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Two Possible Caterpillar Mimicry Complexes in Neotropical Danaine Butterflies (Lepidoptera: Nymphalidae)

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ABSTRACT Caterpillar mimicry is surprisingly scarce, despite many examples of apparently defended, aposematic species. Here, we describe two possible examples of caterpillar mimicry in two tribes of the Neotropical Danainae: Danaini and Ithomiini. The first example, from the Caribbean island of Hispaniola, includes two subtribes of Danaini: *Danaus plexippus* (L.), *Danaus gilippus* (Cramer), *Danaus cleophile* (Godart) (Danaina), *Anetia briarea* (Godart), and *Anetia jaegeri* (Ménétriés) (Itunina). The first two widespread *Danaus* species have unusually dark phenotypes on Hispaniola, which we suggest are the result of mimicry with endemic Caribbean danaines. The second example, from the upper Amazon of eastern Ecuador, involves four subtribes of Ithomiini: *Forbestra olivencia* (Bates) (Mechanitina), *Hypothyris fluonia* (Hewitson), *Hypothyris semifulva* (Salvin) (Napeogenina), *Ithomia amarilla* Haensch (Ithomiina), *Hyposcada anchiala* (Hewitson), *Oleria sexmaculata* (Haensch) (Oleriina), and *Pseudoscada florula* (Hewitson) (Godyridina). *Hyposcada illinissa* (Hewitson) (Oleriina) is a possible additional member. This mimicry ring shows a color pattern known only from the upper Amazon, with the caterpillar having a yellow body and bright blue anterior and posterior segments, and this pattern has clearly evolved at least four times in the Ithomiini. We suggest that precise mimicry among caterpillars may be rarer than among adult butterflies because of a lack of sexual selection to drive the initial evolution of bright colors in larvae. We also suggest that the evolution of warning colors in protected caterpillars is more difficult than in butterflies, because a novel, conspicuous caterpillar is less able to avoid capture than the more agile adult.

KEY WORDS Apocynaceae, immature stages, larval mimicry, life history, Solanaceae

Predation pressure on caterpillars is evidently high, contributing to a diverse array of adaptive responses (Dempster 1984). Caterpillar defenses include crypsis or protective resemblance to inedible items such as bird droppings (e.g., Futahashi and Fujiwara 2008), chemical camouflage (e.g., Portugal and Trigo 2005), development of false eyes to startle predators (e.g., Janzen et al. 2010), physical defenses including spines and hairs (e.g., DeVries 1987), behavioral strategies (e.g., Gentry and Dyer 2002), spatial (e.g., Murphy 2004), and temporal avoidance (e.g., Stefanescu et al. 2003), recruitment of ant defenders through mutualisms (Pierce et al. 2002; Rico-Gray and Oliveira 2007), and chemical defense (Brower 1984, Trigo 2000, Opitz and Müller 2009). Shifts in dominant predators throughout the life cycle (Dempster 1984) often lead to ontogenetically distinct defensive strategies (Nentwig 1985, Futahashi and Fujiwara 2008, Higginson and Ruxton 2010). Bright warning coloration, or aposematism, often accompanied by gregariousness, has also evolved in many species that are physically and/or supposedly chemically defended (Sillén-Tull-

berg 1988). Such warning coloration implies the importance of vertebrate predators with keen color vision, believed principally to be birds, which are key selective agents on caterpillars (Holmes 1990, Hooks et al. 2003, Van Bael et al. 2007) and are even considered potential biological control agents of caterpillar pests (Sanz 2001, Mols and Visser 2002).

Under such a scenario, therefore, it is surprising that few cases of either Batesian (Bates 1862) or Müllerian (Müller 1879) mimicry, phenomena so widespread among adult butterflies, have been reported among caterpillars (Berenbaum 1995). Conspicuous warning color patterns in larvae, such as a striped black-and-white body and a red head, or an orange body with black projections, occur commonly throughout the Lepidoptera (Wagner 2005, Conner 2009, Janzen and Hallwachs 2009). Demonstrating that similar patterns result from mimicry, however, can be difficult. For example, although Berenbaum (1995) suggested that larvae of *Papilio polyxenes* F. (Papilionidae) are mimetic of *Danaus plexippus* (L.) (Nymphalidae), Brower and Sime (1998) argue convincingly, on the basis of phylogenetic, biogeographic, and ecological evidence, that any resemblance is merely incidental. Other cases of caterpillar mimicry involve both putative Batesian and Müllerian systems and are listed in Table 1.

