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AN ILLUSTRATED KEY TO THE SILVANIFORM
HELICONIUS (LEPIDOPTERA: NYMPHALIDAE)¹
WITH DESCRIPTIONS OF NEW SUBSPECIES

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INTRODUCTION

The group of Nymphaline butterflies classified under the general name "silvaniform heliconians" represents one of the most difficult taxonomic groups in the Lepidoptera. The fact that their wing colors and patterns are extremely plastic, responding rapidly to local selective pressures usually linked to Müllerian mimicry rings, make traditional classification based on these color-patterns laborious and often contradictory. The importance of developing a reasonable, orderly, and accurate systematic arrangement for the group derives from the fundamental significance of the mimicry in the ecology of these organisms, and of many related insects in the mimicry rings. The knowledge of the correct ordering of the silvaniforms could lead (and, indeed, already has led) to new insights into the evolution and stabilization of mimicry and polymorphism in Neotropical butterflies (Brown and Benson, 1974; Papageorgis, 1975; Brown, 1976a; Benson, Brown and Gilbert, 1976).

Studies of patterns and morphology in the silvaniforms have indicated that closely related subspecies (and even members of a single population) can show as much morphological and color-pattern difference as distinct species (this has also been found to be true in other mimetic butterflies; see d'Almeida, 1951; Fox, 1949, 1960, 1967; and Brown, 1976b). On the other hand, certain minor elements of color-pattern in select wing areas shown to be of utility in the taxonomy of other heliconians and also in the ithomiines (especially forewing spaces M₃-Cu₁ and Cu₁-Cu₂, and the base of the ventral hindwing), have now been shown to

¹ Contribution number 13 of the Programa de Ecología, Instituto de Biología, Universidad Estadual de Campinas.

be useful in reliable superficial separation of silvaniform species. The final solution to the tangle, however, has only come through extensive biosystematic work in the field and insectary. This has shown that near-identical adults can have very easily distinguishable eggs or larvae, and that the insects themselves perceive behavioral barriers between species which are invisible to the taxonomist who works only on museum specimens.

Full discussion of the mimetic polymorphisms, genetics, and speciation-despeciation phenomena observed in the silvaniform *Heliconius* is reserved for future papers of a more general biological nature. This paper describes the basis for systematic ordering of the silvaniforms, and presents a key for the separation of all named forms (to 1976), with illustrations of each of these and of important variations and intergradations. This foundation is necessary for the derived discussion of the unique and fascinating biological processes associated with the past and present lives of these butterfly species.

BRIEF HISTORY OF SILVANIFORM SYSTEMATICS

Traditional taxonomy of the silvaniforms tended to regard all sympatric and visually separable forms as full species. Thus, Weymer's classical revision (1894), which also discussed mimicry between known silvaniforms and sympatric ithomiines, presented most names as species (a total of 70), with only 21 additional minor forms placed as associated "varieties." The first serious attempt at ordering these many names into species-groups was that of Stichel and Riffarth (1905), who recognized 22 species in all. This logical arrangement permitted these and other authors to properly identify and describe new forms, assigning them to known species or defining them as new species, and a large number of new taxa appeared in the following twelve years. By the time the volume of the "Lepidopterorum Catalogus" corresponding to the Helconiini (Neustetter, 1929) appeared, 25 species and nearly two hundred named forms were recognized.

In this same period, however, more analytic forces were also at work. The first to examine the morphology of the silvaniforms was Eltringham (1917), in a classic paper which noted the near impossibility of species separations by male genitalia. Although

Kaye (1917) contested Eltringham's reduction of the number of species, he later (1924) used the weight of his extensive field experience and large collection to propose that the silvaniforms represented only three highly variable and polytypic species. Michael (1926) then reported interesting observations on intergradations and even matings between very different silvaniforms in lowland Peru; he remarked (p. 186, in translation) that "A new revision of this especially difficult group will probably be long in coming, as this can only be based on zealous and successful studies in the field ("on the spot"), and rearing of the caterpillars." By the time Neustetter prepared his catalogue, only he was describing new silvaniforms. The confusion apparently led to a moratorium of new descriptions until a satisfactory systematic arrangement could be achieved for the group; no new names were proposed for forty years, though representatives of unnamed subspecies were not lacking in major collections.

A comparison of the numbers of distinct silvaniforms described in various periods anterior to the present work, reflects the activity in the taxonomy of the group:

- (a) Period of primitive description (Linné, Cramer, Fabricius, Hübner)
(1758-1846, 89 years) 9 names = 0.1/year
- (b) Period of early exploration (Doubleday, Westwood, and Hewitson)
(1847-1861, 15 years) 6 names = 0.4/year
- (c) Period of more intense, often personal exploration (Bates, the Felders, Butler, Godman, Salvin, etc.)
(1862-1882, 21 years) 30 names = 1.4/year
- (d) Period of expanding systematic interest (dominated by Weymer, also Staudinger)
(1883-1896, 14 years) 47 names = 3.4/year
- (e) Period of understanding and ordering the names (mostly Stichel and Riffarth)
(1896-1906, 10 years) 18 names = 1.8/year
- (f) Period of rapid expansion and description (Riffarth, Neustetter, Joicey, Kaye, Boulet and Le Cerf, and others)
(1907-1917, 11 years) 35 names = 3.2/year

- (g) Period of exhaustion of new forms and beginning of uncertainty about the group
(1918-1924, 7 years) 4 names = 0.6/year
- (h) Period of supplementary description, mostly of minor varieties (Neustetter, also Hall, Michael, Apolinari Maria)
(1925-1932, 8 years) 27 names = 3.4/year
- (i) Period of confusion and moratorium
(1933-1972, 40 years) no names

The next rational attempt at ordering the silvaniforms came only with Emsley's revision of the genus (1965). This analysis was based largely on the distribution of androconial scales on the male hindwing. Emsley recognized a total of four species, one of these (*H. hecale*) being restricted to the nominate subspecies. Although there are fairly large differences between the analysis presented here and that of Emsley, he did see many types in the British Museum (Natural History), and his arrangement provided a solid base for further work on the group. Two species recognized in the present paper were not separated by Emsley: all forms of *H. pardalinus* were joined to "aristionus," and all forms of *H. ismenius* were included under "numatus." The morphological characters illustrated by Emsley for the latter species are actually those of *ismenius* only, not applying to the Amazonian or southern subspecies he included. Emsley correctly joined *numata* and *silvana* under "numatus," but truncated this species westward, separating the upper Amazonian forms as "aristionus." The races of *H. hecale* were placed by Emsley in all three of his other species, being concentrated under "ethillus" and "aristionus." Most forms of *ethilla* were correctly joined under "ethillus" in Emsley's analysis.

MATERIALS AND METHODS

When Emsley's otherwise excellent revision was used to order the long series of silvaniforms in the Museu Nacional in Rio de Janeiro, much confusion resulted. A large number of forms was dissected by standard methods; this only served to slightly rearrange the confusion. Attempts at determination of androconial distribution revealed wide variation in series apparently homogeneous in color and pattern, and appreciable discrepancies from the distributions reported. This character proved very difficult to

evaluate, even when massive scale removal was employed to detect scattered androconia, and was not judged to be any more useful than the valve shape in understanding the species.

Personal consultation with Dr. Emsley did not lead to the resolution of these problems. The other major systematist in the Heliconiini, Dr. John R. G. Turner of the University of York, England (now Stony Brook, New York), stated that he had not arrived at a satisfactory understanding of speciation patterns in the silvaniforms, and was not dedicating further time to their study. The problem thus appeared available, but almost insoluble, except perhaps through the development of new taxonomic methods applicable in the group.

Fortunately, these new methods were indeed available, in the form of modern biosystematics. Although cytological studies proved fruitless (all species having identical chromosome complements), laboratory and field work was facilitated for this author, favorably located in the Brazilian tropics with opportunities for wide travel in other parts of the Neotropics. This provided singular conditions for a biosystematic approach to silvaniform taxonomy, which was carried forward in the years 1966-1976, with methods of field and insectary work already described (Brown, 1972a; Brown and Benson, 1974).

Most major public *Heliconius* collections were also visited. Notable exceptions were those in Paris, Berlin, and Vienna; the Museum National d'Histoire Naturelle (**PM**) sent many photographs and the types of *intermedia* and *boulleti* (courtesy of P. Viette and H. de Lesse), the Zoologisches Museum der Humboldt-Universität (**HM**) mailed seven key type specimens for study in Brazil (through H. J. Hannemann), and H. Holzinger provided photographs of the Neustetter types in the Naturhistorisches Museum, Wien (**VM**), and of other important specimens in this and in his own collection (**HH**) (see also Holzinger and Holzinger, 1974). Especially useful collections examined, including large numbers of types and carefully identified material, were those of the British Museum (Natural History) (**BM**) (R. I. Vane-Wright, P. R. Ackery and R. L. Smiles) and the Allyn Museum in Sarasota, Florida, including the W. J. Kaye collection (**AA**) (Lee D. Miller). Other large museums with important series studied were

the American Museum of Natural History in New York (**AM**) (F. H. Ringe), the Carnegie Museum in Pittsburgh (**CM**) (H. A. Clench), and the Museu Nacional in Rio de Janeiro (**MN**) (A. R. do Rêgo Barros). Smaller collections seen, with appreciable new information, included the United States National Collection in Washington, D.C. (**NM**) (W. D. Fields), the Facultad de Agronomia in Maracay, Venezuela (**FA**) (F. Fernández Yépez), the Museu Javier Prado in Lima, Peru (**JP**) (G. Lamas M.), the Cornell University collection (**CU**) (J. D. Franclemont), the Museu Goeldi in Belém, Pará (**MG**) (R. Arlé), the Instituto Oswaldo Cruz in Rio de Janeiro (**IO**) (J. Jurberg), the Departamento de Zoologia of the Universidade Federal do Paraná (**DZ**), including the R. F. d'Almeida collection (**RA**) (O. H. H. Mielke), the Museu de Zoologia of the Universidade de São Paulo (**MZ**) (U. R. Martins de Souza), and the personal collections of Gordon Small in Panamá (**GS**), L. W. Harris in Lima (**LH**), E. W. Schmidt-Mumm in Bogotá (**SM**), David Gifford in Edinburgh (**DG**, photos only), Ricardo Diringhofen in São Paulo (**RD**), Koroku Negishi in Kanazawa, Japan (**KN**, photos only), and W. W. Benson in Campinas, São Paulo (**WB**), as well as abundant material collected or obtained by this author (**KB**).

The two-letter combinations representing the collections in the paragraph above plus **CZ** (Museum of Comparative Zoology, Harvard University, not visited) are used throughout this paper, including in the descriptions of new subspecies and on the key illustrations.

The collection of the **MN** was initially used for basic research leading to the development of a working hypothesis for silvaniform systematics. The very complete representation in the **MN** of Brazilian forms, which are poorly represented in essentially all other major collections, proved to be an important new element in the rational understanding of speciation in the group. The problem was approached through the application of the following methodology:

- (a) *For separation and identification of good species:*
 - (1) identification of significantly different and non-intergrading entities in all possible localities at the peripheries of the Neotropics;

- (2) correlation of these with useful pattern or morphological characters wherever possible, seeking especially minor elements of color-pattern; all major elements linked to mimetic association with ithomiines or other heliconians in the respective regions were discounted from consideration. The criterion of minor color-pattern elements was suggested both by Emsley's revision (1965) and by the classic works of Forbes (1924, 1927, 1948) and Fox (1960, 1967) on the mimetic ithomiines *Melinaea*, *Forbestra*, and *Mechanitis*. These butterflies, while varying greatly in overall color and pattern and showing monotonous genital structure like the silvaniforms, often preserve relatively insignificant characters throughout the range of a species. One such character is that which Forbes (1924) designated the "comma-mark" in forewing spaces M_3 - Cu_1 and Cu_1 - Cu_2 . These spaces proved to be of singular utility in silvaniform systematics, and indeed may be shown to be important in a wide variety of Lepidoptera. Other important minor elements discovered in the silvaniforms were the presence or absence of red basal dots on the ventral surface of the hindwing (much used by Emsley); the form and location of subapical markings on the forewing (Fox, 1960); the presence or absence of white marginal streaks dorsally or ventrally; the form of the hindwing median and marginal black bands; and the general shape of the wings, the average size, and the intensity or quality of the orange, red, or brown coloration;
 - (3) preliminary association of these peripheral forms into possible polytypic species, based on the useful and generalizable characters encountered.
- (b) *For subspecies identification and association with species:*
- (1) judicious application of the criteria developed for species recognition, derived from the above analysis of peripheral populations, to neighboring and differentiated populations, using wherever possible specimens from locali-

ties well inside of adjacent proposed Quaternary forest refuges (Brown, Sheppard and Turner, 1974; Brown, 1976, 1977);

- (2) once corresponding forms were identified (at times with necessity to discount or disregard some of the initially supposed "general species characters"), search for intermediate specimens or intergrading series, from localities in the regions between the supposed refuges. If such transitional forms could be found, clear association of the two original entities was presumed;
 - (3) extension of the same sort of analysis continuously farther into the center of the Neotropical region, attempting wherever possible to close the gaps with other peripheral forms;
 - (4) in cases where no intermediate forms were discovered between apparently adjacent and probably conspecific entities (from the analysis above), conservation of the association only if large and important physiogeographic barriers, operating in many other organisms, could be demonstrated in the intervening area;
 - (5) eventually, attempt to link up as many of the peripheral populations as possible, giving an overall picture of the range and variation of the supposed species, with modifications as necessary to the concepts developed during the initial stages of the analysis (for a discussion of criteria used for subspecies status in polytypic continental species, see Brown, 1976a).
- (c) *For identification of species not present at the peripheries:*
Proposal of an additional species if, and only if, in complicated polymorphic series from central localities, an important form could not be assigned to any of the peripheral species, there existing no intergrades with sympatric morphs of any of these; local adaptive polymorphism was, however, accepted as possible (Brown and Benson, 1974).
- The working hypothesis thus developed indicated a total of six or possibly seven species in the group (Brown and Mielke, 1972: 26), not including *nattereri* (Fig. 1), a very primitive and geo-

graphically restricted silvaniform already discussed (Brown, 1972b); nor *atthis* (Fig. 2), a very closely related southwestern isolate of *ethilla* (possibly still conspecific) confined to western Ecuador and adjacent Colombia and Peru; nor *elevatus/luciana/besckei* (Fig. 3), a complex of possible silvaniform origin which has, however, deviated widely in color-pattern from typical members of the group (see Turner, 1966 and Brown and Mielke, 1972), and may in fact be closely related to *H. cydno*.

The problem was then taken into the field in an attempt to formulate a necessary and independent antithesis. As many of the forms as possible were studied in nature, observing especially general behavior (including courtship, foodplant preferences, social chasing, and roosting), and were taken into the insectary for the study of early stages (which, in some cases, proved to be far more distinct than the adults, but which also showed appreciable variation; Figs. 4-6). The adults derived from rearing studies were, whenever possible, placed in outdoor insectaries for further studies of behavior and genetic analyses (whenever spontaneous matings were obtained). These experiments are still underway, and will be reported in a future paper.

The working hypothesis developed from analysis of the MN material and of other large collections was changed in only one important particular (other than minor rearrangement of some forms and subspecies) by the biological studies in the field: three of the possible species (*numata*, *silvana*, and *aulicus*) had to be recombined (Brown and Benson, 1974). A summary analysis of the useful characters discovered, and differentiation patterns observed in the five species now recognized (*numata*, *ismenius*, *par-dalinus*, *hecale*, and *ethilla*) is presented below.

