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Mimicry, obscure colors, and secondary sexual colors were important classes of observations that were analyzed by nineteenth century biologists from several vantage points. Adherents of the doctrine of special creation of fixed species believed animal colors to be evidence of design; Darwin and Wallace and their successors suggested that a natural process, natural selection, had produced the adaptations. Letters to the editor of Nature and discussions at the Royal Entomological Society of London record the controversy between biological world-views. There was, however, little unity between Darwin and Wallace on the development of coloration. Darwin emphasized the sexual function of color which Wallace largely discounted. Wallace emphasized the protective function of color. The source of their differences may be traced to their sources of data. Darwin had relied upon the variations of domestic animals to understand

wild species which Wallace believed must be studied directly rather than by domestic analogy. Darwin used sexual selection and the inherited effects of acquired characters to account for most of the cases of dimorphic coloration in animals and of racial colors in man, setting his view of the origin of colors in both animals and man irreconciably apart from that of Wallace. The controversy on the uses of color in animals shows the differences of opinion between Darwinians as well as between Darwinians and creationists, and provides a way of studying some of the distinctive features of nineteenth century biology.

The Coloration of Animals: A Nineteenth Century Controversy

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INTRODUCTION

The existence of unexplored episodes in the history of the theory of natural selection was a surprise. The accumulation of biographical information, historical treatises, and autobiographical reminiscences on the topic of Darwin and Darwinism is massive, as a cursory glance at the Dar-Daz drawer of any library card catalog will confirm. It was not the abundance of literature that impressed me most, but the comparative dearth of histories and biographies of Darwin's colleague and co-discoverer of natural selection, Alfred Russel Wallace. It is a common myth that Wallace was not only Darwin's junior partner, but his silent partner, whose views were similar, if not exact copies of Darwin's. Wilma George's biography of Wallace presented a good case for a very different view.

Her Biologist Philosopher[1], is the only book that attempts to couple an analysis of Wallace's scientific contributions with a survey of his life-events. Gerald Henderson's dissertation Alfred Russel Wallace: His Role and Influence in Nineteenth Century Evolutionary Thought,[2] focuses on the anthropological aspects of Wallace's research and differences with Darwin. Wallace's autobiography, My life,[3]

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[1] Wilma George, Biologist Philosopher. A Study of the Life and Writings of Alfred Russel Wallace (London: Abelard-Schulman, 1964).

[2] Gerald Henderson, Alfred Russel Wallace: His Role and Influence in Nineteenth Century Evolutionary Thought (Ann Arbor, Michigan: University Microfilms, 1960).

made other attempts at descriptive accounts of his life superfluous, but analysis of both his life and writings has been long overdue. H. Lewis McKinney's work emphasizes Wallace in the role of co-discoverer of natural selection and unravels some of the mysteries about the extent and direction of influence between Darwin and Wallace prior to 1858. McKinney's article "Alfred Russel Wallace and the Discovery of Natural selection, "[4] and one by Barbara G. Beddall, [5] "Wallace, Darwin and the Theory of Natural Selection, "[5] contain quotations from and references to Wallace's unpublished "Species Notebook," the publication of that notebook will be helpful to students of Wallace's scientific thought. Of all the works on Wallace's progress toward discovery of a mechanism of evolution, articles by Professor C. F. A. Pantin[6] on the Essays of 1855 and 1858 were particularly helpful in conjunction with Barbara Beddall's synthetic treatment of the earlier period of Wallace's writings and interaction with Darwin.

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[3] Alfred Russel Wallace, My Life. A Record of Events and Opinions. 2 vols. (London: Chapman & Hall, 1905).

[4] H. Lewis McKinney, "Alfred Russel Wallace and the Discovery of Natural Selection", Journal of the History of Medicine 21:333-357, 1966.

[5] Barbara G. Beddall, "Wallace, Darwin, and the Theory of Natural Selection. A Study in the Development of Ideas and Attitudes, " Journal of the History of Biology 1:261-323, 1968.

[6] C. F. A. Pantin, "Alfred Russel Wallace: His Pre-Darwinian Essay of 1855, " Proceedings of the Linnean Society of London 171:139-153, 1960, and "Alfred Russel Wallace, F. R. S., and His Essays of 1858 and 1855. " Notes and Records of the Royal Society of London 14: 67-84, June, 1959.

Darwin as an individual has become confusingly synonymous with the orthodox view of evolution by natural selection. The name, "Darwinism," focuses attention on Darwin as symbolic leader and spokesman for the doctrine of organic evolution under natural law rather than on the content of his contributions to biology, and in the process tends to detract from the work of other scientists who were "Darwinians" from the first.

The moderation of Sir Gavin DeBeer's Charles Darwin: A Scientific Biography,[7] is a welcome contrast to several other relatively recent biographical works on Darwin which tends to suffer from excesses in either praising or blaming Darwin uncritically. Michael T. Ghiselin's The Triumph of the Darwinian Method[8] amalgamates the contributions of Darwin and other Darwinians, implying that Darwinian techiques for verification of theories were of Darwin's private invention. On the other side, C. D. Darlington blames Darwin for completely befouling the issues so that his views might be favorably received by representatives of any and all positions on the sources and directedness of

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[7] Gavin DeBeer, Charles Darwin: A Scientific Biography (Garden City, New York: Doubleday, 1965).

[8] Michael T. Ghiselin, The Triumph of the Darwinian Method (Berkeley: University of California Press, 1969).

variation[9] at least an equally negative picture of Darwin is found in Jacques Barzun's Darwin, Marx, Wagner[10]. Gertrude Himmelfarb's, Jacques Barzun's and sometimes William Irvine's verbal portraits of Darwin are rather ungenerous charicatures. Barzun has attempted to judge the many from the few, that is, to understand the historical period by an investigation of representative individuals. Both Darwin and the Darwinian Revolution[11] and Victorian Minds by Gertrude Himmelfarb contain positive attempts to understand the man by understanding the ethos of his times. Irvine in Apes, Angels, and Victorians[12] has looked at the role of Thomas H. Huxley, "Darwin's bulldog," as the real hero of the evolution controversy. All of these are valuable assets in the diversification of perspectives on Darwin and the history of evolution. The common element in them is that Darwin's phychological foibles are brought to the fore in a manner that negates or neglects his worthy contributions.

It has been the intention here to steer between the equally dangerous shoals. Darwin's lack of generosity in his relationships with Wallace, especially, does detract from Darwin's usually cordial and gentlemanly

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[9] C. D. Darlington, "The Origin of Darwinism," Scientific American 200:60-66, 1959.

[10] Jacques Barzun, Darwin, Marx, Wagner (2nd ed.; Garden City, New York: Doubleday & Co., 1958).

[11] Gertrude Himmelfarb, Darwin and the Darwinian Revolution, The Norton Library, (New York: W. W. Norton, 1968) and Victorian Minds Harper Torchbooks (New York: Harper & Row, 1970).

[12] William Irvine, Apes, Angels, and Historians, Meridian Books (New York: World Publishing Co., 1970).

manner. It does not, however, denigrate Darwin's contributions to science, to suggest that Wallace ought also to be given credit for his scientific and philosophical work on evolution and natural selection. There is little doubt but that Wallace by his self-effacing conduct contributed to his own eclipse under Darwin's shadow. It falls, then, upon biographers and students of "Wallaces" to deny Wallace's own word that credit for the theory is due to Darwin alone.

Articles in the journal, Victorian Studies, have added substantially to the elucidation of Darwin as a Victorian; since ideas are best studied in situ, within an intellectual matrix, the perspective of historians of the Victorian Period are welcome and helpful, especially essays by Walter Cannon,[13] Donald Fleming,[14] Walter Houghton,[15] and John Passmore.[16]

The papers which were most helpful in gleaning a general idea of the philosophy of evolution were those by Feibleman,[17] Passmore, Mandelbaum,[18] and especially Ellegard,[19] and Hull.[20]

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[13] Walter Cannon, "The Bases of Darwin's Achievement: A Reevaluation," Victorian Studies 5:109-134, 1961.

[14] Donald Fleming, "Charles Darwin, the Anaesthetic Man," Victorian Studies 4:219-234. 1961.

[15] Walter Houghton, "Victorian Anti-Intellectualism," Journal of the History of Ideas 113:291-313, 1952.

[16] John Passmore, "Darwin's Impact on British Metaphysics," Victorian Studies 3:19-40, 1959.

[17] James K. Feibleman, "Darwin and Scientific Method," Tulane Studies in Philosophy 8:3-14, 1960.

Historical writing can only reflect the actual events of the past in barest outline. The discussion among the nineteenth century scientists on the colors of animals has to the present been so abbreviated that even the outline is but vaguely discernible. Darwin and Wallace were never the only scientists involved in the theorizing or in submitting observational and experimental evidence. The colors of animals was the topic of an open forum in which natural selection and even natural law was tested. The emotional pitch on evolution was still high in 1862 when Bates put forth his theory of mimetic resemblances. The discussion of mimicry, protection, and selection among animals was a conscious examination of natural selection, on the order of a critical test. The timing of Bates' announcement suggests the importance of the theory and the testimony of participants in the subsequent debate adds credibility to the "test case" theory. The transactions of the Royal Entomological Society contain a rich literature on the assimilation of evolutionary theory into the framework of working hypotheses used by field collectors and laboratory taxonomists. The participation of Wallace, Bates, Meldola and other prominent Darwinians in the entomological argumentation on theories of color constitutes an important difference from Darwin whose examples of choice were drawn not from wild butterflies but from domestic productions.

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[18] Maurice Mandelbaum, "The Scientific Background of Evolutionary Theory in Biology," Journal of the History of Ideas 28:342-361, 1960.

Mary Alice Evans' "Mimicry and the Darwinian Heritage"[21] is an important application of the history of ideas principle to coloration phenomena, which is particularly susceptible to that kind of analysis. The shifts and nuances of meaning and theory related to various color phenomena need to be traced out on the model so well illustrated by Arthur O. Lovejoy's Great Chain of Being,[22] and described by George Boas' The History of Ideas.[23]

The balance of influences inside and outside biological investigation was in a state of flux during both the writing and reception of the Origin of Species. Various views of social evolution were beginning to vie with more orthodox ideas of ethics, religion, and social policy; research in geology, paleontology, embryology, and comparative anatomy had prepared many scientists to at least consider the possibility of a dynamic rather than a static biological world. The idea that evolution

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[19] Alvar Ellegard, "The Darwinian Theory and Nineteenth Century Philosophies of Science," Journal of the History of Ideas 28:362-393, 1957.

[20] David L. Hull, "The Metaphysics of Evolution," British Journal of the History of Science 3:309-337, 1967.

[21] Mary Allice Evans, "Mimicry and the Darwinian Hertiage," Journal of the History of Ideas 28:362-393, 1965.

[22] Arthur O. Lovejoy, Great Chain of Being, Harper Torchbooks (New York: Harper & Row, 1960).

[23] George Boas, The History of Ideas (New York: Charles Scribner's Sons, 1969).

was "in the air" is undoubtedly true, but it does not explain why only two scientists, Darwin and Wallace plucked it, not from the air, but from long research in the tropics and from reading in the social sciences.

That both internal and external factors have a place in narrative histories of science, has been apparent in this study of the history of theories of animal coloration. The integration of gestalt psychology with the idea of philosophical frameworks has been worked out by Norwood Russel Hanson in Patterns of Discovery,[24] and the applications of the idea of "pattern" in scientific revolutions to Thomas S. Kuhn,[25] The Structure of Scientific Revolutions.

This essay is only an abstract of a more comprehensive work which could, indeed should, be done. The zoogeographical aspects of Wallace's research are not adequately explored here, yet it is certain that animal distribution was important in both his discovery of natural selection and his application of it. The updating of theories of coloration into the twentieth century and the "genetic period" of biological history would be a fitting sequel to this study. The life and writings of many nineteenth century biologists, especially Raphael Meldola and Edward Poulton, have not been adequately analyzed or appreciated.

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[24] Norwood Russell Hanson, Patterns of Discovery (Cambridge: University Press, 1969).

[25] Thomas S. Kuhn, The Structure of Scientific Revolutions, 2nd edition, enlarged (Chicago: Chicago University Press, 1970).

This research was undertaken in hope that by studying a single data-class, known in the nineteenth century before a mechanism for evolution had been announced and then reevaluated after 1858-59, the change in description of empirical observation would be indicative of a deeper change; a change of mind, of basic conceptual terms. Bates, Wallace, and Darwin were probably most influential in turning the discussion of animal coloration into a definitive trial of natural selection as a unified and universal theory.

THE COLORATION OF ANIMALS: A NINETEENTH CENTURY CONTROVERSY

CHAPTER I

SOCIAL AND INTELLECTUAL CLIMATE

The reciprocal influence of men and their times is one of the most important and, simultaneously, most complicated aspects of the history of science. History, does not lend itself to the precise dissections of the laboratory. The separation of nerves and bloodvessels from their muscular matrix bears only symbolic similarity to the artificial segregation of a group of nineteenth century scientists from the Victorian milieu of which they were a part. Darwin and Wallace were Victorians as well as naturalists, who were influenced by their predecessors and contemporaries besides being an influence upon their own and later generations of scientists. In tracing influences, the central issue is that of tacit belief and no belief is stronger than an assumption nor more difficult to dissect free from its interacting and interlocking stubstrate. The historiography of thought can never be done once-for-all time, but it relies upon the continually shifting equilibrium between data and interpretation. "Hard data" is, in the history of evolution, as in all history, an extremely scarce commodity and the equilibrium is far out of balance on the side of interpretation rather than that of "fact". The acceptance and denial of evolution by natural selection is

a good example of the simultaneous use of different conceptual frameworks by two groups whose membership was not distinct but rapidly changing and frequently overlapping. The discussion of the coloration of animals, is a small chapter in the history of the testing and assimilation of the Darwinian paradigm, which exemplifies both the similarities and differences among Darwinians of the time. The scientists utilized prevalent theoretical beliefs and introduced new ones; it is the introduction of novelty along with the preservation of the useful aspects of old schemes that makes the history of Darwinism exciting. No criticism was disqualified, but the rules of the warfare were Victorian.

Confidence in a moral code based on literal interpretation of the Bible was steadily undercut during the Victorian Period by new doubts as to the inerrancy of the Bible based on the compelling evidence of higher criticism of biblical documents and by scientific evidence of the antiquity of the earth. The question before Victorian society was "If the Bible contains errors in history is it reliable as a moral guide?" Industrialization and the urban poverty which accompanied it only accentuated the pain of rising religious skepticism and contributed to the general malaise of the times. One of the manifestations of this spirit of discontent was "Victorian Anti-Intellectualism,"[26] having as a primary symptom retreat into work as an escape from the agony of solitary thought.

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[26] Walter E. Houghton, "Victorial Anti-Intellectualism," Journal of the History of Ideas 13:291-313, 1952.

> ... enormous production, far greater than anything we are now accustomed to had one source in their confidence that the human mind could resolve every problem however difficult, and that the individual could influence the course of events regardless of all impersonal political or economic forces. But another service was the temptation to bury their doubts and anxieties under the distractions of objective and constant activity. This is reflected by the frantic intensity with which they often work, so different from the quiet, steady production that rests on inner peace and assurance. They cannot sit still -- they dare not, and they cannot work calmly.[27]

It is not surprising that anxiety typified Victorian attitudes. The religious foundations upon which the emotional tranquility of many individuals depended were shaken. The furor touched off by the declaration of natural selection as the mechanism for evolutionary change was so intense that it is certainly indication that it had touched a sensitive nerve. The fear of religious skepticism was so great that challenges to traditional religious beliefs were met by overzealous counterattacks.

Darwin, as a central and symbolic figure in the nineteenth century, is an ideal example of one man's participation in the Victorian ethos. His autobiography contains an outline sketch of his perception of himself and is a valuable document in Victorian studies as well as in the history and philosophy of science.[28] In a revealing attempt at self analysis Darwin wrote:

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[27] Walter E. Houghton, "Victorian Anti-Intellectualism," p. 312.

[28] Nora Barlow, ed., Autobiography of Charles Darwin 1809-1882. With Original omissions restored (New York: W. W. Norton & Co., 1969). [Hereinafter referred to as Autobiography.].

> My mind seems to have become a kind of machine for grinding general laws out of large collections of facts, but why this should have caused the atrophy of the brain alone, on which the higher tastes depend, I cannot conceive. A man with a mind more highly organized or better constituted than mine, would not I suppose have thus suffered; and if I had to live my life again I would have made a rule to read some poetry and listen to some music at least once a week; for perhaps the parts of my brain now atrophied could thus have been kept active through use. The loss of these tastes is a loss of happiness, and may possibly be injurious to the intellect, and more probably to the moral character, by enfeebling the emotional part of our nature.[29]

Perhaps Darwin's voluminous correspondence and massive output of energy to produce his books despite debilitating illness is best understood as representating Victorian reliance upon facts and a corresponding lose of a sense of the sublime.[30] One of the few facts which may be stated with certainty is the one that the idea of natural selection did

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[29] Barlow, ed., Autobiography. p. 139.

[30] Darwin was no anti-intellectual; he certainly deserves exemption from that category: The point which merits emphasis is that intellectual pursuits were held in generally low esteem, especially if they conflicted with religious beliefs. Donald Fleming's brilliant essay ("Charles Darwin, the Anaesthetic Man," Victorian Studies 4:219-236.) clearly shows that Darwin's retreat from music and art was one aspect of a general rejection of religious experience; an experience in which Darwin was not unique. Jacques Barzun's Darwin, Marx, Wagner (Rev. 2nd ed. Garden City, New York: Doubleday & Co., 1958), and Morse Peckham's article "Darwinism and Darwinisticism" (Victorian Studies 3:41-54) points to the common theme in Victorian art and literature--including Darwin's thought, the loss of the ability to love (Coleridge and Byron) and the inability to be loved (Wagner's Flying Dutchman).

not arise by itself, but it was conceived and defended by human agents in a social milieu.

The methodology of science and the philosophy it represented was in metamorphosis in the middle of the nineteenth century. Although Darwin liked to think of his collection of data as being upon "true Baconian principles, and without any theory"[31] his contributions to biological science were daringly speculative. Fact, not theories, were in vogue and Darwin's approach mingling the two was anathema to the popular idea that observations may be made without theoretical bias and that this fact-gathering was the only scientific method. Departure from the well-worn Baconian method of induction was considered as Ellegard has said, "almost morally reprehensible."[32] It is to

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[31] Barlow, ed., Autobiography, p. 119.

[32] Alvar Ellegard, "The Darwinian Theory and Nineteenth Century Philosophies of Science," Journal of the History of Ideas 28:362-393. p. 364. This article contains a fairly detailed evaluation of the elements of Mill' and Whewell's philosophy which Darwin incorporated into his scientific method. Several other articles treat the topic of Darwin's scientific method. James K. Fiebleman, "Darwin's Scientific Method," Tulane Studies in Philosophy 8:3-14 and John Passmore, "Darwin's Impact on British Metaphysics," Victorian Studies 3:41-54. Michael T. Ghiselin's The Triumph of the Darwinian Method (Berkeley: University of California Press, 1969) contains a discussion of Darwin's science in which he rather anachronistically asserts that Darwin was a scientist in the hypothetico-deductive model.

Darwin's credit that he was willing to risk loss of status in the service of science. He agreed with the philosophers of science, Whewell and Mill, who had begun to advance the new idea that inductive science had concern with hypotheses as well as with observations. Darwin's mixture of hypothesis and observation is made clear in this reaction to an attempt to separate them:

> How profoundly ignorant B must be of the very soul of observation! About thirty years ago there was much talk that geologists ought only to observe and not theorise; and I well remember some one saying that at that rate a man might as well go into a gravel pit and count the pebbles and describe the colours. How odd it is that anyone would not see that all observation must be for or against some view if it is to be of any service![33]

Darwin did not consider himself a philosopher. He wrote, "My power to follow a long and purely abstract train of thought is very limited; I should, moreover never have succeeded with metaphysics or mathematics,"[34] nonetheless, his philosophic contributions to science must not be underestimated. Darwin, like Mill, but contrary to Whewell, avoided explanations in terms of their Final Causes or of Vital Forces. His theories approached conformity to the law of parsimony, that

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[33] Francis Darwin and A. C. Seward, eds., More Letters of Charles Darwin, 2 vols. (London, John Murray, 1903). Letter to Henry Fawcett, Sept. 18, 1861.

[34] Barlow, ed., Autobiography, p. 140.

principle of using the minimum number of assumptions or premises.[35]

The impact of the Darwinian method on philosophy has been interpreted by a wide spectrum of contemporary scholars. Opinion varies from Walter Cannon,[36] on the right, who sees Darwin as the legitimate offspring of the natural theologians to Michael Ghiselin,[37] on the left, who considers Darwin solidly within the camp of the hypothetico-deductive

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[35] See Bert James Loewenberg, "The Mosaic of Darwinian Thought", Victorian Studies 3:3-18 and David L. Hull, "The Metaphysics of Evolution, "British Journal of the History of Science 3:309-337. Loewenberg sees Darwin's chief contribution as a reversal in the priority of Being and Reality. "As Darwin viewed the world of Reality, Being possessed no antecedent priority . . . Being and permanence were conceived, not as ultimate coordinates of temporal change within an antecedent transcendental system. " p. 287. Hull's view is similar, he sees Darwin, on the subject of species, as neither an essentialist nor a nominalist but incorporating elements of both.

