

Derby, "is interesting, and the success of those who do succeed is lasting. What general, what orator, what statesman, what man of letters can hope to leave a memory like that of Darwin? An invalid in health, a man who seldom stirred from home, a man until his later years very little known to the outer world, but who, from his quiet study, revolutionized the thought of Europe, and will be remembered as long as Newton and Bacon. If fame be ever worth working for—I do not say it is—that kind of fame is surely, of all, the most durable and the most desirable. Well, I have perhaps digressed from our proper subject, for it is not likely that we have a future Darwin in this room, but it is no exaggeration to say that, as a rule, no man who has taken to science as the work of his life regrets the choice, while men who have done important work in other lines feel like Renan, who, at the height of his literary eminence, tells us in his autobiography that he has often regretted that science, rather than historical research, had not been the object of his early pursuit."

MIMICRY.¹

THE relationship of mimicry to other animal colours can only be explained by giving a short account of the latter.

I. The commonest use of colour is for concealment (*cryptic*), enabling an animal (1) to escape its enemies, or (2) to approach its prey. In these (1) protective (*procryptic*) or (2) aggressive (*anticryptic*) resemblances, animals seek concealment by a likeness to some object which is of no interest to enemies or prey respectively. Similar effects may be produced by the use of foreign objects with which the animal covers itself to a greater or lesser extent (*allocryptic*).

EXAMPLES.—(1) *Procryptic Colours*. A green pipe-fish (*Siphonostoma typhle*) conspicuous in the water, but well concealed among the leaves of *Zostera*: the brown lappet moth (*Gastropacha quercifolia*), conspicuous on a smooth deal board, but well concealed among dead leaves.

(2) *Anticryptic Colours*. A large frog (*Ceratophrys cornuta*) from tropical South America, which almost buries itself in a hole in the ground, while the head, which is exposed, harmonizes with the surroundings. In this position it waits till the small animals on which it feeds approach or even walk over it.

(3) *Allocryptic Colours*. A small English crab (*Stenorhynchus phalangium*) which decks itself with pieces of seaweed: another small English crab (*Hyas coarctatus*) was shown with and without its covering of pieces of seaweed (*Ulva*, &c.).

Mimicry is closely related to the colours illustrated above, but differs in that the animal resembles an object which positively repels its enemies or positively attracts its prey rather than one which is of no interest to either. It is better, therefore, to defer its consideration until after the description of the colours which form the models for mimicry.

II. The second great use of colour is to act as a warning or signal (*sematic colour*), repelling enemies by the indication of some unpleasant or dangerous quality (*aposematic* or *warning colours*), or signalling to other individuals of the same species, and thus assisting them to escape from danger (*episematic* or *recognition colours*). In a very interesting group of cases (*allosematic*), the animal warns off its enemies by associating with itself some other animal with unpleasant qualities and warning colours.

EXAMPLES.—(1) *Aposematic Colours*. The two unpalatable English moths (*Spilosoma urticae* and *S. mendica*, female), when disturbed, assume attitudes which serve to display their conspicuous yellow and black colours. Portchinski has recently shown that an unpalatable European chrysalis (*Limenitis populi*) bears the most detailed resemblance to a chrysalis which has been pecked and rejected by a bird. The American skunks (*Mephitis mephitis*, *Conepatus mapurito*, &c.) possess the power of emitting an intolerable stench, and are extremely conspicuous black and white mammals.

(2) *Episematic Colours*. In the common rabbit the white tail serves as a beacon to other individuals, pointing the way to the burrow.

(3) *Allosematic Colours*. A hermit crab (*Pagurus bernhardus*) is commonly found with a sea anemone (*Sagartia parasitica*) attached to its shell; in another hermit crab (*Pagurus prideauxii*)

the association is more constant, and the sea anemone (*Adamsia palliata*) is specialized for life on the shell of the crustacean. Two crabs (*Polydectes cupulifer* and *Melia tessellata*), described by Möbius in some of the islands round Madagascar, invariably held a sea anemone in each claw. Two other groups of animals, sponges, and ascidians, in addition to sea anemones, are avoided by the enemies of the Crustacea, and these are also made use of by the latter. Thus the hermit crab (*Pagurus cuanensis*) is found in shells which are covered with a (generally) brightly-coloured sponge (*Suberites domuncula*): Möbius also describes a hermit crab (*Ascidiophilus caphyraformis*) which lives in a case formed by an ascidian.

III. Mimicry may be defined as false warning or signalling colours (*pseudosematic*), repelling enemies by the deceptive suggestion of some unpleasant or dangerous quality (*pseudaposematic*) or attracting prey by the deceptive appearance of something attractive to them (*pseudepisematic*). Even foreign objects commonly associated with some well-defended and aggressive species may be mimicked by a comparatively defenceless form (*pseudallosematic*).

EXAMPLES.—(1) *Pseudaposematic Colours*. The various degrees of complexity with which protective mimicry occurs in insects was shown by examples of Indian and African Lepidoptera.