The next step in the systematic analysis was association of each recognized subspecies with an available name. Where this proved to be impossible, new subspecies names were proposed (Brown, 1973, 1976a, this paper).² The remaining and available names

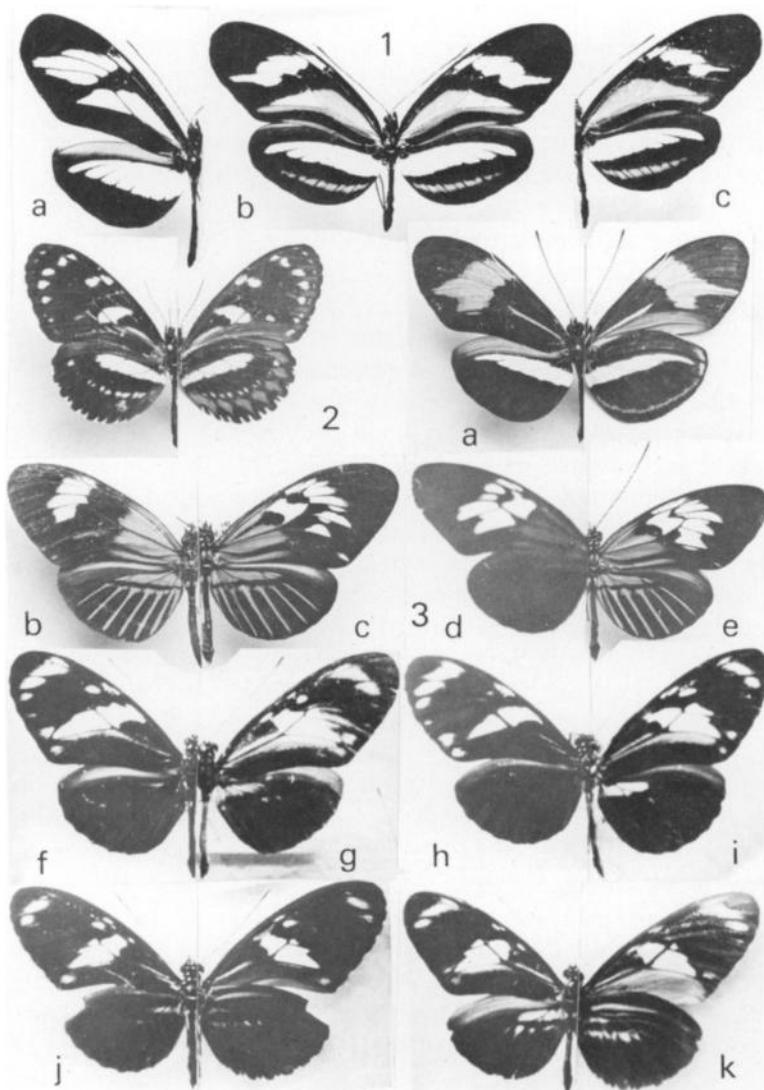
² I am grateful to Gerardo Lamas Müller, Museo Javier Prado, Universidad Nacional Mayor de San Marcos, Apartado 1109, Lima, Peru, and Francisco Fernández Yépez, Facultad de Agronomía, Universidad Central de Venezuela, Maracay, Aragua, Venezuela, for permission to include joint descriptions of new silvaniform subspecies in this paper, thereby completing the formal naming of presently recognized taxa.

were then either synonymized (rarely) or, wherever possible, assigned to transitional forms or intrapopulational variants. In the case of extensively polymorphic species like *numata*, some names were conserved with a "weak subspecific" status, even when no pure or even predominant populations could be found, providing they seemed to represent important morphs occurring in populations over large areas, probably derived in isolated refuges in the past, and not easily explainable by simple gene recombination from other sympatric forms. For operational determination, a "weak subspecies" in the case of *Heliconius* was defined as a significant morph, preferably of identifiable evolutionary history (through evident color-pattern association with a mimicry complex largely restricted to a well-defined core area for evolution), which over a reasonable area (more than 2500 Km²) occurred in a proportion above $\frac{3}{2n}$ in all known populations, where n = the number of recognizable conspecific morphs which occur in proportions exceeding 0.10 in the populations. Thus, if a series of populations in a defined geographical region shows two principal morphs, and one of these is distinctly mimetic and represents over 75% of the individuals ($\frac{3}{2 \times 2} = 0.75$), it is regarded as a

FIGURE 1.—*Heliconius nattereri* C. & R. Felder, a protosilvaniform. a, male; b, female (= fruhstorferi" Riffarth); c, female variety, all dorsal, from Santa Teresa, Espírito Santo, collection of the author, about 0.6× life size, black, yellow and orange (females).

FIGURE 2.—*Heliconius atthis* Doubleday, a postsilvaniform very close to *ethilla*, male, dorsal (left) and ventral (right) wing surfaces, Santo Domingo de los Colorados, western Ecuador, collection of the author, 0.6× life size, black and yellow, orange ventrally.

FIGURE 3.—*Heliconius elevatus* Nöldner subspecies, *H. besckei* Ménétriés, and *H. luciana* Lichy subspecies. a, *besckei*, male, dorsal (left) and ventral (right) wing surfaces, Itatiaia, Rio de Janeiro, collection of the author; b, *e. elevatus* × *pseudocupidineus* Neustetter, male, dorsal, Tingo María, Peru, collection of the author; c, *e. aquilina* Neustetter, male, dorsal, Riozinho, Rondônia, collection of the author; d, *e. roraima* Turner, male, dorsal, Roraima, in the AMNH; e, *e. perchlora* Joicey & Kaye, male, dorsal, Riozinho, Rondônia, collection of the author; f, *l. luciana*, holotype male, dorsal, Raudal "Los Tiestos," Alto Orinoco, Amazonas, Venezuela, in the FAM; g, *l. luciana*, male, dorsal, Mantecal, Rio Cuchivero, in the H. Skinner collection; h, *l. luciana*, paratype female, dorsal, same data as holotype;



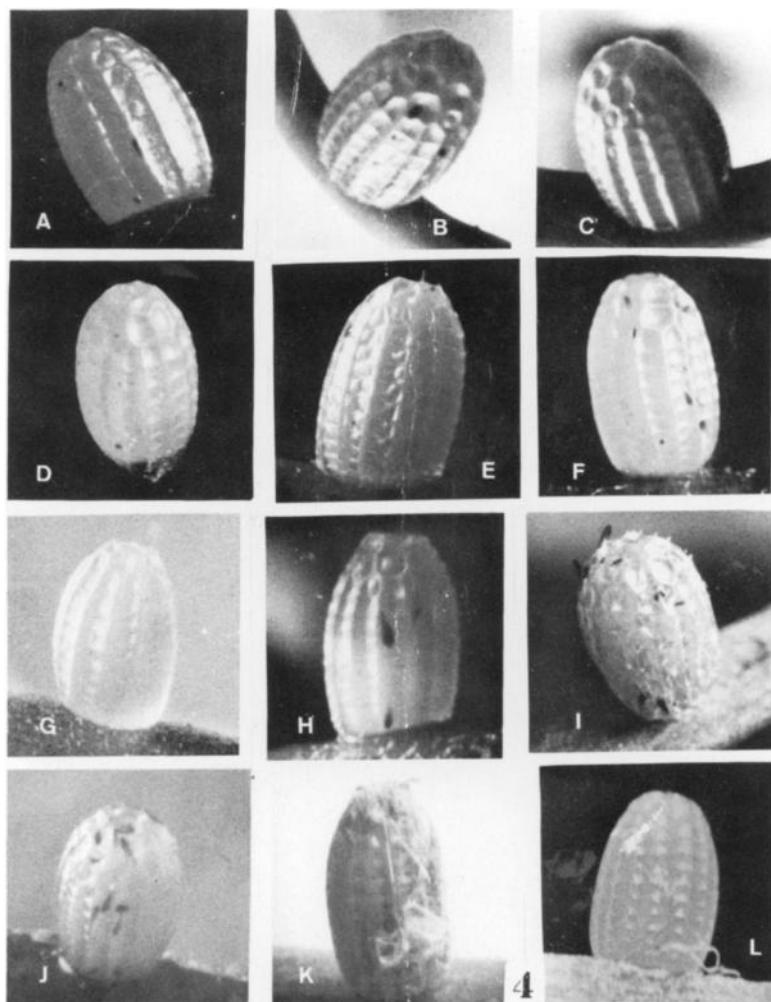
i, *I. watunna* Lichy, male, dorsal, same data as (g); j, *I. watunna*, female, dorsal (left) and ventral (right) wing surfaces, Boca Aguas Negras, Guaniamo, Bolívar, in the FAM; k, *I. watunna*, male, dorsal (left) and ventral (right) wing surfaces, same data as (j). All about $0.6 \times$ life size, black, white (f, g, h) or yellow, and orange to red.

"weak subspecies." If there are five morphs in proportions above 10% of the populations, the one (or two) with proportion over 0.30 will be regarded as a "weak subspecies." In most cases, these names should not be considered as modern geographical subspecies, but rather as biologically important mimetic morphs (Brown and Benson, 1974).

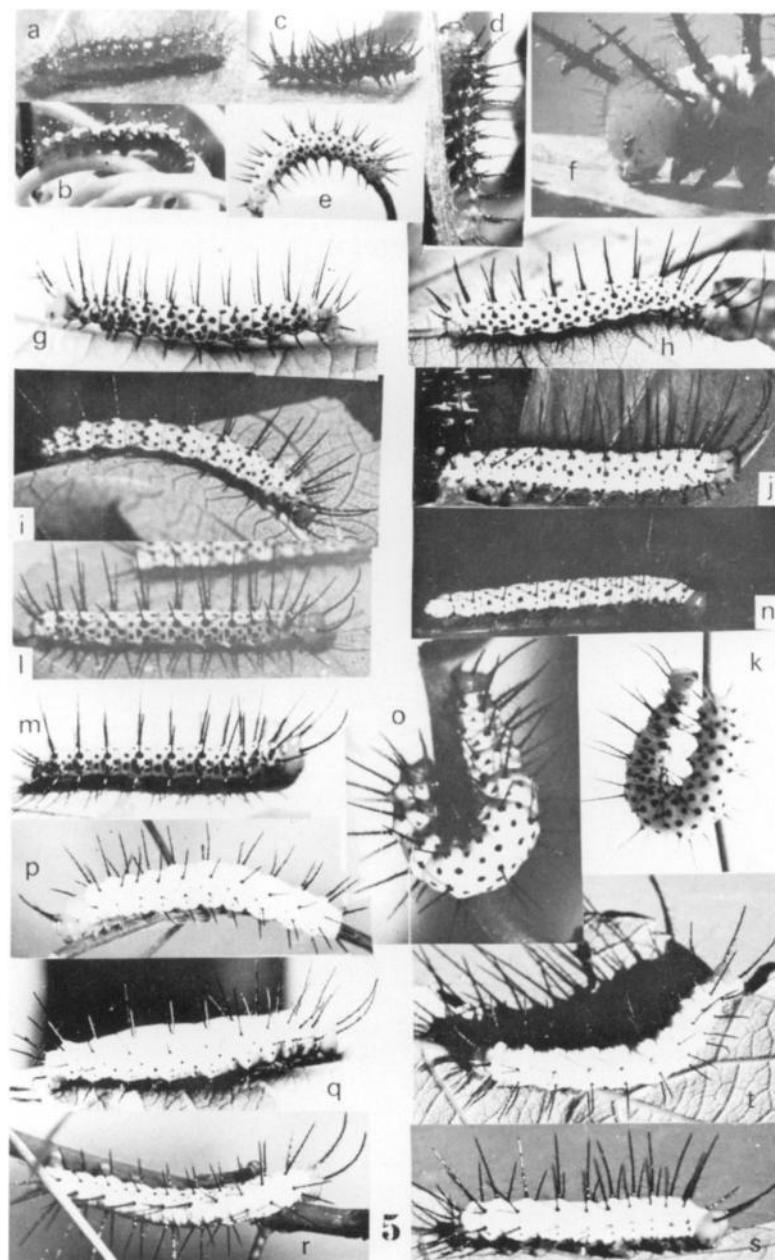
Finally, the resulting systematic order was crystallized into a dichotomous taxonomic key, and at least one specimen (preferably a type, and also a recent specimen when possible) was chosen to illustrate each available name, and also important unnamed or transitional forms. This key is presented after the systematic discussion below, along with accompanying illustrations.

As a typological orientation is not practical in the study of these highly polymorphic species, and indeed could even obscure the inherent importance of their variability, often well demonstrated in syntypic series, no lectotypes are designated in this work; however, the first illustrated specimen for any taxon whose holotype is not shown is subjectively considered to be "representative" of the strictest application of the name. All specific epithets are retained in the author's original spelling, following our expressed policy in this group (Turner, 1967; Brown and Mielke, 1972). Because the judgment as to whether a name is a good subspecies or an intrapopulational variant is often a subjective matter in the highly vagile and polymorphic silvaniforms, no effort has been made here to revalidate names of dubious taxonomic status or to designate new combinations as such. Modern redescription, with substitution of authorship, of older taxa originally called "varieties," "forms," or "aberrations," perfectly adequately described before the codification of the international rules, represented by satisfactory extant type-material, and often in widespread use today, seems to be an unfortunate practice at best. In the heliconians it could easily lead to an ambitious modern revisor becoming the author of the majority of the taxa in the tribe, including some with

FIGURE 4.—Eggs of silvaniform *Heliconius*, 20× life size, strong yellow (taxon, locality, number of vertical ribs, number of regular horizontal ribs): a, *nattereri*, Santa Teresa, Espírito Santo, 14-9; b, *numata aulicus*, San Esteban, Venezuela, 17-7; c, *numata peeblesi*, Barinitas, Venezuela, 17-8; d, *numata ethra*, Linhares, Espírito Santo, 14-8; e, *numata aristiona*, Santa Clara,



east Ecuador, 14-11; f, *ismenius* "faunus," Quibdó, Chocó, Colombia, 14-11; g, *ismenius metaphorus*, Santo Domingo, west Ecuador, 13-9; h, *ismenius ismenius*, Victoria, Caldas, Colombia, 14-11; i, *pardalinus lucescens* × *radiosus*, Km.2 Manaus-Manacapuru road, Amazonas, Brazil, 16-9; j, *hecale melicerta*, Victoria, Caldas, Colombia, 17-10; k, *hecale quitalena*, Santa Clara, east Ecuador, 14-11; l, *ethilla chapadensis*, Buriti, Mato Grosso, 16-11. Note variation in ribbing within species and consequent uselessness of this character in taxonomic analysis.



species-category. It seems a far better policy, much more in line with nomenclatural stability and scientific humility, to give not only the "benefit of the doubt" (Mayr, 1969:362), but also that of the authorship of the name, to the describer before 1961, even when an "erroneous" category was originally used.

SPECIATION AND DIFFERENTIATION IN THE SILVANIFORMS

Silvaniform *Heliconius* are easily confused with Ithomiinae of the mimetic genera *Melinaea* and *Mechanitis*, and sometimes even with the smaller Ithomiinae in the genera *Hypothenemis*, *Callithomia*, and *Hyposcada* (some especially close pairs are illustrated in Brown and Benson, 1974). They have been found mixed with these ithomiines in essentially all collections examined. Separation is possible by a variety of readily observed characters. The form of closure of the hindwing cell is different in *Heliconius* and Ithomiinae; the forewing comma-marks have a different fundamental form; and in male ithomiines, there is a well-developed hair-pencil near the costal margin of the dorsal hindwing, while in silvaniforms the corresponding region is silvery-colored, not bear-

FIGURE 5.—Larvae of silvaniform *Heliconius*, black, white, and yellow; younger larvae dark brown (taxon, instar, locality, scale): a, *ethilla narcaea*, 1st, Rio de Janeiro, 4 \times ; b, *numata aulicus*, 1st, San Esteban, Venezuela, 4 \times ; c, *hecale annetta*, 2nd, San Esteban, 2 \times ; d, *numata aristiona*, 2nd to 3rd molt, Santa Clara, east Ecuador, 3 \times ; e, *pardalinus butleri*, 3rd to 4th molt, Iquitos, Peru, 1 \times ; f, *numata silvana*, 5th, Belém, Pará, Brazil, 5 \times ; g, *numata aulicus*, 4th, San Esteban, 1.6 \times ; h, *numata euphone*, 5th, Limoncocha, east Ecuador, 1 \times ; i, *numata silvana* (ex *nubifer*), 5th, Km. 2 Manaus-Manacapuru road, Amazonas, Brazil, 1 \times ; j, *numata superioris* \times *robigus* hybrid, 5th, insectary, 1 \times ; k, *numata mirus*, 5th, Colonia Hardeman, north of Montero, Bolivia, 1 \times ; l, *numata ethra*, 5th, Linhares, Espírito Santo, 1 \times ; m, *numata ethra*, 4th, Linhares, 1.6 \times ; n, *pardalinus lutescens* \times *radiosus*, 5th, Km. 2 Manaus-Manacapuru road, 1 \times ; o, *pardalinus butleri*, 5th, Iquitos, Peru, 1.5 \times ; p, *ethilla narcaea*, 4th to 5th molt, Petrópolis, Rio de Janeiro, 1.4 \times ; q, *ethilla metalilis*, 5th, San Esteban, 1 \times ; r, *ethilla chapadensis*, 5th, Buriti, Mato Grosso, 1 \times ; s, *hecale melicerta*, 4th, Quibdó, Chocó, Colombia, 1.4 \times ; t, *hecale melicerta*, 5th, Quibdó, 1 \times . Note that *numata* and *pardalinus* larvae are usually heavily spotted (as are *ismenius*, not illustrated), with variable development of dark side and ventral color and yellow anal cap; while *ethilla* and *hecale* larvae are usually much more lightly spotted.

ing hairs (Figs. 7-9). On the dorsal thorax, ithomiines possess orange patagia, while *Heliconius* bear yellow spots.