[36] Walter Cannon, "The Bases of Darwin's Achievement: A Reevaluation, " Victorian Studies 5:109-134. This interesting article presents the thesis that the "triumph of Darwinism is the triumph of a Christian way of picturing the world over the other ways available to scientists. " p. 109. The sides of the argument for Cannon are not the evolutionists against the special (miraculous) creationists, but rather realists versus the Platonists.

[37] Ghiselin, The Triumph of Darwinian Method. Ghiselin has attempted to prove that Darwin was a thoroughly modern scientist it is on this a priori basis that the book is constructed. It contains several incautious references to Darwin personally that are more properly attributed to other Darwinians, Wallace, and Bates, conspicuously. In an attempt to counteract recent books which have tended to discredit Darwin's intellect or personality Ghiselin has swung the pendulum so far in praise of Darwin as to be incredible.

philosophers. The variety of literature discussing Darwin and his method serves only to underscore his important impact upon modern science.

Darwin shared the Victorian interest in the practical uses of science without participating in the anti-intellectualism of the period, which may be associated with the well established fact that the Industrial Revolution in England resulted, not from scientific theories, but from empirical inventions. "Book-learning" and experts, theoreticians, were held in low regard. In mid-nineteenth century ideas without a practical purpose were perceived as useless and wisdom as simply practical knowledge.[38]

> The glory of Baconian philosophy was its practical aim, the multiplying of human sufferings, physical enjoyments and physical sufferings; and as a result, it has wonderfully succeeded--witness its tremendous fruits in the nineteenth century.[39]

Darwin, the Victorian man, was a Counter-Victorian scientist. However, unconsciously, Darwin freed inductive science from its strict Baconian limitations--using both hypothesis and observation for the broader purpose of explanation. His method includes the inescapable dichotomy between justification of an hypothesis and its invention. Facts may be accumulated in support of theory, but this statistical method contrary to Baconian methods of doing science, does not apply to the

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[38]Gertrude Himmelfarb, Victorian Minds. Harper Torchbook (New York: Harper & Row, 1970). This book contains a good discussion of the Victorian ethos expecially regarding the "angst" which typified it.

[39]Houghton, "Victorian Anti-Intellectualism, p. 300.

discovery of theories. Although Darwin's logic is not always tight, not is his attempt to refrain from telelogy entirely successful, Darwin's science has added elements of a new metaphysics of science which were radically different and quite as difficult for him to accept as for others.[40]

The new metaphysics of science was the substratum on which the theory of evolution by natural selection is based; it is, moreover, one of the aspects of Darwin's thought most criticized in the nineteenth century. The group of scientists who took the name of "Darwinians may be understood abstractly as a cluster of people working under the new paradigm of Darwin's philosophy of science.[41] The discussion of animal colors is a fairly clear window on the debate between Darwinists on the inside of the paradigm and those on the outside.

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[40] David L. Hull, "The Metaphysics of Evolution, pp. 336-337. Darwin's introduction of the idea of evolving lineage made clear distinction between species impossible. This was as difficult for Darwin himself to accept or to explain to the satisfaction of fellow biologists, since for him as for them, "A hazy border was no border at all." p. 336.

[41] The idea of paradigms as explanatory, inclusive conceptual systems is that of The Structure of Scientific Revolutions by Thomas S. Kuhn.

Biographical Background

Charles Darwin (1809-1882) and Alfred Russel Wallace (1923-1913) were separated by more than the fourteen years difference in their birth dates. The distance between them was one of social class and of opportunity that nearly always accompanies differences in economic status.

Darwin's father, Robert Darwin, was a respected physician in Shrewsbury and by careful investments he was able to accumulate adequate wealth to comfortably support his family and to free his children from the necessity of earning their own livings. As a student Charles Darwin had shown little aptitude or interest in scholarship and had great difficulty in deciding upon a career. It was decided that he should become a physician but he left Edinburgh University after two years, having abandoned hope of a career in medicine. He also never became an Anglican clergyman although he completed his degree at Cambridge with that intention. His friends at Cambridge were not scholars, but "a sporting set, including some dissipated low-minded young men".[42]

Darwin's university education, although not a period of energetic study did put him in the acquaintance of the well known botanist,

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[42] Barlow, ed., Autobiography, p. 60.

Professor John Stevens Henslow, who encouraged Darwin's interest in natural history,[43] and recommended him for the position of naturalist aboard the survey ship the HMS Beagle. The society level of the Darwin amily, his university education and, finally, the Beagle voyage set Darwin at a distinct advantage for life as a naturalist in contrast to the biography of Alfred Russel Wallace.

Wallace's early years were spent quite differently. He was the eighth child of an increasingly impoverished family. His father, Thomas Wallace, had through a series of poor investments steadily reduced the family income to less than 100 pounds per year. As a result, upon reaching the age of fourteen Wallace was expected to earn his own living. Instead of leisurely summers spent in recreation Wallace worked in a carpenter's shop than took up surveying as his brother's assistant. While a surveyor he learned a little geology, mapmaking and became interested in learning the names of wildflowers. His personal knowledge of the problems of urban workers and of the rural peasant sparked his interest in socialism. Before the age of twenty Wallace had opportunity to learn several trades ranging from watchmaking to surveying and a little architectural design. What leisure he had was spent on botanical collections even though his brother considered this

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[43] The importance of Darwin's relationship to Henslow may be most clearly seen in the letters which were exchanged. The correspondence is presented in full in: Nora Barlow, ed., Darwin and Henslow: The Growth of an Idea. Letters 1831-1860 (Berkeley: University of California Press, 1967).

pursuit a waste of time. Wallace's early independence made him dislike business or employment which required subjecting himself to supervision of any kind. He taught surveying and English in Leicester but disliked it, having a natural shyness and embarrassment about his lack of education in the classics. The period (1844-1846) was not without its rewards, it was at this time that he met Henry Walter Bates, a young entomologist, who taught Wallace the rudiments of beetle collection and classification. In 1847 after reading W. H. Edwards' book A Voyage up the Amazon,[44] Bates and Wallace decided upon an adventure in South America which could be paid for by the sale of specimens upon their return.

The letters between Bates and Wallace reveal Wallace's seriousness of purpose for study in the tropics, transcending the secondary purposes of adventure and excape from a teaching career which he disliked. In September of 1847 he wrote,

> I begin to feel rather dissatisfied with a more local collection; little is to be learnt by it. I should like to take some one family to study thoroughly, principally with a view to the theory of the origin of species. By that means I am strongly of opinion that some definite results might be arrived at . . . There is a work published by the Ray Society I should much like to see, Oken's 'Elements of Physiophilosophy'. There is a review of it in the Athenaeum. It contains some remarkable views on my favorite subject -- the variations, arrangements, distribution, etc., of species.[45]

Wallace's autobiographical reflections are almost totally devoid of bitterness for his early poverty and lack of education. He saw early hardships as an important factor in the molding of character and helpful in choosing a life work.

> Had my father been a moderately rich man and had supplied me with a good wardrobe and ample pocket-money; had my brother obtained a partnership in some firm in a populous town or city, or had established himself in a profession, I might never have turned to nature as a solace and enjoyment of my solitary hours, my whole life would have been differently shaped, and though I should, no doubt have given some attention to science, it seems very unlikely that I should have ever undertaken what at that time seemed rather a wild scheme, a journey to the almost unknown forests of the Amazon in order to observe nature and make a living by collecting. All this may have been pure change, as I long thought it was, but of late years I am more inclined to Hamlet's belief, when he said --
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> 'There's a divinity that shapes our ends,
> Rough-hew them how we will.'[46]

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[44] William H. Edwards, A Voyage Up The River Amazon, Including a Residence at Para (London: John Murray, 1847). This book is filled with exciting passages, of which the following is a sample. "Promising indeed to lovers of the marvalous is that land where the highest of earths' mountains seek her brightest skies, as though their tall peaks sought a nearer acquaintance with the most glorious of stars; where the mightiest of rivers roll majestically through primeval forests of boundless extent, concealing, yet bringing forth the most beautiful and varied forms of animal and vegetable existence; where Peruvian gold has tempted, Amazonian women have repulsed; the unprincipled adventurer; and where Jesuit missionaries and luckless traders have falled victims to cannibal Indians and epicurean anacondas." p. 11.

[45] Alfred Russel Wallace, My Life. 2 vols. (London: Chapman & Hall, 1905), pp. 256-257.

[46] Ibid., p. 197.

One of the few similarities between Darwin and Wallace was that each of them began his career as a naturalist with an expedition to tropical America. Neither of them had upon his departure any clear idea of what the tropics would be like nor what his experience there would mean for his career. For Darwin the Beagle voyage came after university study at both Edinburgh and Cambridge and was another major change in his plans for a career--or in his plans to avoid a career. Wallace, similarly had no committment to any profession but had great fondness for field collecting, facility in the use of tools, resourcefulness and self-reliance. Darwin's and Wallace's motivations for an expedition to South America were quite similar. Collecting and natural history was the first love of both Darwin and Wallace although the background events which made them free to go on an extended adventure were radically different. Wallace's journey began in 1848; Darwin's voyage had ended in 1837. By the time Wallace set out looking for an answer to the mystery of the origin of species Darwin had already formulated a solution to the puzzle. But Wallace could not have known that.

Many of the similarities between the theories developed by Wallace and Darwin directly relate to their mutual study of wild species, more precisely, tropical, wild species. For Darwin the impressive stock of endemic species on the Galapagos archipelago was of signal importance in the development of his theory. The variation of finches and turtles

from island to island separated only by narrow straits only served to augment his doubts about the special creation of animal species.[47] Darwin's early reliance on wild species for evidence of natural selection became blurred in his later thought as he increasingly relied upon species under domestication to understand natural phenomena by analogy. The prominent role which domestication phenomena play in Darwin's theory in comparison with natural phenomena is the point of major variance between Darwin and Wallace. The discussion of the analogy between domestic and wild species runs through their correspondence like a recurring symphonic theme. It is precisely the difference between Wallace's exclusive reliance upon animals in the state of nature and Darwin's reliance upon domestic species for evidence that separates them. Domestication is the watershed. Perhaps the disparity in importance of wild phenomena stems from the fact that Wallace's experience in the tropics was longer then Darwin, is but this is too simple to exhaust the truth.

Wallace's information on the diversity of species which was gathered during four years in South America was richly augmented by seven years in the Malay Archipelago. Wallace lost nearly all his

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[47] Charles Darwin, Journal of Researches into the Natural History and Geology of the Countries Visited During the Voyage of the HMS Beagle Round the World Under the Command of Capt. FitzRoy (New York: Harper & Bros., 1946). Chapter 17.

notes and collections and nearly lost his life also when the ship on which he was returning caught fire. After two years in London, during which he put together a small book on palms[48] and a volume entitled Travels on the Amazon and Rio Negro[49] he determined to try again. His latter book was diminished by the destruction of most of his collections. Darwin complained in a letter to Bates in 1961, "I was a little disappointed in Wallace's book on the Amazon; hardly facts enough."[50] If Darwin was "a little disappointed" Wallace was utterly unsatisfied with his lack of progress at solving the problem of the origin of species, and was determined to have another try at it. Practical considerations entered into Wallace's decision to go collecting and exploring again--there were no academic positions open to one with no university degree, social standing and only scanty evidence of success as a collector.

It is an understatement to call Wallace's Malayan collection substantial. "Formidable" more nearly describes it--125,660 different species, of which a sizeable number had never been described.[51] The

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[48]Wallace, Palm Trees of the Amazon (London: [privately printed], 1853).

[49]Alfred Russel Wallace, A Narrative of Travels on the Amazon and Rio Negro (London: Reeve & Co., 1853).

[50]Francis Darwin, ed., Life and Letters of Charles Darwin, 3 vols. (London: John Murray, 1888). Letter to H. W. Bates, Dec. 3, 1861. II, p. 380.

[51]Wilma George. Biologist Philosopher. A Study of the life and Writings of Alfred Russel Wallace (London: Abelard-Schuman, 1964). p. 48. Wallace found over 900 new species of Longicorn beetle alone.

tropics in splendid diversity provided Wallace with a repertory of experiences and of factual data on which his success as a theoretician, zoogeographer, and general biologist was based. His theories were founded on animals in their natural state, rarely utilizing as Darwin often did, the analogy from domestication to buttress his arguments. Pantin's evaluation is a fair one that:

> Except for their prolonged experience of strange and untamed land there seems little in common between this [history of Wallace] and the history of Charles Darwin. But each was in fact a naturalist and each as a young man became interested in that extraordinarily varied and variously adapted group of insects, the beetles. Each spent long periods of solitude in the tropics face to face with natural facts and with his own imagination.[52]

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[52] Pantin, "Alfred Russel Wallace, F. R. S., and His Essays of 1858 and 1855," Notes and Records of the Royal Society 14:76-84, p.68.

CHAPTER II

The Development of Natural Selection

Although Darwin's curiosity had been profoundly stirred by the Beagle voyage and had settled upon natural history as a vocation he had not yet found the answer to the mystery of transmutation of species.

The road to discovery of important ideas is seldom straight and many stones remained unturned in 1837. Darwin's search for the mechanism of organic evolution was systematic; he kept reading notes and comments in a series of four notebooks and these record both the seeking and the finding of the mechanism of evolutionary change.

The variation of animals was a good place to begin, and the first notebook, opened in July, 1837 and completed in February, 1838, contained his thoughts on the role of sexual reproduction, "generation", in producing variations.

> We see the young of living beings become permanently changed or subject to variety, according to circumstances, seeds of plants sown in rich soil, many kinds are produced through new individuals produced by buds are constant, hence we see generation here seems a means to vary or adaptation . . . therefore, generation to adapt and alter the race to changing world.[1]

Already Darwin had perceived sexual reproduction as the source of variability. Sexual reproduction, the primary repository of individual variation from parental forms, is consistently linked with an apparently

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[1] Gavin DeBeer, ed., "Darwin's Notebooks on Transmutation of Species, Part I, First Notebook. (July, 1837-Feb., 1838)", Bulletin of the British Museum (Natural History) Historical Series 2(2), 1960. pp. 3-4.

opposite idea that generation provided stability to the breeding population and, therefore, to the species. The "beautiful law of intermarriages" of which Darwin wrote, was the law of blending inheritance which tends to prevent freakish variations from persisting in the population. Even in 1837 Darwin perceived that sexual reproduction was the agent that maintained the balance between variation and stability, tending to "adapt and alter" the group in a slowly changing environment and lending cohesiveness among the members of the interbreeding population.

Darwin was not fully satisfied with his first attempt to understand secual generation and the problem is posed again in the second notebook.

> It would be curious to know whether variety could be transmitted more easily in those born without coitus, than with . . . generation may be viewed as condensor. Must (on my theory)-- . . . But the acts of condensing must alter method of generation. Heaven knows how. This reaction takes place in every organ. Hence method of generation is very good general character in those animal where much change has been added, as it speaks to amount of change only and not kind.[2]

Outcrossing, inbreeding, and the communication of traits from one generation to another was a life-long study for Darwin. His early work on the topic reveals a dissatisfaction with his own understanding; each of the notebooks contains many entries on the topic. Although he believed that the "final cause" of sexual crossing was the obliteration

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[2] Gavin DeBeer, M. J. Rowlands, and B. M. Skamovsky, eds., "Darwin's Notebooks on Transmutation Species, Part VI. Pages Excised by Darwin." Bulletin of the British Museum (Natural History) Historical Series 3(5), 1967. Pages Excised from the Second Notebook, p. 162.

of variations also produced by generation, his dissatisfaction remained.

> The weakest part of my theory is the absolute necessity that every organic being should cross with another--to escape it in any case we must draw such a monstrous conclusion, that every organ is become fixed and cannot vary--which all facts show to be absurd. [3]

The notebooks contain information gleaned from a prodigious quantity of reading and the entries mention many diverse subjects including both wild and domestic animals and plants. Some merely make note of curious phenomena without theoretical remark, following the pattern which Darwin recommended in his autobiography as "true Baconian principles." Many of his comments, however, are replete with theoretical meaning, often relying upon a restrained use of analogy. The most striking is the analogy between domestic and wild species.

> It is a beautiful part of my theory, that domesticated races of organics are made by precisely same means as species--but later for more perfectly and infinitely slower-- No domesticated animal is perfectly adapted to external condition. -- (Hence great variation in each birth) from man arbitrarily destroying certain forms and not others. [4]

Domestic analogy pervades Darwin's works from the writing of the notebooks until the end of his career as a biologist. The early mention of

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[3] Gavin DeBeer, ed., "Darwin's Notebooks on Transmutation of Species. Part IV. Fourth Notebook. October, 1838-July 10, 1839," Bulletin of the British Museum (Natural History) Historical Series 2 1960. pp. 71-73.

[4] Ibid. pp. 71-72.

domestic species gains its significance in part from the fact that he later elaborated upon it in a two volume work, The Variation of Animals and Plants Under Domestication[5] with considerable mention of the topic in On The Origin of Species[6] and in Descent of Man.[7]

Darwin had filled three of his notebooks before reading Malthus' Essay on Population[8] at the end of September, 1838. He had already established many elements of his viewpoint, which he had been calling "my theory" since the second notebook. From study of both individuals and populations Darwin was convinced that variations were inheritable, and that competition was an important factor. Since the voyage of the Beagle Darwin had considerable awareness that animals change in relation to their ecological relationships. Although the puzzle had been partly worked out, a key piece was missing; it was hidden between the lines of Malthus' essay on man.

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[5] Charles Darwin, Variation of Animals and Plants Under Domestication, 2 vols. (London: John Murray, 1868).

[6] Charles Darwin, On the Origin of Species (London: John Murray, 1859).

[7] Charles Darwin, The Descent of Man and Selection in Relation to Sex (London: John Murray, 1871).

[8] Thomas R. Malthus, Essay on the Principles of Population, 2 nd. ed. (London: Macmillan, 1798).

> In October 1838, that is fifteen months after I had begun my systematic enquiry, I happened to read for amusement Malthus on Population, and being well prepared to appreciate the struggle for existence which everywhere goes on from long-continued observation of the habits of animals and plants, it at once struck me that under these circumstances favorable variations would tend to be preserved, and unfavorable ones to be destroyed. The result of this would be the formation of new species. Here, then, I had at last got a theory by which to work.[9]

On September 28, 1838 Darwin made the following entry in his notebook; which reveals the ecological basis for his discovery.

> Population is increasing at geometrical ratio in FAR SHORTER time than 25 years--yet until the one sentence of Malthus no one clearly perceived the great check amongst men . . . The final cause of all this wedging, must be too sort out proper structure, and adapt it to changes--to do that for form, which Malthus shows is the final effect (by means however of volition) of this populousness on the energy of man. One may say that there is a force like a hundred wedges trying to force every kind of adapted structure into the gaps in the economy of nature, or rather forming gaps by thrusting out weaker ones.[10]

Professor Ernst Mayr has emphasized that Darwin's most profound contribution was his use of "population thinking" instead of "typological-thinking."[11] From Darwin's earliest synthesis of theory of natural

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[9] Barlow, ed., Autobiography, p. 120.

[10] DeBeer, Rowlands, and Skramovsky, eds., "Pages Excised by Darwin," Excised from the Third Notebook, p. 135.

selection it was devoid of Platonic idealism and firmly based on changes within populations. Evolution by natural selection includes both the death of the weaker and the survival of the stronger in the struggle for live, but the whole warfare is in direct relationship to the environment, the "oeconomy of nature."

Since Darwin opened his series of notebooks with the self-conscious purpose of working out a theory of transmutation it is enlightening to pay careful attention to his early discussion of animal coloration which may be approached from either a theoretical or observational standpoint. It is not surprising that Darwin included entries on animal colors; they are both external and variable and bright colors are characteristic of both domestic and wild species. The advantage of certain patterns of colors was already well acknowledged.[12]

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[11] Ernst Mayr, "Introduction," to On the Origin of Species by Charles Darwin (Cambridge, Mass.: Harvard University Press, 1966), pp. xi-xxiii. Darwin's biology has only scant traces of Platonic-types, or what Mayr has called "eidos." Peter J. Vorzimmer has recently pointed out that Darwin limited the principle of utility, underlying natural selection, to individuals, which Wallace extended to populations. Darwin was, then, a "population-thinker" in terms of divergent evolution and in opposition to typology, but not with respect to the principle of utility. Peter J. Vorzimmer, Charles Darwin: The Years of Controversy. The Origin of Species and its Critics, 1859-1882 (Philadelphia: Temple University Press, 1970). pp. 206-208.

[12] DeBeer, ed., "Darwin's Second Notebook on mutation of Species," p. 85. "With respect to question which is adaptation, examine ptarmigan, hare becoming white in winter of Arctic countries few will say it is direct effect, according to physical laws, such as sulphuric acid disorganized wood."

Darwin's concern for the laws of heredity, and for natural law in general, prevented him from slipping into a cavalier dismissal of coloration as too variable a trait to be subject to law. Nor did he assume the direct action of the environment. Darwin was well aware that the effect of the environment could be learned with certainty by experimental isolation of some members from their normal environment.[12a] The notebook entries were made by a serious student of biological science whose "graduate program" had been taken aboard the HMS Beagle.

Although Darwin's notebooks were completed in England they contain many references to observations from the Galapagos, Tierra del Fuego, and the Andean Cordillera. His discovery of the missing piece to the species puzzle was put into its place shortly after the second anniversary of his landing in Falmouth. South America and the stimulus it's unique fauna and flora provided much of the impetus behind Darwin's change from a dilettante collector to a professional scientist.

