THE COLOURS OF ANIMALS AND PLANTS.

I.—THE COLOURS OF ANIMALS.

THERE is probably no one quality of natural objects, from which we derive so much pure and intellectual enjoyment as from their colours. The "heavenly" blue of the firmament, the glowing tints of sunset, the exquisite purity of the snowy mountains, and the endless shades of green presented by the verdure-clad surface of the earth, are a never-failing source of pleasure to all who enjoy the inestimable gift of sight. Yet these constitute, as it were, but the frame and background of a marvellous and ever-changing picture. In contrast with these broad and soothing tints, we have presented to us in the vegetable and animal worlds, an infinite variety of objects adorned with the most beautiful and most varied hues. Flowers, insects, and birds, are the organisms most generally ornamented in this way; and their symmetry of form, their variety of structure, and the lavish abundance with which they clothe and enliven the earth, cause them to be objects of universal admiration. The relation of this wealth of colour to our mental and moral nature is indisputable. The child and the savage alike admire the gay tints of flower, bird, and insect; while to many of us their contemplation brings a solace and enjoyment which is both intellectually and morally beneficial. It can then hardly excite surprise that this relation was long thought to afford a sufficient explanation of the phenomena of colour in nature; and although the fact that—

> "Full many a flower is born to blush unseen,
> And waste its sweetness on the desert air—"

might seem to throw some doubt on the sufficiency of the explanation, the answer was easy,—that in the progress of discovery, man would, sooner or later, find out and enjoy every beauty that the hidden recesses of the earth have in store for him. This theory received great support, from the difficulty of conceiving any other use or meaning in the colours with which so many natural objects are adorned. Why should the homely gorse be clothed in golden raiment, and the prickly cactus be adorned with crimson bells? Why should our fields be gay with buttercups, and the heather-clad mountains be clad in purple robes? Why should every land produce its own peculiar floral gems, and the alpine rocks glow with beauty, if not for the contemplation and enjoyment of man? What could be the use to the butterfly of its gaily-painted wings, or to the humming bird of its jewelled breast, except to add the final touches to a world-picture, calculated at once to please and to refine mankind? And even now, with all our recently acquired knowledge of this subject, who shall say that these old-world views were not intrinsically and fundamentally sound; and that, although we now know that colour has "uses" in nature that we little dreamt of, yet the relation of those colours to our senses and emotions may be another, and perhaps more important use which they subserve in the great system of the universe?

We now propose to lay before our readers a general account of the more recent discoveries on this interesting subject; and in doing so, it will be necessary first to give an outline of the more important facts as to the colours of organised beings; then to point out the cases in which it has been shown that colour is of use; and lastly, to endeavour to throw some light on its nature, and the general laws of its development.

Among naturalists, colour was long thought to be of little import, and to be quite untrustworthy as a specific character. The numerous cases of variability of colour led to this view. The occurrence of white blackbirds, white peacocks, and black leopards; of white blue-bells, and of white, blue, or pink milkworts, led to the belief that colour was essentially unstable, that it could therefore be of little or no importance, and belonged to quite a different class of characters from form or structure. But it now begins to be perceived that these cases, though tolerably numerous, are, after all, exceptional; and that colour, as a rule, is a constant character. The great majority of species, both of animals and plants, are each distinguished by peculiar tints which vary very little, while the minutest markings are often constant in thousands or millions of individuals. All our field buttercups are invariably yellow, and our poppies red, while many of our butterflies and birds resemble each other in every spot and streak of colour through thousands of individuals. We also find that colour is constant in whole genera and other groups of species. The Genistas are all yellow, the Erythrinas all red, many genera of Carabidæ are entirely black, whole families of birds—as the Dendrocolaptidæ—are brown, while among butterflies the numerous species of Lycæna are all more or less blue, those of Pontia white, and those of Callidryas yellow. An extensive survey of the organic world thus leads us to the conclusion that colour is by no means so unimportant or inconstant a character as at first sight it appears to be; and the more we examine it the more convinced we shall become that it must serve some purpose in nature, and that besides charming us by its diversity and beauty it must be well worthy of our attentive study, and have many secrets to unfold to us.

In order to group the great variety of facts relating to the colours of the organic world in some intelligible way, it will be best to consider how far the chief theories already proposed will account for them. One of the most obvious and most popular of these theories, and one which is still held, in part at least, by many eminent naturalists, is, that colour is due to some direct action of the heat and light of the sun, thus at once accounting for the great number of brilliant birds, insects, and flowers, which are found between the tropics. But here we must ask whether it is really the fact that colour is more developed in tropical than in temperate climates, in proportion to the whole number of species; and even if we find this to be so, we have to inquire whether there are not so many and such striking exceptions to the rule, as to indicate some other causes at work than the direct influence of solar light and heat. As this is a most important question, we must go into it somewhat fully.

It is undoubtedly the case that there are an immensely greater number of richly-coloured birds and insects in tropical than in temperate and cold countries; but it is by no means so certain that the *proportion* of coloured to obscure species is much or any greater. Naturalists and collectors well know that the majority of tropical birds are dull-coloured; and there are whole families, comprising hundreds of species, not one of which exhibits a particle of bright colour. Such are the Timaliidæ of the Eastern and the Dendrocolaptidæ of the Western hemispheres. Again, many groups of birds, which are universally distributed, are no more adorned with colour in the tropical than in the temperate zone; such are Thrushes, Wrens, Goatsuckers, Hawks, Grouse, Plovers, and Snipe; and if tropical light and heat have any direct colouring effect, it is certainly most extraordinary that in groups so varied in form, structure, and habits as those just mentioned, the tropical should be in no wise distinguished in this respect from the temperate species. The brilliant tropical birds mostly belong to groups which are wholly or almost wholly tropical—as the chatterers, toucans, trogons, and pittas; but as there are perhaps an equal number of groups which are wholly dull-coloured, while others contain dull and bright-coloured species in nearly equal proportions, the evidence is by no means strong that tropical light or heat has anything to do with the matter. But there are also groups in which the cold and temperate zones produce finer-coloured species than the tropics. Thus the arctic ducks and divers are handsomer than those of the tropical zone, while the King-duck of temperate America and the Mandarin-duck of N. China are the most beautifully coloured of the whole family. In the pheasant family we have the gorgeous gold and silver pheasants in N. China and Mongolia; and the superb Impeyan pheasant in the temperate N. W. Himalayas, as against the peacocks and fire-backed pheasants of tropical Asia. Then we have the curious fact that most of the bright-coloured birds of the tropics are denizens of the forests, where they are shaded from the direct light of the sun, and that they abound near the equator where cloudy skies are very prevalent; while, on the other hand, places where light and heat are at a maximum have often dull-coloured birds. Such are the Sahara and other deserts where almost all the living things are sand-coloured; but the most curious case is that of the Galapagos islands, situated under the equator, and not far from South America where the most gorgeous colours abound, but which are yet characterised by prevailing dull and sombre tints in birds, insects, and flowers, so that they reminded Mr. Darwin of the cold and barren plains of Patagonia. Insects are wonderfully brilliant in tropical countries generally, and any one looking over a collection of South American or Malayan butterflies would scout the idea of their being no more gaily-coloured than the average of European species, and in this they would be undoubtedly right. But on examination we should find that all the more brilliantly-coloured groups were exclusively tropical, and that, where a genus has a wide range, there is little difference in coloration between the species of cold and warm countries. Thus the European Vanessides, including the beautiful "peacock," "Camberwell beauty," and "red admiral" butterflies, are quite up to the average of tropical beauty in the same group, and the remark will equally apply to the little "blues" and "coppers;" while the alpine "apollo" butterflies have a delicate beauty that can hardly be surpassed. In other insects, which are less directly dependent on climate and vegetation, we find even greater anomalies. In the immense family of the Carabidæ or predaceous ground-beetles, the northern forms fully equal, if they do not surpass, all that the tropics can produce. Everywhere, too, in hot countries, there are thousands of obscure species of insects which, if they were all collected, would not improbably bring down the average of colour to much about the same level as that of temperate zones.

But it is when we come to the vegetable world that the greatest misconception on this subject prevails. In abundance and variety of floral colour the tropics are almost universally believed to be pre-eminent, not only absolutely, but relatively to the whole mass of vegetation and the total number of species. Twelve years of observation among the vegetation of the eastern and western tropics has, however, convinced me that this notion is entirely erroneous, and that, in proportion to the whole number of species of plants, those having gaily-coloured flowers are actually more abundant in the temperate zones than between the tropics. This will be found to be not so extravagant an assertion as it may at first appear, if we consider how many of the choicest adornments of our greenhouses and flower-shows are really temperate as opposed to tropical plants. The masses of colour produced by our Rhododendrons, Azaleas, and Camellias, our Pelargoniums, Calceolarias, and Cinerarias,—all strictly temperate plants—can certainly not be surpassed, if they can be equalled, by any productions of the tropics.[1] But we may go further, and say that the hardy plants of our cold temperate zone equal, if they do not surpass, the productions of the tropics. Let us only remember such gorgeous tribes of flowers as the Roses, Peonies, Hollyhocks, and Antirrhinums, the Laburnum, Wistaria, and Lilac; the Lilies, Irises, and Tulips, the Hyacinths, Anemones, Gentians, and Poppies, and even our humble Gorse, Broom, and Heather; and we may defy any tropical country to produce masses of floral colour in greater abundance and variety. It may be true that individual tropical shrubs and flowers do surpass everything in the rest of the world, but that is to be expected, because the tropical zone comprises a much greater land-area than the two temperate zones, while, owing to its more favourable climate, it produces a still larger proportion of species of plants, and a great number of peculiar natural orders.

Direct observation in tropical forests, plains, and mountains, fully supports this view. Occasionally we are startled by some gorgeous mass of colour, but as a rule we gaze upon an endless expanse of green foliage, only here and there enlivened by not very conspicuous flowers. Even the orchids, whose gorgeous blossoms adorn our stoves, form no exception to this rule. It is only in favoured spots that we find them in abundance; the species with small and inconspicuous flowers greatly preponderate; and the flowering season of each kind being of short duration, they rarely produce any marked effect of colour amid the vast masses of foliage which surround them. An experienced collector in the Eastern tropics once told me, that although a single mountain in Java had produced three hundred species of Orchideæ, only about 2 per cent. of the whole were sufficiently ornamental or showy to be worth sending home as a commercial speculation. The alpine meadows and rock-slopes, the open plains of the Cape of Good Hope or of Australia, and the flower-prairies of North America, offer an amount and variety of floral colour which can certainly not be surpassed, even if it can be equalled, between the tropics.

It appears, therefore, that we may dismiss the theory that the development of colour in nature is directly dependent on, and in any way proportioned to the amount of solar heat and light, as entirely unsupported by facts. Strange to say, however, there are some rare and little-known phenomena, which prove that, in exceptional cases, light does directly affect the colours of natural objects, and it will be as well to consider these before passing on to other matters.

