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THE COLORS OF ANIMALS AND PLANTS.[1]

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I. THE COLORS OF ANIMALS.

THERE is probably no one quality of natural objects from which we derive so much pure and intellectual enjoyment as from their colors. 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 marvelous 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 color 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 color 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,

[1] From Macmillan's Magazine.

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 colors 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 gayly-painted wings, or to the humming-bird of its jeweled 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 color has "uses" in nature that we little dreamed of, yet the relation of those colors 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 colors of organized beings; then, to point out the cases in which it has been shown that color is of use; and, lastly, to endeavor to throw some light on its nature and the general laws of its development.

Among naturalists color was long thought to be of little import, and to be quite untrustworthy as a specific character. The numerous cases of variability of color led to this view. The occurrence of white blackbirds, white peacocks, and black leopards, of white bluebells, and of white, blue, or pink milkworts led to the belief that color 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 color, 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 color through thousands of individuals. We also find that color 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 color 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 colors 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 color 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 color 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-colored birds and insects in tropical than in temperate and cold countries; but it is by no means so certain that the *proportion* of colored to obscure species is much or any greater. Naturalists and collectors well know that the majority of tropical birds are dull colored; and there are whole families, comprising hundreds of species, not one of which exhibits a particle of bright color. Such are the Timaliidæ of the eastern and the Dendrocolaptidæ of the western hemisphere. Again, many groups of birds, which are universally distributed, are no more adorned with color in the tropical than in the temperate zone: such are thrushes, wrens, goat-suckers, hawks, grouse, plovers, and snipe; and if tropical light and heat have any direct coloring 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 colored, while others contain dull and bright colored 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-colored 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 Northern China are the most beautifully colored of the whole family. In the pheasant family we have the gorgeous gold and silver pheasants in Northern China and Mongolia, and the superb impeyan pheasant in the temperate Northwest Himalayas, as against the peacocks and fire-backed pheasants of tropical Asia. Then we have the curious fact that most of the bright-colored 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-colored birds. Such are the Sahara and other deserts, where almost all the living things are sand colored; 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 colors abound, but which are yet characterized 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 gayly colored 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 colored 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 color 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 color the tropics are almost universally believed to be preëminent, 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 gayly colored 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 color 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 equaled, by any productions of the tropics.[1] But we may go further, and say that the

[1] It may be objected that most of the plants named are choice, cultivated *varieties*, far surpassing in color 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 color. 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 color almost as much as the cultivated varieties, and the same may be said of 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 color 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 favorable 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 color, 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 favored 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 color 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 two 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 color which can certainly not be surpassed even if it can be equaled between the tropics.

It appears, therefore, that we may dismiss the theory that the development of color 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

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 nursery-men 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.

are some rare and little-known phenomena which prove that, in exceptional cases, light does directly affect the colors 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 color of the chrysalis of the small cabbage butterfly (*Pontia rapæ*), when the caterpillars were confined 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 whitewashed 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 colors. 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 colored plate) in the Transactions of the Entomological Society, 1874, page 519. The caterpillar feeds on the orange-tree, and also on a forest tree (*Vepris lanceolata*) which has a lighter green leaf, and its color 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 neighboring tree, but it is probably often attached to larger branches; and Mrs. Barber has discovered that it has the property of acquiring the color, 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 color; 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 colored 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 color 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 color 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 color occurs in animals, the action is quite involuntary; but among some of the higher animals the color 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 color 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 upward either together or separately. When no pressure is exerted the color 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 defenseless, and its power of changing its color to harmonize with surrounding objects is essential to its existence. Here, too, as with the pupa of *Papilio Nireus*, colors such as scarlet or blue, which do not occur in the immediate environment of the animal, cannot be produced. Somewhat similar changes of color occur in some prawns and flat-fish, according to the color of the bottom on which they rest. This is very striking in the chameleon shrimp (*Mysis chamæleon*), which is gray when on sand, but brown or green when among sea-weed of these two colors. 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 color of the soil wherever they are found, while several caterpillars which feed on two or more plants vary in color accordingly. Several such changes are quoted by Mr. R. Meldola in a paper on Variable Protective Coloring in Insects,[1] 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 color as that of the food plant.

These peculiar powers of change of color and adaptation are, however, rare and quite exceptional. As a rule there is no direct connection between the colors 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 under surface would be equally invisible against the light of the clouds and sky. Again, the gorgeous colors 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 under wings of many moths, which are exposed only at night, contrast remarkably with the sombre tints of the upper wings, which are more or less exposed to the various colors 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 colors that everywhere meet us in the animal and vegetable world. Let us, therefore, take a wider view of these colors, 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 colors of living organisms, seems to be best expressed by a division into five groups, as follows: —

[1] Proceedings of the Zoölogical Society of London, 1873, page 153.

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

The nature of the first two groups, protective and warning colors, has been so fully detailed and illustrated in my chapter on Mimicry and other Protective Resemblances among Animals [1] that very little need be added here except a few words of general explanation. Protective colors are exceedingly prevalent in nature, comprising those of all the white arctic animals, the sandy-colored 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 colors 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-colored *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 toward 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 conspicous 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 colors 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 colored; yet when feeding on the heather it so harmonizes with the foliage and flowers as to be almost invisible. Every day fresh cases of protective coloring 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.

[1] Contributions to the Theory of Natural Selection, page 45.

