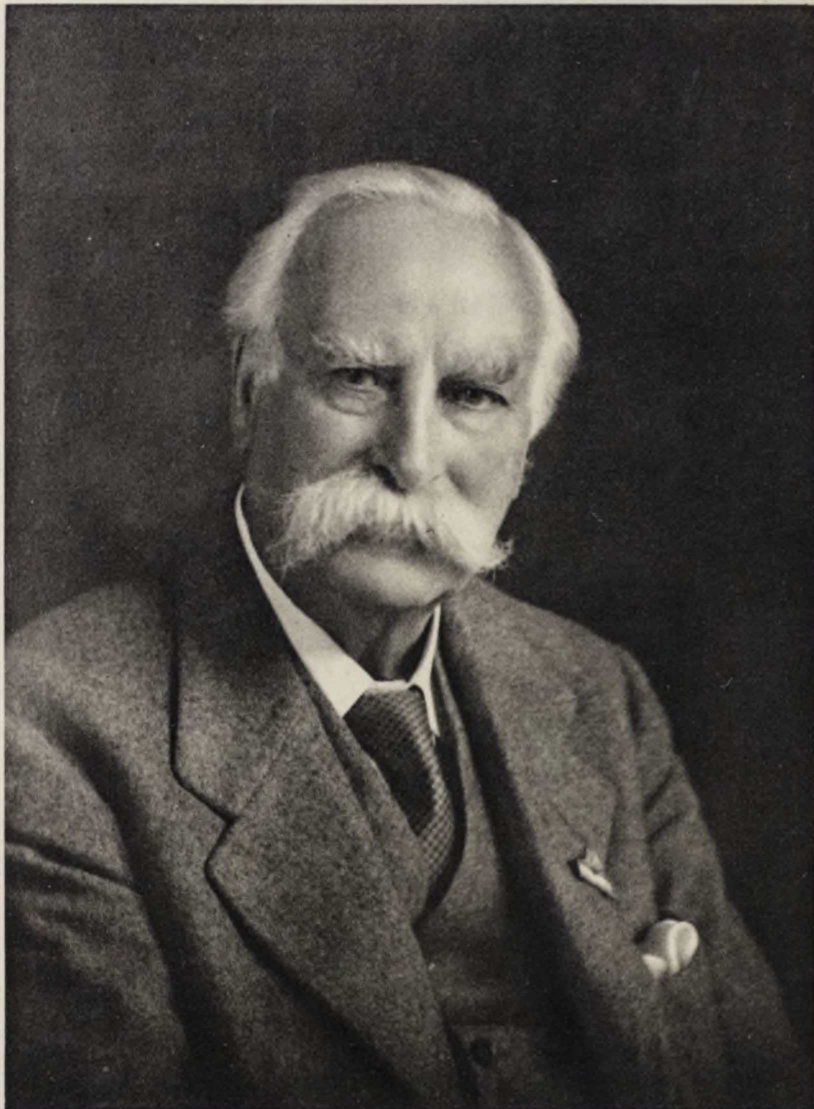

E. B. Poulton.

EDWARD BAGNALL POULTON

1856–1943

Edward Bagnall Poulton, who died on 20 November 1943, was born at Reading on 27 January 1856. His father, William Ford Poulton, an architect, was a man of great industry and energy: his mother, 'simply for the love of the work set herself to write a large volume on the history of England'.

Edward considered that his love of science was inherited from his father's family. Before he was ten he had been to two boarding schools of which he wrote, 'the memories that remain are of punishments only and the broad principle that every natural inclination was wrong and dangerous. . . . A few months before my tenth birthday I was sent, in the autumn of 1865, to my third school' newly opened by Mr W. M. Watson at Oakley House, Reading, at which the pupils were chiefly sons of Nonconformists. He spoke of the seven years spent there as a boarder as 'a long dreary interval in a happy life'. There was little regular teaching of science, and Poulton's comment was: 'Being interested in science of all kinds, and kept very much alone in this section of my work, it is probable that the puzzling out of difficulties in books and in the little laboratory was a valuable discipline'. However, towards the end of his schooldays he benefited much by the teaching of J. N. Gordon, a Demy of Magdalen, who encouraged him to enter for a Science Demyship in 1872: he was unsuccessful, but 'learnt a great deal about the proper books to read'. At the end of 1872 he began work in his father's office: his mother, however, always longed for him to go to Oxford. The experience in the office improved his natural gift for drawing but 'my heart was in science, especially in zoology, and late at night I used to read the books of which I had heard at the Magdalen examination'.

This was found out, and his father agreed to his trying for a scholarship at Oxford in the autumn. Thus it came about that in the summer of 1873 he went over to Oxford thrice a week to work in the University Museum. Of this time he wrote: 'I attended Rolleston's lectures and at once felt the irresistible grip of his individuality. He burst in upon my life as something stupendous and magnificent . . . the shock of such a glorious surprise at the outset of life altogether stimulating and inspiring. It is the deepest debt I owe to Rolleston's memory.'

Poulton gained a scholarship at Jesus College, came into residence in 1873 and took a first class in the Honour School of Zoology in 1876, after which he held a demonstratorship until the middle of 1879. But Rolleston as a chief was very different from the brilliantly inspiring lecturer and Poulton found him hard and unsympathetic. The conditions of the demonstratorship were arduous, and the stipend small, and there was little time for research, nor did Rolleston ever suggest any.

In January 1877 Poulton was forced by pecuniary needs to work for the Burdett-Coutts scholarship in geology which brought him into touch with Professor Joseph Prestwick. He gained the scholarship in 1878 and resigned from his demonstratorship in 1879. Under Prestwick's supervision he conducted his first research on tertiary remains and it might have seemed that his foot was set on the geological ladder. Fortunately for zoology, although this geological work gave him the keenest pleasure he had the feeling all the time that he would come back to zoology. This happened in 1880 when he became lecturer to Keble College, and afterwards to Jesus College. Keble gave him a tutorship which he held until 1889 when he resigned from both college appointments in order to have more time for his own work.

Rolleston died in 1881 and H. N. Moseley was appointed in his place as Linacre Professor. Poulton found him as helpful towards research as Rolleston had been difficult, and having mentioned that he was interested in the organs of taste in mammalian tongues received the offer from Moseley of material from the Challenger Expedition. That conversation, and the gift of the material, Poulton wrote, 'did more for me than all the terms I had been with Rolleston. The start is the difficulty. After that, fresh paths lead off in every direction, bewildering in their number and in the variety of their rival fascinations.' But, as he wrote, 'although the work on lowest Mammalia gave me the greatest pleasure and interest, I felt from the first that sooner or later the passionate enthusiasm of childhood would again spring into life'. His early love for insects had been fostered by visits to the Hope Collections under the care of Professor Westwood at Oxford when preparing in 1873 for his examination. But it was the *living* insect that attracted him, and Westwood's morphological and taxonomic studies did not seem to open a path to investigation. It is amusing to note here that Westwood was not in favour of Darwinism, and warned the young man against its dangers. Fortunately the seed fell on stony ground, and Poulton became a leading exponent of Darwin's particular contribution to the theory of evolution, and by means of the very creatures which Westwood studied. The first stimulus came in 1878 when Poulton read Wallace's Essays on Natural Selection which 'aroused a lifelong delight in the facts and theories of Protective Resemblance, Warning Colours and Mimicry'. A few years later, in Meldola's translation of Weissmann's *Studies in the theory of descent* he was interested to find that some observations he had made as a boy upon the colour of the caterpillar of the 'eyed hawk moth' were in accord with Weissmann's own studies. This led him into investigations upon the colour and structure of insects, many of which bore upon more general aspects of biology, such as heredity and evolution. He therefore undertook to organize a translation of Weissmann's papers upon heredity and kindred subjects, which was published in 1889. The need of a textbook to which students of the coloration of insects could be referred led him to write, in 1890, *The Colours of Animals*, a book in which new lines of research were suggested, and it set him at once in the front line of

Darwinians. Westwood died in 1893 and Poulton was elected to the Hope Professorship of Zoology at Oxford which he held for forty years. Under his leadership this department of the University Museum became a world-renowned centre for the study of the coloration of insects, and there emanated from it a stream of correspondence with field naturalists and students of evolution by which Poulton stimulated observations and discussion.

During his tenure of the chair he wrote the book *Charles Darwin and the theory of Natural Selection* and collected together in the form of two books (*Charles Darwin and the Origin of Species* and *Essays on Evolution*) numerous essays and addresses. He also wrote a vivid account entitled *Viriamu Jones and other Oxford memories* from which numerous personal details have been quoted for this memoir. It was the hope of his friends that, on retirement, he would embody his studies in a new and comprehensive work, but when 1933 came he found himself unable to face the task, and could not break off his correspondence. 'I must do what I am impelled to do and act on what I feel are responsibilities' he replied to the present writer, who in 1934 enquired whether the eagerly anticipated work would materialize. Thus he will be known in the future by the work of younger naturalists inspired by him, and by his very numerous contributions to journals rather than as the author of authoritative tomes. For some years after his retirement he continued as before, but family bereavements aged him much, his memory faded and his powers weakened. He was interested to the last in the activities of the department for which he had done so much, and his end was easy, for he passed away quietly after a few days of increasing failure of the worn-out heart.

