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# THE BIOLOGY OF *HELICONIUS* AND RELATED GENERA

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## OVERVIEW AND PERSPECTIVES

Biological studies of mimetic Neotropical butterflies in the nymphalid tribe Heliconiini have twice come full cycle in the past 100 years. Bates's classic writings (6, 7), reflecting observations during his lengthy stay on the Amazon, used these insects in a proposal of the phenomenon of mimicry and in support of Darwinian paradigms of adaptation and evolution. During the following thirty years, field biological studies of heliconians were relegated to second place behind heated arguments about "mimicry" in museum specimens; an important exception was the pioneering work of the brothers Fritz and Wilhelm Müller in southern Brazil (100-105). Most papers in this period involved taxonomic description of the seemingly endless phenotypes in the tribe. In the early 1900s, however, a synthesis of heliconiine systematics (119, 121) opened the way for field studies during subsequent years by Kaye (87, 88), Michael (95, 96), Collenette (43), Moss (98), Beebe (in 112), and others. Both these biological studies (primarily undertaken by European visitors to the Neotropics) and the systematic work, which by then was mostly restricted to naming new individual forms and aberrations, were interrupted in the pre-World War II period. Modern biological studies began in the 1950s in Trinidad and since have expanded to many countries, institutions, and areas of investigation. Heliconiini are now laboratory animals; experimental methods and biological theory have derived great benefit from the detailed study of field and captive populations of these butterflies. The affirmation of Turner (155) that they are the "best studied terrestrial invertebrates of no economic importance outside the Drosophilidae" must be qualified, however. The pests *Agraulis vanillae* and *Dione juno* are the

principal enemies of passion fruit crops from California to Argentina (16, 72, 74, 91, 92) and are difficult to control without ecological techniques (30, 72). In addition, self-regulating forest *Heliconius* populations have been proposed for the control of a pest species of passion vine in Hawaii (J. Waage, J. T. Smiley, and L. E. Gilbert, in preparation).

This review covers the ten Neotropical genera in the tribe, but not Palearctic members (*Cethosia*, possibly also *Vindula* and other relatives). It summarizes the recent phase of biological work on these insects, trends in the present state of knowledge, and the most promising areas for future research. A comparison of basic biological data for all 65 species is provided to aid in the selection of study organisms for projected research. Turner's bibliography (155) covers the important literature on the Heliconiini through 1976–1977; only half of its 317 entries could be quoted here, but other papers through early 1980 have been included.

## FOUNDATIONS FOR BIOLOGICAL RESEARCH ON THE HELICONIINI

Turner (143) reviewed pre-Linnaean publications on heliconians [which include an early adult painting by Petiver (111) and life-history sketches by Merian (94)] and important biological work before the 20th century. Classical systematic work benefitted from the incisive thinking of Stichel and Riffarth (118, 119, 121) on species-groups, Dixey and Moulton (53, 99) on mimicry, Eltringham (60) on male genitalia, and Joicey and Kaye (82, 83, 88) on subspecies intergradations. The tribe was later catalogued by Neustetter (107) and Stichel (120). New morphological and morphometric techniques were brought to bear on heliconian systematics by Michener (97) and Comstock & Brown (22, 44) during and after World War II.

Several life histories were published in the nineteenth century by Jones (84, 85) and the Müllers (100, 103, 105). Nocturnal communal roosting of adults, first mentioned by Edwards (56), was later described by Jones (86), Poulton (112), Carpenter (41), and Moss (98). Odor production by heliconians was investigated by F. Müller (101, 102, 104), Eltringham (61), and Barth (4, 5). Migratory behavior on a large scale northward was noted by Randolph (113) and O'Byrne (109) in central North America for one species (*Agraulis vanillae*) and on a small scale southward by Beebe (9) in the Venezuelan coastal cordillera for many species. Long-term studies of field behavior were conducted by Kaye (87, 88), Michael (95, 96), and Collenette (43). Other references to early works are included in Turner's reviews (143, 155).

The still rapidly expanding recent phase of biological investigation of Heliconiini began in William Beebe's tropical research station at Simla,

Trinidad in the 1950s. The basic groundwork on juvenile biology and host-plant relationships was provided by Beebe, Crane, Fleming, and Alexander (2, 3, 11, 65) after the domestication of numerous local heliconian species in large, open-air, semi-natural insectaries (50, 51, 63). Jocelyn Crane initiated ecological and ethological studies (48, 49) that soon branched into a multitude of physiological and biochemical investigations (8, 126–139) and fundamental experiments on the phenomena of aposematism and mimicry (20, 21). Philip Sheppard, John Turner, and Michael Emsley followed Beebe's lead (10) in an investigation of the genetics of Müllerian mimicry (63, 115, 144, 146, 148–150, 158) which continues to occupy an increasing number of scientists. The systematics of the whole tribe were revised by Emsley (62–64) and Turner (141, 142, 145), who reduced the 117 species in Neustetter's (107) and Stichel's (120) catalogues to 55. The basic data produced during twenty years of heliconian research at Simla laid the foundations for almost all the present research on the tribe and provided the initial stimulus and orientation for most modern workers in the area.

## TRENDS AND RESULTS IN MODERN RESEARCH

Descriptive morphology and biology of the heliconians have now advanced to the stage where the entire tribe can be analyzed in comparative terms for a large number of features (Figures 1–4, Tables 1–3).

### *Biosystematics* (Figure 1)

Studies of juvenile biology (2, 3, 11, 24, 25, 34–36, 38, 39, 65, 76, 93, 106, 116, 117, 145, 165), genetics (10, 33, 36, 63, 115, 124, 144, 148, 150, 157–159, 162), field ecology (13, 14, 16, 27, 35, 36, 39, 57, 64, 69, 70, 76, 93, 96, 116, 147), and biogeography (26, 28, 29, 31, 39, 40, 44, 62, 64, 89, 140, 146, 156) have given a broad base for the present biosystematic arrangement of species and subspecies in the tribe Heliconiini (1, 31). In large part, the biological data have served to confirm the (primarily) morphologically-based systematics of Emsley (62, 64), although detailed observations of local and broad sympatries led to an increase in the number of species recognized in the tribe from 55 to 65 (26, 31, 39). Biological and morphological characters agree well in indicating the phylogeny and relative antiquity of modern species (Figure 1). The arrangements of difficult groups of sister-species like *Eueides* (26, 38, 79, 80, 118), the silvaniform *Heliconius* (27, 33), the *cydno* superspecies (39, 78), and the *sapho*-group (26, 34, 39) have been extensively tested and refined in field and laboratory work over the past decade. Remaining problems that need more investigation include the probable division of *Philaethria dido* into a number of sibling species, the rela-