A few years ago Mr. T. W. Wood called attention to the curious changes in the colour of the chrysalis of the small cabbage butterfly (*Pontia rapæ*) when the caterpillars were confined

[1] It may be objected that most of the plants named are choice cultivated *varieties*, far surpassing in colour the original stock, while the tropical plants are mostly unvaried wild *species*. But this does not really much affect the question at issue. For our florists' gorgeous varieties have all been produced under the influence of our cloudy skies, and with even a still further deficiency of light, owing to the necessity of protecting them under glass from our sudden changes of temperature; so that they are themselves an additional proof that tropical light and heat are not needed for the production of intense and varied colour. Another important consideration is, that these cultivated *varieties* in many cases displace a number of wild *species* which are hardly, if at all, cultivated. Thus there are scores of *species* of wild hollyhocks varying in colour almost as much as the cultivated varieties, and the same may be said of the pentstemons, rhododendrons, and many other flowers; and if these were all brought together in well-grown specimens, they would produce a grand effect. But it is far easier, and more profitable, for our nurserymen to grow *varieties* of one or two species, which all require a very similar culture, rather than fifty distinct *species*, most of which would require special treatment; the result being that the varied beauty of the temperate flora is even now hardly known, except to botanists and to a few amateurs.

in boxes lined with different tints. Thus in black boxes they were very dark, in white boxes nearly white; and he further showed that similar changes occurred in a state of nature, chrysalises fixed against a white-washed wall being nearly white, against a red brick wall reddish, against a pitched paling nearly black. It has also been observed that the cocoon of the emperor moth is either white or brown, according to the surrounding colours. But the most extraordinary example of this kind of change is that furnished by the chrysalis of an African butterfly (*Papilio Nireus*), observed at the Cape by Mrs. Barber, and described (with a coloured plate) in the *Transactions of the Entomological Society*, 1874, p. 519. The caterpillar feeds on the orange tree, and also on a forest tree (*Vepris lanceolata*) which has a lighter green leaf, and its colour corresponds with that of the leaves it feeds upon, being of a darker green when it feeds on the orange. The chrysalis is usually found suspended among the leafy twigs of its food-plant, or of some neighbouring tree; but it is probably often attached to larger branches, and Mrs. Barber has discovered that it has the property of acquiring the colour, more or less accurately, of any natural object it may be in contact with. A number of the caterpillars were placed in a case with a glass cover, one side of the case being formed by a red brick wall, the other sides being of yellowish wood. They were fed on orange leaves, and a branch of the bottle-brush tree (*Banksia, sp.*) was also placed in the case. When fully fed, some attached themselves to the orange twigs, others to the bottle-brush branch; and these all changed to green pupæ; but each corresponded exactly in tint to the leaves around it, the one being dark the other a pale faded green. Another attached itself to the wood, and the pupa became of the same yellowish colour; while one fixed itself just where the wood and brick joined, and became one side red, the other side yellow! These remarkable changes would perhaps not have been credited, had it not been for the previous observations of Mr. Wood; but the two support each other, and oblige us to accept them as actual phenomena. It is a kind of natural photography, the particular coloured rays to which the fresh pupa is exposed in its soft, semi-transparent condition, effecting such a chemical change in the organic juices as to produce the same tint in the hardened skin. It is interesting, however, to note that the range of colour that can be acquired seems to be limited to those of natural objects to which the pupa is likely to be attached; for when Mrs. Barber surrounded one of the caterpillars with a piece of scarlet cloth no change of colour at all was produced, the pupa being of the usual green tint, but the small red spots with which it is marked were brighter than usual.

In these caterpillars and pupæ, as well as in the great majority of cases in which a change of colour occurs in animals, the action is quite involuntary; but among some of the higher animals the colour of the integument can be modified at the will of the animal, or at all events by a reflex action dependent on sensation. The most remarkable case of this kind occurs with the Chameleon, which has the power of changing its colour from dull white to a variety of tints. This singular power has been traced to two layers of pigment deeply seated in the skin, from which minute tubes, or capillary vessels, rise to the surface. The pigment-layers are bluish and yellowish, and by the pressure of suitable muscles these can be forced upwards either together or separately. When no pressure is exerted the colour is dirty white, which changes to various tints of bluish, green, yellow, or brown, as more or less of either pigment is forced up and rendered visible. The animal is excessively sluggish and defenceless, and its power of changing its colour to harmonise with surrounding objects is essential to its existence.

Here too, as with the pupa of *Papilio Nireus*, colours such as scarlet or blue, which do not occur in the immediate environment of the animal, cannot be produced. Somewhat similar changes of colour occur in some prawns and flat-fish, according to the colour of the bottom on which they rest. This is very striking in the Chameleon Shrimp (*Mysis Chamæleon*), which is grey when on sand, but brown or green when among sea-weed of these two colours. Experiment shows, however, that when blinded the change does not occur, so that here too we probably have a voluntary or reflex sense action. Many cases are known among insects in which the same species has a different tint according to its surroundings, this being particularly marked in some South African locusts which correspond with the colour of the soil wherever they are found; while several caterpillars which feed on two or more plants vary in colour accordingly. Several such changes are quoted by Mr. R. Meldola, in a paper on Variable Protective Colouring in Insects (*Proceedings of the Zoological Society of London*, 1873, p. 153), and some of them may perhaps be due to a photographic action of the reflected light. In other cases, however, it has been shown that green chlorophyll remains unchanged in the tissues of leaf-eating insects, and being discernible through the transparent integument produces the same colour as that of the food plant.

These peculiar powers of change of colour and adaptation, are however rare and quite exceptional. As a rule there is no direct connection between the colours of organisms and the kind of light to which they are usually exposed. This is well seen in most fishes, and in such marine animals as porpoises, whose backs are always dark, although this part is exposed to the blue and white light of the sky and clouds, while their bellies are very generally white, although these are constantly subjected to the deep blue or dusky green light from the bottom. It is evident, however, that these two tints have been acquired for concealment and protection. Looking *down* on the dark back of a fish it is almost invisible, while to an enemy looking *up* from below the light undersurface would be equally invisible against the light of the clouds and sky. Again, the gorgeous colours of the butterflies which inhabit the depths of tropical forests bear no relation to the kind of light that falls upon them, coming as it does almost wholly from green foliage, dark brown soil, or blue sky; and the bright underwings of many moths which are only exposed at night, contrast remarkably with the sombre tints of the upper wings which are more or less exposed to the various colours of surrounding nature.

We find, then, that neither the general influence of solar light and heat, nor the special action of variously tinted rays, are adequate causes for the wonderful variety, intensity, and complexity, of the colours that everywhere meet us in the animal and vegetable world. Let us therefore take a wider view of these colours, grouping them into classes determined by what we know of their actual uses or special relations to the habits of their possessors. This, which may be termed the functional or biological classification of the colours of living organisms, seems to be best expressed by a division into five groups as follows:—

Animals	1. Protective colours.	
	2. Warning colours.	*a.* Of creatures specially protected.
		b. Of defenceless creatures, mimicking *a.*
	3. Sexual colours.	
	4. Typical colours.	
Plants .	5. Attractive colours.	

The nature of the two first groups, Protective and Warning colours, has been so fully detailed and illustrated in my chapter on "Mimicry and other Protective Resemblances among Animals," (*Contributions to the Theory of Natural Selection*, p. 45), that very little need be added here except a few words of general explanation. Protective colours are exceedingly prevalent in nature, comprising those of all the white arctic animals, the sandy-coloured desert forms, and the green birds and insects of tropical forests. It also comprises thousands of cases of special resemblance—of birds to the surroundings of their nests, and especially of insects to the bark, leaves, flowers, or soil, on or amid which they dwell. Mammalia, fishes, and reptiles, as well as mollusca and other marine invertebrates, present similar phenomena; and the more the habits of animals are investigated, the more numerous are found to be the cases in which their colours tend to conceal them, either from their enemies or from the creatures they prey upon. One of the last-observed and most curious of these protective resemblances has been communicated to me by Sir Charles Dilke. He was shown in Java a pink-coloured *Mantis*, which, when at rest, exactly resembled a pink orchis-flower. The Mantis is a carnivorous insect which lies in wait for its prey, and by its resemblance to a flower the insects it feeds on would be actually attracted towards it. This one is said to feed especially on butterflies, so that it is really a living trap and forms its own bait! All who have observed animals, and especially insects, in their native haunts and attitudes, can understand how it is that an insect which in a cabinet looks exceedingly conspicuous, may yet, when alive in its peculiar attitude of repose and with its habitual surroundings, be perfectly well concealed. We can hardly ever tell by the mere inspection of an animal, whether its colours are protective or not. No one would imagine the exquisitely beautiful caterpillar of the Emperor-Moth, which is green with pink star-like spots, to be protectively coloured; yet when feeding on the heather it so harmonises with the foliage and flowers as to be almost invisible. Every day fresh cases of protective colouring are being discovered even in our own country, and it is becoming more and more evident that the need of protection has played a very important part in determining the actual coloration of animals.

The second class — the warning colours — are exceedingly interesting, because the object and effect of these is, not to conceal the object, but to make it conspicuous. To these creatures it is *useful* to be seen and recognised, the reason being that they have a means of defence which, if known, will prevent their enemies from attack-them, though it is generally not sufficient to save their lives if they are actually attacked. The best examples of these specially protected creatures consist of two extensive families of butterflies, the Danaidæ and Acræidæ, comprising many hundreds of species inhabiting the tropics of all parts of the world. These insects are generally large, are all conspicuously and often most gorgeously coloured, presenting almost every conceivable tint and pattern; they all fly slowly, and they never attempt to conceal themselves: yet no bird, spider, lizard, or monkey (all of which eat other butterflies) ever touch them. The reason simply is that they are not fit to eat, their juices having a powerful odour and taste that is absolutely disgusting to all these animals. Now, we see the reason of their showy colours and slow flight. It is good for them to be seen and recognised, for then they are never molested; but if they did not differ in form and colouring from other butterflies, or if they flew so quickly that their peculiarities could not be easily noticed, they would be captured, and though not eaten would be maimed or killed. As soon as the cause of the peculiarities of these butterflies was recognised, it was seen that the same explanation applied to many other groups of animals. Thus bees and wasps and other stinging insects are showily and distinctively coloured; many soft and apparently defenceless beetles, and many gay-coloured moths, were found to be as nauseous as the above-named butterflies; other beetles, whose hard and glossy coats of mail render them unpalatable to insect-eating birds, are also sometimes showily coloured; and the same rule was found to apply to caterpillars, all the brown and green (or protectively-coloured species) being greedily eaten by birds, while showy kinds which never hide themselves—like those of the magpie-, mullein-, and burnet-moths—were utterly refused by insectivorous birds, lizards, frogs, and spiders. (*Contributions to Theory of Natural Selection*, p. 117.) Some few analogous examples are found among vertebrate animals. I will only mention here a very interesting case not given in my former work. In his delightful book entitled *The Naturalist in Nicaragua*, Mr. Belt tells us that there is in that country a frog which is very abundant, which hops about in the day-time, which never hides himself, and which is gorgeously coloured with red and blue. Now frogs are usually green, brown, or earth-coloured, feed mostly at night, and are all eaten by snakes and birds. Having full faith in the theory of protective and warning colours, to which he had himself contributed some valuable facts and observations, Mr. Belt felt convinced that this frog must be uneatable. He therefore took one home, and threw it to his ducks and fowls; but all refused to touch it except one young duck, which took the frog in its mouth, but dropped it directly, and went about jerking its head as if trying to get rid of something nasty. Here the uneatableness of the frog was predicted from its colours and habits, and we can have no more convincing proof of the truth of the theory than such previsions.

The universal avoidance by carnivorous animals of all these specially protected groups, which are thus entirely free from the constant persecution suffered by other creatures not so protected, would evidently render it advantageous for any of these latter which were subjected to extreme persecution to be mistaken for the former, and for this purpose it would be necessary that they should have the same colours, form, and habits. Strange to say, wherever there is an extensive group of directly-protected forms (division *a* of animals with warning colours), there are sure to be found a few otherwise defenceless creatures which resemble them externally so as to be mistaken for them, and which thus gain protection as it were on false pretences, (division *b* of animals with warning colours). This is what is called "mimicry," and it has already been very fully treated of by Mr. Bates (its discoverer), by myself, by Mr. Trimen, and others. Here it is only necessary to state that the uneatable Danaidæ and Acræidæ are accompanied by a few species of other groups of butterflies (Leptalidæ, Papilios, Diademas, and Moths) which are all really eatable, but which escape attack by their close resemblance to some species of the uneatable groups found in the same locality. In like manner there are a few eatable beetles which exactly resemble species of uneatable groups, and others which are soft, imitate those which are uneatable through their hardness. For the same reason wasps are imitated by moths, and ants by beetles; and even poisonous snakes are mimicked by harmless snakes, and dangerous hawks by defenceless cuckoos. How these curious imitations nave been brought about, and the laws which govern them, have been discussed in the work already referred to.

The third class—Sexual Colours—comprise all cases in which the colours of the two sexes differ. This difference is very general, and varies greatly in amount, from a slight divergence of tint up to a radical change of coloration. Differences of this kind are found among all classes of animals in which the sexes are separated, but they are much more frequent in some groups than in others. In mammalia, reptiles, and fishes, they are comparatively rare and not great in amount, whereas among birds they are very frequent and very largely developed. So among insects, they are abundant in butterflies, while they are comparatively uncommon in beetles, wasps, and hemiptera.