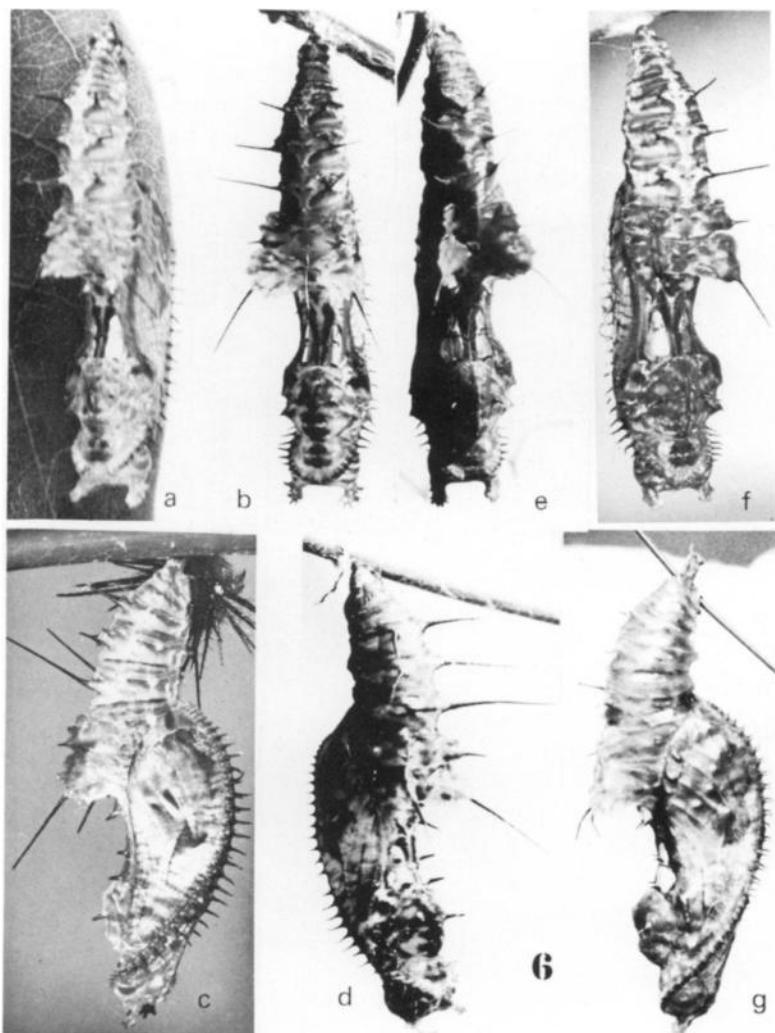
A. *Heliconius numata* (Figure 11, distribution map), one of the two silvaniform species present at the southern limits of the Neotropics (but not invading dryer or subtropical areas as does the other, *H. ethilla*), has been the subject of a detailed study of adaptive polymorphism and Müllerian mimicry (Brown and Benson, 1974). The principal morphs were illustrated in that publication, and the behavior of the adults and characteristics of the early stages were discussed.

Most but not all *numata* morphs show a simplified comma-mark, a bar under vein Cu_1 , occasionally doubling back in a hook at the inner end (as in *ethilla*, but usually not so strongly); some, especially "silvana"-type morphs, have a black triangle at the margin (Fig. 8). Almost never is a complete submarginal light spot present, unless the whole comma-mark is obsolescent. Never has a red basal spot been seen on the ventral hindwing; the spot at the inner angle of forewing space M_3-Cu_1 is only very rarely elongated distally over vein M_3 to assume a teardrop-shaped form; the hindmarginal black bar on the forewing, when present and extending to the anal angle, may be slightly clubbed distally, but essentially never forms a broad arrowhead isolating a submarginal anal spot as is frequent in *pardalinus*, *hecale*, and *ethilla*.

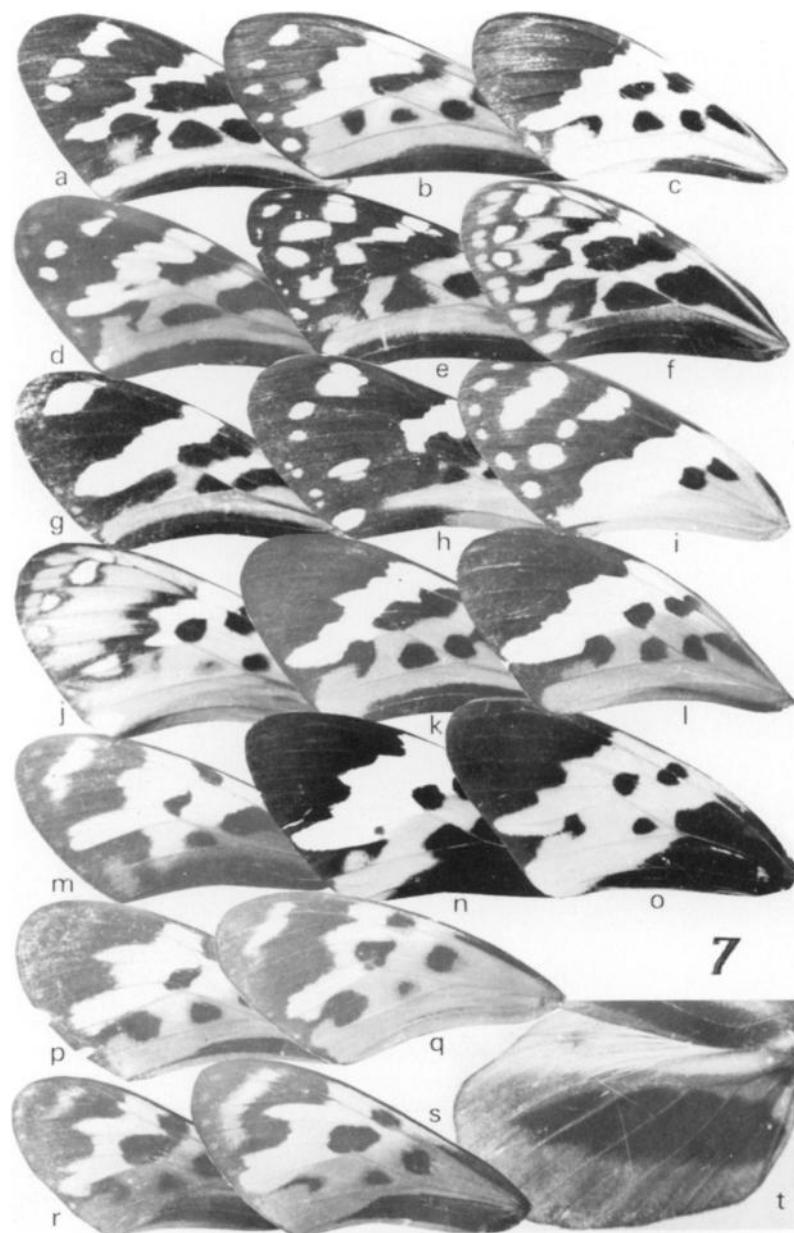
The tip of the male genital valve (TMGV) is extremely elongated in southern races (*n. ethra* and *n. robigus*); these also bear a clear brand on the inner margin of the ventral forewing of the male. These characters are variable in Amazonian *numata*; some have an elongate TMGV, but many others have the valve shorter and the terminal process thicker (Figure 10). The brand can appear in both males and females of *numata*, as well as those of *hecale* and *ethilla*, and is variable in its expression.

Association of the many widely different morphs of *numata* has been possible principally through observation of their voluntary association in the field and in the insectary. Intergrading series, often including a variety of named forms, connect many of the principal morphs of *numata*. In some cases, however, switch-

FIGURE 6.—Pupae of silvaniform *Heliconius*, light to dark brown, all 2× life size (taxon, locality): a, *numata ethra*, Linhares, Espírito Santo;



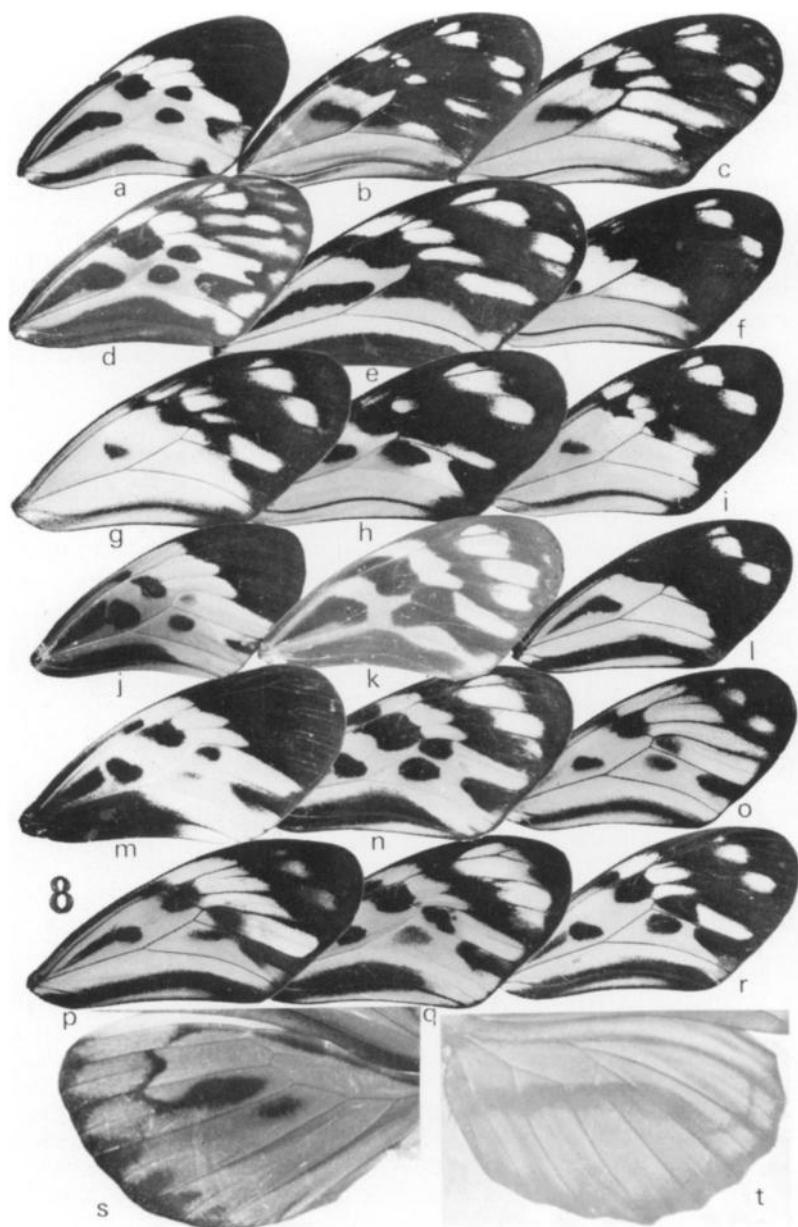
b, *numata robigus* × *superioris* hybrid, insectary; c, *numata messene*, Rio Negro, Meta, Colombia; d, *numata euphone*, Limoncocha, east Ecuador; e, *pardalinus lucescens* × *radiosus*, Km. 2, Manaus-Manacapurú Road, Amazonas, Brazil; f, *hecale melicerta*, Santa Rita, near Colón, Panamá; g, *hecale zuleika*, Rincon, Costa Rica (photo W. W. Benson). Note variation in length and angling of abdominal spines, which are not good taxonomic characters.



genes or supergenes determine the different patterns, and conspecificity was confirmed only after rearing one form out of eggs expressed from another, and appropriate genetic experiments (Brown and Benson, 1974). These programs are still incomplete, but it is now possible, with the aid of the refuge model (Brown, 1976) and the study of mimicry rings in the field, to define the significant races of *numata* and their probable origins. Totally sympatric morphs, which do not occur anywhere in pure populations today but were apparently derived from mimetic pressure in some well-defined refuge, are considered as "weak subspecies" (see definition above), not acceptable in the usual geographic sense because of extensive dispersal and mixing. For some of these, relatively pure populations may still be found in core areas of past refuges.

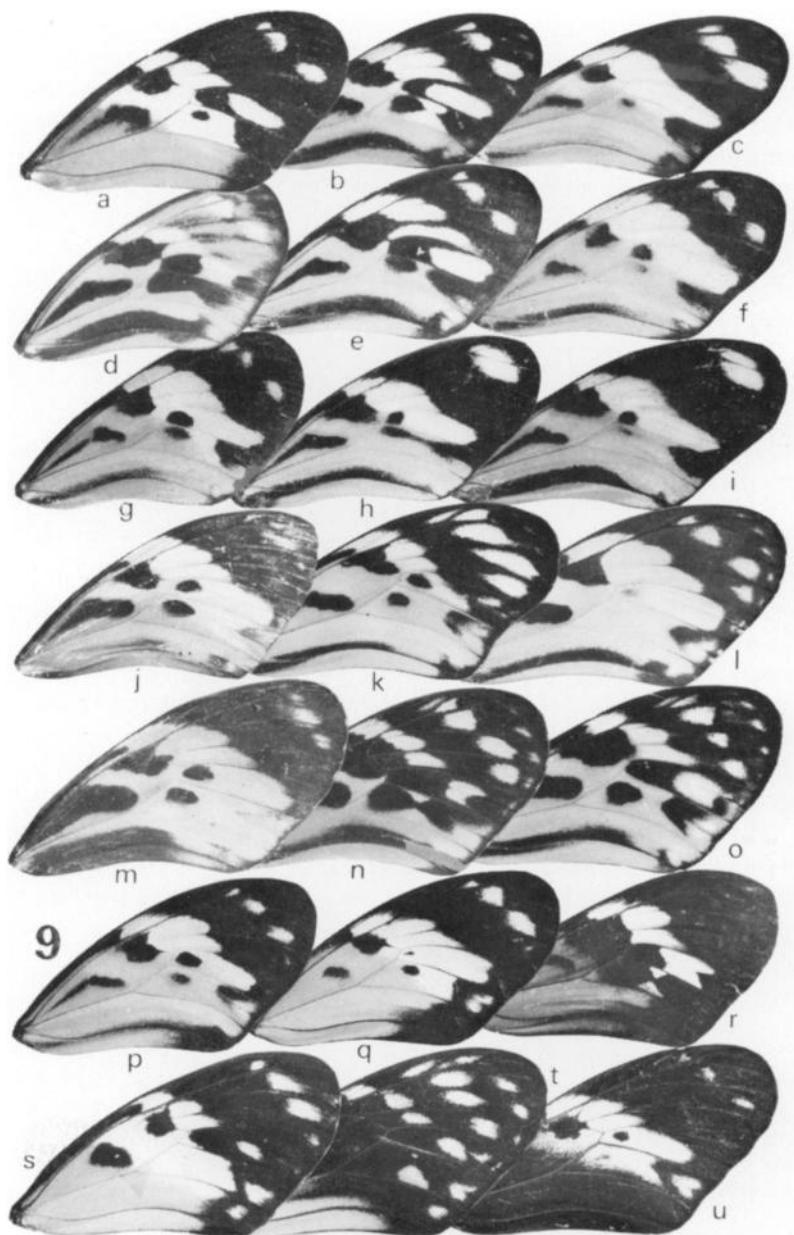
The species occurs in monomorphic populations at the peripheries of its range: a new subspecies (described below) in extreme northeastern Venezuela, which grades to *n. aulicus* in north-central Venezuela, which in turn grades to *n. peeblesi* in southwestern Venezuela; *n. messene* at higher elevations in the Colombian Andes; *n. aristiona* at higher elevations in the Andes of Ecuador, Peru, and Bolivia; *n. zobrysi* in the dry southeastern Amazon; and *n. ethra* and *n. robigus* in eastern and southeastern Brazil, respectively. Toward the center of the Neotropics, all of these subspecies except the last two intergrade with other races; the conspecificity of the east Brazilian and Amazonian subspecies has been established, however, by appropriate crosses in the insectary, to the third generation (Brown and Benson, 1974). In the

FIGURE 7.—Comma-marks and hair-pencil in the Ithomiinae mimetic of silvaniform *Heliconius*. a, *Melinaea ethra zamora*; b, *M. mnasias* ssp. nov.; c, *M. mnasias comma*; d, *M. ethra sola*; e, *M. ethra dodona*; f, *M. ethra cydon*; g, *M. ethra ethra*; h, *M. ethra mnemopsis*; i, *M. ludovica ludovica*; j, *M. ludovica aurantia*; k, *M. marsaeus pothete*; l, *M. menophilus zaneka*; m, *Mechanitis polymnia caucaensis*; n, *Melinaea marsaeus messenina*; o, *M. marsaeus mothone*; p, *Mechanitis polymnia bolivarensis*; q, *M. mazaeus beebei*; r, *M. mazaeus* form; s, *M. mazaeus visenda*; t, hindwing of same, showing male hair-pencil. The useful area in taxonomy (spaces M_3 - Cu_1 and Cu_1 - Cu_2) includes Forbes' "comma-mark" distally, and isolated pattern elements basally, which are often good subspecies or species markers, varying less than overall mimetic pattern. For nomenclature see Brown, 1977.



