

DANAUS CHRYSIPPUS AND ITS POLYMORPHIC MÜLLERIAN MIMICS IN TROPICAL AFRICA (LEPIDOPTERA: NYMPHALIDAE: DANAINAE)

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ABSTRACT.— Theoretically, Müllerian mimicry, in which there is convergence of coloration between unrelated unpalatable species, should lead to uniformity in appearance, not polymorphism. Hence the discovery in Africa of polymorphic Müllerian mimics in the Danainae and Acraeinae suggested an evolutionary problem of special interest. Field and laboratory work in Uganda and Sierra Leone in 1964-72 demonstrated a statistical association between the occurrence and relative frequencies of corresponding colour forms in *Danaus chrysippus* and *Acraea encedon* which was deemed as confirmation of the Müllerian relationship between the two species. There were, however, certain anomalies which at the time could not be resolved. Later (1976), it was discovered that what had been called *A. encedon* is in reality two sibling species, *A. encedon* and a new one, named as *A. encedana*. The two differ in the structure of both male and female genitalia and in the coloration and the food-plants of the larvae. Some color forms are shared, others are restricted to one species only. The recognition of the additional species has enabled a re-assessment of the polymorphic Müllerian association between *D. chrysippus* and the two *Acraea* species. What emerges is that throughout tropical Africa there is a close mimetic association between *D. chrysippus* and *A. encedana*, and a much weaker (in places, non-existent) association between *D. chrysippus* and *A. encedon*. The possible origin of the mimetic and non-mimetic polymorphism in all three species is discussed in terms of hybridization of previously allopatric and monomorphic populations which have met as a consequence of recent expansions of geographical range resulting from forest clearance and the spread of savanna-like conditions.

KEY WORDS: *Acraea*, Acraeinae, Commelinaceae, *Danaus*, Ethiopian, genetics, Ghana, Leguminosae, mimicry, Nigeria, polymorphism, Sierra Leone, Tanzania, Uganda, West Africa.

INTRODUCTION

Müllerian mimicry involves convergence in coloration between two or more species of usually unrelated animals to an extent that potential predators cannot discriminate between them. The coloration is usually bold and conspicuous and all the species in the association are known or believed to be unpalatable, although not necessarily equally so. Theoretically, Müllerian mimicry should not lead to polymorphism in coloration; in contrast, Batesian mimicry, which involves unpalatable models and palatable mimics, often results in polymorphism in the mimics in which each of several color forms resembles an unpalatable model. Almost all known examples of mimicry in butterflies fit one or other of these two categories, but it is acknowledged that there is no absolutely rigid distinction between them, and that in many mimetic associations it is not always clear whether the mimicry is Müllerian or Batesian.

The monarch or milkweed butterflies, Danainae, are generally recognized as being unpalatable to predators and many species (especially in the tropics) are models for Batesian mimics which are often polymorphic; some species are also involved in Müllerian associations with other unpalatable butterflies. The existence in tropical Africa of a danaine, *Danaus chrysippus* (Linnaeus), which is conspicuously polymorphic in parts of its geographical range but monomorphic in other parts, and the

occurrence of corresponding polymorphic forms in an unpalatable acraeine, *Acraea encedon* (Linnaeus), suggested an evolutionary problem of special interest and worthy of examination.

We started investigations in Uganda in 1962 and in 1964-66 conducted a large-scale capture-mark-release project to obtain estimates of the relative frequency of the corresponding polymorphic forms of the two species. We later extended investigations to Sierra Leone, Ghana and Tanzania, and to a lesser extent elsewhere in tropical Africa. We designed breeding experiments to determine the genetics of the polymorphisms, and undertook ecological work which led us to the conclusion that these butterflies, both of which are open country (savanna) species, had expanded their geographical range and increased in abundance as a result of human destruction of the forest and the conversion of much of the forest region to a savanna-like agricultural environment. The results appeared between 1965 and 1991 in some 40 scientific publications. Not all of these are directly relevant to the problem of polymorphic Müllerian mimicry; those that are include Owen (1970, 1971), Owen and Chanter (1969), and Owen and Smith (1991).

