BULLETIN OF THE ALLYN MUSEUM

Published by
THE ALLYN MUSEUM OF ENTOMOLOGY
Sarasota, Florida

Number 26 28 February 1975

THE HELICONIANS OF BRAZIL (LEPIDOPTERA: NYMPHALIDAE)

PART VI. ASPECTS OF THE BIOLOGY AND ECOLOGY OF *HELICONIUS DEMETER,* WITH DESCRIPTION OF FOUR NEW SUBSPECIES

Keith S. Brown, Jr.

Departamento de Zoologia, Instituto de Biologia, Universidade Estadual de Campinas, C. P. 1170, Campinas, São Paulo, Brazil 13.100; and Centro de Pesquisas de Produtos Naturais, Instituto de Ciências Biomédicas, C. C. M., Universidade Federal do Rio de Janeiro, Ilha do Fundão, Rio de Janeiro ZC-32, Brazil

and

Woodruff W. Benson

Centro de Pesquisas de Produtos Naturais, Instituto de Ciências Biomédicas, C. C. M., Universidade Federal do Rio de Janeiro, Ilha do Fundão, Rio de Janeiro ZC-32, Brazil

INTRODUCTION

The rare mimetic species *Heliconius demeter* Staudinger was the subject of a recent taxonomic revision (Turner, 1966), in which a new subspecies was described *(H. d. beebei* from Guyana) and the complicated synonymy of the other three subspecies *(demeter, bouqueti* Nöldner, and *eratosignis* Joicey & Talbot) was summarized. In the most recent complete revision of the genus (Emsley, 1965), the species was placed near *Hel. ricini* (L.) in the *sara*-group. The unusually small wingspans of *demeter* and *ricini* had led many earlier authors to place them both in the genus *Eueides,* but they are in fact very distant from members of this part of the tribe.

All of the known subspecies of *demeter* except *eratosignis* were illustrated in a recent compilation of photographs of little-known *Heliconius* (Turner, 1973); *eratosignis* was pictured as part of a mimetic group from Rondônia in southwestern Brazil (Brown, 1973); the types of this form (in the British Museum (Natural History)) are shown in Figure **1.** The present paper discusses some additional systematic facets, and unusual aspects of the juvenile biology and adult ecology of *demeter.*

SYSTEMATICS

H. demeter, still a little-known species which is very localized in the field, is nonetheless probably present but hiding among its co-mimics in many collec-

tions. A wide variety of minor and somewhat variable characters (small size, yellow rather than red basocostal line on the ventral forewing, elongated hindwing basal red dots, white hindwing submarginal spots (the last two better expressed ventrally), greenish diffusion around the yellow forewing band in males, strongly undulate hindwing border especially in females) has been used to recognize *demeter*. All of these, however, fail in some populations or individuals. A rapid and reliable separation of *demeter,* especially the very easily misidentified females, from all sympatric and similar heliconians, especially the near-identical *erato* forms, is as follows:

(1) if hindwing nonrayed (northern middle Amazon and western Guyana, possibly southern Suriname): forewing ventral costal line yellow, head markings all white, underside ground color not gray-suffused, no or very faint submarginal spots on ventral hindwing, and a *small yellow basal spot on the dorsal forewing below the anal vein.*

(2) If hindwing rayed: in eastern Guianas, middle Amazon south of the river, upper Rio Negro, and Peru, *forewing ventral costal line yellow* (red elsewhere) and a *red basal patch on the hindwing;* (males only); in all populations, underside color black, head markings all white, and *red-orange ray between hindwing cubital and anal veins simple,* not divided basally (as in *erato* or *Eueides eanes* subspecies) to enclose a black oval (in males, best seen on the ventral surface). *H. aoede* and *H. xanthocles* also have this ray unforked, but have shortened abdomens, bearing much more prominent yellow annular rings and segmental spots.

At least four previously unrecognized subspecies of *demeter* exist (see **Map**). Four specimens from the south shore of Rio Negro across from Manaus, and a female from an unspecified locality (labelled "Peru"), represent a pattern transitional between those of *bouqueti* and *demeter,* with a semi-compacted square forewing band centered over the end of the discal cell. These are apparently a new mimetic subspecies from the south-central Amazon area, described below.

The farthest east population of unrayed *demeter,* from Terra Santa, near the western frontier of Pará, shows a dramatic reduction in the yellow forewing band elements, which in extreme individuals are limited to a few widely separated spots. This population, apparently separated geographically from *d. beebei* (which is known from farther west in Manaus, and farther north in Guyana), is here named as a new, probably isolated subspecies.

The population of *d. eratosignis* in southeastern Rondônia includes many individuals with a full square yellow forewing band ("Bolivian type") along with typical specimens possessing a more dispersed group of reduced yellow spots (see Brown, 1973, Figure 20M). The former pattern predominates further southwest in northern Bolivia, constituting a local mimetic population. Two males from Caranavi at 800 m. on the Rio Coroico and 50 Km. northeast of La Paz, are available as types of this form; besides the Riozinho transitions to *eratosignis,* a pair transitional between the Bolivian subspecies and *d. demeter* is known from Acre.

A similar form, bearing however a yellow forewing costal line and showing many additional differences from the Bolivian type, has been discovered (one pair only known) in the upper Rio Uaupés in extreme northwestern Brazil. It should also occur in other parts of the upper Rio Negro area, as far as eastern Colombia.

Heliconius demeter turneri K. Brown and Benson, NEW SUBSPECIES

(Figures 2, 3; Map)

Adult male: forewing 33-36 mm. Similar to *H.d. bouqueti* (Figure 3; Map), but forewing yellow band square, compacted, centered over end of discal cell, where a much reduced black "V" divides the yellow area; yellow spot in cell reduced to an hourglass-shaped mark. Forewing yellow area only slightly indistinct,

greenish, at edges. Dennis red-orange; ventral costal line yellow. Hindwing rayed (rays longer in the anal region), with a moderately developed red-orange basal patch (smaller than that in *bouqueti,* more like that in *demeter*), and paired white intervenal submarginal spots ventrally, in the median and cubital regions. Head markings white, body markings yellow, similar to those in the nominate subspecies.

Adult female with clear hindwing rays (no basal patch) hindwing border undulate, paired white intervenal submarginal spots on the ventral hindwing, not continued apically of vein M_1. Forewing yellow band very squared, centered over end of discal cell, but quite broken into clear spots by black over the veins: consisting of a yellow area between the subcostal and radial veins divided into three by diagonal veins R_1 and R_2, an hourglass-shaped mark in the end of the discal cell, a semi-

