

What kind of signals do mimetic tiger moths send? A phylogenetic test of wasp mimicry systems (Lepidoptera: Arctiidae: Euchromiini)

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Mimicry has been examined in field and laboratory studies of butterflies and its evolutionary dynamics have been explored in computer simulations. Phylogenetic studies examining the evolution of mimicry, however, are rare. Here, the phylogeny of wasp-mimicking tiger moths, the *Sphecosoma* group, was used to test evolutionary predictions of computer simulations of conventional Müllerian mimicry and quasi-Batesian mimicry dynamics. We examined whether mimetic traits evolved individually, or as suites of characters, using concentrated change tests. The phylogeny of these moth mimics revealed that individual mimetic characters were conserved, as are the three mimetic wasp forms: yellow *Polybia*, black *Polybia* and *Parachartergus* mimetic types. This finding was consistent with a 'supergene' control of linked loci and the Nicholson two-step model of mimicry evolution. We also used a modified permutation-tail probability approach to examine the rate of mimetic-type evolution. The observed topology, hypothetical Müllerian and Batesian scenarios, and 1000 random trees were compared using Kishino–Hasegawa tests. The observed phylogeny was more consistent with the predicted Müllerian distribution of mimetic traits than with that of a quasi-Batesian scenario. We suggest that the range of discriminatory abilities of the predator community plays a key role in shaping mimicry dynamics.

Keywords: comparative biology; Arctiinae; Müllerian mimicry; evolution of mimicry

1. INTRODUCTION

Mimicry is one of the most intriguing phenomena in evolutionary biology. H. W. Bates (1862) proposed that palatable butterfly species 'copied' the appearance of poisonous butterflies and that birds selected for this resemblance. Franz Müller (1879) demonstrated mathematically that many unpalatable species could gain protection by converging visually on a single form. These predictions form the basis of traditional mimicry theory. Palatable species that imitate noxious species are called Batesian mimics; unpalatable species that converge on a single appearance are termed Müllerian mimics. However, cases of Batesian and Müllerian mimicry are apparently rare in nature (Ritland 1991; Ritland & Brower 1991).

One reason that these scenarios are not observed is that models and mimics rarely fall into palatability extremes, as described by traditional mimicry theory (Fisher 1958; Sheppard 1960; Brower & Brower 1964; Brower *et al.* 1968; Turner 1987). All mimics fall somewhere along a palatability spectrum, between completely unpalatable and palatable. In classic Batesian mimicry, the model is completely unpalatable, while the mimic is completely palatable. Thus, the difference in palatability is maximized between the model and the mimic. In cases of Müllerian mimicry, palatability differences are minimized, that is, both the model and mimic are unpalatable. Further, Batesian and Müllerian mimetic systems also differ in their

selection pressure on the model species (Turner 1987; Huheey 1988). Batesian models suffer increased predation and a decrease in fitness, due to misinformed predators that encounter palatable mimics. Müllerian models benefit from decreased predation and increased fitness as the result of a predator experience with co-occurring unpalatable mimics.

These differences in fitness under Batesian and Müllerian systems predict selection for two different evolutionary outcomes. Batesian systems should select for novel forms in the model species (Gilbert 1983). Novel model forms 'escape' from parasitic mimics. The mimic, in turn, is then selected for the novel form and the mimic 'chases' the model through evolutionary time (Gilbert 1983; Joron & Mallet 1998; Holmgren & Enquist 1999). The mimic is likely to converge on the model's form, because the mimic evolves faster than the model. Additionally, as the population density of mimics increases relative to the population of models, predators are more likely to encounter mimics rather than models, encouraging further predation (Brower 1960; Huheey 1964; Charlesworth & Charlesworth 1975). This evolutionary scenario predicts a rapid rate of form evolution in the mimic over time. The evolutionary outcome to Batesian mimicry is a phylogenetic pattern of multiple shifts in mimetic type (figure 1*a*).

