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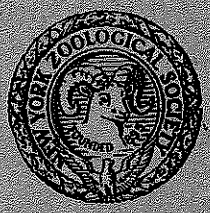

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The Heliconians of Brazil (Lepidoptera: Nymphalidae). Part II.[1] Introduction and General Comments, with a Supplementary Revision of the Tribe.

(Plates I-VI; Text-figures 1-12; Map)

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The Lepidopterous tribe Heliconiini has recently become very useful in biological and genetic investigations. For this reason, it was important to obtain information on many previously little-studied species in the Amazon Basin and southern Brazil, and to clarify the systematics of the tribe in the light of this new information.

There are 18 species in the tribe normally found in extra-Amazonian Brazil, with seven more appearing marginally on the borders of the Amazon Basin. They demonstrate rather little variation or subspeciation over this area of nearly four-million square kilometers. In the mountains of the southeast, especially in subtropical areas, they undergo dramatic and cyclical annual variations in abundance, reaching their peak in late summer and fall (February through June).

The 37 species of Heliconiini found over the four-and-a-half million square kilometers of Amazonian Brazil are often very variable, and in many cases broken into multiple subspecies which often show parallelism in color-pattern with those of other species throughout the area; the subspecific divisions closely follow those observed in other animal groups and ascribed to Pleistocene weather changes. Many Amazonian heliconians demonstrate striking polymorphisms in single populations.

In light of new biological and distribution data, and with relation to Emsley's systematic revisions (*Zoologica*, 1963-1965), a total of 12 good species must be added to the tribe, and a further two must be recombined; the total number of species is now 66. A few remaining systematic uncertainties still remain, which could modify this number by two or three.

INTRODUCTION

THE LEPIDOPTEROUS TRIBE Heliconiini (Nymphalidae: Nymphalinae; also frequently referred to as a subfamily, Heliconiinae) has recently attracted much attention as a convenient and varied tool for biological and genetic investigations (M. G. Emsley, 19th Annual Meeting of the Lepidopterists' Society, Washington, D.C., June 15-18, 1968). A long series of papers has been published by the Department of Tropical Research of the New York Zoological Society on many aspects of heliconian life, taxonomy, mimicry, behavior, physiology, and genetics: Alexander, 1961a, 1961b; Baust, 1967; Beebe, 1955; Beebe, Crane, and Fleming, 1960; Brower, Brower, and Collins, 1963; Crane, 1954, 1955, 1957; Crane and Fleming, 1953; Emsley, 1963, 1964, 1965, 1970; Fleming, 1960; Sheppard, 1963; Swihart, 1963, 1964, 1965, 1967a, 1967b, 1968; Turner,

[1] Part I of this series: see K. Brown, 1970. Part III: see following paper.

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1968a, 1971; and Turner and Crane, 1962. These papers have resulted in a thorough knowledge of the 14 heliconian species normally present in Trinidad.

We have recently initiated biochemical studies on Brazilian heliconians (K. Brown, 1965, 1967; K. Brown and Domingues, 1970; Tokuyama *et al.*, 1967) and thus have had to develop a similarly thorough knowledge of the species present in this area. We succeeded in delineating food-plants and observing at least some part of the early stages of all 18 heliconian species normally present in extra-Amazonian Brazil (Appendix I). Most species proved to be readily bred in captivity and reasonably resistant to disease, parasitism, and handling. A few species, however, were not tractable even under the most ideal conditions. These included the four high-flying and uncommon-to-very-rare species, *Philaethria wernickei, Eueides pavana, Heliconius nattereri,* and *H. silvana ethra.* Partial to complete information on early stages, either observed in nature or reared from fertile eggs expressed from wild-caught females, and food-plants is nonetheless available for these species (Appendix I).

This paper presents a general view of the tribe in Brazil, with detailed comments on various species. It includes some specific corrections and additions to Emsley's recent papers (1963, 1964, 1965) on the Heliconiini, including comments on non-Brazilian species, and thus amounts to a complete supplementary revision of the tribe. The paper also contains a complete synopsis of the species occurring in extra-Amazonian Brazil and preliminary food plant data for them, as well as a brief list of the heliconians of the Brazilian Amazon. Part III includes a description of the biology of the key primitive species *Heliconius nattereri,* and a graphical formulation of the possible geohistorical evolution of the genera *Heliconius* and *Eueides.* Three new subspecies from the central Brazil plateau (Appendix I) will be fully described in Part IV. Part V is a revision and discussion of the mimetic silvaniforms (the first half of Emsley's "*numatus*-group"); its taxonomic conclusions are incorporated into the nomenclature used in this part.

Taxonomy

The taxonomy of the Heliconiini was revised by Emsley in 1963-1965, reducing the recognized number of species in the tribe from 116 to 55. Useful papers have since been published by Turner (1966, 1967b, 1967c), clarifying the systematic positions and variations of *Heliconius demeter* and *H. elevatus,* and the nomenclature of *Dryas iulia.* Emsley's papers require a few further clarifications, corrections, and additions in light of new information about Brazilian and extra-Brazilian heliconians, which brings the total number of recognized species in the tribe back up to 66 (see below and Appendix III). We also will separate the genus *Eueides* from *Heliconius* on morphological, biological, karyological, behavioral, and chemical grounds.

Emsley (1965) revised, where appropriate, the endings of all names in *Heliconius* and *Eueides* to masculine gender or genitive case. The inadvisability of such modifications of the endings of originally described specific names to agree with the supposed gender of an often changeable genus has been defended by Turner (1967d), with specific reference to the heliconians. His comment on the modification of *vesta* to *vestus* ("Scandal in Temple. Vestal Virgins say *We are just good friends*") is truly classic and defends our preference, followed in this series of papers, for leaving all names as originally proposed by their authors.

Variation

One of the principal reasons that heliconians have been so useful to biologists is that they vary extremely in bright and colorful wing-patterns. The perfectly parallel variation of the common species, *Heliconius erato* and *H. melpomene,* over essentially all of tropical America and through at least 20 distinct basic color-patterns and over 200 named forms (Emsley, 1964; Turner, 1970), is material to astonish the layman, confound the collector, and delight the geneticist. The variability in *erato* and *melpomene* expresses itself most luxuriantly at the borders of the Amazon Basin (map, page 71). Here, the blue to black ground color, with one or two red forewing bands and often a yellow hindwing stripe, typical of the extra-Amazonian forms of these two species, encounters the radically different Amazonian dennis-rayed pattern (Plate VI, figs. 63 and 64), also displayed by many other Amazonian *Heliconius* and *Eueides* species.[3] The complexity of forms occurring in a small area (northeastern Bolivia, central Ecuador, south-central Colombia, and French Guiana-Surinam are especially noteworthy) challenges the imagination. The transition zone between the Amazonian and extra-Amazonian color-patterns has yet to be thoroughly investigated in any part of Brazil, with the possible exception of the Obidos-Santarém area (Plate VI, fig. 64).

In central Mato Grosso, the start of pattern plasticity has been recorded in the literature (Talbot, 1928) and documented by us. Unusual variations of *erato* and *melpomene* frequently turn up there, along with several other species

normally confined to Amazonia and carrying the dennis-rayed pattern. However, at least 95 per cent of the populations are within normal limits of *H. erato phyllis* and *H. melpomene burchelli*. In June, 1971, apparently monomorphic populations of *H. erato phyllis* and of the dennis-rayed *H. e. venustus* and *H. melpomene penelope* were traced to within 100 Km of each other in western Mato Grosso, with no signs of hybridization being observed. By October, a wandering *phyllis* had apparently crossed the very inhospitable dory grassland between these colonies and introduced its genes into the northern *venustus* population, which showed over 30 percent of individuals with hybrid characters. In this area, however, the subspecies may be effectively separated by the grassland ridge of the Serra dos Parecis, unlike in lowland Bolivia where they hybridize extensively.

Two extra-Amazonian species (*Heliconius silvana ethra* and *H. ethilla narcaea*) show a moderate north-south variation that has resulted in the separation of weak but recognizable subspecies. Intergradation occurs, however, well into "typical" populations both north and south of any arbitrary boundary. These are the only two species that are appreciably polymorphic in extra-Amazonian Brazil. Four named forms of *silvana ethra* may be found in a single population in Espírito Santo, and six named forms plus dozens of minor individual variants of *ethilla narcaea* can be found in southern Minas Gerais. Appreciable variation is also evident in some populations of Amazonian heliconians marginal in central Mato Grosso (Appendix I, B and Plate VI). The total amount of polymorphic variation, however, is small, especially in relation to that observed in Amazonian populations, particularly silvaniforms (see Part V of this series).

Zoogeography

While heliconians usually conform to major zoogeographic barriers, they are relatively strong flyers and we frequently have observed them crossing unfavorable terrain, ascending mountains, or apparently moving deliberately from one area to another. They are therefore not as useful as, say, the Ithomiinae for detection of finer zoogeographic boundaries (Fox, 1967).

In extra-Amazonian Brazil (map), the only barrier noticeably separating the heliconians is the divide formed by the high southeast coastal mountains, a geohistorically significant boundary affecting many groups of plants and animals. This restricts the tropical *Philaethria dido, Eueides vibilia, Heliconius melpomene nanna,* and *H. silvana ethra* and largely restricts *H. sara apseudes* to the coastal plains and foothill canyons north of Santa Catarina (where the high mountains are close to the ocean), and substantially restricts *Dione moneta* to the Paraná-Paraguay River Basin, Santa Catarina, and Rio Grande do Sul. The two subtropical species *Eueides pavana* and *Heliconius besckei* are native to the coastal and adjacent mountains which form this divide. Isolated and undifferentiated colonies of *besckei* (and of many other southeastern mountain butterfly species, some of which have evolved into recognizable subspecies) may be found in the Brasília area, northern Goiás, and isolated highlands in northeastern Brazil. The exceedingly rare and declining primitive species *Heliconius nattereri* (Parts I and III of this series) is confined to a very few select areas of undisturbed extensive virgin forest in eastern Brazil (Littoral-median region = northern Espírito Santo, eastern Bahia, and possibly eastern Minas Gerais, Alagôas, Sergipe, and Pernambuco). Other than the species mentioned above and marginal species (see below), the remaining nine heliconian species may be expected in nearly all parts of extra-Amazonian Brazil, with the exception of a very few high, cold, or excessively dry regions. Some species, notably *Dione juno, Dryadula phaetusa,* and *Philaethria wernickei,* while widespread, tend to be very strongly localized.

[3] This pattern is apparent in the female of *Eueides vibilia unifasciatus,* in *E. eanes* and *tales,* and in *Heliconius aoede, burneyi, egeria, astraea, xanthocles, doris* (red forms), *elevatus, melpomene, timareta*+ (except nominate form), *erato,* and *demeter* (species marked here with a cross are not known from the Brazilian Amazon and are in all cases marginally Amazonian, from higher elevations on the eastern slopes of the Andes). Four additional *Heliconius* species (*hierax*+, *himera*+, *clysonymus*+, and *ricini*) show a similar though simpler black-yellow-red pattern, which easily may be confused in the field with that of the dennis-rayed heliconians. *Eueides lampeto* and *isabella,* and the six species of silvaniform *Heliconius* [*ismenius*+, *silvana, numata* (= *aristiona*), *hecale* (= *quitalena*), *ethilla,* and *pardalinus*; see Part V for clarification of taxonomy], have a related black-yellow-orange pattern which suggests partial mimetic association with the dennis-rayed species (see Emsley, 1964: 281). Species in these two genera known from the Amazon Basin which do not show a black-yellow-red (or orange) pattern are almost all either orange with black bars and wing bands: *Eueides lybia, aliphera,* and *procula edias*+, and *Heliconius metharme, wallacei, hecuba*+, *heurippa*+, *luciana, cydno*+, *hermathena, telesiphe*+, *charitonia*+, *sara, leucadia, antiochus,* and *congener*+. See map, figures, and Appendix II.

Altitudinal transitions seem to present only imperfect barriers to many heliconian species in extra-Amazonian Brazil, certainly with much less importance than as implied in Emsley (1964, 1965). *Agraulis vanillae maculosa* flies from sea level to the highest areas in southern Brazil (near 3000 meters). In the genus *Heliconius*, the Andean species *telesiphe* was mentioned by Emsley (1965) as the only species normally flying at elevations above 1300 meters. In southern Brazil, however, *H. besckei* is found from sea level (locally) to its mecca at 800 to 1600 meters. From there it ranges upward in summer to more than 2000 meters. In late summer, even *H. erato phyllis* can be found breeding at nearly 2000 meters elevation, many kilometers from the nearest valley below 1300 meters. Many additional *Heliconius* species (*hierax, hecuba, heurippa, timareta, cydno, himera,* and *clysonymus,* as well as some local races of *erato* and *melpomene*) also have been found by us and by other collectors in the 1300-2500 meter range on the Amazonian slopes of the Andes in Bolivia, Peru, Ecuador, and Colombia. However, it does seem that heights above 2500 meters are impassable for *Heliconius* other than *telesiphe* (though not for *Agraulis* or *Dione*).

Cyclic Annual Variations in Abundance

Many field observations suggest that most heliconians undergo great annual variations in abundance that are partially but not wholly related to extensive new growth on the passifloraceous foodplants, and possibly accompanied by appreciable range expansions. They commonly appear in late summer and fall in areas where they do not survive or are drastically reduced in numbers in winter. A similar pattern has been observed in the two North American subspecies of *Agraulis vanillae,* and has been suggested for *Dione moneta* in Texas (Gilbert, 1969).

Several areas of intermediate elevation have progressively increasing numbers of tropical heliconians from January (mid-summer) into late May or June, followed by disappearance (or great reduction) during the winter and spring. Areas at 600 to 1200 meters elevation in the coastal mountains, such as Curitiba (Paraná), Petrópolis (Rio de Janeiro), and Santa Teresa (Espírito Santo), provide good vantage points for observing this. In Curitiba, at 900 meters elevation, *Heliconius sara apseudes* and *H. erato phyllis* begin appearing only in summer; by early fall they are frequent, but they seem to disappear with the first winter frosts. Both species fly all year around in the neighboring lowland areas; no definite information is available suggesting seasonal diapause mechanisms in *Heliconius* species in Brazil. *H. silvana robigus* and *H. sara apseudes* appear only in January and may be found only through May on the seaward slope of the coastal mountains in Petrópolis, an area 1000 meters in elevation and without winter frosts. In relatively warm Santa Teresa, at 600 to 800 meters elevation and above a rich tropical tableland area, *Eueides vibilia, Heliconius melpomene nanna, H. sara apseudes, H. silvana ethra, and H. nattereri* are encountered principally from January through June; they sometimes are very common in March and April, depending upon the year. These five species have actually been observed by K. B. moving up and down the seaward face of the mountains; and they appear first each summer at lower elevations near where larger streams run down the mountain-face.

The increased abundance of the mountain species *Eueides pavana* and *Heliconius besckei* at sea level near the foothills in winter, when they are not commonly encountered on the colder mountaintops, may result from a diminished upward movement of individuals from these populations during the cooler months.

The Chapada de Guimarães in central Mato Grosso seems to have an invasion of Amazonian species from lowland northern Mato Grosso in fall. The marginal species mentioned in the section below all have been found in this region rarely or not at all from September to February, commonly in May to July.

Finally, Prof. Dr. Heinz Ebert of Rio Claro, São Paulo, has observed that the southwestern species *Dione moneta* is common in central São Paulo in March to June, but very rare or absent there during the rest of the year. Whether local populations simply build up in fall, or the species invades from the south or west in response to unusual weather conditions or population pressure, has yet to be established.

A general discussion of the annual variation of butterfly frequencies in Brazil has also been published recently by Dr. Ebert (1970).

Marginal Species in Extra-Amazonian Brazil

The borders of the Amazon Basin in northeastern and central Brazil (map) are not well-marked zoogeographical barriers, being visible essentially as a gradual change from humid forest to more dry and open vegetation, and a number of normally Amazonian species of heliconian (Appendix I, B and II and Emsley, 1965) cross them into adjacent areas of the extra-Amazonian region.

Two areas have received special attention. One is the Cuiabá region of central Mato Grosso. Although in the basin of the Paraguay River, this region has a large influx of Ama-

zonian Lepidoptera, especially in the highlands ringing Cuiabá from the north (Rosário Oeste, Melguira, Serragem, Nobres, Tombador, Quebó) around through the northeast (Chapada de Guimarães, Buriti) to the east (São Vicente). Amazonian heliconians found by us to be marginal in this area include *Eueides vibilia unifasciatus, Heliconius sara thamar, H. melpomene burchelli, H. wallacei flavescens, H. ethilla* as a new subspecies (see Part IV of this series), *H. xanthocles melete,* and *Eueides isabella isabella.* The first three of these species also are found locally as far as the Paraná drainage in central and western Goiás, and *H. sara thamar* has been captured in the San Francisco River drainage in northwest Bahia (Rio Sapão; specimens in the Carnegie Museum).

In the northwesternmost tributaries of the Paraguay River in central-western Mato Grosso, between the swampy Pantanal around Cáceres and the high grassy ridge of the Serra dos Parecis, is an eastward extension of the north Bolivian rain forest, which is in turn contiguous with the general Amazonian forest (Hylaea) down the Rio Guaporé. Here the flora and fauna are very strongly Amazonian. In the heliconians, *H. erato* remains as the southern subspecies *phyllis;* but the Amazonian species *H. numata* (many variants), *H. silvana* as subspecies *mirus, H. aoede* as a new subspecies (Part IV), *H. burneyi,* and *H. leucadia* were all discovered in a few hours' collecting on the upper Rio Branco, a major tributary of the Rio Cabaçal, in June 1971. The last species was also found in the upper Rio Jaurú to the west, only a few kilometers from the upper Rio Guaporé, which flows to the Amazon within the Hylaea. Additional north Bolivian species which might be found with more intensive collecting in the Cabaçal-Jaurú area include *Philaethria dido* (known from coastal extra-Amazonian Brazil but not from the interior), *Eueides lybia* (possibly observed already on the Rio Branco), *Heliconius doris, H. hecale* (members of the *sisyphus* subspecies complex), and *H. elevatus perchlora.*

A further four species have been recorded as occurring in the "Cuyabá-Corumbá River System," a rather ill-defined area which may or may not be restricted to the Paraguay drainage in central Mato Grosso (not the Corumbá River in southern Goiás, however): *Heliconius ricini, H. astraea* as a new subspecies (Part IV) (one in the British Museum, *fide* J. R. G. Turner, and one in the Kaye collection, now part of the Allyn collection), *H. elevatus schmassmanni* (which may only be a variation of Neustetter's *aquilina*), and *H. demeter eratosignis* (for the last two, see Joicey and Talbot, 1925). We have searched in essentially all habitats in central Mato Grosso without locating any of these species. They would not invade from the northwest where the lowland Hylaea extends into extra-Amazonian Brazil, since here they were not found south of the Pimenta Bueno area in southeastern Rondônia (map). In this region, still 400 Km north of the Cabaçal-Jaurú forests, *Heliconius erato* makes a transition from the dennis-rayed, open-forewing-banded form, *amazona,* to the reduced dennis-rayed, compact-forewing-banded form, *venustus* (Plate VI, fig. 63).