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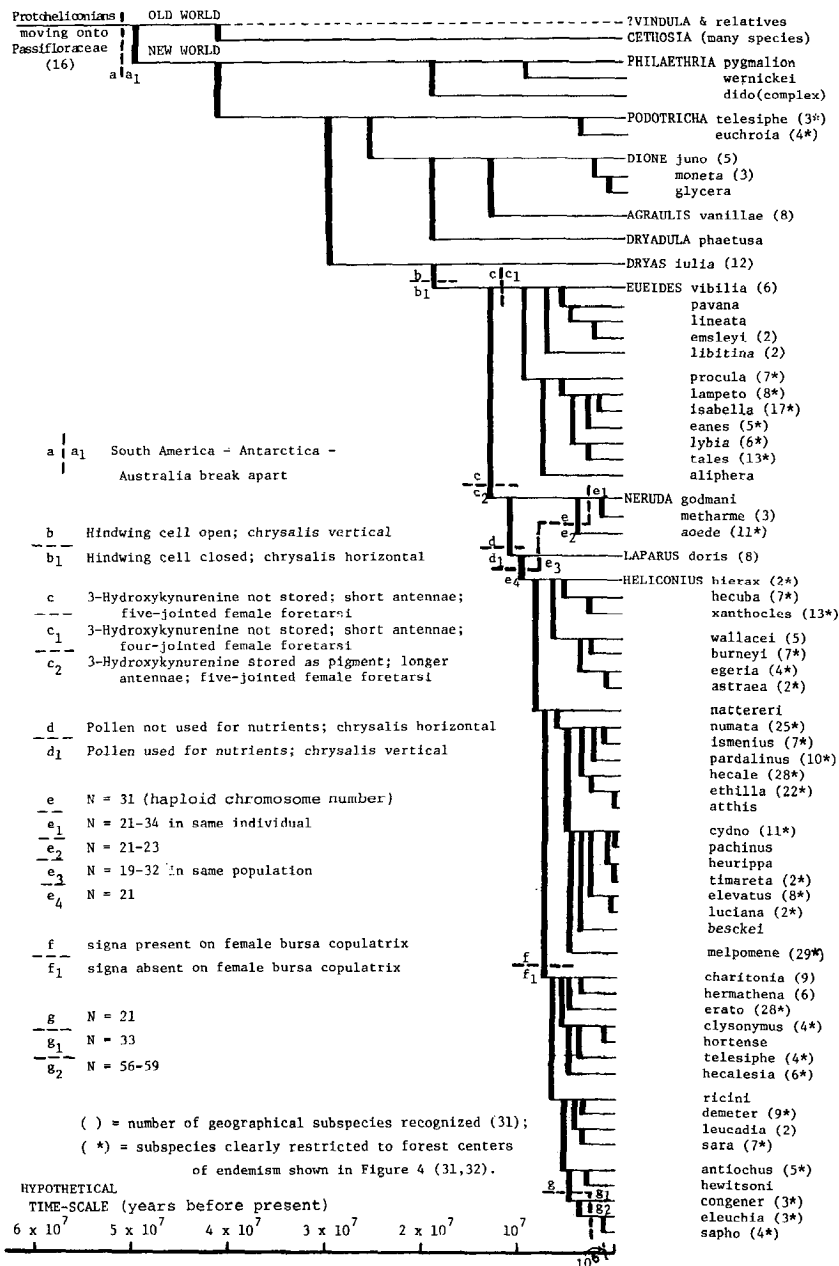


Figure 1 Postulated phylogeny of the Heliconiini (schematic) [Original interpretation based on that in (24), recent data, and available biosystematic information].

tionships between *Eueides lineata*, *E. emsleyi*, and *E. libitina*, the affinities of *Heliconius egeria* and *H. astraea*, the complex speciation and despeciation phenomena observed in the silvaniforms (27), and the degrees of inter-fertility of members of the *H. cydno* group, of *H. atthis* with *H. ethilla*, of *H. hortense* with *H. clysonymus*, and of *H. hewitsoni* with *H. antiochus*.

### *Captive Cultures*

The Simla group solved the major problems in rearing heliconians in the tropics (50, 51, 63); the domestication of the butterflies in temperate-zone greenhouses was later accomplished with success in Britain (151, Sheppard, Cook) and New York (Turner) and especially Texas (69, 70) in North America. The butterflies adapt well to captivity with the help of flowers (including preferred natural pollen sources), supplementary feeders of honey water, many passion vines, over 80% humidity and moderate tropical temperatures (20–30° C), protection from wind and predators, and a patchy illumination structure combining strong but diffuse brightness and deep shade. Care and good fortune in the choice of founding stock also helps; best are relatively undisturbed populations from open woods with understory flowers and considerable daily and yearly variation in environment. Field-captured males and females almost always outperform reared individuals in courtship and pollen gathering, if not necessarily in adaptation to captivity; inbreeding leads to appreciable loss of viability. Intersub-specific crossing can give increased larval survivorship, but also at times impaired adult performance and skewed sex ratios (33).

Various authors have published basic methods for obtaining stock in the field (33, 57, 63, 116, 147, 150, 151, 162, 167). Adults may be maintained alive for many weeks during field research if they are kept cool and humid in hanging cages or in envelopes and are fed daily. Eggs and larvae encountered in the field may show a high rate of parasitism (57, 70, 72), so cultures are often established from adult females. Larvae grow well in closed humid plastic dishes with daily food and air renewal and are quite resistant to disease.

### *Juvenile Biology* (Figure 2, Tables 1–2)

The biology and behavior of the early stages of several species was first thoroughly described from work at Simla (2, 3, 11). Many recent papers have included descriptions of juvenile biology as adjuncts to systematic (24, 25, 27, 38, 39, 145), biogeographical (34), evolutionary (14, 16), or ecological (35, 36, 93, 106, 116, 163–165) investigations. Chaetotaxy of first instar larvae was first described by Fleming (65) and has been expanded recently by M. Johnson and J. Turner (in preparation). Presently, information on

juveniles (Table 1) is essentially complete for all species except *Neruda godmani* and *metharme*, *Eueides lampeto*, and *Heliconius hecuba*, *H. luciana*, and *H. telesiphe* (partial only) and *Eueides emsleyi*, *E. libitina*, and *E. eanes* and the high-Andean *Podotricha euchroia* and *Heliconius hierax* (lacking).

Eggs (Figure 2A–G), if exposed on tendrils, are placed out of reach of predators. Eggs are often imitated by round yellow plant structures that discourage placement of “more” eggs by ovipositioning females of species with cannibalistic larvae, which eat eggs and smaller caterpillars (16, 70; K. Williams and L. Gilbert, submitted). Larvae are often cryptic in early instars and brightly colored when mature (Figure 2H–Q). Pupae (Figure 2R–W) are usually regarded as cryptic and are well armed with spines (145). Morphological characters of juveniles vary appreciably within a species (and sometimes even within a population) (2, 3, 11, 27, 35), often in apparent response to biotic factors or light regimes. For example, eggs of a single species vary greatly in size and number of ridges (27); pupae also vary and may be light or dark (24, 36); caterpillars of *H. erato chestertonii* have a dark side stripe unknown in other *erato* larvae; and different larval colors and behaviors in two subspecies of *H. demeter* (35) have been attributed to the presence or absence of other common Heliconiine larvae in the same regions. Adaptive color-pattern mimicry among larvae (Figure 2O–Q, Table 2) has been suggested on several occasions (35, 36, 38, 145). The numbers and traits given in Tables 1–2, therefore, should be regarded as potentially very flexible in individual populations or subspecies.

### Genetics, Evolution, and Mimicry (Figure 3)

The ability to maintain *Heliconius* in captivity has permitted a variety of genetic experiments to be performed. Work has mostly concentrated on the strongly polytypic and mutually mimetic species, *H. melpomene* and *H. erato* (150, 158; P. Sheppard, J. Turner, K. Brown, W. Benson, and M. Singer, submitted), and led to new theories on the evolution, stabilization, and genetics of Müllerian mimicry (157). Density-dependent factors in mimicry, combined with temporal and spatial heterogeneity in the mimetic environment, were proposed to explain wide-scale polymorphism in

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**Figure 2** Early stages of heliconian butterflies. A–G, eggs, 8 × life size: A, *Eueides tales*, near hatching; B, *Neruda aoede*; C, *Heliconius xanthocles*; D, *H. timareta*; E, *H. telesiphe*; F, *H. demeter*; G, *H. eleuchia*. H–Q, larvae: H, *Heliconius timareta*, first instar; I, *Philaethria wernickei* first instar; J–Q, fifth instars: J, *Philaethria pygmalion*; K, *Dione glycera*; L, *Eueides vibilia*; M, *Eueides lybia*; N, *Eueides pavana*; O, *Eueides tales*; P, *Heliconius demeter eratosignis*; Q, *Heliconius heurippa*. R–W, pupae: R, *Philaethria pygmalion*; S, *Eueides vibilia*; T, *Heliconius wallacei*; U, *Heliconius heurippa*; V, *Heliconius hecalesia*; W, *Heliconius sara*. A, J, M, O, P, T, V, W illustrated in previous publications; others not.