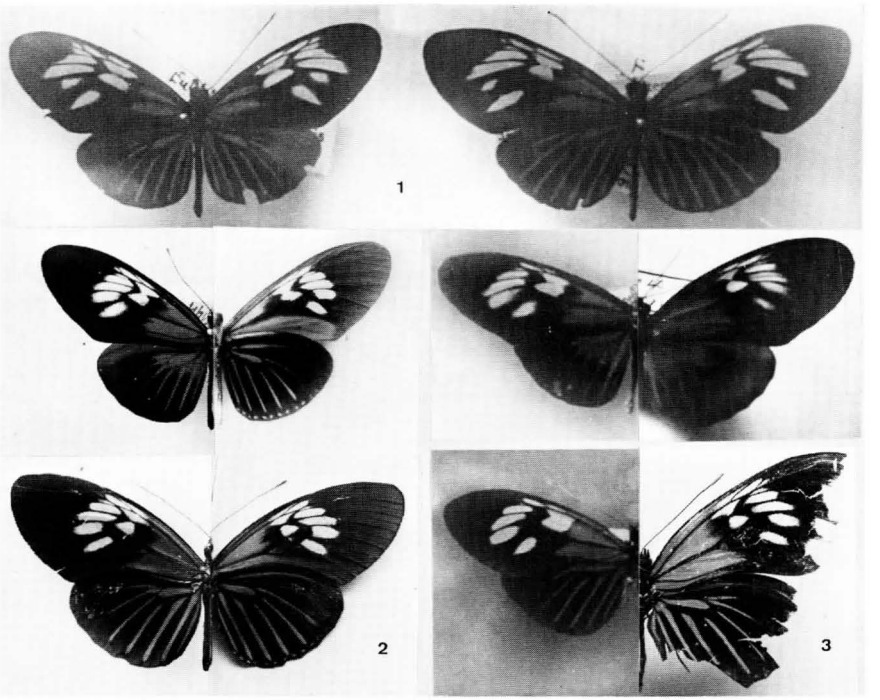


Figure 1: male and female syntypes of *Heliconius demeter eratosignis,* "Cuyabá-Corumbá River System" (= southeastern Rondônia for these specimens, see Brown and Mielke, 1972); British Museum (Natural History). Figure 2: *Heliconius demeter turneri* nov., holotype male (upper figures) and allotype female (lower figures), dorsal (left) and ventral (right) wing surfaces; British Museum (Natural History) and Allyn Museum of Entomology. Figure 3: comparison of *H.d. turneri* (right wings, upper paratype male in the Museu Nacional, Rio de Janeiro, "Rio Trombetas" (error = across from Manaus), lower paratype female captured by K. Brown across Rio Negro from Manaus) and *H. d. bouqueti* (left wings, upper male, lower female, Saut Sabbat, Guyane Française, W.W. Benson collection). All butterflies are black, yellow, and red-orange, and are reduced to about three-quarters life size.

continuous extra-cellular band divided by veins M_1, M_2 and M_3 with distinctly undulate but subparallel borders, and an isolated spot in the inner part of Cu_1-Cu_2 with length similar to that of the elements of the postdiscal band (~4 mm.). Other markings as in the male; forewing 36-38 mm.

HOLOTYPE ♂ in the British Museum (Natural History), "Ypiranga, Rio Madeira" (=Uypiranga, across and up the Rio Negro from Manaus, Amazonas, Brazil), captured by H. Boy, from the Miles Moss collection. Mentioned by Turner (1966) as a *d. bouqueti,* from which this subspecies is separated by a thousand kilometers of intervening nonrayed populations (see **Map**), as well as the shape of the forewing yellow area.

ALLOTYPE ♀ in the Allyn Museum of Entomology, Sarasota, Florida, same locality (as "Uypiranga"), from LeMoult unsorted material.

Paratypes: One male in the Museu Nacional, Rio de Janeiro, No. 4/154, from "Trombetas" (erroneous, = south of Manaus; the Rio Trombetas area is probably occupied by the following-described subspecies; other material in the M.N. with this label is characteristic of the hybridization area across the Rio Negro from Manaus, see below); one female in the American Museum of Natural History, New York, labelled only "Peru", probably an error; one female in the collection of K. S. Brown, Jr., Campinas, São Paulo, captured in a clearing in dense woods, west of Km. 4 of the Manaus-Manacapurú road, south bank of the Rio Negro, 6-XI-71. The first and last of these paratypes are figured in comparison with *H. d. bouqueti* from Guyane Française (Figure **3**).

The subspecies is dedicated to Dr. John R. G. Turner of the State University of New York, Stony Brook, who greatly advanced our knowledge of this rare heliconian species. It is expected to occur in other parts of the middle Amazon south of the Rios Negro and Amazonas, along with similar-appearing subspecies of other *Heliconius,* and may bear a somewhat more opened forewing band in populations farther eastward, resembling more *bouqueti.* In the population observed across the Rio Negro from Manaus, sympatric mimetic species were polymorphic populations of *Eueides tales* and *Heliconius aoede, burneyi, egeria, erato,* and *melpomene,* mostly rayed and many with a compact square yellow forewing band as in *turneri;* the mimetic complex is illustrated in Figure **4**. Other sympatric heliconians were *Agraulis vanillae vanillae* (with appreciable infusion of genes from *v. lucina*[1]), *Philaethria dido, Dryadula phaetusa, Dryas iulia titio,*[2] *Eueides lybia lybia,* and *Heliconius wallacei* (polymorphic), *numata (silvana, superioris, nubifer, maeon,* etc.), *hecale fortunatus, pardalinus* cf. *lucescens, sara thamar,* and *a. antiochus; hermathena* is also known from the immediate area, in dryer habitats. The *demeter* foodplant across from Manaus is probably *Dilkea* sp. (a primitive member of the Passifloraceae), very common in the area, but several *Passiflora (Astrophea)* would also be available.

Heliconius demeter terrasanta, K. Brown and Benson, NEW SUBSPECIES

(Figures 5, 6; Map)

Adult male: forewing 39-41 mm. (by far the largest of the *demeter* subspecies).

[1] In an earlier paper (Brown and Mielke, 1972, part II of this series), *lucina* was separated from *Agraulis vanillae* as a good species, based on morphological, distributional, biological and behavioral characters. Recent information has indicated that, although these characters are real, the two forms are perfectly interfertile, forming intergrading populations where they meet. A long series from Vista Hermosa, La Macarena, Meta, Colombia shows full and independent intergradation of all characters which differentiate *vanillae* from *lucina.* Further intergrading populations can be found in the middle to upper-middle Amazon (Manicoré, Tefé), the southwest Amazon (Acre), and central Peru (Chanchamayo); the last two of these represent meeting grounds of *lucina* and *v. maculosa.* Thus, we are now inclined to regard the distinctive form *lucina* Felder as merely a well-differentiated but still interfertile subspecies of *vanillae,* occupying the central upper Amazon, an area corresponding to the Napo refuge of many recent authors.

[2] As F. M. Brown has recently shown that *i.iulia* was described from an Antillean (Grenada) population of the species (Brown and Heineman, 1972), the mainland subspecies, formerly regarded as nominate, must now bear Stichel's name *titio* (type-locality Bolivia).

Very similar to *H.d. beebei* (Figure **6**), but forewing yellow band reduced to a widely disjunct series of spots, one in each of the following spaces: end of discal cell (usually divided longitudinally into two), Sc-R_1, R_1-R_2, R_5-M_1, M_1-M_2, M_2-M_3, M_3-Cu_1, and Cu_1-Cu_2, forming a very open inverted "U". Dennis red, forewing ventral costal line yellow, basodorsal yellow spot below the anal vein. Hindwing black, often with 2-4 short basal red streaks dorsally, and no or at most very faint paired white submarginal spots ventrally, along with four red basal spots, rather elongated, and a yellow costal stripe.

Adult female similar, but usually with forewing spots slightly smaller, hindwing border more undulate, and forewing more rounded (length 35-40 mm.).

Head and body markings as in nominate subspecies.

