THE

COLOURS OF ANIMALS

THEIR MEANING AND USE

ESPECIALLY CONSIDERED IN THE CASE OF INSECTS

BY

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ETC.

WITH CHROMOLITHOGRAPHIC FRONTISPIECE

AND SIXTY-SIX FIGURES IN TEXT

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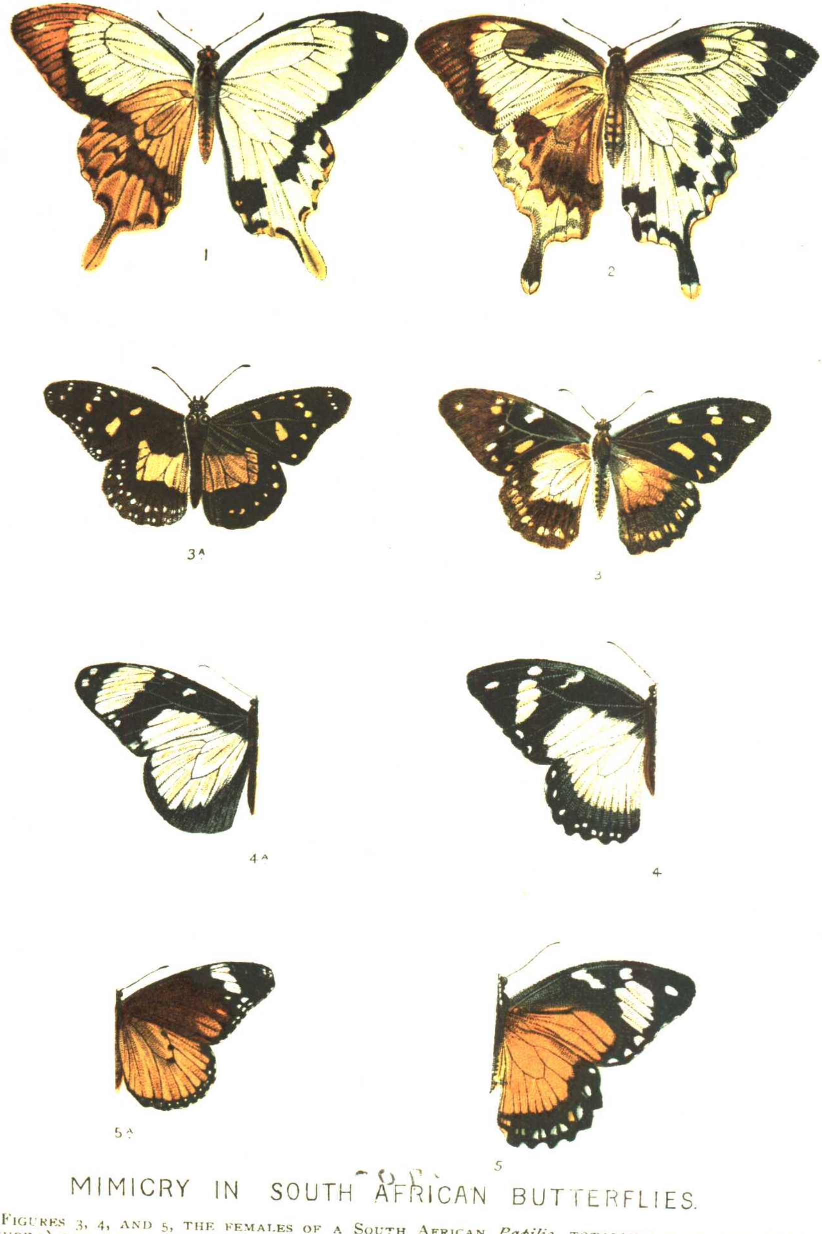

MIMICRY IN SOUTH AFRICAN BUTTERFLIES.

Figures 3, 4, and 5, the females of a South African *Papilio*, totally unlike the male (Figure 1), but mimicking respectively three species of the unpalatable genus, *Danais* (Figures 3a, 4a, and 5a). The female (Figure 2) of a nearly allied *Papilio*, in Madagascar, is not mimetic,

DESCRIPTION OF PLATE

The figures have been copied, by kind permission of the author, and the council of the Linnean Society, from the plates accompanying Mr. Roland Trimen's paper, 'On some Remarkable Mimetic Analogies among African Butterflies.' ('Linn. Soc. Trans.' vol. xxvi. pp. 497, *et seqq.*)

All figures are represented one-half of their natural size. The appearance of the under side of the wings is shown on the left hand of the four upper figures.

