

and Columbia; of the former one was by Mr Lucas on specimens collected by Mr Barraud and the other by Dr H. Scott in 1923 on those he collected in the Pyrenees.

One paper occurs on the Rhyncota by Dr Chapman on specimens collected by Mr Kirkaldy.

With regard to the countries in which collecting took place France appears the most popular with 91 articles on the subject; Switzerland comes next with 76; Italy has 37 and Spain 22. Greece has 13, Germany and the Tyrol 11 each, Turkey and Austria 8, 4 each are concerned with Norway and Belgium and 3 with Hungary. Finland, Bulgaria and Portugal are dealt with in 2 each and Malta in 1. These are all the European countries mentioned except for a few notes on Orthoptera in Holland. Although Sweden has been visited and reported on elsewhere we have no paper on the subject. Denmark and Holland seem to be left severely alone; this is strange as both are so easy of access; perhaps some entomologist may be found enterprising enough to visit them.

Outside Europe but still near it we find 3 papers on Algeria, 7 on Egypt, 13 on Syria (including Palestine) and 5 on Asia Minor. Further afield 2 treat of Persia, 6 of India (including Mr Sevastopulo's descriptions of Indian larvae found in Calcutta), 2 of Ceylon and 1 each of Java, Kurdistan and Hong Kong. Various parts of Africa are dealt with in 5 papers, and Central and South America in 13. These do not include the wide range visited by Dr Burr and cited above in writing of the Orthoptera. Contributors to the *Ent. Rec.* therefore cover a wide range and must advance in no slight degree the knowledge of distribution of species.

---

## FIFTY YEARS IN OUR STUDY OF PROTECTIVE RESEMBLANCES AS EXEMPLIFIED IN THE ORDER INSECTA.

By SIR EDWARD B. POULTON, D.Sc., M.A., F.R.S., Hon. Life Pres.  
R.E.S.L., F.R.E.S., F.L.S., &c.

In attempting to bring forward a brief account of work and discussion upon Protective Resemblance, Warning Colours, and Mimicry, both Batesian and Müllerian, during the past half century, it is, I think, well to devote a brief section to their earlier history.

One of the most significant of the early statements upon Protective Resemblance was that made by A. R. Wallace in his section of the joint essay on Natural Selection read before the Linnean Society on July 1st, 1858:—"Even the peculiar colours of many animals, more especially of insects, so closely resembling the soil or leaves or bark on which they habitually reside, are explained on the same principle; for though in the course of ages varieties of many tints may have occurred, *yet those races having colours best adapted to concealment from their enemies would inevitably survive the longest.*" Much earlier than this W. J. Burchell wrote of "the intention of Nature" in giving to the Chameleon its power of changing colour, and to a pebble-like Acridian and Mesembryanthemum a resemblance protecting them from their natural enemies (1). He also wrote of plants "in this arid country, where every juicy vegetable would soon be eaten up," being given "an acrid or poisonous juice, or sharp thorns, to preserve the species from annihilation" (2). Both Protective and Aggressive Resemblances were also



recognised by Erasmus Darwin who wrote:—"The colours of many animals seem adapted to their purposes of concealing themselves either to avoid danger, or to spring upon their prey" (3). The Variable Protective Resemblance of the Octopus was observed by Charles Darwin in the Cape de Verde Islands in 1832. Writing a little later to Henslow, he referred to its "most marvellous power of changing its colours, equalling any chameleon, and evidently accommodating the changes to the colour of the ground which it passed over" (4). Wallace first suggested the meaning of the conspicuous Warning Colours of insects in reply to a letter from Darwin who was puzzled by the brilliant appearance of many caterpillars which could not be explained by Sexual Selection. The interpretation offered—an advertisement of distastefulness—received confirmation from the experiments of Jenner Weir and A. G. Butler (5), and has been the subject of investigation and discussion up to the present day. The superficial resemblances between insects of different groups were known long before the publication of Bates' classical memoir on Mimicry, the best examples known to me being those recorded by W. J. Burchell in his manuscript notebooks and on labels in his collections made in S. Africa (1810-15) and Brazil (1825-30).

