



*Theories of Mimicry, as illustrated by African Butterflies.*

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H. W. Bates, in his epoch-making paper ('Trans. Linn. Soc.' vol. xxiii. 1862), first gave an intelligible theory of mimicry, and accounted for the superficial resemblances which had been known for so long by supposing that the most dominant, well-defended, and conspicuous forms in a country become the models towards which natural selection leads many of the weaker hard-pressed species in the same locality. The material on which Bates' theory was formed was confined to tropical America, and his generalisation remained incomplete until it could be applied to the other great tropical regions. This want, however, was soon supplied by A. R. Wallace for the East ('Trans. Linn. Soc.' vol. xxv. 1866), and by Roland Trimen for Africa ('Trans. Linn. Soc.' vol. xxvi. 1870).

In Bates' original paper a certain class of facts—frequently mentioned and abundantly illustrated—cannot be explained under his theory of mimicry. This is the strong resemblance which is apt to exist between the dominant forms themselves, and which is as minute and as remarkable as the resemblance of the weaker for the stronger species. Bates pointed out that this was unsolved by his theory, and both he and Wallace were compelled to suggest the direct action of some unknown local influence as the possible cause. There the matter rested until Fritz Müller, in a paper published in Kosmos for May 1879, suggested an explanation, viz., that the dominant forms gain an advantage by this resemblance, inasmuch as it facilitates the education of their enemies by giving them fewer patterns to learn. The necessary waste of life by which the education of young birds, &c., is brought about is here divided between the various species of a closely convergent group, instead of being contributed by each member independently. The chief sub-families of butterflies which in tropical America appear to be specially distasteful to insect-eating animals, and which are specially mimicked by others, are the *Danainæ*, *Ithomiinæ*, *Heliconinæ*, and *Acræinæ*. Of these the second and third are confined to this part of the world. The resemblances which Fritz Müller explained are those which occur very commonly between the *Danainæ*, *Ithomiinæ*, *Heliconinæ*, and less commonly the *Acræinæ* of any locality. In order to complete this theory it was necessary to test its application in other parts of the world.

In the East the butterflies which take the place of the four above-named sub-families belong almost exclusively to the *Danainæ*, the *Acræinæ* being represented by very few species. The *Danainæ* are, however, extremely rich in species, and F. Moore first pointed out in 'Proc. Zool. Soc.', 1883, p. 201, that there is the same relationship between the species of this dominant group that obtains between those of tropical America. Not only do *Danainæ* of very different genera closely resemble each other, but there is often a strong likeness between the species belonging to the two chief divisions of the sub-family—the *Danaina* and *Euploeina*. As in America, these resemblances are always between the species of the same locality.

While, however, Müller's theory received full confirmation from the facts observed in India and the tropical East generally, no attempt has been made until now to apply it to the African lepidopterous fauna. I have therefore examined this fauna from the Müllerian standpoint, and find that in it too the same relationship can be traced.

The dominant distasteful groups of Africa are the *Acræinæ*, which have their metropolis here, and the *Danainæ*. The latter are chiefly represented by the species of the peculiar African genus *Amauris*, and by the abundant and widespread *Danais* (*Limnas*) *chrysippus*. I first looked for evidence of convergence between the *Acræinæ* and *Limnas chrysippus*, and soon found what appeared to

be evident traces of it. Such species as *Planema esebria* (certain forms of), *Acræa petraea* (female), *A. oppidia*, and, above all, *A. encedon* (*lycia*) bear a considerable resemblance to *L. chrysippus*, inasmuch as all of them possess a dark tip to the fore wing crossed by a white bar, as in the Danaïne butterfly. Looking at the near allies of these species and at the *Acræinæ* as a whole, we may feel confident that this black-and-white tip is not an ancestral character of the group, but a comparatively recent modification. Again, the fact that this character is sometimes more strongly developed in, and sometimes confined to, the female sex agrees with the corresponding relationships in other parts of the world, and furthermore supports the conclusion as to the recent acquisition of the markings.

