to the active influence of some external stimulus may, when repeated for many generations, cause a change in the gametes corresponding to the change in the soma, and finally come to be developed because of this change in the gametes before the original stimulus begins to act on the individual, or long after the original stimulus has ceased altogether. In other words, are not acquired characters inherited—so far as a single generation is concerned we know that generally such inheritance is not evident—but were some inherited characters, especially those whose functions or structure are adaptive, originally acquired under the influence of external stimuli?

DR KAMMERER'S EXPERIMENTS ON THE INHERITANCE OF ACQUIRED CHARACTERS

The experiments of Dr Paul Kammerer, carried out chiefly in the years 1900-1914, have aroused widespread interest among biologists and have given rise to acute controversy. The experiments were carried out in the Biologische Versuchsanstalt in Vienna, and were described and recorded by their author in a series of long papers in the *Archiv. für Entwicklungsmechanik,* and in other periodicals. In 1923 Dr Kammerer came to England and delivered a lecture on his researches and results before the Cambridge Natural History Society, and a little later before the Linnean Society in London, and a report of this lecture was published in *Nature* of May, 12th, 1923.

I will explain here more fully than I have hitherto done my position with regard to these experiments, and make a critical examination of them in some detail. My scepticism concerning them has been regarded with some disapproval by extreme Lamarckians, and as I was already opposed to the universal application of the principles of genetics and mutation to the evolution of all characters, I am not entirely in favour with either party in the controversy.

Experiments on Alytes obstetricans. One of the subjects of Kammerer's experiments was the Midwife Toad, *Alytes obstetricans*, in which he stated that he had produced epidermic callosities on the anterior limbs in the male by causing it to change its habits and mate in the water, instead of mating on land as it does in the natural state, in which it is destitute of such callosities. The majority of other Anura perform the sexual amplexus in water, and the males not only have thicker and stronger 'arms' or fore-legs than the females, but, like the common frog, have epidermic callosities on the 'hands' or fore-feet and sometimes on the arms as well. These thickenings of the epidermis have been variously termed thumb-pads, nuptial pads, nuptial excrescences, *brosses copulatrices* in French and *brunstschwielen* in German. Usually the surface, consisting of the horny outer layer of the epidermis, is brown or black in colour, and raised into pointed horny papillæ. In this country Kammerer's claims concerning his results were opposed by Dr William Bateson, and supported with equal confidence and emphasis by Prof. E. W. MacBride. Although I published some criticisms of other experiments of Dr Kammerer's, I took no part in the Alytes controversy, with the exception of some unreported remarks in the discussion following Dr Kammerer's lecture at the Linnean Society's rooms in 1923, the reason being that I had come to no definite conclusion on this case, not having thoroughly studied and considered the evidence which Dr Kammerer had published on the subject.

Alytes obstetricans is a small toad which is common in France, Belgium, Switzerland, and West Germany. It owes its name to the fact that the male receives the strings of eggs from the female and carries them about attached to his hind legs. The sexual amplexus and discharge of the eggs take place on land, whereas in other Anura they occur in water. *Alytes obstetricans* is the only European species which breeds on land, and the male carrying the eggs continues to lead a terrestrial life, hiding in holes or under stones in the daytime, and only occasionally at night entering the water. Fertilization as in other Anura is external and takes place when the eggs are discharged from the cloaca of the female. The remarkable breeding habits were first observed by Demours in the Jardin des Plantes at Paris in 1744, and described in more detail by de l'Isle in 1876 from observations made in the neighbourhood of Nantes. According to G. A. Boulenger,[1] during the lumbar amplexus the male passes its hind feet alternately over the cloaca of the female, and also makes movements of friction with its 'fingers', the digits of its fore-feet. Finally, the male contracts violently, presses strongly the flanks of the female, and the eggs escape suddenly with noise and as though by explosion, to fall between the posterior limbs of the male. Then the male releases his hold of the loins of the female and seizes

[1] *Les Batraciens.* Bibliothèque de Zoologie, A. Douin et Fils. Paris, 1910, p. 217.

her by the base of the head. It is at this moment that the male secretion is discharged. Then ensues a pause of ten to fifteen minutes, after which the male attaches the eggs to his legs by plunging the feet alternately into the mass

Kammerer's account is somewhat different. He states[1] that in Anura in general, excluding Alytes, the male clasps the female round the loins or the axillæ and presses the load of eggs from her body by work lasting for hours or days. If this is correct, the term *obstetricans* would be almost as appropriate to ordinary frogs and toads as to Alytes, but it is difficult to understand how lumbar pressure could possibly press the eggs out of the abdomen, since the constriction occurs between the mass of eggs and the cloacal outlet. Kammerer also states that in Alytes the contraction and extension of the legs of the male help to pull the egg-strings out of the abdomen, which is quite contrary to de l'Isle's description as quoted by Boulenger. The eggs of Alytes are large with much yolk, and comparatively few in number (18-86). The amplexus is of short duration and occurs at night; so that the coupling of the sexes, the discharge and fertilization of the eggs, are all accomplished within a few hours, whereas in most other cases the male grips the female for several days.

Kammerer[2] states that at ordinary temperatures (17° C., 62° F.) specimens in captivity continue to breed in the same way on land. The eggs are adhesive when laid, as in the common frog, and this causes them to adhere to the legs of the male. In the common frog and in other frogs and toads which breed in the water, the adhesive covering of the eggs absorbs water as soon as they are expelled from the oviducts of the

[1] Archiv. f. Entwicklungsmechanik, Bd. xxviii, 1909.

[2] Ibid., p. 447.

female, swells up and ceases to be adhesive. When Alytes in captivity is kept at 25°-30° C. (77° to 86° F.) some of them spawn on land, but the eggs do not adhere to the legs of the male, owing to the surfaces drying too rapidly, but are left lying on the ground. The majority of the animals, however, take to the water and mate and spawn there, and the gelatinous coverings immediately swell up and do not adhere to the legs of the male. The offspring of specimens which have spawned only once or twice in water, if restored to ordinary temperature, lay their eggs on land, but if derived from later spawnings they spawn in water. If the abnormal conditions are continued for several generations the eggs become more numerous, the tadpoles become smaller and develop three pairs of gills instead of one pair, like the ordinary Alytes, and the males in the third and fourth generation develop rough black swellings on the inner edge of the first digit of the 'hand', the muscles of the fore-arm being at the same time hypertrophied. The nuptial pad on the first digit or inner side of the hand, and the thicker fore-arm are the secondary sexual characters of the male in the common frog and other species which spawn in the water, and the fact that the pad was not developed in Kammerer's experiments till the third and fourth generation would show that the effect was accumulated by heredity. The pads were only fully developed in the breeding season, as in the common frog. Bateson's chief reasons for not fully accepting this result as proved are that Kammerer failed to produce specimens when requested, and that his figures of the structures were inadequate. In his 1909 paper the figures are outline diagrams, and show a black mark on the inner side of the first digit; while in the 1919 paper[1] a photo-

[1] Archiv. f. Entwicklungsmechanik, Bd. 45, 1919.

graph is given of the modified Alytes lying on its back with its head towards the camera and its fore-legs stretched out. Apparently the photograph is taken from a dead and preserved specimen, but whatever the photograph was, the printed reproduction of it is indistinct and unsatisfactory. Bateson (*Nature*, July 3rd, 1919) described the outer side of digit IV as conspicuously thickened, but Prof. MacBride (*Nature*, June 23rd, 1923) stated that Dr Kammerer agreed with him that this thickening was merely a patch of dirt adhering to the fourth finger. This leaves nothing visible in the photograph but an indistinct pad on the wrist of the right hand. At the Linnean Society meeting on April 30th, 1923, at which Dr Kammerer delivered his lecture, he exhibited a specimen of the modified Alytes preserved in a glass jar. I was unable to see the condition of the 'hands' on the specimen in the jar as I stood among a number of people all trying to examine it, but Dr Bateson stated (*Nature*, June 2nd, 1923) that all he saw was a broad dark mark across the *palm* of the left hand. I do not know if this specimen was that shown in the photograph of the 1919 paper; there is a black patch extending from the carpal pad over the ventral surface of the wrist visible in that photograph.

In Kammerer's 1919 paper it is stated that the greater the number of males of the fourth and fifth generations which came into the breeding condition, the oftener it was seen that the callosities extended beyond the original area, the inner side of the first digit and the metacarpus at the base of the first digit, (the so-called ball of the thumb), over the surface of the lower arm as far as the elbow, with great variability in different individuals, and between the two arms of the same individual. The photograph (Fig. 2, Pl. X.) criticized by Dr Bateson, is described as showing a male of F_5 generation, in high breeding condition, in which a large callosity extends over a great part of the radial side of the lower arm, and also over the 'thumb ball', but leaves the phalanges free. At successive breeding seasons in the same male the callosities may extend, e.g. from tip of finger to whole finger, then to thumb ball or base of first digit and finally to the neighbouring part of the lower arm. Kammerer considers the arm-pads especially important, because they are absent in most Anura, but present in Bombinator, the aquatic relative of the terrestrial Alytes.

The nuptial swellings of male Anura, according to Kammerer in his 1909 paper, serve to enable the male to hold the female more firmly. In water the amphibian skin, however warty, becomes slippery, not only through being wet, but because of the slimy secretion. In Alytes copulating on land the swellings would undergo retrogressive change because the drier skin would render callosities unnecessary. Therefore, when the nuptial pads appear in the third and fourth generation of Alytes copulating in water, this fact signifies the inheritance of a functional adaptation. All this in my opinion is irrelevant to the question of Lamarckism. What we require to discover is not the use or benefit of the modification, but the cause of it. The use or benefit is only important for the theory or concept of selection. It is true that an adaptation means a structure or co-ordination of structures adapted to produce a certain result, but the Lamarckian theory is that the functional use came first and involved special stimuli whether acting directly and mechanically or by increasing or diminishing the activity of muscles, which stimuli themselves caused the structural changes by hypertrophy or atrophy. In the case of the callosities of Anura it may be presumed that the stimulus was intermittent pressure or friction, for that is known to be, at least in Vertebrata, the general cause of epidermic hypertrophy and the formation of a thicker layer of the horny outer portion.

When we try to discover what is the special stimulus to which the development of these nuptial callosities is attributed by Kammerer, it is surprising to find that he nowhere gives a detailed description of the position of the fore-legs of the male in the amplexus, that is to say, he does not consider exactly which part of the fore-limbs are in contact with the female. Both in Kammerer's own writings and in those of the biologists who have taken part in the controversy concerning his results there is a tendency to confuse the term adaptation with the term acquired character, and to introduce teleological ideas as in the part of Kammerer's 1909 paper referred to above. For example, Prof. MacBride in *Nature*, May 22nd, 1919, writes: "In all these water-breeding forms of anura the male is provided with a horny patch situated on the hand below the index-finger in order to enable him to retain his hold of the female when he clasps her under the water".

However, in his 1919 paper Kammerer definitely concludes that the development of callosities on the fore-leg of Alytes is due to the direct stimulus of friction acting on the skin. He discusses the general influence of the increased temperature, and of the water as a medium, and satisfies himself that they cannot be the cause of the modification. The cause of the hypertrophy of the epidermis is, then, the greater intensity and longer duration of the skin friction in the amplexus in water than on the land.[1] Boulenger's recent observations of the animal in the natural state give 43 minutes for the duration of the embrace,

[1] Archiv. f. Entwicklungsmechanik, Bd. 45, 1919, p. 340.

Dähne's in the terrarium $1\frac{1}{2}$ hours. Kammerer himself observed that the coupling of Alytes in water lasted four to five hours, while in those left under normal conditions in captivity it never lasted more than one hour. V. Bedriaga[1] states that the amplexus of the tree-frog Hyla can be completed in six to ten hours, although the coupled pair may swim about for three or four days. The amplexus in water also, on account of the greater slipperiness of the female's skin, due to the water and increased secretion, causes greater exertion on the part of the male, greater pressure, and therefore more stimulation to the male epidermis.

Kammerer admits that as the normal Alytes is in all probability descended from ancestors which possessed nuptial callosities and bred in water, therefore the development of callosities in the course of a few generations in Alytes made to breed in water must be in part attributed to atavism. In other words the character is not quite newly acquired, but is in part the re-development of a structure, a tendency to which was possibly retained in the hereditary constitution. It has been objected on this ground that the result of the experiment does not prove the inheritance of an acquired character, but merely that the genetic factor was always there, but was only called forth by the external stimuli : the phenotype is different, the genotype the same. From this point of view the case would be analogous to that of the axolotl, which, though breeding for many generations in the larval form, can in any individual under appropriate conditions resume the adult form with its definite characters. But, on the other hand, if the neoteny or prolongation of the larval form and

[1] Kammerer, Archiv. f. Entwicklungsmechanik, Bd. 45, 1919, p. 330.

its power of reproduction in the axolotl were the result of a cumulative effect of conditions extending over many generations, there was heredity of the effect of external conditions, and so also with Alytes.

In studying Dr Kammerer's memoirs on Alytes, and the controversy concerning them, there are two distinct things to be considered: (*a*) the evidence concerning the epidermic modifications which he describes; (*b*) the causes to which they are to be attributed. With regard to (*a*) we have seen that the illustrations of them, which have been published, are not very satisfactory, and that according to the descriptions given the structures themselves are rather indefinite, and not very closely similar to those which occur normally in other Anurous Amphibia. In his reply (*Nature*, August 18, 1923) to Bateson's letter, Kammerer states it was incorrect to assert that the black colour was restricted to the palmar aspect of the left hand in the specimen exhibited at the Linnean Society Lecture: that actually the pad extended to the dorsal aspect also. But it is certain that no Anuran has been described with a nuptial callosity extending right across the palm of the hand, although in many cases, as in the common frog, the callosity on the inner edge of the hand extends to some extent both on to the palmar and dorsal surface. On the other hand, I think that the photos of microscopic sections in Pls. X and XI of the 1919 paper cannot be ignored, especially Figs. 7 and 9 of Pl. XI, which show the enlarged glands and a few horny papillæ like those which occur in normal nuptial callosities. We are bound to accept Dr Kammerer's statement that these sections were made from the skin of the first finger of *Alytes obstetricans*, after breeding for some generations in water. Difficult as the experiments are, and long as is the time required to get three or four generations, it is much to be desired that some biologist should repeat them, and give more detailed descriptions and more satisfactory illustrations of the results.

With regard to (*b*), the causes to which the modifications are to be attributed, it seems to me that not only Dr Kammerer himself, as mentioned above, but Dr Bateson and Prof. MacBride confuse the ideas of adaptation and causes of adaptation. In German the English 'adaptation' is supposed to be rendered by 'anpassung'. But Kammerer often uses this word as though it meant a process by which the individual organism becomes adapted to the requirements and conditions of its life by the actions which the requirements call forth, and the effect of the conditions themselves. A blacksmith's arm becomes stronger as the result of the exercise of its muscles, and therefore automatically becomes more adapted to its work. The epidermis of his hand becomes thicker under the influence of friction with his tools, and so more adapted to the use of those tools. Anpassung in this sense means, therefore, the modification of the individual by functions and external conditions, in the assumption that the modification is in general adaptive. In English, on the other hand, adaptation means the relation to function or utility of the structure and characters which are due to the hereditary or congenital constitution of the animal, as the hind legs of the frog or kangaroo are adapted for jumping, the teeth of the tiger for killing or tearing flesh, the teeth of the ox for masticating vegetable foods. In such cases the structure is extremely efficient for its proper and natural function, and almost useless for any other. The word adaptation, then, has two meanings, an apparatus or mechanism (the structure adapted) and a process: the relation of an organ or system of organs to its function, or to the outside world, and the process by which this relation or adaptation was produced. The word, like its German equivalent, anpassung, etymologically implies the process of adapting, and so may lead to logical fallacy, because it may contain a *petitio principii*, or begging of the question. The fact is the utility of structures and characters in the animal's natural mode of life, the question is the process by which this utility, whether of mechanism or mere existence, was produced. The word adaptation, or anpassung, tends to suggest the assumption that the utility in structure has been produced by the animal's mode of life and the influence of external conditions, the very conclusion that has to be proved. There may be differences of opinion on the question whether all characters are adaptive or only some, but there is complete agreement with regard to some characters. The great problem is the evolution of adaptation, which has been discussed and investigated from Darwin's time till now. Biologists are often in general agreement with regard to the function and utility of adaptive structures, and at the same time in direct opposition to one another with regard to the mode in which such structures have been evolved. In his 1919 paper Kammerer discusses at considerable length whether the epidermic hypertrophy of the hands and arms of the male Alytes in his experiments could have been due either to the effect of life in the water, or to the higher temperature in which the animals were intentionally kept, and states the evidence which, in his opinion, is sufficient to show that the results in question could not have been due to either of these conditions alone, or to both. It is evident that neither water nor temperature would explain the nuptial callosities of Anura in general, because in the first place they differ in different genera and species, and, in the second place, those conditions would not explain the occurrence of the callosities on the parts used to hold the female, and their occurrence in the male sex only. On the other hand, it might be possible that if Alytes was descended from ancestors which had nuptial callosities, the effect of aquatic life during reproduction or of a higher temperature would be to cause these structures to reappear. Kammerer, however, concludes that the development of the callosities in his experiments could only be due to the effect of friction with the skin of the female in the amplexus.

It is therefore surprising to find that in reply to Bateson's criticisms concerning the specimen of Alytes exhibited at the Linnean Society Lecture of April 30th, 1923, Kammerer (*Nature*, August 18th, 1923) completely abandons his previous position and virtually gives up the Lamarckian explanation of the nuptial pads of Anura altogether. He does not deny that the pad in his specimen of Alytes was on the palmar aspect of the hand, but asserts that not only his Alytes, but also other Batrachians, and especially the other Discoglossidæ, have pads on places which never come into contact with the female. "*Bombinator pachypus*, for example, develops pads on two or three toes of the hind foot". It is, however, by no means certain that these toes in *Bombinator pachypus* do not come into contact with the female. They are very probably used in friction against the hind legs or the cloacal region of the female. Dr Kammerer proceeds as follows: "I willingly admit that the traditional explanation of the pads, namely, that they are produced by friction with the skin of the female, may possibly be a fable. . . . It is by no means impossible that life in water produces the pads. If this were so we should have a case of direct passive production, but not of active adaptation. The correctness of my observations, and their relevance to the theory of heredity, is not affected whichever explanation is adopted ".

It is difficult to be certain whether in the above quotation Kammerer intends the word traditional to apply to the callosities produced on Alytes in his own experiments, or to those of Anura in general. Clearly there could be no tradition with regard to Alytes, for the modification had never been produced in this genus before. But Kammerer may have meant that the popular and traditional Lamarckian idea with regard to the pads of Anura in general may be a fable and, therefore, not the explanation of the experimental result in Alytes, that this must then be attributed to ' life in water ', which would be a case of direct passive production and not active adaptation.

In his 1919 paper (p. 353), Kammerer uses the German terms *direkte passive Bewirkung* and *indirecte aktiver Anpassung.* To an English biologist in search of definite concepts and statements these terms appear vague and obscure. By careful reading, however, it is possible to find out what the writer means by them. Direct passive influence means the effect of an external condition, such as temperature, on the gametocytes within the animal, so that the fertilized eggs when produced develop into offspring showing some change or modification. Kammerer writes that the changed function of a well-defined part of the body can hardly be transferred to the germ-plasm by direct parallel influence. Warmth can certainly reach the ovary directly; that the influence of the water can do so is less probable, but that they can effect there the same changes which show themselves on the surface through the use of a specialized structure is scarcely to be harmonized with our biological experience.

Therefore he concludes that the pads affect the gametes and become hereditary through the soma. Indirect active adaptation means the modification of function by the environment, and the modification of structure by the function. Thus, the effect of the watery medium is to make the friction of the skin of the male's hands greater and more prolonged, and this increased friction causes hypertrophy of the epidermis. An English Lamarckian would say that the epidermic hypertrophy was the direct result of the friction, and that the hypertrophy of the muscles of the arm was the result of increased functional exercise; therefore, an indirect effect in comparison with that on the epidermis. It will be seen that the quotations given above from Kammerer's letter in *Nature*, August 18, 1923, are in complete contradiction to those just cited from his 1919 paper.

It is evident that 'direct passive production' of the nuptial pads in Alytes, meaning some unexplained influence of the water surrounding the animal upon the gametocytes within the testis, would not be Lamarckism at all as the word is understood by biologists at the present time. The 1919 paper is entitled *Vererbung erzwungener Formveränderungen*, the heredity of enforced changes of structure. This is not quite the same verbally as the heredity of acquired characters. But even Weismann, the most uncompromising opponent of the inheritance of acquired characters, admitted the direct influence of conditions on the germ cells within the body as a cause of hereditary change. Thus, when Kammerer asserts that the relevance of his results to the theory of heredity is not affected whichever explanation is adopted, the statement is quite irrational. The whole biological world has been in acute controversy over the question, whether the results could be accepted as evidence of the inheritance of modifications produced by the direct action of stimuli on the soma, and Kammerer now states that this question is not affected if these results are explained by an entirely different process. The truth obviously is that the whole relevance of his results to the theory of heredity depends on which of the explanations mentioned by him is accepted or proved to be correct.

RELATION OF NUPTIAL PADS IN ANUROUS AMPHIBIA TO ONE ANOTHER AND TO THE FEMALE SKIN

With regard to the problem of the nuptial pads in general it had some time ago occurred to my mind that, on the assumption that the pads in the male were due to friction with the skin of the female, it was surprising that no modification was perceptible on the part of the female skin which is in contact with the male pads during amplexus. The friction, being mutual, would be expected to produce epidermic hypertrophy in both sexes over the regions which come into contact. During the breeding season of 1926, I made a careful examination of pairs of *Rana temporaria* in amplexus, and took photographs of some.[1] I found that the male grasped the female more tightly when the couple were taken out of the water, and that when they were placed on a board on the male's back, after being held for a few minutes till they became quiet, they would continue without movement for a minute or two, so that it was easy to make a photographic exposure, the lens of the camera being directed vertically downwards.

