

Diversity in mimicry: paradox or paradigm?

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Visual mimicry is a textbook case of natural selection because it is both intuitively understandable and has repeatedly evolved in a range of organisms: it is the ultimate example of parallel evolution. In many mimetic groups, particularly butterflies, a huge variety of colour patterns has arisen, even in closely related species. There has been much recent controversy over explanations of this variety. Mimicry is today a broad field of evolutionary study; here we discuss the evolution of its diversity in predator-prey systems.

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Although mimicry is often presented merely as an undergraduate showcase for darwinian selection, it is a microcosm for evolutionary theory in general, with ramifications into the evolution of polymorphism, transitions between adaptive peaks, origins of biodiversity, and the evolution and maintenance of community patterns. The classical view of mimicry and frequency-dependent selection, found in most textbooks, is as follows: predator aversion to the appearance of warningly coloured (aposematic) species is exploited by edible prey – Batesian mimics – which evolve to resemble their models^{1,2}. Batesian mimics should lose protection when common because they hide among superficially similar models whose unpalatability maintains the validity of their warning colours – if the edible mimics become too common the predators would soon learn to ignore the colouration. Rare mimetic morphs should be fittest because of this diversifying frequency-dependent selection, leading to the possibility of stable polymorphisms if several distinct models are imitated by a single species. Conversely, aposematic models are best protected when common (purifying frequency-dependent selection) – rare or new variants suffer the heaviest predation, because they are not recognized as distasteful by predators. Unpalatable species are therefore expected to be monomorphic. Purifying selection should also act across the species boundary, leading to Müllerian mimicry where pairs of unpalatable species benefit from mutual resemblance³ (i.e. selection for monomorphism at an interspecific level). Although still generally accepted, these traditional ideas of frequency-dependent selection in Batesian and Müllerian mimicry are now under strong attack.

Polymorphism in Batesian mimicry

Polymorphism is often cited in textbooks as an important, almost diagnostic, characteristic of Batesian mimicry. However, although Batesian mimicry seems fairly common (but see Ref. 4), mimetic polymorphism is relatively rare. The best-studied cases have all been swallowtail butterflies (Papilionidae)^{5–11}, in which mimicry is often limited to females. As well as involving frequency-dependent selection against common mimetic morphs, sexual dimorphism will also be favoured by sexual selection^{7,8,11} or preferential predation on females^{9,12} (Box 1).

Why is Batesian polymorphism so rare? It could be that mimics are usually strongly selected towards a single highly abundant or noxious model^{13,14}. Another likely explanation is that mimetic polymorphism requires a very peculiar genetic architecture – a single mimetic ‘switch’ gene or ‘supergene’, which very few species attain. The traditional idea that mimetic polymorphism evolved via the

microevolutionary construction of a tightly linked supergene now seems untenable. Batesian polymorphism requires new colour genes to be tightly linked from the beginning. Without this, tighter linkage will not evolve because recombination will destroy the adaptive polymorphism before it is stabilized^{6,15}. Most genetic architectures are probably not suitable, resulting in mostly monomorphic mimicry from which novel, poorly adapted mutants cannot escape. Batesian mimicry encounters what Turner⁶ calls an evolutionary ‘sieve’, beyond which few species will pass to become polymorphic.

The coevolutionary chase

One of the main attributes of Batesian mimicry, and a reasonable part of its definition, is that the mimic is deleterious to its model^{2,13,16,17}. The model could therefore escape its mimic by evolving a new warning pattern. However, this escape is probably transient, because mutant models could soon attract new mimics. A coevolutionary chase might therefore arise between models and mimics, similar to the evolutionary ‘arms race’ described for host-parasite interactions^{2,18}. Huheey¹⁶ suggested a coevolutionary chase could cause morph and race differentiation in models (as in *Heliconius erato* and *H. melpomene*), eventually leading to the coexistence of several mimetic patterns in a community. Similarly, although new hypotheses are now being tested¹⁹, Smith *et al.*²⁰ explained polymorphism in the distasteful *Danaus chrysippus* as an escape from an overload of palatable *Hypolimnas* mimics. More recently, equations for the coevolution of a pair of mimetic species have been developed²¹, showing that cyclical coevolution of model and mimic is possible if interspecific interactions (i.e. benefit of mimicry to the mimic and cost of Batesian mimicry to the model) are stronger than intraspecific interactions (i.e. aposematism and palatability).