Guianas occurs the nominate, dark-hindwing *n. numata*, which intergrades northwestward to the new subspecies through form "guiensis," and southward to the common Amazonian *n. superioris* (mostly as form "maecenas" in the lower Amazon where the two meet). Over the entire Amazon Basin, the recessive supergene-morph *n. silvana* occurs together with various forms of *n. superioris*. The former rigorously represents the oldest correct name for the Basin populations, if only one of the supergene morphs should be regarded as a subspecies, but *superioris* is often predominant in populations westward, and is best conserved with subspecies status. *Silvana* also occurs northward into the Guianas as a supergene-morph of *n. numata*; although it is predominant in Belém, *silvana* is nearly absent in the populations of a new subspecies (described below) inhabiting the Marajó Island, across the mouth of the Rio Pará from Belém. Over most of the central and western Amazon Basin, and northward into the Guianas, occur all-orange forms (*n. mavors*, a "weak subspecies" at best); these may have spread eastward from the upper Amazon, where they seem to predominate genetically in many of the confusing polymorphic populations found there today. Using the refuge map (Brown, 1976) to sort out the origins of mimetic forms in today's highly mixed populations, the following acceptable though sometimes "weak" races can be identified: *n. euphrasius* (Putumayo refuge), *n. aurora* (Loreto), *n. euphone* (Napo), *n. lenaeus* (Abitagua), *n. ignotus/talboti* supergene pair (Marañón), *n. staudingeri* (Huallaga), *n. arcuella/illustris/timaeus* triplet (Ucayali), *n. lyrcaeus* (Inambari), *n. leopardus* (Yungas), *n. mirus* (Guaporé), *n. jiparanaensis* (Rondônia), and *n. nubifer* (Tefé). Further important mimetic morphs, such as *n. isabellinus*, *n. idalion*, *n. seraphion*, *n. geminatus*, *n. spadicarius*, and *n. gradatus*,

FIGURE 8.—Comma-marks in silvaniform *Heliconius* (*numata*, *ismenius*, and *pardalinus*), and hindwing venation of same compared with mimetic Ithomiinae. a, *p. sergestus*; b, *i. ismenius*; c, *i. ismenius* form "hoppi"; d, *p. pardalinus*; e, *i. telchinia*; f, *i. metaphorus*; g, *n. silvana*; h, *n. mirus*; i, *n. robigus*; j, *n. euphrasius*; k, *n. aurora*; l, *n. ethra*; m, *n. aristiona*; n, *n. aurora*; o, *n. mavors*; p, *n. superioris*; q, *n. aurora*; r, *n. superioris*; s, hindwing of *Melinaea menophilus zaneka* (note cell closure); t, hindwing of *Heliconius pardalinus sergustus*. Forewings life size, hindwings twice life size in Figures 7-8.



although conceivably derivable from combinations of characters of other forms, often appear in rather concentrated populations; they are of uncertain origin, and are conserved here as "weak subspecies." The mimetic Bolivian "splendidus" results from combination of characters from sympatric *n. leopardus* and *n. aristizona*, showing that all apparent mimicry is not necessarily selected for homozygous genetic condition.

Each of the great river deltas of South America harbors an endemic subspecies of *numata*; both are still undescribed. North of the Orinoco Delta occurs

***Heliconius numata holzingeri* K. Brown and**

F. Fernández Yépez, n. ssp. (Key and Ill., 81aa).

Sexes similar, except for hindwing costal androconial area in male. FW 39-42 mm. Forewing typical of *n. numata* or *n. superioris* (form "maecenas"). Hindwing orange with a black marginal band and broad club-shaped median bar, cutting off a basocostal orange triangle and a subapical yellow spot, strongly narrowed near the anal margin. Ventral surface similar to dorsal, with white streaks in the margin, especially on the hindwing.

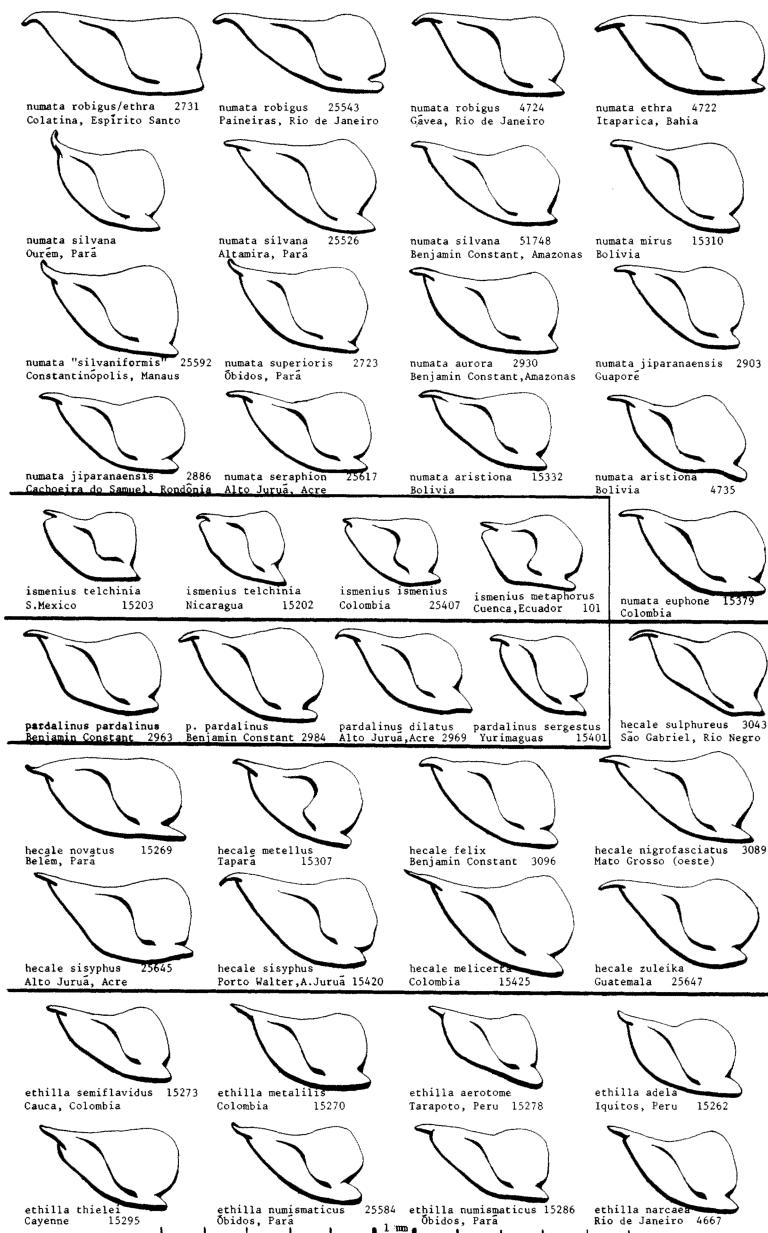
HOLOTYPE. — Venezuela (Monagas), Caripito ($10^{\circ}07' N.$, $63^{\circ}05' W.$), male, 19-VII-37, in the American Museum of Natural History, ex coll. Frank Johnson. PARATYPES: same locality, one male, 3-IV-69 (KN); one female, 16-III-42 (FA), coll. Wm. Beebe. Further specimens caught by Beebe are reputed to exist in American collections, but have not been seen.

The northeastern part of the Ilha do Marajó, at the mouth of the Amazon, is inhabited by a very distinct and unusual subspecies of *numata*, which is unique in not co-occurring with very similar large Ithomiine butterflies; possibly as a result of this, its color-pattern has converged on that of other sympatric *Heliconius*.

***Heliconius numata sourensis* K. Brown, n. ssp. (Key and Ill., 91a).**

Male. — FW 35-45 mm. Orange dorsally, orange-brown ventrally. Forewing with small to obsolete yellow subapical spots, a narrow yellow

FIGURE 9. — Comma-marks in silvaniform *Heliconius* (*hecale* and *ethilla*).
a, *e. claudia*; b, *e. semiflava*; c, *e. adela*; d, *e. aerotome*; e, *e. metalilis*; f, *e. thielei* (holotype); g, *e. eucoma*; h, *e. narcaea*; i, *e. narcaea*; j, *h. vittatus*; k, *h. humboldti*; l, *h. ennius*; m, *h. ithaca*; n, *h. quitalena*; o, *h. felix*; p, *h. paraensis* \times *vetustus*; q, *h. novatus*; r, *h. metellus*, form "boyi"; s, *h. melicerta*; t, *h. zuleika*; u, *h. hecale*. Life size.



postmedian band, and heavy black spots across the median area. Hindwing with a characteristic yellow anvil-shaped mediocostal patch on the ventral surface, and a strong black median bar; otherwise like *n. superioris*.

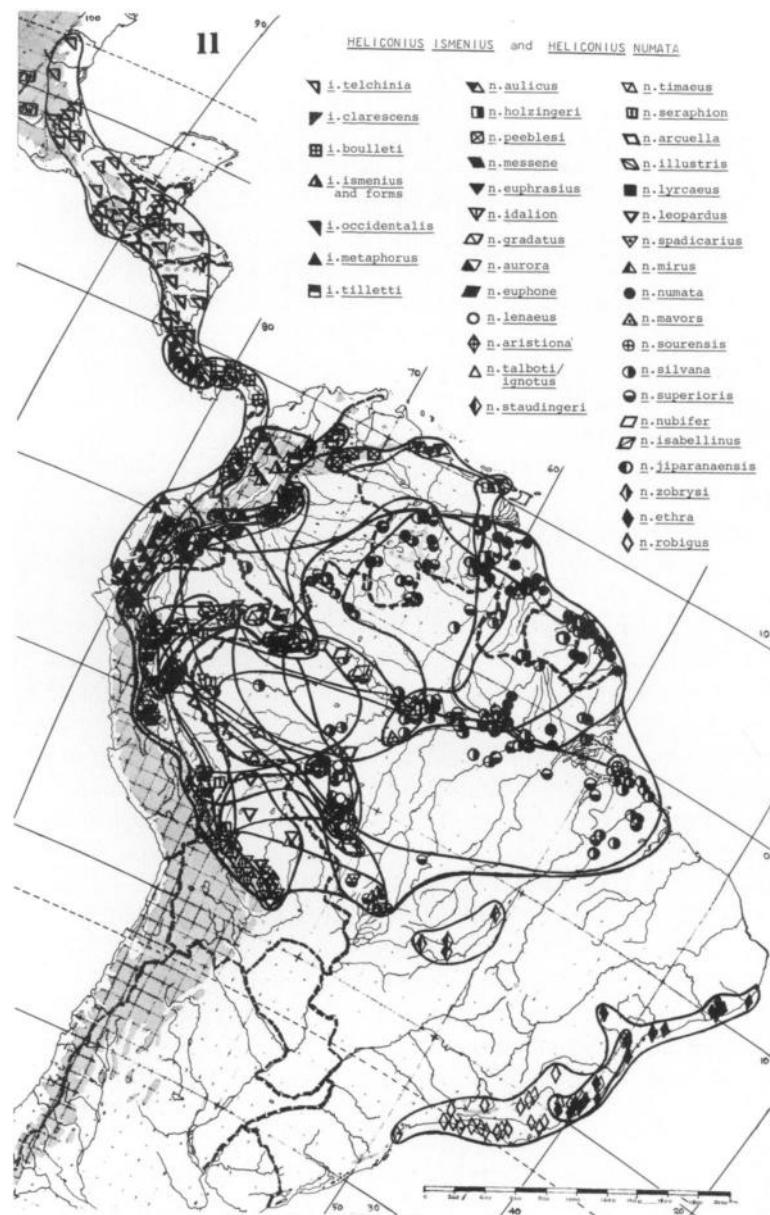
Female.—FW 42-45 mm. Deep red-brown both dorsally and ventrally. Forewing median black elements fused to form a black transverse band from the end of the cell to the margin of space Cu₁-Cu₂, with a basally-directed tab representing the spot in the inner angle of this same space.

HOLOTYPE.—Brazil (Pará), Ilha do Marajó, scrubby woods to north of Soure airport (0°40' S., 48°32' W.) surrounded by grassy swamps, male, 17-I-75, donated to the Museu Nacional (Rio de Janeiro), K. Brown leg. *PARATYPES*: same locality and collector, two males and two females, 17-I-75, donated to the Museu Nacional; one male and one female, 18-I-75, donated to the AM; one male and one female, 18-I-75, donated to the AA; eight males and nine females, 17-I-75, one male and four females, 16-I-75, five males and two females, 18-I-75, in the collection of the author; Amparo, Soure (same area), four males and two females, 9-13-VI-54, Zoologisches Sammlung der Bayerischen Staates, W. Forster leg.; “Ile de Marajó,” one male and one female in the BM, Levick Bequest, acc. 1941-83.

The reddening of the ground-color (especially in the female) and the fusion of the forewing median black elements to give a transverse bar and isolate the yellow postdiscal band, produce an overall color-pattern distinctly mimetic of that of sympatric *Heliconius erato estrella*, rather than of ithomiines, which were not captured in the range of *sourensis*. The population sampled included a very small (perhaps 5%) proportion of *silvana*-morphs, resembling form “divisus” (72cc; one illustrated), but showing affinity with *sourensis* in the ventral color-pattern; they should be considered an integral part of the gene-pool and are included as paratypes. A male of this morph was captured on 17-I-75 *in copula* with a recently emerged typical female of *sourensis*.

The larva of *numata* is almost always heavily spotted with black (though much lighter in the Marajó population); in northwestern populations, it bears a prominent yellow cap on the final ab-

FIGURE 10.—External aspect of right male genital valves of silvaniform *Heliconius* (with sacculus shape shown within). All in the Museu Nacional, Rio de Janeiro (taxon, number, locality). Bristles eliminated to emphasize only outline and tip shape.



dominal segments (Figures 5g, h). The isolated southeastern populations (coastal Brazil) have darker greenish-colored larvae, with much black pigment ventrally and even laterally (Fig. 5l, m), and some black spots on the head, resembling those of the primitive and sympatric silvaniform *H. nattereri* (Brown, 1972b). In the Amazon Basin and Bolívia, larvae often possess both northern and southern regional characters, or show one or the other to varying extents. Larval genetics have not yet been studied in detail. Foodplant range is the widest known in the genus *Heliconius*, but a heavy concentration on the more primitive *Grandailla* (other than Lobatae and Kermesinae) is evident (55% of all known records, the rest distributed among four other *Passiflora* subgenera and two other passifloraceous genera) (Benson, Brown and Gilbert, 1976).

Further details on this unusual species, including behavior, have been published (Brown and Benson, 1974), or are reserved for future biological papers.

B. *Heliconius ismenius* (Figure 11, distribution map) replaces *H. numata* in the northern Neotropics (as far as southern Tamaulipas in Mexico; L. Gilbert, pers. comm.). It is the only silvaniform cleanly identifiable by adult morphology. The TMGV is very short, almost melpomeneform, rounded with the dorsal process not projecting beyond the end of the valve (Figure 10); this can usually be seen by external examination under a good stereo microscope, without dissection. The character can be traced from northern *i. telchinia* (Mexico to northwestern Panamá) through Chiriquí-endemic *i. clarescens* and Darién *i. boulleti* (intergrades are well-known), to a polymorphic series (including nominate and albinic *i. ismenius*) occurring through Colombia with an isolate on the west coast (weak subspecies *i. occidentalis*), to *i. metaphorus* in western Ecuador. A recently discovered peripheral subspecies, occurring in extreme western Venezuela and described below, is close to *i. boulleti* in pattern. Adults of either sex can be recognized by a combination of the wide separation of the two pairs of yellow (or white) subapical spots on the forewing, and the black distal part of forewing space Cu₁-Cu₂ (Figure 8), bearing no centered light submarginal dot (at most a small orange area in the lower part of the space).