I found that when the male was about equal to

[1] *On the Nuptial Callosities of Frogs and Toads from the Lamarckian Point of View.* Journ. Linn. Soc., vol. xxxvi, 1927.

the female in size the nuptial pads were in contact with each other, and not only in contact with the female skin. The more the female struggled the more tightly were the pads of the male pressed together. In this case, therefore, mutual friction between the pads is one of the mechanical stimuli related to the development of the pads. I then examined the specimens of Anura in the British (Natural History) Museum, and compared them with the figures of the nuptial excrescences and the amplexus given by G. A. Boulenger.[1] I found that mutual contact between the excrescences did not occur in all cases. In *Bufo vulgaris*, for instance, the male is much smaller than the female, and the hands of the male are far from meeting on the ventral side of the female. Each hand is doubled into a fist which makes a depression in the female skin in the upper part of the axillar. The callosities in the toad, however, are much less developed than those in the frog. They occur on the inner side of the metacarpus, on the whole of the dorsal surface of the first and second digit, and on the inner surface of the third digit. These are the parts of the hand in contact with the female. No distinct callosities were visible on the skin of the female in the depression formed by the hands of the male, but the skin here is very warty, and the epidermis probably thicker than in the male callosities.

In the other European genera placed by Boulenger in the families Discoglossidæ and Pelobatidæ the amplexus is lumbar. In Discoglossus there is a black callosity on the inner or radial edge of the metacarpus and on the dorsal surface of the first digit, and also a slight one on the inner and dorsal surface of the second digit. The fingers did not actually meet below the female in the preserved specimens in amplexus,

[1] *Les Batraciens.* Bibliothèque de Zoologie, Paris, 1910.

but probably did so in life. In both sexes there are minute epidermic papillæ close together on the ventral surface, and larger blunt warts on the dorsal surface. In these epidermic excrescences there is evidence of a reciprocal effect between male and female, for the ventral papillæ of the male and the dorsal warts of the female are both hypertophied where they come into contact with one another in the lumbar amplexus, that is in the anterior ventral region of the male and the posterior dorsal region of the female.

Of Bombinator there are two species, *B. igneus*, known as the fire-bellied toad from the red colour of its ventral skin, and *B. pachypus* in which the ventral skin is yellow. I examined a pair of the latter species preserved in the state of amplexus. There are two black callosities on the inner side of the fore-arm, the proximal one the larger, and also slight ones on the inner edge of the first, second and third digits. Only the tips of the digits meet beneath the loins of the female, though it is possible that in life the digital callosities of the two sides meet each other. The radial callosities here are not in contact with each other, but with the skin of the female, but the latter is thick and warty. There are also small pads on the ventral surface of the second, third and fourth toes of the hind feet as mentioned above in the discussion of Kammerer's experiments.

Pelodytes, which is common in France, offers the most striking example of mutual contact between callosities in the male. The amplexus being lumbar and the loins very narrow, the arms of the male meet beneath the female from the elbow to the inner fingers. There is an elongated pad on the radial surface of the lower arm, and on the inner sides of the first two digits, and the radial pads are in contact with each other during amplexus. The palms of the hands are turned away from the ventral surface of the female, and there can be little doubt that the two inner fingers come into contact with each other. On the other hand there is an oval pad on the ventral surface of the upper arm and another smaller on the pectoral surface of the male where the arm is joined to the body. These two pads certainly do not come into contact with each other, but with the skin of the female. The male Pelodytes has also minute papillæ on the ventral surface like those of Discoglossus: a band parallel to the edge of the lower jaw and a number closely crowded on the posterior part of the ventral surface of the body, and on the ventral surface of the thighs. These latter parts are behind the ventral region of the male which comes into contact with the female, but they doubtless undergo friction with the dorsal part of the legs of the female. Lastly, there are slight longitudinal thickenings on the ventral surface of the toes.

Pelobates, of which there are two species in France, *P. fuscus* and *P. cultripes*, is the genus of the spade-footed toads, having a flat projection with a hard horny edge on the inner side of the heel, which is adapted to the habit of digging themselves into soft soil backwards. This organ is instructive, because it forms an epidermic hypertrophy present in both sexes, obviously related to pressure and friction against the soil, and similar in nature to the amplexual callosities confined to the male sex in most of the Anura. Pelobates is remarkable because it has no amplexual callosities of the ordinary kind. The amplexus is lumbar, and during the breeding season there are, according to Boulenger, little granular excrescences, not coloured black, scattered on the upper surface of the fore-arm and fingers. These may represent nuptial epidermic hypertrophy in a very rudimentary form, and the upper or dorsal surface as well as the radial surface of the male fore-arm comes into contact with the female skin, but there is no pad. On the outer surface of the upper arm, which does not come into contact with the female skin, there is a large oval gland, to which the garlic-like smell of the male is probably due. In *P. cultripes* at the Museum I could scarcely make out either the gland or granular excrescences, though they were very distinct in *P. fuscus*. Kammerer, in making the statement that Alytes is the only anuran of Europe which spawns on land, and the only one which has no nuptial pads, has overlooked the case of Pelobates which has no pads. Certainly the minute granular excrescences mentioned above do not resemble the usual nuptial pads, and are not on the inner or radial surface, as is the case in other genera. Pelobates, however, spawns in the water. It is probable that the cause of the difference between Pelobates and other genera is the short duration of amplexus in the former. G. L. Boulenger[1] states that pairing takes place in ponds or deep ditches, and that the eggs are expelled immediately after the female is seized, or within a few days. Miss Durham, in *The Frog-book*, New York, 1907, states that the American spade-foot is likely to remain in water for breeding only one night or two. Dr Gadow, in his account of Amphibia in the *Cambridge Natural History*, says about a week.

Pelobates, therefore, seems to be, with regard to terrestrial habits, intermediate between Alytes and other Anura. Although I have not found a full description of its behaviour the evidence tends to show that both the duration of the amplexus and the whole time spent in the water in the breeding season have been much reduced, and the absence of ordinary

[1] *Batrachians of Europe*, Roy. Soc. 1897.

callosities corresponds to this reduction. The case of Pelobates, however, proves that mere amplexus in the water is not sufficient to cause the development of callosities, either by the direct influence of the aqueous medium, nor by the greater difficulty of holding the female, as Kammerer supposes.

DR KAMMERER'S EXPERIMENTS ON SALAMANDRA MACULOSA AND S. ATRA

We have next to consider Kammerer's experiments on the European Salamanders. There are two species of these: *Salamandra maculosa* and *S. atra*. In both species fertilization is internal and the young are born alive, but in *S. maculosa* the young pass from the uterus into water, are provided with gills, and spend the first stage of their existence as aquatic larvæ. Kammerer has made experiments to find the effect of external conditions on the duration of intra-uterine development, but I propose to consider these later, and to examine first his experiments on the coloration of *S. maculosa*. These are recorded in detail in a long paper published in 1913,[1] and illustrated by 12 plates. The observation of specimens captured under natural conditions has shown that two colour varieties occur, one in which yellow markings are irregularly distributed over a black ground colour (*forma typica*), and the other in which the yellow markings are larger in area and symmetrically arranged, especially a longitudinal band on either side of the mid-dorsal line (*forma tæniata*). Systematists regard these two types as independent of external illumination

[1] *Das Farbkleid des Feuersalamanders (Salamandra maculosa, Laurenti) in seiner Abhängigkeit von der Umwelt.* Zeitschr. f. Entwicklungsmechanik, Bd. 36, 1913.

or other external conditions. Kammerer claims to have proved that the *forma tæniata* is produced from the *forma typica* by exposure to a yellow ground. His chief experiments consisted in keeping specimens on yellow loam, or on black garden soil well illuminated, from a stage of growth reached shortly after metamorphosis to adult and sexually mature condition, and continuing the treatment for one or more successive generations produced by the original animals.

Each of the Plates II to XIII in the memoir here considered contains figures representing nine stages of growth and coloration of the *same* specimen, with the exception that in a few cases some of the stages may be wanting. The original material, referred to as the P or parent generation consisted of specimens from the beechwoods near Vienna, where only spotted Salamanders with quite irregular asymmetrical markings occur. For the experiment with yellow loam specimens which had little yellow in their original coloration were chosen. With regard to age they were about a year old. The experiment continued from May 12th, 1903, to May 23rd, 1907, or four years. The specimens were so different from each other in the distribution of the spots that it was easy to distinguish the particular specimen whose changes of coloration were to be recorded in the figures at half-yearly or yearly intervals. The changes in the specimen figured in Plate II are an example of the changes which all the specimens underwent. In the last stage the yellow areas were much increased on the back of the specimen, less so on the ventral surface and flanks, but the arrangement was still quite irregular. The yellow extends across the head in three places, across the body in two, on the tail the yellow is median.

Plate III shows the development of yellow coloration in a female which was the offspring of the specimen in Plate II, and was kept under similar conditions, i.e. on yellow loam. The surprising fact is that in this specimen the yellow marking consists of symmetrical longitudinal stripes ; it belongs, as Kammerer himself points out, to the *forma tæniata*. This contrast in marking between parent and offspring is visible in the earliest stages of the latter, in which there are paired longitudinal rows of small spots on the back and a single row on the tail. There is no apparent reason why the effect of a yellow ground should be to change the pattern of the marking in the offspring, while it had no such effect in the parent. Assuming that the effect of light reflected from a yellow ground surface is to increase the amount of yellow pigment in the animal's skin, then the inheritance of this increase would be the inheritance of a somatic modification, an example of what has been called Lamarckism ; but the manifestation of a new marking, a striped instead of an irregularly spotted pattern, in the offspring of the animals placed upon a yellow ground-surface is not the inheritance of a somatic modification, but an induced mutation, which is quite a different thing. With regard to the male parent, which is not mentioned by Kammerer, it must be presumed that it was of the irregularly spotted kind, and exposed to the yellow ground in the same way as the female. In the parent specimen the effect of the yellow ground was to increase the total amount of the yellow pigment in course of time. In the striped offspring the total amount of yellow in the latest stage seems distinctly greater than in the parent, and this might possibly be due to an inherited effect in addition to the effect of the yellow ground acting directly on the specimens of the F_1 generation.

The hereditary effect which is stated to have occurred in the experiments must of course be compared with the heredity of the varieties, whether merely individuals or races, occurring in nature. Kammerer states on the evidence of the young taken in nature and those obtained by breeding controls—

1. That the offspring of irregularly spotted individuals (*forma typica*) taken in the Vienna Forest are always irregularly spotted. In other words, *forma typica* always breeds true.

2. That the symmetrically marked specimens of *forma tæniata* obtained at Vorwohle in Brunswick also breed true; asymmetrically spotted individuals resembling *forma typica* never appear among the progeny.

3. That striped forms produced artificially also breed true to striping, and further that striped produces striped even when the natural striped race is crossed with the artificially produced striped form.[1]

This last statement is truly remarkable and inevitably suggests doubt. We are asked to believe that the striped marking is produced by a yellow ground from the irregular spotting not in the individual lifetime, but in the F_1 generation, and having been so produced is immediately in the next or F_2 generation completely inherited. Not only is such inheritance contrary to the general experience concerning the effect of conditions, but there is no apparent relation between the influence of yellow environment and the pattern of the yellow marking as distinct from

[1] Kammerer, 1913, pp. 125, 128.

the extent of the yellow colour in the animal's skin.

The experiment of E. G. Boulenger described in a paper published in 1921 [1] dealt only with individuals not with heredity. The experiment was made only on larvæ, and he used painted aquaria instead of merely soil of different colours. He had a gravid specimen of the *forma tæniata*, stated to have come from Western Germany, which gave birth to 32 young. Half of these larvæ were placed in aquaria 16 in. square, painted orange yellow, the other half in similar aquaria painted black. When all the larvæ were completely metamorphosed, or very nearly so, nine survived in the yellow aquaria, eleven in the black. According to Boulenger's description those in yellow light not only had much more yellow colour in the skin than the mother, but this colour was in irregular markings with spots united together across the middle line, and with one exception all of them agreed with the *forma typica* and not with *tæniata*. The larvæ which had been reared in black aquaria were darker than the mother with smaller and more numerous spots, and these spots were arranged, in a bilaterally symmetrical pattern, as in *forma tæniata*. Boulenger believed that the larvæ reared by him in yellow light would in course of time assume the *tæniata* marking, but he had no evidence for this. The figures given do not seem to me to support these conclusions. The specimens reared in yellow light undoubtedly show larger areas of yellow colour, but most of them distinctly retain the *tæniata* pattern.

We have next to consider the Mendelian experiments made by Kammerer on the heredity of the

[1] E. G. Boulenger, *Experiments on Colour Changes in the Spotted Salamander, S. maculosa*, Proc. Zool. Soc., 1921, pt. 1.

different markings. The results in the F_1 generation were as follows—

1 P *typica* × natural *tæniata*.

F_1 All *typica*. (*typica* dominant)

2 P *typica* × artificial *tæniata*.

F_1 With double, symmetrical, row of spots. (Intermediate.)

This again is surprising. The natural *tæniata* is recessive, but the experimentally produced *tæniata* is not recessive. It would follow from this that the natural *tæniata* is not the direct result of conditions, since its inheritance is different from that of the artificial *tæniata*.

The results in the F_2 generation were as follows—

3 F_1 *typica* × F_1 *typica*, both from No. 1 above.

F_2 231 *typica* 77 *tæniata*.

Precisely 3 to 1.

4 F_1 double row of spots × ditto, from No. 2 above.

F_2 234 specimens with double row of spots from brood to brood more distorted.

Great range of variation, but no segregation.

The natural *tæniata*, therefore, shows perfect Mendelism, the artificial *tæniata* none at all.

My review and criticism of Kammerer's published papers up to this point were already written when, on Sunday, October 11th, 1926, I was astonished to read in the *Observer* a communication from Vienna containing the tragic story of his death, stating that he had committed suicide and left a letter in which he gave his reason for doing so, namely that he had found that the specimen of Alytes supposed to exhibit an experimentally developed nuptial pad, which he exhibited in Cambridge and London in 1923, had been without his knowledge fraudulently injected with Indian ink beneath the skin of the fore-foot, as asserted by Dr Noble in an article in *Nature*, August 17th, 1926. Some biologists may be of opinion that this surprising admission makes any further discussion of Kammerer's work unnecessary, that it is superfluous to give any attention in future to any of his experimental evidence. As the preceding pages however were written before I knew of any reason to suspect actual fraud in connexion with Alytes or any other of Kammerer's specimens, I will leave the above criticisms of his publications as I wrote them, and complete as briefly as possible my review of his work, with the same object as when I began, namely, assuming his experimental results to be correctly described, to consider how far his arguments and reasoning are sound.

The fact that Mendelian segregation occurs when naturally spotted Salamandra is crossed with the naturally striped, but not when it is crossed with experimentally striped, suggests that in the former case the striped character is gametic, i.e. represented by some 'factor' or 'gene' in the reproductive cells, while in the latter it is not. But if the striping resulting from experiment is not gametic, what becomes of the heredity?

On the other hand, in the experiments on ovarian transplantation, Kammerer found that the soma of the naturally striped female had no influence on the ova derived from a spotted female, but the artificially striped soma made the ova derived from a naturally spotted female behave as though they came from a striped female. Here we have a complete gametic change due to the somatic influence of an induced or 'acquired' character, while according to the Mendelian experiments there was little or no evidence of gametic change. Kammerer concludes that somatic induction is only exerted by a new character, while he concludes from the Mendelian experiment that the new character does not obey the Mendelian law, while the old character does. All these conclusions are mutually contradictory. If the new characters effected complete somatic induction, it would logically be expected that the gametes in an artificially striped female would show Mendelian segregation. Kammerer's results cannot be accepted without corroboration.

Kammerer's experiments on the reproduction of *Salamandra maculosa* and *S. atra* were described in two memoirs which appeared in 1904 and 1908, of which the later is the more important with regard to heredity.[1] Neither of these species occurs in the British Islands. The stage at which the young are born varies according to the height of the region in which the animals naturally live. In the plains or hilly land of slight elevation *S. maculosa* is ovoviviparous, laying a large number of eggs in the water from which larvæ of 23 to 25 mm. length are hatched within a few minutes and continue to live in the water for several months. In hilly or mountainous regions of greater elevation a similar number of larvæ 25 to 30 mm. long are born alive in water; they

[1] Archiv. f. Entwicklungsmechanik, Bd. 17, 1904 and Bd. 25, 1908.

possess already four legs and short gills, and their subsequent history is similar to that of the larvæ hatched from eggs. *S. atra* lives in the higher regions of the Alps, and is therefore often known as the Alpine Salamander. It is normally viviparous, and gives birth on land to only two fully developed young Salamanders 30 to 40 mm. in length. Thus, the larval life and the metamorphosis, consisting chiefly in the loss of the gills and gill-slits and development of the lungs, are passed in *S. atra* within the uteri. A large number of eggs as in *S. maculosa* are produced and fertilized, but the majority of these die at an early stage of development, and only two, one in each oviduct, survive till birth, the yolk of the others serving as food for these two. Kammerer found in nature in intermediate regions also intermediate conditions with regard to birth: Alpine Salamanders with two young in each oviduct instead of one, producing, therefore, four at a birth and these not quite so fully developed as in normal cases; and, on the other hand, spotted Salamanders in high localities having in their oviducts comparatively few larvæ advanced in development, nourished by the yolk of other eggs which had not developed.

Kammerer found that by reversing the natural conditions of the two species he could reverse the characteristics relating to the birth of the young. By raising the temperature of the surroundings from 30° to 37° C., and increasing the moisture, he made *S. maculosa* ovoviviparous; by lowering the temperature, and reducing the water supply he gradually reduced the number of young and prolonged the antenatal development until finally only two were born which were already metamorphosed. Conversely, by raising the temperature and supplying water-basins and keeping the surroundings saturated with water he made *S. atra* produce from three to nine young, which had not completed their metamorphosis.

The next problem was to rear the young born under the altered conditions till they were sexually mature, and to see if there was evidence in their progeny of inheritance of the altered mode of reproduction. Kammerer was able to rear the young animals obtained from his experiments by feeding them on fibres of raw meat, on which diet they grew quickly and reached in two years the size of sexually mature animals. They showed, however, no signs of breeding, and when specimens were killed and dissected it was seen that the sexual organs were very small and undeveloped, and covered with an enormous mass of fat. He therefore had constructed open-air enclosures, 4.5 metres (about 14 ft. 6 in.) long, 3 metres (about 9 ft. 9 in.) broad, and 1.10 to 1.20 metres (3 ft. 8 in. to 4 ft.) deep. Each enclosure was provided with a water-basin sunk in the ground, 0.5 metre (1 ft. 7 in.) deep. In May, 1905, 26 *S. maculosa*, born at an abnormally late stage of development in consequence of want of water and low temperature, and 26 *S. atra*, born at an abnormally early stage in consequence of abundance of water and high temperature, were placed in such enclosures. In the summer of 1906 and subsequently some of the females in the enclosures were seen to be gravid, and were then removed to indoor terraria, some with and some without a water-basin, in order to observe carefully the condition of the young at the time of birth. The results in the two species separately may be thus summarized—

S. maculosa. The first birth produced five young, having an average length of 45 mm. instead of 25 mm., as in the normal new-born larvæ of the species. These larvæ had gills and a fin-membrane on the tail, and were set free by the mother in the water-basin, but they completed their metamorphosis ten days after birth instead of spending months in the aquatic larval state like the larvæ of the wild *S. maculosa*. In the second birth from a female of which the mother had been experimentally treated there were only two larvæ, also produced in the water, a little less developed than those of the first 'litter', but still much more advanced than the normal larvæ of the species. One of these was preserved, the other lived from its birth on December 19th, 1906, till May 18th, 1907, without metamorphosis. The third birth consisted of four young of only 26 mm. length, i.e. no longer than normal larvæ, but they were produced on the ground, not in water. They proved incapable of aquatic life and in less than a month completed their metamorphosis in moist surroundings, namely, damp moss or water only 2 to 3 mm. deep. In the fourth case, only two young were produced as in *S. atra*. The mother had been put into an indoor terrarium without water-basin, and thus may be said to have been under the same conditions as her own mother, but this would not apply to the conditions in the open air terrarium, in which she had been previously kept. The two larvæ were 40 and 41 mm. in length and were completely metamorphosed, having no trace of gills or tail fin-membrane. Kammerer considers that the two first litters show definite and certain evidence of an inherited effect of the change (extension of intrauterine development) produced experimentally in the previous generation.

S. atra. The first female in which parturition occurred produced three young, the last of which was dead. These young had long well-developed gills and were born in the water, they had also a caudal fin-membrane. Born on the 25th April, they continued to live in the water till the 27th May, when one of them commenced its metamorphosis and left the water. It was 40 mm. in length at birth and 44 mm. when completely metamorposed, a little longer than the new-born young of *S. atra* in the natural condition. A second female produced five young in the water in May, 1907. These were smaller than those of the first birth, measuring from 21 to 23 mm. in length. One of them underwent metamorphosis on the 9th and 10th June, while the others continued in the aquatic condition when the paper which I am quoting was written. Control specimens kept under similar conditions in another open-air terrarium, and derived from parents reproducing normally, continued to produce two fully metamorphosed young at a birth as in their normal habitat. This is evidence that the production of unmetamorphosed larvæ in the offspring of parents in which the same change had been experimentally produced, was due to inherited effect.

