

CHRIS D. JIGGINS



THE ECOLOGY & EVOLUTION OF
Heliconius
Butterflies

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Preface

I had been working in the western part of Ecuador for about three months before I got around to heading east, taking the road from Baños, high in the Andes and overshadowed by volcanoes, down through the narrow valley towards Puyo. At the time, this road was famous with backpackers because of a waterfall that fell right onto the middle of the road. Travellers who opted for the open-air option and sat on the roof of the bus would get soaked on the way down. My first stop was in a town called Shell—in the 1930s, it was a frontier oil town, named after the oil company responsible for its establishment. I walked through the dusty streets towards a stream just at the edge of the town, which I had heard was a good place to collect *Heliconius*.

It was getting towards dusk, and sure enough, as I waded along the shallow stream, there was suddenly a gentle fluttering of butterflies all around me. I had come across a roost of *Heliconius erato*, just starting to gather before settling on a twig to sleep together for the night. Even by this stage, early in my PhD, I felt that I was starting to get to know this species fairly well. I had already collected several hundred of them across south-western Ecuador, as part of my PhD project.

But these butterflies were wildly different. For a few moments I was completely confused—I knew the shape, the flight pattern, even the strange habit of gathering in streams at dusk. But the butterfly I knew from western Ecuador, *Heliconius erato cyrbia*, was iridescent blue with red patches. These butterflies had pink and white spots. I had seen lots of pictures, so logically I knew that these were *Heliconius erato notabilis*, a geographic race of the same species. But nothing quite prepared me for the dramatic difference in appearance between what I was familiar

with and what was fluttering around my head. It was the moment in which the geographic variation in form that *Heliconius* are famous for came vividly to life. I hope that in this book I can convey some sense of the awe that I felt that day about the unusual biology of these butterflies.

Along the way, I hope to address some current questions in evolutionary biology, and highlight areas in which we remain ignorant. In the first chapter, I outline some of the questions that work on *Heliconius* has helped to address, or in some cases might contribute to in the future. These topics are largely focused on the genetic basis for adaptation and speciation that have been the motivation for my own work on *Heliconius*. However, this brief overview of topics is not meant to be comprehensive, and throughout the book I will also describe many other areas of ongoing and past *Heliconius* research.

The second chapter introduces the butterflies and their relationships, as well as briefly summarizes the history of *Heliconius* research (with not a little trepidation, as I have certainly missed some moments that others would consider critical). The next four chapters review many aspects of the basic biology of *Heliconius*, before moving on to wing pattern evolution and finally speciation.

This book is based on the premise that a complete understanding of any topic in biology—but evolution particularly so—requires an intimate understanding of the natural biology of the organism studied. I therefore review the different aspects of *Heliconius* natural history that have been studied over the years, before coming back to the topics of speciation and the genetic basis of adaptation, which have come to the fore in *Heliconius* research. I hope that readers primarily interested in the latter

will gain a richer understanding of *Heliconius* speciation biology from reading about the ecology and natural history of these butterflies. Conversely, readers interested in the natural history of these brightly coloured butterflies—so common in tropical butterfly displays around the world—will hopefully be pleasantly surprised to learn that they are also the subject of evolutionary studies in genomics and developmental biology.

It has taken me a long time to write this book. Looking back through emails, I found that my first correspondence with Ian Sherman at OUP dates back to November 2005. In the meantime, *Heliconius* research has surged ahead. I had originally planned that the book would summarize the older literature on the natural history of *Heliconius*, and only briefly touch upon later developments. However, the genomic and developmental studies have

progressed so much that I now feel compelled to include more of them here than was originally planned. Undoubtedly, some of these sections will become dated fairly quickly, but I hope that our understanding of wing pattern development and speciation genomics is sufficiently advanced now that the basics will remain relevant for some time to come.

One of the sources of inspiration as I was thinking of writing this book was Peter Grant's *Ecology and Evolution of Darwin's Finches*. In his Preface, Grant mentions a number of other systems that might also be excellent case studies for understanding biological diversification, one of which is *Heliconius* butterflies. Over 30 years after the first publication of the *Ecology and Evolution of Darwin's Finches*, I am hoping that the butterflies can finally catch up with the finches.

Acknowledgements

This book has been several years in gestation, and over that period very many people have contributed. I am grateful to Margarita Beltran, Grace Wu, Luana Maroja, John Davey, Markus Möst, Adriana Briscoe, Richard Merrill, and Claire Mérot for reading chapters. Special thanks to Arnaud Martin and Joe Hanly, who provided very constructive comments on the development chapter, and Richard Merrill and Simon Martin, for reading and commenting on the final two chapters. Patricio Salazar wrote an introduction to his PhD thesis that was very helpful in thinking about the history of *Heliconius* wing pattern genetic studies. Other members of my group and the wider *Heliconius* community have contributed; I am grateful to Camilo Salazar, Carolina Pardo-Diaz, Krzystof Kozak, Laura Ferguson, Simon Baxter, Jamie Walters, Ana Pinharanda, Kathy Darragh, Emma Curran, Liz Evans, Nicola Nadeau, Denise Dellaglio, Arnaud Martin, Marcus Kronforst, Ricardo Papa, Robert Reed, Susan Finkbeiner, Kanchon Dasmahapatra, Violaine Llaurens, Catalina Estrada, and Tim Thurman for various discussions.

I am especially grateful to Keith Willmott, Andrei Sourakov, and Tom Emmel at the MacGuire Center, University of Florida, for providing access to the Neukirchen collection in order to take photos of specimens. I am also indebted to Walter Neukirchen for amassing such a wonderful collection of perfect specimens. Thanks to Derya Akkaynak for help with image manipulation. Gerardo Lamas generously shared his most recent taxonomy for the group, reproduced here in updated form as Chapter 12.

In Panama, I am grateful to Liz Evans and Oscar Paneso for raising caterpillars and keeping an

eye out for unusual species that helped with obtaining images of early stages. I thank Ana Carolina Aymone, Arnaud Martin, Harald Krenn, Neil Rosser, Keith Willmott, Adriana Briscoe, Richard Wallbank, Steven Montgomery, and Andrei Sourakov for sharing figures and images, and Patricio Salazar, Krzystof Kozak, Joe Hanly, and Claire Mérot for the use of unpublished figures and data from their respective PhD theses. I also thank the Tupper library and staff, notably Angel Aguirre and Elizabeth Sanchez, for support in obtaining obscure literature while I was in Panama.

I thank the institutions that have supported me during the writing, especially St John's College and the Department of Zoology in Cambridge, but also the Smithsonian Tropical Research Institute in Panama, where the bulk of the writing was completed. I also thank Ian Sherman, Helen Eaton and Lucy Nash at OUP for their continued patience and support and Indumadhi Srinivasan for support in the final stages.

I thank my colleagues in the *Heliconius* community who carried out the research described here and have provided many stimulating conversations over the years; in particular, Mathieu Joron, Owen McMillan, Richard Merrill, Mauricio Linares, John Turner, Larry Gilbert, and Jamie Walters deserve a special mention. Most importantly, I thank Jim Mallet, who got me hooked on *Heliconius* in the first place and who certainly should have written this book himself.

Finally, I thank my family, Margarita, Catalina, and Manuela, and my parents, Roger and Sylvia, who have supported my time spent on this project. And finally, my brother Frank, whose scepticism spurred me on to finish the project.

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Plate 1 Variation in early stages—Larvae (see Figure 2.1a on page 12)

From top: *H. cydno*; *H. charithonia*; *H. hecale*; *H. erato*; *Eueides aliphera*; *Philaethria dido*; *Heliconius doris*; *Agraulis vanillae*; *Dryas iulia* (bottom left). All specimens were raised and photographed in Gamboa, Panama. Images are not precisely scaled but scale bar indicates approximately 1 cm.



