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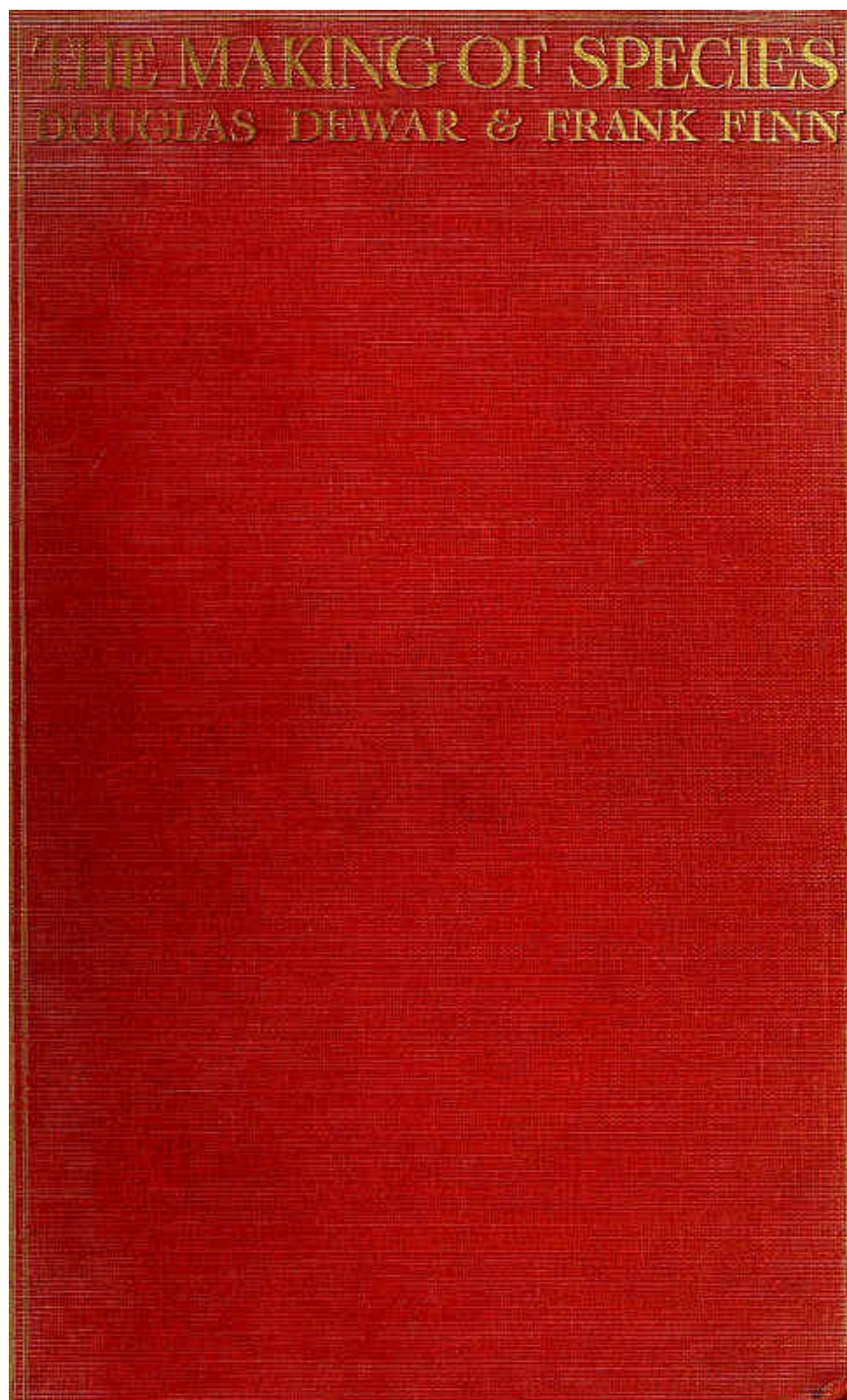
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HEX CURASSOW FEEDING YOUNG BIRD, WHICH HAS THE PLUMAGE OF THE HENS OF THE GLOBOSE CURASSOW, ITS FATHER'S SPECIES

THE MAKING OF SPECIES

BY DOUGLAS DEWAR, B.A. (Cantab), I.C.S., F.Z.S.
AND FRANK FINN, B.A. (Oxon), F.Z.S., M.B.O.U.
WITH FIFTEEN ILLUSTRATIONS

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[v]

PREFACE

Post-Darwinian books on evolution fall naturally into four classes. I. Those which preach Wallaceism, as, for example, Wallace's *Darwinism*, Poulton's *Essays on Evolution*, and the voluminous works of Weismann. II. Those advocating Lamarckism. Cope's *Factors of Evolution* and the writings of Haeckel belong to this class. III. The writings of De Vries, forming a group by themselves. They advocate the theory that species spring suddenly into being; that new species arise by mutations from pre-existing species. IV. The large number of books of a more judicial nature, books written by men who decline to subscribe to any of the above three creeds. Excellent examples of such works are Kellog's *Darwinism To-Day*, Lock's *Recent Progress in the Study of Variation, Heredity, and Evolution*, and T. H. Morgan's *Evolution and Adaptation*.

All four classes are characterised by defects.

Books of the two first classes exhibit the faults of ardent partisanship. They formulate creeds, and, as Huxley truly remarked, "Science commits suicide when it adopts a creed." The books which come under the third category have [vi] the defects of extreme youth. De Vries has discovered a new principle, and it is but natural that he should exaggerate its importance, and see in it more than it contains. But, as time wears on, these faults will disappear, and the theory of mutations will assume its true form and fall into its proper place, which is somewhere between the dustbin, to which Wallaceians would relegate it, and the exalted pinnacle on to which De Vries would elevate it.

In the present state of our knowledge, books of Class IV. are the most useful to the student, since they are unbiassed, and contain a judicial summing-up of the evidence for and against the various evolutionary theories which now occupy the field. Their chief defect is that they are almost entirely destructive. They shatter the faith of the reader, but offer nothing in place of that which they have destroyed. T. H. Morgan's *Evolution and Adaptation*, however, contains much constructive matter, and so is the most valuable work of this class in existence.

Zoological science stands in urgent need of constructive books on evolution—books with leanings towards neither Wallaceism, nor Lamarckism, nor De Vriesism; books which shall set forth facts of all kinds, concealing none, not even those which do not admit of explanation in the present state of our knowledge.—It has been our aim to produce a [viii] book of this description.

We have endeavoured to demonstrate that neither pure Lamarckism nor pure Wallaceism affords a satisfactory explanation of the various phenomena of the organic world. We have further, while recognising the very great value of the work of De Vries, tried to show that that eminent botanist has allowed his enthusiasm to carry him a little too far into the realm of speculation. We have followed up the exposure of the weak points of the theories, which at present occupy the field, with certain suggestions, which, we believe, throw new light on many biological problems.

Our aim in writing this book has been twofold. In the first place we have attempted to place before the general public in simple language a true statement of the present position of biological science. In the second place, we have endeavoured to furnish the scientific men of the day with food for reflection.

Even as the British nation seems to be slowly but surely losing, through its conservatism, the commercial supremacy it had the good fortune to gain last century, so is it losing, through the unwillingness of many of our scientific men to keep abreast of the times, that scientific supremacy which we gained in the middle of last century by the labours of Charles Darwin and Alfred Russell Wallace. To-day it is not among Englishmen, but among Americans and [viii] Continentals, that we have to look for advanced scientific ideas.

Even as the Ultra-Cobdenites believe that Free Trade is a panacea for all economic ills, so do most English men of science believe that natural selection offers the key to every zoological problem. Both are living in a fool's paradise. Another reason why Great Britain is losing her scientific supremacy is that too little attention is paid to bionomics, or the study of live animals. Morphology, or the science of dead organisms, receives more than its due share of attention. It is in the open, not in the museum or the dissecting-room, that nature can best be studied. Far be it from us to deprecate the study of morphology. We wish merely to insist upon the fact, that the leaders of biological science must of necessity be those naturalists who go to the tropics and other parts of the earth where nature can be studied under the most favourable conditions, and those who conduct scientific breeding experiments. Natural selection—the idea which has revolutionised modern biological science—came, not to professors, but to a couple of field-naturalists who were pursuing their researches in tropical countries. It is absurd to expect those who stay at home and gain most of their [ix] knowledge second-hand to be the pioneers of biological science.

We fear that this book will come as a rude shock to many scientific men. By way of consolation we may remind such that they will find themselves in much the same position as that occupied by theologians immediately after the appearance of the *Origin of Species*.

At that time theological thought was cramped by dogma. But the clergy have since reconsidered their position, they have modified their views, and thus kept abreast of the times. Meanwhile scientific men have lagged behind. The blight of dogma has seized hold of them. They have adopted a creed to which all must subscribe or be condemned as heretics. Huxley said that the adoption of a creed was tantamount to suicide. We are endeavouring to save biology in England from committing suicide, to save it from the hands of those into which it has fallen.

We would emphasise that it is not Darwinism we are attacking, but that which is erroneously called Neo-Darwinism. Neo-Darwinism is a pathological growth on Darwinism, which, we fear, can be removed only by a surgical operation.

Darwin, himself, protested in vain against the length to which some of his followers were pushing his theory. On p. 657 of the new edition of the *Origin of Species* he wrote: "As my conclusions have lately been much misrepresented, [x] and as it has been stated that I attribute the modification of species exclusively to natural selection, I may be permitted to remark that in the first edition of this work, and subsequently, I placed in a most conspicuous position—namely, at the close of the Introduction—the following words: 'I am convinced that natural selection has been the main but not the exclusive means of modification.' This has been of no avail. Great is the power of steady misrepresentation; but the history of science shows that this power does not long endure."

Notwithstanding this protest the Wallaceians continue on their course, and give to the world a spurious Darwinism. It is our belief that were Darwin alive to-day his sympathies would be with us, and not with those who call themselves his followers. It was one of Darwin's strong points that he never avoided facts. If new facts came to light which were incompatible with a theory of his, he promptly modified his theory. Since his death a number of new facts have come to light which, in our opinion, plainly indicate that the theory of natural selection as enunciated by Darwin needs considerable modification.

We have in this book set forth certain of these facts and indicated the directions in which the Darwinian theory [xi] seems to require modification.

This volume originated as the result of several conversations we, the joint authors, had last summer. We discovered that we had a great many ideas in common on the subject of evolution. This seemed strange, seeing that our education had not been on the same lines. One of us took a degree in natural science at Cambridge, and subsequently entered His Majesty's Indian Civil Service, but continued his zoological studies in India as a hobby. The other, a naturalist from childhood, nevertheless took a classical degree at Oxford, then received a technical zoological training, adopted zoology as a profession, and held for some years a position in the Natural History Museum at Calcutta.

Our conversations revealed that we were both of opinion that biology is in an unhealthy condition, especially in England, and that the science sorely needs some fresh impetus. Neither of us had the time to attempt, single-handed, to give the required impetus, but as one of us happened to be home on eighteen months' leave, we thought we might undertake the task in collaboration.

We felt that we might collaborate the more successfully because the large number of facts collected by the one of us form the necessary complement to the philosophical studies of the other.

We have endeavoured, so far as possible, to avoid technical terms, and have made a special point of quoting, [xii] wherever practicable, familiar animals as examples, in order that the work may make its appeal not only to the zoologist but to the general reader.

It may, perhaps, be urged against us that we have quoted too freely from popular writings, including those of which we are the authors. Our reply to this is that the study of bionomics, the science of living animals, occupies so small a place in English scientific literature that we have been compelled to have recourse to popular works for many of our facts; and we would, moreover, point out that a popular work is not necessarily inaccurate in its information.

In conclusion, we would warn the reader against the danger of confounding Inference with Fact. The failure to distinguish between the two has vitiated much of the work of the Wallaceian school of biologists.

Facts are always to be accepted. Inferences should be scrutinised with the utmost care.

In making our deductions, we have endeavoured to act without bias. We shall, therefore, welcome any new facts, be they consistent with, or opposed to, our inferences.

D. D.
F. F.

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THE MAKING OF SPECIES

[1]

CHAPTER I RISE OF THE THEORY OF NATURAL SELECTION AND ITS SUBSEQUENT DEVELOPMENT

Pre-Darwinian Evolutionists—Causes which led to the speedy triumph of the theory of Natural Selection—Nature of the opposition which Darwin had to overcome—Post-Darwinian biology—Usually accepted classification of present-day biologists as Neo-Lamarckians and Neo-Darwinians is faulty—Biologists fall into three classes rather than two—Neo-Lamarckism: its defects—Wallaceism: its defects—Neo-Darwinism distinguished from Neo-Lamarckism and Wallaceism—Neo-Darwinism realises the strength and weakness of the theory of Natural Selection, recognises the complexity of the problems which biologists are endeavouring to solve.

Darwinism and evolution are not interchangeable terms. On this fact it is impossible to lay too much emphasis. Charles Darwin was not the originator of the theory of evolution, nor even the first to advocate it in modern times. The idea that all existing things have been produced by natural causes from some primordial material is as old as Aristotle. It was lost sight of in the mental stagnation of the Middle Ages. In that dark period zoological science was completely submerged. It was not until men shook off the mental lethargy that had held them for many generations that serious attention was paid to biology. From the moment when men began to apply scientific methods to that branch of knowledge the idea of evolution found supporters. [2]

Buffon suggested that species are not fixed, but may be gradually changed by natural causes into different species.

Goethe was a thorough-going evolutionist; he asserted that all animals were probably descended from a common original type.

Lamarck was the first evolutionist who sought to show the means whereby evolution has been effected. He tried to prove that the efforts of animals are the causes of variation; that these efforts originate changes in form during the life of the individual which are transmitted to its offspring.

St Hilaire was another evolutionist who endeavoured to explain how evolution had occurred. He believed that the transformations of animals are effected by changes in their environment. These hypotheses were considered, and rightly considered, insufficient to explain anything like general evolution, so that the idea failed for a time to make headway.

[3]

Strength of Darwin's Position

As knowledge grew, as facts accumulated, the belief in evolution became more widespread. Hutton, Lyell, Spencer, and Huxley were all convinced that evolution had occurred, but they could not explain how it had occurred.

Thus, by the middle of last century, all that was needed to make evolution an article of scientific belief was the discovery of a method whereby it could be effected. This Darwin and Wallace were able to furnish in the shape of the theory of natural selection. The discovery was made independently, but Darwin being the older man, the more influential, and the one who had gone the more deeply and carefully into the matter, gained the lion's share of the credit of the discovery. The theory of natural selection is universally known as the Darwinian theory, notwithstanding the fact that Darwin, unlike Wallace, always recognised that natural selection is not the sole determining factor in organic evolution.

From the moment of the enunciation of his great hypothesis, Darwin's position was an exceedingly strong one. Everything was in his favour.

As we have seen, the theory was enunciated at the psychological moment, at the time when zoological science was ripe for it. Most of the leading zoologists were evolutionists at heart, and were only too ready to accept any theory which [4] afforded a plausible explanation of what they believed to have occurred.

Hence the rapturous welcome accorded to the theory of natural selection by the more progressive biologists.

Another point in Darwin's favour was the delightful simplicity of his hypothesis. Nothing could be more enticingly probable. It is based on the unassailable facts of variation, heredity, and the tendency of animals to multiply in numbers. Everybody knows that the breeder can fix varieties by careful breeding. Darwin had simply to show that there is in nature something to take the part played among domesticated animals by the human breeder. This he was able to do. As the numbers of species remain stationary, it is evident that only a small portion of the animals that are born can reach maturity. A child can see that the individuals most likely to survive are those best adapted to the circumstances of their life. Even as the breeder weeds out of his stock the creatures not suited to his purpose, so in nature do the unfit perish in the everlasting struggle for existence.

In nature there is a selection corresponding to that of the breeder.

It is useless to deny the existence of this selection in nature, this natural selection. The only disputable point is whether such selection can do all that Darwin demanded of it.

The man in the street, then, was able to comprehend the theory of natural selection. This was greatly in its favour. [5] Men are usually well disposed towards doctrines which they can readily understand.

The nineteenth century was a superficial age. It liked simplicity in all things. If Darwin could show that natural selection was capable of producing one species, men were not only ready but eager to believe that it could explain the whole of organic evolution.

The simplicity of the Darwinian theory has its evil side. It has undoubtedly tended to make modern biologists superficial in their methods. It has, indeed, stimulated the imagination of men of science; but the stimulation has not in all cases been a healthy one.

So far from adhering to the sound rule laid down by Pasteur, "never advance anything that cannot be proved in a simple and decisive manner," many modern naturalists allow their imagination to run riot, and so formulate ill-considered theories, and build up hypotheses on the most insecure foundations. "A tiny islet of truth," writes Archdale Reid, "is discovered, on which are built tremendous and totally illegitimate hypotheses."

Another source of Darwin's strength was the vast store of knowledge he had accumulated. For twenty years he had been steadily amassing facts in support of his hypothesis. He enunciated no crude theory, he indulged in no wild [6] speculations. He was content to marshal a great array of facts, and to draw logical conclusions therefrom. He was as cautious in his deductions as he was careful of his facts. He thus stood head and shoulders above the biologists of his day. He was a giant among pigmies. So well equipped was he that those who attempted to oppose him found themselves in the position of men, armed with bows and arrows, who seek to storm a fortress defended by maxim guns.

Nor was this all. The majority of the best biologists of his time did not attempt to oppose him. They were, as we have seen, ready to receive with open arms any hypothesis which seemed to explain how evolution had occurred. Some of them perceived that there were weak points in the Darwinian theory, but they preferred not to expose these; they were rather disposed to make the best of the hypothesis. It had so many merits that it seemed to them but reasonable to suppose that subsequent investigation would prove that the defects were apparent rather than real.

Opponents of Darwin

We hear much of the “magnitude of the prejudices” which Darwin had to overcome, and of the mighty battle which Darwin and his lieutenant Huxley had to fight before the theory of the origin of species by natural selection obtained acceptance. We venture to say that statements such as these are misleading. We think we may safely assert that scarcely ever has a theory which fundamentally changed the prevailing scientific beliefs met with less opposition. It would have been a good thing for zoology had Darwin not obtained so easy a victory. [7]

Sir Richard Owen, a distinguished anatomist, certainly attacked the doctrine in no unmeasured terms, but his attack was anonymous and so cannot be considered very formidable. Far more important was the opposition of Dr St George Mivart, whose worth as a biologist has never been properly appreciated. His most important work, entitled the *Genesis of Species*, might be read with profit even now by many of our modern Darwinians.

For some time after the publication of the *Origin of Species* Mivart appears to be almost the only man of science fully alive to the weak points of the Darwinian theory. The great majority seem to have been dazzled by its brilliancy.

The main attack on Darwinism was conducted by the theologians and their allies, who considered it to be subversive of the Mosaic account of the Creation. Now, when one whose scientific knowledge is, to say the best of it, not extensive, attacks a man who has studied his subject dispassionately for years, and invariably expresses himself with extreme caution, the onslaught can have but one result—the attacker will be repulsed with heavy loss, and the onlookers will have a higher opinion of his valour than of his common sense. [8]

The theologians were in the unfortunate position of warriors who do not know what it is against which they are fighting; they confounded natural selection with evolution, and directed the main force of their attack against the latter, under the impression that they were fighting the Darwinian theory.

It was the misfortune of those theologians that it is possible to prove that evolution, or, at any rate, some evolution has occurred; they thus kicked against the pricks with disastrous results to themselves. When this attack had been repulsed men believed that the theory of natural selection had been demonstrated, that it was as much a law of nature as that of gravitation. What had really happened was that the fact of evolution had been proved, and the theory of natural selection obtained the credit. Men thought that Darwinism was evolution. Had the theologians admitted evolution but denied the ability of natural selection to explain it, the Darwinian theory, in all probability, would not have gained the ascendancy which it now enjoys.

Evolution and Natural Selection

To us who are able to look back dispassionately upon the biological warfare of the last century, Darwin’s opponents—or the majority of them—appear very foolish. We must, however, bear in mind that at the time of the publication of the *Origin of Species* both natural selection and evolution were comparatively unknown ideas. Darwin had to fight for both. He had to prove evolution as well as natural selection. Many of the facts adduced by him supported both. It is, therefore, not altogether surprising that many of his opponents failed to distinguish between them. [9]

A glance at the *Origin of Species* will suffice to show how considerable is the portion of the book that deals with the evidence in favour of evolution rather than of natural selection.

Of the fourteen chapters which make up the book no fewer than nine are devoted to proving that evolution has occurred. It has been truly said, that for every one fact biologists have found in support of the special theory of natural selection they have found ten facts supporting the doctrine of evolution. Darwin, then, was in the position of a skilled barrister who has a plausible case and who knows the ins and outs of his brief, while his opponents stood in the shoes of inexperienced counsel who had but recently received their brief, and who had not had the time to master the details thereof. In such circumstances it is not difficult to predict which way the verdict of the jury will go.

Darwin, moreover, had a charming personality. Never was a man with a theory less dogmatic. Never was the holder of a theory more careful of the expressions he used. Never was a scientific man more ready to give ear to his opponents, to meet them half way, and, where necessary, to compromise. Darwin was not afraid of facts, and was always ready to alter his views when they appeared to be opposed to facts. The average scientific man of to-day makes facts fit his theory; if they refuse to fit it he ignores or denies them. [10]

Darwin continually modified his views; when he found himself in a tight place he did not hesitate to resort to Lamarckian factors, such as the inheritance of the effects of use and disuse and of the effects of environment. He conceded that natural selection was insufficient to account for all the phenomena of organic evolution, and advanced the theory of sexual selection in order to account for facts which the major hypothesis seemed to him incapable of explaining.

Darwin, moreover, having ample private means, was not obliged to work for a living, and was therefore able to devote the whole of his time to research. The advantages of such a position cannot be over-estimated, and, perhaps, have not been sufficiently taken into account in apportioning the praise between Darwin and Wallace for their great discovery.

Huxley

To all these factors in Darwin's favour we must add his good fortune in possessing so able a lieutenant as Huxley. [11]

Huxley was an ardent evolutionist, an able writer, and a brilliant debater. A man of his mental calibre was able, like a clever barrister, to make out a plausible case for any theory which he chose to take up. While nominally a strong supporter of the Darwinian theory, he was in reality fighting for the doctrine of descent. Had *any* plausible theory of evolution been enunciated, Huxley would undoubtedly have fought for it equally earnestly.

A firm believer in evolution, Huxley was, as Professor Poulton says, confronted by two difficulties,—first, the insufficiency of the evidence of evolution, and, secondly, the absence of any explanation of how the phenomenon had occurred. The *Origin of Species* solved both these difficulties. It adduced much weighty evidence in favour of evolution, and suggested a *modus operandi*. Small wonder, then, that Huxley became a champion of Darwinism. But, as Poulton writes, on page 202 of *Essays on Evolution*, “while natural selection thus enabled Huxley freely to accept evolution, he was by no means fully satisfied with it.” “He never committed himself to a full belief in natural selection, and even contemplated the possibility of its ultimate disappearance.” To use Huxley's own words: “Whether the particular shape which the doctrine of evolution, as applied to the organic world, took in Darwin's hands, would [12] prove to be final or not, was, to me, a matter of indifference.”

The result of the fortuitous combination of the circumstances which we have set forth was that in a surprisingly short time the theory of natural selection came to be regarded as a law of nature on a par with the laws of gravitation. Thus, paradoxical though it seems, practical certainty was given to a hitherto uncertain doctrine by the addition of a still more uncertain theory.

“At once,” writes Waggett, “the theory of development leapt from the position of an obscure guess to that of a fully-equipped theory and almost a certainty.”

Darwin thus became a dictator whose authority none durst question. A crowd of slavish adherents gathered round him, a herd of men to whom he seemed an absolutely unquestionable authority. Darwinism became a creed to which all must subscribe. It still retains this position in the popular mind.

Growing Opposition to Darwinism

The ease with which the theory of natural selection gained supremacy was, as we have already said, a misfortune to biological science. It produced for a time a considerable mental stagnation among zoologists. Since Darwin's day the science has not made the progress that might reasonably have been expected, because the theory has so captivated the minds of the majority of biologists that they see everything through Darwinian spectacles. The wish has been in [13] many cases the father to the observation. Zoologists are ever on the lookout for the action of natural selection, and in consequence frequently imagine they see it where it does not exist. Many naturalists, consciously or unconsciously, stretch facts to make them fit the Darwinian theory. Those facts which refuse to be so distorted are, if not actively ignored or suppressed, overlooked as throwing no light upon the doctrine. This is no exaggeration. A perusal of almost any popular book dealing with zoological theory leaves the impression that there is nothing left to be explained in the living world, that there is no door leading to the secret chambers of nature to which natural selection is not an “open sesame.”

But the triumph of natural selection has not been so complete as its more enthusiastic supporters would have us believe. Some there are who have never admitted the all-sufficiency of natural selection. In the British Isles these have never been numerous. In the United States of America and on the Continent they are more abundant. The tendency seems to be for them to increase in numbers. Hence the recent lamentations of Dr Wallace and Sir E. Ray Lankester. Modern biologists are commonly supposed to fall into two schools of thought—the Neo-Darwinian and the Neo-Lamarckian.

The former are the larger body, and pin their faith absolutely to natural selection. They deny the inheritance of [14] acquired characters, and preach the all-sufficiency of natural selection to explain the varied phenomena of nature. The Neo-Lamarckians do not admit the omnipotency of natural selection. Some of them allow it no virtue. Others regard it as a force which keeps variation within fixed limits, which says to each organism, “thus far shalt thou vary and no farther.” This school lays great stress on the inheritance of acquired characters, especially on the inheritance of the effects of use and disuse.

The above statement of the recent developments of Darwinism is incomplete, for it fails to include those who occupy a middle position. If it be possible to classify a large number of men of which scarcely any two hold identical views, it is into three, rather than two, classes that they must be divided.

Speaking broadly, evolutionists of to-day may be said to represent three distinct lines of thought. For the sake of classification we may speak of them as falling into three schools, which we may term the Neo-Lamarckian, the Wallacean, and the Neo-Darwinian, according as their views incline towards those held by Lamarck, Wallace, or Darwin.

The Neo-Lamarckian School

As adherents of the Neo-Lamarckian school, we cite Cope, Spencer, Orr, Eimer, Naegeli, Henslow, Cunningham, Haeckel, Korchinsky, and a number of others. It may almost be said of these Neo-Lamarckians that each holds a totally distinct theory of evolution. So heterogeneous are their views that it is difficult to find a single article common to the evolutionary belief of all. It is commonly asserted that all Neo-Lamarckians are agreed, firstly, that acquired characters are transmissible; and, secondly, that such transmission is an important factor in the production of new species. This assertion is certainly true of the great bulk of Neo-Lamarckians, but it does not appear to hold in the case of those who believe that evolution is the result of some unknown inner force. So far as we can see, a belief in the inheritance of acquired characters is not necessary to the theories of orthogenesis held by Naegeli and Korchinsky. For that reason it would possibly be more correct to place those who hold such views in a fourth school. Since, however, a number of undoubted Neo-Lamarckians, as, for example, Cope, believe in an inner growth-force, it is convenient to regard Naegeli as a Neo-Lamarckian. His views need not detain us long. Those who wish to study them in detail will find them in his *Mechanisch-physiologische Theorie der Abstammungslehre*. [15]

Naegeli believes that there is inherent in protoplasm a growth-force, which makes each organism in itself a force making towards progressive evolution. He holds that animals and plants would have become much as they are now even if no struggle for existence had taken place. "To the believers in this kind of . . . orthogenesis," writes Kellog (*Darwinism To-day*, p. 278), "organic evolution has been, and is now, ruled by unknown inner forces inherent in organisms, and has been independent of the influence of the outer world. The lines of evolution are immanent, unchangeable, and ever slowly stretch toward some ideal goal." It is easy to enunciate such a theory, impossible to prove it, and difficult to disprove it. [16]

It seems to us that the fact that, so soon as organisms are removed from the struggle for existence, they tend to degenerate, is a sufficient reason for refusing to accept theories of the description put forth by Naegeli. More truly Lamarckian is Eimer's theory of orthogenesis, according to which it is the environment which determines the direction which variation takes; and the variations which are induced by the environment are transmitted to the offspring.

Orr's Views

Spencer and Orr preach nearly pure Lamarckism. The former, while fully recognising the importance of natural selection, considered that sufficient weight has not been given to the effects of use and disuse, or to the direct action of the environment in determining or modifying organisms. [17]

The similarity of the views of Orr and Lamarck is best seen by comparing their respective explanations of the long neck of the giraffe. Lamarck thought that this was the direct result of continual stretching. The animal continually strains its neck in the search for food, hence it grows longer as the individual grows older, and this elongated neck has been transmitted to the offspring. Orr writes, on page 164 of his *Development and Heredity*: "The giraffe seems to present the most remarkable illustration of the lengthening of the bones as the result of the frequent repetition of such shocks. As is well known, this animal feeds on the foliage of trees. From the earliest youth of the species, and the earliest youth of each individual, it must have been stretching upwards for food, and, as is the custom of such quadrupeds, it must have constantly raised itself off its forefeet, and, as it dropped, must have received a shock that made itself felt from the hoofs through the legs and vertical neck to the head. In the hind legs the shock would not be felt. It is impossible to imagine that an animal which, during the greater part of every day of its life (both its individual and racial life), performed motions so uniform and constant, would not be peculiarly specialised as a result. The forces acting upon such an animal are widely different from the forces acting upon an animal which eats the grass at its feet like an ox, or one which must run and climb like a goat or a deer, and the resultant modifications of growth in the several cases must also be different. The principle of increased growth in the direction of the shock, resulting from superabundant repair of the momentary compression, explains how the giraffe acquired the phenomenal length of the bones of its forelegs and neck; and the absence of the shock in the hind-quarters shows why they remained undeveloped and absurdly disproportionate to the rest of the body." [18]

Inheritance of Acquired Characters

It seems to us that a fatal objection to all these Neo-Lamarckian theories of evolution is that they are based on the assumption that acquired characters are inherited, whereas all the evidence goes to show that such characters are not inherited. In these days, when scientific knowledge is so widely diffused, it is scarcely necessary to say that all the characteristics which an organism displays are either congenital or inborn, or acquired by the organism during its lifetime. Thus a man may have naturally a large biceps muscle, and this is a congenital character; or he may by constant exercise develop or greatly increase the size of the biceps. The large biceps, in so far as it has been increased by exercise, is said to be an acquired character, for it was not inherited by its possessor, but acquired by him in his lifetime. We must bear in mind that the period in the life history of an organism at which a character appears, is not necessarily a test as to whether it is congenital or acquired, for a great many congenital characters, such as a man's beard, do not appear until some years after birth. As we have seen, the Neo-Lamarckians believe that it is possible for an organism to transmit to its offspring characters which it has acquired during the course of its existence. But, as we have already said, the evidence goes to show that such characters are not inherited. For example, the tail of the young fox-terrier is not shorter than that of other breeds of dogs, notwithstanding the fact that its ancestors have for generations had the greater portion of their caudal appendage removed shortly after birth. [19]

We do not propose to discuss at any great length the vexed question of the inheritance of acquired characters, for the simple reason that the Neo-Lamarckians have not brought forward a single instance which indubitably proves that such characters are inherited.

