SCIENCE

VOL. 74 FRIDAY, OCTOBER 9, 1931 No. 1919

SCIENCE: A Weekly Journal devoted to the Advancement of Science, edited by J. MCKEEN CATTELL and published every Friday by

THE SCIENCE PRESS
New York City: Grand Central Terminal

Lancaster, Pa. Garrison, N. Y.
Annual Subscription, $6.00 Single Copies, 15 Cts.

SCIENCE is the official organ of the American Association for the Advancement of Science. Information regarding membership in the Association may be secured from the office of the permanent secretary, in the Smithsonian Institution Building, Washington, D. C.

A HUNDRED YEARS OF EVOLUTION[1]

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THINKING over the subject of this address, I have been encouraged by a metaphor given me by Oliver Wendell Holmes at a delightful dinner of the Boston Saturday Club in January, 1894—"Memory in old age is a palimpsest with the records beneath standing out more clearly than those above." And, indeed, memories of my first British Association, at York in 1881, are clearer than those of many in later years. It was a great meeting, as befitted the fiftieth anniversary, and nearly every sectional president had been a president of the association. It also marked a turning-point in evolutionary controversy, being, I believe, the last meeting at which opposition was offered to evolution as apart from its motive cause or causes. From 1881 onwards the battles in this section have been over Lamarckism and natural selection and their factors, especially heredity; over the size of the steps and the rate of progress. Evolution itself has been generally accepted. It was different at York in 1881. Dr. Wright's indignation, when the reptilian affinities of *Archeopteryx* were explained in the geological section, was stirred by the hated doctrine which gave meaning and life to the demonstration. I well remember, too, how Professor O. C. Marsh, discussing one of the meetings in this section with a young and inexperienced naturalist, said that he had felt rather anxious about the way in which his paper on the Cretaceous toothed birds of America would be received by the president, Sir Richard Owen. His fears were, however, groundless, and all was well.

The difference between the controversies raised in the first and the second of these half-centuries of evolution reminds us that long before Darwin saw his way to an explanation of evolution he was satisfied that evolution was a fact; reminds us, too, that we are celebrating another great centenary, for he sailed in the *Beagle* on December 27, 1831, thus entering upon the five years' voyage which, in his own words, "was by far the most important event in my life, and

[1] Address of the president of Section D—Zoology, British Association for the Advancement of Science, London, September, 1931.

has determined my whole career"—the voyage which provided him with the evidence that evolution is a fact. The idea of natural selection as a motive cause did not come to him until October, 1838, just two years after his return.

The independent discovery and publication of the principle of natural selection by Dr. W. C. Wells[2] in 1818 and by Patrick Matthew in 1831 followed a very different course, for neither of these men realized the significance of the idea which had come to him. Wells wrote that he had ventured to expound it, "though at the hazard of its being thought rather fanciful than just," and Matthew half apologizes for the amount of space which has been taken from his main subject. He was, nevertheless, anxious to claim credit when, twenty-nine years later, the importance of the discovery was revealed to him in the *Gardener's Chronicle* reprint of the *Times* review of the "Origin," the review of which Huxley said, "I wrote it, I think, faster than I ever wrote anything in my life." It is interesting to speculate upon what might have happened if the author had called his book "Arboriculture and Naval Timber" instead of the more severely technical "Naval Timber and Arboriculture"; for, with the former title, the work might well have been consulted by Darwin who would have been led by the table of contents to discover its significance.

Robert Chambers' "Vestiges of the Natural History of Creation," which appeared in 1844, undoubtedly includes illuminating thoughts far in advance of the time. Thus, more than once, the author writes of organic life "pressing in" when suitable conditions arose, "so that no place which could support any form of organic being might be left for any length of time unoccupied," and he also speaks of withdrawals when the appropriate conditions pass away. Then, too, Anton Dohrn's "Functionswechsel" is foreshadowed in the conclusion that "organs, while preserving a resemblance, are often put to different uses. For example: the ribs become, in the serpent, organs of locomotion, and the snout is extended, in the elephant, into a prehensile instrument." And, contrasted with this, the author points to the performance of the same functions by "organs essentially different," and then to the consideration of rudimentary structures and the recognition that "such curious features are most conspicuous in animals which form links between various classes." Of great interest, too, is the forcible rebuke administered to those who maintain that an animal origin for man is a degrading thought.

[2] Wells, like Matthew and Chambers, was a Scotsman. He was born (May 1757) of Scottish parents in Charlestown, South Carolina. In the troubled times preceding the Declaration of Independence his father, to quote his own words, "obliged me to wear a tartan coat, and a blue Scotch bonnet, hoping by these means to make me consider myself a Scotchman. The persecution I hence suffered produced this effect completely."

It was a credulous age and we need not be astonished at the author's belief in a spontaneous, or as he preferred to call it, "aboriginal," generation of clover in waste moss ground treated with lime, and his opinion that an explanation based on the presence of dormant or transported seed was "extremely unsatisfactory"; or, again, his acceptance of the hypothesis, held by some authorities at the time, that parasitic entozoa were produced from "particles of organized matter" within the host, such a development being, he considered, "in no small degree favorable to the general doctrine of an organic creation by law." The authorship of the "Vestiges" was revealed in Alexander Ireland's introduction to the 12th edition, published in 1884, thirteen years after Chambers' death. The secrecy appears to have been mainly due to a rule, laid down in the Chambers' publishing business, that "debatable questions in politics and theology" should be avoided.

I have devoted some little time to the "Vestiges," which I think has hardly received its due, although Darwin fully acknowledged its importance in preparing many minds for a belief in evolution. We know, too, that the author warmly supported the Darwinian cause in the controversy which arose over the "Origin," and that it was his advocacy which rendered possible the great encounter at Oxford in 1860; for when Huxley told him that he did not mean to attend the meeting of the section on June 30—"did not see the good of giving up peace and quietness to be episcopally pounded," "Chambers broke into vehement remonstrances, and talked about my deserting them. So I said, 'Oh! if you are going to take it that way, I'll come and have my share of what is going on.'" And after the meeting, J. R. Green wrote to his college friend, Boyd Dawkins—"I was introduced to Robert Chambers the other day and heard him chuckle over the episcopal defeat."

Owing to the kindness of Lady Boyd Dawkins and Dr. Leonard Huxley, I am able to print a very interesting and hitherto unpublished letter in which Huxley confirmed the well-known description of the debate given by Green:

4 Marlborough Place,
Abbey Road, N.W.
June 11, 1883.

My dear Boyd Dawkins,

Many thanks for the extract from Green's letter. His account of the matter appears to me to be accurate in all essentials, though, of course, I can not be sure of the exact words that were used on either side.

It is curious that your letter should have reached me this morning, when in a couple of hours I shall start for Cambridge for the purpose of delivering the Rede Lecture on the subject of "Evolution." I should not have chosen this topic of my own mere motion. But I found that nothing else would satisfy the expectations of Cam-

bridge! Truly "the whirligig of time brings its revenges."

I am,

Yours very sincerely,

T. H. HUXLEY.

Robert Chambers' work appears to have provided the stimulus which led to the preparation of an interesting and surprising manuscript[3] by the younger J. Searles Wood. It was found by my friend, Sir Sidney Harmer, among his father's papers, and bears a note, dated 1866 and signed J.S.W., Jr., stating that it "was written about 1848 or 1849 and the pencil alterations made at the time." The paper, however, bearing a water-mark of 1850, supplies a rather comforting correction, for the author was not born until 1830, and at eighteen or nineteen must have been a very precocious youth to have written such a manuscript. Searles Wood, who was a great admirer of Lamarck, was evidently stirred by the immense success of the "Vestiges" and doubtless especially by the statement that the hypothesis of the French naturalist "deservedly incurred much ridicule, although it contained a glimmer of truth." The manuscript is, however, far more than a defense of Lamarck: it contains powerful arguments in favor of evolution, based upon the very grounds which convinced Darwin himself—the "wonderful relationship in the same continent between the dead and the living," and between island species, especially in the Galapagos, and those of the nearest continental area. It will be remembered that Darwin's pocket-book for 1837, referring to this very evidence, contains the words, "These facts (especially latter) origin of all my views." At the side of a page on which the argument on island life is developed, Searles Wood had noted—"When I wrote this, Mr. Darwin had not broached his hypothesis and was not known to be any other than a believer in creation. J.S.W. Jr. 1866." Darwin's "Journal" was first published in 1839, the second edition in 1845, but I have not heard of any reader except Searles Wood who recognized, before the appearance of the Darwin-Wallace Essay and the "Origin," that organic evolution was an irresistible conclusion from the facts recorded by the author. Other important arguments, brought forward in the manuscript, will, I am sure, be read with the utmost interest when it appears in the Linnean proceedings.

A curiously interesting event in 1858, the year of the Darwin-Wallace Essay, was the appearance of "Omphalos," so well described, with the eager expectation and bitter disappointment of its author, in Sir Edmund Gosse's "Father and Son." It is unnecessary to repeat on this occasion the often told and never-to-be-forgotten story of the Joint Essay and the Linnean Society's celebration of its fiftieth anniversary, when Wallace protested in noble and inspiring words against the undue credit which he considered had been allotted to him for his share in the discovery of natural selection—a discovery brought to him, as it was brought to Darwin, by the reading of Malthus "On Population."