Figure 1.—The male of *Papilio merope* (now called *P. cenea*; the name *P. merope* being restricted to the West African form), from Knysna, Cape Colony. A closely allied butterfly (*P. meriones*), with a very similar male, is found in Madagascar.

Figure 2.—The female of *Papilio meriones*, from Madagascar. The male is almost exactly like Figure 1. The black bar on the costal margin of the fore wing of the female probably represents the beginning of the darkening which has been carried so far in the females of the African *P. merope* and *P. cenea*.

Figure 3.—First or *cenea*-form of female of *Papilio merope* (now called *P. cenea*), from Knysna, Cape Colony. The female is totally unlike the male of the same species (Figure 1), but closely mimics an unpalatable butterfly, *Danais echeria*, prevalent in its locality. The appearance of the latter is shown in Figure 3*a*. The mimetic resemblance is seen to be very striking on both upper and under sides of the wings. A local variety of the *Danais* is also mimicked by a corresponding variety of the *Papilio*.

Figure 4.—Second or *hippocoon*-form of female of *Papilio merope* (now called *P. cenea*), from Graham's Town, Cape Colony. This variety mimics the southern form of the unpalatable *Danais niavius*, shown in Figure 4*a*.

Figure 5.—Third or *trophonius*-form of female of *Papilio merope* (now called *P. cenea*), from Knysna, Cape Colony. This variety mimics the abundant and unpalatable *Danais chrysippus* shown in Figure 5*a*.

In a closely allied species of Papilio from West Africa (the true *Papilio merope*) the male closely resembles Figure 1, while there are two mimetic varieties of female. The *hippocoon*-form is like Figure 4, except that it is larger and the white patch on the hind wing is smaller; corresponding in both these respects to the West African variety of *Danais niavius*. The *trophonius*-form resembles Figure 5. There is no *cenea*-form of this species. For further details see pp. 234–38.

PREFACE

I HAVE adopted a general title, 'The Colours of Animals,' in order to indicate the contents of this volume, although the vast majority of the examples are taken from insects, and indeed almost invariably from a single order, the Lepidoptera. The examples are, however, employed merely to illustrate principles which are of wide application.

I have purposely abstained from multiplying instances when a little observation or even reflection will supply them in large numbers. For example, the ordinary Protective Resemblances of mammals and birds are barely alluded to, on this account. On the other hand, more difficult problems, such as the change of colour in arctic mammals, or the meaning of the colours of birds' eggs, are treated at far greater length. My object in both cases is the same: to stimulate observation in a subject which will amply repay investigation, from the scientific value of the results, and the never-failing interest and charm of the inquiry.

Variable Protective Resemblance in insects is treated in considerable detail, for the reasons given above, and because much of the work is so recent that no complete account can be found outside the original memoirs.

My chief object has been to demonstrate the utility of colour and marking in animals. In many cases I have attempted to prove that Natural Selection has sufficed to account for the results achieved; and I fully believe that further knowledge will prove that this principle explains the origin of all appearances except those which are due to the subordinate principle of Sexual Selection, and a few comparatively unimportant instances which are due to Isolation or to Correlation of Growth.

In support of these views I have endeavoured to bring together a large amount of experimental evidence in favour of the theories as to the various uses of colour. Further experiments are still greatly needed.

In the chapters on 'Sexual Selection' I have argued in favour of Darwin's views, and have attempted to defend them against recently published attacks.

At the conclusion of the volume I have brought forward a detailed classification of the various uses of colour, in which new, and, I believe, more convenient terms are suggested. Definitions and examples are also given in the classification, which is, in fact, a brief abstract of the whole book.