Mr J. T. Cunningham, in a paper of great value and interest, entitled "The Heredity of Secondary Sexual Characters in relation to Hormones: a Theory of the Heredity of Somatogenic Characters," which appeared in vol. xxvi., No. 3, of the *Archiv für Entwicklungsmechanik des Organismen*, states: "The dogma that acquired characters cannot be inherited . . . is founded not so much on evidence, or the absence of evidence, as on *a priori* reasoning, on the supposed difficulty or impossibility of conceiving a means by which such inheritance could be effected." Such appears certainly to be true of some zoologists, but we trust that Mr Cunningham will do us the justice to believe that our opinion that the inheritance of acquired characters does not play an important part in the evolution of, at any rate, the higher animals, is based, not on the ground of *a priori* reasoning, but on facts. All the evidence seems to show that such characteristics are not inherited. If, as Mr Cunningham thinks, all secondary sexual characters are due to the inheritance of the effects of use, etc., how is it that no Neo-Lamarckian is able to bring forward a clear case of the inheritance of a well-defined acquired character? If such characteristics are habitually inherited, countless examples should be forthcoming. Fanciers in their endeavours are constantly "doctoring" the animals they keep for show purposes; and it seems to us certain that if acquired characters are inherited, breeders would long ago have discovered this and acted upon the discovery. If Neo-Darwinians are charged with refusing to believe that acquired characters are inherited because they "cannot conceive the means by which it could be effected," may it not be said with equal justice that many Neo-Lamarckians believe that acquired characters are inherited, not on evidence thereof, but because if such characters are not inherited it is very difficult to account for many of the phenomena presented by the organic world? [21]

In many of the lower animals, as, for example, the hydra, the germinal material is diffused through the organism, so that a complete individual can be developed from a small portion of the creature. In such circumstances it seems not improbable that the external environment may act directly on the germinal substance, and induce changes in it which may perhaps be transmitted to the offspring. If this be so, it would seem that some acquired characters may be inherited in such organisms. Very many plants can be propagated from cuttings, buds, etc., so that we might reasonably expect some acquired characters to be hereditary in them. The majority of botanists appear to hold Lamarckian views; but on the evidence at present available, it is doubtful whether such views are the correct ones.

Plants are so plastic, so protean, so sensitive to their environment that their external structure appears to be determined by the external conditions in which they find themselves quite as much as by their inherited tendencies. In this respect they differ very considerably from the higher animals. The peacock, for example, presents the same outward appearance [1] whether bred and reared in Asia or Europe, in a hot or cold, a damp or a dry climate. The same plant, on the other hand, differs greatly in outward appearance according as it is grown in a dry or a damp soil, a hot or a cold country. In his recent book *The Heredity of Acquired Characters in Plants*, the Rev. G. Henslow cites several examples of the celerity with which plants react to their environment. On page 32 he writes: "The following is an experiment I made with the common rest-harrow (*Ononis spinosa*, L.) growing wild in a very dry situation by a roadside. I collected some seeds, and also took cuttings. These I planted in a garden border, keeping this well moist with a hand-light over it, and a saucer of water, so that the air should be thoroughly moist as well. Its natural conditions were thus completely reversed. They all grew vigorously. The new branches of the first year's growth bore spines, proving their hereditary character, but instead of their being long and stout, they were not an inch long, and like needles. This proved the spines to be a hereditary feature. In the second year there were none at all; moreover, the plants blossomed, and, taken altogether, there was no appreciable difference from *O. repens*, L." [23]

From this experiment Professor Henslow draws the inference that acquired characters tend to be inherited in plants. In our opinion the experiment affords strong evidence against the Lamarckian doctrine. Here we have a plant which has, perhaps, for thousands of generations developed spines owing to its dry environment. If acquired characters are inherited we should have expected this spiny character to have become fixed and persisted under changed conditions, for some generations at any rate. But what do we find? By the second year the thorns have entirely disappeared. All the years during which the plant was exposed to a dry environment have left no stamp upon it. The fact that the new branches of the first year's growth bore small spines is not, as Professor Henslow asserts, proof of their hereditary character. It merely shows that the initial stimulus to their development occurred while the plant was still in its dry surroundings.

In the same way all other so-called proofs of the heredity of acquired characters break down when critically examined.

In our opinion "not proven" is the proper verdict on the question of the possibility of the inheritance of acquired characters in the higher animals. One thing is certain, and that is that acquired characters are not commonly inherited in those organisms in which there is a sharp distinction between the germinal and the somatic cells. [24]

It is nothing short of a misfortune that Haeckel's *History of Creation*, which seems to be so widely read in England, should be built on a fallacious foundation. It seems to us that this work is calculated to mislead rather than to teach.

Our attitude is not quite that of the Wallaceian school, which denies the possibility of the inheritance of acquired characters. In practice, however, the attitude we adopt is as fatal to Lamarckism in all its forms as the dogmatic assertions of the Wallaceians. It matters not whether acquired characters are very rarely or never inherited. In either case their inheritance cannot have played an important part in evolution. All those theories which rely on use-inheritance as a factor in evolution are therefore in our opinion worthless, being opposed to facts. Our attitude, then, is that the inheritance of acquired characteristics, if it does occur, is so rare as to be a negligible quantity in organic evolution.

We may add that the position which we occupy will not be affected even if the Lamarckians do succeed eventually in proving that some acquired characters are really inherited. Such proof would merely help to elucidate some of the problems which confront the biologist. Thus the question of the inheritance of acquired characters, while full of interest, has no very important bearing on the question of the making of species. [25]

The Wallaceian School

The Wallaceians hold the doctrines which have been set forth above as those of the Neo-Darwinian school. It is incorrect to call those who pin their faith to the all-sufficiency of natural selection Neo-Darwinians, because Darwin at no time believed that natural selection explained everything. Darwin moreover was a Lamarckian to the extent that he was inclined to think that acquired characteristics could be inherited. His theory of inheritance by gemmules involved the assumption that such characters are inherited. It is Wallace who out-Darwins Darwin, who preaches the all-sufficiency of natural selection. For this reason we dub the school which holds this article of belief, and to which Weismann, Poulton, and apparently Ray Lankester belong, the Wallaceian school. Weismann has put forth a theory of inheritance, that of the continuity of the germ plasm, which makes this inheritance a physical impossibility. We believe that the Wallaceians have erred as far from the truth as the Lamarckians have, because, as we shall show hereafter, a great many of the organs and structures displayed by organisms cannot be explained on the natural selection hypothesis. Those who pin their faith to this, needlessly increase the difficulty of the problem which they have to face. [26]

There remains the third school, to which we belong, and of which Bateson, De Vries, Kellog and T. H. Morgan appear to be adherents. This school steers a course between the Scylla of use-inheritance and the Charybdis of the all-sufficiency of natural selection. It may seem surprising to some that we should class De Vries as a Neo-Darwinian, seeing that he is the originator of the theory of evolution by means of mutations, which we shall discuss in Chapter III. of this work. As a matter of fact the theory of mutations should be regarded, not as opposed to the theory of Darwin, but as a theory engrafted upon it. De Vries himself writes:—"My work claims to be in full accord with the principles laid down by Darwin." Similarly Hubrecht writes in the *Contemporary Review* for November 1908: "Paradoxical as it may sound, I am willing to show that my colleague, Hugo de Vries, of Amsterdam, who a few years ago grafted his *Mutations Theorie* on the thriving and very healthy plant of Darwinism, is a much more staunch Darwinian than either Dr Wallace himself, or the two great authorities in biological science whom he mentions, Sir William Thistleton Dyer and Professor Poulton."

Complexity of the Problem

Having classified ourselves, it remains for us (the authors of the present work) to define our position more precisely. [27]
 Like Darwin we welcome all factors which appear to be capable of effecting evolution. We have no axe to grind in the shape of a pet hypothesis, and consequently our passions are not roused when men come forward with new ideas seemingly opposed to some which already occupy the field. We recognise the extreme complexity of the problems that confront us. We look facts in the face and decline to ignore any, no matter how ill they fit in with existing theories. We recognise the strength and the weakness of the Darwinian theory. We see plainly that it has the defect of the period in which it was enunciated. The eighteenth century was the age of cocksureness, the age in which all phenomena were thought to be capable of simple explanation.

This is well exemplified by the doctrines of the Manchester school as regards political and economic science. The whole art of legislation was thought to be summed up in the words *laissez faire*. The whole sphere of legitimate government was asserted to be the keeping of order and the enforcing of contracts. Experience has demonstrated that a State guided solely by these principles is wretchedly governed. A large proportion of recent Acts of Parliament limits the freedom of contract. Such limitations are necessary in the case of contracts between the weak and the strong. [28]
 Similarly the earlier economists considered political economy a very simple affair. They asserted that men are actuated by but one motive—the love of money. All their men were economic men, men devoid of all attributes save an intense love of gold. Experience has shown that these premises are not correct. Love of family, pride of race, caste prejudices are more or less deeply implanted in men, so that they are rarely actuated solely by the love of money.

The Aim of the Biologist

Thus it is that the political economy of to-day as set forth by Marshall is far more complex and less dogmatic than that of Ricardo or Adam Smith. Similarly the political philosophy of Sidgwick is very different to that of Herbert Spencer. So is it with the theory of organic evolution. The theory of natural selection is no more able to explain all the varied phenomena of nature than is Ricardo's assumption that all men are actuated solely by the love of money capable of accounting for the multifarious existing economic phenomena. Even as the love of wealth is an important motive of human actions, so is natural selection an important factor in evolution. But even as the majority of human actions are the resultant of a variety of motives, so are the majority of existing organisms the resultant of a complex system of forces. Even as it is the duty of the economist to discover the various motives which lead to human actions, so is it [29]
 the duty of the biologist to bring to light the factors which are operative in the making of species.

[30]

CHAPTER II

SOME OF THE MORE IMPORTANT OBJECTIONS TO THE THEORY OF NATURAL SELECTION

Brief statement of Theory—Objections to the Theory fall into two classes—Those which strike at the root of the Theory—Those which deny the all-sufficiency of Natural Selection—Objections which strike at root of Theory are based on misconception—Objections to Wallaceism—The Theory fails to explain the origin of Variations—Natural Selection called on to explain too much—Unable to explain beginnings of new organs—The Theory of change of function—The co-ordination of variations—The fertility of races of domesticated animals—Missing links—Swamping effects of intercrossing—Small variations cannot have a survival value—Races inhabiting same area—Excessive specialisation—Chance and Natural Selection—Struggle for existence most severe among young animals—Natural Selection fails to explain mimicry and other phenomena of colour—Conclusion, that scarcely an organism exists which does not possess some feature inexplicable on the theory of Natural Selection as held by Wallace and his followers.

“The burden of proof is on him who asserts” is a rule of evidence which the man of science should apply as rigidly as does the lawyer.

It is therefore incumbent upon us to prove our assertion that the theory of natural selection does not afford an adequate explanation of all the varied phenomena observed in the organic world.

Theory of Natural Selection

The theory of natural selection is so generally understood, that to set it forth in detail in this place would be quite superfluous.

Darwin, it will be remembered, based his great hypothesis on the following observed facts:—

1. No two individuals of a species are exactly alike. This is sometimes called the law of variation.
2. All creatures tend in a general way to resemble their parents in appearance more closely than they resemble individuals not related to them. This may be termed the law of heredity.
3. Each pair of organisms produces in the course of a lifetime, on an average, many more than two young ones.
4. On an average the total number of each species remains stationary.

From (3) and (4) follows the doctrine of Malthus, namely, that many more individuals are born than can reach maturity.

Darwin applied this doctrine to the whole of the animal and the vegetable kingdoms.

In his introduction to *The Origin of Species* he writes:—“As many more individuals of each species are born than can possibly survive; and as, consequently, there is a frequently recurring struggle for existence, it follows that any being, if it vary, however slightly, in any manner profitable to itself, under the complex and sometimes varying conditions of life, will have a better chance of surviving, and thus be naturally selected. From the strong principle of inheritance, any selected variety will tend to propagate its new and modified form.” [32]

In other words, the struggle for existence amongst all organic beings throughout the world, which inevitably follows from the high geometrical ratio of their increase, results in the survival of the fittest, that is to say, of those best adapted to cope with their enemies and to secure their food. Since organisms are thus naturally selected in nature, we may speak of a natural selection which acts in much the same way as the human breeder does. Darwin's theory, then, is that all the variety of organisms which now exist have been evolved from one or more forms by this process of natural selection.

Various Anti-Darwinian Views

The objections which have been urged against the theory of natural selection fall into two classes.

- I. Those which strike at its root, which either deny that there is any natural selection, or declare that it is not capable of producing a new species.
- II. Those which are directed against the all-sufficiency of natural selection to account for organic evolution.

Those of the first class need not detain us long, although among those who formulate them are to be found some eminent men of science. [33]

Delage alleges that selection is powerless to form species, its function is, according to him, limited to the suppression of variations radically bad, and to the maintaining of a species in its normal character. It is thus an inimical factor in evolution, a retarder rather than an accelerator of species-change. It merely acts by preserving the type at the expense of the variants, and so acts as a brake on evolution.

Korschinsky, while possibly not denying that selection occurs in nature, declares that its influence on evolution is *nil*, or, if it has any influence, that it is a hindering one.

Eimer similarly denies any capacity on the part of natural selection to create species.

Pfeffer urges a very different objection. He says that if such a force as natural selection existed it would transform species much more rapidly than it does!

Now, in order that the above objections can carry any weight, one of two sets of conditions must be fulfilled.

Either all organisms must be perfectly adapted to their environment, and this environment must never change, or there must be inherent in each species a kind of growth-force which impels the species to develop in certain fixed directions. In either of these circumstances natural selection will be an inhibitory force, for if the normal organism is perfectly adapted to its environment, all variations from the type must be unfavourable, and natural selection will weed out the individuals that display them. No careful student of nature can maintain, either that all animals are perfectly adapted to their environment, or that this never changes. Hence those who deny that natural selection is a factor in the making of species, assume the second set of conditions, that species develop in certain fixed directions, being impelled either by internal or external forces. How far these ideas are founded on fact we shall endeavour to determine when speaking of variation. It must suffice at present to say that even if any of these views of orthogenesis be established, natural selection will have, so to speak, a casting vote, it will decide which series of species developing along preordained lines shall survive and which shall not survive. [34]

Thus we reach by a different line of argument the conclusion we arrived at in the last chapter: namely, there is no room for doubt that natural selection is a factor in the making of species.

We must now pass on to the second class of objections, those which are urged against the all-sufficiency of natural selection. So numerous are these that it is not feasible to consider them all. A brief notice of the more important ones should suffice to satisfy any unbiassed person; firstly, that natural selection is an important factor in evolution; secondly, that the position taken up by Wallace and his followers, that natural selection, acting on minute variations, is the one and only factor in organic evolution, is untenable. [35]

Darwinism does not explain Variation

1. It has been urged that the Darwinian theory makes no attempt to explain variation, and that, until we know what it is that causes variations, we are not in a position to explain evolution. This of course is quite true, but the objection is scarcely a fair one, since, as we have seen, Darwin freely admitted that his theory made no attempt to explain the origin of variations. It is not reasonable to object to a theory because it fails to explain phenomena with which it expressly states that it is not concerned. On the other hand, the objection is one that must be reckoned with, for, as we shall see, it makes a great difference to the importance of natural selection as a factor in evolution if variations appear indiscriminately in all directions, as Darwin tacitly assumed they do, or whether, as some biologists believe, they are determinate in direction, being the result of a growth-force inherent in all organisms.

2. Very similar to the above-mentioned objection is that which points out that it is a long journey from Amoeba to man. It is difficult to believe that this long course of development from the simple to the complex is due to the action of a blind force, to the survival of those whose fortuitous variations happen to be best adapted to the environment. The result seems out of all proportion to the cause. There must be some potent force inherent in protoplasm, or behind organisms, impelling them upwards. This objection is as difficult to refute as it is to establish. It is purely speculative. [36]

3. A very serious objection to the Darwinian theory is that the beginnings of new organs cannot be explained by the action of natural selection on fortuitous minute variations, and natural selection can act on an organ only when that organ has attained sufficient size to be of practical utility to its possessor. When once an organ has come into being it is not difficult to understand how it can be improved, modified and developed by natural selection. But how can we explain the origin of an organ such as a limb by the action of natural selection on minute variations?

Theory of Change of Function

The theory of the change of function goes some way towards meeting the difficulty, for by means of it we are able to understand how certain organs, as, for example, the lung of air-breathing animals, might have come into existence. This is said to have been developed from the swimming-bladder of fishes. This bladder is, to use the words of Milnes Marshall, "a closed sac lying just underneath the vertebral column. In many fish it acquires a connection by a duct with some part of the alimentary canal. It then becomes an accessory breathing organ, especially in those fish which are capable of living out of water for a time, e.g. the *Protopterus* of America. An interesting series of modifications exists connecting the air-bladder with the lung of the higher vertebrates, which is undoubtedly the same organ." [37]

This theory, however, does not seem adequate to explain the origin of all organs. It does not explain, for example, how limbs developed in a limbless organism. Wallace tried to avoid the difficulty by asserting that it is unreasonable to ask a new theory that it shall reveal to us exactly what took place in remote geological ages and how it took place. To this the obvious reply is, firstly, that we ought not to give unqualified acceptance to any theory of evolution until it does afford us such explanations, and, secondly, that the theory of the origin of species by means of natural selection is no longer a new one.

Latterly, however, Wallace appears to have given up all hope of being able to account for the origin of new organs by means of natural selection, for he states on page 431 of the issue of the *Fortnightly Review* for March 1909: “It follows—not as a theory but as a fact—that whenever an advantageous variation is needed, it can only consist in an increase or decrease of some power or faculty already existing.” Now, in order for an increase or decrease to occur, there must be something in existence to be increased or diminished. Wallace, it is true, speaks here only of powers and faculties; but it can scarcely be supposed that he believes that variations as to structure are intrinsically different from those relating to powers and faculties. [38]

4. Herbert Spencer urges, as an objection to the theory of natural selection, that favourable variations in one organ are likely to be counterbalanced by unfavourable variations in some other organ. He maintains that the chances are enormous against the occurrence of the “many coincident and co-ordinated variations” that are necessary to create a life or death determining advantage.

This objection was urged by a writer in the *Edinburgh Review* in January 1909, and even by Wallace himself in the *Fortnightly Review* last March against the mutation theory. This objection, strong though it appears on paper, exists only in the imagination of the objector.

Those who urge it display a misunderstanding of the manner in which natural selection acts, and ignorance of the phenomenon of the correlation of organs.

[39]

Correlation

Natural selection deals with an organism as a whole. Its effect is to permit those creatures to survive which, taken as a whole, are best adapted to their environment.

Physiologists insist with ever-increasing emphasis that there is more or less correlation and inter-connection between the various parts of an organism.

The several organs of an animal are not so many isolated units. It is impossible to act on one organ without affecting some or all of the others.

Variations in a given direction of one organ are usually accompanied by correlated variations in some of the other organs. If strength be of paramount importance to an animal, natural selection will tend to preserve those individuals which exhibit strength to a marked degree, and this exhibition of strength may be accompanied by other peculiarities, such as short legs or a certain colour, so that natural selection will indirectly tend to produce individuals with short legs and having the colour in question, and it may happen that this particular colour is one that renders the animal more conspicuous than the normal colour does. Nevertheless, on account of the all-needful strength which accompanies it, those animals so coloured may survive while those of a more protective hue perish. Thus, paradoxical though it seems, natural selection may indirectly be responsible for characteristics which in themselves are injurious to the individual. This is probably the case as regards the decorative plumage of some male birds. The phenomenon of correlation was recognised by Darwin, and has, we believe, played an important part in the making of species. We shall deal more fully with the subject in a later chapter. [40]

5. An oft-urged objection to the theory of natural selection, and one which weighed very strongly with Huxley, is that breeders have hitherto not succeeded in breeding a variety which is infertile with the parent species. If, Huxley asked, breeders cannot produce such a thing, how can we say we consider it proved that natural selection produces new species in nature? This objection, however, loses much of its force in view of the fact that many perfectly distinct species are quite fertile when bred together. We shall recur to this in Chapter IV.

6. The fact that palæontology has hitherto failed to yield links connecting many existing species is a classical objection to the theory of the origin of species by gradual evolution.

Missing Links

Wallace states this objection as follows, on page 376 of his *Darwinism*: “Many of the gaps that still remain are so vast that it seems incredible to these writers that they could ever have been filled up by a close succession of species, since these must have been spread over so many ages, and have existed in such numbers, that it seems impossible to account for their total absence from deposits in which great numbers of species belonging to other groups are preserved and have been discovered.” [41]

Wallace's reply is to the effect that in the case of many species palæontology affords abundant evidence of the gradual change of one species into another, the foot of the horse being a well-known case. The genealogy of this noble quadruped can be traced from the Eocene four-toed *Orohippus*, through the *Mesohippus*, the *Miohippus*, the *Protohippus*, and the *Pliohippus*, until we reach the one-toed *Equus*.

Wallace further points out that in order that the fossil of any organism may be preserved, the "concurrence of a number of favourable conditions" is required, and against this the chances are enormous. Lastly, he urges the imperfection of our knowledge of the things that lie embedded in the earth's crust.

The objection based on the lack of "missing links" loses some of its force if we accept the theory that species sometimes arise as sports. Thus, suppose a species with well-developed horns produces as a mutation a hornless variety, which eventually replaces the horned form, we should look in vain for any forms intermediate between the parent and the daughter species. On the other hand, it is significant that just where the links are most needed they [42] are missing. For example, the splint bones of the horse, taken in conjunction with the feet of existing tapirs, which have four toes in front and three behind, would have led us to infer, without the help of the geological record, that the horse was a descendant of a polydactyle ancestor. When, however, we come to the origin of birds, bats, and whales, palæontology fails to give us any assistance, so that we are in the dark as to the origin of such really important modifications.

7. The swamping effects of inter-crossing is an objection which has been repeatedly urged against the Darwinian theory.

This objection is not so serious as it appears at first sight. Darwin and Wallace maintain, firstly, that natural selection acts by eliminating all individuals except those which present favourable variations. The favoured few alone survive and mate with one another, so that there is here no question of the swamping effects of inter-crossing, none but well-adapted individuals being left to mate with one another.

The objection gains greater force when directed against the theory that evolution proceeds by sudden jumps. But in this connection we must bear in mind that the experiments of Mendel and his followers have demonstrated that some of the offspring of crosses may resemble their pure ancestors and breed true *inter se*. Nor is this all. [43]

Recurrent Mutations

Experience shows that where a mutation, or sport, or discontinuous variation occurs, it frequently repeats itself; for example, the black-winged sport of the peafowl has occurred several times over and in different flocks of birds. The sport or mutation must have a definite cause. There must be something within the organism, something in the generative cells, which causes the mutation to arise; and hence, on *a priori* grounds, we should expect the same mutation to arise about the same time in many individuals. It seems legitimate to infer that things have been quietly working up to a climax. When this is reached there results a mutation. Therefore we should expect sudden mutations to appear simultaneously in a number of individuals. To this important subject we shall return.

8. An almost insuperable objection to the theory that species have originated by the action of natural selection on minute variations, is that such small differences cannot be of a life-or-death value, or, as it is usually called, a survival value to their possessor. But if evolution is the result of the preservation by natural selection of such slight variations, it is absolutely necessary that each of these should possess a survival value.

As D. Dewar has pointed out, on page 704 of vol. ii. of *The Albany Review*, it is only when the beast of prey and its victim are evenly matched as regards fleetness and power of endurance that small variations in these qualities can have a survival value. But in the rough and tumble of the struggle for existence the victim and its foe are but rarely well-matched. Take as an example the case of a flycatcher. "This bird," writes D. Dewar, "will sometimes take three or four insects in the course of one flight; all are captured with the same ease, although the length of wing in each victim varies. So great is the superiority of the bird that it does not notice the difference in the flying powers of its puny quarry." It is unnecessary to labour this point. [44]

9. Species or varieties differing considerably in colour may exist side by side, as the hooded and carrion crows, the white and dark breasted forms of the Arctic skua, the pale and dark forms of the fulmar petrel, the grey and rufous forms of the American scops owl (*Megascops asio*).

It is true that preponderance of one form or another in certain districts points to some advantage possessed by one over the other, but, for all we know, it may be due to heredity, and in any case the co-existence of the two types in part of their range, or at certain seasons, shows that selection is not at all rigorous.

The same argument applies to the co-existence of very differently-coloured species with generally similar habits, such as that of the jaguar and puma in South America, and the five very differently-coloured flycatchers in the Nilgiri Hills. [45]

Leaf-butterflies

In short, there is abundant evidence to show that considerable differences in colour do not appear to have any effect on the chances of survival in the struggle for existence of those that display them. Yet this is precisely what the supporters of the Darwinian hypothesis cannot afford to admit, for they then find it impossible to account for the origin of such a form as *Kallima*, the leaf-butterfly, by the action of natural selection. As most people are aware, this creature displays a remarkable resemblance to a decaying leaf. "These butterflies" (there are several species which show the marvellous imitation), writes Kellog, on page 53 of *Darwinism To-day*, "have the under sides of both fore and hind wings so coloured and streaked that when apposed over the back in the manner common to butterflies at rest, the four wings combine to resemble with absurd fidelity a dead leaf still attached by a short petiole to the twig or branch. I say absurd, for it seems to me the resemblance is over-refined. Here for safety's sake it is no question of mimicking some one particular kind of other organism or inanimate thing in nature which birds do not molest. It is simply to produce the effect of a dead leaf on a branch. Leaf-shape and general dead-leaf colour-scheme are necessary for this illusion. [46] But are these following things necessary? namely, an extra-ordinarily faithful representation of mid-rib and lateral veins, even to faint microscopically-tapering vein tips; a perfect short petiole produced by the apposed 'tails' of the hind-wings; a concealment of the head of the butterfly so that it shall not mar the outlines of the lateral margin of the leaf; and finally, delicate little flakes of purplish or yellowish brown to mimic spots of decay and fungus-attacked spots in the leaf! And, as culmination, a tiny circular clear spot in the fore-wings (terminal part of the leaf) which shall represent a worm-eaten hole, or a piercing of the dry leaf by flying splinter, or the complete decay of a little spot due to fungus growth! A general and sufficient seeming of a dead leaf, object of no bird's active interest, yes, but not a dead leaf modelled with the fidelity of the waxworkers in the modern natural history museums. When natural selection has got *Kallima* along to that highly desirable stage when it was so like a dead leaf in general seeming that every bird sweeping by saw it only as a brown leaf clinging precariously to a half-stripped branch, it was natural selection's bounden duty, in conformance to its obligations to its makers, to stop the further modelling of *Kallima* and just hold it up to its hardly won advantage. But what happens? *Kallima* continues its way, specifically and absurdly dead-leafwards, until to-day it is a much too fragile thing to be otherwise than very gingerly handled by its rather anxious foster-parents, the Neo-Darwinian selectionists." It is obvious that if natural selection has produced so highly specialised an organism as the dead-leaf butterfly, every minute variation must be of value and have been seized upon by natural selection. [47]

A Dilemma

Thus the Wallaceians are on the horns of a dilemma. If they assert, as they appear to do, that every infinitesimal variation has a survival value, they find it difficult to explain the existence, side by side of such forms as the hooded and carrion crows, to say why in some species of bird both sexes assume a conspicuous nuptial plumage at the very time when they stand most in need of protective coloration, why the cock paradise flycatcher is chestnut for the first two years of his life and then turns as white as snow. If, on the other hand, the Wallaceians assert that small variations are unimportant and have no survival value, they are, as Kellog points out, in trouble over the close and detailed resemblance which the *Kallima* butterflies bear to dead leaves.

10. An objection to the Darwinian theory which has been advanced by Conn, Henslow, D. Dewar, and others, is that the selection theory fails to take into account the effects of chance. "If," writes D. Dewar on page 707 of *The Albany Review*, vol. ii., "the struggle for existence were of the nature of a race at a well-regulated athletic meeting, where the competitors are given a fair start, where there is no difference in the conditions to which the various runners are subjected, then indeed would every variation tell. I would rather liken the struggle for existence to the rush to get out of a crowded theatre, poorly provided with exits, when an alarm of fire is given. The people to escape are not necessarily the strongest of those present. Propinquity to a door may be a more valuable asset than strength." [48]

Or again, we may take the imaginary case of some antelopes being pursued by wolves. The chase, being prolonged, brings the antelopes to a locality with which they are not familiar. The foremost of the herd, the most swift, and therefore the individual which should stand the best chance of survival, suddenly finds himself on soft boggy ground, which, owing to the depth to which his feet sink into the soil, seriously impedes his progress. His fellow antelopes, now outdistanced, seeing his predicament, take another course and soon leave him behind, to fall an easy prey to his foes. Here we have a case of the perishing of the most fit as regards the important point of speed.

The Effects of Chance

Writing of plants, Professor Henslow says, on page 16 of *The Heredity of Acquired Characters in Plants*: “As the whole of the animal kingdom ultimately lives upon the vegetable, plants must supply the entire quantity of food supplied, not to add innumerable vegetable parasites as well, for both young and old. Myriads of germinating seeds perish accordingly, being destroyed by slugs and other mollusca, and ‘mildews,’ etc. But far more seeds and spores—about 50,000,000 of these it is calculated can be borne in a single male-fern—never germinate at all. They fall where the conditions of life are unfavourable and perish. This misfortune is not due to any inadaptiveness in themselves, but to the surrounding conditions which will not let them germinate. Thus thousands of acorns and other fruits, as of elder, drop upon the ground in and by our hedges, road-sides, copses, and elsewhere; but scarcely any or even no seedlings are to be seen round the trees.” [49]

Every year thousands of birds perish in the great migratory flight, others succumb in a cyclone, a fierce tropical storm, a prolonged drought, a severe frost. Here death overtakes multitudes, all that dwell in a locality, the weak and the strong, the swift and the slow alike.

This objection may be met by saying that in the long run it is the fittest that will survive. This is true. The objection is nevertheless of importance in showing how exceedingly uncertain must be the action of natural selection if it have but small variations upon which to work. In such circumstances the mills of natural selection may grind surely, but they must grind very slowly. [50]

11. We must bear in mind that the struggle for existence is most severe among young animals, among creatures that are not fully developed. Nature pays no attention to potentialities. The weak go to the wall in the conflict, even though, if allowed time, they might develop into prodigies of strength.

Moreover, and this is an important point, death in the case of young creatures overtakes broods and families rather than individuals.

The above-cited objections to the theory that species have originated by the action of natural selection on minute variations, are mostly of a general nature; let us now notice briefly a few more concrete objections. We shall not devote much space to these in the present chapter, since we shall be continually confronted with them when dealing with the subject of animal colouring.