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Table 1. Proposed cases of caterpillar mimicry

Mimicry	Model/co-mimic	Mimic/co-mimic	Reference
Batesian	<i>Euphydryas phaeton</i> (Drury) Nymphalidae	<i>Chlosyne harrisii</i> (Scudder) Nymphalidae	Bowers (1993)
Batesian	<i>Papilio memnon</i> L. Papilionidae	<i>Cerura erminea</i> (Esper) Notodontidae	Bowers (1993)
Batesian	<i>Dendrolimus pini</i> (L.) Lasiocampidae	<i>Hyloicus pinastri</i> (L.) Sphingidae	Pelzer (1992)
Müllerian	<i>Acraea terpsichore</i> (L.) Nymphalidae	<i>Acraea alicia</i> (Sharpe) Nymphalidae	Carpenter (1913)
Müllerian	<i>Acraea alciopae</i> Hewitson Nymphalidae	<i>Acraea orestia</i> Hewitson Nymphalidae	Carpenter (1913)
Müllerian	<i>Acraea macarista</i> (Sharpe) Nymphalidae	<i>Acraea poggei</i> Dewitz, <i>Acraea arenaria</i> (Sharpe) Nymphalidae	Carpenter (1913)
Müllerian	<i>Heliconius melpomene</i> (L.), <i>Heliconius numata</i> (Cramer) Nymphalidae	<i>Eueides tales</i> (Cramer) Nymphalidae	Brown and Holzinger (1973)
Müllerian	<i>Eueides</i> spp. Nymphalidae	<i>Josia</i> spp. Notodontidae	Brown and Holzinger (1973)
Müllerian	<i>Meris alticola</i> Hulst Geometridae	<i>Neoterpes graefiaria</i> (Hulst) Geometridae	Poole (1970)
Müllerian	<i>Parnassius apollo</i> (L.) Papilionidae	<i>Glomeris guttata</i> Risso Diplopoda	Deschamps-Cottin and Descimon (1996)
Müllerian	<i>Heliconius hewitsoni</i> Staudinger Nymphalidae	<i>Eueides vibilia</i> (Godart) Nymphalidae	Mallet and Longino (1982)

We suggest that multiple criteria, individually or in concert, might be used to support a hypothesis of caterpillar mimicry, including the following:

- 1) Behavioral or physical traits that suggest that models are protected, such as gregariousness, bright warning coloration, exposed feeding or observed rejection by predators. Gregariousness is perhaps the simplest trait to score and may benefit protected prey by reducing the chances of an individual encountering inexperienced predators (Leimar et al. 1986) and by limiting attacks through predator satiation (Sillén-Tullberg and Leimar 1988). Furthermore, gregariousness may increase the effectiveness of aposematic signals in unpalatable prey (Gamberale and Tullberg 1996).
- 2) Phylogenetic evidence that one or more distinctive warning signal elements are uniquely derived in putative mimics (and perhaps their descendants). For example, Brower and Sime (1998) point out that putative mimetic pattern elements evolved in basal members of the *Papilio machaon* L. group that had probably never had contact with putative model *D. plexippus*, arguing against mimicry.
- 3) Ecological and biogeographic evidence that putative mimics co-occur in space and time, at multiple scales, from microhabitat to geographic region. Demonstrating that species that mimic one another (co-mimics) co-occur more often than non-mimics would strengthen any such observations.
- 4) Concordant geographic change in warning signal among co-mimics and models, such as is observed in most mimicry rings involving adult butterflies. Notable examples of the latter include the precisely matching hybrid zones separating co-mimetic subspecies of the Neotropical *Heliconius erato* (L.) and *Heliconius melpomene* (L.) (Sheppard et al. 1985), and the geographically restricted mimetic female morphs of *Papilio dardanus* Brown in Africa (Ford 1936). Importantly, this kind of evidence supports mimicry even among closely related species that share the same ancestral warning color pattern (Willmott and Mallet 2004).
- 5) Experimental evidence that a warning color pattern reduces the frequency of attacks on co-mimics

by predators that have sampled a protected individual, ideally in natural surroundings. Thus, larvae are in some way unprofitable (not necessarily unpalatable) and bear a color pattern that can be learnt and avoided.

Although convincing experimental evidence is difficult to obtain for a range of predators in natural conditions, fulfillment of either criterion two or 4, especially in conjunction with other criteria or evidence for host plant toxicity, makes a hypothesis of mimicry reasonable.

Larval mimicry is a potentially rewarding field for research, but very few cases are yet reported that will permit rigorous testing. In particular, confinement of our knowledge of larval mimicry to only a few species, typically only a species pair in each case, hinders the kinds of comparative analyses that have recently begun to elucidate the evolution and ecology of adult butterfly mimicry rings (Mallet and Gilbert 1995, Becaloni 1997a, DeVries et al. 1999, Elias et al. 2008, Hill 2009). Here, we therefore describe two likely larval mimicry complexes among Neotropical members of the tribes Danaini and Ithomiini (Nymphalidae, Danaeinae). Because these groups are some of the best studied nymphalids, integrating ecological, phylogenetic and biogeographic data should in future permit novel tests of the larval mimicry hypothesis in these two groups.

Materials and Methods

Study Groups. The Danaini include ≈ 150 species of relatively large, colorful butterflies in tropical and temperate regions throughout the world, with the highest species diversity in the oriental region (Ackery and Vane-Wright 1984). Both immature stages (Wiklund and Sillén-Tullberg 1985) and adults (Brower 1958, Chai and Srygley 1990, Pinheiro 1996) are unpalatable and warningly colored, and adults are extensively involved in both Müllerian and Batesian mimicry rings (Ackery and Vane-Wright 1984). In the Americas, the Danaini include only 13 species in three genera, *Danaus* Kluk, *Lycorea* Doubleday, and *Anetia* Hübner (Lamas 2004). Adult mimicry is typically limited, with the exception of *Lycorea*, which is a member

of diverse mimicry complexes with ithomiines and heliconiines (e.g., Beccaloni 1997b).