In view of the known parallelism of forewing band modifications in Amazonian dennis-rayed *Heliconius* (Appendix II), it would be expected that *demeter, astraea,* and *elevatus* would similarly acquire a compact square forewing yellow patch in areas adjoining the northwestern Paraguay Basin. Indeed, the Pimenta Bueno population of *elevatus* already shows about 50 per cent of the subspecies *perchlora* with this compact band. The four species may invade from the northeast into the extreme upper Rio Cuiabá, in a forested highland which gives birth also to five major Amazonian rivers, or into the northeastern Pantanal, where highly suitable lowland forest habitat exists. However, in northeastern Mato Grosso, the Hylaea is 400 Km north of the Cuiabá river system, connected with it only by sparse riparian forests very poor in Heliconiini. We are inclined to regard the specimens labelled "Cuyabá-Corumbá River System" as originating from northern Mato Grosso or eastern Rondônia; until these species are confirmed in extra-Amazonian Brazil, they will remain on the hypothetical list. Here we place also *H. antiochus,* which lives commonly in northeastern Mato Grosso, even well south of the Hylaea in typical *erato phyllis/melpomene burchelli* territory (the dry southeastern Amazon).

The second area is in northern Ceará, where a number of mountain ranges (Serras de Ibiapaba, Uruburetama, Maranguape, and Baturité) break the palm-grassland plain and provide oases for unusual butterfly life. Also included in this marginal region is the area of Dom Pedro in southern Maranhão, but not northwestern parts of Maranhão which are decidedly Amazonian. Dr. Dmitro Zajciw collected these areas in 1962-1963, and donated many of his specimens to the Museu Nacional in Rio. His material includes *Heliconius erato phyllis, H. melpomene burchelli, H. ethilla* near *eucoma,* and *H. ricini.* The last three are not known from further southeast along the Brazilian coast. Other species known from central Maranhão and probably present in the extra-Amazonian portion, which has not yet been visited by the

authors, are *Eueides lybia* and *i. isabella,* and *Heliconius doris, wallacei, burneyi, numata, sara thamar,* and *antiochus.*

Two Andean butterflies have been recorded in Misiones in Argentina (Hayward, 1951) and might eventually be found in western Paraná or Santa Catarina: *Heliconius numata* (= *aristiona,* see Part V of this series) *splendidus* and *Dione glycera.* To our knowledge, however, neither of these has yet been captured in Brazil.

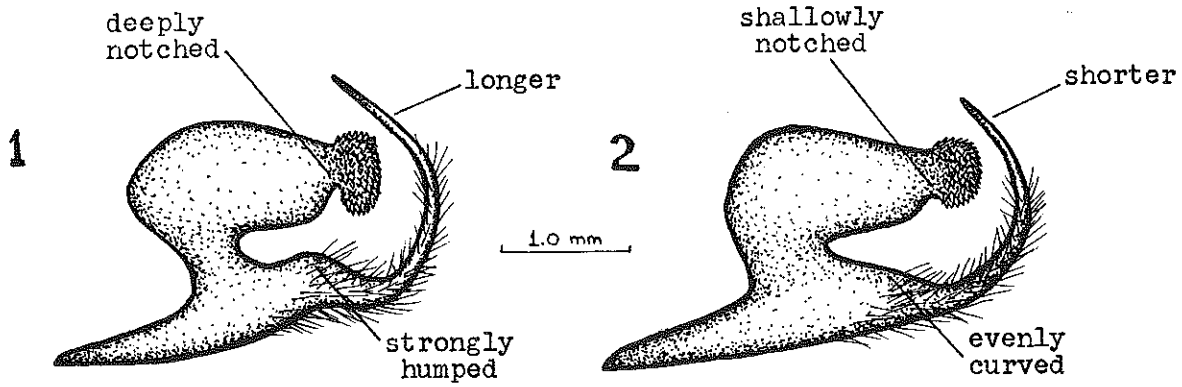
Some Specific Comments on the Species

Philaethria dido and *P. wernickei,* two large black-and-green species very similar on the dorsal wing surface, are clearly distinct on the ventral surface and have consistently different male genital valves (Text-figs. 1 and 2). Furthermore, they are sympatric at least over all of the lower and middle Amazon Basin (*wernickei* as subspecies *pygmalion*) and along the east coast of Brazil as far south as Rio de Janeiro (the Museu Nacional in Rio contains long series of both species from a number of localities). They may be readily distinguished, at times even in flight, by the under surface of the hindwing (Plate I, figs. 1 and 2): *dido* has a much redder groundcolor (*wernickei* is black or gray), large silvered intervenal marginal spots (*wernickei* has only a series of faint submarginal whitish streaks), and a long white costal stripe limited by the subcostal vein (*wernickei* has a short white streak which drops below the vein and covers the black upper border of the green area). The flight of *dido* tends to be higher, more rapid, and less interrupted than that of *wernickei;* both species may be frequently encountered on hilltops. The mature larva of *wernickei* is much more deeply and richly colored than that of *dido* (Beebe, Crane, and Fleming, 1960), with a dark brick-red head and prolegs (orange in *dido*); the pupae of the two species are nearly identical.

Agraulis lucina (Felder), a singular form from the upper Amazon and Andean slopes, should be separated from *A. vanillae,* with which it has been treated as conspecific in the past. The former possesses a dramatically different color-pattern on both wing surfaces and its wings are of a distinctly different shape from those of *A. vanillae* (Plate I, figs. 3 and 4). The two species occur sympatrically in much of the Brazilian upper Amazon and on the Andean slopes of Peru, Ecuador, Bolivia, and Colombia.

In the areas where they commonly fly together, occasional specimens of *vanillae* (*catella* Stichel) show a coagulation of the dark markings on the dorsal wing surface and a reduction of the silvering on the ventral surface, looking thereby somewhat like *lucina* (Plate I, figs. 3 and 4). However, *catella* retains the light forewing apex, broader hindwing, and dark distal spot in hindwing space Rs-M_1, all typical of *vanillae.* In these same areas, occasional specimens of *lucina* are more heavily silvered ventrally, adding to the impression that the two species intergrade. Indeed, they may well interbreed occasionally where they meet, though they occupy different ecological habitats; *vanillae* lives in open areas and second growth, while *lucina* lives in forest clearings.

The overall behavior of *lucina* in the field is closer to that of *Dione juno* or *D. moneta,* which it also mimics in color-pattern, than to



Text-figure 1. *Philaethria dido,* male, left genital valve, external.

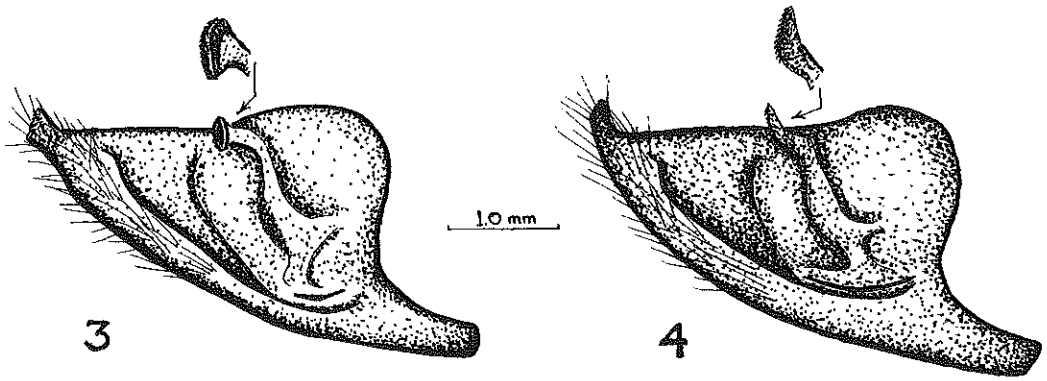
Text-figure 2. *Philaethria wernickei* or *P. w. pygmalion,* male, left genital valve, external.

that of *vanillae*. The egg of *lucina*, expressed with difficulty from the female, is noticeably smaller and more spherical than that of *vanillae*, and a number of expressed eggs failed to hatch. This suggests that the eggs of *lucina* may be laid in clusters, as are those of *juno* (but not those of *vanillae*). Male genitalia of *lucina* could be consistently distinguished from those of *vanillae* (including *catella*) by the form of the process on the inner face of the valve. In *lucina*, the upper flange of the process is flared upward and narrowly serrated, while the lower posterior edge bears no teeth. In *vanillae*, the upper flange is curved inward and heavily serrated, and the lower posterior edge is usually denticulate (Text-figs. 3 and 4).

Eueides pavana, poorly represented in museums, is not at all rare in southeastern Brazil, occurring frequently in all the mountain area and sparsely down foothill canyons to the outwash plains at sea level. Its tendency towards high flight makes it somewhat difficult to capture.

Two color phases of the female exist, evidently in nearly equal numbers. One resembles the orange male, and the other is a pale straw color. Intermediates with the forewing light-colored and part or all of the hindwing orange (Plate I, fig. 5) also may be encountered. The species is sympatric with *Eueides vibilia* over much of the low-altitude part of its range (up to 800 meters, including the city of Rio de Janeiro); the dimorphic female of *vibilia* is quite similar in appearance to *pavana*, and both participate in the mimetic complex of *Actinote* spp. (distasteful Acraeinae), being almost indistinguishable from these on the wing (Plate I, fig. 5).

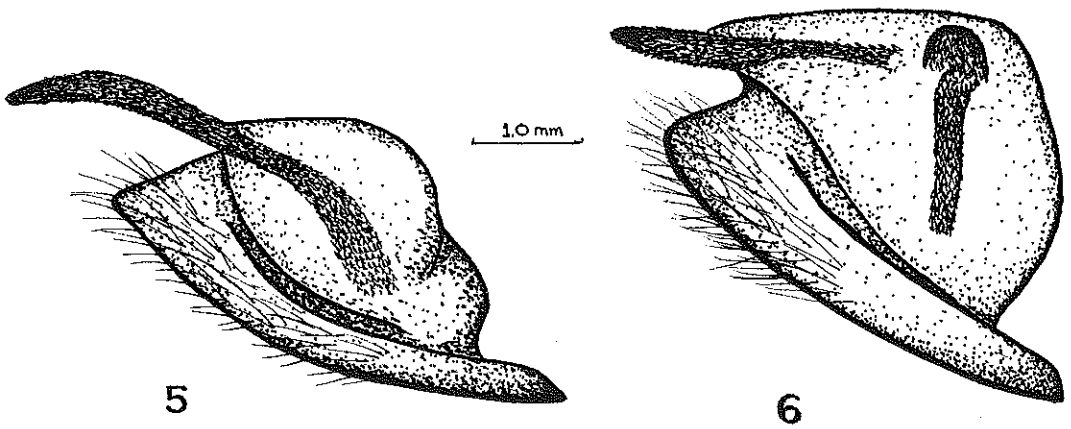
Eueides vibilia is also sympatric with the morphologically very similar *Eueides lampeto* in the Guianas (*l. copiosus*, Plate I, fig. 6), the Brazilian Amazon (*l. copiosus* and *l. lampeto*), and at various points on the eastern slopes of the Andes. As both species are quite localized and not frequently taken by commercial collectors, their micro-sympatry is not easy to prove. The two differ appreciably in size (*lampeto* is appreciably larger), wing-shape, and color-pattern. All races of *lampeto* demonstrate a large diffuse dark spot at the inner angle and an inward-directed dark triangle at the margin of forewing space Cu_1-Cu_2 (a wing area very useful in taxonomy both in heliconians and ithomiines) and heavy dark intervenal postcellular marks on the hindwing, lacking in *vibilia*. No intermediates are known from areas where the species fly near each other. The egg of *E. lampeto carbo* (Coroico, Bolivia, 1600 m) was totally dissimilar to that of *E. vibilia unifasciatus* from nearby Mato Grosso and Rondônia. The egg of *lampeto* is larger, creamy yellow instead of white with a pink cap as in *vibilia*, closely resembles that of *E. isabella*, and is laid singly rather than in large rafts as in *vibilia*. The appearance and individual feeding-pattern of the solitary first-stage larva of *lampeto* are very similar to those of gregarious *vibilia* larvae; both may be distinguished by the light-colored rather than black head from all other known first-stage *Eueides* larvae except *E. aliphera*. Thus, we regard *lampeto* and *vibilia* as closely related but distinct species.



TEXT-FIGURE 3. *Agraulis vanillae*, male, left genital valve, internal, and detail of upper flange of process.
TEXT-FIGURE 4. *Agraulis lucina*, male, left genital valve, internal, and detail of upper flange of process.

Heliconius egeria and *H. astraea,* represented in long series in the Museu Nacional, Rio, consistently show great differences in the male genital-valves (Text-figs. 5 and 6; see also Emsley, 1965), and usually in wing-shape and color-pattern. They apparently are sympatric at least at São Paulo de Olivença on the upper Amazon and at Manicoré on the Rio Madeira, where they do not intergrade morphologically, and so probably should be treated as separate species. Some middle and upper Amazonian and Venezuelan *egeria* (*e. hyas* Weymer) look very much like south-middle Amazonian *astraea* (which lack a name, having been assigned to *e. hyas* in the past; see Part IV for description) (Plate III, fig. 11); *egeria* usually has a more pointed forewing, with the hindwing rays more abbreviated and vein Cu red (in *astraea,* always black). However, as the color-patterns of the two are quite variable, and sometimes closely approach each other where the species fly together, examination of the genitalia is advisable for positive identification.

It is worthy of note that the Amazonian dennis-rayed heliconians (*Eueides tales* and *eanes*, and *Heliconius aoede, burneyi, egeria, astraea, xanthocles, elevatus,* and *demeter*) may be found flying together with red-forewing-band extra-Amazonian subspecies of *erato* and *melpomene,* not only in central Mato Grosso (*e. phyllis* and *m. burchelli* with *aoede* new subsp., *burneyi, xanthocles melete,* and possibly *astraea* new subsp., *elevatus schmassmanni,* and *demeter eratosignis* in the northern part of the state), but also in Peru (*e. favorinus* and *m. amaryllis* with *aoede cupidineus, xanthocles melior, burneyi huebneri,* and *elevatus pseudocupidineus,* and *Eueides tales calathus* at Tingo Maria), north-central Colombia (*e. guarica* and *m. melpomene* with *burneyi lindigii* and *xanthocles flavosia* and polymorphs, and *Eueides eanes* and *tales cognatus* above Villavicencio), and in northern Pará, southeastern Venezuela and adjacent Guyana (*e. hydara* and *m. melpomene* with *aoede* near *astydamia* and *a. aoede, b. burneyi* and *b. catherinae, e. egeria* and *e. hyas, x. xanthocles, x. vala,* and *x.* subsp. incog., *elevatus barii, e. tumatumari,* and *e. roraima,* and *demeter bouqueti* and *d. beebei,* and *Eueides tales surdus* in Obidos to Itacoatiara and northward, Bolivar and western Guyana, and coastal Surinam and Guyane; see also map, fig. 64, and Masters, 1969; many of these species are polymorphic in this area for dennis only/dennis-ray). Upper Amazonian subspecies of *xanthocles* (*x. melete, x. melittus, x. melior,* and *x. flavosia,* plus several additional named and unnamed morphs) are unusual in lacking the subapical yellow forewing band typical of the lower Amazonian and Orinocan *x. xanthocles* and *x. vala* (*x. paraplesius* and the southeast Venezuelan race, probably new, are intermediate, showing partial fusion of the two yellow bands). They also possess many of the minor characters (Emsley, 1965) of *H. aoede:* paired intervenal submarginal white spots, a longer an-



TEXT-FIGURE 5. *Heliconius egeria,* male, left genital valve, internal.
TEXT-FIGURE 6. *Heliconius astraea,* male, left genital valve, internal.

terior red basal spot, and a longer yellow costal stripe on the ventral surface of the hindwing; and prominent yellow lateral dots and intersegmental annuli on the abdomen. The males, however, have typical *xanthocles* genitalia and broad, rounded forewings, while sympatric subspecies of *aoede* (in southwestern Brazil, lowland Peru, and Venezuela) have the genitalia and deep triangular forewing, with an exceptionally broad androconial area on the costal half of the upper hindwing, typical of that species. Females in these areas may be quite difficult to distinguish.

In Mato Grosso, males of *xanthocles melete* have a rapid, fluttery flight, often quite high above the ground, and cover a large area in their promenading. The species is thus somewhat reminiscent of *H. nattereri* (see Part I and Part III), another primitive *Heliconius* occurring in extra-Amazonian Brazil, although in *xanthocles* the sexes are identical, though differing in flight habits.[4] It was not possible to express fertile eggs from the short abdomens of either *H. aoede* or *H. xanthocles* females, suggesting that the eggs may be laid all at once, and the caterpillars may be gregarious. This is so in *H. antiochus, H. sara,* and *Eueides vibilia,* other species with short abdomens, which give no fertile expressed eggs.

Some Notes on the *Melpomene*-group

Four species must be added to the *melpomene*-group as defined by Emsley in 1965 as part of the "*numatus*-group".[5] One of the two Brazilian species (*H. besckei*) was mentioned as probably distinct in Emsley's 1965 revision; later experiments have confirmed its specific status. The second species (*luciana,* which may be shown to be conspecific with *elevatus*), is unusual in that it escaped detection until 1960 (Lichy).

The tropical and subtropical habitat preferences of *H. melpomene* and *H. besckei,* respectively, in southern Brazil, do not often permit their occurrence at the same locality. Three areas where they have been found flying together are central Espírito Santo (in river valleys and up the mountain slopes to at least 1000 meters, principally in late summer), the foothill canyons near Rio de Janeiro (where *melpomene nanna* is very scarce), and the Brasília area in the central plateau (where *besckei* flies with *m. burchelli*). The two may also be found together over much of southern Mato Grosso and in northern Goiás and other isolated mountain areas in northeastern Brazil. Typical *besckei* also have been recorded as far west as Santa Cruz de la Sierra in Bolívia, where they fly with a polymorphic population of *melpomene* in which the predominant subspecies *amandus* is partially infused with genes from the Amazonian *penelope*.