The species is very close to *numata* in behavior (the males promenading rapidly through heavy moist forest, fairly high above the ground), and is almost allopatric with this species; however, the TMGV is appreciably shorter in *ismenius* than *numata*. Reliable recent records indicate that *ismenius ismenius* and *numata messene/euphrasius/euphone* occur together in select localities of the eastern face of the east Colombian Cordillera (Florencio, Villavicencio). Both in Texas (observations of L. Gilbert) and in Rio de Janeiro, sexually active and insectary-adapted males of *ismenius* ignored virgin females of *numata* placed in the same compartments with them. Although interfertility between the two species may eventually be established, it seems preferable to maintain them separate for the time being.

Close approximation of very different color-patterns of *numata* (*n. aulicus*, *n. peeblesi*) and *ismenius* is seen in western Venezuela, where a new subspecies of the latter was discovered in January 1976:

Heliconius ismenius tilletti K. Brown and

F. Fernández Yépez, n. ssp. (Key and Ill., 65aa).

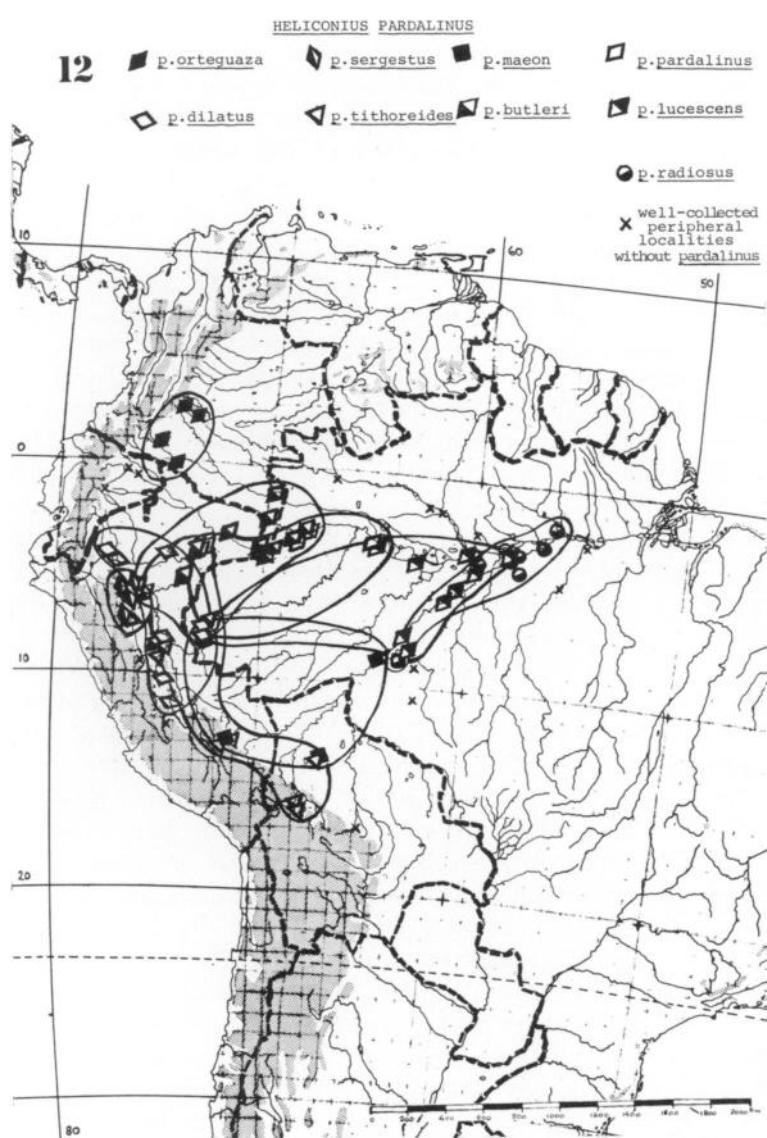
FW 40-46 mm. Sexes similar (except for the lack, in the female, of the silvery androconial patch on the dorsal hindwing costa). Very close to *i. boulleti* (65a), most consistently distinguishable by the brighter orange-yellow ground-color (in *boulleti*, redder and darker), and the shape of the outer edge of the broad yellow forewing median band, which in *tilletti* is sharply angled upon crossing vein Cu₁ (in *boulleti*, usually smoothly curved from costa to vein Cu₂), or occasionally projecting distad in space M₃-Cu₁. Hindwing with a wide to very wide black border and no median band.

HOLOTYPE. — Venezuela (Zulia), Estación Catatumbo near Tres Bocas (8°37' N., 72°36' W.), 150 m., male, 19-I-76, in the Facultad de Agronomía, Maracay, Venezuela, J. Salcedo leg. **PARATYPES:** four males and four females, same data as holotype, in the FA; three males and a female, in the collection of the author; one male donated to the AM, and one donated to the BM, K. Brown leg.

The subspecies is named in honor of the botanist Stephen S. Tillett of the Facultad de Farmacia, Universidad Central de Venezuela, organizer of the excursion in which it was discovered and specialist in Passifloraceae biosystematics.

In Mexico, the mature larva of *ismenius* is heavily spotted with black, with a well-marked yellow cap on the 8th and 9th abdominal segments, much like that of more northwestern populations of *numata*. However, in Venezuela the larva is more lightly marked, with less yellow on the abdomen, thus differing markedly from that of neighboring populations of *numata aulicus*. The presently known foodplants are in the *Passiflora* subgenera *Distephana* and *Granadilla* (Benson, Brown and Gilbert, 1976; pers. obs.).

C. *Heliconius pardalinus* (Figure 12, distribution map) is the only good "central" silvaniform species, absent on the peripheries of the Neotropics. All races bear a red basal dot on the ventral hindwing between veins Cu₂ and 1A, as in *ethilla* and many *hecale*, usually (except in peripheral populations) large, diffuse, and poorly separated from the orange or mahogany coloration of the rest of the space. All races except extreme western *p. sergestus* are very heavily marked with black or dark brown pigment. The comma-mark is a heavy paraboloid spot in the middle of space Cu₁-Cu₂ (Figure 8), leaving a large orange or yellow submarginal block; in *p. sergestus*, however, it appears more hooked like that of *ethilla*, which is especially confusing because the local race of *ethilla* (*e. aerotome*) is heavily marked with a *pardalinus*-like comma-mark (fortunately, both of the forms grade eastward to other well-defined and typical subspecies, permitting unambiguous association). The genital valve tends to be shorter in *pardalinus* than in other silvaniforms (Figure 10), with a narrow curved dorsal process, but this character is not as reliable as the color-pattern elements. Most forms show a deeply dentate black margin on the hindwing; in *p. sergestus*, the teeth, when present, extend discally between the veins, a character unique in silvaniforms. Some specimens are deceptively similar to *hecale* forms, but usually can be reliably identified by careful examination of color-pattern elements. A difficult case is the middle Amazonian *p. radiosus*, the only race which possesses white streaks in the ventral hindwing margin, and which in some specimens is not clearly distinguishable from some phenotypes of the sympatric *hecale fortunatus*, especially form "spurius." The race occurs in riverside woods from Manaus downriver to Obidos, and is common near



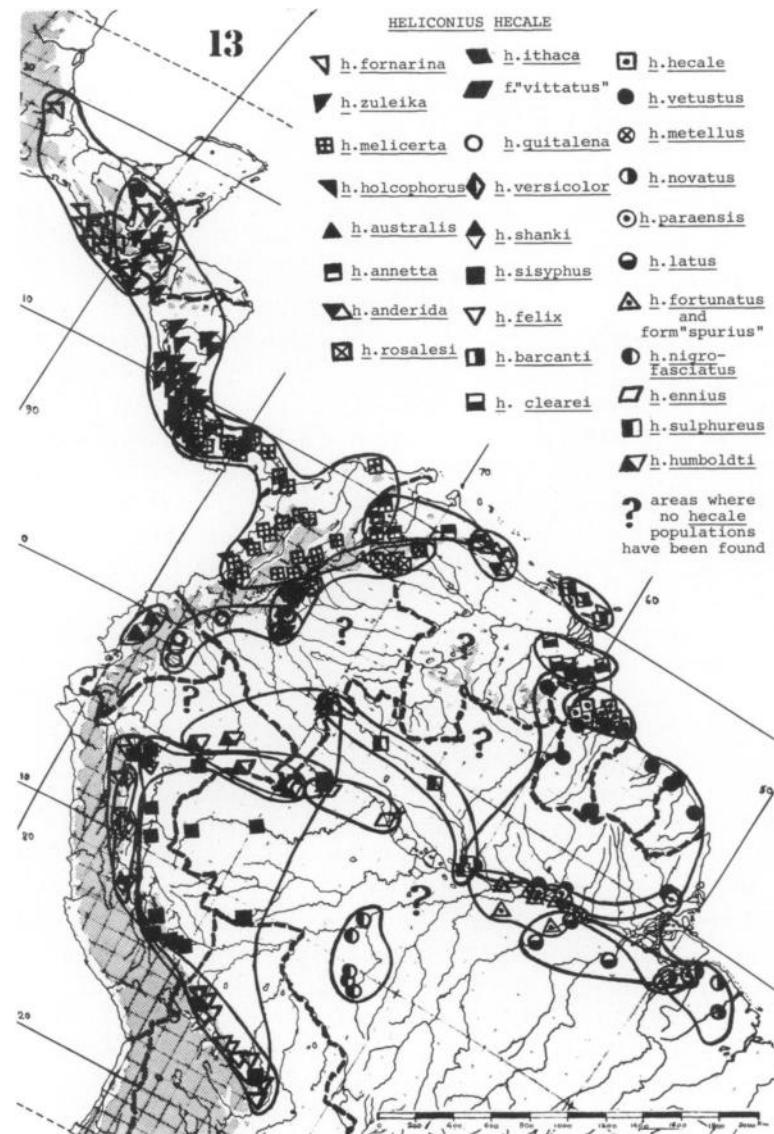
Itacoatiara. Although careful inspection usually permits identification as to species, it seems possible that *pardalinus* and *hecale* may be able to hybridize in this region ("peripheral sympatric hybridization," see Woodruff, 1973), though they are clearly separate in the upper Amazon. The case obviously merits a detailed study, which will be undertaken as soon as the opportunity appears.

The Rio Madeira area is inhabited by *p. lucescens*, which grades into nominate *p. pardalinus* near Tefé. Westward, the principal color becomes orange rather than brownish-red (*p. butleri*); the black markings may then be reduced on the dorsal hindwing (*p. dilatus*), or on the ventral hindwing (*p. tithoreides* and its form "garleppi"). Further obsolescence of hindwing markings gives the weak subspecies *p. maeon* (western Brazil to Madre de Diós). Most populations of these subspecies are polymorphic, and the species appears to be quite mobile; it is unlikely that *p. dilatus* ever occurs in pure populations. At the northwestern limits of the species, however, *p. sergestus* occurs nearly pure on the Rio Hual-laga and Rio Mayo, and the yellow-washed *p. orteguaza* is nearly pure in south-central Colombia.

The species distinctly prefers low areas and swamps, and the males promenade rapidly at medium elevations, like those of *numata*. It seems to occur in highly localized colonies, far separated from neighboring populations, and in which it can be quite frequent. Colonies in Amazonian floodable swamps ("igapó" or "várzea") are possibly frequently eliminated by seasonal high water, which covers the foodplants.

Larvae of *pardalinus*, from *p. butleri* in Iquitos and a Manaus female of a *p. lucescens* \times *radiosus* type, were nearly indistinguishable from *numata* larvae (Figure 5n, o), heavily spotted with black with a dark yellow head and bearing a diluted yellow cap on the dorsal extremity of the abdomen and considerable dark pigment ventrally (especially in the third and fourth instars). This suggests that *pardalinus*, in spite of superficial resemblance to *hecale*, may in fact be an isolate from a long-past speciation cycle of upper Amazonian *numata* stock. Although the larvae obtained used standard silvaniform foodplants in *Passiflora* (*Granadilla*) and *P. (Distephana)*, the natural host of *pardalinus* may in

SILVANIFORM HELICONIUS



many areas be the primitive *P. (Astrophea) spinosa* and close relatives, specialists in Amazonian floodable swamps which apparently can survive high water and profit by dispersal of fruits

along the river.

D. *Heliconius hecale* (Figure 13, distribution map), the second species occurring in the northern Neotropics, is strongly melanic both there and in the nominate and related subspecies in coastal eastern Venezuela and Guyana. The TMGV is elongate (Figure 10); most individuals are large (FW 44-48 mm.), and bear strong, bright orange colors. The comma-mark in the outer part of forewing space Cu₁-Cu₂ is highly characteristic (Figure 9), being either a narrow hook or arrowhead, or a broad spot in the middle of the space (like that of *pardalinus*), always cutting off a submarginal light spot which extends well into the upper half of the space (sometimes best observed ventrally; obsolescent in east-central Colombia). This character is shown by very occasional *ethilla* and *numata*, but only rarely is there any ground for confusion of these forms with *hecale*. Northern forms (México to Colombia and western Ecuador) bear no white subapical streaks on the ventral forewing and no red basal spot on the ventral hindwing, while southern forms (Amazonian and Orinocan regions) usually show these characters, but the two subtypes intergrade cleanly in Venezuela and eastern Colombia. Indeed, clear intergradation has been seen between almost all known adjacent *hecale* races, from Mexican *h. fornaria* to west Ecuadorian *h. australis*, east Bolivian *h. felix*, northeastern Venezuelan *h. barcanti*, east Amazonian *h. novatus*, and southwestern Brazilian *h. nigrofasciatus*. Many of the transitional forms between *h. fornaria* (Mexico and Guatamala) and *h. zuleika* (Costa Rica), and between the latter and *h. melicerta* (Panamá and Colombia) bear names; some of the latter are very similar to sympatric *ismenius* forms produced by mixture of *i. telchinia* and *i. bouletti* genes, but can always be separated by the light submarginal spot in forewing space Cu₁-Cu₂. *Melicerta* grades eastward through many named forms, including the weak subspecies *h. annetta*, to central Venezuelan *h. anderida*, long recognized as conspecific with *h. fornaria* and the other northwestern forms, due to these clear transitions. A discontinuity of 400 Km. exists between *h. anderida* and the east Venezuelan melanic forms, corresponding to two broad dry river valleys with very little *Heliconius* habitat; indeed, this discontinuity blocks many other species in the genus, though it is crossed by

more dry-adapted forms like *H. ethilla* and *H. ricini*. Intergradation from *h. anderida* thus occurs southwestward through the upper Orinocan area, including a new subspecies (described below) and the transitional forms "indecisa" and "cajetani," leading to "vittatus" (light form) and *h. ithaca* (dark form) from the eastern Colombian Andes. In the Serranía La Macarena, *h. ithaca* intergrades with *h. quitalena*, which is found southward into Ecuador. The conspecificity of *h. quitalena* with other upper Amazonian forms, here divided into weak subspecies *h. sisyphus*, *h. felix*, and *h. humboldti*, has long been acknowledged, because of the extensive intergradation of these four, especially in northeastern Peru; many names have been applied to the variations which result, and at least one well-marked local subspecies (described below) remains unnamed. From extreme western Brazil eastward, these forms grade into *h. ennius* (near Tefé) and *h. sulphureus* (on the Rio Negro), which in turn show transitions to *h. fortunatus* (Manaus area), *h. latus* (Rios Tapajós and Xingu), *h. paraensis* (eastern Pará), and *h. vetustus* (north of the Amazon into the Guianas); all four of these last subspecies meet and mix near Obidos, Pará. A most strange and isolated subspecies, *h. metellus*, is confined to the island of Tapará in front of Santarém, where the river Tapajós empties into the Amazon; intergrades are known on the mainland, and indeed the nominate form shows some gradation to *h. latus*, not evident in the usually encountered form "boyi." Eastward, *h. paraensis* intergrades near Belém with *h. novatus*, which is found on east into Maranhão. The principal form of the Guiana highlands, *h. vetustus*, undergoes an abrupt and amazing transition, possibly determined by a single gene (K. Brown, in preparation), to the albomelanic *h. hecale*, where the upland forest meets the coastal swamp in northern Guyana; the two may be found together, though in different levels of the forest, near the Georgetown airport (Timehri) in favorable seasons. Finally, northwestward along the coast, a whiter race *h. clearei* predominates in southeastern Venezuela (at times also sympatric with *h. vetustus*), being replaced by *h. barcanti* north of the Orinoco Delta.