The tribe Ithomiini, recently included in the Danaeae (Wahlberg et al. 2009), contains ≈ 360 species distributed from sea level to 3,000 m from Mexico to southern Brazil and Argentina. Ithomiines are inhabitants of humid forest, where they are particularly abundant in the understory. Adults of all species are believed to be unpalatable (Brown 1984) and participate in mimicry with other ithomiines or putatively unpalatable butterflies, especially the Heliconiinae (Chai and Srygley 1990), dominating these mimicry rings in species diversity and abundance (Beccaloni 1997b).

Although there are few published observations of predation on unpalatable tropical butterflies in nature (e.g., Brower 1988), the primary predators driving the evolution of mimicry are believed to be insectivorous birds, being the only abundant predators with suitably developed color vision to explain precise mimicry (Chai 1986, Langham 2004).

Field Methods. Danaeae immature stages and adults were studied in 1995 by A.S. above Mata Grande in the Cordillera Central of Dominican Republic (Santiago Province, 1,000–1,200 m, 19° 18' N, 70° 54' W). Eggs were collected on *Asclepias nivea* L. (Apocynaceae) and reared to adult in resealable plastic bags with fresh leaves of the natural host plant provided every 2–3 d.

Ithomiini were studied in 2005 at Napo Wildlife Center (NWC) and surroundings in eastern Ecuador (Orellana Province, 240–300 m, 0° 31.43' S, 76° 23.41' W) by K.R.W., M.E., and colleagues (Elias et al. 2008). The study site was topographically complex and covered with wet lowland rain forest, mostly undisturbed except along the edges of the Río Napo and Río Añangu. Supplementary information comes from further studies in 2001–2002 and 2006 at cloud forest localities in eastern Ecuador (Sucumbíos and Zamora-Chinchi, 1,000–3,000 m) (Willmott and Mallet 2004; Willmott and Lamas 2006, 2008). Individuals were located by searching many individual plants in known ithomiine host plant families, Solanaceae, Apocynaceae and Gesneriaceae (Willmott and Freitas 2006; Beccaloni et al. 2008). Eggs and larvae were collected and reared as described above. Photographs were taken of each instar, and cast larval skins, head capsules, and specimens of larvae and pupae were preserved, where possible, in locally available industrial alcohol (ethanol) and are deposited in the Florida Museum of Natural History, Gainesville, FL. Voucher host plant specimens were collected and are deposited in the Natural History Museum, London, United Kingdom; and the Museo Ecuatoriano de Ciencias Naturales, Quito, Ecuador. Additional information on the height above ground, host plant height, density, and microhabitat also were recorded. Data on the systematics and distribution of Ithomiini come from research in progress by Willmott and Lamas to revise several ithomiine genera (Willmott and Lamas 2006, 2008).

Results

Danaeae. Five danaine species were observed flying together in the study locality in Dominican Republic: the widespread *Danaus plexippus* and *Danaus gilippus* (Cramer) and the Caribbean endemics *Danaus cleophile* (Godart), *Anetia jaegeri* (Ménétriés), and *Anetia briarea* (Godart). All of these species, except *A. briarea*, are known or suspected to feed on *A. nivea* at the study site. Larvae of *D. plexippus* (Fig. 1A), collected as eggs from the latter host plant, had much broader dark bands than typical individuals from continental United States (Fig. 1B; Warren et al. 2010). *D. gilippus* larvae in the continental United States usually bear a banded white, black, and yellow pattern (e.g., Fig. 1D; Warren et al. 2010) similar to *D. plexippus* but also occur very rarely as a darker phenotype (e.g., Calhoun 1996). This darker phenotype was uniformly observed at the Dominican Republic study site (Fig. 1C). *D. cleophile*, observed ovipositing on *A. nivea* during the study, is described as “velvety black . . . with narrow bands of yellow lying at the junction of the segments” (Brown and Heineman 1972, p. 94), a description closely matching the observed Dominican Republic larvae of *D. plexippus* and *D. gilippus*. Several larvae of *A. jaegeri* were reared from the same host plant. These larvae were described by Sourakov and Emmel (1996) and bear multiple narrow black and white rings (Fig. 1F). Finally, adults of *A. briarea* also were found in the same habitat, although no immature stages were encountered. In the fourth instar, *A. briarea* larvae have a banded black-and-white pattern similar to *A. jaegeri* (Fig. 1F) and the mainland *A. thirza* Geyer (Llorente et al. 1993), which changes in the fifth instar (Fig. 1E) to a pattern that seems predominantly dark with more dispersed white bands.