The effect of the Darwin-Wallace Essay upon Canon Tristram and the appearance, a few weeks before the "Origin," of his paper on the ornithology of the Sahara was brought before this section by Professor Newton at Manchester in 1887, and by the author himself at Nottingham in 1893. It is, however, desirable to emphasize its significance afresh in view of recent attempts to throw doubt on the value of concealing coloration in desert areas. Tristram was led to a belief in natural selection when he read the Essay in the light of a recent experience of many months in the Algerian Sahara, where he had observed that "the upper plumage of every bird, . . . and also the fur of all the small mammals, and the skin of all the Snakes and Lizards, is of one uniform isabelline or sand colour," and had come to realize the absolute necessity for the vast majority of the species to be thus concealed upon the uniform surface of the desert. Precisely the same necessity had been recognized in South Africa nearly half a century earlier by Burchell, when he observed the protective resemblance of a *Mesembryanthemum* and a grasshopper to pebbles, and the defensive value of thorns and acrid secretions in a bare dry country "where every juicy vegetable would soon be eaten up by the wild animals." Burchell's mention of plants with an "acrid or poisonous juice" suggests the meaning of the conspicuousness of the relatively few black, slow-moving insects which have been thought to throw doubt upon the whole theory of protective coloration in the desert. The problem is complex and the struggle for existence is waged in many ways, important among them being the physiological adaptations by which the imperative need for moisture is satisfied—a subject on which much light has been thrown by P. A. Buxton.

Coming now to the meetings of the British Association and of this section in the second half-century, we are naturally led to the discussion, "Are Acquired Characters Hereditary?" at Manchester in 1887, when Weismann, Ray Lankester, Hubrecht and many others spoke; and to the same subject at Newcastle in 1889 when Francis Galton and Fairfield Osborn, our welcome guest to-day, took part in the debate.

It was only natural that Weismann's conclusions should rouse intense opposition, for they undermined the foundations on which so much evolutionary theory had been erected. I remember Sir William Turner's

[3] Presented by Sir Sidney Harmer, F.R.S., to the Linnean Society of London. It is hoped that the manuscript will be published in the Proceedings of the Society when the rather difficult task of editing has been completed.

words at one of our meetings about this time—"Whoever believes that acquired characters are not transmitted looks upon life with a single eye"—not in the Biblical sense, but implying monocular vision; also Lawson Tait's dogmatic statement at a meeting of the Midland Institute at Oxford in 1890, that a believer in Weismann's conclusion "says that the sun shines black." One result of the new doctrine—the collapse of Herbert Spencer's "Synthetic Philosophy," so largely built upon Lamarckian principles—was especially distressing to those who remembered a beneficent power in teaching the world to think; remembered, too, what it had done for themselves in earlier years. But not all naturalists were startled and amazed when Weismann "awoke us from our dogmatic sleep." I well remember Ray Lankester's reply when I first mentioned the subject to him—"I believe Weismann is right. I have always doubted the statement that acquired characters are transmitted." And his two old Oxford friends, H. N. Moseley and Thiselton-Dyer, were also ready to follow Weismann from the first. Two sayings of Weismann may be recalled here—how the "Continuity of the Germplasm," the theory which first led him to doubt the accepted views on heredity, came to him when he discovered that "there was something which had to be carefully preserved" throughout the development of a hydrozoon, *viz.*, that unexpended portion of the parental germ-cell which will give rise to the germ-cells of the offspring. Shielded and "carefully preserved" as was this carrier of hereditary qualities, how improbable was the conclusion, that it would be effected by the happenings in distant parts of the organism, how doubly improbable the supposition that the effect would reproduce the result of these happenings in the offspring. All this is, of course, well known, but it is interesting to recall it as told by Weismann himself. His other remark was to the effect that if acquired characters could be transmitted, we should not be obliged to search for the evidence. It would have been obvious everywhere.

Although, as my friend and colleague, Professor Goodrich, has written—"these conclusions of Weismann . . . are the most important contribution to the science of evolution since the publication of Darwin's "Origin of Species,"[4] it was soon realized that the statement of the problem required revision and that Weismann's terms "Blastogenic" and "Somatogenic" were inaccurate; for the germinal or inherent characters are no less dependent on external causes than the somatic or acquired characters. This criticism was developed by Adam Sedgwick in his address to this section at Dover in 1899 and by Goodrich at Edinburgh in 1921; also, between these two addresses, by Archdall Reid. Furthermore, in the spring of 1890, when I was giving a course of university extension lectures on "Evolution and Heredity" at Gresham College, the same idea was expressed in an answer written by one of the students. I was very fortunate in my audience, which included Professor A. G. Tansley, F.R.S., Wilfrid Mark Webb and W. Platt Ball.[5] The last-named student, in one of his answers, wrote to the following effect, if I may trust a memory of over forty years—"Acquired characters are due to external causes acting upon inherent potentialities; inherent characters are due to inherent potentialities acted upon by external causes." The distinction, which seems at first sight difficult and confusing, is very clearly shown by a simple diagram given by Professor Goodrich,[6] who considers that the expression "acquired character" should be dropped. Its history is, however, so interesting—Erasmus Darwin (1794), Lamarck (1809), Prichard (1813)—and its use still so general that we may hope for its continuance, considering especially the vital importance in every-day life of the facts which it describes. It is difficult to imagine Johannsen's term—"phenotype"—replacing it in discussing the problems of education or crime.

In mentioning the name of the illustrious anthropologist, James Cowles Prichard, I may remind the section that the non-transmission of acquired characters was maintained by him in the second edition (1826) of his great work, "Researches into the Physical History of Mankind."[7] I have recently studied the first edition (1813) and find that the same conclusion was affirmed at this earlier date. Thus, on page 195, the author states, "the changes produced by external causes in the appearance or constitution of the individual, are temporary, and in general acquired characters are transient and have no influence on the progeny." Again, on page 232, arguing that age-long exposure to heat did not cause the dark color of tropical races, he continues "and this fact is only an instance of the prevalence of the general law, which has ordained that the offspring shall always be constructed according to the natural and primitive constitution of the parents and therefore shall inherit only their connate peculiarities and not any of their acquired qualities"—a very remarkable statement to find in a book published eighteen years before the first meeting of the British Association. I must also mention on this occasion the paper[8] contributed to

[4] "Living Organisms," Oxford, pp. 50, 51, 1924.

[5] Author of "The Effect of Use and Disuse," "Nature Series," London. The excellent term "Use-inheritance" to signify "the direct inheritance of the effects of use and disuse in kind," was suggested in this book.

[6] *Ibid.*, p. 54. See also p. 62, n. 1.

[7] *Science Progress*, April, 1897. Reprinted in *Essays on Evolution*, Oxford, 1908.

[8] *Abstract of a Comparative Review of Philological and Physical Researches as Applied to the History of*

the second meeting at Oxford in 1832, in which Prichard contends, in opposition to Cuvier, "that the various tribes of men are of one origin."

The rediscovery of Mendel's work—epoch-making although the birth of the epoch was long delayed—produced an immense effect on the papers and discussions in this section. Much of the controversy in the first and second decades of this century arose out of the belief that only large variations—or as they were called, "mutations," using an old word with a new meaning—are subject to Mendelian inheritance, and to the related belief that small variations are not inherited at all. But towards the end of this period the foundations of the controversy vanished, for as Professor H. S. Jennings[9] pointed out in 1917, the work of W. E. Castle and T. H. Morgan proved that the smallest characters are hereditary, so that "the objections raised by the mutationists to gradual change through selection are breaking down as a result of the thoroughness of the mutationists' own studies." To give a single illustration—between a red-eyed and a white-eyed fruit-fly (*Drosophila*) seven gradations of color intervene, each of them "heritable in the normal Mendelian manner." Furthermore, in the middle member of this series, "Bridges has found seven modifying factors, each of which alters its intensity and gives rise to a secondary grade of color. Now each [all] of these modifying factors are described 'specifically as mutations; as actual changes in the hereditary material.'" The author finally concludes that "Evolution, according to the typical Darwinian scheme, through the occurrence of many small variations and their guidance by natural selection, is perfectly consistent with what experimental and paleontological studies show us"; indeed, it appears to him to be "more consistent with the data than does any other theory," a conclusion confirmed by Dr. R. A. Fisher's recent work, "The Genetical Theory of Natural Selection." Mendelian heredity also provided an effective answer to a difficulty by which Darwin had been greatly troubled—the supposed "swamping effect of intercrossing" on which Fleeming Jenkin had written a powerful article.[10] Moreover, it can not be doubted that Mendelian research, by demonstrating the paramount importance of germinal qualities, played a great part in promoting the general acceptance of Weismann's teaching.

A mistaken belief prevailed in the early years of the Mendelian rediscovery that a new theory of evolution had been revealed to the world and that Darwinism had been abandoned. The true position was emphatically stated by Miss E. R. Saunders at the Cardiff Meeting in 1920—"Mendelism is a theory of heredity; it is not a theory of evolution."

I need not dwell upon the paleontological evidence for continuous evolution, as Professor Osborn is here and we shall soon have the pleasure of listening to one who can tell us of the conclusions to be inferred from the matchless record of past ages in the great museum of which he is the director.