In all of these areas, no signs of intermediate characters have been found in many dozens of *melpomene* and *besckei* examined. Eggs of *besckei* from Petrópolis (1000 meters, near Rio de Janeiro) were bred through to adults on *Passiflora sidaefolia.* The egg, larva, and pupa were very similar to but distinct from those of *melpomene* (see Beebe, Crane, and Fleming, 1960). It should be noted, however, that these early stages are subject to much permissible variation, and that striking differences were observed by the first author in the size, color, and patterns of the eggs, larvae, and pupae of geographically separated but indubitably conspecific populations and subspecies of *Heliconius melpomene, H. erato, H. wallacei,* and many silvaniform *Heliconius.* Furthermore, male *besckei* showed no response to virgin females of *H. melpomene flagrans* in Trinidad (Emsley, 1970); indeed, they showed no reaction to any exclusively red-banded heliconians, but indulged in social chasing with red-and-yellow banded *H. erato phyllis* reared there from a previous shipment from Rio.

In life, *H. besckei* tends to have a higher and more fluttery flight, but also with more planing, than *H. melpomene.* The tip of the male genital valve in *besckei* is elongated, silvaniform rather than melpomeneform, similar to that observed in the closely allied and evidently allopatric species *H. elevatus* (Turner, 1967b). The ventral hindwing costal streak and basal spot complex are so different between *besckei* and *elevatus,* however, that it is highly unlikely that they could be conspecific. They may eventually be found flying together in central or southwestern Mato Grosso, meeting-ground of the Amazonian and southeastern forms of *melpomene* which these two species resemble in their respective ranges.

The existence of closely parallel species in the *melpomene* group and the *sara* group, *H. cydno —H. sapho*[6] and *H. pachinus—H. hewitsoni,* suggested the possibility of a *melpomene*-linked species parallel to the *sara*-linked *H. antiochus.* This species, *luciana* Lichy, was finally discovered in southern Venezuela in the late 1950s. A single female of *luciana,* from near Bôa Vista in the Brazilian territory of Roraima, on the southern slope of the Venezuelan highlands, is present in the collection of the Museu Nacional, Rio. The wing-pattern of this specimen is very similar to that of the sympatric and common *H. antiochus alba* on the dorsal surface. However, there are elements in common with *cydno* and *elevatus* (both in the *melpomene* group)

[4] A further presumably quite primitive heliconian species observed to have very similar large-scale promenading behavior is *Heliconius hecalesia formosus* in Panama.

[5] We have observed the complete sympatry of *Heliconius heurippa* with *H.m. melpomene* (Plate II, fig. 8) in the Rio Negro area above Villavicencio, Colombia, where they are among the 32 species of heliconian present (of a total of 51 so far recorded, with six more expected, in Colombia—a very high percentage of the 66 species in the tribe). We are grateful to Dr. E. W. Schmidt-Mumm and his brother Helmut of Bogotá for opportunities to visit the latter's property on the Rio Negro in 1969 and 1971. Here, *H. heurippa* and *H. melpomene* fly together in the altitude range 600 to 1600 meters, with *melpomene* found principally on the forest edge at lower elevations, and *heurippa* principally in clearings within the forest at higher elevations. However, they are frequently observed together. The eggs of *heurippa* (expressed from females) had more vertical ridges (17-18) than those of *melpomene*; the caterpillars and pupa, reared from these eggs showed many small but consistent differences from the corresponding early stages of *melpomene*. We judge *heurippa* to be a good "splinter species," probably originally arising from a yellow-banded ancestor of *melpomene* (see Emsley, 1964). The red outer band of *heurippa* is very inconspicuous in the field, and not likely to be useful in courtship recognition (see below, in text).

Heliconius cydno, a closely related species which also could be regarded as involved in the ancestry of *heurippa,* and which has nearly identical field behavior with the latter species, lacks the red basal dot pattern on the ventral surface of the hindwing shared by *melpomene* and *heurippa,* having in its place a variable U-shaped red-brown marking across the middle of the wing. *H. cydno* is absent from the restricted area where *heurippa* flies above Villavicencio, but could reach it, as have *H. erato guarica, m. melpomene,* and *charitonia bassleri,* presumably by going around to the north in southwestern Venezuela, or across several low passes in the southeastern Colombian cordillera. *H. cydno* in near-typical forms is definitely present on the southeastern slopes of the Venezuelan cordillera at Barinitas, and (together with another central valley species, *H. ismenius,* which has also been recorded near Villavicencio) on the Amazonian slopes of the eastern Colombian cordillera above Florencia. In the central valleys of Colombia, the morphologically very close *cydno* and *melpomene* are common, fly together, and occasionally hybridize, producing little-known intermediate forms; these either strongly resemble *melpomene* (*rubellius, seitzi*; K. B. took one of these in Victoria, Caldas, on Jan. 21, 1971, in normal courtship with a female *melpomene,* not recognizing the hybrid until it was in the net), or have the double yellow-and-red forewing band as in *heurippa* and strongly resemble *cydno* in the field (*wernickei, emilius*). All of the hybrids have at least part of *cydno*'s U-shaped red-brown mark on the ventral hindwing (this is variable enough in the parent populations of *cydno* to admit its near absence in a hybrid, however); all show reduced but clear red basal spots intermediate between the three large dots of *melpomene* and the lack of spots of *cydno.* No hybrids are known to us from the *heurippa* area to the east of the eastern cordillera, and *heurippa* does not show hybrid characters other than the double-colored band.

The polymorphic yellow-banded species *Heliconius timareta* is completely sympatric, with no signs of intergradation, with the very different *H. melpomene plesseni* (and occasionally, with some of its intergrades to *H. m. aglaope*) in eastern Ecuador between 1000 and 1800 meters (Plate II, figs. 9 and 10). The field behavior of *timareta* is very similar to that of *heurippa* and *cydno*; it flies fairly high above the ground, and indulges extensively in repetitious promenading over set courses. It is found much more inside the steep pre-montane forest than is the sympatric *melpomene,* which prefers edges and riverbanks. *H. timareta* should be regarded as another distinct "splinter species," isolated at moderate elevations in the eastern Ecuadorian river valleys, and possibly closer systematically to *cydno* than to *melpomene.* Reproductive isolation from *melpomene* almost surely takes place by a color-courtship mechanism (see below, in text).

[6] The species regarded as *sapho* in Emsley (1965) is divisible into at least two fully sympatric species (Plate II, fig. 7) with dramatically different flight habits and behavior. One, represented by *sapho* and probably by *leuce,* occurs from southern Mexico to western Ecuador, flies high and slowly, frequently visits flowers, and is quite attached to one place both when feeding and when occupying a territory. The other, rep-

resented by *eleuchia* and *primularis,* and probably *eleusinus* and *ceres,* occurs from central Panama (Colon) to western Ecuador, and flies low, rapidly, and in a straight line, not stopping at flowers or remaining over long periods in one area. We are grateful to Dr. E. W. Schmidt-Mumm of Bogotá for detailed information on the sympatry and habits of these species in Colombia; we have fully confirmed his observations in Panama, Ecuador, and in museum collections. Dr. Tarsício Escalante of México also provided key information on the field behavior of *H. sapho leuce.* Where *sapho* and *eleuchia* fly together (Panama, central Colombia, and western Ecuador), they show no intergradation and rarely occupy the same habitats in the forest; in these areas, the latter species invariably has a shorter red costal streak and anterior red basal spot on the ventral surface of the hindwing, in relation to those of the former. Where only one form in the complex is known (*leuce* from México to Costa Rica, and *eleusinus* and its yellow morph *ceres* along the west coast of Colombia), this form shows the field behavior of *sapho* but the shorter red spots of *eleuchia.* Tentatively, *leuce* is placed with the former species; a short series from Nariño in extreme southwestern Colombia, present in the Instituto Oswaldo Cruz in Rio, strongly suggests intergradation of *primularis* with *eleusinus* through *ceres* and varieties; we thus tentatively place these three forms together with *eleuchia.*

A further very different-appearing and allopatric form which flies east of the Andes in Colombia, Ecuador, and northern Peru, *H. congener,* has the field habits and shortened red basal spots of *eleuchia.* If its reported chromosome number (33) is correct (de Lesse, 1967; presently being reconfirmed), it should stand as a good species. The allopatric *H. hewitsoni,* known only from the "Chiriqui" faunal region in southern Costa Rica and northwestern Panama, seems to merit its presently accepted specific status. There are thus most probably four species in the *sapho*-complex, apparently still in rapid evolution as the most recent major group in the Heliconiini.

Heliconius cydno also shows a separation into forms (*c. chioneus* and *c. cydnides*) which closely resemble *sapho* and *eleuchia* in Colombia. We have little field experience with the forms related to *cydnides,* and cannot completely eliminate the possibility that *cydno* may eventually be divisible into more than one species when more information becomes available, although this seems unlikely. In addition, *cydno* has some very unusual related forms in Colombia (*c. hermogenes* in the upper Magdalena valley, *c. weymeri* and its form *gustavi* in the Cauca Valley) which do not resemble members of the *sapho*-complex, but approach other species of *Heliconius* (notably *hecalesia* and *erato chestertonii*) flying in the same areas. Kaye (1917) argued for the separation of these forms, which also frequently show a diminished or absent U-shaped red-brown mark on the ventral hindwing surface, from *cydno.* In defense of the unity of the species *cydno,* the following facts are presented: (1) *weymeri* and *gustavi* are evidently conspecific with *cydnides* and *cydno zelinde,* since complete intergradation among all of these forms is evident in series taken west of the cordillera northwest of Cali where low passes permit them to meet and mix (some forms illustrated in Holzinger & Holzinger, 1968); and (2) the intergradation of *c. cydno* and *hermogenes* can be seen in many intermediate specimens known from the middle Magdalena valley, and *hermogenes* apparently meets and intergrades with *weymeri* in select areas of the central cordillera. Thus, present evidence suggests the existence of but a single, if highly variable, species, *cydno,* in this complex.

An additional member of Emsley's *sara*-group, *H. hygiana,* is evidently interfertile with *H. clysonimus.* A polymorphic population exists northwest of Cali, Colombia, at high altitudes on the Pacific slope of the western cordillera, which includes occasional specimens of near-typical *clysonymus* and *hygiana,* a number of intermediates in color and pattern, and several unique endemic forms as well; morphologically, members of this population are nearer *hygiana,* but intermediate characters can be seen. It is probable that these two species, which have identical and quite singular field behavior among members of the genus, should be combined in spite of their appreciable morphological differences (Emsley, 1965; Holzinger and Holzinger, 1970). *H. hygiana* occurs from central-western Colombia through western Ecuador, at moderate to high elevations; *H. clysonimus* is known from similar elevations from Costa Rica to eastern Venezuela and southern Ecuador, but is sparse in central Colombia. It has been found on the inner face of the western cordillera near Cali, and in eastern Nariño; in these areas, where it can cross the western cordillera through passes below 2000 meters, it can meet and apparently occasionally interbreed with *hygiana.* The two are perhaps best regarded as "semi-species," very closely related in an evolutionary sense and not yet with perfect reproductive isolation in spite of long and nearly complete geographic isolation. For more details on the intermediate population northwest of Cali, see Holzinger and Holzinger, 1970.

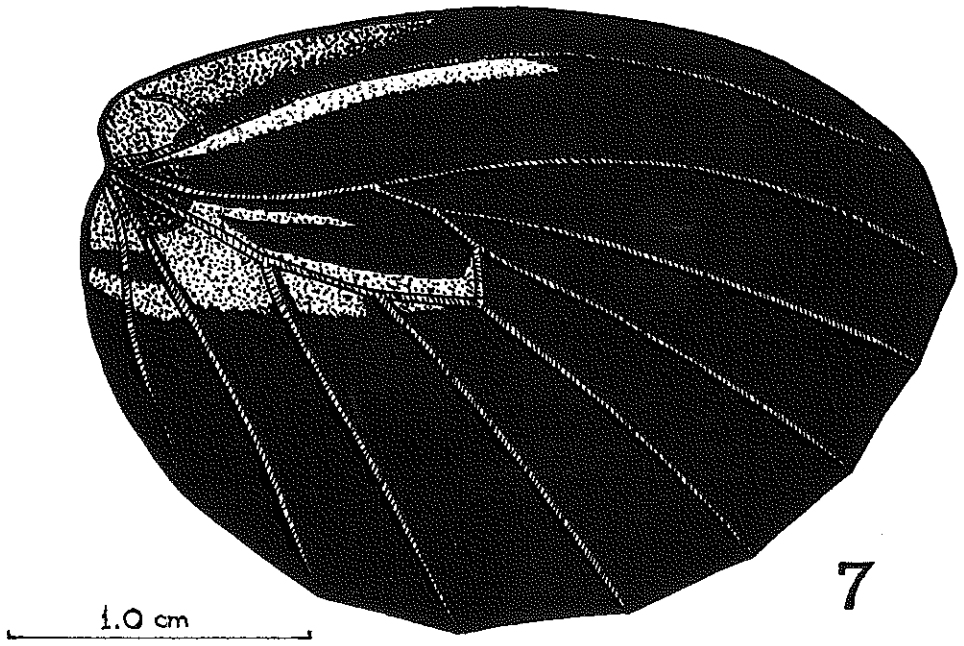
on the ventral surface of the hindwing. In particular, there are a yellow streak under vein Sc-R_1 shared in the genus only by *elevatus,* and part of the unusual U-shaped red-brown bar of *cydno* (Text-fig. 7). This female was dissected; the bursa copulatrix has signa (Text-fig. 8) placing the species clearly within the *melpomene*-group (Emsley, 1965). The metapretarsus (Text-fig. 9) has paronychial processes nearly equal in length, and the abdominal processes (Text-fig. 10) are narrow, strongly curved at the base, and recurved near the outer tip, further confirming the placement of the species near *cydno* and *elevatus* in the *melpomene*-group.

In January 1970, K. B. examined the type-series of *luciana* (two pairs) in the Facultad de Agronomia, Universidad Central de Venezuela, Maracay, courtesy of Dr. Francisco Fernández Yépez of the Facultad. Although dissection of a male was not performed, the tip of the valve was examined under a 80x microscope and proved to be typically silvaniform, very similar to that of *H. elevatus,* but not like the abbreviated tip of the valve in *cydno.*

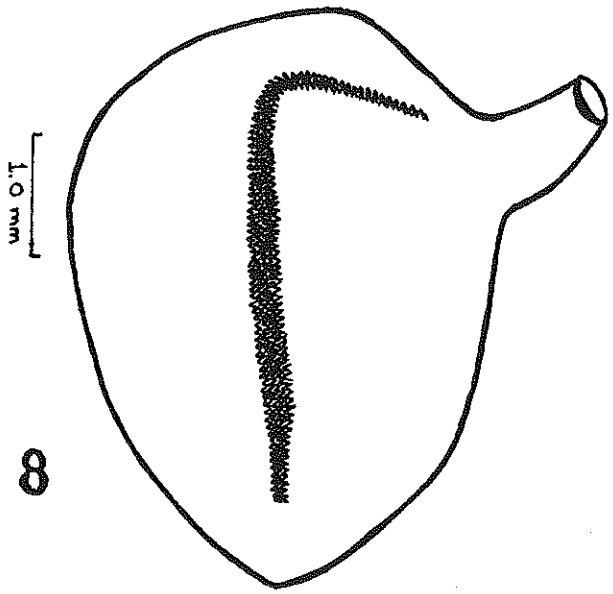
A most unusual series of *luciana* was taken by Mr. Harold Skinner of La Victoria, Venezuela, in April 1968 at Mantecal on the upper Rio Cuchivero in Bolivar, Venezuela, well north of the type-locality of the species. No two specimens of this series are alike; included are the typical white-banded form, a variety of yellow-banded forms with very variable forewing band shape and spots, and variable markings at the base of the hindwing, and one specimen which even has long yellow rays on the hindwing. We illustrate on Plate III (figs. 12-15), in addition to the type-series of *Heliconius luciana,* eight specimens from this series taken by Mr. Skinner.

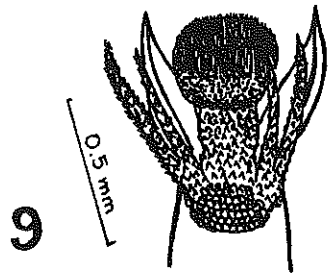
In early 1970, a party of six collectors, including Mr. Skinner and Dr. Fernández Yépez, returned to Mantecal and captured a further fourteen *luciana,* all yellow-banded. According to Dr. Fernández Yépez, the species flies quite high above the ground and is difficult to capture except when it descends to flowers. Sr. Francisco Romero R., another member of the party, described the males as flying at more than ten meters of height above the ground, descending only occasionally to chase other passing *Heliconius* or species with similar flight or appearance.

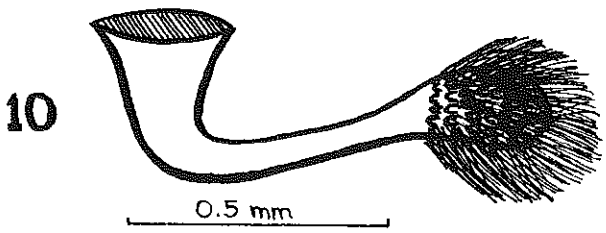
In February 1970, K. B. was privileged to obtain through the kindness of Mr. Skinner a single male (Plate III, fig. 15) from the Mantecal series of *luciana.* The genital valves of this specimen (Text-fig. 11) are very close to those of *elevatus,* but show a somewhat less elongated



TEXT-FIGURE 7. *Heliconius luciana,* paratype female in the Museu Nacional, Rio de Janeiro, from Bôa Vista, Roraima, hindwing, ventral, schematic.