Plate 2 Variation in early stages—Pupae (see Figure 2.1b on page 13)

First row: *Heliconius cydno* prepupa; *H. cydno* pupa (side, front); *H. hecale* pupa (side, front); *H. charithonia*. Second row: *Agraulis vanillae* (side, front); *H. erato* (side, front); *H. hecalesia* (side, front). Third row: *Eueides aliphera* (side, front); *Dryas iulia* (side, front); *Philaethria dido* (side, front). All specimens were raised and photographed in Gamboa, Panama. Images are not precisely scaled but scale bar indicates approximately 1 cm.

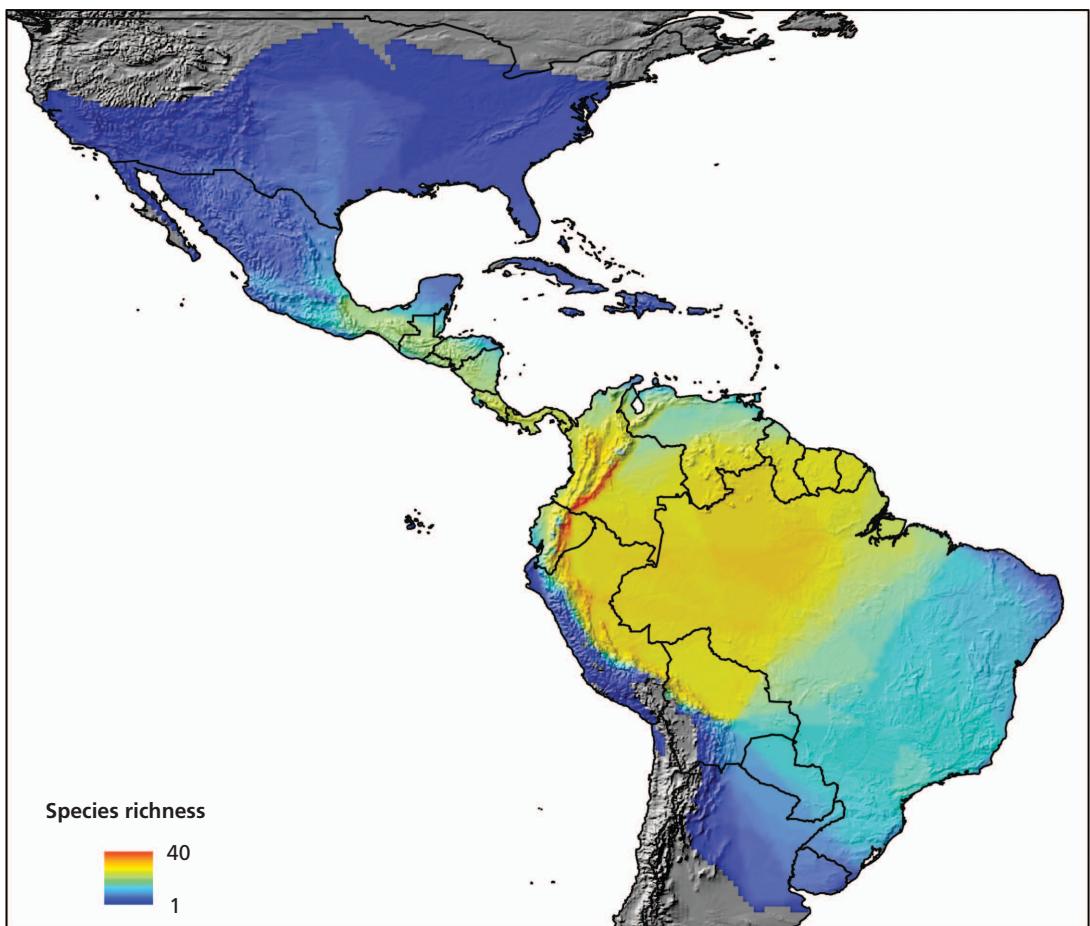


Plate 3 Patterns of species richness (see Figure 2.2 on page 15)

The diversity of heliconiine species reaches a peak in the upper Amazon, where lowland Amazonian taxa overlap with Andean species. This region corresponds to peak diversity in many taxa. Image courtesy of Neil Rosser.



Plate 4 Main wing pattern forms (see Figure 2.5 on page 20)

Representative taxa are shown for major wing patterning forms with upper (ventral; above) and underside (dorsal; below) wing patterns. Note that this is not a definitive classification of pattern diversity, but rather is intended as a rough guide to the terms that will be used throughout the book to refer to different types of patterns. Row 1, Postman: *H. ricini insulanus*, *H. erato hydara*; Dennis-ray: *H. xanthocles napoensis*; Sara: *H. leucadia pseudorheia*; Row 2, Cydno: *H. cydno cydrides*, *H. eleuchia eleusinus*, Metharme: *H. metharme metharme*, Nattereri: *H. nattereri*; Row 3, Tiger: *H. numata silvana*, *H. pardalinus titthoreides*, *H. numata aristonia*, Hecuba: *H. hecuba hecuba*; Row 4, Dryas: *Dryas iulia alcionea*, Agraulis: *Agraulis vanillae maculosa*, Philaethria: *Philaethria dido dido*, Eueides: *Eueides lybia olympia*. Note that the genus *Eueides* contains a large diversity of wing patterns including forms with postman, dennis-ray, tiger, and dryas patterns. Scale bar = 1 cm.



Plate 5 Oviposition behaviour (see Figure 3.1 on page 28)

Heliconius charithonia laying on *Passiflora biflora* and *Heliconius melpomene melpomene* laying on *Passiflora menispermifolia*. Both photographs were taken in the insectary in Gamboa, Panama.



Plate 6 Caterpillar feeding strategies (see Figure 3.2 on page 33)

(A) *Heliconius doris* caterpillars feed in a coordinated manner in large groups. Third-instar caterpillars are shown in the main image and fifth-instar caterpillars are shown inset. (B) Early-instar caterpillars of *Dryas iulia* cut a narrow strip of leaf and sit at the end of the hanging thread. This is a strategy to avoid the attention of ants patrolling the leaves. (C) Caterpillars of *Dione juno* are a crop pest on commercial *Passiflora edulis*. They are highly gregarious but do not feed in such a coordinated manner as *H. doris*. (D) Early-instar caterpillars of *Eueides aliphera* scrape the underside of leaves, leaving characteristic 'windows' of translucent cuticle in the leaf.

