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| Citation | Mallet, James, and Kanchon K. Dasmahapatra. 2012. "Hybrid Zones and the Speciation Continuum in <i>Heliconius</i> Butterflies ." <i>Mol Ecol</i> 21 (23) (November 21): 5643–5645. doi:10.1111/mec.12058. |
| Published Version | doi:10.1111/mec.12058 |
| Citable link | http://nrs.harvard.edu/urn-3:HUL.InstRepos:25288054 |
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Hybrid zones and the speciation continuum
in *Heliconius* butterflies

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20 **2012. *Molecular Ecology* 21 (in press).**

21

22 **Commentary on: Arias CF, Rosales C, Salazar C et al. (2012) Sharp**
23 **genetic discontinuity across a unimodal *Heliconius* hybrid zone.**
24 ***Molecular Ecology*, 21 (in press).**

25 **Tropical butterflies in the genus *Heliconius* have long been models in**
26 **the study of the stages of speciation. *Heliconius* are unpalatable to**
27 **predators, and many species are notable for multiple geographic**
28 **populations with striking warning colour pattern differences associated**
29 **with Müllerian mimicry. There is a speciation continuum evident in**
30 ***Heliconius* hybrid zones, across which mimicry patterns are often**
31 **different, but where hybrids are common and little else differs, through**
32 **to 'bimodal' hybrid zones with strongly marked molecular differences**
33 **with few hybrids, through to 'good' sympatric species. Now Arias et al.**
34 **(2012) have found an intermediate case in Colombian *Heliconius cydno***
35 **showing evidence for assortative mating and molecular differences, but**
36 **where hybrids are abundant.**

37

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

48

49 It is less well known that Bates, who was particularly interested in the
50 origin of species after reading Darwin's works, was also the first to

51 document a hybrid zone and assess its implications for understanding the
52 continuum of speciation (Bates 1863). He carried out this work on a hybrid
53 zone between colour pattern races of *Heliconius melpomene* in the Brazilian
54 Amazon. Recent work with heliconiines has shown how mimicry and
55 speciation are closely intertwined across the adaptive radiation in this
56 group (McMillan *et al.* 1997; Linares 1997; Jiggins *et al.* 2001; Arias *et al.*
57 2008). Now a new paper closes the gap between species and geographic
58 races still further (Arias *et al.* 2012).

59

60 Speciation appears to be more of a problem for humans to understand
61 than it is for the organisms that do it. Learned books tell us that speciation
62 was a conundrum not solved by Darwin, and one that is not clearly
63 understood even today. Nonetheless, many intermediate stages of ongoing
64 speciation are evident both below the species level (ecotypes, ecological
65 races, and host races) and above the species level (involving hybridization
66 and gene flow between species, and hybrid speciation). Speciation clearly
67 exists as a continuum across the species boundary, and assessing these
68 intermediate stages is key to understanding the process.

69

70 Studies involving the genus *Heliconius* have been major recent contributors
71 to our knowledge of the speciation continuum. An early study used hybrid
72 zone dynamics to measure the strong natural selection on mimicry, and
73 showed how this selection could stabilize narrow zones of hybridization
74 between Peruvian geographic races of *H. erato* differing in mimetic colour
75 pattern. Similar results are also evident from the coincident hybrid zone
76 between races of its co-mimic *H. melpomene* (Mallet *et al.* 1990). Recent
77 studies have shown that virtually no genomic differences exist across these
78 Peruvian hybrid zones, except at fixed differences in a handful of genomic
79 regions controlling the colour pattern and mimicry shift (Counterman *et al.*
80 2010; Nadeau *et al.* 2012), suggesting that in many cases mimetic shifts may
81 be a first stage of divergence towards speciation. However, mating of the
82 geographic races within each species is random in the centre of each
83 hybrid zone, so the contribution of the evolution of geographic races like
84 those in Peru to speciation was still unclear. *Heliconius cydno* is a species
85 with widespread mimicry polymorphisms, such as in *H. cydno weymeri*
86 studied here in the southern Cauca Valley (Fig. 1). In an Ecuadorean
87 population of this species, colour pattern contributes to assortative mating
88 among mimetic morphs in one direction of cross (Chamberlain *et al.* 2009).
89

90 How such racial divergence might contribute to speciation was further
91 studied along a wet-dry ecotone in Ecuador. A narrow hybrid zone
92 between *H. (erato) himera* and *H. erato cyrbia*, which were previously
93 regarded as conspecific, was rather different in character than the Peruvian
94 hybrid zones in *H. erato* and *H. melpomene*. In particular, there were strong
95 differences in mtDNA and nuclear markers across the hybrid zone. Within
96 the hybrid zone multilocus genotypes, including colour pattern loci,
97 formed a bimodal distribution. Phenotypic hybrids between the taxa,
98 although present, formed only about 10% of the population in the centre of
99 the hybrid zone. This was largely due to assortative mating and ecological
100 differences between the taxa, because no hybrid inviability or sterility was
101 found (Jiggins *et al.* 1997; McMillan, Jiggins, and Mallet 1997). Clearly,
102 considerable progress towards speciation has been achieved because the
103 bimodality of the genotypic distribution shows that two clusters of
104 genotypes coexist without collapsing, albeit in a narrow zone of contact.
105 As a result, *H. himera* and *H. erato* were thereafter classified as separate
106 species.