Müllerian systems, by contrast, should select for convergence on one visual form, because unpalatable models and mimics reinforce predator learning. Negative predator experiences would reinforce predator learning and result in minimal predation on members of the mimicry ring. Any deviation from this Müllerian form would lead to a novel experience for a predator, a potential predation event, and would decrease the fitness of the new mimetic

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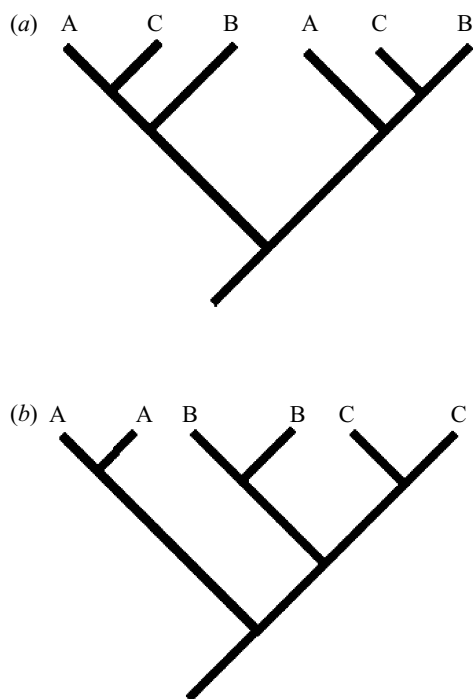


Figure 1. Phylogenetic hypotheses representing two mimetic scenarios. (a) Batesian mimicry; (b) Müllerian mimicry (A, B, C: three mimetic species with three different forms).

form (Turner 1977; Mallet & Singer 1987). Selection, through decreased fitness, acts against novel forms in either the mimic or model. This evolutionary scenario predicts few changes in mimetic type over time. That is, a phylogeny of Müllerian mimics should have minimal shifts between mimetic types (figure 1b).

Drastic shifts among forms would be possible if loci involved in mimicry were linked developmentally (Goldschmidt 1945; Charlesworth & Charlesworth 1975; Charlesworth 1994). The Nicholson two-step theory (Nicholson 1927; Mallet & Joron 1999) suggests that mimetic forms evolve in this manner. First, jumps to different mimetic forms are coordinated by a supergene complex. 'Supergenes' (Clarke & Sheppard 1960; Turner 1977) are responsible for linked developmental gene cascades and can cause drastic, concerted changes in phenotype with just small changes in a developmental pathway. Genetic modifiers, acting at several loci, which tailor individual species to local mimicry rings, subsequently perfect these large phenotypic changes. This process should only result in extremely precise mimics and transitional stages should not occur (Mallet & Joron 1999). Shifts in mimetic type could result from local differences in spatial and temporal distribution of mimicry rings. It is easy to imagine that a Müllerian mimic would be selected to shift forms if its mimicry ring does not coincide in time or space (Mallet & Gilbert 1995; Joron & Mallet 1998; Mallet & Joron 1999).

Most recently, Speed (1993) revived discussion of another category of mimicry, quasi-Batesian (Q.-B.) from Huheey (1988) and Pough *et al.* (1973). Q.-B. mimicry occurs when members of a mimicry ring differ in palatability, such that one species is more palatable (Pough *et al.* 1973; Huheey 1988; Speed 1993). Computer simulations of Q.-B. mimicry systems are indistinguishable from

the evolutionary dynamics of conventional Batesian mimicry (Speed 1993). More unpalatable models have reduced fitness, due to more palatable Q.-B. mimics that some predators can consume. Selection then favours differentiation of the model to escape predation. Model differentiation then selects for polymorphism in the less distasteful (more palatable) mimics, leading to mimic and model polymorphism (Brower & Brower 1964; Pough *et al.* 1973; Huheey 1988; Speed 1993). Speed (1993) proposed Q.-B. mimicry to explain unexpected polymorphism that occurs in presumed Müllerian systems of unpalatable model-mimic rings (e.g. *Heliconius doris* L., *H. sara* F. and other *Heliconius* species; Mallet (1999)). This evolutionary scenario predicts a more rapid rate of form diversification, approaching the rate of a Batesian system. Thus, a phylogeny of a Q.-B. mimic is predicted to have multiple changes in mimetic type, similar to the Batesian phylogenetic pattern.