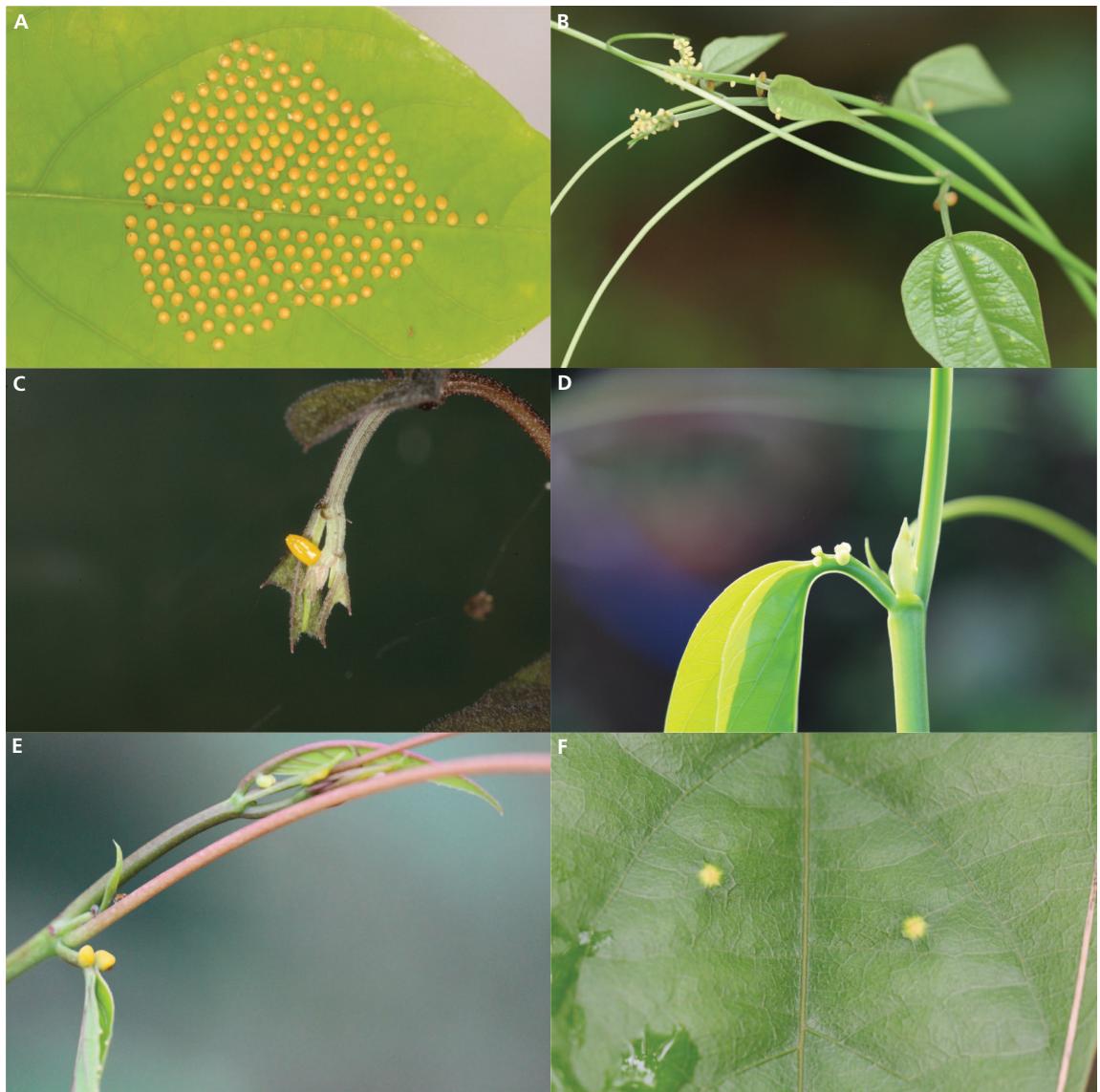


Plate 7 Eggs and egg mimics (see Figure 3.4 on page 40)

(A) Egg cluster of *H. doris* on *P. ambigua*; (B) eggs of *H. sara* on *P. auriculata*; (C) single egg of *H. erato* on *P. biflora*; glands on the petiole of (D) *P. quadrangularis* and (E) *Passiflora* spp. and on the leaf blade of (F) *P. auriculata* act as egg mimics to deter oviposition by *Heliconius* females.



Plate 8 Pollen-feeding behaviour (see Figure 4.2 on page 49)

(A) *H. melpomene aglaope* processing a pollen load. Note the large-grained *Psiguria* pollen on the proboscis. (B) The first flower on an inflorescence of *Psiguria warczewiczi* is relatively large, and (C) subsequent flowers get smaller. (D) A single inflorescence of *Psiguria bignoniaceae* with over 250 flower scars, indicating almost a year of continuous flower production.



Plate 9 Roosting behaviour of *H. erato* (see Figure 5.3 on page 60)

One female is shown fanning a group of four individuals already roosting together. This photograph was taken in an insectary in Gamboa.

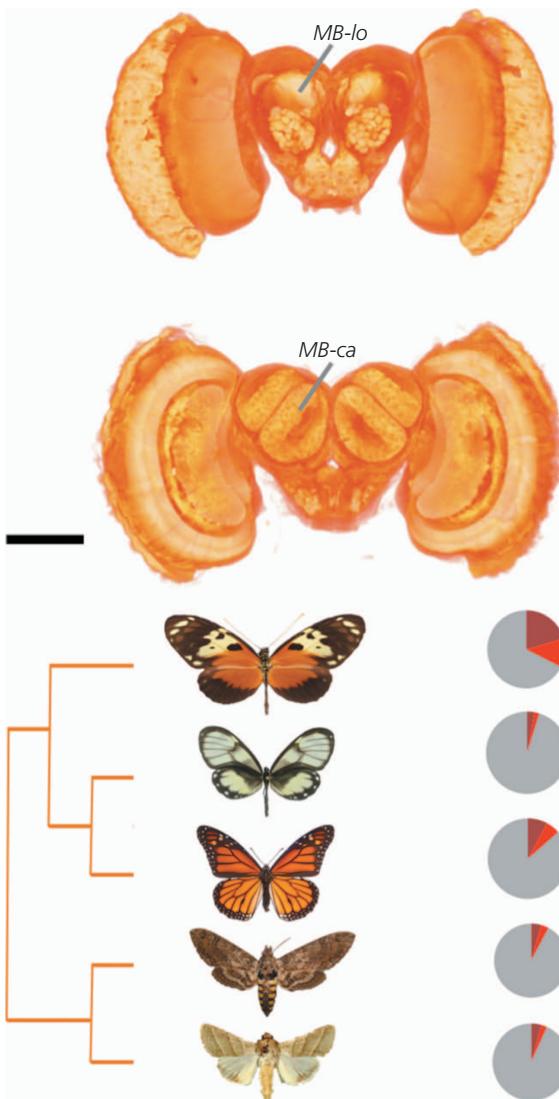


Plate 10 Expansion of mushroom bodies in *Heliconius* butterflies (see Figure 6.1 on page 67)

(A) 3D surface rendering of the brain of *H. hecale* (shown left, scale = 2.5 mm) viewed from the anterior (top) and posterior (bottom) indicating the mushroom body lobes (MB-lo) and calyx (MB-ca). Scale = 500 µm. (B) Phylogenetic tree showing relationships between *H. hecale*, *Godyris zavaleta*, *Danaus plexippus*, *Manduca sexta*, and *Heliothis virescens* (top to bottom) (Merrill et al., 2015; Montgomery et al., 2016).