The Origin of Mimicry

12. Natural selection, as we shall see, fails to account for the origin of what is known as protective mimicry. Some insects look like inanimate objects, others resemble other insects which are believed or known to be unpalatable. Those creatures displaying this resemblance to other objects or creatures, and deriving profit therefrom, are said to “mimic” the objects or creatures they copy. They are also called “Mimics.” It is easy to understand the profit that these mimics derive from their mimicry. When once the disguise has been assumed we can comprehend how natural selection will tend to improve it by eliminating those that mimic badly; but it seems to us that the theory fails utterly to account for the origin of the likeness. [51]

13. Similarly, the Neo-Darwinian theory fails to explain the colours of the eggs of birds laid in open nests, why, for example, the eggs of the accentor or hedge-sparrow are blue and those of the doves are white.

14. The theory fails to give a satisfactory explanation of the phenomena of sexual dimorphism. Why, for example, in some species of doves and ducks, the sexes are alike, while in other species with similar habits they differ in appearance.

15. It fails to explain why the rook is black and why the jackdaw has a grey neck.

These and many other objections we shall deal with more fully in the chapter on animal colouration. It must suffice here to mention them, and to say that our experience teaches us that scarcely a single species of bird or beast exists which does not display some characteristic which is inexplicable on the theory that natural selection, acting on small variations, is the one and only cause of organic evolution.

[52]

CHAPTER III VARIATION

The assumption of Darwin and Wallace that variations are haphazard in origin and indefinite in direction—If these assumptions be not correct Natural Selection ceases to be the fundamental factor in evolution—Darwin's views regarding variation underwent modification—He eventually recognised the distinction between definite and indefinite variations, and between continuous and discontinuous variations—Darwin attached but little importance to either definite or discontinuous variations—Darwin's views on the causes of variations—Criticism of Darwin's views—Variations appear to occur along certain definite lines—There seems to be a limit to the extent to which fluctuating variations can be accumulated—De Vries' experiments—Bateson on "discontinuous variation"—Views held by De Vries—Distinction between continuous and discontinuous variations—The work of De Vries—Advantages enjoyed by the botanist in experimenting on the making of species—Difficulties encountered by the animal breeder—Mutations among animals—The distinction between germinal and somatic variations—The latter, though not transmitted to offspring, are often of considerable value to their possessor in the struggle for existence.

Nature of Variation

As we have already seen, the Darwinian theory, unlike that of Lamarck, does not attempt to explain the origin of variations. It is content with the fact that variations do occur.

Although Darwin did not try to explain how it is that variation occurs, and was very guarded in the expressions he used concerning it, he assumed that variations are indefinite in variety and occur indiscriminately in all directions, as the following quotations from the *Origin of Species* will show: "But the number and diversity of inheritable deviations of structure . . . are endless" (page 14, ed. 1902). "The variations are supposed to be extremely slight, but of the most diversified nature." "I have hitherto sometimes spoken as if the variations so common and multiform with organic beings under domestication, and in a lesser degree to those under nature, were due to chance. This, of course, is a wholly incorrect expression, but it serves to acknowledge plainly our ignorance of the cause of each particular variation" (page 164). [53]

Wallace is far less guarded in his expressions. On page 82 of his *Darwinism* he speaks of "the constant and large amount of variation of every part in all directions . . . which must afford an ample supply of favourable variations whenever required."

The double assumption that variations are for all practical purposes haphazard in origin and indefinite in direction is necessary if natural selection is to be the main factor in evolution. For if variations be not haphazard, if they are definite, if there be a directive force behind them, like fate behind the classical gods, then selection is not the fundamental cause of evolution. It can at most effect, not the origin of species, but the survival of certain species which have arisen as the result of some other force. Its position is changed; it is no longer a cause of the origin of new organisms, but a sieve determining which of certain ready-made forms shall survive. Evidently, then, we shall not be able to fully understand the evolutionary process until we have discovered how it is that variations are caused. In other words, we must go considerably farther than Darwin attempted to do. [54]

Before proceeding to inquire into the true nature of variations, it behoves us to set forth briefly the ideas of Darwin on the subject. We shall then be in a position to see how much progress has been made since the days of that great biologist.

It is not at all easy to discover exactly what were Darwin's views on the subject of variation. A perusal of his works reveals contradictions, and gives one the impression that he himself scarcely knew his own mind upon the subject. This should not be a matter for surprise.

We must remember that Darwin had to do pioneer work, that he had to deal with altogether new conceptions. Such being the case, his ideas were of necessity somewhat hazy; they underwent considerable modification as fresh facts came to his knowledge.

Definite and Indefinite Variability

Towards the end of his life Darwin recognised that variability is of two kinds—definite and indefinite. Indefinite variation is indiscriminate variation in all directions around a mean, variation which obeys what we may perhaps call the law of chance. Definite variation is variation in a determinate direction—variation chiefly on one side of the mean. Darwin believed that these determinate variations were caused by external forces, and that they are inherited. He thus accepted Lamarckian factors. “Each of the endless variations,” he writes, “which we see in the plumage of our fowls, must have had some efficient cause, and if the same causes were to act uniformly during a long series of generations on many individuals, all probably would be modified in the same direction.” [55]

But Darwin was always of opinion that this definite variability, this variability in one direction as the result of some fixed cause, is far less important, from an evolutionary point of view, than indefinite variability, that it is the exception rather than the rule, that the usual result of changed conditions is to let loose a flood of indefinite variability, that it is almost exclusively upon this that natural selection acts.

Darwin also recognised that variations differ in degree, even as they do in kind. He perceived that some variations are much more pronounced than others. He recognised the distinction between what are now known as continuous and discontinuous variations. The former are slight departures from the normal; the latter are considerable deviations from the mean or mode; great jumps, as it were, taken by nature, as, for example, the pea and the rose combs of fowls, which were derived from the normal single comb. [56]

Monstrosities

“At long intervals of time,” wrote Darwin, “out of millions of individuals reared in the same country and fed on nearly the same food, deviations of structure so strongly pronounced as to deserve to be called monstrosities arise, but monstrosities cannot be separated by any distinct line from slighter variations.” Therefore it is evident that he regarded the difference between continuous and discontinuous variations as not one of kind, but merely of degree. To the discontinuous variations Darwin attached very little importance from an evolutionary point of view. He looked upon them as something abnormal.

“It may be doubted,” he wrote, “whether such sudden and considerable deviations of structure such as we occasionally see in our domestic productions, more especially with plants, are ever permanently propagated in a state of nature. Almost every part of every organic being is so beautifully related to its complex conditions of life that it seems as improbable that any part should have been suddenly produced perfect, as that a complex machine should have been invented by a man in a perfect state. Under domestication monstrosities sometimes occur which resemble normal structures in widely different animals. Thus pigs have occasionally been born with a sort of proboscis, and if any wild species of the same genus had naturally possessed a proboscis, it might have been argued that this had appeared as a monstrosity; but I have as yet failed to find, after diligent search, cases of monstrosities resembling normal structures in nearly allied forms, and these alone bear on the question. If monstrous forms of this kind ever do appear in a state of nature and are capable of reproduction (which is not always the case), as they occur rarely and singly, their preservation would depend on unusually favourable circumstances. They would, also, during the first and succeeding generations cross with the ordinary form, and thus their abnormal character would almost inevitably be lost.” But, in a later edition of the *Origin of Species*, Darwin seems to contradict the above assertion: “It should not, however, be overlooked that certain rather strongly marked variations, which no one would rank as mere individual differences, frequently recur owing to a similar organisation being similarly acted on—of which fact numerous instances could be given with our domestic productions. In such cases, if the varying individual did not actually transmit to its offspring its newly acquired character, it would undoubtedly transmit to them, as long as the existing conditions remained the same, a still stronger tendency to vary in the same manner. There can also be little doubt that the tendency to vary in the same manner has often been so strong that all the individuals of the same species have been similarly modified without the aid of any form of selection. Or only a third, fifth, or tenth part of the individuals may have been thus affected, of which fact several instances could be given. Thus Graba estimates that about one-fifth of the guillemots in the Faroe islands consist of a variety so well marked, that it was formerly ranked as a distinct species under the name *Uria lacrymans*. In cases of this kind, if the variation were of a beneficial nature, the original form would soon be supplanted by the modified form, through the survival of the fittest.” Here we seem to have a plain statement of the origin of new forms by mutation. [57] [58]

Minute Variations

Again, we read (page 34): “Some variations useful to him (*i.e.* man) have probably arisen suddenly, or by one step; many botanists, for instance, believe that the fuller’s teasel, with its hooks, which cannot be rivalled by any mechanical contrivance, is only a variety of the wild *Dipsacus*; and this amount of change may have suddenly arisen in a seedling. This is known to be the case with the turnspit dog.” [2] But, as we have already said, Darwin at no time [59]

attached much importance to these jumps made by nature as a factor in evolution. He pinned his faith to the minute, indefinite variations which he believed could be piled up, one upon another, so that, if allowed sufficient time, either nature or the human breeder could, by a continued selection of these minute variations, call into being any kind of organism. The importance of selection, he writes, “consists in the great effect produced by the accumulation in one direction, during successive generations, of differences absolutely inappreciable by an uneducated eye” (page 36). On page 132 he writes: “I can see no limit to the amount of change, to the beauty and complexity of the coadaptations between all organic beings . . . which may have been effected^[3] in the long course of time by nature’s power of selection.” He expressly states, on page 149, that he sees no reason to limit the process to the formation of genera alone.

Although the theory of natural selection does not attempt to explain the causes of variation, Darwin paid some [60] attention to the subject. He believed that both internal and external causes contribute to variation, that variations tend to be inherited whether the result of causes within the organism or outside it. He believed that the inherited effect of use and disuse was a cause of variation, and cited, as examples, the lighter wing-bones and heavier leg-bones of the domestic duck and the drooping ears of some domestic animals. He supposed that animals showed a greater tendency to vary when under domestication than when in their natural state, attributing the supposed greater variability to the excess of food received, and the changed conditions of the life of domestic animals. Nevertheless, he was fully alive to the fact that “nearly similar variations sometimes arise under, as far as we can judge, dissimilar conditions; and, on the other hand, dissimilar variations arise under conditions which appear to be nearly uniform.” In other words, the nature of organisms appeared to Darwin to be a more important factor in the origin of variations than external conditions. Evidence of this is afforded by the fact that some animals are more variable than others. Finally, he frankly admitted how great was his ignorance of the causes of variability. Variability is, he stated, governed by unknown laws which are infinitely complex.

Lines of Variation

It will be convenient to deal with each of Darwin’s main ideas on variation separately, and to consider to what [61] extent they seem to require modification in the light of later research.

Firstly, Darwin believed that variations arise in what appears to be a haphazard manner, that they occur in all directions, and seem to be governed by the same laws as chance. It is our belief that we are now in a position to make more definite statements regarding variation than Darwin was able to.

Biologists can now assert definitely that variations do not always occur equally in all directions. The results of many years of the efforts of practical breeders demonstrate this. These men have not been able to produce a green horse, a pigeon with alternate black and white feathers in the tail, or a cat with a trunk, for the simple reason that the organisms upon which they operated do not happen to have varied in the required direction. It may perhaps be objected that breeders have no desire to produce such forms; had they wished to do so, they would probably have succeeded. To this objection we may reply that they have not managed to produce many organisms, which would be highly desirable from a breeder’s point of view, as, for example, a blue rose, hens that lay brown eggs but do not become broody at certain seasons of the year, or a cat that cannot scratch.

As Mivart well says, on page 118 of his *Genesis of Species*, “Not only does it appear that there are barriers which [62] oppose change in certain directions, but that there are positive tendencies to development along certain special lines. In a bird which has been kept and studied like the pigeon, it is difficult to believe that any remarkable spontaneous variations would pass unnoticed by breeders, or that they would not have been attended to and developed by some fancier or other. On the hypothesis of indefinite variability, it is then hard to say why pigeons with bills like toucans, or with certain feathers lengthened like those of trogons, or those of birds of paradise, have never been produced.”

There are certain lines along which variation seems never to occur. Take the case of the tail of a bird. Variable though this organ be, there are certain kinds of tail that are seen neither in wild species nor domesticated races. A caudal appendage, of which the feathers are alternately coloured, occurs neither in wild species nor in artificial breeds. For some reason or other, variations in this direction do not occur. Similarly, with the exception of one or two of the “Noddy” terns, whenever a bird has any of its tail feathers considerably longer than the others, it is always the outer pair or the middle pair that are so elongated. It would thus appear that variations in which the other feathers are especially lengthened do not usually occur. The fact that they are elongated in two or three wild species is the more significant, because it shows that there is apparently nothing inimical to the welfare of a species in having, say, the [63] third pair of tail feathers from the middle exceptionally prolonged.

Breeders’ Boasts

This is a most important point, and one which seems to be ignored by the majority of scientific men, who appear to be misled by the boastful talk of certain successful breeders. Thus, on page 29 of the *Origin of Species*, Darwin quotes, with approval, Youatt's description of selection as "the magician's wand, by means of which he may summon into life whatever form and mould he pleases." Darwin further cites Sir John Sebright as saying, with regard to pigeons, that he would "produce any given feather in three years, but it would take him six years to obtain head and beak."

If it were possible absolutely to originate anything by selection, horticulturists would almost certainly ere this have produced a pure black flower. The fact that not a single mammal exists, either in nature or under domestication, with scarlet, blue, or green in its hair, appears to show that, for some reason or other, mammals never vary in any of these directions.

The fact that so few animals have developed prehensile tails seems to indicate that variation does not often occur in that direction, for obviously a prehensile tail is of the very greatest utility to its possessor; so that there can be little room for doubt that it would be seized upon and preserved by natural selection, whenever it occurred. [64]

As E. H. Aitken very truly says, "so early and useful an invention should, one would think, have been spread widely in after time; but there appears to be some difficulty in developing muscles at the thin end of a long tail, for the animals that have turned it into a grasping organ are few and are widely scattered. Examples are the chameleon among lizards, our own little harvest mouse, and, pre-eminent among all, the American monkeys" (*Strand Magazine*, Nov. 1908).

Even as there are many variations which seem never to occur in nature, so are there others which occur so frequently that they may be looked for in any species. Albinistic forms appear now and again in almost every species of mammal or bird; while melanistic sports, although not so common, are not by any means rare.

Every complete manual on poultry gives for each breed a note of the faults which constantly appear, and which the fancier has to watch carefully for and guard against. The fact that these "faults" occur so frequently in each breed shows how strong is the tendency to vary in certain definite directions. It is true that some of these faults are in the nature of reversions, as, for example, the appearance of red hackles in the cocks of black breeds of poultry. On the other hand, some certainly are not reversions, such as the appearance of a white ring in the neck of the female of the Rouen duck, which should resemble the Mallard as regards the plumage of the neck. Again, the tendency of Buff Orpingtons to assume white in the wings and tail must be regarded as a variation which is not in the nature of a reversion. In short, the efforts of all breeders are largely directed to fighting against the tendencies which animals display towards variation in certain directions. [65]

Albinistic Variations

This tendency to vary in the direction of whiteness may account for many of the white markings which occur in nature, as, for example, the white tails of the Sea Eagle (*Haliaeetus albicilla*) the Nicobar Pigeon (*Caloenas nicobarica*), and many hornbills. Provided that such variations are not too great a handicap to their possessors in the struggle for existence, natural selection will allow them to persist.

It was the belief of Linnæus, based on experience, that every blue or red-coloured flower is likely to produce a white variety, hence he held that it is not safe to trust to colour for the identification of a botanical species.

On the other hand, white flowers are not likely to produce red varieties, and we believe we may positively assert that they never produce a blue sport. Similarly, white animals appear not to give rise to colour varieties. [66]

We are never surprised to find that an ordinary upright plant produces as a sport or mutation a pendulous, or fastigiate form. These aberrant varieties, be it noted, occur in species which belong to quite different orders.

De Vries points out that lacinated leaves appear in such widely separated trees and shrubs as the walnut, the beech, the hazel-nut, and the turnip.

Another example of the definiteness of variation is furnished by what Grant Allen calls the "Law of Progressive Colouration" of flowers.

On pp. 20, 21 of *The Colours of Flowers*, he writes, "All flowers, as we know, easily sport a little in colour. But the question is, do their changes tend to follow any regular and definite order? Is there any reason to believe that the modification runs from any one colour toward any other? Apparently there is. . . . All flowers, it would seem, were in their earliest form yellow; then some of them became white; after that a few of them grew to be red or purple; and finally a comparatively small number acquired the various shades of lilac, mauve, violet, or blue."

Over-development

So among animals there are many colour patterns and structures that appear in widely different genera, as, for example, the magpie colouring in birds. With this phenomenon we shall deal more fully when speaking of animal colouration. There is certainly no small amount of evidence which seems to indicate that, from some cause or other, an impetus has been given to certain organs to develop along definite lines. The reduction of the number of digits in several mammalian families which are not nearly related is a case in point. This phenomenon is, as Cope points out, observed in Marsupials, Rodents, Insectivores, Carnivores, and Ungulates. He, being a Lamarckian, ascribes this to the inherited effects of use. Wallaceians attribute it solely to the action of natural selection. The assumption of a growth-force or tendency for the development of one digit at the expense of the others, would explain the phenomenon equally well. And it is significant that many palæontologists are believers in some kind of a growth-force. In the case of certain extinct animals we seem to have examples of the over-development of organs. "Palæontology," writes Kellog on p. 275 of his *Darwinism To-day*, "reveals to us the one-time existence of animals, of groups of animals, and of lines of descent, which have had characteristics which led to extinction. The unwieldiness of the giant Cretaceous reptiles, the fixed habit of life of the crinoids, the coiling of the ammonites and the nautili, the gigantic antlers of the Irish stag—all these are examples of development along disadvantageous lines, or to disadvantageous degrees. The statistical studies of variation have made known numerous cases where the slight, as yet non-significant (in a life-and-death struggle) variation in pattern of insects, in dimensions of parts, in relative proportions of superficial non-active areas, are not fortuitous, that is, do not occur scattered evenly about a mean or mode according to the law of error, but show an obvious and consistent tendency to occur along certain lines, to accumulate in certain directions."

It seems to us that the only proper attitude to adopt in the present state of our knowledge is, not to call in to our aid an unknown growth-force, but simply to say that there is evidence to show that variations frequently occur along certain definite lines only.

Speed of Racehorses

Darwin's second assumption was that there is no limit to which variations may be accumulated in any direction; that by adding one minute variation to another through countless generations new species, new genera, new families may arise. This assumption, if applied to continuous or fluctuating variations, seems opposed to facts. All the evidence available goes to show that there is a definite limit to which minute variations can be accumulated in any given direction. No one has succeeded in breeding a dog as large as a horse, or a pigeon with a beak as long as that of a snipe. In the case of racehorses, which have been selected so carefully through a long period of time, we seem to have reached the limit of speed which can be attained by the multiplication of insignificant variations. We do not wish to dogmatise, but we believe that of late years there has not been any material increase in the speed of our racehorses.

Mr S. Sidney says, on page 174 of *Cassell's Book of the Horse*: "As far as form went (*pace* Admiral Rous), the British racehorse had reached perfection in 1770, when 'Eclipse' was six years old." He quotes the measurements of the skeleton of "Eclipse" in the Museum of the Royal College of Surgeons as evidence of this. All the efforts of breeders, then, have failed appreciably to improve the form of the British racehorse in the course of over a century and a quarter.

Experiments of De Vries

De Vries has made some important experiments with a view to determining whether or not there is a limit to the amount of change which can be induced by the selection of fluctuating or continuous variations as opposed to mutations. "I accidentally found," he writes, on page 345 of *Species and Varieties: their Origin by Mutation*, "two individuals of the 'five-leaved' race (of clover); by transplanting them into my garden I have isolated them and kept them free from cross-fertilisation with the ordinary type. Moreover, I brought them under such conditions as are necessary for the full development of their character; and last, but not least, I have tried to improve their character as far as possible by a very rigid and careful selection. . . . By this method I brought my strain within two years up to an average of nearly 90 per cent. of the seedlings with a divided primary leaf (such seedlings averaging five leaves in the adult). . . . This condition was reached by the sixth generation in the year 1894, and has since proved to be the limit, the figures remaining practically the same through all the succeeding generations. . . . I have cultivated a new generation of this race nearly every year since 1894, using always the strictest selection. This has led to a uniform type, but has not been adequate to produce further improvement." Similarly, De Vries found in the bulbous buttercup (*Ranunculus bulbosus*) a strain varying largely in the number of petals; therefore he tried by means of continuous selection of those flowers having the largest number of petals to produce a double flower, but was not able to do so. He succeeded in evolving a strain with an average number of nine petals, some individuals having as many as twenty or thirty; but even by breeding only from these last he could not increase the average number of petals in any generation beyond nine. This was the limit to be obtained by the most rigorous selection of fluctuating variations.

Selection, based on fluctuating variation, does not, asserts De Vries, conduce to the production of improved races. “Only temporary ameliorations are obtained, and the selection must be made in the same manner every year. Moreover, the improvement is very limited, and does not give any promise of further increase.” Notwithstanding prolonged efforts, horticulturists have not yet succeeded in breeding a biennial race of either beetroots or carrots that does not continually give rise to useless annual forms. Writing of the beet, De Vries says useless annual varieties “are sure to return each year. They are ineradicable. Every individual is in the possession of this latent quality, and liable to convert it into activity as soon as the circumstances provoke its appearance, as is proved by the increase of annuals in the early sowings”—that is to say, in circumstances favourable to the annual variety.

It will be urged perhaps that these experiments, which seem to show that there is a limit to which a species can be modified by the accumulation of fluctuating variations, cannot have been properly carried out, because all the various breeds of pigeons and other domestic animals clearly show that extraordinary differences not only can, but have [72] actually been produced by the selection of such variations. This objection is based upon the assumption that breeders have in the past dealt only with fluctuating variations. This assumption does not appear to be justified. It is exceedingly probable that most, if not all, the varieties of domesticated animals have originated in mutations. Take, for instance, the modern turbit pigeon; this has been derived from the old Court-bec, described and figured over two centuries ago by Aldrovandus.

De Vries goes so far as to assert that the various races of pears are all mutations; that each distinct flavour is a mutation, and that it is impossible to produce a new flavour by selecting fluctuating variations. Thus it would appear that in every case of the production of a new breed a mutation has occurred which has attracted the fancy of some breeder, and he has seized upon this and perpetuated it.

All the evidence available tends to show that there is a limit—and one which is quickly reached—to the amount of change that can be produced by the selection of fluctuating or continuous variations. We, therefore, seem driven to the belief that evolution is based on the kind of variation which Professor Bateson terms “discontinuous variation” and Professor De Vries calls “mutation.”

[73]

Bateson on Variation

As long ago as 1894 Bateson published his *Materials for the Study of Variation*, in which he set forth a large number of cases of discontinuous variation which he had collected. He pointed out that species are discontinuous, that they are sharply separated one from another, whereas “environments often shade into one another and form a continuous series.” How, then, he asked, if variations are minute and continuous, have these discontinuous species arisen? May not variation prove to be discontinuous, and thus make it clear why species are discontinuous?

On page 15 of the above-cited work we find: “The preliminary question, then, of the degree of continuity with which the process of evolution occurs has never been decided. In the absence of such a decision, there has nevertheless been a common assumption, either tacit or expressed, that the process is a continuous one. The immense consequence of a knowledge of the truth as to this will appear from a consideration of the gratuitous difficulties which have been introduced by this assumption. Chief among these is the difficulty which has been raised in connection with the building up of new organs in their initial and imperfect stages, the mode of transformation of organs, and, generally, the selection and perpetuation of minute variations. Assuming, then, that variations are minute, we are met by this familiar difficulty. We know that certain devices and mechanisms are useful to their possessors; but from our knowledge of [74] natural history we are led to think that their usefulness is consequent on the degree of perfection in which they exist, and that if they were at all imperfect, they would not be useful. Now it is clear that in any continuous process of evolution such stages of imperfection must occur, and the objection has been raised that natural selection cannot protect such imperfect mechanisms so as to lift them into perfection. Of the objections which have been brought against the theory of natural selection this is by far the most serious.”

Bateson further pointed out that chemical compounds are not continuous, that they do not merge gradually each into the next, and suggested that we might expect a similar phenomenon in the organic world.

Elsewhere he says: “Let the believer in the efficacy of selection operating on continuous fluctuations try to breed a white or a black rat from a pure strain of black-and-white rats, by choosing for breeding the whitest or the blackest; or to raise a dwarf sweet pea from a tall race by choosing the shortest. It will not work. Variation leads and selection follows.”

Work of Bateson and De Vries

But Bateson's views fell upon stony ground, because zoologists are mostly men of theory and not practical breeders. They laboured under the delusion that mutations or "sports" are rare in nature, and that when these do happen to occur they must of necessity be swamped by inter-crossing. [75]

However, the discovery of the Abbé Mendel's account of his experiments on breeding mongrel sweet peas has opened the eyes of many zoologists, so that they have at last learned what practical breeders have known for untold years—namely, that sports have a way of perpetuating themselves. Moreover, Mendel was able to give a theoretical explanation of his discoveries, with the result that the believers in discontinuous variation have largely increased in number of late.

While we are unable to see eye to eye with Professor Bateson in all things, we gladly recognise the immense value of his work. Had his statements in 1894 received the attention they merited, zoological theory would to-day be considerably more advanced than it actually is.

Professor De Vries has gone farther than Bateson, having engrafted upon the Darwinian hypothesis the theory of mutations. He has done no small amount of experimental work, and has undoubtedly thrown much new light on the ways in which species arise. He is purely a botanist, so that he argues only from plants. Nevertheless, we believe that some of his conclusions are applicable to animals. We are far from accepting his theory of mutations *in toto*. We are, however, convinced that he, like Bateson, is on the right track. There can be no doubt that a great many new forms have originated suddenly, by jumps, and not by imperceptibly slow degrees. Before giving a list of the names of some of the races, both plant and animal, which appear to have come into existence suddenly, it will be of advantage to consider for a little some of the more important conceptions of De Vries. [76]

Varieties and Elementary Species

That eminent botanist, as we have already seen, insists on the distinction between fluctuating variations and mutations. The former correspond, for all practical purposes, to the continuous variations of Bateson, and the latter seem to be equivalent to his discontinuous variations.

According to De Vries, all plants display fluctuating variation, but only a small percentage exhibit the phenomenon of mutation. The most daring of his conceptions is, that the history of every species is made up of alternating periods of inactivity, when only fluctuating variations occur, and of activity when "swarms of species" are produced by mutation, and of these only a few at the most survive; natural selection, which De Vries likens to a sieve, determining which shall live and which shall perish.

As we have seen, De Vries does not believe that new species can arise by the accumulation of fluctuating variations. By means of these the race may be greatly improved, but nothing more can be accomplished. These variations follow Quetelet's law, which says that, for biological phenomena, deviations from the average comply with the same laws as the deviations from the average in any other case, if ruled by chance alone. [77]

Very different in character are mutations. By means of these, new forms, quite unlike the parent species, suddenly spring into being. Mutations are said by De Vries to be of two kinds—those that produce varieties and those which result in new elementary species.

According to De Vries, those species of plants which are in a state of mutation (he refers to the species of the systematic botanists) are of a composite nature, being made up of a collection of varieties and elementary species. His conception of a variety is a plant that differs from the parent plant in the loss or suppression of one or more characters, while an elementary species differs from the parent form in the possession of some new and additional character. But we will allow him to speak for himself: "We can consider (page 141 *Species and Varieties*) the following as the principal difference between elementary species and varieties: that the first arise by the acquisition of entirely new characters, and the latter by the loss of existing qualities, or by the gain of such peculiarities as may already be seen in other allied species. If we suppose elementary species and varieties originated by sudden leaps and bounds, or mutations, then the elementary species have mutated in the line of progression, some varieties have mutated in the line of retrogression, while others have diverged from the parental types in a line of digression or in the way of repetition. . . . The system (of the vegetable kingdom) is built up of species; varieties are only local and lateral, never of real importance for the whole structure." [78]

De Vries asserts that these elementary species, when once they arise, breed true, and show little or no tendency to revert to the ancestral form. We can, says De Vries, ascertain only by experiment which plants are in the mutating state and which are not. The great majority, however, are not at present in the mutating state.

Mutations

The distinction between fluctuating variation and mutation has been roughly illustrated by the case of a solid block of wood having a number of facets, on one of which it stands. If the block be tilted slightly it will, when the force that has tilted it is removed, return to its old position. Such a gentle tilt may be compared to a fluctuating variation in an organism. If, however, the block be tilted to such an angle that when left to itself the block does not return to its old position, but tips over and comes to rest on another facet, we have a representation of the kind of change indicated by a mutation. [79]

The analogy is far from perfect, for it makes it appear that the smallest mutation must of necessity involve a departure from the normal type more considerable than that of the largest fluctuating variation. Now, although mutations ordinarily consist in considerable deviations from the mean or mode of the type, while continuous variations are usually minute deviations, it sometimes happens that the extreme fluctuations are more considerable than some mutations. Hence "fluctuating" describes this latter kind of variation more accurately than "continuous" does.

The test, then, of a mutation is not so much the amount of deviation as the degree in which it is inherited. Mutations show no tendency to a gradual return to the mean of the parent species; fluctuating variations do display such a tendency. A mutation consists, as M. E. East says, in the production of a new mode or centre for linear fluctuation; it is, as it were, a shifting of the centre of gravity; the centre about which those fluctuations which we call continuous variations occur.

As it is of considerable importance thoroughly to grasp the true nature of mutations or discontinuous variations, and as some writers do not appear to realise wherein lies the essential difference between the two kinds of variation, we will, at the risk of appearing tedious, give a further illustration. Let A be a species of bird of which the average length of the wing is 20 inches, and let us suppose that individuals belonging to that species occur in which the length of the wing varies as much as 3 inches each side of the mean; thus it is possible to find individuals of this species with a wing as short as 17 inches, or as long as 23 inches. Let B be another species of which the average length of the wing is 17 inches, and let us suppose that a 3-inch variation on each side of the mean be found to occur. Individuals belonging to species B will occur which have a wing as short as 14 inches, or as long as 20 inches. Thus some individuals of the short-winged species will have longer wings than certain individuals of the long-winged species. Similarly, certain individuals of a species which display a mutation may show less deviation from the mean than some individuals showing a very pronounced fluctuating variation. In other words, even as by measuring the length of wing in the above example it was not always possible to say whether a given individual belonged to species A or B, so is it not always possible to say by looking at an individual that shows a considerable departure from the mean whether that departure is due to a mutation or a fluctuating variation. [80]

Law of Regression

It is only by watching the effect of the peculiarity on the offspring of its possessor that we are able to determine the nature of the variation. Where the peculiarity is due to a fluctuating variation the offspring will display the peculiarity in a diminished degree; but if the peculiarity be due to a mutation, the offspring are likely to display it in as marked a degree as the parent.

Fritz Müller and Galton conducted independently enquiries into the amount of the regression shown by the progeny of parents which have deviated from the average by fluctuating variation.

Müller experimented with Indian corn; Galton with the sweet pea.

Each found that where the deviation of the parents is represented by the figure 5, that of their offspring is usually 2, that is to say, the deviation they display is, on the average, less than half that of their parents.