(a) Both sexes of the Indian *Papilio agestor* closely resemble the much commoner and nauseous butterfly *Euplaea tytia*.

(b) An Indian moth (*Epicopeia philenora*) similarly mimics an unpalatable butterfly (*Papilio protenor*), but in this case the male moth mimics the appearance of the male butterfly, and the female moth that of the female.

(c) If the mimicking species became common relatively to the mimicked, the deception would be liable to be detected. We therefore find that two or more models are often mimicked by the same species. Thus the male of the Indian *Elymnias leucocyma* mimics *Euplaea binotata*, while the female mimics the female of *Euplaea linnei*. Both these *Euplaeas* are also imperfectly mimicked by day-flying moths (*Amesia midama*). So also the male of the Indian *Papilio castor* mimics *Papilio chaon*, while the female mimics *Euplaea core*: in the south, *Papilio chaon* is absent, and BOTH sexes of the species (*Papilio dravidarum*) which represents *P. castor*, mimic *E. core*.

(d) Female butterflies are exposed to more dangers than the swiftly-flying males, and we find many instances in which the former are mimetic, although the latter are not. Thus the female of *Hypolimnas bolina* mimics *Euplaea core*, while the male is non-mimetic. The same is true of *Hypolimnas misippus*, the female of which mimics *Danais chrysippus*. Two forms closely allied to the latter (some regard them as merely varieties) are also mimicked by the former.

(e) The mimetic females also often resemble two or more different species of nauseous butterflies. Thus the female of *Papilio pammon* appears in two forms, mimicking respectively *Papilio Hector* and *P. aristolochae*; while the females of *Euripus halitherses* (the male of which is probably mimetic) mimic *Euplaea rhadamantus* and *Euplaea deione*.

(f) There are also striking examples in which the non-mimetic ancestor of a mimetic species has been preserved, e.g. in an adjacent island. Thus the female of *Elymnias undularis* mimics *Danais genutia* in Sikkim and North-East India; in Rangoon and Burmah there is a variety of the latter with white hind wings which is as common as the typical form, and the female of *E. undularis* is beginning to mimic this variety; in South India *E. undularis* is represented by *E. caudata*, in which the male is also beginning to mimic *D. genutia*, and the female is a more perfect mimic than in the other localities; in the Andaman Islands *E. cottonii* represents *E. undularis*, and both sexes appear to be non-mimetic, while *D. genutia* has never been recorded from this locality. A still more wonderful example is found in Africa and adjacent islands. *Papilio meriones* of Madagascar is non-mimetic, and the sexes are alike; the same is true of a closely-allied species, *P. humbloti*, recently discovered in Grand Comoro, and of *P. antinorii* recently found in Abyssinia. A very nearly related species in West Africa has a closely similar non-mimetic male, while two forms of female mimic *Danais chrysippus* and *Danais niavius*. In South Africa *Papilio cenea* has an almost identical male, while the females mimic *D. chrysippus*, the southern form of *D. niavius*, and two varieties of *D. echeria*.

(g) There are also examples which show the origin of mimicry, in which the resemblance is very imperfect, but, nevertheless, sufficient to afford protection. The blue *Euplaeas* of

¹ Abstract of Lecture delivered by Edward B. Poulton, F.R.S., on Friday, September 5, at the Leeds meeting of the British Association.

India, &c. (such as *E. harrisi*, *E. linnæi*, *E. splendens*, and *E. irawada*) form a very characteristic group, while their general type of appearance is imperfectly mimicked by a group of day-flying moths (*Ameletus midama*, *A. aliris*, *A. sanguiflua*). It is extremely probable that the wonderfully close likeness of many mimetic species arose by gradual stages from some general resemblance to a type of colour or pattern possessed by some large group of unpalatable insects.

The above-cited examples are some of them well-known, they were chosen to illustrate the various different ways in which mimicry occurs.

Evidence for the evolution of mimetic resemblance has also been forthcoming as the result of recent and hitherto unpublished work.

Many moths have lost the scales which are characteristic of the order of insects to which they belong, so that their wings become transparent, and they mimic stinging insects such as wasps or hornets. This is the case with two British hawk-moths (*Hemaris fuciformis* and *bombyliiformis*). It is known that when these moths emerge from the chrysalis, the transparent parts of their wings are thinly covered with scales which are shaken off during the first flight. The loss of the scales has now been shown to be due to the rudimentary nature of the stalk at the base of the scale and of the socket in which the stalk is inserted; a closely-allied Indian moth (*Hemaris hylas*) was still more completely denuded of scales, but in it also the rudimentary sockets were found to be thinly scattered over the transparent part of the wing. These facts suggested that all moths with transparent wings may be found to repeat, in the course of their own individual lives, the history of the change by which the transparency has been attained by the species. Investigation has supported this suggestion. The examination of two British moths which resemble hornets or wasps was especially instructive. In one of these (*Sesia apiformis*) the mimicry is not so perfect as in the other, and is therefore presumably of more recent date; in this moth the rudimentary scales which fall off are comparatively perfect, while in the other species (*S. bembeciformis*) they are far more degenerate, inasmuch as they have been useless to the species for a far longer period of time. It is interesting to note that these degenerate scales have not been reduced in size in either species, but are, on the contrary, much larger than the scales which are retained for the whole life of the moth. In the allied "clearwings" of the genus *Trochilium*, the transparency of the fore wing has been attained by the trans-

parency of scales which are retained as well as by the loss of scales.