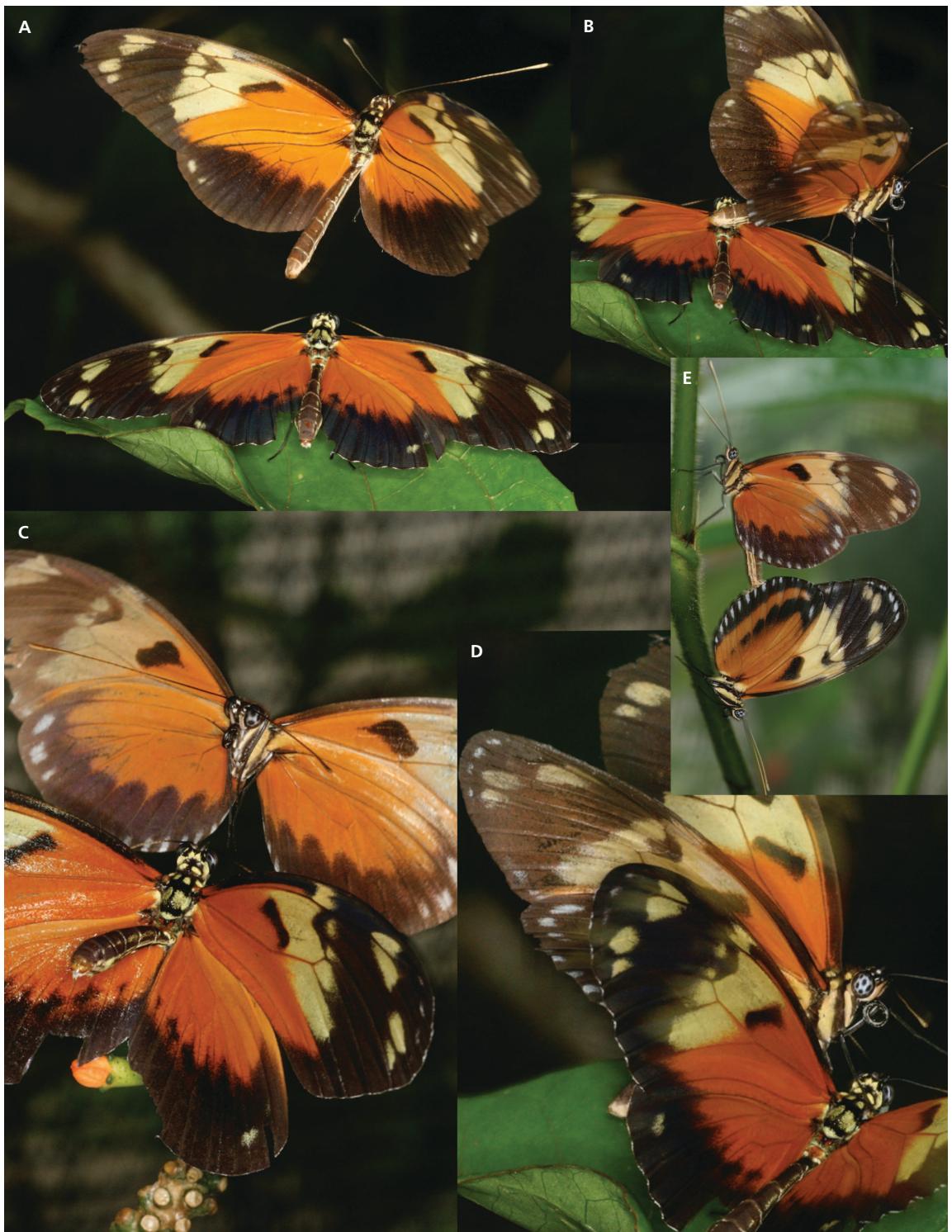


Plate 11 Mating behaviour and courtship sequence (see Figure 6.4 on page 74)

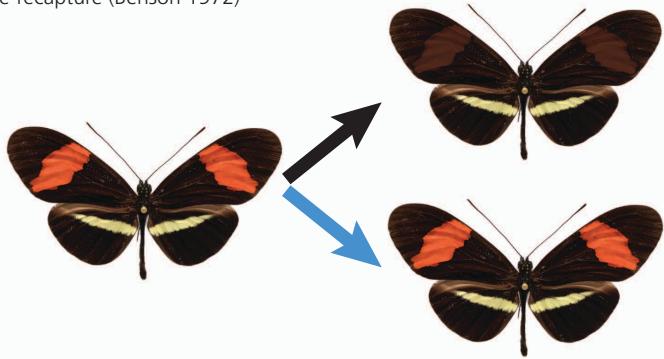
A courting pair of *H. ismenius* are shown at various stages in the courtship. (A) The male hovers over the female fanning his wings; (B) the male lands beside or even on top of the female; (C) the female can reject males by raising her abdomen and opening her pheromone glands; (D) the male attempts to mate by landing beside the female and bending his abdomen towards her; (E) during mating the male and female can stay attached for several hours. Note that panel E shows a different pair of individuals.



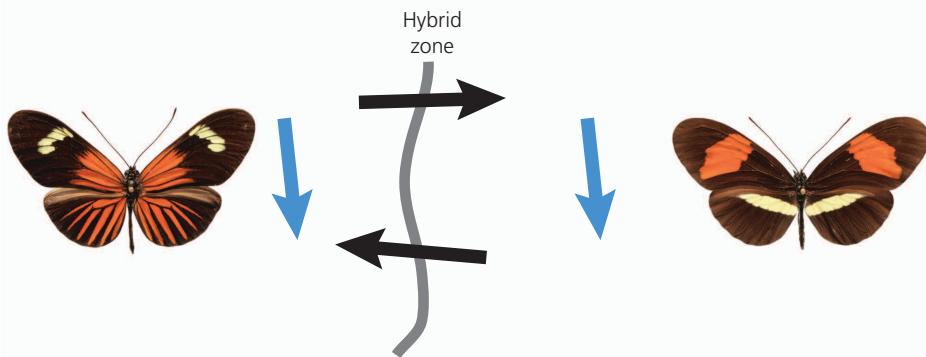
Plate 12 The behavioural sequence of pupal mating in *H. charithonia* (see Figure 6.6 on page 77)

Three males are shown contesting for a position on a female pupa (A), one in flight and two perched on the pupa. As the female begins to emerge, the male inserts his abdomen into the pupal case (B and C). In the inset (B), one male attempts to mate (left) while a second male is perched on the pupa (right). Finally, as the female ecloses from the pupa, she is already mating (D). Photos courtesy of Andrei Sourakov.

a) Mark-release-recapture (Benson 1972)



b) Mark-move-recapture across a hybrid zone (Mallet et al. 1989a)



c) Mark-move-recapture between polymorphic populations (Kapan 2001)

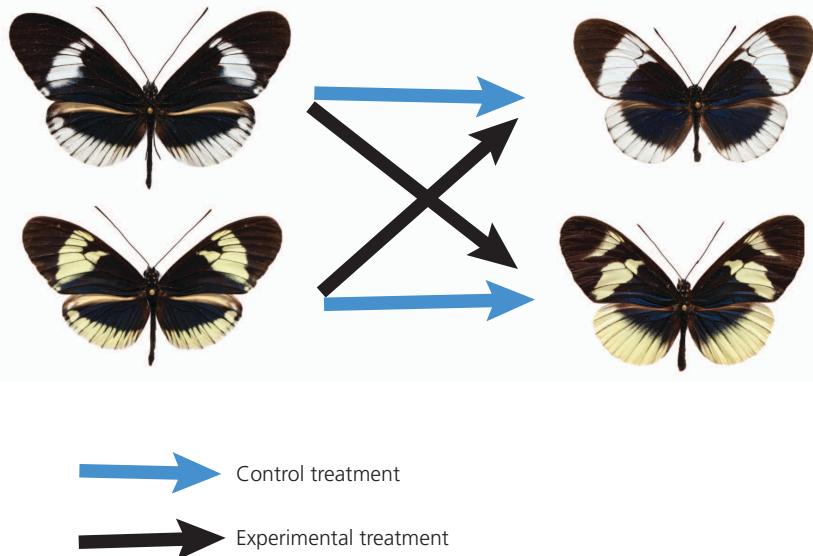


Plate 13 Summary of field tests of mimicry selection in *Heliconius* (see Figure 7.1 on page 92)

(A) Benson blacked out the forewing band of *Heliconius erato* in Costa Rica, with control butterflies similarly manipulated without a colour change; (B) Mallet moved butterflies across a wing pattern hybrid zone in Peru, with control butterflies being moved a similar distance but within the same wing pattern range; (C) Kapan moved polymorphic *Heliconius cydno* adults between populations with different morph frequencies, demonstrating that the locally abundant morph showed higher fitness. See text for full details and references.



Plate 14 Sympatric mimicry rings (see Figure 7.2 on page 94)

Coexisting mimetic species found in central Panama with upper (ventral; above) and underside (dorsal; below) wing patterns. Top row: *H. hecale melicerta*, *H. ismenius bouletti*, *H. sara magdalena*; second row: *H. cydno chioneus*, *H. sapho sapho*, *H. doris obscurus*; third row: *H. erato demophoon*, *H. melpomene rosina*, *H. hecalesia longarena*.