ANOMALOUS RESULTS AND THEIR SOLUTION

Work in Uganda in 1964-66 indicated a statistical correlation between the frequencies of matching polymorphic forms of *D.*



Plate 1. Last instar larvae: 1. *Acraea encedon*. 2. *Acraea encedana*.

chrysippus and *A. encedon* (Owen and Chanter, 1969), but there were certain anomalies which at the time could not be satisfactorily explained. Similar and additional anomalies occurred in 1966-70 when we analysed the situation in Sierra Leone (Owen and Chanter, 1971), and we were left with a strong feeling of having missed a vital aspect of the population biology of one or both species. The problems we recognized were:

1. During genetic experiments, we failed to breed and therefore to ascertain the mode of inheritance of one of the commoner color forms of *A. encedon*. Thus while it was possible to obtain fertile matings between individuals from sites as far apart as Sierra Leone, Ghana and Uganda, it was impossible to secure successful matings between individuals from two Sierra Leone sites. Attempted matings were observed between butterflies of different color forms, but none was successful. At the time it was suggested that some degree of reproductive isolation had developed between butterflies from different sites from within Sierra Leone and that *A. encedon* was in the process of incipient speciation (Chanter and Owen, 1972; Owen *et al.*, 1974).

2. In West Africa west of Nigeria, *D. chrysippus* is monomorphic. At some sites in Sierra Leone, hardly any of the polymorphic color forms of *A. encedon* matched the local form of *D. chrysippus*, while at other sites there was a 100% match; this meant that the degree of Müllerian mimicry varied incomprehensibly from place to place (Owen and Chanter, 1971). In the Gambia, at the western limit of the range of the two species, both are monomorphic, with no match in coloration.

3. In Uganda, the relative frequency of the polymorphic forms of *A. encedon* varied from site to site, even between sites separated by only a few km, yet the relative frequency of the four polymorphic forms of *D. chrysippus* was stabilized over a large

area. If indeed these two unrelated butterflies are Müllerian mimics it was (at the time) difficult to explain why one species should exhibit inter-site differences in the relative frequency of forms while the other did not.

4. When two species are involved in a Müllerian association, each is both model and mimic; this does not imply that each is equally unpalatable, but it would be incorrect to speak of one as the model and the other as the mimic. In *A. encedon* a high but geographically variable proportion of color forms do not correspond with any forms known in *D. chrysippus*; we designated these forms as "non-mimetic". A parallel situation does not occur in *D. chrysippus*, and so the occurrence of non-mimetic *A. encedon* was something of a puzzle.

The next event had been partly predicted from our failure to obtain matings between certain color forms of *A. encedon*. Pierre (1976a) separated what we had been calling *A. encedon* into two species, *A. encedon* and an undescribed one which was named *A. encedana* Pierre. The adult butterflies are almost identical and often occur at the same sites, but they differ markedly and consistently in the structure of male and female genitalia, illustrated in Pierre (1976a, 1976b). The larvae are strikingly different: those of *A. encedon* are mainly black (Fig. 1, Pl. 1) and feed on *Commelina*, a monocotyledon (Commelinaceae), while those of *A. encedana* are mainly yellow (Fig. 2, Pl. 1) and feed on *Desmodium*, a member of the Leguminosae, a very different and unrelated plant. Some of the polymorphic forms previously ascribed to *A. encedon* occur in both species, some are restricted to *A. encedon*, others to *A. encedana*. There is nothing to suggest that *D. chrysippus* is other than a single species, and hence the anomalies arose because what we had considered one species is in reality two.

The failed breeding experiments can now be explained: the color form which would not mate with *A. encedon* belonged to *A. encedana* and we were thus attempting to cross two species. The discovery of the second species clearly indicates that in our early work in Uganda and to a lesser extent in Sierra Leone, we had confused two species, the result of which is that the statistical analysis of inter-site differences in the relative frequencies of color forms and of Müllerian mimicry with *D. chrysippus*, particularly in Uganda, but also in other areas, requires re-assessment. All the work (both field sampling and laboratory breeding) on *D. chrysippus* stands as it is, and all genetic work on *A. encedon* is sound: we simply happened by chance to establish laboratory stock of *A. encedon* rather than *A. encedana*.