Although Müllerian and Batesian mimicry have been examined extensively in butterflies (Turner 1977, 1981, 1987; Gilbert 1983), mimicry is not as well studied in other insects. Further, mimicry has been examined in a comparative framework by mapping mimetic characters onto phylogenies to show mimetic form convergence in unrelated taxa (Brower 1995, 1996; Miller 1996). These seminal comparative studies did not examine, however, whether the pattern of mimic evolution was consistent with either Müllerian or Batesian predictions.

Tiger moths (Lepidoptera: Arctiidae) are an excellent insect lineage for examining the evolution of mimicry and mimetic characteristics. Tiger moths are often involved in mimicry rings (Scoble 1992) and the chemical basis of their unpalatability is well studied in model species (Eisner & Meinwald 1995). Many tiger moths are known to sequester and transfer plant secondary compounds from larval to adult stages for defence against vertebrate predators (see the review in Weller *et al.* 1999).

We chose to focus on *Sphecosoma* and related moth genera, which are among the most precise wasp mimics found in Arctiidae (figure 2). An additional advantage is that this system involves multiple model-mimic systems within a single lineage. Adult moths mimic different genera and species of polybiine wasps (Hymenoptera: Vespidae) and display three different, recognizable mimetic forms: (i) black *Polybia*, (ii) yellow *Polybia*, and (iii) *Parachartergus* (figure 2). These three forms are sympatric with each other, as well as with putative wasp models. Although plant hosts are not known for all moth species in this study, euchromiine larvae have been recorded from host plants containing cardiac glycosides or pyrrolizidine alkaloids (Kitching & Rawlins 1999). It is reasonable to assume that the adults have some chemical protection, although the degree of protection is unknown. Thus, two mimicry scenarios are possible: (i) conventional Müllerian mimicry or (ii) Q.-B. mimicry (Speed 1993).

Both of these mimicry scenarios have phylogenetic predictions that can be tested with the phylogeny of the *Sphecosoma* group. If these moths are Müllerian mimics, then mimetic type will be phylogenetically conserved (figure 1b), that is, few shifts will occur among the three types of wasp mimics. In addition, mimetic traits (characters) should also be phylogenetically conserved and evolve as suites of linked traits. Imperfect mimics

Table 1. Comparison of observed mimicry characters with randomly generated character distributions (character states listed beneath).

(*Significantly different at $\alpha < 0.05$; *L*, length; CI, consistency index; s.d., standard deviation).

character	<i>L</i>	CI	mean length \pm s.d. 1000 random characters	mean CI \pm s.d. 1000 random characters
mimetic type (0) <i>Pepsis</i> , (1) <i>Parachartergus</i> , (2) black <i>Polybia</i> , (3) yellow <i>Polybia</i>	6*	0.5*	14.5 \pm 2.21	0.19 \pm 0.04
wasp waist (0) absent, (1) coloration, (2) 2nd abdominal segments narrowed, (3) 3rd abdominal segments narrowed	4*	0.5*	11.7 \pm 1.6	0.15 \pm 0.04
wings (0) scaled, (1) partiallyhyaline, (2) hyaline with yellowish hue, (3) clear hyaline, black veins & fringe, (4) clear hyaline, black veins, no fringe	12*	0.33*	21 \pm 1.6	0.18 \pm 0.01
palpal brush (0) present, (1) absent	3*	0.33*	11.8 \pm 1.2	0.09 \pm 0.01
swollen tibia ^a (0) present, (1) absent				
tufted hind tarsi (0) scaled normally, (1) tufts of scales	2	1.0*	3.0 \pm 1.2	0.4 \pm 0.2
thorax colour (0) black, (1) yellow, (2) black & yellow stripes, (3) black with yellow spots, (4) metallic	7*	0.43*	13.4 \pm 1.4	0.17 \pm 0.04
abdomen colour (0) black, (1) yellow, (2) black & yellow stripes, (3) black with yellow spots, (4) black with white basal spots, (5) metallic	8*	0.5*	14.6 \pm 1.6	0.21 \pm 0.04

^a Swollen tibia were only present in the outgroup taxon *Orcynia calcarata* Walker (*Pepsis* mimic).