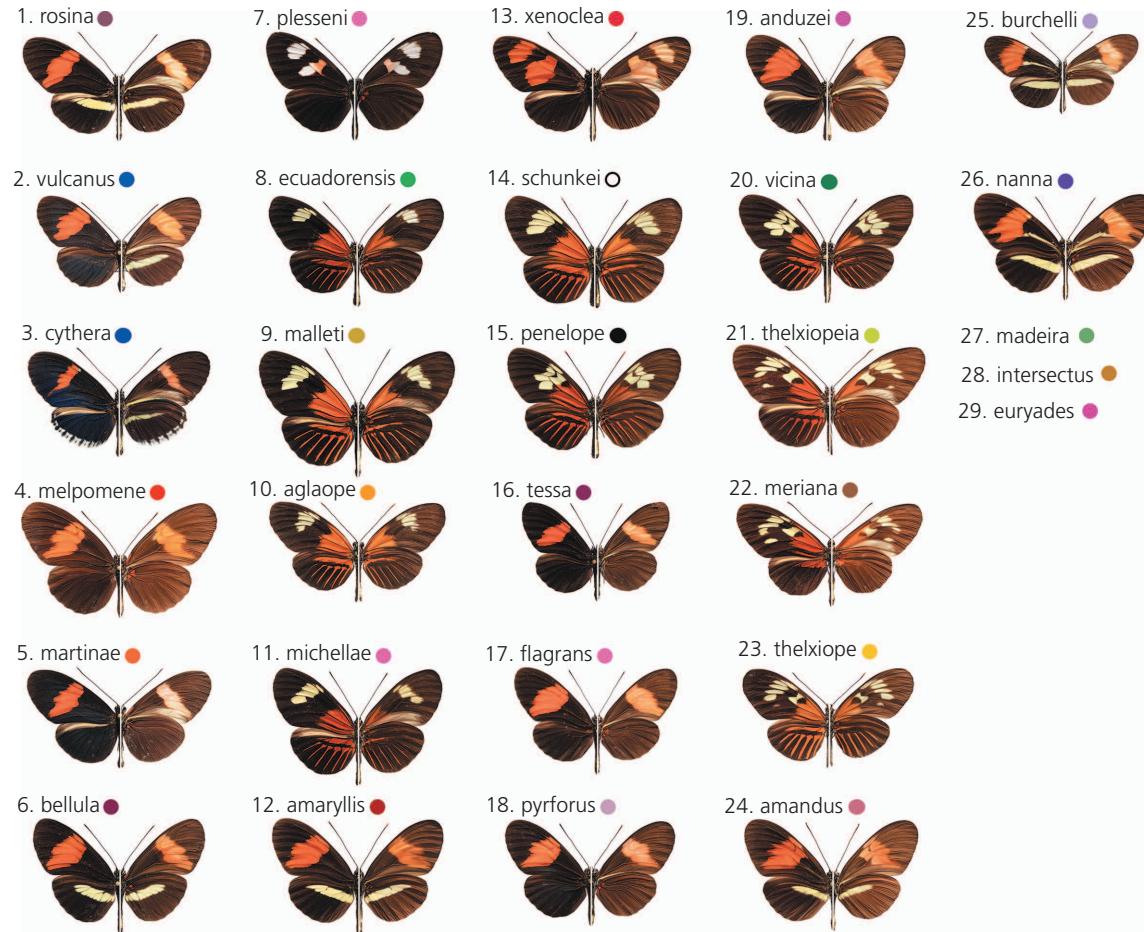


Plate 15 Distribution of geographic races of *Heliconius melpomene* (see Figure 7.3a on page 97)

Three forms lack images: *madeira* is similar to *thelxiopia*; *intersectus* is the Isla de Marajó form with a distal yellow band otherwise similar to *thelxiopia*; *euryades* is a postman form similar to *melpomene*. Note that *H. m. martiniae* is polymorphic for the hindwing yellow band, with some individuals looking very similar to *H. m. rosina*. On the map, some specimens from the Neukirchen collection labelled as *n. ssp. × vicina* hybrids from the central Amazon are here assigned to the race *vicina*. I have not examined these specimens, and the extent of the race *vicina* may not extend as far east as indicated. Butterflies are shown with dorsal (left) and ventral (right) images. Geographic distribution data were compiled by Neil Rosser and maps drawn using CartoDB.