MÜLLERIAN MIMICRY IN UGANDA AND SIERRA LEONE

We dissected 361 *Acraea* specimens, mostly from a random sample obtained in 1991 from the same sites as those examined in 1964-66; also a few from a random sample obtained in 1971, and a few from selected specimens retained from the 1964-66 mark and release project. This enabled re-arrangement of the Müllerian association with three species rather than two. The result is shown in Plate 2. The color forms of *D. chrysippus* and *A. encedon* have in the past received Latin names and, as before, we use these, sometimes in combination with descriptive English names. Pierre (1976b) cleverly invents similar names for *A.*



Plate 2. Corresponding color forms of *Acraea encedon*, *Danaus chrysippus* and *Acraea encedana*. *A. encedana*: 1. *encedana*, 2. *alcippina*, 3. weak *alcippina*, 4. *dairana*, 5. *alcippina-dairana*. *D. chrysippus*: 6. *aegyptius*, 7. *alcippus*, 8. weak *alcippus*, 9. *dorippus*, 10. *albinus*. *A. encedon*: 11. *encedon*, 12. *daira*.

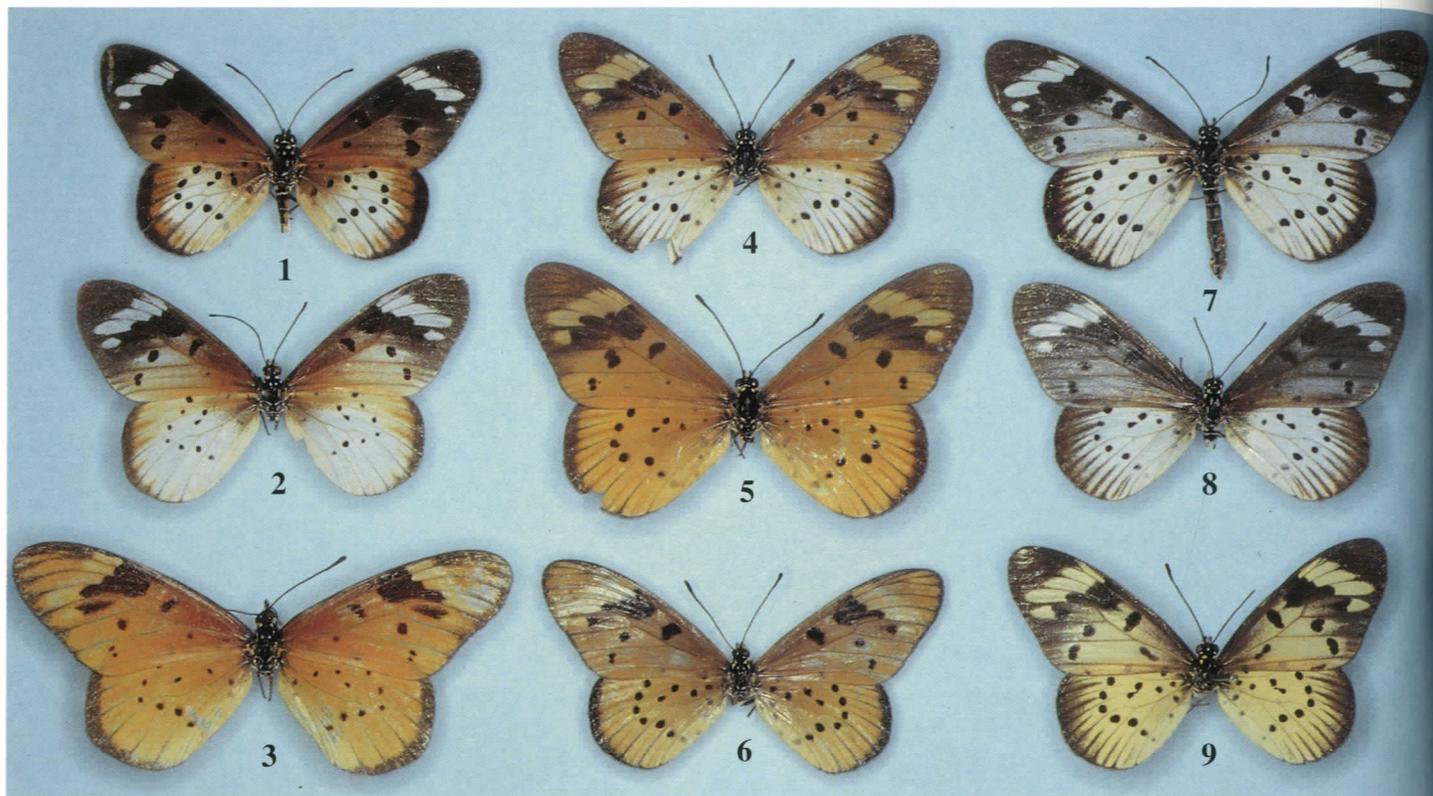


Plate 3. Non-mimetic and weakly-mimetic forms of *Acraea encedon* and weakly mimetic forms of *Acraea encedana*. *A. encedana*: 1. suffused *alcippina*, 2. white *alcippina*, 3. *encedana-dairana* (all weakly-mimetic). *A. encedon*: 4. *commixta*, 5. *infuscata*, 6. *encedon-daira* (all weakly-mimetic); 7. *lycia*, 8. suffused, *lycia*, 9. *sganzini* (all non-mimetic).

encedana which draw attention to similarities with corresponding forms in *A. encedon*. One form, *alcippina*, previously ascribed to *A. encedon*, occurs only in *A. encedana*, and so the original name is retained.

There are essentially four forms of *D. chrysippus*: *aegyptius*, *alcippus*, *dorippus* and *albinus*. What we have called weak *alcippus* in Plate 2 is a variable heterozygote between *aegyptius* and *alcippus*; the white in the hindwing of weak *alcippus* may be considerably smaller in extent than shown in Plate 2. The four forms in *D. chrysippus* are matched by four forms in *A. encedana*, and weak *alcippus* is