The important subject of geographical races or subspecies will be discussed next Tuesday, and I will now only refer to the splendid work of the Tring Zoological Museum under the guidance of Lord Rothschild, Dr. Hartert and Dr. Jordan, and the conclusions published in their journal in 1903.[11] "Geographical varieties . . . represent various steps in the evolution of daughter-species"; and "whoever studies the distinctions of geographical varieties closely and extensively, will smile at the conception of the origin of species *per saltum*."

The age of the earth, as estimated by Lord Kelvin and Professor Tait, was one of Darwin's "sorest troubles." "I should rely much on pre-Silurian times," he wrote in 1871, "but then comes Sir W. Thomson, like an odious spectre." Lord Salisbury's treatment of this subject in his address at Oxford in 1894 will be remembered by many. Entirely accepting the fact that Darwin had "disposed of the doctrine of the immutability of species," he ridiculed the demands which evolution by natural selection makes upon the bank of time. "Of course if the mathematicians are right, the biologists can not have what they demand. If, for the purposes of their theory, organic life must have existed on the globe more than a hundred million years ago, it must, under the temperature then prevailing, have existed in a state of vapor. The jelly-fish would have been dissipated in steam long before he had had a chance of displaying the advantageous variation which was to make him the ancestor of the human race." I venture to refer to this difficulty, although a difficulty no longer, because it provides a good illustration of the help which so often comes to us at these meetings, and also recalls a vigorous personality, our kindly treasurer for many years, Professor John Perry. Walking together on the Sunday of the Leeds Meeting in 1890 he explained to me the evidence on which Thomson and Tait had relied, and said that he believed the argument founded on the cooling of the earth to be sound. When, however, he heard Lord Salisbury's address four years later, and decided to re-examine the evidence, he soon discovered that an important consideration had been overlooked.

the Human Species. The abstract occupies fifteen pages of B.A. Reports, vol. i. (including the first two meetings).

[9] *Journ. Washington Acad. Sci.*, vol. vii, No. 10, p. 281, May 19, 1917; *American Naturalist*, vol. li., p. 301, May, 1917. The statements here reproduced are quoted from a brief summary of these two papers in *Proc. Ent. Soc. Lond.*, 1917, p. lxxxv.

[10] *North British Review*, June, 1867.

[11] *Nov. Zool.*, vol. x, p. 492, 1903.

With his kind help I chose this subject, together with the biological evidence for the age of the habitable globe, for my address at Liverpool in 1896. In the following year as we were traveling across Canada after the Toronto meeting and the chance of collecting insects for a few minutes at each station could not be resisted, Lord Kelvin said to his wife: "My dear, I think we must forgive Poulton for thinking that the earth is so very old when he works so hard in one day out of all the endless millions of years in which he believes!" A quarter of a century later "The Age of the Earth" was the subject of a joint discussion at Edinburgh, when the Thomson-Tait limitation of time was abandoned in consequence of researches on radio-activity.

We now come to biological criticisms of evolution by natural selection, especially those urged by my friend Sir John Farmer in his presidential address to the botanical section at Leicester in 1907,[12] and concisely restated in 1927.[13] In the latter publication the theory of evolution as it was held forty years ago, and, I may add, very nearly as it is held to-day, was described as "the notion that the basis of evolutionary change in living forms lay in the gradual summation of almost imperceptibly small variations, and that, in fact, specific change was attributable to selection and accumulation of these small variations as the result of environmental conditions." Except for the implied restriction of selection to "almost imperceptibly small variations," the statement appears to express fairly the opinion of many believers in natural selection at the centenary of the British Association. One main criticism of this belief was that it led to "the facile teleology, which, like a noxious weed, had overgrown the solid framework of evolutionary doctrine." But this was not a necessary nor, in my opinion, a common result of the evolutionary beliefs of those years. Let me give two examples of teleological interpretations offered forty years ago, interpretations which are anything but "noxious weeds," being extremely interesting in themselves and pointing directly to further researches and a further strengthening of the "solid framework."

On his return from a visit to Ceylon and Southern India in 1889 and 1890 Sir John Farmer gave at Oxford a most interesting lecture on his experiences. I recall two of his observations which have always seemed to me most illuminating. One concerned a *Loranthus,* which is so successful that it threatens the very existence of certain introduced trees. It possesses a viscid fruit which adheres to stem and leaves; then from the seed the embryo puts out a sucker borne at the end of a rather thick stalk which curls down and fixes itself to anything it touches. The stalk then straightens and the fruit, containing the germinating seed, is borne aloft. If, however, as he believed, the sucker becomes attached to an unsuitable surface, the stalk bends over again and makes another attempt to reach a living structure which can be penetrated, and if this fails the process continues, causing the fruit to travel in search of favorable opportunities, naturally denied to those which he often saw thickly covering the telegraph wires in the Nilgiri Hills.[14]

The second observation was made upon flowering plants which depend for cross-fertilization on insect-visitors and the honey which attracts them. Such flowers are well known to be robbed by insects which bite their way in and steal the honey without doing their work. Now Sir John Farmer observed that in certain species this difficulty was met by the development, on the outside of the flower, of special glands attractive to a bodyguard of ants so that the lazy visitors would be compelled to seek the proper entrance and the thieves driven away. This observation has always seemed to me especially significant, as showing how the simple operation of natural selection may simulate a rather elaborate process of reasoning. We may wonder whether it would have satisfied the zoologist of whom Darwin wrote to Lyell: "Dr. Gray of the British Museum remarked to me that *'selection* was obviously impossible with plants! No one could tell him how it could be possible!' And he may now add that the author did not attempt it to him!"

But if either or both of these interpretations should be disproved, if the ants in these and other analogous associations should be shown, as some believe, to be parasites doing no useful work for the plant—what then? Well, once again hypothesis will have played a fruitful part in stimulating and guiding research.

An often repeated objection to natural selection is the difficulty or impossibility of accounting for the earliest stages of useful structures. It is, of course, unwise to attempt an explanation of an unknown origin. We can only await further discoveries, and oftentimes admit that there is little hope of success. But the difficulty is frequently completely met by Anton Dohrn's principle of "change of function." A new function is often taken over by an organ adapted to perform another, the two at first overlapping and the younger gradually supplanting the older. The various uses of vertebrate limbs supply a good illustration.

Another valuable principle, working in association with Anton Dohrn's, is the "Organic Selection" of Mark Baldwin, Lloyd Morgan and Fairfield Osborn. The power of individual adaptability "acts as the

[12] An answer to the criticisms in this address appeared in the Introduction to *Essays on Evolution,* Oxford, p. xliv, 1908.

[13] *Proc. Roy. Soc.,* B., vol. 101, pp. i, ii, 1927.

[14] My friend has kindly refreshed my memory on some of the details.

nurse by whose help the species . . . can live through times in which the needed inherent variations are not forthcoming." But this power of adaptability is itself a product of selection. "The external forces which awake response in an organism generally belong to its inorganic (physical or chemical) environment, while the usefulness of the response has relation to its organic environment (enemies, prey, etc.). Thus one set of forces supply the stimuli which evoke a response to another and very different set of forces."[15]

What other theories of evolution have been offered to us by those who would reject or limit the power of natural selection? Some of them have been mentioned by a writer in a recent number of *Nature*[16]—"orthogenic variations," "established organic architecture," "metabolic routine," "laws of growth" and "conditions of organic stability." Others were named in Sir Peter Chalmers Mitchell's Huxley Memorial Lecture in 1927, and I agree with his description of them as a "brood of imaginary vital forces, gods placed in machines to account for modes of working we do not understand"; although, in many instances, some supposed manifestation of an internal developmental force receives a ready explanation along the lines suggested by H. W. Bates in his classical paper:[17]

> The operation of selecting agents, gradually and steadily bringing about the deceptive resemblance of a species to some other definite object, produces the impression of there being some innate principle in species which causes an advance of organization in a special direction. It seems as though the proper variation always arose in the species, and the mimicry were a predestined goal. [Then, after mentioning other suggested hypotheses, he concludes that all are] untenable, and the appearances which suggest them illusory. Those who earnestly desire a rational explanation, must, I think, arrive at the conclusion that these apparently miraculous, but always beautiful and wonderful, mimetic resemblances, *and therefore probably every other kind of adaptation in beings*,[18] are brought about by agencies similar to those we have here discussed.

The writer in *Nature* who marshalled his array of supposed developmental forces contrasted with them "the old nightmare view of evolution as a chapter of accidents." Well, a nightmare is not uncommon as a result of imperfect digestion!

The concluding section of the address will be almost entirely devoted to recent work with a direct bearing on Darwinian evolution—the researches upon mimicry and allied subjects undertaken by a band of brother naturalists widely scattered over the world. My greatest scientific interest and delight have been found in this work, and to it for nearly fifty years all available time has been given. The preparation lies far back in childhood, for my earliest memories are of living insects; and then at a fortunate period I read Professor Raphael Meldola's translation, with his valuable notes, of Weismann's "Studies in the Theory of Descent." He soon became my dear friend, and for nearly a quarter of a century I relied "probably even more than I am myself aware upon his sympathy and help."[19]

I would ask any naturalist who feels inclined to criticize the amount of space given to insect-mimicry in this address, to remember the words of H. W. Bates—"The process by which a mimetic analogy is brought about in nature is a problem which involves that of the origin of all species and all adaptations."[20]

The evidence for evolution by natural selection to be briefly described is in large part associated with the name of Fritz Müller, the illustrious German naturalist of whom Sir Francis Darwin wrote—"The correspondence with Müller, which continued to the close of my father's life, was a source of very great pleasure to him. My impression is that of all his unseen friends, Fritz Müller was the one for whom he had the strongest regard."[21] These words enable us to realize the special value and interest of Darwin's letters to Fritz Müller, the noble gift which the British Association has received within the last few months from Professor Fairfield Osborn.