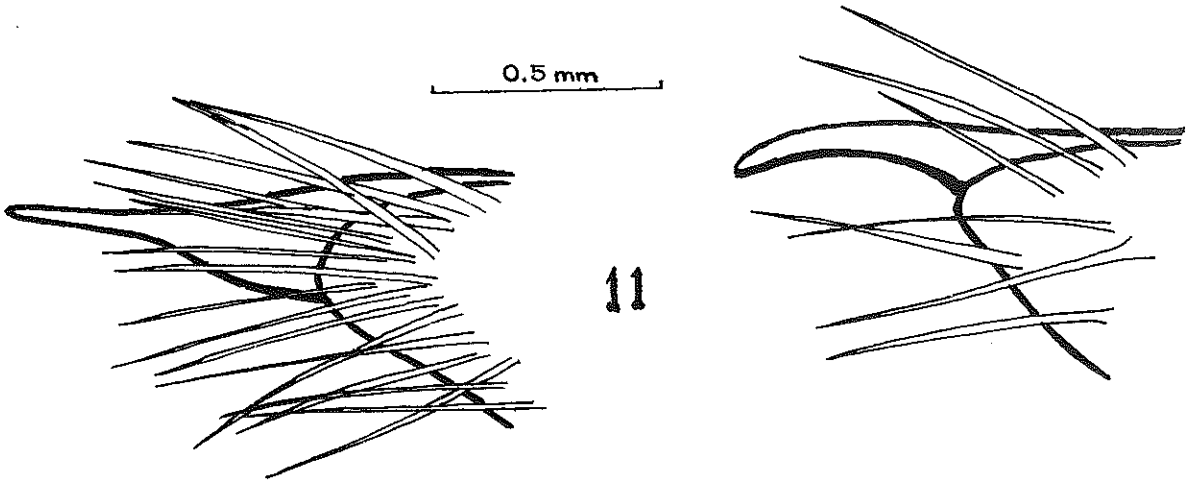




TEXT-FIGURE 8. *Heliconius luciana,* same female, bursa copulatrix.
TEXT-FIGURE 9. *Heliconius luciana,* same female, metapretarsus.
TEXT-FIGURE 10. *Heliconius luciana,* same female, abdominal process.

general form, a narrower dorsal process, and no apical tuft of bristles regarded as typical in *elevatus* genitalia (Turner, 1967b). However, as these characters have all been shown to be variable in the silvaniform valves, though the thickness of the dorsal process is usually reliable, we also compared female genitalia of the two species. The form of the signa on the bursae copulatrices is indistinguishable in the two, but *elevatus* possesses a vulvar plate markedly more lobed at the corners, and abdominal processes (Text-fig. 12) thicker, less curved at the base, and less recurved near the tip than those of *luciana*. These minor morphological differences between the two species are accompanied by significant differences in both major and minor elements of color-pattern between *luciana* and the nearest races of *elevatus* (*tumatumari* and *roraima*; Turner, 1967b, and Masters, 1969). *H. luciana,* in contrast to *elevatus,* possesses inclined rather than vertically arranged elements in the forewing subapical band; no dennis, but a yellow hindwing bar; usually a yellow stripe along the forewing cubitus; usually several red basal dots on the ventral hindwing; small or absent postcellular yellow elements on the forewing; and in most specimens a light submarginal spot in forewing space Cu_1-Cu_2, an element which we have found significant in correlation of the silvaniforms (see Part V). All of these facts lead us to regard *luciana* as specifically distinct from *elevatus*. However, at least one yellow-banded *luciana* has been taken at San Juan de Manapiare, 100 Km southwest of Mantecal (map), which could easily be interpreted as an intermediate between typical *H. luciana* from farther south and *H. elevatus roraima* from farther east. Both species are presently so little-known that they have not been found flying in the same area; *luciana* has been found in Venezuela to the west of areas occupied by *elevatus,* and the latter species has not yet been captured in Roraima, Brazil. Thus, until more collecting in intermediate areas or interbreeding can be performed, we cannot completely eliminate the possibility of *luciana* being conspecific with *elevatus*. Further specimens of *luciana* captured in 1971 in central Venezuela and Bôa Vista conform to previous patterns, not casting new light on the problem; a population was discovered in Bolivar with equal representation of yellow and white-banded individuals.

It is of considerable interest that these five parallel species to *melpomene* within its same group (*H. timareta, heurippa, elevatus, luciana,* and *besckei*) apparently retain yellow as a courtship-release color, while red is distinctly the important color in *melpomene* (Emsley, 1964, 1970; Crane, 1957). The first three of the species have bright yellow forewing bands in all known forms, and maintain these, in the first with complete suppression of red (in the nominate form), in spite of being sympatric with red-banded forms of *melpomene*. The rare *luciana,* also sympatric with red-banded *erato* and *melpomene* in all its known localities, exists in yellow-banded and white-banded morphs. Either color is probably equally effective in courtship release, as they have similar reflectance and are interchangeable in many silvaniform heliconians such as *ismenius* and *hecale*



TEXT-FIGURE 11. *Heliconius luciana,* male from Mantecal, Rio Cuchivero, Bolivar, Venezuela, H. Skinner leg., tip of genital valve (at right), compared with valve tip of *Heliconius elevatus tumatumari* (at left), from north of Obidos, Pará (the latter has the dorsal process, normally curved inward toward the dorsal midline, straightened out for comparison).

(Part V). *H. besckei,* as mentioned above, seems to respond socially to yellow but not to red (Emsley, 1970). Yellow is presumably a more ancient color (Emsley, 1964), typical of the genus *Heliconius* and present in all of its members (chemical composition 3-hydroxy-L-kynurenine; K. Brown, 1967, and Brown and Domingues, 1970). This color predominates in the male of the most primitive *Heliconius, H. nattereri.* Thus, these five species parallel to *melpomene* may have been "left behind" in an evolutionary sense when *melpomene* appeared as a widespread and red-responding species, or they may have developed independently from the more primitive silvaniforms, which at least the last three resemble morphologically more than they do *melpomene.*

The *Silvana*-group in Extra-Amazonian Brazil

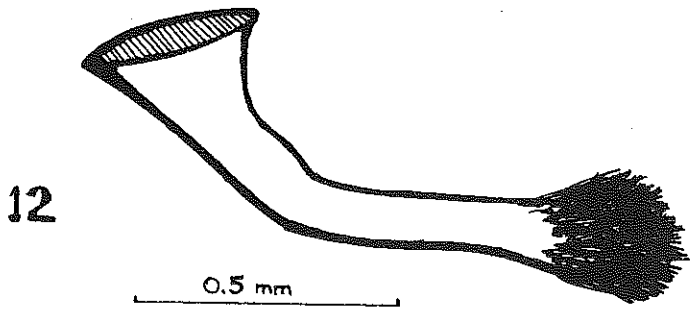
Our use of *silvana* and *ethilla* as species names, and the former as a group name for the silvaniforms of older authors, rests on data which is detailed in the fifth part of this series. With respect to the latter, a cross of *narcaea* from Rio de Janeiro with Trinidadian *ethilla* revealed good fertility in the offspring of the F_2 backcross to the latter, thus confirming their conspecificity as suggested by morphological studies (Emsley, 1965).

The polymorphism of *ethilla narcaea* in Rio was clarified by rearing eggs obtained from a female of the rare dark form *satis*; five adults, including three *narcaea* and two *satis,* were obtained from seven eggs. We thus believe that *satis* is merely a dark color-variant with a single gene or closely linked genes controlling its three constant color-pattern differences from *narcaea* (*N*-locus?—Turner, 1968 and 1971, and Sheppard, 1963).

In the cooler interior of Brazil, *narcaea* locally intergrades smoothly to the striking form *polychrous,* which has an excess of yellow on both wings, with almost complete suppression of orange. A very few areas are known where *polychrous* is nearly monomorphic, but it usually flies together with *narcaea* and interbreeds freely with it.

Kaye (1917) mentioned the existence of an unusual brand on the inner margin of the ventral surface of the forewing of male *robigus* and *ethra,* absent in Amazonian *silvana,* and on this basis, coupled with the extremely elongated genital valves of the first two forms, separated these from *silvana.* We have verified in the collection of the Museu Nacional that this brand is present in all *ethra* and *robigus,* and also, to a varying degree, in over half of all Amazonian *silvana.* The form of the genital valve in Amazonian *silvana* is also extremely variable, frequently being as elongate as those of the southern subspecies. Both the brand and the genitalia are variable characters in many subspecies of *H. numata, hecale,* and *ethilla.* The caterpillar and chrysalis of some *ethra* are noticeably different from those of Amazonian and Bolívian *silvana,* but these differences do not surpass those observed in geographically isolated subspecies of other *Heliconius.* In spite of the essentially complete geographical isolation of *ethra* from *silvana,* we regard the possibility of reproductive isolation between the two as very small, and thus maintain them for the present as a single species.

Recent breeding results have suggested that, in spite of many constant differences in pattern, behavior, and early stages, the silvaniform species *numata* and *silvana* may interbreed freely in some areas of the Amazon Basin, where they are sympatric and common over nearly six million square kilometers. In this paper, and until more extensive field and insectary experiments can be completed, the two species are still maintained as distinct.



Text-figure 12. *Heliconius elevatus tumatumari,* female, Obidos, abdominal process.

An Explanatory Note on Materials and Methods

We have based our conclusions on examination and study *in vitro,* with standard biological dissection methods, of all known heliconians, and extensive field experience with 59 of the 66 species recognized in the tribe. A biological rather than narrowly morphological definition of the species is advanced and, in the systematic ordering of these species, considerable weight has been placed upon *in loco* observations of adult behavior and micro-sympatry, and on characters of the early stages where these are known. Field observations and breeding were realized in Panama, Jamaica, Colombia, Venezuela, Trinidad, Guyana, Ecuador, Peru, Bolivia, and all areas of Brazil except the extreme northeast and the upper Rio Negro. Dr. Woodruff W. Benson also contributed additional field information from Costa Rica and Guyana. Complete Heliconiini collections were examined in the Museu Nacional in Rio de Janeiro; the Facultad de Agronomia in Maracay, Venezuela; the Allyn Collection (including the W. J. Kaye collection) in Sarasota, Florida; the Carnegie Museum in Pittsburgh, Pennsylvania; the Cornell University Entomology Department in Ithaca, New York; and the U.S. National Museum in Washington, D.C. Partially complete collections were studied of each of the authors, and of the Departamento de Zoologia in Curitiba, the Museu Goeldi in Belem, the Instituto Oswaldo Cruz in Rio, the Universidade Federal Rural of Rio de Janeiro, P. Gagarin and the late R. F. d'Almeida in Rio, L. W. Harris in Lima, E. W. Schmidt-Mumm in Bogotá, G. Small in the Canal Zone, F. Romero and H. Skinner in Venezuela, and W. Benson from Costa Rica and Guyana, among others. Further discussion of methodology is presented in Part III.

Summary

1. The taxonomy, variation, and zoogeography of heliconians are discussed, with particular reference to the 18 species regularly occurring in extra-Amazonian Brazil.

2. Significant cyclical annual variations in the abundance of species are noted, especially in the more subtropical areas and on the margins of the Amazon Basin; some possible mechanisms for these variations are discussed.

3. The following systematic changes are suggested in the tribe Heliconiini as defined and revised by Emsley (1963, 1964, 1965), based upon morphological study of museum specimens, field observation, breeding experiments, and proof of gross sympatry over large areas with or without evident intergradation:

a. *Philaethria wernickei,* and its Amazonian subspecies *P. w. pygmalion,* are separated from *P. dido.*

b. *Agraulis lucina* is separated from *A. vanillae*; the apparently transitional form *A. v. catella* may result from occasional hybridization, but appears to be true *vanillae.*

c. *Eueides lampeto* is separated from *E. vibilia*; the relationship of the latter to *E. pavana* is discussed.

d. *Heliconius astraea* is separated from *H. egeria*; where the two are sympatric, they are often nearly indistinguishable in color-pattern, but differ morphologically.

e. *Heliconius heurippa, H. timareta* and its forms, and *H. besckei* are separated from *H. melpomene.*

f. *Heliconius luciana* is added to the list of species, and fully discussed; its relationship to *H. elevatus,* still not perfectly defined, is explained.

g. *Heliconius eleuchia* with its subspecies *primularis,* and probably with *eleusinus* and its yellow morph *ceres,* are separated from *H. sapho. Heliconius congener* is also regarded as separate from *H. sapho.*

h. The species *H. hygiana* and *H. clysonymus* appear to be interfertile where they occasionally meet in western Colombia; the two are combined to form a single species *clysonymus*, though *hygiana* may be best regarded as a nearly isolated semi-species.

4. The probable use of yellow as a courtship-release color by five *Heliconius* species, closely parallel to the red-responding *H. melpomene,* is suggested.

5. A complete synopsis of known and hypothetical extra-Amazonian heliconian species in Brazil is presented, with behavioral and food-plant data and geographical distribution given for each species (Appendix I).

6. A brief synopsis of the heliconian species known from Amazonian Brazil is presented (Appendix II); the approximate divisions of the Amazonian subspecies of *erato* are defined, with indication of hybridization zones (map).

7. A brief summary of the systematic conclusions of this paper and of Part V (on the silvaniforms), which brings the number of species recognized in the tribe Heliconiini up to 66, is presented, with indication of the systematic problems still imperfectly resolved in the tribe (Appendix III).

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APPENDIX I

A Synopsis of the Heliconians of Extra-Amazonian Brazil

In polymorphic species, only significant colormorphs with well-established names are included in this synopsis.

Ranges are given for extra-Amazonian Brazil only. Abbreviations used for states are those standardized for use in Brazil: BA, Bahia; CE, Ceará; DF, Distrito Federal; ES, Espírito Santo; GO, Goiás; GB, Guanabara (city of Rio de Janeiro, formerly the Distrito Federal before the creation of Brasília); MA, Maranhão; MG, Minas Gerais; MT, Mato Grosso; PB, Paraíba; PR, Paraná; PE, Pernambuco; RJ, Rio de Janeiro; RS, Rio Grande do Sul; RN, Rio Grande do Norte; SC, Santa Catarina; SP, São Paulo. See map.

Indications of preferred flowers are: R = red (*Lantana, Gurania,* red *Bidens, Passiflora coccinea,* Poinsettia, Bromeliaceae); M = magenta (*Passiflora kermesina*); B = blue (*Stachytarpheta,* many *Eupatorium*); Y = yellow (*Oxypetalum,* yellow *Bidens,* many Compositae); W = white (many *Eupatorium,* Orchidaceae, Compositae).

The larval food-plants represent a very preliminary list. The passifloraceous species have been identified by the authors, by Dr. W. W. Benson, by Dr. C. M. Biezanko, and by Appariciο P. Duarte, following Killip's recent revision and Masters in Martius, *Flora Brasiliensis,* and more recent studies in Brazil, especially by Sacco; and by Dr. Stephen S. Tillett of Barquisimeto, Venezuela, following Killip and his own investigations. Tentative identifications are indicated with a question mark; several of the species used as food-plants by Brazilian heliconians are undoubtedly new. All the information on food-plants for Santa Catarina and Rio Grande do Sul is taken, with permission, from Biezanko, 1969. Food-plant records are based on field observations, usually on several occasions and in different areas, of feeding larvae and ovipositing females. For earlier works on the immature stages of Brazilian heliconians, see Turner (1967a).

A. NORMALLY EXTRA-AMAZONIAN HELICONIANS

Philaethria Billberg, 1820.

dido (Linné, 1763) (Plate I, fig. 1). Eastern coastal lowlands in forest at least from PB to RJ; not certain if present in the extreme south or in the interior (possibly marginal in central MT). Very localized and rather rare south of ES. Hilltops, though not strongly. Flowers W, Y, B, rarely R. Caterpillars solitary: *Passiflora mucronata* (ES); refused *P. alata, P. speciosa* (whose close relative *P. vitifolia* is accepted in Colombia and Panama), *P. violacea, P. jileki,* and *Tetrastylis ovalis* (ES).

wernickei wernickei (Röber, 1906) (Plate I, fig. 2, and Plate IV, fig. 16). Entire area in forest and on edges, commoner southward (but rare in coastal RS), very rare in central plateau except in central MT (where flies in cerrado near gallery forests); usually quite localized. Intergrades perceptibly to *w. pygmalion* (Fruhstorfer, 1912) northward. Hilltops. Flowers W, Y, B, R. Caterpillars solitary: *Passiflora sidaefolia* (GB, RJ), *P. coerulea* (SC, RS), *P. suberosa* (RS), *P. elegans* (RS), *P. mansii* (MT).

Dryadula Michener, 1942.

phaetusa (Linné, 1758) (Plate IV, figs. 20 and 21). Entire area in open country (fields, marshes, and scrublands), strongly localized but common where found. Flowers W, Y, R. Caterpillars solitary: *Passiflora mucronata* (GB), *P. misera* (BA), *P. mansii* (MT).

Agraulis Boisduval and LeConte, 1833.

vanillae (Linné, 1758) *maculosa* (Stichel, 1907) (Plate IV, figs. 17 and 18). Entire area, common to abundant, in open country only or in large cultivated areas within the forest. Flowers R, B, W, Y. Caterpillars solitary but tolerant: *Passiflora ichthyura* (ES), *P. mucronata* (GB), *P. edulis* (GB, BA, DF), *P. odontophylla* (?) (ES), *P. kermesina* (ES), *P. speciosa* (ES), *P. violacea* (ES), *P. quadrangularis* (GB, ES), *P. coerulea* (SC, RS), *P. mansii* (MT).

Dione Hübner, 1819.

juno juno (Cramer, 1779) (Plate IV, fig. 19). Entire area in forest clearings, but very rare in interior plateau; quite localized but common where encountered. Hilltops. Flowers R. Caterpillars strongly gregarious with coordinated behavior: *Passiflora edulis* (GB, RJ, BA), *P. alata* (GB, ES), *P. speciosa* (ES), *P. odontophylla* (?) (ES), *P. coerulea* (SC, RS).

juno suffumata Hayward, 1931. Isolated populations in the Brasília area; to be expected elsewhere in south-central Brazil (described from Paraguay). Both fore- and hindwings heavily suffused with black from margins inward; some specimens in populations in central MT tend towards this suffusion. Flowers R, B. Caterpillars gregarious: *Passiflora cornuta* (DF), *P. alata* (DF).

moneta moneta Hübner, 1825 (Plate IV, fig. 22). Southwestern MG, western SP and PR, and SC and RG, common in late summer and fall in open country and cleared areas within the forest. Perches in afternoon, and roosts at night on projecting tips of grass in open areas. Flowers R, W, Y. Caterpillars solitary: *Passiflora violacea* (SP).

Dryas Hübner, 1807.

juno juno (Cramer, 1779) (Plate IV, fig. 23 and 24). Entire area in all habitats, less common in interior plateau. Flowers R, W, Y, B. Caterpillars solitary and cannibalistic: *Passiflora organensis* (GB), *P. truncata* (GB, SP), *P. sidaefolia* (GB), *P. misera* (BA), *P. capsularis* (GB, SP), *P. quadrangularis* (RS), *P. coerulea* (RS), *P. edulis* (GB, RS).

Eueides Hübner, 1816.

aliphera aliphera (Godart, 1819) (Plate IV, fig. 28). Entire area, strongly localized, almost always encountered very near its food-plant. Flowers W, Y. Caterpillars solitary but tolerant: *Passiflora violacea* (GB, RJ, SP, MG, ES, BA, DF), *P. coerulea* (RS), *P. quadrangularis* (RS), *P. coccinea* (MT), *P. sidaefolia* (GB).

vibilia vibilia (Godart, 1819) (Plate I, fig. 5). Very local on coastal plain in deep forest, up to moderate elevations in the coastal mountains and river-valleys, south at least to PR. Observed in apparent unidirectional migration in late summer in ES, from the valley of the Rio Doce SE over the mountains towards the coast. Flowers W, Y, B. Caterpillars gregarious: *Passiflora odontophylla* (?) (ES).

pavana Ménétriés, 1857 (Plate I, fig. 5). Locally common in forest in the Serra do Mar and Serra da Mantiqueira at 600 to 1500 meters elevation, from central ES and central MG south to SC, also locally down to foothills and outwash plains at sea level. Flowers W, Y. Caterpillars solitary: *Passiflora sidaefolia* (RJ).

isabella (Cramer, 1781-2) *dianasa* (Hübner, 1806) (Plate IV, fig. 25). Entire area in forest, uncommon. Becomes plastic northward, showing an increasing percentage of yellow and/or divided subapical elements on the forewing (intergradation to *i. isabella*). Hilltops. Flowers W, Y, rarely R, B. Caterpillars solitary but tolerant: *Passiflora edulis* (GB, RJ), *P. alata* (GB), *P. odontophylla* (?) (ES).