In 1842 when Darwin committed his theory to an outline prose sketch, he began with a section entitled "On Variation Under Domestication" in which the importance of the inheritance of

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[12a] Ibid., p. 86, "The only way of judging whether structure is owing to habits on hereditary is to see whether a large family has it, and one member of that family having it with very different habits.

characters impressed directly by the environment was clearly recorded.

> An individual organism placed under new conditions [often] sometimes varies in a small degree and in very trifling respects such as stature, fatness sometimes colour, health, habits in animals and probably disposition. Also habits of life develop certain parts. Disuse atrophies. [Most of these slight variations tend to become hereditary.][13]

The early sketch contains passages which are equally reminiscent of the "Notebooks on Transmutation" and foreshadow the Origin of Species published seventeen years later. The brief discussion of sexual selection is particularly similar to that found in the Origin.

> Besides selection by death, in bisexual animals . . . the selection in time of fullest vigour, namely struggle of males; even in animals which pair there seems a surplus and a battle, possibly as in man more males produced than females, struggle of war or charms. Hence that male which at that time is in fullest vigour, or best armed with arms or ornaments of its species, will gain in hundreds of generations some small advantage and transmit such characters to its offspring. So in female rearing its young, the most vigorous and skillful and industrious, instincts best developed, will rear more young, probably possessing her good qualities, and a greater number will thus be prepared for the struggle of nature. Compared to man using male of good breed . . .[14]

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[13] Charles Darwin, Sketch of 1842, p. 41. In Evolution by Natural Selection by Charles Darwin and Alfred Russel Wallace. (Cambridge: University Press, 1958). According to DeBeer, the brackets indicate that Darwin erased these from the original manuscript and perhaps show that on second thought he preferred not to be so definite on the subject of inheritance of acquired variation, at least at the outset of the paper.

Sexual selection conferred an advantage upon succeeding generations just as natural selection does, but it was more limited in its scope of operation. It was primarily related to the variation of sexual traits and to the struggle between males; consequently, the effect of sexual selection tended to be greater in the males rather than in the species at large. Darwin's "trademark", the analogy from domestication, characterized nearly all his discussions of sexual selection. Although the idea of sexual selection has given only a small place in the total argument for evolution by natural selection; it was a place destined for subsequent enlargement in Darwin's total theory of evolution. The Essay of 1844 contained an amplified discussion of sexual selection; it ought not be overlooked that the passage on sexual selection was chosen to be a part of his earliest publication on the mechanism of evolution.[15] There are at least five major aspects to Darwin's delineation in the Essay of a "second agency" of selection. (1) It is less intense than normal

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[14] Ibid., pp. 48-49. Darwin's two types of sexual selection, "war or charms" are already distinct in the same way as in the Origin, 1st edition, pp. 88-90.

[15] In the joint Darwin-Wallace papers, "On the Tendency to Form Varieties and on the Perpetuation of Varieties and Species by Natural Means of Selection," Proceedings of the Linnean Society of London 3:45-62, p. 50. The Essay of 1844 is found in extenso in Evolution by Natural Selection by Charles Darwin and Alfred Russel Wallace (Cambridge: University Press, 1958), pp. 91-257.

selection; (2) It is most effective in excess male to female ratio; (3) It usually acts in concert with natural selection but may occasionally oppose it; (4) Artificial selection is analogous to sexual selection; (5) The effects are usually confined to one sex rather than distributed equally.

The early essays are important because of the insight they provide on Darwin's own mental processes and development as he elaborated and documented the theory in preparation for eventual publication. Neither of the essays were intended for publication, except in the event of his death. They are also interesting because they present in miniature many of the topics discussed in great detail in the Origin. Darwin's work after 1844 was predominantly horizontal, that is, extension and application of his hypothesis rather than development of new theories. The essays are particularly relevant to the discussion of animal coloration because of the dichotomy between the province of sexual selection and of natural selection. Protective colors fall within the domain of natural selection and the bright colors of sexual dimorphism in that of sexual selection. Darwin's discussion of animal colors emphasized the independence of the two agencies of selection rather than sexual selection as a special case of natural selection.

Darwin's preliminary studies and essays did not lead directly to revision and publication but were followed by a long interlude

during which he was occupied by systematic and anatomical work on barnacles.[16] During the eight year course of study on Cirripedia Darwin became a trained naturalist instead of merely a collector and observer.[17]

Darwin was reluctant to publish anything on transmutation without amassing evidence to present in his own defense and to countermand all possible objections. The publication of Vestiges of the Natural History of Creation[18] in 1844 evoked a general outcry against "irreligious speculation" which rejected the literal truth of the Genesis account of creation. Darwin was too cautious and too wise to publish his own work when one treating the same general topic was under widespread attack. At the end of 1844 Darwin put his work on species aside and for the next ten years undertook other projects of which the work on Cirripedia was the longest, but included his book on the geology of South America[19] and another edition of his Journal of Researchers.[20]

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[16] Charles Darwin, A Monograph on the Sub-class Cirripedia (London: Printed for the Ray Society 1851-1854).

[17] Barlow, ed., Autobiography, pp. 117-118.

[18] [Robert Chambers], Vestiges of the Natural History of Creation (New York: Wiley & Putnam, 1845).

[19] Charles Darwin, Geological Observation on South America (London: John Murray, 1846).

[20] Charles Darwin, Journal of Researches, 2nd ed. (London: John Murray, 1845).

When Darwin laid aside his manuscript on transmutation to begin the study of barnacles, Alfred Russel Wallace, the other main character in the drama of the discovery of natural selection, was beginning his collection of beetles in the country surrounding Leicester. On the surface Darwin and Wallace had little in common except a great love for field biology. Their temperaments and backgrounds were different, yet their ideas were remarkably similar. Their topics of interest so strategically and repeatedly overlapped that Darwin exclaimed in a letter to Wallace, "It is curious how we hit on the same ideas."[21] It was indeed.

Wallace and his companion, Henry Walter Bates, self-taught naturalists though they were, began their tropical researches in an aggressive, determined spirit.[22] They were learners, not merely commercial collectors. Each of them kept careful notes of his travels and observations. Bates' book, The Naturalist on the River Amazons,[23] is a classic of the travel narrative genre. Bates was

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[21] Marchant, James, ed., Alfred Russel Wallace's Letters and Reminiscences, 2 vols. (London: Cassel & Co., 1916). Letter, Darwin to Wallace, April 29, 1867. I, p. 152.

[22] Barbara G. Beddall, ed., Wallace and Bates in the Tropics (London: Macmillan, 1969).

[23] Henry Walter Bates, The Naturalist on the River Amazons. (London: John Murray, 1864). (Reprinted 1964 by University of California Press: Berkeley).

first of all an entomologist and his major theoretical contributions are in that field. His discovery of mimicry in 1862 is the contribution for which he is best remembered.[24]

Wallace's South American expedition did not end as successfully as Bates; whose collections arrived in tact. On his return to England the brig, the Helen, caught fire and was totally destroyed; consequently Wallace lost his entire collection of specimens and almost all of his notes which would have enhanced his own travel narrative and constituted the factual basis for further theoretical works. Fortunately, experience cannot be destroyed, even by fire, and Wallace was determined to continue in scientific research.

After a two-year interlude Wallace undertook a second expedition to the Malay Archipelago which was more productive for him as a collector, and also as a theoretical biologist. When he was in Sarawak, Borneo he made his first published contribution on the subject of organic evolution with the article "On the Law which has Regulated the Introduction of New Species."[25] His law clearly stated "Every species has come into existence coincident both in time and

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[24]Bates defined mimicry as the resemblance in external appearance, shapes and colours between members of widely distinct families. Beyond Bates' narrow definition, Batesian mimicry includes the class of phenomena in which unprotected and generally unpalatable insects resemble protected, unpalatable species. The first mention of the mimicry phenomena are in Bates, "Contributions to an Insect Fauna of the Amazon Valley," Linnean Society Journal (Zoology) 6:73-77.

space with a pre-existing closely-allied species."[26] Natural classification systems must be a forked or many branched line like the "twigs of a gnarled oak." The analogy between similar species on the phylogenetic tree was, near the common antetype actually an affinity. Wallace's autobiographical account gives the details of how the article came to be written.

> On wet days I had nothing to do but to look over my books and ponder over the problem which was rarely absent from my thoughts. Having always been interested in the geographical distribution of animals and plants, having studied Swainson and Humboldt, and having now myself a vivid impression of the fundamental differences between the Eastern and Western tropics; and having also read through such books as Bonaparte's "Conspectus" . . . and several catalogues of insects and reptiles in the British Museum (which I almost knew by heart), giving a mass of facts as to the distribution of animals over the whole world, it occurred to me that these facts had never been properly utilized as indications of the way in which species had come into existence. The great work of Lyell had furnished me with the main features of the succession of species in time, and by combining the two I thought that some valuable conclusions might be reached. I accordingly put my facts and ideas on paper . . .[27]

In 1855 Wallace had synthesized from the evidence of zoogeography, taxonomy, and uniformitarian geology the "when" and "where" of the transmutation problem, but discovery of the "how" of specification was still four years into the future.

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[25] A. R. Wallace, "On the Law Which has regulated the Introduction of New Species," Annals and Magazine of Natural History 16:184-196, 1855.

[26] Wallace, "On the Law . . . ," p. 186.

The Sarawak Essay of 1855 illustrated a view of science as a combination of fact and theory. In "On the Law" Wallace is no strict Baconian, but fully within the perspective now called Darwinian. Wallace was dealing with broad categories under an even broader hypothesis. He set forth the limits of his law:

> This law agrees with, explains and illustrates all the facts connected with the following branches of the subject: 1st. The system of natural affinites. 2 nd. The distribution of animals and plants in space. 3rd. The same in time, including all the phaenomena of representative groups, and those which Professor Forbes supposed to manifest polarity. 4th. The phaenomena of rudimentary organs.[28]

For Wallace, equally with Darwin, science is legitimately explanatory and hypothenis is co-equal with observation. The Sarawak Essay was written in opposition to Edward Forbes' platonistic Theory of Polarity,[29] which tends to confirm Walter Cannon's thesis that the sides in the evolution controversy were actually drawn between empiricists and

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[27] A. R. Wallace, My Life, I, pp. 354-355.

[28] Wallace, 1855, "On the Law which has regulated the Introduction of New Species," Annals and Magazine of Natural History, 16:186.

[29] Walter Cannon, "The Bases of Darwin's Achievement: A Reevaluation," Victorian Studies 5:109-134, 1961. Forbes divided fossil history into two divisions, the paleozoic and the neozoic. If one imagined oneself as in the time period dividing the two periods one would find that the production of new "genera-ideas" per unit time was at a minimum. Looking back into the paleozoic one would see an increase in the number of new genera ideas the same would be true looking forward in time toward the present, but the genera-ideas would be different. On either side of the division of fossil period one may see an increasingly richness in genera-ideas.

platonists rather than between believers in evolution and believers in special creation. Forbes' Theory of Polarity, like the typological classifications of Swainson and others, was a total alternative to the phylogenetic system of taxonomy or the uniformitarian evolutionary principle of geology. Forbes' death prevented the discussion which Wallace had expected his article to evoke; the essay was generally ignored or criticized.

> Soon after this article appeared, Mr. Stevens wrote me that he had heard several naturalists express regret that I was "theorizing" when what we had to do was to collect more facts.[30]

Observational science was still the only widely accepted activity for the naturalist.

The essay of 1855 was not all theory, both geographical and geological evidence was marshalled in defense of the new law and in opposition to Forbes' idealistic law of polarity. Geographical distribution was employed to account for evidence in spatial terms and geology to account for temporal evidence. Wallace had made a powerful argument for evolution; Thomas Huxley writing in Darwin's Life and Letters said: "On reading it ["On the law which has regulated the Introduction of New Species"] afresh, I have been astonished to

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[30] Wallace, My Life, I, p. 355.

recollect how small was the impression it made."[31] Huxley's statement seems to confirm Professor Pantin's retrospective assertation that the Sarawak essay was "perhaps the most important Pre-Darwinian essay on the origin of species apart from the works of Lamarck."[32]

During his stay in the Malay Archipelago, Wallace wrote an extensive, unpublished sketch of his theory which was, in large part, inspired by Lyell's publications. The "Species Notebook" was one phase of Wallace's preparation of a book tentatively titled "Organic Law of Change."[33] His work on species continued despite disappointment that his essay had evoked little response.

Although the Sarawak Essay had the effect of alienating colleagues who denounced his "theorizing", covertly it made a deep impression on a few major scientists. Charles Lyell opened his own species notebook two months after Wallace's essay was published. As if to confirm the implication of Wallace's influence, Lyell wrote Wallace's name at the top of his first page.[34]

In 1857 Wallace wrote another essay, "Note on the Theory of Permanent and Geographical Varieties"; it was an attempt to grapple

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[31] Thomas H. Huxley, "On the Reception of the Origin of Species," in Life and Letters of Charles Darwin, ed. by Francis Darwin, II, p. 185.

[32] Pantin, "Alfred Russel Wallace, F. R. S., and His Essays of 1858 and 1855," p. 71.

with the indistinct border between species and varieties which he understood as incipient species.

> On continents the individuals of one kind of plant disperse themselves very far, and by the difference of stations of nourishment and of soil produce varieties, which at such a distance not being crossed by other varieties and thus brought back to the primitive type, become at length permanent and distinct species. Then if by chance in other directions they meet with another variety equally changed in its march, the two have become very distinct species and are no longer susceptible of intermixture.[35]

Dispersal, isolation, eventual sterility of hybrids, and speciation were Wallace's primary interests in 1857.

The pursuit of a mechanism for organic evolution was long and tortuous, it was thirteen years from his first mention of evolution as a topic for research until his synthesis of a complete theory of natural selection in Ternate, 1858.

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[33] Wallace's Species Notebook is being prepared for publication by H. Lewis McKinney and he gives Wallace's projected title for his book in "Alfred Russel Wallace and the Discovery of Natural Selection." Journal of the History of Medicine 21:342-343, 1966.

[34] Leonard G. Wilson, ed., Sir Charles Lyell's Scientific Journal on the Species Question (New Haven: Yale University Press, 1970).

[35] From Wallace's Species Notebook, p. 90, Quotation taken from "Wallace, Darwin and the theory of Natural Selection" by Barbara G. Beddall. Journal of the History of Biology 1:287, 1968. Beddall's article is the most analytical and most comprehensive publication emphasizing Wallace's development and discovery of natural history Its value is especially great because passages are included from Wallace's species notebook which is not available at the present time.

Darwin read Wallace's essay in 1855 and was one of few to give him any encouragement. Their correspondence had begun shortly before the publication of Wallace's essay and Wallace had revealed to Darwin the progress he had made in the study of the origin of species. Wallace's side of the correspondence is missing but it is possible to infer the content of his letters from Darwin's replies. From their first letters, the subject of domestic and wild varieties was a primary concern, other subjects in early letters included sterility of hybrids and the direct effects of climatic conditions; subjects on which there was recurring discussion and on which agreement was rare. The difference of opinion on the sterility of hybrids reflected their differing beliefs on the influence of geographical barriers in the production of speciation and the adaptive value of sterility. The subject of environmental influence was related to the Lamarckian elements in Darwin's thought. Wallace, from the beginning of his theorizing on evolution, did not give any credence to the idea that climatic conditions directly cause variations. Even with such central differences Darwin was correct to state "we hit on the same ideas." If their differences were striking their similarities were equally important.

Darwin had been warned by Charles Lyell in 1856 not to delay in publishing a sketch of his views of natural selection. Lyell's appeal had been reinforced by Joseph Hooker; the conclusion of the matter

was that Darwin did nothing but "most heartily to wish that Lyell had never put this idea of an Essay into my head."[36] Darwin had confided most of the salient points of his theory to Asa Gray in 1855, but in writing to Wallace he said, "It is too long a subject to enter on my speculative notions."[37] Lyell's advice to Darwin to publish a statement on natural selection would not of itself suggest that Lyell perceived that Wallace was close to his own solution of the species puzzle if it were not also known that Wallace's influence via the "Essay of 1855" induced Lyell to open his own notebook on species. The tone of Darwin's letters was cordial; he did not betray any anxiety that Wallace would publish a theory and destroy his priority as well as his originality. Darwin's friendliness was not, however, unmixed with caution. Although his views had not been too long to put into a letter to Asa Gray; they were too long to write to Wallace. It is an easy leap to the conclusion that Darwin was well aware that Wallace and he "hit on the same ideas."

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[36] F. Darwin, ed., Life and Letters of Charles Darwin, II, p. 71.

[37] James Marchant, ed., Alfred Russel Wallace: Letters and Reminiscences, I, p. 109.

Wallace's third letter to Darwin contained the essay, a complete sketch of his ideas on the mechanism of evolution by natural selection, entitled "On the Tendency of Varieties to Depart indefinitely from the Original Type." Wallace's autobiographical account of his discovery of natural selection emphasized the "flash of light" aspect; but it took more than 10,000 miles of travel and more than ten years of study to ready his mind for the flash of insight.

> At the time in question I was suffering from a sharp attack of intermittent fever, and every day during the cold and succeeding hot fits had to lie down for several hours, during which time I had nothing to do but to think over any subjects then particularly interesting to me. One day something brought to my recollection Malthus's "Principles of Population," which I had read about twelve years before. I thought of his clear exposition of "the positive checks to increase"--disease, accidents, war, and famine--which keep down the population of savage races to so much lower an average than that of more civilized peoples. It then occurred to me that these causes or their equivalents are continually acting in the case of animals also . . . Why do some die and some live? And the answer was clearly, that on the whole the best fitted live.[38]

The new theory was quickly written out in order to complete the essay before the next mail departed. The essay was sent to Darwin along with a letter, now missing, requesting Darwin to forward the essay to Charles Lyell if he thought it sufficiently important. "Your words have come true with a vengeance--that I should be forestalled,"

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[38] Wallace, My Life, I, p. 361-362.

Darwin wrote in the letter which had Wallace's essay enclosed with it. Lyell and Hooker shared the responsibility with Darwin of deciding upon a judicious procedure. They decided to publish Wallace's essay with fragments of Darwin's work which established them as co-discoverers of natural selection. Although the major biographies of Darwin have rendered the joint-publication an oft-told tale it is more than a mere anecdote in the history of evolution since the circumstances of publication defined the terms of Darwin and Wallace's relationship to each other and to posterity in regard to priority. Research into the incident has been hampered by the disappearance of crucial documents--the letters to Darwin from Wallace, Hooker, and Lyell regarding the essay, and the manuscript of Wallace's essay are all missing and as Barbara Bedall points out, "The facts, consequently are difficult to determine and the circumstances have been variously interpreted."[39] The ambiguity which has resulted has led to many disagreements among scholars. George Sarton[40] and Loren Eiseley[41]

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[39]Bedall, "Wallace, Darwin and the Theory of Natural Selection," p. 299. It has been difficult to determine why these letters should be missing when Darwin saved others from the same time period. It may be that they were destroyed or lost in some way not involving Darwin himself, but there is an atmosphere of mystery in the whole issue.

[40]George Sarton, "Discovery of the Theory of Natural Selection," Isis, 14:134. What he says is, in itself, true enough. Darwin and Wallace were not simply great discoverers; they were great men." It misrepresents the situation which was not one of chivilrous behavior, but of frustration and necessity.

have asserted the nobility of the participants; a point of view which Barbara Beddall has rightly modified.[42] Wallace had no knowledge of what Darwin had done with his paper for a long time after the publication. It ought to be remembered that Wallace had not requested publication either by Darwin or Lyell, merely their reactions to his theory. That Wallace never stressed his equality as co-discoverer is evident in both his correspondence and in his references to "Darwinism" as synonymous with the theory of Natural Selection. Wallace wrote Bates that he was glad for the publication of the Origin of Species since it relieved him of the necessity of elaborating the theory.[43] His claim was not that he was Darwin's equal in discovery

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[41] Loren Eiseley, Darwin's Century, Anchor Books (Garden City, New York: Doubleday & Co., 1961), p. 292. "When Wallace sent his theory to Darwin and there occurred that mutual nobility of behavior so justly celebrated in the annals of Science."

[42] Beddall, "Wallace, Darwin and the Theory of Natural Selection," p. 301. "This was not an occasion of 'mutual nobility' nor was it a monument to the natural generosity of both the great biologists," [Julian Huxley in Alfred Russel Wallace, "Dictionary of National Biography, Supplement 1912-1921" (London: Oxford University Press, 1927), p. 547] as is so often claimed. It was clearly not mutual because Wallace's paper was read without his knowledge or consent, and he knew nothing about it until October. Nor does it seem to have been particularly noble. However just Darwin's claims to priority, he was a gainer, not a loser, from the decision. Wallace had no opportunity to be either noble or generous."

[43] Marchant, Alfred Russel Wallace: Letters and Reminiscences, I, p. 59. Letter, Wallace to Bates, December 24, 1860.

but that he was second to none as an adherent of the doctrine of evolution by natural selection.

Wallace fully grasped the difference between his own understanding of natural selection and that of others like Patrick Matthews and William Wells. It is the difference between a line drawn tangent to a circle and one drawn solidly through the diameter. With the essay, "On the Tendency of Varieties to Depart Indefinitely from the Original Type," Wallace showed that his understanding and application of natural selection was on the center. Professor Pantin's summary is appropriate.

