Zoological Journal of the Linnean Society (1996), *116:* 317–332. With 8 figures

A new mimetic species of *Heliconius* (Lepidoptera: Nymphalidae), from southeastern Colombia, revealed by cladistic analysis of mitochondrial DNA sequences

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Received September 1994, accepted for publication April 1995

A new species of *Heliconius* and a new geographical race of *Heliconius melpomene* are described from the vicinity of Mocoa, Dpto. Putumayo, Colombia, based on molecular and morphological characters. The new species, *H. tristero*, is a close relative of *H. cydno*, a geographically differentiated species which lacks red coloration and engages in Müllerian mimicry with other blue and yellow *Heliconius* species in Central and northwestern South America. *H. tristero* has switched mimetic associations, instead mimicking the local, sympatric forms of two widespread mimetic species, *H. erato* and *H. melpomene*. This discovery provides evidence that the splinter species *H. heurippa, H. tristero* and *H. timareta* represent phenotypically divergent members of the *H. cydno* group that are endemic to successive river valleys on the eastern slope of the northern Andean Cordillera. The nominal taxon *Heliconius amaryllis bellula* Stichel, currently misapplied to both *H. tristero* and *H. melpomene* populations from the Mocoa region of Colombia, is considered here to represent a hybrid between *H. heurippa* and *H. tristero*. The Mocoa *melpomene* race is formally named *Heliconius melpomene mocoa*, new subspecies.

ADDITIONAL KEY WORDS: — morphology – Müllerian mimicry – phenotypic variation – mtDNA COII.

CONTENTS

INTRODUCTION

Heliconius butterflies are well-known for their aposematic wing patterns, Müllerian mimicry, and remarkable intraspecific geographical polymorphism. Although

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genetical theory suggests that Müllerian mimics benefit from phenotypic monomorphism (Ford, 1953), some *Heliconius* species have evolved a dozen or more distinct geographical races with radically different colour patterns (Emsley, 1964; Brown *et al.*, 1974; Sheppard *et al.*, 1985; Brower, 1994b, 1996). This paradoxical diversification is dramatically evident among races of the mimetic species pair, *H. erato* (L.) and *H. melpomene* (L.). These two species have been crossed extensively to elucidate the genetic basis of shared patterns of phenotypic variation (Sheppard *et al.*, 1985 and references therein; Mallet, 1989; Nijhout *et al.*, 1990). Similarly, *H. cydno* Doubleday is subject to geographical covariation with other *Heliconius* species, that together form a separate, blue-and-white or blue-and-yellow series of local mimicry complexes in northwestern South America and Central America (Eltringham, 1916; Brown, 1979; Linares, 1989).

Historically, the taxonomy of *Heliconius* has been severely hampered by the overzealous efforts of typologically-minded systematists working with bewildering arrays of vaguely-labelled museum specimens representing not only the various geographical races but also recombinant phenotypes captured in zones of interracial hybridization. The proliferation of names was dramatic: Neustetter's (1929) catalogue listed 593 *Heliconius* "species, subspecies et formae". An infamous example of such flagrant splitting is the vast collection of named forms from the *H. erato* and *H. melpomene* hybrid zones along the Maroni river in Suriname and French Guiana (many collected by inhabitants of the French penal colony there) (Oberthür, 1902; Joicey and Kaye, 1917, 1918).

As collections have grown and our understanding of *Heliconius* biogeography and genetics has improved, the proliferation of names has slowed substantially. The most recent new species (*H. luciana*) was described from southern Venezuela, by Lichy (1960). The development of refugium theory (Haffer, 1969; Brown *et al.*, 1974; Brown, 1979) has promoted the recognition of numerous subtly defined geographical races from putative areas of endemism (e.g. Brown & Fernandez Yepez, 1984; Lamas, 1984; Holzinger & Holzinger, 1989; Neukirchen, 1993), but the species-level taxonomy of the genus appears to be reasonably stable.

Until recently, Brown's (1981) phylogeny has provided the accepted hypothesis of relationships among heliconiine species and genera, but my cladistic analyses of *Heliconius* mitochondrial DNA sequences at inter- and intraspecific levels (Brower, 1994a,b, 1996) offer new and partially conflicting perspectives. A surprising result from the mtDNA survey of *H. erato* and *H. melpomene* geographical races (Brower,1996) is the identification of the new species and race described below, which casts new light on the evolution of mimetic wing patterns in these remarkable butterflies. Although nomenclatural conservatism is desirable for the preservation of stability in classification, demonstration of non-monophyly demands the revision of traditional groups. To this end, more changes in *Heliconius* classification are undoubtedly in store as additional data become available corroborating novel hypotheses of relationships, such as the paraphyly of *Heliconius* with respect to *Eueides* (Brower, 1994a), and of *H. melpomene* with respect to *H. cydno* (Brower, 1996).

MATERIAL AND METHODS

Butterflies used in the mtDNA studies were collected from numerous sites in Central and South America (Brower, 1994a, 1996). Specimens relevant to this study

were collected near Mocoa, Prov. Putumayo, Colombia, with the assistance of Dr Mauricio Linares. Standard protocols for specimen preparation and DNA manipulation and analysis are described in Brower (1994a). Mitochondrial sequences spanning 945 bases of the COI and COII genes were sequenced for 35 individual *H. melpomene* representing 13 geographical races, and for seven individuals representing six races or splinter species in the *H. cydno* group. (Brower, 1996). Phylogenetic analysis of molecular data was conducted using PAUP version 3.1 (Swofford, 1990). Multiple heuristic searches with random addition were conducted to generate a consensus tree of numerous equally parsimonious cladograms. Methodological details of the phylogenetic analyses are also discussed in Brower (1994a, 1996). Additional specimens from southeastern Colombia were sequenced for parts of the same mitochondrial fragment, to determine their affinity to those in the published cladogram.