Box 1. Sex-limited mimicry: why are males nonmimetic?

For some species, in which mimicry is restricted to females, such as *Papilio glaucus*, *P. dardanus* and *P. memnon*, selection pressures on wing patterns must differ between the sexes. Any one or a combination of several ideas may explain this:

Sexual selection via female choice: if nonmimetic males are preferentially chosen by females, mimicry in males would be at a sexually selected disadvantage⁶. For example, in the sexually dimorphic *P. glaucus*, males that were experimentally blackened to look like females had a lower mating success than normal yellow males⁷.

Sexual selection via male–male competition: experimental removal of the inner yellow submarginal band in male *P. polyxenes*, resulting in female-like males, did not affect female choice^{10,11}. In this species, males are territorial ‘hilltoppers’ and wing pattern is critical to success in male–male encounters – experimentally altered males had more difficulty establishing territories, and the territories they did win were of lower quality than those held by yellow-banded males¹¹.

Potential predation is higher in females: a third possibility is that females gain more from mimicry because their behaviour makes them more vulnerable to predators. Females of mimetic and nonmimetic butterflies have been shown to be more heavily attacked than males, presumably because of their less agile escape flight and more predictable behaviour near foodplants. This behaviour difference would lead to greater advantages for mimicry in females than in males, and could contribute to sexual dimorphism¹².



Fig. 1. What is a mimicry ring? A mimicry ring is a group of sympatric species sharing a common warning pattern. In Amazonian Ecuador, mimetic ithomiine butterflies (Nymphalidae) belong to about eight discrete mimicry rings^{36,43}, in which more than 120 species of sometimes distantly related taxa participate, including other butterflies (especially Riodinidae and Pieridae) and even day-flying moths. These rings are similar to the Amazonian rings first studied by Bates¹, who noted the strong resemblances between mimics (particularly Pieridae and *Napeogenes*) and more abundant Ithomiinae (for example *Melinaea*, *Mechanitis*, *Ithomia* and *Oleria*). Here, a limited selection from four of these mimicry complexes are shown, each ring is in a block of two columns having four to five insects per column. The majority are ithomiines; other lepidopteran families are noted in brackets. Orange tip ring, top left block: first column, *Napeogenes sylphis caucayensis*, *Hypoleria lavinia chrysodonia*, *Hypoleria sarepta aureliana*, '*Hypoleria*' *orolina orolina*; second column, '*Hypoleria*' *seba oculata*, '*Pseudoscada*' *florula aureola*, *Ithomiola cascella cascella* (Riodinidae), *Dismorphia theucharila f. erythoe* (Pieridae). Small dark transparent mimicry ring, top right block: third column, *Hyposcada illinissa ida*, *Hyposcada kena kena*, *Oleria agarista agarista*, *Oleria assimilis assimilis*; fourth column, *Oleria gunilla lota*, *Oleria lerda lerda*, '*Oleria*' *sexmaculata sexmaculata*, *Oleria tigilla tigilla*. Small yellow transparent mimicry ring, bottom left: first column, *Ithomia salapia salapia*, *Ceratiscada hymen* ssp. n., *Pteronymia vestilla sparsa*, *Godyris zavaleta matronalis*; second column, *Scada recchia ethica*, *Aeria eurimedea negricola*, *Napeogenes inachia avila*, *Moschoneura pinthias amelia* (Pieridae), *Ithomia derasa*. Yellow bar tiger mimicry ring, bottom right: third column, *Melinaea menophilus cocana*, *Mechanitis mazaeus fallax*, *Mechanitis messenoides messenoides*, *Napeogenes achaea achaea*; fourth column, *Melinaea Hypothyris anastasia honesta*, *Hypothyris mamercus mamercus*, *Hypothyris moebiusi moebiusi*, *Callithomia alexirrhoe* ssp. n. Reproduced, with permission, from the Natural History Museum and Dr G.W. Beccaloni.