> The intuitive discovery of a new principle may seem to us as though it must be 'all-or-nothing'. Either you discover natural selection, or you do not. That is not in fact so. We may grasp a notion, but only imperfectly and inconsistently perceive its implications; and thereby fail to raise its significance above that of a multitude of trivial things in our mind. It is as though one found and recognized a key but failed to realize the implication of the doors it would unlock. There is, I believe, a close relation between this and poetic imagery. The same image which in the hands of an indifferent poet--or a great poet in an indifferent moment--gives us no more than evanescent pleasure, can in the hands of the really great transform our view of human life.[44]

Wallace was not a usurper of Darwin's priority, but a colleague in the scientific enterprise.

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[44]Pantin, "Alfred Russel Wallace, F. R. S., and His Essays of 1858 and 1855," p. 73.

The joint papers consist of an abstract of Darwin's Essay of 1844 his letter to Asa Gray, 1857,[45] and Wallace's essay, "On the Tendency of Varieties to Depart Indefinitely from the Original Type," prefaced by an letter from Hooker and Lyell explaining the unusual circumstances surrounding the publication. The joint publication is a convenient point for refocusing attention on the different uses Darwin and Wallace made of domestication phenomena and for the different uses of coloration in animals as illustrative of the natural selection hypothesis.

Darwin chose to include in his published abstract a passage on sexual selection taken almost verbatim from the 1844 essay. Coloration, as Darwin used it was (1) frequently subject to sexual selection and (2) a paradigm example of the production of traits in the state of nature which is analogous to the artificial selection of the breeder.

From the outset, Wallace treats domestic varieties as distinct from wild. Domestic breeds do not depart indefinitely from the original type. Although they may vary considerably from their parental stock if left to themselves they will tend to revert to their

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[45] Although mainly a reiteration of points in the abstract, the letter to Gray is more succinct and includes a statement on divergence not found in the 1844 essay and which John L. Brooks ["Reassessment of A. R. Wallace's Contribution to the Theory of Organic Evolution," American Philosophical Yearbook of 1968:534-535 (1968)] contends is evidence of Wallace's influence.

original type rather than continue to vary in the direction the breeder had chosen. Nothing could more clearly illustrate the difference between Darwin and Wallace, than the use of domestic analogy.

Darwin, for whom natural selection was analogous to the nursery man's "roguing," wrote:

> It is wonderful what the prinnciple of selection by man, that is the picking out of individuals with any desired quality, and breeding from them, and again picking out, can do.[46]

> I think it can be shown that there is such an unnerring power at work in Natural Selection . . . which selects exclusively for the good of each organic being.[47]

Wallace's argument cames from quite a different direction.

> We see, then, that no differences as to varieties in a state of nature can be deduced from the observation of those occurring among domestic animals. The two are so much opposed to each other in every circumstance of their existance, that what applies to the one is almost sure not to apply to the other.[48]

The same mechanism, natural selection, at work in both domestic and build species will act differently, even oppositely. In wild animals the tendency will be to diverge progressively from parental

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[46] Darwin, "On the Tendency of Species to form Varieties; and on the Perpetuation of Varieties and Species by Natural Means of Selection," Proceedings of the Linnean Society, London 3:50, 1858.

[47] Ibid., p. 51.

[48] Ibid., p. 61.

types and in domestic varieties to revert to the ancestral form. Wallace used color phenomena in three allied but distinct ways in his essay. (1) Color is used as representative of variations which have definite effects on the habits and capacities of the animals possessing them. In this case the animals protection may be enhanced or diminished by a small change of coloration. (2) Color represents the action of the natural selection principle, in contrast to Lamarckian influences. Animals bearing the best protective coloration are not victims of their predators. There is no volition, no direct action of the environment; coloration exemplifies natural selection and natural selection alone. (3) Similar "colour, texture of plumage and hair, form of horns or crests,"[49] etc., may be preserved in species which, through divergence, have other, more important differences if no more perfectly adapted form arises in the population. External and internal characters, vital and superficial traits are equally subject to the principle of natural selection.

Although the Proceedings of the Linnean Society for July 1, 1858, was a turning point for biological science, there was little response from the company of naturalists who heard the reading of the Darwin-Wallace papers or from those who read the publication. The history of science contains a surfeit of cases in which a new idea, even a

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[49] Wallace, "On the Tendency . . . , " p. 62.

brilliant idea, had to wait for acceptance and in the case of Mendel's genetics, even for discussion. Darwin and Wallace's theory did not have to wait long, the next year Darwin's magnum opus was published and the battle was joined.

On the Origin of Species was hastily completed; Wallace had unknowingly compelled Darwin to publish. Darwin considered the Origin of Species an abstract of his views--each chapter of the book was an outline of a topic for a projected book-length work. The intellectual circumstances in 1859 were not very different from those during which Darwin wrote the Essay of 1844 and Sir Gavin DeBeer's comment is appropriate 1859 also:

> It is a matter for wonder that with the meager materials at his disposal he was able to steer a straight course across a largely uncharted ocean of ignorance, with rocks of falsehood right across his path.[50]

The prospects for immediate acceptance of a theoretical work were poor even if no religious questions were raised. Much of the evidence which is presently used in support of Darwins hypothesis was not available.[51] Especially significant was the inadequate notion of the

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[50] DeBeer, Charles Darwin, A Scientific Biography, p. 131.

[51] Gavin DeBeer in the "Foreward" to Evolution by Natural Selection by Charles Darwin and Alfred Russel Wallace (Cambridge: University Press, 1858) pp. 2-3. Sir Gavin DeBeer gives an impressive list of what was not known in 1858. (1) no knowledge of chromosomes or meiosis, (2) no knowledge of mimicry (3) no knowledge of the homology of the body cavity, genital ducts and kidneys, (4) no knowledge of the segmentation of vertebrates, (5) similarity of

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"laws of heredity" which Darwin used; blending inheritance was not particularly useful for prediction and Darwin had to confess that the laws of variation were not well known. Although the force of Darwin's argument was diminished without the unequivocal support of particulate genetics, precise laws of inheritance, paleontological, embryological and anatomical evidence his achievent is undiminished, but rather an even greater monument to his ability as a theoretician.

Although the Origin of Species was a theoretical work, it is filled with facts from all quarters of natural history and its impact depended as much upon its inclusiveness as upon its innovativeness. Darwin, more than anyone else must be given credit for the earliest elaboration of the theory of natural selection. It is little wonder that Darwin became the symbolic leader of nineteenth century evolutionists. The Origin of Species was the great headland against which the waves of criticism crashed and the Origin itself showed considerable erosion.

There is considerable literature on the subject of Darwin's trend toward Lamarckism in later editions of the Origin; a traditional

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[51](Continued) Ascidian tadpoles and vertebrates and between hemichordates and echinoderm larvae and not been discovered many vestigial organs were not understood. (7) botanists had not realized the significance and existence of alternation of generations in plants, (8) little paleontological support, (9) age of earth was still considered in biblical terms, (10) no comparative serology. The ocean of ignorance was a wide and dangerous place.

interpretation being that the criticisms offered by Fleeming Jenkin (1867) on the "swamping-out" of favorable variations[52] caused Darwin to turn towards Lamarckian explanations. The first edition of the Origin controverts this belief since it contains numerous instances of Darwin's use of the inheritance of acquired characters.[53] Darwin's increasing reliance upon Lamarckism is rendered most graphic by an examination of the variorum edition of the Origin of Species,[54] Jacques Barzun's statement is badly overdrawn, nevertheless it expresses the fundamental nature of the changes in Darwin thought between 1859 and 1872.

> In the middle versions of the Origin of Species there was a dash of all the disputed hypotheses--a little Lamarckian use and disuse, a little Buffonian change by direct action of the environment, and a little curtsey before the Creator, who is mentioned by name. Natural selection nevertheless dominated the scene.[55]

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[52] Fleeming Jenkin, "The Origin of Species," North British Review 96:149-171, 1867.

[53] Ernst Mayr has included a list of references to use and disuse in the introduction of the facsimile reprint of the first edition of the Origin of Species. p. xxxvi.

[54] Charles Darwin, The Origin of Species. A Variorum Test. by Morse Peckham (Philadelphia: University of Pennsylvania Press, 1959).

[55] Jacques Barzun, Darwin, Marx, Wagner, Revised 2nd ed. (Garden City, New York: Doubleday & Co., 1858). p. 57.

Perhaps the changes Darwin made in successive editions of the Origin of Species are more fairly attributed to flexibility than to weakness; certainly many of the criticisms could not go unanswered. There were questions in the 1960's that seemed unanswerable by the theory of natural selection. Some modifications were required in response to valid criticism and Darwin, who was not impervious to attacks on his theory, was steadily driven to contract the borders of the domain of natural selection in order to retrench. The widening Lamarckian sphere was a by-product of Darwin's move to save natural selection, not an act of surrender. Explanation based on old Lamarckian ideas was not embraced by Darwin in the positive sense, but was ceded or defaulted to Lamarckian categories when natural selection proved inadequate. When Darwin could not explain phenomena by using natural selection he found alternatives. It was an honest, scientific choice.

His treatment of sexual selection does not change appreciably throughout the course of six editions of the Origin, in spite of the fact that the subject of other secondary agents of selection was given increased space and attention in later editions. The full elaboration of sexual selection was reserved for The Descent of Man, published in 1871. Although the discussion of sexual selection was abbreviated in the Origin, nevertheless its scope was broad, its effects reaching as low in the phylogenetic scale as to be in evidence

in the appendages and colors of beetles.

Darwin's discourses on coloration in animals were usually, but not always, related to sexual selection; coloration in domestic species is excessively variable, having no bearing on survival in the artificial state. The emphasis on domestic species is reflected by his references to color as "that most fleeting of characters,"[56] and as a "trifling character"[57] with respect to most domestic breeds Darwin is quite right, but in the wild state an animal's color may seem the difference between survival and death. In such species color is highly stable, being regulated by natural selection; a fact which Darwin does not ignore.

> It may be said that natural selection is daily and hourly scruitizing, throughout the world, every variation, even the slightest; rejecting that which is bad, preserving and adding up all that is good; silently and insensibly working, whenever and wherever opportunity offers, at the improvement of each organic being in relation to its organic and inorganic conditions of life. . . Hence, I can see no reason to doubt that natural selection might be most effective in giving the proper colour to each kind of grouse, and in keeping that colour, when once acquired, true and constant.[58]

Darwin did not overlook either the reality nor the importance of protective coloration; it is a matter of emphasis. Wallace, Bates,

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[56] Darwin, On the Origin of Species, p. 39-40.

[57] Ibid., p. 410.

[58] Darwin, On the Origin of Species, pp. 84-85.

Meldola and many other evolutionists perceived color phenomena from the perspective of natural selection; whereas Darwin's view tended to be from the alternative vantage point of sexual selection, a more specialized, less severe form of selection.

Darwin weathered a considerable onslaught of criticism on the subject of sexual selection from supporters of his idea of natural selection. There was concern on Wallace's part that Darwin had been led astray by his application of domestic phenomena to wild species. Darwin's made extensive use of anthropomorphic language in the Origin of Species with the affirmation that he intended it only as a literary device. Not all his associates were either comforted or convinced.

> Nature, like a careful gardener, thus takes her seeds from a bed of a particular nature, and drops them in another equally well fitted for them.[59]

> Those who have closely attended to birds in confinement well know that they often take individual preferences and dislikes.[60]

The concept of female 'choice' in beetles, salmon, alligators, etc., the analogy of nature to a gardener or an animal breeder was difficult for Baconian scientists to accept, even with the assurance that the animals choice is unconscious.

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[59] Darwin, On the Origin of Species, p. 388.

[60] Ibid., p. 89.

Sexual selection has two aspects; the first of them Darwin called the "Law of Battle." The struggle for reproduction assures the continuation within the species of the attributes of the most vigorous animals. On the individual level sexual selection is less rigorous than natural selection. Failure to reproduce is not synonymous with the failure to survive; it does mean, however, that the inheritable characters of that animal are not perpetuated. In sexual selection the race is to the swift and the battle to the strong. The law of battle is an extension and specialization of natural selection and was not generally criticized by Darwin's fellow evolutionists. The struggle for existence on the individual plane was governed by natural selection; sexual selection was the struggle for existence at the species level, on a broader level of space and time.

Darwin's concept of sexual selection, however, greatly transcended the law of battle; it was the supplementary conclusions which made him susceptible to criticism, especially his use of anthropomorphic language implying volition in birds and insects. Not only did sexual selection depend upon domestic analogy which was suspect, but it also became intangled in ambiguities of a semantics and metaphors. The distinction between the human breeder making a selection and the choice of the wild female bird was not always clear.

On the one hand, sexual selection depends upon the persistence of similar 'tastes' in female animals for many succeeding generations

in order to produce a result analogous to artificial selection; Darwin's example of the pied cock which was attractive to the hens seems to contradict this point of view.[61] The pied cock was a deviant from the normal and Darwin admitted that birds "take individual preferences." The idea of sexual selection demands a uniformity or community of taste in order to have significant net effect over the period of thousands of generations.

Bantams and peacocks in captivity present frail evidence for the conclusion that Darwin asserted:

> Thus it is, as I believe,
>
> > That when the males and females of any animal have the same general habits of life, but differ in structure, colour, or ornament, such differences have been mainly caused by sexual selection.[62]

The division of labor among birds makes it difficult to assert with certainty the actual degree of similarity between their habits. Darwin did not name explicit criteria for "the same general habits." Darwin's views on sexual selection had to wait for a better explication of important details.

Darwin's argument for sexual selection needed tightening; the language was anthropomorphic and troubled by an inconsistent use of the utility principle which he used at need, rather in the manner

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[61] Darwin, On the Origin of Species, p. 89.

[62] Darwin, On the Origin of Species, p. 89.

of an ad hoc hypothesis, used to fill a breach in logical sequence. Statements like "I can see no good reason to doubt that female birds, by selecting during thousands of generations, the most melodious or beautiful males, according to their standard of beauty, might produce a marked effect, "[63] are the inverse of the Baconian method by which proof was derived from the overwhelming preponderance of evidence necessitating a certain explanation. Nature's laws are self explanatory to the Baconian scientist who observes correctly. Darwin was well aware that his strong suspicions would not be enough to convince other naturalists. The correspondence between Darwin and Bates, Wallace, J. J. Weir, Raphael Meldola, etc., contans many requests for information on animal coloration and sexual selection.[64]

Darwin used color phenomena to illustrate the laws of inheritance, especially in the discussion of reversion to ancestral type.[65] Darwin's implicit point of view was that protective coloration illustrated a primitive condition which may be regained by ferel animals. The emphasis in the Origin of Species is on color as it is used in courtship

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[63] Ibid., [italics mine, M. L. B.]

[64] Some of Darwin's inquiries were in preparation for forthcoming books, others were related to long-term discussions between the correspondents.

[65] Darwin's discussion of the frequent reappearance of blue markings in domestic pigeons, similar to ancestral rock-pigeon (On the Origin of Species, pp. 22-25), is a sample.

rituals and in intra-male contests for reproduction as well as on the aesthetic aspects of female choice. The protective function of color did not receive extensive treatment except as a typical primitive condition frequently seen reemerging in atavism and in "going wild."

The controversy on which process of selection, sexual or natural, governed coloration was chiefly a post-Origin discussion. The Origin of Species, however, was the setting against which succeeding scenes were played; yet, the Descent of Man contains the entirity of Darwins views on sexual selection. The two works were an interlocking unit; the Origin of Species was the scenario of which both Variation of Animals and Plants Under Demestication and Descent of Man was the full script.

The diversity of animal colors and the familiarity of students of natural history with them made coloration ideally suitable for Darwin's discussion of variation in his great work Variation of Animals and Plants Under Domestication. This work was one of only two cases in which he was able to utilize all the material he had gathered on the topic (the other being Descent of Man). The first volume presented a systematic discussion of the whole gamut of domestic animals including a section in which the colors of each was described and analyzed. In general, the approach taken in the Origin is continued in Variation; colors provided paradigm examples of reversion of primordial condition.

Darwin's Variation was the end-product of a long chain in investigations which began with entries in the "Notebooks on Transmutation of Species." Darwin's published correspondence showed that he adopted the practice of asking his correspondants for information from their areas of expertise and many questions on domestication are included among them. Peter Vorzimmer has recently published a series of questions which Darwin compiled and had privately printed and distributed, in 1839.[66] The queries are mainly related to problems of heredity and the results of various kinds of crosses. Vorzimmer points out that the questions may be seen as "Deductive manifestation of Darwin's own view of how the phenomena of hereditary transmission might bear upon his transmutation hypothesis."[67] The information received could have been incorporated into the Sketch of 1842 which was briefly outlined sometime prior to that year. The Sketch of 1842 and the longer Essay of 1844 as well as the Origin of Species had the variation under domestication as the first chapter and springboard for discussion. Natural selection was an abstraction and not available in the same sense that Darwin's cote of pigeons was accessible for study. Variation was the common element of both wild and domestic

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[66] Peter J. Vorzimmer, "Darwin's Questions about the Breeding of Animals," Journal of the History of Biology 2:269-281.

[67] Vorzimmer, "Darwin's Questions about the Breeding of Animals," p. 272.

breeds; the analogy was a convenient and useful one and Darwin relied greatly on it. In uniformitarian fashion, one would expect present-day processes to be at work in the past. Domestication was a well-known process and similar mechanisms in wild animal did not seem to be an unreasonable assumption; in many ways Darwin was right. His inability to distinguish between environmental modifications and hereditary ones led him to make erroneous conclusions. Equally damaging to his argument was the idea that domestic species are more variable than wild species; the conditions of the domestic state, he believed, caused the increase number of variations.[68] The apparent greater variability was accounted for by the survival of those in artificial state which would have perished under the operation of natural selection.

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[68]See Arne Muntzing, "Darwin's Views of Variation Under Domestication in the Light of Present-Day Knowledge," Proceedings of the American Philosophical Society 103:190-219, for a complete discussion of Darwins views on Domestication. "Darwin's thesis that species when domesticated start to vary on account of the variable conditions of life and excess of food is essentially or entirely wrong." p. 217. This statement has been disputed by a number of geneticists as Peter Vorzimmer states, "The Assumption of greater variability under domestication notwithstanding, the importance of the point lies in the fact that Darwin believed it was the conditions of the domestic state itself that produced this greater variation. As a point of information, those who aver greater variation in the domestic state are unanimous in their belief that this is not related to Darwin's "external conditions, but to factors such as "gene pools", "genetic homeostatis," etc., in Charles Darwin: The Years of Controversy, The Origin of Species and its Critics, 1859-1882 (Philadelphia: Temple University Press, 1970), p. 274.

Darwin's Variation was the vehicle for his presentation of the "Provisional Hypothesis of Pangenesis."[69] Pangenesis, like Ptolemaic astronomy functioned well on the empirical level, with a certain amount of tinkering with details. It was a fairly effective hypothesis at the time when there were no other viable alternatives. Wallace and many others adopted the thesis in the "provisional" manner in which Darwin offered it. Darwin's Lamarckism was unabated in the Variation, the environment was considered to the cause of variation. Habit, use, disuse, and other unknown external influences have a role in inheritable modifications. Pangenesis was as compatible with Lamarckian as with Darwiniam explanations.

Coloration was not treated as an independent topic, but as representing a variable, "trifling" class of phenomena, usually in connection with domestic atavism or with sexual selection. The analogy from domestication was a central theme in Darwin's work, but he did not believe the analogy was a perfect one. He did more than almost any other nineteenth century evolutionist in the battle with the inadequate pre-Mendelian laws of inheritance. The Variation of Animals and Plants Under Domestication is a monument to Darwin's attempt to solve intricate, difficult problems. Pangenesis was an inadequate answer but no one had a better hypothesis to offer at the

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[69] Darwin, Variation of Animals and Plants Under Domestication, Chapter 27, pp. 349-399.

time; blending inheritance had to be replaced by another system before substantial progress could be made in solving Darwin's second puzzle, the Laws of Inheritance.

CHAPTER III

COLORS AS A TEST FOR NATURAL SELECTION

At the beginning of his book, Colouration in Animals and Plants (1886), Alfred Tylor stated poetically the pre-Darwinian attitude animal colouration:

> Before Darwin published his remarkable and memorable work on the Origin of Species, the decoration of animals and plants was a mystery as much hidden to the majority as the beauty of the rainbow ere Newton analyzed the light. That the world teemed with beauty in form and color was all we knew; and the only guess that could be made as to its uses was the vague and unsatisfactory suggestion that it was appointed for the delight of man. [1]

Although the system of natural laws governing the colors of animals was poorly understood before Darwin and Wallace's declaration of a new law behind the adaptation of species to the environment; it was still a topic of considerable discussion and interest. The laws of adaptation had not been found, but there was suspicion about their probably existence.

In 1859 Andrew Murray read a paper before the British Association containing no reference or comment indicating influence or acquaintance with Darwin and his views, yet it epitomized the

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[1] Alfred Tylor, Colouration in Animals and Plants, ed. By S. B. J. Sketcherly, (London: Albaster, Passmore and Sons, 1886). Tylor, 1824-1884, geologist, discussed the psychological aspects of color perception and colour responses in animals as well as a survey of the diversity of color in various major groups of animals and plants.

awareness that color phenomenom constituted a significant class of data operating on unknown, but nonetheless real, laws of nature.[2] His article contained a plea for other naturalists to join him in ferretting out the hidden laws. Many nineteenth century naturalists, includint Andrew Murray, believed that the world and its complement of organic species was designed by a Creator whose creative activity was like that of a Divine Legislator. The enterprise of science consisted in the discovery of these laws. There are also hints in Murray's article of a kind of Newtonianism; the belief that there is a great law of adaptation analogous to the law of universal gravitation. The great law of biology causes comparable associations of fauna and flora in different parts of the world with the same general climatic properties. The rhea of South America, the Australian emu, and the African ostrich live on separate continents, but their habitats have similar ecological characteristics. Murray saw the similarities of the ostrich, emu, and rhea as the result of universal law; their differences were also explained under another law that "nature never repeats herself." The essential point was that the disguises of nature could be important for unravelling general laws and for distinguishing

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[2] Andrew Murray, "On the Disguises of Nature; Being An Inquiry into the Laws which regulate External Form and Colour in Plants and Animals." Edinburgh New Philosophical Journal 11:66-90. 1860. Murray, 1812-1878, was President Royal Horticultural Society 1858-1859, also Fellow Royal Society of Edinburgh and Fellow of the Linnean Society.

mutable "laws of life" from permanent and irrevocable laws of creation."