The phenomena of sexual variations of colour, as well as of colour generally, are wonderfully similar in the two analogous yet totally unrelated groups of birds and butterflies; and as they both offer ample materials, we shall confine our study of the subject chiefly to them. The most common case of difference of colour between the sexes, is for the male to have the same general hue as the females, but deeper and more intensified; as in many thrushes, finches, and hawks; and among butterflies in the majority of our British species. In cases where the male is smaller the intensification of colour is especially well pronounced, as in many of the hawks and falcons, and in most butterflies and moths in which the coloration does not materially differ. In another extensive series we have spots or patches of vivid colour in the male which are represented in the female by far less brilliant tints or are altogether wanting; as exemplified in the gold-crest warbler, the green woodpecker, and most of the orange-tip butterflies (*Anthocharis*). Proceeding with our survey we find greater and greater differences of colour in the sexes, till we arrive at such extreme cases as some of the pheasants, the chatterers, tanagers, and birds-of-paradise, in which the male is adorned with the most gorgeous and vivid colours, while the female is usually dull brown, or olive green, and often shows no approximation whatever to the varied tints of her partner. Similar phenomena occur among butterflies; and in both these classes there are also a considerable number of cases in which both sexes are highly coloured in a different way. Thus many woodpeckers have the head in the male red, in the female yellow; while some parrots have red spots in the male, replaced by blue in the female, as in *Psittacula diopthalma*. In many South American Papilios green spots on the male are represented by red on the female; and in several species of the genus *Epicalia*, orange bands in the male are replaced by blue in the female, a similar change of colour as in the small parrot above referred to. For fuller details of the varieties of sexual coloration we refer our readers to Mr. Darwin's *Descent of Man*, chapters x. to xviii., and to chapters iii. iv. and vii. of my *Contributions to the Theory of Natural Selection*.

The fourth group—of Typically-coloured animals—includes all species which are brilliantly or conspicuously coloured in both sexes, and for whose particular colours we can assign no function or use. It comprises an immense number of showy birds, such as Kingfishers, Barbets, Toucans, Lories, Tits, and Starlings; among insects most of the largest and handsomest butterflies, innumerable bright-coloured beetles, locusts, dragon-flies, and hymenoptera; a few mammalia, as the zebras; a great number of marine fishes; thousands of striped and spotted caterpillars; and abundance of mollusca, star-fish, and other marine animals. Among these we have included some, which like the gaudy caterpillars have warning colours; but as that theory does not explain the particular colours or the varied patterns with which they are adorned, it is best to include them also in this class. It is a suggestive fact, that all the brightly coloured birds mentioned above build in holes or form covered nests, so that the females do not need that protection during the breeding season, which I believe to be one of the chief causes of the dull colour of female birds when their partners are gaily coloured. This subject is fully argued in my *Contributions*, &c., chapter vii.

As the colours of plants and flowers are very different from those of animals both in their distribution and functions, it will be well to treat them separately: we will therefore now consider how the general facts of colour here sketched out can be explained. We have first to inquire what is colour, and how it is produced; what is known of the causes of change of colour; and what theory best accords with the whole assemblage of facts.

The sensation of colour is caused by vibrations or undulations of the etherial medium of different lengths and velocities. The whole body of vibrations caused by the sun is termed radiation, and consists of sets of waves which vary considerably in their dimensions and their rate of vibration, but of which the middle portion only is capable of exciting in us sensations of light and colour. Beginning with the largest and slowest rays or wave-vibrations, we have first those which produce heat-sensations only; as they get smaller and quicker, we perceive a dull red colour; and as the waves increase in rapidity of vibration and diminish in size, we get successively sensations of orange, yellow, green, blue, indigo, and violet, all fading imperceptibly into each other. Then come more invisible rays, of shorter wave-length and quicker vibration, which produce, solely or chiefly, chemical effects. The red rays, which first become visible, have been ascertained to vibrate at the rate of 458 millions of millions of times in a second, the length of each wave being $\frac{1}{36900}$th of an inch; while the violet rays, which last remain visible, vibrate 727 millions of millions of times per second, and have a wave-length of $\frac{1}{64516}$th of an inch Although the waves vibrate at different rates, they are all propagated through the ether with the same velocity (192,000 miles per second), just as different musical sounds, which are produced by waves of *air* of different lengths and rates of vibration, travel at the same rate, so that a tune played several hundred yards off reaches the ear in correct time. There are, therefore, an almost infinite number of different colour-producing vibrations, and these may be combined in an almost infinite variety of ways, so as to excite in us the sensation of all the varied colours and tints we are capable of perceiving. When all the different kinds of rays reach us in the proportion in which they exist in the light of the sun, they produce the sensation of white. If the rays which excite the sensation of any one colour are prevented from reaching us, the remaining rays in combination produce a sensation of colour often very far removed from white. Thus green rays being abstracted leave purple light; blue, orange-red light; violet, yellowish green light, and so on. These pairs are termed complementary colours. And if portions of differently coloured lights are abstracted in various degrees, we have produced all those infinite gradations of colours, and all those varied tints and hues which are of such use to us in distinguishing external objects, and which form one of the great charms of our existence. Primary colours would therefore be as numerous as the different wave-lengths of the visible radiations if we could appreciate all their differences, while secondary or compound colours caused by the simultaneous action of any combination of rays of different wave lengths must be still more numerous. In order to account for the fact that all colours appear to us capable of being produced by combinations of three primary colours—red, green, and violet—it is believed that we have three sets of nerve fibres in the retina, each of which is capable of being excited by all rays, but that one set is excited most by the larger or red waves, another by the medium or green waves, and the third set chiefly by the violet or smallest waves of light; and when all three sets are excited together in proper proportions we see white. This view is supported by the phenomena of colour-blindness, which are explicable on the theory that one of these sets of nerve-fibres (usually that adapted to perceive red) has lost its sensibility, causing all colours to appear as if the red rays were abstracted from them. It is another property of these various radiations, that they are unequally refracted or bent in passing obliquely through transparent bodies, the longer waves being least refracted, the shorter most. Hence it becomes possible to analyse white or any other light into its component rays; a small ray of sunlight, for example, which would produce a round white spot on a wall, if passed through a prism is lengthened out into a band of coloured light exactly corresponding to the colours of the rainbow. Any one colour can thus be isolated and separately examined, and by means of reflecting mirrors the separate colours can be again compounded in various ways, and the resulting colours observed. This band of coloured light is called a *spectrum*, and the instrument by which the *spectra* of various kinds of light are examined is called a *spectroscope*. This branch of the subject has, however, no direct bearing on the mode in which the colours of living things are produced, and it has only been alluded to in order to complete our sketch of the nature of colour.

The colours which we perceive in material substances are produced either by the absorption or by the interference of some of the rays which form white light. Pigmental or absorption-colours are the most frequent, comprising all the opaque tints of flowers and insects, and all the colours of dyes and pigments. They are caused by rays of certain wave-lengths being absorbed, while the remaining rays are reflected and give rise to the sensation of colour. When all the colour-producing rays are reflected in due proportion the colour of the object is white, when all are absorbed the colour is black. If blue rays only are absorbed the resulting colour is orange-red; and generally, whatever colour an object appears to us, it is because the complementary colours are absorbed by it. The reason why rays of only certain refrangibilities are reflected and the rest of the incident light absorbed by each substance, is supposed to depend upon the molecular structure of the body. Chemical action almost always implies change of molecular structure, hence chemical action is the most potent cause of change of colour. Sometimes simple solution in water effects a marvellous change, as in the case of the well-known aniline dyes; the magenta and violet dyes exhibiting, when in the solid form, various shades of golden or bronzy metallic green. Heat again often produces change of colour, and this without effecting any chemical change. Mr. Ackroyd has recently investigated this subject,[1] and has shown that a large number of bodies are changed by heat, returning to their normal colour when cooled, and that this change is almost always in the direction of the less refrangible rays or longer wave-lengths; and he connects the change with molecular expansion caused by heat. As examples may be mentioned mercuric-oxide, which is orange-yellow, but which changes to orange, red, and brown when heated; chromic-oxide, which is green, and changes to yellow; cinnabar, which is scarlet, and changes to puce; and metaborate of copper, which is blue, and changes to green and greenish yellow. The colouring matters of animals are very varied. Copper has been found in the red of the wing of the turaco, and Mr. Sorby has detected no less than seven distinct colouring matters in birds' eggs, several of which are chemically related to those of blood and bile. The same colours are often produced by quite different substances in different groups, as shown by the red of the wings of the burnet-moth changing to yellow with muriatic acid, while the red of the red-admiral-butterfly undergoes no such change.

These pigmental colours have a different character in animals according to their position in the integument. Following Dr. Hagen's classification, epidermal colours are those which exist in the external chitinised skin of insects, in the hairs of mammals, and, partially,

1 "Metachromatism, or Colour-Change," *Chemical News*, August, 1876.

in the feathers of birds. They are often very deep and rich, and do not fade after death. The hypodermal colours are those which are situated in the inferior soft layer of the skin. These are often of lighter and more vivid tints, and usually fade after death. Many of the reds and yellows of butterflies and birds belong to this class, as well as the intensely vivid hues of the naked skin about the heads of many birds. These colours sometimes exude through the pores, forming an evanescent bloom on the surface.

Interference colours are less frequent in the organic world. They are caused in two ways: either by reflection from the two surfaces of transparent films, as seen in the soap-bubble and in thin films of oil on water; or by fine striæ which produce colours either by reflected or transmitted light, as seen in mother-of-pearl and in finely-ruled metallic surfaces. In both cases colour is produced by light of one wave-length being neutralised, owing to one set of such waves being caused to be half a wave length behind the other set, as may be found explained in any treatise on physical optics. The result is, that the complementary colour of that neutralised is seen; and as the thickness of the film or the fineness of the striæ undergo slight changes almost any colour can be produced. This is believed to be the origin of many of the glossy or metallic tints of insects, as well as of those of the feathers of some birds. The iridescent colours of the wings of dragon-flies are caused by the superposition of two or more transparent lamellæ; while the shining blue of the Purple-Emperor and other butterflies, and the intensely metallic colours of humming-birds are probably due to fine striæ.

This outline sketch of the nature of colour in the animal world, however imperfect, will at least serve to show us how numerous and varied are the causes which perpetually tend to the production of colour in animal tissues. If we consider, that in order to produce white all the rays which fall upon an object must be reflected in the same proportions as they exist in solar light, whereas if rays of any one or more kinds are absorbed or neutralised the resultant reflected light will be coloured, and that this colour may be infinitely varied according to the proportions in which different rays are reflected or absorbed, we should expect that white would be, as it really is, comparatively rare and exceptional in nature. The same observation will apply to black, which arises from the absorption of all the different rays. Many of the complex substances which exist in animals and plants are subject to changes of colour under the influence of light, heat, or chemical change, and we know that chemical changes are continually occurring during the physiological processes of development and growth. We also find that every external character is subject to minute changes, which are generally perceptible to us in closely allied species; and we can therefore have no doubt that the extension and thickness of the transparent lamellæ, and the fineness of the striæ or rugosities of the integuments, must be undergoing constant minute changes; and these changes will very frequently produce changes of colour. These considerations render it probable that colour is a normal and even necessary result of the complex structure of animals and plants, and that those parts of an organism which are undergoing continual development and adaptation to new conditions, and are also continually subject to the action of light and heat, will be the parts in which changes of colour will most frequently appear. Now there is little doubt that the external changes of animals and plants in adaptation to the environment are much more numerous than the internal changes, as seen in the varied character of the integuments and appendages of animals—hair, horns, scales, feathers, &c. &c.—and in plants, the leaves, bark, flowers, and fruit, with their various appendages,—compared with the comparative uniformity of the texture and composition of their internal tissues; and this accords with the uniformity of the tints of blood, muscle, nerve, and bone throughout extensive groups, as compared with the great diversity of colour of their external organs. It seems a fair conclusion that colour *per se* may be considered to be normal, and to need no special accounting for, while the absence of colour (that is, either *white* or *black*), or the prevalence of certain colours to the constant exclusion of others, must be traced, like other modifications in the economy of living things, to the needs of the species. Or, looking at it in another aspect, we may say, that amid the constant variations of animals and plants colour is ever tending to vary and to appear where it is absent, and that natural selection is constantly eliminating such tints as are injurious to the species, or preserving and intensifying such as are useful.