Applying this rule to the hypothetical case given above, if two individuals of species A having a length of wing of 20 inches be bred together, their offspring will, on an average, have a length of wing of 20 inches, since neither parents showed any deviation from the mean. On the other hand, the offspring of 20-inch-wing individuals of species B would show, on an average, a length of wing of only about 18¼ inches. They tend to return to that mode from which their parents had departed. [81]

But suppose that the deviation of the parents in this case had been due, not to fluctuating variation, but to a mutation; this would mean that, owing to some internal change in the egg that produced each parent, 20 inches became the normal length of wing; that the normal length of wing had suddenly shifted from 17 inches to 20 inches.

The result of this would be that their offspring would have on an average a wing-length of 20 inches instead of 18¼ inches, that the centre of variation as regards length of wing had suddenly shifted from 17 to 20, that, in future, all fluctuating variations would occur on either side of 20 inches, instead of on either side of 17 inches as heretofore.

Thus a variation is a fluctuating one or a mutation according as it does or does not obey Galton's Law of Regression.

De Vries's Dictum

De Vries says that it is of the essence of mutations that they are completely inherited. This statement, although substantially true, fails to take into consideration the factor of fluctuating variation. For example, in the above instance if the two individuals of species B had mutated into forms with a 20-inch wing, their offspring will nevertheless vary *inter se*, some of them will have wings shorter than 20 inches and others wings more than 20 inches in length. But [83] the average wing-length of the offspring of the two mutating individuals will be 20 inches.

So much, then, for the practical difference between a mutation and a fluctuating variation. In Chapter V. we shall discuss the possible causes of the difference. By way of anticipation we may say that the suggestion we shall make is that a mutation is due to some rearrangement in the particles which represent that part of the organism in the fertilised egg, whereas a fluctuating variation is caused by variations in the particles themselves.

De Vries, it should be noted, bases his theory largely on experimental evidence. His dictum is "the origin of species is an object of experimental observation." He has, we consider, proved conclusively that among plants mutations sometimes occur, and, further, that in a mutating plant the same mutation tends to occur again and again. This latter is a most important fact, because it goes some way towards overcoming the difficulty urged by Darwin that isolated sports must be swamped by continual crossing with the normal type. If mutations arise in swarms, as De Vries asserts they do, then any particular mutation is likely, sooner or later, to cross with a similar mutation and so be able to perpetuate itself.

[84]

Mutating Plants

The classical example of a mutating plant is the evening primrose of the species *Oenothera lamarckiana*. This is described by De Vries as a stately plant, with a stout stem, attaining often a height of 1.6 metres or more. The flowers are large and of a bright yellow colour, attracting immediate attention, even from a distance. "This striking species," he writes, in *Species and Varieties* (p. 525), "was found in a locality near Hilversum, in the vicinity of Amsterdam, where it grew in some thousands of individuals. Ordinarily biennial, it produces rosettes in the first, and stems in the second year. Both the stems and the rosettes were seen to be highly variable, and soon distinct varieties could be distinguished among them.

"The first discovery of this locality was made in 1886. Afterwards I visited it many times, often weekly or even daily, and always at least once a year up to the present time. This stately plant showed the long-sought peculiarity of producing a number of new species every year. Some of them were observed directly in the field, either as stems or rosettes. The latter could be transplanted into my garden for further observation, and the stems yielded seeds to be sown under like control. Others were too weak to live a sufficiently long time in the field. They were discovered by sowing seed from indifferent plants of the wild locality in the garden. A third and last method of getting still more new [85] species from the original strain was the repetition of the sowing process, by saving and sowing the seed which ripened on the introduced plants. These various methods have led to the discovery of over a dozen new types, never previously observed or described." Some of these De Vries regards as varieties, in the sense in which he uses the words; others, he maintains, are real progressive species, some of which are strong and healthy, others weaker and apparently not destined to be successful. All these types proved absolutely constant from seed. "Hundreds of thousands of seedlings may have arisen, but they always come true and never revert to the original *O. lamarckiana* type. But some of them, however, are, like their parent form, liable to mutations." The case of the evening primrose is by no means an isolated one. De Vries cites several other instances of plants in a mutating state. "The common poppy," he says (p. 189), "varies in height, in colour of foliage and flowers; the last are often double or laciniated. It may have white or bluish seeds, the capsules may open themselves or remain closed, and so on. But every single variety is absolutely constant, and never runs into another when the flowers are artificially pollinated and the visits of insects excluded." Similarly the garden carnation sometimes gives rise to the wheat-ear form. "In this variety," writes De Vries (p. 228), "the flower [86] is suppressed, and the loss is attended by a corresponding increase in the number of pairs of bracts. This malformation results in square spikes, or somewhat elongated heads, consisting only of the greenish bracts. As there are no flowers, the variety is quite sterile, and, as it is not regarded by horticulturists as an improvement on the ordinary bright carnations, it is seldom multiplied by layering. Notwithstanding this it appears from time to time, and has been seen in different countries and at different periods, and what is of great importance for us, in different strains of

carnations. Though sterile, and obviously dying out as often as it springs into existence, it is nearly two centuries old. It was described in the beginning of the eighteenth century by Volckamer, and afterwards by Jaeger, De Candolle, Weber, Masters, Magnus, and many other botanists. I have had it twice at different times and from different growers." Similarly, the long-headed green dahlia arose twice over some years ago in the nursery of Messrs Zocher & Co.

Further, the peloric Toad-flax (*Linaria vulgaris peloria*) is, De Vries informs us, "known to have originated from the ordinary type at different times and in different countries under more or less divergent conditions." And, as this variety is wholly barren, it must in each instance have had an independent origin. Lastly, the purple beech seems to be a [87] mutation which has originated at least three times over.

Mutation Theory Criticised

Every one interested in biological theory should read both *Species and Varieties* and *Plant Breeding* by De Vries, works which are of incalculable value to the horticulturist and agriculturist as well as to the biologist.

While not wishing to detract in any way from the truly splendid work done by De Vries, we feel constrained to bring several charges against him.

Firstly, he suffers from the complaint that seizes nine out of ten originators of new theories. He pushes his theory to extreme lengths; he allows his imagination to run away with him. We do not think that on the evidence available he is justified in asserting that every species passes through alternating periods of comparative quiescence and periods in which it throws off, as mutations, swarms of elementary species. He is justified in asserting that discontinuous variation is by no means an uncommon phenomenon, but further than this it does not seem safe to go at present.

Secondly, he ought to lay more stress on the fact that *Oenothera lamarckiana* is a plant which does not appear to be known in the wild state, and that it is therefore possibly a hybrid plant, and the so-called elementary species which it gives off may be merely the varieties out of which it has been built up. Boulenger and Bailey have both studied this [88] plant, and they have not been able to witness all the mutations of which De Vries speaks, so that the former says, "The fact that *Oenothera lamarckiana* was originally described from a garden flower, grown in the Paris *Jardin des Plantes*, and that, in spite of diligent search, it has not been discovered wild anywhere in America, favours the probability that it was produced by crossing various forms of the polymorphic *Oenothera biennis*, which had been previously introduced in Europe."

Definition of a Species

It has further been objected that, even if these various forms which Lamarck's evening primrose throws off are true mutations, they ought not to be called new species, for they do not differ sufficiently from the parent species to deserve the name of new species. The reply to this criticism is that De Vries asserts that mutations produce new elementary species, which are not the same things as new species in the ordinary sense of the term. Most Linnæan species differ from one another to a far greater extent than do elementary species. It seems to us quite plain that new species arise, not by a single mutation, but by two or three successive mutations which occur in various parts of an organism.

First arises a well-marked variety, by a single mutation. Subsequent mutations follow, so that a distinct race is [89] produced. And, finally, fresh mutations occur, so that a new species is eventually produced.

What De Vries calls an elementary species the majority of systematists would call a well-marked variety.

We may take this opportunity of remarking that the definition of a species is one on which naturalists seem unable to agree.

So vast is the field of biology, that now-a-days biologists are compelled to specialise to some extent. Thus we have botanists, ornithologists, those who devote themselves to the study of mammals, those who confine themselves to reptiles, or insects, or fishes, or crustaceans, or bacteria, etc.

Now each class of systematists has its own particular criterion of what constitutes a species. Ornithologists do not seem very exacting. Most of them appear to consider a constant difference of colour sufficient for the formation into a species of the birds that display such a variation. Those who study reptiles, on the other hand, do not allow that a mere difference in colour is sufficient to promote its possessor to specific rank. Into these nice questions we cannot enter. For our purpose a species is a group of individuals that differ from all other individuals in displaying certain well-marked and tolerably constant characters, which they transmit to their offspring.

Our contention, then, is that new species, in the ordinarily-accepted use of the term, do not arise as a rule by one sudden bound (although they may sometimes do so), but are the result of the accumulation of several mutations or discontinuous variations. Some of these mutations are exceedingly well marked, while others are so small as to be indistinguishable from the more extreme fluctuating variations. Before passing on to consider some cases of well-marked mutations which have occurred among animals and plants, we should like to take this opportunity of pointing out that as regards experiments in evolution the botanist is far more favourably situated than the zoologist. [90]

The botanist is able to reproduce many species vegetatively, *e.g.* by cuttings, and is thus easily able to multiply examples of mutation. He can also reproduce the great majority of plants by self-fertilisation, and so experiences no difficulty in “fixing” a new form. Again, plants are far easier to control than animals; as a rule they can be transplanted without any impairment of their capacity for breeding. Moreover, they produce a greater number of offspring than the most prolific of the higher animals. The animal breeder is thus at an obvious disadvantage as compared with the horticulturist. It is only with great difficulty that he can fix the mutations which appear in his stock.

[91]

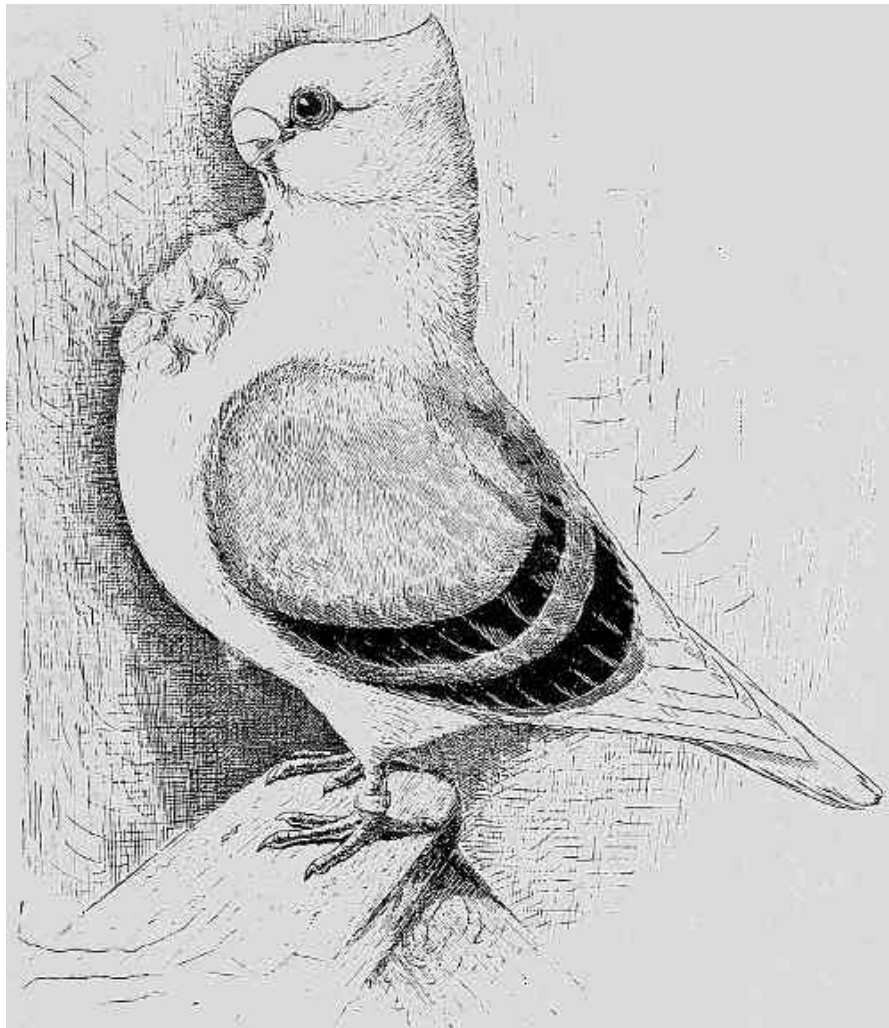
“Scatliff Strain” of Turbit

The history of the production of the “Scatliff strain” of turbit affords a good example of the kind of difficulties that confront the breeder.

Pigeon fanciers require that the ideal turbit shall have, among other things, an unbroken “sweep,” that is to say the line of the profile from the tip of the beak to the back of the head should be the arc of a circle. As a rule this line is broken by the overgrowth of the wattle at the base of the beak. Mr Scatliff, however, has succeeded in breeding a strain which possesses the required description of profile.

“In the year 1895,” writes Mr H. P. Scatliff on page 25 of *The Modern Turbit*, “I visited Mr Houghton’s lofts and purchased three or four extra stout and short-beaked stock birds. . . . The following year I mated one of these to one of my own black hens, and reared one of the most successful show birds ever bred, viz. ‘Champion Ladybird,’ a black hen. . . . Most of the leading judges and many turbit breeders remarked upon this hen’s wonderful profile, which seemed to improve as she got older instead of getting worse, as is usual in rather coarse-wattled birds. I, too, had remarked this, and it opened my eyes to a point in turbit breeding which I had never heard mentioned by any turbit judges or breeders, and which I believe I am now pointing out for the first time in print, viz. that the feathers over her beak wattle which formed her front *grew from the top and right to the front of her wattle, and not from slightly behind*, as in almost every other turbit of her day; thus, as the wattle developed and grew coarser, the front became more developed, and made her head larger without in any way spoiling the sweep of the profile. [92]

“The same year ‘Ladybird’ was bred I bred eight others from the same pair, and with one exception all turned out to be hens. There was only one other hen, however (a dun), that had this same point, but in a lesser degree than ‘Ladybird,’ and from these two hens nearly all my blacks, and several of my blues are descended.”



A TURBIT BELONGING TO MR. H. P. SCATLIFF

Mr Scatliff, having “spotted” this point, looked about him for another bird having the peculiarity, with the object, if possible, of fixing the same in his strain. He discovered this point in a pigeon belonging to Mr Johnston of Hull, and purchased the bird for £20. But it died in the following spring without producing for Mr Scatliff a single young one. The next year Scatliff found that a bird belonging to a Mr Brannam had the required peculiarity and so purchased him for £20. But that cock, too, died before anything was bred from him. Nothing daunted, Scatliff found that another of Brannam’s cocks displayed the same peculiarity, so purchased him in 1899 for £15, but he also died before the year [93] was out. Meanwhile Scatliff had, by mating up “Ladybird” with the most likely of his own cocks, succeeded in producing one or two young cocks with the desired point. By breeding these with their mother “Ladybird” and their offspring again with “Ladybird,” Scatliff eventually succeeded in breeding some turbits, both blacks and duns, with the required peculiarity fully developed, but not before he had spent a further sum of £55 on two other cocks, both of which died before they could be mated with the famous “Ladybird.” However, amid all his misfortunes, Scatliff informs us that he bought one bird, by name “Amazement,” which did assist him in fixing his strain. Thus Scatliff spent considerably over £100 in purchases, and took eight years fixing the peculiarity in question. Had “Ladybird” been a flower, the peculiarity could probably have been fixed in one generation by self-fertilisation.

This furnishes an excellent example of the trouble which breeders will take, and the expense to which they will go in order to produce a desired result. Nevertheless, it appears to be the fashion for scientific men to decry the work of the breeder.

Let us now pass on to consider the cases of mutations which are known to have occurred among animals.

[94]

MUTATIONS AMONG ANIMALS

Some instances of great and sudden variation in domesticated animals have become classical, and been detailed in almost every work on evolution. These are, firstly, the celebrated hornless Paraguay cattle. This hornless breed, or rather the ancestor of the breed, arose quite suddenly.

Many domestic horned breeds of animals, especially sheep and goats, throw off hornless sports. Were a hornless breed of buffalo found in nature, it would undoubtedly be ranked a new species, and the Wallaceians would doubtless exercise much ingenuity in explaining how natural selection had brought about the gradual disappearance of the horns; and palæontologists, being baffled in their search for intermediaries between the hornless species and their horned ancestors, would complain of the imperfection of the geological record.

It may, perhaps, be argued that this hornless mutation was a direct result of the unnatural conditions to which the Paraguay cattle were subjected, it may be asserted that since there are no species of hornless cattle in nature, such mutations have never occurred under natural conditions, and hence the Paraguay cattle prove nothing. As a matter of fact, we know that in nature a great many mutations occur which are not perpetuated because not beneficial to the species. A hornless individual in the wild state would stand but little chance in fighting for females against his horned brethren. We must keep clearly in mind that the theory of mutation does not seek to abolish natural selection; it merely affords that force something substantial to work upon. [95]

The second classical example of a leap taken by nature is furnished by the Franqueiro breed of long-horned cattle in Brazil. These furnish us with an example of a mutation in the other direction. Then there is the Niata or bull-dog breed of cattle, which are also South American. These instances would seem to indicate that cattle are what De Vries would call "in a mutating state" in that part of the world.

The other classical examples of great and sudden variations are the Ancon sheep of Massachusetts, the Mauchamp breed of Merino sheep, the tufted turkeys, and the long-haired race of guinea-pigs.

The "wonder horses," whose manes and tails grow to an extraordinary length, so as to trail on the ground, may perhaps be cited as a race which originated in a sudden mutation. They are all descendants of a single individual, Linus I., whose mane and tail were respectively eighteen and twenty-one feet long. But in this case it is important to note that the parents and grandparents of Linus I. had exceptionally long hair. [96]

Mutations among Birds

Coming now to birds we find several undoubted examples of mutations, or new forms which have come suddenly into being.

The black-winged peafowl, whose peculiarities were commented on by Darwin, afford a striking example of this phenomenon. These birds breed true when mated together, and are known to have arisen from common peafowl in no less than nine instances. The cocks have the wings (except the primary quills), black glossed with blue and green, and have the thighs black, whereas, in the ordinary peacock, the same part of the wing is nearly all mottled black and pale buff, and the thighs are drab. The black-winged hen, on the other hand, is nearly white, but has a black tail and black speckling on the upper surface of the body, while her primary quills are cinnamon coloured as in male peafowl, not drab as in the normal hens. The young are white when hatched, the young cock gradually assuming the dark colour as he matures.

This mutation, which, in one case quoted by Darwin, increased among a flock of peafowl until the black-winged supplanted the ordinary kind, is so distinct in appearance in all stages that it was formerly supposed to be a true species (*Pavo nigripennis*), of which the wild habitat was unknown.

The Golden Pheasant (*Chrysolophus pictus*) produces, in domestication, the dark-throated form (*C. obscurus*), in which the cock has the throat sooty-black instead of buff, and the scapulars or shoulder feathers black instead of red. Moreover, the two middle-tail-feathers are barred with black and brown like the lateral ones, while in the ordinary form they are spotted with brown on a black ground. The hens have a chocolate-brown ground-colour instead of yellow-ochre as in the normal type. The chicks are likewise darker. [97]

The common duck, in domestication, when coloured like the wild mallard, sometimes produces a form in which the chocolate breast and white collar of the drake are absent, the pencilled grey of the abdomen reaching up to the green neck. In this mutation the duck has the head uniformly speckled black and brown, and lacks the light eye-brow and cheek-stripes found in the normal duck. Both sexes have the bar on the wing dull black instead of metallic blue.

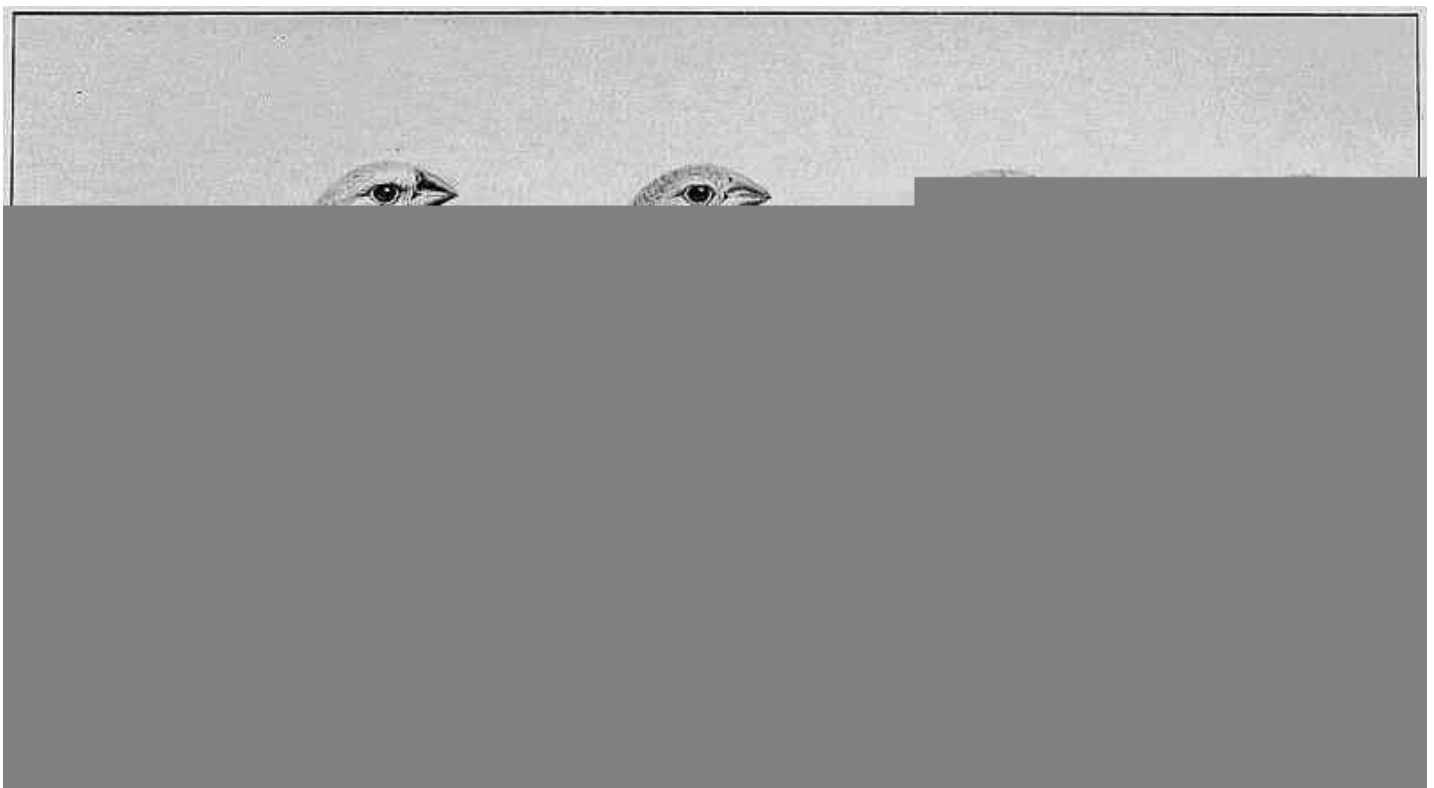
The ducklings which ultimately bear this plumage are sooty-black throughout, not black and yellow like normal ones.

The phenomenon of mutation is not confined to animals in a state of domestication. The common Little Owl of Europe (*Athene noctua*) has produced the mutation *A. chiaradiæ* in the wild state. In this the irides are dark, instead of yellow as in the normal type, and the plumage of the back of the wings is longitudinally streaked with white instead of barred. Several examples of this form were found, along with normal young, in the nest of one particular pair of little owls in Italy, but the whole family were foolishly exterminated by local ornithologists. [98]

The reed bunting (*Emberiza schæniclus*) exists in two distinct forms—one having a much stouter bill than the other (*E. pyrrhuloides*). This probably is an example of a mutation.

The rare yellow-rumped Finch (*Munia flaviprymna*), of Australia, has displayed a tendency to change into the allied and far commoner chestnut-breasted Finch (*M. castaneithorax*) during the lifetime of the individual (*Avicultural Magazine*, 1907). Conversely, the male of the common Red-billed Weaver (*Quelea quelea*) of Africa has been found in its old age to assume the characters of the comparatively rare *Q. russi*, its black throat becoming pale buff as in that form.

Everyone is familiar with the chequered variety of the common blue-rock pigeon, in which the wings are regularly mottled with black instead of being barred. This form sometimes occurs among wild birds, so that it has been described as a distinct species. It is important to note that there are red, dun, and silver chequers as well as blue ones.



YELLOW-RUMPED AND CHESTNUT-BREASTED FINCHES, WITH SPECIMENS IN TRANSITIONAL STATE

On the left, the yellow-rumped finch; on the right, the chestnut-breasted; birds in state of change in the middle.

A well-marked mutation which appears regularly in nature is the red-headed variety of the beautiful Gouldian Finch (*Pöephila mirabilis*) of North Australia. Normally the head of the cock is black, but in about ten per cent. of the individuals the cock has a crimson head, while that of the hen is dull crimson and black. [99]

Mutations which occur with such regularity are certainly rare. On the other hand, there are certain mutations which we may expect to see appear in any species of plant or animal.

Albinistic forms are a case in point, and less frequently we see white varieties which are not pure albinos, because the eye retains some at least of the normal pigment. As examples, we may cite white dogs, cats, fowls, horses, ducks, geese, and Java sparrows among domesticated animals, and the white forms of the Amazonian dolphin and of the giant Petrel of the South seas (*Ossifraga gigantea*) among wild creatures.

In a white mutation the eye may lose all its pigment, and then we have a true albino. Such forms on account of their imperfect vision cannot survive in a state of nature, hence no wild pink-eyed species are known.

Or the eye may display a partial loss of pigment, as, for example, in the white domestic forms of the common goose, the Chinese goose, and the Muscovy duck. Finn saw a case in which the eyes of a pink-eyed rabbit changed after death into this type of eye—that is, with the pupil black and the iris blue. It is to be observed that this kind of eye sometimes occurs in coloured horses, rabbits, and dogs. Finally, we have white mutations in which the eye loses none of the pigment. These are abundant in nature, and probably most of the white species of birds—as, for example, some egrets, swans, etc.—arose in this way.^[4] Pure white species are comparatively uncommon in nature, because, except in snow-clad regions, white creatures are easily seen by their adversaries. Most white birds are of considerable size, and well able to look after themselves. [100]

Similarly black mutations occur frequently among animals, both under domestication and in a state of nature. All are familiar with black dogs, cats, horses, fowls, ducks, pigeons. Black mutations, however, do not occur nearly so frequently as white ones. So far as we are aware no black mutation has been recorded among canaries, geese, guinea-fowl, ferrets, Java sparrows or doves, all of which produce white mutations.

On the other hand, in the wild state black species occur more frequently than normal-eyed white forms. This is probably because such creatures are less conspicuous than white ones. As examples of black mutations which occur in nature, we may cite black leopards, water rats, squirrels, foxes, barking deer (*Cervulus muntjac*), hawk-eagles, harriers, peppered moth (*Amphidasys betularia*), etc. [101]

That many black species have arisen as sudden mutations from lighter-coloured animals seems tolerably certain from the facts that in Malacca the black leopard forms a local race; that some of the Gibbon apes are as often black as light coloured; that the American black bear is sometimes brown, while the other bears, when not brown, are almost invariably black.

Color Mutations

Not uncommon, although rarer than black or melanistic forms, are reddish or chestnut varieties. These occur both among tame and wild animals. Among domesticated creatures, sandy cats, “red” pigeons, buff fowls, chestnut horses, red guinea pigs afford examples of this mutation. Among wild animals many of the species of squirrel, not naturally red, produce red mutations; and some of the grey owls—as, for example, the Indian race of the Scops (*Scops giu*)—throw off a red or chestnut form. As everyone knows, some species are normally red.

Green or olive species not unfrequently throw off yellow mutations. As examples of these we may cite yellow canaries, yellow budgerigars (*Melopsittacus undulatus*), goldfish, golden tench, and the golden form of the common carp among captive animals; and among animals in a state of nature, yellow forms have been recorded of the rose-ringed Paroquet (*Palaeornis torquatus*), the green woodpecker, the pike, and the eel. These lutinistic forms usually have normally coloured eyes. Sometimes, but only very rarely, these yellow forms throw off white sports—as, for example, the “silver” form of the goldfish. Finn has seen a white variety of the common carp. White canaries are excessively rare, while white budgerigars are unknown. [102]

It is worthy of note that entirely yellow species of birds and fish are unknown. We would suggest that the explanation of this is that yellowness is correlated with some physical characteristic unfavourable to an organism exposed to the struggle for existence; hence individuals which are yellow are not permitted to survive. In some species of moths individuals occur in which the parts normally red are yellow. According to Bateson, a chalk pit at Madingly, near Cambridge, has long been known to collectors as a habitat of a yellow-marked form of the six-spot Burnet Moth (*Zygaena filipendulae*). These lutinistic forms are not confined to one genus of Butterflies. Moreover, in the Pin-tailed Nonpareil Finch (*Eythura prasina*) of the Eastern Archipelago the red tail and other red parts of the plumage are not infrequently replaced by yellow in wild individuals of either sex and of any age. In the blue-fronted Amazon parrot (*Chrysotis aestiva*)—a most variable bird—the normally red edge of the pinion is sometimes yellow. [103] Bateson, in his *Materials for the Study of Variation*, gives other examples of this kind of variation.

Mutations among Invertebrates

As further instances of mutations among animals which have been observed in nature, we may mention the *valezina* form of the female of the Silver-washed Fritillary Butterfly (*Argynnis paphia*) and the *helice* form of the female Clouded-yellow Butterfly (*Colias edusa*).

The common jelly-fish is an organism which frequently throws off sports, and some zoologists are of opinion that the medusoid *Pseudoclytia pentata* arose by a discontinuous variation from *Epenthesis folleata* or a closely allied form. Thomson discusses this particular case at some length on pages 87-89 of his *Heredity*, and gives it as his opinion that the evidence in favour of this latter having arisen as a mutation is “exceedingly strong.”

Mutating Species

It is our belief that many species of birds which occur in nature have been derived from other species which still exist, but as no one has ever seen the mutation take place, we cannot furnish any proof thereof. We merely rely on the fact that the species in question differ so slightly from one another that there seems every likelihood that they have suddenly arisen and managed to establish themselves alongside of the parent species. [104]

The Curassows, *Crax grayi*, *C. hecki*, each of which is only known by a very few specimens, appear to be mutations of the female of the globose Curassow, *Crax globicera*. The fact that when a female *hecki* bred in the London Zoological Gardens with a male *globicera*, the solitary young one which lived to grow up was a pure *globicera*, renders the assumption almost certain.

The Chamba Monaul (*Lophophorus chambanus*) seems to be a mutation of the male of the common Monaul or Impeyan Pheasant (*Lophophorus impeyanus*), the common species of the Himalayas.