Wings, abdomens and appendages from each specimen examined were glued with rubber cement to a 1 × 3 cm card so wing patterns and morphological features are visible. The reassembled 'specimens' were dried and pinned in insect drawers. These vouchers are deposited in the Cornell University Insect Collection (Ithaca, New York; CUIC Lot 1220). Abdomens were later removed from the cards for dissection. All voucher specimens are individually coded to match corresponding wings, genitalia slide and DNA sample. Purified DNA samples are in the possession of the author, preserved at –20°C. Additional material for morphological comparison was obtained from the collections of the American Museum of Natural History (AMNH, New York) and the Zoologisches Museum der Humboldt Universität (HUZM, Berlin).

Genitalia and abdominal pelts were prepared from dried voucher and museum material following the procedures of Miller (1987a,b). Abdomens were removed from the specimens, soaked with 70% EtOH, then boiled for 5 minutes in 10% KOH. They were then transferred to 70% EtOH, and cleared of scales and soft tissues with a fine paintbrush and forceps under a dissecting microscope. The right pleural membrane was slit with iridectomy scissors, and the terminalia were separated from the abdomen. The aedeagus was removed from the rest of the genitalia and the vesica was teased out with fine forceps. Structures were stained in Chlorazol Black (ICN Pharmaceuticals) to enhance contrast. Drawings were made under EtOH using a Zeiss SV8 stereo microscope with a drawing tube attachment. Structures were mounted on slides in Canada Balsam slide mounts.

RESULTS AND DISCUSSION

Discovery of a new mimetic Heliconius *species*

The *H. melpomene* race that occurs in the vicinity of Mocoa, Colombia has been named *bellula* Stichel (1923). In phylogenetic analysis of mtDNA sequences thought to include three specimens of this race, putative *bellula* individuals fell into two distinct haplotype classes (Brower, 1996). One sequence appeared within an undifferentiated clade containing numerous Amazonian *H. melpomene* races, while the other two were included among races of *H. cydno* and its relatives (Fig. 1). Subsequent analysis of additional representatives from the original field samples supports this initial distinction: four additional '*bellula*' specimens are unambiguously placed on the

cladograms, their partial sequences being identical to or differing only by autapomorphies from members of the Amazonian *H. melpomene* clade (data not shown).

Specimens of *H. cydno, H. heurippa* Hewitson and *H. pachinus* Salvin were included in the study initially as outgroups, to provide a root for inferring relationships among races of *H. melpomene*, but resultant cladograms from unrooted analyses (Brower, 1996; Fig. 1) indicated that relationships among *H. cydno* and *H. melpomene* were more complex than the simple sister species arrangement proposed by Brown (1981). *H. melpomene* appeared to be paraphyletic or even polyphyletic with respect to *H. cydno* and its relatives, depending on the disposition of the anomalous *bellula* sequences (Brower, 1996). It became obvious from the mtDNA results that '*H. melpomene bellula*' is a polyphyletic entity. There are two ways to explain this result.

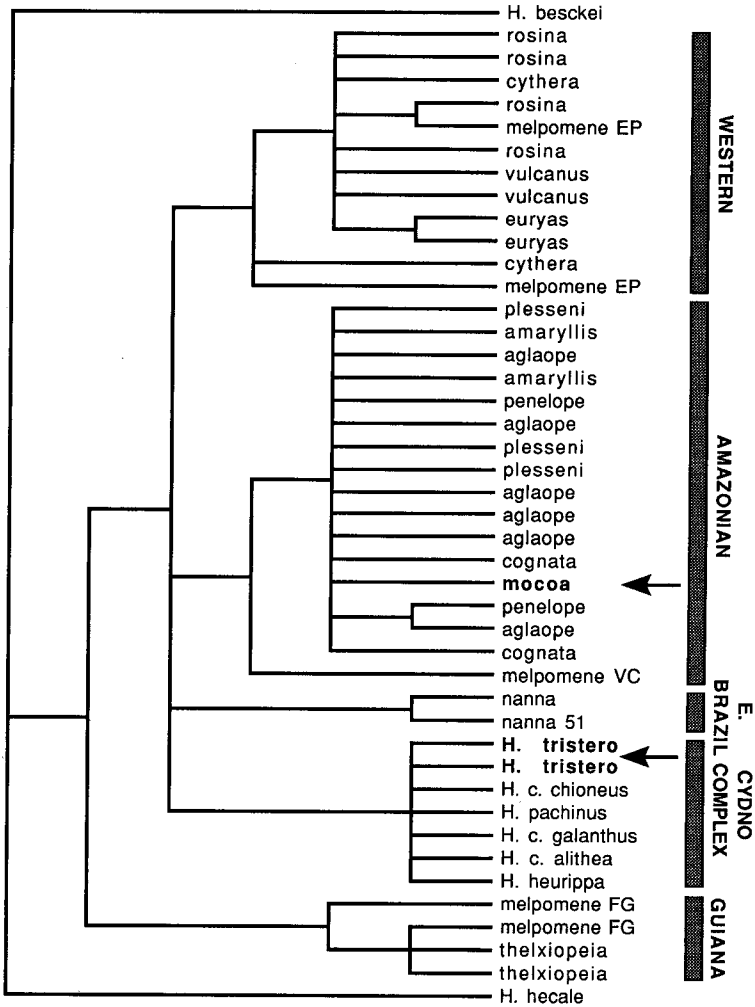


Figure 1. Strict consensus of 2744 trees, reflecting relationships among representatives of *Heliconius melpomene, H. cydno, H. heurippa* and *H. pachinus*, based on mtDNA cytochrome oxidase subunit 1 and 2 sequences (after Brower, 1996). The positions of the '*H. melpomene bellula*' individuals are indicated by the arrows, in the Amazonian *H. melpomene* clade ('*mocoa*'), and the *H. cydno* clade ('*H. tristero*').