> There is yet a further step, which the advocates of a modification of species might not hesitate to take--viz. to abandon the idea (of a Law of Disguises) altogether as a law of creation and confine it to a rule of life. . . There may be truth to the idea that changes in species do arise from the modifications of climate, food, etc.; but I confess that, in the present state of my information on the subject, I am not inclined to look upon such instances as cases where such modification has taken place, but rather as instances of the exercise of the original law I have assumed, or of some other such law of equivalent force and application.[3]

Without using the Darwinian paradigmMurray explored the whole spectrum of resemblances of animals to other animals and to inanimate substrates, e. g. of insects to bark and moths to bees. Unlike his predecessors, Murray was not satisfied with the easy teleology that clear-wing months impersonate bees in order to enter hives unnoticed.[4] The purposes of the resemblences in both behavior and color may be absolutely clear without illuminating at all the law or means by which the similarities are acquired. The resemblance of the hare to the "benty braes" on which it grazes is no less remarkable than the moth's bee disguise. In his conclusion Murray enumerated three major points regarding natural disguises. (1) That perfect

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[3]Murray, "On the Disguises of Nature...," p. 80.

[4]Kirby and Spence, Introduction to Entomology (London: Longman, Hurst, Rees, Orme and Brown, 1818) is a classic in the teleological approach to biology.

imitations of objects occur. (2) That disguises are not exceptional or rare, but found in every class of animals and in some so often as to constitute a rule. (3) There is a purpose in it and that purpose is the concealment of the animal bearing the disguise.

> What is this law? I cannot tell:. . . It would appear as if there were a genius loci, whose subtle and pervading essence spread itself around, penetrating and impregnating the denizens of the place with its facies--possibly only affecting some, the conditions of whose entry on existence render them more liable to receive its impression than others; more probably affecting all, some more and some less. How this mysterious influence may operate, it may be bootless to inquire; but is it unphilosophical, or inconsistent with the simplicity and grandeur of nature, to suppose that one great idea should contain elements of laws which regulate all the different constituent parts of the created world? [5]

In the end he could only conclude that similar conditions produce similar animals and plants. His tone was not pious or didactic in the manner of the Bridgewater Treatises:[6] it was not Murray's aim to prove that animal disguises were part of a benevolent design. His object was rather to uncover the law of nature behind the disguise; special creation was an implicit idea and his search for laws was within the Christian "gestalt," not that of evolution.

Murray's world view was more closely tied to the past than to the future of biological thought. His area of investigation was,

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[5] Murray, "On the Disguises of Nature. . . ," p. 77.

[6] The Bridgewater Treatises were a series of eight works on natural theologians in the tradition of William Paley's well-known book on natural theology and the argument from design.

however, extremely timely. The coloration of animals possessed many characteristics which suited it for study with a view to discovering general laws. On this point, Murray and the evolutionists, like Wallace and Bates, were on equal ground.

Wallace, as a gatherer of specimens, came into daily contact with animals of every hue. Animal colors are often pleasing and interesting aesthetically, quite apart from scientific motives; the suitability of the phenomena as a test for a new theory is at quite another level of inquiry. Appreciation of animal disguises may have begun as a simple matter of curiosity and delight, but that was not where the matter ended. Darwin had referred to colors as a most "fleeting of characters" and Wallace had called them "unimportant;" neither of them, however, intended his remarks to imply that color was of no stability or importance in all cases. The mutability of colors is apparent in domestication, when natural camouflage is no longer at issue and many variations from parental type appear and persevere. In the wild state unfavorable variations are eliminated from the population by the survival of the fittest, rendering the colors of the breeding population quite stable. The externality and observability made coloration accessible to easy investigation. It was, and is, however, the extreme diversity of colors that makes them interesting; the range of color is broad both within closely allied groups and throughout the entire animal kingdom. The explanatory value of

natural selection was tested in the years following 1859 and one of the tests it endured was that of animal coloration in all of its ramifications. Alfred Russel Wallace was at the forefront of the discussions on coloration; he had been interested in deriving the general laws of coloration from a great mass of data before his discovery of natural selection. His belief that the theory of natural selection was adequate to explain color phenomena is obvious from his first publications. Murray's law depended upon an unknown, "X" quantity analogous to universal gravitation, but for Wallace that law was natural selection.

Discussion of the laws of coloration had begun without Darwin, Wallace, or the beliefs associated with the word "Darwinism." The question of evolution by natural selection rather quickly became the dividing line of the topic; one was either a Darwinian or one was not. Scientific work was done by partisans of separate world-views. Membership in the Darwinian camp quickly grew in the 1860's as did the assimilation of scientific data under the "paradigm" of natural selection. As interesting as were the "disguises in nature" which Murray had described, his paper did not provoke profound reaction. In 1862, Henry Walter Bates, Wallace's former companion in the Amazon, made a discovery which broadened the discussion of coloration to include biologists and theoreticans in many fields.[7]

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[7]Henry Walter Bates, "Contributions to an Insect Fauna of the Amazon Valley, --Lepidoptera:--Heliconinae." Transactions of the Linnean Society of London, 23:495-566, 1862. With an abstract

Upon analysis of his Amazonian specimens Bates was forced to conclude that the similarity between distantly related species of butterflies was too perfect to be coincidental. He called likenesses between different species "mimetic analogy" and believed it to be the protective resemblance of a palatable insect to a form protected from predators by being distasteful to them, what was to be an important evidence for natural selection slipped quietly into the scientific literature in the middle of a general article on the whole Heliconinae family, as part of Bates' series of articles on the insect life of the Amazon Valley.[8] Bates' modest claim that his discovery of a new phenomenon "involves questions of the greatest scientific interest"[9] was no exaggeration. Darwin immediately recognized the significance of mimicry as an unequivocal evidence for natural selection and wrote a letter congratulating Bates, but rather justifiably added:

> I have one serious criticism to make, and that is about the title of the paper; I cannot but think that you ought to have called prominent attention in it to mimetic resemblances.[10]

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appearing in the Journal of the Linnean Society of London. 6:73-77. (1862).

[8] Bates series "Contributions to an Insect Fauna of the Amazon Valley" had begun in 1858 and continued until 1870.

[9] Bates, "Contributions to an Insect Fauna of the Amazon Valley" Journal of the Linnean Society of London, p. 74.

[10] Francis Darwin, ed., Life and Letters, II, p. 393. Letters to Darwin Bates, November 20, 1962.

By this time, Bates was respected as a naturalist and his ideas received consideration by others, but the support of Darwin and Wallace added authority to Bates' new theory. His article contained no mention of natural selection explicitly, which was as important as if he had made it a central topic. Bates' work was founded on an evolutionary assumption that in the struggle for existence only favorable variations persist; in the case of his mimicry, likeness of a palatable butterfly species to a protected species had arisen on the basis of the preservation of apparently random variations.

> The likeness of a beetle or lizard to the bark of the tree on which it crawls cannot be explained as an identical result produced by a common cuase acting on the tree and the animal; one is evidently adapted to the other. The infinite variety of resemblances between insects and plants or inorganic substances--between predaceous animals and their victims--the adaptation of organs or functions to the object or habits they relate to--are all of the same nature. They are adaptations either of the whole outward dress or special parts, all having in view the welfare of the creatures that possess them . . . The means by which the existence of species is maintained are of endless diversity; and amongst them may be reckoned the resemblance of an otherwise defenseless species to another whose flourishing race shows that it possesses peculiar advantages.[11]

The basis of mimicry was the protection of the mimicking species by capitalizing upon the exemption of unpalatable species from predation, especially from birds. It is consequently an advantage to a palatable group to be deceptively similar to a protected species. The

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[11] Bates, "Contributions to an Insect Flora of the Amazon Valley--Lepidoptera, Heliconinae," Transactions of the Linnean Society, p. 74.

selection of variations tending to produce the mimicry and the eliminations of intermediate modifications fit well with Darwin's account of natural selection. The thrust of Bates' own argument was as much a negative as a positive one; mimicry was not the result of Buffonian direct influence or Lamarckian inheritance of acquired characteristics. Neither was it a remarkable example of design, but mimicry was a product of natural law alone. The old ideas of volition of the animals themselves or of directed variation had no part in Batesian mimicry as originally expounded; they were two points of omission that Darwin fully appreciated.

> 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 marvellous, and you connect excellently a host of analogous facts. . . I am rejoiced 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. You will find, I should think, that Wallace will fully appreciate it.[12]

Darwin did not let the matter rest with the "mob of naturalists without souls," but took steps to insure that the significance of Bates' discovery did not go unappreciated. In an unsigned review in the Natural History Review Darwin summarized and analyzed Bates'

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[12] Francis Darwin, (ed.) Life and Letters, II, p. 391-393. Letter, to Darwin Bates, November 20, 1862.

"Contributions" with emphasis on the difficulties which mimicry posed for a creationist view.[13] The creationist was forced, Darwin said, to admit that some species were created in their present state and others have become imitators by the laws of variation. The article was an attempt on Darwin's part to drive a wedge into the creationist ideology; if they were forced to admit small modifications the likelihood of their accepting larger changes would be greatly increased. Darwin's arguments were predicted on the assumption that consistency was a high priority goal for his opponents as well as for himself.

> Not many naturalists will be content thus to believe that varieties and individuals have been turned out all ready made, almost as a manufacturer turns out tyos according to the temporary demand of the market.[14]

Although Bates' discovery could be understood as the culmination of Murray's request for aid in the search for laws of nature's disguises, it was a discovery under quite a different conceptual frame than Murray had anticipated.

Darwin's prediction that Wallace would appreciate Bates' new theory was abundantly confirmed. Wallace applied the theory of mimetic resemblances to the Papilionidae of the Malay Archipelago.

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[13] Charles Darwin, "A Review of Mr. Bates' paper on Mimetic Butterflies," Natural History Review 1863:219-224.

[14] Ibid., p. 219.

The Papilionidae are a complex group requiring attention, not only to the phenomenon of mimicry, but also to a remarkable constellation of races, varieties, subspecies, and polymorphism in a number of species. The occurence of mimicry in various degrees of perfection ranging from only general resemblance to exact duplication was evidence that partial resemblance to an unpalatable form may be adequate to preserve mimickers from predation.

> This form of Papilio which mimics Drusilla varies much, and there is therefore material for natural selection to act upon so as ultimately to produce a copy as exact as in the other cases.[15]

Wallace not only extended Bates' mimicry hypothesis to Malaysian examples but he used mimicry as a clue to understand the processes by which dimorphic forms were produced. The genetic basis of Wallace's idea was quite inadequate to the task he chose, but the issue was clear that the differences between the sexes was related to the differences in the necessity of protection.

> The reason why the females are more subject to this kind of modification than the males is, probably, that their slower flight, when laden with eggs, and their exposure to attack while in the act of depositing their eggs upon leaves, render it especially advantageous for them to have some additional protection. This they at once obtain by acquiring a resemblance to other species which, from whatever cause, enjoy a comparative immunity from persecution.[16]

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[13] Alfred Russel Wallace, "On the Phenomena of Variation and Geographical Distribution as Illustrated by the Papilionidae of the Malayan Region," Transactions of the Linnean Society 25:1-71, 1865. p. 21

14 [14] Ibid. p. 22

Wallace's extension of mimicry to Malayan Papilionidae was not the only geographical advancement of Bates' idea; Roland Trimen found mimicry among butterflies in Africa and Thomas Belt reported similar mimicry in tropical Central America.[17] The apparent universality of mimicry lent force to the theory which explained it.

The central theme of the earliest statements on mimicry was its Darwinism in contradistinction to Lamarckianism or creationism. The importance of Batesian mimicry as a test case for natural selection has not been emphasized by historians of the period, nor has the role of H. W. Bates in bringing forward an important idea for the history of evolution been adequately appreciated[18] in retrospective treatments.

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[17] Roland Trimen, "On some remarkable mimetic analogies among African Butterfiles," Transactions of the Linnean Society 26: 497-522. Trimen, 1840-1916, was President Entimological Society 1897-1898.

Thomas Belt, The Naturalist in Nicaragua. London: J. M. Dent, 1874. Thomas Belt, 1832-1878, geologist and traveler.

[18] Mary Alice Evans, "Mimicry and the Darwinian Heritage," Journal of the History of Ideas 26:211-220, 1965. This is the only recent, general article on the history of mimicry which makes an attempt to place it in its central place in the history of evolution and as a persistent biological "idea." Its brevity necessitated a certain amount of unavoidable superficiality on the history of mimicry from Artistotle to the present. One point of fact requires comment. M. A. Evans wrote, "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 advantage of the first slight changes." (pp. 216-217) This is an underestimation of the early Darwinians' attention to important detail. It was well known that partial resemblance was of survival value and the suspicion was

The entomologists of the 1860's and 1870's were not remiss in understanding the importance of mimicry for their science. The Proceedings of the Royal Entomological Society of London abound in references to mimicry and the minutes of their informal discussions are very informative "windows" on the opinions of scientists which are mostly known in their carefully composed writings. Extemporaneous judgments are often more illuminating than studied expositions.

A discussion was held in 1864 about the wing forms of three groups of butterflies that Wallace had collected in the Celebes; a summary of the session was inserted into the Proceedings of the Royal Entomological Society of London.[19] Wallace's butterflies from the Celebes had falcate wings which distinguished them from varieities on other islands. Along with the exhibit, Wallace had given a theor etical explanation of the aberrant, curved wings. His hypothesis was that some peculiarity of the Celebes environment favored the curved wing

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common (among Darwin, Wallace, Bates, etc.) that mimicry may have originated when predators were less discriminating giving even slight similarity great advantage. Many cases of mimicry involve species already sharing general similarity in size, shape, and behavior. Geneticists added greatly to the precision of mimicry theory, but the evolutionists had their own explanations both for the first change and for the extinction of certain intermediate forms.

[19] A. R. Wallace, "Effects of locality in producing change of form in insects," Proceedings of the Royal Entomological Society of London 1864:21-23.

form which facilitated turning while in flight. Different insects preserve their existence by resorting to a variety of protective devices, one by possessing unpleasant odor or taste, another by natural camouflage, and others by flight. The Celebesian Papilio form, Wallace believed had evolved the curved wing form enabling it to elude its enemies.

> Prof. (J. O.) Westwood, after remarking upon the pleasure he always derived from Mr. Wallace's speculations, whether he agreed with them or not, said that he was unable to follow Mr. Wallace in tracing the phenomenon to the causes assigned by him; arched wings were not necessarily, or even generally, accompanied by the greatest rapidity of flight; and if the original form of the butterfly must be varied, if one species must imitate another, he thought it far more probable that the variation would consist in getting stronger muscles to their bodies, as in the species Charaxes he had that evening exhibited, rather than in minute change in the curve of the wing.[20]
>
> Capt. Cox thought that the swiftest fliers had the straightest wings.
>
> Mr. Newman also was unable to connect an arcuate wing with rapidity of flight. . .
>
> Mr. Baly said that the arched form of wing might be advantageous in giving a greater power of twisting and turning about, rather than in giving greater rapidity of flight; and that, he thought, was what Mr. Wallace had suggested.[21]

If natural selection was to succeed as a law of universal change it must be applicable at the level of butterfly wings. Bates, Westwood

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[20] John Obediah Westwood (1805-1893), entomologist and palaeographer, honorary life-president of the Royal Entomological Society, 1893ff.

[21] Wallace, "Effects of locality. . ." p. 22.

and Newman, Wallace were highly regarded entomologists who had many years of experience in both taxonomic and field entomology and their interaction was profitable for their scientific development. The mettle of Wallace's hypotheses was tested in the fire of critical judgment; observation and theory must corroborate each other.

The discussions were held regularly, with many different topics at issue and Batesian mimicry was among them. Bates had made statements to the effect that mimicry was necessary for the very subsistence of mimicking species; Professor Westwood gave a series of seven objections to Bates' view attacking mimicry at its most vulnerable points.[22] (1) Mimickers in so low a ratio to modes as 1 in 1000, could scarcely exist and certainly not flourish. (2) There were many non-mimetic Pieridae in the same territory with the Heliconidae which were flourishing. (3) Many species which were equally subject to the attacks of birds have not "attempted" mimicry of Heliconidae. (4) Some species of protected Heliconidae resembled each other.[23] (5) Mimicry by the female Pieridae was common, (6) Bates' theory

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[22] A. R. Wallace. "Exposition of the Theory of mimery of adoptive resemblances as explaining anomalies of sexual variation" Zoologist 2:573-576, 1867. Also see Wallace "On the Pieridae of the Indian and Australian Regions." Transactions Entomological Society 1867:301-415.

[23] Scientists were well aware of the phenomenon which became called, "Mullerian mimicry" after 1879, . Until Muller the resemblances among protected species were accounted for by evolutionists as the effects "unknown local causes."

suggested that the Heliconidae must have existed prior to mimicry by Pieridae; yet he (Bates) also inferred that the Heliconidae were still changing. (7) Mimicry was improbable on the doctrine of chance.

> Each species tending towards distinct and equally peculiar species, would by a logician be pronounced impossible. The admission that the God of Nature created these species in their present mimetic conditon for some wise but hidden purpose disposed of all difficulty.[24]

On the surface it was mimicry theory that was under examination, but at the interior of the matter natural selection and the reign on natural law was also at stake. In fact, the "trial" of mimicry was the "competency hearing" for natural selection.

By 1870 the Origin of Species had been issued in a succession of five editions; the journals were filled with what St. George Mivart called the odium theologicum and the odium antitheologicum. Few naturalists seemed to have reserved judgment; it was every man to his own opinion. The principle that current events are more complex than the written, oversimplifications of history reflects is eminently true of the discussion of evolution by natural selection. There were not merely evolutionists and non-evolutionists, that is, the team of Darwin against the team of Agassiz; evolutionists came in all degrees ranging from Ernst Haeckel whose evolution was totally materialistic and aggressively anti-religious to Asa Gray who believed that

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[24]Wallace "Exposition of the theory..." pp. 273-276.

evolution and orthodox Christianity were compatible. A relatively common compromise position was that evolution had occurred in the past as well as in the present but that natural selection was incompetent as the major mechanism for evolution. St. George Mivart had settled on this compromise as both scientifically and theologically satisfying.[25] In the later 1860's and 1870's evolution began to be accepted, and natural selection rejected as sufficient to explain org organic change. Mivart summarized virtually all the best arguments brought against natural selection. One of his major objections was that natural selection was unable to account for the incipient stages of useful structures--mimicry was one of his examples.

Mivart's criticism of Batesian mimicry was picked up by Arthur Bennett in his review of Genesis of Species for Nature.[26] In an extremely sympathetic review, Bennett took the same basic stance as Mivart had with respect to natural selection, adding in the review many of his own ideas. For both author and reviewer natural selection had been ascribed too great a role in the origin of species by its

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[25] St. George Mivart, "On the Genesis of Species" (London: Macmillan and Co., 1871). For Mivart's part in the evolution controversy see his biography by Jacob W. Gruber, A Conscience in Conflict. The life of St. George Jackson Mivart. (New York: Columbia University Press, 1960).

[26] Arthur Bennett, "The Genesis of Species. A review," Nature, 3:270-273, 1871. (Alfred William Bennett, 1833-1902) Botanist and Fellow of the Linean Society.

early advocates, conspicuously, Darwin, Wallace, and Bates. Evolution was quite a separate issue, one on which Bennett was willing to go even farther than Mivart.

> Under Mr. Mivart's first head, he deals with the subject of mimicry, contending that Natural Selection is incompetent to account either for the first or last stages of such wonderful instances of protective resemblance as thus represented... We think the author could have supported his case with arguments of even greater force, had he extended his observations to the vegetable kingdom.[27]

For Mivart and Bennett the idea of a force in nature analogous to human intelligence was more feasible than undirected natural selection, rooted as it was in natural law exclusively.

> Should the enquiries which are now being energetically pursued on every side result in our acquiring more accurate knowledge of such a force, it will be safe to predict that to it will then be ascribed a more easy and natural solution of many phenomena which we are now forced to attribute to Natural Selection.[28]

A. W. Bennett filled the gap which Mivart had left open by publishing his own extension of mimicry theory to plants in which he redoubled his attack on natural selection.[29] The element which he found most objectionable in Darwinian theory was the notion that each form of life exists for its own advantage solely. There are many examples of

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[27] Bennett, "The Genesis of Species: A review," Nature 3:272, 1871.

[28] Ibid., p. 273.