I have to thank the Councils of various scientific societies for the courteous permission to copy figures from their respective publications. The figures in the coloured plate are copied from the plates accompanying Mr. Roland Trimen's paper in the 'Transactions of the Linnean Society,' vol. xxvi. pp. 497–522. Figures 18, 19, 20, 21, and 22 are copied from the plate accompanying Mr. R. Bowdler Sharpe's paper in the 'Proceedings of the Zoological Society,' 1873, pp. 414 *et seqq.* Figures 3, 4, 5, 6, 7, 8, 11, 14, 58, 60, 61, 62 are copied from the plates and woodcuts accompanying my papers in the 'Transactions of the Entomological Society,' 1884, 1885, 1887, and 1888. Figures 25, 26, and 27 are copied from the plate accompanying Mrs. Barber's paper in the 'Transactions of the Entomological Society,' 1874, pp. 519 *et seqq.* Figures 29 and 30 are copied from the plate and woodcuts accompanying my paper in the 'Philosophical Transactions of the Royal Society,' vol. 178 (1887), B, pp. 311–441. Figures 15, 16, 53, 54, 63, 64, 65, 66 are copied from the woodcuts and plates accompanying G. W. and E. G. Peckham's paper in the 'Occasional Papers of the Natural History Society of Wisconsin,' vol. i. (1889), Milwaukee. Figures 55 and 56 are copied from the plates accompanying Professor Weismann's 'Studies in the Theory of Descent,' translated by Professor Meldola. Figure 10 is copied from one of the plates accompanying Dr. Wilhelm Müller's 'Südamerikanische Nymphalidenraupen' ('Zoologische Jahrbücher,' J. W. Spengel, Jena, 1886). Figure 42 is copied from Vogt ('The Natural History of Animals': English translation: Blackie and Son). Figures 44 and 45 are copied from the plates accompanying Curtis's 'British Lepidoptera.' The remaining figures are original. Figure 17 was kindly lent me by Dr. A. R. Wallace, to whom it had been sent by Mr. Wood-Mason. In preparing the drawings of the original figures I have been greatly assisted by my wife, my sister Miss L. S. Poulton, Miss Horman Fisher, Mr. Alfred Sich, Mr. Alfred Robinson, and especially by Miss Cundell.

I have almost invariably referred to original papers from which facts or conclusions have been adopted; so that any reader having access to a scientific library may easily gain possession of further details. Not wishing to overburden the book with such notes, I have abstained from referring constantly to my own papers, although most of the examples are taken from them. A list of my papers which deal with the colours of insects is therefore printed below.

'Transactions Entomological Society,' London, 1884, pp. 27–60
" " " " 1885, " 281–329
" " " " 1886, " 137–179
" " " " 1887, " 281–321
" " " " 1888, " 515–606
'Philos. Trans. Royal Society,' vol. 178 (1887), B, pp. 311–441
Abstract of the above in 'Proceedings Royal Society,' 1887, vol. xlii. pp. 94–108
'Proceedings Royal Society,' 1885, vol. xxxviii. pp. 269–315
" " " 1886, vol. xl. pp. 135–173
'Proceedings Zoological Society,' 1887, pp. 191–274

Short papers or notes (exclusive of those which are mere abstracts of the above) :—

'Proceedings Entomological Society,' London,				1887,	pp. l–li
,,	,,	,,	,,	1887,	,, lxi–lxii
,,	,,	,,	,,	1888,	p. v
,,	,,	,,	,,	,,	pp. viii–x
,,	,,	,,	,,	,,	,, xxvii–xxviii
,,	,,	,,	,,	1889	,, xxxvii–xl

'Journal of the Victoria Institute,' 1888, vol. xxii., 'On Mimicry.'

It is my pleasant duty to thank many friends for their kind assistance. I owe to Professor Meldola more than I can possibly express: his writings first induced me to enter upon this line of investigation, and I have had the benefit of his great experience and wise advice during the whole of the time that I have been at work. Nearly every subject touched upon in this volume has been discussed with him.

Professor Westwood has always been most kind in helping me with the literature of the subject, with which he has so intimate an acquaintance, and in giving me the free use of the Hope collection at Oxford. Professor E. Ray Lankester has read the proof-sheets dealing with the classifications of the uses of colour, and has offered valuable suggestions. Several beautiful examples were suggested to me by Professor C. Stewart. Dr. Günther, Mr. Roland Trimen, Mr. Oldfield Thomas, Mr. R. Bowdler Sharpe, Mr. F. E. Beddard, Mr. W. W. Fowler, and Mr. A. H. Cocks have been very kind in answering questions upon their special subjects. Sir John Conroy has kindly helped me in explaining the physical questions involved in the first chapter. I am especially pleased to speak of the help received from my former pupils Mr. W. Garstang and Mr. R. C. L. Perkins, who have supplied many valuable instances, which are specified in the volume, where other kind assistance is also duly acknowledged.