One possibility is non-correspondence of the mtDNA cladogram with the 'species phylogeny', due to ancestral polymorphism or introgressive mitocondrial gene flow across the *H. cydno-H. melpomene* species boundary (reviewed in Doyle, 1992; Brower & DeSalle, 1994; Brower, 1996). Although they are close relatives, *H. melpomene* and *H. cydno* are broadly sympatric biological species (*sensu* Mayr, 1940), and, as noted above, belong to different mimicry complexes. The separation of sampled taxa into well-supported and biogeographically plausible monophyletic groups (Fig. 1) suggests that the single observed instance of incongruence is not due to ancestral polymorphism (Brower, 1996).

What about introgression? *H. cydno* and *H. melpomene* are partially interfertile, and hybridization is known from captive populations and has been reported occasionally in nature (Nijhout *et al.*, 1990). However, because female butterflies are heterogametic, F1 females are likely to have reduced fecundity (Haldane, 1922), impeding gene flow of maternally-inherited mtDNA across the species boundary during hybrid matings (Sperling, 1993). Nijhout *et al.* (1990) reported sterile F1 females in the *H. cydno* × *H. melpomene* crosses they performed. If this is generally the case, then mitochondrial DNA cannot introgress across species boundaries between these two species. Therefore, the only way to obtain the observed distribution of mitochondrial and phenotypic characters as a product of recent gene flow between species is for all the nuclear alleles responsible for the generation of the wing pattern to have migrated as a unit from *H. melpomene* autosomes into *H. cydno*. This seems highly implausible, given the complex, polygenic control of wing pattern diversification within both species (Sheppard *et al.*, 1985; Linares, 1989; Nijhout *et al.*, 1990; Mallet, 1993). These arguments effectively rule out character incongruence between mtDNA and the phenotype as an explanation for the polyphyly of '*H. melpomene bellula*'.

An alternative explanation is that '*H. melpomene bellula*' is in fact two distinct taxa. This would represent a new case of mimetic convergence between members of the *H. cydno* complex and the *H. melpomene* and *H. erato* clades. To confirm the separate identities of the mimics, male genitalia from the '*H. melpomene bellula*' material were examined (Fig. 2). Male genitalia of *H. cydno* and *H. melpomene* have been examined and illustrated by prior authors (Eltringham, 1916; Emsley, 1965), but these authors' taxonomy was so muddled and conclusions drawn so vague as to make their data impossible to evaluate. Eltringham (1916: 113) stated "...in so far as may be judged from the genitalia there is no reason to suppose that the forms now included under the Cydnoformes and Melpomeneformes ... really constitute more than one species." Emsley (1965) apparently felt that *H. cydno* and *H. melpomene* were distinct based on differences in the valvae, but it is unclear which races of each species he dissected. This is a critical problem, since *H. melpomene* is evidently paraphyletic with respect to *H. cydno* (Brower, 1996), and the range of morphological variation among *H. melpomene* races may be larger than that between the two species

In the current study, several morphological characters which divide the '*bellula*' specimens into two discrete groups were found, reflecting the same divisions observed in the mtDNA. (Fig. 2, Table 1). Representatives of other members of the *melpomene-cydno* clade were also dissected (Fig. 3). The distinction between *H. melpomene* and the *H. cydno* groups was supported, although several characters that are consistently different between the modest samples of the two '*bellula*' taxa studied here show substantial and potentially confounding variation among allopatric races of both *H. cydno* and *H. melpomene*. Prior hypotheses of relationships (Emsley, 1965;

Brown, 1972) have suggested that *H. heurippa* and *H. timareta* Hewitson are splinter species of *H. melpomene*. The evidence from mtDNA and male genitalic morphology (morphology only for *H. timareta*) that they are members of the *H. cydno* group corrobates the biogeographical observation that each occurs with a sympatric race of *H. melpomene* which it does not mimic (Brown & Mielke, 1972). While *H. timareta* displays a *melpomene*-like 'dennis-ray' wing pattern, it is only in the Mocoa region (as far as we know) that the mimicry between *H. melpomene* and *H. cydno* representatives has become so fine-tuned that the two species have been conflated by systematists, based upon their wing patterns. Given that many examples of interspecific and intraspecific wing pattern convergence among *Heliconius* butterflies (Eltringham,

