Mimicry and the Darwinian Heritage

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Source: *Journal of the History of Ideas*, Apr. - Jun., 1965, Vol. 26, No. 2 (Apr. - Jun., 1965), pp. 211-220

Published by: University of Pennsylvania Press

Stable URL: https://www.jstor.org/stable/2708228

MIMICRY AND THE DARWINIAN HERITAGE

By Mary Alice Evans*

"Dear Bates," wrote Darwin in 1862, three years after *The Origin of Species* had been published, "I have just finished, after several reads, your paper. In my opinion it is one of the most remarkable and admirable papers I ever read in my life. The mimetic cases are truly marvelous, and you connect excellently a host of analogous facts. The illustrations are beautiful, and seem very well chosen. . . . I rejoice that I passed over the whole subject in the *Origin,* for I should have made a precious mess of it. You have most clearly stated and solved a wonderful problem. . . . Your paper is too good to be largely appreciated by the mob of naturalists without souls, but rely on it, that it will have lasting value, and I cordially congratulate you on your first great work." [1] Darwin thus expressed his appreciation of the work of Henry W. Bates, who made mimicry "an established element in Darwinism" [2] by showing that the phenomenon was an excellent example of adaptation through natural selection.

Long before 1859, the colors of plants and animals had been noticed, particularly if they were bright, or if they helped an organism blend into its background. For example, Aristotle knew that an octopus could change its color so as to look like the adjacent stones. Seasonal color changes of northern animals were known to Theophrastus. Pliny recorded the ability of the chameleon to assume the color of its surroundings. In the seventeenth century, Francesco Redi, while working with insects in his experiments on spontaneous generation, made note of stick-like insects. However, little was known of the importance of color, and nothing of how color patterns had come about.

Erasmus Darwin, grandfather of Charles Darwin, and for his time an interesting and capable biologist in his own right, wrote: "The efficient cause of the various colours of the eggs of birds, and of the hair and feathers of animals, is a subject so curious, that I shall beg to introduce it in this place. The colours of many animals seem adapted to their purposes of concealing themselves either to avoid danger, or to spring upon their prey. Thus the snake and wild cat, and leopard, are so coloured as to resemble dark leaves and their lighter interstices; birds resemble the colour of the brown ground, or the green hedges, which they frequent; and moths and butterflies

* I would like to thank Mrs. Joan McGrath, one of my former students at Wellesley College, for the initial idea and inspiration for this paper.

[1] *Life and Letters of Charles Darwin,* ed. F. Darwin (New York, 1959), II, 183–5.

[2] W. L. Distant in "Obituary" (for Bates), *Proc. Royal Geogr. Soc.,* XIV (April 1892), 252.

are coloured like the flowers which they rob of their honey."[3] He also noted that "many animals in countries covered with snow become white in winter, and are said to change their colour again in the warmer months, as bears, hares, and partridges."[4] Erasmus Darwin's observations were good, but his hypotheses as to how the colors came to be are of little value except historically. He discussed color in his chapter on generation, saying that the retina of the eye transmitted the colors the animal was seeing through fibers to the skin, which in turn caused the feathers, etc., to take on the colors noted by the retina. He gave the chameleon as the best example. He added that the egg shells were colored "by the imagination of the female parent."[5] He must have sensed the inadequacy of the last statement, at least, for he went on to say that all was not explained, but that conjectures could lead to further discoveries.

Naturalists coming after Erasmus Darwin described more examples of protective coloration, especially among insects, but perhaps they lacked his imagination or courage to offer explanations of the development of such phenomena. In *An Introduction to Entomology,* W. Kirby and W. Spence, in a chapter on "Means of Defence of Insects,"[6] mentioned the use of color and form to either deceive, dazzle, alarm or annoy enemies. They also said that some insects were protected by being able to conceal themselves, such as the caterpillars which resembled twigs, and flies which resembled bumblebees, so they could enter the bees' nest and lay their eggs. In 1819, W. S. MacLeay[7] noted the likeness of some flies to bees and wasps, not only in structure, but also in life history. He further pointed out that these similarities were due not to the fact that the two different groups were closely related, for they were not, but to what he called "analogy," which we now call convergent evolution. Subsequent workers added further evidence mainly to substantiate MacLeay.[8]

In the first edition of *The Origin of Species,* Charles Darwin, in the chapter on natural selection, included the following: "Although natural selection can act only through and for the good of each being, yet characters and structures, which we are apt to consider as of very trifling importance, may thus be acted on. When we see leaf-eating insects green, and bark-feeders mottled-grey; the alpine ptarmigan white in winter, the red-grouse the colour of heather, we must believe that these tints are of service to these birds and insects in preserving them from danger."[9] In later editions of his book, Darwin attempted

[3] *Zoonomia* (3rd Amer. Ed., Boston, 1809), I, 401. [4] *Ibid.*, 402. [5] *Ibid.*, 403.