There are two main reasons why coevolutionary chase is unlikely to drive mimicry diversification. First, the evolutionary rate of the mimic should be much higher than that of the model, because the mimic usually gains more from mimicry than the model loses. Consequently, a model cannot escape by gradually evolving a new pattern because the mimic will quickly catch up^{6,22}. Second, given that the model is the source of the protective (warning) colour in the first place, it will

be under strong purifying selection and, as in any aposematic system, rare variants will be strongly disfavoured. A strong constraint would thus prevent the evolution of novelty in the model, which will be trapped by its own pattern. There are two options for the model: either it becomes a Müllerian mimic in another more protected mimicry ring (Fig. 1) where it would gain immediate protection^{6,18}, or (possibly) it evolves a pattern via genetic drift that 'jumps' out of the mimic's reach.

Faster evolution of the parasite is a general feature of host-parasite systems, whose coevolution is thought to be one of the major forces driving the evolution of higher organisms. In mimicry, although adaptation will tie species together, the arms race will be severely hampered because of the purifying frequency-dependent selection on the model^{18,22,23}. Coevolution will also be constrained because the model is usually more common, and so the interspecific effect of mimics on the model will be weaker than the intraspecific effect of other model individuals. Mimicry will rarely evolve past these sieves¹⁸, leading to unilateral, noncoevolutionary mimicry, and stasis.

Müllerian mimicry: why polymorphism?

Most unpalatable species are monomorphic, as predicted by theory, apart from in narrow hybrid zones between geographical races^{24,25}. However, some supposedly Müllerian mimics are polymorphic over extensive geographical areas. Among classic but still unresolved examples are *D. chrysippus* and *Acraea encedon/encedana* in sub-Saharan Africa¹⁹ and *Heliconius numata* in the Amazon Basin²⁶. How can we explain this paradoxical mimetic polymorphism under purifying selection?

Importance of palatability and abundance

Similarity of a pair of distasteful species does not necessarily imply Müllerian mimicry. Huheey (Refs 16, 27 and earlier papers) held the radical view that if species differ in unpalatability, then the stronger suffers from the presence of the weaker, which dilutes the unpalatability of the mimicry ring. The mimetic relationship would then become effectively Batesian, giving the potential for coevolutionary chase. Huheey^{16,27} was roundly criticized^{28,29}, in part because his models predicted that mutualistic Müllerian mimicry could never exist, except at the limit of identical palatability. Alternative models reaffirmed the traditional view of a sharp discontinuity between Batesian and Müllerian mimicry^{17,30}. However, mimics that are less unpalatable could indeed, in theory, raise the probability of attack on their more unpalatable models. Speed¹³ has rejuvenated the argument that this could lead to polymorphism evolving in the mimic. Because this type of Müllerian mimicry could be diversifying, the effect has been termed quasi-Batesian¹³ or Speedian¹⁸ mimicry.

These ideas of quasi-Batesian mimicry depend on revised assumptions about predator behaviour (see later), and they also incur some evolutionary problems.