(i.e. those with narrow waists and scaled wings) would be selected against and should not be observed. However, if these moths are Q.-B. mimics of their wasp models, mimetic type should be phylogenetically labile (figure 1a). That is, multiple phylogenetic shifts should occur among the three mimetic types. Further, traits associated with mimicry (clear wings, wasp waist, coloration) should be uncoupled over evolutionary time to allow for rapid convergence on changing models, and imperfect mimics would exist. We examine these phylogenetic predictions resulting from Müllerian and Q.-B. dynamics on a moth phylogeny constructed using morphological characters not involved in mimicry.

2. MATERIAL AND METHODS

To generate a phylogeny of the *Sphecosoma* generic group, we sampled adults of 48 species within 16 genera (Simmons 2001). The ingroup included 41 (of 89 described) species and the outgroup consisted of three genera (five euchromiine species). Although all of the 89 described species were examined, only species represented by both male and female specimens were included in the analysis. Species represented by only one sex were omitted to avoid artefacts created by missing data (Kitching *et al.* 1998). In total, 52 adult morphological characters were described with 195 states (26 multistate characters).

In addition, eight characters (29 states) related to mimicry were scored (table 1; figure 2). Characters related to mimicry were mapped onto the phylogeny rather than included in the data matrix, because unrelated species (i.e. *Pleurosoma*, *Sphecosoma cognatum* Walker, *Mymecopsis polistes* (Möschler)) converge on similar wasp model forms independently (clear wings, wasp waist). Phylogenetic trees were constructed using maximum parsimony (MP) with PAUP* (Swofford 2000). In all searches, 10 replicates of random-taxa additions were performed to uncover hidden topology islands (Maddison *et al.* 1984). Characters were treated as unordered. We obtained 24 trees (length, 408; consistency index, 0.41; retention index, 0.64). The strict consensus with Bremer indices (decay indices; Bremer 1988; Donoghue *et al.* 1992) is shown in figure 3a. The different resolutions of the polytomies do not affect character mapping or other results. Details of specimen preparation, non-mimetic character descriptions are available from Simmons upon request or are described elsewhere (Simmons 2001). The data matrix can be found at www.entomology.umn.edu/museum/databases/matrices/Simmons&Weller2002.nex.

The three mimetic types (black *Polybia*, yellow *Polybia* and *Parachartergus*) and individual mimetic characters (table 1) were mapped onto the strict consensus tree using MACCLADE 4.0 (Maddison & Maddison 2000). We used the option 'show all parsimonious states' at each node. To examine if the individual mimetic characters evolved as suites, or independently, we per-