Before accepting the evidence given as sufficient proof of the inheritance of the changed conditions it is necessary to apply careful logical reasoning to the experiments and their results. If we consider first the case of *Salamandra atra* in the natural state in which the production of metamorphosed young is probably a new characteristic in comparison with the production of aquatic larvæ in *S. maculosa*, the first question is whether this new characteristic is hereditary. It has been maintained, as already mentioned, by opponents of Lamarckism that the evidence supposed to be obtained by such experiments as those of Kammerer on Salamandra is self-contradictory. It is urged that the change produced by changed conditions shows that the original character was not inherited and that the inheritance in the offspring of the specimens experimentally modified is in contradiction to the absence of inheritance in the parental specimens themselves. To represent the matter by symbols, it is stated that an animal with character A living under conditions *x* is exposed to conditions *y*, and the character becomes A^1. The A^1 is placed again under conditions *x*, or some intermediate condition between *x* and *y*, and the character A^1 is in some degree repeated by heredity in the offspring. The new character A^1, to use the technical terms which have been proposed, is phenotypic or the direct effect of external conditions on the development of the soma, not genotypic or the result of special factors or genes in the gametes or reproductive cells. How then can it be believed that the new phenotype will persist or has persisted when the old conditions are restored? If the new character were inherited after the influence of new conditions on one generation, the old character which had been under the influence of the old conditions for countless generations could not have been changed.

The above reasoning is logically sound, and therefore the only question can be whether any degree of heredity was exhibited in the change by which a specimen of *S. atra* came to give birth to aquatic gill-breathing larvæ instead of metamorphosed air-breathing young. Kammerer does not seem to have fully appreciated this point, but he states that the change was gradual, that it was difficult to bring about the aquatic parturition for the first time, and that in a series of successive parturitions the number of larvæ born increased and the stage at which they were born became less advanced. There was, therefore, some slight degree of inherited effect, for a resistance to the change and a progressive development of the change in the individual can only be regarded as due to inheritance from the wild parents.

When, however, we examine closely the evidence presented by Kammerer as proof that the change in gestation was inherited by the offspring of specimens in which the change had been experimentally produced we cannot accept it as conclusive. It is naturally difficult in such experiments with living animals to keep them under precise and constant conditions; but even so, more definite details of temperature and moisture might have been given. From Kammerer's account, as it stands, it would seem that the specimens of the two species of the filial, or to use the Mendelian symbol, F_1, generation were kept under the same conditions. They were reared in indoor terraria, and fed on the same food to the age of about 2¼ years, then placed in the large outdoor enclosures till they showed signs of pregnancy, and then again brought into indoor terraria. It is true that one of the latter was without a water-basin, and kept only moderately damp, but only one birth is recorded as occurring in this. If we compare the birth-records for the two species in terraria provided with a water-basin we find them very similar, as the following comparisons will show—

S. maculosa. 7th August, 1906. 5 larvæ more advanced than those born in the natural state, born in the water, average length 45 mm., instead of 25 mm., as in natural larvæ. Metamorphosed on 16th August.

S. atra. 25th April, 1907. 3 larvæ, one dead. 44 and 35 mm. long, metamorphosed 28th May.

S. maculosa. 1-2 May, 1907. 4 larvæ, comparatively small, only 26 mm. in length, unable to live in water, but lived in wet moss, etc. Born on dry ground. Metamorphosed 26th May.

S. atra. 2-3 May, 1907. 5 larvæ in water, 21 to 23 mm. long, one metamorphosed 9th to 10th June. The normal length of young of *S. atra* born in nature is 38 to 40 mm. long.

In both species there were great differences in the size of the larvæ at the two births, but not so much difference in the duration of the larval life. The great similarity between the species in these births might possibly be due to the same conditions acting on both, and might be regarded as indicating that the ordinary natural differences of gestation are not to any marked degree inherited. The differences between the two births in the same species might be due to the influence of the artificial conditions of captivity in disturbing the normal course of gestation.

Of the other two births in *S. maculosa*, one consisting of only two young was otherwise similar to the first of those mentioned above; the other was different from all the others in both species, consisting of only two young completely metamorphosed and born in the entire absence of water. The latter condition might be sufficient to account for the result. Kammerer regards it as evidence that the delayed parturition induced experimentally in the mother of this specimen has been inherited. There are two possible ways of testing whether any inheritance occurs in this case. We may assume that the retention of the young till after metamorphosis in *S. atra* is the new character, and the birth of aquatic larvæ in *S. maculosa* the primitive feature. Absence of water and lower temperature, according to Kammerer, caused the new character to appear in specimens of *S. maculosa*, but only somewhat gradually. One way of testing the heredity would be to place the offspring under the same experimental conditions and observe if the new feature, delayed parturition, appeared earlier, was produced with greater facility, than in the parents. Kammerer did not adopt this method, except in one instance, for the specimens of the parental generation were kept without a water-basin, while the offspring or F_1 generation were kept in terraria provided with a water-basin, in three cases, and without it in only one case. In this single individual it may be considered that the same condition, absence of water, produced greater effect in the offspring than in the parent, not only in the fact that fully metamorphosed young were produced at the first pregnancy, but in the fact that the number of young which had been more than two in the parent was reduced to two in the offspring. One individual however is not very strong evidence.

The other method would be to place the offspring under the same conditions as the *S. maculosa* in the natural state, and this was done so far as the presence of a basin of water is concerned in the case of the other three individuals. Two of these produced few larva in an advanced stage, and metamorphosed after only 9 days in one case, in the other remained in the larval condition for 5 months. The third birth, in which the larvæ were much smaller and yet could not live in water, seems quite abnormal. Kammerer concludes that these cases show that adaptation to the want of water was inherited in some degree, but there was a gradual reversion to the original character proportioned to the length of time that the animals were exposed to conditions like the original. But we do not know how far the conditions in the indoor terraria really reproduce those of nature, in the humidity of the air for example.

In the case of the offspring of *S. atra*, individuals which had become adapted to giving birth to aquatic larvæ, only one method was tried, namely, repetition of the same conditions, so far as presence of water was concerned. They produced young in the water like their parents, three in one case, and five in the other, metamorphosis taking place in one individual but not in the others, about a month after birth. Kammerer considers that this was evidence of partial heredity, reversion to the ancestral habit being shown by the smaller number of young than in the parents. He states also that a number of individuals, the progeny of parents which reproduced in the normal manner, and which served as controls, again produced two fully metamorphosed young at a birth. They were kept in one of the open-air enclosures, but Kammerer does not state that they were brought into an indoor terrarium before parturition. He does not give sufficient details to prove that the control was decisive. We are asked to believe that the gestation of natural *S. atra* was so feebly inherited as to be altered in the individuals placed in moist warm conditions in the presence of water, while the alteration was inherited by the offspring of these individuals which were placed also in the presence of water.

It certainly does not appear that the evidence for inheritance in the F_1 generation was conclusive. What is proved by the experiments as described is that the difference in gestation between the two species is due to the difference of external conditions. That there is some resistance in either case to the modification of the natural gestation of each species towards that of the other, is evidence that the natural gestation is in some degree hereditary, though the heredity does not appear to be very strong.

It seems to me that this case is similar to that of the absence of colour from the lower sides of flat fishes investigated experimentally by myself.[1] After several months' exposure to light the lower sides became more or less pigmented, in some cases the colour extending over nearly the whole of the lower side. The degree of pigmentation after the same period of exposure varied considerably in different individuals, all the individuals in the first experiments described in the *Phil. Trans. Memoir* being flounders (Pleuronectes flesus), but there was evidence that all individuals became pigmented sooner or later. There was evidence of heredity in the resistance to the development of the pigment. A number of specimens in process of metamorphosis were put into the apparatus illuminated from below, and the completion of the process, including the disappearance of the pigment (chromatophores) from the lower side was not affected. The only reasonable conclusion is that the absence of pigmentation from the lower side in the natural state is due to the absence of light-incidence, while the long exposure necessary to produce pigment on the lower side experimentally is evidence that the character originally acquired has become to a considerable degree hereditary. My experiments did not extend to the next generation, as I did not obtain offspring from the modified specimens.

KAMMERER'S EXPERIMENTS ON PROTEUS ANGUINUS

Kammerer also experimented on the subterranean amphibian, *Proteus anguinus*, which lives in underground waters in the limestone caves of Dalmatia,

[1] J. T. Cunningham and C. A. MacMunn, *On the Coloration of the Skins of Fishes, especially of Pleuronectidæ*, Phil. Trans. 184 B, 1893.

J. T. Cunningham, *Additional Evidence on the Influence of Light in producing Pigment on the lower Sides of Flat-fishes.* Journ. Mar. Biol. Assn., vol. iv. (N.S.) 1895-97, p. 53.

and is not only almost completely colourless, but also blind, the eyes being vestigial and concealed beneath the skin. The animal is aquatic throughout life, having three external gills, and two gill-clefts on each side. It has short slender legs with three toes on the fore-foot and two on the hind foot. The body is long and slender, when adult reaching a maximum length of one foot. Kammerer found that at any temperature below 15° C. Proteus was viviparous, and as the waters of its native habitat do not reach this temperature this must be its normal mode of reproduction, but at any temperature above that limit it lays eggs which hatch into larvæ, but these are unable to survive very long.

When first captured and removed into daylight, the skin of Proteus is almost devoid of pigment and appears flesh-coloured on account of the blood-vessels within it. Only a small amount of yellow and reddish pigment is present. After exposure to daylight for some time, brown and blue-black pigments develop and the skin becomes dark, but red light has no effect in developing pigment. Kammerer states that the offspring of pigmented animals, whether they are born in the light or after long stay in darkness, are again pigmented, but whether this is supposed to be entirely due to heredity or not is not clear. Remarkable results were obtained by experiments on the influence of light on the development of the eyes. In the new-born young the eye is in a rudimentary stage, consisting of the secondary optic vesicle and the rudiment of the lens. In the dark the eye increases in size only 1.6 times and does not keep pace with the rest of the body so that in the adult it is disproportionately small, and thick glandular skin develops over it. The secondary vesicle persists, and choroid and sclerotic develop, but the lens disappears. By keeping the animal in strong daylight, interrupted by periods of exposure to red artificial light, Kammerer was able to produce a much greater development of the eye. Daylight alone caused so much pigmentation of the skin over the eye that its development was not much affected. But under daylight and red light alternately the eye-ball increased fourfold, the lens increased 18 times in length and 12½ times in breadth, and developed its fibrous structure, cornea and sclerotic were differentiated and also choroid and iris. One specimen under exclusively red light developed still larger eyes, but they were colourless and unpigmented. It would seem from this that the development of the eye and that of pigment depend on different parts of the spectrum. The evidence shows that the degeneration of the eye is due to the darkness, or absence of the light stimulus, and this is probably true for all cave animals such as the blind fish (*Amblyopsis*) and the blind crayfish of the Kentucky caves. Kammerer says nothing of the heredity of the experimentally developed eyes, but it is difficult to believe that the degree of degeneration of the eye found in normal Proteus in its native habitat is the direct effect of the absence of light on each individual, without the cumulative effect of heredity.

CHAPTER VI

SECONDARY SEXUAL OR SEX-LIMITED CHARACTERS

Two of the most fundamental processes of life are cell-fusion and cell-division, and we know very little of either beyond the superficial, visible movements which they involve. By cell-fusion I mean the union of two cells into one, which occurs periodically, and in many cases is essential for the production of new individuals and the continued succession of generations. The union is conjugation, which is called when, in unicellular organisms, the two cells are similar, isogamy ; when the two are differentiated, anisogamy, or fertilization. Here we have the almost if not quite universal phenomena of sex and growth. The essential fact of sex is the difference between the small motile cell in fertilization, the spermatozoon or sperm, and the large motionless cell, the ovum. In the higher animals the sperms and ova are produced in distinct organs, ovary and testis or spermary, which may be in the same individual, but are usually in separate individuals. The rest of the body is distinguished as the soma. In many of the lower animals, e.g. the common starfish, there is no visible difference between male and female except the difference between ovary and testis. We are so accustomed in the higher and more familiar animals to regard the whole individual as male or female that we overlook the fact that the differences between the sexes in the soma are secondary, and often wanting. Their secondary nature when present is also very evident from the facts that in many animals, such as the earth-worm and the snail, male and female reproductive organs or gonads are present in the same individual, while in others such as the oyster the same individual and the same gonad changes from one sex to the other. The majority of flowers in the higher plants are also bisexual. Secondary sexual differences, therefore, are not in themselves essentially sexual, although they are associated with the presence of the sexual organs. They may be called somatic sexual characters, and as they are connected with sexual relations they have been called epigamic, but this term is only appropriate to those characters which are definitely associated with courtship and mating, such as the nuptial plumage of birds. From the point of view of heredity and genetics they are called sex-limited characters, to distinguish them from other characters which have nothing to do with sexual functions or habits, but only with sex-determination, and these are called sex-linked characters, e.g. colour-blindness.

In some of the lower animals such as certain marine worms, sponges, hydroids, medusæ and corals, the ova and sperms escape from the parent body into the surrounding water by simple rupture either directly to the exterior or through the natural cavities and apertures. In other cases, especially where fertilization is external, there are special ducts and other organs to ensure fertilization, and these constitute one class of sex-limited characters, namely, those directly connected with the generative organs. In the next class are those which are related to courtship, and in the next those which are used in fighting with rival males. In another class are those which are not in the strictest sense sexual at all, but parental, their function being the nourishment and protection of the offspring by one sex or the other. It is interesting to note that in the human species some of the characters which we are accustomed to regard as essentially female are parental rather than sexual.

It has long been known that the perfect development of these characters and organs depends on the presence of normal ovaries or testes. But it is a recent discovery that the explanation of this is that the development of the sex-limited characters is under the influence of chemical compounds of unknown composition originating in the reproductive organs and carried in the blood and other circulating liquids. These 'hormones' are the internal secretions of the reproductive organs. The dependence of the sex-limited characters on these internal secretions has an important bearing on the question of Lamarckism, for it can be explained on Lamarckian principles and in my opinion on no others. My theory[1] is briefly as follows. The characters—which are usually excessive developments of some external structure such as antlers of stag or tail of peacock—correspond to an external stimulation associated with the sexual habits and occurring only when the sexual hormone is present. The parts stimulated to excessive growth at the beginning of the evolution themselves gave off waste substances into the circulating fluids of the body, and these substances may be regarded as an internal secretion having in its composition some ingredients peculiar to the particular tissues from which they were derived. This internal secretion was present in the blood and lymph which permeated the gonads as well as other parts of the body, and the theory

[1] J. T. Cunningham, *Heredity of Secondary Sexual Characters*. Archiv. f. Entwicklungsmechanik, 1908.

assumes that it acted as a stimulus to the particular parts of the gametes which corresponded to those parts of the soma from which the internal secretion arose. In modern genetics it is supposed that each character, it may be the shape of a fowl's comb for example, is determined by a special part of a single chromosome in the nucleus of ovum or sperm. Such special part of a chromosome is called a gene. My theory assumes that the gene or genes which determined the growth of the frontal bone of an ancestral stag before stags had antlers, was or were stimulated by the internal secretion from the frontal bone in which some slight outgrowth had developed in consequence of the stimulation due to mechanical irritation or injury incurred in fighting with other stags. In the following generation the frontal bone and the skin covering it had a slight tendency to develop outgrowths, which was due to the stimulation of the corresponding genes in the sperms of the father. But the tendency to growth only produced actual growth when the hormone derived from the functional testis was also present, because it was only when this hormone was present that the special genes had been stimulated. The hereditary tendency would thus be increased by the repetition of the external stimulation in each generation.

This mutual interaction of the hormone derived from the testis and the internal secretion derived from the excessive growth of tissues caused by external stimulation would explain the otherwise unexplained wonderful facts concerning the heredity and development of sex-limited characters. They are inherited by both sexes, but only fully developed in one, e.g. the male, and this normal development only occurs when the hormone of the active testis is present. In course of time the hereditary tendency has increased from generation to generation so that the secondary character develops under the influence of the testis hormone without the external stimulation which was the original cause of the development. But the habits and actions of the animals which involved the stimulation still continue, as in the fighting of stags and the erection of the peacock's tail.

There is a remarkable difference in the effects of removal of the reproductive organs between birds and mammals. In the latter, castration of the male prevents the normal development of the sex-limited male characters. In the common fowl on the other hand castration causes reduction in the size of the comb and wattles, but does not prevent the growth of the spurs nor cause the development of plumage similar in colour and structure to that of the hen. On the other hand, when the ovary of the female is removed, whether duck or hen, she at the next moult develops plumage of the male character. There are certain breeds of fowls, Henny game, Sebright Bantams, and Campines for example, in which the cocks are hen-feathered instead of having the usual male plumage. Prof. Morgan[1] made the remarkable discovery that castration of these cocks caused resumption of the normal characters of male feathering. Thus the normal cocks have male plumage whether the testes are present or removed and normal hens develop male plumage if the ovaries are removed. On the other hand we have a variation in which although functional testes are present the plumage has the female character, and castration in this case has the same effect as the removal of the ovaries in the normal hen,

[1] T. H. Morgan. *Genetic and Operative Evidence relating to Secondary Sexual Characters.* Carnegie Institute of Washington, Pub. 285, 1919.

namely, the replacement of female plumage by the male. Prof. Morgan drew the conclusion that hen-feathering was due to the presence, in the testes of the hen-feathered breeds, of cells like those in the ovary of the hen which produced a hormone having the property of suppressing or inhibiting the development of the characters of the male plumage.

This is a reasonable conclusion, but Prof. Morgan goes much further and writes: "We are coming to realize that the hereditary genes generally have more than a single effect on the characters of the animal. The secondary sexual characters may then be only by-products of genes whose important function lies in some other direction. If, for example, the secretion produced by the cells of the male gonad have an important influence on his output of energy or strength or activity, their secondary influence over certain parts of the body would not call for any further explanation on the modern view of natural selection. If the secretions of the female bird have some direct relation to her physiological processes that are important in the development of the oviduct, for example, it would be a matter of no importance from an evolutionary point of view if that same secretion suppresses in her the development of the high colour shown by the male". It is obvious that this argument suggests no reason why the hormone from the testis should cause strength or activity in the male, nor in the second place why it should have a secondary influence over other parts of the body. Moreover, it misses altogether the essential question, which is what determines the particular parts of the body to be affected by the secondary influence of the hormone, why the front of the head in the stag and the tail in the peacock, and why in many animals, no parts are affected.

According to Prof. Morgan's reasoning, therefore, the sex-limited characters are purely accidental. His statement seems to me to involve two fallacies. In the first place, it makes no attempt to explain why the characters in question have a definite relation to the sexual habits of the animal, and that it is just the characters having this external relation which are affected by the hormones from the gonads. In the second place, his remarks imply that the internal secretion of the testis is specific for different animals, producing antlers in stags, beard in man, tail in peacock and so on. The evidence on the contrary is that the internal secretion of the testis in one mammal is similar to that in another. Just as the effect of thyroid extract depends on the normal development of the animal into which it is introduced, and not on the animal from which it is taken, so the action of testis secretion is to call forth the organs or characters which are latent in the constitution of the animal in which the secretion is produced. Pezard [1] quotes Bouin and Ancel as having shown experimentally that extract of testes of pig, horse, etc., have effects on castrated guinea pigs, causing them to develop the same characters of skeleton and generative organs as entire males, while he himself found that injection of extract of the cryptorchid testes of swine into castrated cocks had the effect of increasing the size of the comb to that of entire males, and in one case the animal began to crow and to exhibit the pugnacious instincts of the normal cock. It is evident, therefore, that the effect of the internal secretion of the testis is to stimulate the development of characters latent in the hereditary constitution of each particular animal, and that the evolutionary

[1] Pezard, *Caractères sexuels secondaires chez les oiseaux.* Bull. Biologique de la France et de la Belgique, tome 52, 1918.

origin of such characters is quite a different question.

The influence of the sexual hormones is as we have seen different in birds from what it is in mammals. The male plumage in fowls, pheasants and ducks is not dependent on the testis hormone ; it requires for its suppression not merely the absence of this, but also the presence of the hormone from the ovary. This is not a refutation of the Lamarckian theory. The theory does not claim to explain secondary sexual differences of colour, but with regard to structural characters of plumage, especially length of feathers, it is only necessary to assume that the heredity has become stronger, so that the development persists in the absence of the testis hormone, although it is unable to take place in the presence of the ovarian secretion, which was of course never present when the stimulation to which the excessive development of the male plumage is attributed was applied. This stimulation was the irritation of the papillæ from which the feathers grow by the erection and movement of the feathers in the display of courtship. The origin of hen-feathering in cocks cannot be explained by the Lamarckian theory. It obviously does not correspond to any change of stimulation, it is a change of heredity unrelated to external stimulation of feathers. This means that it must have arisen as a mutation, and the mutation must have consisted in the production by the testis of a hormone similar to that of the ovary. This alone explains why the castration of hen-feathered cocks has the same effect as the removal of the ovaries from normal hens, namely the development of male plumage. Morgan and others have thought that they could see in preparations of the testes of hen-feathered cocks the interstitial cells which are absent in normal cocks and present in ovaries, but these observations have not been confirmed by other investigators. Some may ask why, if it be admitted that hen-feathering is due to a mutation, may not the ordinary relations of male characters to the testis hormone have owed their origin to mutation. The reply is that the effect of the mutation in the case of hen-feathering is merely a change in the limitation of the ovarian hormone and its production by the testis, not the origin of a new hormone or a new sex-limited character. It throws no light on the origin of the structural characters, and supplies no reason why sexual hormones should have any effect on them. We have at present no evidence of the origin of such a character as the antlers of stags with its relation to the testis hormone by mutation.

Dr F. A. E. Crew and Mr A. W. Greenwood[1] have recently recorded and discussed a peculiar case of change of plumage following operation in a hen chick of the Brown Leghorn breed. The ovary of the chick was removed when it was four days old, and chopped-up testis from a brother of the same age was inserted into the left side of the body cavity. When the chick developed the adult plumage, which would be at the age of four to six months, this plumage was that of a normal cock, although the original sex was female. But, at the next moult, at the age of seventeen months, the bird developed henny plumage, although the comb and wattles continued to show male characters. Post-mortem investigation showed that there was a large mass of normal active testicular tissue on the left side, and also a small mass of ovarian tissue on the site of the original ovary. On the right side where in a normal hen the ovary is quite vestigial and undeveloped there was a small mass of testicular tissue.