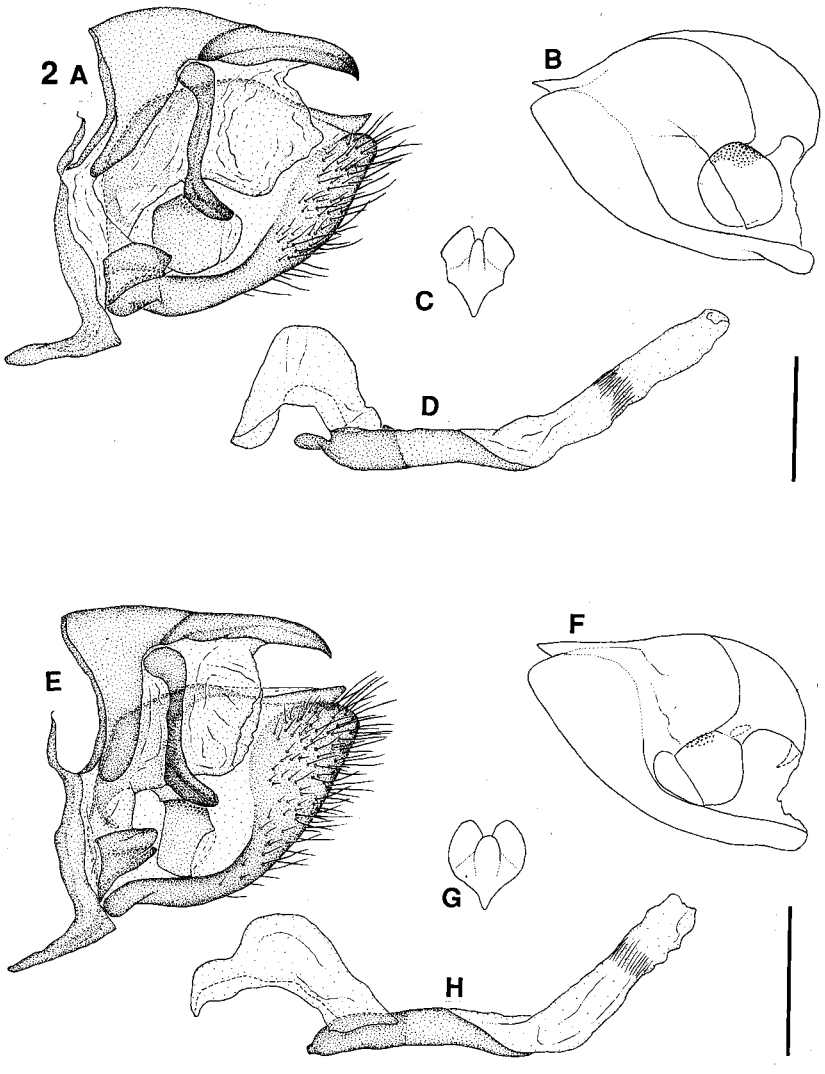


Figure 2. Genitalia of holotype male specimens of *H. tristero* (A–D) and *H. melpomene mocoa* (E–H). A, lateral view from left valve and aedeagus removed. B, left valve, medial surface (setae omitted). C, juxta, posterior view. D, aedeagus with vesica extended. E, lateral view with left valve and aedeagus removed. F, left valve, medial surface (setae omitted). G, juxta, posterior view. H, aedeagus with vesica extended. All parts to scale (scale bars = 1 mm).

TABLE 1. Morphological characters identified in this study that separate *H. melpomene* and *H. cydno* group members generally, and separate *H. melpomene mocoa* and *H. tristero*, in particular

	State			
Character	*H. tristero*	*cydno* group	*H. melpomene mocoa*	other *H. melpomene*
Male Genitalia:				
valve shape	broad	broad	narrow	narrow
valve vestiture	sparse	sparse	dense	generally dense
Valve pocket size	large	large	small	variable
denticulation on pocket	extensive	extensive	reduced	variable
posterior dorsal process	small	small	large	variable
heel on aedeagus	large	small or absent	small	small or absent
gnathos, posterior aspect	narrow	variable	broad	variable
Wing Patterns:				
red in FW discal cell	barely	(absent)	distal 1/4	variable
red color (varies with age)	more orange	more orange	more carmine	variable

1916; Emsley, 1965; Brower, 1996), it seems more reasonable to hypothesize that the mimetic colour patterns exhibited by the two clades are independently-derived within each lineage, rather than that the patterns are homologous, and shared as the result of complex patterns of gene flow or selective maintenance of ancient polygenic phenotypes.

Two entities: which is bellula*?*

H. melpomene bellula (Fig. 4) and two additional forms collected at the same time, from the same general region (f. *permira*, f. *degener*, Figs 5 and 6), were described by Stichel (1923). Stichel considered all these taxa to be forms of *H. amaryllis* Felder & Felder, which was reduced to subspecific status within *H. melpomene* by Eltringham (1916). All recent literature (Brown, 1979; Sheppard *et al.*, 1985; Brower, 1996) refers to *bellula* as a race of *H. melpomene*. The three holotypes were borrowed from the Zoologisches Museum der Humboldt Universität (Berlin) and dissected (the *permira* type could not be dissected because its abdomen was missing), to ascertain their identity with respect to the two classes of morphological character states identified in Table 1. Genitalic characters of the *bellula* (Fig. 3) and *degener* (not shown) types clearly group these specimens within the *H. cydno* clade. Based on its wing pattern, the *permira* type appears to be a phenotypic intermediate between *bellula* and *degener*, and is presumably also a *cydno*. Thus, as the taxonomy currently stands, the *H. melpomene* race from Mocoa is unnamed, and the *H. cydno* relative is incorrectly identified as a subspecies of *H. melpomene*.

One approach would be to raise *H. melpomene bellula* Stichel to species status. However, Stichel's type specimen and description do not correspond to the current concept of *H. melpomene bellula*: the specimen displays small yellow spots (Stichel's, [1923: 262] "schwefelgelbes Fleckchen") at the proximal subcostal edge of the red forewing patch (Fig. 4). Although specimens of these geographically-restricted taxa are rare in collections (the only specimens other than those I collected that I have been able to examine are the three types and one additional specimen lacking locality data, from HUZM), recent illustrations (Brown, 1979; Turner, 1981; Sheppard *et al.*, 1985; Mallet, 1993) and specimens collected by the author to show no yellow on the

forewing at all. The yellow spot is also absent in the sympatric mimic, *H. erato dignus* Stichel.