The populations of *hecale* occurring in the lower parts of the Perené River in Peru (part of the Chanchamayo refuge) are well-

differentiated; that they represent a good subspecies was suggested to this author by Gerardo Lamas Müller of the Universidad Nacional Mayor de San Marcos (Lima), who is the senior author of this taxon:

Heliconius hecale shanki G. Lamas M. and

K. Brown, n. ssp. (Key and Ill., 14aa).

FW 44-47 mm. Similar to *H. h. felix*, but readily recognized by the extensive yellow pigment present on the wings, reducing the orange to a very few areas. The yellow color infuses the basal and median regions of the forewing and the median band of the hindwing, and forms broad lunules in the submarginal area of the hindwing. The over-all effect is very similar to that of the sympatric ithomiine, *Tithorea harmonia neitha*, which however has a much wider range than *h. shanki*.

HOLOTYPE. — Peru (Junin), Shanki, Rio Satipo, 750-850 m., male, VIII/75, in the Museu Javier Prado, UNMSM, Lima, Peru, H. Rojas V. leg. PARATYPES: same data as holotype, ten males in the JP; one male in the collection of the author; one male donated to the Museu de Zoologia, Universidade de São Paulo (MZ); Satipo, 750 m., three males, VI-75, in the collection of the FA, H. Rojas V. leg.; three males, 18-X-40, 20-X-40, and 23-X-40, in the RA collection (now in the DZ), Pedro Paprzycki leg.

In southwestern Venezuela, there occurs commonly an undescribed subspecies of *hecale*, which shows transitional characters between adjacent subspecies (*annetta/anderida* and *ithaca/“vittatus”*):

Heliconius hecale rosalesi K. Brown and

F. Fernández Yépez, n. ssp. (Key and Ill., 19a).

Male. — FW 36-42 mm. Forewing distinctively marked with a clean, Y-shaped yellow median band showing a very reduced or obsolescent black spot in the inner angle of space Cu₁-Cu₂; base entirely orange except for cell dagger; small comma-spot in submarginal area of space Cu₁-Cu₂, anal spot, and three or four subapical spots yellow. Hindwing dorsally orange with a fairly narrow (5-7 mm.) black border and a variable black median spot-band, weaker anally, at times reaching only to vein M₃. Costal stripe (below silvery androconial area) and apex black, with a yellow subapical dot. Hindwing ventrally very dark, ground color red-brown, black median band heavy and complete.

Female. — FW 38-43 mm. Similar to male, but darker red-brown dorsally, with a more complete hindwing median band.

HOLOTYPE. — Venezuela (Barinas), Reserva Forestal de Tiocoporo (about 8°00' N., 70°50' W.), 230 m., 22-28/V/68, male, in the Facultad de Agronomia, Universidad Central de Venezuela, Maracay, M. Gélbez and J. Salcedo leg. PARATYPES: Same data as holotype, two females in the FA; (Barinas) Barinitas (8°45' N., 70°25' W.), 525 m., two males, 14/I/76, in the FA, K. Brown leg.; two males and one female, 14/I/76, in the collection of the author; (Barinas) Reserva Forestal Caparo, Campamento Cachicamo, 100 m., two males and a female, 6-14/VIII/69, in the FA, J. Salcedo and F. Zambrano leg.; (Tachira) La Morita (7°31' N., 71°58' W.), 300 m., one male, 10-IV-72 (A. Dáscoli, A. Montange & J. Salcedo leg.), two males and one female 3-VIII-72 (J. Terán and J. Salcedo leg.), in the collection of the author; one male 3-VIII-72, one male 8-14/IV/72 (collectors as above), one female 13-17/V/72 (J. Terán and J. Salcedo leg.), in the collection of H. Holzinger, Vienna; one female, 8-14/IV/72, in the FA; (Apure) La Ceiba, Selva de San Camilo (7°23' N., 71°45' W.), one female, 8-I-55, in the FA, F. Fernández Yépez and C. J. Rosales leg.; (Táchira) San Joaquin de Navay (7°38' N., 71°44' W.), 225 m., six males and two females, 21/XII/70, in the collection of K. Negishi, Kanazawa, Japan; two males, 1/III/71, one male, 4/III/71, and one female, 29/IV/71, in the FA, A. and M. Gadou leg.; (Táchira) Carretera San Cristóbal-Barinas, cruce San Domingo, (7°35' N., 72°05' W.), one female, 16/II/72, in the FA, C. J. Rosales leg.; (Mérida), generalized, two males in the NM; Mucuchachí (8°09' N., 71°21' W.), one male in the BM, Joicey Bequest, acc. 1934-120.

The subspecies is dedicated to C. J. Rosales, present director of the Facultad de Agronomia and frequent collector of this and other interesting Lepidoptera in many parts of Venezuela.

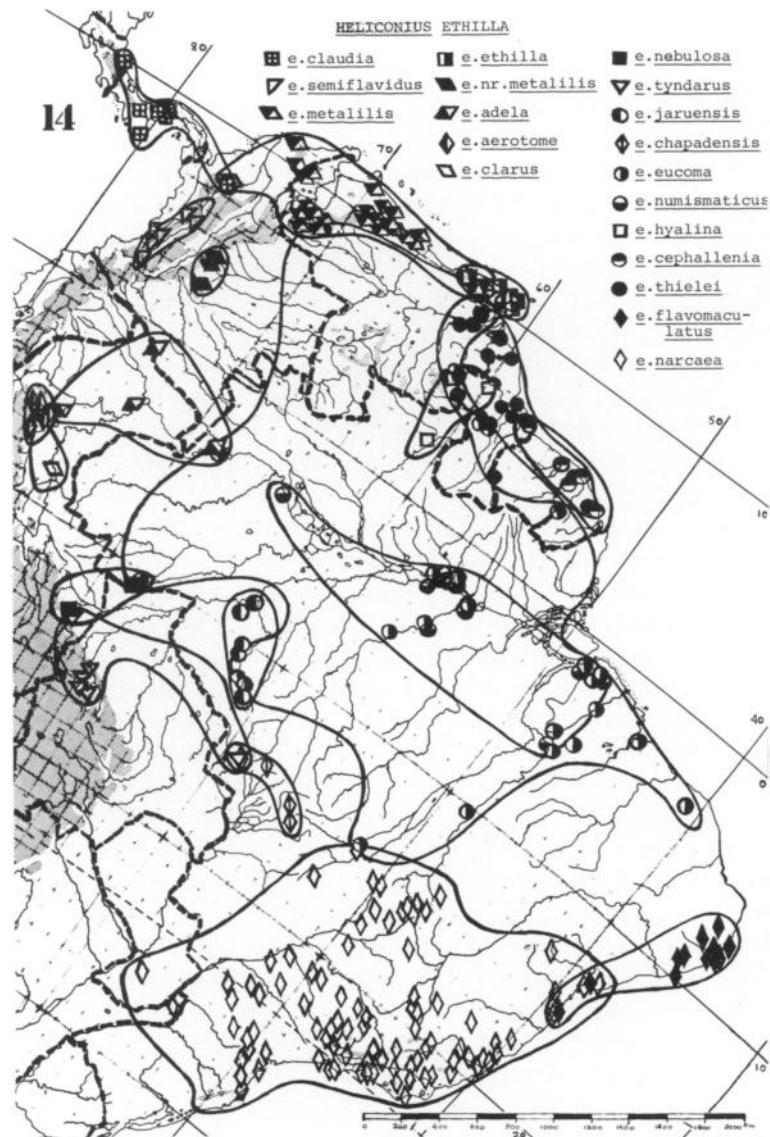
Some adults of various races of *hecale* adapt well to insectaries and even live happily in windowless laboratories (Gilbert, 1975), but all Amazonian and most northern stock we have reared has behaved in a most refractory fashion in the insectary, beating against the roof until either dead or so tattered as to be nonair-worthy. Some *h. hecale* adapted well to captivity, as would be expected from consideration of the undergrowth-frequenting behavior of this melanic race. In the field, *hecale* is normally

strong- and fast-flying, and very difficult to capture except at flowers, where in dense populations, or in occasional low-level male flyways. In the afternoon, adults tend to congregate at specific or favored points on the forest floor, often where rays of sun reach the ground, flying around slowly or sitting until near dusk, when they spiral rapidly upward and disappear near the canopy, where they may roost (observations of W. W. Benson on *zuleika* and on *ithaca/quitalena*, and of the author on *nigrofasciatus*). The species is likely to be found in locally dense populations, well separated geographically and often even genetically from nearby populations, and often showing particular characters of behavior and color-pattern. The large number of transitional forms known (many named) indicates, however, that extensive mixing of these localized populations must occur occasionally, perhaps under very special conditions or catastrophic circumstances. The mixed character of the *melicerta* populations in the Panamá Canal Zone was strong a hundred years ago, with many unusual *zuleika*-infused forms dominating; it is very faint there today, but a similar hybrid zone has been located by G. Small 100 miles to the west, in Veraguas province. A few immigrants, brought in by a storm, could probably play havoc with color-patterns in a nearby but strongly differentiated population. The effect would be expected to die out slowly through selection against non-mimetic or non-adapted genes, over a period of several months to several decades, depending upon the nature and degree of the selection.

The mature larva of *hecale* is very lightly spotted with black (Fig. 5s, t), in some populations almost pure white, and never shows a yellowing of the final abdominal segments. Foodplants are heavily concentrated in the *Passiflora* subgenus *Distephana* (45% of all records, the rest in three other subgenera, mostly *Granadilla*) (Benson, Brown and Gilbert, 1976).

E. *Heliconius ethilla* (Figure 14, distribution map) is the only representative of the silvaniforms present in subtropical Brazil, as the subspecies *e. narcaea*. The latter name, in fact, has page preference over *ethilla* in Godart's "Encyclopédie Méthodique," but it seems best to follow now widespread usage for the species name, initiated by Emsley, the first reviser to detail the conspecificity of these two entities. The species is characterized by a bar-like

SILVANIFORM HELICONIUS



comma-mark under forewing vein Cu₁, recurved at its inner extremity to form a hook or projection downward and distally, which normally does not reach vein Cu₂ unless the comma-mark is very

heavy and blacked-in (Fig. 9); this character is also occasionally present in *numata*. Very rarely, in some Amazonian individuals, a small light spot appears submarginally in the upper part of the space, making the comma-mark look more like that of *hecale*. Two far western races (*e. aerotome* and *e. clarus*) have the comma-mark obsolescent; they are both small with rounded wings, like the other Andean races *e. nebulosa* and *e. tyndarus*, and all of these intergrade eastward with the typical Amazonian *e. eucoma*. Essentially all *ethilla* can be recognized by the single small red basal dot on the ventral hindwing, between the cubital and anal veins. However, in the northwestern race *claudia*, this is smudged and diffuse, easily confused with the mahogany color of the ventral surface; and a number of Amazonian and Guianan specimens lack this dot, and thereby are easily confused with *numata*. Careful comparison of forewing color-pattern elements, especially if effected on a series of sympatric *ethilla* and *numata*, usually leaves no doubts about identification of individuals. The hindmarginal bar in *ethilla* tends to terminate in a submarginal arrowhead near the anal angle, appreciably wider than the bar; this character is almost never seen in *numata* except in Bolivia, where the sympatric *ethilla tyndarus* is easily recognized. The subapical spots of *ethilla*, especially of *e. eucoma* types with a wide postmedian band, are small and characteristically shaped, with the second very close to the first (costal) one and typically squarish. The spot in the inner angle of space M_3-Cu_1 in Amazonian *ethilla* not of the *eucoma* phenotype is teardrop-shaped, projecting distally over vein M_3 , a character very rare in *numata*. Any of these characters, combined with the *ethilla* hook-shaped comma-mark, usually suffices for identification even if the red basal dot is obsolescent. Sympatric *hecale* also may bear a red basal dot, but are usually larger than *ethilla* and in very few areas bear a similar color-pattern; most can be rapidly recognized by the comma-mark, which also serves to separate *pardalinus* which all have the red basal dot, usually large and not well separated from the orange color in the space.

The TMGV can be used occasionally for identification of *ethilla*: although the valve is of normal length, the projecting dorsal process tends to be straight, blunt, and thick, while in *hecale*

and *numata* it is usually more elongate, narrower, and curved downward or inward; unfortunately, the variability in this character does not permit more than corroboratory usage (Figure 10).

Complete intergradation has been observed for essentially all adjacent *ethilla* races. Panamanian *e. claudia* intergrades through "mentor" to Colombian and Venezuelan *e. metalilis*, which in turn shows clear transitions to Cauca Valley *e. semiflavidus*, Amazon Basin *e. eucomae/numismaticus*, Guianan *e. thielei*, and Trinidadian *e. ethilla*. *E. thielei* grades southward through *e. hyalina* in Roraima to *e. eucomae* in the Amazon Basin, which intergrades with *e. narcea* and *e. flavomaculatus* in eastern Brazil, *e. chopardensis* in west-central Brazil, and *e. tyndarus* in northern Bolivia; westward, intergrades are evident to *e. nebulosa* in Acre and southeastern Peru, and to *e. clarus* in central Peru. The last grades northward to *e. aerotome*; the restricted *e. adela* in northeastern Peru shows intermediates eastward to *eucomae* types.

A new subspecies of *ethilla*, very near to *e. eucomae*, has recently been studied in southwestern Brazil:

***Heliconius ethilla jaruensis* K. Brown, n. ssp. (Key and Ill., 56aa).**

FW 35-40 mm. Sexes similar. Readily distinguishable from the otherwise very similar *e. eucomae* by the presence of orange scaling between the broad yellow postmedian band and the three small yellow subapical dots on the forewing, present dorsally and ventrally, usually as three or four orange streaks but occasionally much reduced (especially dorsally) or expanded into a continuous patch (especially ventrally). Hindwing median bar strongly dentate, in some specimens broken into intervenal streaks; marginal black band smooth and narrow.

HOLOTYPE. — Brazil (Rondônia), Jaru ($10^{\circ}27' S.$, $62^{\circ}27' W.$), male, 3-VIII-75, donated to the Museu Nacional, Rio de Janeiro, K. Brown, leg. **PARATYPES:** same locality, one female, 29-VII-75, two males and a female, 30-VII-75, one female, 1-VIII-75, one male and one female, 2-VIII-75, in the collection of the author; one female, 8-IX-76, in the collection of N. W. Benson, Campires; Cachoeira do Samuel ($8^{\circ}45' S.$, $63^{\circ}27' W.$), one female, 26-VII-75, in the collection of the author, one female, no. 2/898, in the MN; from Calama, Rio Madeira ($8^{\circ}03' S.$, $62^{\circ}52' W.$), one female in the BM (W. Hoffmans; Rothschild Bequest, acc. 1939-1); from Jaru, one male, 30-IX-75, donated to

the AM, one female, 3-X-75, donated to the AA, K. Brown leg.

Adult males of *ethilla* have the characteristic habit of promenading over small areas, in the presence of other males and without extensive chasing, either on ridgetops or (most typically) in open clearings in woods near water, not far from the ground (1-4 m.), with a slow, lazy flight interrupted frequently by perching with wings closed (to 30° open on cold days) on exposed leaves. This field behavior almost always surely differentiates *ethilla* from sympatric *numata* and *hecale*, which have far wilder promenading habits; *ethilla* also adapts to scrub and to dry woods much better than these species, and may be found as well in cities, gardens, and very small woodlots. As would be expected from this, it adapts well in the insectary, and shows differentiation patterns not always clearly linked to forest refuges; it is often commonest in relatively poor vegetation in marginal areas, where it apparently can best compete with other silvaniforms.

The west Ecuadorian *Heliconius atthis* (Fig. 2) is very closely related and allopatric to *ethilla*, and has near-identical larvae showing foodplant preferences in the same group as *ethilla*. However, its color-pattern and behavior are sufficiently distinct from those of any *ethilla* to justify its maintenance as a separate species.

A very thorough, but non-comparative study of population dynamics, adult behavior, and reproductive biology of Trinidadian *e. ethilla* has been published recently (Ehrlich and Gilbert, 1973). It is probable that *ethilla* is the most evolved, nervously complex, and adaptable of the silvaniforms, and these traits are shown well in the study.

Insectary courtships and matings among the subspecies *e. claudia*, *e. ethilla*, *e. eucoma*, *e. tyndarus*, and *e. narcaea* (conducted by M. G. Emsley, P. M. Sheppard, L. E. Gilbert, and this author) have helped to confirm the unity of the species. Detailed genetic work, however, has been confined to date to studies of the yellow/brown dimorphism present in numerous populations. In both Trinidadian *e. ethilla* (Turner, 1968) and south Brazilian *e. narcaea*, the yellow form is controlled by a single gene (or gene-complex), and is recessive to the brown ("depuncta" and "satis," respectively). The yellow is more extensive in the Trinidad than the Brazilian form, while the pattern modifications are more ac-

centuated in the latter, suggesting that the genes involved are related but non-identical, with their effects appreciably differentiated in the respective genetic backgrounds of the different races.