This view is in accordance with the well-known fact, of colours which rarely or never appear in the species in a state of nature continually occurring among domesticated animals and cultivated plants; showing us that the capacity to develop colour is ever present, so that almost any required tint can be produced which may, under changed conditions, be useful, in however small a degree.

Let us now see how these principles will enable us to understand and explain the varied phenomena of colour in nature, taking them in the order of our functional classification of colours (p. 389).

Theory of Protective Colours.—We have seen that obscure or protective tints in their infinitely varied degrees are present in every part of the animal kingdom, whole families or genera being often thus coloured. Now the various brown, earthy, ashy, and other neutral tints are those which would be most readily produced, because they are due to an irregular mixture of many kinds of rays; while pure tints require either rays of one kind only, or definite mixtures in proper proportions of two or more kinds of rays. This is well exemplified by the comparative difficulty of producing definite pure tints by the mixture of two or more pigments, while a hap-hazard mixture of a number of these will be almost sure to produce browns, olives, or other neutral or dirty colours. An indefinite or irregular absorption of some rays and reflection of others would, therefore, produce obscure tints; while pure and vivid colours would require a perfectly definite absorption of one portion of the coloured rays, leaving the remainder to produce the true complementary colour. This being the case we may expect these brown tints to occur when the need of protection is very slight or even when it does not exist at all, always supposing that bright colours are not in any way useful to the species. But whenever a pure colour is protective, as green in tropical forests or white among arctic snows, there is no difficulty in producing it, by natural selection acting on the innumerable slight variations of tint which are ever occurring. Such variations may, as we have seen, be produced in a great variety of ways; either by chemical changes in the secretions or by molecular changes in surface structure, and may be brought about by change of food, by the photographic action of light, or by the normal process of generative variation. Protective colours therefore, however curious and complex they may be in certain cases, offer no real difficulties.

Theory of Warning Colours.—These differ greatly from the last class, inasmuch as they present us with a variety of brilliant hues, often of the greatest purity, and combined in striking contrasts and conspicuous patterns. Their use depends upon their boldness and visibility, not on the presence of any one colour; hence we find among these groups some of the most exquisitely-coloured objects in nature. Many of the uneatable caterpillars are strikingly beautiful; while the Danaidæ, Heliconidæ, and protected groups of Papilionidæ conprise a series of butterflies of the most brilliant and contrasted colours. The bright colours of many of the sea-anemones and sea-slugs will probably be found to be in this sense protective, serving as a warning of their uneatableness. On our theory none of these colours offer any difficulty. Conspicuousness being useful, every variation tending to brighter and purer colours was selected, the result being the beautiful variety and contrast we find.

But when we come to those groups which gain protection solely by being mistaken for some of these brilliantly coloured but uneatable creatures, a difficulty really exists, and to many minds is so great as to be insuperable. It will be well therefore to endeavour to explain how the resemblance in question may have been brought about. The most difficult case, which may be taken as a type of the whole, is that of the genus *Leptalis* (a group of South American butterflies allied to our common white and yellow kinds), many of the larger species of which are still white or yellow, and which are all eatable by birds and other insectivorous creatures. But there are also a number of species of *Leptalis*, which are brilliantly red, yellow, and black, and which, band for band and spot for spot, resemble some one of the Danaidæ or Heliconidæ which inhabit the same district and which are nauseous and uneatable. Now the common objection is, that a slight approach to one of these protected butterflies would be of no use, while a greater sudden variation is not admissible on the theory of gradual change by indefinite slight variations. This objection depends almost wholly on the supposition that when the first steps towards mimicry occurred, the South American Danaidæ were what they are now, while the ancestors of the Leptalides were like the ordinary white or yellow Pieridæ to which they are allied. But the danaioid butterflies of South America are so immensely numerous and so greatly varied, not only in colour but in structure, that we may be sure they are of vast antiquity and have undergone great modification. A large number of them, however, are still of comparatively plain colours, often rendered extremely elegant by the delicate transparency of the wing-membrane, but otherwise not at all conspicuous. Many have only dusky or purplish bands or spots, others have patches of reddish or yellowish brown —perhaps the commonest colour among butterflies; while a considerable number are tinged or spotted with yellow, also a very common colour, and one especially characteristic of the Pieridæ, the family to which *Leptalis* belongs. We may therefore reasonably suppose that in the early stages of the development of the Danaidæ, when they first began to acquire those nauseous secretions which are now their protection, their colours were somewhat plain, either dusky with paler bands and spots, or yellowish with dark borders, and sometimes with reddish bands or spots. At this time they had probably shorter wings and a more rapid flight, just like the other unprotected families of butterflies. But as soon as they became decidedly unpalatable to any of their enemies, it would be an advantage to them to be readily distinguished from all the eatable kinds; and as butterflies were no doubt already very varied in colour, while all probably had wings adapted for pretty rapid or jerking flight, the best distinction might have been found in outline and habits; whence would arise the preservation of those varieties whose longer wings, bodies, and antennæ, and slower flight rendered them noticeable, — characters which now distinguish the whole group in every part of the world. Now it would be at this stage that some of the weaker-flying Pieridæ which happened to resemble some of the Danaidæ around them in their yellow and dusky tints and in the general outline of their wings, would be sometimes mistaken for them by the common enemy, and would thus gain an advantage in the struggle for existence. Admitting this one step to be made, and all the rest must inevitably follow from simple variation and survival of the fittest So soon as the nauseous butterfly varied in form or colour to such an extent that the corresponding eatable butterfly no longer closely resembled it, the latter would be exposed to attacks, and only those variations would be preserved which kept up the resemblance. At the same time we may well suppose the enemies to become more acute and able to detect smaller differences than at first. This would lead to the destruction of all adverse variations, and thus keep up in continually increasing complexity the outward mimicry which now so amazes us. During the long ages in which this process has been going on, many a *Leptalis* may have become extinct from not varying sufficiently in the right direction and at the right time to keep up a protective resemblance to its neighbour; and this will accord with the comparatively small number of cases of true mimicry as compared with the frequency of those protective resemblances to vegetable or inorganic objects whose forms are less definite and colours less changeable. About a dozen other genera of butterflies and moths mimic the Danaidæ in various parts of the world, and exactly the same explanation will apply to all of them. They represent those species of each group which at the time when the Danaidæ first acquired their protective secretions happened outwardly to resemble some of them, and have by concurrent variation, aided by a rigid selection, been able to keep up that resemblance to the present day.[1]

[1] For fuller information on this subject the reader should consult Mr. Bates's original paper, "Contributions to an Insect-fauna of the Amazon Valley," in *Transactions of the Linnean Society*, vol. xxiii. p. 495; Mr. Trimen's paper in vol. xxvi. p. 497; the author's essay on "Mimicry," &c., already referred to; and, in the absence of collections of butterflies, the plates of Heliconidæ and Leptalidæ, in Hewitson's *Exotic Butterflies*, and Felder's *Voyage of the "Novara,"* may be examined.

Theory of Sexual Colours.—In Mr. Darwin's celebrated work, *The Descent of Man and Selection in Relation to Sex*, he has treated of sexual colour in combination with other sexual characters, and has arrived at the conclusion that all or almost all the colours of the higher animals (including among these insects and all vertebrates) are due to voluntary sexual selection; and that diversity of colour in the sexes is due, primarily, to the transmission of colour-variations either to one sex only or to both sexes, the difference depending on some unknown law, and not being due to natural selection.

I have long held this portion of Mr. Darwin's theory to be erroneous, and have argued that the primary cause of sexual diversity of colour was the need of protection, repressing in the female those bright colours which are normally produced in both sexes by general laws; and I have attempted to explain many of the more difficult cases on this principle ("A Theory of Birds' Nests," in *Contributions*, &c., p. 231). As I have since given much thought to this subject, and have arrived at some views which appear to me to be of considerable importance, it will be well to sketch briefly the theory I now hold, and afterwards show its application to some of the detailed cases adduced in Mr. Darwin's work.

The very frequent superiority of the male bird or insect in brightness or intensity of colour, even when the general tints and coloration are the same, now seem to me to be due to the greater vigour and activity and the higher vitality of the male. The colours of an animal usually fade during disease or weakness, while robust health and vigour adds to their intensity. This intensity of coloration is most manifest in the male during the breeding season, when the vitality is at a maximum. It is also very manifest in those cases in which the male is smaller than the female, as in the hawks and in most butterflies and moths. The same phenomena occur, though in a less marked degree, among mammalia. Whenever there is a difference of colour between the sexes the male is the darker or more strongly marked, and difference of intensity is most visibled uring the breeding season; (*Descent of Man*, p. 533). Numerous cases among domestic animals also prove, that there is an inherent tendency in the male to special developments of dermal appendages and colour, quite independently of sexual or any other form of selection. Thus, "the hump on the male zebu cattle of India, the tail of fat-tailed rams, the arched outline of the forehead in the males of several breeds of sheep, and the mane, the long hairs on the hind-legs, and the dewlap of the male of the Berbura goat," are all adduced by Mr. Darwin as instances of characters peculiar to the male, yet not derived from any parent ancestral form. Among domestic pigeons the character of the different breeds is often most strongly manifested in the male birds; the wattle of the carriers and the eye-wattles of the barbs are largest in the males, and male pouters distend their crops to a much greater extent than do the females, and the cock fantails often have a greater number of tail-feathers than the females. There are also some varieties of pigeons of which the males are striped or spotted with black while the females are never so spotted (*Animals and Plants under Domestication*, I. 161); yet in the parent stock of these pigeons there are no differences between the sexes either of plumage or colour, and artificial selection has not been applied to produce them.

The greater intensity of coloration in the male—which may be termed the normal sexual difference, would be further developed by the combats of the males for the possession of the females. The most vigorous and energetic usually being able to rear most offspring, intensity of colour, if dependent on, or correlated with vigour, would tend to increase. But as differences of colour depend upon minute chemical or structural differences in the organism, increasing vigour acting unequally on different portions of the integument, and often producing at the same time abnormal developments of hair, horns, scales, feathers, &c., would almost necessarily lead also to variable distribution of colour, and thus to the production of new tints and markings. These acquired colours would, as Mr. Darwin has shown, be transmitted to both sexes or to one only, according as they first appeared at an early age, or in adults of one sex, and thus we may account for some of the most marked differences in this respect. With the exception of butterflies, the sexes are almost alike in the great majority of insects. The same is the case in mammals and reptiles, while the chief departure from the rule occurs in birds, though even here in very many cases the law of sexual likeness prevails. But in all cases where the increasing development of colour became disadvantageous to the female, it would be checked by natural selection, and thus produce those numerous instances of protective colouring in the female only, which occur in these two groups of animals.

There is also, I believe, a very important purpose and use of the varied colours of the higher animals, in the facility it affords for recognition by the sexes or by the young of the same species; and it is this use which probably fixes and determines the coloration in many cases. When differences of size and form are very slight, colour affords the only means of recognition at a distance or while in motion, and such a distinctive character must therefore be of especial value to flying insects which are continually in motion, and encounter each other, as it were, by accident. This view offers us an explanation of the curious fact, that among butterflies the females of closely-allied species in the same locality sometimes differ considerably, while the males are much alike; for as the males are the swiftest and the highest fliers and seek the females, it would evidently be advantageous for them to be able to recognize their true partners at some distance off. This peculiarity occurs with many species of *Papilio*, *Diadema*, *Adolias*, and *Colias*. In birds such marked differences of colour are not required, owing to their higher organisation and more perfect senses, which render recognition easy by means of a combination of very slight differential characters. This principle may, perhaps, however, account for some anomalies of coloration among the higher animals. Thus, Mr. Darwin, while admitting that the hare and the rabbit are coloured protectively, remarks that the latter, while running to its burrow, is made conspicuous to the sportsman, and no doubt to all beasts of prey, by its upturned white tail. But this very conspicuousness while running away, may be useful as a signal and guide to the young, who are thus enabled to escape danger by following the older rabbits, directly and without hesitation, to the safety of the burrow; and this may be the more important from the semi-nocturnal habits of the animal. If this explanation is correct, and it certainly seems probable, it may serve as a warning of how impossible it is, without exact knowledge of the habits of an animal and a full consideration of all the circumstances, to decide that any particular coloration cannot be protective or in any way useful. Mr. Darwin himself is not free from such assumptions. Thus, he says: "The zebra is conspicuously striped, and stripes cannot afford any protection on the open plains of South Africa." But the zebra is a very swift animal, and, when in herds, by no means void of means of defence. The stripes therefore *may* be of use by enabling stragglers to distinguish their fellows at a distance, and they *may* be even protective when the animal is at rest among herbage—the only time when it would need protective colouring. Until the habits of the zebra have been observed with special reference to this point, it is surely somewhat hasty to declare that the stripes "cannot afford any protection."