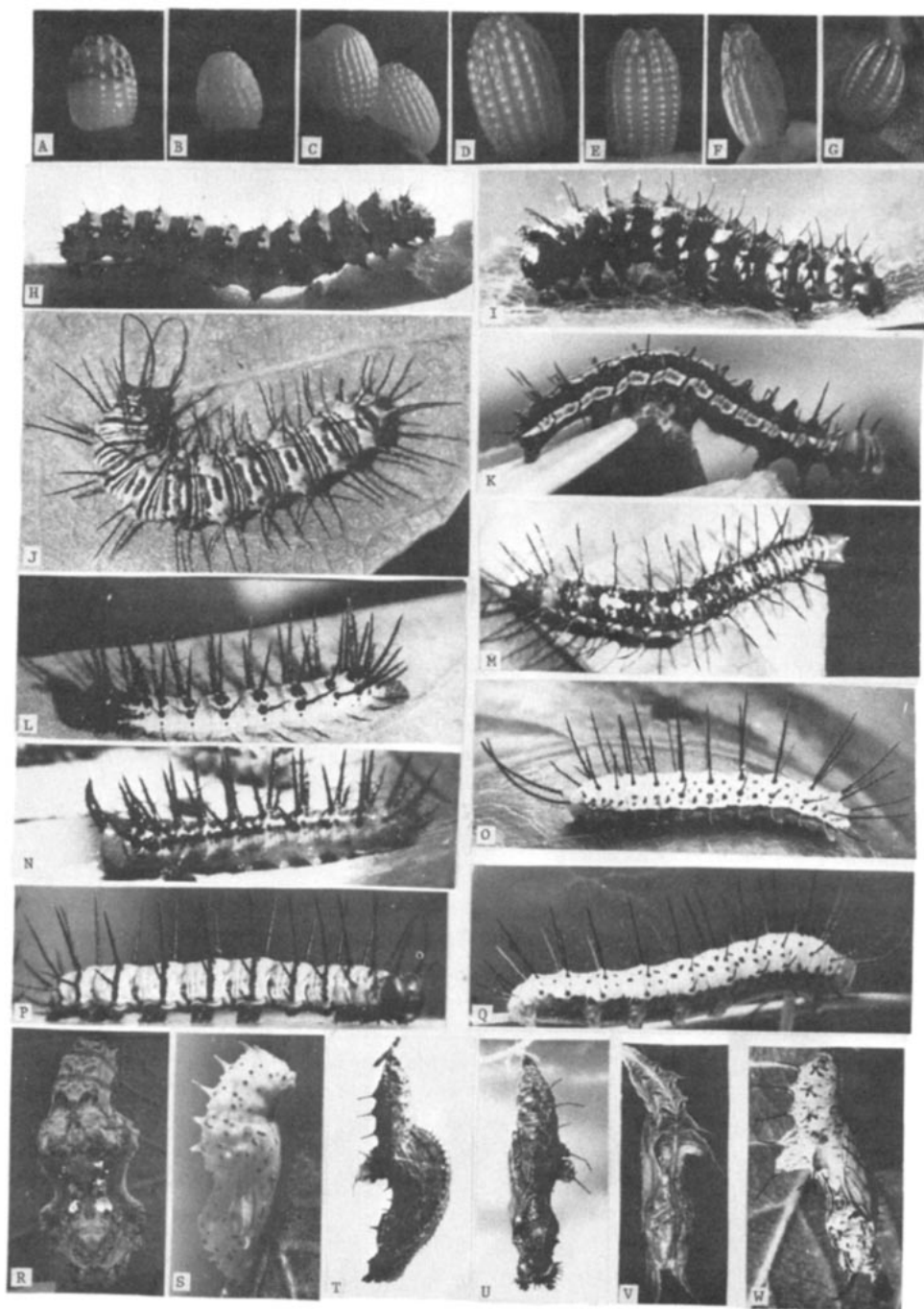


Table 1 Morphological characteristics of heliconian eggs, larvae, pupae and adults<sup>a</sup>

Genus, species	Special refer- ences	Egg			Mature (5th Instar)
		Color	Height/ diamet- er (mm)	Vert/ horiz. ridges	Summary of color - pattern (ground color, bands, stripes or spots, scoli, head, anal cap)
<i>Philaethria</i>					
<i>pygmalion</i>	36	Ye	1.5/1.1	20/8	Wh/BkRe-b, BkWhRe-sc, Re-hd
<i>vermickiei</i>	36	Ye	1.5/1.1	20/8	Wh/BkRe-b, Bk-sc, YeOr-hd
<i>dido</i> complex	11	Ye	1.6/1.2	22/12	Wh/BkRe-b, BkWhRe-sc, Ye-hd
<i>Podotricha</i>					
<i>telesiphe</i>	LG, KB	YeWh	1.0/0.8	20/14	GrWh/Ye-st, Bl-sp, BkWhYe-sc, Ye-hd
<i>euchroia</i>		?	?	?	?
<i>Dione</i>					
<i>juno</i>	11, 106	Re	1.0/0.7	12/5	Br/Or-sp, Bl-sc+hd
<i>moneta</i>	KB, JM	Wh	1.1/0.8	14/7	Bk/Ye to GrWh-sp+st, Bk-sc, BkWh-hd
<i>glycera</i>	KB	Ye	1.2/0.9	16/10	Bk/Ye-st, Or-sp, Bk-sc, BkOr-hd
<i>Agraulis</i>					
<i>vanillae</i>	11	Ye	1.1/0.8	16/13	Bk/OrYeWh-sp+st, Or or BkOr-hd
<i>Dryadula</i>					
<i>phaetusa</i>	11	Ye	1.7/1.1	17/20	Bk/Or-hd
<i>Dryas</i>					
<i>iulia</i>	11, 165	Ye	1.2/1.0	20/13	Br/ReWh-sp, BkYe-sc, BrWh-hd
<i>Eueides</i>					
<i>vibilia</i>	KB	ReWh	1.0/0.8	16/6	Ye/Bl-sp+sc+hd
<i>pavana</i>	KB	Wh	1.0/0.8	18/10	GrYe/Bk-sp+st, Bk-sc, Or-hd
<i>lineata</i>	JM	GrWh	0.9/0.8	20/11	GrYe/BkWh-sp+st+sc, Or-hd+ac
<i>emsleyi</i>		?	?	?	?
<i>libitina</i>		?	?	?	?
<i>procula</i>	KB	Cr	0.8/0.8	16/10	Bk/Ye-sp+st, Bk-sc, BkWh-hd
<i>lampeto</i>	KB	Cr	1.1/0.8	16/9	?
<i>isabella</i>	11, 165	Cr	1.0/0.9	16/8	Bk/OrYe-st, Wh-b, BlWh-sc+hd, Or-ac
<i>eanes</i>		?	?	?	?
<i>lybia</i>	165, KB	Cr	1.0/0.7	12/8	Br/Ye-st, Bk-sc, Or-hd+ac
<i>tales</i>	38, 145	Cr	1.1/0.8	16/9	Wh/Bk-sp, Or-hd+ac
<i>aliphera</i>	11, 165	Cr	0.6/0.6	19/8	Ye/BkOrWh-b+st+sc+hd
<i>Neruda</i>					
<i>godmani</i>	KB	Wh	0.9/0.7	18/8	?
<i>metharme</i>	KB, WB	Wh	1.0/0.7	17/12	?
<i>aoede</i>	25, 145, WB	Wh	0.9/0.7	16/10	Ma/Wh-sc, Bk-hd
<i>Laparus</i>					
<i>doris</i>	11, 145	Ye	1.1/0.8	24/14	Ye/Bk-b+sc+hd
<i>Heliconius</i>					
<i>hierax</i>		?	?	?	?
<i>hecuba</i>	KB	?	?	?	GrYe/Bk-b+sc+hd
<i>xanthocles</i>	93, KB	Ye	1.1/0.9	24/14	Ye/Bk-b+sc+hd



Table 1 (Continued)