[1] *Henny feathering in an ovariotomised hen with active testis grafts.* Proc. Roy. Soc., B. vol. 99, 1926.

The authors conclude that the character of the plumage is not determined by the internal secretion of the ovary, but by the demands made by the gonads on the general metabolism, the ovary normally making the greater demand, that in this individual the increased amount of testicular tissue exerted demands on the body equivalent to those of an active ovary. It seems to me that this conclusion is illogical. There is nothing to indicate that the testes of hen-feathered cocks are making greater demands on the body metabolism than those of normal cocks. The fact that the first plumage in the experiment of Crew and Greenwood was of the male character would be expected on the theory of the influence of internal secretion of the gonads, because the ovary had been removed. The subsequent reversion to the female plumage would be the natural effect of the development and enlargement of the small remnant of ovarian tissue left when the ovary was removed. It is admitted by the authors that ovarian tissue and oocytes were present. It is more probable that the change of plumage was the effect of recrescence of ovarian tissue than of the increase in size and activity of the testicular grafts.

The assumption that all the phenomena of evolution are adequately explained by the occurrence of mutations and natural selection is in my opinion conclusively disproved by the facts known concerning sex-limited characters in Vertebrates. The assumption fails to explain the relations of these characters to external stimuli on the one hand, and to internal secretions on the other. It gives no reason why the antlers of a stag used in fighting other stags should be affected by an internal secretion of the testes any more than the animal's hooves.

THE DISLOCATION OF THE TESTES IN MAMMALS

In mammals alone of all the classes of Vertebrata the male gonads do not remain in their original position in the abdomen, attached to the primitive embryonic kidney known as the Wolffian body, or mesonephros, but together with the latter undergo during fœtal life a gradual change of position, moving backwards and downwards until they finally occupy pouches of the abdominal wall, the scrotal sacs, situated on either side of the middle line anterior to the ventral portion of the ring of bone formed by the pelvic girdle. The mesonephros or embryonic middle kidney is attached to the testis in the adult forming an appendage known as the epididymis, consisting of a coiled duct continued into the vas diferens. Until recently no physiologist had discovered any function for the scrotum, or any valid explanation of the change of position of the testes in mammals. In medical terminology, in relation to the erect position of the human body this change is known as the 'descent of the testes'. In other mammals the movement is backwards and downwards, and the most appropriate term for the change of position is dislocation. The feature is so obvious and familiar in man and mammals that the significance of its absence in other vertebrates is not always realized. As no utility or advantage arising from the scrotal pouches and the position of the testes within them in mammals was known, in other words no reason had been discovered why it should be necessary or advantageous for mammals to have scrotal pouches when other vertebrates have the testes in the abdominal cavity, I maintained in a previous publication[1] that it was impossible to

[1] *Hormones and Heredity*, Constable & Co., London, 1921.

explain the evolution of this peculiarity by the theory of Natural Selection. It must be explained as a mutation or by some Lamarckian hypothesis. A mutation means a change of structure which is not directly related to a special stimulus of external origin, but mutations as a general rule do not involve a considerable change in the individual development comparable to the dislocation of the testes.

We have to inquire therefore if there is anything in the mode of life of mammals which might possibly cause dislocation of the male reproductive organs and not the female, on the theory that the change originally due to external stimulus would if repeated in every generation become hereditary, originally a somatic effect would become gametic. It has been suggested or supposed that the dislocation might be due to rise of pressure in the abdominal cavity resulting from the evolution and action of the diaphragm which is also peculiar to mammals. But a general rise of pressure would not tend to cause a movement of the testes in any particular direction, even supposing that abdominal pressure is higher in mammals than in birds, of which there is no evidence. In 1903 Dr W. Woodland[1] put forward the theory that the dislocation of the testes and formation of scrotal sacs could be explained as the result of the galloping or leaping action which is characteristic of most mammals when moving at their greatest speed. In this mode of locomotion the whole body is thrown off the ground in a succession of leaps or bounds. At each impulse the body is thrown violently upwards and forwards, the more or less loose organs in the abdomen are, on the principle of inertia, as it were left behind—that is, are pressed backwards and downwards in relation to the body. Then the body descends

[1] Proc. Zool. Soc., 1903, pt. 1.

again forwards and downwards, its movement being arrested for a moment when the limbs touch the ground. The abdominal organs in this part of the leap are pressing at first upwards and backwards, and at the moment when the limbs reach the ground, they are jerked violently downwards. The general effect, therefore, on the abdominal organs is to move them backwards and downwards. But the testes have been shown to have greater specific gravity than any of the other abdominal organs, e.g. the liver, and at the same time are more loosely attached to the inner surface of the abdominal wall. For this reason the testes only have been affected by the mechanical impulse, and not the other organs. The response to this mechanical impulse has evidently been, not a rupture of the suspending membrane as Dr Woodland suggested, but a process of growth by which the membrane suspending the organ from the peritoneum remained intact, but changed position with the testis, for it still remains with the same attachments to testis and peritoneum within the scrotal sac in the final position.

One difficulty in this theory is that the mesonephros is not suspended in the abdominal cavity, but closely covered by the peritoneum, and the kidney, originally developed behind the mesonephros, not only remains in the abdomen, but has a relatively more anterior position in the adult, than in the embryo. The testis, however, is somewhat firmly attached to the mesonephros in consequence of the fact that efferent ducts pass from the testis into it, and the mesonephros itself becomes at an early stage converted almost entirely into a much-coiled duct which is attached to the testis by membrane.

The fact that, as an individual abnormality, it occurs in many mammals, such as the commoner domestic forms, horse, bull, pig, sheep, etc., that the dislocation of the testes fails to take place in development, gives rise to other questions, and this condition of cryptorchidism, as it is called, has been under investigation recently. It has long been known that cryptorchidism usually involves sterility. The animal is incapable of effecting fertilization, though showing the ordinary sexual instinct and being fully capable of sexual union. It is found that the cryptorchid testes do not produce spermatozoa, that the seminal tubules within them are degenerate, not exhibiting normal spermatogenesis. In 1922 it was suggested by Dr Crew of Edinburgh, and Mr Carl Moore of Chicago[1] that the cause of this aspermatic condition was the higher temperature of the abdominal cavity as compared with the cavity of the scrotal sac. In the interior of the abdominal cavity the temperature is the maximum temperature of the body ; in the scrotal cavity it is some degrees lower. The difference varies ; in the abdomen the temperature is constant, in the scrotum there is a loss of heat over the surface, the supply of blood is not very great, and the communication with the abdominal cavity is only at the anterior end. The loss of heat is therefore greater than in the interior of the abdomen, and varies with the external temperature. The temperature of the scrotum, therefore, is seldom, if ever, as high as that of the interior of the body ; observation shows that it is in this climate from 2 to 8 °C. below that of the abdomen. It is found experimentally that when the testis of a Rodent, e.g. rabbit, guinea-pig, or rat, in which animals the inguinal canal has a wide opening into the abdominal cavity, is artificially removed from the scrotum to

[1] F. A. E. Crew, *A Suggestion as to the Cause of the Aspermatic Condition of the imperfectly descended Testis*. Journal of Anatomy, vol. lvi., pt. ii., Jan. 1922. Carl R. Moore, Anat. Record. Phil. 1922.

the latter cavity and prevented from returning, the seminal tubules soon degenerate and spermatogenesis ceases. Seven days are sufficient to produce marked evidence of the change in microscopic structure, and at the end of three weeks the seminal tubules are quite disorganized. It has been shown also that merely enclosing the scrotum in wrappings to prevent loss of heat is sufficient to cause cessation of spermatogenesis.

In consequence of these facts Mr Carl Moore claims that the function of the scrotum has now been discovered. It is to keep the testes at the lower temperature which is necessary for normal spermatogenesis. He maintains that if the dislocation of the testes and the scrotal pouches had not been evolved, the Mammals would have become extinct, and these peculiarities are therefore not merely an advantage, but a necessity. A little consideration will show that the argument is fallacious. There can be no doubt that mammals are descended from primitive Reptiles which were cold-blooded, and Moore's idea seems to be that when in the course of evolution mammals became warm-blooded it was necessary to save the testes from exposure to the higher temperature by means of the scrotal sacs. But there are many mammals in which the testes are normally abdominal, namely, sloths, seals, elephants, Cetacea, and the primitive Monotremata. The birds also have a temperature considerably above that of mammals, and yet retain the testes in the original position in the abdominal cavity. A temperature of 104 ° F, as in the common fowl, is not therefore incompatible with spermatogenesis, and the only logical conclusion is that the evolution of the scrotum has nothing to do with the necessity of keeping the testes at a lower temperature, but that as the scrotum was evolved spermatogenesis became adapted to a lower temperature and cannot now continue at the higher temperature of the abdomen. In the Rodents the testes are retracted within the abdomen occasionally, and this temporary contact with the higher temperature has no ill effect.

DYSHARMONIC, HETEROGONIC, OR DIFFERENTIAL GROWTH

The relation between sexual or sex-limited characters and the sexual hormones has been recently studied from another point of view, namely, the rate of growth of the sex-limited structure in comparison with the rate of growth of the whole body. The attention of biologists was directed to this subject by Prof. Charles Champy in 1924, in a book [1] containing numerous illustrations, original observations, and novel ideas. In Coleoptera and other insects it had long been noticed that the conspicuous excrescences of the males are larger in proportion to the body, in other words more developed, in the larger specimens than in the smaller. Lameere [2] attributed the differences to differences in the supply of nourishment to the larvæ, some obtaining more food, some less. But there is no reason why a better supply of food to the larva should by itself necessarily alter the proportion of the excrescence to the body; they might both be increased, but retain the same proportion. Champy gives a table showing the relative lengths of the elytra, taken as proportional to the total size of the body, and the length of the projecting mandibles in the common stag-beetle. In specimens whose elytra measured 20 mm. the mandibles were 10 mm. long; in specimens with elytra of 29 mm. the mandibles

[1] Ch. Champy, *Sexualité et Hormones*. Paris, Gaston Doin, 1924.

[2] Lameere, Bull. scientif. France et Belg. 1915.

were 30 mm. long. In the first case the mandible was half as long as the elytron; in the second it was 1 mm. longer than the elytron. In some cases, as in the common earwig, it has been found that the variations in the secondary sexual characters do not form a continuous series, but fall into two groups which are distinguished as high males and low males. Champy says that this kind of variation is in opposition to the idea of a phenomenon of evolution which should tend towards variations in various directions. He remarks that it will be regarded as a case of orthogenesis, but that this is merely to give a name to the thing, not to explain it. He believes it to be a 'variation d'ordre purement nutritive', and therefore calls the phenomenon dysharmony of growth, or anisoplasia. It will be evident that although the differences here considered are differences between individual insects each higher stage must have passed through the lower stages in the same individual, either in the pupa or in the later larval condition, and therefore the condition seen in any one specimen is the result of a higher rate of growth in the sexual excrescence than in the rest of the body.

In the Coleoptera the projections on the head or thorax and the enlarged mandibles which usually constitute the secondary sexual characters are well developed externally, like the other appendages, in the pupa, and are visible through the pupal cuticle. There is little if any increase of size in these outgrowths in the imago as compared with the pupa. But the outgrowths develop internally beneath the skin in the later stages of the larva, and thus we see that the greater proportional size of any such outgrowth in the largest individual is the result of the outgrowth increasing at a greater rate than the rest of the body, although the growth is not externally visible, as it is in the horns of a ruminant or the claws of a crab. Generally, though not always, the same kind of dysharmony is found on comparing species with one another—that is to say, the larger species have disproportionately larger excrescences.

Champy points out that dysharmony is the same phenomenon which has been studied by the palæontologists under the name orthogenesis. Cope and Osborn have pointed out how in series of the same genus in geological succession the size of body often increases while the specialized structures increase to a disproportionate degree. Osborn refers to series of the giant mammal Titanotherium as an example. The palæontologists consider such cases as exhibiting evolution in a definite direction ; according to Champy the phenomenon is purely nutritive, the only evolution being an increase in total size of which the relative enormity of special structures is the necessary consequence. He points out that the palæontologists have found that the giant forms with the most enlarged special structures are the last terms of the series, the type having then become extinct, and this according to Champy is the necessary result of the dysharmony, a further increase in general size involving such increased size and weight of the excrescences that life becomes impossible.

Champy discusses the case of the calling crab, formerly known as Gelasimus, but now by application of the absurd laws of priority as Uca, in which one of the large pincer claws, or chelæ, sometimes the right sometimes the left, is of enormous size compared with the other claws and with the body. Here the growth or rather the visible increase in size occurs only at the successive moults in the same individual, while in the insect it appears externally at one moult. He represents in Uca as well as in the insects the relation between the size of the special structure and the body graphically in curves.

Champy, reviewing the numerous experiments which have been made to ascertain the relation of the testicles and ovaries to epigamic structures in Vertebrates, concludes that there is certainly a sexual hormone derived from the testis and another from the ovary, and that its effect is 'all or nothing'. A certain minimum amount of testis tissue in the form of grafted fragments or regenerated growth is sufficient to maintain such sexual characters as the comb and wattles of a cock or the thumb-glands of a frog ; less than this has no effect and more has no greater effect : the dysharmonic growth does not vary with the quantity of testis tissue, but in some cases is much modified by conditions of nutrition, i.e. by the amount of nutriment available, and also in some animals by obscure conditions associated with captivity as compared with freedom in the natural state. The action of the sexual hormones is, therefore, qualitative and not quantitative. Champy concludes from his studies that the development of the sexual differences is for the most part due to a sensitivity, positive or negative, to the hormones emitted by the sexual organs, that it is this sensitivity which varies racially and specifically and that nothing indicates that the hormones vary. Although he does not consider the question of evolution itself his view evidently agrees with my opposition to Morgan's suggestion that epigamic characters are to be regarded as by-products of the hormones.

The last Section of Champy's volume is devoted to the theory of Bouin and Ancel, adopted by Steinach, that the sexual hormone in the male has its origin in the special cells of the interstitial or intertubular tissue of the testis. Champy rejects this theory entirely on several grounds. He points out, firstly, that the development of intertubular tissue varies much in different animals. In pig and horse the cells are large, in Rodents and other Mammals very small. In adult birds they are extremely small. In *Rana esculenta* the tissue is abundant, in *R. temporaria* very scanty. Among fishes the tissue is well developed in Selachians and most Acanthopterygians, absent in Cyprinidæ and Salmonidæ. He refers to experimental evidence in frogs as the most decisive evidence against the theory. Partial castration is followed by the development of testicular nodules with spermatozoa in some cases, none in others, and always without the special cells in the intertubular tissue; yet the glands of the thumb which depend on the testis hormone are fully developed. Champy holds that the intertubular cells, whose development is generally in inverse proportion to that of the seminal cells, contain reserves of nutriment for the latter. When spermatogenesis is proceeding these reserves are given up to nourish the spermatic cells; when spermatogenesis ceases spermatic cells are absorbed and material derived from them is deposited in the intertubular cells. Champy concludes that the hormone is derived from the testis in general, and that there is no need to seek for it a special cellular origin, but it is evident from many of his statements that he attributes it chiefly if not exclusively to the reproductive cells within the tubules.

The subject of dysharmonic growth has been studied further by Prof. T. H. Morgan and by Prof. J. S. Huxley, who calls it heterogonic growth. The latter gave a lecture on the subject at the Oxford meeting of the British Association in 1926. With Morgan he investigated the growth of the large claw of the fiddler or calling crab, Uca (Gelasimus) at Wood's

Hole, Mass. and by himself that of the claw of the large spider-crab (Maia) at Plymouth in this country. It was found that where the ratio of the two rates of growth, that of the organ to that of the body, remains constant, as in these two cases, the ratio is represented by the formula $y = bx^k$, in which $y =$ the weight of the organ, $x =$ the weight of the rest of the body, and b and k are constants. Champy constructed graphic curves for some of his cases of dysharmonic growth, and points out that they are not far removed in form from a parabola. Huxley's formula, though not representing a parabola except when the constant k is 2, represents curves which are paraboloid in character. Huxley remarks concerning the special outgrowths of Coleoptera, that since they only appear in the imaginal stage we must postulate the formation at a heterogonic rate of some substance which determines the size of these organs. As pointed out above, however, the organs are already formed to some degree in the pupa, and not merely a determining substance, but the material of the actual tissues of the organs must have been developing in the later larval stages.

Huxley proceeds to maintain that this heterogonic growth throws important light on several subjects in Biology, namely on taxonomy or classification, certain forms or races being merely size variations, on polymorphism in ants etc., on embryology with regard to recapitulation, and on evolution with regard to orthogenesis, i.e. evolution in a direct line of modification. Without wishing to deny the importance of the more precise knowledge of heterogonic growth which has been obtained by the researches of Champy, Morgan and Huxley, I think it is necessary to realize that they do not afford any explanation of the phenomena with which they deal, but merely describe them. With regard more precisely to epigamic structures, Huxley does not even mention that they are confined to one sex. Champy added considerably to our exact knowledge of the relation of the growth to the sexual hormone. But neither he nor Huxley considers the question why these particular outgrowths occur in a particular family, genus or species and not in others, why they are thus affected by the sexual hormone, and why they are related to special functions and to the sexual habits of the species. It was known before that in many cases, as in the antlers of stags, these structures were larger and more complicated in the older animals than in the younger, although the constant relation to the growth of the body had not been distinctly ascertained. Deer hunters and foresters have always known that the antlers of successive years in the same stag are not only larger in proportion to the body, but have a larger number of branches, and as trophies they are prized according to the number of ' points ' they show. In extreme old age the development of the antler again declines in some degree. It is also a fact, as mentioned by Huxley, that in the same species such as the Red Deer, the largest geographical races such as the Wapiti or Canadian race (which it is not necessary to regard as a distinct species) develop the largest antlers, not in the same proportion to the weight of the body as in smaller forms, but in greater proportion. The Irish elk was of great size with relatively enormous antlers, and there is reason to believe that its extinction was the consequence of this heterogonic growth, the great size involving such a disproportionate size and weight of antlers that the animal succumbed to this handicap in the struggle for existence.

But there is one important peculiarity in the case of antlers which those who have studied heterogonic growth have omitted to consider, namely, the annual shedding and recrescence of these massive structures. If Huxley's formula is true for antlers, it can only be applied to the succession of fully developed antlers in successive years. This represents the rate of increase in size in proportion to the body, but not of the same antlers. Each pair of antlers accomplishes its whole growth in a few months, and the formula for this differential growth, if ascertained, would be very different from that of the increase of size in excessive fully developed antlers. If we take the excrescences of the Coleoptera, the antlers of Cervidæ, and the chela of the calling crab, we have three very distinct types of heterogonic growth. In the first case the external excrescences appear for the first time in the pupa, are complete in the imago, and undergo no change afterwards; in the second the excrescences are shed and redeveloped annually; in the third the same chela grows continuously throughout life, although the visible increments of size appear only at the successive ecdysis or moults of the shell. Now the shedding and recrescence of the antler has nothing whatever to do with differential growth. We might regard the growth of the body during the recrescence as zero in comparison with that of the antler. There probably is an increase of weight of body, and possibly of size too, during the period when the antler is growing, but these increases are so slight in comparison with the rate of growth of the antler that the latter might be regarded as growing from a body of constant size, as the nails and hair grow in an adult human being. This remarkable process of shedding and recrescence is not to be explained as the result of a 'mechanism for heterogonic growth', as other changes are explained by Huxley. I have shown elsewhere[1] that it is

[1] *Sexual Dimorphism in the Animal Kingdom*, London, 1900, pp. 78 *et. seq.*

related to the fact that the external skin and the periosteum (together known as the 'velvet') which cover the antler during growth are shed when the growth is complete, being actually rubbed off by the action of the stag itself, that this denudation of the bone surface causes the death of the bone, and that the phagocytes at the base of the antler absorb the dead bone there, so that the whole drops off, and a new antler grows from the scar of the old one. In the Bovidæ on the other hand, the external skin is not removed, the epidermis forms a layer of horn, and growth of both horn and bony core is continuous and slow. Heterogonic growth also affords no explanation of the relation of the antlers to fighting between rival stags. All these various facts are explained by the Lamarckian theory and shown to be connected with one another.