Although I have ventured to disagree with my friend Dr. A. R. Wallace upon the subject of 'Sexual Selection,' I wish to acknowledge how very much I owe to his writings, which I have very frequently quoted. I have also made great use of the late Thomas Belt's extremely interesting and suggestive 'Naturalist in Nicaragua.'

Among recent papers I wish especially to mention that by G. W. and E. G. Peckham, of Milwaukee, U.S.A. The minute observation of these authors upon the courtship of spiders of the family *Attidæ* is a model for investigation in a subject which has never before been attacked systematically.

Above all, I should wish to acknowledge, although I can never fully express, the depth of my indebtedness to the principles which first made Biology a science, the principles enunciated by Charles Darwin. It is common enough nowadays to hear of new hypotheses which are believed (by their inventors) to explain the fact of evolution. These hypotheses are as destructive of one another as they are supposed to be of Natural Selection, which remains as the one solid foundation upon which evolution rests. I have wished to express this conviction because my name has been used as part of the support for an opposite opinion, by an anonymous writer in the 'Edinburgh Review.'[1] In an article in which unfairness is as conspicuous as the prejudice to which it is due, I am classed as one of those 'industrious young observers' who 'are accumulating facts telling with more or less force against pure Darwinism.'[2] On the strength of this and other almost equally strange evidence, the Reviewer triumphantly exclaims, 'Darwin, the thanes fly from thee!' In view of this public mention of my name, I may perhaps be excused for making the personal statement that any scientific work which I have had the opportunity of doing has been inspired by one firm purpose—the desire to support, in however small a degree, and to illustrate by new examples, those great principles which we owe to the life and writings of Charles Darwin, and especially the preeminent principle of Natural Selection.

E. B. P.

OXFORD: *Dec.* 28, 1889.

[1] *Edinburgh Review.* Article V. April 1888, pp. 407–47.

[2] p. 443. The bias of the writer appears in a most singular manner upon this page. In the short space of seventeen lines the following adjectives are divided between five writers and their works:—industrious, illustrious, gifted, well-read, acute, intelligent, brilliant, thoughtful. I need hardly say that all five writers are believed by the Reviewer to oppose the theory of Natural Selection.

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THE

COLOURS OF ANIMALS

CHAPTER I

THE PHYSICAL CAUSE OF ANIMAL COLOURS

Colours due to absorption

THE colours of animals are produced in various ways. By far the commonest method is the *absorption* of certain elements of light by means of special substances which are called *pigments*, or *colouring matters*. The colour of each pigment is due to those elements of the light which it does not absorb, and which can therefore emerge and affect the eye of the spectator. Black is, of course, caused by the absorption of all the constituents of light, so that nothing reaches the eye. The colour of red pigment, like that of red glass, depends upon the fact that red is less absorbed than any other element of the light which passes through. If a sheet of red glass be placed upon white paper, the light traverses the glass, is reflected from the surface of the paper, re-traverses the glass, and emerges. Similarly, in painting, bright effects are produced by covering a surface of Chinese white with the desired colour. The light passing twice through the thickness of the colour, absorption is far more complete than when only one thickness is traversed, as in a piece of red glass held up to the light. Absorption being more complete, the red colour is deeper. Animal pigments are nearly always twice traversed by the light, and therefore a very thin layer produces a considerable effect.

Animal colours are therefore generally due to precisely the same optical principle which causes the colour of a wall-paper, a carpet, or a picture. Certain transparent animals are, however, for the most part coloured by light which passes but once through them, upon the same principle as the colours of a stained-glass window. The beautiful transparent blue of many pelagic animals, such as the Portuguese Man-of-war (*Physalia*), is caused in this way.