H. W. Bates' paper explaining the resemblances between the butterflies of the Amazons was published in *The Transactions of the Linnean Society* for 1862, four years after the Darwin-Wallace Essay on Natural Selection was read in 1858. It was followed in the *Linnean Transactions* of 1865 by Wallace's description of analogous resemblances between Malayan butterflies, and in 1868 by Roland Trimen on those between the butterflies of S. Africa. Ten years later Fritz Müller first brought forward his hypothesis, explaining a large proportion of the examples of Mimicry as produced by the advantageous resemblance between distasteful species rather than by the resemblance of a palatable mimic to its distasteful model (6).

The year before the Jubilee period the earlier experimental work on the protective value of insect colours was brought together by the present writer (7). Much help was given by Jenner Weir and Raphael Meldola, whose name must always be remembered in the history of evolutionary thought during the early years of the period and for many before it. His work as Darwin's "general agent" in Entomology is briefly described in this journal (8). The immensely important discovery of protective counter-shading, explaining the meaning of the white undersides of animals, was first published in 1895 by Abbott H. Thayer in the April and October issues of "The Auk," the American journal of Ornithology, and a condensed account of the two articles appeared in "Nature" (1902). The author communicated a paper on the subject to the *Ent. Soc. Lond.* in 1903 (p. 553), discussed by the present writer on p. 570. The subject was expanded and finely illustrated in "Concealing Coloration in the Animal Kingdom," 1909, by his son, Gerald H. Thayer, with a second edition in 1918 (9). The number of publications on the concealing (Procryptic) adaptations of insects is so large that, in this brief article, I feel that I must not do more than refer to W. A. Lamborn's discovery of the method by which the larva of an African Tabanid fly prevents the wide cracks formed in the dry season from invading the clay cylinder in which the pupa lies hidden, and thus exposing it to attack (10). In a paper (11) read before the Lin-



nean Society in 1898 I attempted to describe under different heads the chief general characteristics of Mimetic Resemblances, Batesian and Müllerian, and to show that the evolution of each one had required the operation of Natural Selection. After the lapse of 40 years I venture to quote a sentence from A. R. Wallace's letter written 28th December 1898, the day on which Roland Trimen also sent congratulations:—"It is the completest, and most conclusive article that has yet appeared, and to all who *will* read and *can* reason, it is absolutely unanswerable."

Probably the most important contribution to our subject in the Jubilee years and one which has been largely responsible for the dominant position of Africa as a field for Bionomic research in the present century, is the Memoir (12) by G. A. K. Marshall (now Sir Guy) on observations and experiments on insects during the period 1896-1901. An American friend, after reading it, wrote to me:—"It is the paper we have all been waiting for." In spite of its length, close on 300 pages, and the great variety of the subjects treated, the memoir is remarkably easy to consult being provided with an elaborate but very clear table of contents and a separate index. It is of course impossible to attempt any account of this admirable work, but I cannot help referring to the first three plates illustrating the injuries to be found upon the wings of butterflies, which, when the specimens are fresh and unworn, must nearly always have been inflicted by enemies, especially birds. This evidence, powerfully enforced by Marshall's later publication on "Birds as a factor in the Production of Mimetic Resemblance among Butterflies" (13), led on to very many observations recorded by Prof. Hale Carpenter, Collenette, Lamborn and others.

The late R. Shelford, while Curator of the Sarawak Museum, wrote on the "Mimetic Insects and Spiders from Borneo and Singapore" (14), a paper of especial importance because of the variety of insect families which are considered and illustrated by fine coloured plates. Ten years later he published "Mimicry amongst the Blattidae" (15), describing and figuring many "Mimetic Cockroaches and Beetle models"—striking examples in a family which had rarely if ever been studied from this point of view. A very interesting nesting association between birds and social insects—Aculeates and Termites—is described by J. G. Myers (16), who concludes (p. 19) that the wasps, bees and ants "are all among the most vicious species" and holds that "association of birds with aculeates and of the latter *inter se*, corresponds to some definite ecological need," and that "we are justified in assuming that this need is protection." The long list of references also proves that this association has been observed by many naturalists.