Based on these observations, we suggest that the unusually dark phenotypes of the widespread *D. plexippus* and *D. gilippus* in Dominican Republic result from mimicry with the three Caribbean-endemic danaines observed at the study site. The endemic danaines have similar banded patterns that are notably darker than those of the first two species in the continental United States, and we consider the following in evaluating whether this dark, banded coloration is a warning color pattern and mimetic:

- 1) The black larval coloration is distinctive against the host plant leaves where these larvae feed, and unpalatability of all species in the putative mimicry ring is probable based on their close phylogenetic relationship, shared host plant, and evidence that *D. plexippus* larvae, at least, are unpalatable to birds (Brower et al. 1967, Wiklund and Sillén-Tullberg 1985).
- 2) The dark larval coloration observed in Hispaniolan danaines is widespread throughout the Danaeae, also occurring, for example, in the mainland *A. thirza* (Llorente et al. 1993) as well as in other members of *Danaus* (e.g., Bascombe et al. 1999). It is therefore not clear whether the dark color patterns of Hispaniolan danaines represent an ancestral or recently derived trait. However, the fifth

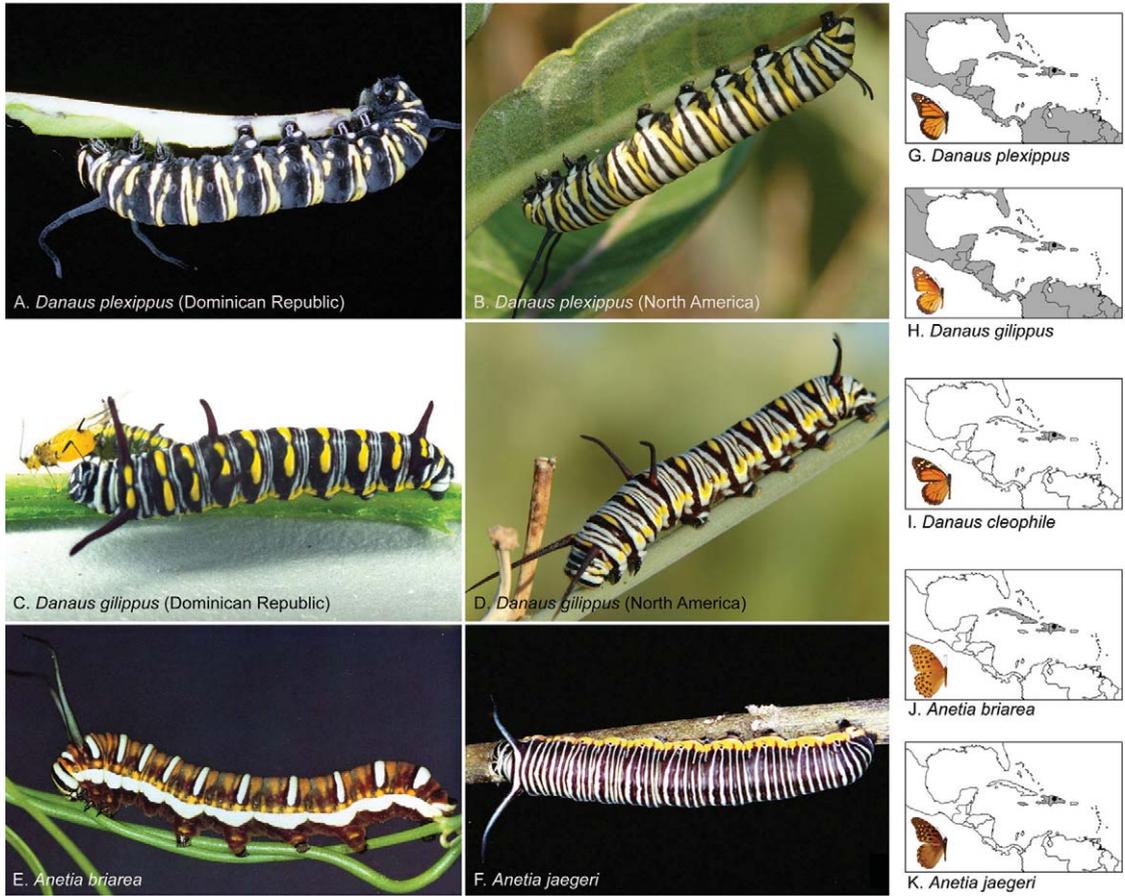


Fig. 1. (A–F) Putative Danaini dark-banded caterpillar mimicry complex from Dominican Republic (A, C, E, and F), with geographically distinct phenotypes (B and D). (A) *D. plexippus*, Dominican Republic. (B) *D. plexippus*, Wisconsin, North America. (C) *D. gilippus*, Dominican Republic. (D) *D. gilippus*, Arizona, North America. (E) *Anetia briarea*, fifth instar, Dominican Republic. (F) *Anetia jaegeri*, fifth instar, Dominican Republic. (G–K) Approximate distributions of the five Dominican Republic danaines recorded at the study site (black dot). Distribution data from Ackery and Vane-Wright (1984), Smith et al. (1994), and www.butterfliesandmoths.org. Caterpillar images B and D courtesy of Gene Hanson, image E courtesy of Linda S. Fink; butterfly images from Warren et al. (2010). (Online figure in color.)

instar of *A. briarea* (Fig. 1E) is even darker than earlier instars (Brower et al. 1992), which resemble *A. jaegeri* (Fig. 1F) and *A. thirza* (Llorente et al. 1993). The particularly dark pattern of the fifth instar of *A. briarea* might thus represent a unique derived trait which at least enhances its similarity to *D. cleophile* (based on Brown and Heineman’s (1972) description of the latter).