HOLOTYPE ♂ and ALLOTYPE ♀ donated to the Museu Nacional, Rio de

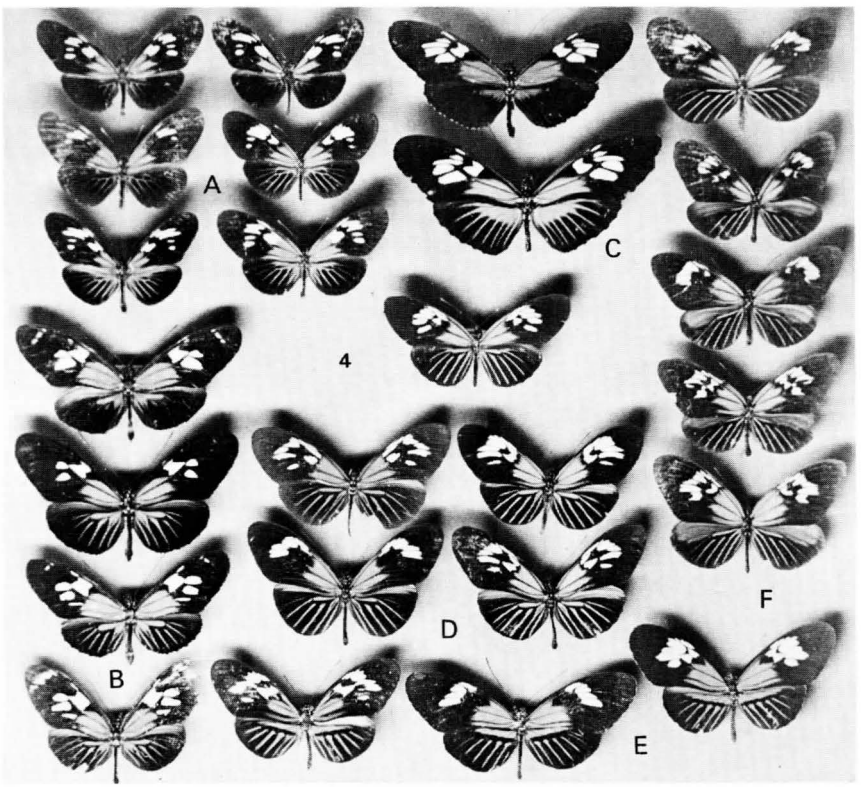


Figure 4: mimetic complex of Heliconiini flying together with *H. demeter turneri* across from Manaus, Amazonas: A, six forms of *Eueides tales* (*tales* x *pythagoras* x *calathus*, see Brown and Holzinger, 1973); B, four forms of *Heliconius burneyi* (*burneyi* x *catherinae* x *ada*); C, two forms of *H. egeria* (*egeria* x *hyas*); D, four forms of *H. erato* (*amazona* x *lativitta* x *reductimacula*); E, three forms of *H. melpomene* (*madeira* x *aglaope* x *vicinus*); F, five forms of *H. aoede* (*faleria* x *lucretius* x *bartletti*). The zone represents a mixture of the genes of subspecies from four areas: the northern and southern lower Amazon, and the northern and central upper Amazon. All butterflies black, yellow, and red-orange, reduced to about two-fifths life size.

Janeiro; small woods 3 Km. north of Terra Santa, Pará, Brazil, 3-II-73, and 12 Km. NW of Terra Santa, 2-II-73, respectively; W.W. Benson, *leg.*

PARATYPES (Figure **6**): One ♂ each, same data as holotype, donated to the British Museum (Natural History), the Allyn Museum of Entomology, the American Museum of Natural History, and the Museu de Zoologia da Universidade de São Paulo. Six ♀, same data; two ♂, same locality, 10-II-73; two ♀, same locality, 11-II-73; and one ♂, same data as allotype, W.W. Benson collection, Rio de Janeiro. One ♀, 3 Km. NW of Terra Santa, W.W. Benson *leg.*, and two ♂, bred from eggs laid by this female, Keith S. Brown Jr. collection, Campinas, São Paulo.

The paratypes vary somewhat in the size of the yellow markings, and the amount of green suffusion around them (which is minimal to absent); two examples are shown in Figure **6** (right wings), together with an *H. d. beebei* from Manaus, north of the Rio Negro, in the Reserva Ducke of the Instituto Nacional de Pesquisas da Amazônia (upper left).

The most abundant sympatric heliconian at the locality of the holotype of *terrasanta* was *H. aoede astydamia,* as a form also possessing very reduced yellow spots in the forewing "U"-band (Figure **6**, lower left); as this form is also known occasionally from the Guianas and Manaus, it is not judged to be worthy of a new name. Other heliconians found were *H. burneyi catherinae, erato hydara* x *amalfreda* (polymorphic hybrid population), *melpomene melpomene,* and *numata* forms.

No *demeter* populations were found in extensive explorations of suitable habitats near Faro, about fifty kilometers west of Terra Santa on the Pará/ Amazonas border, and we know of none captured in Óbidos to the east, from where

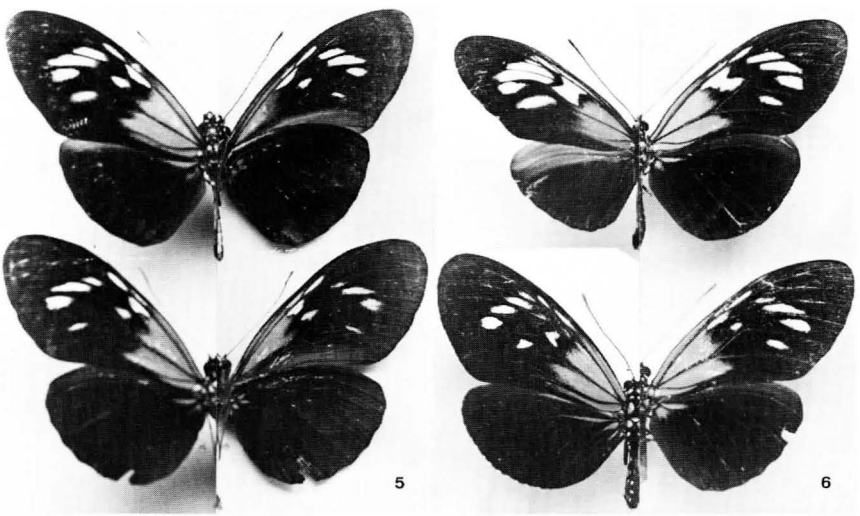


Figure 5: *Heliconius demeter terrasanta,* holotype male (upper) and allotype female (lower), dorsal (left wings) and ventral (right wings); Museu Nacional, Rio de Janeiro, W.W. Benson leg.; Terra Santa, Pará. Figure 6: *H.d. terrasanta,* two female paratypes (right wings), Terra Santa, 3-II-73, representing extremes of variation in forewing markings; *H.d. beebei* male, Reserva Ducke, Manaus, K. Brown coll. (upper left); and *H. aoede astydamia* with extremely reduced markings on FW, Terra Santa, 3-II-73, W.W. Benson coll. (lower left). All black, yellow, and red, reduced to three-quarters life size.

many thousands of similar-appearing *Heliconius* have been sent out in recent years (**Map**); this may indicate narrow geographic isolation of this subspecies and complete discontinuity from populations of *d. beebei.*

The subspecies is named after the type locality, placing emphasis on the fact that even "well studied" areas in the "vast and homogeneous" Amazonian forest region are likely to produce locally differentiated races or isolates of sedentary tropical organisms, and thus permit studies on incipient evolution of species in the present context.

Heliconius demeter ulysses K. Brown and Benson, NEW SUBSPECIES

(Figures 7, 8; Map)

HOLOTYPE ♂ (Figure **7**): forewing 35 mm. Similar to *H. d. eratosignis* (Figure **1**), but forewing yellow band fused to a single square patch, centered over the end of the discal cell, divided only by light black scaling over the veins and a black "V" at end of cell, and with the elements in the discal cell and spaces M_3-Cu_1 and Cu_1-Cu_2 enlarged and confluent with the rest of the yellow area. Slight green diffusion both discally and distally of the yellow patch. Dennis (divided into three by veins) and well-developed rays (clear, with no red basal patch) red-orange, forewing ventral costal line red, hindwing submarginal white spots poorly developed. Body markings as in nominate subspecies. Caranavi, La Paz, Bolivia, 800 m.; flowers by road to Alcoche, 3 Km. NW of center of town, 6-X-74. Donated to the Allyn Museum of Entomology; K. Brown *leg.*

One paratype ♂, very broken but otherwise identical, same flowers and date, in the collection of K. Brown, Campinas, São Paulo.

The collecting area was a steep south-facing hillside covered with second growth and scrub; sympatric *Heliconius* species were *erato venustus* (abundant), *melpomene penelope* (frequent; these two very similar in color-pattern to *ulysses), sara thamar* and *wallacei flavescens* (frequent), *hecale felix* and *numata aristiona* (infrequent). The types were captured in mid-afternoon (3 PM) of a cloudy day; no further specimens were seen three days later, on a sunny afternoon.