Many honours came to him, the first being the Presidency of the Oxford Union in 1879. Elected to the Royal Society in 1889 he served twice on the Council, was Vice-President in 1909–1910, and Darwin medallist in 1914. The Linnean Society made him President from 1912–1916, he had served thrice on the Council, twice being Vice-President: the Linnean Medal was awarded him in 1922. Entomological activities being his chief interest his association with the Entomological Society of London was prolonged and intimate: he presided over it in 1903–1904, 1925–1926, and in the centenary year 1933, when it became a Royal Society and bestowed upon him the honour, conferred upon only two other men, of election to Honorary Life President. He presided over the second International Entomological Congress at Oxford in 1912 and over the Association of Economic Biologists in 1922–1923: his long association with the British Association, in which he had presided over Section D in 1931, was crowned by his presidency at London in 1937. He gave the Romanes lecture at Oxford in 1915, and the first 'Huxley' lecture at the Royal College of Science in 1925. A Knighthood was conferred on him in 1935. The Swedish Academy of Science made him a Foreign Member and he was Commander (Class II) of the Swedish order of the Pole Star. He was Hon. LL.D., Princeton: Hon. D.Sc. of Durham, Dublin, Reading: an honorary member of the Entomological Society of Belgium, the Spanish Royal Natural History Society, and the New York Academy of Science, and was a corresponding member of the Academy of Natural Science, Philadelphia, the Boston Natural History Society and the American Entomological Society.

Such was Poulton's career: what of the man himself? The writer did not come into close personal touch with him until 1913, but his autobiographical notes reveal a most human personality of abounding vigour and joy in living interests. A big man, with penetrating blue eyes and large eyebrows and moustache, he was capable of considerable physical endurance, though he never shone at games. Walks from Oxford to Reading, a distance of twenty-eight miles, were accomplished in seven hours.

He used to ride from Reading to Oxford, for a day's work, on the high bicycle with 56-inch wheel, returning in the evening: he had ridden in the Inter-University cycle races.

He was a prominent member of the 'Union' at Oxford and was elected President in 1879: until prevented by increasing age he was a regular attendant at dining clubs in Oxford and London. Spending all his adult life at Oxford he took an active part in university affairs, served as Pro-Proctor, and on Hebdomadal Council, and was prominent in movements for the betterment of science teaching and wider outlook. The meetings of the British Association from 1881 onwards found him a regular attendant and a doughty fighter in evolutionary controversy. It was said by an old friend that he could forgive anything except disbelief in evolution [by natural selection].

Truth was sacred, and inaccurate or slipshod work roused his fierce antagonism, and he could not pass over the kind of argument which belittled the subject he was prepared to defend with all the vigour of which he was capable. The claims of the early 'Mutationists', extravagant as they seemed to him, particularly infuriated him. Yet he himself, with enthusiasm and imagination, would sometimes go further than to some seemed logically permissible, though, it may be said, his vision was often justified by subsequent work.

Without imagination much is missed in nature but even he quoted examples of his own unimaginative failure to note the significance of some minute detail which meant nothing to him at the time. This quality which made him so inspiring, was linked with lack of mathematical and statistical ability. A just criticism of some of his papers is that he did not give adequate numerical data by which to judge the real significance of the statements he made. He was content to say, for example, that butterflies of a certain area differed from their kin in another area by having a larger spot, but no measurements were given, although photographs of a few selected specimens were shown. But as regards other detail he was indefatigable: a reviewer of his book on Viriamu Jones wrote, 'We feel that the passion for scientific accuracy and detail that is everywhere displayed makes the reading somewhat forced and unnatural'. This attention to detail led Poulton to devise very complicated titles for his communications, one of which (80) is selected as an example: he liked a title to tell the whole story. Generous in disposition he saw to it that due credit was given to the authors of notes communicated by him to scientific societies, and indeed would deliberately make the most of a quite trifling observation to give encouragement to a young unknown naturalist.

The subject of help and encouragement was frequently mentioned in his obituary notices of others; and never did any one who had freely received give more freely. Like many largely generous people he had absurd foibles of economy: he rarely bought paper for his MSS., but utilized the backs of old forms and circulars or spent in the aggregate an enormous amount of time in cutting out blank areas and pasting them together. The completed MS. must often have been a nightmare to the printer, with extra tags containing additional notes gummed on the edges.

His interest in science was mainly in the living creature, its problems and reactions, and he would probably never have become such an authority had he kept to geology. Living things, as the preacher said at his funeral service, 'were God's creatures, their lives like his were sacred. He found in Nature a deep religious experience . . . if he had to kill it was always to make a sacrificial offering . . . on the altar of truth.'

Such a man is born for friendship, and Poulton had many friends. His intimacy with Viriamu Jones (first Vice-Chancellor of the University of Wales) is described in his book (133) which also gives many autobiographical details. Ray Lankester, R. Meldola, H. F. Osborn, James Mark Baldwin were intimates with whom he discussed evolutionary topics: R. C. L. Perkins was a pupil of his at Jesus College. He knew, and admired greatly, Alfred Russel Wallace and Roland Trimen.

Poulton was greatly blessed in his marriage with Emily Palmer, eldest daughter of George Palmer of Reading, who became his wife in 1881. They met when he was conducting his first geological research, and after marriage she was with him at Dowkerbottom cave. Their hospitable house at Oxford and holiday home in the Isle of Wight saw many friends, and the five children were a great happiness. But grievous happenings brought sorrows: the eldest daughter, Hilda, who married Dr E. W. Ainley Walker, died in 1917. Ronald, the second son, the famous Rugby International, was killed in France in 1915. After this sadness, when the war was over, the death by a bicycle accident of his youngest daughter Janet (Mrs C. P. Symonds) in 1919 was a grievous shock. The eldest son, Edward, after a highly successful medical career, was Physician at Guy's hospital when a functional cardiac complaint of long standing brought his life suddenly to an end in 1939: in the same year Lady Poulton died. Their second daughter, Margaret (Mrs Maxwell Garnett) alone remains. Thirteen grandchildren and six great grandchildren were a great solace to Sir Edward in his old age, and his loving nature found happiness in memories.

Poulton's writings were very many, and a selection has been made for the bibliography, grouped by subjects.

With his passion for detail it is not surprising that minute anatomy attracted him, and from 1883–1889 and again in 1894 he was engaged in histological research. He traced the evolution of taste-bulbs in the tongues of marsupials (5, 7) deriving gustatory sense organs from ordinary epithelial upgrowths.

Specialization came by modification of the covering epithelium and formation of a fold surrounding the chief sense organ. Compound filiform papillae found in *Perameles* were characteristic of marsupials, but he found indications of transition between the condition in these animals and in the Monotreme, *Ornithorhynchus*, the duck-billed platypus (6). The tongue of this has taste bulbs of peculiar form at the end of papillary processes and Poulton suggested that this exposed condition was likely to cause damage and that the circumvallate papilla of higher animals was a response to the need for protection. Studies of the hair of *Ornithorhynchus* made it desirable to obtain a very young specimen and Dr W. K. Parker kindly lent Poulton a series of sections through the head from which he made the important discovery that true teeth exist in this lowliest of mammals but never come through the gum and are replaced in the adult by horny plates (11). *Ornithorhynchus* served also as material for another study (9), in which he concluded that in the minute structure of the Graafian follicle in the ovary there is a significant difference between marsupials and monotremes, contrasting with the transition in the condition of the gustatory organs which has already been mentioned. A study of the structure and origin of hair followed (12) and from *Ornithorhynchus* he concluded that there is no essential difference in the development of a hair or feather, both being derived from reptilian scales: there is a succession of hairs in *Ornithorhynchus* forming a parallel with the shedding of scales in reptiles. Poulton pointed out that in the primitive bird *Archaeopteryx* the feathers are typically avian, but the skeleton differs profoundly from that of a typical bird. Similarly, the hair of *Ornithorhynchus* shows far less difference from that of other mammals than does its skeleton. This persistence of the epidermic characters of the class when other class characters are failing suggested a persistence beyond the limits of the class and led Poulton to believe that both feathers and hairs were, as regards essential structure, existent in the Reptilian ancestors of birds and mammals.

Two papers on the external morphology of the lepidopterous pupa (13, 14) show Poulton as a student of the evolutionary significance of degeneration. He discovered that the sex of a pupa is revealed by its external genitalia and commented on the fact that this had never been observed before. The degenerate condition of the females of certain moths had begun with the antennae and may go so far as to produce a mere helpless egg-bag. Degeneration of the wing goes further in the imago than in the pupa. An analogous condition was shown very many years later by W. A. Lamborn in the female of *Papilio dardanus*. The male has the usual 'swallow-tails' but not its mimetic female. However, Lamborn found that in the pupa of the female the outline of the wing provides a space for the ancestral tail which has ceased to exist in the imago. Degeneration of wings occurs in females of species which do not require them for obtaining food, for oviposition, or finding the males. Such females are readily found by the males in which there is compensatory hypertrophy of the antennae, so that the sedentary degenerate females can develop larger bodies and lay more eggs. The next series of researches (15–30) concerned the colours, markings and habits of caterpillars and chrysalises and revealed Poulton as an extremely observant naturalist who took a keen delight in his studies, and saw evolutionary significance in the smallest characters. Thus the oblique stripes on the sides of the Hawk-moth caterpillars are derivable from scattered pale dots, and play a part in concealment. The caudal horn is the result of fusion of paired spines. He commented on the interest of the various means of escape from cocoons and suggested that the Puss moth used a softening fluid: many years later O. Latter showed that potassium hydroxide is used.

The significance of attitude in connexion with form and colour was a point which Poulton never ceased to urge, and at an early date he discovered that the caterpillar of *Selenia illunaria* illustrates this in a very interesting way. During its last three stages the colouring and form of the larva are similar, yet in the third stage the appearance of the resting larva is different from that of the later stages, and the difference is correlated with a position upon leaves or twigs respectively. Such a correlation is of fundamental importance for warning coloration and mimicry, and is often overlooked by critics of the current explanation of these phenomena.