Heliconius Kluk, 1802 (1780?).

nattereri C. and R. Felder, 1865 (illustrated in Part I and Part III of this series). Very rare and local in large tracts of virgin forest in the "Amazonian island" of lowland BA, ES, and possibly eastern MG. Prefers steep, humid areas where its foodplant is giving abundant fresh growth. Female =

fruhstorferi Riffarth, 1898. Flowers R, M, B, rarely W. Caterpillars solitary but tolerant: *Tetrastylis ovalis* (ES).

silvana (Cramer, 1781) *ethra* (Hübner, 1827-31) (Plate V, figs. 34-37). Coastal belt from PE south to central ES in deep primary forest, rarely up river valleys and foothill canyons to 900 meters elevation. Includes form *brasiliensis* Neustetter, 1907, and many additional minor varieties. Quite localized. Flowers R, W. Caterpillars solitary: *Tetrastylis ovalis* (BA).

silvana robigus Weymer, 1875 (Plate V, fig. 38). Coastal belt from southern BA (overlapping with *ethra*) to SC (occasional) in deep forest, rarely up to 900 meters elevation in foothill canyons, very rare and localized southward. Flowers R, W. Caterpillars solitary: *Passiflora alata* (GB), *P. sidaefolia* (GB), *P. rhamnifolia* (GB).

ethilla Godart, 1819 *narcaea* Godart, 1819 (Plate V, figs. 40-43, 45, 46). Entire area in many habitats (but prefers forest), north to southern BA and DF, northwest to eastern MT, and south to western RS. Form *satis* Weymer, 1884 (fig. 45) appears very rarely in all populations (commoner locally, up to five percent of populations, in ES, MG, RJ, and GB). Form *polychrous* C. and R. Felder, 1865 (figs. 43 and 46) is commoner in the central plateau and in SP, predominant in some populations westward. Ridgetops. Flowers R, M, B, rarely W, Y. Caterpillars solitary: *Passiflora sidaefolia* (GB), *P. alata* (GB, DF), *P. kermesina* (GB, ES), *P. jileki* (ES), *P. rhamnifolia* (GB), *P. nitida* (DF), *P. cornuta* (DF), *Tetrastylis ovalis* (ES).

ethilla flavomaculatus Weymer, 1894 (Plate V, fig. 39). Coastal belt from PB south to southern BA. Flowers R. Caterpillars solitary: *Passiflora recurva* (PE), *P. kermesina* (PE).

besckei Ménétriés, 1857 (Plate V, fig. 47). Mountains in forest above 700 meters elevation from central ES (possibly BA and PE, locally), northern GO, and southern MT (at lower elevations) south to western RS, also occasionally down foothill canyons to outwash plains at sea level. Flowers R, B, rarely W, Y. Caterpillars solitary to semi-gregarious, tolerant: *Passiflora sidaefolia* (RJ), *P. villosa* (RJ), *P. coerulea* (SC), *P. organensis* (RJ).

melpomene (Linné, 1758) *nanna* Stichel, 1899 (Plate V, fig. 48). Eastern coastal belt in forest from RN south to ES, rarely to GB and occasionally to SC, also up mountains and river valleys to 1000 meters elevation. Flowers R. Caterpillars solitary: *Passiflora alata* (young, soft, shaded plants) (ES), *P. misera* (ES, BA), *P. violacea* (BA), *Tetrastylis ovalis* (ES).

erato (Linné, 1758) *phyllis* (Fabricius, 1775) (Plate V, figs. 50 and 51). Entire area in all habitats, common. Becomes plastic (including form *phyllides*) in central MT. Forms *artifex* and *cohaerens* appear normally in all populations. Adults roost communally at night, in groups of three to 20 individuals. Flowers R, B, rarely W, Y. Caterpillars solitary and cannibalistic: *Passiflora truncata* (GB), *P. organensis* (GB, RJ, ES), *P. jileki* (ES), *P. violacea* (BA), *P. misera* (ES), *P. sidaefolia* (GB), *P. alata* (SC, RS, but rejected in GB), *P. capsularis* (GB, ES, GO), *P. coerulea* (RS), *Tetrastylis ovalis* (ES).

sara (Fabricius, 1793) *apseudes* (Hübner, 1806) (Plate IV, fig. 32). Coastal plain in oceanside hammocks, forest, and second growth, from PB to SC, up mountains, common; very sparse in interior of São Paulo (Loreto) and MG (Belo Horizonte). Adults roost communally at night in groups of up to 40 individuals. Flowers W, Y, R, B. Caterpillars strongly gregarious: *Passiflora mucronata* (GB, ES), *P. sidaefolia* (GB), *P. rhamnifolia* (GB), *P. edulis* (RJ), *Tetrastylis ovalis* (ES).

B. Marginally Extra-Amazonian Heliconians

Eueides Hübner, 1816

vibilia (Godart, 1819) *unifasciatus* Butler, 1873 (Plate IV, figs. 26 and 27). Marginal, locally abundant in fall and early winter, in forest and scrub in central MT and southwestern GO. Populations include a few percent of *v. vibilia* and many intermediates. Flowers W, Y, B. Caterpillars gregarious with coordinated behavior: *Passiflora mansii* (MT).

isabella isabella (Cramer, 1781-2) (Plate VI, figs. 52-55). Marginal, local, in central MT; to be expected in MA, CE. Polymorphic. Flowers W, B, R.

Heliconius Kluk, 1802 (1780?)

aoede (Hübner, 1809-13) manuscript subspecies, K. Brown (see Part IV of this series). One specimen from the Rio Branco, tributary of the Rio Cabaçal (Paraguay drainage) in west-central MT, a male taken in the afternoon of a cloudy day flying together with very similar-appearing ithomiines in heavy riparian forest, 400 meters elevation. Flowers R, W. Caterpillars probably gregarious.

wallacei Reakirt, 1866 *flavescens* Weymer, 1890 (Plate IV, fig. 29). Marginal in forest in central MT, to be expected in MA. One record of form *parvimaculata* Riffarth, 1900 from SC may be a labeling error. Flowers R, W, B. Caterpillars semi-gregarious: *Passiflora coccinea* (MT); *wallacei* is closely associated with this species and its very close relatives throughout its range in the Amazon and Orinoco Basins.

burneyi (Hübner, 1827-31) near *burneyi* (Plate VI, fig. 60). One specimen known from Cáceres in west-central MT; one male observed for over 30 minutes on high yellow flowers on the Rio Branco, tributary of the Rio Cabaçal, in June 1971. To be expected elsewhere in central MT and in MA.

xanthocles Bates, 1862 *melete* C. and R. Felder, 1865 (Plate IV, fig. 30). Regular in fall and winter in forests by streams in highland central MT. Flowers R. Caterpillars probably gregarious.

silvana (Cramer, 1781) *mirus* Weymer, 1894 (Plate VI, fig. 59). Marginal, well-established in west-central Mato Grosso (Rio Branco/Rio Cabaçal, 400 meters).

numata (Cramer, 1780-82) *superioris* Butler, 1875 and many forms near this (Plate VI, figs. 56-58). Marginal, common in west-central MT (Rio Branco/Rio Cabaçal, 400 meters); to be expected elsewhere in central MT. Caterpillars solitary: *Passiflora coccinea* (MT), *P. glandulosa* (MT), accepted *P. tricuspis* (MT).

ethilla Godart, 1819 *eucoma* (Hübner, 1827-31) (Plate V, fig. 44). Marginal in western CE and southeastern MA (D. Zajciw); may appear in west-central MT (Rio Cabaçal).

ethilla manuscript subspecies, K. Brown (see Part IV). Marginal but regular, frequent in fall, in deep forest near streams in highland central MT. Males promenade in small clearings. Flowers R, B. Caterpillars solitary: *Passiflora cornuta* (MT), *P. glandulosa* (MT).

melpomene (Linné, 1758) *burchelli* Poulton, 1910 (Plate V, fig. 49). Borders of Amazon Basin, in forest and cerrado, in MA, CE, GO, DF, and MT; becomes plastic, occasionally even with dennis and ray, in central MT. Flowers R, B. Caterpillars solitary: *Passiflora cornuta* (DF), *P. mansii* (MT), probably *P. tricuspis* (MT).

ricini (Linné, 1758) (Plate IV, fig. 32). Marginal in MA and CE; possibly marginal but unlikely in central MT ("Cuyabá-Corumbá River System").

sara (Fabricius, 1793) *thamar* (Hübner, 1806) (Plate IV, fig. 33). Locally common in forest and second growth on the borders of the Amazon Basin in MT, central and southern GO, DF, and extreme northwestern BA (Rio Sapão). To be expected in MA and CE. Flowers W, Y, R, B. Caterpillars gregarious: *Passiflora mansii* (MT).

leucadia Bates, 1862 *pseudorhea* Staudinger, 1896 (Plate VI, fig. 61). Marginal in west-central MT (Rio Branco/Rio Cabaçal and upper Rio Jaurú).

C. Hypothetically Extra-Amazonian Heliconians

The following species are either tenuously recorded from extra-Amazonian Brazil, with no recent and reliable confirmation, or else occur commonly in the indicated areas adjacent to extra-Amazonian Brazil, or have been recently recorded from these areas by reliable authorities. None has yet been captured by the authors in the area under consideration.

Dione glycera (C. and R. Felder, 1861). Misiones, Argentina (Hayward, 1951).

Eueides lybia lybia (Fabricius, 1775). Maranhão, Rondônia; possibly seen on the Rio Branco, MT, in June 1971.

Heliconius astraea Staudinger, 1896 manuscript subspecies, K. Brown (see Part IV). Rondônia and northern MT; "Cuyabá-Corumbá River System."

Heliconius doris doris (Linné, 1771) and form *delila* (Hübner, 1813). Maranhão, northern Mato Grosso and Rondônia.

Heliconius numata (Cramer, 1780-82) *splendidus* Weymer, 1894. Misiones, Argentina (Hayward, 1951).

Heliconius hecale (Fabricius, 1775) *sisyphus* Salvin, 1871 and variants. Northern Bolivia west of the Rios Cabaçal and Jaurú.

Heliconius elevatus Nöldner, 1901 *schmassmanni* Joicey & Talbot, 1925 (? = *aquilina* Neustetter, 1925) and *H.e. perchlora* Joicey & Kaye, 1917. Rondônia and northern MT; "Cuyabá-Corumbá River System."

Heliconius demeter Staudinger, 1895 *eratosignis* Joicey and Talbot, 1925. Southeastern Rondônia; "Cuyabá-Corumbá River System."

Heliconius antiochus (Linné, 1767) *alba* Riffarth, 1900. Northeastern Mato Grosso (common), Maranhão.

APPENDIX II

A Brief List of the Heliconians of Amazonian Brazil

The Amazonian region of Brazil is so little-explored that it would be most premature and foolhardy to present a definitive list or a complete synopsis of the subspecies at this time. A large network of highways, now under construction and to be finished by the mid-1970s, will permit a far more thorough investigation of Amazonian heliconians by the end of this decade. This list presents only a preliminary tally of the species and ranges known to date, with indications of the principal subspecies present where these are reasonably well defined. Marginally Amazonian species like *besckei* are omitted.

Many Amazonian heliconian populations are noted for their polymorphism. This phenomenon is perhaps most marked in *Heliconius numata,* discussed in detail along with other Amazonian silvaniforms in Part V of this series. Some examples of polymorphism in Amazonian heliconians are illustrated on Plate VI.

The Amazonian area of the map has been divided and patterned according to present information on the interaction of the subspecies of *Heliconius erato* in the Amazon Basin. Relatively monomorphic areas are indicated by pure patterns, blend zones (see Plate VI, figs. 63 and 64) by overlapping patterns; much of the Brazilian upper Amazon is a blend zone for three major subspecies, and the named form *lativitta* Butler 1877 is a typical hybrid from this area which shows signs of influence of all three of these subspecies (*amazona, emma,* and the *reductimacula-donatia-venustus* complex). The various color-patterns of *erato* in the Amazonian area are closely followed by those of the other dennis-rayed heliconians (*Eueides tales* and *eanes, Heliconius aoede, burneyi, egeria, astraea, xanthocles, elevatus,* Amazonian *melpomene,* and *demeter*). However, some startling exceptions to this generalized parallelism are known, presumably due to individual differences in the genetic mechanisms by which each species achieves the desired patterns.

Where *erato* and *melpomene* are red-banded in the north-central and southeastern parts of the Amazonian basin, the other dennis-rayed species may exist in unchanged form. They also may be replaced by closely related species (like the substitution of *luciana* in the north and *besckei* in the south for *elevatus*), or may be absent (as in most of Amazonian Goiás). The definition of the blend areas necessarily is approximate until detailed studies can be made along the new roads. Evidence accumulated over 50 years also indicates that both the position and the composition of these hybrid zones is constantly changing, in dynamic equilibrium with the monomorphic zones which give rise to them and with natural selection phenomena which vary within them from year to year.

Philaethria dido (Linné, 1763) (Plate I, fig. 1). Entire area except dry southeastern Amazon (*erato phyllis* area), quite frequent in heavy forest and clearings; very high flyer.

Philaethria wernickei (Röber, 1906) *pygmalion* (Fruhstorfer, 1912) (see Plate I, fig. 2). Upper Rio Negro and Uaupés, and southern Rondônia eastward through entire middle and lower Amazon.

Dryadula phaetusa (Linné, 1758) (Plate IV, figs. 20-21). Entire area, localized in open or marshy areas.

Agraulis vanillae (Linné, 1758) (Plate IV, figs. 17 and 18; Plate I, figs. 3-4). Entire area, but rare and local westward where following species flies. Principally nominate subspecies, except in southern Amazon [*v. maculosa* (Stichel, 1909)].

Agraulis lucina Felder, 1862 (Plate I, figs. 3-4). Upper Amazon only, from Uaupés, Tefé, and eastern Acre westward, in forest clearings.

Dione juno juno (Cramer, 1779) (Plate IV, fig. 19). Entire area though quite localized, in forest clearings; southwestern populations show appreciable variation in dark markings.

Dryas iulia iulia (Fabricius, 1775) (Plate IV, figs. 23-24). Entire area, frequent in all habitats.

Eueides aliphera aliphera (Godart, 1819) (Plate IV, fig. 28). Entire area, very localized, common along streams.

Eueides vibilia (Godart, 1819) (Plate I, fig. 5; Plate IV, figs. 26-27). Nominate subspecies rarely encountered in lower and middle Amazon; *v. unifasciatus* Butler, 1873 locally common in upper Amazon. Intermediates with partial forewing subapical bands are common in populations of both subspecies in the Amazon Basin.

Eueides lampeto Bates, 1862 (Plate I, fig. 6). Nominate subspecies very local and rare in upper Rio Solimões (above Tefé); *l. copiosus*

Stichel, 1906 recently discovered north of Obidos.

Eueides eanes eanes Hewitson, 1861. Not rare in extreme western Amazonas and Acre.

Eueides isabella isabella (Cramer, 1781-2) (Plate VI, figs. 52-55). Entire area but quite local; strongly polymorphic, especially southwestward.

Eueides lybia lybia (Fabricius, 1775). Entire area but rarer westward and southward; local in dryer areas and secondary forest, always found very near its food-plant.

Eueides tales (Cramer, 1775-6). Locally common in forest and second growth; the rather variable subspecies *pythagoras* Kirby, 1900 (dennis-ray), *tales* and *surdus* Stichel, 1903 (dennis only), *aquilifer* Stichel, 1903 (condensed FW yellow patch), and *calathus* Stichel, 1902 (FW yellow band distal to cell) follow the *erato* variations indicated in map. Not known outside the Hylaea in the dryer southeastern Amazon (Goiás).

Heliconius metharme (Erichson, 1848). Very local, from western Pará northwestward and southwestward to Uaupés, Benjamin Constant and western Acre.

Heliconius aoede (Hübner, 1809-13). Entire area except dryer southeastern Amazon. Subspecies *aoede* (dennis-ray), *astydamia* (Erichson, 1848) (dennis only), *faleria* Fruhstorfer, 1910 (partially coagulated FW yellow band), *lucretius* Weymer, 1890 (condensed FW yellow patch) and a new subspecies with reduced dennis (see Part IV), and *bartletti* Druce, 1876 (FW yellow band distal to cell) closely follow *erato* variations (Map I). Generally uncommon and local, in heavy moist forest.

Heliconius wallacei Reakirt, 1866 (Plate IV, fig. 29; Plate VI, fig. 62). Entire area, common wherever *Passiflora coccinea* and related species grow, many habitats. Usually *flavescens* Weymer, 1890; white-banded forms [*clytia* (Cramer, 1775-6) and *elsa* Riffarth, 1899] and *w. wallacei* are more frequent in the northern Amazon; polymorphic populations (*colon* Weymer, 1890; *parvimaculata* Riffarth, 1900, and many other forms) occur in the lower middle Amazon.

Heliconius burneyi (Hübner, 1827-31) (Plate VI, fig. 60). Entire area except extreme southeast, rather localized; very high flyer. Subspecies *burneyi* (dennis-ray), *catherinae* Staudinger, 1885-8 (dennis only), *ada* Neustetter, 1925 (partly coagulated FW yellow band with reduced subapical elements), and *huebneri* Staudinger, 1896 (condensed and reduced FW yellow patch and wider HW rays) occupy areas roughly corresponding to *erato* variations, though much discrepancy from parallelism is seen and the overall variation of *burneyi* is less (see Map I).

Heliconius egeria (Cramer, 1775-6) (Plate III, fig. 11). Rare and local, from Belém west in heavy forest to Uaupés, western Amazonas and northern Rondônia; very high-flyer. The rayed subspecies *hyas* Weymer, 1884 is a variable element in many populations, predominant in the Rio Madeira region; its northern form with a more compact FW band, *asterope* Zikán, 1937, is found on the upper Rio Negro.

Heliconius astraea Staudinger, 1896 (Plate III, fig. 11). Rare and local in southwestern and extreme western Amazon, in heavy forest or along rivers; habits as in *egeria* and *burneyi*. Nominate subspecies in western Amazonas above Tefé; new subspecies (see Part IV) in the Rio Madeira area, south to well beyond the range of *egeria hyas*.

Heliconius xanthocles Bates, 1862 (Plate IV, fig. 30). Entire area except extreme southeastern Amazon. Subspecies *vala* Staudinger, 1885-8 (dennis-ray), *xanthocles* (dennis only), *paraplesius* Bates, 1867 (partly coagulated FW yellow band), *melete* Felder, 1865 (condensed FW yellow patch), and *melittus* Staudinger, 1896 (FW band distal to cell) closely follow *erato* variations (Map I).