Additional males and females (Figure **8**) are known as part of the population of *d. eratosignis* in Riozinho, southeastern Rondônia, 700 Km. farther east in an area where *erato* is present as a mixture of *amazona* (mimicked by *eratosignis*) and *venustus* (mimicked by *ulysses*) (Brown and Mielke, 1972; Brown, 1973). The new subspecies should be found in monomorphic form in northeastern Bolivia (north La Paz, Beni, north Santa Cruz, perhaps Pando), southwestern Rondônia (on the Guaporé side of the Serra dos Pacaás Novos), and possibly extreme western Mato Grosso (Cáceres to Vilhena), wherever there are pure populations of *erato venustus* and *melpomene penelope.* In Acre, where *erato* and other dennis-rayed species possess a narrow forewing band outside the cell, *demeter* should occur as the nominate subspecies (near the specimen shown in Figure **9**, which however probably has some infusion of genes from *turneri*) or as transitions between this and *ulysses.* The latter type is shown by two specimens in the Museu Nacional, Rio, one male from Alto Juruá, Acre, No. 4/155, and one female from Xapuri, Acre, collected by J. Oiticica Filho (Figure**10**).

The subspecies is named for its association with *H. melpomene penelope;* Ulysses (=Odysseus) was Penelope's wandering husband of the Greek Odyssey (Homer).

Heliconius demeter zikani K. Brown and Benson, NEW SUBSPECIES

(Figure 11)

HOLOTYPE ♂: forewing 36 mm. Basal dennis strongly reduced, leaving only scattered red-orange scaling between the veins; median area of forewing

with a large quadrangular yellow patch, as in *d. ulysses,* consisting of poorly separated spots in the end of the discal cell and in spaces Sc-R_1, R_1-R_2, R_2-R_5, R_5-M_1, M_1-M_2, M_2-M_3, M_3-Cu_1, and Cu_1-Cu_2, the last five of these extending far distally as diffuse greenish areas (yellow over blue-black scales), nearly reaching the outer margin - the most extensive green diffusion known in any *demeter* form. Hindwing with somewhat shortened rays and a moderately expressed red-orange basal patch, leaving the cubital veins black but uniting the rays out to shortly distal of the cell, as in nominate subspecies. Underside with a clear yellow forewing square patch corresponding to the non-diffuse part of the dorsal area, yellow costal line on the forewing and costal stripe of the hindwing, well-expressed dennis in

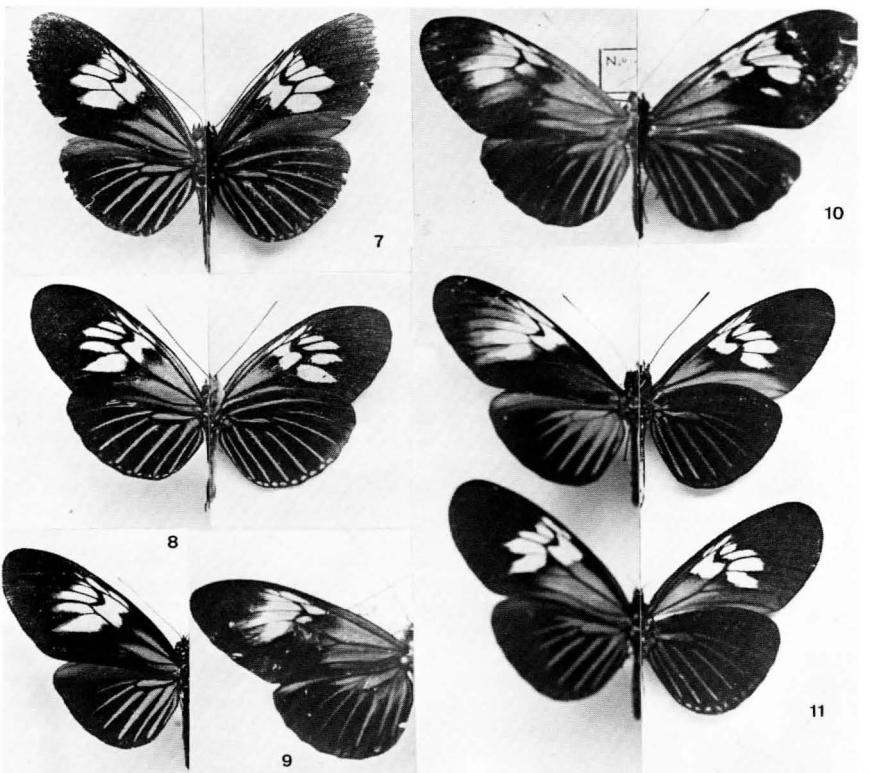


Figure 7: *Heliconius demeter ulysses,* holotype male, dorsal (left) and ventral (right) wing surfaces; Caranavi, La Paz, Bolivia, 6-X-74; Allyn Museum (K. S. Brown leg.). Figure 8: *Heliconius demeter ulysses,* female as part of a polymorphic population, dorsal (left) and ventral (right) wing surfaces, Riozinho, Rondônia, K. Brown coll., and a male from the same series (lower left), dorsal. Figure 9: *H.d. demeter* with some *turneri* infusion, male, dorsal, Eirunepé, Amazonas (middle Juruá) (Museu Nacional). Figure 10: *H. demeter* (*demeter* x *ulysses*), male (left), Alto Rio Juruá, Acre, and female (right), Xapuri, Acre (Museu Nacional). Figure 11: *H. d. zikani,* holotype male (upper) and allotype female (lower), dorsal (left) and ventral (right) wing surfaces, Jauareté, Rio Uaupés, Amazonas, J. F. Zikán leg., I-1937 (Museu de Zoologia, Universidade de São Paulo). All butterflies black, yellow, and red-orange; diffuse areas of males green; reduced to about three-quarters life size.

the discal cell (in contrast to the dorsal reduction), and fully developed but poorly expressed (faint) red rays on the hindwing; very faint white submarginal spots anally of vein M_2, and four red basal spots as in other subspecies.

ALLOTYPE ♀: forewing 36 mm. Very similar to male, but with forewing yellow patch clear and compact (no green diffusion) on both surfaces, no red basal patch uniting the clear hindwing rays, and large dennis on dorsal forewing (appreciably more extensive than in *ulysses*), uniting with the yellow patch in the cell and space Cu_1-Cu_2, but absent in the costal third of the cell.

Both from Jauareté, upper Rio Uaupés (frontier of Colombia), I-37, J.F. Zikán leg.; in the Museu de Zoologia, Universidade de São Paulo.

Sympatric heliconians at the type-locality included at least the mimetic species *H. erato reductimacula, H. egeria asterope,* and *H. aoede lucretius,* in addition to *H. metharme* and *H. numata silvana.*