[29] Arthur W. Bennett, "Mimicry in Plants," Popular Science Review 9:1-10, 1872.

harmonious interactions between species which Bennett found incompatible with Darwinism; for him there was no other recourse than to explain mimicry in both plants and animals as evidence of harmonious design, "Which it may take centuries of unwearied observation and laborious toil before we discover the key by which we may be able to unlock it."[30]

Bennett's published arguments with natural selection and the Darwinian interpretation of mimicry did not begin with his Nature review, but in 1870 when he published an article on the mathematical improbability of mimicry occurring spontaneously;[31] the chances, as he calculated it were, conservatively, ten million to one. His attack was not a carefully guarded raid on some Darwinian outpost, but a direct assault on the fortress of central examples for natural selection. Mimicry was forced into the role of double agent, working both for natural selection and for cosmic design. The integration of natural law and design was basic to Bennett's attack on natural selection; the discovery of natural laws was based on the lawfulness of the Creator's work. Natural laws either work consistently or they do not; Bennett considered weaknesses in natural selection theory probable cause to

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[30] Bennett, "Mimicry in Plants," p. 10.

[31] Alfred W. Bennett, "The Theory of Natural Selection from a Mathematical Point of View." Nature 3:30-33, 1870.

doubt its total veracity. Although Darwin had repeatedly admitted that natural selection was not the source of variations, variations spontaneously arise in an apparently random order and natural selection acted upon them to preserve beneficial variations and eliminate unfavorable ones. Bennett maintained that if natural selection could not even explain the origin of variation, it was even less capable of accounting for the origin of species. Unless natural selection was everything it was nothing.

The origin of variation, the usefulness of incipient stages, the mathematical improbability of favorable variations arising by chance, inexplicable symbioses in nature, and inconsistencies among Darwinians were some of Bennett's objections to natural selection.[32] Neither Bates nor Wallace had employed mathematics in their discourses on mimicry and the introduction of mathematical considerations shifted the discussions to rather uncomfortable grounds for the Darwinians. It was clearly time for a move in their own defense. Although scientific criticisms constituted his primary argument, metaphysical suppositions were of nearly equal importance. Bennett presupposed directional variations, guided by an organizing intelligence. A third level of Bennett's attack was that of an almost aesthetic or moral aversion to natural selection and the Darwinian denial of design.

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[32] Bennett specifically criticized Wallace for inconsistency in limiting natural selection with respect to man.

> It is the carrying into Natural Science of the Hobbesian principle of Self-love.[33]

Even in a discussion of mimicry and mathematics the odium antitheologicum looms like a spectre.

Wallace could not be expected to take Bennett's direct criticism without retort; his reply was swift and appeared in the next week's issue of Nature as a point-by-point rebuttal.[34] He attempted to clarify what he considered to be a basic semantic confusion in Bennett's article between "species" and "variety" or "individual." Bennett had indicated that the Darwinians had no solution to the problem of the origin of variation and, consequently, none on the origin of species--a point which Wallace contended. Wallace held that natural selection was an integral part of the origin of species because of its important part in producing and perpetuating stable forms and eliminating spontaneous, unstable variations. The laws governing variation itself, although unknown, did not refute the law of natural selection in its limited task of preserving useful variations. On mimicry, Wallace's arguments with Bennett were both observational and theoretical. He pointed to the common occurrence of mimicry among Leptalis and the similarity of general form between model and mimic,

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[33] Bennett, "The Theory of Natural Selection from a Mathematical Point of View," p. 33.

[34] A. R. Wallace, "Natural Selection--Mr. Wallace's Reply to Mr. Bennett," Nature 3:49-50, 1870.

giving even a small increase in likeness great potential for deceiving predators. Instead of disputing Bennett's mathematics, Wallace's main disagreements were on the assumptions on which Bennett's figures were based. Bennett had argued:

> Suppose there are twenty different ways in which a Leptalis may vary, one only of these being in the direction ultimately required, the chance of any individual producing a descendant which will take its place in the succeeding generation varying in the required direction, is 1/20; the chance of this operation being repeated in the same direction in the second generation is $1/20^2$ or 1/400; the chance of this occurring for ten successive generations. . . is $1/20^{10}$, or about one in ten billions.[35]

To which Wallace replied:

> There are three great oversights in this one short sentence. The first, is, that each Leptalis produces, ont one only, but perhaps twenty or fifty offspring; the second is, that the right variation has, by the hypothesis, a greater chance of surviving than the rest; and the third that at each succeeding generation the influence of heredity becomes more and more powerful, causing the chance of the right variation being reproduced to become greater and greater.[36]

By making use of examples of variation under domestication, Wallace contended that the modifications of color necessary to produce mimicry are of a superficial nature as may be observed by the vararіability of domestic animals. Since color is independent of structure, color changes may be very great yet involve comparatively little rearrangement of internal organs and may come about in fewer steps than could

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[35] Bennett, "The Theory of Natural Selection...", p. 31.

[36] Wallace, "Natural Selection--Mr. Wallace's Reply to Mr. Bennett," p. 49.

be expected without the culling effect of natural selection. A. W. Bennett had argued against natural selection on the basis of the mathematical improbability of advantageous variations and Wallace had accepted battle on his terms; Wallace was soon engaged from another side also.

Andrew Murray's article, "Mimicry and Hybridization," appeared in Nature the following month.[37] In this memoir he accounted for all mimicry phenomena in animals on the basis of analogy from hybridization studies in plants.[38] The laws of mimicry, the identity of the ranges of mimic and model, and the relatively prevalence of model and scarcity of mimics could be explained equally well on the basis of interbreeding. If mimics were hybrid forms of the model and some absent parental type, the idea of descent would account for the mimicking animal's presence in the same territory with its progenitor. Murray was not content with the presentation of a merely competetive view, but sought to show that hybridization was a better explanation for mimicry than natural selection. Natural selection could not, Murray believed, account for the identity of ranges between model and mimic since the basis for mimicry (as stated by Bates, Wallace, and

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[37] Andrew Murray, "Mimicry and Hybridization" Nature 3:154-156, 1870.

[38] Ibid., p. 154. "There is not a phase or a fact in the mimicry in question, for which I cannot produce the exact counterpart in the hybridization of plants."

Trimen) was the preservation of adaptive variations, which gave immunity from predation and most of the predators of butterflies had ranges in excess of the boundaries of the insect's distribution. The models and mimics should, therefore, take up separate territories since the mimic would receive the same advantage as if confined to its model's territory. The small ratio of the number of mimics to the models was accounted for by the fact that hybridization was an exception explaining the case in which there was less than one mimic for each 1,000 models.

The argument for hybridization hung upon the validity of an analogy drawn from plant breeding experiments and applied to insects, as well as upon the equally tenuous idea of one-sided crosses in which one of the parental stocks is unknown. Murray ascribed to the additional idea that hybrids tend to resemble the female parent more than the male. If, therefore, the model species were the female parental line the hybrid resulting from the cross would tend to resemble that species more than the male parent. The presence of male traits would explain any difficulties or variability in the hybrid. In many species the female is a mimic, but the male is not. On the hybridization theory this could be explained as clear proof of the one-sided cross hypothesis; males resemble males and females resemble females. Should this explanation be inadequate, sexual dimorphism may also be explained by climatic influences affecting the two sexes

differently. Murray believed "most of Mr. Wallace's instances are of this character."[39] A point with which Wallace most heartily disagreed.

The controversy in the pages of Nature in the year 1871, began to widen as naturalists submitted observations of their own on protective resemblances of many kinds in an attempt to resolve the increasing ambiguity of animal disguises. The Darwinian side of the discussion was taken by J. P. Mansel Weale whose information was based on South African specimens.[40]

Although Weale had said at the outset of his letter, "I am anxious to avoid Mr. Bennett's reproach of being an 'ultra-Darwinian'," he could find no instance of hybridization between representatives of different classes although there were cases of mimicry between very distinct insect taxa. Weale cited the example of a spider mimic with an ant model which was quite inexplicable on the usual limitations of interbreeding, as Arthur G. Butler of the British Museum confirmed in his own letter to the Nature editor. The likelihood, he said, of hybridization between sub-orders, families, or genera of Lepidoptera were about the same as the probability of a successful cross between a horse and a rabbit. Should, for the sake of argument, the cross be

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[39] Murray, "Mimicry and Hybridization," p. 156.

[40] J. P. Mansel Weale, "Protective Resemblances," Nature 3: 507-508, 1871.

successful it would be infertile, and should, by chance, the hybrid be fertile, its offspring would revert to one of the ancestral types. Hybridity and mimicry were incompatible ideas for Butler; even if hybridization were assumed possible the predicted results would be at odds with actual observations. He strongly opposed the idea of the analogy from plant hybridizations as the basis for conclusions about insects.

> If the fertilisation of flowers and butterflies were the same, hybrids might be as common in the one case as the other, and the results attained might be more nearly alike; but as butterflies are not fertilised through the transmission of pollen by external agencies, and as they seem to have a decided preference for mates belonging to their own peculiar species, hybridisation must needs be a thing almost unknown amongst them.[41]

There the Nature discussion remained; the lines were drawn between those who accepted natural selection as an adequate hypothesis and those who did not, either substituting hybridization as an alternative or simply calling the source of mimicry "unknown causes" or "intelligent design." The participants in the discussion had stealthily avoided direct confrontation on the sensitive topic of God or even "Cosmic Intelligence." In his letter in the columns of Nature five years later, in 1876, John Joseph Murphy imputed the variable coloration of arctic animals, chameleons, and certain fish to the activity of

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[41] Arthur G. Butler, "Mimicry versus Hybridity, ", Nature 3: 165, 1870. (Arthur Gardner Butler, 1844-1925, Fellow of the Linnean Society, Fellow of the Zoological Society).

a "guiding intelligence."[42] It was like opening an old wound.

Of the letters in response, Francis Darwin's was first as representing the opposite point of view of undirected variation and natural selection.[43] A rather uneasy balance was struck between the protective functions and other factors controlling coloration, for example, anger, sexual passion, illness, local irritants, and nerve stimulations, to explain the rapid changes of color in lizards and fish. Darwin explained the white winter fur of the ermine as due to direct environmental causes analogous to the "temporary greyness of the eyebrow accompanying frontal neuralgia."[44]

The common element in the letters attempting a reconciliation of natural selection and protective coloration was the dichotomy between variation and selection which Murphy had not clearly expressed, nor apparently had he understood that variation was spontaneous and random, whereas natural selection is systematic and concerned with the preservation of favorable variations.[45] The eminent entomologist Raphael Meldola expressed succinctly the train of Darwinian argument

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[42] Joseph John Murphy, (1827-1894), "Protective Mimicry," Nature 14:309, (1876).

[43] Francis Darwin, "Protective Mimicry," Nature 14:329-330, 1876.

[44] Ibid., p. 329

[45] A point made by Thomas R. R. Stebbing (1835-1926) in Nature 14:330 and repeated by Raphael Meldola (1849-1915), Ibid.

for Mr. Murphy's benefit and that of the general Nature reader:[46] (a) Natural selection works for the exclusive good of a species, i.e. favorable variations are selected, no matter how the variations arise; most of the causes of variations are unknown. (b) Consider a species having protective coloration under one set of circumstances placed in another set of circumstances on a seasonal cycle in which its original colors are disadvantageous to its survival, "it becomes advantageous to the species to possess a power of adaptation."[47] Only by some innate, adaptive power can the animal survive the varifying external conditions. It is upon this adaptive power, as Meldola called it, that natural selection had operated. Variable colors are produced by the same means as permanent protective coloration which Murphy did not dispute could be attributed to natural selection.

The debate was conducted by turns, oscillating between two poles of opinion. The definition of "mimicry" was redefined to suit the writer's purposes but frequently interpreted to include both the resemblance of an animal to an inanimate surface or plant as well as the similarity between animals of separate taxa. Discussion had suffered from the imprecise definitions of words, but even more from the lack of clarity in understanding the main terms of the argument.

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[46] Raphael Meldola, "Protective Mimicry", Nature 14:330.

[47] Ibid.

"Natural selection" and "mimicry" had assumed emotional content which made its scientific and metaphysical implications difficult to separate. Neither side was content with the answers of the other. Bennett was not satisfied with Wallace's answer to the mathematical improbability of mimicry by natural selection. On the other side Butler considered the non-Darwinian hypothesis of hybridization to have been undercut by essential inadequacies as an explanatory hypothesis and by a lack of confirmating evidence in animals of a phenomenon found in plants. Both camps were vulnerable and reinforcements were welcome.

Fritz Muller, who had espoused the idea of natural selection in the 1860's,[48] published an article on mimicry in Brazilian butterflies as explained by natural selection. The American Naturalist published an English abstract of the German memoir.[49] The struggle for existence completely explained, not only mimicry and protective colors of all other kinds, but also the advanced sharp-sightedness found among predators. Natural selection worked without bias, on both prey and predator. It was the principle of natural selection which made it probable that the early steps in mimicry were useful to the possessors of mimicking colors. The watchful insectivores may not have been so

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[48] Fritz Muller, Facts and Arguments for Darwin, Translated by W. S. Dallas (London: John Murray, 1869).

[49] Fritz Muller, (1822-1897) "Mimicry in Butterflies Explained by Natural Selection," American Naturalist 10:534-536, 1876.

discriminating at the beginning of mimicry; visual acuity of the hunters had increased in proportion with the elusiveness of the insect food-supply.

The publication of Muller's abstract in the American Naturalist was the first of several articles in that journal on mimicry and natural selection. The "trial" of natural selection had had a temporary change in venue. The site of the debate was shifted to the American Naturalist when A. W. Bennett, who had been an antagonist natural selection in the Nature series, issued his rejoinder in the American revival of the debate.[50] Although the title of his article was a question, "Is Protective Mimicry Due to Natural Selection?", his answer was a resounding, "No!" The attack centered on the admissions of "perfectly unexcpetionable" authorities such as Wallace, Bates, Muller, and Huxley, of inadequacies in the present state of natural selection to explain the whole body of mimicry data. Bennett made his opponents speak against their own theories, by the clever use of selected quotations. He attributed likenesses between different insect species to similarities in physical environmental conditions as was common practice to explain unexpected resemblances between plant forms. There was no reference to "guiding intelligence" although Bennett chose allies from the ranks of theologically oriented scientists,

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[50] Alfred W. Bennett, "Is Protective Mimicry Due to Natural Selection?", American Naturalist 11:3-7, 1877.

especially St. George Mivart, author of Genesis of Species, and J. J. Murphy, author of Habit and Intelligence,[51] who "argued much more forcibly than I can do against the adequacy of natural selection to account for the phenomena in question."[52]

It is not surprising that a representative of the Darwinian position made some rejoinder in the American press. The response took the form of a treatise by Wallace on the whole gamut of color phenomena found in the animal and plant kingdoms.[53] In this article Wallace treated mimicry as a case of false warning colors, with emphasis on the protective aspects of color and upon the basis of natural selection in a general utility principle. Wallace's essay had the effect of rendering the entire discussion much more complex; coloration was not simply illustrative of natural selection in opposition to intelligent design nor in distinction to sexual selection. Colors may have several functions which are utilized simultaneously or in alternation, steadily throughout the life cycle or periodically as in courtship rituals.

Raphael Meldola, Secretary of the Royal Entomological Society, figured importantly in the discussion of animal coloration because of his own contributions and also as the translator of Fritz Muller's

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[51] J. J. Murphy, 1827-1894, Habit and Intelligence, (London: Macmillen, 1869).

[52] Bennett, "Is Protective Mimicry. . .?" p. 6.

[53] A. R. Wallace, "The Colors of Animals and Plants." American Naturalist 11:641-662, 713-728, 1877.

German-language publications. Meldola's "Entomological Notes Bearing on Evolution"[54] the doctrine of natural selection with special mention of Muller's contributions, which were not generally available in English translation. Meldola realized the importance of understanding color as a multiple-use phenomenon. The perception of insect coloration by insects is of greater importance to science than the hu human perception of color in insects. Observation and experimentation on insects were the solutions to much of the quibbling about the protective versus the sexual function of color.

> Without further observation it cannot be assumed in this case that the colour is displayed as a sexual attraction, since it is well known that colour is displayed for other purposes, such as for protection, when the colour is a signal of distastefulness (as with brightly coloured larvae, and those species which serve as models for mimicry), or for giving resemblance to some coloured objects, such as flowers.[55]

A trait acquired for protection may be turned to a second purpose by natural selection; an insectivorous insect may have developed resemblance to a flower to avoid detection by an enemy and in the process find that its coloration is a successful lure for insect prey. Wallace had called the second use of color, "alluring coloration." Meldola cited an Indian Mantis, Gongylus, as an example of this phenomenon.

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[54]Raphael Meldola, "Entomological Notes Bearing on Evolution," Annals and Magazine of Natural History 1:155-161, 1878.

[55]Meldola,"Entomological Notes. . ." p. 156.

> The object of the bright colouring of the under surface of the prothoracic expansion is evident its purpose being to act as a decoy to the insect, which, mistaking it for a corolla, fly directly into the expectant, serrated, sabre-like, capitorial arms of the simulator.[56]

Meldola well appreciated the relationship of observations upon insects to natural selection as an explanatory theory. The colors an insect bears were not isolatable from the other aspects of its life-cycle, but must be perceived as an integrated unit. Perception, habits, and instincts were equally as important as coloration, and internal as well as external causes affect the evolution of traits such as coloration. Meldola was better prepared than many lesser scientists to appreciate the complexity of animal colors and the variety of their relationships to natural selection.

> A case like that of Gongylus is of the highest interest--can, in fact, be only completely appreciated by the believer in natural selection. . . natural selection took advantage of the underside of the foliaceous expansions and coloured them by minute gradations till they acquired their present floral tints and markings; hand in hand with this modification of colour, habits tending to complete the deception were gradually acquired, till the marvellous coordination which we now behold was perfected.[57]

For Meldola only the "believer" could fully appreciate the meaning of Gongylus' colors. The situation is like that of Kohler's

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[56] Ibid. pp. 160-161. Meldola was quoting statements made at a meeting of the Asian Society of Bengal (Proceedings Asian Soc. Bengal, Aug. 1877).

[57] Meldola, "Entomological Notes. . . " p. 161.

Goblet-and Faces.[58] Two men may view the same picture and "see" different figures. What one believes makes a difference; sense-data is only part of understanding. Meldola's view of insect life was from the perspective of a committed evolutionist and even more particularly, of evolution by natural selection.

Wallace's book of essays, Contributions to the Theory of Natural Selection contained a systematic review and refutation of the major objections to Batesian mimicry that had been brought forward at that time.[59] First, Professor Westwood admitted mimicry as a fact but believed that each species had been created in that state for the purpose of protecting it. Second, Andrew Murray in "Disguises of Nature" was inclined to believe that the similar conditions of food, climate, and so forth acted to produce mimicry. Finally, it had been suggested also that heredity or reversion to ancestral type might have produced mimicry. Neither Murray's belief that mimicry resulted from environmental conditions, nor the objection that it was a manifestation of hereditary reversion explained the fact the mimicry did not appear equally in all groups subject to the same conditions. The common occurrence of mimicry in the female alone was a case in

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[58]Wolfgang Kohler, Gestalt Psychology, (New York: H. Liveright, 1929).

[59]A. R. Wallace, Contributions to the Theory of Natural Selection, 2nd ed. (New York:Macmillan, 1871). Ch. 3 "Mimicry and other Protective Resemblances Among Animals." pp. 45-129. (Hereinafter referred to as Contributions.)

point. "Reversion" did not explain resemblance between members of different orders just as "similar conditons" did not explain the limitations of resemblance to the exterior of the animal only.

Besides the usual arguments against design there were some unique problems for the advocates of the special creation of mimicking species. There were, for example, many imperfect mimics; the mimicry of butterflies from the Malay Archipelago and South America varied along a gradient from general similarity to duplication even of neuration in the wings. The fine gradations of mimicry strongly suggested a natural process. The special creationist would be forced to affirm that few mimics had been created in proportion to the models since mimicry was found in rare species many of which approach extinction. A third objection to the creationist idea was that it led to rather strange views on the personality of the Creator, who chose to create one species in masquerade instead of providing each its own protection in a less circuitous way; the origin of mimicry by variation and subsequent modification by natural selection is comparatively more cirect and simple hypothesis. The reality of Bates' discovery as well as its applicability to natural selection was well defended from critics who removed it from the sphere of science by elevating it to the level of religious faith as well as from those scientists who reduced mimicry to an adventitious circumstance.

Wallace and Bates had hit upon a stratagem when they undertook

the study of butterflies with a view toward unravelling the laws of species' origin. In his Contributions Wallace included a chapter on "The Malayan Papilionidae or Swallow-Tailed Butterflies, as Illustrative of the Theory of Natural Selection" in which he reviewed the distinctive features of the family with respect to taxonomy, geographic distribution, and special variations which exemplified natural selection.[60] The Papilionidae are so diverse as to have representative examples of at least six forms or degrees of variation, (1) simple variability, (2) polymorphism or dimorphism, (3) local form, or variety, (4) coexisting variety, (5) race or sub-species, and (6) species. The variability of the family is important not only for its taxonomic interest, but because of its relationship to geographical considerations of speciation. The many islands of the Malay Archipelago were not formed simultaneously as is reflected by the dissimilarities in the fauna and flora from island to island. The discontinuity of the land mass is further complicated by two distinct zoogeographical realms, the Australian and the Oriental. Because of slight differences in physical and ecological relationships between each island and its near neighbors, Wallace attributed many local variations to the action of inexplicable local causes. In 1879 Wallace had reason to retract one of his examples of the influence of environment on color in Papilionidae.

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[60] Wallace, Contributions, Ch. 4, pp. 130-200.