The power possessed by caterpillars of adjusting their colour to the surroundings deeply interested Poulton and he experimented on a large scale to ascertain how this protective mechanism worked. He distinguished, in 1884 (15), between two types of protective coloration; either to the surroundings as a whole (general) or to some particular part (special). Another point made for the first time was the value of dimorphism in the struggle for existence. The practical advantage is that more effort is required from an enemy searching for food for the discovery of two types than of one, for experience makes it easier to find one that has become familiar. For a species it may be a matter of indifference which individual is destroyed: what matters is that one shall be left to maintain the species. This point was developed later in considering Intraspecific selection.

During these studies Poulton came very near to anticipating the fundamental principle of concealment through countershading established later by the artist naturalists Thayer, father and son. He himself in later days commented on his failure to notice the real significance of the following two points. He found that in the stick-like caterpillar of a Geometrid moth small fleshy protuberances obliterate the cleft between the body and the twig on which it rests. There remains a furrow indicated by darker shadow, but the perception of this shadow is prevented by the lighter colour of the processes neutralizing the darkness. Two years later, in 1888 (25), Poulton perceived that the flat, leaf-like appearance of the obese pupa of the Purple Emperor butterfly was due to the same principle: the effect of roundness is neutralized by increased lightness compensating for the shadow by which the roundness of an object is judged. Poulton took the matter no further, and it was Abbot H. Thayer who demonstrated this general principle in the concealment of animals by the lighter countershading of the underside whereby the solidity is masked.

Another principle foreshadowed by Poulton is the presence in one species of two races differing only in physiological characters. He showed in 1885 (16) that the green colour of larvae is due to the colour of the blood being derived from the chlorophyll of the food plant: it gives a spectrum nearer to that of unaltered chlorophyll in leaves than is the spectrum of chlorophyll in alcoholic solution. The food plant may produce a tendency in the larva to be coloured in a certain way but this is met by a tendency in the larva itself towards another direction. Larvae bred from the egg showed that the variety towards which a larva is tending may be modified by the food plant: when such a change has been produced and the food is again changed some considerable effect may be produced towards the original tendency. Poulton suggested that the tendency becomes cumulative as the larvae of successive generations feed upon the same food plant. A long series of generations might result in a distaste for other food plants, so that larvae from eggs laid on the wrong plant would wander and die. Thus, Natural Selection would lead the female to lay eggs on the appropriate plant and separation (of two races) would be complete. Mere proximity of one food and distance from other kinds might produce some tendency in this direction and two varieties might become locally distinct. If such were stereotyped there would result a species with specific difference in the larva alone.

These passages, in 1885, which have not been sufficiently recognized, foreshadowed the idea of 'Physiological races' first clearly enunciated by Hopkins in 1917.

The hereditary transmission of these larval tendencies was shown in a later paper (18) for larvae with very strong tendencies towards a whitish form produced in the next generation only a single yellowish larva out of seventy-five. Experiments were devised to test the self-adapting power: larvae fed in the dark on white stems from which all green leaf-tissue had been stripped were all white. Poulton showed (27) by sewing leaves together so that the larva was only exposed to the underside, that although all the leaf was eaten as usual the colour of the surface and not its substance when eaten is the agent influencing larval colours. The ultimate predominance of one larval tint depends upon the time that that tint predominated in the environment. This, Poulton said, 'implies an entirely new resource in the various schemes of larval protection by resemblance to environment'. The larva has acquired a power, relatively immediate in action, by which it responds to environmental changes, and which is not the result of modifications in the existing pigmentary mechanism as in the chamaeleon but depends upon some neuro-chemical mechanism affecting absorption and utilization of pigment derived from the food plant.

The means by which the newly formed pupa of a butterfly assumes a colour most in harmony with its surroundings were experimentally investigated by Poulton (22, 23, 26, 28). It had been vaguely supposed that the fresh moist skin was in some way sensitive to the surrounding colours and through some unknown mechanism responded accordingly. This is obviously impossible when a larva pupates during darkness and pupal coloration is assumed before light comes. Poulton showed that it is the larva which is sensitive, especially while it rests quietly before suspending itself: by altering the surroundings at this stage he obtained pupae which mostly agreed in tint with the intensity of the light they received from their surroundings. The effect of conflicting colours on different parts of the larva was tested and it was concluded that the effect is not produced through the eyes or other especial sense organ but the whole skin is susceptible. The brilliantly gilded appearance of chrysalids of the Tortoiseshell butterfly and its kin was the subject of a Royal Institution lecture in 1893 (24) and Poulton commented on it again in 1927 (30). At one time supposed to be due to the presence of internal parasites, the gilded appearance can be artificially produced by exposure to high light or to the reflection from gilt surfaces: it is due to lamellae between which is fluid. The effect is screened in a normal dark pupa by the dark pigment which is illuminated by light reflected from the lamellae.

The next series of papers concerns heredity, in which his early interest was shown by a letter to *Nature* in 1884 on the inheritance of abnormal toes in cats; this was the first of many letters to that journal during the course of his life. The exaggerated claims of mutationists roused him vehemently and in the prefaces to *Essays on Evolution* and *Charles Darwin and the Origin of Species* he protested that the earlier writings on variation by a leading mutationist were 'injurious to biological science and a hindrance in the attempt to solve the problem of evolution'. In 1916 (39) he referred to the absurdity of the opinion expressed by Bateson at the meeting of the British Association at Melbourne, when naturalists were invited to contemplate the process of evolution as just an unpacking from that illimitable warehouse—the unicellular ancestor. At the 1913 meeting of the Association (38) he pointed out the confusion existing in the use of the term 'Mutation', and suggested that the only way to put matters right was by restoring the term to its rightful owner Waagen—a measure of justice for which geologists had long been contending. A devout disciple of Weismann he wrote much against the inheritance of acquired characters and devoted an address to showing how the study of insects controverts that theory (35). One example may be cited. Lamarckians claim that the complex adaptive instincts of insects presuppose the accumulation of experience through many generations, but Poulton asked how could this possibly apply to the cocoon-making instinct of a caterpillar? A chrysalis within a cocoon is obviously incapable of any experience in regard to a structure it never makes and upon which it depends for protection. It is not from insects which had *most* experience of enemies that descendants have come but precisely the reverse: the prime necessity for an insect is to avoid an experience altogether.

Poulton considered the doctrine of the continuity of germ plasm so important that in 1909 (46) he wrote in a review of the centenary of Darwin, 'The only fundamental changes in the doctrine given to us in 1858–1859 are those brought about by the researches and the thoughts of Weismann; and these have given to the great theory which will ever be associated with the names of the two illustrious English naturalists a position far higher than that ever assigned to it by Darwin himself'.

The importance of the Mendelian principle was clearly appreciated by Poulton and he was always pleased when his correspondents in Africa bred families of butterflies in which he was able to show segregation (36, 39, 71).

For many years he bred successive generations of the Magpie moth, *Abraxas grossulariata* L. in his own fashion, but as he sought no expert guidance the material has proved genetically valueless. But it had a bearing (40) on the much discussed question of those days, whether quite small variations are heritable, which was denied by the early mutationists. He pointed out that the mere fact that 'geographical races' can be distinguished by quite small differences shows the local inheritance of such characters (39).

Poulton took a prominent part in the early 'Mutation' controversies and fiercely contested the claims of the early protagonists. Thus, R. H. Lock commented upon Bateson and Gregory's demonstration of the pin-eyed condition of the primrose flower as a Mendelian dominant as follows. 'We have here the solution . . . of a biological problem to which Darwin devoted the greater part of a volume.' Depreciatory references to Darwin such as this always aroused Poulton's antagonism and he proceeded (131, introduction) to 'enquire what Darwin *did* achieve in the pages referred to; for Lock only leads his readers to infer that the great naturalist failed to find a solution'. After summarizing all that the discovery of the meaning of heterostyled flowers really implied Poulton asked, 'What had Bateson and Gregory done to make their work the only possible solution of the problem upon which Darwin had made all these fruitful investigations?'

After a simple explanation of what is meant by 'dominance' Poulton continued: 'What does the 'solution'amount to? Merely this—the knowledge that the two conditions, 'thrum-eye' and 'pin-eye', so far as they follow Mendelian laws, do not combine in successive generations, but may be shown by an appropriately managed experiment gradually to become divided between two groups of individuals. . . . Darwin had clearly proved that both forms exist in Nature, and that in fact the offspring do arrange themselves in two groups of approximately equal numbers. The gametic explanation of this, although intensely interesting, carries us no step further on the road of Evolution. Furthermore, Darwin showed what is the meaning of the heterostyled condition in the life of the plant, and thus explained how it was that the character has been selected and incorporated into the structure of the species.

'To look on this record and on that and maintain that Darwin failed to solve the problem which the Mendelian has now solved is, to put it as mildly as possible, unreasonable and absurd.'

Similarly Poulton took exception to 'the appropriation by Bateson of Weismann's conclusions'. Bateson (*Rep. Brit. Ass.* p. 579, 1904), discussing the blue Andalusian fowl, wrote: '*Selection* will never make the blues breed true. . . . If the selectionist reflect on this experience he will be led straight to the centre of our problem. There will fall, as it were, scales from his eyes, and in a flash he will see the true meaning of fixation of type, variability and mutation, vaporous mysteries no more.' Poulton commented as follows (131, introduction): 'This is really no novelty, no falling of scales from the eyes, for we have been aware, ever since Weismann's researches and illuminating thought on the germ cells, that no characters except those predetermined in the germ are available for evolution. . . . I fully admit the importance of Mendel's discovery in increasing our knowledge of the constitution and relationships of germ cells but this by no means justifies the appropriation under his name of results which the present generation owes to Weismann.'