The second class — the warning colors — 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 recognized, the reason being that they have a means of defense which, if known, will prevent their enemies from attacking 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 colored, 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 touches them. The reason simply is that they are not fit to eat, their juices having a powerful odor and taste that is absolutely disgusting to all these animals. Now, we see the reason of their showy colors and slow flight. It is good for them to be seen and recognized, for then they are never molested; but if they did not differ in form and coloring 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 recognized, 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 colored; many soft and apparently defenseless beetles, and many gay-colored 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 colored; and the same rule was found to apply to caterpillars, all the brown and green (or protectively colored 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.[1] 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

[1] Contributions to Theory of Natural Selection, page 117.

never hides himself, and which is gorgeously colored with red and blue. Now, frogs are usually green, brown, or earth-colored, feed mostly at night, and are all eaten by snakes and birds. Having full faith in the theory of protective and warning colors, 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 colors 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 colors, form, and habits. Strange to say, wherever there is an extensive group of directly protected forms (division *a* of animals with warning colors) there are sure to be found a few otherwise defenseless creatures which resemble them externally so as to be mistaken for them, and which thus gain protection as it were on false pretenses (division *b* of animals with warning colors). 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 defenseless cuckoos. How these curious imitations have been brought about, and the laws which govern them, have been discussed in the work already referred to.

The third class — sexual colors — comprise all cases in which the colors 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 color, as well as of color 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 color 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 color 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 color 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 color 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 colors, 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 colored 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 color 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-colored animals — includes all species which are brilliantly or conspicuously colored in both sexes, and for whose particular colors 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-colored 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 colors ; but as that theory does not explain the particular colors 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 colored 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 color of female birds when their partners are gayly colored. This subject is fully argued in my Contributions, etc., chapter vii.

As the colors 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 color here sketched out can be explained. We have first to inquire what is color, and how it is produced ; what is known of the causes of change of color ; and what theory best accords with the whole assemblage of facts.

The sensation of color is caused by vibrations or undulations of the ethereal 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 color. 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 color ; 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 four hundred and fifty-eight millions of millions of times in a second, the length of each wave being $\frac{1}{36900}$ of an inch; while the violet rays, which last remain visible, vibrate seven hundred and twenty-seven millions of millions of times per second, and have a wave-length of $\frac{1}{64516}$ 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 color-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 colors 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 color are prevented from reaching us, the remaining rays in combination produce a sensation of color 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 colors. And if portions of differently colored lights are abstracted in various degrees, we have produced all those infinite gradations of colors, 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 colors 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 colors, 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 colors appear to us capable of being produced by combinations of three primary colors, — 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 small 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 color-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 colors 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 analyze 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 colored light exactly corresponding to the colors of the rainbow. Any one color can thus be isolated and separately examined, and by means of reflecting mirrors the separate colors can be again compounded in various ways, and the resulting colors observed. This band of colored 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 colors of living things are produced, and it has only been alluded to in order to complete our sketch of the nature of color.

The colors 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 colors are the most frequent, comprising all the opaque tints of flowers and insects, and all the colors 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 color. When all the color-producing rays are reflected in due proportion the color of the object is white; when all are absorbed the color is black. If blue rays only are absorbed the resulting color is orange-red; and generally, whatever color an object appears to us, it is because the complementary colors 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 color. Sometimes simple solution in water effects a marvelous 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 color, 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 color 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 coloring 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 coloring matters in birds' eggs, several of which are chemically related to those of blood and bile. The same colors 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 colors have a different character in animals, according to their position in the integument. Following Dr. Hagen's classification, epidermal colors are those which exist in the external chitinized skin of insects, in the hairs of mammals, and, partially, in the feathers of birds. They are often very deep and rich, and do not fade after death. The hypodermal colors 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 colors sometimes exude through the pores, forming an evanescent bloom on the surface.

Interference colors 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 colors either by reflected or transmitted light, as seen in mother-of-pearl and in finely-ruled metallic surfaces. In both cases color is produced

[1] Metachromatism, or Color-Change, Chemical News, August, 1876.

by light of one wave-length being neutralized, 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 color of that neutralized is seen; and, as the thickness of the film or the fineness of the striæ undergoes slight changes, almost any color 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 colors 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 colors of humming-birds are probably due to fine striæ.

This outline sketch of the nature of color 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 color 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 neutralized, the resultant reflected light will be colored, and that this color 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 color 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 color. These considerations render it probable that color 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 color 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, etc.) 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 color of their external organs. It seems a fair conclusion that color *per se* may be considered to be normal, and to need no special accounting for, while the absence of color (that is, either *white* or *black*), or the prevalence of certain colors 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 color 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 colors 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 color 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 color in nature, taking them in the order of our functional classification of colors (page 650).

Theory of Protective Colors.—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 colored. 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 colors. An indefinite or irregular absorption of some rays and reflection of others would, therefore, produce obscure tints; while pure and vivid colors would require a perfectly definite absorption of one portion of the colored rays, leaving the remainder to produce the true complementary color. 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 colors are not in any way useful to the species. But whenever a pure color 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 colors, therefore, however curious and complex they may be in certain cases, offer no real difficulties.

Theory of Warning Colors.—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 color; hence we find among these groups some of the most exquisitely colored objects in nature. Many of the uneatable caterpillars are strikingly beautiful; while the Danaidæ, Heliconidæ, and protected groups of Papilionidæ comprise a series of butterflies of the most brilliant and contrasted colors. The bright colors 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 colors offer any difficulty. Conspicuousness being useful, every variation tending to brighter and purer colors 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 colored but uneatable creatures, a difficulty really exists, and to many minds is so great as to be insuperable. It will be well, therefore, to endeavor 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 toward 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 color 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 colors, 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 color among butterflies, —while a considerable number are tinged or spotted with yellow, also a very common color, 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 colors 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 color, 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 color 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 neighbor; 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 colors 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]

(To be concluded.)

[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, etc., 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.