matched by weak *alcippina* (genetics not known, but probably also a heterozygote). Only two forms of *A. encedon* enter the Müllerian association, which immediately suggests that in Uganda *D. chrysippus* and *A. encedon* are less closely associated than *D. chrysippus* and *A. encedana*. Tentatively, we do not postulate Müllerian mimicry between the two *Acraea* species as we suspect the polymorphism evolved before speciation occurred.

Plate 3 shows three color forms of *A. encedana* and three of *A. encedon* considered as poor mimics as they cannot be accurately matched with corresponding forms of *D. chrysippus*. In Uganda, all of these forms are relatively infrequent but forms *commixta* and *infuscata* of *A. encedon* are frequent in West Africa.

As shown in Plate 3, there are three non-mimetic forms of *A. encedon*, one of which, *lycia*, is relatively frequent in Uganda and even more frequent in West Africa. No non-mimetic forms have been found in *A. encedana*, adding to the supposition that this species is more closely associated with *D. chrysippus* than *A. encedon*.

Armed with the knowledge that some color forms are restricted to *A. encedon*, some to *A. encedana*, while others are shared, we were able to estimate the frequency of the two species (previously considered as one) in the 1964-66 mark and release project. The precise statistical details as to how this was done will appear in a forthcoming paper. The result is that the inter-site differences in the frequency of color forms in what at one time was considered *A. encedon* were mainly due to differences in the relative frequency of the two species at each site. In each species, with only two exceptions which could result from sampling errors, the frequency of color forms is homogeneous across sites, as is the frequency of color forms in *D. chrysippus*. The establishment of homogeneity in all three species in the Kampala region eliminates the problem of what we had thought as heterogeneity in *A. encedon* and homogeneity in *D. chrysippus* (Owen and Chanter, 1969).