These words were published in 1908, but Poulton lived to see that the apparent disharmony between Darwinians who hold that evolution has proceeded by small steps, and Mutationists who hold that it has advanced by large ones, could be reconciled, and in 1917 drew the attention of the Entomological Society to some remarks by Jennings upon the heritable gradation of colour in the eye of *Drosophila* by means of which 'one could obtain, by the mutationists' own statement, the continuously graded results which selection actually gives. What more can the selectionist ask?' All this controversy is now merely historical, but Poulton played a big part in it and saw its closure by R. A. Fisher with the concept of evolution within the gene complex and the development by E. B. Ford of the principle of factor interaction.

Poulton wrote much upon evolution (see series E in Bibliography) and made the study of mimetic resemblances his special subject. It will be remembered that H. W. Bates was one of the first to apply the Darwin-Wallace principle, and greatly delighted Darwin in 1862 by his enunciation of the theory of mimicry. Certain insects endowed with unpleasant qualities have benefited by the association of those deterrents with conspicuous coloration and habits which enhance it. Other species, not necessarily nearly related, have similar coloration without the deterrent qualities and Bates suggested that they live by the unsavoury reputation of the 'models' which they mimic. Fritz Müller in 1870 pointed out equally close resemblances between the models themselves, and explained this as due to the necessary education of enemies by experimental tasting. If a warning coloration were adopted by a great number of species they would all benefit because the enemy would destroy comparatively few of each in learning the meaning of the common pattern. This is now known as 'Müllerian' resemblance and is not mimicry in the strictest sense. The relation between protective (cryptic), warning (aposematic), false warning (pseudaposematic) and common warning (syn-aposematic) coloration is set out in a table in Poulton's classical work *The Colours of Animals* (129). These logical terms, devised by Arthur Sidgwick, should be more commonly used, for 'mimicry' is frequently and erroneously used to include synaposematic as well as pseudaposematic resemblance, which in principle are fundamentally distinct. Poulton adroitly compared the former to the use of a common trade-mark by the members of a 'combine' manufacturing the same type of goods, whereas the latter is comparable to the fraudulent use by a struggling small firm of a trade-mark belonging to a successful big firm. Pseudaposematic resemblance implies deceit which is not a necessity in the other class. The result of synaposematic resemblance in nature is to make it easier for an enemy to learn what should be avoided if better food is obtainable: the other class makes it more difficult for an enemy to select his food. Synaposematic coloration of insects benefits the enemy, but pseudaposematic coloration makes life more difficult for him. It is clear that pseudaposematic and special procryptic coloration are of the same order: both, as Poulton said, are 'apatetic', i.e. deceitful. There is no reason for discussing mimicry as if it were a peculiar phenomenon requiring a special explanation. In later years (101) Poulton added the term 'parasematic' for markings enticing an enemy to seize an insect at some point at which no vital damage is done, e.g. the eyelike spots often seen in butterflies at the base of a tail on the hind wing.

Mimicry was a platform upon which fierce controversy with the mutationists raged at one time. The claim put forward by Punnett that mimicry is simply a case of a similar set of pattern factors producing similar mutations in model and mimic was refuted by Poulton (39). Although the patterns may appear similar they are not so in reality: the margin of the pale areas in models is sharply cut, in the mimic 'woolly'. This same relationship holds good between male and female of a species, irrespective of mimicry, and is significant in regard to the much greater prevalence of mimicry in the female sex. The hard outline Poulton termed 'eulegnic', the soft 'dyslegnic'. The mutationist's argument just mentioned is an example of a common failure on the part of critics to see mimicry from a wide view-point: a more comprehensive knowledge of the subject would show that while such an argument *may* apply to two butterflies it fails to cover the case of a caterpillar mimicking a snake, or a beetle resembling a seed.

Again, a common and ill-informed explanation of mimicry is that, by the terms of the current theory, model and mimic inhabit the same area. What more likely than that environmental conditions produce similar results? To refute this facile argument Poulton used the great association of Lycid beetles and their mimics. These soft beetles, related to our glow-worm, found all over the hot countries, are marked in simple patterns of black and red-brown and fulfil all the canons of aposematic species. Wherever they occur they are resembled by insects of other orders, some as remote in connexion as flies or wasps. The colours of the adults being laid down in the immature stages, which in these numerous species are passed under the most diverse conditions of food, light and humidity, cannot possibly be due to similar environmental conditions.

Another refutation of the theory of parallel mutations is provided by the different chemical constitution of pigments in model and mimic, a subject in which Poulton took much interest since it was first demonstrated by Gowland Hopkins in 1895. Much work has recently been done by E. B. Ford on this subject in the Hope Department.

Mimicry is a subject for field naturalists and Poulton continually stressed the need for observation and experiment under natural conditions. Attitude and movements are as important as shape and colour and Poulton considered that mimicry may often have begun by a chance resemblance in movements to some other creature disliked or feared. This is particularly exemplified by spiders which mimic ants, in spite of the fundamental morphological difference between them. The great traveller Burchell in 1828 in Brazil made the following note (112) on a spider. 'Black—runs and seems like an ant with large extended jaws.' It is significant that the distinguished arachnologist, W. S. Bristowe, particularly emphasizes the value of mimicry of the quick *movements* of ants in protecting spiders against their greatest enemies, other spiders. The characteristic movements of an ant are readily perceived by a spider's sensory front legs, and the corresponding mimetic movements of an ant-like spider would have the same effect: it seems possible that ant mimicry arose first from habit and movement, and when ant-like appearance had been secured additional protection would be afforded against enemies of spiders which did not like ants.

Resemblance to ants has been produced in a variety of ways and this production of a similar end by different means is characteristic of natural selection. Poulton was particularly pleased with another example of this provided by the caterpillars of two moths of very different groups (85). The hymenopterous parasites (Braconidae) of caterpillars when full fed frequently cover the empty skin of their former host with a cluster of small, conspicuous, white or yellow cocoons. The caterpillar of *Norasuma kolga* Druce (Bombycidae) before constructing its cocoon spins a loose web bearing several oval masses of yellow silk closely resembling Braconid cocoons. Within the loose network the *Norasuma* spins its own cocoon, the little yellow masses on its surface then deceptively suggesting that the caterpillar has been destroyed by parasites.

Exactly the same suggestion is conveyed by the caterpillars of species of *Deilemera* (Hypsidae) which eject *per anum* small objects like bubbles which are then affixed with silk to the outside of the cocoon. So deceptive is the appearance that it has deceived experienced naturalists. Poulton's explanation was that the conspicuous sham Braconid cocoons serve as a warning to birds that the caterpillar has been destroyed by parasites. Experience will have taught the enemy that such parasitic cocoons cover an empty skin of the former host and that the cocoons themselves contain so small an amount of nutriment that if other food is readily available it is waste of time to try to open them.

If mimicry is due to the operation of natural selection, and no other explanation has been devised which covers so vast an accumulation of facts, it behoves Darwinians to produce evidence as to the selecting agent.

Here is another point on which the critics of this explanation often trip up, for they commonly consider mimicry in butterflies alone. Since it is held that birds are the selective agents causing butterfly mimicry it is often said that there is inadequate evidence that birds prey on butterflies. G. A. K. Marshall collected numerous direct observations and a large amount of indirect evidence founded on symmetrical injuries to the wings of butterflies. C. F. M. Swynnerton, in Rhodesia, for many years accumulated notes and observations on the subject which he submitted to Poulton with whom he corresponded. His experiences leave no room for doubt that birds do selectively prey upon butterflies, but that the observer must know how to observe. In 1920 Poulton received an observation of prime importance from W. A. Lamborn in Africa who found the imprints of a bird's beak on the wings of a butterfly which he had seen the bird tear off when eating the body. Poulton published the observation at once with the characteristic remark that 'it was thought better to make the letter public without delay in order that the new method of investigation might be known and pursued as soon as possible'. He subsequently communicated notes on many such specimens, and this study has been carried considerably further by G. D. Hale Carpenter who, by analysis of nearly a thousand examples of beak-marks in butterflies of different groups, has produced significant statistical evidence of selection. But, even if no bird had ever been proved to attack a butterfly, the theory of mimicry would not be upset, for mimicry is a phenomenon of widespread occurrence among other orders of insects.

The prey that bats select for themselves was studied by Poulton (99). The long-eared bat in particular has a habit of taking the moths it captures to a regular roosting place under which the nipped-off wings can be collected in abundance. It was found that the wings of moths with the characters of 'distasteful' species are seldom present.

If certain insects are distasteful to vertebrate enemies it may be supposed that other predators are less fastidious, for there must be *some* check on numbers. Thus the prey of predacious insects attracted Poulton's attention (95) and studies commenced by him and afterwards developed by B. M. Hobby show that insect predators exert little choice on the whole, and certainly do not avoid the distasteful insects.

The word 'distasteful' must always be considered as *relative*, for there can be no *absolute* inedibility. A common fallacy is to suppose that the theory of warning coloration is upset because, for instance, a bird has been seen to eat a wasp. This is very superficial reasoning. Poulton very frequently pointed out that of all forms of protective devices the commonest is cryptic coloration; for it is safest not to be seen at all. But, in the presence of abundance of relatively more edible species, it has paid certain species provided with unpleasant taste or deterrent devices to be conspicuous so that they can be recognized and left alone when food of better quality is readily obtainable. Thus, warning (aposematic) colours and the consequential mimicry are features of the teeming life of the tropics.