Many of Fritz Müller's letters on insect mimicry and allied subjects were sent by Darwin to Professor Meldola, who communicated the observations to the Entomological Society of London,[22] of which he was an honorary secretary.

Whenever I have brought some striking example of insect mimicry to Sir Ray Lankester, my dear friend and the friend of many here, his comment was always the same—that it was a convincing proof of evolution by natural selection, and that he was unable to understand how any naturalist could come to a different conclusion. And yet, as we know, many have done so and probably many do so still. I hope, therefore, that it may be interesting and perhaps convincing to some unbelievers to refer to the two plates recently

[15] Poulton in *Proc. American Assoc. for Adv. Sci.*, vol. xlvi, p. 241, 1897.

[16] Vol. 127, p. 479, March 28, 1931.

[17] *Trans. Linn. Soc. Lond.*, vol. xxiii. (1862), Pt. III (1862), Mem. XXXII, p. 514.

[18] Italicized for the purpose of this address.

[19] "Essays on Evolution," p. ix. This work is dedicated to Raphael Meldola.

[20] *Ibid.*, p. 511.

[21] "Life and Letters of Charles Darwin," London, vol. iii, p. 37, 1887.

[22] Darwin's letters to Meldola, including ten referring to Fritz Müller, are printed in "Charles Darwin and the Theory of Natural Selection," Poulton, London, 1896. The originals, with many of F. Müller's letters, were presented by Professor Meldola to the Hope Library, Oxford Univ. Museum.

published in the Transactions of the Entomological Society.[23]

The moth model and butterfly mimic, beautifully illustrated on plate XIV, really speak for themselves; but it must be explained that the resemblance between the patterns is much closer on the upper surface of the wings than on the under; that the orange patch evidently becomes a conspicuous warning mark (aposeme) in which the position of rest when the insects hang with drooping wings and the under side of the body is uppermost; that the position of the mimic's patch on the parts of the wings which cover the body and not on the body itself, as in the model, is evidence of selective elimination guided by the sense of sight; also that model and mimic fly together round the tops of trees, the former being much the commoner. I owe this most interesting example to my kind friend, Dr. Karl Jordan, of the Tring Zoological Museum.

The second example, shown on plate XV, is of a very different kind, but I think equally interesting and convincing. The oval yellow masses of silk spun on the outside of their cocoons by the caterpillars of the W. African Bombycid moth, *Norasuma kolga,* closely resemble the cocoons constructed by Braconid parasites which have devoured a larva or pupa. The appearance is, I believe, well known to nearly everyone and is especially common in the autumn, when the dead or dying caterpillars of the Large Garden White butterfly may be seen on walls and fences, bearing the yellow cocoons of the parasitic larvae which have destroyed them. It has sometimes been thought that the object of the pretended Braconid cocoons is to deceive the female Bracon in her search for caterpillars in which to deposit her eggs, but this is most improbable because these parasites are guided by other delicate senses in addition to sight, which perhaps is not employed for this purpose; above all, because the eggs which are the ultimate cause of parasitic cocoons like the pretended ones, would have been laid far back in the life of the victim. It is probable that the conspicuous yellow color is advantageous to the parasites, for the small cocoons are very tough and contain but a small amount of food. A few experiments, perhaps a single one, would teach a bird that a cocoon bearing these yellow masses contains only a shrunken skin, and also that the yellow cases themselves are not worth opening. The yellow warning color is advantageous to the parasites "because enemies are all the more readily discouraged from making attempts which would incidentally lead to the destruction of some of them. Hence the obvious advantages conferred by false cocoons of parasites when mistaken for real ones."[24] This interesting adaptation was discovered by my old friend, Dr. W. A. Lamborn, O.B.E., who, a little earlier, had found another example in which the same deceptive resemblance was brought about in a totally different way. The cocoon of another West African moth (*Deilemera antinorii*) he observed to be covered with little yellowish spheres so very like Braconid cocoons that he kept them and watched for the parasites to emerge. It was finally discovered that the "cocoons" are spheres of hardened froth evacuated by the *Deilemera* caterpillar and then attached with silk to the outside of its cocoon. The late Mr. G. F. Leigh, of Durban, was similarly deceived by an allied East African species and threw away three or four cocoons, thinking they had been parasitized.

What interpretation can be suggested for adaptations such as these, except the selection and accumulation of small variations? And it is to be remembered that even in the mimetic butterfly of Plate XIV the associated instinct—the attitude assumed at rest—is an essential element in the resemblance, while in the construction of the false cocoons shown on Plate XV, the instinctive actions are nearly everything. It is also to be remembered that these actions are prophetic, destined for the protection of a future pupal stage. This fact is so interesting and significant in its bearing on theories of evolution that I venture to bring before you two other especially striking examples, although, of course, prophetic activities are displayed by every caterpillar in spinning its cocoon or otherwise preparing for pupation.

The larva of an African Tabanid fly (*T. biguttatus*) lives and becomes a pupa in mud which, in the dry season, is traversed by cracks so wide that they would often expose the insect in its most helpless stage. But Dr. Lamborn discovered that the maggot has prepared for this danger. It carves out a cylinder from the surrounding mud, making a line of weakness by means of a close spiral tunnel; then it enters just below the top of the cylinder and pupates in its center. The pupa when mature bores its way through the hard mud covering and the fly emerges. Dr. Lamborn was led to his discovery by observing the tops of the cylinders, of about the size of a penny, often with the pupal shell protruding from the center; also by noticing that the cracks running in all directions stopped short when they reached the cylinders. I feel sure that you will agree with the words written by Professor J. M. Baldwin when he read the account

[23] *Trans. Ent. Soc. Lond.*, vol. lxxix (pls. xiv and xv, 1931). The cost of reproduction has been borne by the Fund for Promoting the Study of Organic and Social Evolution, presented to Oxford University by my dear friend Professor James Mark Baldwin.

[24] *Trans. Ent. Soc. Lond.*, vol. lxxix., p. 397, 1931. This paper gives full references to all the observations here referred to in the description of pls. xiv and xv, as well as others necessarily omitted.

of this instinctive behavior—"As to the discovery of Lamborn, it seems *complete*—one of those rare cases of a single experience being sufficient to establish both a fact and a reason for the fact! It is beautiful."[25]

The other observation is also of especial interest, being an arresting example of the attainment of the same end by a different and unusual means. In leaving their cocoons some insects gnaw their way out, others make use of holes drilled by pupal spines, as in the last-mentioned Tabanid fly. The well-known "Puss-moth" (*Dicranura vinula*) has been shown by O. H. Latter to soften the hard cocoon with a secretion of caustic potash. Many caterpillars in spinning their cocoons make special provision for easy emergence and difficult entrance, on the reversed principle of the lobster-pot, a beautiful example being our own "Emperor Moth" (*Saturnia pavonia*). Now these preparations are made in spinning the cocoon, but the caterpillar of an Indian moth allied to our "Lappet Moth" first nearly finishes its cocoon and then deliberately bites two slits in it. As Lt.-Col. F. P. Connor[26] has written: "It was a striking fact to observe how the larva, after all but completing the cocoons, always "remembered" to destroy part of its laboriously built home by biting out two deep clefts at one end, and how the valve-like door thus made was patiently tested several times to make certain of its being of the right size, and then carefully closed on the inside with a little soft silk which would not interfere with the emergence of the imago." In testing the opening the caterpillar extended "half its body out of the cocoon to assure itself that the vent was large enough." How is it possible to apply any Lamarckian theory of inherited experience or of effort and improvement following from experience, to examples like these? The experience of ease or difficulty in emergence in the last example, of failure or success in evading enemies in the others, will come, not in the stage which made the preparation but in a later one, and should it come, the chances of handing on its lessons would be negligible. "The prime necessity for an insect, as for all animals which can not in any real sense contend with their foes, is to avoid experience of them altogether."[27] And the cocoon-making activities described above are preparations, made long beforehand, for the avoidance of experience.

I propose now to refer briefly to some of the objections which have been raised against the opinion that protective and mimetic resemblances have arisen by natural selection, and to consider alternative suggestions. Dr. Paul Vignon, in his fine and beautifully illustrated monograph[28] on the leaf-like Long-horned Grasshoppers (*Tettigoniidae*) of tropical America, comes to the conclusion that the detailed resemblance to decayed leaves or leaves apparently mined or eaten by caterpillars, is useless, his reason being that other species with the much simpler likeness to uninjured leaves are able to hold their own in the struggle with greater success, as shown by their comparative abundance. Therefore he considers the details as a "decoration" unnecessary in the life of the insect, agreeing with Brunner's theory of "Hypertely."[29] I believe, on the contrary, that the detailed resemblance to one out of many different appearances which the same object may present—*e.g.*, to a leaf gnawed into a particular shape by a caterpillar—would often mean safety to a rare, hard-pressed species but great danger to a common one; for the sharp senses of enemies would quickly detect the meaning of that one shape, and then a special search would be made for it.[30] I am sure, however, that every one will share the author's hopes for further observations on the living insects in their natural surroundings.