- 3) All putative mimics occur together in time and space, with four of the danaine species feeding or ovipositing on the same host plant species in the same area.
- 4) The distinctive color pattern of *D. plexippus* and *D. gilippus* on Dominican Republic are the only examples of which we know where an aposematic larval color pattern seems to have varied geographically to match putative co-mimics. Sympatric *D. cleophile*, *A. jaegeri*, and *A. briarea* also bear similar dark patterns, and these three species co-occur only on Hispaniola (Fig. 1). Given that all species

except *A. briarea* also occur on Jamaica, we would expect Jamaican *D. plexippus* and *D. gilippus* to have a similar dark larval color pattern. Unfortunately, we have been unable to find any precise descriptions of the early stages of these species on Jamaica (Brown and Heineman 1972). The fifth instar *D. plexippus* on Guadeloupe (Zagatti et al. 2010) and on Puerto Rico (Warren et al. 2010) is also very similar to that observed on Hispaniola, but we have otherwise not observed this phenotype outside the Caribbean.

Ithomiini. Immature stage data were obtained in the field for 32 of the 57 ithomiine species recorded at NWC (Fig. 2; Supp Table 1 [online only]) and from publications for an additional nine species (Brown and Freitas 1994, Hill and Tipan 2008). Of the 41 species for which some data were available, 19 seem to be mostly cryptic (Fig. 2), being entirely green, or olive-green to buff, often with diffuse pale yellow lateral markings

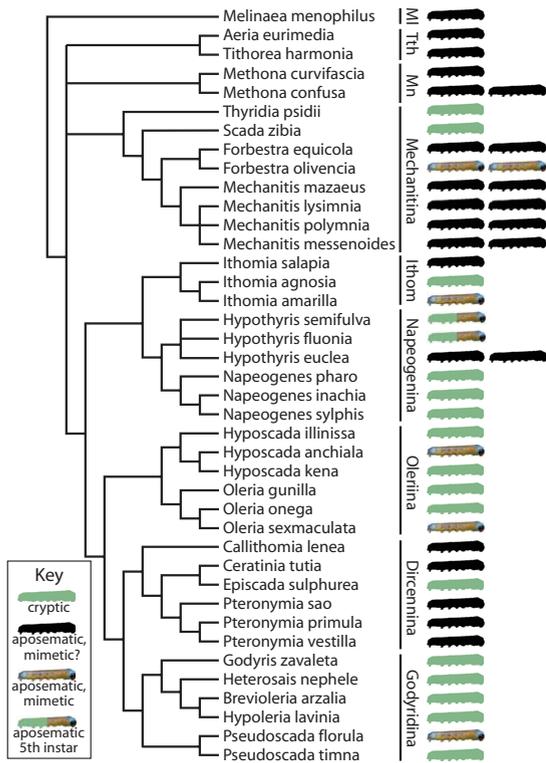


Fig. 2. Cladogram for Ithomiini caterpillar community studied at NWC, showing phylogenetic distribution of cryptic (green), aposematic, possibly mimetic (black) and aposematic, mimetic (yellow-blue) caterpillar color patterns. Subtribal names abbreviated as follows: MI, Melinaeina; Tth, Tithoreina; Mn, Methonina; Ithom, Ithomiina. Double caterpillars indicate gregariousness. Cladogram is reduced from that in Elias et al. (2008) based on DNA sequence data. (Online figure in color.)

(Fig. 3D, F, H, and M). *Hypothesis mamercus* (Hewitson) (all taxonomic authorities for ithomiine names are in Supp Table 1 [online only]) was cryptic in early instars, but because no data were available for the late fifth instar (see below), it is omitted from Fig. 2. The remaining 22 species, representing all tribes and 14 genera (Fig. 2), seem to be warningly colored to some extent, at least in the fifth instar, with many exhibiting color patterns that include black, white, and yellow bands or mosaics. Although mimicry might be involved among some of the black-, white-, and yellow-patterned caterpillars, these patterns are geographically widespread and not sufficiently similar to provide strong evidence of mimicry. By contrast, five of the warningly colored species in four different subtribes [*Forbestra olivencia* (Bates), *Ithomia amarilla* Haensch, *Hyposcada anchiala* (Hewitson), *Oleria sexmaculata* (Haensch), and *Pseudoscada florula* (Hewitson)] (Figs. 2; 3A, C, I, L, and N) exhibited a particularly novel color pattern in which the body is a greenish yellow with bright blue anterior (T1-T2) and posterior (A9-A10) segments. In *F. olivencia*, this coloration was present from at least the third instar,

whereas in the remaining species it became intense only in later instars (fourth to fifth). The late fifth instar to prepupa of two otherwise cryptic species, *Hypothesis fluonia* (Hewitson) and *H. semifulva* (Salvin) (Fig. 3E and G), developed similar but more subdued coloration with the blue coloration replaced by bluish gray. We tentatively classified *Hyposcada illinissa* (Hewitson) as cryptic, even though this species also shows a similar but less intense coloration in the fifth instar (Fig. 3J).

Evidence for the blue-yellow color pattern being aposematic and mimetic comes from several anecdotal observations.

