APPENDIX S1

CASE SCENARIOS OF BATESIAN MIMICRY EVOLUTION

The Yellow-banded sphinx Proserpinus flavofasciata (Sphingidae)

The moth P. flavofasciata flies in the northern part of North America. It is a Batesian mimic of bumblebees and is the only species in its genus that has evolved mimicry (Rubinoff and Le Roux 2008). The models are sympatric Bombus species belonging to a Müllerian mimicry complex, the core of which includes B. vagans, B. bimaculatus, and B. perplexus (Plowright and Owen 1980). Other Batesian mimics in the ring could be the polymorphic sphingid Hemaris diffinis, the syrphid fly Hadromyia grandis and the robber flies Laphria thoracica and L. flavicollis.

In North America, at least three different bumblebee mimicry rings have been identified, having different patterns of yellow on a dark background (Plowright and Owen 1980). Because there is greater pattern similarity within than between the species in these rings, it is likely that the size and organization of the yellow areas are important for predator recognition. In general, yellow is a conspicuous and common warning coloration (Cott 1940). For the P. flavofasciata mimetic appearance (Fig. 3C), body coloration is likely to be more important than wing coloration, because sphingids hover above flowers when foraging, rendering the wing pattern less distinct because of fast movement of the wings. Furthermore, P. flavofasciata is most likely to share time and space with the bumblebee models during foraging.

In the scenario of mimicry evolution in P. flavofasciata (Fig. 3), the ancestral appearance (Fig. 3A) is similar to the sister species, P. proserpina (Rubinoff and Le Roux 2008), which shares a greenish-grey and cryptic color pattern with the majority of the Proserpinus species, giving phylogenetic support to the scenario. The postulated feature mutation consists in a pronounced increase of yellow pigmentation of the thoracic scales (Fig. 3B). The mutation corresponds to a qualitative change into a passable mimic, which
predators might categorize as unprofitable. After the feature saltation, fine-tuning of the appearance increases the mimetic resemblance (Fig. 3C). Among the changes are increased melanism of the body and a shortening, broadening and rounding of the abdomen. Hairiness of the body is a common character of bumblebee mimics, including *P. flavofasciata*, and is most likely polygenically determined. Because there are presumed bumblebee mimics that are not hairy (e.g., carrion beetles, Silphidae), the character seems not to be crucial for mimicry.

**The Red-spotted purple *Limenitis arthemis astyanax* (Nymphalidae)**

The species *L. arthemis* includes a non-mimetic form – the White-banded admiral *L. a. arthemis* – and the unbanded forms *L. a. astyanax* and *L. a. arizonensis* that are Batesian mimics of the Pipevine swallowtail, *Battus philenor* (Platt and Brower 1968, Platt et al. 1971, Platt 1975). There is experimental evidence that the members of the *L. arthemis* complex are edible to birds and that the unbanded *L. a. astyanax* is a Batesian mimic of *Battus philenor* (Platt et al. 1971). There is also geographical concordance between the mimic and its model (Ries and Mullen 2008).

Several studies confirm the monophyly of the species complex *L. arthemis*, but the phylogeography and evolutionary relationships of the component populations have been debated (Mullen 2006, Mullen et al. 2008, Prudic and Oliver 2008, Savage and Mullen 2009). It is not yet established whether a mimetic form evolved only once, or more than once, or whether there has been an evolutionary reversal to a non-mimetic white-banded form. There is, however, agreement that a white-banded form was ancestral and that mimicry evolved from this form. White banding is the rule among Palaeartic *Limenitis* species, within which the monophyletic group of North American *Limenitis* species are nested (Mullen 2006, Prudic and Oliver 2008). The function of the white bands is usually assumed to be disruptive (Platt and Brower 1968, Platt 1975), although this has not been experimentally verified.
Our scenario (Fig. 4) uses the generally accepted idea of a white-banded ancestral state (Fig. 4A). The feature mutation, resulting in melanin covering most of the white bands (Fig. 4B), is supported by the observation that white banding is controlled by a major locus, at which the unbanded allele is dominant but has incomplete penetrance (Platt and Brower 1968, Platt 1975, Mullen et al. 2008). The scenario is in agreement with previous views that a reduction of the white bands was a first step in the evolution of mimicry (Platt and Brower 1968, Mullen et al. 2008). The mimetic importance of the feature is further supported by dorsal wing melanism being shared by several mimics of *B. philenor*, such as the females of *Papilio troilus* and *Papilio polyxenes* (Brower 1958), and by field experiments in which the appearance of males of the saturniid moth *Callosamia promethea* was manipulated (Sternburg et al. 1977, Jeffords et al. 1979).