A corollary of this is the fact that in species of butterflies which appear in different colours at different seasons the dry-season form is usually procryptic; the wet-season form may be very conspicuous. It was G. A. K. Marshall in correspondence with Poulton (134) over five years who first bred in South Africa the bright salmon-pink wet-season form of *Precis octavia* Cr. from the dark blue dry-season form with procryptic lower surface.

Other species were also bred, and Poulton in a detailed study (93) showed how the conspicuous pattern and colouring of a wet-season form can be derived from the cryptic dry-season coloration: the two forms had previously been classified as distinct species. Poulton's comments (l.c. 458–459) on this important result are characteristic. 'Under the shock of Mr Marshall's discovery . . . the systematist may well feel doubts about the foundations upon which his science has been erected. In these distracting circumstances a firm belief in natural selection will be found to exercise a wonderfully calming and steadying influence.'

Polymorphism was a subject constantly before Poulton, and his appreciation of its value in conferring protection by increasing the amount of work to be done by a searching enemy has been mentioned in the account of his work on caterpillars. In the case of mimetic butterflies polymorphism is often pronounced, and in some cases the species mimicked have different habitats. Thus a mimetic species may obtain protection in one area from the presence of a species absent from another area in which the mimic is represented by a different form.

Some mimetic species, such as *Papilio polytes* L. may exist in the absence of the model, and it may justly be asked, why, if it can hold its own, should it have become a mimic? Poulton argued that it is a successful species kept up by selection, but the development of a mimetic appearance need not necessarily increase the *numbers* of the species. What happens is that 'certain variations formerly unchecked now tend to fall into the surviving percentage and, once started, the further stages of transformation were effected in the same way' (39). When *polytes* spreads beyond the range of the model, or the model disappears, the *constitution*, not the amount, of the surviving percentage is changed: it is the species, not the individual, that is concerned. The process is the selection of a pattern borne by a butterfly, rather than a butterfly bearing a pattern. For this process, to which Poulton had drawn attention many years before, J. H. Huxley introduced the term 'intraspecific selection' (50).

The study of polymorphic mimics in equatorial Africa had important results, entirely due to Poulton's enthusiasm in getting friends to collect on a large scale. C. A. Wiggins collected at Entebbe, on the north coast of Lake Victoria, the various members of a large and complex association in which the Nymphaline genus *Pseudacraea* closely mimicked different species of the Acraeine genus *Bematistes*, formerly known as *Planema*. Some years later G. D. Hale Carpenter sent similar large collections from the Sese Isles in the great lake.

Poulton when studying the former collection (68) showed that it was extremely probable that several different 'species' of *Pseudacraea* were forms of one polymorphic species, for they were connected by rare intermediates. The mimetic *Pseudacraea* far outnumbered by the models, were faithful mimics. The collections from the Sese Isles, however, were found by Poulton, and later shown in detail by Hale Carpenter, to be in the opposite condition. *Pseudacraea* far outnumbered the *Bematistes* and were extremely variable, non-mimetic intermediates being abundant.

Poulton hailed these facts as of first importance, claiming that they afforded strong presumptive evidence that mimicry *is* maintained by natural selection, for in the locality where the species of *Bematistes* were insufficiently numerous to confer any advantage by resemblance to them the variation in *Pseudacraea* was uncontrolled. The proof by breeding that the forms of *Pseudacraea* were conspecific was obtained by Hale Carpenter who cabled the news to Poulton (70). He received it with great excitement and wrote that it caused him a sleepless night!

This phenomenon, uncontrolled variation in a polymorphic mimetic species when the model is inadequate to protect, was also noted by Poulton in his favourite butterfly, *Papilio dardanus* Brown, and later was firmly established on a statistical basis by E. B. Ford.

The subject of mimicry is closely linked with geographical variation on which Poulton wrote much. His studies of mimicry began with North American species and one of his chief points was the error of attributing mimicry to a similar response to environmental conditions. The common milkweed butterfly (*Danaus plexippus* L.) of North America has a type of coloration characteristically Asiatic but unique in America: it is evidently derived from Asia. Yet this product of Asiatic conditions, far from responding to its new environment, has apparently influenced a species indigenous to America, and therefore by hypothesis the result of American conditions, to change its American facies for one resembling the Asiatic intruder.

A detailed and important study of the island races of certain butterflies in Fiji (79) led Poulton to conclude that several waves of immigrants had entered the Fijian archipelago from the islands to the west and had produced changes in the earlier established species.

An address in 1914 (74) was devoted largely to the forms and geographical distribution of *Papilio dardanus*, which in another monographic study (78) he called 'the most interesting butterfly in the world'. Poulton said, 'By this single great example I hope to make clear one chief aim of the Hope Department—the study of specific change in relation to geographical distribution and to the organic environment'.

A study of the many forms of *Hypolimnas bolina* L. in the Pacific (79) resulted in the suggestion that a certain species of *Euploea* (*E. euphon* F.) had probably at one time existed on the Chagos Islands where it is now unknown. *Euploea*, an Asiatic genus, seems at one time to have found its way towards Africa, for four species are known from the islands north and east of Madagascar. The butterflies of Mauritius and Bourbon (104) provide evidence of the 'extraordinary effect of one of the most dominant and distasteful types of the oriental region'. Ethiopian species of *Amauris*, *Salamis* and *Papilio* [*s. l.*] in these islands all exhibit, in the modification of their appearance from that of their nearest allies, the influence upon them of *Euploea*. Moreover, on the Chagos Isles far to the north-east of the Mascarene isles, there exists a peculiar form, *euphonoides* Poulton, of *Hypolimnas bolina* which differs considerably from any other form in the whole enormous range of that species. The difference is in the direction of mimicry of *Euploea euphon* F. now known only in Mauritius where it is mimicked by *Papilio phorbanta* L. Poulton suggested that '*Euploea euphon* and *E. mitra* Moore of the Seychelles reached their present locality by way of the Laccadive, Maldive and Chagos groups and the islands between them; thence westward and south westward by many other scattered islands. The route of the invading *euphon* clearly passed through the Chagos group, and it is not an extravagant exercise of the imagination to see in the race *bolina euphonoides* the persistent effect of its residence in these islands.'

Thus has a wandering butterfly left footprints on the sands of time.

Another study (109) concerned the Ethiopian races of the holarctic common small copper butterfly which, occurring only on the eastern highlands, is probably a pluvial relict.

The subject of sexual selection greatly interested Poulton and the knowledge that has been accumulated about the epigamic displays and scents in insects has been largely due to his enthusiasm. Having no olfactory sense himself he had to depend upon the observations of others, particularly F. A. Dixey, F.R.S. and G. B. Longstaff. It was Fritz Müller who drew attention from 1876 onwards to the different scents emitted from special organs on the wings of male Lepidoptera. H. Eltringham, F.R.S., while working in the Hope department, with masterly technique elucidated the minute structure of the abdominal brushes and glandular wing-patches in certain Dànaine butterflies.

Observations in the field by W. A. Lamborn and G. D. Hale Carpenter showed the whole process whereby scent is picked up by the protrusible anal brush from the secreting patches on the wings and afterwards discharged into the air around the female by energetic protrusion of the brush while the male flutters above her. The fact that this process has only once been observed in the case of *Danaus chrysippus* L., possibly the commonest butterfly in the world, is an illuminating example of our ignorance of the ways of living creatures. Poulton pointed out in 1907 (54) that numerous observations have shown that the mimetic appearance of a female butterfly may momentarily deceive the male but that the error is quickly detected on closer approach. In synaposematic associations between species of genera such as *Euploea*, *Amauris*, *Heliconius*, valuable time may be lost to a male by attempts to pair with a wrong female. Possibly the great differences in position, size and shape of the male scent-glands on the wings afford a ready means of identification by the opposite sex. An observation by W. A. Lamborn was considered by Poulton to be of great significance as affording a possible explanation of the variability of secondary sexual characters (56). This observer saw a nest of the African wasp *Synagris cornuta* L. on which a large male with enormous mandibles frustrated the attempts of others to alight. It was guarding a cell from which a female emerged, to be immediately seized by the large male, which apparently attempted coitus with it but was alarmed by the observer and flew off. The other males showed astonishing differences in mandibular development; they were terrorized by the larger specimen which definitely effected marriage by capture. Poulton commented that the immense mandibles may be a disadvantage in obtaining food, and that the emergences of the females cover a period long enough for this to tell, so that the males with smaller mandibles have an advantage in the end through *natural* selection while the others score at the beginning through *sexual* selection in battles between males.

Observations on the courtship habits of predacious flies of the family Empididae, carried out with great patience by A. H. Hamm, for long assistant in the Hope Department, were shown by Poulton to form a complete series of evolutionary stages in the use of prey (55). In the first the captured insects serve as food for both sexes without relation to pairing: then as a gift provided by the male and devoured by the female while pairing; finally the prey is no longer fed upon by the female but serves as a lure and stimulus to her and may even be replaced by some vegetable fragment. The climax is reached in an elaborate cocoon spun by the male around the prey and replacing the latter as an object of attraction: Hamm even found that merely an empty cocoon would be accepted.

An astonishing application of the use of a scent to attract the male insect has been described by Mrs E. Coleman in an Australian orchis. The flower apparently produces a scent so like that of the female of a certain species of 'Ichneumon fly' that the male insect actually enters the flower backward in an attempt to copulate with the supposed female and thereby picks up the pollinia on his abdomen, to carry them to another flower. Poulton suggested (57) that, while it was obvious that the plant benefited, the less obvious benefit to the insect lay in the fact that males emerge from the pupa before females and the scent of the flower keeps them in a state of readiness to mate when the female does appear. In 1887 he had already suggested that late emergence of females from pupae is advantageous by causing complete rivalry among large numbers of males for each of the females as they emerge.