Huxley's reasoning concerning the relation of heterogonic growth to development and to recapitulation in particular is in my judgment fallacious. All development which is not merely an increase in size without change of the proportions of parts and organs implies, and is the result of, difference in the rate of growth of the several parts, and this is especially true of the rapid change of structure which is known as metamorphosis. I do not know the particular cases of Brachiopods to which Huxley refers in the abstract of the lecture to which I am referring, contained in the Sectional Transactions in the *Journal of the British Association Meeting*, 1926, but he states that the half-grown and young stages represent the adult stages of an earlier and a much earlier form respectively, and that this can be shown to be due to the new type being produced by differential growth in certain regions of the shell. If this means that the new characters are merely the continuation of a differential growth which began in the young stage and are, therefore, the necessary consequence of increase of size of the whole animal it would be true that there had been in this case no change in the direction of evolution. But when Huxley states that many cases of recapitulation are direct consequences of differential growth of parts, I would reply that all development, not merely all recapitulation, is the direct consequence of differential growth. Huxley next considers vestigial organs which he explains as due to negative heterogonic growth: "wherever a vestigial organ recapitulates past history by starting of greater relative size than that which it finally reaches the recapitulation may be equally well put down to negative differential growth being the simplest biological method for producing an organ of smaller size". Huxley appears to mentally visualize the matter in this way: the organ may not be actually smaller in the adult individual, but only relatively so, and thus it is simpler for it to develop almost to its complete size at an early stage, and then to grow at a slower rate than the rest of the body, or not at all. But why should this be simpler? Would it not be equally simple for the organ to develop directly to the same relative size in the young animal which it has in the adult, and then to continue to grow at the same rate as the body? Another statement in the Abstract cited is: "Thus, recapitulation of growth stages may be only recapitulatory as an accident, the essential fact being the convenience of differential growth as a developmental mechanism". This last phrase, 'convenience of differential growth' has to my mind no scientific meaning whatever. Huxley has made no attempt to show that differential growth is a simpler method of developing a small part or organ, or to explain what he means by the 'convenience' of this kind of growth. The term seems to be due to a personification of Nature, which is not a scientific proceeding. We must discuss growth and development in terms of cause and effect. A vestigial organ means one that is without function or utility, and therefore the simplest way of dealing with it would be to omit it altogether; there is no necessity or advantage in its presence, so far as the survival of its possessor is concerned. We see that it has been inherited from the animal's ancestors, and heredity is the cause of its presence. Heredity is also the cause of the greater relative size and development of the structure in the earlier stages of life, which is a more complex and indirect mode of reaching the final size, not a simpler way, and certainly affords no convenience to the individual. A useless vestige such as that of the eye in the blind-fish (Amblyopsis) of the Kentucky caves, might just as well be entirely absent in the embryo as it virtually is in the adult. If the eye is entirely functionless, and useless for vision in the adult, why is it more 'convenient' that the rudiment of the lens and retina should be developed in the embryo as in other fishes and degenerate at later stages? There is no essential difference, only a difference of degree, between useless vestigial organs, and the entire absence of organs in the adult which are developed as rudiments in the embryo. Why is it 'convenient' that teeth which are entirely absent in the adult should be developed in the upper jaw of the calf, in the jaws of whalebone whales, and in those of Ornithorhynchus, and then disappear by negative heterogonic growth in the course of the development of the individual? The facts of mutation show that negative differential growth is not a necessary mode of reducing or eliminating an organ formerly present in the adult ancestors of a given race. Absence of wings as a mutation in Drosophila, absence of pigment in albinos, absence of horns in polled cattle, absence of limbs in all stages of development in all snakes except Pythonidæ, show that organs may be entirely lost without recapitulation. The only rational explanation of negative differential growth in relation to reduction or loss of organs is that disuse and absence of external stimulation has caused gradual decrease of the organ in the individual in each generation with cumulative effect due to the heredity of the process. The case of the development of the urinogenital system in mammals, to which Huxley refers, is in a different category, organs developed in one sex being reduced in the other and vice versa. But here the mesonephros, which is equally developed in both sexes in the embryo, becomes vestigial in the female, and is developed into the epididymis, an essential organ, in the male. This is obviously due to the fact that in the male the organ in the course of evolution has become adapted to the discharge of the sperms, while in the female the oviduct has had a different history. Other instances of rudimentary parts in one sex representing parts fully developed in the other, e.g. clitoris in the female, mammary glands in the male, have nothing to do with recapitulation; they are organs originating in the evolution of mammals, and their rudimentary condition in one sex is due to heredity controlled by the hormones from the ovary and testis respectively. They are in fact typical examples of sex-limited characters. Few, if any, biologists who have considered the matter would agree with Huxley that, if the development of the mammalian urinogenital system were recapitulatory, we should be led to the conclusion that the ancestral mammal was hermaphrodite. Hermaphroditism properly means that ovary and testis are present in the same individual, and of this there is no indication except in rare individuals at any stage of mammalian development, but embryologists are agreed that the similarity of the two sexes in the embryonic condition of the excretory system, putting aside the copulatory organ and the mammary glands, recapitulates the condition in the ancestral vertebrate, not the ancestral mammal. In the adult frog, and the tailless Amphibia generally we find a primitive embryonic and ancestral condition of the excretory system persisting throughout life ; the mesonephros is equally developed in both sexes, and in both is the functional excretory organ, while the metanephros, which is the functional kidney in mammals, is not differentiated. With regard to the male and female genital ducts in mammals, the male duct being the duct of the mesonephros is necessarily recapitulated in the female with that organ. We have thus only the oviduct in the male embryo left to suggest a resemblance to the recapitulation of a hermaphrodite condition. But the oviduct, to judge from the rather obscure indications in the earliest stages of primitive vertebrates, was originally derived from the duct of the pronephros or original kidney, and this organ with its duct was naturally developed in both sexes. The fact, therefore, that the oviduct is more developed in the embryo of the male mammal than in the adult is no indication that it ever served for the passage of eggs in a hermaphrodite ancestor.

Striking cases of recapitulation occur in the development of many animals, e.g. that of the crab with vestigial tail from a larva with tail like a lobster's, of the degenerate sessile Barnacle from an active larva similar to that of many other Crustacea, of the degenerate Ascidian or Sea-squirt fixed to a rock from an active larva with characters similar to those of the early stage of a Vertebrate. But the most important case from its fundamental character and from its occurrence in Vertebrata, including man, is that of the gill-slits and gill-arches in the higher Vertebrates. It seems to me impossible to doubt that in this respect the embryo of reptile, bird, or mammal repeats the larval stage of its amphibian ancestor, or that the amphibian larva, e.g. the tadpole of the frog, repeats the adult character of the ancestral fish. Now in the metamorphosis of the amphibian the gill processes disappear, the gill-slits close up and cartilages and arteries of the arches are reduced and adapted to new functions. Before metamorphosis the arches develop in proportion to the body; in the embryo there must be local differential growth, but nothing like the simple increase in size of the claw of the calling crab. During metamorphosis there is negative heterogonic growth of the gill structures, positive of the lungs and of the legs. But it can scarcely be said that the growth of these organs bears a constant relation to that of the body, for in the later stages of metamorphosis in the frog the body is diminishing. It is evident, then, that the metamorphosis is a recapitulation of the process by which the fish became adapted to terrestrial existence, and that it consists of the differential growth of various organs, but the latter fact affords no explanation of the process. The question is, what caused the differential growth, and how was it that the changes of growth corresponded in the organs of locomotion and respiration with the changed conditions of life?

Similar considerations apply to the case of the flat-fishes or Heterosomata. Here the lower eye changes its position from the lower to the upper side of the head, and this is due to the differential increase of the tissues between the dislocated eye and the lower side of the mouth. Special growth of the ectethmoid and frontal bones on the outer side of the dislocated eye forms a new arch of bone between that eye and the mouth. The growth of the dorsal fin forwards takes it to the outer side of the dislocated eye instead of along the original axis of symmetry between the eyes. Huxley stated that many cases of recapitulation were the direct consequences of differential growth. My reply is that all changes in development are the consequences of differential growth, and it has long been recognized that such changes may be recapitulatory or not. For example, there is no reason for believing that the gills of certain aquatic insect larvæ are organs which were present in the ancestors of insects. But the important problems are what were the causes of the origin of the differential growth, and what the explanation of recapitulation. Adam Sedgwick pointed out long ago that recapitulation occurred in the embryo, when the embryo, as in the higher Vertebrata, represented the larval stage of the ancestor, to which I added the additional conclusion that recapitulation in larval forms only occurred when the larval form as in Amphibia continued to live under the same or nearly the same conditions as the ancestor, while in cases such as snakes the mode of life was similar from birth or hatching throughout life, and there was neither metamorphosis nor recapitulation. It may be added that in such cases as the aquatic larvæ of insects, it is the larvæ which have adopted new habits and evolved new adaptations, so that the adult resembles the ancestor more than does the larva.

This brings us to the subject of orthogenesis as understood by H. F. Osborn, and other palæontologists. In the Titanotheriidæ, according to Osborn,[1]

[1] *Origin and Evolution of Life.* New York, Charles Scribner's Sons, 1918, p. 263.

several distinct lines independently develop horns and show subsequent disproportionate increase of horn-size with increase of body size. Huxley urges that to explain the facts we need only postulate (1) the existence within the group of a developmental mechanism for differential horn-growth, and (2) an increase of body-size during geological time. With regard to the increase of the proportional size of horns in the same line of descent this would cover the facts, but how are we to explain the origin of horns in the first place? Osborn tells us that eleven principal branches of the family radiate from the earliest known form *Eotitanops*, which is small and hornless. Are we then to suppose that the mechanism for heterogonic growth was in existence before the horns first appeared? I know no reason for such a supposition, and therefore we have still to find the cause of the origin of the horns in Titanotheres as in other cases. Apparently these outgrowths, nasal and paired in Titanotheres, were not confined to the male sex, but there can be little doubt that they were used for fighting as in existing Bovidæ, and that thus in the one case, as in the other, both the origin and the heterogonic growth can be explained on Lamarckian principles as the result of the mechanical stimulation caused by fighting. It is reasonable to suppose that fighting with the head required a certain size and weight of body, and that this is the reason of the absence of horns in the smallest and most ancient forms. It is somewhat more difficult to understand why similar horns should arise, as Osborn tells us they did, independently in different times in different branches of the family, but even this is not incompatible with the Lamarckian explanation, for the animals being all of similar form and habits it is quite conceivable that when in the course of evolution they reached a sufficient size and weight they would begin to fight with their snouts in the same way.

The horses, according to the palæontologists, exhibit a similar orthogenetic evolution in independent branches of the genus, that is to say in independent lines of descent. Thus Osborn states that "during a period of not less than 500,000 years the horses of France, Switzerland and North America evolve in these widely separated regions in a closely similar manner and develop closely similar characters in approximately a similar length of time." Here we have heterogonic growth of the toes in opposite directions associated with increase of body-size in the course of evolution. The earliest known fossil horses (Hyracotherium of the Lower Eocene) are four-toed, having lost the first digit, and are of very small size. The subsequent evolution consisted in the continual increase of size in the third toe and decrease of the second, fourth and fifth. The fifth toe was entirely eliminated in about a million years, three-toed horses (Hipparion, Oligocene) had the third toe largest and a smaller on each side, while in the existing form the lateral toes have disappeared altogether, only the metacarpals and metatarsals belonging to them remaining. Could we explain this evolution of the horse by increase in the size of the body associated with developmental mechanisms for positive heterogonic toe-growth for the middle toe and negative heterogonic growth for the lateral toes? In this case of the horses we have examples of most of the phenomena mentioned by Huxley in different animals, namely, increase and decrease in proportional size of a part with increase of size of the body, recapitulation, vestigial organs and orthogenesis. Heterogonic growth expresses the facts in some degree, but it does not explain them. If we consider the third digit we see that it has increased in proportion as the size of the body increased in evolution, while at the same time the lateral digits have decreased in proportion to the size of the body. In this case and in that of the Titanotheres we have to distinguish between the increase (or decrease) in relative size of the organs considered in the series of adult forms of succeeding generations, and, on the other hand, the continuous increase in relative size in the same individual as in the chela of Gelasimus. Of the latter kind of growth little or no evidence in the fossil skeletons of the Titanotheres is mentioned by the palæontologists. It is interesting to consider how far it occurs in the existing horse. Actual observation of changes of this kind in the embryo has not been carried out very extensively. Embryological research usually stops at the stage when the principal systems of organs are differentiated, and does not follow their further development in detail. Moreover, specimens of the fœtus of the horse are not easy to obtain. Prof. Cossar Ewart, however, has published descriptions of the bones of the fore-limb in embryo horses of 20 to 50 mm. in length.[1]

In the smaller of these embryos the ulna was complete and entirely separate from the radius, whereas in the adult it is reduced to the olecranon process and distally united with the radius. In the embryo of 35 mm. length the distal end of the second metacarpal when the connective tissue surrounding it was removed was found to contain distinct rudiments of all three phalanges of the second digit. The metacarpal of the third digit was much shorter in proportion to its thickness than in the adult, exhibit-

[1] J. C. Ewart, *Development of the Skeleton of the Limbs of the Horse*. Journ. of Comp. Pathology and Therapeutics, 1894, Journ. Anat. and Physiol., vol. xxviii, 1894.

ing, therefore, both heterogonic growth in the individual and recapitulation. The development of the horse's leg and foot does not, however, completely recapitulate the stages of evolution seen in Hyracotherium and Hipparion. We must distinguish therefore between such heterogonic growth in the individual, continued throughout life, as is seen in the large claws of Gelasimus and heterogonic growth in evolution as in the toes of the horse. A young individual of a larger species of Gelasimus of a certain body-size would have the enlarged chela of about the same relative size as that of another form in which that body-size was the maximum. Here again the real problem is what were the causes of the change in the relative sizes of the toes in the horse, and it is evident that the results are related to change in the stimulation to growth produced by change in speed of locomotion.

The degree to which the sole of the foot is raised off the ground corresponds in mammals to increased rapidity of movement, the effect being to increase the leverage and mechanical efficiency of the limb. Probably, considering the speed of digitigrade animals such as wolves, something must be attributed to bulk and rigidity of body in explaining why, in the ungulates, the support of the body was ultimately transferred to the tips of the toes covered by the hooves. In wolves, the body is light and flexible, and is used as a spring alternately flexed and extended ; in the ungulates the speed is more exclusively due to the leverage of the legs themselves. When the animal stood and moved entirely on the tips of its toes the change involved greater strains on the bones of the toes and on the original horny claw. The stimulation of the latter caused change of growth and increase of size, transforming it into the hoof.

The strains on the bones necessarily fell on the middle toes, while the outer ones were less used. Thus, on the theory that the effects of use and disuse are in time inherited we have the explanation of the positive heterogonic growth of the central toes and negative heterogonic growth of the outer toes. The difference between the odd-toed horses and the even-toed ungulates is obviously due to the fact that in the former the centre of support in the foot was through the middle of the third toe, in the latter between the third and fourth. The difference between the adaptive changes in the development and evolution of the horses and the continuous outgrowth of secondary sexual structures such as the claw of Gelasimus and the antler in stags is that in the latter the stimulation is of a more local and intense kind. In Gelasimus I do not profess to decide whether the principal stimulus to growth is external impact of the claws against each other in fighting or the internal stimulus of exercise of the muscles. We know that Gelasimus constantly waves the enlarged claw with a rhythmical movement, and that growth of muscles results from exercise or functional activity. There is an obvious difference between the adjustment in the size of internal bones to strains of weight sustained, and the tension of tendons, and the exostosis due to violent irritation of the superficial periosteum, as in the antlers of stags.

The post-natal development of the body in the human species offers a striking and interesting example of differential growth of various parts, which has been studied and measured with some care in connexion with physiology and medicine. The proportions of head, legs, arms, and body at different ages are shown in a diagram to the scale of 1 : 25 in Prof. Roaf's *Text Book of Physiology*, London, 1924, p. 578, and by another method in Feldman's *Antenatal and Postnatal Child Physiology*, Fig. 63. In the latter the whole body is shown as of the same size at each stage, so that the difference of proportion is more conspicuous.

In the adult the height of the head is $\frac{1}{7}$ th of the total height from crown of head to sole of feet=70 in.

Actual height of head, 10 in.

In the new-born infant the height of the head is $\frac{1}{4}$ of the total height=20 in.

Actual height of head, 5 in.

The legs, on the other hand, are shorter than the body at birth and considerably longer than the body in the adult. There is a point here which requires further exact investigation, and which might well engage the attention of those who are studying the subject of differential growth. It seems evident that both the head and the posterior limbs have increased greatly in proportion to the body in the recent evolution of man; the face has of course decreased, but the brain and therefore the cranium have increased. Yet at the time of birth the head and with it the brain have their *maximum* relative size, the legs their minimum. Similar facts are noticed in other animals. For example, the legs have increased in length in the last stages of evolution in the horse, but they seem to attain their greatest *relative* size in the new-born foal, in which they are very long in proportion to the body. Again, in the chick of the common fowl just before hatching, the head is about equal in length to the body, and the eyes are relatively enormous, while in the adult fowl the head is relatively very small. In some cases, therefore, it appears that the most specialized organ (brain in man) attains a relatively large size at an early stage, in others (legs in man), at the end of development. In the former case we have negative heterogonic growth; in the other, positive.

In general the precise study of differential growth which has recently been carried on is of great importance and value, but it is a fallacy to regard it as an explanation of anything. Its value lies in being a more extensive and more precise description of the biological phenomenon to be explained. There is a tendency in modern biology to suppose that when structures and functions have been measured and the results expressed in curves, graphs, or mathematical formulæ, the causes of them have been discovered. But no more can be obtained from a mathematical calculation than is put into it at the beginning, mathematics afford an exact and concise method of expressing measurements and relations. It is true that there is probably no such thing as a final or ultimate explanation; every attempt may be a stage or approximation to a deeper explanation, every cause discovered may be due to a deeper cause. Nevertheless, description and explanation are different categories. The description of the motions of the planets in their orbits round the sun is one thing, but these motions have to be explained by the principle of inertia or persistence of velocity and the mutual attraction of the bodies themselves, i.e. gravitation. Then the cause of gravitation has to be sought, and the Einstein theory claims to supply it. The final word has probably not been uttered on this question. It may be considered in a sense that the great size of an elephant or an oak is explained by its continued growth, and the relative size of parts by their differential growth. But this is in no sense a real explanation. The question is, what is the cause of the process which Huxley calls "a mechanism for heterogonic growth"?

It has been indicated in the preceding pages that all development and metamorphosis is due to differential growth, and therefore we are only considering some particular problems of heredity, development, and especially evolution. The ultimate causes of cell-nutrition, cell-division, and growth we do not know ; they are fundamental phenomena of life. But we know that individual development is inherited from parents and ancestors with modifications and variations in the succession of generations. In investigating differential growth, therefore, the problems to consider are the modifications and variations by which the processes we see in existing and extinct animals arose. It is not only an advantage, but a necessity, in following this investigation to compare the different processes and find how far it is possible to classify them. The cases originally studied by Champy were all secondary sexual characters, and it was to these that the term dysharmony was applied by him. Thus, we have one class of cases of differential growth. But if we take these typical examples of secondary sexual structures investigated by Champy, and those who have followed him, namely, the projections in male Coleoptera, the antlers of stags, and the chelæ of Gelasimus (Uca) and other Crustacea, we see that they show very different kinds of growth. The first two types are both excrescences, they are new outgrowths from the general structure of the body as seen in the majority of the class of animals to which their possessors belong. But the excrescences of insects are permanent when once developed, while antlers are shed and redeveloped every year. The enlarged chelæ of Gelasimus and other Crustacea, on the other hand, are enlargements of appendages normally present in Decapod Crustacca, not excrescences at all, and the same is true of the mandible in stag-beetles. In some of the Brachyura (Inachus) there are three stages in the differential growth of the chelæ, small crabs with chelæ of the male form, but not much enlarged in proportion to the body, middle-sized males which have chelæ similar in form and size to those of females of similar size, and large males with much enlarged chelæ. In the middle males the testes are in a quiescent state and reduced in size, so that here as in other cases the variations in the rate of differential growth at different periods of life appear to be dependent on the variations in the activity of the testis. Champy points out that sexual characters which are specially adaptive, such as the specialized antennæ of male insects (Saturnia, a moth, Tetralobus, a beetle), the copulatory organs of the crayfish (Astacus), show little dysharmony.

Here, as I have pointed out elsewhere,[1] we have a more limited relation between growth and external stimulation than in structures common to both sexes, for the intense external stimulation in the case of antlers and probably of the excrescences in insects is confined to the males, and in the enlarged chela of Gelasimus the intense functional activity is not only confined to the males, but confined to one side of the body. The relation to the testicular hormone (or whatever plays a corresponding part in insects and crustacea) explains why the special growth though inherited by both sexes only normally takes place in the male sex.

On the other hand, we have the vast number of cases of differential growth in development and metamorphosis, to some of which I have already referred, and most of which are associated with recapitulation. It does not seem possible to divide these into different classes according to the nature of the

[1] Cunningham, *Hormones and Heredity*, London, 1921.

structures or the kind of growth. It is evident, however, that they are related to adaptation and changes of adaptation. How far the differential growth continues throughout life in these cases has not been precisely ascertained, but it is evident that in most cases it does not. There are of course many cases among the lower Vertebrata, and perhaps Invertebrata, in which the characters of the older individuals differ in some degree from those of the younger, but the asymmetry of the flat-fish, the size of the toes in the horse, the proportions of the limbs and body in man, or other mammals, or birds, do not much if at all change after full development. Notwithstanding all the differences which have been mentioned, I think the important common factor in all these cases is not the differential growth itself, but adaptation. Adaptation is determined by external conditions which under pressure of multiplication of individuals causes difference and change of habits, and involves passive and active (functional) stimulation, and the rate of growth is determined by the stimulation. This principle applies equally to the secondary sexual characters such as antlers and chelæ, etc., for here the stimulation is due to fighting confined to the males and continuing throughout life. Huxley found that the legs behind the chelæ were also larger in the male than in the female, and concludes that the excessive growth of the chelæ induces over-growth in the neighbouring parts, probably by the diffusion of chemical substances. There is at present no evidence for this assumption, especially as the size of the third maxillipeds which are next to the chelæ anteriorly are not at all affected. It seems much more probable that the legs behind the chela are also to some degree involved in the great activity of the chela, and that their slight increase of size is related to this. In

Gelasimus the striking fact is the enormous enlargement of one chela as compared with that of the other, and this is obviously related to the greater functional activity of the one as compared with the other. Whether the Lamarckian theory or the inheritance of modifications determined by stimulation is true or not, it is certain that all the phenomena are more satisfactorily explained on this hypothesis than on any other.

All this special study of heterogonic growth is part of the study of changes in the development of the organism after the embryonic or fœtal stage. From the point of view of evolution it does not afford any new evidence concerning the causes of the changes which have occurred, but it is valuable because it shows more clearly what these changes are. It exhibits characters not as stationary structures, but as processes of growth in relation to one another, and to the body as a whole. We have to inquire not merely what was the cause of the evolution of the extraordinary projections of male Coleoptera, of antlers in stags, of the enlarged chela of one side in Gelasimus, but what was the cause of their differential growth. With regard to non-sexual cases of metamorphosis and recapitulation little has been added to what we knew before. But the point I wish to insist upon is that each case offers a separate problem. The idea of selection from all possible variations has been abandoned by many biologists; the concept of mutation does not explain why some cases of growth are influenced by the sexual hormone, others are not, and does not explain the various peculiarities of differential growths in different cases. We still have to consider the explanation of the evolution of each case, why horns arose from hornless ancestors in Titanotheres, deer, oxen, sheep, antelopes, etc., why the horns were nasal in Titanotheres, frontal in other cases, why antlers are annually shod and reproduced, why the claw of one side and not the other in Gelasimus increases disproportionately to the body throughout life, why horses show an orthogenesis in evolution of the toes without the continuous differential growth seen in horns, how the terrestrial vertebrate was evolved, and why the process is recapitulated in the metamorphosis of the frog and the embryonic development of the Sauropsida and Mammalia, and thousands of other questions. In all such cases the differences of structure and growth correspond to differences of external stimulation.