On the subject of the protective resemblance to leaves I can not resist the temptation to say a few

[25] *Proc. Ent. Soc. Lond.*, vol. v., p. 14, 1930. Lamborn's discovery is published in *Proc. Roy. Soc.*, B., vol. 106, p. 83, pl. v, 1930. As this address was being written a letter arrived from my friend at Fort Johnston, Nyasaland, telling me that he has just bred another Tabanid fly, at present undetermined, from a mud cylinder like that of *T. biguttatus*.

[26] *Journ. Bombay Nat. Hist. Soc.*, vol. xxvi., p. 691, 1919.

[27] The arguments in this paragraph were brought forward in the unpublished discussion "Are Acquired Characters Hereditary?" at the Manchester Meeting, September 5, 1887 (*Report*, p. 755). The later occasions on which they were developed and recorded are mentioned on p. 155, n. 1, of *Essays on Evolution*, where they are reprinted (pp. 117, 118, 154–160).

[28] *Arch. du Mus.*, 6, V, p. 57, 1931. See also his *Introduction à la Biologie Experimentale. Les êtres organisés. Activités, instincts, structures.* Encyclopédie Biologique, VIII, Paris, 1930.

[29] Professor J. M. Baldwin has kindly written the following note on a subject (recalled by Dr. Vignon's memoir) we had discussed together: "The continued lack of enthusiasm for natural selection in France seems at first glance remarkable. It seems inconsistent with the French love of logical "clearness and distinctness" given as the criteria of truth by the French philosopher Descartes, for whom his countrymen have the greatest veneration. But the tendencies shown in the work of Delage and Giard in the last generation appear still in the publications of such thinkers as Le Roy and Brunschweig. Naturally I take no account of special researches of younger biologists with which I am not familiar. The philosophical writers, at least, retain a diluted Lamarckism, somewhat hesitant, it is true, and always on the defensive. It is part of the vitalism expressed by Bergson in the terms 'élan vital' and 'évolution créatrice.' The positivism of Auguste Comte is still completely demoded, except in the sociological work of Durkheim and Lévy Bruhl, in which the question of the method of biological evolution has no place. The revolt against Bergsonian vitalism in the intellectual world has been directed against its mysticism, but has not extended itself to questions of biology."

[30] *Proc. Ent. Soc. Lond.*, p. cxlv, 1924.

words about W. J. Kaye's discovery of the part played by the dead-leaf-like under surface of the tropical American butterfly *Protogonius*.[31] The upper side of this butterfly roughly resembles the conspicuous warning pattern of the predominant mimetic association of its locality, changing when the pattern changes as we pass from one area to another—always a mimic although always a poor one. At rest, with folded wings, the resemblance to a dead leaf is perfect. Now Kaye observed that when the open wings of these butterflies were seen from below against the sky the appearance was that of the upper surface, so that at first he thought they must be flying upside down. When, however, he examined them he found that the apparently opaque dead-leaf-like under side was completely overwhelmed by the stronger contrasts of the upper surface. The wings of *Protogonius* were shown in this section at Liverpool in 1923, when a friend who does not greatly favor an interpretation based on natural selection, pointed out rather triumphantly that the dark and the light parts of the two patterns correspond respectively. But this is precisely the kind of result which affords proof of evolution by selection. The two patterns certainly have a common plan, but by stippling here, softening there, and the addition of delicate tints in streaks and washes, the conspicuous, strongly contrasted mimetic pattern of the upper surface is replaced on the under by a beautiful and detailed likeness to a dead leaf.

Before considering the objections to the theory of mimicry it is necessary to devote a little time to Fritz Müller's interpretation of the resemblances which Bates was unable to explain. His difficulty was caused by the remarkably detailed likeness between many species in the two groups which he called *Danaoid* and *Acraeoid Heliconidae,* groups really widely separated and now known respectively as the *Ithomiinae* and the *Heliconinae,* both conspicuous and distasteful, and providing models for other butterflies and moths, yet often mimicking each other, the *Heliconinae* being commonly mimetic, the *Ithomiinae* rarely. Bates was referring to these resemblances in the following sentence: "Not only, however, are *Heliconidae* [*viz.,* both the *Danaoid* and *Acraeoid* groups] the objects selected for imitation; some of them are themselves the imitators; in other words, they counterfeit each other, and this to a considerable extent."[32] The theory of mimicry which bears Fritz Müller's name was suggested by him in 1879.[33] Briefly, the theory rests on the advantage of a combined advertisement in saving lives that would have been lost in the experimental attacks of enemies. Batesian mimicry, on the other hand, rests on the advantage of a false advertisement, leading a palatable insect to escape because mistaken for a distasteful one. Much controversy has arisen over the mathematical aspect of the problem, but this can not be considered on the present occasion. I have been led to believe that Müllerian mimicry is more important than Batesian because models and mimics are so commonly found in the same presumably distasteful group, and because the resemblances which were not explained by Bates' theory are so much commoner than he supposed. Thus the distasteful Heliconine butterflies, among which he recognized mimics of the Ithomiines, are also themselves divided into groups, of which one mimics the other so perfectly that the real difference was for many years unsuspected.[34] And this is equally true but far more striking in the Heliconine mimics of Ithomiines because the patterns are very elaborate, so much so indeed that these mimics are among the most remarkable in the world.

One or two more examples which suggest the prevalence of Müllerian mimicry may be mentioned. The intricacies of systematics being unnecessary for the appreciation of the argument, I propose to reduce them to a minimum. The "White Admirals" of the northern belt have been separated into different genera, but they are all nearly related with very similar life-histories. They are, except when modified by mimicry, dark butterflies with conspicuous white markings displayed in a sailing flight. In Europe they are mimicked by the female of our "Purple Emperor" and other butterflies, including a black-and-white invader (*Neptis*) from the south, this latter butterfly belonging to a group which itself provides models for mimicry. Any doubt about the mimetic resemblance of the female Emperor is dispelled when we remember that numerous allies of these Admirals in tropical America (*Adelpha*) are there mimicked by females of butterflies allied to the Emperors (*Chlorippe*). In North America some of the White Admirals possess the black-and-white pattern, one (*astyanax*) is a mimic of a distasteful Swallowtail (*P. philenor*), but at the same time is considered by Scudder to be the model for a female Fritillary. Others are beautiful imitations of Danaine invaders from the Old World, and the mimicry is so recent that one of these (*archippus*) and also *astyanax* can breed with their black-and-white ancestor (*arthemis*)

[31] *Ibid.,* p. xcviii, 1922; p. xxxvii, 1923. See also p. xl for Lord Rayleigh's notes on the optical interpretation.

[32] *Ibid.,* p. 507.

[33] *Kosmos.* The paper was at once translated by Meldola and published in the *Proc. Ent. Soc. Lond.,* p. xx, 1879. A preliminary paper containing everything essential to his theory of mimicry was published by Fritz Müller in *Zool. Anzeiger* (Carus), I, pp. 54, 55, 1878. Translation by E. A. Elliott in *Proc. Ent. Soc. Lond.,* p. xxii, 1915.

[34] W. J. Kaye in *Proc. Ent. Soc. Lond.,* p. xiv, 1907; H. Eltringham in *Ibid., Trans.,* p. 101, pls. XI–XVII, 1916.

and produce intermediate offspring.[35] There is finally a species (*lorquini*) on the Pacific Coast which is a mimic of a southern invader (*californica*) closely related to the tropical American Adelphas. This last, too, is of especial interest because the mimicry is only developed where the two butterflies overlap, and dies away to the north and east where *lorquini* spreads beyond the range of its model.[36]

We have seen that the Adelphas of the New World are models, but the corresponding African representatives of the White Admirals, the Pseudacraeas, are, with one or two exceptions, mimics, resembling certain Acraeine butterflies conspicuous in their localities, and in two instances Danaines, one of the models being *D. chrysippus.*

These tangled relationships of models and mimics in the great group of "White Admirals" and their allies are in my opinion impossible to reconcile with the Batesian theory, but in every way consistent with the Müllerian. It will be necessary to return to the African Pseudacraeas, a little later, but I will first mention one more example which, I believe, supports the same conclusion.

During the meeting of the Association at Toronto in 1897, I met Dr. Gustav Gilson, of Brussels, who was about to visit Fiji and very kindly promised to collect butterflies for me. Among the specimens received were two species of *Euploea,* one of which had obviously been modified in mimicry of the other. Now the Euploeas are among the most distasteful and most commonly mimicked butterflies in the world, and I became extremely anxious to obtain more specimens from different islands of the Fijian and other groups. Finally, after waiting more than twenty years I received a very kind letter from Mr. Hubert W. Simmonds, who had heard of my wants, which he then proceeded to supply most generously and efficiently, enabling me to study this and other equally interesting problems. There is not now the possibility of describing the results,[37] but I will mention, as bearing on the Müllerian theory, that the mimicking *Euploea* of Fiji is found to be a model on Wallis Island, and the model of Fiji its mimic; while on Fortuna Island, 150 miles away, the Wallis model is absent, while the other *Euploea* is present, but unmodified by mimicry.