Heliconius doris (Linné, 1771). Entire area, principally along major rivers. Forms *delila* (Hübner, 1813), *metharmina* Staudinger, 1896, and *amathusius* (Cramer, 1777) occur in all populations, but are commonest in far western and southwestern Amazon. Essentially no green forms have been found in the Brazilian part of the Amazon Basin. This species has been placed by recent authors in a separate subgenus (*Laparus* Billberg, 1820).

Heliconius silvana (Cramer, 1781) (Plate VI, fig. 59; Plate V, figs. 34-37). Entire area except southeast Amazon, quite common. Grades smoothly into subspecies *mirus* Weymer, 1894 in southern Rondônia; some eastern (Belém) specimens seem to grade towards *ethra* (Hübner 1827-31); far western specimens have larger subapical spots on the FW (as does the sympatric *numata aurora*).

Heliconius numata (Cramer, 1780-2) (Plate VI, figs. 56-58). Entire area except extreme southeast, locally abundant, highly polymorphic. Forms which may deserve weak subspecific rank include *superioris* Butler, 1875 (middle Amazon southward), *aurora* Bates, 1862 (far west), *euphone* Felder, 1862 (south-

west), and *zobrysi* Fruhstorfer, 1910 (southeast); *silvaniformis* Joicey and Kaye, 1917 is a strong element in far eastern populations. Some southwestern specimens have a black suffusion on the distal half of the FW as in *silvana mirus*. Dissimilar specimens in which the yellow has been entirely replaced by orange occur in all populations; the extreme of these is *arcuella* Druce, 1874, commoner westward; the orange form of *superioris* is *isabellinus* Bates, 1862; of *zobrysi* is *seraphion* Weymer, 1894. The very dark hindwing of nominate *numata* appears in all populations, but is commoner northeastward.

Heliconius ethilla Godart, 1819 (Plate V, figs. 39-46). The subspecies *eucoma* (Hübner, 1827-31) and its dark variety *numismaticus* Weymer, 1894 occupy almost the entire area, except for the southeast (*e. narcaea* Godart, 1819 and its form *polychrous* Felder, 1865), southwest (*nebulosa* Kaye, 1916), and south-central Amazon (new subspecies, see Part IV). The Guianian subspecies *thielei* Riffarth, 1900 may appear in the northeastern and north-central parts of the Amazon Basin.

Heliconius hecale (Fabricius, 1775). Entire area except southeastern and south-central Amazon. Strongly fragmented into locally differentiated populations with apparently rather limited gene-flow, which may be regarded as good subspecies: *novatus* Bates, 1867 (Belém; erroneously rechristened *schulzi*); *xinguensis* Neustetter, 1925 (lower Rio Xingú); *paraensis* and *latus* Riffarth, 1900 (Obidos area); *vetustus* Butler, 1873 (north of Obidos into Guianian highlands); *metellus* Weymer, 1894 (near Santarém); *fortunatus* Weymer, 1884 (north of Manaus); *spurius* Weymer, 1894 (south and east of Manaus, a minor element as far east as eastern Pará); *sulphureus* Weymer, 1894 (Rio Negro); *ennius* Weymer, 1890 (south and west of Manaus); *nigrofasciatus* Weymer, 1894 (Rondônia and Acre); *sisyphus* Salvin, 1871 and forms *concors, jonas*, etc., Weymer, 1894 (extreme west and southwest); *humboldti* Neustetter, 1928 (extreme west north of the Solimões), and probably many more to be discovered.

Heliconius pardalinus Bates, 1862. Principally from extreme western Amazonas (*pardalinus*) east to Rondônia and Manaus (form *lucescens* Weymer, 1894 commoner), possibly to Obidos and Santarém; also southwest to Acre (*maeon* Weymer, 1890 and *dilatus* Weymer, 1894).

Heliconius elevatus Nöldner, 1862. Entire area except southeast and north-central Amazon, but extremely rare and localized. Subspecies *barii* Oberthür, 1902 (dennis-ray), *roraima* Turner, 1967 and *tumatumari* Kaye, 1906 (dennis only, the former with a condensed FW yellow patch), *aquilina* Neustetter, 1925 and (or=?) *schmassmanni* Joicey and Talbot, 1925 (partly coagulated FW yellow elements), *perchlora* Joicey and Kaye, 1917 (condensed FW yellow patch), and *elevatus* (FW band mostly distal to cell) follow fairly well the divisions of *erato* (see Map I).

Heliconius luciana Lichy, 1960 (Plate III, figs. 12-15). Known only from near Bôa Vista in northern Roraima, where sympatric with the very similar and abundant *antiochus* and uncommon *wallacei elsa*.

Heliconius melpomene (Linné, 1758) (Plate II, figs. 8 and 10; Plate V, fig. 49). Entire Amazon Basin, locally abundant but often absent from large areas. Subspecies *thelxiope* (Hübner, 1806) (dennis-ray), *meriana* Turner, 1967 (dennis only), *madeira* Riley, 1919 (partly coagulated FW yellow band), *vicina* Ménétriés, 1857 (condensed FW yellow patch), *penelope* Staudinger, 1897 (same with reduced dennis), *aglaope* Felder, 1862 (FW band distal to cell), *melpomene* (red forewing band), and *burchelli* (red forewing band and yellow hindwing stripe) fairly closely accompany the corresponding variations of *erato* (Map I), with a few notable exceptions in and near hybridization zones.

Heliconius hermathena Hewitson, 1853. Very rare and local in northern central Amazon from Santarém (or perhaps Belém?), Maués, and Manicoré to the far west (São Gabriel, Rio Negro). At Faro, occurs principally as subspecies *vereatta* Stichel, 1912, almost identical in color-pattern to *melpomene melpomene*; transitions are known between the nominate and mimetic subspecies.

Heliconius erato (Linné, 1758) (Plate V, figs. 50-51; Plate VI, figs. 63-64; Map I). Entire Amazon Basin, common. Major subspecies *amazona* Staudinger, 1896 (dennis-ray), *amalfreda* Riffarth, 1900 (dennis only), *estrella* Bates, 1862 (dennis-ray with reduced forewing band), *reductimacula* Bryk, 1953 (condensed FW yellow patch), *venustus* Salvin, 1871 (same with reduced dennis), *emma* Riffarth, 1901 (FW band distal to cell), *hydara* Hewitson, 1867 (red forewing band), and *phyllis* (Fabricius, 1775) (red forewing band and yellow hindwing stripe) are represented with approximate ranges and blend areas in Map I.

Heliconius ricini (Linné, 1758) (Plate IV, fig. 31). Maranhão and Amapá westward to Roraima (Bôa Vista) and Rondônia.

Heliconius demeter Staudinger, 1896. Almost entire area of Hylaea (excludes southeastern and north-central Amazon), but extremely local; at times common where found. Subspecies *bouqueti* Nöldner, 1902 (dennis-ray, with males imitating *egeria*), *beebei* Turner, 1966 (dennis only), *eratosignis* Joicey and Talbot, 1925 (partly coagulated FW yellow band and clearer rays), and *demeter* (FW band mostly distal to cell) closely follow the variations of *erato* (see Map I).

Heliconius sara (Fabricius, 1793) *thamar* (Hübner, 1806) (Plate IV, fig. 33). Entire area, common in many habitats.

Heliconius leucadia Bates, 1862 (Plate VI, fig. 61). Entire area from Maranhão to Uaupés, Benjamin Constant and Acre, always local and very much less frequent than *sara*. The nominate subspecies, with a white HW border, predominates over *pseudorhea* Staudinger, 1896 only in some populations northwestward.

Heliconius antiochus (Linné, 1767) *alba* Riffarth, 1900. Entire area except extreme southeast, commoner at the borders of the Hylaea in Mato Grosso and in Roraima. Form *zobeide* Butler, 1869 is most frequent in the lower middle Amazon; *salvinii* Dewitz, 1877 may be found in extreme northeastern Roraima.

APPENDIX III

Systematic Changes, and Remaining Uncertainties

The new systematic arrangement of the silvaniform *Heliconius* is presented in Part V of this series. A total of six species is recognized (*ismenius, silvana, numata, hecale, ethilla,* and *pardalinus*), two more than those recognized by Emsley (1965) and with *hecale* much expanded. The largest uncertainties that still remain in the revision of this extremely complicated mimetic group, other than the placement of certain little-known subspecies, are the relationships of *Heliconius numata* to the *H.n. aristiona* and *H.n. aulicus* complexes, of *H. silvana* to *H.s. ethra,* and of these two species to each other; and of the northern *H. hecale* group of subspecies to the *H.h. quitalena* complex of the Amazon Basin.

The following species are added by the present paper to Emsley's lists of 1963, 1964, and 1965, defining the tribe Heliconiini:

Philaethria wernickei (separated from *P. dido*).

Agraulis lucina (separated from *A. vanillae*).

Eueides lampeto (separated from *E. vibilia*).

Heliconius astraea (separated from *H. egeria*).

Heliconius besckei (separated from *H. melpomene*).

Heliconius heurippa (separated from *H. melpomene*).

Heliconius timareta (separated from *H. melpomene*).

Heliconius luciana (added, provisionally being maintained separate from *H. elevatus*).

Heliconius eleuchia (separated from *H. sapho*).

Heliconius congener (separated from *H. sapho*).

The two species *Heliconius hygiana* and *H. clysonymus* are recombined, the latter name taking precedence over the former.

A number of taxonomic uncertainties still exist in the tribe. We have seen no specimens of the Peruvian *Dione miraculosa* Hering, 1926; from its original description, it may be a good species, isolated in southwestern Peru on the Pacific slope of the Andes. *Eueides procula* Doubleday, 1848 and *E.p. edias* Hewitson, 1861, while morphologically distinguishable, are connected in western Venezuela by a graded series (*E.p. luminosus* Stichel, 1903) and are probably conspecific. The situation of the *Eueides lybia* complex, however, is less clear; *E. lybia lybia, E. l. olympia* (Fabricius, 1793) and *E. l. lybioides* Staudinger, 1876 are allopatric, not connected by graded series, and morphologically distinguishable. While we favor maintaining them together, they may prove to be not interfertile. *Heliconius hecuba,* with which we have very limited field experience, may be separable into two sympatric species, though apparent intergrades are known in collections; the extremes of variation between *hecuba* Hewitson, 1857 at one end and *cassandra* Felder, 1862 at the other end of a sympatric population are quite far apart in many ways. Finally, until *H. hecalesia* and *H. longarena* are found flying together, the considerable possibility that they may be conspecific (linked by *H. h. gynaesia*) cannot be eliminated.

EXPLANATION OF PLATES

Plate I

Figure 1. *Philaethria dido,* Rio de Janeiro, ventral surface of hindwing, twice life size. Black, red, and green.

Figure 2. *Philaethria wernickei,* Curitiba, Paraná, ventral surface of hindwing, twice life size. Black and green.

Figure 3. Upper left (upside down): *Agraulis vanillae maculosa,* Xapuri, Acre.

Upper right: *Agraulis vanillae catella,* Xapuri, Acre.

Lower: *Agraulis lucina,* Alto Rio Juruá, Acre (identical to specimens from Xapuri).

All in the Museu Nacional, Rio. Dorsal, life size. Black and orange.

Figure 4. Six *Agraulis* from near La Merced, Junín, Peru, all ventral, life size. Orange, yellow, silver, and black.

Left row: three variations of *A. vanillae maculosa.*

Lower right: *A. vanillae catella* (note orange FW apex).

Upper and middle right: *A. lucina.* We also have specimens of *lucina* from this area with as much ventral silvering as the *catella* illustrated. All in the collection of G. Harris, Lima, Peru.

Figure 5. Upper left: *Eueides pavana,* male, Xerém, Rio de Janeiro.

Middle left: *Eueides pavana,* orange female, Petrópolis, Rio de Janeiro, 900 meters.

Lower left: *Eueides pavana,* intermediate female, Parque Nacional de Itatiaia, Rio de Janeiro (900 meters).

Upper center: *Eueides pavana,* yellow female, Belo Horizonte, Minas Gerais (1100 meters).

Middle center: *Eueides vibilia vibilia,* female, Conceição da Barra, Espírito Santo.

Lower center: *Actinote pyrrha* (Fabricius) (Acraeinae), male, Rio de Janeiro.

Upper right: *Eueides vibilia vibilia,* male, Conceição da Barra, Espírito Santo.

All dorsal, three-quarters life size. Black, yellow, and orange.

Figure 6. Types (upper male, lower female) of *Eueides nigrifulva* Kaye = *E. lampeto copiosus* Stichel, Potaro River, British Guyana, dorsal, one-half life size. Black and orange. From the Allyn Museum of Entomology.

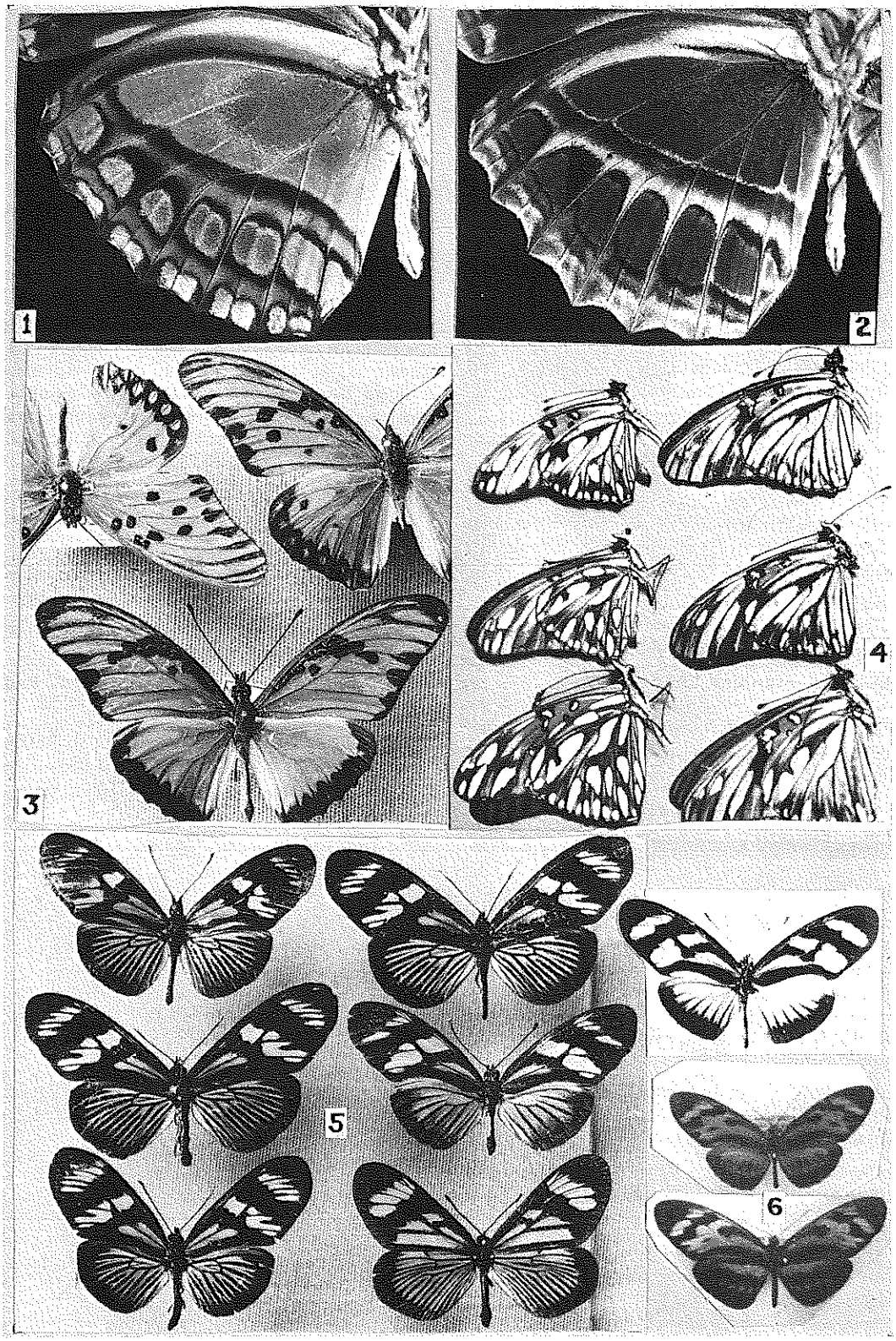


PLATE I

Plate II

Figure 7. Upper left: *Heliconius congener* Weymer, 1890, Abitagua, Oriente, Ecuador (1100 meters). Iridescent blue and yellow.

Middle left: *Heliconius sapho sapho* (Drury, 1782), Victoria, Caldas, Colombia. Iridescent blue and white.

Lower left: *Heliconius eleuchia*(?) *eleusinus* Staudinger, 1885-8, highway from Medellin to Quibdó, northwestern Colombia. Black and white with reduced blue iridescence.

Upper right: *Heliconius eleuchia eleuchia* Hewitson, 1854, Victoria, Caldas, Colombia. Iridescent blue, yellow forewing bands, white hindwing border.

Middle right: *Heliconius eleuchia primularis* Butler, 1869, Santo Domingo, western Ecuador. Iridescent blue and yellow.

Lower right: *Heliconius hewitsoni* Staudinger, 1875, Agua Buena, Puntarenas, Costa Rica. Deep blue-black and yellow.

All dorsal, two-thirds life size.

Figure 8. Left: *Heliconius melpomene melpomene,* Rio Negro, Meta, Colombia, 900 meters. Black and red.

Right: *Heliconius heurippa* Hewitson, 1854, Rio Negro, Meta, Colombia, 900 meters. Black, red, and yellow. Both dorsal, two-thirds life size.

Figure 9. *Heliconius timareta* Hewitson, 1867, polymorphic population from the Rio Topo between Baños and Puyo, Ecuador, 1400 meters. Identical forms fly in the Abitagua, upper Santa Clara, and upper Rio Arajuno areas at 1000 to 1300 meters, and up the slopes of the valley of the Rio Pastaza to 1800 meters, in heavy humid forest.

Upper left: nominate form (black and yellow). Upper right: form *richardi* Riffarth, 1900 (black, yellow, and red).

Lower: two forewing band variants of form *contiguus* Weymer, 1890. Black, yellow, and red.

All dorsal, four-fifths life size. In the Carnegie Museum, Pittsburgh.

Figure 10. Intergradation of forms of *Heliconius melpomene* in eastern Ecuador. All forms may be found flying together on the northern escarpment of the Abitagua highlands, such as near Santa Clara (600-1000 meters), and Arajuno (500-1000 meters). The last two are found widely at higher elevations on the Rio Pastaza, such as at the Rio Topo, and elsewhere in eastern Ecuador at comparable levels. The first subspecies is widespread in the upper Amazon Basin of Brazil, Peru, Ecuador, and Colombia. The width of the blend zone near Santa Clara does not exceed twenty kilometers in horizontal and 500 meters in vertical dislocation.