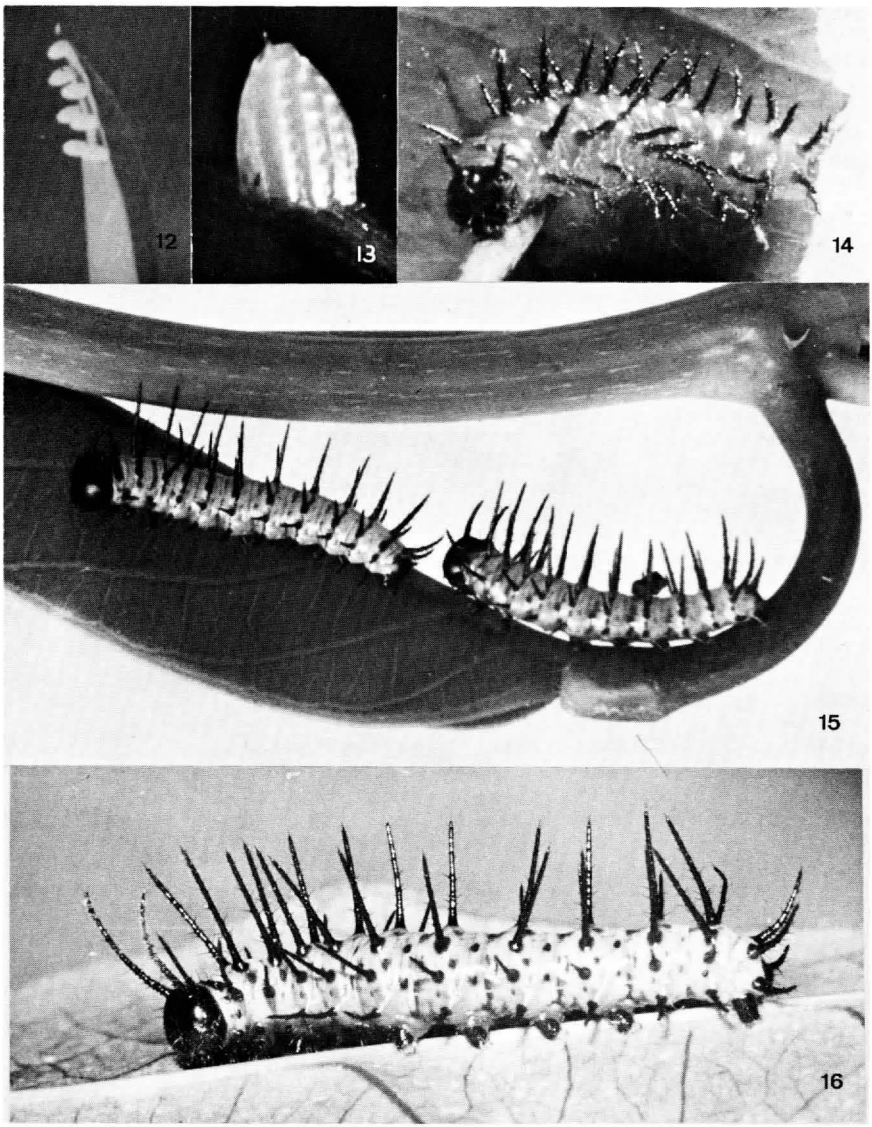
The subspecies is named for its original discoverer, J. F. Zikán, one of the most active of Brazilian lepidopterists in the period 1920-1940.

Based on the observed distribution patterns of Amazonian mimicry systems, all the expected mimetic forms of *demeter* have now been discovered, except for the very narrow yellow-banded type which may still be found in the Huallaga and upper Ucayali valleys in Peru (though known specimens from these areas are near typical *d. demeter*). In addition, the unexpected form *terrasanta* demonstrates the occurrence of microevolution in the species, in response to local selective pressures in isolated populations, and points out the processes responsible for the broader evolutionary trends in tropical populations. Following the recent suggestion of the derivation of heliconian mimicry rings in isolated Quaternary forest refugia (Brown, Sheppard and Turner 1974; Brown, in preparation), the races would correspond to the following core areas for evolution and differentiation: *demeter,* Napo; *turneri,* Tapajós; *zikani,* Imeri; *eratosignis,* Madeira; *beebei,* Guyana; *bouqueti,* Cayenne; and *ulysses,* Beni. In each area, the race that is present takes part in an extensive Müllerian and Batesian mimicry ring, consisting of dennis-(rayed) heliconians and other butterflies. The geographically restricted *d. terrasanta* also converges on a local form of *H. aoede,* with a reduced yellow area on the forewing. Thus, *demeter* is certainly properly characterized as a mimetic *Heliconius.*

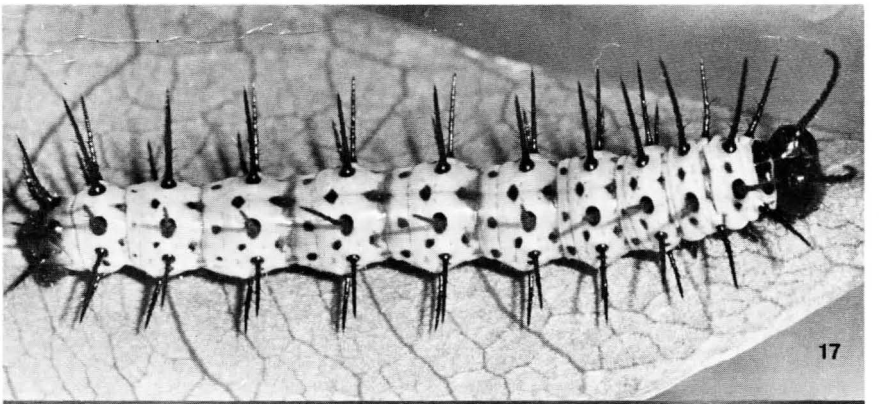
The most interesting fact is that it is also a rare *Heliconius.* While some other members of the Müllerian mimicry groups in which *demeter* participates are quite local in their distribution, none can really be called rare. The description of five new subspecies of *demeter* in the last ten years testifies to the infrequency of its encounter wtih collectors; very few major world collections have over five specimens representing one to three of these subspecies. In the following sections, we will examine some of the background for the understanding of the sparse distribution of *demeter* over the ten million square kilometers of its known range.

JUVENILE BIOLOGY

The early stages of *demeter* were discovered by W.W.B. near Terra Santa, Pará (north bank of the Amazon River on the lower Rio Nhamundá; *d. terrasanta*), on *Dilkea* sp., in February 1973; and in the region of Riozinho, Rondônia (Km. 992 of the Cuiabá-Porto Velho highway, 490 Km. southeast of the latter city; *d. eratosignis*), on *Passiflora (Astrophea)* sp. nr. *citrifolia,* in July 1972. During August and September of 1970, W.W.B. also had the opportunity to observe populations of *d. bouqueti* in several localities of Guyane Française. The adults were very rarely encountered in well-developed moist forest, but locally dense populations were present in sandy soiled, more open forest situations, which had been subjected to limited clearing. These populations consisted largely of females which looked identical to, and behaved very much like the abundant and much more widespread *H. erato erato.* At the most dense *demeter* population, on the Cayenne-St. Laurent road at the turnoff of Mana (near Saut Sabbat), a *Passiflora (Astrophea)* sp. near *citrifolia,* essentially identical to the foodplant of *eratosignis* in Rondônia, was



Figures 12-23: juvenile forms of *Heliconius demeter* (form, amplification, subspecies, locality when necessary): 12, egg raft, 3x, *eratosignis,* Riozinho; 13, egg, 20x, *beebei,* Manaus; 14, second instar larva, 8x, *terrasanta* (from egg in insectary); 15, third instar larvae, 5x, *eratosignis*; 16, fourth instar larva, 5x, *terrasanta;* 17, fifth instar larva (dorsal), 3x, *terrasanta;* 19, fifth instar larvae, lateral, 2.5x, *eratosignis;* 20, fifth instar larvae, dorsal, 2.5x, *eratosignis.*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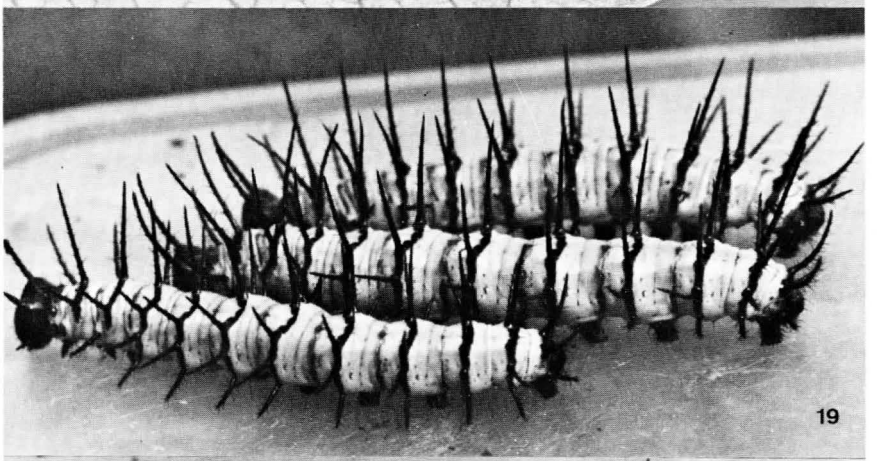
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abundant; it is almost certain that *bouqueti* was using this host plant at this site (although only early stages of *H. sara thamar* were discovered on the plant), and/or *Dilkea,* which at that time was unknown to the observer.