[35] *Proc. Ent. Soc. Lond.*, p. xciv, 1916. Abstract of W. L. W. Field's three valuable papers in *Psyche.*

[36] *Trans. Ent. Soc. Lond.*, p. 447, 1908. *Lorquini* and its model are represented on pl. XXV, which also shows a reciprocal approach of the latter towards its mimic. Owing to the kindness of Commander C. M. Dammers I have been provided with Mimicry in the N. American "White Admirals," here very briefly summarized, is the opportunity of renewing this investigation with far more extensive material, considered in detail in the above paper and in *Proc. Acad. Nat. Sci. Philadelphia,* p. 161, January, 1914.

[37] A full description appears in *Trans. Ent. Soc. Lond.*, p. 564, pls. XXIX–LIII, 1923.

The year before Fritz Müller proposed his theory of mimicry in 1878, he published a paper which was probably the preparation for it—the paper in which he explained the meaning of the gregarious habit in certain distasteful insects. Thus, writing of the dull brown caterpillars of two American butterflies, he suggested that the social habits "which lead them to congregate in large numbers make up for their want of color, since their offensive odor then gives timely warning to an approaching enemy."[38] This interpretation has recently been adopted for the interesting and hitherto puzzling habits of *Heliconius charithonia,* which collects into crowded groups on bare twigs in the evening, as was first recorded by Philip Gosse in Jamaica in 1851 and since then by numerous observers. *H. charithonia,* which belongs to the distasteful Heliconines referred to on page 354, and is itself mimicked by other butterflies,[39] has been carefully studied by Dr. F. M. Jones, and its gregarious habits described in detail in his paper "The Sleeping Heliconias of Florida."[40] He here suggests that the warning characters may be rendered more effective at night "by the close proximity of large numbers, under these conditions readily recognizable by form, color, or *scent,* as identical in kind and inedible; for thus the injury or destruction of one of the group might conceivably work for the protection of the many." It may be added that the choice of leafless twigs for a resting-place obviously enhances the conspicuousness of the assemblage.

We must now return to one of the African Pseudacraeas, a wide-ranging species (the Linnean *eurytus*) which subdivides into a number of local forms mimicking the local Acraeine models. This species is represented in Uganda by a race (*hobleyi*) so significant in its bearing on evolution by selection that it is necessary to give a little time to it. *Eurytus hobleyi* appears in three forms—two, with male and female alike, mimicking two Acraeine butterflies (*Planema*) differing in color but also with male and female alike. The third, with male and female very different, mimics a third *Planema,* the sexes resembling the corresponding sexes of the model. Now these four mimetic forms —for the male and female of the last were believed to be of different species—have all been described and named as distinct, and there was great astonishment and even some incredulity when Dr. Karl Jordan, relying on structural features, pronounced them to be one. After many efforts to test this conclusion by

[38] *Kosmos,* December, 1877. Translation by Professor R. Meldola in *Proc. Ent. Soc. Lond.*, pp. vi, vii, 1878.

[39] W. J. Kaye in *Proc. Ent. Soc. Lond.*, vol. v, p. 89, 1930.

[40] "Natural History," *Journ. American Mus. Nat. Hist.*, vol. xxx., p. 635. A full abstract, with references to other observations, in *Proc. Ent. Soc. Lond.*, vol. vi., p. 4, 1931.

breeding, a cable was received from Dr. Hale Carpenter on Bugalla Island (N.W. Victoria Nyanza), giving the information which proved that Dr. Jordan was right.

Many other families were then bred by Dr. Carpenter, and these, with his captured specimens, showed that, in the islands, the three forms run into each other, being connected by an abundance of transitional varieties which are extremely rare on the adjacent mainland of Uganda. The significance of this is obvious when it is realized that the models are for some unknown reason comparatively scarce on the islands.[41]

The same conclusion is enforced by the wonderful families of *Papilio dardanus,* bred by Dr. V. G. L. van Someren and Canon K. St. Aubyn Rogers from localities near Nairobi. Now in the families of this butterfly that have been bred in other parts of Africa—by Carpenter in Uganda, by Lamborn on the W. and E. coasts, by Swynnerton in S. E. Rhodesia, and by Leigh in Natal, the mimetic forms of the females are sharply separated—a fact which led to the mistaken conclusion that these patterns appeared fully formed and complete, each as a single variation. But in the Nairobi families, as in the Pseudacraeas of the Uganda islands, all kinds of transitional forms appear and, most striking of all, the *trophonius* female mimicking the Danaine *D. chrysippus* has not been bred but only its primitive ancestor *lamborni,* and this has appeared often, although very rare in other localities. Here, too, the same explanation holds, for Dr. van Someren and Canon Rogers have observed that for some cause, perhaps the elevation, the Danaine models are much scarcer than their mimics, and can not be supposed to influence the selective elimination as in other parts.

These two striking examples offer, I believe, convincing evidence of the power of selection in the evolution and preservation of mimetic patterns; also that the evolution was by small variational steps. The remarkable families of *Hypolimnas bolina,* bred by Mr. H. W. Simmonds in Fiji, supply further evidence in favor of this last conclusion.[42]

Admitting, as claimed and, I believe, proved above, that selection is essential for the evolution of mimicry, nevertheless the abundance of mimetic forms when their models are rare, and still more when they are absent altogether, does make it difficult to feel confident that natural selection, in its accepted sense of survival of the fittest, has always been the cause. This doubt was first raised in my mind by the consideration of the Oriental butterfly, *Papilio polytes,* and led to the belief that in this and probably other predominant species the absence of the model finally leads to the disappearance of the mimetic pattern, "although the species that bore it remains as abundant as before. The survival or extinction of the species is not affected: all that has happened is the survival or extinction of a pattern borne by a certain proportion of the individuals of the species. When these disappear, other individuals with another pattern take their place."[43] For this process Professor Julian Huxley has suggested the term "intraspecific selection," to be contrasted with natural selection which ensures the survival of the species in its organic environment and, therefore, in a struggle which is *inter*specific. Mr. A. J. Nicholson[44] has independently proposed a similar hypothesis but seeks to carry it much further, so as to cover all examples of mimicry and protective resemblance. My reasons for disagreeing with this opinion are given in the above-mentioned paper on intraspecific selection.

Certain criticisms which have been brought against the theory of mimicry have followed from the erroneous assumption that the warning colors of the models imply complete immunity from attack, even by parasites, an assumption unfortunately made by Haase in his important and valuable work.[45] Of course no species enjoys absolute immunity, and if it did so the enjoyment would be brief, for it would rapidly destroy its own means of existence. Furthermore we know, as my friend Dr. Hale Carpenter showed to this section at Birmingham in 1913, that the species distasteful to insectivorous animals (although not by any means entirely free from this danger) are specially subject to parasitic attack. At the same city, in 1886, I brought before this section the theory of a compensating principle[46] which would check the increase of distasteful insects; for when other food became scarce they too would be devoured, and then their conspicuous appearance and slow movements would lead to their easy capture. This theory was supported by experiments which proved that insectivorous animals, when they are sufficiently hungry, will in fact eat the distasteful species, although often with signs of disgust. The experimental method, necessarily employed in testing the above-mentioned hypothesis, and also of much value when other evidence is wanting, was criticized by W. L. McAtee in a paper published in 1912.[47] I

[41] *Trans. Ent. Soc. Lond.,* p. 706, 1912; p. 606, 1913; p. 84, 1920; p. 469, 1923.

[42] *Trans. Ent. Soc. Lond.,* pls. XLV–LIII, 1923.

[43] Poulton in *Proc. Zool. Soc. Lond.,* p. 1037, 1928. The term "Intraspecific Selection" was introduced in this paper, which also quotes the essential passages from the paper (*Bedrock,* vol. ii., No. 3, p. 295, October, 1913, in which the hypothesis was first suggested.

[44] "A New Theory of Mimicry in Insects," *Australian Zoologist,* vol. v., pt. 1, p. 10, pls. I–XIV, November, 1927.

[45] *Untersuchungen über die Mimicry,* Stuttgart, 1891–3.

[46] Considered in detail in a paper published in the following year: *Proc. Zool. Soc. Lond.,* p. 191, 1887.

[47] "The Experimental Method of Testing the Efficiency of Warning and Cryptic Coloration in Protecting Ani-

was probably mistaken in not at once writing a detailed reply to these criticisms, which were not only directed against the conclusions drawn from experimental feeding, but also against other conclusions on which the theory of mimicry is founded. On the other hand, there was much to be said for waiting until far more evidence had been collected, and now, after nearly twenty years, it may be fairly maintained that such evidence has been forthcoming.