Mortality and the nature of mimicry does not depend only on relative palatability – mimicry is very strongly influenced by relative abundance³ and recognition accuracy³¹. Müller long ago showed that the relative benefits for a mimetic pair varies as the square of their relative abundances³ (Box 2). Suppose that species A is much more palatable than species B, leading to ten times the asymptotic predation rate on A than on B when each is alone (and at equal densities). The mimetic relationship would then be very ‘unfair’ because A induces more predation on B than vice versa. Species A is consequently a potential quasi-Batesian mimic of B (Ref. 13). Assume now that A is ten times as abundant as B: predator encounters would involve A ten times as often as B, so B will benefit 100 times more than A from sharing in the education of predators (Box 2). Type A is then the ‘model’, even though it is more palatable than B. This very powerful frequency-dependent effect will typically influence the outcome of the mimetic association much more strongly than merely the frequency-independent effect of relative palatability. Whether quasi-Batesian mimicry¹³ exists commonly will depend strongly on typical patterns of relative abundance and colour pattern similarity³¹, as well as on relative palatability.

Importance of predator behaviour

The palatability of prey in evolutionary models is defined by the way predators react³². Various types of learning have been assumed, mostly tacitly, by the authors already cited^{3,12,16,17,21,22,24,27–31}, but how predators actually learn is still unclear^{13,15,18,33}. To investigate how predator behaviour influences the outcome of mimicry, Monte Carlo simulations, incorporating a range of possible theories of predator behaviour, were run³³ (also M.P. Speed and J.R.G. Turner, unpublished). Palatability was assumed to be measured by ‘asymptotic attack rate’, which is the proportion of individuals attacked when local predators reach an equilibrium between learning and forgetting¹³. A three-zoned mimicry spectrum (classical Batesian and Müllerian mimicry separated by a quasi-Batesian mimicry zone) is predicted by many parameter combinations, including those closest to current theories of cognition and learning. Mildly unpalatable species (having, by Speed’s definition, a nonzero asymptotic attack rate) behave like Batesian mimics and can evolve towards polymorphism. Only very strongly unpalatable species will become Müllerian mimics with purifying selection in the model. If these results are correct, true Müllerian mimicry could be rare.

Box 2. Müller’s mathematical model of mimicry

In perhaps the earliest application of mathematical arguments to evolution (1879), Müller³ showed (in a footnote) that each member of a pair of unpalatable species could benefit from mimicry, and also that the ratio of advantages for mimicry was greatly in favour of the rarer species (in proportion to the square of the ratio of abundances). Müller assumed that both species are equally unpalatable (n represents palatability in the following equations); however, similar results clearly hold for unequal palatabilities also. Few now read the original, so it is worth quoting Müller’s footnote directly:

Let a_1 and a_2 be the numbers of two distasteful species of butterflies in some definite district during one summer, and let n be the number of individuals of a distinct species which are destroyed in the course of a summer before its distastefulness is generally known. If both species are totally dissimilar, then each loses n individuals. If, however, they are undistinguishably similar, then the first loses $a_1n/(a_1+a_2)$ and the second $a_2n/(a_1+a_2)$. The absolute gain [in numbers] by resemblance is therefore for the first species $n - a_1n/(a_1+a_2) = a_2n/(a_1+a_2)$; and in a similar manner for the second, $a_2n/(a_1+a_2)$. This absolute gain, compared with the occurrence of the species, gives for the first, $g_1 = a_2n/(a_1(a_1+a_2))$, and for the second species, $g_2 = a_1n/(a_2(a_1+a_2))$ [g_1 and g_2 are the per capita fitness advantages of Müllerian mimicry once it has gone to completion], whence follows the proportion, $g_1:g_2 = a_2^2:a_1^2$.

In Speed’s analysis¹³, the prey is unpalatable if the asymptotic probability of predation is lower than the naive attack probability (set arbitrarily as 0.5). A more sensible view of unpalatability would be defined as any palatability that reduces predation upon experience, regardless of the naive attack rate. Only when the asymptotic probability of attack reaches zero do we have this kind of unpalatability. Here, the degree of unpalatability would affect only the rate of learning¹⁷. If this criticism is fair, ‘quasi-Batesian’ mimicry is actually normal Batesian mimicry, explaining why it is evolutionarily Batesian!