- 1) Larvae of *F. olivencia* are moderately gregarious, occurring mostly in groups of two to four individuals (with clusters of up to 13 eggs observed; Hill 2006; K.R.W. and M.E., personal observation), a trait typically associated with aposematism and presumably unpalatability (Sillén-Tullberg 1988).
- 2) The blue-yellow color pattern is highly distinctive, being unknown among well-studied ithomiine communities in adjacent montane Ecuador (e.g., Willmott and Mallet 2004), as well as throughout the remainder of the range of the Ithomiini. For example, Brown and Freitas (1994) figure ithomiine larvae for many species from several countries, especially southeastern Brazil, with no evidence of a similar pattern elsewhere. In eastern Ecuador, the pattern has apparently evolved at least four times, in the subtribes Mechanitina, Ithomiina, Oleriina, and Godyridina. In *Forbestra* Fox, *F. equicola* (Cramer) also has aposematic, gregarious larvae, but these are black, white, and yellow (Brévi-gnon 2003), whereas the immature stages of the only other congener, *F. proceris* (Weymer), are unknown. *Mechanitis* F., the sister genus to *Forbestra* (Willmott and Freitas 2006), also has gregarious and aposematic larvae but of different color pattern (Figs. 2 and 3B). The color pattern of *Ithomia amarilla* (Fig. 3C) differs sharply from known congeners, which typically resemble *Ithomia agnosia* Hewitson (Fig. 3D), although *Ithomia salapia* Hewitson is also aposematic, being black with yellow rings (K.R.W. and M.E., personal observations). The early fifth instar color patterns of *H. fluonia* (Fig. 3F) and *H. semifulva* (Fig. 3H) are typical of the genus, and it is possible that late instars of species in other regions also may resemble the putative mimics in Fig. 3E and G, which would suggest that resemblance in this case could be purely incidental. Similarly, *H. illinissa* is not strikingly different from the fifth instar of the closely related montane *Megolera orestilla* (Hewitson) (Willmott and Lamas 2008), and resemblance may perhaps be fortuitous. However, the intense blue anterior and posterior segments of *H. anchiala* are not known in any other congener or member of the subtribe, except the sympatric *O. sexmaculata* (Fig. 3L). Finally, *P. florula* differs dramatically from the sympatric congener *Pseudoscada timna* (Hewitson), which has a color pat-



Fig. 3. Putative Ithomiini yellow-blue caterpillar mimicry complex from eastern Ecuador (left column), with nonmimetic phenotypes (right column). Range maps based on distribution data compiled by K.W. (unpublished data). All specimens from Napo Wildlife Center, 250 m, Napo, Ecuador, except K, from Reserva Arcoiris, 2,100 m, Zamora-Chinchipe, Ecuador. (A) *Forbestria olivencia* (Mechanitina). (B) *Mechanitis messenioides* (Mechanitina). (C) *Ithomia amarilla* (Ithomiina). (D) *Ithomia agnosia* (Ithomiina). (E) *Hypothyris fluonia*, late fifth instar (Napeogenina). (F) *Hypothyris fluonia*, early fifth instar. (G) *Hypothyris semifulva*, late fifth instar (Napeogenina). (H) *Hypothyris semifulva*, early fifth instar. (I) *Hyposcada anchiala* (Oleriina). (J) *Hyposcada illinissa* (Oleriina). (K) *Megoleria orestilla* (Oleriina). (L) *Oleria sexmaculata* (Oleriina). (M) *Oleria onega* (Oleriina). (N) *Pseudoscada florula* (Godyridina). (O) *Pseudoscada timna* (Godyridina). (Online figure in color.)

tern typical of its genus (Brown and Freitas 1994) and of the closely related genus *Greta* Heming (Willmott and Freitas 2006).

- 3) All of the proposed mimics are sympatric, being recorded from a single site of $\approx 1 \text{ km}^2$, where all occur in forest understory. The geographic ranges of the proposed mimics also broadly overlap in the upper Amazon basin (Fig. 3); although *H. illinissa* and *H. anchiala* also have Transandean records, *P. florula* has disjunct subspecies in the Guianas and southeastern Brazil, and *H. fluonia* also extends to the lower Amazon and Guianas. Some closely re-

lated but nonmimetic sympatric species also have similar ranges (e.g., *O. onega* Hewitson) but more often represent species at the edge of a largely submontane distribution (e.g., *I. agnosia* and *P. timna*) (Fig. 3).

Discussion

Danaini. Little is known about the palatability of danaine larvae beyond studies with *D. plexippus* (e.g., Wiklund and Sillén-Tullberg 1985), but the correlation between warning coloration and typically toxic

asclepiad host plants among many Danaini suggests that most species are chemically defended. Four of the five species at the Dominican Republic study site fed on the same host plant and are probably Müllerian mimics, whereas the natural host plant of *A. briarea* is not known (Brower et al. 1992).

The hypothesized shift to a darker warning coloration in *D. plexippus* and *D. gilippus* may have resulted from the abundance of other dark danaine larvae on Hispaniola, which contains the highest species richness for this tribe in the Caribbean. The Caribbean endemics *D. cleophile*, *A. briarea*, and *A. jaegeri* are relatively common in upland forests (Smith et al. 1994), certainly no rarer than the widespread *D. plexippus* and *D. gilippus*. The apparent occurrence of dark *D. plexippus* larvae on Guadeloupe (Zagatti et al. 2010) and Puerto Rico (Warren et al. 2010), which lack endemic Caribbean danaines, suggests that Caribbean *Danatus plexippus megalippe* (Hübner) colonized these islands from Hispaniola if the dark larval phenotype is indeed mimetic. Clearly, however, much more research on the distribution of larval phenotypes and butterfly phylogeography throughout the Caribbean is needed.