[6] Vol. II (2nd ed., London, 1818). Letter XXI, 218–269.

[7] *Horae Entomologicae* (London, 1819), Pt. II, 365.

[8] For more details, read the historical introduction to "Natural Selection the Cause of Mimetic Resemblance and Common Warning Colours" in *Essays on Evolution* by E. B. Poulton, Oxford: Clarendon, 1908, 220–224.

[9] Reprint of 1st ed., London, 1859, reprinted 1950, 72–73.

to clear up some of the objections to his ideas regarding adaptation through natural selection saying: "Insects are preyed on by birds and other enemies, whose sight is probably sharper than ours, and every grade in resemblance which aided an insect to escape notice or detection would tend towards its preservation; and the more perfect the resemblance so much the better for the insect." [10] Thus Darwin at last provided the explanation of the mechanism for the development of protective resemblance and indirectly of mimicry.

Today the terms "protective resemblance" and "mimicry" have come to have specialized meanings. When an animal escapes predation by resembling its environment, it is said to have protective resemblance. As examples of this might be cited the walking stick and the dead leaf butterfly, with those mentioned in the previous paragraph. The resemblance of one animal to another animal, instead of to its physical environment, is termed mimicry. Mimicry is probably best known among butterflies, but it also occurs in other insects, spiders, fish, birds, lizards and other vertebrates and invertebrates.[11]

In 1848 two young Englishmen sailed for Brazil for a joint expedition up the Amazon River with the purpose of investigating the natural history of this rich, tropical area. One of these men was A. R. Wallace, who later, independently of Darwin, arrived at the idea of evolution through natural selection, and thus became joint author with Darwin when their idea was first presented to the Linnaean Society in 1858. The other man was Henry W. Bates. Wallace and Bates had met in Bates's home town, Leicester, where Wallace had gone to teach English. Bates, in the tradition of his family, was managing a manufacturing business, and was considered to be quite successful. Business, however, did not completely satisfy him, and whenever possible he escaped from his desk by going to the library to read, or by going to the fields and woods to collect butterflies, and later beetles. Bates's enthusiasm was such that he caused Wallace, who had been interested only in plants, to take up beetle collecting, too. Thus, Bates and Wallace, though still in their twenties, soon became informed students of the local flora and fauna, and then wanted to do more than mere local collecting. They wanted to study plant and animal families thoroughly, with a view to the theory of their origins. The two friends discussed various schemes for exploring some unharvested region, and finally Wallace suggested to Bates that they try the Amazon. They could pay for the trip by collecting extensively and selling duplicate specimens in London, and meanwhile also gather facts. Consequently, on this Brazilian trip, both men made extensive notes and collections which they took home—Wallace after approximately four years, and Bates after eleven. Wallace meanwhile had

[10] Reprint of 6th ed. (Oxford Univ., 1872, reprinted 1956), 237.

[11] Probably the most comprehensive scientific treatise on this subject today is that of H. B. Cott's *Adaptive Coloration in Animals* (London, 1940), 508 pp.

gone to the Malayan Archipelago, where he continued to study the plants and animals of the tropics.

In 1862, Bates published a paper [12] in which he described some of the butterflies he had collected around the Amazon. He had found, within a large family of conspicuously marked butterflies (Danaidae), some similarly marked ones which belonged to a different family (Pieridae). The Danaidae are tropical butterflies, except for a few like the more northern monarch, and are brilliantly colored and marked with black, red, yellow, blue or orange brown. The members of the Pieridae family are found almost everywhere, are white, yellow or orange, and have simple wing patterns. These are commonly called "whites" or "sulphurs," and may have been the inspiration for the word "butterfly." The general or ancestral wing of the Pieridae is in no way reminiscent of the Danaidae in shape or color. However, some species have markedly departed from the usual pattern and taken on the shape and color of some of the bright Danaidae. Bates called the Pieridae with the danaid pattern "mimics"; the specific Danaids which were copied he called "models." He attempted to explain this resemblance by saying that the colorful models were distasteful to birds, and once a particular bird had attempted to eat one and discarded it, the bird would no longer prey on the Danaid or anything remotely resembling it. The Pieridae did not have the acrid body secretions which are so distasteful to predators, so that any slight change in adaptation to make a Pierid more like a Danaid would be favored in natural selection. Bates's generalizations were soon extended to other parts of the world (usually in the tropics) and to other animals in papers published by Wallace,[13] Thomas Belt,[14] and others who observed similar cases of mimicry. In *The Descent of Man,*[15] first published in 1871 and considered to be a sequel to *The Origin of Species,* Darwin included a brief discussion of mimicry.