It will have been clear from what has been said that Poulton's enthusiasm and helpful correspondence with observers and collectors in the field did as much to advance knowledge as his own studies, and something must be said of the work done by his associates and friends whose notes he communicated to the Royal Entomological Society with his own illuminating and inspiring comments.

G. A. K. Marshall for five years in Rhodesia studied insects in the field (134), paying especial attention to mimetic associations, the prey of insectivores, and especially the question whether birds eat butterflies as to which he had no doubt that they do. His part in the unravelling of the tangle of seasonal forms has been discussed. One outstanding result was the number and size of Müllerian or synaposematic associations, and Poulton, as he accumulated more and more experience of mimetic relationships, concluded that by far the greater number of cases had at least a Müllerian element: Batesian mimicry seems to be rare. C. F. M. Swynnerton in Southern Rhodesia for many years conducted tests and experiments on the relative edibility of insects to birds, and provided Poulton with much information on the subject of birds preying on butterflies, together with large collections.

W. A. Lamborn, in Nigeria, devoted particular attention to insects associated with ants (135) especially the Liptenine section of the Lycaenid butterflies: he had a genius for breeding insects of all kinds from the larvae and made many most interesting discoveries on the life histories of minute Diptera and Homoptera. A friend of his, C. O. Farquharson, followed his example and Poulton, after his death at sea in the last war, communicated his important and numerous observations on ants and their associates for publication (136). The great collections made in Kenya and Uganda by C. A. Wiggins, in Kenya by V. G. L. van Someren and K. St A. Rogers, and in Rhodesia by C. F. M. Swynnerton, gave Poulton special experience of African butterflies with the result that the Hope Department became known as a rich storehouse of material and a fruitful source of knowledge of the bionomics and geographical forms of African butterflies.

The same can be said of the Fiji and Solomon islands whence came great collections from R. A. Lever and H. W. Simmonds, enabling Poulton to contribute important evolutionary studies on these interesting areas.

Another naturalist correspondent was R. W. C. Shelford in Borneo who greatly enlarged the knowledge of Bornean insect life and contributed much material for the study of mimicry in the Hope Department. After his untimely death Poulton edited his notes in the form of a book (137).

Finally, something must be said of his assiduity in the care and enlargement of the famous collections bequeathed to the university by the Rev. F. W. Hope, containing many 'type' specimens. Poulton was a great beggar and collected large sums, contributing freely himself, for the purchase of cabinets to house the ever-growing collections. Nothing came amiss to him; he would accept anything and discard nothing so that the department when he retired was overwhelmed with specimens of all degrees of value in apparent confusion, unsorted, unidentified and hard to find.

Being always of a hopeful disposition he never seemed to realize that it was impossible for a university to maintain a general collection of insects, more or less in competition with the British Museum. Himself not a taxonomist he welcomed the help of any expert who could be tempted to come to Oxford and make order out of chaos, but such visitors were infrequent and his successor was forced to decide on a change of policy and abandon the task of trying to do what Hope himself *could* do nearly a hundred years ago.

Among the treasures of which Poulton took charge were the collections made by the great traveller Burchell, presented to the museum in 1865. Poulton took much trouble to get the specimens identified and reported upon. He wrote of them that they were furnished with such accurate notes that they made possible 'a trustworthy standard by which to measure the rate of future change; for one great justification of the immense funds which are expended on museums is that they will serve this very purpose for generations yet to come'.

Poulton's great attention to detail led him to take infinite pains over preparing the labels without which specimens are worse than useless. He had each label printed in duplicate; one, attached to the specimen, of best quality hand woven paper so that it would not perish. The duplicate, of less choice paper, was pinned alongside the specimen. This system, probably unique, makes the geographical study of a species a pleasure instead of the neck-breaking effort to get a glimpse of a label close under the specimen on a short pin.

The outstanding feature of Poulton's long life of devotion to natural history was his readiness to help and encourage others, and a slightly shortened quotation from his own remarks on this subject is appropriate (119). 'The essential motive of investigation is the overwhelming desire to find out, to satisfy the craving for knowledge, not knowledge in general but of some special kind. . . . The problems encountered in the investigation of living insects are so infinitely complex that the student must seek for all possible help from other workers in other sciences as well as his own. He knows from his own experience the uselessness of superficial study; and study over too wide an area must be superficial. Therefore he asks for help from the specialist in subjects of which he knows but little. And he becomes willing, nay delighted, to render to such students the help which his own specialized work enables him to give. He is thus led to pursue to the uttermost his own researches in his own part of the great field without any inclination to encroach on the sections where others are at work—to give help and receive help, to take a keen and friendly interest in the investigations going on around him and to welcome the same interest in his own. Specialization pursued in this spirit, so far from being narrow and narrowing, is broadening as an education and broadening as a social force; for it leads to mutual appreciation instead of mutual jealousy.' It is not surprising that, taking this view, Poulton considered the definition of specialist as 'one who knows ever more and more about less and less' to be a libel.

This memoir has been written during the middle of the struggle which makes the war of 1914–1918 seem relatively unimportant. Some words in addresses given by Poulton during that time may fittingly be quoted as being applicable also at the present time.

'The great problem of problems after the war—will be the attempt to create an atmosphere sympathetic to the teachings of science' (114). In 1915 (113) he had spoken with great feeling of 'the spirit of all others the most antagonistic to science [the spirit of the advocate] . . . The advocate labours to give to his case, whether true or false, the appearance of truth: the scientific man labours to strip off appearance and discover whether the true or false is hidden beneath.'

He sought the truth—and Truth hath loved him well.
Probing the mysteries of Nature's mind
He shared with others what he found to tell;
The secret processes of living kind.

G. D. Hale Carpenter

SELECTED REFERENCES

The 137 items, selected as the more important of Poulton's writings, are arranged in the following groups:

A. Geology. Nos. 1–4.
B. Morphology. Nos. 5–14.
C. Colours, etc., of larvae and pupae. Nos. 15–30.
D. Heredity. Nos. 31–40.
E. Evolution. Nos. 41–53.
F. Sexual selection. Nos. 54–57.
G. Mimicry. Nos. 58–87.
H. Insect bionomics. Nos. 88–103.
I. Geographical distribution. Nos. 104–110.
J. Miscellaneous. Nos. 111–122.
K. Obituaries. Nos. 123–128.

L. Books. Nos. 129–133.
M. Contributions by others, edited, or with important comments, by Poulton. Nos. 134–137.

A large number of contributions of smaller size to the Royal Entomological Society of London are not listed. The full title of *Transactions* or *Proceedings* of this society is given only for the first of each: subsequently they are quoted merely as *Trans.* or *Proc.*

A. Geology

1. On mammalian remains and tree trunks in quaternary sands at Reading. *Quart. J. Geol. Soc.* **36,** 296–306, 1 fig. (1880).
2. A preliminary account of the working of Dowkerbottom Cave, in Craven, during August and September 1881. *Proc. Geol. Soc. Yorkshire,* **7,** 351–368 (1881).
3. A preliminary account of the working of Dowkerbottom Cave, in Craven, during August 1881. *Rep. Brit. Ass.* **1881,** 622–623 (1882).
4. A naturalist's contribution to a discussion upon the age of the earth. (Presidential address to section D.) *Rep. Brit. Ass.* **1896,** 808–828 (1896).

B. Morphology

5. The tongue of *Perameles nasuta,* with some suggestions as to the origin of taste bulbs. *Quart. J. Micr. Sci.* **23,** 69–86, pl. 1 (1883).
6. The tongue of *Ornithorhynchus paradoxus*: the origin of taste bulbs and the parts upon which they occur. *Quart. J. Micr. Sci.* **23,** 453–472, pl. 32 (1883).
7. On the tongues of the Marsupialia. *Proc. Zool. Soc. Lond.* **1883,** 599–628, pl. 54–55 (1883).
8. On the tactile terminal organs and other structures in the bill of *Ornithorhynchus. J. Physiol.* **5,** xv–xvi (1884).
9. The structures connected with the ovarian ovum of Marsupialia and Monotremata. *Quart. J. Micr. Sci.* **24,** 118–128, pl. 5 (1884).
10. True teeth in the young *Ornithorhynchus paradoxus. Proc. Roy. Soc.* **43,** 353–356, 1 fig. (1888).
11. The true teeth and horny plates of *Ornithorhynchus. Quart. J. Micr. Soc.* **29,** 9–48, pl. 2–4 (1888).
12. The structure of the bill and hairs of *Ornithorhynchus paradoxus*; with a discussion of the homologies and origin of mammalian hair. *Quart. J. Micr. Sci.* **36,** 143–199, pl. 14, 15, 15A (1894).
13. The external morphology of the Lepidopterous pupa: its relation to that of the other stages and to the origin and history of metamorphosis. Parts I–III. *Trans. Linn. Soc. Lond.* (2), **5,** 187–212, pl. 20–21 (1890).
14. The external morphology of the Lepidopterous pupa: its relation to that of the other stages and to the origin and history of metamorphosis. Parts IV–V. *Trans. Linn. Soc. Lond.* (2), **5,** 245–263, pl. 26–27 (1891).