Given the widespread presence of dark color patterns throughout the Danaini, it is of course possible that the dark Caribbean phenotype in *D. plexippus* and *D. gilippus* represents an ancestral state, and that there is selection for paler forms in the continental United States. Without any obvious selective advantage for pale continental coloration, however, and given that the pale form is much more widespread, we prefer the hypothesis of a shift in color pattern in the Caribbean.

Ithomiini. The Ithomiini mimicry ring perhaps represents Batesian or mixed Batesian–Müllerian mimicry, with *F. olivencia* the most obvious unpalatable model. All basal ithomiine clades (Tithoreina, Methonina, Melinaeina, and *Athesis* Doubleday + *Patricia* Fox) have brightly colored larvae, whereas most species in the more derived subtribes Napeogenina, Ithomiina, Oleriina, Dircennina, and Godyridina have cryptic larvae (Fig. 2) (Brown and Freitas 1994, Willmott and Freitas 2006). Within the transitional Mechanitina, both cryptic and bright color patterns occur, but aposematism probably was present in the ancestor of *Mechanitis* + *Forbestra* because these sister genera are both aposematic (Fig. 2). Widespread bright larval coloration among basal Ithomiini clades suggests that their larvae are protected, and *Methona* Doubleday and *Mechanitis*, at least, are unpalatable to chicks (Massuda and Trigo 2009). The pyrrolizidine alkaloids that protect adult Ithomiini (Brown 1984) are known only in *Tithorea* Doubleday larvae (Trigo and Brown 1990, Trigo et al. 1996), but different compounds might well be involved in other genera, such as the tropane alkaloids present in *Placidina* d'Almeida (Freitas et al. 1996) and as yet unknown compounds in *Methona* (Massuda and Trigo 2009). The gregariousness and appearance of aposematic coloration in early instars of *F. olivencia* (Hill 2006) are both consistent with the hypothesis that its larvae are unpalatable.



Fig. 4. Possible model for the Ithomiini yellow-blue caterpillar mimicry complex: sawfly species (Hymenoptera: Symphyta) observed near study site at Ecuador, Sucumbíos, Garzacocha, by R. Hill. (Online figure in color.)

In all of the remaining putative mimics, the larvae are solitary, members of clades that largely have cryptic larvae, and cryptic until the later instars. In *Ithomia* Hübner, all known larvae of species in the clade containing *I. amarilla* (Mallarino et al. 2005) are cryptic (Brown and Freitas 1994; Fig. 3D). In *Hypothyris* Hübner, *H. euclea* is also aposematic (Young 1977, Brown and Freitas 1994), but there is no evidence that it forms a clade with the two putative mimics described here, *H. fluonia* and *H. semifulva* (C. Arias, unpublished data). Delaying warning coloration until later instars in palatable species should reduce the relative abundance of Batesian mimics, because late instars are less abundant than early instars and thus result in fewer attacks on all individuals by naïve predators.

Notwithstanding the previous discussion, conspicuous larval coloration is relatively common in the derived tribe Dircennina, in *Callithomia* Bates, *Ceratinia* Hübner, and in all three *Pteronymia* Butler & Druce at the Ecuadorian study site (and elsewhere; Brown and Freitas 1994; K.R.W. and M.E., personal observations), although none of these species is involved in the blue-yellow mimicry ring (Fig. 2). Most ithomiines, including all Dircennina, feed on Solanaceae, a plant family with diverse secondary chemicals (Brown 1987), and the likelihood that larvae of at least some of these species are chemically protected seems high. For example, Dyer (1995) found that cryptic *Greta morgane oto* (Hewitson) (Ithomiini: Godyridina) caterpillars were unpalatable to ants. It is clear, therefore, that assays of larval palatability are needed, and the fact that larvae of *F. olivencia* were not significantly more abundant in the study site than those of putative Batesian mimics (K.R.W. and M.E., unpublished data) suggests that at least some Müllerian mimicry is probably involved. Finally, additional likely models are the later instars of a sawfly species (Hymenoptera: Symphyta) that was observed by R. Hill (personal communication) at Garzacocha, a site several kilometers from the study site (Fig. 4). Sawfly larvae have various behavioral and chemical defenses (Boevé and Pasteels 1985, Vlieger et al. 2004) and are often gregarious and aposematic. According to Hill, the sawfly larvae at Garzacocha rested and fed on the underside of fern leaves (Pteridophyta), in the same areas as larvae of *F. olivencia*.