It also seems likely that intermediate asymptotes of predation rate will be rare. This is consistent with some empirical results. For example, birds respond non-linearly to a palatability spectrum of pastry baits¹⁷, and asymptotic predation rates are often either near 0% or 100%, with a sharp boundary between what a predator likes or tolerates and what it always rejects². Classical Müllerian and Batesian mimicry would then be the most abundant types of mimicry¹⁷, with only a very small parameter space in which quasi-Batesian mimicry is even possible^{13,16}. It would be worthwhile designing new sets of experiments to investigate whether intermediate rates of asymptotic predation on natural prey do exist and, if so, how common they are.

Spatiotemporal heterogeneity

Variations in relative abundance (Box 2) and distastefulness might change or even reverse respective roles in mimicry: a Müllerian (or quasi-Batesian) mimic could itself become a model if temporarily more abundant than the species it mimics. This may cause geographical variation in mimetic pattern^{6,25} and dramatic switches from diversifying to purifying number-dependent selection³⁴ in the quasi-Batesian mimicry zone^{31,35} (if such a zone exists). The nature of the mimetic relationship can be variable in time and space; it is ‘contextually defined’³⁵. Can

such environmental heterogeneity select for stable polymorphisms and interspecific diversity of mimicry?

Brown and Benson²⁶ explained the extraordinary diversity of *H. numata* colour patterns as an adaptation to a highly unpredictable mimetic environment. In this unpalatable Amazonian species there are up to 11 sympatric morphs in any one area, and about 38 morphs over its whole range. Each sympatric morph mimics a separate species of *Melinaea* (lithobiinae, tiger pattern mimicry ring, Fig. 1). *Melinaea* are clearly the models for *H. numata*^{1,26} but are tremendously variable in abundance. Polymorphism in *H. numata* is therefore explained as a bet-hedging strategy, which ensures survival in an unpredictable mimetic environment. It is likely that spatial, as well as temporal, heterogeneity in model frequency contributes to the stability of the *H. numata* polymorphism²⁶. However, there is no experimental evidence for this explanation³⁶. More theoretical work is also needed because it is possible that stochastic variability should typically cause the eventual loss of all except one morph in a locality.

The relative abundances of sympatric morphs of the Müllerian mimics *Acraea* spp. and *D. chrysippus* in Africa also vary geographically. There is little correlation between morph frequencies of these co-mimics, making the putative Müllerian association between *Acraea* and *Danaus* difficult to understand²⁰. Because the evolutionary chase explanation²⁰ was unconvincing, Owen *et al.*¹⁹ recently reassessed the mimetic relationship after *A. encedon* was discovered to include a sibling species, *A. encedana*. They showed that *A. encedon* only weakly follows the morph frequencies of *A. encedana* and *D. chrysippus* despite the resemblance of some morphs. In contrast, frequencies of *A. encedana* morphs are closely correlated with those of *D. chrysippus*. Recent contact in Eastern Africa of previously isolated geographical races has been suggested as a nonadaptive cause of polymorphism in these species¹⁹.