The Three-coloured Mannikin (*Munia malacca*) of South India is probably simply a white-bellied form of the widely-ranging Black-headed Mannikin (*M. atricapilla*), which has the abdomen chestnut like the back. Intermediate wild-caught forms have been recorded.

The African Cordon-bleu (*Estrela phœnicotis*) and Blue-bellied Waxbill (*E. cyanogastra*) would also seem to be mutations, as almost the only difference between them lies in the fact that the male of the former has a crimson cheek-patch, which is wanting in the latter.

The Ringed Finch (*Sticteptera annulosa*) of Java, and Bichenov's Finch (*S. bichenovii*) of Australia, only differ in the former having the rump black, while in the latter it is white, and this difference appears to be of the nature of a mutation. [105]

So, it might be urged, is the pure white breast of the male Upland Goose (*Chloëphaga magellanica*), which part, in the very similar *C. dispar*, is barred as in the females, the latter form being probably the ancestor.

The differences between the silver-grey-necked Crowned Crane of the Cape (*Balearica chrysopelargus*) and the dark-necked species of West Africa (*B. regulorum*) seem also to be not more than could be accounted for by mutation.

Peculiar forms, such as a rabbit with a convoluted brain or a mouse with a peculiar pattern of molar teeth, have been come upon by anatomists.

The above-cited mutations are all very considerable ones, and we do not profess to have mentioned a tenth part of those which have actually been recorded.

We trust that we have collected and set forth sufficient evidence to show that the phenomenon of discontinuous variation is a very general one, and this would seem to tell against the hypothesis of De Vries that species pass through alternate periods of comparative stability and periods when swarms of mutations appear. We think it more probable that all species throw off at greater or less intervals discontinuous variations, and that it is upon these that natural selection acts. [106]

We further hope that we have succeeded in making clear what we believe to be the very sharp distinction between continuous and discontinuous variations, even when the latter are inconsiderable, as frequently happens.

Somatic and Germinal Variations

Before leaving the subject of variation it is necessary to notice the distinction, which Weismann was the first to emphasise, between somatic and germinal variations.

Every adult organism must be regarded as the result of two sets of forces; inherited tendencies or internal forces, and the action of environment or external forces. The differences which the various members of a family show are due in part to the initial differences in the germinal material of which they are composed, and in part to the differences of their

environment. The former differences are the result of what we may call germinal variations, and the latter the result of somatic variations. It is scarcely ever possible to say of any particular variation that it is a germinal or a somatic one, because even before birth a developing organism has been subjected to environmental influences. One of a litter may have received more nourishment than the others. Nevertheless, any marked variation which appears at birth is [107] probably largely germinal. According to Weismann and the majority of zoologists, there is a fundamental difference between these germinal and somatic variations, in that the former tend to be inherited, while the latter are never inherited. Weismann believes that very early in the formation of the embryo the cells which will form the generative organs of the developing organism are separated off from those cells which will go to build up the body, and become as much isolated from them as if they were contained in a hermetically-sealed flask, so that they remain totally unaffected by any changes which the environment effects in the somatic cells. Therefore, says Weismann, acquired characters cannot be inherited.

While the majority of zoologists believe that acquired characters are not inherited, probably not many will go so far as Weismann and declare that the environment cannot exercise *any* effect whatever on the germ cells.

Somatic Variations

Even though acquired characters or variations are not inherited, it does not follow that they do not play an important part in evolution. Acquired variations are the result of the way in which an organism reacts to its environment. If an organism is unable to react to its environment it must inevitably perish. If it is able to react, it matters not, so far as the chances of survival of the organism are concerned, whether the adaptation is the result of a congenital variation or [108] a somatic one. This will be rendered clear by a hypothetical example. Let us suppose that a certain mammal is forced, owing to the intensity of the struggle for existence, to migrate into the Arctic regions. Let us further suppose that this organism is preyed upon by some creature that hunts by sight rather than by scent. Let us yet further imagine that this predacious species is swifter than our animal, on which it preys. It is obvious that, other things being equal, the more closely the creature preyed upon assimilates to its surroundings the more likely is it to escape the observation of its foes, and so to survive and give birth to offspring. Now suppose that the glare from the snow-covered ground bleaches its coat. This whitening of the fur is a somatic variation, one which is induced by the environment. Such an animal will be as difficult to see, if the bleaching is such as to render it snow-white, as if its whiteness were due to a germinal variation. Thus, as regards its chances of survival, it matters not whether its whiteness be the result of germinal or somatic variation. But if the whiteness is due to a somatic variation, its offspring will show no tendency to inherit the variation; they will have in turn to undergo the bleaching process. If, on the other hand, the whiteness is due to a germinal variation, the offspring will tend to inherit this peculiarity and to be born white. In such a case, it is [109] unlikely that the fur of an organism which is naturally coloured will be completely bleached by the snow, and, even if it be, the bleaching process will take time, meanwhile the creature will be comparatively conspicuous. So that those which are naturally whiter than the average, that is to say, those in which the tendency to whiteness appears as a germinal variation, will be less conspicuous than those which tend to be the ordinary colour. Thus the former will enjoy a better chance of survival, and will be likely to transmit their whiteness to their offspring in so far as it is due to a germinal or congenital variation.

Thus, although none of the whiteness due to somatic variations is transmitted to the offspring, such variations are of considerable importance to the species, as they enable it to survive and allow time for the germinal variations in the required direction to appear.

That this case need not be purely hypothetical is shown by the fact that dun domestic pigeons, which are of an earthy-brown colour when fresh moulted, soon fade in the sun to a dull creamy hue. Thus a coloration adapted to an ordinary soil could soon be suited to a desert environment. The ruddy sheldrake also, normally a bright chestnut-coloured bird, and one that haunts exposed sunny places, in many cases fades very much, becoming almost straw-coloured.

Many variations which organisms display are of a mixed kind, being in part the result of inner forces and in part [110] due to the action of the environment. In so far as they are due to this latter they do not appear to be inherited.

Thus, although we cannot say of many variations whether they are germinal, or somatic, or of a mixed kind, it is of great importance to keep continually in mind the fundamental differences between the two kinds.

Some somatic variations are due to the direct action of the environment; they are merely the expression of the manner in which an organism responds to external stimuli.

What is the cause of germinal variations? This is a question to which we are not yet in a position to give a satisfactory answer.

The attempt to explain their origin plunges us into the realm of theory. This doubtless is a realm full of fascination, but it is an unexplored region of extreme darkness, in which, we believe, it is scarcely possible to take the right road until more of the light of fact has been shed upon it.

In the chapter dealing with inheritance we shall indicate the lines along which it is likely that future progress will be made.

[111]

CHAPTER IV HYBRIDISM

The alleged sterility of hybrids a stumbling-block to evolutionists—Huxley's views—Wallace on the sterility of hybrids—Darwin on the same—Wallace's theory that the infertility of hybrids has been caused by Natural Selection so as to prevent the evils of intercrossing—Crosses between distinct species not necessarily infertile—Fertile crosses between species of plants—Sterile plant hybrids—Fertile mammalian hybrids—Fertile bird hybrids—Fertile hybrids among amphibia—Limits of hybridisation—Multiple hybrids—Characters of hybrids—Hybridism does not appear to have exercised much effect on the origin of new species.

The alleged sterility of the hybrids produced by crossing different species has long proved a great stumbling-block to evolutionists. Huxley, in particular, felt the force of this objection to the Darwinian theory. If the hybrids between natural species are sterile, while those of all the varieties which the breeder has produced are perfectly fertile, it is obviously quite useless for evolutionists to point with pride to the results obtained by the breeder, and to declare that his products differ from one another to a greater extent than do many well-recognised species.

"After much consideration, and with no bias against Mr Darwin's views," wrote Huxley to the *Westminster Review* in 1860, "it is our clear conviction that, as the evidence now stands, it is not absolutely proven that a group of animals having all the characters exhibited by species in nature, has ever been originated by selection, whether natural or artificial. Groups having the morphological nature of species, distinct and permanent races, in fact, have been so produced over and over again; but there is no positive evidence at present that any group of animals has, by variation and selective breeding, given rise to another group which was in the least degree infertile with the first. Mr Darwin is perfectly aware of this weak point, and brings forward a multitude of ingenious and important arguments to diminish the force of the objection. We admit the value of these arguments to the fullest extent; nay, we will go so far as to express our belief that experiments, conducted by a skilful physiologist, would very probably obtain the desired production of mutually more or less infertile breeds from a common stock in a comparatively few years; but still, as the case stands at present, this little 'rift within the lute' is not to be disguised or overlooked." [112]

Alleged Sterility of Hybrids

Similarly Wallace writes, at the beginning of chapter vii. of his *Darwinism*: "One of the greatest, or perhaps we may say the greatest, of all the difficulties in the way of accepting the theory of natural selection as a complete [113] explanation of the origin of species, has been the remarkable difference between varieties and species in respect of fertility when crossed. Generally speaking, it may be said that the varieties of any one species, however different they may be in external appearance, are perfectly fertile when crossed, and their mongrel offspring are equally fertile when bred among themselves; while distinct species, on the other hand, however closely they may resemble one another externally, are usually infertile when crossed, and their hybrid offspring absolutely sterile. This used to be considered a fixed law of nature, constituting the absolute test and criterion of a species as distinct from a variety; and so long as it was believed that species were separate creations, or at all events had an origin quite distinct from that of varieties, this law could have no exceptions, because if any two species had been found to be fertile when crossed and their hybrid offspring to be also fertile, this fact would have been held to prove them to be not species but varieties. On the other hand, if two varieties had been found to be infertile, or their mongrel offspring to be sterile, then it would have been said—These are not varieties, but true species. Thus the old theory led inevitably to reasoning in a circle, and what might be only a rather common fact was elevated into a law which had no exceptions." [114]

Thus the sterility of hybrids was a zoological bogey which had to be demolished. The plan of campaign adopted by Darwin and Wallace was, firstly, to try to disprove the assertion that the hybrids between different species are always sterile, and secondly, to find a reason for the alleged sterility of these hybrids.

Fertile Hybrids

Darwin succeeded in obtaining some examples of crosses between botanical species which were said to be fertile. These he quotes in chapter viii. of *The Origin of Species*. As regards animals, he met with less success. "Although," he writes, "I do not know of any thoroughly well-authenticated cases of perfectly fertile hybrid animals, I have some reason to believe that the hybrids from *Cervulus vaginalis* and *reevesii*, and from *Phasianus colchicus* and *P. torquatus* and with *P. versicolor* are perfectly fertile. There is no doubt that these three pheasants, namely, the common, the true ring-necked, and the Japan, intercross, and are becoming blended together in the woods of several parts of England. The hybrids from the common and Chinese geese (*A. cygnoides*), species which are so different that they are generally ranked in distinct genera, have often been bred in this country with either pure parent, and in one single instance they have bred *inter se*. This was effected by Mr Eyton, who raised two hybrids from the same parents but from [115] different hatches; and from these two birds he raised no less than eight hybrids (grandchildren of the pure geese) from one nest. In India, however, these cross-bred geese must be far more fertile; for I am assured by two eminently capable judges, namely, Mr Blyth and Captain Hutton, that whole flocks of these crossed geese are kept in various parts of the country; and as they are kept for profit, where neither pure parent species exists, they must certainly be highly fertile.^[5] . . . So again there is reason to believe that our European and the humped Indian cattle are quite fertile together; and from facts communicated to me by Mr Blyth, I think they must be considered as distinct species."

Darwin does not seem to have been very satisfied with the evidence he had collected, for he said: "Finally, looking to all the ascertained facts on the intercrossing of plants and animals, it may be concluded that some degree of sterility, both in first crosses and in hybrids, is an extremely general result; but that it cannot, under our present state of [116] knowledge, be considered as absolutely universal."

Similarly Wallace writes: "Nevertheless, the fact remains that most species which have hitherto been crossed produce sterile hybrids, as in the well-known case of the mule; while almost all domestic varieties, when crossed, produce offspring which are perfectly fertile among themselves."

Darwin resorted to much ingenious argument in his attempt to explain what he believed to be the almost universal sterility of hybrids, as opposed to mongrels or crosses between varieties. He pointed out that changed conditions tend to produce sterility, as is evidenced by the fact that many creatures refuse to breed in confinement, and believed that the crossing of distinct wild species produced a similar effect on the sexual organs. He expressed his belief that the early death of the embryos is a very frequent cause of sterility in first crosses.

Wallace thus summarises Darwin's conclusions as to the cause of the sterility of hybrids: "The sterility or infertility of species with each other, whether manifested in the difficulty of obtaining first crosses between them or in the sterility of the hybrids thus obtained, is not a constant or necessary result of species difference, but is incidental on unknown [117] peculiarities of the reproductive system. These peculiarities constantly tend to arise under changed conditions owing to the extreme susceptibility of that system, and they are usually correlated with variations of form or of colour. Hence, as fixed differences of form and colour, slowly gained by natural selection in adaptation to changed conditions, are what essentially characterise distinct species, some amount of infertility between species is the usual result."

A Biological Bogey

But Wallace has not been content to let the matter remain where Darwin left it. He has boldly tried to make an ally of this bogey of the infertility of hybrids. On page 179 of *Darwinism* he argues, most ingeniously, that the sterility of hybrids has been actually produced by natural selection to prevent the evils of the intercrossing of allied species. We will not reproduce his argument for the simple reason that it is now well-known, or should be well-known, that hybrids between allied species are by no means always sterile. The doctrine of the infertility of hybrids seems to have been founded on the fact that the hybrids best known to breeders, namely the cross between the ass and the horse, and those between the canary and other finches, are sterile.

[118]

FERTILE CROSSES BETWEEN SPECIES OF PLANTS

In the case of plants the number of fertile hybrids between species is so large that we cannot attempt to enumerate them. De Vries cites several instances in Lecture IX of his *Species and Varieties: Their Origin by Mutation*.

One of these—the hybrid between the purple and the yellow species of Lucerne which is known to botanists as *Medicago media* is, writes De Vries, “cultivated in some parts of Germany on a large scale, as it is more productive than the ordinary lucerne.” Other examples of perfectly fertile plant hybrids cited by De Vries are the crosses between *Anemone magellanica* and *A. sylvestris*, between *Salix alba* and *Salix pentandra*, between *Rhododendron hirsutum* and *R. ferrugineum*.

He gives an instance of a hybrid—*Egilops speltaeformis*, which, though fertile, is not so fertile as a normal species would be. It is worthy of note that Burbank of California has obtained a hybrid between the blackberry and the raspberry, which is not only fertile, but quite popular as producing a novel fruit.

STERILE PLANT HYBRIDS

De Vries does not cite nearly so many examples of sterile hybrids, presumably because they are not so easy to find. He mentions the sterile “Gordon’s currant,” which is considered to be a hybrid between the Californian and the Missouri species. He also gives *Cytisus adami* as an absolutely sterile hybrid, this being a cross between two species of Laburnum—the common and the purple. [119]

In the case of animals the known hybrids are so much less numerous that we are able to furnish a list which may be taken as fairly exhaustive.

FERTILE MAMMALIAN HYBRIDS

Taking the mammals first, we find that, in addition to those cited by Darwin, there are several recorded cases of crosses between well-defined species which are fertile.

There is the hybrid between the brown bear and the polar bear, which is perfectly fertile. In the London Zoological Gardens there is a specimen of this hybrid, also one of this individual’s offspring by a pure polar bear.

The stoat has been crossed with the domestic ferret, a descendant of the polecat, a very distinct species; the resulting hybrids have nevertheless proved fertile.

The bull American bison produces with the domestic cow hybrids known as “cataloes,” which are fertile. The reverse cross of the domestic bull with the bison cow does not, however, succeed at all, which reminds us of what happens in the case of finch-hybrids.

Bird fanciers when crossing the canary with wild species of finch, almost invariably use a hen canary as the female parent, because domesticated female animals breed more readily than do captive wild ones. [120]

The domestic yak breeds frequently in the Himalayas with the perfectly distinct zebu or humped cow of India, and the hybrids are fertile. Yet the zebu and the Indian buffalo, living constantly side by side in the plains of India, never interbreed at all.

Among wild ruminants of this hollow-horned family, the Himalayan Argali (*Ovis ammon*) ram, a giant sheep of the size of a donkey, has been known to appropriate a herd of ewes of the Urial (*O. vignei*), a very distinct species of the size of a domestic sheep. Many hybrids were born, and these, in turn, bred with the pure urials of the herd.

In our parks the little Sika deer of Japan (*Cervus sika*), a species about the size of the fallow-deer, with an even more marked seasonal change of colouration and antlers having only three tines, breeds with the red deer, and the hybrids are fertile.

In certain parts of Asia Minor the natives cross the female one-humped camel with the male of the bactrian or two-humped species. The hybrids (which are one-humped) will breed with the pure species; but, although the hybrids are strong and useful, the three-quarter bred beasts are apparently of little value. [121]

FERTILE BIRD HYBRIDS

Coming to birds, we are confronted by a longer list of fertile hybrids. This is the natural outcome of the fact that a greater number of bird species have been kept in captivity.

The oldest known fertile hybrid is that between the common and Chinese geese above cited, but many others have since been recorded. Even among birds so seldom bred, comparatively, as the parrot family, a fertile hybrid has been produced, that between the Australian Rosella Parrakeet (*Platycercus eximius*) and Pennant's Parrakeet (*P. elegans*). The hybrid was first described as a distinct species, the Red-mantled Parrakeet (*P. erythropeplus*). These two parrakeets, though nearly allied, are very distinct; Pennant's being coloured red, blue, and black, with a distinct young plumage of uniform dull green; the rosella in addition to the above colours displays much yellow and some white and green. It is, moreover, considerably smaller and has no distinct youthful dress.

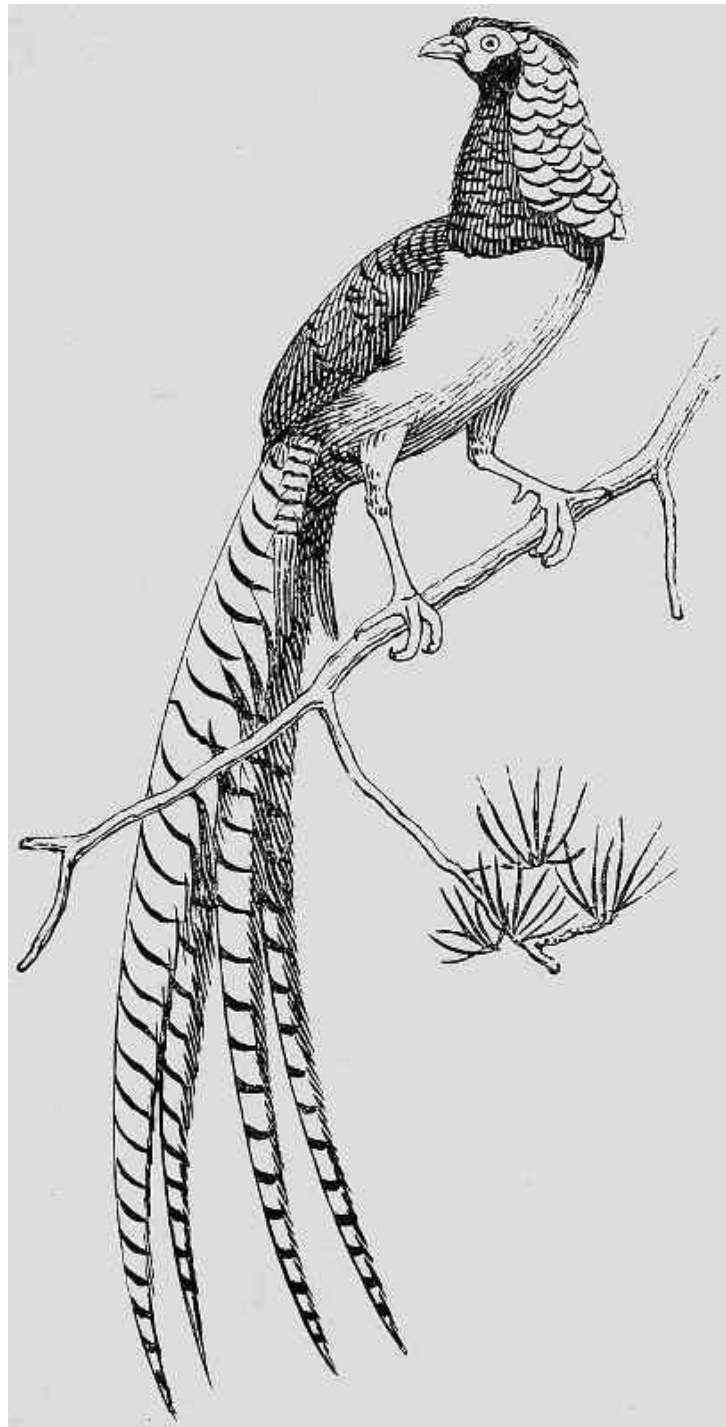
The Amherst Pheasant (*Chrysolophus amherstiae*) and the Gold Pheasant (*C. pictus*) have long been known as producing hybrids which are fertile either *inter se* or with the parents. Here the species are still more distinct; not only are the leading colours of the Amherst white and green, instead of red and gold, but it is a bigger bird with a larger tail and smaller crest, and a bare patch round the eyes. [122]

The Pintail Duck (*Dafila acuta*) and the Mallard or Wild Duck and its domestic descendants (*Anas boscas*), when bred together, produce hybrids which have been proved fertile between themselves and with the pure pintail. Any sportsman or frequenter of our parks can see for himself the distinctness of the species concerned.

The Pied Wagtail (*Motacilla lugubris*) and the Grey Wagtail (*M. melanope*) have produced hybrids in aviaries, which have proved fertile. The two species are distinct in every way, as all British ornithologists know.

The Cut-throat Finch (*Amadina fasciata*) and Red-headed Finch (*A. erythrocephala*) of Africa have hybridised in aviaries, and the produce has proved fertile. The red-headed finch, among other differences, is far larger than the cut-throat, and the males have the head all red, not merely a throat-band of that colour.

The Japanese Greenfinch (*Ligurinus sinicus*) which is not green, but brown and grey, with bolder yellow wing- and tail-markings than our larger European greenfinch, has produced fertile hybrids with this latter bird.



MALE AMHERST PHEASANT

The chief colours of this species (*Chrysolophus amherstiae*), are white and metallic green, so that it is very different in appearance from its near ally the gold pheasant.

The Red Dove of India (*Oenopopilia tranquebarica*) has produced hybrids with the tame Collared Dove (*T. risorius*) and these have bred again when paired with the red species. *O. tranquebarica*, although presenting a general similarity to the collared dove, is truly distinct, being much smaller, with a shorter tail, and displaying a marked sex-difference (the male only being red, and the female drab). Its voice is also utterly unlike the well-known penetrating and musical *coo* of the Collared Dove. [123]

There is a large class of fertile wild hybrids produced between forms differing only in colour, such as those between the Hooded Crow (*Corvus cornix*) and Carrion Crow (*Corvus corone*), the various species of *Molpastes* bulbuls, and the Indian Roller (*Coracias indica*) and Burmese Roller (*C. affinis*). Indeed, it may be said that wherever two such colour-species meet they hybridize and become more or less fused.

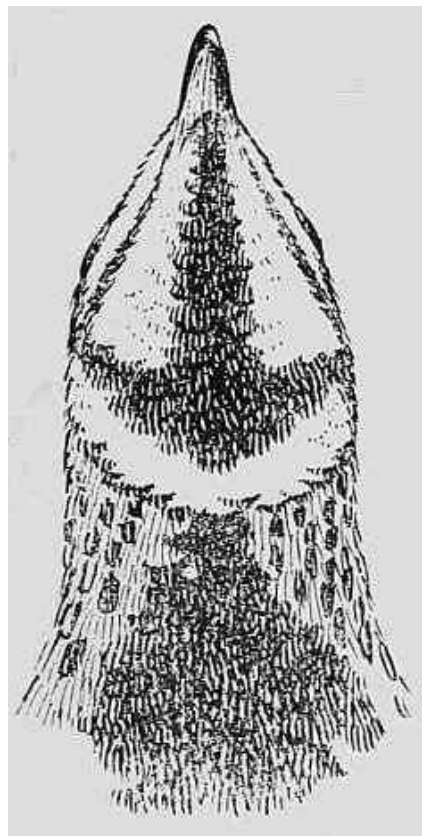
In this connection sportsmen, as mentioned by Darwin, performed unconsciously a most interesting experiment when, more than a century ago, they introduced largely into their coverts the Chinese Ring-necked Pheasant (*Phasianus torquatus*) and the Japanese *P. versicolor*. So freely has the former bred with the common species already present there (*Phasianus colchicus*) that nowadays nearly all our English pheasants show traces of the cross in the shape of white feathers on the neck, or the green tinge of the plumage of the lower back. The influence of the Japanese Green Pheasant (*P. versicolor*) has been very slight. [124]

It is, of course, open to anyone to assert that such crosses are not true hybrids, as the species are not fully distinct, but mere colour-mutations.

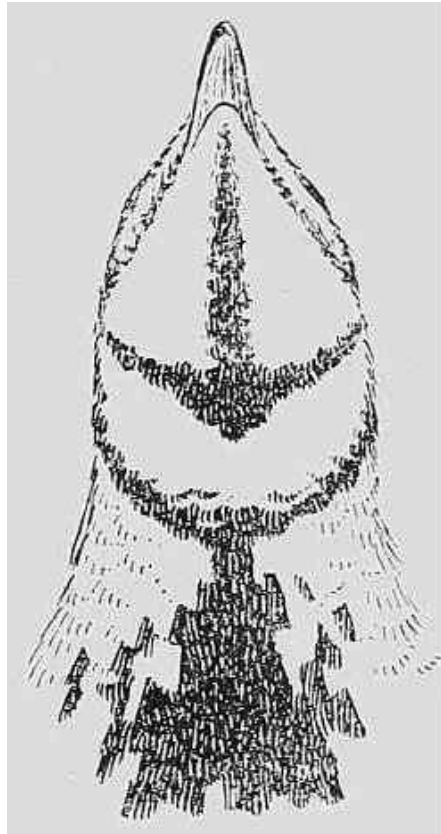
The fact of the intermingling, however, is a fatal blow to the theory of recognition marks, since it demonstrates that merely distinctive colouring is not a preventative of cross-breeding. To this matter we shall return later.

FERTILE HYBRIDS AMONG AMPHIBIA

Our Crested Newt (*Molge cristata*) and the Continental Marbled Newt (*M. marmorata*) interbreed in France, in the wild state, and the resulting hybrid was at first described as a distinct species, under the name of *Molge blasii*. These two newts differ greatly in appearance. In the Marbled Newt the colouration is brilliant green and black above, and shows no orange below, thus differing much from that of the Crested Newt, which is black above and mottled with orange beneath, while the crest of the breeding-male of this species lacks the notches which are so conspicuous in that of the Crested Newt.



HARLEQUIN QUAIL
(*Coturnix delegorguei*)



RAIN QUAIL
(*Coturnix coromandelica*)

The markings on the throats of these quails are of the type usually put down as “recognition marks,” but as the Harlequin Quail is African and the Rain Quail Indian, the two species cannot possibly interbreed. The pattern, then, can have no “recognition” significance.

INSECTS

Among insects, M. de Quatrefages states that the hybrid progeny of the silk-moths *Bombyx cynthia* and *B. arrindia* are fertile for eight generations when bred *inter se*. [125]

LIMITS TO THE POSSIBILITIES OF HYBRIDISATION

Hybrids can apparently only be produced between species of the same natural family. The stories of cat-rabbits, deer-ponies, fowl-ducks, and similar distant crosses invariably break down on close examination. A belief in such remote crosses characterized the ancient “bestiaries,” and still lingers, as witness the falsely-reputed crosses alluded to above.

This belief has no doubt arisen from the fact that the domestic breeds of dogs, fowls, etc., are popularly confounded with truly distinct species. Mongrels are well known to be readily produced, and hence the notion arises that hybrids between the most widely-separated species are possible.

In practice, the most remote cross of which authenticated specimens exist is that between the red grouse and the domestic fowl (bantam cock). It is true that the grouse are commonly ranked by ornithologists as a family distinct (*Tetraonidae*) from that of the pheasants and partridges (*Phasianidae*), to which the fowl belongs; but the relationship is admittedly very close, and we doubt if general zoologists would countenance the maintenance of the families as distinct. Ornithologists are notoriously apt to over-rate small differences when drawing up a classification. It would be therefore safe to say, in the present state of our knowledge, that species belonging to different natural families cannot hybridize. [126]

In some cases multiple hybrids have been produced. Thus, at the London Zoological Gardens, many years ago, a hybrid between the Gayal of India (*Bos frontalis*) and the Indian humped cow mentioned above was put to an American bison, and produced a double hybrid calf.

M. G. Rogeron of Angers bred many hybrids from a male pochard and a duck bred from a Mallard and a Gadwall.

More recently, Mr J. L. Bonhote has succeeded in combining the blood of five wild species of ducks in one individual.

Mr J. T. Newman has also bred turtle-doves containing the blood of three distinct species.

A cross, which usually results in sterile offspring, may in very rare cases produce a fertile individual; thus, Mr A. Suchetet once succeeded in obtaining a three-quarter-bred bird from the not uncommon hybrid of the tame pigeon and tame collared dove (*Turtur risorius*), which is usually barren, by pairing it with a dove; but the bird thus produced, when again paired with a dove, was itself sterile. Some of the cases here given seem to encourage Darwin's view [127] that domestication tends to eliminate sterility; but it is doubtful if this can be upheld. The hybrid between the Muscovy duck (*Cairina moschata*) and common duck is usually, at all events, sterile, like that between the pigeon and dove; yet all these birds have been long domesticated. The hybrid between the fowl and the guinea-fowl is likewise barren, nor has the long domestication of the horse and ass lessened the sterility of the mule.

Characters of Hybrids

Some facts may be noted respecting the characters of hybrids. In the first place, it is important to notice that the characters of the hybrid vary according to the sexes of the species concerned; thus, the "hinny," which is bred from a horse and a she-ass, is a different animal from the true "mule," which is bred from the jackass and mare, and is inferior to it.

Similarly, Mr G. E. Weston, a great authority on British cage-birds and their hybrids, informs us that when hybrids are bred from a male canary and a hen goldfinch or siskin—contrary to the almost universal practice of using the hen canary for crossing—the progeny are inferior in size and colour to the hybrids obtained in the ordinary way.

Hybrids, in animals at all events, differ from crosses between mutations or colour-variations in not exhibiting the phenomenon of alternative inheritance; they do not follow one parent or the other exclusively, but always exhibit [128] some blending of the characters of both, which is, after all, what might have been expected, since well-defined species usually differ in more than one character.

Thus, the cross between the Amherst and gold pheasants chiefly resembles the latter, but has the ruff white as in the Amherst, while the crest, though in form it resembles that of the gold species, is not yellow as in that species, nor red as in the Amherst, but of an intermediate tint, brilliant orange.

The mule between the horse and ass, as all know, combines the shapes of the two parents, though in colour it follows the horse rather than the ass.