One obvious question is why only some of the conspicuously colored caterpillars at NWC adopt the blue-yellow pattern, whereas others have a geographically widespread black, yellow, and white pattern (Brown and Freitas 1994, Willmott and Freitas 2006). Among adult ithomiines, mimicry rings are at least partially segregated by microhabitat (DeVries et al. 1999, Elias et al. 2008, Hill 2009), flight height (Beccaloni 1997a, Elias et al. 2008), and season (DeVries et al. 1999), perhaps partly because of host plant distribution (Beccaloni 1997a, Willmott and Mallet 2004). Notably, in many of the previously proposed cases of caterpillar mimicry the models and mimics occur in restricted habitats (e.g., Deschamps-Cottin and Desimon 1996) or on the same host plants (Poole 1970, Mallet and Longino 1982, Pelzer 1992). Larvae occupying narrower niches are exposed to a limited fraction of the total predator population and are therefore perhaps more likely to evolve mimicry, because the chances of encountering educated predators is higher. At NWC, however, there is no immediately obvious similarity among the microhabitats of the host plants for the eight species (M.E. and K.R.W., unpublished data).

However, it is notable that the geographic ranges of two of the most remarkable mimics, *I. amarilla* and *O. sexmaculata*, are narrowly confined to a small region in the western Amazon. *P. florula*, also a notable mimic, has a disjunct range, with a population confined to a similar area in the western Amazon, and other populations in the Guianas and southeastern Brazil. If, as we suggest below, mimicry evolves much more rarely in larvae than in adults, then the most likely warning color pattern for a caterpillar to display is that which is most common throughout its geographical range. Species with broad ranges are therefore most likely to adopt already widespread patterns, whereas those with restricted ranges are more likely than widespread species to adopt existing patterns that are unique to a small region. Thus, in caterpillars, shared host plants among co-mimics (Poole 1970, Mallet and Longino 1982, Pelzer 1992, and Danaini reported here) may result in mimicry because of similarity of geographic range rather than similarity of microhabitat.

Evolution of Caterpillar Mimicry. Four main hypotheses have been suggested to account for the rarity of known cases of mimicry among lepidopteran larvae (Berenbaum 1995, Brower and Sime 1998). Poor knowledge of tropical lepidopteran immature stages must surely contribute to the paucity of documented cases of caterpillar mimicry (Berenbaum 1995). Furthermore, the tendency for caterpillar researchers (ourselves included) to study taxonomically limited hosts or herbivores must lead to cases of cross-taxon mimicry being frequently overlooked. For example, the blue-yellow ithomiine pattern discussed here is also very similar to that of a presumably highly toxic (Murphy et al. 2010) Amazonian stinging slug caterpillar (Limacodidae), whose photograph we discovered by chance at <http://www.onlineadventure.com/photos/1964>. Although the full distribution of this limacodid is unknown, it occurs at least partly within

the range of the majority of supposedly mimetic ithomiines in Fig. 3.

Brower and Sime (1998) suggested that because many caterpillars are host plant specific, host plants will form a part of the predator's search image. Thus, predators learn to avoid specific combinations of plant-caterpillar color pattern rather than the color pattern itself. Although this is an interesting and plausible hypothesis, it is potentially relevant only to Batesian mimicry. If color pattern was a reliable indicator of unpalatability, then host plant phenotype would cease to be an important cue for identification of edible prey. However, in the Ithomiina example we describe here, which we argue is likely to represent Batesian mimicry, there is little obvious phenotypic similarity among the host plants.

We suggest an additional hypothesis that focuses on the initial evolution of aposematic coloration. Explaining the origin of aposematic coloration in protected species is a challenge because the benefits of warning coloration become significant only when the aposematic pattern is abundant (e.g., Mallet and Singer 1987). In adult butterflies, novel color patterns probably arise frequently through sexual selection, because many butterflies are brightly colored even if not mimetic or aposematic. Such patterns also may incidentally provide a crude resemblance to a protected species that can be refined by selection for mimicry (Mallet and Singer 1987). Obviously, larvae lack the mechanism of sexual selection to provide an initial benefit for bright coloration to outweigh the disadvantages of increased visibility to predators, and this might limit the evolution of larval mimicry. The role of sexually selected color patterns in the evolution of mimicry could be examined by testing whether mimicry in adult butterflies arises more frequently in clades containing species that have bright coloration for sexual signaling. Furthermore, we suggest that a novel aposematic pattern in a cryptic, but protected, butterfly is more likely to become widespread if it evolves in the adult rather than larval stage. This is because adult butterflies are more likely than caterpillars to be able to escape capture once identified as a potential prey item. Several studies have experimentally documented the selective value of mimicry in adult butterflies (Mallet and Barton 1989, Kapan 2001), and similar studies could be conducted on caterpillars. Finally, J. Mallet (personal communication) suggested that number dependence and apparency might explain rarity of caterpillar mimicry. Because caterpillars are smaller and move less than adult butterflies, they are more likely to escape detection by using crypsis, whereas the relative rarity of adults means that they gain more from mimicry by reducing the fraction sacrificed during predator learning.

The example of *Danaus* described here is the only example of which we know where larval aposematic coloration is geographically variable, matching local models. This rarity of precise local mimicry, such a striking phenomenon in adult butterflies, itself contributes to why larval mimicry is so rarely documented.

Much of this discussion is necessarily speculative with the hope of stimulating further research. The putative ithomiine larval mimicry ring documented here is one of the most diverse known, and the excellent knowledge of ithomiine phylogeny, ecology, and distribution should permit future comparative analyses to test more rigorously what ecological traits most favor the evolution of larval mimicry.

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