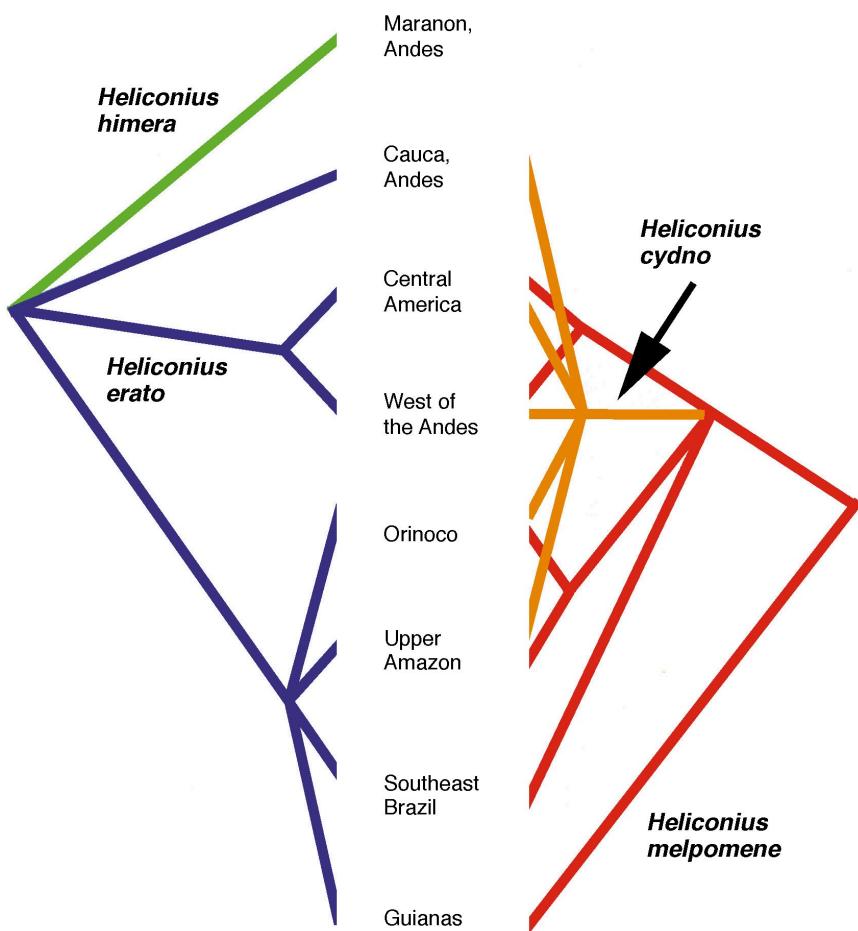


Fig. 2. Did *Heliconius erato* and *H. melpomene* coevolve? Simplified consensus cladogram of geographical races of *H. erato* (and *H. himera*), compared with that of *H. melpomene* (and *H. cydno*)³⁷. Mitochondrial DNA sequences of *H. erato* and *H. melpomene*, which mimic each other virtually everywhere they occur, did not share a common biogeographical history, invalidating the hypotheses of coevolution or codifferentiation from a common ancestral pattern. Adapted, with permission, from Ref. 37.

Geographical divergence and coevolution in Müllerian systems

Müllerian mimicry with mutual benefits, if it occurs, seems an excellent candidate for coevolutionary mutualism. A variety of colour patterns might have codifferentiated from an ancestral pattern. Among classic examples is the spectacular racial divergence in *H. erato*, mirrored with amazing accuracy by *H. melpomene*. As these two species belong to different phylogenetic groups within the same genus, coevolution is a very tempting explanation for parallel race formation. Cladograms based on knowledge of wing-pattern loci are almost identical in *H. erato* and *H. melpomene*, as expected if the two species had strictly coevolved⁶. However, recent evidence^{37,38} suggests that *H. erato* could have a different ancestral pattern from *H. melpomene*. In any case, a concordant cladogram does not imply coevolution, because one species could have colonized the other's pre-existing pattern of diversity using a similar route. Both species might be expected to have similar

genetic control of wing patterns simply because they are related, so that shared branching patterns could result from common genetics rather than coevolution^{6,39}. To clarify the evolutionary history of the pair, Brower³⁷ sequenced mitochondrial DNA from both species. Cladograms of races based on mitochondrial DNA are not concordant in the two species (Fig. 2), revealing that *H. melpomene* and *H. erato* did not share a common biogeographical history, and that at least some of the mimicry was not coevolutionary.