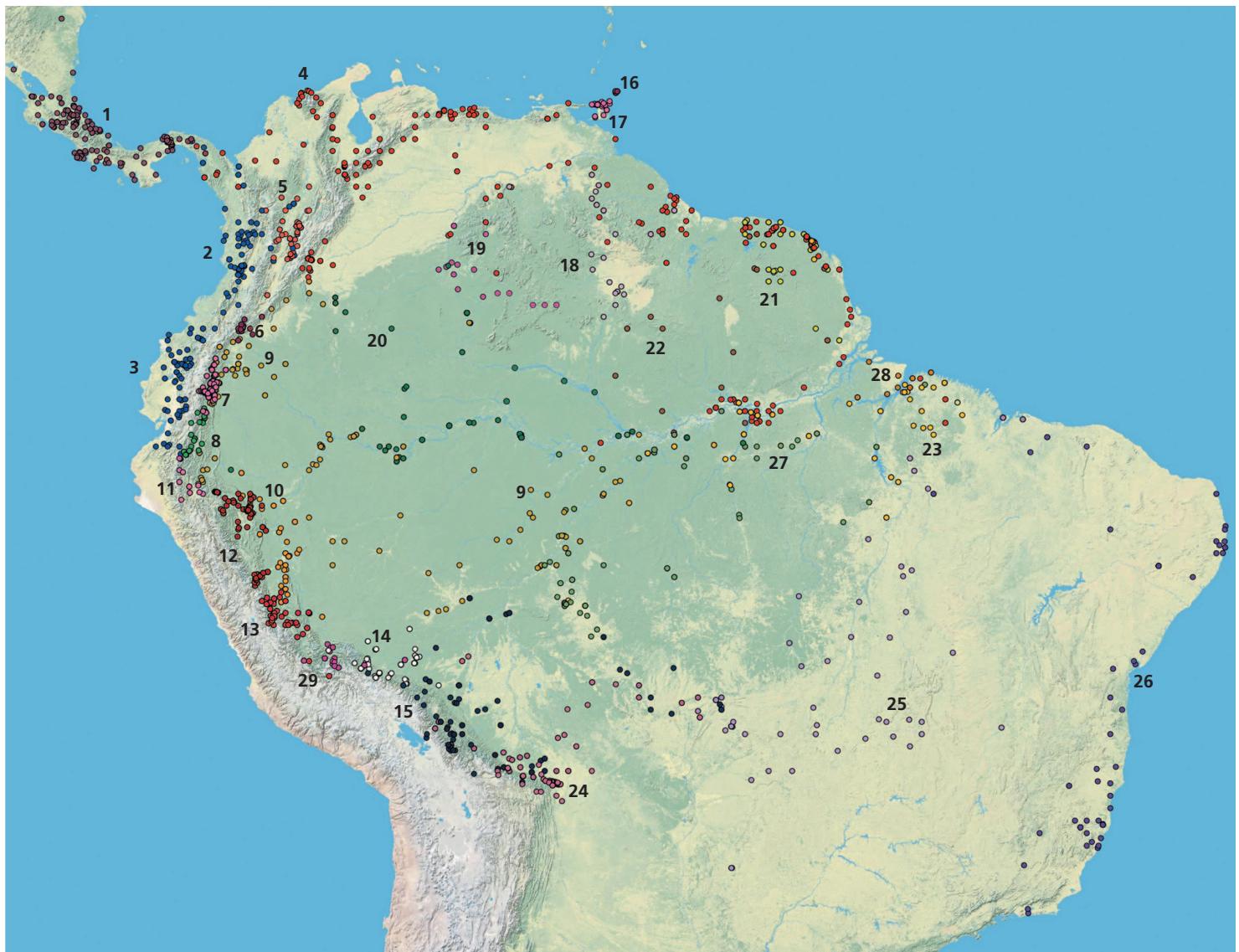


Plate 15 *Continued*

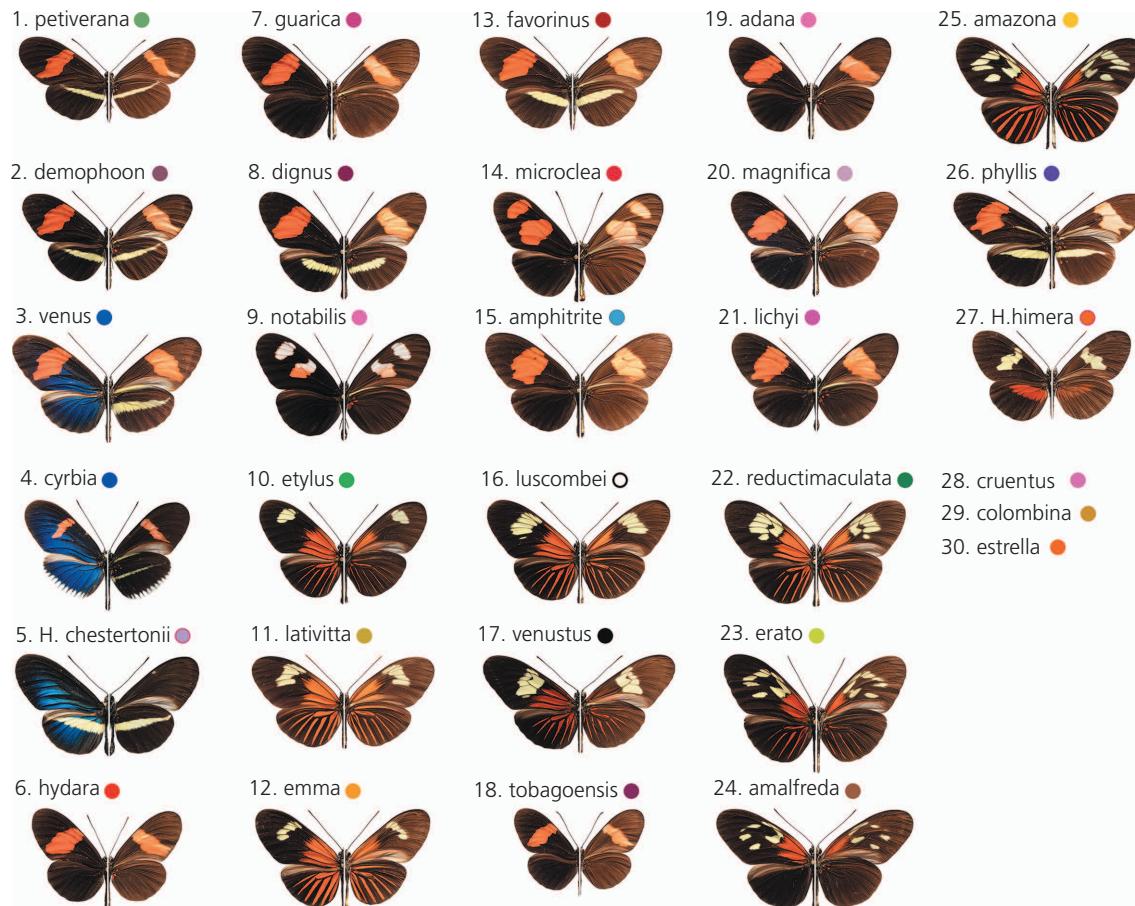


Plate 16 Distribution of geographic races of *Heliconius erato* (see Figure 7.3b on page 98)

Three forms lack images: *cruentus* is similar to and somewhat intermediate between *petiverana* and *demophoon* with a broad and slightly shorter hindwing yellow bar; *colombina* is similar to *demophoon*; *estrella* is the Isla de Marajó form with a distal yellow band otherwise similar to *erato*. Butterflies are shown with dorsal (left) and ventral (right) images. Geographic distribution data were compiled by Neil Rosser and maps drawn using CartoDB.