Larva		Pupa			Adult (62,64)		
Prothoracic plate	Head scoli/height	Head appendages	Segments with: Reflective spots Large flanges		♂ Genital valve tip & process	♂ Androconial distribution	♀ Signa shape (bursa)
dk,br	2.3	Short	3T;1,2A	3A	Very long curved V spike	Almost all FW, HW veins	Broad U, one arm thicker
dk,br	2.3						
dk,sl	2.3	↓	↓	↓			
dk,br	2.0	"Non-Heliconius"	(LG)		Short V bulb	FW, central HW veins	Narrow L, arms 4:1
?	?	?	?	?			
dk,br	0.1	Short	Absent	3,4A	D and V spikes	FW, central HW veins (-HW cubital)	Broad chb, slight S-curve
	1.2	↓	2A	3-7A			
	0.4		2A	3,4A			
	1.2	↓	Absent	3,5A	V tri	FW veins	Broad J
	1.3	Medium	1,3T;1,2A	3,4A	2 D spikes	FW veins	Large L
dk,sl	0.9	Absent	3T,1A	3A	Rounded	FW+ant HW vn	Broad V
dk,br	2.0	Hooks	Absent	Absent	D short, V tri	HW SC,R	Broad L Straight Broad L
	1.0	↓	↓	↓			
	1.0	↓	↓	↓			
?	?	?	?	?	D mod + hook, V tri		
?	?	?	?	?			
dk,4-pt	2.0	Long Hooks	Absent	Absent	D medium, V tri		
?	?	?	?	?			
dk,4-pt	1.7	Long Hooks	Absent	Absent	V,D blunt		
?	?	?	↓	↓	D mod,V tri		
dk,sl	3.0	Hooks	↓	↓	D+V long	HW SC,R+mb	Narrow V
dk,sl	4.0	↓	↓	↓	D+V long	HW SC,R+mb	Broad V
dk,br	2.5	↓	↓	↓	D mod,V pnt	HW SC+R+mb+Cu	Broad V
?	?	?	?	?	Rounded, V tri	HW vnt+ant mb	Narrow sickle curve
?	?	?	?	?			
dk,br	Absent	Knobs	Absent	Absent		(broad)	
dk,br	0.1	Knobs	Absent	Absent	D knob	HW ant mb	Narrow J
?	?	?	?	?	D mod, curved D sh, V tri	HW ant vnt+mb	Broad J
dk,br	1.0	?	?	?			
	0.3	Short	1A	2-7A	D sh, V round	HW SC,R + mb	Narrow L

**Table 1** Morphological characteristics of heliconian eggs, larvae, pupae and adults<sup>a</sup> (Continued)

Genus, species	Special refer- ences	Egg			Mature (5th Instar Summary of color - patter (ground color/bands, stripes o spots, scoli, head, anal cap)
		Color	Height/ diamet- er (mm)	Vert/ horiz. ridges	
<i>Heliconius</i>					
<i>wallacei</i>	11,145	Cr	1.1/0.9	18/11	Ma/Ye-sc, Br-hd
<i>burneyi</i>	145, WB	Cr	1.1/0.9	18/11	MaBk/Ye-sc, Bk-hd
<i>egeria</i>	KB	Cr	1.2/0.9	16/13	Or/Bk-sc+hd
<i>astraea</i>	25, KB	Cr	1.2/0.9	16/13	Or/Bk-sc+hd
<i>nattereri</i>	24	Ye	1.1/0.8	14/11	Wh/Bk-sp+sc, YeBk-hd
<i>numata</i>	27	Ye	1.4/0.9	16/10	Wh/Bk-sp+sc, Or-hd+ac
<i>ismenius</i>	27	Ye	1.3/0.8	14/12	Wh/Bk-sp+sc, Or-hd+ac
<i>pardalinus</i>	27	Ye	1.4/0.9	16/11	Wh/Bk-sp+sc, Or-hd+ac
<i>hecale</i>	27, 164	Ye	1.9/0.9	16/13	Wh/Bk-sc, Or-hd
<i>ethilla</i>	11, 25, 27	Ye	1.3/0.9	16/13	Wh/Bk-sc, Or-hd
<i>atthis</i>	27, KB	Ye	1.3/0.8	17/13	Wh/Bk-sc, Or-hd
<i>cydno</i>	163, KB	Ye	1.8/1.0	14/10	Wh/Bk-sp+sc, Or-hd
<i>pachinus</i>	JS	Ye	1.6/1.0	16/10	Wh/Bk-sp+sc, Or-hd
<i>heurippa</i>	KB, WB	Ye	1.6/1.0	18/11	Wh/Bk-sp+sc, Or-hd
<i>timareta</i>	KB	Ye	1.7/1.1	18/14	Wh/Bk-sp+sc, Or-hd
<i>luciana</i>	KB	Ye	1.5/1.1	15/14	?
<i>elevatus</i>	KB	Ye	1.4/1.1	15/12	Wh/Bk-sp+sc, Or-hd+ac
<i>besckei</i>	KB	Ye	1.2/0.9	14/10	Wh/Bk-sp+sc, Or-hd
<i>melpomene</i>	11, KB	Ye	1.5/1.0	15/12	Ye or Wh/Bk-sp+sc, Or-hd
<i>charitonia</i>	LG, KB	YeWh	1.2/0.8	14/11	Wh/Bk-sp or b+sc, BkYe or BlWh
<i>hermathena</i>	36	Ye	1.3/0.7	16/13	Re/BkWh-sp+b, Bk-sc, Re-hd
<i>erato</i>	11	Ye	1.5/0.9	16/11	Wh/BkOr-sp, Bk-sc, Ye-hd
<i>clysonymus</i>	145, JS	Ye	1.5/1.0	15/12	Wh/BkOr-sp, Bk-sc, Ye-hd
<i>hortense</i>	LG	Ye			Wh/BkOr-sp, Bk-sc, Ye-hd
<i>telesiphe</i>	KB	Ye	1.6/0.8	15/14	?
<i>hecalesia</i>	34, JS	Ye	1.2/0.8		Ye/Bk-sp+sc+hd
<i>ricini</i>	11, KB	Ye	1.2/0.7	17/15	Ye/Bk-sp+sc+hd
<i>demeter</i>	35	Ye	1.3/0.7	14/10	Ye/Bk-sp or b+sc+hd
<i>leucadia</i>	KB	YeWh	1.0/0.8	14/10	Br/Bk-b+sc+hd
<i>sara</i>	11, 36	Ye	1.1/0.7	13/7	Ye or Br/Bk-b+sc+hd
<i>antiochus</i>	KB	Ye	1.1/0.8	12/10	Ye/Bk-sc+hd
<i>hewitsoni</i>	JS, JM	Ye	1.2/0.8	11/10	YeGr/Ye-sc, Bk-hd
<i>congener</i>	KB	YeWh	1.0/0.7	11/10	Ye/Bk-sc+hd
<i>eleuchia</i>	KB	YeWh	1.0/0.8	11/11	
<i>sapho</i>	LG, KB, JS	YeWh	1.0/0.7	11/10	↓

<sup>a</sup> Abbreviations: ? = no information available; Colors, Ye = yellow, Wh = white, Cr = cream, Re = re Or = orange, Br = brown, Bk = black, Ma = maroon, Gr = green, dk = dark, lt = light; b = bands or ring sp = spots, st = longitudinal stripes; sc = scoli, hd = head, ac = anal cap; Prothoracic plate, br = broa sl = slender, pt = partite; Pupal segments, T = thoracic, A = abdominal; Valve shape, D = dorsal, V ventral, tri = triangular, sh = short, mod = moderate length, pnt = pointed; Androconia, FW = forewin

Table 1 (Continued)