When two remote species, one or each of which possesses some distinctive structural peculiarity, are crossed, the hybrid does not inherit such points. The guinea-fowl has a helmet, and a pair of wattles on the upper jaw; the common fowl a comb, and a pair of wattles on the lower jaw; but in the hybrid no comb, helmet, or wattles are present.

The Muscovy drake has a bare red eye-patch, and the male of the common duck curled middle-tail feathers; in the hybrid neither of these peculiarities is reproduced.

In a cross between nearly-related forms, the peculiarity of one species may be reproduced in a modified form in [129] the hybrid; for instance, in that between the blackcock (*Tetrao tetrix*) and the capercaillie (*T. urogallus*), the forked tail of the former reappears to a small extent in the hybrid.

Very interesting are those cases in which the hybrid resembles neither parent, but tends to be like an altogether distinct species, or to have a character of its own. Thus the hybrids between the pied European and chestnut African sheldrakes (*Tadorna cornuta* and *Casarca cana*), now in the British Museum, bear a distinct resemblance to the grey Australian sheldrake (*C. tadornoides*). In pheasants, also, the crosses between the common and gold, common and Amherst, gold and Japanese, and gold and Reeves' pheasants, widely different as all these birds are in colouration, are remarkably alike, being all chestnut-coloured birds with buff median tail-feathers. These may be seen in the British Museum. This phenomenon, together with the above-noted disappearance of specialised features in hybrids, is possibly comparable to the "reversion" observed when widely-distinct domestic breeds are crossed, and so may give us an idea of the appearance of the ancestors of the groups of species concerned.

In the few cases wherein several generations of hybrids have been bred *inter se*, there seems to have been no reversion to the original pure types, such as happens when colour-forms are crossed. [130]

M. Suchetet bred hybrid gold = Amherst pheasants for four generations, and they retained the hybrid character. The young bred by Darwin from a pair of common = Chinese geese hybrids “resembled,” he says, “in every detail their hybrid parents.”

Wild Hybrids

When hybrids have been—as has far more usually been the case—bred back to one of the pure stocks, the hybrid characters have shown, as might be expected, a tendency quickly to disappear. The three-quarter-bred polar bear now in the London Zoological Gardens is a pure polar save for a brown tinge on the back. A three-quarter Amherst = gold pheasant in the British Museum is a pure Amherst save for the larger crest, and a patch of red on the abdomen. When three-quarter-bred pintail = common duck hybrids were bred back to the pintail, the offspring “lost all resemblance to the common duck.” In the case of the Argali-urial herd of wild sheep above-mentioned, after the usurping Argali ram had been killed by wolves, the hybrids bred with the urials, with the result that the herd renewed the appearance of pure urial.

Thus, except in the very improbable case of a family of hybrids going off and starting a colony by themselves, the effect of hybridism on the evolution of species seems likely to have been *nil*. It is, however, curious that three-quarter-bred animals have rarely, if ever, been recorded in a state of nature, though a good many wild-bred hybrids are on record. [131]

This points to some unfitness for the struggle for existence even in a fertile hybrid. It is necessary to emphasise the fact that wild hybrids are always exceedingly rare as individuals, in spite of what has been said as to the number of recorded crosses.

More hybrid unions have been noted among the duck family than anywhere else in the animal kingdom. Nevertheless Finn never once saw a hybrid duck for sale in the Calcutta market, although for seven years he was constantly on the look-out for such forms; nor does Hume record any such specimen in his *Game Birds and Wild Fowl of India*.

The hybrid which occurs most commonly as an individual is that between the blackcock and capercailzie, which is recorded yearly on the Continent; but it appears to be sterile, and so has no influence on the species.

Wild hybrids between mammals are far rarer even than bird hybrids, the only ones which seem to be on record being those between the Argali and Urial above alluded to; those between the brown and blue hares and the common and Arctic foxes.

A consideration of the phenomena of hybridism thus leads us to the conclusion that, although many hybrids are fertile, the crossing of distinct species has exercised little or no effect on the origin of species. Even where allied species, like the pintail and the mallard ducks, whose hybrid offspring is known to be fertile, inhabit the same breeding area and occasionally interbreed in nature, such crossing does not, for some reason or other, appear to affect the purity of the species. [132]

Very different, of course, is the effect of crossing a mutation within a species with the parent form; the offspring are, as we shall see, likely to resemble one or other of the parents; so that, if the mutation occur frequently enough and be favourable to the species, the new form may in course of time replace the old one.

[133]

CHAPTER V INHERITANCE

Phenomena which a complete theory of inheritance must explain—In the present state of our knowledge it is not possible to formulate a complete theory of inheritance—Different kinds of inheritance—Mendel's experiments and theory—The value and importance of Mendelism has been exaggerated—Dominance sometimes imperfect—Behaviour of the nucleus of the sexual cell—Chromosomes—Experiments of Delage and Loeb—Those of Cuénot on mice and Castle on guinea pigs—Suggested modification of the generally-accepted Mendelian formulae—Unit characters—Biological isomerism—Biological molecules—Interpretation of the phenomena of variation and heredity on the conception of biological molecules—Correlation—Summary of the conception of biological molecules.

We have seen that variations may be, firstly, either acquired or congenital, and, secondly, fluctuating or discontinuous. We have further seen that acquired variations—at all events in the higher animals—do not appear to be inherited, and therefore have not played a very important part in the evolution of the animal world. Discontinuous congenital variations or mutations are the usual starting points of new species. It is not unlikely that fluctuating congenital variations, although they do not appear to give rise directly to new species, may play a considerable part in the making of new species, inasmuch as they may, so to speak, pave the way for mutations. [134]

We are now in a position to consider the exceedingly difficult question of inheritance. We know that offspring tend to resemble their parents, but that they are always a little different both from either parent and from one another. How are we to account for these phenomena? What are the laws of inheritance, whereby a child tends to inherit the peculiarities of its parents, and what are the causes of variation which make children differ *inter se* and from their parents?

Scores of theories of inheritance have been advanced. It is scarcely exaggerating to assert that almost every biologist who has paid much attention to the subject has a theory of inheritance which differs more or less greatly from the theory held by any other biologist.

As regards the phenomena of heredity we may say *Tot homines tot sententiæ*.

Phenomena of Inheritance

For this state of affairs there is a good and sufficient reason. We are not yet in possession of a sufficient number of facts to be in a position to formulate a satisfactory theory of inheritance. A complete theory of heredity must explain, among other things, the following phenomena:—

1. Why creatures show a general resemblance to their parents.
2. Why they differ from their parents. [135]
3. Why the members of a family display individual differences.
4. Why the members of a family tend to resemble one another more closely than they resemble individuals belonging to other families.
5. Why "sports" sometimes occur.
6. Why some species are more variable than others.
7. Why certain variations tend to occur very frequently.
8. Why variations in some directions seem never to occur.
9. Why a female may produce offspring when paired with one male of her species and not when paired with another male of the species.
10. Why organisms that arise by parthenogenesis appear to be as variable as those which are sexually produced.
11. Why certain animals possess the power of regenerating lost parts, while others have not this power.
12. Why most plants and some of the lower animals can be produced asexually from cuttings.
13. Why mutilations are not inherited.
14. Why acquired characters are rarely, if ever, inherited.

15. Why the ovum puts forth the polar bodies.
16. Why the mother-cell of the spermatozoa produces four spermatozoa.
17. Why differences in the nature of the food administered to the larvæ of ants determines whether these shall develop into sexual or neuter forms. [136]
18. Why the application of heat, cold, etc., to certain larvæ affects the nature of the imago, or perfect insect, to which they will give rise.
19. Why the females in some species lay eggs which can produce young without being fertilised.
20. Why some species exhibit the phenomena of sexual dimorphism, while others do not.
21. In addition to all the above, a satisfactory theory of inheritance must account for all the varied phenomena which are associated with the name of Mendel. It must explain the various facts with which we have dealt in the chapter on hybridism, why some species produce sterile hybrids when intercrossed, while others give rise to fertile hybrids, and yet others form no offspring when crossed; why the hinny differs in appearance from the mule, etc.
22. It must explain all the facts which constitute what is known as atavism.
23. It must account for the phenomenon of prepotency.
24. It must explain the why and the wherefore of correlation.
25. It must tell us the meaning of the results of the experiments of Driesch, Roux, and others.
26. It must render intelligible the effects of castration on animals. [137]

Existing Theories Unsatisfactory

Now, no existing theory of heredity can give anything approaching a satisfactory explanation of all these phenomena.

It is for this reason that we refrain from critically examining, or even naming, any of them.

We are convinced that in the present state of our knowledge it is not possible to formulate anything more than a provisional hypothesis.

It must not be thought that we consider the various theories that have been enunciated to be of no value. Erroneous hypotheses are often of the greatest utility to science, for they set men thinking and suggest experiments by means of which important additions to knowledge are made.

We now propose to set forth certain facts of inheritance, and from these to make a few deductions—deductions which seem to be forced upon us.

We would ask our readers to distinguish carefully between the facts we set forth, and the conclusions we draw therefrom. The former, being facts, must be accepted.

The interpretations we suggest should be rigidly examined, we would say regarded with suspicion, and all possible objections raised. It is only by so doing that any advance in knowledge can be made.

By inheritance we mean that which an organism receives from its parents and other ancestors—all the characteristics, whether apparent or dormant, it inherits or receives from its parents. Professor Thomson's definition—"all the qualities or characters which have their initial seat, their physical basis, in the fertilised egg cell"—seems to cover all cases except those where eggs are parthenogenetically developed. [138]

The first fact of heredity which we must notice is that inheritance may take several forms. This is apparent from what was set forth in the chapter dealing with hybrids.

Types of Crosses

In considering the phenomena of inheritance it is convenient to deal with crosses in which the parents do not closely resemble one another, because by so doing we are able readily to follow the various characters displayed by each parent. It may, perhaps, be urged that such crosses occur but rarely in nature. This is true. But we should bear in mind that any theory of inheritance must explain the various facts of cross-breeding, so that, from the point of view of a theory of inheritance, crosses are as important as what we may term normal offspring. As inheritance is so much easier to observe in the former, it is but natural that we should begin with them. Our deductions must, if they be valid ones, fit all cases of ordinary inheritance, *i.e.* all cases where the offspring results from the union of parents which closely resemble one another. Now, when two unlike forms inter-breed, their offspring will fall into one of six classes. [139]

I. They may exactly resemble one parent, or rather the type of one parent, for, of course, they will never be exactly like either parent; they must of necessity display fluctuating variations. The cases in which the offspring exactly resemble one parent type in all respects are comparatively few. They occur only when the parents differ from one another in one, two, or at the most three characters. Thus when an ordinary grey mouse is crossed with a white mouse the offspring are all grey, that is to say, they resemble the grey parent type. Although they are mongrels or hybrids, they have all the appearance of pure grey mice. This is what is known as unilateral inheritance.

II. The offspring may resemble one parent in some characters and the other in other characters. They may have, for example, the colour of one parent, the shape of the other, and so on. Thus if a pure, albino, long-haired, and rough-coated male guinea-pig be crossed with a coloured, short-haired and smooth-coated female, all the offspring are coloured, short-haired, and rough-coated. That is to say, they take after the father in being rough-coated, but after [140] the mother in being pigmented and short-haired. This form of inheritance is usually seen only in crosses between two types which differ in but few of their characters.

III. The offspring may display a blend of the characters of the two parents. They may be intermediate in type. They are not of necessity midway between the two parents; one of the parents may be prepotent. The crosses between the horse and the ass show this well. Both the mule, where the ass is the sire, and the hinny, where the horse is the sire, are more like the ass than like the horse; but the hinny is less ass-like than the mule. The offspring between a European and a native of India furnishes a good case of blended inheritance; Eurasians are neither so dark as the Asiatic nor so fair as the European.

IV. The offspring may show a peculiarity of one parent in some parts of the body and the peculiarity of the other parent in other parts of the body. This is known as particulate inheritance. The piebald foal, which is the result of a cross between a black sire and a white mare, is a good example of such inheritance. This does not appear to be a common form of inheritance.

V. The usual kind of inheritance is perhaps a combination between the forms II. and III. In such cases the [141] offspring display some paternal characters and some maternal ones, and some characters in which the maternal and paternal peculiarities are blended. An example of inheritance of this description is furnished by a cross between the golden and the amherst pheasants.

VI. The offspring may be quite unlike either parent. For example, Cuénot found that sometimes a grey mouse when crossed with an albino produces black offspring.

Mendel's Experiments

The first two kinds of inheritance were carefully investigated by Gregor Johann Mendel, Abbot of Brunn. The results of his experiments were published in the Proceedings of the Natural History Society of Brunn, in 1854, but attracted very little notice at the time.

Mendel experimented with peas, of which many varieties exist. He took a number of varieties, or sub-species, which differed from one another in well-defined characters, such as the colour of the seed coat, the length of the stem, etc. He made crosses between the various varieties, being careful to investigate one character only at a time. He found that the offspring of such crosses resembled, in that particular character, one only of the parents, the other parent apparently exerting no influence on it. Mendel called the character that appeared in the off-spring dominant, and the character [142] which was suppressed, recessive. Thus when tall and short varieties were crossed the offspring were all tall. Hence Mendel said that tallness is a dominant character, and shortness a recessive character. Mendel then bred these crosses among themselves, and found that some of the offspring resembled one grandparent as regards the character in question while some resembled the other, and he found that those that showed the dominant character were three times as numerous as those that displayed the recessive character. He further found that all those of the second generation of crosses which displayed the recessive character bred true; that is to say, when they were bred together all their descendants exhibited this characteristic. The dominant forms, however, did not all breed true; some of them produced

descendants that showed only this dominant character, others, when crossed, gave rise to some forms having the dominant character and some having the recessive character.

It is thus evident that organisms of totally different ancestry may resemble one another in external appearance. In other words, part of the material from which an organism is developed may lie dormant.

Mendelism

From the above results Mendel inferred, in the case of what he called alternating characters, that only one or other [143] of the pair can appear in the offspring, that they will not blend. If both parents display one of the opposing characters, the offspring will of course show it. But if one parent display one character and the other the opposing character, the hybrid offspring will display one only, and that which is dominant. The other character is suppressed for the time being. When, however, these hybrids are bred *inter se*, their gametes or sexual cells split up into their component parts, and then the recessives are free to unite with other recessives and thus produce offspring which show the recessive character.

His results can be set forth in symbols.

Let T stand for the tall form and D for the dwarf form. Since the offspring are composed of both the paternal and maternal gamete, we may represent them as TD. But dwarfness is, as we have seen, recessive, so that the offspring all look as though they were pure T's. When, however, we come to breed these TD's *inter se*, the gamete or sex-cell of each individual crossed breaks up into its component parts T and D, which unite with other free T or D units to form TD's or TT's or DD's. What are the possible combinations? A D of one parent may meet and unite with a D of the other parent, so that the resulting cells will be pure D, *i.e.* DD, and will give rise to pure dwarf offspring. Or the D [144] gamete from one parent may unite with a T gamete from the other parent, and the result will be a TD cross, but this, as we have seen, will grow up to look like a pure T, *i.e.* will become a tall organism. Similarly, a T gamete from one parent may unite with a T gamete of the other, and produce a pure tall form, or it may unite with a D and produce a hybrid TD, which gives rise to a tall form. Thus the possible combinations of offspring are DD, DT, TD, TT, but all these three last contain the dominant T gamete, and so develop into tall offspring; therefore, *ex hypothesi*, we shall have three tall forms produced to one dwarf form, but of these three tall forms two are not pure, and do not breed true. Mendel's experimental results accorded with what we should expect to obtain if the above explanation were correct. Hence the inference that there is such a splitting of the gametes in the sexual act seems a legitimate one.

Mendel's experiments are of great importance, for they give us some insight into the nature of the sexual act. But, as is usual in such cases, Mendel's disciples have greatly exaggerated the value and importance of his work. It is necessary to bear in mind that Mendel's results apply only to a limited number of cases—to what we may call balanced characters. In the case of characters which do not balance one another, which are, so to speak, not diametrically [145] opposed to one another, Mendel's law does not hold. A second important point is, that the dominance is in many cases not nearly so complete as it should be if the Mendelian formula correctly represented what actually occurs in nature. Further, the segregation of the gametes does not appear to be so complete as the above hypothesis requires it to be. The phenomena of inheritance seem to be far more complex than the thorough-going Mendelian would have us believe.

Let it be noted that it is not to the facts of Mendelism, but to some portions of what we may call the Mendelian theory, that we take exception.

Maturation of the Germ-cells

Before passing on to consider some of the later developments of Mendelism, it is necessary for us to set forth briefly certain of the more important facts regarding the sexual act which the microscope has brought to light. We propose to state these only in the merest outline. Those who are desirous of pursuing the subject farther are referred to Professor Thomson's *Heredity*.

The germ cells, like all other cells, consist of a nucleus lying in a mass of cytoplasm. The nucleus is composed of a number of rod-like bodies, which are called chromosomes, because they are readily stainable.

These chromosomes appear, under ordinary circumstances, to be joined together end to end, and then look like a [146] rope in a tangle.

When a cell is about to divide into two, these chromosomes become disjoined and can then be counted, and it is found that each cell of each species of animal or plant has a fixed number of these chromosomes. Thus the mouse and the lily

have twenty-four chromosomes in each cell, while the ox is said to have sixteen of them per cell.

When a cell divides into two, each of these chromosomes splits by a *longitudinal* fissure into two halves, which appear to be exactly alike. One-half of every chromosome passes into each of the daughter cells, so that each of these is furnished with exactly half of each one of the rod-like chromosomes. In the cell division, which takes place immediately before the male gamete or generative cell meets the female gamete, the chromosomes do not divide into equal halves, as is usually the case. In this division half of them pass into one daughter cell and half into the other daughter cell, so that, prior to fertilisation both the male and the female gametes contain only half the normal number of chromosomes. In the sexual act the male and the female chromosomes join forces and then the normal number is again made up, each parent contributing exactly one half.

[147]

Experiments of Delage and Loeb

Biologists, with a few exceptions, seem to be agreed that these chromosomes are the carriers of all that which one generation inherits from another. Thus the cardinal facts of the sexual act are, firstly, prior to fertilisation the male and the female gamete each part with half their chromosomes; and, secondly, the fertilised cell is composed of the normal number of chromosomes, of which one-half have been furnished by each parent. Thus the microscope shows that the nucleus of the fertilised egg is made up of equal contributions from each parent. This is quite in accordance with the observed phenomena of inheritance.

But Delage has shown that a non-nucleated fragment of the ovum in some of the lower animals, as, for example, the sea-urchin, can give rise to a daughter organism with the normal number of chromosomes when fertilised by a spermatozoon. Conversely, Loeb showed that the nucleus of the spermatozoon can be dispensed with. Thus it seems that either the egg or the spermatozoon of the sea-urchin contains all the essential elements for the production of the perfect larva of a daughter organism. We are, therefore, driven to the conclusion that the fertilised ovum contains two sets of fully-equipped units. Only one of these seems to contribute to the developing organism. If this set happens to be composed of material derived from one only of the parents, we can see how it is that we get unilateral inheritance [148] in the case of a cross. Where, however, the units from the two parents intermingle, although only one set is active in development, the result will be blended inheritance. Thus, we may regard the fertilised egg as made up of two sets of characters—a dominant set, which is active in the production of the resulting organism, and a recessive set, which appears to take little or no part in the production of the organism.

This is quite in accordance with Mendelian conceptions.

Let X be an organism having the unit characters *A B C D E F G*, and let Y be another organism having the unit characters *a b c d e f g*.

Now suppose that these behave as opposed Mendelian units, and that the unit characters in italics are dominant ones. Then the resulting individual will resemble each parent in certain unit characters. It may be represented by the formula *A B c d E f G*, but it will contain the characters *A b C D e F g* in a recessive form, so that its complete formula may be

written $\left. \begin{array}{l} a B c d E f G \\ A b C D e F g \end{array} \right\}$

When these hybrids are paired together it will be *possible* to get such forms as $\begin{array}{cc} A B C D E F G & a b c d e f g \\ A B C D E F G & a b c d e f g \end{array}$ and $\begin{array}{cc} a b c d e f g & A B C D E F G \\ a b c d e f g & A B C D E F G \end{array}$ which exactly resemble the respective grandparents, and these should breed absolutely true, if the segregation of the [149] gametes is as pure as the Mendel's law seems to require.

Experiments of Cuénot and Castle

There are, however, certain facts, which recent experimenters have brought to light, that seem to show that the segregation is not so complete as the law requires. For example, the so-called pure extracted forms may be found, when bred with other varieties, to have some latent characters. Thus Cuénot observed that extracted pure albino mice, that is to say, those derived from hybrid forms, did not all behave alike when paired with other mice. Those which had been bred from grey × white hybrids behaved, on being crossed, differently to those that had been bred from black × white hybrids; and further, those derived from yellow × white hybrids yielded yet other results on being intercrossed. Castle records similar phenomena in the case of guinea-pigs, and accordingly draws a distinction between recessive and latent characters. Recessive characters are those which disappear when they come into contact with a dominant character, but

reappear whenever they are separated from the opposing dominant character. Latency is defined by Castle as “a condition of activity in which a normally dominant character may exist in a recessive individual or gamete.”

The ordinary Mendelian pictures a unit character in a cross that obeys Mendel's law, as follows:— $\frac{D}{R}$, the [150]
dominant character only showing. It seems to us that each unit character should be represented as a double entity, thus $\frac{D(R)}{R(D)}$, the portion within the bracket being latent. The cross would appear to be represented by the formula $\frac{D(R)}{R(D)}$, since the union appears to take the form of the transfer of the dormant latent characters. Now an extracted pure recessive will, on this hypothesis, bear the formula $\frac{R(D)}{R(D)}$. When such recessives are crossed the two dormant portions will ordinarily change places, and never appear, so that these extracted recessives will, under ordinary circumstances, appear to be as pure as the true pure recessives, which are represented by the formula $\frac{R(R)}{R(R)}$. Now, suppose that, from some cause or other, it is possible for the latent D to change places with the visible R, it is obvious that the impure nature of the extracted and hitherto apparently pure recessives will become manifest. This seems to be what happens under certain circumstances to the extracted albino mice. They possess latent the character of their dominant ancestor. [151]

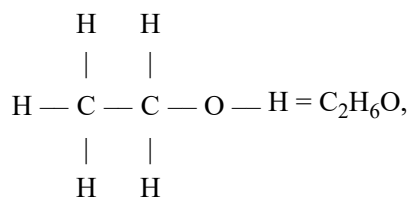
Unit Characters

Mendelian phenomena force upon us the conclusion that organisms display a number of unit characters, each of which behaves in much the same way as a radicle does in chemistry, inasmuch as for one or more of these characters others can be substituted without interfering with the remaining unit characters. For example, it is possible to replace the chemical radicle NH_3 by the radicle Na_2 ; e.g. $(\text{NH}_3)_2\text{SO}_4$ (ammonium sulphate) may be transformed into Na_2SO_4 (sodium sulphate).

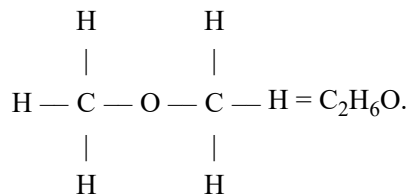
The conclusion that each organism is composed of a number of unit characters, which sometimes behave more or less independently of one another, is one which most biologists who have studied the phenomena of inheritance appear to have arrived at. Zoologists are mostly of opinion that these characters, or rather their precursors, exist as units in the fertilised egg. Very varied have been the conceptions of the nature of these biological units. Almost every biologist has given a name to his particular conception of them. Thus we have the gemmules of Darwin, the unit characters of Spencer, the biophors of Weismann, the micellæ of Naegeli, the plastidules of Haeckel, the plasomes of Wiesner, the idioblasts of Hertwig, the pangens of De Vries, and so on. It is unnecessary to extend this list. It must suffice that almost every investigator of the phenomena of inheritance believes in these units, and calls them by a different name. Moreover, each clothes them with characteristics according to his taste or the fertility of his imagination. [152]

Chemical Molecules

These units behave in such a way as to suggest to us an analogy between them and the chemical molecules. The sexual act would appear to resemble a chemical synthesis in some respects. One of the most remarkable phenomena of chemistry is that of isomerism. It not infrequently happens that two very dissimilar substances are found, upon analysis, to have the same chemical composition, that is to say, their molecules are found to be composed of the same kind of atoms and the same number of these. Thus chemists are compelled to believe that the properties of a molecule are dependent, not only on the nature of the atoms which compose it, but also on the arrangement of these within the molecule. To take a concrete example: Analysis shows that both alcohol and ether are represented by the chemical formula $\text{C}_2\text{H}_6\text{O}$. In other words, the molecule of each of these compounds is made up of two atoms of the element Carbon, six of the element Hydrogen, and one of the element Oxygen. Now, every chemical atom possesses the property which chemists term valency, in other words, the number of other atoms with which it can directly unite [153] is strictly limited. All atoms of the same element have the same valency. Monovalent atoms are those which can, under no circumstances, unite with more than one other atom. The Hydrogen atom is an example of such an atom. Divalent atoms, as, for example, that of Oxygen, can unite with one other atom of similar valency or with two monovalent atoms. Similarly, a trivalent atom, such as that of Nitrogen, can unite with three monovalent atoms. A tetravalent atom, such as that of Carbon, can combine with four monovalent atoms. There are also pentavalent and hexavalent atoms. Now, by indicating the valency of any given atom by a stroke for each monovalent atom with which it is able to combine, chemists have been able to represent the molecule of every compound, or, at any rate, of every inorganic compound, by what is known as a graphic or structural formula. Thus, ethylic alcohol is represented by the formula:—



and methylic ether by the structural formula:—



The formulæ indicate a very different arrangement of the nine atoms which compose the molecule in each case. [154]
 And to this different arrangement the differing properties of the two compounds are supposed to be due. A rough illustration of the phenomenon of isomerism is furnished by written language. Thus, three different words can be made from the letters t, a, and r, *e.g.* tar, art, and rat. They also form tra, which does not happen to be an English word, although it might have been one.

Experiments of Gräfin von Linden

Among organisms we sometimes observe a phenomenon which looks very like isomerism. The classical example of this is furnished by the butterflies *Vanessa prorsa* and *Vanessa levana*.

At one time these were supposed to belong to different species, since they differ so greatly in appearance. *Vanessa levana* is red, with black and blue spots. *Vanessa prorsa* is deep black, with a broad yellowish-white band across both wings. It is now known that the *levana* is the spring form and the *prorsa* the summer and autumn form of the same species. The pupæ of *levana* produce the *prorsa* form, but Weismann found that after being placed in a refrigerator they emerged, not as *prorsa*, but partly as *levana* and partly as another form intermediate in many respects between *levana* and *prorsa*. Weismann also succeeded, by exposing the winter pupa to a high temperature, in making it give rise [155] to the *prorsa* form, and not to the *levana* form, as it would ordinarily do.

Similar results have been obtained with the seasonally dimorphic *Pieris napi*. Standfuss, the Gräfin von Linden, and others have obtained like results in the case of other seasonally dimorphic butterflies. In some instances it has been proved that the change in the pigment is a purely chemical one; a similar transformation can be effected in the extracted pigment. But, we must bear in mind that the changes which are induced in this way are not confined to colour; they occur in the marking and shape of the wing.

Even more remarkable is the fact that in some sexually dimorphic species a change of temperature alters the female, so as to cause her to have the outward appearance of the male. For example, it has been found that warmth changes the colours of the female *Rhodocera rhamni* and *Parnassius apollo* into the colours of the male.

By applying rays of strong light, electric shock, or centrifuge, the Gräfin von Linden was able to change the colours of the butterflies to which the caterpillars gave rise. Pictet experimented on twenty-one species of butterflies, or rather on their caterpillars, and found that in nearly all cases when the caterpillars ate unusual food, they developed into butterflies with abnormal colouring. Schmankewitsch made the discovery that, in the case of the crustacean [156] *Artemia*, he could produce either of two species according to the amount of salt in the water in which these creatures were placed. He declared that the anatomical differences between the species *Artemia salina* and *Artemia milhausenii* depended solely on the percentage of the salt in the surrounding water. He further stated that by adding still more salt he could change the *Artemia* into a new genus—*Branchipus*. More recent observers have cast doubt upon these results of Schmankewitsch. They, however, admit that the degree of salinity of the water has some effect on the form of the *Artemia*, although they suggest that factors other than concentration affect the result. In any case, it is now well-known that changes in the environment effect changes in the colouring of many crustacea. Pictet has shown that the alternating wet and dry seasons in some tropical countries are the cause of, or stimulus that induces, seasonal dimorphism in some butterflies. He was able to effect changes in the colouring of certain species by means of humidity.

The most important cases, from our point of view, are those in which the application of heat or cold to a pupa has affected the colour, shape, etc., of the emerging butterfly. Here we have but one factor, that of temperature. All the material for the formation of the butterfly is already stored up in the pupa. The unit characters, or their precursors, [157] are all there, and they take one form or another according to the stimulus applied.

Biological Isomerism

Phenomena of this kind can, we think, be accounted for only on the assumption that the unit characters affected are each developed from a definite portion of the fertilised egg, that each of these portions, these precursors of the unit characters, is, like a chemical molecule, made up of a number of particles, and that upon the arrangement of these particles in its precursor in the egg depends the form that the unit character derived from it will take. One arrangement of these particles gives rise to one form of unit character, while another arrangement will give rise to a totally different form of unit character.

Thus, some organisms seem to display a biological isomerism akin to chemical isomerism, save that the particles which in organisms take the place of chemical atoms are infinitely more complex.

In other words, the precursors in the fertilised egg of each of these unit characters behave in some respects like chemical molecules.

In order to avoid the manufacture of fresh terms we may speak figuratively of the germ cells as being composed of biological molecules, which in their turn are built up of biological radicles and atoms. These behave in some ways [158] like chemical molecules, radicles, and atoms, as the case may be.

Biological Molecules

It seems legitimate to regard each unit character in the adult as the result of the development of one or more of the biological molecules which compose the nucleus of the fertilised egg. These biological molecules are, of course, a million-fold more complex than chemical molecules. Each biological atom must contain within itself a number of the very complex protoplasmic molecules. This view of the structure of the germ cell seems to force itself upon the observer. Notwithstanding this, the conception will have no value unless it seems to throw light on the various phenomena of heredity, variation, etc.

Let us then try to interpret some of these.

Each chemical element is made up of atoms which are all of the same kind, but no two elements are made up of the same kind of atoms, although chemists are now inclined to conceive of all the various kinds of atoms as made up of varying amounts of some primordial substance. In any case, the molecules of chemical compounds are made up of various kinds of atoms. With biological atoms the case would seem to be different. All would appear to be made up of the same kind of substance, and the differences shown by the various unit characters that go to make up an [159] organism would seem to be due to the different numbers and the varying arrangement of the biological atoms which compose the molecules from which unit characters are derived. This would be quite in accordance with the chemical notion of allotropy. Thus, the graphite and the diamond molecules are both made up of the same kind of atoms.