Bates observed in his paper that there were certain types of mimicry which he could not explain. Some species, which were models for mimicry, also mimicked other models. This was explained for the first time in a paper published in 1879 by Fritz Müller.[16] Müller,

[12] "Contributions to an Insect Fauna of the Amazon Valley. Lepidoptera: Heliconidae," *Trans. Linn. Soc., Lond.,* XXIII, 495–566. Also, for a most delightful description of the Brazilian trip, see Bates's *The Naturalist on the River Amazons.* Reprint of unabrid. edit. (New York: Appleton, 1892), 389 pp. (with a memoir of the author by Ed. Clodd). Later edition reads "... *Amazon.*"

[13] "On the Phenomena of Variation and Geographical Distribution as Illustrated by the Papilionidae of the Malayan Region," *Trans. Linn. Soc., Lond.,* XXV, 1865–66, 1–77.

[14] See *The Naturalist in Nicaragua* (London, 1874), 403 pp. This is modeled after Bates's classic, but contains many more examples of mimicry as well as some good records of the effectiveness of mimicry on would-be predators.

[15] 2nd ed. (New York, 1874), 329–331.

[16] "Ituna and Thyridia: a Remarkable Case of Mimicry in Butterflies," trans.

though a German by birth, spent most of his life in Brazil. He seems to have been a man of many talents. Among other things he studied medicine, though he apparently never practiced it, and physiology with Johannes Müller (no relative). He studied crustacean larval forms and noted that the larvae of higher crustaceans resembled the larvae of lower ones. Later, with his brother Hermann, he studied pollination and the accompanying modifications of insects and flowers. He became a firm supporter of Darwin, and the little book he wrote called *Für Darwin* [17] was the instrument which aroused the controversial figure of Ernst Haeckel into developing the recapitulation theory far beyond anything Darwin would have recognized. But this is another episode in the history of biology which, though fascinating, does not concern us here. Müller reasoned that since young birds and other animals must learn by experience which prey are not palatable, where these (the prey) are complexes of many similarly colored species, the amount of loss of individuals (*i.e.*, the number of models and mimics eaten) will be spread out over the several groups involved. Thus today we speak of two forms of mimicry: Batesian and Müllerian. Batesian mimicry involves a palatable and an unpalatable form; Müllerian involves two or more unpalatable forms. In actuality, however, the distinction is not always so clear or simple—one reason being that palatability is relative. [18]

Almost as soon as the theory for the evolution of mimicry was proposed, there were men who criticized it. Much of this was aimed indirectly at Darwin. The chief defender of mimicry was Edward B. Poulton, Hope Professor of Zoology at Oxford University. His book, *The Colours of Animals,*[19] attempted to explain the origin of all types of coloration by natural selection, and it made its author famous as one of the leading Darwinians. Poulton was an excellent naturalist, a very careful observer, well-liked by students and contemporaries (he was knighted in 1935), and most intolerant of slipshod work and of those who attacked the truth as he saw it.[20] But he apparently did not like or understand mathematics and the then young science of genetics. Thus a good many of his later papers were devoted to rather vigorous denunciations of "Batesonians," men who believed mimicry had come about in one large change, or mutation, today usually called a discontinuous mutation or saltation. Early workers in mimicry believed that it had evolved slowly in small mutational steps, but this did not explain the lack of intermediate forms, or the

by Meldola, *Proc. Ent. Soc. Lond.*, xx–xxix.

[17] Leipzig, 1864. Trans. by Dallas, London, 1869, 144 pp.