The wonderful display and endless variety of colour in which butterflies and birds so far exceed all other animals, seems primarily due to the excessive development and endless variations of the integumentary structures. No insects have such widely expanded wings in proportion to their bodies as butterflies and moths; in none do the wings vary so much in size and form, and in none are they clothed with such a beautiful and highly-organized coating of scales. According to the general principles of the production of colour already explained, these long-continued expansions of membranes and developments of surface-structures must have led to numerous colour-changes, which have been sometimes checked, sometimes fixed and utilised, sometimes intensified, by natural selection, according to the needs of the animal. In birds, too, we have the wonderful clothing of plumage—the most highly organised, the most varied, and the most expanded of all dermal appendages. The endless processes of growth and change during the development of feathers, and the enormous extent of this delicately-organised surface, must have been highly favourable to the production of varied colour-effects, which, when not injurious, have been merely fixed for purposes of specific identification, but have often been modified or suppressed whenever different tints were needed for purposes of protection.

To voluntary sexual selection, that is, the actual choice by the females of the more brilliantly-coloured males, I believe very little if any effect is directly due. It is undoubtedly proved that in birds the females do sometimes exert a choice; but the evidence of this fact collected by Mr. Darwin (*Descent of Man*, chap. xiv.) does not prove that colour determines that choice, while much of the strongest evidence is directly opposed to this view. All the facts appear to be consistent with the choice depending on a variety of male characteristics, with some of which colour is often correlated. Thus it is the opinion of some of the best observers that vigour and liveliness are most attractive, and these are no doubt usually associated with intensity of colour. Again, the display of the various ornamental appendages of the male during courtship may be attractive, but these appendages, with their bright colours or shaded patterns, are due probably to general laws of growth and to that superabundant vitality which we have seen to be a cause of colour. But there are many considerations which seem to show that the possession of these ornamental appendages and bright colours in the male is not an important character functionally, and that it has not been produced by the action of voluntary sexual selection. Amid the copious mass of facts and opinions collected by Mr. Darwin as to the display of colour and ornaments by the male birds, there is a total absence of any evidence that the females admire or even notice this display. The hen, the turkey, and the peafowl go on feeding while the male is displaying his finery, and there is reason to believe that it is his persistency and energy rather than his beauty which wins the day. Again, evidence collected by Mr. Darwin himself proves that each bird finds a mate under any circumstances. He gives a number of cases of one of a pair of birds being shot, and the survivor being always found paired again almost immediately. This is sufficiently explained on the assumption that the destruction of birds by various causes is continually leaving widows and widowers in nearly equal proportions, and thus each one finds a fresh mate; and it leads to the conclusion that permanently unpaired birds are very scarce; so that, speaking broadly, every bird finds a mate and breeds. But this would almost or quite neutralize any effect of sexual selection of colour or ornament, since the less highly-coloured birds would be at no disadvantage as regards leaving healthy offspring. If, however, heightened colour is correlated with health and vigour, and these healthy and vigorous birds provide best for their young, and leave offspring which, being equally healthy and vigorous, can best provide for themselves, then natural selection becomes a preserver and intensifier of colour. Another most important consideration is, that male butterflies rival or even excel the most gorgeous male birds in bright colours and elegant patterns; and among these there is literally not one particle of evidence that the female is influenced by colour or even that she has any power of choice, while there is much direct evidence to the contrary (*Descent of Man*, p. 318). The weakness of the evidence for sexual selection among these insects is so palpable that Mr. Darwin is obliged to supplement it by the singularly inconclusive argument that, "Unless the females prefer one male to another, the pairing must be left to mere chance, and this does not appear probable (*l.c.*, p. 317)." But he has just said—"The males sometimes fight together in rivalry, and many may be seen pursuing or crowding round the same female;" while in the case of the silk-moths, "the females appear not to evince the least choice in regard to their partners." Surely the plain inference from all this is, that males fight and struggle for the almost passive female, and that the most vigorous and energetic, the strongest-winged or the most persevering, wins her. How can there be chance in this? Natural selection would here act, as in birds, in perpetuating the strongest and most vigorous males, and as these would usually be the more highly coloured of their race, the same results would be produced as regards the intensification and variation of colour in the one case as in the other.

Let us now see how these principles will apply to some of the cases adduced by Mr. Darwin in support of his theory of voluntary sexual selection.

In *Descent of Man*, 2nd ed., pp. 307-316, we find an elaborate account of the various modes of colouring of butterflies and moths, proving that the coloured parts are always more or less displayed, and that they have some evident relation to an observer. Mr. Darwin then says—"From the several foregoing facts it is impossible to admit that the brilliant colours of butterflies, and of some few moths, have commonly been acquired for the sake of protection. We have seen that their colours and elegant patterns are arranged and exhibited as if for display. Hence I am led to believe that the females prefer or are most excited by the more brilliant males; for on any other supposition the males would, as far as we can see, be ornamented to no purpose" (*l.c.*, p. 316). I am not aware that any one has ever maintained that the brilliant colours of butterflies have "commonly been acquired for the sake of protection," yet Mr. Darwin has himself referred to cases in which the brilliant colour is so placed as to serve for protection; as for example, the eye-spots on the hind wings of moths, which are pierced by birds and so save the vital parts of the insect, while the bright patch on the orange-tip butterflies which Mr. Darwin denies are protective, may serve the same purpose. It is in fact somewhat remarkable how very generally the black spots, ocelli, or bright patches of colour are on the tips, margins, or discs of the wings; and as the insects are necessarily visible while flying, and this is the time when they are most subject to attacks by insectivorous birds, the position of the more conspicuous parts at some distance from the body may be a real protection to them. Again, Mr. Darwin admits that the white colour of the male Ghost-moth may render it more easily seen by the female while flying about in the dusk, and if to this we add that it will be also more readily distinguished from allied species, we have a reason for diverse ornamentation in these insects quite sufficient to account for most of the facts, without believing in the selection of brilliant males by the females, for which there is not a particle of evidence. The facts given to show that butterflies and other insects can distinguish colours and are attracted by colours similar to their own, are quite consistent with the view that colour, which continually tends to appear, is utilised for purposes of identification and distinction, when not required to be modified or suppressed for purposes of protection. The cases of the females of some species of *Thecla*, *Callidryas*, *Colias*, and *Hipparchia*, which have more conspicuous markings than the male, may be due to several causes: to obtain greater distinction from other species, for protection from birds, as in the case of the yellow-underwing moths, while sometimes—as in *Hipparchia*—the lower intensity of colouring in the female may lead to more contrasted markings. Mr. Darwin thinks that here the males have selected the more beautiful females, although one chief fact in support of his theory of voluntary sexual selection is, that throughout the whole animal kingdom the males are usually so ardent that they will accept any female, while the females are coy, and choose the handsomest males, whence it is believed the general brilliancy of males as compared with females has arisen.

Perhaps the most curious cases of sexual difference of colour are those in which the female is very much more gaily coloured than the male. This occurs most strikingly in some species of *Pieris* in South America, and of *Diadema* in the Malay islands, and in both cases the females resemble species of the uneatable Danaidæ and Heliconidæ, and thus gain a protection. In the case of *Pieris pyrrha*, *P. malenka*, and *P. lorena*, the males are plain white and black, while the females are orange, yellow, and black, and so banded and spotted as exactly to resemble species of Heliconidæ. Mr. Darwin admits that these females have acquired these colours as a protection; but as there is no apparent cause for the strict limitation of the colour to the female, he believes that it has been kept down in the male by its being *unattractive* to her. This appears to me to be a supposition opposed to the whole theory of sexual selection itself. For this theory is, that minute variations of colour in the male are *attractive* to the female, have always been selected, and that thus the brilliant male colours have been produced. But in this case he thinks that the female butterfly had a constant aversion to every trace of colour, even when we must suppose it was constantly recurring during the successive variations which resulted in such a marvellous change in herself. But if we consider the fact that the females frequent the forests where the Heliconidæ abound, while the males fly much in the open, and assemble in great numbers with other white and yellow butterflies on the banks of rivers, may it not be possible that the appearance of orange stripes or patches would be as injurious to the male as it is useful to the female, by making him a more easy mark for insectivorous birds among his white companions? This seems a more probable supposition, than the altogether hypothetical choice of the female, sometimes exercised in favour of and sometimes against every new variety of colour in her partner.

The full and interesting account given by Mr. Darwin of the colours and habits of male and female birds (*Descent of Man*, chapters xiii. and xiv.), proves that in most, if not in all cases, the male birds fully display their ornamental plumage, before the females and in rivalry with each other; but on the essential point of whether the female's choice is determined by minute differences in these ornaments or in their colours, there appears to be an entire absence of evidence. In the section on "*Preference for particular Males by the Females*," the facts quoted show indifference to colour, except that some colour similar to their own seems to be preferred. But in the case of the hen canary, who chose a greenfinch in preference to either chaffinch or goldfinch, gay colours had evidently no preponderating attraction. There is some evidence adduced that female birds may, and probably do, choose their mates, but none whatever that the choice is determined by difference of colour; and no less than three eminent breeders informed Mr. Darwin that they "did not believe that the females prefer certain males on account of the beauty of their plumage," Again, Mr. Darwin himself says: "as a general rule colour appears to have little influence on the pairing of pigeons." The oft-quoted case of Sir R. Heron's peahens which preferred an "old pied cock" to those normally coloured, is a very unfortunate one, because pied birds are just those that are not favoured in a state of nature, or the breeds of wild birds would become as varied and mottled as our domestic varieties. If such irregular fancies were not rare exceptions the production of definite colours and patterns by the choice of the female birds, or in any other way, would be impossible.

We now come to such wonderful developments of plumage and colour as are exhibited by the peacock and the Argus-pheasant; and I may here mention that it was the case of the latter bird, as fully discussed by Mr. Darwin, which first shook my belief in "sexual," or more properly "female" selection. The long series of gradations, by which the beautifully shaded ocelli on the secondary wing-feathers of this bird have been produced, are clearly traced out, the result being a set of markings, so exquisitely shaded as to represent "balls lying loose within sockets,"—purely artificial objects of which these birds could have no possible knowledge. That this result should have been attained through thousands and tens of thousands of female birds all preferring those males whose markings varied slightly in this one direction, this uniformity of choice continuing through thousands and tens of thousands of generations, is to me absolutely incredible. And, when further, we remember that those which did not so vary would also, according to all the evidence, find mates and leave offspring, the actual result seems quite impossible of attainment by such means.

Without pretending to solve completely so difficult a problem, I would point out a circumstance which seems to afford a clue. It is, that the most highly-coloured and most richly-varied markings, occur on those parts of the plumage which have undergone the greatest modification, or have acquired the most abnormal development. In the peacock, the tail-coverts are enormously developed, and the "eyes" are situated on the greatly dilated ends. In the birds of paradise, breast, or neck, or head, or tail-feathers, are greatly developed and highly coloured. The hackles of the cock, and the scaly breasts of humming-birds are similar developments; while in the Argus-pheasant the secondary quills are so enormously lengthened and broadened as to have become almost useless for flight. Now it is easily conceivable, that during this process of development, inequalities in the distribution of colour may have arisen in different parts of the same feather, and that spots and bands may thus have become broadened out into shaded spots or ocelli, in the way indicated by Mr. Darwin, much as the spots and rings on a soap bubble increase with increasing tenuity. This is the more probable, as in domestic fowls varieties tend to become symmetrical, quite independently of sexual selection. (*Descent of Man*, p. 424.)