In the first place it may be granted that, apart from its special value as a test, the experimental method is, in this investigation, very inferior to the direct observation of attacks made upon insects by birds and other enemies in their natural surroundings and undisturbed. It is impossible on this occasion to attempt to give any account of the great number of such records which have accumulated since the appearance of McAtee's criticisms. I will, however, mention two sets of observations. In 1927 Dr. Hale Carpenter kindly sent me the wings of Uganda hawkmoths—twenty-one specimens and seven species—found on the floor of a rest-house where they had been dropped by bats hanging in the roof. This interesting observation suggested an examination of moths' wings dropped by British bats—an ideal means for discovering their true preferences. Wings representing 1,328 moths were collected in sheltered places frequented by bats—probably always by the long-eared bat (*Plecotus auritus*). All the specimens except sixteen belonged to species with protective (procryptic) colors and habits. The exceptions included relatively conspicuous species shown by experiments on other animals to be rather distasteful (sometimes accepted, sometimes refused), also species of which the palatability is unknown. Not a single specimen with a striking warning pattern was present.[48]

The second series of observations is now being undertaken at Vineyard Haven, Massachusetts, by Dr. Frank Morton Jones, who has kindly written to me, explaining the details of the excellent methods he is employing. Insects, chiefly Lepidoptera and Coleoptera, of known species, are exposed on a feeding-tray in a favorable locality and the visits of birds watched at a distance through field-glasses. Thus on June 27 last, of 63 beetles belonging to nine species placed on the tray, there remained in 30 minutes, after 22 bird-visits (three species), 15 beetles of one red-and-black species. Thus 48 beetles of eight species were taken and all the 15 of the ninth species were untouched. Dr. F. M. Jones is also attempting to form a scale of distastefulness by observing the reactions of a common species of ant to the insects employed in the experiments.

One of the chief criticisms made by McAtee, and made in this country also, was the insufficiency of the evidence that butterflies are commonly attacked by birds, the enemies believed to be the selective agents in the evolution of mimicry. McAtee, in support of this objection, quoted the results of an American agricultural investigation in which an enormous number of birds' stomachs had been examined and remains of butterflies found in only an insignificant proportion. This criticism had been in great part met beforehand in a paper[49] published by Sir Guy Marshall in 1909; and more recently C. F. M. Swynnerton[50] and W. A. Lamborn[51] have conclusively shown that butterflies are rapidly reduced to such minute fragments in a bird's digestive tract that examination with the compound microscope is necessary in order to obtain trustworthy results. Furthermore, it is only in recent years that the imprint of a bird's beak on a butterfly's wing has been noticed; but now that attention has been directed to this evidence it is found to be quite common—a good example of the fertile but, for the uncritical, the dangerous principle that an observer only finds what he looks for.

It is possible that the mistaken assumption of the immunity of models has played a part in prompting Dr. Bequaert's interesting paper on the enemies of ants.[52] Admitting the existence of these enemies and the certainty that the list will be immensely lengthened, it still remains that ants are "the most powerful of insects, ever-present and aggressive in all habitable parts of the earth."[53] And it is difficult to reconcile with Dr. Bequaert's opinion that they are valueless as models, the fact that my friend Mr. H. St. J. K. Donisthorpe has, since 1891, discovered, in the nests of British ants, "204 species of insects, spiders and mites new to the country, including 74 new to science. Of these guests 28 are mimics of ants. . . . He has also recorded 34 mimics living independently of ants."[54] I believe that most naturalists will conclude

mals from their Enemies.'' *Proc. Acad. Nat. Sci. Philadelphia*, pp. 281–364, 1912.

[48] *Proc. Zool. Soc. Lond.*, Pt. 2, p. 277, 1929. The interesting plates I–III in *Proc. Ent. Soc. Lond.*, vol. vi., 1931, provide evidence of the same value as that furnished by the rejected wings. They show young cuckoos being fed by fosterers with ''Small Garden White'' butterflies, in Sussex, photographed by Mr. H. F. Chittenden, and Cumberland, by Mr. A. G. Britten. Dr. J. G. Myers' observations on the insect food of the Coati (*Nasua*) were also in large part made under natural conditions (*Ibid.*, vol. v., p. 69, 1930). See also Capt. C. R. S. Pitman's experiments on an African Lemur (*Periodicticus*) on p. 91, and in vol. iv., p. 90, 1929.

[49] *Trans. Ent. Soc. Lond.*, p. 329, 1909. See especially pp. 336, 337.

[50] *Linn. Soc. Journ. Zool.*, xxiii, p. 203, 1919. Abstract in *Proc. Ent. Soc. Lond.*, p. xxxii., 1915.

[51] *Proc. Ent. Soc. Lond.*, p. xxvi., 1920.

[52] *Bull. Am. Mus. Nat. Hist.*, vol. xlv., p. 271, New York, 1922.

[53] *Zoolog. Anz.* (Wasmann-Festband), p. 86, 1929.

[54] *Ibid.*, p. 84. Quoted from ''Guests of British Ants,'' Donisthorpe, London, 1927. The numbers have been brought up to date with the kind help of the author.

from these discoveries in Great Britain and Ireland, and from the remarkable profusion of ant-mimics and ant-associates in the tropics, that in spite of all attacks, these insects possess in the highest degree the qualities which render them valuable as models.

I now propose to direct your attention to certain experiments and observations which throw light on the brain and senses of vertebrate enemies of insects. Although the experiments brought before this section at Manchester in 1887 were few and single, I believe, and I still believe, they were crucial, and proved beyond doubt that the mind and memory of even a reptilian enemy—and of course far more probably an avian enemy—are such as we should expect to find in the selective agents which have brought about the evolution of mimicry in insects. I refer to the chameleon, which, after rejecting a bee which it had captured the moment after its introduction into the cage—after this single experience—would never touch another, although offered from time to time during many months; also to the lizard, which approached a hornet-like clearwing moth with the utmost circumspection, and in finally seizing it kept as far as possible away from the supposed sting, and then, evidently realizing from the texture that the insect was not a wasp or hornet, proceeded to eat it without further caution, and a few days later recognized another at sight and instantly devoured it.

It is not to be hoped that these experiments will carry the same conviction to those who only hear of the results and did not see them; but in recent years other evidence throwing much light on the faculties and behavior of birds has been steadily accumulating.[55]

The conclusions of the distinguished ornithologists, E. C. Stuart Baker and Rev. F. C. R. Jourdain, that the resemblance of cuckoos' eggs to those of the fosterers has been evolved through the selective destruction of the less like by the birds which would otherwise have been victimized, obviously bear closely on the development of a mimetic pattern in insects. The similarity between the two selective processes, both leading to a superficial likeness which changes with the geographical changes of the models, was made the subject of the address to the Entomological Society in January, 1926, and led to the last words addressed to me, although indirectly, by William Bateson, the distinguished ex-president of this section and of the association, whose loss we all deplore. Not many days before his death he was present at the meeting and told a mutual friend that he was much interested in the observations and that they were quite new to him.

Evidence of a different kind, but probably very significant, is provided by the well-known African Honey Guide (*Indicator*) which directs man to a bee's nest and is repaid by a meal on the scattered larvæ. My friend, Dr. Neave, has told me that this bird, when insufficient attention is paid to its directions, becomes so noisy that game is disturbed, and he found it necessary, on hunting expeditions, to detail a couple of natives to follow the Guide and keep it quiet. How far the behavior of the bird is instinctive and how far intelligent is, I believe, unknown, but it is impossible to imagine a more fascinating subject for investigation.

Of more importance, because common to many species and known to exist in all the great tropical areas, is the nesting association between birds and the most formidable of insects—wasps and hornets; also with ants and termites. In the association with wasps naturalists have definitely stated that the birds begin to build close to the already constructed pendent comb of a wasp, while their nests are actually excavated in the termite-mounds and in the huge nests of tree-ants. This most interesting and significant behavior has been summarized for tropical America by J. G. Myers, who has confirmed the older records by his own observations and has also been led to the startling conclusion that at least one wasp tends regularly to make its nest besides the colonies of a tree-ant (*Azteca*). Notes on these associations in Africa have been written by A. Loveridge and V. G. L. van Someren; in India by E. C. Stuart Baker; in Australia by W. B. Alexander.[56]

The behavior briefly described in the last two paragraphs proves, I believe, that birds possess a brain and sense-organs such as would lead them, in seeking their food, to associate the qualities, favorable or unfavorable, with the appearance, and to remember and apply their experience, in fact precisely the powers required by a selective agent in building up a mimetic pattern.

To the above evidence may be added two examples of bird behavior in our own country. The cocoon of the common "Lackey Moth" is thick on the exposed surface but thin where it is spun on to a leaf. Birds have discovered this and peck a hole through the leaf and thin wall in order to abstract the chrysalis.[57] Many naturalists have observed that birds, although they frequently peck their way into the center of "bullet-galls" (often but erroneously called "oak-apples"), never do so when the enclosed insect has emerged, being doubtless guided by the sight of the small round hole or by tapping with the bill.[58]

What other hypotheses have been suggested by those

[55] Nearly all these observations are recorded or quoted with full references in the Proceedings of the Entomological Society of London in recent years, and will be easily traced.

[56] *Proc. Ent. Soc. Lond.*, vol. iv., p. 80, (America) 1929; p. 88 (Africa); p. 89 (India); vol. v., p. 111 (Australia) 1930; vol. vi., p. 34 (India) 1931.

[57] Observed by A. H. Hamm. *Ibid.*, p. xv., 1902.