BIOMETRICAL RESEARCHES OF WELDON ON *CARCINUS MOENAS*

Differential growth is brought out in a very remarkable way in the biometrical investigations on the shore crab, *Carcinus mœnas*, carried out by W. F. R. Weldon, F.R.S., in the years 1894 to 1898.[1]

Weldon and his collaborator, Thompson, made very exact measurements of a large number of the crabs, not in the adult condition, but specimens from 10 to 15 mm. in length of carapace. In each specimen the frontal breadth was measured, that is the distance between the points of the two most anterior teeth on the edge of the carapace outside the orbits and not as stated in a popular account of Heredity recently published,[2] the maximum breadth of the carapace measured between the most posterior lateral teeth.

[1] *Natural Selection in the Shore Crab*, Carcinus *mœnas*. Presidential Address to Section D, Zoology, Report Brit. Assn., Bristol Meeting, 1898, and Proc. Roy. Soc. vol. lvii. 1894.

[2] E. W. Macbride, *Introduction to the Study of Heredity*. Home University Library, London, 1924, pp. 124-127.

Each frontal breadth was then recorded as a fraction of the length of carapace, the latter being taken as 1,000; in other words, the frontal breadths were given in thousandths of the length of the carapace in the median dorsal line. At the beginning of his discussion of the subject Weldon makes the important statement that the mean frontal breadth varies so rapidly with the length of carapace that it was necessary to determine it separately in small groups comprising crabs having a range of only 0.2 mm. in length. In order to consider the data and the conclusions drawn from them it is necessary to give here in full the figures in Table IV of Weldon's Address.

MEAN FRONTAL BREADTH OF MALE *Carcinus Moenas* FROM A PARTICULAR PATCH OF BEACH AT PLYMOUTH IN 1893, 1895, AND 1898.

Length of carapace in mm.	*Mean frontal breadth in carapace length as 1000*		
	1893	1895	1898
10.1	816.70	809.08	
10.3	812.06	804.82	
10.5	807.37	803.27	
10.7	808.98	801.69	
10.9	805.07	799.27	
11.1	802.50	794.12	784.25
11.3	798.18	792.38	787.36
11.5	798.18	792.38	784.00
11.7	794.28	785.29	782.44
11.9	791.45	786.53	780.09
12.1	788.38	780.61	775.25
12.3	783.98	779.50	773.42
12.5	783.99	776.50	767.00
12.7	783.58	773.43	772.43
12.9	777.38	773.63	764.67
13.1	776.63	771.61	760.13
13.3	774.60	766.21	761.29
13.5	766.91	763.96	759.56
13.7	767.63	762.00	757.00
13.9	763.73	759.40	756.10
14.1	758.94	757.00	742.00
14.3	756.90	755.77	747.86
14.5	762.60	754.45	744.44
14.7	753.00	749.84	739.22
14.9	751.32	748.03	742.83

Thus, if we look at the figures for 1893, we see that the mean frontal breadth of crabs from 10.0 to 10.2 mm. in length was 816.70, while that of crabs from 14.8 to 15.0 mm. in length was 751.32. in thousandths of the length. An increase of 4.8 mm. in carapace length involves a *diminution* of 65 thousandths in mean frontal breadth. This, therefore, is an exact measure of the rate at which the frontal breadth decreases in *proportion to* the total length of the body of the crab. The *absolute* measure of the frontal breadth has *increased* at the same time from 8.2 mm. to 11.1 mm. The frontal breadth is therefore growing, but at a slower rate than the total length of the crab—that is to say, the frontal breadth shows a negative heterogonic or differential growth.

The table shows that the mean relative frontal breadth at each small range of length was less in 1895 than in 1893, and again less in 1898 than in 1895. The number of crabs measured in the last of the three years was small, but it will not affect my criticism if we consider the figures in the third column as equally valid with those of the other two. Weldon concluded that the diminution in relative frontal breadth was due to a selective death rate of crabs with the greater frontal breadth at each size. As I pointed out at the time, when the evidence and the deductions from it were published, it is logically impossible to draw any conclusions with regard to selection in the case of a character which is changing in the individual during growth, because it is impossible to distinguish between differences between two individuals and differences in the same individuals at different stages of growth. In every case with few exceptions if we examine the column of figures for 1895 or 1898, we see that the larger the crab the smaller is the survival value of the frontal breadth in proportion to the carapace length. In other words, it would follow from Weldon's argument that the proportional frontal breadths which were fatal to small crabs of a given carapace length permitted the survival of others which were only $\frac{1}{5}$ of a millimetre shorter. If we compare the figures for 1895 with those for 1893, and take any one of the frontal breadth values, that for 14.5 mm. carapace length for example, we see that the mean frontal breadth of 762.60 in 1923 is supposed to have been reduced by selection to 754.45 in 1895, and to 744.44 in 1898. But in the samples of crabs measured in 1895 there are plenty of individuals with a relative frontal breadth much greater than 762.60, namely all those with a carapace length less than 13.7 mm. The figures therefore themselves prove that selection was not in fact taking place with respect to relative frontal breadth. They merely show that crabs of a given frontal breadth were smaller, or of less carapace length, in 1895 than in 1893, and still smaller in 1898. Thus, crabs of about 762/1,000 in frontal breadth in 1893 were 14.5 mm. in carapace length, in 1895 13.7 mm., and in 1898 12.8 mm.

The above seems to me to be the first fallacy in Weldon's argument. The second is that of assuming that the relative frontal breadth would affect the filtration of the water entering the gill-chamber. According to Weldon the decrease in the figures of the second and third columns is due to the death of crabs with the greatest relative frontal breadth and survival of those with least relative frontal breadth, owing to the increase of suspended silt in the water of Plymouth Sound, the narrower relative frontal breadth forming a more efficient filtering apparatus, while the greater relative frontal breadth allows more silt to enter the gill chamber and so impedes respiration. Obviously, the relative frontal breadth could not in itself make any difference in the process of filtration at all; the exclusion of particles of silt of given size must depend on the absolute size of the entrance to the gill chamber, not to the proportion which that size bears to the body-length. If we compare the relative frontal breadths for any given carapace length in the three years we are dealing with absolute breadths; for example, if we take 12.5 mm. of length, then 783.99, 776.50, and 767.00 are all thousandths of this same length, and therefore of decreasing absolute size as well as relative size in the three selected years. But this is not the case for different carapace lengths, although it might have been, i.e. the absolute frontal breadth might have remained constant while the carapace length was increasing by growth. But it does not remain constant. To show this I have converted all the relative frontal breadths into absolute equivalents in mm., and thus transformed Weldon's original table into that shewn on next page (Table II, p. 194).

It is surprising when we consider that Weldon was supporting a hypothesis of filtration of water containing suspended particles of silt, that he did not give the absolute measurements of frontal breadth which he must have taken, instead of converting them into relative breadths or fractions of the body length. Now, if we study the absolute breadths which are given in Table II, we see that while they have decreased for any given carapace length in the three years, they have increased in any one year with the growth in length of carapace; if we compare the figures horizontally and vertically, we see that they decrease in the former direction and increase in the latter. Thus, the supposed mortality of the greater breadths at any one length is contradicted by the

TABLE II

Length of Carapace in mm.	*Frontal breadth in mm.* 1893	1895	1896
10.1	8.248	8.171	
10.3	8.364	8.289	
10.5	8.477	8.434	
10.7	8.656	8.578	
10.9	8.775	8.712	
11.1	8.907	8.814	8.705
11.3	9.019	8.953	8.897
11.5	9.179	9.112	9.016
11.7	9.293	9.187	9.154
11.9	9.418	9.359	9.283
12.1	9.539	9.445	9.381
12.3	9.642	9.587	9.513
12.5	9.799	9.706	9.587
12.7	9.951	9.882	9.809
13.1	10.173	10.108	9.957
13.3	10.302	10.190	10.125
13.5	10.353	10.313	10.239
13.7	10.516	10.439	10.370
13.9	10.615	10.555	10.509
14.1	10.701	10.673	10.462
14.3	10.823	10.807	10.694
14.5	11.057	10.939	10.794
14.7	11.069	11.022	10.866
14.9	11.194	11.145	11.067

increase with growth at all greater lengths. If the greatest frontal breadths at the length of 10.0 to 10.2 mm. with an average breadth of 8.248 mm. were being killed off by a selective death-rate, it would be impossible for any to survive to reach a frontal breadth of 11.194 mm. ; and conversely, if the selective death-rate was acting on the crabs of 14.8 to 15.0 mm. carapace length, with an average frontal breadth of 11.194 mm., then it could scarcely act, if it was due to filtration, on the small crabs of an average frontal breadth of 8.248 mm., for they would have a filtration so much more efficient that they would be exempt from selection in this respect.

It is clear, therefore, that the supposed process of selection could not be taking place, as Weldon supposed, at all these successive stages of growth, and that what the figures show is the differential rate of growth of the frontal breadth, as compared with the carapace length or general size of body. Now if this rate of growth were constant for all conditions and times, i.e. if Huxley's formula, $y = a\,x^{k}$, were the same at different times and under different conditions, then the mean frontal breadth would be constant for a given carapace length. Weldon's measurement in different years shows that this is not the case. We have a different value of mean frontal breadth for the same carapace length in three different years. The decreasing *relative* frontal breadth shown in Weldon's table indicates a stage of development, and thus we see that in 1895 and 1898 the same stage of development was reached at a smaller general size. In other words, crabs of the same size were more advanced in development in 1895 and 1898 than in 1893. It so happens that we have independent evidence from Mr Walter Garstang,[1] at that time on the staff of the Laboratory of the Marine Biological Association at Plymouth, that the physical conditions on the south-west coast of England in 1893 were exceptional. He writes that from the middle of March there were six months of calm seas and almost cloudless skies. He continues: "Under the influence of the great heat the temperature of the Channel waters rose continuously until in August it had attained a point unprecedented for a quarter of a century". "Numbers of semi-oceanic forms which rarely reach our shores arrived in remarkable profusion; even the bottom fauna was influenced."

The third fallacy in Weldon's hypothesis is the

[1] W. Garstang, M.A., *Faunistic Notes at Plymouth during 1893-94*. Journal of the Mar. Biol. Assn., vol. iii, 1893-95.

assumption that smaller frontal breadth implies smaller apertures for the entrance of water and silt. The fact is that water does not enter the gill chamber below the frontal breadth, but farther back at the bases of the large pincher claws, and actually passes out by an aperture below the frontal breadth. W. Garstang in 1897[1] published a paper describing observations from which he concluded that the teeth on the edge of the carapace posterior to the frontal breadth measured by Weldon formed a sieve over the space between the large chelæ and the lower surface of the carapace when the crab was imbedded in the sand, and that this sieve served to keep out particles of sand from the space mentioned, which conducted water to the inhalent branchial apertures at the base of the chelæ. Garstang's sieve would not be fine enough to exclude silt. His conclusion applies chiefly to the Portunidæ, which include Carcinus, the shore crab; but Cancer, the edible crab, is quite as much addicted to burrowing in the sand as the shore crab, and it has no prominent teeth on the lateral edge of the carapace.

But Weldon thought that his hypothesis that the decrease of frontal breadth in the given years was due to a selective death rate caused by increase of sediment in the water was strongly supported by certain experiments which he carried out at the cost of much time and labour, and it is necessary to criticize these experiments. The first, and simpler one, consisted in placing 148 small male crabs in water, with a quantity of very fine china clay kept suspended by stirring. After a number of the crabs had died it was found that the survivors had a lower average frontal breadth than those that died. But it is not stated that the survivors

[1] Walter Garstang, M.A., *Function of Anterolateral denticulations in Sand-burrowing Crabs.* Journal Mar. Biol. Assn. vol. iv. 1895-97.

were, on the average, of the same carapace length as the dead, and it may therefore be assumed that those with the larger frontal breadth (in proportion to length) were smaller, and therefore younger and weaker. The same objection applies to another experiment, in which fine mud from the shore was used, instead of china clay. In a final experiment, Weldon placed a number of small crabs of similar sizes to that of those used in the rest of the investigation, one in each of a number of separate bottles, in clean water, and fed them. The object of this experiment was to protect the crabs from being killed by sediment until they had cast their shells, to find whether in the absence of a selective death-rate the diminution of the average frontal breadth would also be absent. A certain number of the crabs died, which was attributed to the presence of putrid particles of the food, which it was difficult to remove entirely from the bottles. A certain proportion of the crabs survived to cast their shells, and the mean frontal breadth of these shells was less than that of a similar number of wild crabs from the shore. This was considered to be due to the fact that the previous deaths were selective, those with greater frontal breadth being killed by the presence of particles of putrid food. When the new shells had had time to harden, all the surviving crabs were killed and measured, and the mean frontal breadth was found to be greater than that of similar wild crabs from the shore, which was held to be evidence of the absence of a selective death-rate in the absence of silt.

It requires little consideration to perceive that this is not by any means a rigidly logical conclusion from the given data. In the first place the cast shells of the crabs which survived should have been compared, not merely with a similar number of wild crabs from the shore, but with those which had died in the course of the experiment. If the deaths were selective, then the mean relative frontal breadth of those which died should have been greater than that of those that survived, i.e., of the cast shells. This comparison is not given. With regard to the comparison between the cast shells and the wild crabs, Weldon was maintaining that the latter were subject to a selective death-rate from the silt, so that he assumes the selective death-rate due to particles of putrid food was higher than that due to silt, although the evidence of the experiment depended on the assumption that the mortality due to inefficient filtration had been eliminated by the supply of clean water. It may be admitted, however, that in the relation between the cast shells and the same crabs after the moult, there was no room for selection. We may assume that all the crabs which had cast their shells were measured, so that the dimensions could have been compared with those of the cast shells, but this comparison is not given. In any case, it is stated that the same crabs before the moult had a less mean frontal breadth than wild crabs of the same sizes (carapace lengths), and after the moult a greater frontal breadth. There is, of course, an increase in size, i.e., carapace length, at the moult, and the result is held to prove that the wild crabs had been subject to a selective death-rate in relation to frontal breadth during the growth from the one size to the other. But the same result might have been due to a different cause, namely, a greater increase of size at the moult in the crabs under experiment than in those in the natural habitat, so that those of the same size in nature were, on the average, actually older, and therefore had a less mean relative frontal breadth. The crabs fed in the experiment probably had more food than those which had to forage for themselves on the shore, and probably the temperature at which they were kept was higher than that of the shore. The conclusions drawn from the whole investigation were therefore invalid, because the differential growth of the frontal breadth was not taken into consideration.

I have considered this investigation in detail, not merely to prove that it was not, as supposed, evidence of natural selection in actual operation, but because it is a valuable example of heterogonic growth studied with great care and accuracy, showing how such growth may be affected by external conditions.

CHAPTER VII

MIND AND CONSCIOUSNESS

The question of the possibility of inheritance of modifications produced by external stimuli arises in relation to the functions or activities of the nervous system as certainly, if not as obviously, as in relation to structural modifications. There are no visible differences of structure in nerve-fibres or nerve-cells corresponding to differences of faculty, or reflex action, in different individuals, human or animal, and therefore the peculiarities or characters studied consist of reflex actions or responses to stimuli, or the actions of animals in special circumstances. In discussing the questions here considered we cannot avoid passing to some extent within the boundaries of the subject matter of the next section, namely, consciousness and mental phenomena.

The behaviour of man or one of the higher vertebrates can be regarded in two different ways, objectively and subjectively, because the actions to be studied are similar to our own actions which are connected with our own conscious experience, will, and feeling. Those who experiment on the response of animals to stimuli in an exclusively objective manner, are called in America, behaviourists, and treat the animal as an automaton or machine. They observe and record what happens empirically, entirely disregarding what the animal may think or feel. We know that in ourselves reflex actions may be independent of the will, as the knee-jerk, for instance, which we feel, but cannot prevent ; or independent of both will and consciousness, as the contraction and expansion of the pupil of the eye, which we do not feel and cannot control. The behaviourists study the actions of an animal simply as reflex actions.

In the investigations of the physiology of the nervous system, especially of the cerebrum, by Professor Pavlov and his pupils, all reflex actions are divided into two general classes—those which are due to the inherited constitution of the animal, and those which are acquired by the individual animal or man as a result of its own experience, and do not necessarily occur in other individuals of the same species. The two kinds have been distinguished by two technical terms, namely, unconditioned, and conditioned reflexes A conditioned reflex is set up experimentally by applying an additional stimulus simultaneously with, or a little before, the stimulus which gives rise to an unconditioned reflex. For example, a slight blow on the tendon connecting the patella to the tibia, causes the knee-jerk in the human subject. If a bright flash of light is shown at the moment the mechanical stimulus is applied for a number of times in succession, then if the mechanical stimulus is omitted the jerk will be caused by the visual stimulus alone. The secretion of saliva by the parotid gland in the dog was found to be a very convenient reflex for these experiments. It is easy to make a fistula in the duct, and then measure the response to stimulation by counting the number of drops of saliva secreted. Suppose that a sound of a certain pitch was to be used as a stimulus for a conditioned reflex. The production of this sound before the experiment caused no secretion of saliva. Then, at the moment of the production of the sound, a little food was placed in the dog's mouth, and saliva flowed. When this proceeding had been repeated from ten to fifty times the production of the sound without feeding causes the flow of saliva in amount increasing to a certain maximum with the number of times the two stimuli have been repeated. On the other hand, if the secondary or 'conditioned' stimulus be repeated at intervals several times, without being accompanied or followed by the primary stimulus, the conditioned reflex soon ceases; five to seven repetitions at intervals of two to eight minutes are sufficient to effect this extinction.[1]

It is well known that the sight and smell of meat and other foods cause secretion of saliva in dogs, especially young and hungry dogs, in which the saliva often actually drops from the mouth when they are restrained from taking food which is presented to them. Investigation showed that this secretion of saliva is a conditioned reflex acquired by each animal individually[2] and not congenital or unconditioned. Five puppies were removed from their mother and fed exclusively on milk. A separate conditioned salivary reflex was established for each puppy, with different stimuli, visual and auditory, the sound of a metronome in one case, red light in another, and so on. After several months the effect of the sight or smell of meat and other foods was tried, separately and together, and no secretion followed. It is inferred from this that the salivary reflex caused by such sight and smell in ordinary cases in the dog is not inherited, but acquired after birth. This being the case the question arises: how was the unconditioned reflex of salivary secretion to the taste and touch of food in the mouth originally

[1] See Evans, C. Lovatt, *Recent Advances in Physiology*, 1925, p. 339.

[2] *Ibid.*, p. 358.

evolved? Is that also conditioned, and, if so, why does the taste of food cause the secretion of saliva?

It is a somewhat different question whether the establishment of an acquired reflex becomes easier and more rapid in successive generations: whether the establishment in a particular individual implies a change in the nervous system, which is so far inherited that the same change is more quickly produced in the offspring. Experiments in this direction have been made, but apparently full details of them have not been published. The history of the matter so far as I have been able to discover is as follows: Dr G. V. Anrep, Lecturer on Physiology in Cambridge University, has just published (August, 1927) an English edition of a comprehensive work by Pavlov, entitled: *Conditioned Reflexes: An Investigation of the Physiological Activity of the Cerebral Cortex.*[1] The only reference in this volume to the question of heredity is the following footnote:

"Experiments which have been communicated briefly at the Edinburgh International Congress of Physiology, 1923, upon hereditary facilitation of the development of some conditioned reflexes in mice have been found to be very complicated, uncertain and, moreover, extremely difficult to control. They are at present being subjected to further investigation under more stringent conditions. At present the question of the hereditary transmission of conditioned reflexes and of the hereditary facilitation of their acquirement must be left entirely open."

The official Report of the Eleventh International Congress of Physiology, to which the above footnote refers, includes a report of Prof. Pavlov's paper on Inhibition, Hypnosis and Sleep, of which only the last paragraph discusses the experiments mentioned. The

[1] Oxford University Press, 1927.

details of the experiments are not given ; the paragraph is identical with that contained in the Report of the Congress published in the *British Medical Journal* of August 11th, 1923, p. 257, but includes a little more than the corresponding paragraph in the Report in the *Lancet* of August 4th, 1923. In reference to the question whether the experimental establishment of a conditioned reflex showed any hereditary effect if repeated in successive generations, the Report proceeds—

"They had tried to find an answer to that question and had established conditioned food-reflexes in white mice, using the sound of an electric bell. With the first set of wild (!) white mice it was necessary to repeat the combination of ringing the bell and feeding 300 times in order to form well-established reflexes. The next generation formed the same reflexes after 100 repetitions, the third generation after 30, the fourth generation after 10, and the fifth generation after 5 repetitions. The experiment had reached this point when I left Petrograd this summer. On the basis of these results I anticipate that one of the next generations of our mice will show the food-reaction on hearing the sound of an electric bell for the first time. This result would be quite analogous to the well-known fact that a chicken newly hatched tries to pick up any small objects or spots which it sees on the floor."