But the biological atoms are living, that is to say, they are continually undergoing anabolism and katabolism, growth and decay. They exhibit all the phenomena of life, they must grow and divide, and they must absorb nourishment; hence it is not surprising that they should differ slightly among themselves, that they should exhibit the phenomenon of variation. Although probably all are composed of the same living material, no two are exactly alike, hence the molecules formed by them will also differ from one another. Thus we can see why it is that all organisms exhibit fluctuating variations.

Very different are the discontinuous variations or mutations. These would seem to be due to either a rearrangement of the biological atoms in the biological molecule or the splitting up of the latter into two or more molecules. This, of course, is pure hypothesis. Let us take an imaginary example. Suppose that a biological molecule contains eighteen biological atoms, and that these are arranged in the form of an equilateral triangle, six of them going to each side. [160] Suppose now, that from some cause or other they rearrange themselves to form an isosceles triangle, so that only four form the base and seven go to each of the remaining sides. Such an arrangement would give rise to a mutation. Suppose now that, from some cause or other, this triangular biological molecule were to split up into two triangles, each having three atoms to each side, we should obtain a still more marked mutation. We are far from saying that the

atoms in the organic molecule ever take such forms. We have merely attempted to give rough but simple illustrations of the kind of processes which on this hypothesis might be expected to take place in the germ cells or the fertilised eggs.

Let us now consider the sexual act from this aspect. The various molecules (we speak, of course, of biological molecules) of the male parent meet those of the female parent, and a synthesis occurs, which results in the formation of a new organism. When these two sets of gametes meet one another, one of several events may happen. The gametes may refuse to combine. This will occur whenever they are of very different constitution; thus it is that widely differing species will not interbreed. But it may even happen that gametes of individuals of the same species may refuse to coalesce on account of some peculiarity in the composition of one or other of them. Secondly, they may be able to form some sort of a union, but, owing to their diverse nature, the resulting molecules may be so complex that they cannot be broken up into equal halves, and as this seems to be necessary for the sexual act, the resulting organism will be sterile. Thirdly, the two sets of gametes may enter into a proper union, that is to say, form new molecules, but these may be of such different structure to the molecules of the gametes, that the resulting offspring will be quite unlike their parents in appearance. Fourthly, some or all the groups of radicles in each gamete may be united so closely that in the sexual act they do not break up, but enter bodily into the new resulting organism. In these circumstances the inheritance of the offspring will follow Mendel's law. Fifthly, there may be some slight disturbance of the molecule, perhaps one or only a few atoms will be replaced by those of the other gamete. This would give us impure dominance. [161]

Thus this hypothesis appears to be compatible with the various modes of inheritance.

The curious phenomenon known as prepotency would seem also to be quite in accordance with the conception.

In chemical reactions the tendency is for the most stable combinations to be formed, so in nature.

We may probably go farther and say, not only will the most stable biological molecules be formed, but the most stable radicles will dominate the molecule. Hence, if any two animals are crossed and the offspring show alternate inheritance, the resulting organism will, in the case of each unit character, display the most stable of the pair; in other words, it will take after the parent which happens to have the greater stability as regards that particular character. The difference between the mule and the hinny would seem to be explicable on this supposition. If the union were like a simple chemical synthesis it should not make any difference which way the cross were made. But if the species crossed are of varying stability, and if their respective degrees of stability vary with the sex, it is easy to see that it will make a difference how the animals are crossed. [162]

In the cases of creatures that obey Mendel's law, the most stable form of a unit character will presumably be the dominant one.

One of the most curious of the phenomena of inheritance is that of correlation. We shall deal with this more fully in Chapter VIII. It will suffice here to say that certain characters appear to be linked together in organisms. Such seem to be transmitted in pairs. The offspring never exhibits one of such a correlated couple without exhibiting the other also.

It would thus seem that certain combinations of biological atoms, certain molecules, can only exist in conjunction with certain other combinations. This is quite in accordance with the teaching of physiologists regarding the interdependence of the various organs of the body. We have now reached the stage of the fertilised ovum. According to our conception it is a series or conglomeration of the precursors of the unit characters of the adult. These precursors we call biological molecules. Each is of a very complex nature. Each seems to be composed of several portions, only one of which will take part in the building up of the body of the offspring, the other portions remaining latent. We further conceive that it is possible for the various radicles which compose these molecules to arrange themselves in various manners, and with each new arrangement a different form of unit character will be developed. These molecules, then, are built up from radicles derived from both parents, the most stable combinations being formed and one portion of the molecule dominating the whole. Under normal circumstances this dominant portion of the molecule will give rise to a character of a definite type. But it seems that other factors may come into play and cause a rearrangement of the radicles which compose it, and this will result in the formation of a unit character different from that to which it would ordinarily give rise. [163]

But, it may be objected, if the colour of an organism be derived from one of these so-called biological molecules, how is it that it affects the whole organism, or, at any rate, several of the other unit characters? The objection may be met in several ways. In the first place, the colour-forming molecules may split up into as many portions as there are units which it affects, and each portion may attach itself to a unit. Or the property which we call colouration may not be derived from a molecule, it may be an expression in the relative positions of the various molecules in the fertilised egg. Or the colour-determining molecule may secrete a ferment or a hormone, and this may be the cause of the particular colouring of the resulting organism. We do not pretend to say which (if any) of these alternative suppositions is the correct one. But it seems to us that some such conception as that which we have set forth is forced upon us by observed [164]

facts. This conception should be regarded not as a theory, but rather as an indication of the lines along which we believe the study of inheritance could best be made.

The fertilised ovum has nothing of the shape of the creature to which it will give rise. It is merely a potential organism, a something which under favourable conditions will develop into an organism.

Phenomenon of Sex

In the higher animals each individual is either of the male or the female sex. A vast amount of ingenuity has been expended by zoologists in the attempt to ascertain what it is that determines sex. Many theories have been advanced, but no one of them has obtained anything like general acceptance, because its opponents are able to adduce facts which appear to be incompatible with it. [165]

It is tempting to try to interpret the phenomenon of sex on the assumption that the female-producing biological molecule or unit is an isomere of the male-producing cell. Certain facts, however, seem to negative the idea, as, for example, the occasional appearance in an individual of one sex of characteristics of the other sex.

Possibly the attempts to explain the phenomena of sex-production on a Mendelian basis may prove to be more successful. It seems not impossible that each fertilised egg contains material which is capable of developing into male generative organs and material which is capable of developing into female generative organs, but that only one kind of material, that which dominates, succeeds in developing. The number of what are known as "X-elements" that happen to be present in the fertilised egg appear to decide which kind of material is to be dominant.

But the problem of the determination of sex, fascinating though it be, is not one that can be discussed adequately in a general work on evolution. Those interested in the subject are referred to Professor Thomson's *Heredity*, and to the address given by Professor E. B. Wilson, of Columbia University, before the American Association for the Advancement of Science, which was fully reported in the issue of *Science*, dated January 8, 1909. [166]

Stated briefly, then, our conception is, that the fertilised egg is composed of a number of entities, to which we have given the name "biological molecules," because in certain respects their behaviour is not unlike that of chemical molecules.

The units which compose these molecules, being made up of protoplasm, are endowed with all the properties of life, including the inherent instability which characterises all living matter.

We suggest that the continuous or fluctuating variations that appear in the adult organism may be the result of individual differences in the biological "atoms" that compose the molecule.

Discontinuous variations, or mutations, on the other hand, may be the result of a rearrangement of the atoms within the biological molecule. Upon what causes this rearrangement it would not be very profitable to speculate in the present state of our knowledge. To do this would be to inquire into the cause of a re-grouping of entities of the existence of which we are not certain! For aught we know there may be an intracellular struggle for nourishment among the various molecules and among the atoms which compose the molecules. If one molecule enjoys any special advantage over the others the result may be an unusual degree of development of the resulting unit character; in other words, the result will be a variation in the organism. This variation may prove favourable or unfavourable to its possessor. [167]

Struggle for Nourishment

Certain phenomena seem to point to a struggle for nourishment between the germinal and the somatic portions of the egg, between the parts from which the sexual cells of the resulting organism are produced and those which give rise to the body of the organism. Each molecule may strive, so to speak, to increase at the expense of the others. Thus, great size in an organism is likely to be produced at the expense of the germinal cell-forming molecules. In other words, great size in an organism would be incompatible with excessive fecundity. This is what we observe in nature. On the other hand, poor development of bodily tissue, as in the case of intestinal parasites, would be correlated with great fecundity. Some organisms are mere sacs full of eggs.

Success in the struggle for nourishment of one molecule might be shared by the other molecules near to it, hence the phenomena of correlation.

It is thus conceivable that, in a brood consisting of several individuals, a particular molecule or set of molecules in one of the individuals may receive more than its share of nourishment, and this will result in the organs of that [168]

individual which spring from the well-nourished molecules being exceptionally well developed. Thus arises the phenomenon of differences between the members of a litter or brood.

Natural selection will tend to eliminate those individuals in which the resulting variation is an unfavourable one. If the environment is such, as in the case of an internal parasite, that the production of germ cells is the most necessary function of the organism, then those individuals in which the germ-forming molecules increase at the expense of the body-forming ones will tend to be preserved. This would cause the phenomenon which biologists term degeneration. The nourishment of the various biological molecules may possibly depend on their relative positions in the egg. Those in a favourable position will then tend to develop at the expense of the others. This will result in variation along definite lines. Each succeeding generation will tend to an increased development of that particular organ to which the favourably-situated molecule gives rise. This process may continue, as in the case of the horns of the Irish elk, until the development of that particular organ becomes so excessive as to be positively injurious; then natural selection will step in and eliminate the species. But before this happens, something may cause a rearrangement of the biological molecules in the fertilised egg, and thus a mutation may arise, which, so to speak, strikes out a new line. [169]

Origin of Mutations

Finally, on this conception there may be some sort of connection between fluctuating variations and mutations. We can picture the fluctuating variations being piled up, one upon the other, until there results a rearrangement of the atoms in one or more of the biological molecules which, in turn, causes a mutation.

Occasionally this remodelling, as it were, of one biological molecule may affect certain of the other molecules, and thus lead to correlated mutations.

[170]

CHAPTER VI THE COLOURATION OF ORGANISMS

The theory of protective colouration has been carried to absurd lengths—It will not bear close scrutiny—Cryptic colouring—Sematic colours—Pseudo-sematic colours—Batesian and Müllerian mimicry—Conditions necessary for mimicry—Examples—Recognition markings—The theory of obliterative colouration—Criticism of the theory—Objections to the theory of cryptic colouring—Whiteness of the Arctic fauna is exaggerated—Illustrative tables—Pelagic organisms—Objectors to the Neo-Darwinian theories of colouration are to be found among field naturalists—G. A. B. Dewar, Gadow, Robinson, F. C. Selous quoted—Colours of birds' eggs—Warning colouration—Objections to the theory—Eisig's theory—So-called intimidating attitudes of animals—Mimicry—The case for the theory—The case against the theory—"False mimicry"—Theory of recognition colours—The theory refuted—Colours of flowers and fruits—Neo-Darwinian explanations—Objections—Kay Robinson's theory—Conclusion that Neo-Darwinian theories are untenable—Some suggestions regarding the colouration of animals—Through the diversity of colouring of organisms something like order runs—The connection between biological molecules and colour—Tylor on colour patterns in animals—Bonhote's theory of pœcilomeres—Summary of conclusions arrived at.

Since the publication of *The Origin of Species*, naturalists have paid much attention to the colouration of animals and plants, with the result that a large majority of scientific men to-day hold the belief that all, or nearly all, the colours displayed by animals are of direct utility to them, and are therefore the direct result of natural selection; a few would add, "and of sexual selection." [171]

"Among the numerous applications of the Darwinian theory," writes Wallace, "in the interpretation of the complex phenomena, none have been more successful than those which deal with the colours of animals and plants."

Robinson on Protective Colouring

We readily admit that the Darwinian theory has thrown a great deal of light on the phenomenon of animal colouration; it has reduced to something like order what was before Darwin's time chaos. While admitting this we feel constrained to say that many naturalists, especially Dr Wallace and Professor Poulton, have pushed the various theories of animal colouration to absurd lengths. As Dr H. Robinson truly says (*Knowledge*, January 1909), "It seems to have been taken for granted, and some even of Dr Wallace's writings may be interpreted in this sense, that protective colouring is necessary to the continued existence of every species, and that, sexual colouration apart, it is incumbent on naturalists to offer ingenious speculations in this sense to account for the appearance even of the most bizarre and conspicuous beasts. Thence it has been but a short step to the announcement of those speculations as further evidence in favour of natural selection, and of various assumptions made in the speculative process as indisputable facts." [172]

The result of this is that men have ceased to regard the Neo-Darwinian^[6] theories of protective colouration, mimicry, and recognition markings as mere hypotheses which seem to throw light on certain phenomena in the organic world. These theories have assumed the rank of laws of nature. To dispute them would seem to be as futile as to assert that the earth is flat. To take exception to them would appear to be as ridiculous as to object to Mont Blanc. To dare to criticise them is heresy of the worst type.

Be this as it may, scientific dogma or no scientific dogma, scientific opinion or no scientific opinion, we have dared to weigh these theories in the balance of observation and reason, and have found them wanting. We have examined these mighty images of gold, and silver, and brass, and iron, and found that there is much clay in the feet.

We shall devote this chapter to lifting the hem of the garment of sanctity that envelopes each of these images, and so expose to view the clay that lies concealed.

We propose, first, to set forth in outline what we trust will be considered a fair statement of the various theories of animal colouration which are generally accepted to-day, then to show up the various weak points in these, and lastly, to endeavour to ascertain whether there are not some alternative explanations in certain cases to which the generally-accepted theory does not apply. [173]

Cryptic Colouring

Neo-Darwinians divide the various forms of colouration into three great classes:—(1) Cryptic colouring, or protective and aggressive resemblances; (2) sematic colours, or warning and recognition colours; and (3) pseudo-sematic colours, or mimicry. A tabular statement of this scheme of colouring will be found on pp. 293-7 Professor Poulton's *Essays on Evolution*.

As regards class (1), Neo-Darwinians point out that the great majority of animals are so coloured as to make them very difficult to see in their natural environment, hence the whiteness of the creatures which inhabit the snow-bound Arctic regions, the sandy colour of desert animals, the spotted coats of creatures which live among trees, the striped markings of animals which spend their lives amid long grass, and the transparent blueness of pelagic animals. The theory is that all kinds of animals, whether those that hunt or those that are hunted, derive much advantage from being coloured like their environment. The hunted creatures are thereby the better able to elude the vigilance of their foes, while those that hunt are in a position to take their quarry by surprise; so that natural selection has caused them all to assimilate to the hues of their surroundings. Neo-Darwinians point to the fact that some Arctic animals are brown in the summer to match the ground from which the snow has melted, and turn white in winter to assimilate with their snowy background. Naturalists further cite, as evidence in favour of this theory, the case of those creatures which imitate inanimate objects, such as leaves and twigs, and thereby escape the observation of their foes. [174]

Thus, the great majority of animals are supposed to be cryptically coloured, that is to say, coloured so as to be, if not quite invisible, at least very inconspicuous in their natural habitat.

Warning Colouration

It is, however, generally admitted that many creatures are not cryptically coloured. Some, indeed, seem to be coloured in such a way as to render them as conspicuous as possible. The Neo-Darwinians declare that there is a reason for this. "If," writes Professor Milnes Marshall (page 133 of his *Lectures on the Darwinian Theory*), "an animal, belonging to a group liable to be eaten by others, is possessed of a nauseous taste, or if an animal, such as a wasp, is specially armed and venomous, it is to its advantage that it should be recognised quickly, and so avoided by animals that might be disposed to take it as food." [175]

"Hence arises warning colouration, the explanation of which is due to Wallace. Darwin, who was unable to explain the reason for the gaudy colouration of some caterpillars, stated his difficulty to Wallace, and asked for suggestions.

Wallace thought the matter over, considered all known cases, and then ventured to predict that birds and other enemies would be found to refuse such caterpillars if offered to them. This explanation, first applied to caterpillars, soon extended to adult forms, not only of insects, but of other groups as well. . . . Insects afford many admirable examples of warning colours, and many well-known instances occur among butterflies. The best examples of these are found in three great families of butterflies—the *Heliconidæ*, found in South America, the *Danaidæ*, found in Asia and tropical regions generally, and the *Acræidæ* of Africa. These have large but rather weak wings, and fly slowly. They are always very abundant, all have conspicuous colours or markings, and often a peculiar form of flight, characters by which they can be recognised at a glance. The colours are nearly always the same on both upper and under surfaces of the wings; they never try to conceal themselves, but rest on the upper surfaces of leaves and flowers. Moreover, they all have [176] juices which exhale a powerful scent; so that, if they are killed by pinching the body, a liquid exudes which stains the fingers yellow, and leaves an odour which can only be removed by repeated washing. This odour is not very offensive to man, but has been shown by experiment to be so to birds and other insect-eating animals.

“Warning colours are advertisements, often highly coloured advertisements, of unsuitability as food. Insects are of two kinds—those which are extremely difficult to find, and those which are rendered prominent through startling colours and conspicuous attitudes. Warning colours may usually be distinguished by being conspicuously exposed when the animal is at rest. Crude patterns and startling contrasts in colour are characteristically warning, and these colours and patterns often resemble each other; black combined with white, yellow, or red, are the commonest combinations, and the patterns usually consist of rings, stripes, or spots.”

We trust that we shall be forgiven for this lengthy quotation. Our object in reproducing so large an extract is to allow the Neo-Darwinians to speak for themselves. Were we to state their theory in our own words, we might perhaps be charged with stating it inaccurately. We should add that, even as natural selection is supposed to have been the [177] cause of conspicuous colouring in some organisms, so has it caused others to assume intimidating attitudes or emit warning sounds, such as a hiss, when attacked.

Batesian Mimicry

We now come to the third great class of animal colours—mimetic colours. Mimicry is of two kinds, known respectively as Batesian and Müllerian mimicry, after their respective discoverers.

It has been found that some apparently warningly coloured butterflies and other creatures are palatable to insectivorous animals. The explanation given of this is that these showy but edible butterflies “mimic,” that is to say, have the appearance of, show a general resemblance to, species which are unpalatable. This is known as Batesian mimicry. “Protective mimicry,” writes Professor Poulton (*Essays on Evolution*, p. 361), “is here defined as an advantageous superficial resemblance of a palatable defenceless form to another that is specially defended so as to be disliked or feared by the majority of enemies of the groups to which both mimic and model belong—a resemblance which appeals to the senses of animal enemies . . . but does not extend to deep-seated characters, except when the superficial likeness is affected thereby.”

As Wallace has pointed out, five conditions must be satisfied before such protective mimicry can occur:— [178]

“1. That the imitative species occur in the same area and occupy the same station as the imitated. 2. That the imitators are always the more defenceless. 3. That the imitators are always less numerous in individuals. 4. That the imitators differ from the bulk of their allies. 5. That the imitation, however minute, is external and visible only, never extending to internal characters or to such as does not affect the external characters.” (*Darwinism*, Chap. ix.)

Thus the mimic is supposed to deceive his enemies by deluding them into the belief that he is the inedible species which they once tried to eat and vowed never again to touch, so nasty was it. The mimic, then, may be compared to the ass in the lion’s skin. Needless to say, this mimicry is quite unconscious. It is supposed to have been developed by natural selection. Every popular book on Evolution cites many examples of such mimicry. We may therefore content ourselves with mentioning but a few.

Examples of Mimicry

Our common wasps are copied by a beetle (*Clytus arietis*), active in movement and banded black and yellow, and by several yellow-barred hover-flies (*Syrphidæ*); and the bumble-bee by a clear-winged moth (*Sesia fuciformis*). [179] There is, indeed, a whole group of these clear-winged moths, resembling bees, wasps, and other stinging hymenoptera. The common Indian Danaid butterfly, *Danais chrysippus*, is marvellously reproduced by the female of *Hypolimnas misippus*, a form allied to our Purple Emperor. The male of this is black, with white blue-bordered patches,

the female chestnut, edged with black and with white spots at the tips of the wings, as in the *Danais*. Finn has shown experimentally that this species is liked by birds.

Another common Indian Danaid (*D. limniace*), black, spotted with pale green, is imitated, though not very closely, by the female of one of the “white” group, *Nepheronia hippia*. Finn found that this insect was eaten freely by birds, and that the common jungle-babbler (*Crateropus canorus*) was deceived by the mimicry of the female. The very nauseous Indian swallow-tail (*Papilio aristolochiae*) is closely imitated by another swallow-tail (*P. polites*), both having black wings marked with red and white; *P. aristolochiae*, however, has a red abdomen. This difference was not noticed by two species of Drongo-shrikes (*Dicrurus ater* and *Dissemurus paradiseus*), to which the butterflies were offered; but the Pekin robin (*Liothrix luteus*)—a very intelligent little bird—did not fail to pick out and eat the mimic, though it was deceived by the marvellously perfect imitation of *Danais chrysippus*, by the female of the *Hypolimnas*. [180]

Such resemblances can therefore be effective.

The cases of mimicry usually quoted include very few among mammals, probably, as Beddard suggests, because the species of that class are relatively few.

The insectivorous genus *Tupaia* is supposed to mimic the squirrels, which it much resembles as regards form in all respects save the long muzzle; the idea being that squirrels are so active that carnivorous animals find it hopeless to pursue them.

On the other hand, there is a squirrel (*Rhinosciurus tupaoides*) which is supposed to mimic the tupaia! It has a similar long muzzle, and the light shoulder-stripe which is a common marking in tupaia. But why the squirrel, one of the group imitated, should in turn become an imitator is not explained.

The true interpretation of the resemblance is probably that both squirrels and tupaia are adapted to a life in trees. Like profession begets like appearance: the ground-living shrews much resemble mice, and the moles find representatives in mole-like rodents.

Another case, however, wherein true mimicry may have come into play is that of the South American deer (*Cervus paludosus*) which singularly resembles in colouration the long-legged wolf or *Aguara-guazu* (*Canis jubatus*). [181] Both these species are chestnut in colour, with the front of the legs black, and the ears lined with white hair; both inhabit the same regions in South America.

Müllerian Mimicry

The second kind of mimicry—Müllerian mimicry—is where one unpalatable creature resembles another. This form of mimicry is named after Fritz Müller, who suggested the explanation now usually accepted, namely, that “Life is saved by a resemblance between the warning colours in any area, inasmuch as the education of young inexperienced enemies is facilitated, and insect life saved in the process.” “It is obvious,” writes Poulton (p. 328 of *Essays on Evolution*), “that the amount of learning and remembering, and consequently of injury and loss of life involved in these processes, are reduced when many species in one place possess the same aposematic colouring, instead of each exhibiting a different danger signal. . . . The precise statement of advantage was made by Mr Blakiston and Mr Alexander, of Tokio. ‘Let there be two species of insects equally distasteful to young birds, and let it be supposed that the birds would destroy the same number of individuals of each before they were educated to avoid them. Then if these insects are thoroughly mixed and become undistinguishable to the birds, a proportionate advantage accrues to each over its former state of existence. These proportionate advantages are inversely in the duplicate ratio of the respective percentages that [182] would have survived without the mimicry.’”

This is rather a cumbrous method of saying that if there are in a locality a number of young birds, and each of these has to learn by experience which insects are edible and which are not, each will, if it learns by one example, devour one insect of any given pattern. Now, if two species of inedible insects have this pattern, they will between them lose only one member in the educating process of each bird, whereas if each species of insect had a colouration peculiar to itself, each species would lose a whole individual instead of half a one. There can be no doubt that such a livery of unpalatability is of some advantage to its possessors.

It has been shown experimentally that hand-reared young birds have to acquire their knowledge of flavours and colours by experiment.

It is well known that in many species the male and the female are not coloured alike. Such species are said to exhibit sexual dimorphism. In these cases it is usually the male that is more conspicuously coloured. Darwin felt that the theory

of natural selection could not satisfactorily account for this phenomenon, so put forward the supplementary theory of sexual selection. On this hypothesis the females are supposed to be able to pick and choose their mates, and to [183] select the most beautiful and ornamental ones, hence the greater showiness of these in most sexually dimorphic species. Wallace does not accept this theory. He thinks it unnecessary. He looks upon the brilliant colouring of the males as due to their superior vigour; moreover, he says that it is the hen that sits upon the eggs, and so requires a greater degree of protection than the male, and therefore natural selection has not permitted her to develop all the ornaments displayed by the cock. With the phenomenon of sexual dimorphism we shall deal at length in the next chapter.

Danger Signals

Dr Wallace recognizes yet another exception to the rule that animals are cryptically coloured. Many creatures possess on the body markings which tend to render them conspicuous rather than difficult to see. Where such markings occur on gregarious animals, Wallace believes that they have been evolved by natural selection, either to enable their possessors to recognize one another, or to act as a danger signal to their fellows. The white tail of the rabbit is believed by Wallace to serve as a danger signal. The first member of the company to espy the approaching foe takes to his heels, and, as he moves, his white tail catches the eye of his neighbour, who at once follows him, so that, in less time than it takes to tell, the whole company of rabbits is scampering towards the burrow, thanks to the white under-surface of [184] the tail.

Even as Wallace out-Darwin's Darwin, so does Mr Abbott Thayer, an American naturalist and artist, out-Wallace Wallace. That gentleman seems to be of opinion that *all* animals are cryptically or, as he calls it, concealingly or obliteratively coloured. Even those schemes of colour which have hitherto been called conspicuous are, he asserts, "purely and potently concealing" when looked at properly, that is to say, with the eye of the artist.

Lest it be thought unnecessary to criticize a hypothesis which appears to be based upon the assumption that animals see with the eye of the artist, we may say that Professor Poulton writes approvingly of Thayer's theory. He frequently alludes to it in his *Essays on Evolution*, and he published an account of it in the issue of *Nature*, dated April 24, 1902. Moreover the hypothesis has been enunciated in such scientific journals as *The Auk* (1896) and *The Year-Book of the Smithsonian Institution* (1897).

Thayer asserts that all animals, or at any rate the great majority, including many that are usually supposed to be conspicuously coloured, are in reality obliteratively coloured—that is to say, coloured in such a way that the effects of light and shade are completely counteracted, with the result that they are invisible.

[185]

Obliterative Colouring

It is possible, says Mr Thayer, to almost obliterate a statue in a diffused light, by putting white paint on the surfaces in darkest shadow and dark paint on the most brightly lighted parts, all in due proportion. Now this is precisely what nature is supposed by Mr Thayer to have done for all her creatures.

It is well known that a great many animals, as for example the Indian black-buck and the hare, are coloured on the upper side and white below. This is called by Mr Thayer the principle of the gradation of colour. It runs, he declares, all through the animal world, and is "the main essential step toward making animals inconspicuous under the descending light of the sky."

Animals, he contends, are not protectively coloured to look like clods or stumps or like surrounding objects, they are simply obliteratively coloured—coated, as it were, with invisible paint.

To quote from *The Century Magazine* (1908): "Whales, lions, wolves, deer, hares, mice; partridges, quails, sandpipers, larks, sparrows; frogs, snakes, fishes, lizards, crabs; grasshoppers, slugs, caterpillars—all these animals, and many thousands more, crawl, crouch, and swim about their business, hunting and eluding, under cover of this strange obliterative mask, the smooth and perfect balance between shades of colour and degrees of illumination."

Nature having thus visually unsubstantialized the bodies of animals, so that, if seen at all, they look flat and [186] ghostly, does not stop there. From solid-shaded bodies they have been converted, as it were, into flat cards or canvases, and, to complete the illusion of obliteration, pictures of the background—veritable pictures of the more or less distant landscape—have been painted on their canvases! Such in effect are the elaborate "markings of field and forest birds."

Again he writes: "Brilliantly changeable or metallic colours are usually supposed to make the birds that wear them conspicuous, but nothing could be further from the truth. Iridescence is, indeed, one of the strongest factors of concealment. The quicksilver-like intershifting of many lights and colours, which the slightest motion generates on an iridescent surface, like the back of a bird or the wing of a butterfly, destroys the visibility of that wing or back as such and causes it to blend inextricably with the gleaming and scintillating labyrinthine-shadowed world of wind-swayed leaves and flowers."

According to Thayer, the skunk, which for years has been an important item of the stock-in-trade of the advocates of the theory of warning colouration, is an excellent example of obliterative colouring, since its enemies are supposed to mistake for the sky-line the line of junction between the white fur of the back and the dark fur of the sides. [187] Similarly the crocodiles are supposed to mistake a flamingo for the sky at sunrise or at sunset!

There is doubtless something in this theory of obliterative colouration.

Any one can see, by paying a visit to the South Kensington Museum, that an animal which is of a lighter colour below than above, is less conspicuous in a poor light than it would be were it uniformly coloured. There is then no doubt that this scheme of colour, which is so common in nature, has some protective value.

To this extent has Mr Thayer made a valuable contribution to zoological science. But when he informs us that obliterative colouring is a "universal attribute of animal life," we feel sorely tempted to poke fun at him.

We would ask all those who believe in the universality of obliterative colouring to observe a flock of rooks wending their way to their dormitories at sunset.

Let us now pass on to the examination of the more orthodox theories of animal colouration.

OBJECTIONS TO THE THEORY OF CRYPTIC COLOURING

Before criticising the theory of cryptic colouring, we desire to state distinctly that we admit that, where other [188] things are equal, it is of advantage to all creatures which hunt or which are preyed upon to be inconspicuous. If difficult to distinguish amid their natural surroundings, the former are likely to secure their prey readily, and the latter have a chance of escaping from their enemies. Our quarrel is with the theory of cryptic colouring as it is enunciated by many Neo-Darwinians, with the theory that every hue, every marking, every device displayed by an organism is of utility to the organism and has been directly developed by natural selection.

The extreme advocates of the theory of cryptic colouring have greatly exaggerated the degree in which animals are assimilated to their natural environment.

Fauna of Polar Regions

We grant that a great many creatures, which when seen in a menagerie appear very conspicuous, are the reverse of conspicuous when standing motionless amid their natural surroundings. As Beddard has pointed out, it is often not easy to find a sixpenny piece which has been dropped on the carpet, but the reason for this is, not that the coin is protectively coloured, but that any small object, no matter how coloured, is difficult to distinguish amid a variegated environment. The assumption of a white winter coat by many organisms that live in northern latitudes has been cited, again and again, as showing how important it is for an animal to be protectively coloured. If, it is urged, those creatures that [189] live in lands which are covered in snow for half of the year have become white in winter by the action of natural selection in order to escape their foes, it is obviously of paramount importance to all creatures that they should be cryptically coloured. Popular books on natural history convey the impression that during winter the snow-clad, ice-bound Arctic regions are peopled by a fauna whose fur or hair rivals in whiteness the snowy mantle of the earth. The impression thus conveyed is misleading. It is true that an unusually large percentage of the animals that inhabit the polar regions are white in winter, but the majority of the creatures which dwell there do not assume the white garb of winter.

As the fauna of the polar regions is a small one, we are able to give lists of all the birds and mammals which dwell in the Arctic and the Antarctic regions. We have arranged these in three columns. In the first are placed those creatures which are white throughout the year, in the third those that retain their colour through the winter, while the middle column contains those forms which change their colouring with the season.

ARCTIC FAUNA.