In the scenario, the feature mutation is followed by an increase in the areas of blue-green iridescent structural color and a decrease in the areas (spots) of orange-red pigment, producing a perfected mimic (Fig. 4C), and this is a temporal sequence that agrees with previous views (Platt and Brower 1968). The extents of blue-green iridescence and orange-red spots appear to be polygenically determined (Platt 1975) and show substantial variation in the field (Platt and Brower 1968). The changed wing shape (Fig. 4C), resembling that of the model (Fig. 4D), represents mimetic fine-tuning of another, most likely polygenic, trait.

**The Mocker swallowtail *Papilio dardanus* (Papilionidae)**

*P. dardanus* has a wide distribution across sub-Saharan Africa and is divided into subspecies or races (Clark and Vogler 2009). The species exhibits female-limited polymorphism (Clark and Vogler 2009), mainly controlled by an autosomal locus with at least 11 alleles (Nijhout 2003). The locus is sometimes referred to as the mimicry locus, because the majority of the morphs are Batesian mimics of different aposematic models. The geographic ranges of the mimetic morphs are determined by the ranges of their models, such that the same female morph can occur in several subspecies. This supports the idea that at least some of the morphs are older than the present geographic diversity and that
there may have been a single origin of mimicry in the species (Clark and Vogler 2009), although more than one origin is also possible (Nijhout 2003). There has been some uncertainty about the precise phylogenetic position of *P. dardanus* (Vane-Wright et al. 1999, Zakharov et al. 2004), but a recent analysis comes to the conclusion that *P. dardanus* and *Papilio phorcas* are sister species (Clark and Vogler 2009). Both species are sexually dimorphic and have female-limited polymorphism, which means that these traits could be ancestral in *P. dardanus* (Clark and Vogler 2009, Vane-Wright et al. 1999, Kunte 2008).

The females of *P. phorcas* are not mimetic, nor are the females of other closely related *Papilio* species (Kunte 2008), so that mimicry most likely evolved in the line leading to *P. dardanus* (Clark and Vogler 2009, Kunte 2008).

Several lines of evidence indicate that the original *P. dardanus* mimetic appearance was similar to the current allopatric female morphs hippocoon and hippocoonides, and also the morph niavioides, and that the aposematic butterfly *Amauris niavius* (Danaidae) was the original model (Clarke and Sheppard 1960, Nijhout 2003) (the current *P. dardanus* morphs hippocoon, hippocoonides and niavioides mimic the subspecies *A. n. niavius*, *A. n. dominicanus*, and *A. n. aethiops*, respectively). The morphs hippocoon and hippocoonides are common, wide spread and centrally distributed, and have the ‘bottom recessive’ homozygous genotype at the mimicry locus (Clarke and Sheppard 1960). The significance of the recessivity lies in the idea that other mimicry alleles at the locus subsequently originated and spread as dominant mutants (Clarke and Sheppard 1960), a phenomenon sometimes referred to as Haldane’s sieve (Turner 1981).

In our scenario (Fig. 5), a hippocoon-like mimetic form evolved from an ancestral non-mimetic ancestor. There are two crucial ingredients needed for such a scenario: on the one hand the appearance of the ancestral non-mimetic female morph and on the other a feature saltation transforming the ancestral female into a passable mimic of *A. niavius*. The ancestral female appearance has been proposed to either be close to the current male *P. dardanus* appearance (Clarke and Sheppard 1960), because there are populations of *P. dardanus* where females and males are quite similar (Clark and Vogler 2009), or to be close
to the current appearance of the light yellow female morph of the sister species *P. phorcas* (Nijhout 2003). We propose an ancestral appearance somewhere between these two possibilities. Thus, we reconstruct the ancestral appearance of *P. dardanus* females based on the assumptions that they were similar to their sister species and that there was genetic coupling between male and female characters during the evolution of the male *P. dardanus* appearance; the males of *P. dardanus* deviate substantially from *P. phorcas* males, and also from the typical *Papilio* male appearance.