The experimental method of investigating the palatability of protectively coloured and the unpalatability of conspicuous (Aposematic) insects and the validity of the results obtained were criticised by W. L. McAtee in 1912 (17) and again in 1932 (18), the years in which I wrote a reply (19). A few months later, on December 7th, the subject was discussed at the Entomological Society of London. The full report appears on pp. 79-105. Dr McAtee's rejoinder was communicated to the Society on 4th October 1933, appears in Pt. II of the *Proceedings*, pp. 113-120, and was followed by replies on 2nd May 1934, pp. 21-40, and by H. B. Cott's paper with four plates, pp. 109-120, including a brief ter-



minimal note stating that I did not propose to continue the discussion.

The following publications by four naturalists are of much significance in relation to Dr McAtee's criticisms.

I wish that space permitted an adequate account of Dr Frank Morton Jones' paper on "Insect Coloration and the Relative Acceptability of Insects to Birds" (20), describing experiments conducted on the island of Martha's Vineyard, Massachusetts, in 1930 and 1931. A feeding-tray was set up at the edge of an extensive woodland and supplied with water and food so that birds of several species were attracted to it; then from time to time freshly killed insects were placed upon the tray instead of or in addition to the other food and the visits recorded, having been observed from a distance through field-glasses. The extremely careful discussion of the evidence obtained led the author to conclude that, although insect acceptability to birds is relative, coloration has material influence upon it. Further experiments also proved that certain insects feeding on poisonous plants are refused by ants as well as by birds and also indicated that in these instances, but not in others, the deterrent qualities are derived from the plants. Two years later Dr Morton Jones published an account (21) of further experiments in the same locality in 1932-33, and in S. Florida during March and April 1933. The results of the earlier work were confirmed and the conclusion reached that "acceptability of insects is determined, not primarily by numbers and availability, but by bird preferences" (p. 452).

An important paper (22) published by Dr H. N. Kluijver in 1933 proves that the Starlings of two colonies near Wageningen, Holland, certainly show preferences and discrimination in selecting insect food for their young; also that McAtee has not convincingly shown that so-called protective adaptations are of no importance. R. Carrick in his very interesting and convincing "Experiments to test the efficiency of protective adaptations in insects" (23) proved that a bark-like geometrid larva motionless on a bare twig of hawthorn fixed near a nest containing young, was unseen by the parent wren but seized when lying on a tray below the nest. Finally, Prof. F. B. Isely has conducted extremely interesting and successful experiments upon the "Survival Value of Acridian Protective Coloration" (24), exposing the insects upon plots of differently coloured soil and recording the effect of attack by enemies upon those which harmonised with the surroundings as compared with those which contrasted.

I had hoped to conclude with brief reference to Prof. Hale Carpenter's replies to recent criticisms of natural selection as applied to insect ecology and to the evidence of bird attacks on butterflies which he has collected; also to the fine work of very many naturalists, especially in Africa, but the limit imposed by the editors is already much overpassed and I must regretfully bring this imperfect statement to a close.

#### REFERENCES.

1. *Travels in the Interior of Southern Africa*, Vol. I, Lond., 1822, pp. 310, 311.
2. *Ibid.*, p. 226. The same conclusions appear in a letter written by Darwin to G. H. Lewes in 1868 (*More Letters*, 1903, i, 308).
3. *Zoonomia*, i, 509, Lond., 1794.
4. *Life and Letters*, 1887, i, 235, 236.
5. See *Life and Letters*, iii, 93, 94, 1887, for two of Darwin's letters to Wallace in 1867; also the footnotes on p. 94.