The mature larva of *ethilla* is very lightly marked, often pure white before the fourth instar is reached (Figure 5p, q, r). Food-plants, while quite varied, are strongly concentrated in the *Passiflora* subgenus *Granadilla*, series Lobatae and Kermesinae, groups not known to be used by other silvaniforms (36% of all records, the rest in three subgenera and a separate genus) (Benson, Brown and Gilbert, 1976).

There follows an illustrated key to the silvaniforms, first a short key for rapid (and not always certain) species separations, then a full one for identification of races, transitional forms, and variants. Not all specimens will pass through the key satisfactorily, and some will fall out in the wrong place, because the extremes of variation in color-pattern of some of the races, and all transitional forms known or possible, could not be efficiently included. If in doubt, examination of a series, or careful comparison with the illustrations, is often necessary. A number of unusual and generally unkeyable forms, all representing transitions of *H. numata*, are presented together in the final (twentieth) plate associated with the Key, facing the final text page. The author will be glad to identify any difficult specimens, preferably from clear 2× black-and-white photos of both surfaces (with the base of one of the hindwings clearly and totally visible), and locality data; usually it is not necessary to examine the specimen itself, now that external species and race characters have been recognized, correlated with internal and biological characters, and ordered within each species.

When the sexual diethism which characterizes the majority of the silvaniform *Heliconius* (Brown, 1972b; Brown and Benson, 1974; Fig. 1) is matched by dimorphism in color-pattern, both sexes are illustrated. In most cases, however, the sexes are similar in appearance. In the Illustrations, left-hand wings (pointing left) represent type-specimens, right-hand wings others; each picture is identified by a key number, form name, sex, collecting locality, and initials of collection where deposited presently.

Finally, all names applied up until 1976 to the silvaniforms (a total of 211) are listed, both as a checklist under the respective

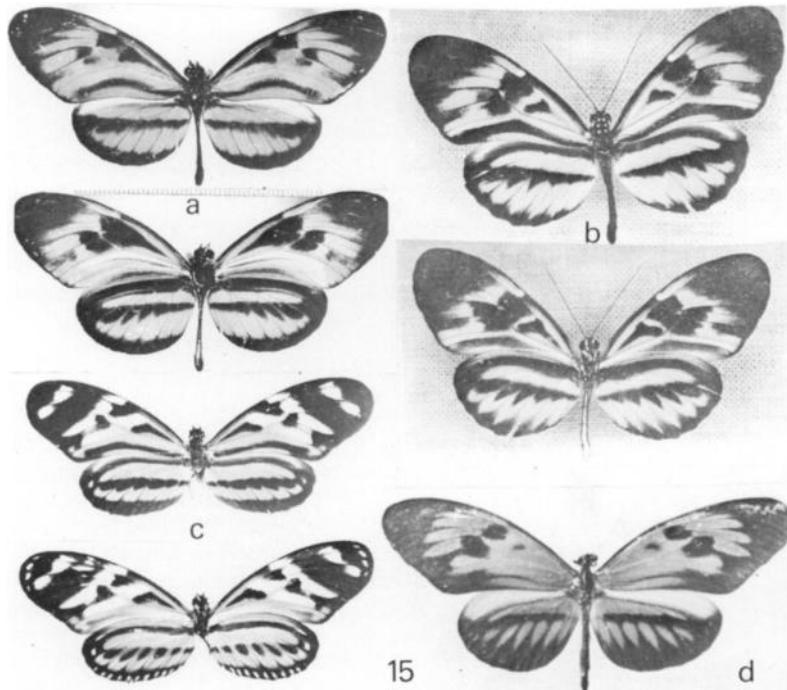


FIGURE 15.—Interspecific hybrids between silvaniforms and other *Heliconius* (three samples from the BM, one duplicated in a very recent collection). a, *Heliconius hippola* Hewitson, dorsal (upper) and ventral (lower), ?Peru; b, a near-identical specimen caught by E. W. Schmidt-Mumm on the Rio Negro above Villavicencio, Colombia, apparently a hybrid between *H. ethilla metalilis* and *H. m. melpomene*; c, a hybrid between *H. ethilla narcaea* and *H. numata ethra*, dorsal (upper) and ventral (lower), caught in Leopoldina (= Santa Leopoldina, Espírito Santo), from the Riffarth collection, now in the BM; d, *Heliconius seraphini* Talbot, dorsal, Guyane, St. Laurent, apparently a hybrid between *H. numata numata* and *H. melpomene thelxiopeia*, in the BM.

species (with presumed refuge derivation), and as an alphabetical index to all forms, which includes code letters indicating the degree of study of the entity by this author and the location of the type (when known), and assignment to one of the five species, or definition as a transitional or infrasubspecific form, or a synonym, depending upon each case.

A number of interspecific hybrids between silvaniforms and *H. melpomene* or relatives are known. These will be fully treated in a future paper, but illustrations are included here of the named hybrids *hippola* and *seraphini*, as well as of an *ethilla narcaea* × *numata ethra* hybrid in the BM, which bears a still unpublished name of Riffarth (Figure 15).

Selected types of seventy-six silvaniforms in the BM, including many of the specimens illustrated here and also the two named hybrids, have very recently been figured in Ackery and Smiles' catalogue (1976).

KEY TO HELICONIUS SPECIES (SIMPLIFIED)

Succession mandatory; (not as above understood after each diagnosis)

1. Forewing comma-mark either filling entire margin of space Cu_1-Cu_2 , or else lying over vein Cu_1 and filling most of the two adjacent spaces, leaving elongated spots along the central parts of veins M_3 and Cu_2 ; forewing subapical spots present as two widely separated pairs, each with one large internal and one smaller external spot; tip of male genital valve shortened and rounded, with dorsal process not projecting beyond end of valve, usually visible without dissection; Mexico through Panamá, central and western Colombia to western Ecuador and extreme western Venezuela *ismenius*
(Key and Illustrations 60-65)
2. Hindwing marginal black strongly dentate (more than two-thirds of its width), or if very narrow, frayed inward between the veins; a large and diffuse red spot at the base of space Cu_2-1A of the ventral hindwing, usually poorly separated from the adjacent orange or red-brown by black; Amazon Basin from Óbidos to the lower Andes of Colombia, Peru, and northern Bolivia *pardalinus*
(Key and Illustrations 4, 29, 36-41)
* Occasional *hecale* forms, usually much larger and more brightly colored than *pardalinus*, will key out here; essentially all have well-developed white streaks on the ventral hindwing margin, possessed only by lower middle Amazonian *pardalinus*.
3. Forewing "comma-mark" in space Cu_1-Cu_2 either absent, or else in the form of an arrowhead with one arm along Cu_1 , or a recurved paraboloid spot in the middle of the space, always cutting off a submarginal spot which extends into the upper (Cu_1) half of the space; usually large in size, bright in color;
 - (a) no submarginal white streaks on ventral forewing; second subapical yellow or white spot on FW placed well distal of first, forming a nearly straight line with third; no red basal dot on ventral hindwing; comma-mark a clear, narrow arrowhead; Mexico through Panamá, Colombia, western Ecuador and Ven-

ezeula to northern Guyana *hecale* (*hecale*-group)
 (Key and Illustrations 7-9, 16-24)

- (b) subapical white streaks present on ventral forewing; second subapical yellow spot on forewing placed more nearly under first (when series present); often a small red basal dot on ventral hindwing; comma-mark obsolescent, or a broad paraboloid spot in middle of space Cu₁-Cu₂; entire Amazon and southern Guianan area from Andean Colombia, Ecuador, Peru and Bolivia to Guyane, Pará, and Maranhão
 *hecale* (*quitalena*-group)
 (Key and Illustrations 1, 10-14, 26-34)

* *Ethilla aerotome* and *e. clarus* will also key out here; from central Peru, they are recognized by a broad median and narrow marginal bands on the hindwing, and the forewing apex often heavily suffused with orange.
 ** Some *numata* from Ecuador and Peru will key out here also. They are smaller, duller in color, usually have a doubled marginal/submarginal series of black marks on the hindwing (or only the latter) rather than a narrow black border as in sympatric *hecale*, and never show a red basal dot on the ventral hindwing (variably present in *hecale*).

4. A distinct red basal spot in space Cu₂-1A of the ventral hindwing, usually separated (except in Panamá) from the orange color of the space by black; even if this is not present, forewing hindmarginal bar often terminating in an arrowhead-shaped expansion near the anal angle; central Panamá through Venezuela, the Guianas, and the Amazon Basin (rarer or absent in some areas westward) to northern Argentina *ethilla*
 (Key and Illustrations 3, 42-58)
5. No red basal spot on the ventral hindwing; comma-mark usually a bar under Cu₁, or a marginal triangle; forewing hindmarginal bar absent, truncated, or tapering smoothly at anal angle, except in Bolivia in forms possessing much yellow in cell and space Cu₁-Cu₂; northern Venezuela through Amazon, Orinoco, and Guiana areas, along eastern face of Andes to Bolívia, south in central Brazil to central-west Goiás, and along Brazilian coast to 25° south;
 (a) No continuous postdiscal band on forewing; comma-mark usually a marginal triangle (entire range of species except for northern and western Venezuela and higher elevations in the Andes) *numata* (*silvana*-group)
 (Key and Illustrations 70-73)
- (b) A continuous postdiscal band on the forewing;
 (b1) Hindwing dark bands interrupted before apex, or if most of hindwing dark, no continuous orange subcostal stripe present; northern Venezuela south through western Brazil to northern Bolivia *numata* (*aristiona*-group)
 (Key and Illustrations 67-69, 75-80, 84, 88-90, 93a, 94-97, 100-105, and 109-112)



- (b2) Hindwing dark bands extending heavily and continuously to apex; if most of HW dark, a continuous orange subcostal stripe present; eastern Venezuela, Guianas, and northern Brazil *numata* (*numata*-group)
 (Key and Illustrations 81, 86,
 92, 93aa, 99, 106-107, and 113)

6. More than one red spot on the ventral hindwing; pattern elements tending to include fuzzy, sharply truncate, or blended elements
 hybrids between silvaniforms and other members of the genus *Heliconius* (Fig. 15).

KEY TO THE SPECIES, SUBSPECIES, AND FORMS OF SILVANIFORM *HELICONIUS*

Based on external characters of the dorsal wing surface, unless otherwise indicated. Individual specimens will sometimes key out erroneously, and the examination of a series from a single population is recommended, when possible; comparison with the photographs should be helpful in the resolution of more difficult cases. Standard abbreviations: FW = forewing, HW = hindwing, ap. = apical, subap. = subapical, pmed. = postmedian, med. = median, marg. = marginal, submarg. = submarginal; N, E, W, S, NE, SW etc. (compass points); C = central; R. = Rio or river; f. = form (intrasubspecific category).

- 1 a. Comma-mark in the outer half of FW space Cu₁-Cu₂ obsolete or obsolescent, represented usually by a shadowy line curving inward between the orange submarg. and lower part of the space, and the yellow inner upper part of the space (E-C Colombia, in Meta and Boyacá) *hecale ithaca*

b. HW mostly black, at times with yellow streaks or dots (commoner at higher elevations).

c. FW pmed. yellow band broad and continuous *ithaca*
 (= f. "sulphureofasciata")

cc. Spots in inner angles of FW spaces M₃-Cu₁ and Cu₁-Cu₂ enlarged, the upper of these fused with the ap. area along veins M₃ and Cu₁, breaking yellow pmed. band f. "caketani"

* Further unnamed forms have variable amounts of yellow on the HW, reduction of yellow on the FW, FW subap. dots large or scattered, or enlarged or reduced black areas on FW and HW.

* Very occasional *numata messene* (84a) will key out here; they almost always show orange (not yellow) subap. spots or patches on the HW, never seen in *ithaca* forms, and never have orange between yellow and black in the upper half of the submarg. area of FW space Cu₁-Cu₂.

bb. HW crossed by a narrow or broad orange area between black med. and marg. bands (commoner at lower elevations).

- d. FW heavily marked as in "cajetani" (cc) f. "indecisa"
- dd. FW with a complete, broad yellow pmed. band.
 - e. Dark med. and marg. bands on HW barely separated by orange f. "hero"
 - ee. Dark med. and marg. bands on HW well separated by orange.
 - f. HW med. band heavy and continuous f. "vittatus"
(= f. "nigroapicalis")
 - ff. HW med. band broken into a series of separated triangles, pointed distally f. "marius"

* Occasional specimens of *hecale sisyphus*, *h. felix*, and related forms (34) may key out here; they generally have a much narrower FW pmed. band than *ithaca* forms.

** Very occasional lightly marked *numata euphone* (102c) types will also appear here; usually, their horizontal bar-shaped comma-mark under FW vein Cu₁ is discernible, and they are often predominantly orange-washed and have a very broad black FW apex.

- aa. Comma-mark present as a curved spot, horizontal bar, arrowhead, marg. triangle, or other well-defined black mark 2
- 2(1) a. Comma-mark obsolescent marginally (replaced by orange), heavy in center of FW space Cu₁-Cu₂, usually continuous to the inner angle of the space; FW barely twice as long as broad; FW hindmarg. bar heavy, enlarged terminally (near the anal angle); HW med. band broad and strongly dentate, but marg. black band smooth; a small red dot at the base of space Cu₂-1A on the ventral HW 3
 - aa. Not as in descriptor a 4
- 3(2) a. FW pmed. and subap. regions with much yellow scaling (Tarapoto region in C Peru) *ethilla aerotome*
 - aa. FW heavily washed with orange, essentially eliminating all yellow scaling (Pucallpa region in E-C Peru) .. *ethilla clarus*
- 4(2) a. FW with a continuous yellow pmed. band, and a hindmarg. black bar which is strong basally but ends abruptly at $\frac{2}{3}$ wing length; HW with a diffuse but continuous non-dentate med. bar, and either very reduced marg. black or else teeth extending distad between the veins; a large diffuse red basal spot on the HW between veins Cu₂ and 1A (Tarapoto area southward, in C Peru) *pardalinus sergestus*
 - b. FW apex completely black *sergestus*
 - bb. An irregular yellow streak in FW ap. area f. "ninacura"

* Transitions to other *pardalinus* forms show variable subap. spots.