[58] *Ibid.*, vol. iii., p. 50, 1928; vol. iv., p. 10, 1929.

who reject evolution by natural selection as the explanation of mimicry and allied adaptations? Some naturalists believe that the resemblances in question are accidental and of no biological significance. This opinion, although defended by such an eminent entomologist as Professor Handlirsch,[59] is not likely to be held by any one who has seriously considered examples such as those brought before you to-day, or has studied the geographical distribution of mimetic associations. Chance resemblances are, of course, bound to occur among the immense number of butterfly patterns throughout the world, but these will be as frequently found between the species of different countries as between those of the same country. Such truly chance likenesses in patterns have been examined by my friend, Dr. F. A. Dixey,[60] and have been shown to be relatively few and only to exist at all when the patterns are relatively simple. The distinguished mathematician, the late Professor Study, of Bonn, who was deeply interested in mimicry, has shown, in two of his last papers, the impossibility of an explanation based upon chance resemblance, and I believe that the same conclusion will be reached by any one who reads the chapter on mimicry in Dr. R. A. Fisher's recent work.

The view has sometimes been held that mimetic resemblances are due to model and mimic independently passing through the same stage of evolution, either as a whole or in the mimetic features only; or, as Darwin once suggested, "that the process probably commenced long ago between forms not widely dissimilar in color.[61] I remember, at the Leeds meeting in 1890, when Professor Patrick Geddes suggested the former interpretation, that the late Lord Rayleigh remarked, "How would you apply your explanation to the resemblance of insects to bark, or twigs, or leaves?"[62] It is strange that this fatal objection did not occur to Darwin, for Bates himself in the great paper had written: "I believe . . . that the specific mimetic analogies exhibited in connection with the *Heliconidæ* are adaptations—phenomena of precisely the same nature as those in which insects and other beings are assimilated in superficial appearance to the vegetable or inorganic substance on which, or amongst which, they live. The likeness of a beetle or a lizard to the bark of the tree on which it crawls can not be explained as an identical result produced by a common cause acting on the tree and the animal."[63]

Before concluding, a few lines must be devoted to recent work on sexual selection, first briefly introduced as a factor in evolution by Darwin in the Joint Essay. Nothing would have interested and pleased him more than discoveries which, following the splendid pioneer work of Fritz Müller, have been made in the epigamic structures and behavior of insects—the extensive observations on the scents of male butterflies, by Dixey and Longstaff, and on their scent-scales by Dixey; the structure and use in courtship of the scent-brushes of male Danaine butterflies, by Eltringham, Lamborn and Hale Carpenter; the extraordinary brushes protruded from the back of the head by the males of *Hydroptila* (Trichoptera), by M. E. Mosely and Eltringham; the courtship of Empid flies, including the spinning of a cocoon as a wedding gift by the male *Hilara,* by Hamm and Eltringham;[64] the fertilization of orchids (*Ophrys*) by male bees (*Andrena*) which, emerging before the other sex, are attracted by female-like appearances, and probably scent, of the flowers, by Pouyanne, confirmed by M. J. Godfrey and by Mrs. Coleman, who has observed the fertilization of an Australian orchid (*Cryptostylis*) by a male Ichneumonid (*Lissopimpla*), similarly attracted to the flower.

On two occasions I have been present when the late Lord Balfour expressed his opinion on the theories of evolution we have been considering to-day, and I am sure that naturalists will be glad to hear the conclusions reached by his keen and penetrating intellect on subjects in which, although without the time, or indeed the inclination to probe far into details, he took the keenest interest. We know that, even before he went to Cambridge in 1866, he had read and admired the "Origin," and we have been told by his nephew, Lord Rayleigh, of his "extraordinary faculty for getting hold of the essentials of a subject without apparently feeling the need for systematic study.[65]

Over forty years ago, when the results of Weismann's researches were extinguishing the Lamarckian element which had been added to the Darwin-Wallace theory, I heard Lord Balfour say that to him, as a student of philosophy, the new teachings on the scope of heredity were more interesting than the old. Again, in 1927, a few months before his eightieth birthday and before he began to dictate the charming

[59] *Handbuch der Entomologie.*

[60] *Proc. Ent. Soc. Lond.,* p. lx., 1913. As regards chance likeness in form, Bates wrote in his great paper (p. 514 n.): "Some orders of insects contain an almost infinite variety of forms, and it will not be wonderful, therefore, if species here and there be found to resemble each other, although inhabiting opposite parts of the earth, and belonging to widely different families. Such analogies are accidental, and can have nothing at all to do with the evidently intentional system of resemblances, carried on from place to place, which I have discussed."

[61] *Essays on Evolution,* p. 233 n.

[62] *Proc. Ent. Soc. London.,* p. xcv., 1925–26.

[63] *Ibid.,* p. 508.

[64] *Ent. Monthly Mag.,* p. 177, 1913; *Proc. Roy. Soc.,* B., vol. cii., p. 327, 1928. All the other observations are recorded, with full references to earlier publications, in the *Trans.* or *Proc. Ent. Soc. Lond.*

[65] *Proc. Roy. Soc.* B., vol. 107, p. viii., 1930.

but too brief "Chapters of an Autobiography," he said that, looking back, he was impressed by the fact that nothing suggested in later years had replaced or modified the Darwinian theory of evolution.

And now in conclusion, speaking at the close of the second half-century of our society's life, and speaking as one who owes more than he can express to the kindness and help received at these meetings, I can not do better than remind you of prophetic words spoken at Oxford in 1832. Professor Adam Sedgwick, responding after his nomination as president at Cambridge in the following year, said that the work of the association at the meeting which had just been held could not but tend "to engender mutual friendship, mutual forbearance, mutual kindness and confidence"; and, for the future, "he looked forward with full assurance to the happy results of this union between men of similar sentiments and similar pursuits, who possess one common object—the improvement of mankind by the promotion of truth."

SCIENTIFIC EVENTS

THE INTERNATIONAL GEOLOGICAL EXPEDITION

AN international expedition under the sponsorship of Princeton University will make a concentrated study next winter of the geological structure of the West Indies, it was recently announced by Professor Richard M. Field, of Princeton University, director of the expedition.

The U. S. Navy is cooperating in the project and will place a submarine at the disposal of the expedition. The submarine will assist the investigators in obtaining as nearly stable conditions as possible for under-water gravity tests. The U. S. Coast and Geodetic Survey, the Royal Society of Great Britain and the National Research Council are other national organizations cooperating with Princeton University in the expedition.

The data which the expedition will obtain during its ten weeks' stay in the West Indies are expected not only to aid in determining the relative stability of the islands and the manner in which they have been formed, but also to throw further light on the origin of the major inequalities on the earth's surface, particularly the origin of folding and faulted mountain ranges.

About 5,000 miles of submarine profiles will be measured and 30 or 40 gravity-at-sea stations will be established. The submarine will be used in this phase of the expedition's work. The new "three-pendulum" apparatus, which is the latest device for determining the difference in gravity at different points on the surface of the earth, will be used in the work of "weighing" the islands and the "deeps." The data to be obtained may also be of assistance in determining the location of earthquakes.

Land gravity stations will be established by the U. S. Coast and Geodetic Survey with the help of Mr. Hugh Matheson, of Miami, Florida. The plans also call for the drilling of bore-holes to determine the structure of the islands.

Soundings and charts which the expedition will make will be of assistance to ships navigating in the West Indian waters in the future. The expedition will begin work early in February.

The personnel of the advisory staff and of the expedition is as follows:

Navigation: Rear-Admiral W. R. Gherardi, chief hydrographer, U. S. Navy; Hugh Matheson, Miami, Florida.

Geophysics: Rear-Admiral Gherardi; Dr. William Bowie, chief, U. S. Geodetic Survey; Dr. F. Vening Meinesz, Geodetic Survey of the Netherlands; Dr. F. E. Wright, U. S. Geophysical Laboratory; George W. Littlehales, hydrographic department, U. S. Navy.

Tectonics or mountain building: Dr. Arthur Keith, U. S. Geological Survey; Professor E. B. Bailey, chairman of the department of geology of the University of Glasgow; Professor Owen Thomas Jones, chairman of the department of geology, Trinity College, Cambridge, England; Professor R. T. Chamberlin, chairman of the department of geology of the University of Chicago; Professor Walter H. Bucher, professor of geology at the University of Cincinnati; Professor W. T. Thom, associate professor of geology at Princeton University, senior geologist, U. S. Geological Survey, and chairman of the petroleum committee of the National Research Council.

Oceanology: Professor Edwin Grant Conklin, chairman of the department of biology of Princeton University; Dr. Charles Fish, director of the Buffalo Museum of Science; Professor Ulric Dahlgren, professor of biology at Princeton University.

Sedimentation: Professor Alexander Hamilton Phillips, chairman of the department of geology of Princeton University; Professor Richard M. Field, associate professor of geology at Princeton University and director of the International Summer School of Geology; Ernest Dixon, of the Geological Survey of Great Britain; Maurice Black, fellow of Trinity College, Cambridge, England; Dr. Edward M. Kindle, chief of the division of paleontology, Geological Survey of Canada; Professor John Sandidge, of the department of geology of Princeton University.

Marine Bacteriology: Dr. Selman A. Waksman, microbiologist, State of New Jersey Agricultural Experimental Station, and associate professor of microbiology at Rutgers University.