6. *Zool. Anzeiger* (Carus), I (1878), pp. 54, 55. Translation in *Proc. Ent. Soc. Lond.*, 1915, pp. xxii, xxiii.
7. *Proc. Zool. Soc.*, 1887, pp. 191-274.
8. *Ent. Record*, XIII, No. 2, 1901, pp. 75, 76.
9. Both published by The Macmillan Co., New York. On pp. 21-23 of both editions the discoverer and his son generously refer to my early recognition of counter-shading in certain insects, although without any thought of its far-reaching importance. The references given are to *Trans. Ent. Soc. Lond.*, 1887, p. 294, and 1888, pp. 595-7.
10. *Proc. Roy. Soc.*, B, Vol. 106, pp. 83-87, pl. 5, 1930.
11. "Natural Selection the Cause of Mimetic Resemblance and Common Warning Colours," *Linn. Soc. Journ.—Zool.*, XXVI, 558-612, pls. 40-44, 1898. Reprinted, revised, as VIII in "Essays on Evolution," Poulton, Oxford, 1908.
12. *Trans. Ent. Soc. Lond.*, 1902, Pt. III, pp. 287-584, Pls. IX to XXIII.
13. *Trans. Ent. Soc. Lond.*, 1909, Pt. 3, pp. 329-383.
14. *P.Z.S.*, 1902, pp. 230-284, coloured pls. XIX-XXIII.
15. *P.Z.S.*, 1912, pp. 358-376, coloured pl. XLVIII.
16. *Trans. R. Ent. Soc.*, 83, Pt. 1 (June 1935), pp. 11-22, pl. II.
17. *Proc. Acad. Nat. Sci. Phila.*, 1912, pp. 281-364.
18. *Smithsonian Miscellaneous Collections*, Vol. 85, No. 7, 1932, pp. 1-201.
19. *Proc. V. Congr. Internat. Entom.*, Paris, 1932, pp. 33-44.
20. *Trans. Roy. Ent. Soc., Lond.*, Vol. 80, Pt. II (December 1932), pp. 345-385, pls. XVIII-XXVIII.
21. *Trans. Roy. Ent. Soc. Lond.*, Vol. 82, Pt. II (December 1934), pp. 443-453, pls. XVI, XVII.
22. "Bijdrage tot de Biologie en de Ecologie van den Spreeuw (*Sturnus vulgaris vulgaris* L.) gedurende Zijn voortplantingstijd." Published as "Verslagen en Mededeelingen van den Plantenziektenkundigen Dienst te Wageningen," No. 69, 146 pp., Wageningen, Jun. 1933. An abstract of the results of this paper appears in *Proc. Roy. Ent. Soc.*, Vol. VIII (1933-4), pp. 160, 161, 170-172.
23. *Trans. R. Ent. Soc. Lond.*, 85, pt. 4 (May 1936), pp. 131-139, pls. 1-3.
24. *Ecology*, Vol. 19, No. 3, July 1938, pp. 370-389.

## HALF-A-CENTURY OF ORTHOPTERA.

By MALCOLM BURR, D.Sc., F.R.E.S.

When the *Entomologist's Record* was launched, our beloved science had entered upon the last phase of its early period. The task of collecting, naming, and describing material and establishing classification was in full swing and something like a coherent system was crystallising out for most of the orders. Until well into the present century our literature consisted almost exclusively of faunistic catalogues and monographic revisions.

Orthoptera, in spite of their size and attractive appearance, had somewhat lagged behind the other orders, and in 1888 there were few orthopterists in Europe and none in Great Britain. Those who casually picked up our three dozen or so species, such as the Dales, Edward Saunders, George Porritt, C. A. Briggs, and a few others, could hardly find an author to whom to turn for comfort. Curtis' five beautiful plates of some of our outstanding species were already twenty-six years old, and after a reign of half-a-century Stephens was still the authority.

On the Continent the richer fauna was more encouraging, and men whose names stand out were then in full strength. Brunner von Wattenwyl, by birth Swiss but by service a *Hofrath* or Aulic Councillor and a high official in the post and telegraphs of Austria, was busy in Vienna. In both appearance and manner Brunner seemed to me a relict of the seventeenth century, and it was a proud and happy time for me when he took me into the field at Oberweiden, a classic spot, when there was





Poulton, Edward Bagnall. 1938. "Fifty years in our study of protective resemblances as exemplified in the order Insecta." *The entomologist's record and journal of variation* 50, 119–123.

**View This Item Online:** <https://www.biodiversitylibrary.org/item/95161>

**Permalink:** <https://www.biodiversitylibrary.org/partpdf/197940>

**Holding Institution**

Harvard University, Museum of Comparative Zoology, Ernst Mayr Library

**Sponsored by**

Harvard University, Museum of Comparative Zoology, Ernst Mayr Library

**Copyright & Reuse**

Copyright Status: In copyright. Digitized with the permission of the rights holder.

Rights Holder: Amateur Entomologists' Society

License: <http://creativecommons.org/licenses/by-nc-sa/3.0/>

Rights: <https://biodiversitylibrary.org/permissions>

This document was created from content at the **Biodiversity Heritage Library**, the world's largest open access digital library for biodiversity literature and archives. Visit BHL at <https://www.biodiversitylibrary.org>.