Field collected early stages of both the Rondônia and Terra Santa insects were reared from egg to adult on the respective foodplants. *H.d. terrasanta* also placed eggs (in the insectary) on the Rondônia *Astrophea,* which served well as larval food, but the Rondônia females were not observed to lay in the field on local *Dilkea* plants, although these were abundant and microsympatric with the *demeter.*

Early stages from the two areas were similar morphologically (with some variation in length of larval scoli), but the patterns of markings of the mature larvae of the two populations differed greatly; the significance of this is discussed below.

EGG (Figures **12-13**): a bright yellow, elongated ovoid truncated at bottom and deeply sculptured at top, 1.2-1.4 mm. high and 0.6-0.7 mm. in diameter, with 14 vertical and 8-10 horizontal ridges (plus 1-2 in irregular series at top). Laid singly (Terra Santa) or in loose but regularly arranged groups (Rondônia), on a meristem of *Dilkea* or *Passiflora (Astrophea)* nr. *citrifolia,* usually on young leaves, upper surface; duration 2-5 days.

LARVA. First instar uniform light yellow with a yellow-brown to brown head (black pseudoocelli) and translucent setae. Head height 0.5 mm.; maximum length 4 mm.; duration 2-4 days. Gregarious in Riozinho populations (as are all subsequent instars), solitary in Terra Santa.

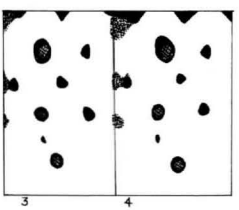
Second instar (Figure **14**) similar but with short black scoli (head lx, thorax up to 1.3x head height, which is 0.8 mm.); prothoracic plate wide, black; head, legs, and anal segment black. Maximum length 7.5 mm.; duration 2-3 days.

Third instar (Figure **15**) similar, stronger yellow, with black head, prothoracic plate, legs, anal segment, and scoli (head 1.5x, thorax 1.4x head height, which is 1.2 mm.); maximum length 12 mm.; duration 2-3 days.

Fourth instar (Figure **16**, of *terrasanta*) developing the pattern of fifth, essentially complete by end of stage - spotted *(terrasanta)* or ringed *(eratosignis)* with black. Head scoli 2x, others 1.5x head height, which is 1.7 mm.; maximum length 20 mm.; duration 2-4 days.

Fifth instar of *terrasanta* (Figure **17**) yellow, with a pattern of rather faint black spots (Figure **18**) identical to that of *erato* larvae; black (strongly bilobed) head, wide prothoracic plate, anal plate, legs, and scoli (head 2x, body up to 1.8x head height, which is 3.0 mm.). Fifth instar of *eratosignis* (Figures **19-20**) yellow, banded strongly around each segment with black, passing through the bases of the scoli (Figure **21**); black, strongly bilobed head, wide prothoracic plate, anal plate, legs, and scoli (maximum 1.6x head height). Maximum length 30 mm. (*eratosignis*) or 35 mm. (*terrasanta*); duration 5-6 days, followed by a day as prepupa.

PUPA (Figures **22-23**) medium gray, highly patterned and sculptured, with black and white fine streaks and reflective spots (paired, dorsal, on the prothorax, metathorax, and first abdominal segment). In general very similar to *erato* or *ricini* pupae (Beebe, Crane and Fleming, 1960), but more slender and finely marked. Long (6 mm.), broad, and well-developed branched spatulate head appendages;



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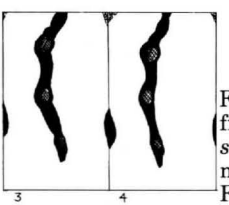

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Figure 18, color-pattern of fifth instar larva of *d. terrasanta* third and fourth abdominal segments, schematic. Figure 21, same, *d. eratosignis.*

dorsolateral flanges on 3AB (large) and 4AB (smaller), bearing long, outward and downward directed, and shorter parallel spines respectively; medium length dorsolateral spines, flanged at base, on 5AB, 6AB, and 7AB; short spines, with tubercles at base, on metathorax and 1AB, 2AB, and along antenna cases (forewing costal sutures); tubercles on wing cases in future cells M_3-Cu_1 and Cu_1-Cu_2. Length 28-32 mm.; duration 8-12 days.

The adult emerges in the very early morning and flies well before midday.

DISCUSSION

A. *Larval Mimicry*

The larval color-patterns observed in Terra Santa and Riozinho are different enough to be associated with separate mimetic groups, if the localized *demeter* caterpillar can be considered to derive benefit from Müllerian mimicry with common and widespread *Heliconius* larvae on the same or nearby foodplants. Certainly the exposed, mobile, and brightly colored heliconian larvae are at least as vulnerable to potential attack by gleaning predators as are the slow-flying, obvious-behaving adults to attack by aerial insectivores. This has apparently caused the development of Müllerian mimetic color-patterns, departing from those

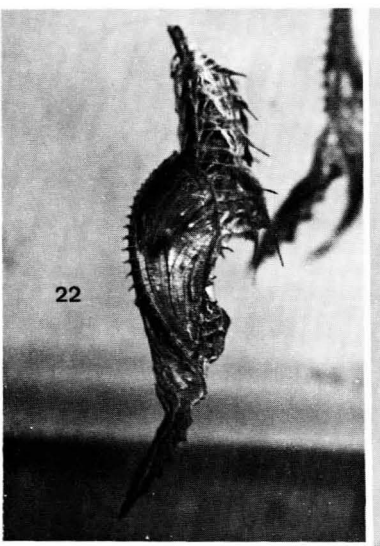
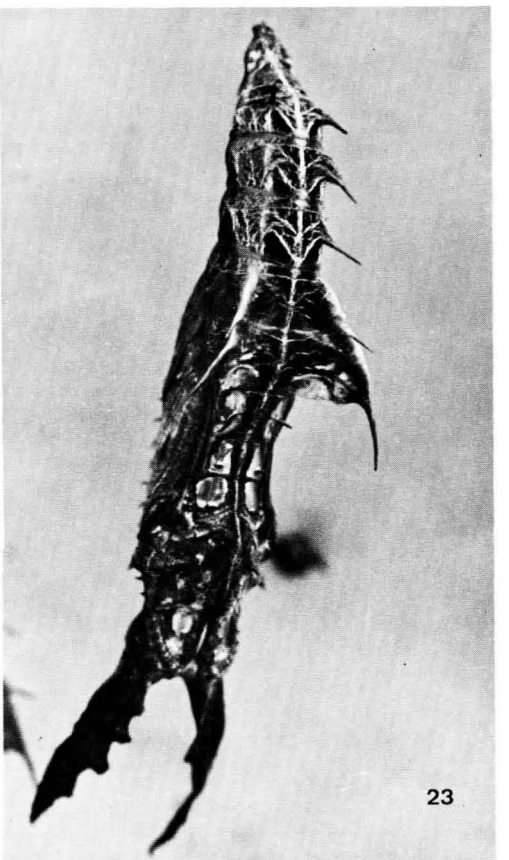


Figure 22: *H. d. eratosignis*, pupa, lateral, 2x; Figure 23, same, dorsolateral, 3.5x (Riozinho, Rondônia).



of close relatives, in larvae of the strongly localized species *Eueides tales* (Brown and Holzinger, 1973) and the rare *Heliconius hermathena* (Brown, 1972; Brown and Benson, in preparation).

The color pattern of the larva of *terrasanta* probably represents the typical or ancestral one to be expected in the majority of *demeter* larvae. It approaches closely that shown in its nearest relatives, such as *H. ricini,* and bears a general similarity to the basic *erato, melpomene,* and *numata* larval spotting arrangements. In contrast, the sharp disruptive banding pattern of *eratosignis* larvae in Rondônia should be considered as a derived condition. We do not know what evolutionary forces have caused it to diverge from the ancestral pattern, but the gregarious caterpillars of *Heliconius doris,* periodically abundant in Riozinho, would be worthy objects for mimetic convergence; they also possess black heads and yellow bodies with annular black bands (Beebe, Crane, and Fleming 1960). It is also possible that no specific mimetic convergence is represented by the Riozinho larval pattern, especially as conspicuous banding is a common phenomenon in gregarious distasteful (aposematic) larvae, presumably functioning by permitting the caterpillars to protect one another through an interlocking and very conspicuous display.