If now we accept the evidence of Mr. Darwin's most trustworthy correspondents, that the choice of the female, so far as she exerts any, falls upon the "most vigorous, defiant, and mettlesome male;" and if we further believe, what is certainly the case, that these are as a rule the most brightly coloured and adorned with the finest developments of plumage, we have a real and not a hypothetical cause at work. For these most healthy, vigorous, and beautiful males will have the choice of the finest and most healthy females, will have the most numerous and healthy families, and will be able best to protect and rear those families. Natural selection, and what may be termed male selection, will tend to give them the advantage in the struggle for existence, and thus the fullest plumage and the finest colours will be transmitted, and tend to advance in each succeeding generation.

There remains, however, what Mr. Darwin evidently considers his strongest argument — the display by the male of each species of its peculiar beauties of plumage and colour. We have here, no doubt, a very remarkable and very interesting fact; but this too may be explained by general principles, quite independent of any choice or volition of the female bird. During pairing-time, the male bird is in a state of great excitement, and full of exuberant energy. Even unornamented birds flutter their wings or spread them out, erect their tails or crests, and thus give vent to the nervous excitability with which they are overcharged. It is not improbable that crests and other erectile feathers may be primarily of use in frightening away enemies, since they are generally erected when angry or during combat. Those individuals who were most pugnacious and defiant, and who brought these erectile plumes most frequently and most powerfully into action, would tend to increase them by use, and to leave them further developed in some of their descendants. If, in the course of this development, colour appeared, we have every reason to believe it would be most vivid in these most pugnacious and energetic individuals, and as these would always have the advantage in the rivalry for mates (to which advantage the excess of colour and plumage might sometimes conduce), there seems nothing to prevent a progressive development of these ornaments in *all dominant races*, that is, wherever there was such a surplus of vitality, and such complete adaptation to conditions, that the inconvenience or danger produced by them, was so comparatively small as not to affect the superiority of the race over its nearest allies. If then those portions of the plumage, which were originally erected and displayed, became developed and coloured, the actual display, under the influence of jealousy or sexual excitement becomes intelligible. The males, in their rivalry with each other, would see what plumes were most effective, and each would endeavour to excel his enemy as far as voluntary exertion could effect it, just as they endeavour to rival each other in song, even sometimes to the point of causing their own destruction.

There is also a general argument against Mr. Darwin's views on this question, founded on the nature and potency of "natural" as opposed to "sexual" selection, which appears to me to be itself almost conclusive of the whole matter at issue. Natural selection, or the survival of the fittest, acts perpetually and on an enormous scale. Taking the offspring of each pair of birds as, on the average, only six annually, one-third of these at most will be preserved, while the two-thirds which are least fitted will die. At intervals of a few years, whenever unfavourable conditions occur, five-sixths, nine-tenths, or even a greater proportion of the whole yearly production are weeded out, leaving only the most perfect and best adapted to survive. Now unless these survivors are on the whole the most ornamental, this rigid selective power must neutralise and destroy any influence that may be exerted by female selection. For the utmost that can be claimed for this is, that a small fraction of the least ornamented do not obtain mates, while a few of the most ornamented may leave more than the average number of offspring. Unless, therefore, there is the strictest correlation between ornament and general perfection, the former can have no permanent advantage; ana if there is (as I maintain) such a correlation, then the sexual selection of ornament for which there is little or no evidence becomes needless, because natural selection which is an admitted *vera causa* will itself produce all the results. In the case of butterflies the argument becomes even stronger, because the fertility is so much greater, and the weeding out of the unfit takes place, to a great extent, in the egg and larvæ state. Unless the eggs and larva which escaped to produce the next generation were those which would produce the more highly-coloured butterflies, it is difficult to perceive how the slight preponderance of colour sometimes selected by the females, should not be wholly neutralised by the extremely rigid selection for other qualities to which the offspring in every stage are exposed. The only way in which we can account for the observed facts is, by the supposition that colour and ornament are strictly correlated with health, vigour, and general fitness to survive. We have shown that there is reason to believe that this is the case, and if so, voluntary sexual selection becomes as unnecessary as it would certainly be ineffective.

There is one other very curious case of sexual colouring among birds—that, namely, in which the female is decidedly brighter or more strongly marked than the male; as in the fighting quails (*Turnix*), painted snipe (*Rhynchæa*), two species of phalarope (*Phalaropus*), and the common cassowary (*Casuarius galeatus*). In all these cases, it is known that the males take charge of and incubate the eggs, while the females are almost always larger and more pugnacious. In my "Theory of Birds' Nests" (*Natural Selection*,

p. 251), I imputed this difference of colour to the greater need for protection by the male bird while incubating, to which Mr. Darwin has objected that the difference is not sufficient, and is not always so distributed as to be most effective for this purpose, and he believes that it is due to reversed sexual selection, that is, to the female taking the usual *rôle* of the male, and being chosen for her brighter tints. We have already seen reason for rejecting this latter theory in every case, and I also admit that my theory of protection is, in this case, only partially if at all applicable. But the general theory of intensity of colour being due to general vital energy is quite applicable; and the fact that the superiority of the female in this respect is quite exceptional, and is therefore probably not of very ancient date in any one case, will account for the difference of colour thus produced being always comparatively slight.

Theory of Typical Colours.—The remaining kinds of animal colours—those which can neither be classed as protective, warning, nor sexual, are for the most part readily explained on the general principles of the development of colour which we have now laid down. It is a most suggestive fact, that, in cases where colour is required only as a warning, as among the uneatable caterpillars, we find, not one or two glaring tints only but every kind of colour disposed in elegant patterns, and exhibiting almost as much variety and beauty as among insects and birds. Yet here, not only is sexual selection out of the question, but the need for recognition and identification by others of the same species, seems equally unnecessary. We can then only impute this variety to the normal production of colour in organic forms, when fully exposed to light and air and undergoing great and rapid developmental modification. Among more perfect animals, where the need for recognition has been added, we find intensity and variety of colour at its highest pitch among the South American butterflies of the families Heliconidæ and Danaidæ, as well as among the Nymphalidæ and Erycinidæ, many of which obtain the necessary protection in other ways. Among birds also, wherever the habits are such that no special protection is needed for the females, and where the species frequent the depths of tropical forests and are thus naturally protected from the swoop of birds of prey, we find almost equally intense coloration; as in the trogons, barbets, and gapers.

Of the mode of action of the general principles of colour-development among animals, we have an excellent example in the humming-birds. Of all birds these are at once the smallest, the most active, and the fullest of vital energy. When poised in the air their wings are invisible, owing to the rapidity of their motion, and when startled they dart away with the rapidity of a flash of light. Such active creatures would not be an easy prey to any rapacious bird; and if one at length was captured, the morsel obtained would hardly repay the labour. We may be sure, therefore, that they are practically unmolested. The immense variety they exhibit in structure, plumage, and colour, indicates a high antiquity for the race, while their general abundance in individuals shows that they are a dominant group, well adapted to all the conditions of their existence. Here we find everything necessary for the development of colour and accessory plumes. The surplus vital energy shown in their combats and excessive activity, has expended itself in ever-increasing developments of plumage, and greater and greater intensity of colour, regulated only by the need for specific identification which would be especially required in such small and mobile creatures. Thus may be explained those remarkable differences of colour between closely-allied species, one having a crest like the topaz, while in another it resembles the sapphire, The more vivid colours and more developed plumage of the males, I am now inclined to think may be wholly due to their greater vital energy, and to those general laws which lead to such superior developments even in domestic breeds; but in some cases the need of protection by the female while incubating, to which I formerly imputed the whole phenomenon, may have suppressed a portion of the ornament which she would otherwise have attained.

Another real, though as yet inexplicable cause of diversity of colour, is to be found in the influence of locality. It is observed that species of totally distinct groups are coloured alike in one district, while in another district the allied species all undergo the same change of colour. Cases of this kind have been adduced by Mr. Bates, by Mr. Darwin, and by myself, and I have collected all the more curious and important examples in my Address to the Biological Section of the British Association at Glasgow in 1876. The most probable cause for these simultaneous variations would seem to be the presence of peculiar elements or chemical compounds in the soil, the water, or the atmosphere, or of special organic substances in the vegetation; and a wide field is thus offered for chemical investigation in connection with this interesting subject. Yet, however we may explain it, the fact remains of the same vivid colours in definite patterns being produced in quite unrelated groups, which only agree, so far as we yet know, in inhabiting the same locality.

Let us now sum up the conclusion at which we have arrived, as to the various modes in which colour is produced or modified in the animal kingdom.

The various causes of colour in the animal world are, molecular and chemical change of the substance of their integuments, or the action on it of heat, light or moisture. It is also produced by interference of light in superposed transparent lamellæ, or by excessively fine surface striæ. These elementary conditions for the production of colour are found everywhere in the surface-structures of animals, so that its presence must be looked upon as normal, its absence as exceptional.

Colours are fixed or modified in animals by natural selection for various purposes; obscure or imitative colours for concealment—gaudy colours as a warning—and special markings, either for easy recognition by strayed individuals, females, or young, or to direct attack from a vital part, as in the large brilliantly-marked wings of some butterflies and moths.

Colours are produced or intensified by processes of development,—either where the integument or its appendages undergo great extension or modification, or where there is a surplus of vital energy, as in male animals generally, and more especially at the breeding-season.

Colours are also more or less influenced by a variety of causes, such as the nature of the food, the photographic action of light, and also by some unknown local action probably dependent on chemical peculiarities in the soil or vegetation.

These various causes have acted and reacted in a vari·ty of ways, and have been modified by conditions dependent on age or on sex, on competition with new forms, or on geographical or climatic changes. In so complex a subject, for which experiment and systematic inquiry has done so little, we cannot expect to explain every individual case, or solve every difficulty; but it is believed that all the great features of animal coloration and many of the details become explicable on the principles we have endeavoured to lay down.

It will perhaps be considered presumptuous to put forth this sketch of the subject of colour in animals, as a substitute for one of Mr. Darwin's most highly elaborated theories—that of voluntary or perceptive sexual selection; yet I venture to think that it is more in accordance with the whole of the facts, and with the theory of natural selection itself; and I would ask such of my readers as may be sufficiently interested in the subject, to read again chapters xi. to xvi. of the *Descent of Man*, and consider the whole theory from the point of view here laid down. The explanation of almost all the ornaments and colours of birds and insects as having been produced by the perceptions and choice of the females has, I believe, staggered many evolutionists, but has been provisionally accepted because it was the only theory that even attempted to explain the facts. It may perhaps be a relief to some of them, as it has been to myself, to find that the phenomena can be shown to depend on the general laws of development, and on the action of "natural selection," which theory will, I venture to think, be relieved from an abnormal excrescence, and gain additional vitality by the adoption of my view of the subject.

Although we have arrived at the conclusion that tropical light and heat can in no sense be considered the cause of colour, there remains to be explained the undoubted fact that all the more intense and gorgeous tints are manifested by the animal life of the tropics, while in some groups, such as butterflies and birds, there is a marked preponderance of highly-coloured species. This is probably due to a variety of causes, some of which we can indicate, while others remain to be discovered. The luxuriant vegetation of the tropics throughout the entire year, affords so much concealment, that colour may there be safely developed to a much greater extent than in climates where the trees are bare in winter, during which season the struggle for existence is most severe, and even the slightest disadvantage may prove fatal. Equally important, probably, has been the permanence of favourable conditions in the tropics, allowing certain groups to continue dominant for long periods, and thus to carry out in one unbroken line whatever developments of plumage or colour may once have acquired an ascendency. Changes of climatal conditions, and pre-eminently the glacial epoch, probably led to the extinction of a host of highly-developed and finely-coloured insects and birds in temperate zones, just as we know that it led to the extinction of the larger and more powerful mammalia which formerly characterised the temperate zone in both hemispheres. This view is supported by the fact, that it is amongst those groups only which are now exclusively tropical, that all the more extraordinary developments of ornament and colour are found. The local causes of colour will also have acted best in regions where the climatal conditions remained constant, and where migration was unnecessary; while whatever direct effect may be produced by light or heat, will necessarily have acted more powerfully within the tropics. And lastly, all these causes have been in action over an actually greater area in tropical than in temperate zones, while estimated potentially, in proportion to its life-sustaining power, the lands which enjoy a practically tropical climate (extending as they do considerably beyond the geographical tropics), are very much larger than the temperate regions of the earth. Combining the effects of all these various causes we are quite able to understand the superiority of the tropical parts of the globe, not only in the abundance and variety of their forms of life, but also as regards the ornamental appendages and vivid coloration which these forms present.