It would be out of place to discuss the details of the causes of colour by absorption. I may, however, mention that vibrations of very different rates are started in the luminiferous ether by the sun, the electric light, &c. A certain series of these vibrations causes the effect of white light when it falls on our retina; but there are vibrations above and below this visible series—vibrations which we cannot see. We can, however, prove their existence in other ways;

and it is certain that some animals can see vibrations which do not affect our eyes.[1] The slowest vibrations that we can see, produce the effect of red, the most rapid the effect of violet, while the intermediate vibrations cause the other well-known colours of the rainbow or the spectrum.

The absorption of certain elements of light therefore means the disappearance of ethereal vibrations with a certain speed. It is believed that these vibrations disappear because their motion has been communicated to the particles of the absorbing body. It is also believed that these particles are in a state of constant vibration, and that the vibrations of ether, which are timed to those of the body, are used up in increasing the motion of the latter.

A white appearance due to light being scattered

The production of white is due to a different principle, for we know that when light passes through a body without any absorption, the body is transparent and invisible rather than white. When all the light passes through, the body is completely invisible. Whiteness is due to reflection of the whole visible series of vibrations, unaccompanied by the absorption of a part of them, as in the production of colours. But regular reflection, viz. reflection from

[1] Sir John Lubbock, *The Senses of Animals*, Chapter X. (International Scientific Series).

a polished surface like that of a mirror, does not cause whiteness: it renders the surface itself invisible, but produces images of surrounding objects. A white appearance is produced by irregular reflection, which causes the light to be scattered or reflected in all directions. To produce such a result there must be an immense number of surfaces in an immense number of different directions. If a coloured substance be reduced to powder of various degrees of fineness, the colour will diminish in intensity, and the whiteness will increase, according to the fineness of the powder; this is because the number of reflecting surfaces is increased, while the thickness of the grains is diminished. This will be clear from the following consideration. When a beam of light falls on a sheet of glass, a known fraction (about 4 per cent.) of the light is reflected back from the first surface: the larger portion, however, enters the glass, and, after suffering a certain amount of absorption, reaches the second surface and is again partially reflected. If the glass be powdered, the number of surfaces will be so immensely increased that all the light will be reflected by a small thickness of the powder. The light reflected from the second surface of each grain of coloured glass will still be coloured by absorption, but not sufficiently to produce any visible results, when the thickness of the grain is very small.

Reflection is the *immediate* cause of whiteness, and the amount of reflection is due to the difference between the refractive powers (viz. the power of changing the direction of rays of light) possessed by the grains of glass and the substance, such as air or water, which lies between them. Thus the refractive powers of glass and water are much nearer than those of glass and air: hence a dry powder will reflect far more than a wet one, and will appear much whiter.

To take a few familiar examples: snow is white, because of the minute globules of air which refract very differently from the crystals between which they are entangled; ice, on the other hand, is transparent. If snow be compressed the air is driven out, and the mass becomes transparent; if ice be powdered it becomes white like snow. The froth of a coloured liquid is not coloured like the latter, but is white. Milk and fat are white because light is scattered from the surfaces of the countless oil globules, which refract very differently from the substance which lies between them. The surface of well-polished glass is almost invisible, because it reflects regularly, but a scratched surface is very visible, because there are surfaces in many different directions, which therefore scatter the light, while the far more numerous surfaces of ground glass scatter the light far more effectually and produce a white appearance.

The white markings of animals are produced in various ways. White hairs and feathers owe their appearance, like snow, to the number of minute bubbles of gas which are contained in their interstices. Fat is also made use of to give a white appearance; and the same result may be obtained by the presence of minute granules, probably akin to pigment, but differing widely from it in optical properties, in that no absorption takes place.

Colours due to thin plates

It has been stated already that when light traverses a sheet of glass surrounded by air, a certain proportion of it is reflected back at the first surface and a certain proportion at the second surface. The light will be reflected in the same direction from both surfaces. It is believed that the vibrations of ether, some of which affect us as light, are in the form of undulations of different lengths; if, therefore, the sheet of glass be sufficiently thin, some of the undulations reflected from the second surface will interfere with those started from the first surface. This will happen when the sheet is of such a thickness that the wave of light reflected from the second surface is half an undulation behind that reflected from the first surface; for then the two sets of undulations will be in opposite directions, and will therefore neutralise each other.

This will be quite clear if we apply the same reasoning to those visible undulations from which the name itself has been borrowed—the waves on the surface of water. If a set of ripples is started by the