MAMMALS.

White.

Polar Bear.

Arctic Fox (some individuals).

White Whale or Beluga.

Changing with the Seasons.

Arctic Fox (most individuals).

Arctic Lemming.

Stoat.

Weasel.

Blue Hare.

Coloured.

Arctic Fox (sometimes).

Reindeer.

Musk-ox.

Glutton.

Moose.

Sable.

Seals.

Walrus.

Narhwal.

Greenland Whale.

BIRDS.

White.

Ivory Gull.

Snowy Owl.

Gyr Falcon.

Snow Goose.

Changing with the Seasons.

Black Guillemot.

Ptarmigans.

Snow Bunting (whitest in summer!)

Razorbill.

Little Auk (throat only becomes white).

Coloured.

Sea Eagle.

Greenland Redpoll (very pale).

All Arctic Geese and Ducks other than Snow Goose.

Raven.

Cormorant.

Brunnich's Guillemot.

Puffin.

Fulmar Petrel.

Ross's Gull.

Glaucous Gull (very pale).

Sandpipers.

ANTARCTIC FAUNA.

MAMMALS.

White.

Antarctic White Seal (*Lobodon carcinophaga*), in some cases.

Changing with the Seasons.

None.

Coloured.

Other Seals than *Lobodon*.

Whales.

BIRDS.

White.

Sheathbill.

Snowy Petrel.

Giant Petrel (some individuals).
 Chick of Emperor Penguin.
 Changing with the Seasons.
 None.
 Coloured.
 Penguins.
 Cormorant.
 Skua Gull.
 Giant Petrel (usually).
 Other Petrels.

It will be observed that the third column contains the largest number of forms. It is thus evident that the whiteness of the Arctic and Antarctic faunas in winter has been greatly exaggerated.

The Arctic fox appears in all three columns, as the creature seems to fall into three races—a permanently white race, a permanently coloured race, and a seasonally dimorphic race.

Of the creatures set forth in the middle column of the above tables all are whiter in winter than in summer with the exception of the snow bunting, who sets at naught the theory of cryptic colouring by turning darker in winter! The [192] same may be said of the Alpine chamois.

The advocates of the theory of protective colouring assert that the creatures which do not turn white in winter are strong and active animals which have no enemies to fear.

This contention is met by F. C. Selous as follows (*African Nature Notes and Reminiscences*, p. 9): “According to the experience of Arctic travellers, large numbers of young musk oxen are annually killed by wolves. . . . Nothing, I think, is more certain than that a far smaller percentage of so-called protectively coloured giraffes are killed annually by lions in Africa than of musk oxen by wolves in Arctic America.”

Another difficulty which confronts the Neo-Wallaceian school is that, *ex hypothesi*, the assumption of the white coat was gradual. Hence the change in the direction of whiteness cannot, in its first beginning, have been of perceptible utility to an organism. How then can natural selection have operated on it?

Pelagic Organisms

The transparency of pelagic organisms is frequently cited as exemplifying cryptic colouring. We all know that the common jelly-fish is as transparent as glass. Floating on the surface of the ocean are millions of tiny organisms, so transparent as to be invisible to the human eye. At first sight this certainly appears to be a remarkable case of [193] protective colouring. Unfortunately, nearly all the more highly developed forms display conspicuous pigment (as in most jelly-fish) in some part of the body.

“An animal floating about in the sea,” writes Beddard, “perfectly transparent, but decked with dense black patches, of the size of saucers, would betray its whereabouts even to the least observant; if the observer were stimulated by hunger or fear, the conspicuousness would not be lessened. . . . Besides the internecine warfare which is continually going on amongst the smaller surface organisms, they are devoured wholesale by the larger pelagic fish, and by whales and other Cetacea. A whale, rushing through the water with open mouth and gulping down all before him, is not the least inconvenienced by the invisibility of the organisms devoured in such enormous quantities; nor do a solid phalanx of herring or mackerel stop to look carefully for their food: they take what comes in their way, and get plenty in spite of ‘protective absence of colouration.’

“If the transparency of the pelagic organisms be due entirely to natural selection, it is remarkable that there is so little modification in this direction among the species inhabiting the bottom at such depths as are accessible to the sun’s rays; the advantage gained by this transparency and consequent invisibility would be equally great. And yet this is not [194] the case; the bulk of the bottom fauna of the coasts are brilliantly coloured animals, and those that show any protective colouring at all appear to be coloured so as to resemble stones or sea-weeds.”^[7]

Before leaving the subject of marine animals, we may point out that the majority of the creatures that live in the everlasting blackness of the depths of the ocean display exceedingly conspicuous colouring, and this colouring seems to be constant. In such cases the colouring cannot be useful as such to its possessors. The same may be said of the colour of blood, or of the colouring of the internal tissues of all organisms. We must not lose sight of the fact that every organism, and every component part thereof, must of necessity be either of some colour or perfectly transparent. It

seems to us that since the appearance of *The Origin of Species* zoologists have tended to exaggerate the importance of colouring to organisms; they frequently speak of it as though it were the one and only factor in the struggle for existence. It is on this account that they feel it incumbent upon them to find ingenious explanations for every piece of colouring displayed by every plant or animal.

Unimportance of Colour

The tendency to exaggerate the importance to an animal of its colouring is doubtless in large part due to the fact [195] that many zoologists are content to study nature in museums rather than in the open. Some of those who observe organisms in their natural surroundings, especially in such favourable localities as the tropics, seem to be of opinion that natural selection has but little influence on the colouration of organisms.

Thus D. Dewar writes (*Albany Review*, 1907): “Eight years of bird-watching in India have convinced me that, so far as the struggle for existence is concerned, it matters not to a bird whether it be conspicuously or inconspicuously coloured, that it is not the necessity for protection against raptorial foes which determines the colouring of a species; in short, that the theory of protective colouration has but little application to the fowls of the air.”

Similarly, F. C. Selous writes, on page 13 of *African Nature Notes and Reminiscences*: “Having spent many years of my life in the constant pursuit of African game, I have certainly been afforded opportunities such as have been enjoyed by but few civilised men of becoming intimately acquainted with the habits and life-history of many species of animals living in that continent, and all that I have learned during my long experience as a hunter compels me to doubt the correctness of the now very generally accepted theories that all the wonderfully diversified colours of animals— [196] the stripes of the zebra, the blotched coat of the giraffe, the spots of the bushbuck, the white face and the rump of the bontebok, to mention only a few—have been coloured either as means of protection from enemies or for the purpose of mutual recognition by animals of the same species in times of sudden alarm.”

So also G. A. B. Dewar—a very close observer of nature in England—writes, in *The Faery Year*: “Few theories in natural history have received more attention of late years than protective or aggressive colour, ‘mimicry,’ and harmony with environment. . . . To doubt this use of colour to animals seems like inviting back chaos in place of cosmos—for abandon the theory, and a world of colour is straightway void of purpose, a muddle of chance. So we all like the theory. Some, however, perceive plans to aid the wearer in every colour, tint, shade, and pattern. We may be sceptical of a good many of the cases they cite in support of colour aid, though attracted by the main idea.”

Writing of the commoner British butterflies, he says: “After a little practice, any man furnished with good eyesight can easily distinguish these butterflies—blues, coppers, small heaths, and meadow browns—from their perches; and so we may be sure that the small beast, bird, or insect of prey, with sense of colour or form, could also distinguish them. [197] . . . Quite often, without even searching for them, I can see cabbage whites and other butterflies asleep on perches to which they by no means assimilate.” Mr G. A. B. Dewar suggests that the safety of the resting butterfly lies in “the position, the couch on high, . . . not the mask of colour or marking.”

Gadow on Coral Snakes

Two short visits to Southern Mexico sufficed to show Dr Hans Gadow that some of the commonly accepted explanations of colour phenomena are not the correct ones.

Thus writing of coral snakes, he says, on page 95 of *Through Southern Mexico*: “They are usually paraded as glaring instances of warning colouration, but I am not at all sure whether this is justifiable. Certainly these *Elaps* are most conspicuous and beautiful objects. Black and carmine or coral red, in alternate rings, are the favourite pattern; sometimes with narrow golden-yellow rings between them, as if to enhance the beautiful combination. But these snakes are inclined to be nocturnal in their habits, and, except when basking, spend most of their time under rotten stumps, in mouldy ground, or in ants’ nests in search of their prey, which must be very small, to judge from the size of the mouth.”

Dr Gadow goes on to show that although black and red are very strong contrasts in the day-time, the combination [198] ceases to be effective in the dark. He suggests that red and black is a self-effacing rather than a warning pattern. He further points out that several kinds of harmless snakes have the same colouring and pattern. “There seems,” he says, “to be no reason why we should not call these cases of mimicry; and yet this is most likely a wrong interpretation, since such harmless snakes are also found in districts where the *Elaps* does not occur, not only in Mexico, but likewise in far-distant parts of the world, where neither elapines nor any other similarly coloured poisonous snakes exist. To interpret this as an instance of ‘warning colours’ in a perfectly harmless snake, which has no chance of mimicry, amounts in such cases to nonsense, and we have to look for a different explanation upon physiological and other grounds.”

It is, to say the least of it, significant that all the opposition to the theory of protective colouration comes from those who observe nature first hand, while the warmest supporters of the theory are cabinet naturalists and museum zoologists.

In the case of nocturnal creatures, as Dr H. Robinson very sagely points out (*Knowledge*, January 1909), the value for protective purposes of any given colouration must depend very largely on the state of the moon. "It was," he writes, "a common experience in the South African War that on overcast or moonless nights the nearly black army great-coat made a picquet sentry invisible at a distance of a few feet. In strong moonlight this garb could be seen at a great distance, whereas a khaki pea jacket, useless on a dark night, answered the requirements of invisibility very well." It is thus evident that the dark colour of the buffalo and sable antelope cannot be protective on both dark and moonlight nights. [199]

The theory of protective colouration is based on the tacit assumption that beasts of prey rely on eyesight for finding their quarry. Raptorial birds certainly do use their eyes as the means of discovering their victims; but the great majority of predaceous mammals trust almost entirely to their power of smell as a means for tracking down their prey.

F. C. Selous Quoted

"Nothing," writes F. C. Selous, on page 14 of *African Nature Notes and Reminiscences*, "is more certain than that all carnivorous animals hunt almost entirely by scent until they have closely approached their quarry, and usually by night, when all the animals on which they prey must look very much alike as far as colour is concerned."

The herbivora—the quarry for the beast of prey—too, have a keen sense of smell, so that they trust their noses rather than their eyes for safety.

No observer of nature can have failed to remark how the least movement on the part of an animal will betray its whereabouts, even though in colouring it assimilates very closely to the environment. So long as the hare squats motionless in the furrow, it may remain unobserved, even though the sportsman be searching for it; but the least movement on its part at once attracts his eye. Thus, in order that protective colouration can be of use to its possessor, the latter must remain perfectly motionless. But, in tropical countries, where flies, gnats, etc., are a perfect scourge, no large animal is, when awake, motionless for ten seconds at a time. The tail is in constant motion, flicking off the flies that attempt to settle on the quadruped. The ears are used in a similar manner. Thus the so-called protective colouring of herbivora cannot afford them much protection. It is further worthy of note that the brush-like tip to the tail of many mammals is not of the same colour as the skin or fur. It is very frequently black. Thus we have the spectacle of a protectively coloured creature continually moving, as if to attract attention, almost the only part of its body that is not protectively coloured! [200]

Sexual Dimorphism

Many species of birds display what is known as seasonal dimorphism, still more display sexual dimorphism.

Seasonally dimorphic birds very often assume a bright livery at the breeding season; this nuptial plumage is by no means invariably confined to the cock, so that we are brought face to face with the fact that some hen birds, that are normally inconspicuously coloured, become showy and easy to see at the nesting time, that is to say, precisely at the season when they would seem to be most in need of protection. [201]

In the great majority of cases of sexual dimorphism among birds the cock is the more showily coloured. Now, if it be a matter of life-and-death importance to a bird to be protectively coloured, we should expect the showily coloured cock birds to be far less numerous than the dull-plumaged hens, since the former are, *ex hypothesi*, exposed to far greater danger than the inconspicuous hens. As a matter of fact, cock birds in practically all species appear to be at least as numerous as the hens. Nor can it be said that this is due to their more secretive habits. As a general rule, cock birds show themselves as readily as the hens; indeed, in the case of the familiar blackbird, the conspicuous cock is less retiring in his habits than the more sombre hen. It may, perhaps, be thought that the greater danger to which the sitting bird is exposed accounts for the fact that hens, notwithstanding their protective colouration, are not more numerous than the cocks. Unfortunately for the supposition, in many sexually dimorphic hens, as, for example, the paradise fly-catcher (*Terpsiphone paradisi*), the showy cock shares the burden of incubation equally with the hen. [202]

It frequently happens that allied species of birds are found in neighbouring countries. The Indian robins, for example, fall into two species. The brown-backed robin (*Thamnobia cambayensis*) occurs north of Bombay, while the black-backed species (*T. fulicata*) is found south of Bombay. The hens of these two species are almost indistinguishable, but the cocks differ, in that one has a brown back, while the other's back is glossy black. The Wallaceian theory of

colouration seems quite unable to explain this phenomenon—the splitting up of a genus into local species—which is continually met with in nature. Equally inimical to the theory of protective colouration is the existence, side by side, of species which obtain their living in much the same manner. On every Indian lake three different species of kingfisher pursue their profession cheek by jowl; one of these—*Ceryle rudis*—is speckled black and white, like a Hamburg fowl; the second is the kingfisher we know in England; and the third is the magnificent white-breasted species—*Halcyon smyrnensis*—a bright-blue bird with a reddish head and a white wing bar. It is obvious that all three of these diversely plumaged species cannot be protectively coloured. It may perhaps be objected that the piscatorial methods of these kingfishers differ in detail. We admit that this is the case, but would maintain, at the same time, that these comparatively slight differences in habit do not account for the very striking differences in plumage. We may also cite the yellow and pied wagtails of our own country, which may be seen feeding in the same meadows. Most familiar and striking of all is the everyday sight of a blackbird and thrush plying their respective avocations within a few yards of each other on the same lawn, differently coloured though they be. [203]

Another weighty objection to the generally accepted theory of protective colouration is that some of the creatures which assimilate most closely to their environment are those which appear to be the least in need of such protection.

Precis Artexia

The butterfly *Precis artexia*, writes F. C. Selous, “is only found in shady forests, is seldom seen flying until disturbed, and always sits on the ground amongst dead leaves. Though handsomely coloured on the upper side, when its wings are closed it closely resembles a dead leaf. It has a little tail on the lower wing, which looks exactly like the stalk of a leaf, and from this tail a dark-brown line runs through both wings (which on the under side are light brown) to the apex of the upper wing. One would naturally be inclined to look upon this wonderful resemblance to a dead leaf in a butterfly sitting with closed wings on the ground amongst real dead leaves as a remarkable instance of protective form and colouration. And of course it may be that this is the correct explanation. But what enemy is this butterfly protected against? Upon hundreds of different occasions I have ridden and walked through forests where *Precis artexia* was numerous, and I have caught and preserved many specimens of these butterflies, but never once did I see a bird attempting to catch one of them. Indeed, birds of all kinds were scarce in the forests where these insects were to be found.” [204]

Similarly D. Dewar writes (*Albany Review*, 1907): “If a naturalist be asked to cite a perfect example of protective colouring, he will, as likely as not, name the sand grouse (*Pteroclorus exustus*). This species dwells in open, dry, sandy country, and its dull brownish-buff plumage, with its soft dark bars, assimilates so closely to the sandy environment as to make the bird, when at rest, practically invisible, at any rate to the human eye. Unfortunately for the theory, this bird stands less in need of protective colouration than any other, for it has wonderful powers of flight. Even a trained falcon is unable to catch it, because it can fly upwards in a straight line as though it were ascending an inclined plane, with the result that the pursuing hawk is never able to get above it to strike.”

[205]

Striped Caterpillars

Lord Avebury, who is a typical Wallaceian, points out the connection that exists between longitudinal stripes on caterpillars and the habit of feeding either on grass or low-growing plants among grass. The inference, of course, is that birds mistake these caterpillars for leaves, or, at any rate, fail to observe them when feeding, not only because they are green in colour, but because their longitudinal stripes look like the parallel veins on the blades of grass. But the butterflies of the family *Satyridae*, as Beddard points out, *all* possess striped larvæ, and these feed chiefly by night, when neither their colouring nor marking is visible, while during the day many of them lie up under stones; other caterpillars of this family feed inside the stems of plants. “Now,” writes Beddard (*Animal Colouration*, p. 101), “in these cases the colour obviously does not matter: if, therefore, the longitudinal striping is kept up by constant selection on account of its utility, and has no other signification, we might expect that in these two species (*Hipparchia semele* and *Enis*), and in others with similar habits, the cessation of natural selection would have permitted the high standard required in the other cases to be lowered—perhaps, even, as has been suggested in the case of cave animals, the colours being useless to their possessors, might have disappeared altogether—but they have not.”

Many exceedingly conspicuous birds—as, for example all the crow-tribe, the egrets, the kingfishers—flourish in spite of their showy plumage. Such creatures, while scarcely constituting a valid objection to the theory of protective colouration, serve to show that protective colouring is not a necessity. An animal otherwise able to take care of itself can afford to dispense with cryptic colouration. “An ounce of good solid pugnacity is a more effective weapon in the struggle for existence than many pounds of protective colouration.” [206]

There used to live in the gardens of the Zoological Society of London a black cat belonging to the manager of one of the restaurants. This animal used to catch birds on the lawn. We believe that not even Mr Thayer will maintain that a black cat is cryptically coloured when stalking on a well-watered lawn! Nevertheless the nigrity of that cat did not prevent it securing a meal.

Colours of Eggs

The case of birds' eggs furnish an excellent example of the lengths to which Wallace and his followers have pushed the theory of protective colouration.

D. Dewar maintains that it is possible to divide birds' eggs that are coloured, as opposed to those that are white, into two classes—those which are protectively coloured and those which are not. The former class includes all those which are laid in shingle or on the bare ground, as, for example, the eggs of the ring-plover and the lap-wing.^[8] [207] He maintains that the variously coloured and speckled eggs that are laid in cup-shaped nests are not protectively coloured at all; he declares that they are usually very conspicuous when in the nest, and, moreover, it would be futile for them to be cryptically coloured, for a bird or lizard that habitually sucks eggs will examine carefully the interior of each nest it discovers.

Needless to say, this view does not appeal to the so-called Neo-Darwinians. Wallace writes, on page 215 of *Darwinism*: “The beautiful blue or greenish eggs of the hedge-sparrow, the song-thrush, the blackbird, and the lesser redpole seem at first sight especially calculated to attract attention, but it is very doubtful whether they are really so conspicuous when seen at a little distance among their usual surroundings. For the nests of these birds are either in evergreen, or holly, or ivy, or surrounded by the delicate green tints of early spring vegetation, and may thus harmonise very well with the colours around them. The great majority of the eggs of our smaller birds are so spotted or streaked with brown or black on variously tinted grounds that, when lying in the shadow of the nest and surrounded by the many [208] colours and tints of bark and moss, of purple buds and tender green or yellow foliage, with all the complex glittering lights and mottled shades produced among these by the spring sunshine and sparkling rain-drops, they must have quite a different aspect from that which they possess when we observe them torn from their natural surroundings.”

The obvious comment on this is that it is very fine and poetic English, but it is not science. It is futile to deny what should be obvious to every field naturalist, namely, that the majority of eggs laid in open nests are most conspicuous.

D. Dewar thus summarises the main facts which show that eggs in nests (as opposed to those laid on the bare ground) are not protectively coloured:—

- “1. Allied species of birds, even though their nesting habits are very different, as a rule lay similarly coloured eggs.
- “2. Eggs laid in domed nests certainly do not need protective colouring, yet many of these are coloured.
- “3. The same is true of many eggs laid in holes in trees or in buildings.
- “4. The protective resemblances of eggs which are laid in the open are apparent to everyone, which certainly is not true of those deposited in nests.
- “5. Many birds lay eggs which exhibit very great variations. [209]
- “6. Some birds lay eggs of different types, and these sometimes differ from one another so greatly that it is difficult to believe that they could have been laid by the same species.”^[9]
7. It not infrequently happens that one species lays in the disused nest of another, and the eggs of the latter are often very different in colouring from those of the former.

We have up to the present considered the theory of general cryptic colouration, which declares that the majority of creatures are so coloured as to be inconspicuous. We have still to deal with the hypothesis of special cryptic colouring.

Certain animals look, when resting, very like an inanimate object, such as a dead leaf or a twig. This resemblance is said to be the result of natural selection, since it enables its possessors to escape destruction; they are seen, but mistaken for something else.

The classical examples of this kind of protective colouring are furnished by the *Kallimas* or leaf-butterflies, which display an extraordinary resemblance to dead leaves.

Other examples are the stick-insects and the lappet moth, which looks like a bunch of dry leaves. It is needless to multiply instances. In every work on animal colouration numbers of such cases are cited. [210]

We may grant that in some cases, at any rate, the resemblance is of value to its possessor, in that it deceives predatory creatures. But it does not follow from this that the likeness has originated through the action of natural selection. In order that there can be selection there must be varying degrees of a tolerable resemblance to select from. How did the initial similarity arise? This is a matter upon which Wallaceians are silent. As Poulton truly says, in discussing the degree of protection afforded by such resemblances, we tacitly endow animals with senses exactly similar to our own. Are we justified in so doing? Most certainly not in the case of the invertebrate animals, especially as regards the arthropods, of which the eyes are constructed very differently from those of human beings.

D. Dewar has often seen a toad shoot out its tongue and touch a lighted cigarette end, apparently mistaking it for an insect. Similarly, he has again and again induced a gecko lizard to chase and try to swallow a piece of black cotton, one end of which was rolled up into a ball. It is only necessary to take hold of the unrolled end of the cotton and place the rolled-up end a few inches from the lizard, and gradually draw it away in order to induce the lizard to attempt to seize it.

[211]

Eyesight of Birds

It would therefore seem that all these elaborate “protective” devices are unnecessary refinements if regarded as a protection against invertebrate, reptilian, and amphibian foes. Birds, on the other hand, appear to have exceedingly sharp eyesight, so that in order to deceive them the resemblance requires to be very close. Indeed, as regards those birds which systematically hunt for their prey among leaves and grass, it seems doubtful whether the alleged “protective” resemblances of caterpillars to twigs, etc., are sufficient to be of much use to them. Thus Beddard writes (on page 91 of *Animal Colouration*): “Judging of birds by our own standard—which is the way in which nearly all the problems relating to colour have been approached—does it seem likely that we should fail to see a caterpillar, perhaps as long or longer than the arm, of an obviously different texture from the branches, and displaying in many cases through its semi-transparent skin the pulsation of the heart, for which we were particularly searching?”

Now, birds certainly feed very largely on caterpillars, while they are but rarely seen to eat butterflies. If, therefore, the aim and object of these special resemblances is the protection of the species, we should expect to see them in a nearly perfect state in caterpillars on which birds feed very largely, and poorly developed in butterflies, which do not appear to be greatly preyed upon by birds, but have to fear chiefly the comparatively dull-eyed lizards and mammals, of [212] which the latter hunt mainly by scent. As a matter of fact, the most striking cases of resemblance to inanimate objects are seen among butterflies, which seem to stand least in need of them.

We have already cited the case of the butterfly *Precis artexia*. Even more marked does the unnecessary elaboration of the likeness seem to be in the Kallima butterflies.

THE THEORY OF WARNING COLOURATION

All biologists admit that there exist some organisms which are not coloured so as to be inconspicuous. Indeed, the colouring of certain species is such as to render them particularly conspicuous. Such species are said to be warningly coloured. They are supposed to be inedible, or to have powerful stings or other weapons of defence, or to resemble in appearance organisms which are thus protected. In the first two cases they are said to be warningly coloured, and in the last they are cited as examples of protective mimicry. With the theory of mimicry we shall deal shortly. We must first discuss the hypothesis of warning colouration.

When animals are unpalatable, or when they possess a sting or poison-fangs, it is, to use the words of Wallace, [213] “important that they should not be mistaken for defenceless or eatable species of the same class or order, since in that case they might suffer injury, or even death, before their enemies discovered the danger or the uselessness of the attack. They require some signal or danger-flag which shall serve as a warning to would-be enemies not to attack them, and they have usually obtained this in the form of conspicuous or brilliant colouration, very distinct from the protective tints of the defenceless animals allied to them” (*Darwinism*, page 232).

Examples of Warning Colouration

For examples of so-called warningly coloured animals, we may refer the reader to Wallace's *Darwinism*, Poulton's *Essays on Evolution*, or Beddard's *Animal Colouration*. An instance familiar to all is our English ladybird. "Ladybirds," says Wallace, "are another uneatable group, and their conspicuous and singularly spotted bodies serve to distinguish them at a glance from all other beetles."

In order to establish the theory of warning colouration, it is necessary to prove that all, or the great majority of conspicuously-coloured organisms, are either unpalatable or mimic unpalatable forms. If this be so, we are able to understand that the possession of gaudy colouring may be of advantage to the individual. But even if this be satisfactorily proved, we must bear in mind that it does not necessarily follow that these warning colours can be accounted for on the theory of natural selection. For, in order to explain the existence of any organ by the action of natural selection, we must be able to demonstrate the utility, not only of the perfected organ, but of the organ at its very beginning, and at each subsequent stage of development. This, as we shall show, is precisely what the Neo-Darwinians are unable to do. We shall have no difficulty in proving that it would be more advantageous even to a highly nauseous creature to have remained inconspicuously coloured rather than to have gradually become more and more conspicuous. [214]

In the first place, let us briefly examine the evidence on which rests the assertion that all gaudily-coloured insects, etc., are unpalatable, or possess stings, or mimic forms which are thus armed.

In England wasps, bees, and ladybirds are familiar examples of conspicuous insects.

The banded black and yellow pattern of the common wasp and the humble bee are regarded as advertisements or danger signals of the powerful sting.

The red-coat with its black spots is similarly believed to be a warning that the ladybird is not fit to be eaten.

Caterpillars are usually coloured grey or brown, so as to be inconspicuous; but numerous exceptions occur which are brightly coloured, and of these individuals many have been experimentally proved to be objectionable as food to most insect-eating animals, being either protected by an unpleasant taste, or covered with hairs or spines. [215]

Familiar cases are those of the abundant and conspicuous black and yellow mottled caterpillars of the European Buff-tip Moth (*Pygæra bucephala*), which are much disliked by birds; and the gaily—coloured Vapourer Moth caterpillar (*Orgyia antiqua*), with its conspicuous tufts of hair. Readers will remember that a few years back these caterpillars were a perfect plague in London, in spite of the abundance of sparrows, which feed freely on smooth green and brown caterpillars.

Oft-cited examples of warning colouration, are the three great groups of mainly tropical butterflies—the *Heliconidæ* of America, the *Acræidæ* of Africa, and the *Danainæ* found all over the world. In all of these the sexes are alike. They are, every one, strikingly coloured, displaying patterns of black and red, chestnut, yellow, or white. In most butterflies the lower surface of the wings is of a quiet hue, in order to render the organism inconspicuous when at rest, but in these warningly coloured groups the under surface of the wings is as gaudy as the upper surface. Their flight is slow. They are tough, and exhale a characteristic odour. [216]

Belt showed that, in Nicaragua, birds, dragonflies, and lizards seem to avoid the Heliconine butterflies, as the wings of these last are not found lying about in places where insectivorous creatures feed, whereas wings of the edible forms are to be found. Moreover, a Capuchin monkey, kept by Belt, always refused to eat Heliconine butterflies.

Finn investigated the palatability of a number of Indian insects. He found that most of the birds with which he experimented objected to the Danaine butterflies; but they disliked still more intensely two butterflies belonging to groups not universally protected—a swallowtail (*Papilio aristolochiæ*) and a white (*Delias eucharis*).

Finn further experimented with the tree-shrew or Tupaia (*Tupaia ellioti*), which feeds largely on insects. He found that this creature refused most emphatically all these warningly-coloured butterflies. It would under no circumstances eat the *Danainæ*, whereas the birds would do so if no more palatable insects were offered to them at the time.

Colonel A. Alcock found that a tame Himalayan bear indignantly refused to eat a locust (*Aularches militaris*) gaily coloured with black, red, and yellow, and exhaling an unpleasant-smelling froth; but this bear readily devoured ordinary brown or green species. [217]

Among cold-blooded vertebrates the common European salamander, with its bright black and yellow markings, is a striking example of warning colouration; its skin exudes, on pressure, a very poisonous secretion.

Colonel A. Alcock has described a small siluroid sea-fish, brightly banded with black and yellow, and armed with poison spines.

A well-known Indian poisonous snake, the banded Krait (*Bungarus cœruleus*), is conspicuously barred with wide bands of black and yellow; and in South America there occur numerous species of coral snakes, in which red is added to these conspicuous colours.

The only known poisonous lizard—the Heloderm of Mexico—is conspicuously blotched with black and salmon-colour.

Among birds, no instances of warning colouration have been recorded, though Professor Poulton has suggested that possibly the striking and contrasted tints of many tropical species may be due to this cause. The suggestion is an ingenious one, but is at present totally unsupported by evidence.

The skunks are often cited as an excellent example of warning colouration among mammals. Skunks are most conspicuously arrayed in black and white—the latter above, not below, as is usual—and have bushy tails, which they carry erect. Although less powerful and ferocious than other members of the weasel family, to which they belong, skunks are notoriously protected by their abundant secretion of a very fetid liquid. [218]

For further examples of warning colouration we would refer the reader to Beddard's illuminating book, entitled *Animal Colouration*.

It should be noticed that in all the cases which we have cited the colouration is not only conspicuous, but is found in both sexes, whereas in many undefended animals the male may be just as strikingly coloured, but the female is not.

We may take it as proved that there is a very general relation between gaudy colouring and inedibility, or rather unpalatability, among insects. It may safely be said that any species of insect which lives, either as an adult or as a larva, in the open will perish in the struggle for existence if, being conspicuously coloured, it is neither inedible nor armed with a weapon such as sting, nor provided with a thick cuticle, nor resembles in appearance some creature which is protected.

Warning Colouring a Drawback

But from this it is not legitimate to conclude, as Neo-Darwinians do, that these brilliant colours have been slowly brought into being by natural selection.

Why should any creature, having by the "luck" of variation and heredity acquired some quality—be it strength, pugnacity, sting, or unpleasant taste—which renders it comparatively immune from persecution, proceed to advertise the fact by assuming a gaudy or striking colour? It would surely be better for such an organism to remain inconspicuous. By becoming showy it is visible to every young bird who, not having yet learned that the creature in question is unfit for food, seizes and perhaps kills it. It is true that the young bird vows that never again will it touch another such organism. But of what avail to the dying example of warning colouration is the resolution of the young bird? Moreover, the organism in question, by being conspicuous, also advertises itself to those few enemies which will eat it. There are always, as Professor Poulton justly remarks, animals which are enterprising enough to take advantage of prey which has at least the advantage of being easily seen and caught. [219]

Conspicuous Animals