(2) *Pseudepisematic Colours*. This division not only includes the examples of aggressive mimicry in which an animal resembles another, and so is enabled to approach and injure it in some way, but also the cases of alluring colouring in which an animal possesses a lure which is attractive to its prey.

Examples of the former are seen in the flies of the genus *Volucella*, which are enabled to lay their eggs in the nests of humble-bees, &c., because of their close resemblance to the latter. The larvæ of the fly feed upon those of the bee.

Examples of alluring colouring. An Asiatic lizard (*Phrynocephalus mystaceus*) possesses pink flower-like structures at the corners of its mouth, it is probable that flies, &c., are thus allured. A terrapin (*Macrolemmys Temminckii*) from the Southern States of America, when hungry, opens its mouth and moves about two filaments at the anterior end of its tongue. These look like worms moving in a crevice in the rocks, and attract prey. The animal is otherwise perfectly motionless, and resembles a weed-covered rock. The fish *Lophius piscatorius* (the angler or fishing-frog) attracts its prey by a brightly coloured lure placed over its large mouth, the rest of the body being concealed. Certain deep-sea fishes allied to *Lophius* (*Cerattus hispidus*, *C. uranoscopus*, &c.) have a phosphorescent lure which attracts the other fish on which they feed.

(3) *Pseudallosematic Colours*. A very striking instance was discovered by Mr. W. L. Sclater in tropical South America. The well-defended and abundant leaf-carrying ants (*Ecodoma*) are mimicked by an immature Homopterous insect possessing a shape and colour which closely resemble the ant together with the piece of leaf it is carrying.

IV. *Epigamic colours* are the bright tints and patterns displayed during courtship. As in other classes of colours the same effects may be produced by the use of foreign objects (*Allepigamic*). Examples are found in the various beautiful or curious objects collected by bower-birds for the decoration of their bowers. Especially interesting in this respect is the *Amblyornis inornata* of New Guinea.

Mutual relationship of the above-mentioned classes of colours. It is clear that I. (*Cryptic*) and III. (*Pseudosemantic*) colours are closely related; they may be conveniently grouped under one head:—*Apatetic* or deceitful colours. The following scheme will be found to represent the mutual relationships:—

I. <i>Apatetic Colours</i> . (Resembling the environment, or some other species, or acting as a lure.)		II. <i>Sematic Colours</i> . (Warning and Signalling.)	III. <i>Epigamic Colours</i> . (Displayed in Courtship.)
A. <i>Cryptic Colours</i> . (Protective and Aggressive Resemblances.)	B. <i>Pseudosemantic Colours</i> . (False Warning and Signalling Colours.)		
(1) <i>Procryptic Colours</i> . (Protective Resemblances.)	(1) <i>Pseudaposematic Colours</i> . (Protective Mimicry.)	(1) <i>Aposematic Colours</i> . (Warning Colours.)	
(2) <i>Anticryptic Colours</i> . (Aggressive Resemblances.)	(2) <i>Pseudepisematic Colours</i> . (Aggressive Mimicry and Alluring Colouring.)	(2) <i>Episematic Colours</i> . (Recognition Markings.)	
<i>Allo-cryptic Colours</i> . (Concealment gained by use of foreign objects.)	<i>Pseudallosematic Colours</i> . (Resemblance to some foreign object associated with mimicked species.)	<i>Allosemantic Colours</i> . (Warning Colours of another Animal made use of.)	<i>Allepigamic Colours</i> . (Display of foreign objects in Courtship.)

The comparatively new terms employed in the lecture were due to the kind help of Mr. Arthur Sidgwick. The beautifully painted lantern slides were due to the great skill and patience of the artist, Mr. H. M. J. Underhill. The examples of *Allo-cryptic* and many of those of *Cryptic* and of *Allosemantic* colours were painted from the living animals in the Marine Biological Laboratory at Plymouth. Colonel Swinhoe had very kindly

suggested good examples of mimicry among Indian butterflies, and had lent from his beautiful collection the specimens for copying. Mr. H. Grose-Smith had kindly lent the African examples. Rev. F. J. Smith had most kindly helped in photographing the examples selected. Mr. W. R. Morfill had kindly translated Portchinski's Russian paper, thus rendering possible the use of some very interesting examples.