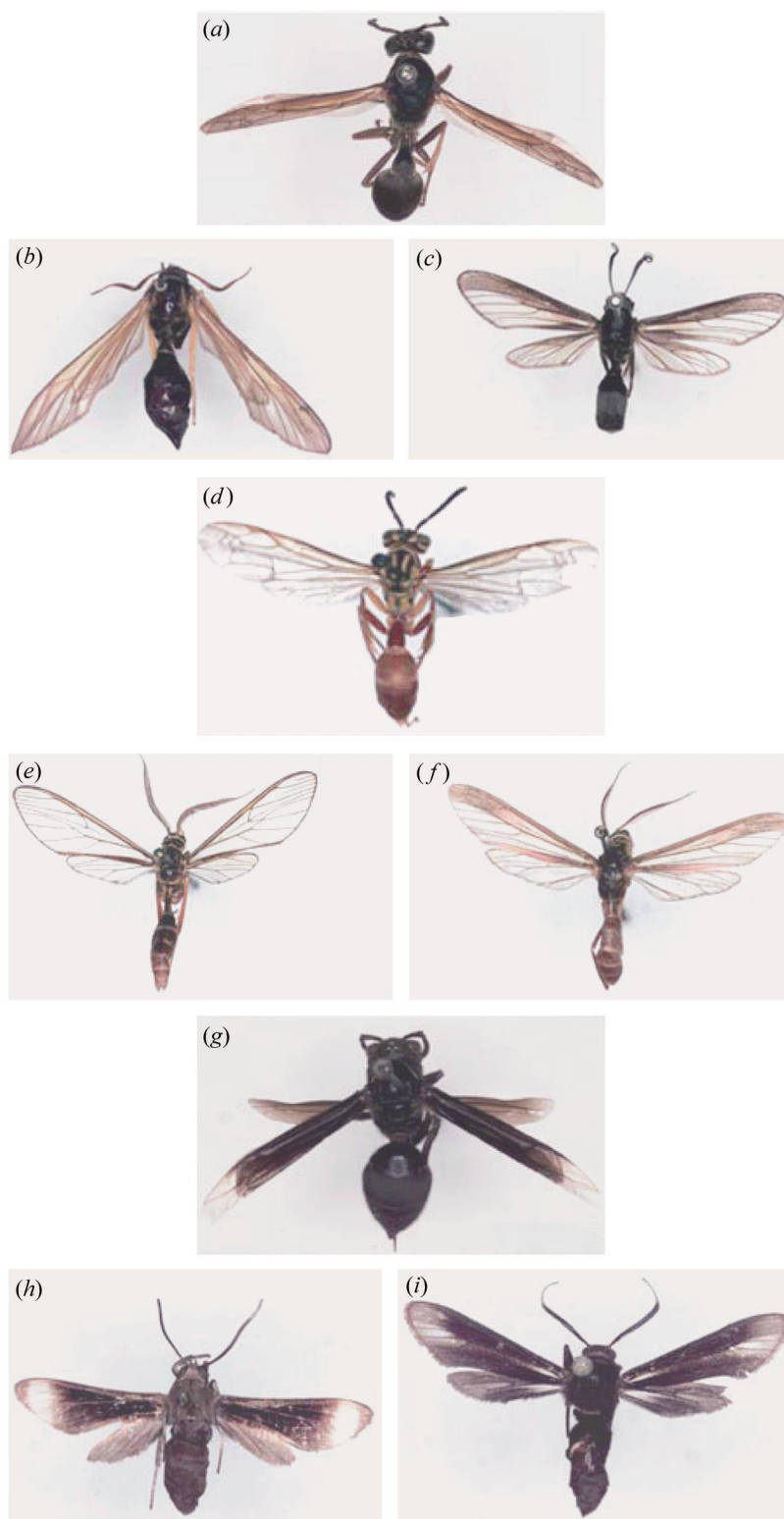


Figure 2. Representatives of three mimicry rings. (a) *Polybia minanum* Ducke (Hymenoptera: Vespidae); (b) *Myrmecopsis caurensis* (Klages); (c) *Myrmecopsis noverca* (Schaus) (Lepidoptera: Arctiidae: Euchromiini); (d) *Agelaia myrmecophila* (Ducke) (Hymenoptera: Vespidae); (e) *Pleurosoma angustata* (Möschler) (Lepidoptera: Arctiidae: Euchromiini); (f) *Myrmecopsis polistes* (Hübner) (Lepidoptera: Arctiidae: Euchromiini); (g) *Parachartergus apicalis* (F.) (Hymenoptera: Vespidae); (h) *Sphecosoma aliena* (Walker) (Lepidoptera: Arctiidae: Euchromiini); (i) *Myrmecopsis strigosa* (Druce) (Lepidoptera: Arctiidae: Euchromiini).

formed concentrated changes tests (MACCLADE 4.0; Maddison & Maddison 2000). Multistate characters were recoded as synthetic binaries for this test. For example, when we examined the correlation between mimetic type (character 1) and waist type (character 2), we coded character 1 as '(0) other forms: (1)

black *Polybia* mimic', and character 2 as '(0) other waists; (1) S2 narrowed'.