It seems evident that the conditioned reflex in this experiment differed to a considerable degree from one in which the response was the involuntary secretion of saliva. Apparently the response in the experiments was some movement of the mice to a particular place where food was given to them, and this is confirmed by the statement of Prof. McDougall, that "Pavlov's procedure had consisted in training white mice to run to their food trough at the sound of a bell ".[1] Prof. McDougall is a well-known specialist in mental philosophy and psychology, and is now Professor of the latter subject at Harvard University, U.S.A. He has carried on experiments on white rats since 1920. When the conclusions drawn from Pavlov's experiments were published as mentioned above, McDougall's had reached the 9th generation of rats, but he states that he continued them because he felt sure that Pavlov's statements were founded on serious error, and he was afterwards informed by Dr Anrep that the positive conclusions of the Russian physiologist were provisionally withdrawn.[2] McDougall claims that the results he has obtained point towards a positive conclusion concerning the validity of the Lamarckian principle, and justify further experimentation. His experiments were made from the subjective or psychological point of view, in contrast to those of Pavlov, which were purely objective. The secretion of saliva is entirely involuntary, and although a flash of light, or the sounding of a note, may be presumed to affect the consciousness of a dog or mouse, the physiologists of Pavlov's school disregard consciousness altogether, and merely consider the sound or sight as an afferent stimulus of the cerebral cortex, which is transmitted to the lower reflex centre at the same

[1] William McDougall, *An Experiment for the Testing of the Hypothesis of Lamarck*. Brit. Journ. Psych. vol. xvii, pt. 4, April 1927.

[2] Dr G. V. Anrep has kindly informed me by letter that a large box was divided into two parts by a partition which was provided with a trapdoor. The mice lived in one part of the box while the other was reserved for feeding, the trapdoor being opened at the sound of a bell. The association of bell and food was repeated from six to ten times a day. Dr Anrep had left Petrograd before the experiments were commenced, but he is informed that after the experiment had continued some time it was not necessary to keep the trapdoor shut, as the mice would not leave their living quarters in search of food unless the bell was sounded. He states however that on repetition of the experiments they failed to give the results described.

time, or just before, the normal afferent stimulus of food in the mouth which gives rise to reflex activity of the salivary gland. In the case of the ' food-reflex ' in the mice experiments, the action of the animals is considered merely as a reflex of the presentation of food, which is observed to follow the sound of an electric bell when the conditioned reflex is established. Prof. McDougall holds that the problems of animal psychology cannot be profitably investigated by these ' behaviouristic ' methods. He considers that the adaptation investigated to test the Lamarckian principle should be one achieved by the intelligent, purposive, efforts of the organism concerned. It seems to me that both the objective and the subjective methods are equally important in themselves, and that it is certainly true that psychological problems cannot be solved by purely objective methods, but on the other hand the inheritance of acquired modifications may occur both in reflex actions, which are automatic and independent of consciousness, and in acquired voluntary and intelligent actions which imply mental faculties.

McDougall's experiments were of two kinds, and were all made on white rats. In the first series the rat was put into water in a tank fitted with two inclined planes, A and B, by which it could escape. These gangways were constructed of ground glass, covered with wire gauze. Each led from a compartment of the tank occupying one-third of the total breadth of the latter, and separated from a middle compartment by a partition in which was an opening five inches long. Under B gangway was a strong glow-lamp, which illuminated it and the chamber to which it led, the rest of the tank being only dimly illuminated. Each rat was placed in the middle tank at the end near the gangways, so that in order to escape it had to swim through either the right or left aperture and reach one of the gangways. The rats showed urgent desire to escape from the water. The wire on gangway B was connected with an interrupted faradaic current, so that the rat received shocks when it came into contact with it. Under these conditions each rat learnt quickly to avoid gangway B, and always take gangway A. But some having taken A from the first and continued to take it, received no shocks at all. To prevent this, a sliding door extending three inches below the surface of the water was placed in the aperture leading to the A chamber, and kept closed for one minute after the rat was put into the water. Under this modified procedure each rat took the B gangway a large number of times, but eventually learnt to avoid B by diving under the door which barred the way on the surface to A.

Two methods of testing were used to ascertain if there was any evidence of the transmission of the results of training : the first was to compare the average number of times each rat took the B—or electrified gangway—before learning to take the A route, in the experimental stock and the untrained controls ; the second method was to make a similar comparison on young rats when put into the tank for the first time. The first method was a test to ascertain whether heredity caused a facilitation of the acquirement of a certain discrimination, the second to ascertain whether the discrimination itself was in any degree inherited independently of training in the individual. After seven generations, of which the first had not been thoroughly trained, and the seventh had not been trained at all, young rats of the eighth generation were tested as to their behaviour the first time they were put into the tank, in comparison with control rats whose ancestors had never been subjected to the tank experiment at all. The following were the results—

I.—210 testings of 35 Control Rats from 6 litters.
Dim A route taken 85 times.
Bright B route taken 125 times.

II.—156 testings of 26 Tank Rats from 7 litters.
Dim A route taken 84 times.
Bright B route taken 72 times.

It seemed, therefore, that in the tank rats there was a distinctly greater avoidance of the illuminated gangway, which might be considered as due to the inherited effect of the training of previous generations; in other words, to the experience of the ancestors or 'ascendants' of an association between the brighter illumination and unpleasant shocks. It was noticed, however, that some, or all, of the members of some litters of the control stock showed a strong bias to one side or the other, which was either a tendency to the right or left direction, or a tendency to the brighter illumination. It was, therefore, just possible that the control stock happened to contain more strains which carried a tendency to choose the bright side—B—than the experimental stock. To eliminate this possible source of error the following modification in the experimental procedure was made.

The wire gauze covering both gangways was so connected with the interrupted current that by turning a switch the current could be sent through either, and at the same time a glow-lamp was placed behind each so that by turning a switch either lamp could be made luminous. Then both currents were switched alternately to the right or left at successive immersions of each rat. Under this system of training the possible association of direction with freedom from shock was eliminated, and the only association was that between bright light and shock. But it was still possible (or at any rate the objection might still be made) that the rats of the experimental stock had a greater innate tendency to avoid the brighter illumination than the controls, and therefore Prof. McDougall considers that it would be necessary to take as criterion the rate at which the offspring of the trained acquired the discrimination as compared with the controls—in other words, to test the question whether there was any hereditary facilitation of acquirement of the discrimination.

The new procedure made the task of the rats more difficult, made a much higher demand on their intelligence. Some of the rats required 330 immersions, or approximately half that number of shocks before they learned to avoid the brighter gangway. Here occurs one of the most interesting and significant points in the results observed by Prof. McDougall, and seems clearly to suggest a psychological process rather than a merely automatic one. Although the effect of the rat's experience was cumulative and was due to the continued repetition of the same event, yet the application of the experience to conduct came almost suddenly and was afterwards almost invariable. For some time before this point was reached the animal would show hesitation and unwillingness to take the illuminated gangway, and yet having reached it take it nearly as often as the other, but at last he would recognize the connexion between bright light and pain, and would decisively turn away and swim to the darker passage. This strongly suggests what we should call reason or intelligence in ourselves, and not merely a reflex mechanism.

With regard to inheritance Prof. McDougall gives the results of testing by both methods indicated above.

I. Results of testing each rat before the beginning of individual training, each rat being tested six times in the fourth week after birth.

	Dim Gangway.	Bright Gangway.
109 tank rats of 10th, 11th, 12th, and 13th generations.	354 times.	300 times.
87 control rats	252 ,,	270 ,,

If to make the difference more obvious we calculate the proportion in each case of the number of times the bright gangway was taken to 100 times of the dim gangway, we have—

	Dim Gangway.	Bright Gangway
Tank rats	100	84
Control rats	100	107

or for every 100 escapes by the dim gangway the tank rats took the bright gangway 23 times less often than the control rats. This certainly seems to be evidence of an inherited aversion for the bright gangway in the tank rats.

Another way is to calculate the percentages of the total number of trials in each case, which gives—

	Dim Gangway	Bright Gangway
Tank rats	54.1%	45.8%
Control rats	48.2%	51.7%

or the tank rats took the bright gangway 8.3 p.c. times less often than the dim gangway, while the control rats took the bright gangway 3.5 p.c. more often.

II. Results of testing 23 tank rats of the thirteenth generation in comparison with 39 control rats with regard to the number of days training required to learn to avoid the bright electrified gangway, each rat being placed in the tank 6 times per day.

	23 Tank Rats.		39 Control Rats.	
Day of Training	*Dim*	*Bright*	*Dim*	*Bright*
1st	62	76	99	135
11th	72	66	108	126
20th	97	41	118	116
30th	115	23	126	108

Prof. McDougall gives the figures for each successive day of the training, but I have selected the days on which (1) the number of times the dim route was taken by the tank rats exceeded those the bright route was taken, (2) the majority of the rats had learned to avoid the bright route altogether, (3) all but two or three rats had learned to avoid the bright route altogether. The difference between the rats of the stock which had been trained for twelve generations previously and the control rats, which were subjected to the treatment for the first time, is sufficiently striking.

Another experiment was carried on by Prof. McDougall during the same period as the tank experiment. His original stock of white rats was divided into two equal portions by dividing each litter at a certain time into two halves, after which the two half-stocks were kept separate and inbred. The half-stock with which the second experiment was made was called half-stock B. The rats used as controls for comparison in testing results were mostly individuals of half-stock T, which had been used for the first experiment, but some of them were unrelated rats newly obtained. The second experiment consisted in forcing the rats to learn to escape from a maze. The usual incentive of food as the reward for escape was considered unsatisfactory because the rat has to be taught that he obtains food when he escapes, and this takes time. The desire to escape from water was therefore used as in the first experiment, but without any alternative paths of escape. The maze was constructed in a tank 3 ft. by 20 in. in area and 20 in. in depth. The tank contained water to a depth of 8 in., and the maze was constructed of vertical walls of sheet zinc. Each rat was taught the route for escape in stages, and the complete route included diving under two partitions extending 3 in. below the surface of the water. If a rat had not succeeded within three minutes he was taken out and allowed to dry and recover, as longer immersion than that was harmful. The training was repeated for seventeen generations, three of which were obtained in each year from 1921 to 1925 inclusive, and two in 1926. The time of immersion of each rat during the first twelve days of training, six immersions each day, was measured with a stop-watch, and recorded. The total times during the first twelve days of training for each rat were thus obtained, and the average total time for each individual rat was then calculated.

The figures show (Table IX, p. 299 *loc. cit.*) that there was a diminution in the average total time spent in the water in the course of the seventeen generations. But the diminution was not quite regular, and the averages for the generations of the same year, February, May, October, showed considerable differences. The average for the May training in the seventeenth generation was higher than that for the same month in any other generation. There are two errors, either typographical or arithmetical, in the averages of column five in Table IX, the second number in the column according to the figures given should be 1044 instead of 1010, and the fourth number should be 813 instead of 846. The average total times of the seventeen generations of the trained rats are distinctly lower than that of the control rats trained only once as a test. Prof.

McDougall considers that the first experiment is superior to the other, and in this he seems to me to be justified. In the first there is one definite association established, the brighter of two similar means of escape being connected with an unpleasant sensation, and the evidence shows that the rats exhibited some degree of inheritance of this association without individual experience, while as a result of individual training the association was established more rapidly and distinctly in successive generations.

RELATION OF MIND TO LIFE AND EVOLUTION

Mr Joseph Needham, to whose views on mechanistic biology we referred in Chapter I, is not a materialist. He does not regard the objects and mechanisms investigated by biology as real, and hold that man and his mind have been evolved from them. He writes : " It is not as if the mechanistic world-view came into our knowledge as something from outside, something given, written on tables of stone, and possessing immutable authority ; on the contrary, it is a product of our own minds, and bears deeply impressed upon it the marks of its origin. Mind, therefore, and all mental processes cannot possibly receive explanation or description in physico-chemical terms, for that would amount to explaining something by an instrument (which is) itself the product of the thing explained ".[1] In this quotation, I have added the two words in brackets, because I think they make the sense clearer.

We have here the full admission of the difficulty which has been obvious to the majority of philosophers and metaphysicians. The question : " Can the

[1] *Science, Religion and Reality*, p. 250.

knowledge of nature be itself a part or product of nature, in that sense of nature in which it is said to be an object of knowledge"? is the first question discussed by T. H. Green, in his *Prolegomena to Ethics*, published in 1883. The knowledge of nature is the aim of scientic research, the nature of knowledge is another and quite different problem.

Mr Needham proceeds to state that the legitimacy of physico-chemical explanations in the realm of physical life has been shown to be well grounded, but as far as mental life is concerned biochemistry and biophysics have no authority. The opinion therefore which seems to him most justifiable is that life in all its forms is the phenomenal disturbance created in the world of matter and energy when mind comes into it. The thought here seems somewhat crude, and inconsistent with the arguments that precede concerning the triumph of mechanistic biology. "Living matter is the outward and visible sign of the presence of mind, the splash made by the entry of mental existences into the sea of inert matter." In that case, what becomes of the mechanism of life? The splash of mental existences seems to be no better or more satisfactory an explanation of vital phenomena than vitalism. According to Mr Needham, the conditions necessary for the action of mind are the properties of the element carbon, and the colloidal state. But this does not explain what is meant by mind. In his further discussion of the subject Mr Needham states that although all living organisms are to be considered as physico-chemical systems, yet at the same time they are as it were musical instruments the keys of which are in all cases played by something, however meagre in mental development it may be. He considers that it is the physical functions of life that physics and chemistry are competent to explain, while such questions as the distribution of animals and the general theory of evolution, which obviously involve the consideration of conscious striving, do not come under their entire dominion. Mr Needham, therefore, himself admits the validity of the criticisms I have made of his argument in the course of the preceding pages, especially that biochemistry and the mechanistic view of life do not explain evolution.

Mr Needham adopts the philosophical view of a relative dualism of matter and spirit, and believes in some kind of psychophysical interaction.

Before we can talk of mind creating a disturbance in the world of matter and energy, we have to consider what mind is. Is such a conception any more valid or legitimate than that of the mind being explained by matter and energy? If the latter are the product of the mind, then the mind cannot very well be conceived as making a disturbance in them: if the mind disturbs its own ideas, the result would presumably be confusion of thought.

It seems to me we must begin the endeavour to investigate mind and consciousness, as Descartes did, with our own experience of our personal consciousness. We have no direct perception of the consciousness of other people, but we may say that we know they have minds and self-consciousness, because we receive by speech, thoughts and ideas from them which are of the same kind as our own. We have in our consciousness percepts and concepts. The percepts are the things perceived, and they appear to be due to effects upon our sense organs. These sensations give us what we call the properties of external bodies. We cannot conceive a consciousness without any percepts. I could not be conscious of myself if I had nothing by which to distinguish myself from anything else. If I had no sensations at all, neither sight, hearing, smell, taste, or touch, nor any internal sensations, how could I think of myself? Concepts are composed of memories and relations of perceptions, and we have no sufficient evidence that they are inherited and can occur without perceptions by the individual. A completely empty consciousness would therefore I presume be unconscious, an empty mind would not be mind at all.

On the other hand, we cannot conceive bodies or objects apart from our sensations. It is true in a philosophical sense that the universe, or nature, is within our minds, although it seems to me that it is not true that it is created by or produced by our minds, or by my mind. When I look at an object and then shut my eyes I no longer see the object. The common sense conclusion may be considered the true one, that the object I looked at is outside my mind, although the sensation I had from it was inside my mind. We cannot conceive of objects apart from the sensations which we receive from them, but we can distinguish a great many ideas or facts of consciousness from the mere properties of matter. Prof. Eddington tells us that the world is to be divided into the metrical and the non-metrical aspects. If we say a rose is red it is easy to understand that the colour is not in the rose, but in the mind. We see a coloured world, the blue of the sky, the green of leaves and grass, the scale of colours in the sunset or the rainbow, but none of these objects have in themselves any colour at all. Our scientific study of light shows us that it is made up of rays of different wave-lengths, and we can measure these wave-lengths. The waves of different lengths are separated by passing through a refracting prism, the shorter wave-lengths forming the violet end of the spectrum and the longer the red end. The difference between them is therefore a difference of degree, just as the difference in sound of a high note and a low note. But the difference between the sensations of red and blue is not a difference of degree, but a difference of kind. We cannot find any unit of colour and say that so many of these units make blue and some other number of them make red. When we hear a siren sounding we can hear first a deep low note rising in pitch to the shrillest sound which is audible, but we feel that all the sounds are differences in one kind of sensation, and we know that the differences of sensation correspond to the differences of wave-lengths or number of vibrations per second. But we do not recognize red as a change of quantity in blue. We can have a scale of red from the lightest to the darkest, analogous to that from the highest to the lowest note, and we may have differences of intensity of red analogous to degrees of loudness in sound-notes, but these differences are quite different from the difference between red and blue. The scientific discussion of colour is to some degree confused by the terms referring to the sensations being transferred to the light rays which produce them. The rays of shorter wave-length are called the violet rays, or the blue rays; those of the larger, the red rays, when what is meant is the rays producing the sensation of red and so on.

We may turn to biology and find that certain cells in the retina of the eye are stimulated by the longer light waves and others by the shorter waves, but the mind is not in the eye. The cells of the retina are connected by nerve fibres with cells in the brain, and it is probably a fact that either the stimulation of different groups of brain-cells, or different frequencies of stimulation of the same group of brain cells correspond to the sensations we call different colours, but that does not explain why quantitative differences of vibration should give rise to such different sensations as those of colour. Although all perceptions are really in the mind, yet the shape, size, weight and movements of objects seem much more external to us than colour, sound, taste and smell. We see objects by the light which they reflect, we feel them by contact, or we feel their resistance to our muscles, and the muscular sense gives us the consciousness of the effort required to move them. But when we look at a rainbow we see no objects at all, we do not recognize its connexion with the raindrops which produce it. When we perceive a sound we do not perceive its source; we trace it to its source by a process of reasoning. A chemical compound such as sodium chloride is represented by many ideas in the mind, its crystalline characters, its composition as a compound of sodium and chlorine, its reactions with other salts and so on. Our knowledge of those qualities is obtained chiefly by sight, but when we taste it we meet with an effect on body and mind which is different from all the others and which is recognized as different. To say that sea-water is salt expresses something different than saying it is liquid, or that a ball is round and smooth We associate smoothness and roundness with the external object, but saltness with a sensation arising in the mouth. We can watch the reaction of sodium chloride and nitrate of silver in a test-tube, but when we taste the sodium salt it has produced a reaction in our own living cells, and we realize this as an effect on ourselves, while we never think of what we see in the test-tube as an effect on our eyes. Similarly in the case of smell, experience teaches us to trace it to its source, but we feel that the sensation is within our minds.

There may be several degrees of deficiency in the colour sense, but the most obvious is the inability to distinguish red and green. It is stated[1] that in some cases colour-blind persons are actually blind to the red end of the spectrum, while others see the whole length of the spectrum, but do not distinguish red in it. In these the longer waves of light produce a sensation of sight, but not of red colour. It seems probable that the stimulation passing along a nerve-fibre is essentially the same in all cases, and that, therefore, the sensation depends on the particular group of brain-cells stimulated. Artificial stimulation of nerve-fibres at any point of their course gives rise to the same result at their termination whatever the nature of the stimulation, whether mechanical or electric for instance. If the sensory or afferent nerves of the leg are stimulated after the foot has been amputated, sensation is felt in the toes, that is to say the stimulation in the brain results in consciousness as a feeling in toes that are no longer there. Artificial stimulation of the auditory nerve causes a sensation of sound, of the optic nerve one of sight. We may suppose, therefore, that stimulation of one group of brain-cells involves the sensation of red, of another that of green, and so on. It is impossible to conceive an element in the consciousness that does not correspond to some action in the brain, for that would imply that the whole of the mind could exist and act independently of the brain. Therefore, hypochromatism, if we limit that term to the condition in which the red end of the spectrum is not seen, might be due to the absence or inefficiency of the group of cells which is associated with the sensation of red. But on the other hand there must be distinct receptors in

[1] H. E. Roaf, *Textbook of Physiology*. Edward Arnold, 1924, p. 418.

the retina for light of different wave-lengths, whether by means of colour screens or otherwise, for if all receptors were stimulated by e.g. red light, then all the optic groups of brain-cells would be stimulated too. Hypochromatism might, therefore, be due to the absence or inefficiency of the receptors for long light-waves.

Heterochromatism, if we use that term for the power to see the whole length of the spectrum, but inability to distinguish red, might be due to the fact that the stimulation of the red group of brain-cells did not produce the red sensation in consciousness. Or it might be due to the fact that the red rays stimulated the receptors in the eye of the other colours as well, so that red could not be seen separately.

Even Prof. Eddington's measurements and observations of scales and clocks are all perceptions by his sense-organs which give rise to percepts or ideas in his mind. Without sensations and perceptions we could have no knowledge of objects, no ideas of them. Therefore, all we know of nature is in our minds, and we can have no knowledge of matter apart from mind. Matter does not exist without mind, and mind or consciousness without perceptions derived from matter (including energy, the two go together) cannot be mind-consciousness. We may believe then that there is some existence which we call matter and energy or nature, or the universe, and there is another existence we call mind, but we cannot have any ideas of them apart from each other : complete separation of them is inconceivable. Of course, it may be objected that the universe was there before we were born, and will be there after we are dead, but we can only conceive of it as it appears to a mind like our own. Knowledge then, or reality, or existence, is not a single thing nor two things which can be known separately, but a relation between two things which are inseparable, the external universe of which we know nothing except its effect on our consciousness, and that consciousness which would be an empty void without percepts derived from the external universe.

Colour, as pointed out above, is a group of sensations which are distinct from the properties of light as revealed by science or reason. But normally the sensation of colour only arises from the stimulation effected by light. If we are right in supposing that there are some number of distinct colour-organs in the grey matter of the brain, the stimulation of one or more of these organs would give rise to the sensation of colour. It is conceivable that a slight pressure from a fragment of bone after a slight fracture of the skull would give rise to a sensation of red, or that the same effect might be produced by micro-organisms in the brain tissue. Even in such cases the sensation would be due to some kinetic energy coming from outside the organ, and producing the same effect as the normal stimulus of light. This suggests the general question of hallucinations of the senses and of the mind, which I can only discuss here very briefly. One test by which a ghost can be distinguished from a real person is whether it can be seen by a number of normal persons at the same time, and that is not quite infallible because of the possibility of suggestion. Another test is whether the impression of sight is confirmed by other senses which indicate the material solidity of the object seen. But in all hallucinations the ideas arise from an excitation of brain-cells which are normally excited by the stimuli derived from external objects.