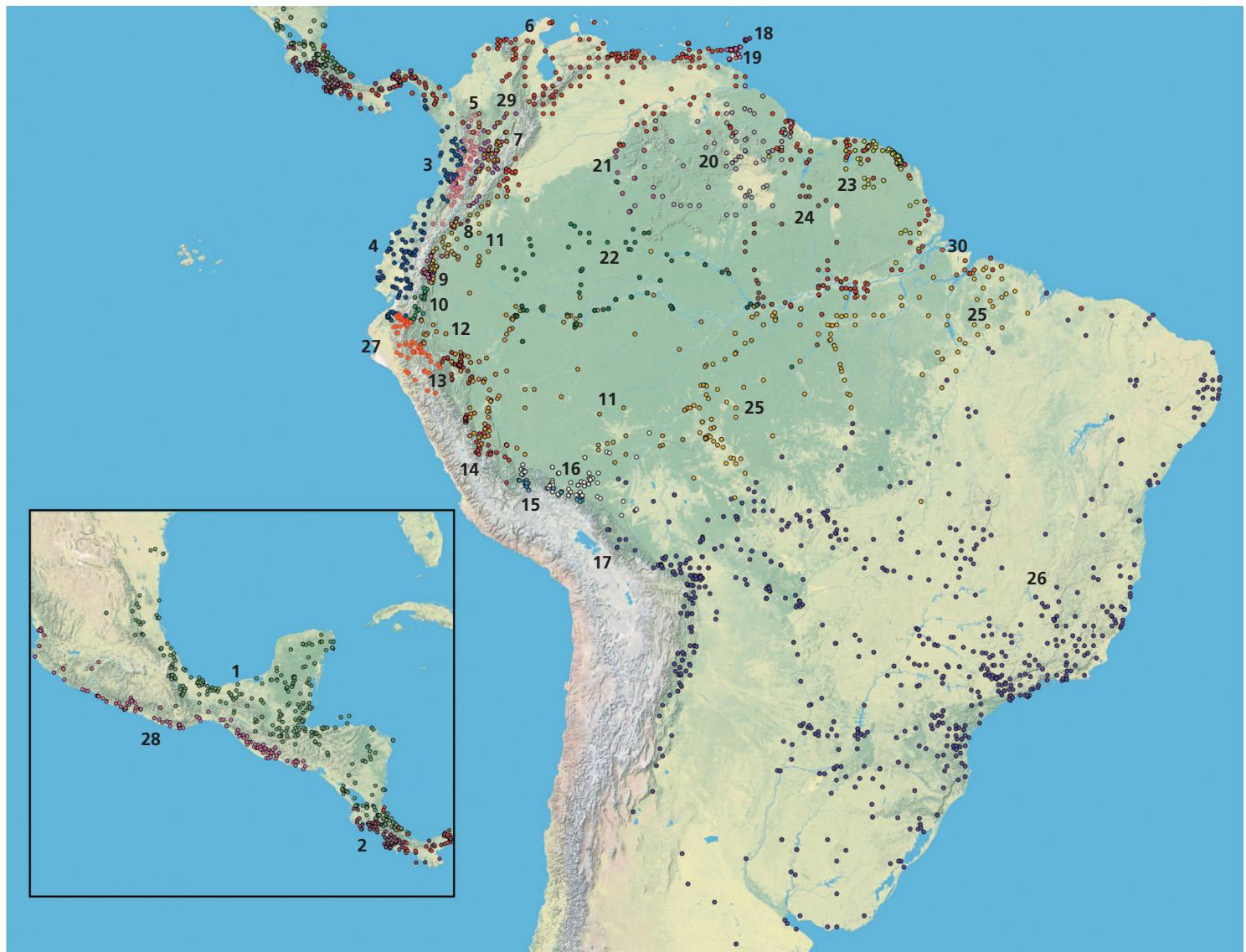


Plate 16 *Continued*

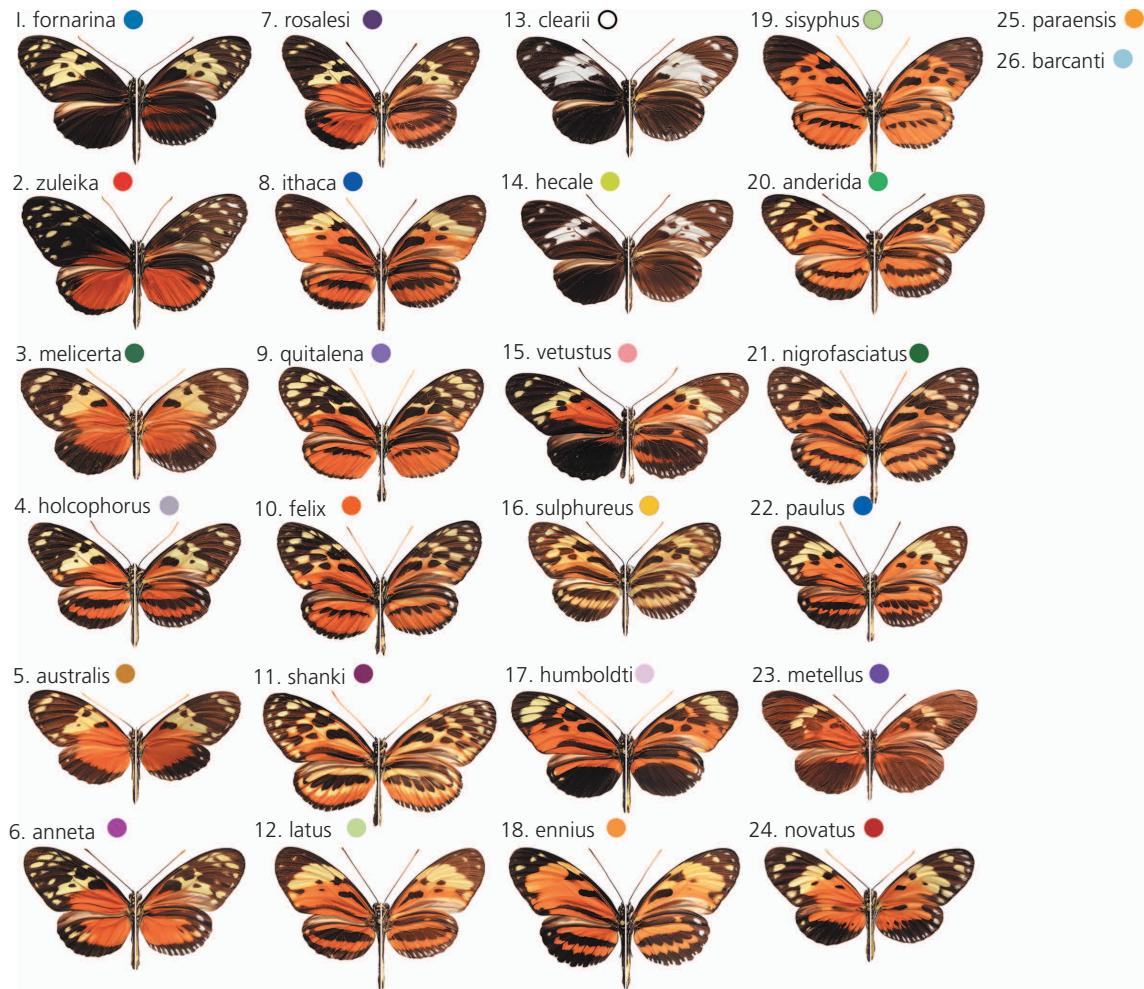


Plate 17 Distribution of geographic races of *Heliconius hecale* (see Figure 7.3c on page 99)

Three forms lack images: *paraensis* is similar to *paulus*; *barcanti* is similar to *clearii*; *zeus* (not mapped) was described from Bolivian specimens and is similar to *felix*; the distributions for these forms are combined. Note that *H. hecale ithaca* also has a form with a black hindwing (not shown) that is mimetic with *H. numata messene*. Butterflies are shown with dorsal (left) and ventral (right) images. Geographic distribution data were compiled by Neil Rosser and maps drawn using CartoDB.