> The resemblance thus produced between widely different insects is sometimes general, but often so close and minute that only a critical examination of structure can detect the difference between them. Yet all are alike protected by the nauseous secretion which renders them unpalatable to birds.[61]

Although Wallace overextended his view of local influences as the cause of apparent mimicry in the Malayan Papilionidae, his study of mimicry, diverse coloration phenomena, taxonomic problems and evolutionary history of the family was a fulfillment of his prophetic remark to Bates in 1847:

> I should like to take some one family to study thoroughly, principally with a view to the theory of the origin of species. By that means I am strongly of opinion that some definite results might be arrived at.[62]

Fritz Muller framed a new hypothesis in 1879 which was to displace "unknown local causes." The new theory was predicted on the idea that it was advantageous for one unpalatable species to resemble another (usually a more abundant) species which is also distasteful.[63] Young birds must learn which species are unpalatable, which results in the destruction of a large number of individuals during the rearing of each generation of birds. The similar colors of the unpalatable

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[61] A. R. Wallace, Natural Selection and Tropical Nature, (London: Macmillan, 1891), 1st edition 1878.

[62] Wallace, My Life, I, pp 256-257.

[63] Fritz Muller, "Ituna and Thyridia; a Remarkable Case of Mimicry in Butterflies," Trans. by R. Meldola Proceedings of the Entomological Society of London 1879:xx-xxix.

species reduces the number sacrificed by each species, loss being proportional to the number of individuals of each species. Benefit, then, is greatest for species with fewest individuals.

Both Wallace and Meldola accepted Muller's theory immediately and published accounts of the new hypothesis for English-speaking naturalists urging their acceptance of the extension of mimicry.[64] The primary objection brought against Mullerian mimicry was that birds and insectivores did not need to acquire discrimination between insects, but that the knowledge was hereditary; therefore, no individuals of protected species would be sacrificed each year as Muller's theory demanded.[65] Since Muller's paper had been from the theoretical point of view, Wallace and Meldola supplied observations to support his hypothesis. As an extension of Batesian mimicry Muller's theory was very compatible with natural selection. It fit so naturally that Wallace exclaimed, "It seems strange to me now that I should not have seen how readily the principle is applicable to these abnormal cases."[66]

Muller had written about distasteful and palatable species as mutually exclusive categories; Wallace modified this idea since some

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[64] A. R. Wallace, "Dr. Fritz Muller on some difficult Cases of Mimicry," Nature 26:86-87, 1882. Raphael Meldola, "Mimicry Between Butterflies of Protected Gernera" Annals and Magazine of Natural History, Series 5, 10:417-425 1882.

[65] W. L. Distant, Nature 26:105.

[66] Wallace, op. cit., p. 87.

birds accept insects which others find nauseous. Distastefulness, like mimicry itself, is a trait found in varying degrees of perfection. An insect species protected by distasteful secretions would benefit from resemblance to species totally protected according to Batesian mimicry as it would also benefit from Mullerian mimicry.

In defense of Muller's theory Wallace and Meldola indulged in another excursion into mathematical proof in an effort to show that the benefit of Mullerian mimicry was greatest for the species with the fewest individuals: "To bring the argument home to entomologists, I will. . . venture to state the case numerically."[67]

> In the former state of affairs (before the resemblance) each species would have lost 1200; now E. Distanti gains 1000 individuals by its resemblance and E. Bremeri only 200. The total number of individuals with which we started was 10,000 of E. Bremeri and 2000 of E. Distanti; so that the last species gains $\frac{1000}{2000}$ or 1/2, and the first species $\frac{200}{10000}$ or only 1/50 of its whole number. The advantage in favour of the rarer E. Distanti, conferred upon it by its being mistaken for E. Bremeri, would thus be twenty-five times as great as the advantage which the commoner E. Bremeri derives from resembling E. Distanti. Surely in such a case the question as to which is the model does not admit of a doubt.[68]

The mathematical details of the problem in proportionate advantage was worked out in collaboration with Thomas Blakiston and Thomas Alexander in several letters, both personal letters to Wallace and

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[67] Meldola, "Mimicry between Butterflies..." p. 422.

[68] Ibid.

published in the Nature columns.[69] There was no doubt about the reality of advantage, but only about its degree and mathematical expression. Muller's law, as the advantage came to be called, was finally expressed as:

> Proportionate advantages are inversely in the duplicate ration of their respective original numbers compounded with the ratio of the respective percentages that would have survived without the mimicry.[70]

In cases of mimicry in which the number of individuals is quite disproportionate the scarcer species may be in the process of becoming extinct, and by acquired resemblance to a flourishing species prolong its existence indefinitely. The significance of the calculation was to show in an irrefutable, quantitative way that advantage "will be measured solely by the fraction of its own numbers saved from destruction, not by the proportion this saving bears to that of the other species."[71]

Mimicry was attacked in the time period of 1862-1882 from several sides. It was criticized as too theoretical, not mathematically precise, and as only apparent and not real. The controversy on animal colors widened to embrace Mullerian as well as Batesian mimicry.

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[69] T. Blakiston and T. Alexander, and "Protection by Mimicry--A Problem in Mathematical Zoology," Nature 29:405-406, 1884.

[70] Ibid., 406.

[71] Wallace, "Difficult cases of mimicry" Nature 26:482.

The adaptive advantage of Muller's new mimicry was more difficult to assess than was Bates' discovery of similarity between a palatable and unpalatable butterflies. The problem was made even more confusing by an error on Wallace's part in the mathematical statement of his first article in support of Mullerian mimicry. The controversy over the reality of mimicry and its relation to natural selection points up the blend of scientific and metaphysical content that typified nineteenth century arguments on evolution by natural selection. The points of view of Wallace and Murray could scarcely be more different; in the language of gestalt psychology, one saw the goblet, the other, faces.

Mimicry and protective colors in insects had dominated the discussion in Nature and in the American Naturalist, but Darwin's Descent of Man,[72] as well as Wallace's Contributions to the Theory of Natural Selection, extended theories of color to include birds and other animals. Darwin, for reasons of health and probably also by choice, had played only a behind-the-scenes role in the discussion of mimicry. The letter from Francis Darwin in Nature was the only foray into public disputation by any representative of the family at Dawn. At the beginning of the talk on colors and natural selection

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[72] Charles Darwin, The Descent of Man and Selection in Relation to Sex, 2 vols. (London: John Murray, 1871). Quotations and page numbers in this paper are from The Origin of Species and the Descent of Man (New York: The Modern Library, n. d.).

Darwin was in the middle of several revisions and editions of the Origin, the publication of Variation of Animals and Plants Under Domestication, and the Descent of Man. His correspondence shows a hearty interest in the success of the Darwinian cause and gratitude to Wallace and Bates for their efforts on his as well as on their own behalf. Darwin was not inclined by either health or disposition to join in disputations; his arguments were not quickly framed and published, but were pondered and published in full in the Descent of Man. Although Muller's discovery of mimicry among protected species of insects came only three years before Darwin's death, he did not fail to appreciate its significance as an evidence of natural selection. The letters exchanged by Darwin and Muller show that Darwin's retirement was never complete nor had his interest in evolution and the triumph of natural law ever abated. Perhaps Darwin stayed out of the debates of the 1870's (except in Descent of Man) because his theory of animal coloration tended to emphasize the sexual function of color much more than its protective function. Darwin wrote to Wallace, "I cannot but think that you push protection too far in some cases."[73] One of several such cases was Wallace's theory of the relationship between birds' nest types and their plumage.

Wallace divided birds' nests into two major types, the enclosed

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[73]Marchant, ed., Alfred Russel Wallace: Letters and Reminiscences, I, 159.

nest and the open nest. There was an interesting correlation between the nest type and sexual dimorphism of the species which he expressed in the form of a general law:

> When both sexes are of strikingly gay and conspicuous colours, the nest is of the first class, or such as to conceal the sitting bird: while, whenever there is a striking contrast of colours, the male being gay and conspicuous, the female dull and obscure, the nest is open and the sitting bird exposed to view.[74]

Female birds were as likely as males to be brightly colored if they are adequately protected; bright hues are suppressed by natural selection in unprotected females.

> The normal action of "sexual selection" is to develop colour and beauty in both sexes, by the preservation and multiplication of all varieties of colour in either sex which are pleasing to the other.[75]

Color is not developed for itself, but for some use either as protection or attraction in each species and in each sex; its modifications are related to its own survival in the struggle for existence. Wallace found support for his view of bird dimorphism based on the disparity of need of the two sexes for protection, "Exactly analogous to what occurs among butterflies,"[76] in that there was not a single instance in the diverse genera of Papilio, Pieris, or Diadema genera of the male alone mimicking the protected Danaidae, or Heliconinae.

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[74]Wallace, Contributions, p. 240.

[75]Wallace, Contributions, pp. 247-248.

[76]Ibid., p. 259

Darwin had struggled longer and more vigorously than had Wallace with the difficulties of the laws of inheritance in both wild and domestic productions. Protection did not explain to his satisfaction the preservation of inheritance of color in one sex only. The appearance of masculine traits in old or diseased females and the presence of feminine characteristics in infertile males suggested the importance of the sexual function of color.

> All these cases have so much in common that they depend, according to the hypothesis of pangenesis, on gemmules derived from each part of the male being present, though latent, in the female; their development following on some slight change in the elective affinitities of her constituent tissues.[77]

Darwin's emphasis on the laws of inheritance and upon the sexual function of coloration separated him from Wallace whose entomological studies could hardly help but stress the complex food-web system and adaptations for self-defense. Wallace's reliance upon the Malayan Papilionidae for examples and for understanding of birds and other animals by analogy was somewhat similar to Darwin's reliance on domestic species for an understanding of wild forms. From knowledge of the laws of variation among accessible forms both Darwin and Wallace tried to make judgements about other forms of animal life.

The debate on colors in animals and plants exposed many of the scientific issues in nineteenth century biology. Pangenesis, Darwin's

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[77] Darwin, Descent of Man, p. 785.

provision of hypothesis of heredity, was an unwieldy predictive tool. Murray's conclusion that mimicry was merely hybridization was based on a serious misunderstanding of the limitations of interbreeding and denial of evolutionary divergence and even of the taxonomic distinctions. Only a few experiments had been devised to test natural selection and its operation in the production of mimicry or other colors. The few that had been attempted were of a casual, uncontrolled kind conducted on a group of ducks or lizards in a pen to which a pan of various insect larvae were presented.

> Three green lizards (Lacerta viridis) which he [A. G. Butler] kept for several years, were very voracious, eating all kinds of food, from a lemon cheesecake to a spider, and devouring flies, caterpillars, and bumble bees; yet there were some caterpillars and moths which they would seize only to drop immediately.[78]

The biology of the 1860's was still oriented toward field biology and taxonomic research in the museums; experimental studies on animal coloration, with a few exceptions, were qualitative rather than quantitative.

No less formidable than the scientific problems of coloration theory was the rift between the natural-ists and the creationists. The metaphysical dichotomy was underscored because the colors of animals had traditionally been a topic for psalms and sermons extolling the inventiveness of Providence. The ground was not easily

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[78] Wallace, Contributions, p. 14.

yielded to those who would replace a Beneficent Creator by the process of the "survival of the fittest." Agreement was not readily achieved on either metaphysical assumptions or scientific interpretations. The inevitable extension of natural selection to man in Darwin's Descent of Man stirred the emotions of Victorians of all persuasions, and the application of coloration theory to man's racial characteristics rekindled the embers of an old fire.

CHAPTER IV

SELECTION AND THE DESCENT OF MAN

One hundred years ago natural history tended to be a solitary activity. Since biology had not been subdivided into rigidly defined specialties, each scientist did his own work and published his own results. A few biologists worked in teams, but research groups and joint publications were exceptions rather than the rule. Nor was the joint publication on evolution by natural selection the result of a team effort. Before 1858 neither Darwin nor Wallace expected his career to be associated with the other's. In a team each member shares the total credit or glory of the discovery because of a contribution to some specific aspect of the investigation. Darwin and Wallace had each independently worked out the total theory. Instead of the glory being doubled; it was halved. Wallace and Darwin were very dissimilar in personality, in social class, and in religious views. They had not intended to be partners; the role had been forced upon them. Consequently, there is no reason to expect that the two should share an identical outlook on scientific matters either, and, in fact, they did not.

Darwin believed that besides natural selection other comparatively minor causes were also active in the modification of species; among

these were use and disuse, habit, correlation of parts and of growth, direct and indirect effects of conditions, and occasional saltations. Although they were mentioned in the yearly editions of the Origin of Species they were confined to a subordinate role; Darwin's expansion of these minor causes in the later editions of the Origin and in Descent of Man and other later writings has been discussed repeatedly and at length by students of Darwin and of Darwiniana. Peter J. Vorzimmer has pointed out in his recent book the interesting correlation in time of Darwin's expansion of his theory of sexual selection and his work on the origin of man.[1] Man is a special creature, separated from other animals by important distinctions which Darwin found difficult to explain by natural selection exclusively. It seemed likely that some special agency of change had been a part of man's origin; and of the development of races and special characteris. Although Darwin extended sexual selection for his study on man it was the series of papers published by Wallace on protective colors that stimulated Darwin's interest in the sexual function of coloration. It is ironic that it should have been Wallace who stimulated Darwin to take a position which was diametrically opposed to his own and which was to constitute a primary source of disagreement and even of some contention between the two.

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[1] Vorzimmer, Charles Darwin: The years of controversy, p. 189.

In 1867, Wallace wrote to Darwin about his plan to publish a work on the origin of man and his racial traits, treating the whole question of sexual and natural modes of selection. Darwin, in an apparent resurgence of the emotions of 1858, was afraid that his originality would again be "smashed"; his return letter to Wallace contained dates and titles of works he had already completed, establishing his priority and territoral rights to the topic of man's descent.

> In my Essay upon Man I intend to discuss the whole subject of sexual selection, explaining as I believe it does, much with respect to man. I have collected all my old notes and partly written my discussion and it would be flat work for me to give the leading idea as exclusively from you.[2]

Wallace again deferred to Darwin by sending him the notes he had prepared for his study on man. Darwin was understandably embarrassed and returned Wallace's notes with an apology for "a touch of illiberality about your paper."[3] Wallace's treatise on man would not, indeed, could not, have been very similar to Darwin's Descent of Man since Wallace was no devotee of the theory of sexual selection. The proposed studies would have been parallel treatments of the same body of data, but the distance between the theories would have been maintained by the force of a priori differences and of mutual repulsion.

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[2] Marchant, Alfred Russel Wallace: Letters and Reminiscences, p. 151. Letter to Wallace from Darwin, April 1867. Wallace's Letters to Darwin are, unfortunately, missing.

[3] Ibid., p. 154. Letter, to Wallace from Darwin. May, 1867.

For Darwin, sexual selection:

> ...depends on the advantage which certain individuals have over others of the same sex and species solely in respect to reproduction. When. . . the two sexes differ in structure in relation to different habits of life, they have no doubt been modified through natural selection, and by inheritance, limited to one and the same sex.[4]

Sexual selection was a junior partner in alliance with natural selection, having "jurisdiction" over the complex of characteristics related to ornamentation and secondary sexual characteristics with little utility to the individual naimal's survival. Sexual selection applied in differing degrees to the whole spectrum of animals from insects to man. Although it may have been his work on man which caused Darwin to extend his view of sexual selection, his treatment of sexual selection in animals required an entire volume of the Descent of Man.

Darwin believed that man was subject to the same agencies of modification as animals without any appeal to either an active Creator or mystical propensity for directed change inherent in matter. Change is natural, but natural selection is not the only natural law at work in either lower animals or man. For example, the proportional lengths of the arms and legs, and the development of the lungs in populations at different altitudes, Darwin believed to be evidence of the inheritance of acquired characteristics inherited following an extended period of excessive use of the part. The inheritance of acquired characters

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[4]Darwin, Descent of Man p. 568.

was a useful way to understand changes in man's structure in the remote past.

> Although man may not have been much modified during the latter stages of his existence through the increased or decreased use of parts, the facts now given show that his liability in this respect has not been lost; and we positively know that the same law holds good with the lower animals. Consequently we may infer that when at a remote epoch the progenitors of man were in a transitional state, and were changing from quadrupeds into bipeds, natural selection would probably have been greatly aided by the inherited effects of the increased or diminished use of the different parts of the body.[5]

Darwin has been criticized for his advancing degree of appeal to use and disuse and the other Lamarckian causes of species modification, but it would more closely approximate the trend of Darwin's later thought to consider his change of direction as toward causes "other than natural selection," rather than as toward "Lamarckian causes," which do not exhaust Darwin's catalogue of other agencies by which changes may occur. His use of the hypothesis of sexual selection was of much the same order as his use of the inherited effects of use of disuse. The point really at issue was the inadequacy of natural selection, not the adequacy of Lamarckian alternatives.

The alternative of sexual selection has two major aspects: first the law of battle and second, female (in most species) choice. The first is a logical extension of natural selection, but the second is

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[5]Darwin, Descent of Man, p. 421.

not. In the law of battle, the animal of greatest physical vigor will almost surely be the victor, assuring the inheritance of the best characteristics by succeeding generations. The utility for the species of this kind of contest was apparent to most Darwinians and its explanation was of general agreement. It was a matter of empirical observation that male animals compete with each other and the conqueror almost invariably "gains his desire."[6] The proliferation of organs and appendages for both defense and offense among animals was ample evidence of some kind of "law of battle" in which the "fittest" is most generally the victor.

The evolution of devices to charm potential mates by "love-notes, songs, and antics,"[7] was variously described in the nineteenth century. Darwin surely understated the situation when he wrote, "Naturalists are much divided with respect to the object of the singing of birds."[8] Many ornithologists doubted that bird songs could have either an exclusively or a predominantly sexual purpose because of the continuation of singing throughout the year even when breeding season was past and, secondly, because of the singing by females found in many species. The use of songs as warning devices and for species recognition for protection were alternatives to Darwin's view. A similar

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[6] Darwin, Descent of Man, p. 704.

[7] Ibid.

[8] Ibid., p. 705.

dichotomy of interpretation surrounded the display by male birds of their plumage.

> Many will declare that it is utterly incredible that a female bird should be able to appreciate fine shading and exquisite patterns. It is undoubtedly a marvellous fact that she should possess this almost human degree of taste. He who thinks that he can safely gauge the discrimination and taste of the lower animals may deny that the female Argus pheasant can appreciate such refined beauty; but he will be compelled to admit that the extraordinary attitudes assumed by the male during the act of courtship, by which the wonderful beauty of his plumage is fully displayed, are purposeless; and this is a conclusion which I for one will never admit.[9]

Others, including Wallace, believed that the vigor and courage of the male was selected rather than his beauty; that health, vigor, and beauty were part of an integrated impression and formed the basis of the unconscious choice, not beauty alone. Beauty, in fact, was of minor importance, since the most fit males were usually also the most beautiful.

In sexual selection the animal species itself played an active part in its own evolution, although not consciously. In sexual selection, as in artificial selection of domestic breeding, unconscious choice, in addition to elements in the environment, produced lasting changes in the character of the species. Man was different from animals only in the degree to which sexual selection was involved in his evolution.

Again, it is ironic that Wallace was bitterly criticized for his

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[9]Darwin, Descent of Man, p. 731.

abandonment of natural selection to explain the origin of man, when for Darwin natural selection was incompetent to explain either. Neither Darwin nor Wallace considered natural selection to be the exclusive means by which species may permanently vary; but the limits which each man drew for the theory of natural selection were quite different. For Darwin the secondary sexual traits, ornamentation of animals, racial traits of man, and so forth, were evidence of sexual selection. Wallace, on the contrary, explained most of the same characters as resulting from natural selection, nor did he appeal to Lamarckian inheritance of acquired characteristics for explanations of difficulties in natural selection--only in the case of man did Wallace admit the inefficacy of natural selection. If natural selection may be equated with "Darwinism", Wallace was more "Darwinian" than Darwin himself.

Wallace's arguments against natural selection as the adequate agent in the transition of ape or proto-ape to man were primarily predicated on the inadequacy of the principle of utility. Natural selection preserves useful variations for man's survival and many of man's traits are either neutral or counter-productive for any survival value; the lack of hair which would be useful for warmth and protection, is an example. The advanced development of man's brain as well as his foot and hand, the origin of the moral sense, and man's ability to do abstract reasoning were inexplicable to Wallace on totally

naturalistic grounds.

> The inference I would draw from this class of phenomena is that a superior intelligence has guided the development of man in a definite direction, and for a special purpose, just as man guides the development of many animal and vegetable forms.[10]

Man's evolutionary history had an important disjunction at an early point in his emergence from anthropoid stock. At some unknown time cultural evolution replaced natural selection as surely as artificial selection had replaced natural selection in the domestication of wild dattle or horses. Man's body ceased to evolve when his mind became complex and clever enough to cope with the hostile environment by building houses, and fashioning garments, weapons and agricultural implements. The evolution of a cooperative social structure obviated the necessity of death for the weak; moral sensitivities replaced the "survival of the fittest."

The difficulties for natural selection posed by the problem of man were not easily solved. The large brain size of primitive people was Wallace's central argument against the natural origin of man. The tribesmen Wallace had known in the Malay Archipelago and in Brazil had lived very primitively, and he did not understand how "an organ quite disproportionate to his actual requirements,"[11] could have

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[10] Wallace, Contributions, p. 359.