Larva		Pupa			Adult (62,64)		
Prothoracic plate	Head scoli/height	Head appendages	Segments with: Reflective spots	Large flanges	♂ Genital valve tip & process	♂ Andro-conial distribution	♀ Signa shape (bursa)
	1.0 1.0 2.0 2.0	Short	3T;1,2A	3,4A	Long D process Very long D Short D	HW vn+mb HW ant mb HW ant area HW ant area	Narrow L, ratio of arms 5:1
dk,sl lt,sl	1.8 2.0 2.0 2.0 1.8 1.7 1.5	Short	1,3T;1,2A	3,4A	Mod D tip (projecting) Short D tip Shortened Thick D tip	FW 1A, HW SC,R FW vn, HW SC+R+mb HW vn+ant mb HW ant mb	Straight L with vertical arm broader, 2x horizontal arm
dk,sl ?	2.0 ?	?	?	?	Short D tip		
lt,sl lt or dk lt or dk	1.6 1.7 1.5	Short	1,3T;1,2A	3,4A	Longer tip Longer tip Mod D tip Short tip	HW vn+ant mb HW vn+ant mb HW ant mb	
dk,sl	1.2 2.0 1.3 1.2 1.3	Long Medium Long		3,4,6,7A 3,4A, sh 3,4,6A 3,4,6,7A 3,4,6,7A	Rounded Mod D tip Mod D tip Rounded Rounded	HW SC+R HW SC,R,M+mb HW SC,R(M)+mb HW SC,R+mb HW SC,R+mb	Absent
?	1.3 ?	?	?	?	D knob	HW SC,R,A+mb	
dk,sl	1.0	Long	3T;1,2A	3-7A	D mod, V tri	HW SC,R(M)+mb	
dk,br	0.8 2.0 0.5 0.4		1,3T;1,2A	3,4,6A 3,4,6A 3,4A	Rounded Rounded Squared Rounded	HW SC,R+mb HW ant mb HW SC,R+mb HW SC,R+mb	
	1.2 0.3 0.3		Absent		Squared Squared Pointed	HW R+mb-SC	

HW = hindwing, ant = anterior (costal) region, vn = veins, mb = membrane, SC, R, M, Cu, A = subcostal, radial, median, cubital, and anal veins respectively; Signa, U, J, L, V indicate shapes.

General references: 11, 24, 25, 26, 27, 34, 35, 36, 38, 39, 62, 64, 93, 145, 163, 165; unpublished data from L. Gilbert, J. Mallet, J. Smiley, and W. Benson; and personal observations, still unpublished (KB).

Genus/group	Dennis-Ray (red, yellow)	Red on FW, (yellow on HW)	Red on HW, yellow on FW	"Tiger", ithomine	Other mimetic*	Blue and yellow, FW	White or yellow on HW & usually FW	Black with yellow bars
<i>Eurides</i>	<i>eanes</i> (pt) <i>vibilla</i> (pt) <i>tales</i>	<i>eanes</i> (pt)	<i>procula</i> (pt) <i>tales</i> (pt)	<i>isabella</i> <i>lampeto</i>	<i>procula</i> <sup>a</sup> <i>vibilla</i> <sup>b</sup> <i>pavana</i> <sup>b</sup>	<i>eanes</i> (pt)	—	—
<i>Neruda</i>	<i>aoede</i>	—	—	—	<i>godmani</i> <sup>c</sup>	<i>metharme</i>	—	—
<i>Heliconius</i> I	<i>doris</i> (pt) <i>xanthochloes</i> (pt)	— —	<i>doris</i> (pt) <i>xanthochloes</i> (pt)	— —	— <i>hecuba</i> <sup>d</sup>	<i>doris</i> (pt) <i>xanthochloes</i> (pt)	<i>doris</i> (pt) —	<i>doris</i> (pt) <i>hecuba</i> (pt)
<i>Heliconius</i> II	<i>burneyi</i> <i>egeria</i> <i>astraea</i>	— — —	— — —	— — —	— — —	<i>burneyi</i> (pt) <i>wallacei</i>	— — —	— — —
<i>Heliconius</i> III	<i>melpomene</i> (pt) <i>timareta</i> (pt) <i>elevatus</i>	<i>melpomene</i> (pt) <i>bosckei</i>	<i>melpomene</i> (pt) <i>timareta</i> (pt)	<i>nattereri</i> ♀ <i>numata</i> <i>hecate</i> <i>ethilla</i> <i>hecalesia</i> (pt)	<i>athysd</i> <i>cydno</i> (pt) <sup>c</sup> <i>cydno</i> (pt) <sup>d</sup>	<i>hecate</i> (pt) <i>timareta</i> (pt) <i>cydno</i> (pt) <i>luciana</i> (pt) <i>leucadia</i> <i>antiochus</i> (pt) <i>congener</i>	<i>cydno</i> (pt)	<i>nattereri</i> ♂ <i>pachinus</i> <i>luciana</i> (pt)
<i>Heliconius</i> IV	<i>erato</i> (pt) <i>demeter</i>	<i>erato</i> (pt) <i>hermathena</i> <i>telesiphe</i>	<i>erato</i> (pt) <i>glycynymus</i> <i>hortense</i> <i>ricini</i>	<i>hecalesia</i> (pt)	<i>hecalesia</i> <sup>c</sup> <i>charitonia</i> (pt) <sup>d</sup>	<i>erato</i> (pt) <i>sara</i> (pt) <i>antiochus</i> (pt) <i>sapho</i> <i>eleuchia</i>	—	<i>hewitsoni</i> <i>sara</i> (pt) <i>charitonia</i> (pt)
Other Genera		<i>Podotricha</i> <i>telesiphe</i>						<i>Philaethria</i> (3 species)
	<i>eanes</i> -24 <i>aoede</i> -24	<i>eanes</i> -23 <i>melpomene</i> -22	<i>tales</i> -4 <i>procula</i> -11 <i>timareta</i> -17	<i>lampeto</i> -30 <i>nattereri</i> -42	<i>procula</i> -6 <i>pavana</i> -43	<i>wallacei</i> -12 <i>cydno</i> -10	<i>cydno</i> -7 <i>cydno</i> -4	<i>nattereri</i> -42 <i>sara</i> -7 <i>hecuba</i> -7
	<i>astraea</i> -36 <i>elevatus</i> -24	<i>erato</i> -43 <i>telesiphe</i> -17	<i>erato</i> -19 <i>glycynymus</i> -11, 19	<i>ethilla</i> -11	<i>hecalesia</i> -4	<i>congener</i> -17	<i>eleuchia</i> -6	<i>pachinus</i> -2

### Other Genera

*Heliconius numata* and other silvaniforms, controlled by supergenes or gene-complexes (33, 144). Like polymorphism and supergenes, sexual dimorphism was not predicted to appear in Müllerian mimicry; where it exists in three species of *Heliconius*, it is correlated with rarity and habitat dissociation between the sexes (24, 34, 35).

Interspecific hybridization is occasional in *Heliconius* populations both in the field and in the insectary; it has also been recorded in *Eueides*, but is most often seen in members of the silvaniform-*cydno-melpomene* group (Brown, in preparation). It usually produces broods, including both sexes, with reasonable viability and some fecundity (especially in backcrosses) and thus can lead to limited introgression and the possibility of some reticulate evolution in the tribe. Long-term genetic experiments, interspecific hybridization, and the appearance of "throwback mutations" in captive populations (150; L. Gilbert, J. Turner, personal communication) all suggest a high degree of shared major color-pattern genes in the members of the genus *Heliconius*, with appreciable modification and epistasis changing or suppressing the expression of genes that are nonetheless present in homologous positions in the different species. These observations permit the tentative extrapolation of phenotypic expressions to genes in species not yet studied in captivity; in one case (*Heliconius hermathena*), this gave some insight into the rate of adaptive color-pattern evolution under favorable local selection in the field (36).

The effectiveness of Müllerian mimicry in nature was supported by painting over the red forewing band of Costa Rican *H. erato petiverana* (making them look like *H. e. chesteronii*) and noting the appreciably greater attack and mortality rates in the altered, nonmimetic individuals (13). The Müllerian-mimetic convergences evident between various members of widely divergent lines in Heliconiini (Figure 3) demonstrate natural selection for the evolution of mimicry, as opposed to pattern similarity due only to common heritage (154). Resemblances effective in protection against predators develop in part by homologous, but more often by analogous mechanisms in the different radiating lines. The development of the Müllerian-mimetic patterns has been related to aspects of the physical environment, especially light distribution and structure, by Emsley (63) and Papageorgis (110) and to biotic selection, on populations isolated in small ecological refuges, by Turner (153, 156, 157); still other hypotheses, equally attractive, await testing with new and more complete data.