Convergence between the *Acræinæ* and *Danainæ* of the genus *Amauris* was next looked for and many examples found. Thus *Acræa johnstoni* of East Central Africa certainly suggests the appearance of one of the *echeria* group, such as *A. hanningtonii*, found in the same locality; while in West Africa *Acræa lycoa* resembles the black-and-white *Amauris damocles* and *A. egialea*. Similar resemblances in the West are to be seen between the large black-and-white females of the numerous species of the *Acræine* genus *Planema* and other *Acræas* in the same locality, such as *A. carmentis* (female) and *A. jodutta* (female), while the species referred to, of both *Acræine* genera, bear some considerable resemblance to an abundant West African black-and-white Danaïne—*Amauris niavius*. Similar relationships occur in the South-East, where *Acræas*, such as *Planema esebria* (white form of female) and *P. aganice* bear considerable resemblance to the abundant black-and-white Danaïnes—*Amauris ochlea* and *A. dominicanus*.

It was of great interest to prove that the members of these convergent groups occur, not only in the same place, but at the same time. Mr. Guy A. K. Marshall has kindly done this work, sending me several groups captured at one place in a single day. At Malvern, near Durban, Natal, on March 6, and again on March 30, 1897, he captured *Limnas chrysippus* and several species of *Acræa*, with the black-and-white tip to the wing. On March 27 he captured, in the same locality, the black-and-white *Planemas* (*Acræinæ*) *P. esebria* and *P. aganice*, together with an abundant black-and-white *Neptis* (*N. agatha*) and a closely similar day-flying moth, *Nyctimeris apicalis*. It is very probable that these latter forms do not mimic in the Batesian sense, but are themselves specially defended and fall into a Müllerian group. Mr. Marshall did not, on that day, capture any of the black-and-white *Danainæ*. Mr. D. Chaplin, however, on April 5, 1896, obtained at Berea, a suburb of Durban, *Amauris ochlea* and *Planema aganice*, as well as *Limnas chrysippus*, with two species of convergent *Acræas* (*A. encedon* and *A. petraea*). Mr. F. D. Godman and Mr. O. Salvin have kindly presented these specimens to the Hope Collection at Oxford.

I think it must be admitted that there is now strong evidence for the same convergence between specially protected abundant African species from the same locality as that which is already well known in the tropical East and in tropical America. Various degrees of perfection exist, and it is in every way probable that the resemblance of some members to the standard of their group is not of long standing, and will improve in the future.

Other facts in the colouring of African Lepidoptera also support this interpretation. Thus certain *Lycænidae* of the genera *Pentila* and *Alana* are known to fly very slowly, and in the case of the latter to feign death when captured—characteristics of unpalatable forms. While they thus differ in habits from *Lycænids* generally, they also differ entirely in their appearance, which rather suggests that of an *Acræa*. The same is true of moths belonging to many groups, and perhaps of the abundant butterflies of the genus *Bybha*. Similarly the large group of Lepidoptera, which has for its centre the abundant day-flying moths of the genus *Aletis*, appears to be moulded upon the colouring and pattern of *Limnas chrysippus*, differing only in an even greater conspicuousness, due to the white spots or rings on the black body, and the highly developed black-and-white border to the hind wing. It is probable that the common species of the genus *Euphadra*, which form some of the most conspicuous members of this group, are themselves specially protected. To take one more example, certain species of the Pierine genus *Mylothris*

are rendered specially conspicuous by the interrupted black border to the hind wings, the interruptions extending along the hind margin of the fore wings. A white butterfly with such a border becomes an extremely conspicuous object, and this appearance of *Mylothris* is mimicked, more or less perfectly, by species from a number of Pierine genera, such as *Nepheronia*, *Belenois*, *Callosune*, &c. This is usually explained as an example of true Batesian mimicry, but it is, perhaps, more probable that the *Pierinae* are very largely a specially protected group, many of the genera of which, so to speak, combine their advertisements, and thus share between them the loss of life which must necessarily ensue during the education of each generation of their enemies.

I think sufficient evidence has been brought forward to show that the theory of mimicry, or rather of common warning (synaposematic) colours, which will always be associated with the name of Fritz Müller, may claim abundant examples in Africa as well as in the other parts of the world in which it has already been proved to hold.