Upper left: *H. melpomene aglaope* Felder, 1862, from near Arajuno. Black, yellow, and orange.

Upper center: form *adonides* Niepelt, 1908. Yellow forewing bands, orange dennis and rays.

Upper right: form *isolda* Niepelt, 1908. White forewing bands, red dennis and rays.

Lower left: form *niepelti* Riffarth, 1907. Red and white forewing bands, red dennis.

Lower center: *H. melpomene plesseni* Riffarth, 1907. Red and white forewing bands.

Lower right: form *pura* Niepelt, 1907. White forewing bands.

All dorsal, two-thirds life size.

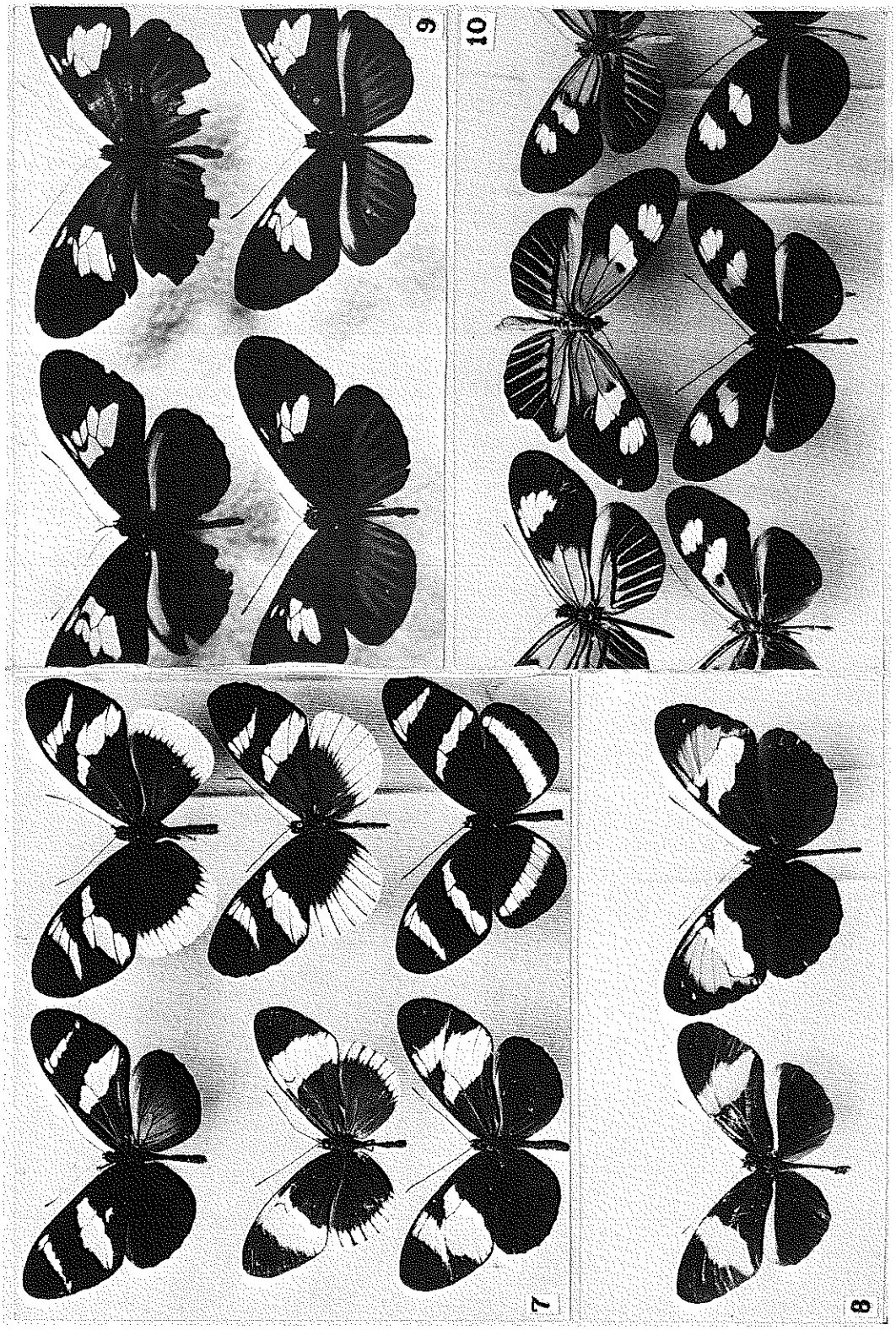


PLATE II

PLATE III

FIGURE 11. *Heliconius egeria* and *astraea* in Brazil.

Upper left and middle left: *H. astraea astraea,* São Paulo de Olivença, Amazonas; typical form.

Lower left: *H. astraea,* new subspecies (see Part IV), Manicoré, Rio Madeira, Amazonas.

Upper right: *Heliconius egeria hyas,* typical form, Maués, Amazonas.

Middle right: *Heliconius egeria asterope,* upper Rio Negro, Amazonas (typical *egeria* genitalia).

Lower right: *H. egeria egeria,* typical, Manicoré, Rio Madeira, Amazonas. Identical specimens are known from São Paulo de Olivença.

All dorsal, one-half life size. Black, yellow, and red. In the Museu Nacional, Rio de Janeiro.

FIGURE 12. Type-series of *Heliconius luciana,* extreme upper Orinoco River, Territorio Amazonas, Venezuela (2°11′ N., 64°12′ W.; Raudal "Los Tiestos").

Upper left: holotype male.

Upper right: allotype female.

Lower left: paratype female.

Lower right: paratype male.

All dorsal, two-thirds life size. Black and white. In the Facultad de Agronomia, Maracay, Venezuela (with permission of Dr. Francisco Fernández Yépez).

FIGURE 13. Six specimens of *Heliconius luciana* from the variable population at Mantecal, Rio Cuchivero, Bolivar, Venezuela. All dorsal, two-thirds life size. Black and yellow except for middle right specimen, which is black and white. Taken from a painting by the collector, H. Skinner of La Victoria, Venezuela, with his permission.

FIGURE 14. *Heliconius luciana,* male, Mantecal, Rio Cuchivero, Bolivar, Venezuela, dorsal, two-thirds life size. Black and yellow. In the Facultad de Agronomia, Maracay (donated by H. Skinner).

FIGURE 15. *Heliconius luciana,* male, Mantecal, Rio Cuchivero, Bolivar, Venezuela. Ventral, two-thirds life size. Black, yellow, and red.

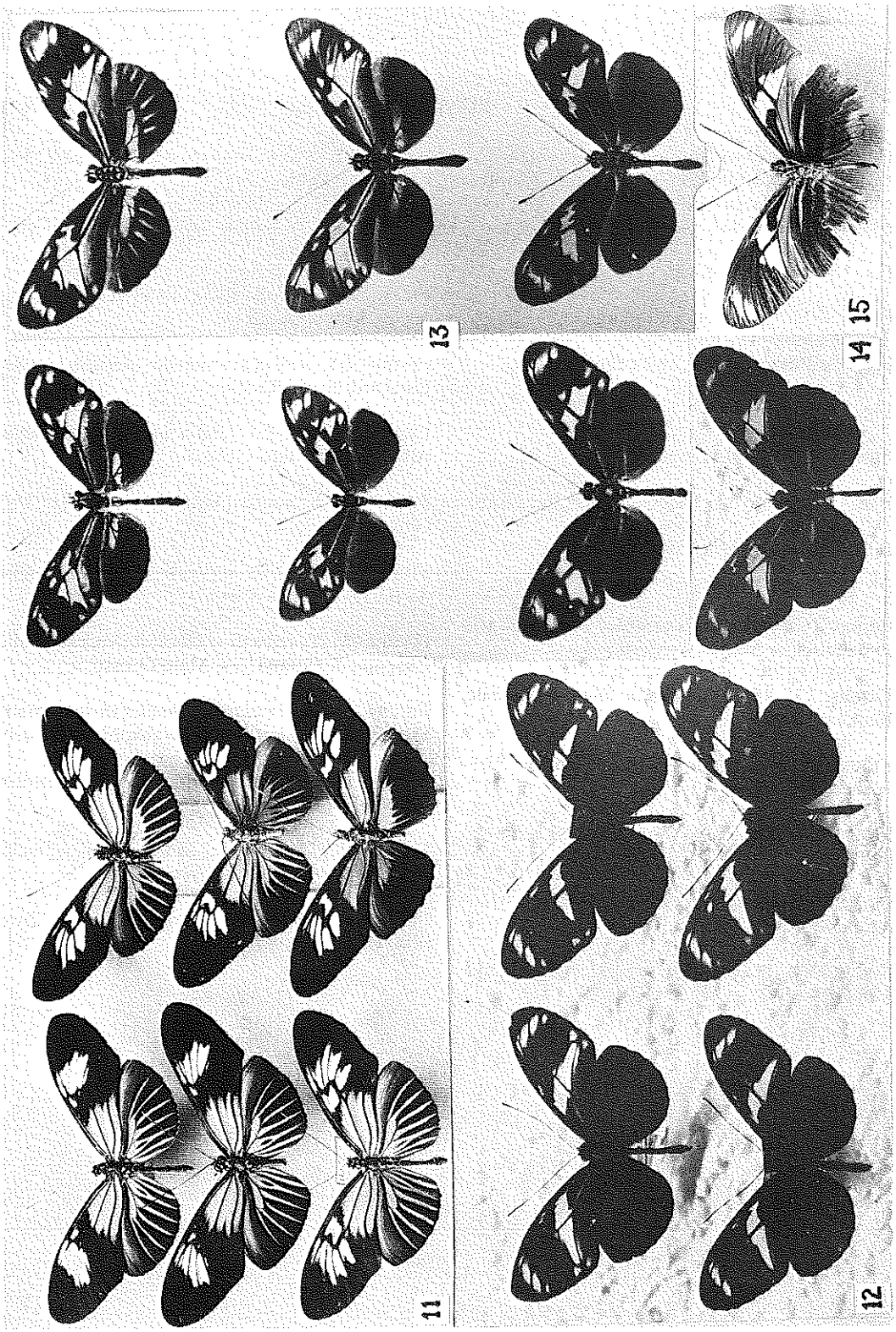


PLATE III

PLATE IV

Heliconians known from extra-Amazonian Brazil and not illustrated on other plates. Primitive genera, *Eueides*, primitive *Heliconius*, and most advanced *Heliconius* (*sara*-group).

Fig. 16: Black and green.

Figs. 17-24, 26: Black and orange.

Fig. 25: Black, orange, and yellow.

Fig. 27: Black, orange, and dull yellow.

Fig. 28: Black and orange.

Figs. 29, 32, and 33: Iridescent blue and yellow.

Figs. 30 and 31: Black, yellow, and red.

All dorsal, two-thirds life size.

FIGURE 16. *Philaethria wernickei wernickei*, Rio de Janeiro.

FIGURE 17. *Agraulis vanillae maculosa*, male, Itanhem, Bahia.

FIGURE 18. *A. vanillae maculosa*, female, Paraopeba, Minas Gerais.

FIGURE 19. *Dione juno juno*, male, Xerém, Rio de Janeiro.

FIGURE 20. *Dryadula phaetusa*, male, Rio Maranhão, Distrito Federal.

FIGURE 21. *D. phaetusa*, female, Barbacena, Minas Gerais.

FIGURE 22. *Dione moneta moneta*, male, Rio Claro, São Paulo.

FIGURE 23. *Dryas iulia iulia*, large male, Canal São Simão, Goiás.

FIGURE 24. *D. iulia iulia*, small female, Paraopeba, Minas Gerais.

FIGURE 25. *Eueides isabella dianasa*, male, Paracatú, Minas Gerais.

FIGURE 26. *Eueides vibilia unifasciatus*, male, Alto Garças, Mato Grosso.

FIGURE 27. *E. vibilia unifasciatus*, female, Alto Garças.

FIGURE 28. *Eueides aliphera*, male, Conceição da Barra, Espírito Santo.

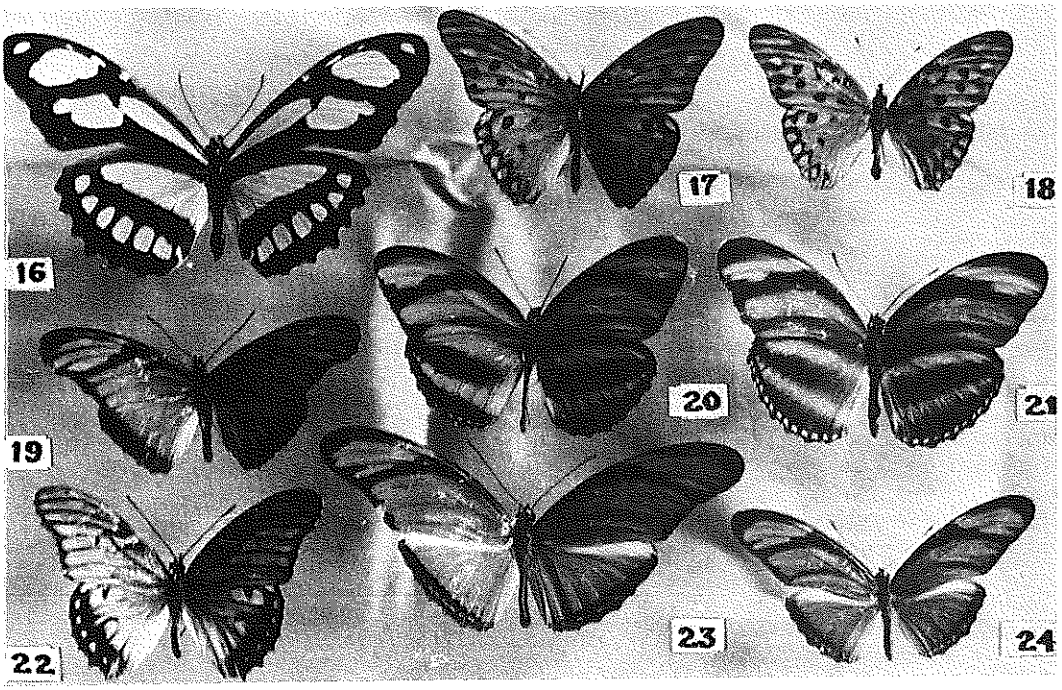
FIGURE 29. *Heliconius wallacei flavescens*, male, Chapada de Guimarães, Mato Grosso.

FIGURE 30. *Heliconius xanthocles melete*, male, São Vicente, 90 km. E. of Cuiabá, Mato Grosso.

FIGURE 31. *Heliconius ricini*, male, Dom Pedro, Maranhão.

FIGURE 32. *Heliconius sara apseudes*, male, Belo Horizonte, Minas Gerais.

FIGURE 33. *Heliconius sara thamar*, male, Brasília, Distrito Federal.



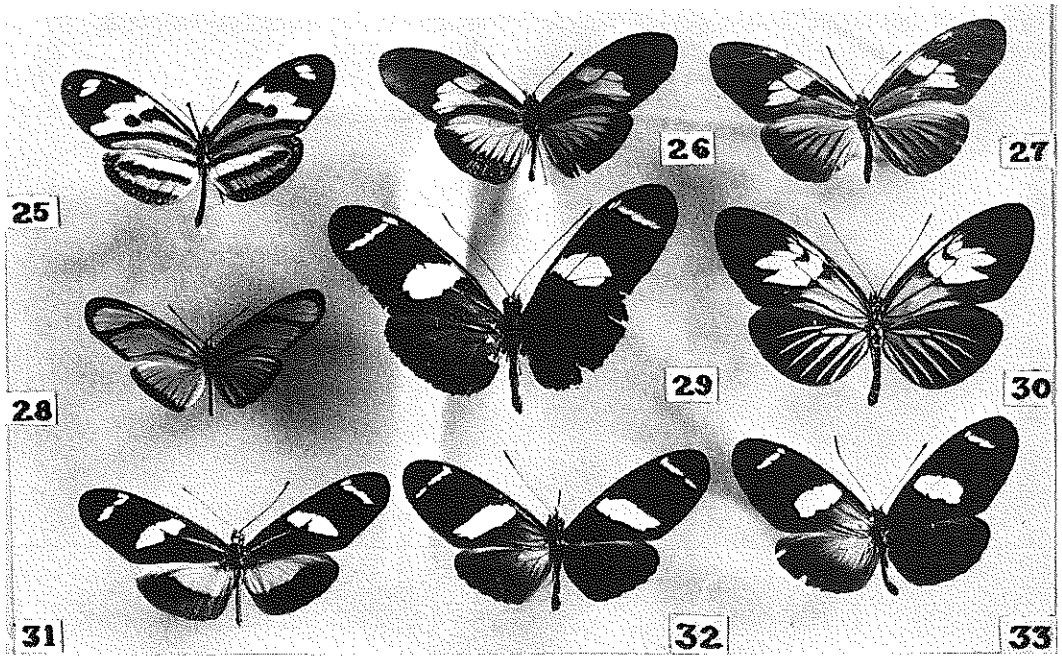


PLATE IV

Plate V

Heliconians known from extra-Amazonian Brazil and not illustrated on other plates (continued). Genus *Heliconius*: *silvana, melpomene,* and *erato* groups.

Figs. 34-46: Black, yellow, and orange, with white subapical spot on forewing in 40-43, 45, and 46.

Figs. 47-51: Black, yellow, and red.

All dorsal, two-thirds life size.

Figure 34. *Heliconius silvana ethra,* male, Conceição da Barra, Espírito Santo.

Figure 35. *H. silvana ethra,* form *brasiliensis,* male, Recife, Pernambuco.

Figure 36. *H. silvana ethra,* variant, male, Conceição da Barra.

Figure 37. *H. silvana ethra,* form *brasiliensis,* variant, female, Conceição da Barra.

Figure 38. *H. silvana robigus,* male, Rio de Janeiro.

Figure 39. *H. ethilla flavomaculatus,* female, Recife, Pernambuco.

Figure 40. *H. ethilla narcaea,* light male, Rio de Janeiro.

Figure 41. *H. ethilla narcaea,* dark male, Santa Teresa, Espírito Santo.

Figure 42. *H. ethilla narcaea,* female, Santa Teresa.

Figure 43. *H. ethilla narcaea,* form *polychrous,* male, Loreto, São Paulo.

Figure 44. *H. ethilla eucoma,* male, Ubajara, Ceará.

Figure 45. *H. ethilla narcaea,* form *satis,* male, Rio de Janeiro.

Figure 46. *H. ethilla narcaea,* form *polychrous,* female, Loreto, São Paulo.