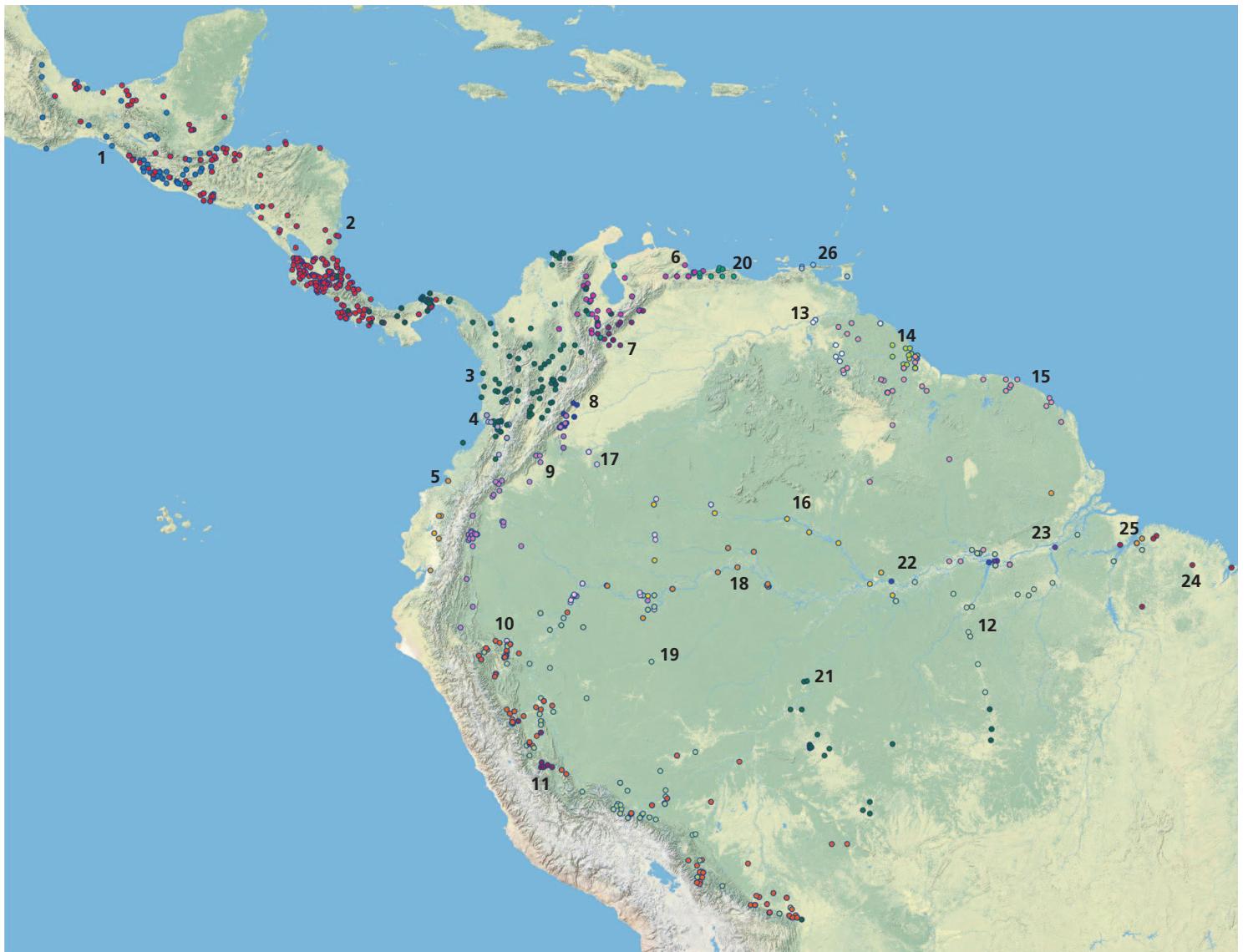


Plate 17 *Continued*

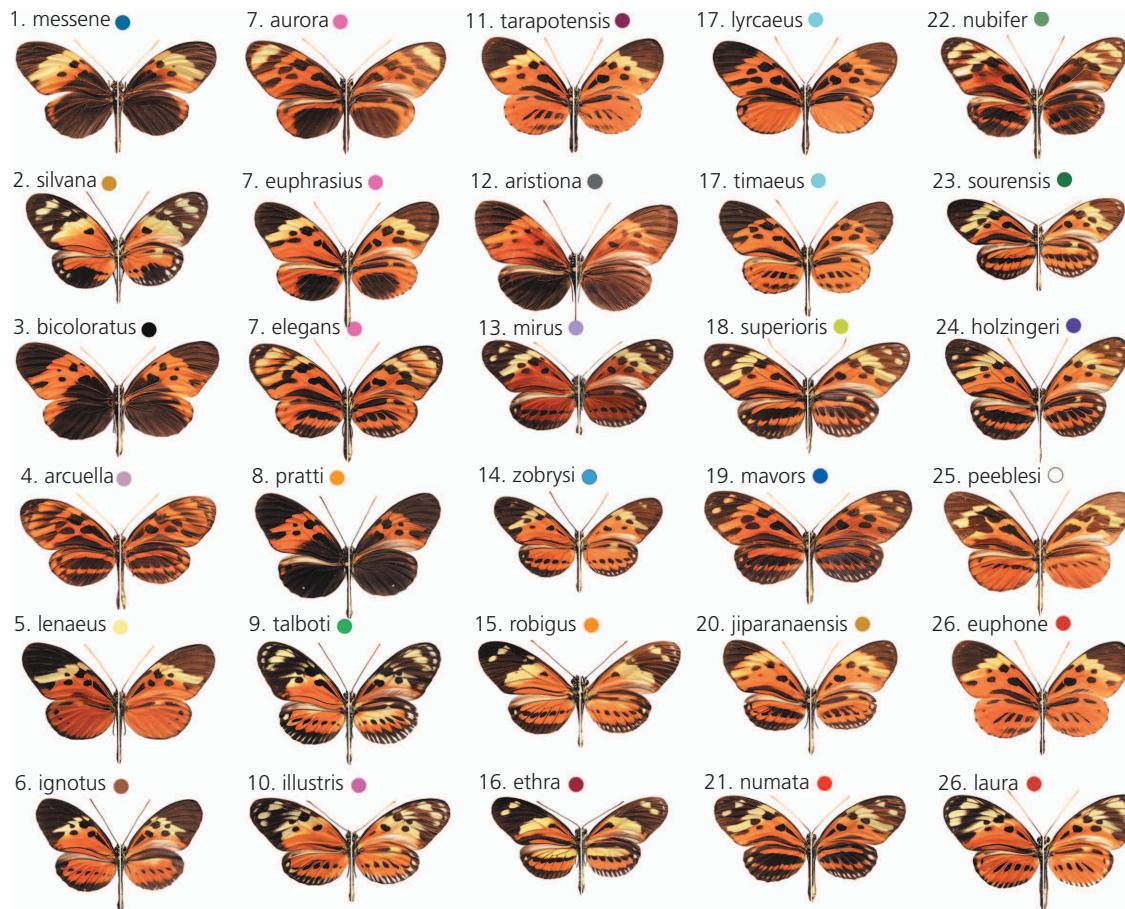


Plate 18 Distribution of forms of *Heliconius numata* (see Figure 7.3d on page 100)

The distinction between geographic races and within-species polymorphism breaks down in *H. numata*. As can be seen from the map, many of these taxa are sympatric forms controlled by alternate alleles at the *P* supergene, but for simplicity I consider all forms as subspecies. Note that some forms are combined for distribution mapping, as these are not distinguished in the available distribution data (*euphrasius*, *aurora*, and *elegans*; *lyrcaeus* and *timaeus*; *euphone* and *laura*). Forms not figured include *aulicus* (labelled as 27, pink circles on map) similar to *peeblesi* but with a more complete yellow forewing band; *geminatus* similar to *elegans* with more clearly defined yellow forewing bands; *isabellinus* similar to *elegans* but with a broad complete median forewing yellow band. Butterflies are shown with dorsal (left) and ventral (right) images. Geographic distribution data were compiled by Neil Rosser and maps drawn using CartoDB.

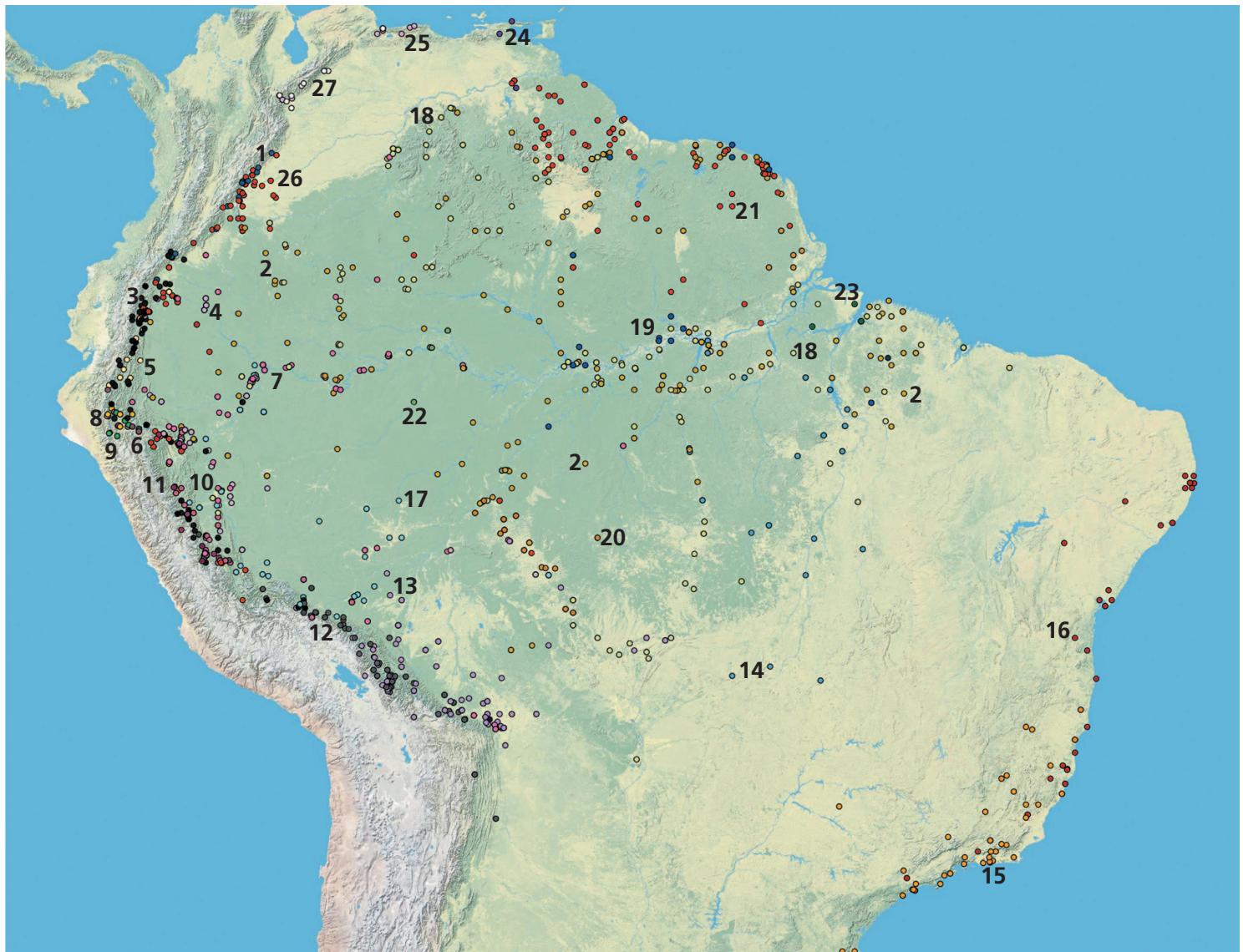


Plate 18 *Continued*



Plate 19 The Amazonian dennis-ray mimicry ring (see Figure 7.4 on page 101)

First row: *H. burneyi huebneri*, *H. aoede auca*, *H. xanthocles zamora*; second row: *H. timareta timareta* f. *timareta*, *H. doris doris*, *H. demeter ucayalensis*; third row: *H. melpomene malletti*, *H. egeria homogena*, *H. erato emma*; fourth row: *H. elevatus pseudocupidineus*, *Eueides heliconioides eanes*, *E. tales calathus*; bottom row: *Chetone phyleis*, a pericopine moth. These butterflies are from populations in both Ecuador and Peru and do not all occur in exactly the same locality.