The ancestral female colouration probably consisted of a light yellow background and a contrasting darker brownish-black pattern, because this kind of colour pattern, with high luminance contrast, occurs both in the light-yellow female morphs of *P. phorcas* and in the males (and some females) of *P. dardanus*. Figure S5 illustrates the basic color patterns of a *P. phorcas* female, a *P. dardanus* male, and an ‘intermediate’ morph representing a reconstructed ancestral *P. dardanus* female (Fig. S5B, corresponding to Fig. 5A). For the apical and basal dark pattern elements on the forewing and hindwing, the intermediate is halfway between the two others. Apart from this, most of the forewing cells of the intermediate is left dark, in a pattern following the variation in forewing cell pigmentation in the *Papilio dardanus* species group (which includes, in addition to *P. dardanus*, also *P. constantinus*, *P. delandei*, *P. phorcas*, and *P. rex*), resulting in the ancestral form in Fig. 5A. Compared to an alternative where the ancestral form is similar to a current *P. phorcas* female (Nijhout 2003) (Fig. S5A), the form in Fig. 5A has greater chances of giving rise to a passable mimic of *A. niavius*.

The feature mutant consists in an increased melanism of interspaces on the forewing, producing a dark bar that divides a light field (Nijhout 2003, Clarke and Sheppard 1960), creating a passable mimic (Fig. 5B). Apart from being present in *P. dardanus* female morphs, such a bar also occurs in the colour patterns in the related *Papilio hesperus* species group. The feature that predators use when categorizing the appearance of the model *A. niavius* as unprofitable could be the light patches, two on each side of the body, separated by a dark pattern (Fig. 5D). This characteristic pattern is shared, with some minor
variations, by a number of species in mimicry rings centred on *A. niavius*. For instance, in West Africa *P. dardanus* hippocoon is regarded as a mimic of *Amauris niavius niavius*, and the model is thought to dominate a large mimicry ring. Other members of the ring, some of which are likely to be unpalatable, could be females of *Bematistes epaea* (Acraeidae), females of *Acraea jodutta* (Acraeidae), *Hypolimnas dubius* form anthedon, (Nymphalidae), *Pitthea famula* (Geometridae), *Pseudoletaion leonis* (Lycaenidae), *Pseudacraea eurytus* female form eurytus (Nymphalidae), *Elymnias bammakoo* form bammakoo (Saturidae) and females of *Papilio cynorta* (Papilionidae) (Owen 1974). In our scenario (Fig. 5), after the feature saltation, there is further fine-tuning of the mimic, which includes a loss of the tails, a whitening of the background colour and modification of the shape of the black pattern (Fig. 5C).

LITTERATURE CITED


Cott, H. B. 1940. Adaptive coloration in animals (Methuen, London).


**FIGURES S1-S5**

**SUPPLEMENTARY FIGURES FOR THE EVOLUTIONARY SIMULATIONS**

**Fig. S1.** Genotype-phenotype mappings for $x_1$ and $x_2$.

**Fig. S2.** Definition of the abdomen shape parameter $x_3$. Increasing values indicate a more elongated abdomen; $d = 1 - 1/x_3$. 
Fig. S3. Evolutionary simulation corresponding to the illustration in Fig. 1B, where the feature region represents a combination of a yellow thorax and a dark abdomen, so that a single-trait saltation to passable mimicry no longer is possible when starting from the non-mimetic prey niche indicated by the green sphere in Fig. 1B. As a consequence, no mimicry evolves over the duration of the simulation (in total 25000 generations). See Fig. 2 for further explanation of the panels. Apart from the changed feature region, parameter values are the same as in the simulation shown in Fig. 2.
**Fig. S4.** Evolutionary simulation corresponding to the illustration in Fig. 1B, where the feature region represents the combination of a yellow thorax and a dark abdomen. The starting point of the mimic-to-be is in the dark sphere in Fig. 1B, where the abdomen is darker, representing a changed non-mimetic prey niche. A single-trait saltation to passable mimicry is now possible, after which mimicry is further improved. See Fig. 2 for further explanation of the panels. Apart from the changed feature region and the changed non-mimetic prey niche, parameter values are the same as in the simulation shown in Fig. 2.
Fig. S5. Reconstruction of an ancestral non-mimetic *P. dardanus* appearance. A current female of *P. phorcas* is shown in (a), a current male of *P. dardanus* is shown in (c), and the intermediate appearance in (b) is the assumed ancestral female *P. dardanus* appearance. See text for further explanation.