A. R. WALLACE.

To be continued.

THE COLOURS OF ANIMALS AND PLANTS.[1]

II.—THE COLOURS OF PLANTS.

The colouring of plants is neither so varied nor so complex as that of animals, and its explanation accordingly offers fewer difficulties. The colours of foliage are, comparatively, little varied, and can be traced in almost all cases to a special pigment termed chlorophyll, to which is due the general green colour of leaves; but the recent investigations of Mr. Sorby and others have shown that chlorophyll is not a simple green pigment, but that it really consists of at least seven distinct substances, varying in colour from blue to yellow and orange. These differ in their proportions in the chlorophyll of different plants; they have different chemical reactions; they are differently affected by light; and they give distinct spectra. Mr. Sorby further states that scores of different colouring matters are found in the leaves and flowers of plants, to some of which appropriate names have been given, as erythrophyll which is red, and phaiophyll which is brown; and many of these differ greatly from each other in their chemical composition. These inquiries are at present in their infancy, but as the original term chlorophyll seems scarcely applicable under the present aspect of the subject, it would perhaps be better to introduce the analogous word Chromophyll as a general term for the colouring matters of the vegetable kingdom.

Light has a much more decided action on plants than on animals. The green colour of leaves is almost wholly dependent on it; and although some flowers will become fully coloured in the dark, others are decidedly affected by the absence of light, even when the foliage is fully exposed to it. Looking therefore at the numerous coloured substances which are developed in the tissues of plants; the sensitiveness of these pigments to light; the changes they undergo during growth and development; and the facility with which new chemical combinations are effected by the physiological processes of plants as shown by the endless variety in the chemical constitution of vegetable products, we have no difficulty in comprehending the general causes which aid in producing the colours of the vegetable world, or the extreme variability of those colours. We may therefore here confine ourselves to an inquiry into the various uses of colour in the economy of plants; and this will generally enable us to understand how it has become fixed and specialised in the several genera and species of the vegetable kingdom.

In animals, as we have seen, colour is greatly influenced by the need of protection from or of warning to their numerous enemies, and to the necessity for identification and easy recognition. Plants rarely need to be concealed, and obtain protection either by their spines, their hardness, their hairy covering, or their poisonous secretions. A very few cases of what seem to be true protective colouring do, however, exist, the most remarkable being that of the "stone mesembryanthemum," of the Cape of

[1] In the first part of this paper I used the term "voluntary sexual-selection" to indicate the theory that many of the ornaments of male animals have been produced by the choice of the females, and to distinguish it from that form of sexual selection which explains the acquisition of weapons peculiar to male animals as due to the selective influence of their combats and struggles for the possession of the females. I find that Mr. Darwin thinks the term "voluntary" not strictly applicable, and I therefore propose to alter it to "conscious" or "perceptive," which seem free from any ambiguity and make not the least difference to my argument.

Good Hope, which in form and colour closely resembles the stones among which it grows; and Dr. Burchell, who first discovered it, believes that the juicy little plant thus generally escapes the notice of cattle and wild herbivorous animals. Mr. J. P. Mansel Weale also noticed that many plants growing in the stony Karoo have their tuberous roots above the soil, and these so perfectly resemble the stones among which they grow that, when not in leaf, it is almost impossible to distinguish them (*Nature*, vol. iii. p. 507). A few cases of what seem to be protective mimicry have also been noted, the most curious being that of three very rare British fungi, found by Mr. Worthington Smith, each in company with common species, which they so closely resembled that only a minute examination could detect the difference. One of the common species is stated in botanical works to be "bitter and nauseous," so that it is not improbable that the rare kind may escape being eaten by being mistaken for an uneatable species though itself palatable. Mr. Mansel Weale also mentions a labiate plant, the *Ajuga ophrydis*, of South Africa, as strikingly resembling an orchid. This may be a means of attracting insects to fertilize the flower in the absence of sufficient nectar or other attraction in the flower itself; and the supposition is rendered more probable by this being the only species of the genus Ajuga in South Africa. Many other cases of resemblances between very distinct plants have been noticed—as that of some Euphorbias to Cacti; but these very rarely inhabit the same country or locality, and it has not been proved that there is in any of these cases the amount of inter-relation between the species which is the essential feature of the protective "mimicry" that occurs in the animal world.

The different colours exhibited by the foliage of plants, and the changes it undergoes during growth and decay, appear to be due to the general laws already sketched out, and to have little if any relation to the special requirements of each species. But flowers and fruits exhibit definite and well-pronounced tints, often varying from species to species, and more or less clearly related to the habits and functions of the plant. With the few exceptions already pointed out, these may be generally classed as *attractive* colours. The seeds of plants require to be dispersed so as to reach places favourable for germination and growth. Some are very minute, and are carried abroad by the wind, or they are violently expelled and scattered by the bursting of the containing capsules. Others are downy or winged, and are carried long distances by the gentlest breeze. But there is a large class of seeds which cannot be dispersed in either of these ways, and are mostly contained in eatable fruits. These fruits are devoured by birds or beasts, and the hard seeds pass through their stomachs undigested, and, owing probably to the gentle heat and moisture to which they have been subjected, in a condition highly favourable for germination. The dry fruits or capsules containing the first two classes of seeds are rarely, if ever, conspicuously coloured, whereas the eatable fruits almost invariably acquire a bright colour as they ripen, while at the same time they become soft and often full of agreeable juices. Our *red* haws and nips, our *black* elderberries, our *blue* sloes and whortleberries, our *white* mistletoe and snowberry, and our *orange* sea-buckthorn, are examples of the colour-sign of edibility; and in every part of the world the same phenomenon is found. The fruits of large forest-trees, such as the pines, oaks, and beeches, are not coloured, perhaps because their size and abundance render them sufficiently conspicuous, and also because they provide such a quantity of food to such a number of different animals that there is no danger of their being unnoticed.

The colours of flowers serve to render them visible and recognisable by insects which are attracted by secretions of nectar or pollen. During their visits for the purpose of obtaining these products, insects involuntarily carry the pollen of one flower to the stigma of another, and thus effect cross-fertilization, which, as Mr. Darwin was the first to demonstrate, immensely increases the vigour and fertility of the next generation of plants. This discovery has led to the careful examination of great numbers of flowers, and the result has been that the most wonderful and complex arrangements have been found to exist, all having for their object to secure that flowers shall not be self-fertilised perpetually, but that pollen shall be carried, either constantly or occasionally, from the flowers of one plant to those of another. Mr. Darwin himself first worked out the details in orchids, primulas, and some other groups; and hardly less curious phenomena have since been found to occur, even among some of the most regularly-formed flowers. The arrangement, length, and position of all the parts of the flower is now found to have a purpose, and not the least remarkable portion of the phenomenon is the great variety of ways in which the same result is obtained. After the discoveries with regard to orchids, it was to be expected that the irregular, tubular, and spurred flowers should present various curious adaptations for fertilization by insect-agency. But even among the open, cup-shaped, and quite regular flowers, in which it seemed inevitable that the pollen must fall on the stigma, and produce constant self-fertilization, it has been found that this is often prevented by a physiological variation — the anthers constantly emitting their pollen either a little earlier or a little later than the stigmas of the same flower, or of other flowers on the same plant, were in the best state to receive it; and as individual plants in different stations, soils, and aspects, differ somewhat in the time of flowering, the pollen of one plant would often be conveyed by insects to the stigmas of some other plant in a condition to be fertilized by it. This mode of securing cross-fertilization seems so simple and easy, that we can hardly help wondering why it did not always come into action, and so obviate the necessity for those elaborate, varied, and highly complex contrivances found in perhaps the majority of coloured flowers. The answer to this of course is, that *variation* sometimes occurred most freely in one part of a plant's organization, and sometimes in another, and that the benefit of cross-fertilization was so great that *any* variation that favoured it was preserved, and then formed the starting-point of a whole series of further variations, resulting in those marvellous adaptations for insect fertilization, which have given much of their variety, elegance, and beauty, to the floral world. For details of these adaptations we must refer the reader to the works of Darwin, Lubbock, Herman Müller, and others. We have here only to deal with the part played by colour, and by those floral structures in which colour is most displayed.

The sweet odours of flowers, like their colours, seem often to have been developed as an attraction or guide to insect fertilizers, and the two phenomena are often complementary to each other. Thus, many inconspicuous flowers — like the mignonette and the sweet-violet, can be distinguished by their odours before they attract the eye, and this may often prevent their being passed unnoticed; while very showy flowers, and especially those with variegated or spotted petals, are seldom sweet. White, or very pale flowers, on the other hand, are often excessively sweet, as exemplified by the jasmine and clematis; and many of these are only scented at night, as is strikingly the case with the night-smelling stock, our butterfly orchis (*Habenaria chlorantha*), the greenish-yellow *Daphne pontica*, and many others. These white flowers are mostly fertilized by night-flying moths, and those which reserve their odours for the evening probably escape the visits of diurnal insects which would consume their nectar without effecting fertilization. The absence of odour in showy flowers and its preponderance among those that are white, may be shown to be a fact by an examination of the lists in Mr. Mongredien's work on hardy trees and shrubs.[1] He gives a list of about one hundred and sixty species with showy flowers, and another list of sixty species with fragrant flowers; but only twenty of these latter are included among the showy species, and these are almost all white flowered. Of the sixty species with fragrant flowers, more than forty are white, and a number of others have greenish, yellowish, or dusky and inconspicuous flowers. The relation of white flowers to nocturnal insects is also well shown by those which, like the evening primroses, only open their large white blossoms after sunset. The red Martagon lily has been observed by Mr. Herman Müller to be fertilized by the humming-bird hawk moth, which flies in the morning and afternoon when the colours of this flower, exposed to the nearly horizontal rays of the sun, glow with brilliancy, and when it also becomes very sweet-scented.

To the same need of conspicuousness the combination of so many individually small flowers into heads and bunches is probably due, producing such broad masses as those of the elder, the gueldre-rose, and most of the Umbelliferæ, or such elegant bunches as those of the lilac, laburnum, horse-chestnut, and wistaria. In other cases minute flowers are gathered into dense heads, as with *Globularia*, *Jasione*, clover, and all the Compositæ; and among the latter the outer flowers are often developed into a ray, as in the sunflowers, the daisies, and the asters, forming a starlike compound flower, which is itself often produced in immense profusion.

The beauty of alpine flowers is almost proverbial. It consists either in the increased size of the individual flowers as compared with the whole plant, in increased intensity of colour, or in the massing of small flowers into dense cushions of bright colour; and it is only in the higher Alps, above the limit of forests and upwards towards the perpetual snow-line that these characteristics are fully exhibited. This effort at conspicuousness under adverse circumstances may be traced to the comparative scarcity of winged insects in the higher regions, and to the necessity for attracting them from a distance. Amid the vast slopes of debris and the huge masses of rock so prevalent in higher mountain regions, patches of intense colour can alone make themselves visible and serve to attract the wandering butterfly from the valleys. Mr. Herman Müller's careful observations have shown, that in the higher Alps bees and most other groups of winged insects are almost wanting, while butterflies are tolerably abundant; and he has discovered, that in a number of cases where a lowland flower is adapted to be fertilized by bees, its alpine ally has had its structure so modified as to be adapted for fertilization only by butterflies.[2] But bees are always (in the temperate zone) far more abundant than butterflies, and this will be another reason why flowers specially adapted to be fertilized by the latter should be rendered unusually conspicuous. We find, accordingly, the yellow primrose of the plains replaced by pink and magenta-coloured alpine species; the straggling wild pinks of the lowlands by the masses of large flowers in such mountain species as *Dianthus alpinus* and *D. glacialis;* the saxifrages of the high Alps with bunches of flowers a foot long, as in *Saxifraga longifolia* and *S. cotyledon*, or forming spreading masses of flowers, as in *S. oppositifolia;* while the soap-

[1] *Trees and Shrubs for English Plantations*, by Augustus Mongredien. Murray, 1870.