We then examined whether the three mimetic types and characters were phylogenetically conserved, using a modification of the permutation-tail probability test (PTP) (Faith & Cranston

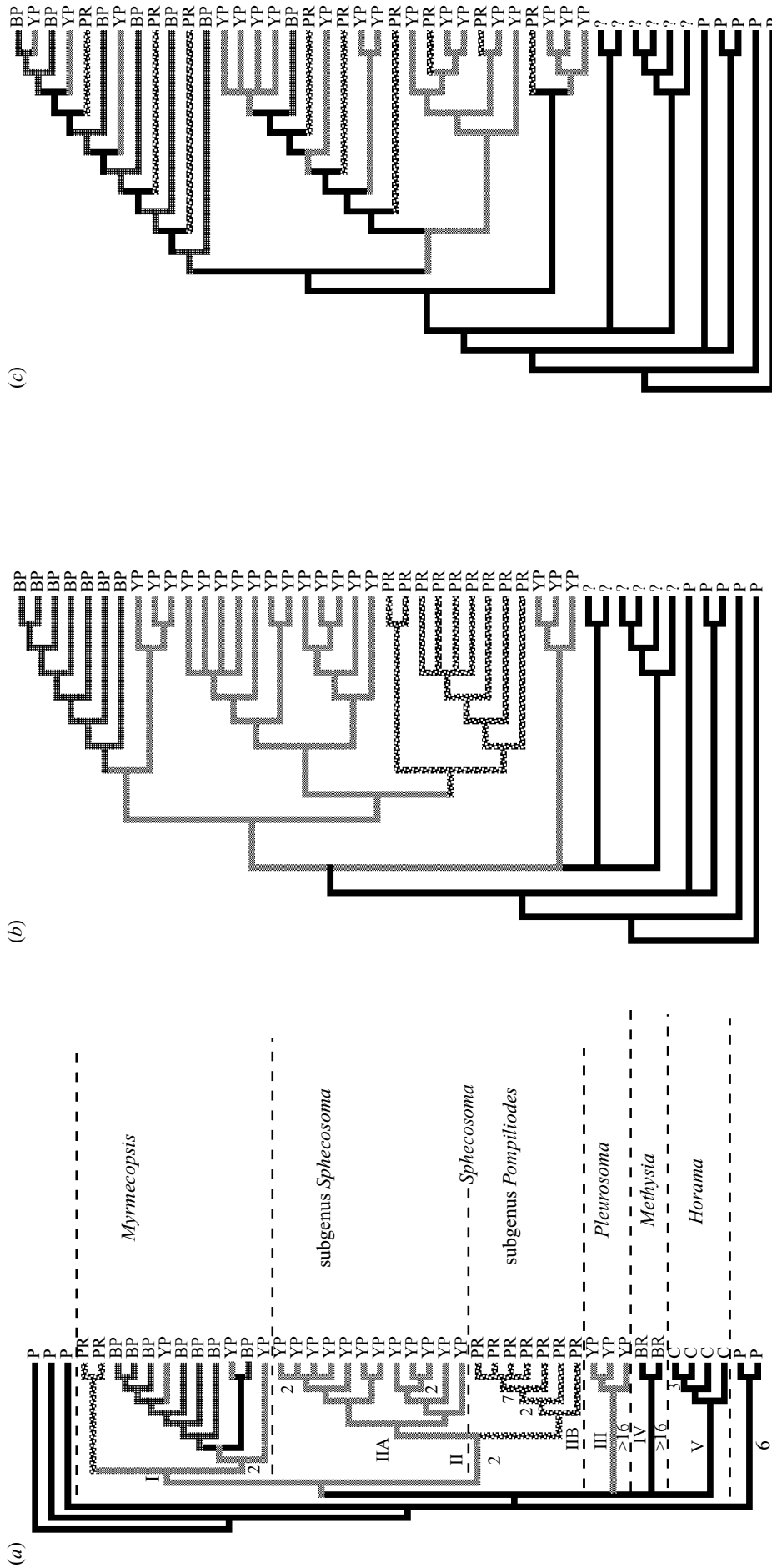


Figure 3. Observed phylogenies and phylogenetic scenarios. (a) Mimetic type mapped on the observed phylogeny of the *Sphecosoma* generic group; (b) Müllerian mimicry; (c) Q-B mimicry (P, *Pepsis* mimic; PR, *Parachartergus* mimic; BP, black *Polybia* mimic; YP, yellow *Polybia* mimic; C, corread bug mimic; BR, braconid wasp mimic; ?, model not determined, I-V, numbers in text; Arabic numbers, Bremer indices).