The retention of a larval pattern resembling that of many heliconian species by the Terra Santa *demeter* may well be related to the more solitary habits of this caterpillar. The also solitary and microsympatric larvae of *erato, melpomene,* and *numata* have the same general aspect as that of *terrasanta,* and may form a "mimetic environment" which maintains the pattern of the last conservative.

Only *H. aoede* eggs were found on the *Dilkea* used by *demeter* in Terra Santa, and these in different habitats. The caterpillar of this species is purple with yellow scoli (Turner 1968), apparently mimicking those of *H. wallacei* and *H. burneyi. H. numata* and *H. melpomene* use *Dilkea* in other parts of their ranges (Brown and Benson, in press), and even *erato* have been found on this primitive plant in western Colombia. The importance of a "mimetic environment" for aposematic caterpillars is further indicated by the Amazonian and Guianan larvae of the very common *H. sara,* which are yellow with black spots like the larva of *terrasanta,* whereas in Trinidad (Beebe, Crane and Fleming, 1960) and Central America (personal observation) they are dark brown or black; this suggests appreciable modification possible under the influence of local conditions.

The fact that other *Heliconius* larvae which are presumed to create the mimetic background for *terrasanta* use different Passifloraceous species does not present any great problem for mimetic advantage to accrue to a similar caterpillar. Since birds are often strata feeders (MacArthur, 1958; MacArthur, Recher and Cody, 1966), it would only be necessary for larvae to occupy similar height positions to enable mimicry to become an effective defense against these predators.

B. *Oviposition Behavior*

It is significant that the subspecies *eratosignis* and *terrasanta* have taken on different oviposition strategies (which in turn has probably affected larval behavior and color-pattern). The former lays eggs in batches on terminal (still folded) leaves of *Passiflora (Astrophea)* (2 cases observed, plus an independent observation of gregariously feeding fifth instar larvae), with perhaps as many as a dozen eggs in a group (Figure **12**). The eggs are spaced in a regular pattern as in *H. doris, Dione juno,* and some *Eueides,* and are not scatter-distributed as is characteristic of closely related advanced *Heliconius* like *sara* and *ricini.* Cluster laying *Heliconius* generally have reduced egg sizes, but the egg of *demeter* is only slightly smaller than that of the solitary laying species such as *erato.* In small-egg but advanced species like *sara* or *antiochus,* the eggs may be difficult to space, and any plant structure provides sufficient surface onto which the eggs may be firmly glued. With its reduced number of larger eggs, *eratosignis* seems to take care in their distribution.

On the other hand, *d. terrasanta* lays its eggs singly, and if more than one egg is placed on the same plant, these are well separated, at least on separate leaves (judging from multiple field and insectary observations). The new growth of *Dilkea* used by *terrasanta* is limited in quantity per plant compared to that of the *eratosignis* foodplant, and this may explain the differences in egg laying strategies of the two populations, if it is assumed that smaller plants will support fewer larvae to pupation and that complete defoliation of a plant would be likely to result in the deaths of all larvae on it. A possible test of this hypothesis would be in the observation of ovipositional behavior in *bouqueti,* which is geographically parapatric to *terrasanta* and/or *beebei* but may possess a larval ecology similar to that of the geographically distant *eratosignis,* judging from its probable foodplant, personal observations, and lore of Guyane collectors indicating local and simultaneous emergence of large broods.

C. *Sexual Dimorphism and Diethism*

The adult butterflies of the different races of *H. demeter* are, as mentioned above, fair to excellent mimics of many sympatric *Heliconius,* especially the co-occurring races of *H. erato.* This mimicry reflects to a great extent the similarities in behavior between these two species, especially their females. For example, *eratosignis* in the transitional cerrado-forest habitats near Riozinho, Rondônia, flies widely with *erato* and occupies the same flight strata, demonstrating very similar behavior patterns. Although the two species use different oviposition plants, the growing tips of the two types of *Passiflora* have very similar habitat and height distributions where *demeter* occurs abundantly. Only by observation of the forewing band in slow-flying or resting individuals could an observer make a fairly confident decision as to which species an individual belonged. Like *erato, d. eratosignis* participates in site specific roosting at night, joining at least with *H. sara* and probably also with other *demeter* and *erato* on occasion. The single roost observed was 3-4 meters above the ground, and under the minimal light conditions it was not possible to determine the complete species composition, beyond observing the *sara* and flushing and capturing a *demeter.* The local *erato* seemed to prefer to roost on lower vegetation along edges, about 1-2 m. above ground level.

The populations of *d. terrasanta* observed occurred in habitats with a striking structural similarity to those of Riozinho — low to medium height, open forests on poor soils, in this case well drained sandy formations. Both sexes flew within the forest along with *H. aoede,* visiting flowers, especially those of rubiaceous shrubs. During the afternoon, activity dropped off and the butterflies moved higher up in the vegetation, spending increasing amounts of time resting on leaves and sunning. The day probably ended with gregarious roosting. Three or four days of occasional removal of individuals from a forest patch three kilometers north of Terra Santa (near the airport runway) greatly reduced the capture rate for both *H. demeter* and *H. aoede,* indicating that the home range and/or rates of dispersal in these species are small. Similar observations were made in the Riozinho populations.

The above mentioned subspecies do not demonstrate appreciable sexual dimorphism, as does for example *d. bouqueti* in Guyane Française. The habitats of this subspecies were characterized by high forests, either virgin or cut out. Soils were sandy and well drained, and the forest was open with a relatively non-humid understory. These are possibly the conditions under with *bouqueti* differentiated, and this may help to explain its sexual dimorphism in pattern and behavior, with dual Müllerian mimicry of other *Heliconius* species. The female of *bouqueti,* like *erato* which it greatly resembles and both sexes of *eratosignis,* flies in the understory and along open edges, looking for oviposition sites and visiting flowers. The male, on the other hand, flies rapidly and high in the treetops, descending to the ground along edges, where it can be infrequently observed and is difficult to

capture. The fact that most known *bouqueti* in collections are males may be ascribed to the excellent mimicry between the female and the abundant *H. erato erato,* which protects her from the collector who usually looks for rarities. Also, there is no doubt that many more females rest in collections than are now known, because they are erroneously placed with *erato;* the second author observed this to be the case even with the collections of experienced Guyane lepidopterists, and the first author found several females thus hidden in the British Museum (Natural History) duplicates. The male of *bouqueti* has a broad red basal patch on the hindwing (Figure 3), which gives it a credible resemblance to the sympatric but much larger *Heliconius egeria,* a species of the forest canopy. It is possible that the male of *bouqueti* has taken to the canopy to permit a more efficient rendezvous with the female, differentiated from that of *erato* and possibly correlated with post-emergence behavior of *bouqueti* females. Even after expanding and drying her wings and initiating flight, the female should seek out a sunny place to harden her wings, and in the higher forest she might ascend to the canopy. The most efficient strategy for the male would be to search this undulent surface rather than confront the volume beneath it, which would also be full of similar-looking temptresses of *erato* to distract his attention. Selection by mating efficiency would tend to rapidly reinforce and stabilize this "rendezvous behavior"; selection by predation would then have promoted mimetic convergence in the male of *bouqueti* to a pattern resembling that of a conspicuous, large, and behaviorally similar species of the canopy, *H. egeria.*[3] The search pattern of *bouqueti* males is also of advantage to the females, since mating will occur more rapidly and the all-important task of egg-laying can be begun sooner.