Stichel's types of other two *bellula* forms (Figs 5 and 6) have characteristics of hybrid specimens (a sparsely-scaled yellow hindwing bar in f. *permira*, suggesting a heterozygote condition (Mallet, 1986); mixed yellow and red banding in f. *degener* that looks very similar to published figures of purported *cydno-melpomene* hybrids (Ackery & Smiles, 1976; Salazar, 1993)). These specimens may represent hybrids between *H. heurippa* and the Mocoa *H. cydno* cognate. Stichel's *H. melpomene bellula* type appears to be a recombinant backcross between such hybrid forms and the parental Mocoa form lacking yellow forewing markings. Because the International Code of Zoological Nomenclature (Ride *et al.*, 1985: Articles 1b, 23h) forbids the use of species group names established on hybrids, and because the modern specimens are in any case diagnosably different from Stichel's *bellula* type, it seems prudent to

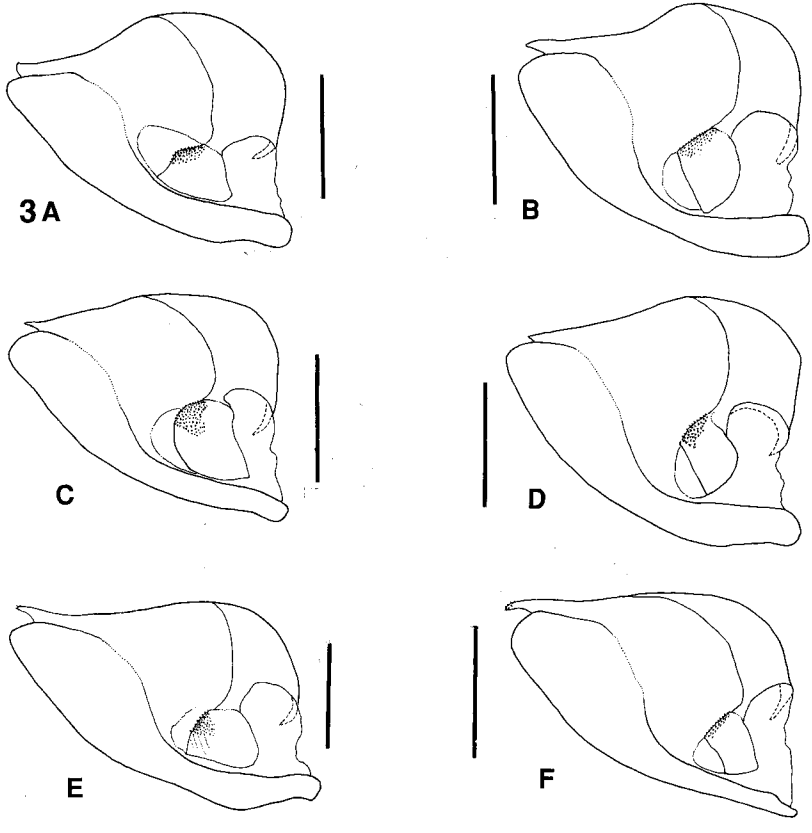
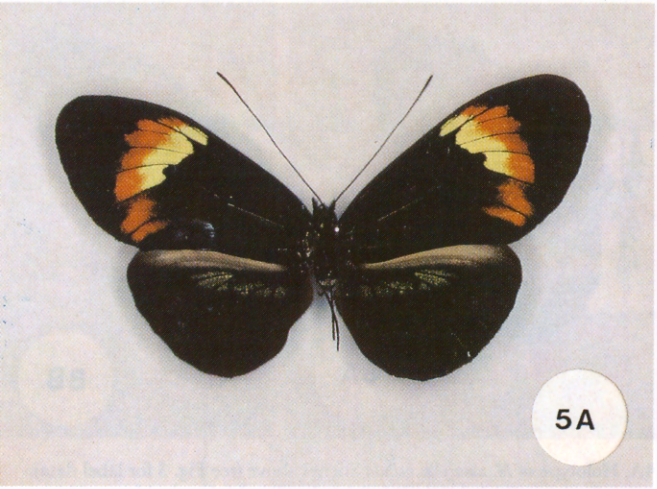


Figure 3. Genitalia of additional male specimens examined in this study. Interior view of left valvae, setae omitted. Institution, label data and specimen codes are listed. A, *H. amaryllis bellula*, holotype (HUZM. 2 labels: "7 VI 21 Rio Guagzayaco Rio Putumayoo Rep. Columbien Werner Hopp."; "*H. amaryllis* f. *bellula* Stichel n. f."). B, *H. heurippa* (AMNH. 4 labels: "Colombia: Cundinamarca, Manzanares, 900 m. 26 Jan. 1946"; "L. Richter, coll., Frank Johnson, donor"; "JRGT 59"; "AB010"). C, *H. cydno weymeri* (AMNH. 3 labels: "Pichinde, Cali 2500 m. VIII 45"; K. von Sneidern coll. donor Frank Johnson"; "AB009"). D, *H. timareta* (AMNH. 2 labels: "Ecuador. Abitagua 1200 m. 3 June 1937"; "AB001"). E, *H. melpomene aglaope* (AMNH. 3 labels: "Jatun Yacu Ecuador 700 m. June 12 1937"; "coll. by Wm. Clark-MacIntyre" "AB007"). F. *H. melpomene plesseni* (AMNH. 4 labels: "Oriente Ecuador"; "coll. by Wm. C. MacIntyre"; "Rio Pastaza watershed, Rio Iuñio 1200 m. 15-IX-37"; "AB008"). Scale bars = 1 mm.