There are many things in the mind beside mere sensations or the ideas of external objects arising from sensations, and this is not a new discovery, but was well known to the philosophers of ancient Greece. In all ages in which philosophy has been considered at all, truth, goodness and beauty have been distinguished. Truth may stand for science, our understanding of the matter and energy of the universe. But what is beauty? The analysis of the vibrations of sound or the investigation of the sense of hearing, however, for they may be carried, do not explain what music is. There is a science of music, which deals with notes and intervals, and to a certain degree explains harmony and discord, but it does not explain the pleasure to be derived from melody or harmony or orchestration. The word pleasure gives the key to the nature of music and of beauty in general. Beauty is connected not merely with our perceptions, but with our emotions or feelings. And an emotion has been stated, apparently correctly, to be some sensation which affects our principal bodily functions through the nervous system. Pleasure stimulates the circulation and gives a feeling of joy in life, pain or fear drains the blood from the face and suggests the approach of death. Beauty, therefore, whether of art, nature, or woman, is that which suggests pleasure and the satisfaction of desire. The æsthetic sense is thus related to the primitive responses of the living organism to the things which are essential or favourable to life, and which stimulate vital processes. The protozoan moves towards food, or towards its mate, or towards oxygen or towards light and warmth, or away from carbon dioxide and so on. The man or wolf when hungry hunts his prey and devours it when he has killed it. There are two ways of regarding such responses. We may consider the animal as an automaton, as T. H. Huxley considered the cray-fish, and its action in seeking or eating food as a reflex action without any consciousness of the stimulation of eyes or other senses, or we may interpret the animal and its action according to our own experience and conclude that the mechanical automatic response has its counterpart in a state of consciousness, in ideas and feelings similar in kind to our own, however rudimentary. Such things then as the satisfaction of hunger give rise to a state of consciousness or a feeling which we call pleasure, and it seems probable that all the refinements and complications of art in civilized human society are founded on this relation of consciousness to the external world.

When we come to goodness in the ethical sense, or ethics, or morality we have to deal with ideas which have their chief importance and development in relation to human society. It is not merely that the solitary lower animal shows no evidence of an ethical sense and that human ethics were probably evolved from instincts similar to those of social animals such as bees and ants, or gregarious mammals such as wolves and monkeys, but that ethical principles and standards are concerned with the relations of human beings to one another in the family or in society. The first four of the ten Mosaic commandments are religious, the other six belong to ethics The first of these concerns the family, the respect and obedience due to parents from their children, the third deals with the sanctity of marriage, the other four with crimes against other members of the tribe. The fundamental moral principles then are the essential conditions of the institution of human society. Without some recognition of rights and duties there could be no society at all. The family is still more primitive and fundamental in ethics than society. Even the lower mammals and birds exhibit highly developed methods of protecting and nourishing their young, and there are some cases among the fishes. Ethics then consist of the recognition of other individuals as conscious beings like oneself, and of the fact that for the sake of social existence desire must not be satisfied at the expense of other members of the tribe although inter-tribal and international ethics have not advanced very far even at the present day.

The three departments of consciousness thus correspond to three faculties, that of understanding, reason, or intelligence, that of feeling or emotion, and that of will or self-control, which in some degree inhibits or controls the response to stimulation and desire. We have now to consider the relation of this consciousness to life.

When I consider my own consciousness, I cannot believe that it was in operation when I was an ovum, or during embryonic development. I doubt if it was in operation just after I was born. It is difficult to believe that a new-born or very young baby is conscious of its own existence or its own 'self', its own ego, although a child a year or two later is intensely desirous of self-realization. If this be so, the question is when does consciousness begin? There is no moment of time and no event which coincides with the beginning of consciousness, and therefore we must believe that it has no beginning in the individual. It must be the development of some rudiment existing in the fertilized ovum. And here it is curious to note that we are apparently explaining mind by things which are only ideas in the mind itself. I must leave it to others to criticize and solve this difficulty, but it seems to me that I do know that other human beings have a mind like my own. Their voices, etc., are only sensations and perceptions, but their words convey thoughts like my own, and I know that the child which is now fully self-conscious was a few years ago a fertilized ovum. Then if we follow the succession of generations we can in them, no more than in the individual, find a moment or an event which marks the beginning of consciousness. The principle of continuity applies here as elsewhere in evolution, and so far as I can see, there is no possibility of separating life and consciousness. The difference between the ' mind ' of an earth-worm or an amœba and of a man may be very great, that of an earth-worm is merely a potentiality rather than an actuality, but the difference must logically be regarded as a difference of degree, not a difference of kind. In this sense even plants may be considered to have the rudiment or potentiality of consciousness and mind.

Life then is always accompanied by some degree of consciousness. In some sense the two may be regarded as different aspects of the same thing. Regarding an animal objectively, as Huxley regarded the crayfish, we may interpret all its life as mechanical, all its actions as automatic. Objectively we can have no evidence of mind in an animal, or even in another person. We can only observe stimuli and reactions—in other words, mechanisms. With this limitation some biologists may believe that we shall one day succeed in explaining all the phenomena of life as physico-chemical processes. It has already been pointed out in previous chapters that we are far from being able to explain development, heredity, and evolution in physico-chemical terms. We cannot explain how root-pressure in plants forces the ascending sap to the summit of tall trees, nor how the urea in the kidneys is excreted against the osmotic pressure, nor how oxygen is excreted into the bladder of a fish which already has a high pressure of oxygen, nor why a crab's leg when lost is replaced by the growth of another. I have attempted to show in this volume that while the processes of life do not present any exceptions to the laws of physics and chemistry, such as the conservation and dissipation of energy, there are features in the phenomena of life which are not found anywhere in inorganic nature. Therefore if we regard living organisms objectively, although they may be mechanisms they are essentially different from any inorganic, non-living mechanisms. In that sense, I am a supporter of vitalism.

On the other hand, we have a knowledge of life which we have not in the case of non-living nature. We have our own inner experience of our own consciousness, which is more real than any other kind of knowledge, and embraces all other kinds. We know that our consciousness, our existence, is bound up with our own life. We must interpret our ideas and sensations as due to a relation between our minds and an outside world, but we cannot justify a dualism of body and spirit in the sense of a dualism of life and consciousness. As already said, we know that other human beings have thoughts and feelings, that is consciousness similar to our own with almost if not quite the same certainty as we know our own consciousness. That being the case, we are justified in attributing mind and consciousness to dogs and other lower animals.

How and where then does consciousness emerge? Every reaction to stimulus, although even in ourselves some reflex actions are both involuntary and unconscious, must be something more than mere mechanism, must contain the rudiment of a conscious sensation. The paths of afferent and efferent stimulation form nerves and become connected with a central brain, and the stimulation of the cells of the brain is accompanied by feeling and consciousness. Thus, we may say that what physiologists often call the irritability of protoplasm or bioplasm contains the germ of consciousness.

If we could only be sure that bioplasm and life originated automatically from non-living matter at a certain stage of inorganic evolution, we might reason further that the germ of life and consciousness was immanent in matter and energy, so that as energy and matter may be different forms of the same thing so life and energy were one. We should conclude that we ourselves are therefore part of the energy of the universe made conscious. It is in any case certain that our own life is the energy which we take in with our food and which was originally derived from the energy of the sun's radiation, and our consciousness is the subjective aspect of that energy.

Finally, a few words may be added on the subject of will as a phenomenon of consciousness. The living body can neither create nor destroy energy. But we are conscious of the power of controlling and directing the energy of our bodies and minds. We can control our movements and the responses to our instincts. Here again there seem to be two aspects.

When we study other people, and to a certain degree ourselves, we can recognize motives and the actions which follow from them, and we can form a theory that there is no such thing as free will, but merely the response to circumstances and temptations determined by hereditary mental constitution. But in the act of forming such a theory we prove that there is some ' ego ' which is free and not determined. In the mind then it would appear that energy becomes conscious of itself and is able to determine whether it will dissipate slowly in the form of heat, or quickly in the form of active exertion, and what the character and direction of that exertion shall be. Otherwise, we must conclude that the self is merely a passive spectator of the automatic responses to stimuli which take place in his own mind, his conduct being determined by the strongest motives and least resistance in relation to his own character and mental attributes, for which he is not responsible.

SELF-DETERMINATION IN HUMAN EVOLUTION

At the end of his Inaugural Address on election to the Professorship of Zoology at King's College, London, Mr Julian Huxley, after a brilliant survey of the newest facts and ideas in Physics, Chemistry, Biology, Psychology and Philosophy, expressed his agreement with the suggestion that science was giving man control of his own evolution. This is an idea which would naturally attract enthusiastic minds, would appeal to the younger people who are apt to exaggerate the importance of modern methods and discoveries, to regard what are called Victorian notions as belonging to the Dark Ages, and to have visions of a near future in which all things will be known, and all ideals realized. But as it is a suggestion made in the name of science, it ought to be carefully analyzed and examined in relation to the scientific evidence bearing upon it.

Eugenics we know, the subject has been for some years before the educated public, and there is an important society for the investigation of it and the promotion of knowledge and interest concerning it. There is also a very considerable literature concerning Eugenics. It means the application of biological knowledge to human reproduction, with the direct purpose of eliminating hereditary defects and undesirable characters and of so preventing some of the worst social evils. It has been proved that not only bodily characters but mental and moral peculiarities are hereditary, and in many cases it has been shown that the heredity follows Mendelian laws. But what exactly are we to understand by control of human evolution? Much evidence has been collected of the heredity of such abnormalities as colour-blindness, brachydactyly or short fingers and toes, polydactyly or possession of supernumerary fingers, feeble-mindedness, insanity, genius, and excess or defect of various mental faculties such as the musical, the mathematical, the artistic. It has been shown especially by American investigators that workhouses, gaols and asylums are largely peopled by those who are descendants of defective parents and forbears. It has been maintained that modern tendencies of civilization favour to an increasing degree the inferior stocks and handicap the superior, that the general effect is the survival of the most unfit. Preventive medicine helps to keep alive children with inherited constitutional defects and with liability to disease. Socialistic legislation to a great extent takes the direction of public expenditure for the benefit of the children of those who are less able to provide for them by their own efforts, and who are improvident and deficient in ambition, industry, and independence. Socialism in practice at the present time usually takes the form of national and municipal expenditure, without any corresponding socialistic production. The people of better stocks cannot afford to have children themselves in any considerable number because they are so highly taxed to provide public services for the benefit of the poor and needy and unfit. Theoretically it is easy to state that if only those with the most perfect and desirable hereditary characters produce offspring, undesirable qualities will be eliminated, and thus, in course of generations, a population of individuals who are healthy in body and mind will be established. Mutations will occur, those which consist of defects or absences of normal qualities must be eliminated, those which are on the positive side or above the previous normal will be allowed to transmit themselves, and so upward evolution will go on. *Sic itur ad astra.*

But in practice, how is this biological science to be applied? Such a control of man's evolution requires the control of man; in other words, if men are to control their own evolution, they must first control themselves. Will the ideal of Eugenics ever be more than a dream? The most powerful influence in evolution is the multiplication of individuals, the increase of population, the fact on which Malthus and Darwin based their enquiries and their conclusions. Increasing populations seek more territory. Emigration affords one kind of relief to congestion, but human history shows only too plainly how the movement of populations in search of new territory led to devastating wars in which the strongest and bravest individuals had the least chance of survival. The tribes and races which were strongest in war and best organized were the victors, and in this sense the inferior were more or less eliminated, but it is by no means certain that the individuals with the most desirable or highest qualities survived. In modern times the rivalry is still partly for territory, but also for markets for exported goods, for supplies of raw materials, and for national power. The Great War, which began in 1914, shows that the danger of war is not less than in former times, while from the biological point of view, probably no war was ever more destructive of individuals who were of the highest quality from the point of view of Eugenics. The destruction of the desirable gametic 'genes' was less than it might have been because the women of the best stocks for the most part escaped.

In considering the possibility of the control of human evolution under peace conditions at the present time we might give attention first to individual highly civilized states, such as our own, or the United States of North America. The tendency of modern legislation as already mentioned is to diminish individual responsibility, to make it possible, if not easy, for people to live without working, to produce families who are provided for by the State, and to maintain institutions for the benefit of those who are genetically below the normal. In addition to this, the exclusion of undesirable aliens is not rigorously carried out. There does not seem much prospect of any conscious attempt or even desire on the part of the general public or the politicians to exercise a control of human evolution in the genetical sense.

If we look at other races of the world, the possibility appears still more remote. I believe the survival of female infants is to some extent prevented in China, and so the increase of population to that extent checked, but it would be absurd to believe that within any period of the future short enough to be worth considering now, the multitudes of the populations in Eastern Asia, India, or Africa will have advanced so far in culture and education as to contemplate the application of principles of Eugenics to themselves.

Prof. Huxley, in referring to man's control of his own evolution, was doubtless speaking as a geneticist. We must therefore enquire what sort of evolution we could produce if we were able to apply the principles of genetics to human reproduction. The science of genetics is based on the heredity of unit characters which are determined by units in the nuclei of the gametes called genes. The units are inherited according to the laws of Mendelism. New characters arise by mutations, and a mutation may be the loss of an old gene or the first appearance of a new one. But according to the orthodox genetical doctrine and excepting the few possible cases of induced mutations mentioned previously, mutations are uncontrolled. We cannot obtain the mutations we require, we are obliged to take those that occur spontaneously. It may be suggested that mutations in all directions would occur in man sooner or later, but there is no evidence of the probability of this, and as the control apparently is merely to discourage the transmission of undesirable genes, there is nothing to show where the mutations that were not positively undesirable would lead. We should have first to decide what improvements, mental, moral, or bodily, were desirable, and then preserve them if mutations in the desired directions occurred. If they did not occur we should be helpless. This can scarcely be called control of evolution. We may consider as actual examples of what is possible firstly such cases as that of the experimental breeding of the American fruit-fly, Drosophila, by T. H. Morgan and his school, and secondly, the breeding of cultivated animals and plants. Most of the mutations which have been recorded in Drosophila have been negative, defects of the eyes, wings, and other organs. In some cases there have been positive mutations such as the presence of two pairs of wings instead of one. But it cannot be said that there has been much evolution of Drosophila in controlled directions. When we study the changes produced by cultivation of plants and animals, it may be urged that they have been changed by human control in directions corresponding to human requirements. The quality and quantity of the wool of sheep, the quality of the flesh of animals used for food, the production of milk and eggs, the strength or fleetness of horses, the quality and size of vegetables and fruits, the beauty of flowers, all these might be cited as examples of remarkable improvement under human control. But, on the other hand, it is obvious that in every species of animal or plant under cultivation a still more conspicuous change is the divergence of the original type into a number of distinct races and varieties distinguished by the most marked and often extraordinary characters which have not been determined in the slightest degree by man's control. Man can only preserve them and propagate them when they appear. We have seen in a previous chapter how little the extraordinary characters of Japanese gold-fish owe to human control. When a gardener wishes to get new varieties he has to wait for a mutation and then cross it with the original form, and usually, he obtains a number of different types, but he cannot foretell what they will be. I myself believe that in some cases, as in the long-tailed Japanese fowls, definite external stimulus has had much to do with the evolution. But here I am considering the relation of human control to the principles which the geneticists assume to be fundamental and universal. It seems to me that the idea of man's control of his own evolution is contradictory to the essential principles of Mendelism and mutation, except in a very much restricted sense of the word control. To take a simple illustration: three of the most familiar defects of civilized man are defects of sight, defects of teeth, and deficiency of hair. Under the conditions of urban civilized life these defects apparently tend to increase. If civilized man can control his own evolution he might ' try his 'prentice han' ' on these three kinds of defect, and earn the gratitude of his posterity. When we consider the question of man's control of his future evolution, it is relevant to consider one aspect of his evolution in the past, namely the differentiation of human races. At present, biological science is unable to tell us how this differentiation was controlled. The racial characters are certainly hereditary, and it is doubtful whether they are all adaptive, or to be attributed to conditions of climate, habit or environment in general. In any case, the geneticist would not admit that effects of environment could be hereditary. If the characters arose by mutation, by what were they determined or controlled? It is possible that by crossing, together with mutation, new varieties of the human species might arise. The segregation of a white race of Panama Indians has actually to a certain degree occurred. But apart from segregation, it is evident that there is little if anything in our knowledge of the diagnostic characters of the races of mankind and their relations to habits and environment, to suggest that the origin of new varieties in the future could be consciously controlled in accordance with the facts and theories of genetics.

I am in complete agreement with Prof. McDougall in his concluding remarks in the paper discussed in the first Section of this Chapter. He expresses the opinion that an answer to the question: Does Lamarckian transmission occur? is imperatively needed by biology and by all the social sciences. He believes that if the Lamarckian principle is valid, the social outlook, the prospect before our civilization, is very much brighter than if it be illusory. It seems to me that there is no justification in the biological knowledge we have at present for speaking of human control of human evolution, unless the effects of external conditions and external stimuli are accumulated by heredity. For if the effects of habits, conditions of life, and training are limited to the individual person, they are powerless in comparison with unforeseen and uncontrolled mutations. In relation to civilization and the improvement of civilized man, the important question which is so generally ignored by modern schools of biology is the evolution of adaptation. In relation to this, I would draw attention to some of Prof. McDougall's remarks in reference to his experiments on rats. He states that there is some slight indication that among the descendants of trained rats, some individuals show well-marked evidence of the effects of ancestral training, while other individuals show no such evidence, that the transmission of effect of training follows a law of segregation reminiscent of Mendel's law, the effect being transmitted to some individuals and not at all to others.

If the above conclusion is sound, it suggests that there is something in common between the phenomena of mutation and the inheritance of the effects of stimuli. It is often tacitly assumed that these effects are similar on all individuals, but there is reason to think it probable that though the effects are in all cases in the same direction, they are greater and more easily produced in some individuals than in others. Exercise in human beings and animals strengthens and enlarges muscles, but some individuals respond more than others to the stimulus. If the chromosomes of the germ cells are affected in some degree we may suppose that they are more modified in the individuals in which the muscles have responded most. Then in breeding, if there is no selection we have pairs of modified chromosomes which may be represented as $b + b$ uniting in fertilization with others to be represented as $a + a$, very slightly modified, and so in the next generation the heredity will be represented by the unions *aa*, *ab*, and *bb*. Thus, the individual differences will tend to increase rather than decrease unless, as seems probable, the conservatism or resistance to change of the less easily modified individuals is ultimately overcome. In any case, the fact that the effects of conditions are inherited in different degrees is, if the above reasoning is correct, no disproof of the Lamarckian doctrine. It has been maintained by rigid adherents of the mutation doctrine that the tameness of domesticated animals is not due to the conditions of domestication and the inheritance of its effects, but entirely to the selection of the less ferocious individuals. The admission, however, that when a number of wild individuals are taken and kept in captivity some are less ferocious and more tameable than others is not inconsistent with the belief that the effects of domestication on the individual are to some degree inherited by the offspring, and therefore cumulative in successive generations.

Prof. McDougall concludes that if the Lamarckian principle is not valid the conflict between eugenics and euthenics (the improvement of the conditions of life) seems destined to continue while our western civilization declines and decays. If Lamarckian transmission occurs he thinks we should be none the less ready to support eugenic research and practice, for seventeen generations of rats would represent about five centuries of human life, and he doubts whether our civilization can maintain itself through five centuries unless some great improvement in the quality of our stock be effected in that time.

To discuss the question of the maintenance of civilization in relation to biology would be a great undertaking, and is far beyond my purpose in the present volume. The term 'improvement of our stock' is somewhat vague, and indefinite. It would certainly include the bodily health and vigour of the population. The question in relation to this is whether improvement can only come from the elimination of the constitutionally abnormal, diseased or inferior types, or will result from preventive medicine, medical care of children, and better conditions of life in general. If Lamarckism is true, the improvement due to external conditions will be cumulative in successive generations; if not, eugenic measures are alone effective, and these are neutralized by the preservation of the congenitally unfit. But even if Lamarckism is true we have to consider that the exercise and training of faculties and functions are more important than mere healthy conditions such as fresh air, sunlight, and food. Civilization means for many decrease in such exercise of bodily and sometimes of mental functions. The richer classes ride in motor-cars and sit in offices till they forget how to walk; the workers ride, if not in their own cars as in the United States, in omnibuses and tram cars, and spend the greater part of the day in factories. Bodily exercise, therefore, has to be provided artificially by games and sports; and biologically such movements as that of boy-scouts, girl-guides, and territorial army training are of the greatest value.

Mental and moral training are also equally necessary. But training will not prevent the production of the mentally deficient and feeble-minded. Biological science does not enable us to assert that such congenital deficiency can be prevented or cured, and all we can do is to consider how the reproduction and multiplication of such defectives can be diminished or abolished.

In modern times the conditions of life of civilized man, which means now nearly the whole of mankind in Europe, Asia, Africa, America, and Australia, are being rapidly altered by the increase of population, the progress of scientific invention and the increasing exploitation of stores of potential energy accumulated in past ages. These changes, although due to human enterprise, are not the result of any deliberate conscious effort to produce new conditions. At the same time we have a great extension of scholastic or literary education, a relaxation of traditional moral restrictions a rapid development during times of peace of the means of mass-destruction of human life. The organization of society has to be and is being adapted to these changing conditions, and it is necessary that we should consider the ideals to be aimed at in the conditions of human life and in human life itself. But in spite of the progress that has been made in the investigation of heredity it is too soon to dogmatize with regard to practical applications of our knowledge of the subject. All we can safely say is that it is a good thing that people should realize the grave responsibility of handing on hereditary defects, whether of body or mind, to the next generation ; that a healthy public opinion with regard to eugenics is highly desirable, and, on the other hand, that the development of the highest faculties, bodily, mental, moral and æsthetic, in the individual is also an ideal worthy of endeavour, while if the effect of training and exercise in the individual is in any degree inherited by the children, so much the better. It is very probable that the neglect of exercise and training causes a loss of faculty which is also in some degree inherited.

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