Turner^{6,25} has applied a noncoevolutionary model to race formation in *Heliconius*: he argues that mimicry rings can differ geographically in their ability to 'capture' species because of 'biotic drift' (stochastic extinction or changes in relative abundance of aposematic species). Species will thus undergo mimetic capture several times in their history, switching pattern again and again, and consequently 'radiating' into different geographical races. Coevolution is not invoked because each species switches rings independently

of less abundant co-mimics and has a different model in each area. Instead, Müllerian mimicry is seen as unilateral colonization by rarer mimics of the protective pattern of more abundant models. This biotic drift leading to intraspecific diversity could have been enhanced if the forest shrank into small refuges, possibly during the last glaciation. Refugia, although not necessary for ring switches, could facilitate extinction or density variation, and consequently accelerate race divergence²⁵. Alternatively, random genetic drift and the shifting balance (i.e. the process by which genetic drift, as well as mutation, provides variation on which selection may act) within model species could account for the local origination of new patterns^{24,25}. Density changes, potentially leading to changes in selection via biotic drift, will also facilitate genetic drift. Once formed in a local area, an advantageous pattern will spread via movement of clines. The shifting balance, although apparently unlikely because it invokes genetic drift, provides a better explanation than biotic drift for the emergence of completely novel colour patterns in the context of purifying selection. Under biotic drift, the pattern diversity should progressively collapse into a single mimicry ring as more and more mimetic captures are affected.

Community patterns

Poorly adapted hybrids between mimetic or aposematic forms will be selected against. Thus, a form of reproductive isolation results from the evolution of new colour patterns. It seems likely, therefore, that mimetic diversity will contribute to the origin of new species; indeed, closely related species often differ in their mimetic allegiance^{1,40} (see also Fig. 1). Understanding the evolution of mimetic diversity might therefore lead to a better understanding of how species evolve from local or racial variants.

The maintenance of a diversity of geographical races in aposematic species, once they have evolved, is easily understood because of the strong purifying selection on either side of steep hybrid zones that separate them²⁴. However, the commonest patterns should always be better protected, so that all mimetic butterflies of similar size in an area evolve towards a single, local pattern. As mimetic captures occur (e.g. when forests are fragmented) we might expect one or two patterns to be increasingly reinforced, resulting in even more captures of Müllerian (and Batesian) mimics leading, ultimately, to a single local mimicry ring.

Nature seems to behave in a completely contrary way; there are abundant, multiple mimicry rings within any

area (Fig. 1). One possible explanation is that each mimicry ring is sustained in a separate microhabitat. *Heliconius* mimicry rings often have little or no diurnal flight stratification in the rainforest canopy^{41,42}. In contrast, there is some stratification of nocturnally roosting *Heliconius*⁴², and of the diurnal flight of ithomine mimicry rings in upper Amazonian Ecuador⁴³. In *Heliconius*, different rings are dominant in low second growth, tall secondary forest and primary forest⁴². Habitat differences are also likely in ithomiines but have still to be studied in detail^{43,44}.

This microhabitat structuring of mimicry, which is correlated with the heights and habitat requirements of the host-plants used by the butterflies⁴³, could allow mimicry rings to remain distinct provided there are sets of predators in different habitats, each of which perceives a different mimicry ring as the most abundant model^{42,43}. However, the major impression a naturalist obtains in the rainforest is of extensive overlap of mimicry rings in flight height and habitat choice^{41–44}. This makes it highly dubious that butterfly communities experience sufficient disruptive predation to maintain a stable mimetic diversity. Alternatively, multiple mimicry rings could be maintained as a result of rapid evolution of novel patterns (as indicated by rampant geographical variation), speciation and sympatry, countered only by slow, sieve-constrained mimetic convergence. Under this interpretation, local mimetic diversity is a result of a dynamic balance between geographical divergence, speciation and mimetic evolution, rather than because it is a stable community optimum. Which explanation is correct is still not clear.

Mimicry: a general model for the evolution of diversity

A major barrier to understanding mimicry is the lack of field studies. For example, there has perhaps been only a single series of appropriately controlled field demonstrations of the advantage of mimicry⁴⁵. Visual mimicry is recognized by human eyes, yet birds see the world differently⁴⁶. Our ability to find mimicry shows that our perceptual systems must be fairly similar to those of the predators causing mimicry, but the differences may explain some of the apparently nonadaptive mimicry that occurs, as in *D. chrysippus* and its mimics. It is also apparent that our understanding of learning is still at such an early stage that we do not know how it affects the evolution of mimicry.