4A

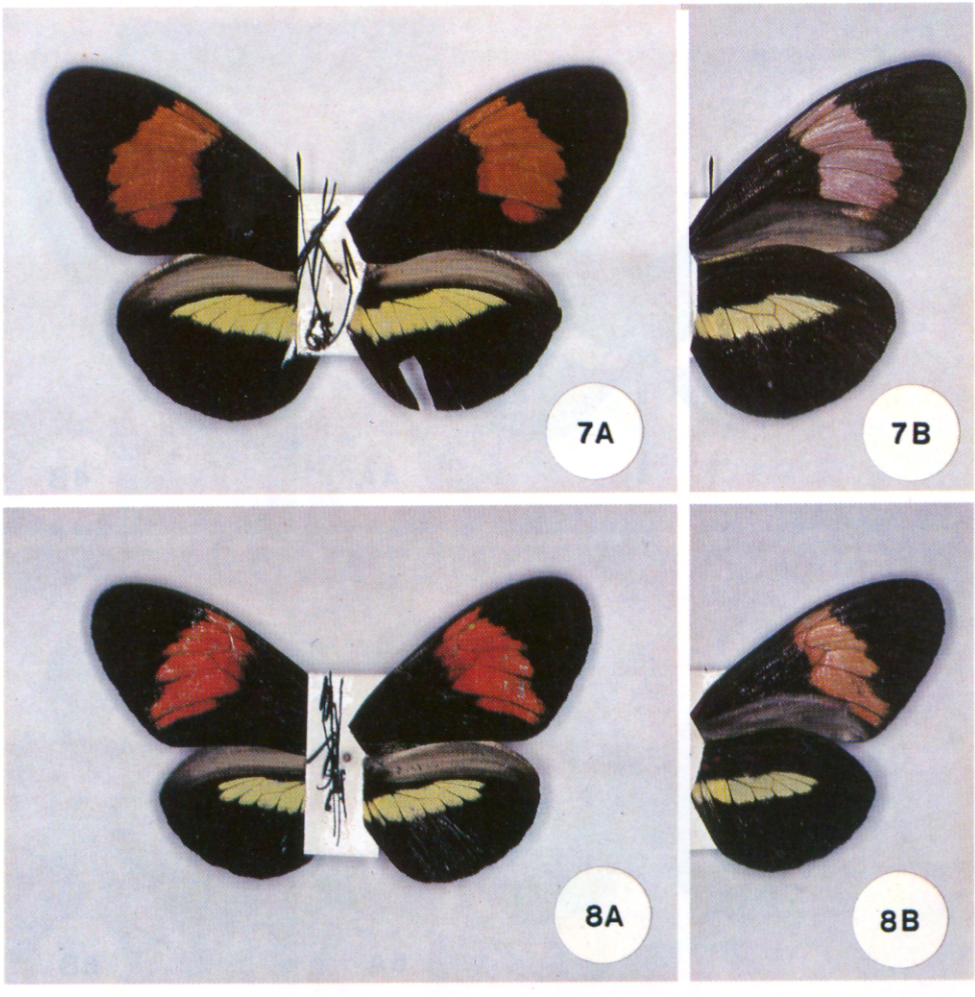

4B


5A


5B


6A


6B



Figures 4–8. Voucher material 4A, Holotype of *H. amaryllis bellula* Stichel above (see Fig. 3 for label data). 4B, below. 5A, Holotype of *H. amaryllis degener* Stichel (HUZM. 2 labels: "Rio Mulato b. Mocoa 500 m. Rep. Colombie Werner Hoppn.", "Hel. amaryllis bellula f. degener f. nova Stichel") above. 5B, below. 6A, Holotype of *H. amaryllis permira* Stichel (HUZM. 2 labels: "Mocoa 530 m. Putumaygebeit Februar 1921 Werner Hopp.", "Heliconius amaryllis bellula f. permira Stichel n. f.") above. 6B, below. 7A, Holotype of *H. tristero* new species, above (see text for label data). 7B, below. 8A, Holotype of *H. melpomene mocoa* new subspecies, above (see text for label data). 8B, below. Detached body parts (legs and antennae) are glued to the card.

establish new taxa for both the *melpomene* race and the *cydno*-like species. The name *bellula* Stichel thus applies only to a hybrid form with yellow forewing spots, corresponding to the original description and Figure 4.

***Heliconius tristero* sp. nov.**

(Figures 2, 7)

Diagnosis

A member of the *H. cydno* species group with a red forewing patch and yellow

hindwing bar, mimicking the pattern of *H. melpomene mocoa* Brower subsp. nov. and *H. erato dignus* Stichel. Female specimens unavailable for examination, but sexes are presumed to share the same colour pattern, as in most other *Heliconius* species.

Male. Anatomically similar to *H. cydno*, FW length 38–42 mm (slightly larger than *H. melpomene*). FW above black ground with irregular orangy-red postmedial band extending proximodistally from distal end of discal cell to R_2-R_3 fork, and laterally from subcosta to CU_2, with a smaller contiguous region continuing into cell CU_2. FW below similar, but with red area slightly reduced, and paler. HW below with black ground colour, androconial distribution as in *H. cydno*. Yellow bar (with black scales on veins) extending from anal margin near base towards apex, similar to form to yellow bar in *H. cydno weymeri* Staudinger. Posterior margin of bar broken by black denticles at veins and medially, between veins. Anterior margin of bar depressed towards posterior within discal cell. HW below similar, with or without basal red spots, and with narrow costal yellow streak.

Genitalia. Figure 2A–D. Valve relatively broad and short, the eversible pocket on its inner surface large and broadly denticulate on its dorsal surface. These two characters appear to hold for all members of the *H. cydno* group examined. Posterior dorsal process of valve small, not extending to apex of valve (a character variable in both the *H. melpomene* and *H. cydno* groups, but consistently different between *H. tristero* and *H. mepomene mocoa*). The large flange at the base of the aedeagus is apparently autapomorphic for *H. tristero*. However, male genitalia of the taxa examined are similar, and display substantial intra-racial variability in form. The valve shape and denticulation on the pocket, as well as degree of setation on the valve apex (*H. melpomene* group specimens are generally hairier than *H. cydno* group members) appear to be the most reliable diagnostic characters.