Isozyme divergence and heterozygosity in *Heliconius* demonstrate little correlation with homozygous color-pattern gene sets in geographical races, suggesting both "classical" and "balanced" modes of evolution within a single genome (159). A sex-linked enzyme is not dosage compensated in

females (the heterogametic sex) of *H. melpomene*, suggesting a possible basis for other sex-limited phenomena such as female mimicry (81).

Preliminary karyological examination of Heliconiini is nearly complete (52, 124, 162; K. Brown, T. Emmel, P. Eliazar, and E. Suomalainen, in preparation), but methods are still lacking for visualization of fine structures of chromosomes. Achiasmatic oögenesis in females has been reported in *H. melpomene* and other species (125, 160; J. Mallet and L. Gilbert, personal communication), but may not be universal in the tribe. The main patterns of chromosome numbers are shown in Figure 1. The outcome of genetic crosses suggests that chromosome arrangements may differ between different subspecies of *H. erato* (A. M. Araujo, K. Brown, and W. Benson, in preparation) and *H. melpomene* (J. Mallet and L. Gilbert, personal communication), with concomitant reduction in viability and fecundity in intraspecific crosses.

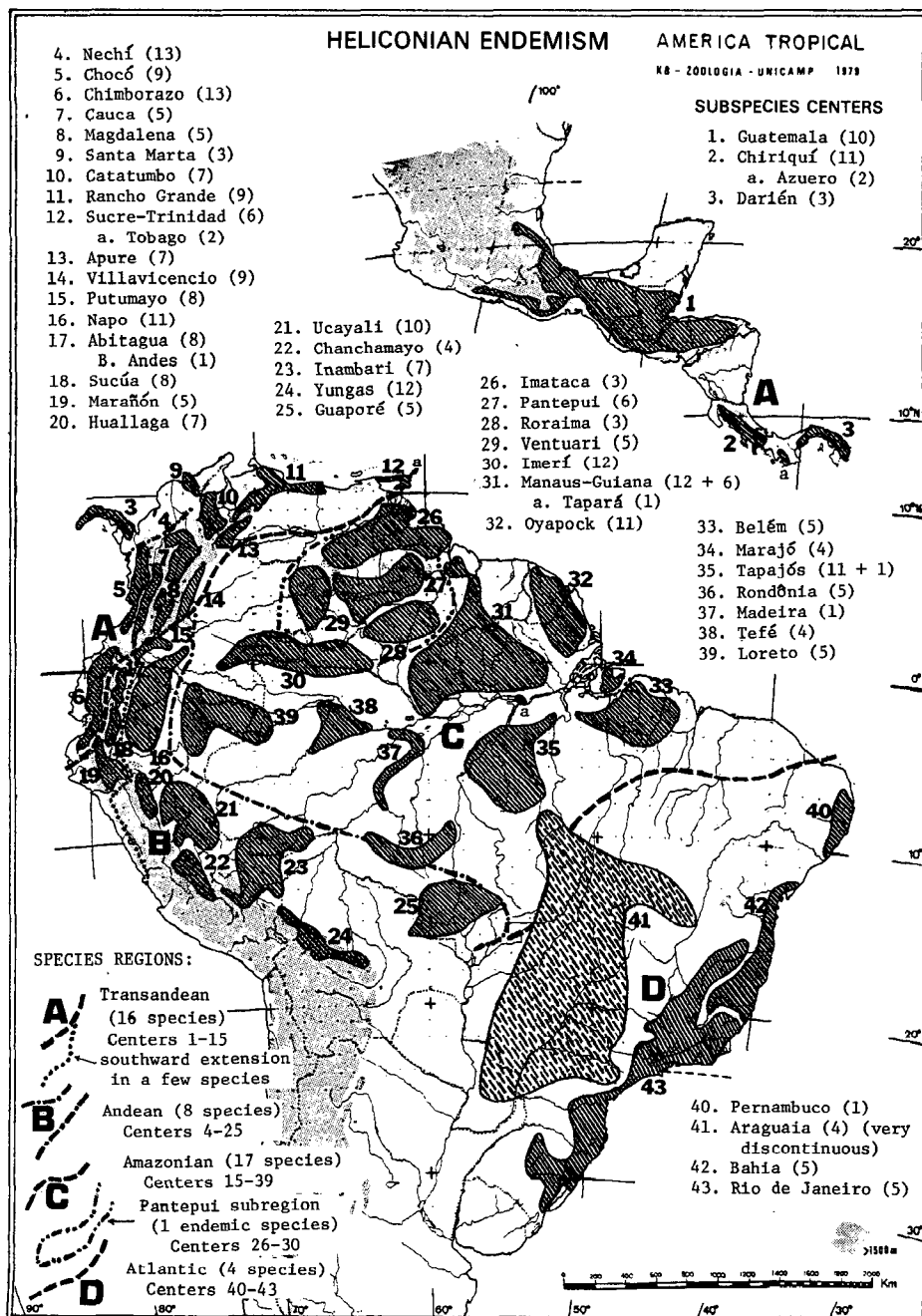
### *Biogeography* (Figure 4, Table 2)

Following early work by Michael (95), Emsley (63), Turner (140, 146), and Sheppard (40), Heliconiini have been used in a broad investigation of geographic patterns of evolution in the Neotropics. The Heliconiini are especially useful for this analysis, since they include widespread polytypic species with marked regional differentiation in color-pattern, which is governed by a few genes and easily related to stabilizing selection in mimetic environments (40). The clear patterns of regional endemism (26, 28, 29, 31, 32, 89, 153) (Figure 4), based on a sampling network of 3500 stations all over the Neotropics, correlated well with areas of high probability for forest continuity during the last glacial maximum, 13,000–20,000 years ago (suggested by independent paleoclimatological, geomorphological, pedological, and phytosociological criteria), but did not correlate with localities of high species diversity (an ecological rather than evolutionary phenomenon) (30–32). Detailed population observations, however, suggest that many of these endemic patterns could be produced by parapatric differentiation in response to modern environmental gradients (15, 66, 161). There seems little doubt that both modern and historical factors are involved in regional

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**Figure 4** Biogeographical division of forest heliconians into four principal species regions (A–D) and 43 important subspecies centers in the Neotropics. The subspecies “centers of endemism” 1–43 are bounded by isoline contours representing one third of the maximum value for corrected endemism. This value was determined for 1520 quadrants of 30' X 30' latitude and longitude by a summation of local endemic subspecies minus double the number of hybridized populations (with invading subspecies from other endemic centers) (31, 32). Numbers in parentheses after the center names are the local endemic subspecies recognized as associated with that center, among the 46 species of forest heliconians analyzed. Note that 46 of the 65 species in the tribe are endemic to one of the four species regions A–D.





endemism patterns; the attempt to identify the causative factors has led to much important parallel research on paleoecology and population ecology, which in some specific cases has uncovered significant new evolutionary phenomena (14, 15, 30–32).

Dispersal undoubtedly plays an important role in many aspects of heliconian biogeography (12, 34, 39, 45, 67). Species with migratory tendencies or very wide-ranging flight, at least under some environmental conditions, include those labelled “Mg” in Table 2; species which are often sedentary include *Neruda aoede* and *Heliconius ethilla*, *H. cydno*, *H. erato*, and *H. hermathena* (13, 36, 45, 57, 116, 147).

### *Population Biology* (Table 2)

Field studies of *Heliconius* often reveal a pattern of small, rather self-contained local populations, composed of long-lived, continually reproducing individuals who learn resource locations by following during the daytime individuals with whom they roost at night (12, 13, 24, 36, 45, 48–50, 57, 75, 116, 147, 152, 166, 167; K. Saalfeld and A. M. Araujo, submitted). Kin selection is thought to operate strongly in such populations (12, 33, 149). Members of some other heliconiine genera are shorter-lived, more dispersive, and exist in larger and more ill-defined populations. The two species of *Podotricha* have dramatically skewed sex ratios (e.g. male:female 10 – 50:1) both in collections (62, 161) and in the field (personal observation), and they may show peculiar biological characteristics. Some sex and age classes, especially younger females, may be highly vagile at some times of the year, possibly representing density-dependent dispersal (31, 39); individuals in these classes are often found sleeping away from the communal roosts (K. Brown and J. Vasconcellos-Neto, unpublished data).