Mimicry still creates almost as much controversy today as it did 136 years ago. The problems that underlie the paradoxical diversity of mimicry are of great interest not just for undergraduates, but also

for students of evolution of all ages. Mimetic organisms have undergone massive diversification where the maintenance of *status quo* is expected. Mimicry therefore provides us with an example of a general problem: the evolution of biological diversity in the face of conservative constraints.

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Dinosaurs for everyone

The Complete Dinosaur

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The editors of this volume sought to produce 'the single most authoritative account of dinosaur palaeontology accessible to the general reader'. To achieve this, they have tasked a broad spectrum of authors to produce chapters each giving an overview of a discrete topic, with the good use of illustrations and a minimum of jargon or assumed knowledge. The style is inevitably uneven, but the aim of communication to the non-specialist has been generally successful. At the same time, I found that chapters on subjects where I had a good knowledge of the literature regularly included previously unpublished work, and/or new thoughts on familiar work. Humour is also used exceptionally effectively: there is a very apt Calvin & Hobbes cartoon, and we find out how many lawyers the *T. rex* of the film 'Jurassic Park' would have to consume to meet its energy needs for a year.

The 34 chapters are organized into six very different sections. The first deals with the history of dinosaur discovery, and is very effective in conveying both the challenges and joys of scientific discovery. The second describes how traces of dinosaurs are recovered and studied. The breadth of

scope here is considerable, from practical details of how to record dinosaur footprints to an explanation of the ways in which molecular techniques can be applied to the study of dinosaurs.

Part 3 deals with the classification of dinosaurs and gives an ordered description of each of the dinosaur groups. The phylogeny is interesting enough in itself, but there is more to the section than this: the development of dinosaur systematics serves as a very illuminating parable of the very human and often far from dispassionate way in which science progresses, and there is plenty of insight into the evolution and physiology of the exceptionally diverse range of creatures which fall into the category of dinosaur.

Section 4 is on what we can infer about how dinosaurs lived from the traces which they have left. Here the level of conceptual difficulty increases somewhat, and lay-readers may struggle in some places, despite strong efforts by authors and editors to keep their explanations as clear as possible. As well as covering the history of a given approach, the authors often present very recent (there are references to papers published in 1997) and previously unpublished pieces of work, whilst also focusing on potential future directions for research. Much of this section concentrates on the likely metabolic rates of dinosaurs and the many implications of this for physiology, behaviour and population-level considerations. Ten to 15 years ago, such discussion would have been much more polarized and heated; in contrast, here authors generally stick to their own angle of enquiry and make little reference to opposing or contradictory viewpoints put forward by other contributors.

Where authors do cross chapter boundaries and discuss the ideas of others, this discussion is generally very polite. Maybe science, or just this reviewer's blood lust, could have been better served by a remit which encouraged contributors to feel free to dissent from views expressed elsewhere in the book.

Section 5 attempts to place the dinosaurs in context by considering the Mesozoic Era more generally, encompassing biogeography, non-dinosaurian vertebrates, and the extinction of the dinosaurs. This last chapter is particularly effective, being co-written by a believer in sudden catastrophe and one who believes that dinosaurs faded away gradually over an extended period. Typical of the book as a whole, the authors find much common ground but raise plenty of issues worthy of further thought and research.

The final section includes a single chapter on the dinosaurs in the media; this provides light entertainment at the end of the book, and includes a useful guide to the best dinosaur web-sites.

This book succeeds magnificently in having something to offer anyone with an interest in dinosaurs, and it shows that dinosaurs continue to present many challenges worthy of research. Furthermore, as the list of contributors to this book demonstrates, scientists from a great diversity of backgrounds can make an important contribution to this effort. Read this book, and you'll want to join them.

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