Hybrid zones and the speciation continuum in Heliconius butterflies

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Hybrid zones and the speciation continuum
in *Heliconius* butterflies

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and

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Tropical butterflies in the genus *Heliconius* have long been models in the study of the stages of speciation. *Heliconius* are unpalatable to predators, and many species are notable for multiple geographic populations with striking warning colour pattern differences associated with Müllerian mimicry. There is a speciation continuum evident in *Heliconius* hybrid zones, across which mimicry patterns are often different, but where hybrids are common and little else differs, through to 'bimodal' hybrid zones with strongly marked molecular differences with few hybrids, through to 'good' sympatric species. Now Arias et al. (2012) have found an intermediate case in Colombian *Heliconius cydno* showing evidence for assortative mating and molecular differences, but where hybrids are abundant.

Hybrid zones in neotropical *Heliconius* butterflies have long fascinated evolutionary biologists, and informed about stages of speciation. Henry Walter Bates was the first to study *Heliconius* on a scientific basis, and he was also the first to explain mimicry among unrelated species via natural selection. Together with Fritz Müller, Bates was able to explain the selective advantage of this mimicry between edible and unpalatable species (Batesian mimicry), and among unpalatable species (Müllerian mimicry): birds, having learnt to avoid the warning colours of one inedible species, thereafter shun other species with convergent or 'mimetic' colour patterns (Bates 1862; Müller 1879).

It is less well known that Bates, who was particularly interested in the origin of species after reading Darwin’s works, was also the first to...
document a hybrid zone and assess its implications for understanding the continuum of speciation (Bates 1863). He carried out this work on a hybrid zone between colour pattern races of *Heliconius melpomene* in the Brazilian Amazon. Recent work with heliconiines has shown how mimicry and speciation are closely intertwined across the adaptive radiation in this group (McMillan *et al.* 1997; Linares 1997; Jiggins *et al.* 2001; Arias *et al.* 2008). Now a new paper closes the gap between species and geographic races still further (Arias *et al.* 2012).

Speciation appears to be more of a problem for humans to understand than it is for the organisms that do it. Learned books tell us that speciation was a conundrum not solved by Darwin, and one that is not clearly understood even today. Nonetheless, many intermediate stages of ongoing speciation are evident both below the species level (ecotypes, ecological races, and host races) and above the species level (involving hybridization and gene flow between species, and hybrid speciation). Speciation clearly exists as a continuum across the species boundary, and assessing these intermediate stages is key to understanding the process.
Studies involving the genus *Heliconius* have been major recent contributors to our knowledge of the speciation continuum. An early study used hybrid zone dynamics to measure the strong natural selection on mimicry, and showed how this selection could stabilize narrow zones of hybridization between Peruvian geographic races of *H. erato* differing in mimetic colour pattern. Similar results are also evident from the coincident hybrid zone between races of its co-mimic *H. melpomene* (Mallet *et al.* 1990). Recent studies have shown that virtually no genomic differences exist across these Peruvian hybrid zones, except at fixed differences in a handful of genomic regions controlling the colour pattern and mimicry shift (Counterman *et al.* 2010; Nadeau *et al.* 2012), suggesting that in many cases mimetic shifts may be a first stage of divergence towards speciation. However, mating of the geographic races within each species is random in the centre of each hybrid zone, so the contribution of the evolution of geographic races like those in Peru to speciation was still unclear. *Heliconius cydno* is a species with widespread mimicry polymorphisms, such as in *H. cydno weymeri* studied here in the southern Cauca Valley (Fig. 1). In an Ecuadorian population of this species, colour pattern contributes to assortative mating among mimetic morphs in one direction of cross (Chamberlain *et al.* 2009).
How such racial divergence might contribute to speciation was further studied along a wet-dry ecotone in Ecuador. A narrow hybrid zone between *H. (erato) himera* and *H. erato cyrbia*, which were previously regarded as conspecific, was rather different in character than the Peruvian hybrid zones in *H. erato* and *H. melpomene*. In particular, there were strong differences in mtDNA and nuclear markers across the hybrid zone. Within the hybrid zone multilocus genotypes, including colour pattern loci, formed a bimodal distribution. Phenotypic hybrids between the taxa, although present, formed only about 10% of the population in the centre of the hybrid zone. This was largely due to assortative mating and ecological differences between the taxa, because no hybrid inviability or sterility was found (Jiggins *et al.* 1997; McMillan, Jiggins, and Mallet 1997). Clearly, considerable progress towards speciation has been achieved because the bimodality of the genotypic distribution shows that two clusters of genotypes coexist without collapsing, albeit in a narrow zone of contact. As a result, *H. himera* and *H. erato* were thereafter classified as separate species.

In Colombia there is a somewhat comparable hybrid zone along a wet-dry ecotone between another two taxa also formerly considered geographic
races of *H. erato*: *H. (e.) chestertonii* and *H. e. venus*. Although considerable hybridization is reported in the hybrid zone, hybrids again remain rare (25%) compared to "pure" colour pattern phenotypes, and both mtDNA and nuclear markers also differ between the taxa (Arias et al. 2008).