[2] *Nature*, vol. xi. pp. 32, 110.

worts, silenes, and louseworts are equally superior to the allied species of the plains.

Again, Dr. Müller has discovered that when there are showy and inconspicuous species in the same genus of plants, there is often a corresponding difference of structure, those with large and showy flowers being quite incapable of self-fertilization, and thus depending for their very existence on the visits of insects; while the others are able to fertilize themselves should insects fail to visit them. We have examples of this difference in *Malva sylvestris, Epilobium angustifolium, Polygonum bistorta,* and *Geranium pratense*—which have all large or showy flowers and must be fertilized by insects,—as compared with *Malva rotundifolia, Epilobium parviflorum, Polygonum aviculare,* and *Geranium pusillum,* which have small or inconspicuous flowers, and are so constructed that if insects should not visit them they are able to fertilize themselves.[1]

As supplementing these curious facts showing the relation of colour in flowers to the need of the visits of insects to fertilize them, we have the remarkable, and on any other theory utterly inexplicable circumstance, that in all the numerous cases in which plants are fertilized by the agency of the wind they never have specially coloured floral envelopes. Such are our pines, oaks, poplars, willows, beeches, and hazel; our nettles, grasses, sedges, and many others. In some of these the male flowers are, it is true, conspicuous, as in the catkins of the willows and the hazel, but this arises incidentally from the masses of pollen necessary to secure fertilization, as shown by the entire absence of a corolla or of those coloured bracts which so often add to the beauty and conspicuousness of true flowers.

The adaptation of flowers to be fertilized by insects—often to such an extent that the very existence of the species depends upon it—has had widespread influence on the distribution of plants and the general aspects of vegetation. The seeds of a particular species may be carried to another country, may find there a suitable soil and climate, may grow and produce flowers, but if the insect which alone can fertilize it should not inhabit that country, the plant cannot maintain itself, however frequently it may be introduced or however vigorously it may grow. Thus may probably be explained the poverty in flowering-plants and the great preponderance of ferns that distinguishes many oceanic islands, as well as the deficiency of gaily-coloured flowers in others. This branch of the subject is discussed at some length in my Address to the Biological Section of the British Association,[2] but I may here just allude to two of the most striking cases. New Zealand is, in proportion to its total number of flowering plants, exceedingly poor in handsome flowers, and it is correspondingly poor in insects, especially in bees and butterflies, the two groups which so greatly aid in fertilization. In both these aspects it contrasts strongly with Southern Australia and Tasmania in the same latitudes, where there is a profusion of gaily-coloured flowers and an exceedingly rich insect-fauna. The other case is presented by the Galapagos islands, which, though situated on the equator off the west coast of South America, and with a tolerably luxuriant vegetation in the damp mountain zone, yet produce hardly a single conspicuously-coloured flower; and this is correlated with, and no doubt dependent on, an extreme poverty of insect life, not one bee and only a single butterfly having been found there.

Again, there is reason to believe that some portion of the large size and corresponding showiness of tropical flowers is due to their being fertilized by very large insects and even by birds. Tropical sphinx-moths often have their probosces nine or ten inches long, and we find flowers whose tubes or spurs reach about the same length; while the giant bees, and the

[1] *Nature*, vol. ix. p. 164.

[2] See *Nature*, September 6th, 1876.

numerous flower-sucking birds, aid in the fertilization of flowers whose corollas or stamens are proportionately large.

I have now concluded this sketch of the general phenomena of colour in the organic world. I have shown reasons for believing that its presence, in some of its infinitely-varied hues, is more probable than its absence, and that variation of colour is an almost necessary concomitant of variation of structure, of development, and of growth. It has also been shown how colour has been appropriated and modified both in the animal and vegetable world, for the advantage of the species in a great variety of ways, and that there is no need to call in the aid of any other laws than those of organic development and "natural selection" to explain its countless modifications. From the point of view here taken it seems at once improbable and unnecessary that the lower animals should have the same delicate appreciation of the infinite variety and beauty—of the delicate contrasts and subtle harmonies of colour—which are possessed by the more intellectual races of mankind, since even the lower human races do not possess it. All that seems required in the case of animals, is a perception of *distinctness* or *contrast* of colours; and the dislike of so many creatures to scarlet may perhaps be due to the rarity of that colour in nature, and to the glaring contrast it offers to the sober greens and browns which form the general clothing of the earth's surface.

The general view of the subject now given must convince us that, so far from colour being—as it has sometimes been thought to be—unimportant, it is intimately connected with the very existence of a large proportion of the species of the animal and vegetable worlds. The gay colours of the butterfly and of the alpine flower which it unconsciously fertilises while seeking for its secreted honey, are each beneficial to its possessor, and have been shown to be dependent on the same class of general laws as those which have determined the form, the structure, and the habits of every living thing. The complex laws and unexpected relations which we have seen to be involved in the production of the special colours of flower, bird, and insect, must give them an additional interest for every thoughtful mind; while the knowledge that, in all probability, each style of coloration, and sometimes the smallest details, have a meaning and a use, must add a new charm to the study of nature.

Throughout the preceding discussion we have accepted the subjective phenomena of colour—that is, our perception of varied hues, and the mental emotions excited by them—as ultimate facts needing no explanation. Yet they present certain features well worthy of attention, a brief consideration of which will form a fitting sequel to the present essay.

The perception of colour seems, to the present writer, the most wonderful and the most mysterious of our sensations. Its extreme diversities and exquisite beauties seem out of proportion to the causes that are supposed to have produced them, or the physical needs to which they minister. If we look at pure tints of red, green, blue, and yellow, they appear so absolutely contrasted and unlike each other, that it is almost impossible to believe (what we nevertheless know to be the fact) that the rays of light producing these very distinct sensations differ only in wave-length and rate of vibration; and that there is from one to the other a continuous series and gradation of such vibrating waves. The positive diversity we see in them must then depend upon special adaptations in ourselves; and the question arises—for what purpose have our visual organs and mental perceptions become so highly specialised in this respect? When the sense of sight was first developed in the animal kingdom, we can hardly doubt that what was perceived was light only, and its more or less complete withdrawal. As the sense became perfected, more delicate gradations of light and shade would be perceived; and there seems no reason why a visual capacity might not have been developed as perfect as our own, or even more so, in respect of light and shade, but entirely insensible to differences of colour, except in so far as these implied a difference in the quantity of light. The world would in that case appear somewhat as we see it in good stereoscopic photographs; and we all know how exquisitely beautiful such pictures are, and how completely they give us all requisite information as to form, surface-texture, solidity, and distance, and even to some extent as to colour; for almost all colours are distinguishable in a photograph by some differences of tint, and it is quite conceivable that visual organs might exist which would differentiate what we term colour by delicate gradations of some one characteristic neutral tint. Now such a capacity of vision would be simple as compared with that which we actually possess; which, besides distinguishing infinite gradations of the *quantity* of light, distinguishes also, by a totally distinct set of sensations, gradations of *quality*, as determined by differences of wave lengths or rate of vibration. At what grade in animal development this new and more complex sense first began to appear we have no means of determining. The fact that the higher vertebrates, and even some insects, distinguish what are to us diversities of colour, by no means proves that their *sensations* of colour bear any resemblance whatever to ours. An insect's capacity to distinguish red from blue or yellow may be (and probably is) due to perceptions of a totally distinct nature, and quite unaccompanied by any of that sense of enjoyment or even of radical distinctness which pure colours excite in us. Mammalia and birds, whose structure and emotions are so similar to our own, do probably receive somewhat similar impressions of colour; but we have no evidence to show that they experience pleasurable emotions from colour itself when not associated with the satisfaction of their wants or the gratification of their passions.

The primary necessity which led to the development of the sense of colour, was probably the need of distinguishing objects much alike in form and size, but differing in important properties;—such as ripe and unripe, or eatable and poisonous fruits; flowers with honey or without; the sexes of the same or of closely-allied species. In most cases the strongest contrast would be the most useful, especially as the colours of the objects to be distinguished would form but minute spots or points when compared with the broad masses of tint of sky, earth, or foliage against which they would be set. Throughout the long epochs in which the sense of sight was being gradually developed in the higher animals, their visual organs would be mainly subjected to two groups of rays—the green from vegetation, and the blue from the sky. The immense preponderance of these over all other groups of rays would naturally lead the eye to become specially adapted for their perception; and it is quite possible that at first these were the only kinds of light-vibrations which could be perceived at all. When the need for differentiation of colour arose, rays of greater and of smaller wave-lengths would necessarily be made use of to excite the new sensations required; and we can thus understand why green and blue form the central portion of the visible spectrum, and are the colours which are most agreeable to us in large surfaces; while at its two extremities we find yellow, red, and violet, colours which we best appreciate in smaller masses, and when contrasted with the other two or with light neutral tints. We have here probably the foundations of a natural theory of harmonious colouring, derived from the order in which our colour-sensations have arisen, and the nature of the emotions with which the several tints have been always associated.[1] The agreeable and soothing influence of green light may be in part due to the green rays having little heating power; but this can hardly be the chief cause, for the blue and violet, though they contain less heat, are not generally felt to be so cool and sedative. But when we consider how dependent are all the higher animals on vegetation, and that man himself has been developed in the closest relation to it, we shall find, probably, a sufficient explanation. The green mantle with which the earth is overspread caused this one colour to predominate over all others that meet our sight, and to be almost always associated with the satisfaction of human wants. Where the grass is greenest, and vegetation most abundant and varied, there has man always found his most suitable dwelling-place. In such spots hunger and thirst are unknown, and the choicest productions of nature gratify the appetite and please the eye. In the greatest heats of summer, coolness, shade, and moisture are found in the green forest glades; and we can thus understand how our visual apparatus has become especially adapted to receive pleasurable and soothing sensations from this class of rays.

The preceding considerations enable us to comprehend, both why a perception of difference of colour has become developed in the higher animals, and also why colours require to be presented or combined in varying proportions in order to be agreeable to us. But they hardly seem to afford a sufficient explanation, either of the wonderful contrasts and total unlikeness of the sensations produced in us by the chief primary colours, or of the exquisite charm and pleasure we derive from colour itself, as distinguished from variously coloured objects, in the case of which association of ideas comes into play. It is hardly conceivable that the material *uses* of colour to animals and to ourselves required such very distinct and powerfully-contrasted sensations; and it is still less conceivable that a sense of delight in colour *per se* should have been necessary for our utilization of it.

The emotions excited by colour and by music, alike, seem to rise above the level of a world developed on purely utilitarian principles.

ALFRED R. WALLACE.

[1] There is reason to believe that our capacity of distinguishing colours has increased even in historical times. The subject has attracted the attention of German philologists, and I have been furnished by a friend with some notes from a work of the late Lazarus Geiger, entitled, *Zur Entwickelungsgeschichte der Menschheit* (Stuttgart, 1871). According to this writer it appears that the *colour* of grass and foliage is never alluded to as a beauty in the Vedas or the Zendavesta, though these productions are continually extolled for other properties. Blue is described by terms denoting sometimes green, sometimes black, showing that it was hardly recognised as a distinct colour. The *colour* of the sky is never mentioned in the Bible, the Vedas, the Homeric poems, or even in the Koran. The first distinct allusion to it known to Geiger is in an Arabic work of the ninth century. "Hyacinthine locks" are black locks, and Homer calls iron "violet-coloured." Yellow was often confounded with green, but, along with red, it was one of the earliest colours to receive a distinct name. Aristotle names three colours in the rainbow—red, yellow, and green. Two centuries earlier Xenophanes had described the rainbow as purple, reddish, and yellow. The Pythagoreans admitted four primary colours—white, black, red, and yellow; the Chinese the same, with the addition of green. If these statements fairly represent the early condition of colour-sensation they well accord with the view here maintained, that green and blue were first alone perceived, and that the other colours were successively separated from them. These latter would be the first to receive names; hence we find purple, reddish, and yellow, first noticed in the rainbow as the tints to be separated from the widespread blue and green of the visible world which required no distinctive colour-appellation. If the capacity of distinguishing colours has increased in historic times, we may perhaps look upon colour-blindness as a survival of a condition once almost universal; while the fact that it is still so prevalent is in harmony with the view that our present high perception and appreciation of colour is a comparatively recent acquisition, and may be correlated with a general advance in mental activity.