107

108 In Colombia there is a somewhat comparable hybrid zone along a wet-dry
109 ecotone between another two taxa also formerly considered geographic

110 races of *H. erato*: *H. (e.) chestertonii* and *H. e. venus*. Although considerable
111 hybridization is reported in the hybrid zone, hybrids again remain rare
112 (25%) compared to "pure" colour pattern phenotypes, and both mtDNA
113 and nuclear markers also differ between the taxa (Arias *et al.* 2008).

114

115 It is extremely difficult for foreigners to obtain permits to collect wild
116 species for DNA-based work in Colombia, and there have been, at least
117 until recently, public order difficulties across much of that country.

118 Mauricio Linares, the senior Colombian author of the current paper, has
119 endured a number of life-threatening situations to obtain valuable data on
120 Colombian *Heliconius* hybrid zones. For a long time his research team has
121 been studying a major hybrid zone between two mimetic races, *H. cydno*
122 *cydnides* and *H. c. weymeri* in the Cauca Valley, sandwiched between the
123 Central and Western Cordilleras of the Andes (Fig. 1). The current paper,
124 from an all-Latin American group, shows some extremely interesting
125 patterns from this hybrid zone. The two races show asymmetrical
126 assortative courtship, and there is also clear mtDNA as well as some
127 evidence for nuclear genetic differences across the zone. Yet hybrids in the
128 centre of the zone appear abundant, giving no evidence for phenotypic
129 bimodality: hence the authors' designation of the hybrid zone as

130 "unimodal" (Arias *et al.* 2012). Along the continuum of speciation, this
131 *Heliconius cydno* hybrid zone therefore sits between bimodal hybrid zones
132 like those of *H. himera* and *H. erato*, and classical clinal hybrid zones like
133 those between Peruvian races of *H. erato* or *H. melpomene* (Table 1).
134
135 The authors also find that the mtDNA haplotypes of the southern race (*H.*
136 *c. weymeri*) are closely related to those of the Pacific coastal race *H. cydno*
137 *zelinde*, whereas the northern *H. c. cydnides* groups with races further east,
138 from the Magdalena Valley. According to the authors, this argues for the
139 current hybrid zone forming by secondary contact as a result of the spread
140 of *H. c. weymeri* accompanied by colour pattern divergence across passes in
141 the Western Andes into the southern Cauca Valley. Here, it met *H. c.*
142 *cydnides* which itself spread from the east. As with most phylogeographic
143 hypotheses, this is hard to prove, especially as it has been shown that some
144 colour patterns in *Heliconius erato* seem to have spread behind moving
145 contact zones while in parapatric contact with another race (Blum 2002), so
146 potentially explaining the existence of multiple, disjunct but otherwise
147 very similar mimicry races up and down the Andes (Hines *et al.* 2011).
148 Nonetheless, the existence of strong mtDNA and some nuclear divergence
149 across this *Heliconius cydno* contact zone argues for greater population

150 restructuring than just a moving colour pattern cline within a continuous
151 geographic range; the authors rightly argue that this is good evidence that
152 the hybrid zone was achieved via secondary contact.

153

154 What is not yet quite clear is whether speciation can take place during
155 complete overlap in sympatry. The existence of regular albeit low-level
156 hybridisation among many sympatric *Heliconius* species (Mallet *et al.* 2007),
157 and the high degree of sympatry among sister species (Rosser *et al.* 2012)
158 argues that sympatric speciation may be common (Neil Rosser *et al.* in
159 prep.). Formation of the hybrid species *Heliconius heurippa* and *H. elevatus*
160 were almost certainly also explained by sympatric transfer of colour
161 pattern genes between species (Mavárez *et al.* 2006; Heliconius Genome
162 Consortium 2012). On the other hand, the existence of a continuum of
163 speciation in parapatric hybrid zones like those studied by Arias *et al.*
164 (2012) (Table 1) suggests that at least some of the speciation is completed in
165 parapatric contact or perhaps, sometimes even in complete geographic
166 isolation.

167

168 Funding is getting more difficult for evolutionary studies in "developed"
169 countries. Meanwhile, strong economic growth in emerging industrial

170 powers like Colombia is contributing to greatly improved strength of their
171 own science base. Further work on problems like these will be done
172 increasingly by indigenous teams like this Colombian research group, with
173 their ready access to high biodiversity in the complex topography of the
174 Andes and adjacent tropical rainforests. This work shows great potential to
175 clarify remaining questions about speciation in *Heliconius* soon.

176 FIGURE LEGEND:

177

178 Figure 1. Mimetic races of *Heliconius cydno* and its Müllerian comimics in
179 the Cauca Valley of Colombia. Left side, top to bottom: *Heliconius cydno*
180 *cydnides*, *H. cydno weymeri* form 'weymeri,' *H. cydno weymeri* form 'gustavi.'

181 Right side, comimics: *H. eleuchia eleusinus*, *Elzunia humboldt*, *H. (erato)*
182 *chestertonii*. Photo by Carlos Arias.

183

184

185



Table 1. The speciation continuum in *Heliconius* butterflies: examples of hybrid zones among species and geographic races.

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

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