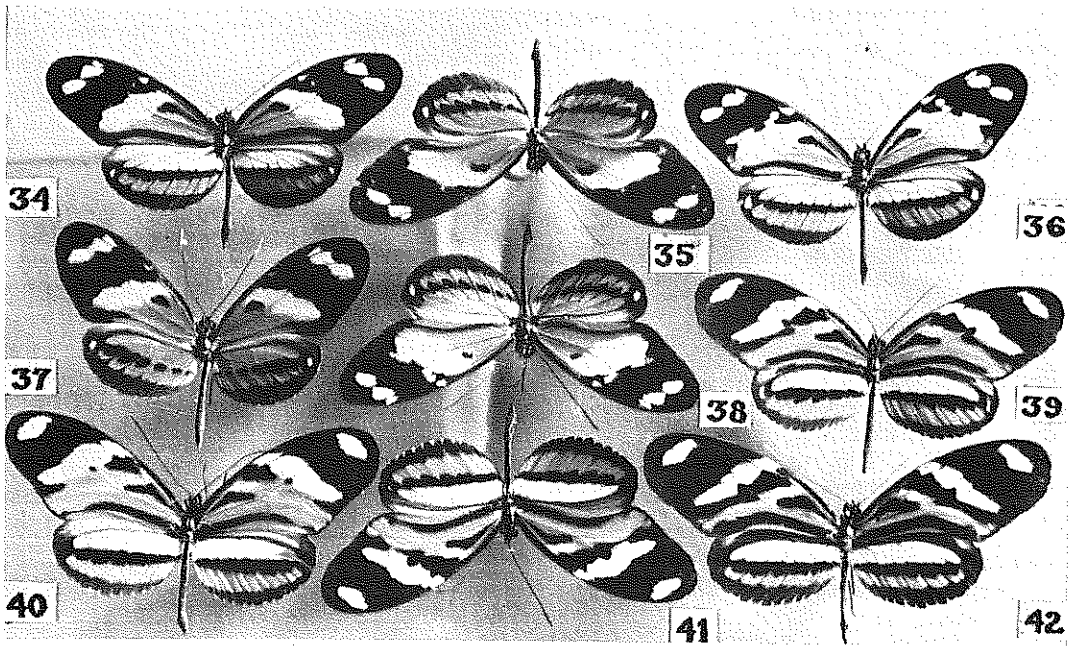
Figure 47. *Heliconius besckei,* male, Brasília, Distrito Federal.

Figure 48. *H. melpomene nanna,* male, Santa Teresa, Espírito Santo.

Figure 49. *H. melpomene burchelli,* male, Rio Maranhão, Distrito Federal.

Figure 50. *H. erato phyllis,* male, Rio de Janeiro.

Figure 51. *H. erato phyllis,* form *artifex* Stichel, 1899, male, Rio de Janeiro.



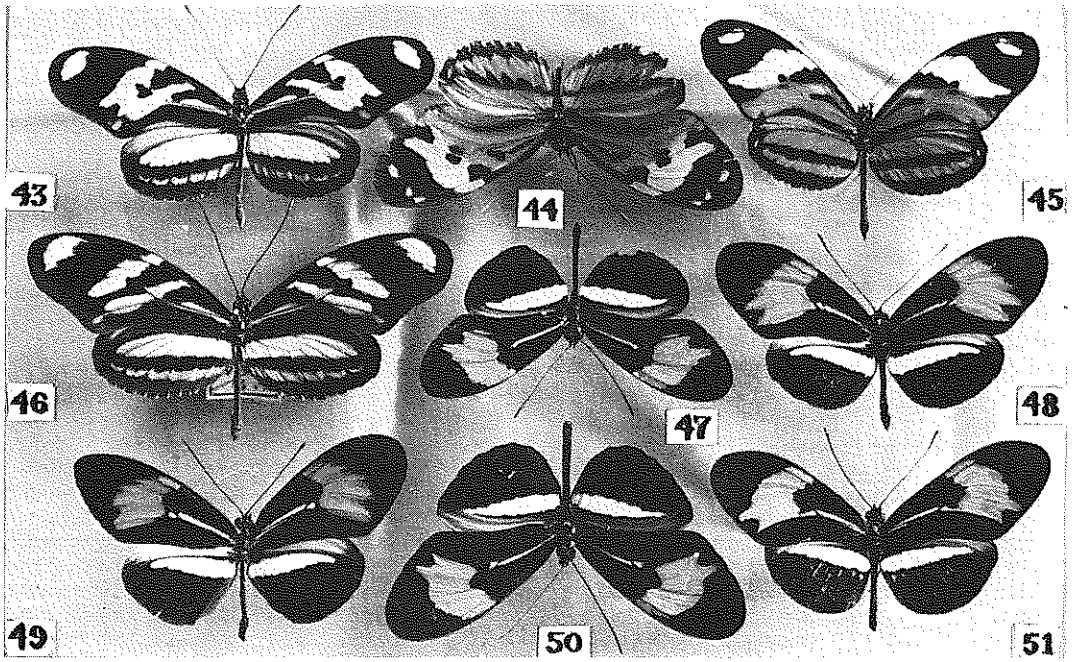


PLATE V

Plate VI

Heliconians marginal in extra-Amazonian Brazil, not illustrated on other plates; polymorphism in Amazonian heliconians.

Figs. 52-60, 63, 64: Black, yellow, and orange to red.

Figs. 61 and 62: Iridescent blue and yellow.

All dorsal, two-thirds life size.

Figures 52-55. *Eueides isabella isabella,* variants from a single polymorphic population, all taken during 90 minutes' collecting on June 2, 1971, over a ten-meter radius in São Vicente, 90 Km. E. of Cuiabá, Mato Grosso, 600 meters. The total sample is 21 specimens.

Figures 56-58. *Heliconius numata* near *superioris* (upper male, middle and lower females), three variants from a fairly stable population, June 7, 1971, 17 Km. N. of Salto do Céu, upper Rio Branco (tributary of the Rio Cabaçal), west-central Mato Grosso, 400 meters.

Figure 59. *Heliconius silvana mirus,* near typical, male, Salto do Céu, Mato Grosso, June 7, 1971.

Figure 60. *Heliconius burneyi* near typical *burneyi,* male, Pimenta Bueno, Rondônia; identical to specimen observed near Salto do Céu, Mato Grosso, 400 meters, June 7, 1971.

Figure 61. *Heliconius leucadia pseudorhea,* male, Patrimônio Nôvo, upper Rio Jaurú, west-central Mato Grosso, 600 meters, June 10, 1971.

Figure 62. Variation in the population of *Heliconius wallacei* flying just north of Obidos, Pará. The second form from the top, plus combinants with a wider band, represents the bulk of the population. All taken in July 1970. Iridescent blue and yellow. Forms with white instead of yellow forewing bands, with all the illustrated band shapes, form up to one-quarter of the populations of *wallacei* in the northern middle Amazon; they may be still more abundant northward, in areas where the white-banded *Heliconius antiochus* is the predominant species of the genus. This polymorphic population of *wallacei* may be found as far southwestward as the Manaus area.

Figure 63. Polymorphic hybrid population of *Heliconius erato* from Riozinho, 28 Km. down the Rio Machado from Pimenta Bueno, Mato Grosso, all taken in August 1970. The subspecies which meet here are *amazona* (upper left) from the northeast and *venustus* (lower right) from the south. A little farther downstream, *emma* also joins the gene pool from the west, producing a continuous series of polymorphic populations all the way down the Rio Madeira to Manaus, up the south bank of the Rio Negro to Barcelos, and westward to São Paulo de Olivença (see map).

Six principal forms can be recognized, for scoring members of populations along the Cuiabá-Pôrto Velho highway between Vilhena and the town of Rondônia, as follows:

(1) *amazona* Staudinger, 1896. Very open yellow band, full orange dennis and rays.

(2) (hybrid). Very open yellow band, dennis restricted to three lines and much redder.

(3) form *constricta* Joicey and Kaye, 1917. Yellow band closed down but still encircling much black, dennis orange and complete.

(4) (hybrid). Same, with dennis red and reduced.

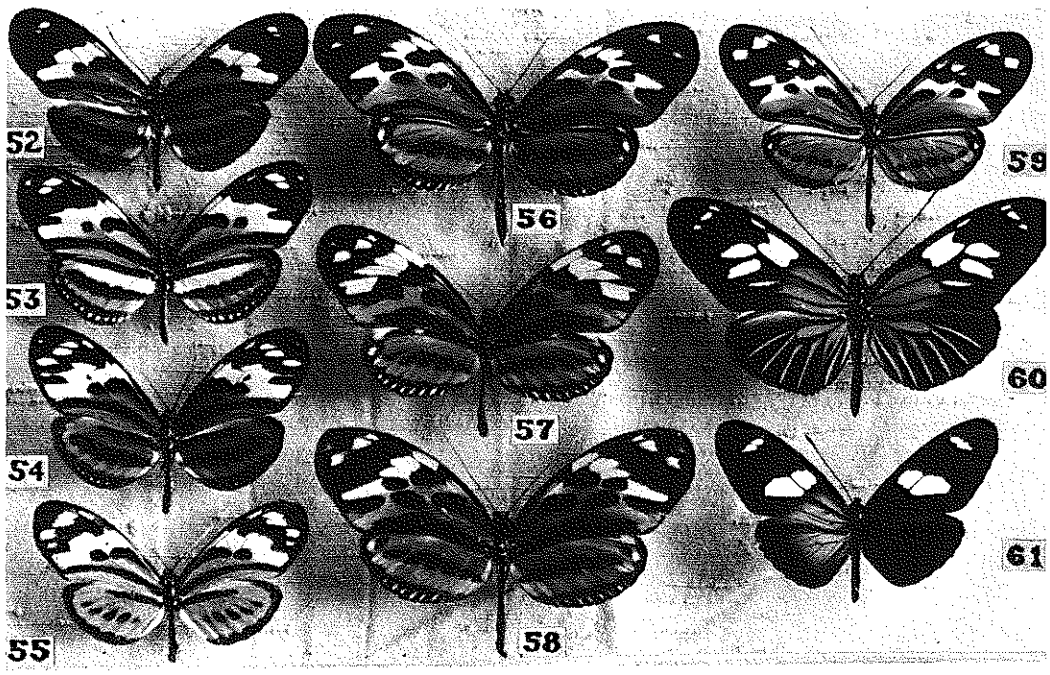
(5) form *donatia* Fruhstorfer, 1910. Forewing yellow band almost totally compacted but still enclosing a small black spot or bar at or extending out from the end of the cell; dennis usually red and reduced.

(6) *venustus* Salvin, 1871. Forewing yellow patch compact, without black in center, and somewhat reduced distally; dennis red and reduced to three lines.

The eight specimens in Fig. 63 would be scored 1 — 2 — 1 — 4 — 4 — 3/5 — 5 — 6.

Analysis of some populations:

Km.	Elev.(m.)	Locality	form 1	2	3	4	5	6	total sample
—200	700	South and west of Vilhena	—	—	—	—	3	12	15
0	600	Vilhena, frontier MT/RO	—	—	—	—	7	12	19
70	400	Km. 70, Vilhena-Pimenta Bueno	—	—	—	1	3	4	8
81	350	Km. 81, Vilhena-Pimenta Bueno	—	—	—	3	25	19	47
190	320	Pimenta Bueno	1	3	—	3	2	1	10
220	300	Riozinho, 1970 season	3	4	8	5	6	1	27
		Riozinho, 1971 trips	16	12	5	8	9	3	53
240	290	Km. 48 east of P. Bueno	3	2	3	1	—	—	9



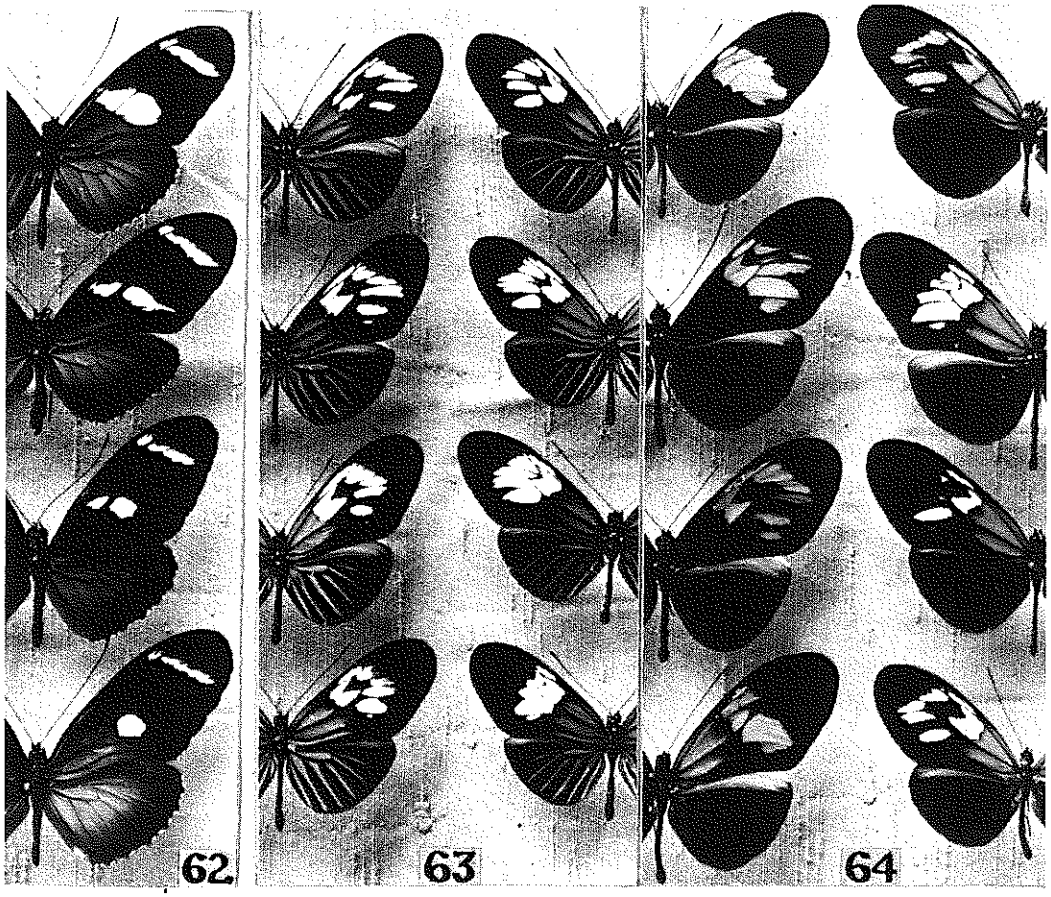
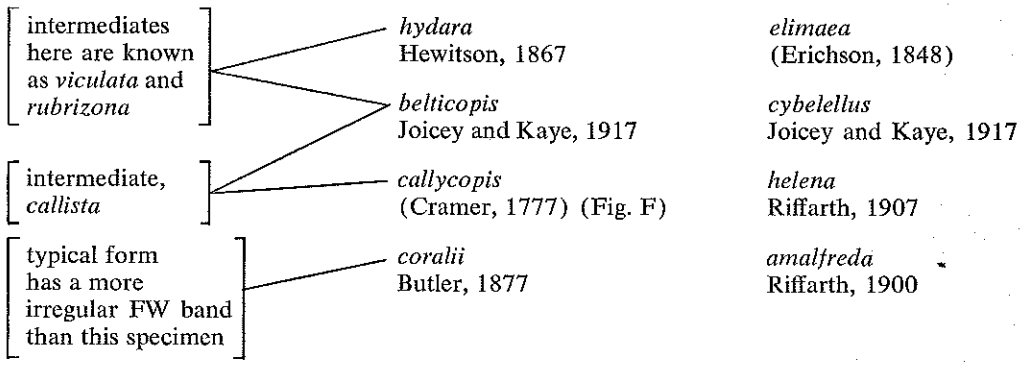


PLATE VI

FIGURE 64. Polymorphic hybrid population of *Heliconius erato* just north of Obidos, Pará. All taken in the same area in July 1970 except *cybelellus* (taken in the area in 1931). The approximate names of the forms are as below; the form *dryope*, with a *hydara* entire red band and dennis, is not illustrated; all forms except *hydara* and *amalfreda* may be considered as hybrid recombinants.



The approximate abundance of the forms in the 1970 population is (starting with the most common; total sample about 150 specimens): *amalfreda — hydara, viculata, rubrizona — helena* and varieties — *belticopis, elimaea,* and *coralii — dryope — callycopis — cybelellus.*

In the Obidos area, *Heliconius melpomene* is abundant and practically monomorphic as *m. melpomene,* with a black ground color and a broad red band on the forewing; a very few individuals have been taken with hybrid characters (dennis, or a mixed red-and-yellow forewing band). The first five illustrated forms of *erato,* and *e. dryope,* are very similar in flight to *m. melpomene,* appearing black with two bright red areas. The last three forms illustrated closely resemble the common sympatric *H. burneyi catherinae* and *H. tales.* Like these latter species, they fly higher, and are encountered more away from the streams, than the red-banded *erato* forms which fly lower and more slowly, with *melpomene* in the areas near permanent water. This double Müllerian mimicry in both behavior and pattern has apparently helped to stabilize an extremely large hybridization zone between *erato hydara* and *e. amalfreda,* covering almost the entire northern half of the lower middle Amazon (see map). This hybrid zone also extends south across the river to Santarém and Maués, where *hydara,* which is apparently able to cross the river, meets not with *amalfreda* but with the rayed *amazona;* these latter two forms, as well as dennis-rayed subspecies of *aoede, melpomene,* and *demeter,* seem to find an impenetrable barrier in the Amazon/Negro Rivers between the Ilha de Marajó and Barcelos. The stronger-flying species (*Eueides tales* and *Heliconius burneyi* and *egeria*) cross the river occasionally (like *erato hydara* and *m. melpomene*), producing populations polymorphic for rays in these species on both sides.

In Itacoatiara, on the north bank of the Amazon 200 Km downstream from Manaus, the hybrid population of *erato* is near its western limit. A sample of 13 specimens caught and another 15 seen indicates almost equal abundance of all of the forms illustrated, plus *dryope.* This suggests that this population may be composed principally of individuals of hybrid parentage, rather than the backcrosses of rarer hybrids to the parent subspecies as in Obidos. In Itacoatiara, the *m. melpomene* population shows greater signs of hybridization than in Obidos, but no yellow-banded individuals were seen or taken in a total sample of over 50. Many specimens, however, had signs of white or yellow in the underside, and one in the upperside, of the forewing red band. About one-quarter of the individuals also showed a dentate red line across the postdiscal area of the hindwing, possibly caused by a gene related to that which transforms *melpomene* rays from triangular to nail-shaped.

In the Manaus area, *erato* is monomorphic as *e. amalfreda.* Across the Rio Negro, only three Km away, the western dennis-rayed population with a polymorphic forewing band is found; there seems to be no gene exchange across the Rio Negro here.