Type material

The holotype male (Fig. 7) bears two labels. The data label reads, "COLOMBIA: Dpt. Putumayo, 6 km N. Mocoa on rd. to Pitalito, quebrada up hillside, 25 March 1992, leg. A. V. Z. Brower, C-15-4." The red holotype label reads, "Cornell University Insect Collection Holotype No. 6896. Heliconius tristero, Brower" The specimen consists of wings, meso- and metathoracic legs, and antennae, glued with rubber cement to a 1 × 3 cm card. The abdomen and genitalia are mounted on a slide, labelled, "Cornell University Insect Collection Holotype No. 6896. Heliconius tristero, Brower (C-15-4)." Both are deposited in the CUIC, Cornell University, Ithaca, NY. One additional male is also deposited at CUIC. Its locality data are: COLOMBIA: Dpto. Putumayo, km. 130-131 on Pasto-Mocoa Rd. (12 km W. Mocoa) roadside cañadas, 24 March 1992, leg. A. V. Z. Brower, C-13-4. This specimen is prepared the same way as the type.

Distribution and habitat

Published distribution maps in Brown (1979) and Sheppard *et al.* (1985) show a range for '*H. melpomene bellula*' corresponding to the upper Rio Putumayo and Rio Caquetá and their tributaries in southern Colombia, with points presumably derived from data on museum material. However, I have been unable to find specimens of either *H. tristero* or *H. melpomene mocoa* in the AMNH, the Natural History Museum (London), the Smithsonian Institution (Washington D.C.), the Allyn Museum (Sarasota, FL), the CUIC, or the Museum of Comparative Zoology at Harvard

University (Cambridge, MA). The type specimens from HUZM (Figs 3–5) list locality data that are plausible, but difficult to place exactly on fairly detailed recent maps (Anonymous, 1990; Healey, 1991).

Presumably, the ranges of *H. tristero*, *H. melpomene mocoa* and *H. erato dignus* are concordant, as is normally the case in local mimetic *Heliconius* races. All three taxa were found in similar second-growth or formerly cultivated (cacao) areas, close to the road, and were associated with the orange flowers of a cucurbit vine (tentatively identified as *Psiguria* or *Gurania*) at one site. All of these sites are characteristic *Heliconius* habitat. The species are all apparently common in appropriate habitat areas within their range, as they were found without difficulty. Mallet (1993) reported hybridization between *H. erato dignus* and *H. erato lativitta* Butler (and referred to hybridization between '*H. melpomene bellula*' and *H. melpomene agalope* Felder & Felder) to the east of Mocoa, near Villa Garzón (Villa Amazonica), Dept. Putumayo, Colombia. Members of the *H. cydno* group tend to occur at higher altitudes than *H. erato* or *H. melpomene* (De Vries, 1987; pers. obs.), and the distribution of *H. tristero* may be limited by ecological factors other than the mimetic tension zone to the east. Additional records and further instances of hybridization with adjacent races (or species) are necessary.

Remarks

The name 'Tristero' derives from Thomas Pynchon's novel, *The Crying of Lot 49*, and refers to a shadowy Renaissance cult figure that inspired a secret, independent postal system in modern suburban California. Because the red forewing patch pattern is referred to as 'postman' (Emsley, 1963), *tristero* seemed an appropriate name for a species that has emulated the local *erato-melpomene* mimicry complex so effectively that it has remained undetected until now.

***Heliconius melpomene mocoa*, subsp. nov.**

(Figures 2, 8)

Diagnosis

A geographical race of *H. melpomene* with a red forewing patch and yellow hindwing bar, mimicking the pattern of *H. tristero* Brower and *H. erato dignus* Stichel. Female specimens unavailable for examination, but sexes are presumed to share the same colour pattern (except for androconia), as in all closely related species.

Male. Anatomically similar to other *H. melpomene*, FW length 35–40 mm (perhaps slightly smaller on average than *H. tristero*, but available samples are too few to draw firm conclusions). FW above black ground with irregular carmine to orangy-red postmedial band extending proximodistally from distal quarter of discal cell to R_2-R_3 fork, and laterally from subcosta to CU_2, with a smaller contiguous bar in anterior half of cell CU_2. FW below similar, but with red area slightly reduced, and paler. HW above with black ground colour, distribution of androconia as in *H. melpomene*. Yellow bar (with black scales on veins) extending from anal margin near base towards apex. Posterior margin of bar broken by black denticles at veins and medially, between veins. Anterior margin of bar depressed towards posterior within discal cell. HW below similar, with narrow costal yellow streak, and with red spots or streaks within and around base of discal cell (the basal red spot in the discal card

is NOT a consistent diagnostic feature of *H. erato*, contra Emsley, 1963 and Beutelspacher Baigts, 1992).

Genitalia. Figure 2E–H. Valve relatively narrow and elongate, eversible pocket small, with a limited area of denticulation on its distal surface. Posterior dorsal process of valve extending to apex and bearing a few small setae. See discussion of differences under *H. tristero* description, above.