C. Colours, etc., in Lepidopterous Larvae and Pupae

15. Notes upon, or suggested by, the colours, markings and protective attitudes of certain Lepidopterous larvae and pupae, and of a phytophagous Hymenopterous larva. *Trans. Ent. Soc. Lond.* **1884,** 27–60, pl. 1 (1884).
16. The essential nature of the colouring of phytophagous larvae (and their pupae); with an account of some experiments upon the relation between the colour of such larvae and that of their food plants. *Proc. Roy. Soc.* **38,** 269–314 (1885).

17. Further notes upon the markings and attitudes of Lepidopterous larvae, together with a complete account of the life-history of *Sphinx ligustri* and *Selenia illunaria* (larvae). *Trans.* **1885,** 281–329, pl. 7 (1885).
18. A further enquiry into a special colour-relation between the larva of *Smerinthus ocellatus* and its food plants. *Proc. Roy. Soc.* **40,** 135–173 (1886).
19. Notes in 1885 upon Lepidopterous larvae and pupae, including an account of the loss of weight in the freshly-formed Lepidopterous pupa, etc. *Trans.* **1886,** 137–179 (1886).
20. (Pigments of ova and larvae.) *J. Physiol.* **8,** xxv–xxvi (1887).
21. Notes in 1886 upon Lepidopterous larvae, etc. *Trans.* **1887,** 281–321, pl. 10 (1887).
22. An enquiry into the cause and extent of a special colour-relation between certain exposed Lepidopterous pupae and the surfaces which immediately surround them. *Phil. Trans. B,* **178,** 311–441, pl. 26 (1887).
23. An enquiry into the cause and extent of a special colour-relation between certain exposed Lepidopterous pupae and the surfaces which immediately surround them. *Proc. Roy. Soc.* **42,** 94–108 (1887).
24. Gilded chrysalides. *Not. Proc. Roy. Instn.* **12,** 33–36 (1887).
25. Notes in 1887 upon Lepidopterous larvae, etc., including a complete account of the life-history of the larvae of *Sphinx convolvuli* and *Aglia tau. Trans.* **1888,** 515–606, pl. 15–17 (1888).
26. Further experiments upon the colour-relation between certain Lepidopterous larvae, pupae, cocoons, and imagines and their surroundings. *Trans.* **1892,** 293–487, pl. 14–15 (1892).
27. The experimental proof that the colours of certain Lepidopterous larvae are largely due to modified plant pigments derived from food. *Proc. Roy. Soc.* (1893), **54,** 417–430, pl. 3–4 (1894).
28. (With F. Merrifield.) The colour-relation between the pupae of *Papilio machaon, Pieris napi* and many other species, and the surroundings of the larvae preparing to pupate, etc. *Trans.* **1899,** 369–433 (1899).
29. Experiments in 1893, 1894, and 1896 upon the colour-relation between Lepidopterous larvae and their surroundings, and especially the effect of lichen-covered bark upon *Odontopera bidentata, Gastropacha quercifolia,* etc. *Trans.* **1903,** 311–374, pl. 16-18 (1903).
30. Brilliantly golden pupae of *Aglais urticae,* L., normally produced on green leaves and stems. *Proc. Ent. Soc. Lond.* **2,** 27–29 (1927).

D. Heredity

31. Observations on heredity in cats with an abnormal number of toes. *Nature, Lond.* **29,** 20–21 (1884).
32. Weismann's theory of variation. *Nature, Lond.* **39,** 412 (1889).
33. On the supposed transmission of acquired characters. *Nature, Lond.* **40,** 610 (1889).
34. Theories of heredity. (Presidential address.) *Midland Naturalist,* **12,** 245–258 (1889).
35. The bearing of the study of insects upon the question, 'Are acquired characters hereditary'? (Presidential address.) *Proc.* **1904,** civ–cxxxii (1905).
36. Heredity in six families of *Papilo dardanus,* Brown, subspecies *cenea,* Stoll., bred at Durban, by Mr G. F. Leigh, F.E.S. *Trans.* **1908,** 427–445, pl. 23–24 (1909).
37. Mimicry and the inheritance of small variations. *Bedrock,* **2,** 295–312 (1913).
38. The term 'Mutation'. *Rep. Brit. Ass.* **1913,** 519–520 (1914).
39. The hereditary transmission of small variations and the origin of butterfly mimicry. (Presidential address.) *Proc. Linn. Soc. Lond.* **128,** 21–52, pl. 1 (1916).
40. Experimental evidence for the hereditary transmission of small variations such as would be required to initiate a mimetic resemblance in butterflies. *Rep. Brit. Ass.* **1922,** 372 (1922).

E. Evolution

41. Theories of evolution. *Proc. Boston Soc. Nat. Hist.* **26,** 371–393 (1895).
42. A remarkable anticipation of modern views on evolution. *Sci. Progr. Twent. Cent.* **1,** 278–296 (1897).
43. The influence of Darwin upon entomology. *Ent. Rec.* (2), **13,** 72–76 (1901).
44. What is a species? (Presidential address.) *Proc.* **1903,** lxxvii–cxvi (1904).
45. The value of colour in the struggle for life. *Darwin and Modern Science,* edited by A. C. Seward (Cambridge), 271–297 (1909).
46. The centenary of Darwin: Darwin and his modern critics. *Quart. Rev.* **211,** 1–38 (1909).
47. Darwin and Bergson on the interpretation of evolution. *Bedrock,* **1,** 48–65 (1912).
48. A remarkable American work upon evolution and the germ theory of disease. (Presidential address.) *Proc. Linn. Soc. Lond.* **1912–1913,** 26–45 (1913).
49. Presidential address, 1914. (Continued investigations into a remarkable American work upon evolution and the germ theory of disease.) *Proc. Linn. Soc. Lond.* **1913–1914,** 23–44 (with appendix) (1914).
50. Intraspecific selection, an attempt to explain the origin and meaning of certain examples of mimicry. *Proc. Zool. Soc. Lond.* **1928,** 1037–1043 (1928).
51. Adaptations which hinder or prevent inbreeding in insects. *Trans. 4th Int. Congr. Ent.* (Ithaca. August 1928), **2,** 582–588 (1929).
52. Insect adaptation as evidence of evolution by natural selection. *Evolution,* edited by G. R. de Beer (Oxford), 1–10 (1938).
53. The conception of species as interbreeding communities. *Proc. Linn. Soc. Lond.* Session 150 (4), 225–226 (1938).

F. Sexual Selection

54. The significance of some secondary sexual characters in butterflies. *Proc.* **1907,** xl–xliii (1907).
55. Empidae and their prey in relation to courtship. (Observations by A. H. Hamm). *Ent. Mon. Mag.* **49,** 177–180 (1913).
56. Mr W. A. Lamborn's observations on marriage by capture by a West African wasp. A possible explanation of the great variability of certain sexual characters in males. *Rep. Brit. Ass.* **1913,** 511–512 (1914).
57. Pollination of an Australian orchid by the male Ichneumonid *Lissopimpla semi punctata,* Kirby. (By Mrs Edith Coleman, edited, with introduction, by E. B. P., appendix by A. M. Lea.) *Trans.* **1928,** 533–539, 1 fig. pl. 23–24 (1928).

G. Mimicry

58. On an interesting example of protective mimicry discovered by Mr W. L. Sclater in British Guiana. *Proc. Zool. Soc. Lond.* **1891,** 462–464, pl. 36 (1891).
59. Theories of mimicry as illustrated by African butterflies. *Rep. Brit. Ass.* **1897,** 689–691 (1898).
60. Protective mimicry as evidence for the validity of the theory of natural selection. *Rep. Brit. Ass.* **1897,** 692–694 (1898).
61. Mimicry in butterflies of the genus *Hypolimnas* and its bearing on older and more recent theories of mimicry. *Proc. Amer. Soc. Adv. Sci.* **46,** 242-244 (1898).
62. Natural selection the cause of mimetic resemblance and common warning colours. *J. Linn. Soc. Lond.* **26,** 558–612, 7 figs. pl. 40–44 (1898).
63. Mimicry and natural selection. *Int. Congr. Zool.* **5,** 171–179 (1902).
64. Mimetic forms of *Papilio dardanus* (*merope*) and *Acraea johnstoni. Trans.* **1906,** 281–321, pl. 17–22 (1906).