Populations of *Heliconius* seem to be regulated largely by egg and early instar larvae mortality [which may come from many sources, including foodplant deterioration or exhaustion, predators, parasitoids, and storms (70, 116)] as well as availability of adult resources, including nectar, pollen, space, and mate location and suitability (17, 75). While population numbers may be exceedingly constant in some rain forest areas (57), fluctuations are commonly observed in more seasonal climate (24, 33, 39), the peak of abundance usually occurring from near the end of the wetter season into the dry season.

**REPRODUCTIVE BIOLOGY AND PHYSIOLOGY** The long reproductive period of adult *Heliconius* is a function of continuous nutrient intake, mainly from pollen, involving a number of physiological, morphological, and ethological adaptations (17, 18, 54, 55, 69–71). *Laparus* and *Heliconius* collect pollen from certain flowers and incubate it with fluid on their

tongues, releasing nitrogenous nutrients which (like labelled amino-acids ministered in parallel experiments) should be rapidly incorporated into eggs and spermatophores (69, 70). Females also obtain nutrients from digestion of male spermatophores to help in egg production (17, 18, 71). The length of the reproductive period varies within the genus *Heliconius* and is apparently much shorter in *Dryas iulia* (17, 54, 55); thus, there exist many different reproductive syndromes within the tribe.

Courtship and mating are complex and variable within the Heliconiini; little has been published recently on comparative ethological characteristics, and almost nothing has been written of chemical or visual signals in natural courtship sequences since Crane's early work (48–50). Certainly the large and complicated *Heliconius* head, including greatly enlarged compound eyes and optic and other sensory ganglia, is important in courtship, food-location and gathering, and the evaluation of host-plant quality (70).

### *Community Ecology*

A series of papers by Gilbert and co-workers relates the community ecology of heliconians to a variety of important concepts, from guild structure and habitat displacement through the organization and succession of tropical forest systems to practical aspects of conservation biology (70, 72–76). The tightly coevolved food webs such as that of the Heliconiini/*Passiflora/Anguria-Gurania* system may represent key units for research on structure, function, and diversity in tropical systems. They also provide a base for conservation planning (the Brazilian government has already included results of heliconian biogeography in the choice of favorable areas for parks and reserves; 28–32, 72, 74); and since the heliconian/Passifloraceae system is an easily monitored and reliable indicator of many ecological processes in tropical communities (30), it may be used in the evaluation of preserved systems and the management of diversity (74). The tight mutualistic relationship between *Heliconius* and its pollen sources *Anguria* and *Gurania* (Cucurbitaceae) may be illustrative of the great importance of such systems in the structure and stability of tropical ecosystems (70, 74); modern ecological theory has largely ignored such interactions, and important models have not taken them into account.

**FOODPLANT UTILIZATION** (Table 3) Many of the dimensions of a larval heliconian's world are determined by the female's choice of oviposition site (16). Recently, this choice has been shown to have a broad ecological component (116, 117), often independent of plant chemistry and larval acceptability. Thus, studies of juvenile biology should include analysis of adult ecology and physiology, as well as plant quality, and should include examination of potential versus realized niche.

**Table 2** Biological characteristics of heliconian larvae, pupae and adults<sup>a</sup>

Genus, species	LARVA (2, 3)			PUPA		ADULT				Social behavior	Normal habitat	Geographical distribution	Normal habitat	Sexual dimorphism	Deme size	Flight habits	Dispersal character	Male puddles?	Preferred flower colors	Mating habits	Nocturnal roosting behavior
	Social-bility	Mimicry	Channels in leaves?	Rests in J-shape?	Usual site	Usual site	Geographical distribution	Normal habitat	Sexual dimorphism												
<i>Philaethria pygmaea</i>	0	+	+	+	+	+	+	+	+	+	Amazon Basin	Field, scrub	-	Md	LR	Ds	+	+	Wh	Ht	SoL
<i>wernickei</i>	0	+	+	+	+	+	+	+	+	+	Southern Brazil	Open forest	-	Md	MR	Mg	+	+	Wh	Ht	SoL
<i>dido</i> complex	0	+	+	+	+	+	+	+	+	+	Widespread	Dense forest	-	La	HR	Ds	++	+	Wh	?	SoL
<i>Podotricha telestoche</i>	0	+	?	?	?	?	?	?	+	+	Southern Andes	Cloud forest	-	La	LR	?	+	Wh	Re	?	?
<i>euchroia</i>	?	?	?	?	?	?	?	?	+	+	Northern Andes	Cloud forest	-	La	MR	Ds	++	?	?	?	?
<i>Dione</i>	+++	-	-	-	-	-	-	-	+	+	Widespread	Open forest	-	La	MR	Ds	+	+	Re	Ht	OG/L/GF
<i>juno</i>	+	-	+	+	+	+	+	+	0	-	Wide(not Amazon)	Scrub, field	-	La	LR	Mg	+	+	Re	?	OG/L/GF
<i>moneta</i>	0	-	+	+	+	+	+	+	0	-	High Andes	Cloud forest	-	La	MR	Ds	+	+	Wh	?	OG/L/GF
<i>glycera</i>	0	-	+	+	+	+	+	+	0	-	High Andes	Cloud forest	-	La	MR	Ds	+	+	Wh	?	OG/L/GF
<i>Agraulis vanillae</i>	0	-	-	+	+	+	+	+	0	-	Widespread	Scrub, field	-	La	LR	Mg	+	+	ReWh	Ml	OG/L/GF
<i>Dryadula phaeus</i>	0	-	+	+	+	+	+	+	+	-	Widespread	Field, marsh	-	La	LE	Mg	±	+	Wh	Tn	OG, SG/UC
<i>dryas</i>	0	-	+	+	+	+	+	+	+	-	Widespread	Forest clearings	-	La	MR	Mg	++	+	ReBl	Ml	OG/L/GF
<i>tulia</i>	0	-	+	+	+	+	+	+	+	+	Widespread	Open forest	++	La	MS	Ds	-	+	Wh	Tn	OG/N/F
<i>Eueides vibidia</i>	+++	+	-	-	-	-	-	-	0	+	South Brazil	Montane forest	+	La	HS	Ds	-	+	Wh	Tn	?
<i>pavania</i>	0	-	+	+	+	+	+	+	?	+	Central America	Forest	-	La	MR	Ds	-	+	Wh	?	?
<i>emslayi</i>	?	?	?	?	?	?	?	?	?	-	Colombia, W Ecuador	Open forest	?	?	HS	Ds	-	?	?	?	?
<i>libitina</i>	?	?	?	?	?	?	?	?	?	-	Guyane, NW Amazon	?	-	?	?	?	?	?	?	?	?
<i>procula</i>	0	+	-	-	-	-	-	-	0	+	Centr. Amer., N Andes	Forest streams	0	+	HR	Pp	-	+	Wh	?	?
<i>lampeto</i>	0	-	-	-	-	-	-	-	0	++	Amazon, Andes	Forest streams	0	+	MR	Ds	-	+	Wh	?	?
<i>isabella</i>	0	-	-	-	-	-	-	-	0	+++	Widespread	Secondary forest	0	±	MR	Ds	-	+	Wh	Ht, Ml	SoL/UF
<i>eones</i>	?	?	?	?	?	?	?	?	+	+++	Upper Amazon	Forest clearings	+	+	MR	Ds	?	?	?	?	?
<i>lybia</i>	0	+	-	-	-	-	-	-	+	+	Centr. Amer.-Amazon	Tall forest, gaps	+	-	MS	Ds	-	+	Wh	Ml	OG/H/UF
<i>tales</i>	0	++	-	-	-	-	-	-	+	+	Amazon, Colombia	Tall forest	+	±	MS	Ds	-	+	Wh	Ml	OG/H/UF
<i>atiphera</i>	0	+	-	-	-	-	-	-	+	-	Widespread	Forest clearings	+	-	MR	Ds	+	+	Wh	Ml	OG/H/UF
<i>Neruda</i>	+++	?	?	?	?	?	?	?	+	-	West Colombia	Deep forest	+	-	MR	Pp	-	+	Re	?	OG/H?
<i>godmani</i>	+++	?	?	?	?	?	?	?	+	-	Amazon Basin	Deep forest	+	±	MS	Mg	-	+	Re	?	?
<i>metharme</i>	+++	+	?	?	?	?	?	?	+	±	Amazon Basin	Deep forest	+	-	MS	Pp	-	+	Re	?	OG/H?
<i>coele</i>	+++	+	?	?	?	?	?	?	+	±	Amazon Basin	Deep forest	+	-	MS	Pp	-	+	Re	?	OG/H?
<i>Leparnus</i>	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...