Table 1 gives color form frequencies in the four mimicry groups in *A. encedana*/*D. chrysippus* in the 1964-66 project. All *D. chrysippus* are mimetically associated with *A. encedana*, but 3.6% of *A. encedana* are considered as poor mimics (Plate 3). The frequencies of the corresponding forms in the four groups are significantly ranked ($p = 0.04$), providing strong evidence of a numerical association.

The relationship between *A. encedon* and *D. chrysippus* is quite different, as shown in Table 2. A quarter of the color forms of *A. encedon* are non-mimetic; these are chiefly the white form *lycia* (Plate 3). Unlike *A. encedana*, there are no white hindwing forms to match *alcippus* and *albinus* in *D. chrysippus*, which means that so far as *A. encedon* is concerned, 40.9% of the *D.*

TABLE 1. Comparison of color form frequencies in *A. encedana* and *D. chrysippus* in the Kampala region of Uganda, 1964-66.

Mimicry groups and color forms	N	%
1. <i>encedana</i> / <i>aegyptius</i>	9599 263	69.5 49.6
2. <i>alcippina</i> / <i>alcippus</i>	2830 198	20.5 37.4
3. <i>dairana</i> / <i>dorippus</i>	751 50	5.4 9.4
4. <i>alcippina-dairana</i> / <i>albinus</i>	196 19	1.4 3.6
Poor mimics (<i>A. encedana</i>)	437	3.6
Total <i>A. encedana</i>	13813	
Total <i>D. chrysippus</i>	530	

TABLE 2. Comparison of color form frequencies in *A. encedon* and *D. chrysippus* in the Kampala region of Uganda, 1964-66.

Mimicry groups and color forms	N	%
1. <i>encedon</i> / <i>aegyptius</i>	1603 263	45.9 49.6
2. <i>daira</i> / <i>dorippus</i>	750 50	21.5 9.4
Poor mimics (<i>A. encedon</i>)	304	8.6
Non-mimetic (<i>A. encedon</i>)	887	25.0
Non-mimetic (<i>D. chrysippus</i>)	217	40.9
Total <i>A. encedon</i>	3544	
Total <i>D. chrysippus</i>	530	

chrysippus are non-mimetic. This leaves two instead of four mimicry groups which are similarly ranked in the frequencies of corresponding forms, but because there are only two groups, a formal statistical association cannot be established. Once again the conclusion is that in Uganda the Müllerian association between *A. encedon* and *D. chrysippus* is much weaker than between *A. encedana* and *D. chrysippus*.

In Sierra Leone, *D. chrysippus* is monomorphic for form *alcippus*; even weak *alcippus* (the heterozygote) is absent. A sample (N = 2517) of *A. encedon* obtained in 1967-70 at a site in Sierra Leone comprised 68.3% non-mimetic *lycia* and 31.7% *commixta*, a poor mimic of *alcippus*. Another sample (N = 71) from another site comprised *A. encedana* only and all were *alcippina*, which means that *A. encedana* and *D. chrysippus* are 100% associated. No weak *alcippina* were recorded, which is of special interest in view of the lack of weak *alcippus* in the same region.

The above figures are given in Owen and Chanter (1971) and Owen *et al.* (1971) as color form frequencies for *A. encedon*, as at the time *A. encedana* had not been differentiated as a separate species. It can now be stated that in Sierra Leone *A. encedon* is dimorphic and is at best only weakly associated with *D. chrysippus*, while the association of *A. encedana* and *D. chrysippus* is monomorphic and complete.

CONCLUSION

Mimicry always involves deception and in this example we ourselves were deceived. The separation of the two *Acraea* species has enabled a better understanding, with fewer anomalies, of what must be one of the most remarkable examples of polymorphic Müllerian mimicry known. When Pierre (1976a, 1976b) discovered there were two species of *Acraea*, he pointed out that much of our work on relative frequencies in the Müllerian association must be in error, but he was unable to correct it. This we have now done, providing ourselves with the satisfaction of re-assessing our own work before someone else had the chance.

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