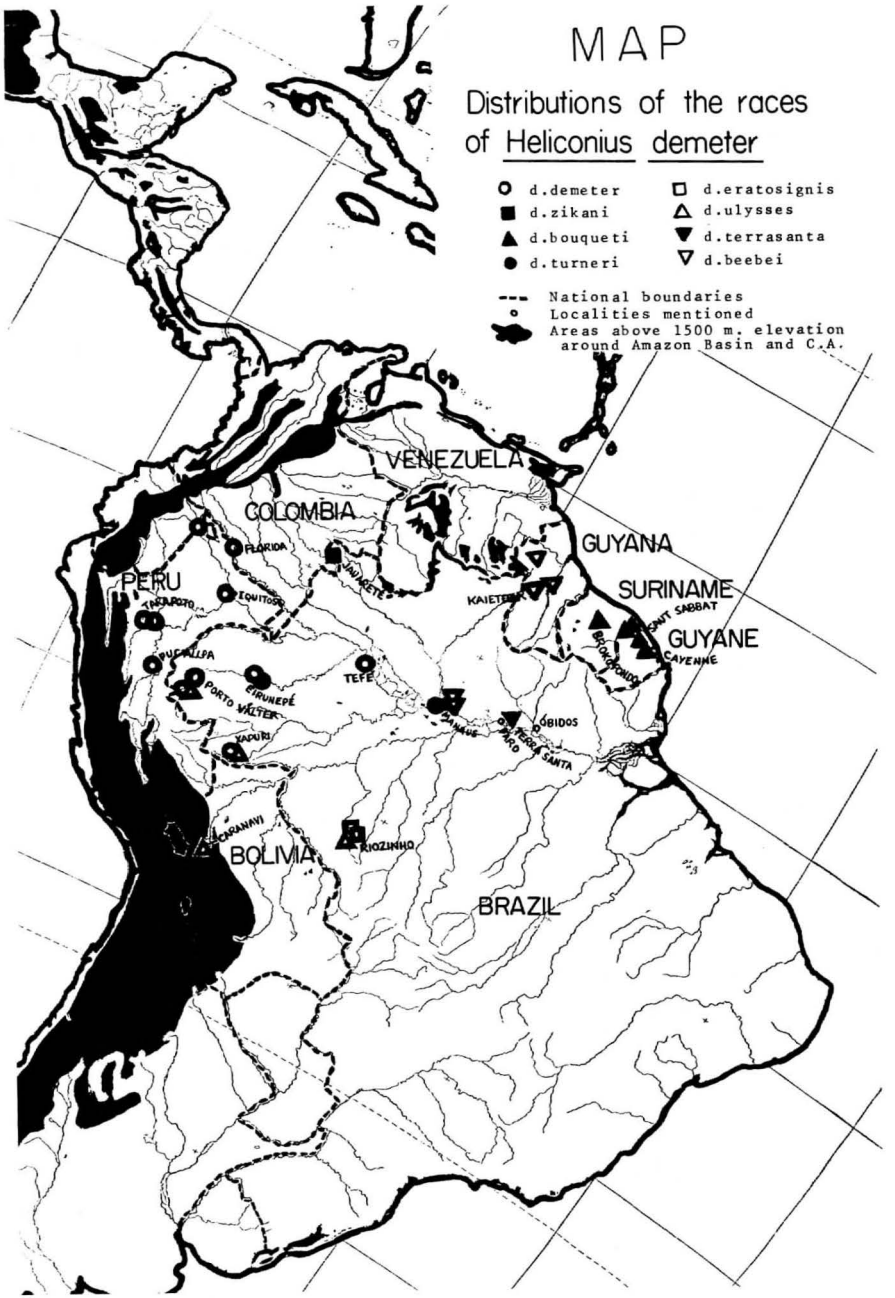
The total pattern of rendezvous in the canopy would be analogous if not homologous to that observed in countless diurnal and crepuscular Lepidoptera on select hilltops (Shields 1967), which has also been shown to occur frequently in other "traditional" sites such as sun-bathed localities along forest edges, in clearings, and anywhere with easily markable and constant physical features (Scott, 1970; Guppy, 1970; personal observation). The pattern proposed here also corresponds closely with that observed in other cases of divergent mimetic sexual dimorphism in heliconians (*e.g., Eueides vibilia* and some *E. procula,* and *Heliconius hecalesia octavia, nattereri* (Brown, 1972), and some *numata*).

Critical information is still lacking, unfortunately, concerning the post-emergence behaivor of *bouqueti* females. The only significant observation in hand is on another, non-sexually-dimorphic *demeter* subspecies: the initial behavior of reared *d. terrasanta* in the insectary suggests seeking of higher levels by young individuals. Whereas the older field-captured mother adapted perfectly to the understory of the twelve-foot-high insectary and lived there for well over a month before falling to a spider, her progeny, both male and female, beat incessantly against the sunlit roof in the fashion of the wildest heliconians *(Philaethria dido, Heliconius nattereri,* and *numata* of *silvana* type), rapidly exhausting themselves and dying within a day or two.

D. *Habitat Distribution*

In most parts of its range, *H. demeter* seems to be very rare and/or strongly localized, encountered in highly restricted habitats. Although detailed observations on behavior and/or foodplant relationships are available for six of the subspecies, these do not give a completely uniform picture of the apparently very narrow preferences of the species. It does seem, however, that *demeter* may often be encountered in marginal or peripheral conditions; the present edaphic climax of

[3]Although the general impression in the field is that *egeria* is rare, the fact that it is the most canopy restricted of all *Heliconius* makes it usually unavailable for observation, much less for identification; capture can normally only be achieved through the use of large red attractact surfaces near the ground, to which the species readily descends. Occasional long periods of canopy observation by the first author have indicated *egeria* to be very frequent in its habitat, which also has a dense population of resident insectivores.


MAP
Distributions of the races
of Heliconius demeter
d.demeter
d.zikani
d.bouqueti
d.turneri
d.eratosignis
d.ulysses
d.terrasanta
d.beebei
National boundaries
Localities mentioned
Areas above 1500 m. elevation
around Amazon Basin and C.A.
VENEZUELA
COLOMBIA
GUYANA
SURINAME
GUYANE
PERU
BOLIVIA
BRAZIL
FLORIDA
KAIETEUR
CAYENNE
TEFÉ
ÓBIDOS
RIOZINHO

the Amazonian forest is apparently not suitable for the development of large populations of the species in competition with others of its genus, and its food-plants, mostly deep forest species, do not survive well in highly disturbed areas.

The butterfly has always been found very uncommonly in the more humid patches of mosaics, whereas dense populations may be observed in more open, often transitional or ecotonal, formations. *H. demeter* may well be considered a species of undisturbed forest understory but one which has difficulty in competing with more adaptable and common heliconians with the same preferences for the few growing tips of young canopy lianas. As a consequence of this, its reproduction is only facilitated in those areas where sufficient light reaches the ground to enable these young lianas to become dense and produce much low growth, and thus permit females to hunt these out effectively.

ACNOWLEDGEMENTS

The authors are grateful to the scientific staffs of the British Museum (Natural History), the Allyn Museum of Entomology, the American Museum of Natural History, the Museu Nacional (Rio de Janeiro), and the Museu de Zoologia da Universidade de São Paulo, for access to the collections under their care, and in some cases loan of material for study and photography. Field work was assisted by Olaf Mielke (Rondônia) and Père Y. Barboutin (Guyane), as well as the Instituto Nacional de Pesquisas da Amazônia (Manaus) and the Expedição Permanente na Amazônia of the Fundação de Amparo à Pesquisa do Estado de São Paulo (Terra Santa). Financial support for the study of Brazilian insects was received from the Conselho Nacional de Pesquisas, the Conselho de Pesquisa e Ensino para Graduados of the U.F.R.J., the Banco Nacional de Desenvolvimento Econômico (FUNTEC 47 and 101), the Ministério do Planejamento (FINEP/FNDCT, contrato 140/CT), and the National Science Foundation (Grant 5389 XI). The manuscript was read by Drs. L. E. Gilbert (Texas), J. R. G. Turner (Stony Brook), and H. Holzinger (Vienna), to whom we extend thanks for their comments.

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