It is extremely difficult for foreigners to obtain permits to collect wild species for DNA-based work in Colombia, and there have been, at least until recently, public order difficulties across much of that country. Mauricio Linares, the senior Colombian author of the current paper, has endured a number of life-threatening situations to obtain valuable data on Colombian *Heliconius* hybrid zones. For a long time his research team has been studying a major hybrid zone between two mimetic races, *H. cydno cydnides* and *H. c. weymeri* in the Cauca Valley, sandwiched between the Central and Western Cordilleras of the Andes (Fig. 1). The current paper, from an all-Latin American group, shows some extremely interesting patterns from this hybrid zone. The two races show asymmetrical assortative courtship, and there is also clear mtDNA as well as some evidence for nuclear genetic differences across the zone. Yet hybrids in the centre of the zone appear abundant, giving no evidence for phenotypic bimodality: hence the authors' designation of the hybrid zone as
"unimodal" (Arias et al. 2012). Along the continuum of speciation, this Heliconius cydno hybrid zone therefore sits between bimodal hybrid zones like those of H. himera and H. erato, and classical clinal hybrid zones like those between Peruvian races of H. erato or H. melpomene (Table 1).

The authors also find that the mtDNA haplotypes of the southern race (H. c. weymeri) are closely related to those of the Pacific coastal race H. cydno zelinde, whereas the northern H. c. cydnides groups with races further east, from the Magdalena Valley. According to the authors, this argues for the current hybrid zone forming by secondary contact as a result of the spread of H. c. weymeri accompanied by colour pattern divergence across passes in the Western Andes into the southern Cauca Valley. Here, it met H. c. cydnides which itself spread from the east. As with most phylogeographic hypotheses, this is hard to prove, especially as it has been shown that some colour patterns in Heliconius erato seem to have spread behind moving contact zones while in parapatric contact with another race (Blum 2002), so potentially explaining the existence of multiple, disjunct but otherwise very similar mimicry races up and down the Andes (Hines et al. 2011).

Nonetheless, the existence of strong mtDNA and some nuclear divergence across this Heliconius cydno contact zone argues for greater population
restructuring than just a moving colour pattern cline within a continuous geographic range; the authors rightly argue that this is good evidence that the hybrid zone was achieved via secondary contact.

What is not yet quite clear is whether speciation can take place during complete overlap in sympatry. The existence of regular albeit low-level hybridisation among many sympatric Heliconius species (Mallet et al. 2007), and the high degree of sympatry among sister species (Rosser et al. 2012) argues that sympatric speciation may be common (Neil Rosser et al. in prep.). Formation of the hybrid species Heliconius heurippa and H. elevatus were almost certainly also explained by sympatric transfer of colour pattern genes between species (Mavárez et al. 2006; Heliconius Genome Consortium 2012). On the other hand, the existence of a continuum of speciation in parapatric hybrid zones like those studied by Arias et al. (2012) (Table 1) suggests that at least some of the speciation is completed in parapatric contact or perhaps, sometimes even in complete geographic isolation.

Funding is getting more difficult for evolutionary studies in "developed" countries. Meanwhile, strong economic growth in emerging industrial
powers like Colombia is contributing to greatly improved strength of their own science base. Further work on problems like these will be done increasingly by indigenous teams like this Colombian research group, with their ready access to high biodiversity in the complex topography of the Andes and adjacent tropical rainforests. This work shows great potential to clarify remaining questions about speciation in Heliconius soon.
FIGURE LEGEND:

Figure 1. Mimetic races of *Heliconius cydno* and its Müllerian comimics in the Cauca Valley of Colombia. Left side, top to bottom: *Heliconius cydno cydnides, H. cydno weymeri* form 'weymeri,' *H. cydno weymeri* form 'gustavi.' Right side, comimics: *H. eleuchia eleusinus, Elzunia humboldt, H. (erato) chestertonii.* Photo by Carlos Arias.
Table 1. The speciation continuum in *Heliconius* butterflies: examples of hybrid zones among species and geographic races.

<table>
<thead>
<tr>
<th>Taxon 1</th>
<th>Taxon 2</th>
<th>Locality</th>
<th>Unimodal /Bimodal /Sympatry</th>
<th>mtDNA divergence</th>
<th>Nuclear divergence</th>
<th>Taxonomic status</th>
<th>References</th>
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<tr>
<td><em>H. erato favorinus</em></td>
<td><em>H. erato emma</em></td>
<td>NE Peru</td>
<td>Unimodal</td>
<td>No</td>
<td>Colour pattern loci only</td>
<td>Geographic races</td>
<td>Mallet et al. 1990; Counterman et al. 2010</td>
</tr>
<tr>
<td><em>H. melpomene amaryllis</em></td>
<td><em>H. melpomene aglaope</em></td>
<td>NE Peru</td>
<td>Unimodal</td>
<td>No</td>
<td>Colour pattern loci only</td>
<td>Geographic races</td>
<td>Mallet et al. 1990; Nadeau et al. 2012</td>
</tr>
<tr>
<td><em>H. cydno cydnides</em></td>
<td><em>H. cydno weymeri</em></td>
<td>Cauca, Colombia</td>
<td>Unimodal</td>
<td>Yes</td>
<td>Some divergence</td>
<td>Geographic races</td>
<td>Arias et al. 2012; this paper</td>
</tr>
<tr>
<td><em>H. erato cyrbia</em></td>
<td><em>H. (erato) himera</em></td>
<td>S Ecuador</td>
<td>Bimodal, 10% hybrids</td>
<td>Yes</td>
<td>Strong</td>
<td>Species</td>
<td>Jiggins et al. 1997</td>
</tr>
<tr>
<td><em>H. erato venus</em></td>
<td><em>H. (erato) chestertonii</em></td>
<td>W Colombia</td>
<td>Bimodal, 25% hybrids</td>
<td>Yes</td>
<td>Yes</td>
<td>Species</td>
<td>Arias et al. 2008</td>
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