1991; Maddison & Slatkin 1991). PTP tests were developed for morphological datasets to determine if character-state distribution departed from random expectations (Faith & Cranston 1991). Although this use of PTP may be questioned (Källersjö *et al.* 1992), others have proposed its use for comparative purposes (Kitching *et al.* 1998). We used a PTP approach for the mimetic characters only. One thousand randomly generated character states for each mimetic character were obtained and we maintained the observed frequencies (i.e. only distribution of states among taxa were changed). The random character distribution was mapped onto the strict consensus tree. We compared the mean length (L) and consistency index (CI) of the reconstructed random characters versus the L and CI for the observed characters using a z score, which tests a hypothesis by comparing a single score with a population mean (Gravetter & Wallnau 1992). If the observed character is *not* conserved, then the L and CI for mimetic characters (table 1) will approach that of random permutations.

To examine if the observed phylogeny was more similar to simulated Q.-B., or to Müllerian phylogenetic patterns, we generated topologies by moving the minimum number of taxa within, and among, clades to obtain the predicted phylogenetic patterns ('move branch' tool option, MACCLADE 4.0). The Müllerian topology minimized changes in mimetic type in that a single origin for each mimetic type was postulated (four changes; figure 3b). The Q.-B. topology maximized changes in mimetic type (15 changes; figure 3c). The L for the non-mimetic characters and overall CIs for these hand-generated topologies were compared with the L and overall CI of the observed, as well as the mean, L and CI of 1000 randomly generated trees using Kishino–Hasegawa (KH) parsimony tests (Kishino & Hasegawa 1989).

3. RESULTS AND DISCUSSION

The phylogenetic pattern of mimicry evolution, and all our comparative tests, suggest that the dynamics of this moth–wasp mimicry system most closely resemble the predicted evolutionary dynamics of a Müllerian mimicry system, not a Q.-B. one. Individual characters related to mimicry appear to be linked in evolutionary time and imperfect mimics are not found in any species examined. These characters are so conserved across the *Sphecosoma* generic group that there is not enough homoplasy in most characters (CI greater than 0.33) to generate significance for the concentrated changes tests ($p > 0.05$). Typically, each mimetic character evolves once in one of the three mimetic types. The character state, once evolved, is usually maintained in all species of the clade (i.e. wasp waist formed by narrow S2). There are two exceptions: striped thorax and completely hyaline wings. The specific patterns of the striped thorax in yellow *Polybia* mimics tend to vary greatly among genera and the striped thorax is lost and re-evolved several times within these mimics. Completely hyaline (clear) wings evolve several times in *Myrmecopsis*, whose species mimic black *Polybia* wasps. Within this clade, the state 'completely hyaline' alternates with 'partially hyaline' wings, instead of with the state 'completely scaled or pigmented'. These results support the Hutchinson two-step model: major shifts in several mimetic characters occur basal to a clade of mimics, then minor modifications of these characters (i.e. wings or thorax

coloration) arise within these clades (Mallet & Joron 1999).

When the individual characters involved in mimicry are summarized as one of three mimetic types, the following evolutionary patterns are observed. Yellow *Polybia* type is the most evolutionarily plastic as this mimetic type originates at least four times (once in *Pleurosoma*, once in *Sphecosoma* and twice in *Myrmecopsis*; figure 3a). The black *Polybia* mimic evolves once within *Myrmecopsis* (figure 3a). The *Parachartergus* mimetic type originates twice: once in the *Pompiliodes* species group and once within *Myrmecopsis* (figure 3a). There are no reversals from the *Parachartergus* mimetic state, unlike the yellow and black *Polybia* types. Other members of the *Sphecosoma* generic group, *Methysia* and *Horama*, mimic braconid wasps and coreid bugs, respectively. Members of the outgroup are spider wasp mimics (Hymenoptera: Pompilidae, *Pepsis*).

To test the qualitative assessment of conserved character evolution more rigorously, we implemented the PTP test such that placement of the three mimetic types (black or yellow *Polybia*, *Parachartergus*) were randomly generated across the tree topology, in the same observed frequencies. If mimetic type is not conserved, then the observed L and CI for mimetic characters and the three mimetic types would approach that of random permutations. The modified PTP test generates a random mimetic-type character with a mean L of 14.5 ± 2.21 steps and a CI of 0.19 ± 0.04 . The observed mimetic-type character (table 1) is significantly shorter (six steps) and has a better fit (CI = 0.5, $p < 0.05$). When the individual mimetic characters are tested in this manner, we obtain similar results (table 1). The PTP tests confirm the observation that mimetic type and associated traits are phylogenetically conserved, as predicted by the traditional Müllerian paradigm.