[illegible]

<sup>a</sup> *Abbreviations:* ? = no information, +/0 = positive, neutral, negative or not present; *Pupa*, U = under; *Deme size*, Sm = small, Md = medium, La = large; *Flight habits*, L = lowerstory, M = middlestory, H = upperstory or canopy, S = slow, E = erratic, R = rapid; *Dispersal*, Pp = philopatric (with home range), Ds = dispersive, Mg = migratory; *Flower colors*, Wh = white or yellow, Re = red, maroon, orange, Bl = blue or violet; *Mating*, Ht = hilltops, MI = females mate multiply, In = intensive female mated, usually not again; *Roosting*, Sol = solitary, OG = loose group, SG = small group, LG = large group (>20), L = lower than 2 m above ground, T = 2–10 m above ground, U = under, G = grass blades, F = leaves, T = twigs or tendrils.

Data taken from 2, 3, 11, 14, 16, 24, 25, 31, 33–36, 38, 39, 41, 43, 48, 50, 57, 63, 67, 70, 93, 116, 143, 144, 145, 152, 163, 164, 165; personal communications from L. Gilberti, J. Mallet, J. Smiley, and W. Benson; personal observations. For special references and other data, see Table 1.

**Table 3** Foodplants of larval *Heliconiini* (expanded from 16)<sup>a</sup>

[illegible]



<sup>a</sup> *Abbreviations:* X = primary natural foodplant, o = secondary natural foodplant, + = accepts in laboratory or insectary experiments, - = unacceptable in laboratory or insectary experiments; U = under older leaves, Y = under younger leaves, L = diverse, mostly on leaves, O = off of plant, B = base of stem, M = meristems (growing shoots), T = tendrils, S = social oviposition (several females on same plant part at same time); ? = unknown.

The massive data on foodplant utilization presented by Benson, Brown & Gilbert (16) is of little use for studies in ecological space and time; the interactions reported in Table 3 must be resolved into local foodplant-usage data sets through new field and laboratory studies. Only in La Selva, Costa Rica (116), and along the Sumaré road in Rio de Janeiro (14, 16) can long-term patterns of resource partitioning in natural heliconian communities be regarded as very well known; comparisons between these data sets and less complete ones, or ones collected over a larger area, should be drawn with due caution. The patterns interpreted in relation to macroclimate by Benson (14) include two data sets from heavy forest where interactions are very difficult to observe; one of these is from an island with a depauperate insect community. Since these patterns are not the same as those seen in two additional equatorial sites in Brazil (personal observation), it is possible that resource utilization patterns are also determined by factors such as disturbance, heterogeneity, and site accessibility. Like other results of presumed competition, between-plant resource patterning in heliconians needs to be investigated by experimental manipulation in the field; present views are still mostly based on negative data.

The physiological and environmental parameters important to the interaction between *Agraulis* and *Passiflora* have been studied in an important work by Copp & Davenport (46, 47) which helps to focus the more anecdotal information widely scattered in other papers (16, 70). Many aspects of the morphology and biology of *Passiflora* can best be understood in terms of interactions with Heliconiini (16, 70; K. Williams and L. Gilbert, submitted); this strengthens the case for powerful coevolutionary pressures between these two groups of organisms (16, 58, 68). Such specific interactions are very useful in broad studies of community ecology (70, 72–76).

Occasional reports exist for the feeding of heliconian larvae on a number of plant families other than Passifloraceae; the only confirmed one is that on the closely related Turneraceae in Costa Rica (D. Janzen, personal communication).

### Biochemistry

Many investigators assume that Heliconiini are distasteful due to sequestration of poisonous chemicals derived from their foodplants (16, 19–21, 70), but no evidence for this has yet been published. Preliminary analysis of *Heliconius* adults has shown presence of cyanogenic glycosides (R. H. Davis and A. Nahrstedt, in preparation), but the presence of these compounds in the larval foodplants of the specimens examined was not determined. Even the strong “witch-hazel” (isocyanide?) scent of mated females has still eluded chemical identification, although female odor has been shown to be

important as a "chemical chastity belt" (71) and may function in intraspecific alarm and interspecific defense roles as well. Also unidentified are the male androconial pheromones and the female pupal odors that attract males. Wing pigments in the Heliconiini are in part polymeric, but some reds have been shown to include pterins (8), and the light yellows in *Neruda*, *Laparus*, and *Heliconius* are the amino-acid 3-hydroxy-L-kynurenine (23, 37). The silver reflective spots of pupae (Figure 2*R*, *T-W*) are physical in nature; spots with a gold color are underlaid by yellow tanning pigments (108).

### *Sensory and Behavioral Physiology*

Many authors have commented on the ability of heliconians to respond to novelty and to learn complex sequences of resource discovery and utilization, both in the field (57, 70) and in captivity (48, 49, 70); Skinnerian experiments of sequencing and color-form discrimination have been reported (48, 49, 127). Extensive investigation of heliconian vision has dominated physiological studies, but some information is also available on hearing (132) and temperature tolerance (42). The details of heliconian visual physiology, implicated in complex behavior patterns, are in accord with daily rhythms of activity (128, 129), the use of red colors in courtship and flower seeking (39, 48, 49, 126, 127), and image processing along multiple channels (77, 90, 114, 122, 123, 128–131, 133–138). Some controversy has developed around the fundamental neurological processes involved in *Heliconius* color vision and learning, but little doubt remains about the existence of unusual physiological processes in these butterflies.

## SYNTHESIS

With an increasingly firm base of systematics, biogeography, and descriptive biology, research on Heliconiini has moved on to complex investigation of physiology, behavior, ecology, and evolution. Primary areas of intense ongoing research in the last decade include natural selection, sociobiology, evolution at and above the population level, interactions with other organisms and implications for tropical communities, development of ecological preferences and behavior patterns, neurophysiology, reproductive biology and physiology, and genetics and mimicry. Heliconians now rival *Euphydryas* butterflies (59, 75) in the amount of new information and concepts they have contributed to population biology. Long-term research on the Heliconiini, aided by accurate identification of organisms, an eye for the unexpected, and complementary laboratory studies, has generated important insights into tropical biological processes:

1. Much variation in fundamental morphology is possible in these organisms; within single widespread species, the variation is often determined by only a few genes and sometimes is capable of interpretation in relation to local selective factors.
2. Historical and modern ecological factors interact with intrinsic features of heliconian populations to determine a wide variety of local characters, community structures, and regional subspecies distributions in the complex and heterogeneous Neotropical forest environment.
3. These long-lived invertebrates with variable and ephemeral resources have developed very complex behavioral physiology, including response to novelty and correlative learning, within a tight social structure.
4. Specific plant-herbivore interactions like those of *Heliconius/Passiflora* may form biological subsystems very useful in the study of community structure and function in the tropics.
5. Müllerian mimicry is a verifiable ecological phenomenon with unexpected genetic and evolutionary facets and may be important to larvae as well as adults of host-specific insects feeding on plants presumed to be poisonous.
6. Classical and balanced modes of evolution, occurring within a single genome, can at the same time maintain variety at weakly selected loci and rapidly fix homozygosis at strongly selected loci.

As heliconian butterflies gain wider acceptance as laboratory animals and continue to attract investigators interested in field biology, their already substantial contribution to scientific theory and knowledge should increase. Their complex nervous system, rapid development, accessibility in the field, and high degree of ecological specificity make them well adapted for future research.

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