Type material

The holotype male (Fig. 8) bears two labels. The data label reads, "COLOMBIA: Dpto. Putumayo, 1–3 km N. Mocoa on rd. to Pitalito, 2nd growth and cacao along Rio Mocoa, on Psiguria, Gurania, 25 March 1992, leg. A. V. Z. Brower, C-14-8." The red holotype label reads "Cornell University Insect Collection Holotype No. 6897. Heliconius melpomene mocoa, Brower". The specimen consists of wings, meso- and metathoracic legs, and antennae, glued with rubber cement to a 1 × 3 cm card. The abdomen and genitalia are mounted on a slide, labelled, "Cornell University Insect Collection Holotype No. 6897. Heliconius melpomene mocoa, Brower (C-14-8)." Both are deposited in the CUIC, Cornell University, Ithaca, NY. Four additional males are also deposited at CUIC. Two bear the same locality data and have been designated paratypes (C-14-4, C-14-6), one specimen has the same locality data as the second *H. tristero* specimen (C-13-6, see above), and the last reads, "COLOMBIA: Dpto. Putumayo, 26 km N. Mocoa on rd. to Pitalito, quebrada up hillside, 25 March 1992, leg. A. V. Z. Brower, C-16-1." All these specimens are prepared the same way as the type.

Distribution and habitat. See above, under *H. tristero* description.

Remarks

This taxon is named here as a subspecies to comply with ICZN Article 45f (Ride *et al.*, 1985). The term 'geographical race' applied to it elsewhere in this article is technically the same, but more apt (see below).

Other taxa examined

In addition to those illustrated in Figure 3, the following male specimens were dissected to examine genitalic morphology. The data labels from pinned material are transcribed in parentheses. *Heliconius cydno cydno* Doubleday ("Colombia: Dpto. Huila, P. N. Arqueologico San Agustín, 1800 m. dry second growth, 26 March 1992, leg. A. V. Z. Brower, Heliconius cydno cydno C-18-1"); *H. cydno gustavi* Staudinger ("Colombia: Dpto. Valle del Cauca, 2 km. W. Saladito on Cali-Buenaventura Rd. (Cauca drainage), 27 March 1992, leg. A. V. Z. Brower, Heliconius cydno gustavi C-20-2"); *H. melpomene melpomene* (L.) ("Buena Vista, East Colomb. 800 m. 29 VII 46", "L. Richter coll., donor Frank Johnson", "AVZB 002"); *H. melpomene plesseni* Riffarth ("La Merced, Ecuador, IV, 36", "coll. by Clark-MacIntyre", "AB004"); *H. timareta* Hewitson ("Ecuador: Abitagua, 1200 m., 3 June 1937", "Abitagua 1200 m, 3 VI 1937", "AB001"); *H. melpomene aglaope* Felder & Felder ("Rio Nanay, Peru, X-26", "Coll. by Guillermo G. Klug", "Coll. F. E. Church", "AB003") (the last specimen appears on the basis of its genitalia to be *H. timareta*). Labels on genitalia slides

correspond to pinned specimen labels. These specimens are housed in the CUIC (Brower material) or the AMNH.

Why is H. melpomene mocoa *a race and* H. tristero *a species?*

Ascribing these two apparently equivalent taxa to different taxonomic levels is problematical. Both occur in the same small geographical region, the ranges of both are geographically bounded by close relatives to the north and south, and there is evidence that both hybridize with adjoining races/species (see above, and Mallet, 1993). The phylogenetic species concepts (Nelson & Platnick, 1981; Cracraft, 1983; Nixon & Wheeler, 1990) argue that species are aggregations of populations diagnosably different from other such aggregations. The criterion of interbreeding, so fundamental to the biological species concept (Mayr, 1940), is only incidentally relevant to the phylogenetic species concept, when interbreeding blurs boundaries among otherwise diagnosable aggregations. *Heliconius* races are clearly diagnosable, as is evident from the diagnoses of hundreds of geographical races with discrete and mappable distributions (Brown, 1979; Sheppard *et al.*, 1985; Mallet, 1993). Each can thus probably be considered a legitimate phylogenetic species (but see Vane-Wright *et al.*, 1975). Indeed, it is ironic that the conflict over species boundaries in *Heliconius* arises only because the butterflies have been so extensively collected. With fewer available data on distributions and hybrid zones, systematists might be perfectly content to recognize each race as a distinct species based on consistent differences in wing pattern and other morphological characters, as is done for other geographically differentiated neotropical taxa (e.g. Miller, 1989). However, the phylogenetic approach circumvents insoluble disputes over what are essentially arbitrary distinctions of classificatory rank, by emphasizing the use of cladograms and the resultant inferred phylogenetic trees to represent relationships among taxa.

I have adopted taxonomic conventions here that will be least disruptive to current *Heliconius* classification. *H. tristero* is considered a species only because its geographically adjacent close relatives, *H. heurippa* and *H. timareta*, have been traditionally considered species as well (Emsley, 1965; Brown, 1981). *H. melpomene mocoa* is considered a geographical race (subspecies) because its geographically adjacent close relatives, *H. melpomene melpomene* and *H. melpomene aglaope* (Felder & Felder) are considered geographical races (Brown, 1979; Sheppard *et al.*, 1985; Mallet, 1993). The mitochondrial DNA data suggest that the degrees of relationship among the *H. melpomene* races and among the *H. cydno* relatives are similar, and that divergence times within each group are also approximately the same (Brower, 1994b, 1996), implying that the taxonomic rank of each group should also be the same. The entire species-level classification of the genus will probably require revision as additional data become available.

ACKNOWLEDGEMENTS

I thank Mauricio Linares for his hospitality and assistance during my expedition to Colombia in March, 1992, and Cal Snyder for his photographic expertise. Wolfram Mey kindly hand delivered Stichel's type material to me from Zoologisches Museum der Humboldt Universität, Berlin. I could not have done the morphological

study without the patient instruction of Jim Miller, to whom I am also indebted for all the wonderful drawings in this paper. He, R. I. Vane-Wright and an anonymous reviewer provided thoughtful criticism that improved the manuscript. I was supported at the AMNH by NSF Environmental Biology Fellowship DEB-9303251.

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