Finally, we investigated whether the observed patterns were more consistent with patterns predicted for the Müllerian model–mimic system or more consistent with a Q.-B. system. To test this, a Müllerian topology was constructed such that each mimetic type evolved once, with the yellow *Polybia* type arising first (figure 3b). We also constructed a Q.-B. topology that maximized changes among mimetic types (figure 3c). Both constructed trees altered the original phylogeny as little as possible. The observed Q.-B. and Müllerian topologies were then compared with each other and with 1000 random trees. We found that the observed and Müllerian trees were not significantly different in length (408 versus 415 steps), however, the Q.-B. tree was significantly longer than both (527 steps, $p < 0.05$). This significance was not due to investigator-introduced randomness, however. The observed Müllerian and Q.-B. topologies were all significantly shorter than the 1000 random trees (length 659–753 steps). Thus, the changes introduced to produce the phylogenetic Q.-B. pattern did not approach randomness.

Comparison of the observed phylogenetic pattern with the expected phylogenetic patterns of different mimicry scenarios suggests that these moths and their wasp models are involved in a classic Müllerian association (Turner 1987). Although these moths are less noxious than their wasp models (they cannot sting), there is no evidence that they are evolving in a Q.-B. manner.

We propose that our results differ from Q.-B. predictions (Huheey 1988; Speed 1993) because of the dynamics of prey-detection abilities of predator communities. Both Huheey and Speed state that Müllerian mimicry is rarely displayed in nature, because no prey items are exactly equal in their degree of palatability. This statement assumes that predators can distinguish slight differences in palatability and find less toxic prey acceptable. Therefore, the predator must be able to link these palatability differences to anatomical differences between models and mimics. Predator perception and accuracy, not palatability, are key factors in these decisions (Chai 1986, 1988; Joron & Mallet 1998; MacDougall & Dawkins 1998).

In addition, a trade-off between mistakes and rewards exists for the predator. The penalty for mistaking a *Parachartergus* wasp for a slightly palatable moth is high. The reward for correctly catching the moth is relatively low (bitter-tasting, scale-covered bodies), particularly when compared with alternative potential prey. Thus, the predator is unlikely to sample mimics, and even if it does, the mimic's palatability does not encourage further predation events.

One factor that we cannot examine with the comparative approach is the effect of local population densities of these moth species relative to their models. If mimics are always rare (population densities low), then one might predict that these mimics would not impact the more numerous, noxious model even if the moths were highly palatable. This situation would result in monomorphic models and mimics, regardless of palatability differences. Computer modelling studies, however, indicate that a counter-intuitive situation should arise (Owen & Owen 1984; Speed 1999). When moderately unpalatable mimics are rare, an increase in predator forgetting occurs. This increase in forgetting results, in turn, in increased predation on the model species (Owen & Owen 1984; Speed 1999). The effect of relative population densities of mimics and models requires further documentation in a natural system.

Indeed, the dynamics of predator communities and those of mimetic assemblages have not, to our knowledge, been addressed, to date. Just as the mimics and models occur on a palatability spectrum, the predators themselves exist in a generalist–specialist spectrum of prey-detection capabilities. We suggest, that in a community dominated by insectivore specialists, the selective pressure for more precise mimics will be increased. A community dominated by specialist insectivores will be able to discern slight differences and may eat prey with some (albeit much lower) chemical defences. In this predator environment, Q.-B. dynamics are predicted to act most intensely on less precise mimics. Conversely, in faunas with fewer obligate insectivores, the selection pressure should be less and imperfect mimics should be more common. In addition, these conditions will shift depending on the composition, palatability and densities of prey species (Speed & Turner 1999). Thus, mimicry dynamics function across historical space (phylogeny), biogeographic space and predator–prey community assemblages.

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