[18] L. de Ruiter, "Some Remarks on Problems of the Ecology and Evolution of Mimicry," *Arch. Néerlandaises de Zool.*, XIII, I Supplé. 1958, 351–368. This is a well-written paper displaying great insight into this subject.

[19] New York: Appleton, 1890, 360 pp.

[20] See "Obituary" written by his successor at Oxford, G. D. H. Carpenter, in *Proc. Linn. Soc., Lond.*, Vol. 156, 1943–44, 219–223.

advantage of the first slight change. When men such as William Bateson and R. C. Punnett (who were working in England with artificial breeding under the recently rediscovered Mendelian laws of inheritance) defended saltation and thus seemed to belittle mimicry, they came under Poulton's disapproving eye, or rather pen.

At the beginning of the present century the genetics being developed in the laboratories, especially in that of T. H. Morgan at Columbia University, seemed to be replacing the theory of evolution defended in the previous century by Darwin and other naturalists. When Bateson said that the investigation of heredity by experimental methods offered the only chance of progress, Poulton was highly incensed. "Bateson's writings appear to me to have introduced a new and most regrettable element into scientific controversy."[21] He then went on to say that such attitudes of dogmatism tended to stifle true scientific curiosity and research. "These attempts to disparage one subject and exalt another naturally raise the question, 'Why do we investigate at all?' . . . The ultimate justification of all scientific research is, 'I do it because it interests me: I want to find out.' Any further motive—the well-being of humanity, the pursuit of gain, the gratification of ambition—only tends to bias and mar the inquiry. We want to know why. This is all. Whither the knowledge we accumulate is tending no one can tell."[22] Thus Poulton rose above the almost forgotten arguments of his day with his universal appreciation of what science is and what a scientist must be. The controversy about the relative merits of field observations and observations made in the laboratories unfortunately goes on in the minds of some today. That both field and laboratory studies are indispensable in natural science should have been obvious long ago. Genetics, once believed by some to have replaced Darwinism, has now become a major facet of evolutionary biology. Poulton spoke with feeling: "Naturalists who are striving to carry on, however imperfectly, a great tradition, can neglect the attempt to depreciate their own work, but they cannot be indifferent to an attack which falls on those who created the tradition —on the founders of modern Biological Science. As for the future, the thoughts of Darwin and Wallace are potent as ever to inspire and direct the labours of the young biologist."[23]

Genetical explanations of mimicry began to be presented around 1915, but the first generally acceptable theory was not made until almost fifteen years later. The distinguished geneticist Sir Ronald A. Fisher, of Cambridge University, wrote a paper in 1927 specifically on mimicry,[24] and then a more generalized treatment of great im-

[21] Poulton, 1908, *op. cit.*, xiii. [22] *Ibid.*, xlvii–xlviii. [23] *Ibid.*, xlviii.

[24] "On Some Objections to Mimicry Theory; Statistical and Genetic," *Trans. Ent. Soc. Lond.*, 75, 269–278.

portance, not just to students of animal color, but to all evolutionists: *The Genetical Theory of Natural Selection.*[25] With the better knowledge of approximately forty years of field observations made by many men, Fisher realized that mimicry involved more than one character. Mimics must not only look like models, they must act like them and live in the same general area. Fisher knew, too, that within certain species there were forms which were mimics of more than one model, as well as some which were non-mimetic; *i.e.*, there was a high degree of polymorphism. Included in this was sexual dimorphism, wherein the female was a mimic, the male non-mimetic, bearing the ancestral pattern of the species. Furthermore, similar patterns, such as the appearance of transparency on the wings of certain butterflies, had been formed in different ways structurally. It became obvious to him that more than one gene had to be involved in mimicry. He concluded that mimicry was controlled by individual genes within a complicated gene-complex. The latter had evolved slowly by natural selection: the first mutation was advantageous to the mimic, and each small mutation thereafter had to be not only advantageous to that mimic, but also of no disadvantage (at least) to the other mimetic or non-mimetic forms of that species. Thus, the resulting resemblances, though multiply-controlled, appeared to be triggered, or "switched on," by one gene.[26]

Mimicry had been primarily an observational study, but the need for experimental studies was becoming increasingly obvious. Some of the first experiments were designed to study the problem of palatability, but later work included breeding experiments to illustrate the specific genetics of mimicry. Neither type of experiment was simple. For example, some of the questions regarding palatability were: What is eaten and what is rejected? How long does it take to learn to distinguish distasteful prey? Are all predators similar in likes and dislikes? To answer these, various workers attempted to perform controlled experiments involving the feeding of models and mimics to predators, such as birds, toads, spiders, ants, lizards, monkeys, etc. However, it has never been easy to be completely objective in this work. One man, W. L. McAtee,[27] after finding the remains of models and mimics in the stomach contents of a large number of birds, implied that the whole idea of palatability was erroneous, and that there was no survival value in mimicry. McAtee's data and conclusions have been severely criticized, but further experimental evidence

[25] (Oxford, 1930), 272 pp.