[11] Wallace, Contributions, p. 343.

evolved on the principle of utility. The brain of savage man represented a "surplusage" of power, having the same potential for philosophical or quantitative reasoning as any European savant. Wallace was eager to deny the accusation that he believed man to be "God's domestic animal." He seldom capitalized the name of the "superior intelligence" to which he credited man's transition from lower animals since his concept was quite unlike the traditional Christian Creator. Wallace's "intelligence" had little in common with either the Jehovah of Genesis who created fixed species, or generalized kinds, nor did it play the role of a Cosmic Gardener, preserving the good and destroying the bad variations. Wallace's assertion of some kind of intelligent intervention in man's biological and psychic development put him into the same category as St. George Mivart, who could not reconcile Catholic theology with Darwinian biology. Wallace found himself in unwilling league with men whose theories of animal origin he rejected.

Neither Darwin nor Wallace felt quite comfortable about their increasing estrangement on the subject of natural selection and on the origin and development of man. Natural selection and sexual selection were the opposing explanations with respect to animals and supernatural origin was opposed to the natural origin of man. During the years when Wallace was becoming increasingly committed to a quasi-religious spiritualism, Darwin wrote that belief in God and the emotions of reverential awe were analogous to the:

> Behavior of a dog when returning to his master after an absence, and, as I may add, of a monkey to his beloved keeper is quite different from that toward their fellows.[12]

With such naturalistic views it is not surprising that Darwin had little regard for Wallace's opinion on a "superior intelligence" directing the development of man.

Wallace was a master of understatement when he wrote in his Contributions:

> It will, therefore, probably excite some surprise among my readers, to find that I do not consider that all nature can be explained on the principles of which I am so ardent an advocate; and that I am now myself going to state objections and to place limits, to the power of "natural selection."[13]

Not only did Wallace's opinions surprise but they appalled some of his colleages. Darwin was among them.

> If you had not told me I should have thought that the comments on man had been added by someone else. As you expected, I differ grievously from you, and I am very sorry for it.[14]

Wallace's reply showed that he believed his opinions on man justified.

> I can quite comprehend your feelings with regard to my "unscientific" opinions as to Man, and because a few years back I should mys f have looked at them as equally wild and uncalled for. I shall look with extreme interest for what you are writing on Man and shall give full weight

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[12] Darwin, Descent of Man, p. 470.

[13] Wallace, Contributions, pp. 332-333.

[14] Marchant, Alfred Russel Wallace: Letters and Reminiscences, p. 199. Letter to Wallace from Darwin April, 1869.

> to any explanation you can give of his probable origin. My opinions on the subject have been modified solely by the consideration of a series of remarkable phenomena, physical and mental, which I have now had every opportunity of fully testing, and which demonstrate the existence of forces and influences not yet recognised by science.[15]

Probably out of deference to Darwin, Wallace waited until after Darwin's death to publish his own magnum opus on descent with modification entitled, Darwinism.[16] It was an attempt at a holistic view of biology; which was an effort to appreciate the relationships between species in the state of nature. The work was published after thirty years of experience as an advocate of a theory he had always insisted upon calling "Mr. Darwin's theory," and it was intended as a tribute to Darwin and to natural selection, notwithstanding his differences from his old friend on the limitations of their theory.

> Even in rejecting that phase of sexual selection depending on female choice, I insist on the greater efficacy of mutual selection. This is pre-eminently the Darwinian doctrine, and I therefore claim for my book the position of being the advocate of pure Darwinism.[17]

The colors of animals and plants constitute a large proportion of Wallace's evidence, interpreted in such a way as to support the theory of natural selection, that is, "pure Darwinism". . . The function of color as protection was the recurring thread woven throughout

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[15] Ibid., p. 200 Letter, Wallace to Darwin, April, 1869.

[16] A. R. Wallace, Darwinism (London:Macmillan, 1889).

[17] Wallace, "Preface," Darwinism, p. iv.

Darwinism. There are, however, many kinds of protective coloration: (1) cryptic colors, (2) warning colors, (3) mimetic (Batesian and Mullerian mimicry) colors, (4) recognition colors,[18] (5) deflexion colors,[19] (6) terrorizing colors,[20] etc., all of which arise in natural populations as a result of the struggle for existence and the survival of the fittest.

During the thirty years of controversy on the purposes of color the grounds of debate had shifted from one purpose or use of color to another. The earliest discussions emphasized natural camouflage (1955-1862) with a second period initiated in 1862 with Bates' announcement of his theory of mimetic analogies (1862-1879). Batesian mimicry was supplanted by the controversial topic of Mullerian mimicry in 1879 (1879-1884). The dialogue between Wallace and the coloration-for-protection advocates and Darwin representing the coloration-for-

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[18] A recognition mark is a "signal flag" used for warning or for keeping a migrating flock together, etc. For example, the upturned tail of the mother rabbit is a signal to the young to follow, its white color having evolved to enhance her visibility to her young in the twilight during which they feed.

[19] Deflection colors or markings distract a predator from the vital parts of the animal possessing them to some expendable part. For example, the eyelike markings on the tail of lizards which can "drop" their tails and escape unharmed.

[20] Terrorizing colors are acquired by defenseless animals to give them the appearance of being dangerous. For example, the larvae of the genus Papilio have a blood-red tentacle which they throw out from the neck in order to frighten their enemies.

reproduction position continued from about 1867 until shortly prior to Darwin's death in 1882. In the years that followed Darwin's death recognition marks were studied. Of greater importance in the latter part of the nineteenth century was the increased level of experimental testing of the theories of animal coloration led by Edward B. Poulton, who built upon work initiated by John Jenner Weir, A. G. Butler, and August Weismann.[21]

Poulton's careful study involving more than 100 species of larvae, on "The Experimental Proof of the Protective Value of Colour and Markings in Insects in Reference to their Vertebrate Enemies,"[22] was a landmark in the critical examination and corroboration of the assumption that colors were useful for protection. Poulton's work introduced important distinctions which both Wallace and Darwin tended to overlook.

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[21] J. J. Weir, "Further Observations on the Relationship Between the Colour and the Edibility of Lepidoptera and their Larvae," Transactions of the Entomological Society of London 1870:337-340. Weir experimented on the edibility of species of insect larvae using many species of birds and lizards. A. G. Butler, "Descriptions of Some New Diurnal Lepidoptera, chiefly Hesperidae," Transactions of the Entomological Society of London 1870:485-520. Butler experimented on the edibility of caterpillars by birds, Lacerta viridis (green lizards), frogs,and spiders. A. Weisman, Studies in the Theory of Descent. Translated and edited by Raphael Meldola. (London: Sampson Low, 1882) also added experimental data.

[22] E. B. Poulton "The Experimental Proof of the Protective Value of Color and Markings in Reference to their Vertebrate Enemies," Proceedings Zoological Society of London 1887:191-274.

> In the sexually mature forms warning colours can be distinguished from sexual colours by their distribution on the surface of the body, by the way in which they are displayed in flight, by their type of pattern, and the colours employed. The sexual colours and patterns are beautiful, the other conspicious. Nevertheless, to the modified taste of a highly conspicuous insect, the warning colours probably possess value as sexual adornments.[23]

The distinction of beautiful and conspicuous was an important one in clarifying the often confusing mixture of uses of animal coloration. Poulton realized more fully than had his teachers that colors are often used in combination and that the mixture of uses may change.

> Just as in a long-contested battle the same position may be taken, lost, and retaken, but never held a second time with quite the same significance as before.[24]

The realization of the complexity of the ecological relationships of animal species dawned slowly, but its realization was important for the growth of the science of biology. In fact, the distribution of animals in a kind of "ecological space" was as important for the advancement of evolutionary thought as the early studies of species distribution in time and space had been for Darwin and Wallace for the discovery of natural selection.

The question in 1859 had been, "Why do animals have the colors they do?" The answers were varied but fell into two distinct groups

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[23] Poulton, "The Experimental Proof," p. 257.

[24] Ibid.

based on a priori committments; some believed that God had created animals in the patterns they now possess while the charter-member Darwinians opted for explanations based on natural law. By 1869 Batesian mimicry had already been assimilated by Darwinian explanations, but the reinterpretation of data by respected creationist scientists such as J. O. Westwood remained a viable alternative. By 1879, opponents of both Mullerian and Batesian mimicry were focusing on scientific arguments based on the laws of heredity and the mathematical improbability of the spontaneous production of mimetic species. In 1889 Wallace published his Darwinism with a sense of triumph that the theory known by that distinguished name had been successfully tested against the vast data of coloration--from the wings of butterflies to the racial colors of mankind.

CHAPTER V

IRRECONCILABLE DIFFERENCES

The rift between Darwin and Wallace on many matters of scientific interest did not pass unnoticed by nineteenth century scholars. Near the end of the century George J. Romanes reviewed the state of evolutionary biology and made the following table of the differences between Darwin's and Wallace's quite distinct theories of natural selection.[1]

The theory of Natural Selection according to Darwin	The theory of Natural Selection according to Wallace
Natural Selection has been the main means of modification, not excepting the case of Man.	Natural Selection has been the sole means of modification, excepting in the case of Man.
(a) Therefore it is a question of evidence whether the Lamarckian factors have cooperated.	(a) Therefore it is antecedently impossible that the Lamarckian factors can have cooperated.
(b) Neither all species nor, a fortiori, all specific charters, have been due to natural selection.	(b) Not only all species, but all specific characters, must necessarily have been due to natural selection.
(c) Thus the principle of Utility is not of universal application, even where species are concerned.	(c) Thus the principle of Utility must necessarily be of universal application, where species are concerned.

[1] George John Romanes, (1848-1894) Darwin and After Darwin, 3 vols. 2nd ed. (Chicago: Open Court Publishing Co., 1897).

(d) Thus, also, the suggestion as to Sexual Selection, or any other supplementary cause of modification, may be entertained and, as in the case of the Lamarckian factors, it is a question of evidence whether, or how far, they have cooperated.	(d) Thus, also, the suggestion as to Sexual Selection, or of any other supplementary cause of modification, must be ruled out; and as in the case of the Lamarckian factors, their co-operation deemed impossible.
(e) No detriment arises to the theory of natural selection as a theory of the origin of species by entertaining the possibility of supplementary factors.	(e) The possibility--and a fortiori the probability--of any supplementary factors cannor be entertained without serious detriment to the theory of natural selection, as a theory of the origin of species.
(f) Cross-sterility in species cannot possibly be due to natural selection.	(f) Cross-sterility in species is probably due to natural selection.[2]

The very nature and integrity of the theory of natural selection, their mutual invention, was in question. Wallace was the closer of the two to the Darwinism which was announced in 1858 since he had remained committed to the universality of the principle of utility he could also remain loyal to its corollary, natural selection. Darwin had changed his mind about the sufficiency of natural selection because the criticisms of his theory given in the 1860's by St. George Mivart, Fleeming Jenkin and others seemed unanswerable.[3] The

[2] Romanes, Before and After Darwin, II, p. 6.

[3] Vorzimmer, Charles Darwin: The years of Controversy, p. 211. "Strangely enough, inspite of all the modifications in his evolutionary thought after 1859, Darwin never accepted a suggestion resulting in any significant change in his theory from his personal friends of the "inner circle" of Darwinians. Instead he made his greatest revision under the influence of his severest critics (Agassiz, Pouchet, Jenkin, and Mivart)."

ultimate incompatibility of Darwin's and Wallace's views on natural selection and on the interpretation of the uses of coloration in animals had a long pre-history. In fact, their final positions were encapsulated in their original premises and earliest statements on evolution by means of natural selection.

One of the prevailing ideas in Darwin's writings was the importance of understanding domestic species in order to appreciate correctly phenomena found among wild species. The argument from domestic analogy was a conspicuous theme of the Origin of Species and more especially of the Variation of Animals and Plants Under Domestication. Darwin's analogy was something like this:

$$\frac{\text{artificial selection}}{\text{domestic breeds}} = \frac{\text{natural selection}}{\text{wild species}}$$

Upon the assumption of the validity of that relationship a second analogy might be derived:

$$\frac{\text{unconscious selection}}{\text{man as selecting agent}} = \frac{\text{sexual selection}}{\text{female animals as agent.}}$$

Wallace remained obdurately opposed to the use of domestic analogies to typify what happens among wild species. He was convinced that the phenomena of one state would most likely not be true of the other. His analogies between animals of different species have natural selection as "common denominator." Variations in wild species have been selected in the struggle for existence by the survival of the fittest. Domestic varieties were a separate question and must

be studied under other principles. The absence of a struggle for life by the intervention of human agents has changed the rules of modification radically; few leaps of analogy between wild and domestic could, in principle, be valid. The only real dichotomy in Wallace's science was the one between man and beast. The action of natural selection was confined to the early stages of man's emergence, but natural selection explained nearly all the modifications selected during the descent of the animals.

There seems to be general agreement among students of Darwin's thought on both sides of the turn of the present century, that Darwin increasingly relied upon explanations other than natural selection. In a sense Darwin moved forward by retreat to the earlier explanations of change offered by Erasmus Darwin, and by J. B. P. de Lamarck, both of whose influence Darwin persistently denied. Darwin declared that his grandfather's, Erasmus Darwin's, evolutionary ideas had had no effect on his own,[4] and that he had taken from Lamarck's writings "not a fact nor an idea."[5] Darwin was introspective enough to acknowledge limitations to his talent for unraveling complex metaphysical and philosophical tangles; but his unacknowledged use of the ideas of his early predecessors lends some credibility to C. D. Darlington's suggestion that:

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[4]Barlow, ed., Autobiography, pp. 49-50.

[5]Francis Darwin, ed., Life and Letters, II, p. 215, Letter, Darwin to Lyell, Oct, 1859,

> No doubt Darwin was able to cut himself off so completely from his historical forerunners because he succeeded so well in separating science from history in his own mind. The science of evolution was real; the history of the idea of evolution was unreal.[6]

However, Darwin had never professed to being a historian; nor could he seem to help feeling possessive of the theory of natural selection and of its applications. Science was Darwin's life, but it was a science science without a history. Darwin denied that the idea of evolution was "in the air"; Nora Barlow has generously written.

> No doubt the isolation of life at Down must have helped to prevent the penetration of opinion from workers in other fields than his own, so that he unconsciously overlooked indications that belief in the permanence of species was waning.[7]

No doubt. In retrospective analysis, however, not only can Lamarck be said to be Darwin's "forerunner" but also his "co-runner" in that Darwin used the ideas that the effects of acquired habit, use and disuse may be inherited in almost the same way Lamarck had used them, minus, however, the sentiment interieur, that volitional propensity for directed modifications. The rise of Lamarckism and the rise of sexual selection, were simultaneous in Darwin's published writings. Neither could Wallace apply natural selection without limit, but in

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[6] C. D. Darlington, "The Origin of Darwinism," Scientific American 200:60-66. p. 64. (May, 1959).

[7] Barlow, ed., Autobiography, p. 153.

denying natural selection he affirmed not earlier scientific paradigms, but heterodox religion.

As time goes on it may be that students of the history of science will judge both Darwin and Wallace as "transitional" characters, in somewhat the same way as Kepler or Harvey typify elements of both their predecessors and of their scientific successors. Darwin had very discernible ties to the theories of his forerunners. Wallace's increasing mysticism has put him into the peculiarly schizoid position of being ultra-Darwinian with respect to animals and non-Darwinian with respect to man's transition from ape to homo.

The discussion of animal colors which began before the discovery of the idea of natural selection, was an important test for the acceptibility of the new explanatory paradigm. It also points to many of the salient features of nineteenth century biology. Darwin and Wallace were two of the more important naturalists interested in discovering the mechanism by which colors are modified, but they were not alone. As the chief proponents of opposing ideas they each had clusters, or constellations, of eminent naturalists as allies. The coloration of animals was a primary "test site," not only to validate or deny explanation in terms of natural law, but also to determine which of several natural laws best fit with observational data. Darwin and Wallace believed different laws or modes of selection were responsible for the development of the variety of

colors, patterns, and decorative appendages found in the zoological kingdom.

Coloration is a matter of applied biology. Armchair speculation would not satisfy nineteenth century naturalists who believed in observational, Baconian science with an almost religious zeal. The question posed was whether or not natural selection could explain color phenomena. Darwinians, armed with Bates' explanation of mimicry, Wallace's work on protective colors of other kinds, and Mullerian mimicry answered in the affirmative.

Natural selection was never an isolated theory, but was constantly tested against masses of data demanding explanation. The coloration of animals was one class of that data which was re-explained on the level of natural law instead of special creation. Wallace's interest in coloration and the correspondence carried on with Darwin shows the growth of significantly different factions among the Darwinian scientists. Bates' discovery of an explanation of mimetic resemblances made the coloration of insects a subject of special interest in the middle 1860's which was reinforced by Muller's contribution in 1879. The application of natural selection to new discoveries as well as the redefinition of old ones proved it to be a flexible and highly inclusive theory.

Darwin's role in the discussion was a mixed one. He had great interest in the extension of natural selection, yet in the discussions of coloration he emphasized instead its inadequacy to explain secondary sexual traits and most cases of sexual dimorphism. He substituted his alternative theory of sexual selection, depending as it does on female choice as well as upon the struggle for reproduction. He did not focus upon the protective aspects of color adapting the animal to the general conditions of life. There is considerable indication that Darwin's idea of sexual selection is a direct transferrence of the concept of artificial selection of domestication which Darwin expanded in relation to the racial and physical traits of man and also of lower animals. Darwin's later writings do not emphasize the productions of tropical nature which also increased his theoretical variance with Wallace. Wallace discounted almost totally the possibility of the learning <u>anything</u> about wild species by analogy from domestic species, since the two conditions have little similarity. This central difference in their scientific premises may even transcend in importance their difference of opinion on man's origin. Wallace also discounted, a priori, the possibility of any second agencies. In that position he was in the good company of others who became known as "neo-Darwinians".

The whole discussion of animal coloration may be examined as an evolving idea, as a set of data toward which attention was directed in a series of ways throughout the latter half of the nineteenth century.

To use the language of Thomas Kuhn's The Structure of Scientific Revolutions, the coloration controversy is an example of the challenge of a new explanatory paradigm, natural selection, to the older views based on special creation of fixed species, with which there had been growing dissatisfaction among scientists. Geological and paeleontological evidence gathered early in the nineteenth century had placed the age of the earth and of living beings at many times the 6000 year span recorded in the book of Genesis. Higher criticism in biblical studies had challenged the literal interpretation of the creation account as well as the traditional Mosaic authorship. Theologically, as well as scientifically, the special creationist position was becoming insecure. The publication of Darwin and Wallace's theory in 1858 and even more important of the Origin of Species in 1859 precipitated a crisis period in biological science as might well be expected of a radical hypothesis. Much of the ideological tension of the 1860's, and even later, was the result of the inevitable clash between the world view of the reactionaries with that of the revolutionaries, representing mutually exclusive paradigms.

The cyclic rise and fall of theories does not lend itself to positivistic security of prized hypotheses, but the Victorians were not accustomed to an instrumentalist, or any other, tentative view of scientific theories. For them a theory must be judged true or false with respect to phenomena, the idea that it might be useful, but natural as to its truth was not entertained. Observations would speak for themselves, There could be no middle, or neutral ground. Darwin, Huxley, Wallace, and their followers, believed in natural selection as objectively true. Murray, Bennett, Westwood, and others were sure it was false. Yet both groups fully acknowledged the resemblances of palatable butterflies to groups protected by the secretion of nauseous substances. But they saw them from very different vantage points and interpreted their perceptions in disjunct terms. The data of animal coloration, like any other data class, is "theory-laden". Although sense-data could be agreed upon, it did not follow that the interpretation of the data would also be unanimous.

The affirmation of some points of view necessitates the denial of others; one cannot be both a mechanist and believe in vital forces simultaneously and to the same degree, nor can one be both a Darwinian with respect to descent with modifications and believe in the absolute fixity of species. A choice is required or some compromise must be negotiated. Evolutionary biology and Christian

theology were never mutually exclusive paradigms, as Asa Gray was quick to point out; but both his science and his theology were re rearranged to accomodate the other.

The theory of natural selection introduced the possibility of expanding natural law to biological phenomena and the coloration of animals was one episode in that extension. The explanation of animal colors on the basis of natural selection was not, in itself, revolutionary; but it had a part in the revolution as one arena of "activism." The controversy over coloration theory was one of the early applications of the paradigm of natural selection which resolved a part of the "crisis" and brought a return to normal science during which observations are made on the basis of an acknowledged or assumed theory and information in support of the theory accrues bit by bit.

The history of theories of coloration may be treated as either a sequence of explanatory paradigms with a focus on the shifts in the philosophy of science or as the history of a recurring idea reappearing sequentially as the societal contest changes. It is true of the idea of coloration of animals, as of other recurring themes, that nineteenth century Victorian England influenced the manner and the form of the discussion of animal colors. Wallace and Darwin's relationship might have ended in a bloody duel if the rules of the society had been quite different. George Boas in an effort to introduce balance

into historical analysis wrote: "The nineteenth century did not get heated up over evolution because it was the nineteenth century or the Victorian Period."[8] He is quite right; periods are not independent of the people and conditions which constitute them. Ideas have never appeared in vacuo, but in social, historical contexts. The controversy over the correct explanation of animal coloration was part of the larger discussion of evolution by natural selection, and secondly, a part of the head-on collision of natural law and super-natural intervention. The history of the theories of animal coloration is a prime example of the shifting edge between observation and explanation, illustrative also of both the evolutionary and the fixed species "gestalt." Perhaps its greatest significance resides in the clear exposure of the schism in interpretation between the equally ardents evolutionists and founders of the theory of evolution by natural means of selection--Charles Darwin and Alfred Russel Wallace.

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[8]George Boas, The History of Ideas (New York: Charles Scribner's Sons, 1969).

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