65. Secondary mimetic resemblance of Ithomiinae to the Danaine genus *Ituna*. *Proc.* **1908,** vii–xi (1908).
66. Mimetic North American species of the genus *Limenitis* (s.l.) and their models. *Trans.* **1908,** 447–488, pl. 25 (1909).
67. Mimicry in the butterflies of North America. *Ann. Ent. Soc. Amer.* **2,** 203–242 (1909).
68. On Dr C. A. Wiggins' researches on mimicry in the forest butterflies of Uganda (1909). *Int. Congr. Ent.* (*Bruxelles*) **2,** 483–508 (1911).
69. Pseudacraeas of the *hobleyi* group on Damba Island as compared with those from the Entebbe district. *Proc.* **1911,** xci–xcv (1912).
70. Polymorphism in a group of mimetic butterflies of the Ethiopian Nymphaline genus *Pseudacraea*. *Nature,* **90,** 36–37 (1912).
71. Mimicry, mutation and mendelism. *Bedrock,* **2,** 42–56 (1913).
72. Mimicry in North American butterflies: a reply. *Proc. Acad. Nat. Sci. Philad.* **66,** 161–195, pl. 5 (1914).
73. The evolution of mimetic resemblance. *Bedrock,* **3,** 34–45 (1914).
74. President's introductory address [on *Papilio dardanus*]. *Int. Congr. Ent. II* (*Oxford*), **2,** 19–36, pl. 1 and 2 (1914).
75. Mimicry and butterflies. *Not. Proc. Roy. Instn. London* (1915), **21,** 372–379 (1918).
76. Pierine butterflies and mimetic moths migrating from one valley to another in Selangor, F.M.S. *Proc.* **1921,** v–vi, pl. A (1922).
77. The terrifying appearance of *Laternaria* (Fulgoridae) founded on the most prominent features of the alligator. *Proc.* **1924,** xliii–xlix, pl. A (1924).
78. *Papilio dardanus*. The most interesting butterfly in the world. *J. E. Afr. Ug. Nat. Hist. Soc. Nairobi,* no. 20, pp. 4–22, pl. 1–3 (1924).
79. Mimicry in the butterflies of Fiji considered in relation to the Euploeine and Danaine invasions of Polynesia and to the female forms of *Hypolimnas bolina* L. in the Pacific. *Trans.* **1923,** 564–691, pl. 29–53, 9 figs. (1924).
80. The likeness to the male *Acraea althoffi althoffi* Dew. closer in the female than the male of the Uganda f. mimetica *dolabella* Hall of *Pseudacraea dolomena albostriata* Lathy. Complexity of the association to which these species belong. Evidence of the attacks of enemies. *Proc.* **1924,** cxl–cxlv (1925).
81. Mimicry in African butterflies of the genus *Charaxes* with a classification of the species. *Int. Congr. Ent. III* (*Zurich*), **2,** 518–575 (1926).
82. The Euploeine associations of the New Hebrides and their relation to those of Fiji. *Proc.* **1,** 47–54, 3 tables (1927).
83. On the male and female forms of the African Pterothysanid moth *Hibrildes norax,* Druce. (Appendix to 'The variability of species in the Lepidoptera, with reference to abundance and sex', by R. A. Fisher & E. B. Ford.) *Trans.* **76,** 380–384, pl. 12 (1928).
84. Ants as models for mimicry. *Zool. Anz.* **82,** 79–86 (1929).
85. Two specially significant examples of insect mimicry. *Trans.* **79,** 395–398, pl. 14–15 (1931).
86. Attempts to disprove the theories of warning colours, mimicry and protective resemblance in insects. *Int. Congr. Ent. V* (*Paris*), **2,** 33–44 (1933).
87. Fifty years in our study of protective resemblances as exemplified in the order Insecta. *Ent. Rec.* **50,** 119–123 (1938).

H. Insect Bionomics

88. Some experiments upon the protection of insects from their enemies by means of an unpleasant taste or smell. *Rep. Brit. Ass.* **1886,** 694–695 (1887).
89. The experimental proof of the protective value of colour and markings in insects in reference to their vertebrate enemies. *Proc. Zool. Soc.* **1887,** 191–274 (1887).

90. Further experiments upon the protective value of colour and markings in insects. *Rep. Brit. Ass.* **1887,** 763–765 (1888).
91. The secretion of pure aqueous formic acid by Lepidopterous larvae for the purpose of defence. *Rep. Brit. Ass.* **1887,** 765–766 (1888).
92. (With Cora B. Sanders.) An experimental inquiry into the struggle for existence in certain common insects. *Rep. Brit. Ass.* **1898,** 906–909 (1899).
93. [Seasonal dimorphism of *Precis*.] *Proc.* **1898,** xxiv–xxvii (1898).
94. A brief discussion of A. H. Thayer's suggestions as to the meaning of colour and pattern in insect bionomics. *Trans.* **1903,** 570–575 (1903).
95. Predaceous insects and their prey. *Trans.* **1906,** 323–409 (1907).
96. A note on the cryptic resemblance of two South American insects, the moth *Dracenta rusina*, Druce, and the Locustid *Plagioptera bicordata*, Serv. *Trans.* **1906,** 533–539, pl. 32 (1907).
97. Transformational deceptive resemblance in insects. *Proc.* **1922,** xlvii–xlix (1923).
98. Protective resemblance borne by certain African insects to the blackened areas caused by grass fires. *Int. Congr. Ent. III* (*Zurich*), **2,** 433–451, Tab. 11 (1926).
99. British insectivorous bats and their prey. *Proc. Zool. Soc. Lond.* **1929,** 277–303 (1929).
100. The Uvarov theory of locust migration and its possible bearing upon butterflv migration. *Proc.* **4,** 16–20 (1929).
101. Paraseme and parasematic as convenient words to describe appearance and behaviour adapted to deflect or mislead an enemy's attack. *Proc.* **5,** 16–17 (1930).
102. Association of birds' nests with nests of insects. *Proc.* **6,** 54–56 (1931).
103. Indirect evidence that parasematic eye-spots are advantageous in the struggle for existence. *J. Ent. Soc. S. Engl.* **1,** 2–3 (1932).

I. Geographical Distribution

104. Mimicry in the butterflies of Mauritius and Bourbon. *Proc.* **1908,** iv–vii (1908).
105. On the species of *Neptis* in the islands to the east and north-west of Madagascar. *Proc.* **1908,** xxxiii–xlii (1908).
106. Contrasts in colouring between certain species of butterflies from the Lagos district and their geographical races at Entebbe. *Proc.* **1911,** lxxxix–xci (1912).
107. The proportions of the female forms of *Papilio polytes*, L., in the different parts of its geographical range. *Proc. Ent. Mtgs. Pusa*, **3,** 903–905 (1920).
108. The proportion of the female forms of *Papilio polytes*, L., in Dehra Dun, United Provinces, and Bihar. *Proc. Ent. Mtgs. Pusa*, **4,** 259–269 (1921).
109. The Ethiopian races of *Heodes phlaeas* L. *Proc.* **1922,** li–lvi (1923).
110. The geographical races of *Charaxes ansorgei*, Rothsch., and their mimetic associations. *Proc.* **7,** 6–9 (1932).

J. Miscellaneous Addresses and Articles

111. C. R. Darwin. Colours of animals. (Articles in) *Encycl. Brit.* (1902).
112. William John Burchell. A lecture to the British and South African Associations. *Rep. Brit. and S. Afr. Ass.* (1905) **3,** 57–110, 1 pl. Capetown (1905).
113. Science and the great war. (Romanes lecture.) Oxford (1915).
114. Eugenics problems after the great war. (Galton lecture.) *Eugen. Rev.* **8,** 34–49 (1916).
115. The inspiration of the unknown. (Presidential address.) *S. East. Nat. Lond.* **1921,** 1–34 (1921).
116. The relation between pure and applied biology. (Presidential address.) *Ann. Appl. Biol.* **11,** 271–277 (1924).
117. Thomas Henry Huxley. (Centenary lecture.) *Nature*, **115,** 704–708 (1925).

118. A hundred years of evolution. (Presidential address, Section D.) *Rep. Brit. Ass.* **1931,** 71–95, pl. 1-2 (1932).
119. Introduction to *The history of the Entomological Society of London,* 1833–1933, by S. A. Neave (London), xxix–xlvi (1933).
120. Evidence that the growth of the Dead-nettle, *Lamium album* L., is stimulated by the presence of the Stinging-nettle, *Urtica dioica* L. *Proc. Linn. Soc.* Session 148, 83–86, pl. 1 (1936).
121. Evidence that the growth of the Dead-nettle, *Lamium album* L., is stimulated by the presence of the Stinging-nettle, *Urtica dioica* L. Further observations. *Proc. Linn. Soc. Lond.* Session **149**, 1–6, pl. 1–2 (1937).
122. The history of evolutionary thought as recorded in meetings of the British Association. (Presidential address.) *Rep. Brit. Ass.* **1937,** 1–23 (1937).

K. Obituary Notices

123. August Friedrich Leopold Weismann, 1834-1914. *Proc. Roy. Soc. B,* **89,** xxvii–xxxiv (1916).
124. Raphael Meldola, 1849-1915. *Proc. Roy. Soc. A,* **93,** xxxii–xxxvii, 1 pl. (1917).
125. Edward Saunders, 1848-1910. *Proc. Roy. Soc. B,* **91,** xii–xvii, 1 pl. (1920).
126. Roland Trimen, 1840-1916. *Proc. Roy. Soc. B,* **91,** xviii–xxvii, 1 pl. (1920).
127. Alfred Russel Wallace, 1823-1915. *Proc. Roy. Soc. B,* **95,** i–xxxv, 1 pl. (1923).
128. Frederick Augustus Dixey, 1855-1935. *Obit. Not. Roy. Soc.* **1,** 465–474, 1 pl. (1935).

L. Books

129. *The Colours of Animals.* London (1890).
130. *Charles Darwin and the Theory of Natural Selection.* London (1901).
131. *Essays on Evolution,* 1889-1907. Oxford (1908).
132. *Charles Darwin and the Origin of Species.* London (1909).
133. *John Viriamu Jones and other Oxford memories.* London (1911).

M. Contributions by others, edited, or with important comments, by Poulton

134. Five years' observations and experiments (1896–1901) on the bionomics of South African insects, chiefly directed to the investigation of mimicry and warning colours. (By G. A. K. Marshall) *Trans.* **1902,** 287–584, pl. 9–23 (1902).
135. On the relationship between certain West African insects, especially ants, Lycaenidae and Homoptera. (By W. A. Lamborn) *Trans.* **1913,** 436–498, pl. 20–29 (1913).
136. Five years' observations (1914–1918) on the bionomics of Southern Nigerian insects, chiefly directed to the investigation of Lycaenid life-histories and to the relation of Lycaenidae, Diptera, and other insects to ants. (By the late C. O. Farquharson) *Trans.* **1921,** 319–448, pl. 9–19, figs. 1–6 (1921).
137. *A Naturalist in Borneo,* by the late R. W. C. Shelford. London (1916).