[26] See de Ruiter, *loc. cit.*, for a clear statement of the specific problems involved here, as well as a discussion of some of the criticisms of Fisher's theory.

[27] "Effectiveness in Nature of the So-called Protective Adaptations in the Animal Kingdom, Chiefly as Illustrated by the Food Habits of Nearctic Birds," *Smithsonian Misc. Coll.*, 85 (1932), 1–210.

in support of mimicry was sadly slow in coming. Among the exceptions is the work of Dr. and Mrs. L. P. Brower of Amherst College. Mrs. Brower did her doctoral thesis at Yale on "Experimental Studies in Some North American Butterflies," [28] where she fed both models and mimics to experimental Florida scrub jays, and only mimics to the control jays. Generally, the control birds ate the butterflies, the experimentals avoided both models and mimics, after the first few encounters. Some similar experiments have been done feeding model and mimic salamanders to bird predators, but with less definite although interesting results.[29]

The relationship between genetics and evolution, as proposed by Fisher in his theoretical explanation of the genetics of mimicry, and consequently polymorphism in general, has gradually been demonstrated experimentally. Such theories as were developed from field observations led to the idea that the gene-complex, or "super-gene," controlling polymorphism, not only produced changes by mutation and selection, but also had a residual variability, in what were called "modifiers," allowing a single species to show local variations, called "races," and thus fit better into the various local environments.[30] Furthermore, polymorphism, whether mimetic or non-mimetic, has proved to have great adaptive value, for a greater genetic diversity permits a greater utilization of a diverse and changing environment.[31]

Off and on in the last thirty years, various biologists have experimented, or tried to, with the genetics of mimicry, but two names stand out: C. A. Clarke and P. M. Sheppard. Their work has been described, along with many others, in fascinating detail by another Englishman, who also has long been interested in mimicry; namely, Professor E. B. Ford of Oxford.[32] Dr. Clarke and Dr. Sheppard have been experimenting with a swallowtail butterfly, *Papilio dardanus,* which is native to southern Africa. It is highly polymorphic, showing ancestral forms, mimics of several different models, and non-mimetic variations. In addition, this species is divided into a number of distinct geographical races. These two geneticists overcame great difficulties in obtaining the necessary stocks (butterflies and eggs were flown in by air), and in breeding these tropical butterflies on a large

[28] This has been published in *Evolution,* XII, 1958, 32-47, 123-136, 273–285. For some other interesting work of the Browers, see their article "Investigations into Mimicry," *Nat. Hist.*, LXXI (April 1962), 9–19.

[29] J. E. Huheey, "Mimicry in the Color Pattern of Certain Appalachian Salamanders," *Journ. Elisha Mitchell Sci. Soc.*, 76 (1960), 246–251.

[30] J. S. Huxley, *Evolution: The Modern Synthesis* (New York, 1943), 123–124.

[31] Ernst Mayr, *Animal Species and Evolution* (Cambridge, Mass.: Harvard, 1963), 250–251. Included here is a brief summary of Dr. T. Dobzhansky's experimental evidence on polymorphism and adaptation in the common fruit fly, *Drosophila.*

[32] *Ecological Genetics* (New York, 1964), 201–246.

scale in their laboratories at the University in Liverpool, England. They crossed various mimetic forms with non-mimetic forms. The resulting hybrids had abnormal color patterns, and thus mimicry was imperfect. When these were bred back to mimetic parents, the mimicry began to reappear. From these experiments of crossing and backcrossing, done patiently over many years, Dr. Clarke and Dr. Sheppard were able to decipher not only the complicated genetical constitution of these various mimics (the super-genes and their modifiers), but also to explain the evolution of the mimetic patterns within this particular species of the butterfly. Professor Ford concludes his discussion of this work by saying: "After many years of discussion, mimicry has been analyzed by Clarke and Sheppard in such a way as to disclose the mechanism of its evolution. . . . The results have demonstrated incontestably the truth of the explanation put forward by Fisher in 1927. . . . Evidently the time has now come for further studies on the ecology of mimicry in the field, carried out in the light of these discoveries." [33]

Through the years many startling examples of mimicry have been described, especially among insects. There is a Brazilian grasshopper which not only is colored like a wasp, but further mimics it by running short distances with expanded wings. There is a longhorn beetle, which, in addition to color, mimics a wasp in curving its abdomen under in such a way as to suggest that it is about to sting. There are spiders which both look and act like ants, even to simulating the walk and the right number of body constrictions. There are records of true bugs which mimic leaf-cutting ants so well that they even appear to be carrying a piece of a leaf.

Mimicry among vertebrate animals is less well known. Among fish, one well-known case involves the common sole and the venomous weever fishes. The latter have black-marked pectoral fins which they raise when molested. The sole, unlike any other member of its own family, also has a black-marked pectoral fin which it raises when threatened.[34] The coral snakes, which are among the deadliest reptiles in the world, are frequent models for mimicry. They have brightly colored rings (usually red, yellow and black) and are mimicked by a number of less venomous snakes, as well as some which are completely harmless.[35] Although little work seems to have been done

[33] *Ibid.*, 246.

[34] J. E. Randall and H. A. Randall, "Examples of Mimicry and Protective Resemblance in Tropical Fishes," *Bull. Marine Sci. of Gulf and Caribbean,* 10 (1960), 444–480.

[35] M. K. Hecht and D. Marien, "The Coral Snake Mimic Problem: A Reinterpretation," *Journ. of Morphol.,* 98 (1956), 335–356. For a discussion of some other snake mimics, read: C. Gans, "Mimicry in Procryptically Colored Snakes of the Genus *Dasypeltis,*" *Evolution,* XV (1961), 72–91.

recently on mimicry among birds, Wallace discussed it, along with snakes and other animals, in several of his books, including *Contributions to the Theory of Natural Selection*[36] and *Darwinism.*[37] He described one family of Malayan orioles, which though normally dull-colored were excellent mimics of the powerful, noisy *Tropidorhynchi* or "Friar-birds," a genus of large honey-suckers. He said: "In each of the great islands of the Austro-Malayan region there is a distinct species of Tropidorhynchus, and there is always along with it an oriole that exactly mimics it. All the Tropidorhynchi have a patch of bare black skin around the eyes, and a ruff of curious pale recurved feathers on the nape, whence their name of Friar-birds, the ruff being supposed to resemble the cowl of a friar. These peculiarities are imitated in the orioles by the patches of feathers of corresponding colours; while the different tints of the two species in each island are exactly the same." [38]

Some of the most remarkable resemblances are the great mimetic assemblages involving several orders of insects. One such is the lycid assemblage. Lycid beetles are an old family, widely distributed, generally orange and black in color, gregarious and sluggish in behavior, and very distasteful to predators. Mimics include moths, wasps, flies, sucking bugs, and other beetles. There are estimates that throughout the world there are many hundreds of species of these mimics, whose larvae vary greatly, but whose adults share the lycid resemblances.[39] These complexes are further complicated by the Batesian and Müllerian elements, which are not always easy to determine or to distinguish. Some of the moths and beetles are odoriferous or distasteful, though not all, and presumably some of the wasps are protected also by a sting, while other mimics would seem to be defenseless except for the lycid resemblance. So far many intricacies of the problem are yet to be completely explained.

Today the study of mimicry continues no less challenging than it was to Bates and the other men who first discovered it among the butterflies and other animals of the tropics. The manner in which adaptations arise, or are lost, through natural selection offers a never-ending source of study to biologists. Mimicry, although it is only one of countless examples, provides a unique opportunity for the study of most of the questions which might arise in connection with the general subject of adaptations.

Museum of Comparative Zoology, Harvard University.

[36] (London, 1870), 75–114, 179–185.

[37] (London, 1889), 239–267.

[38] *Ibid.*, 263–264.

[39] Lycid mimicry is summarized in G. D. H. Carpenter and E. B. Ford, *Mimicry* (London, 1933), 58–59. For some recent work on palatability of lycids and mimics, see E. G. Linsley, T. Eisner, and A. B. Klots, "Mimetic Assemblages of Sibling Species of Lycid Beetles," *Evolution,* XV (1961), 15–29.