- aa. Not as above 5

- 5(4) a. Comma-mark a dark arrowhead or recurved spot, which cuts off a well-marked light submarg. spot, which always extends into the upper (Cu_1) part of the space (*H. hecale*, *H. pardalinus*) 6
 aa. Comma-mark a bar or highly assymetrical arrowhead, filling the upper half of the space submarginally, or else a complete dark marg. triangle, wider along vein Cu_1 (*H. ismenius*, *H. numata*, and *H. ethilla*) 42
- * Some *numata* from Ecuador and Peru have the comma-mark under vein Cu_1 obsolete marginally, with space Cu_1 - Cu_2 completely orange submarginally. They may be recognized by being of smaller size than *hecale*; they lack a red basal dot on the ventral HW, often present in *hecale*; they usually have much orange and/or yellow in the FW subap. area, and a doubled marg./submarg. series of black marks on the dorsal HW (sympatric *hecale* often have a black FW apex and a smooth or dentate but complete black HW marginal band).
- ** Dark specimens of *hecale*, especially *metellus* f. "boyi" (12bb), may have the comma-mark covered by black dorsally, but observable on the ventral surface.
- 6(5) a. HW totally black (except for occasional subap. spots), FW with no orange color on the dorsal surface 7
 aa. Appreciable orange pigment on the dorsal surface, at least on either the FW or the HW 10
- 7(6) a. FW med. band broad and yellow, with two series of yellow subap. spots (or else broad and shadowy, overlaid by dusky scaling) (S Mexico to Honduras, hybridized southward) *hecale fornaria*
 b. FW med. band and subap. spots yellow *fornaria*
 bb. FW markings shadowy, infused with dusky scaling f. "styx"
- * See also f. "bouvieri" (24a).
 aa. FW med. band and single subap. series of spots white 8
- 8(7) a. FW white band narrow, heavily marked with black, to nearly obsolete on the dorsal surface (near Georgetown, Guyana) *hecale hecale*
 b. Base of FW purely black *hecale*
 bb. Base of FW deep red-brown f. "fulvescens"
- * The latter is probably a supergene crossover from *h. vetustus* (12b).
 aa. FW white med. band wider, with reduced or no black spots in the inner corners of spaces M_3 - Cu_1 and Cu_1 - Cu_2 9
- 9(8) a. FW white med. band crossing outer part of discal cell (extreme NW Guyana and extreme E Venezuela, costally) *hecale clearei*
 aa. White band narrowed costally, not entering the discal cell (Paria Peninsula of NE Venezuela, strays to Trinidad) *hecale barcantii*
- 10(6) a. A large yellow subap. patch, surrounded by black, on the



- FW (Iquitos area of NE Peru to extreme NW Brazil) *hecale humboldti*
- b. Med. and marg. areas on HW fused to form a single large black patch covering lower $\frac{2}{3}$ of wing *humboldti*
- bb. Med. and marg. black areas on HW widely separate f. "alexander"
- * Unnamed intermediate forms have the med. and marg. bands confluent, separated only by a series of orange lunules.
- ** A weak subspecies, mixed with other phenotypes in most populations.
- aa. If yellow present on FW, not confined to a large subap. patch 11
- 11(10) a. HW mostly black, with med. and marg. black areas nearly or completely fused, leaving an orange subcostal stripe or baso-costal triangle 12
- aa. HW with med. and marg. black areas separated by orange or yellow, or with med. black bar lacking or vestigial 13
- 12(11) a. FW apex black, lacking subap. spots (Ilha de Tapará, in the Amazon R. facing Santarém, Pará, Brazil) .. *hecale metellus*
- b. Black spots in med. area of FW separated *metellus*
- * A transition between the principal form and other subspecies.
- bb. Black spots in med. area of FW fused, forming a complete band across the FW (normal or principal form) f. "boyi"
- aa. Subap. spots present on FW (Guianas to N Brazil) *hecale vetustus*
- * Some *ethilla thielei* or *e. cephalenia* (48), which usually show a much differing overall pattern from that of *vetustus* (strong hindmarg. bar on FW, HW med. and marg. black areas often not fully confluent), may nonetheless key out here. Most will show a single red basal dot on the ventral HW, absent in *vetustus*.
- ** Occasional recombinants between *humboldti* (10b) and *sisyphus* (34aa) will key out here; they have the FW pmed. band orange.
- 13(11) a. Yellow covering essentially all non-black areas on the FW, including basal region, with orange color almost absent .. 14
- aa. Orange areas present on the FW, or else basal region black 15
- 14(13) a. HW pmed. band mostly orange (R. Negro, Brazil) *hecale sulphureus*
- aa. HW pmed. band with strong yellow lunules (lower R. Perene, Peru) *hecale shanki* n.
- * Some Trinidadian *H. ethilla ethilla* and occasional other yellow-washed *ethilla* subspecies may key out here; they are best separated by locality and/or the presence of a comma-mark filling the upper half of FW space Cu₁-Cu₂ submarginally, or the single red basal dot on the ventral hindwing (also present in some *hecale*).
- 15(13) a. Yellow or white scaling, usually extensive and continuous, across the outer part of the FW discal cell and in space Cu₁-



- Cu_2 ; middle FW subapical spot equidistant from first (costal) and third (distal) spots or closer to latter; no white subap. streaks on the ventral surface of the FW 16
 aa. Little or no yellow in FW discal cell (except in some *h. felix*, 34a); middle subap. spot (when series present) closer to costal than to distal spot; ventral FW with white subap. streaks, or HW black border deeply dentate 25
 16(15) a. Entire basal two-thirds of FW discal cell black; FW usually with four spotted yellow (occasionally white, or reduced) transverse bands; HW dorsally mostly clear orange, with black border less than one-quarter the width of the orange area at vein Cu_1 (Nicaragua to Costa Rica and W Panama)
 *hecale zuleika*
 b. FW spots yellow.
 c. Spots in FW med. and pmed. bands well separated, small.
 d. HW black border narrow, smooth *zuleika*
 dd. HW black border broader, deeply dentate
 f. "dentata"
 cc. FW with med. and pmed. spot-bands enlarged, partly to completely united, somewhat resembling *fornarina* (7b) FW.
 e. HW with a yellow stripe in and above cell
 f. "chrysantis"
 ee. HW with no yellow stripe in discal cell
 f. "discomaculatus"
 bb. FW spots white f. "albipunctata"
 * Unnamed forms have FW spot-bands both yellow and white, partial HW median bands, or an all-dark HW (transition to *fornarina*).
 aa. FW discal cell with much orange between base and (often isolated) midcell spot; dorsal HW with broad black border and/or a partial to complete med. band 17
 17(16) a. Dorsal HW black border much narrower than orange basal area, no med. band dorsally or ventrally (W Ecuador, rare)
 *hecale australis*
 aa. Dorsal HW black border usually almost as wide as orange discal area, or if narrow, a partial to complete med. band present, at least ventrally, fused apically to black border .. 18
 18(17) a. HW black border half the width of the wing, med. band essentially absent (C Panamá to W Venezuela)
 *hecale melicerta*
 b. FW yellow med. band wide and continuous.
 c. One series of FW subap. spots *melicerta*
 cc. Two series of FW subap. spots f. "muzoensis"
 bb. FW med. band broken into two spotted transverse bands



- by black spots at the end of the cell and in space Cu₁-Cu₂ f. "zygia"
- aa. A partial to complete HW med. band present, at least ventrally 19
- 19(18) a. FW heavily marked, with a single series of subap. dots and a clear yellow Y-shaped med. band, the spot in the inner angle of space Cu₁-Cu₂ tending to obsolescence and the anal spots usually small; med. band on HW often reduced and broken dorsally, but complete and heavy ventrally; ground color dorsally bright orange, ventrally darker red-brown (SW Venezuela in Barinas and Táchira) *hecale rosalesi* n.
- aa. If ventral HW bears a broad complete med. band, this is also present dorsally, and ventral surface is not dark red-brown 20
- 20(19) a. A partial dorsal HW med. band, not entering cubital region 21
- aa. Dorsal HW with a nearly to fully complete med. band 22
- 21(20) a. FW yellow med. area heavily marked with black, one or two series of yellow subap. spots, black hindmarg. bar often present from inner angle to center of wing (NW Venezuela) *hecale annetta*
- b. No large yellow submarg. spots on HW *annetta*
- bb. HW dark border including several large yellow submarg. spots, distal of the partial med. band f. "estebana"
- * *Annetta* is a rather weak subspecies, but seems to predominate in extreme western Venezuela, north of the Andes.
- aa. FW med. band heavily or lightly marked with black, FW black hindmarg. bar absent (Panamá, N and W Colombia) transitional forms of *hecale melicerta*
- c. One series of subap. spots on the FW f. "semiphorus"
- cc. Two series of subap. spots on the FW (mostly Panamá).
- d. Two spotted white median bands f. "jucundus" (24c)
- dd. Two spotted yellow med. bands f. "xanthicus" (24cc)
- * As these transitional phenotypes often look very much like *annetta*, the latter is best classified by locality.
- 22(20) a. FW with only one series of light subap. spots and a clear yellow med. band 23
- aa. FW with two series of subap. spots, or if only one series, a broad dusky yellow or white med. band 24
- 23(22) a. FW comma-mark not closing to margin on vein Cu₂; light spot in anal angle of FW not isolated by black (C Venezuela) *hecale anderida*



- b. Weak to obsolescent hindmarg. bar on FW *anderida*
- bb. Strong hindmarg. bar on FW f. "rebeli"
- aa. FW comma-mark closing to margin on vein Cu₂; anal angle dark, completely enclosing a light spot (W Colombia)
..... *hecale holcophorus*
- c. A full hindmarg. bar on FW *holcophorus*
- cc. A weak to obsolescent hindmarg. bar on FW f. "eucherius"
- 24(22) a. A strong, hindmarg. bar on FW (Guatemala)
..... *hecale fornarina*, f. "bouvieri"
- aa. No hindmarg. bar on FW (Panamá) transitions, *h. melicerta* × *zuleika*
- b. One series of subap. spots on the FW, with a single broad white or dusky yellowish med. band f. "albucilla"
- bb. Two series of subap. spots on the FW.
- c. Two spotted white med. bands on FW f. "jucundus"
- cc. Two spotted yellow med. bands on FW f. "xanthicus"
- * Many unnamed forms have other combinations of characters.
- ** These forms are very easily confused with sympatric members of the polymorphic population of *H. ismenius* (*telchinia* × *boulleti*) (64a, 65a). The form of the comma-mark in FW space Cu₁-Cu₂ permits separation; *hecale* forms have a light submarginal spot essentially always lacking in *ismenius* forms.
- 25(15) a. Basal part of space Cu₂-1A on ventral HW with only a small, black-encircled, or no red dot; when red dot present, HW border either not deeply dentate, or including white intervenal streaks at least ventrally (*hecale*, *quitalena*-group) .. 26
- aa. A large well-marked red spot at the base of space Cu₂-1A on the ventral surface of the HW, poorly or not separated from adjacent orange or mahogany color by black scaling; dorsal HW black border deeply dentate, extending discad along the veins (the orange invading two-thirds of the width of the teeth), and not including white streaks dorsally or ventrally; FW usually heavily spotted with black, orange, mahogany, and/or yellow (*pardalinus*) 35
- 26(25) a. Med. band of HW fused to marg. black, obsolescent anally; much yellow in FW space Cu₁-Cu₂ (near Belém, Brazil)
..... *hecale novatus*
(= f. "schulzi")
- aa. Med. band of HW complete, separated from marg. black by orange; little or no yellow in FW space Cu₁-Cu₂ 27
- 27(26) a. Med. and marg. black bands on HW very narrow and widely separated; FW heavily marked, with the comma-mark fused



- to a black spot in the inner part of space Cu₁-Cu₂ (S Colombia to E Ecuador) *hecale quitalena*
 b. Four or five large subap. spots on FW *quitalena*
 bb. Fewer than four (to no), or small subap. spots on FW
 (La Macarena, E-C Colombia)
 transitional forms to *hecale ithaca*
 aa. Med. and marg. black bands on HW either not strongly narrowed and widely separated, or, if narrow, FW comma-mark light, not fused to spot in inner angle of space Cu₁-Cu₂ 28
 28(27) a. Marginal band of HW not including white streaks, wide and strongly dentate (more than half its width), leaving only a narrow orange dentate band between it and a relatively smooth, non-interdigitating median band (middle Amazon, Brazil) 29
 aa. If HW marg. band wide and dentate, usually includes white streaks, and med. band also strongly dentate, interdigitating 30
 29(28) a. FW apex including orange streaks; a well-marked red basal dot on the ventral HW
 *pardalinus radiosus* (40a) or hybrids
 aa. No orange streaks in FW apex or red dot on HW
 *hecale fortunatus*
 b. Black spots in FW med. region faint to absent
 *fortunatus*
 bb. Black spots in FW med. region present, strong
 f. "spurius"
 30(28) a. HW med. and marg. bars smooth, leaving a curved orange bar of almost uniform width between them; usually no white streaks in black marg. bar dorsally (lower Amazon, Brazil) 31
 aa. HW med. and marg. black bars usually with white streaks dorsally, and either dentate, or if smooth, non-parallel, leaving an oval-shaped orange area between them (upper Amazon) 32
 31(30) a. FW comma-mark heavy; HW med. band narrow (C Pará near the Amazon river, from Belém to Santarém)
 *hecale paraensis*
 aa. FW comma-mark light; HW med. band wide and heavy (C Pará well south of the Amazon R.; R. Xingu, R. Tapajós)
 *hecale latus*
 (= f. "xinguensis")
 32(30) a. FW heavily overprinted with black, the med. spots and the comma-mark fused to form a single transverse black band (upper R. Madeira region to Rondônia, Brazil)
 *hecale nigrofasciatus*



- aa. Med. spots on FW not enlarged and fused to a transverse band 33
- 33(32) a. HW heavily marked, but FW lightly marked with black, the spots in the inner corners of spaces M_3 - Cu_1 and Cu_1 - Cu_2 obsolescent, the yellow pmed. band broad, and four subap. spots present (upper middle Amazon near Tefé) *hecale ennius*
- aa. If FW med. spots light, HW also lightly marked, pmed. band on FW mostly orange, and/or FW apex dark 34
- 34(33) a. A wide, clear yellow pmed. band on FW (N Bolivia to C Peru, polymorphic northwards) *hecale felix*
- b. FW apex with reduced or no orange color *felix*
- bb. FW apical area streaked or suffused with orange f. "versicolor"
- * Some *ethilla eucoma* (54b) may key out here; they are best separated by small size, small subap. spots on FW, and comma-mark.
- ** See also *hecale shanki* (14aa).
- aa. No clear yellow pmed. band on FW; yellow, if present, usually confined to ap. area (W Brazil to C and S Peru) *hecale sisyphus*
- c. FW with essentially no yellow color, apex black.
- d. Ground color uniform bright orange *sisyphus*
- dd. Ground color uniform dull orange-brown f. "umbrina"
- cc. FW with yellow subap. dots, sometimes with yellow in pmed. band, especially costally.
- e. Subap. dots well developed, no yellow in pmed. band f. "concors"
- ee. Small yellow subap. dots, pmed. band yellow-dusted f. "jonas"
- 35(25) a. HW relatively lightly marked (more orange than black), with narrow serrate med. and dentate marg. bands, and little marg. black on ventral surface; color bright orange to yellow 36
- aa. Color mahogany brown, or if orange, HW relatively heavily marked, the serrate med. and dentate marg. bands approaching or achieving interdigitation, and much marg. black on the ventral HW 39
- 36(35) a. HW med. band broken into small spots, tending towards obsolescence; FW orange, with apex mostly dark (SE Peru E to extreme SW Brazil) *pardalinus maeon*
- aa. HW med. band continuous, FW with yellow subap. spots 37
- 37(36) a. HW med. band broad, often strongly dentate; well-developed marg. teeth over HW veins (C and S Peru, N Bolivia) *pardalinus tithoreides*



- b. FW with much yellow in med. area *tithoreides*
- bb. Yellow color restricted to FW subap. dots f. "garleppi"
- aa. HW med. bar narrow, smooth; marg. teeth much reduced 38
- 38(37) a. FW heavily suffused with yellow scaling, suppressing almost all orange color (S-C Colombia, perhaps E Ecuador) *pardalinus orteguaza*
- aa. FW with orange pigment in basal and med. areas (N and C Peru to SW Brazil) *pardalinus dilatus*
 - b. FW yellow color confined to subap. area *dilatus*
 - bb. FW with yellow pmed. band, sometimes yellow basally f. "colorata"
- 39(35) a. Yellow on FW restricted to ap. region, HW very dark (Upper Amazon Basin from extreme W Brazil to C Peru) *pardalinus butleri*
- aa. FW with a well-developed yellow pmed. band 40
- 40(39) a. Color orange-brown (lower middle Amazon) *pardalinus radiosus*
- aa. Color reddish to mahogany-brown 41
- 41(40) a. No yellow in FW discal area; HW heavily marked with black (upper Amazon area along the Rio Solimões, near Tefé) *pardalinus pardalinus*
- aa. Yellow across FW cell and space Cu₁-Cu₂; HW lightly marked with black, suffused with mahogany (R. Madeira) *pardalinus lucescens*
- 42(5) a. A large diffuse red basal spot in space Cu₂-1A of the ventral HW; HW with a very broad black margin (over half the wing area); ventral ground color dark reddish-brown; FW crossed by a broad yellow discal/postdiscal band; FW hindmarg. bar absent, inner angle filled with black (C Panamá to extreme NW Colombia) *ethilla claudia*
- * More orange specimens may be distinguished from the very similar and sympatric *hecale melicerta* by the lack of a submarg. spot in space Cu₁-Cu₂ of the FW; and from occasional similar sympatric forms of *ismenius* by the dark inner angle and the dark spot in the inner corner of space M₃-Cu₁ of the FW.
- aa. Not as in descriptor a 43
- 43(42) a. FW ap. area heavily suffused with black (but leaving three small yellow subap. dots), nearly in to discal cell; HW with a very narrow smooth black border and elongate separated med. black spots; small size (SE Peru to Acre, Brazil) *ethilla nebulosa*
- aa. Not as above 44
- 44(43) a. A small red basal dot in space Cu₂-1A of the ventral HW; inner angle of FW usually with a distinct black diamond-shaped mark, linked to the anal bar when present (*H.*



- ethilla*) 45
 aa. No red basal dot on the ventral HW; inner angle of FW not usually having black (if present) diamond-shaped or appreciably wider than anal bar, except in some Bolivian specimens which have yellow in the cell and space Cu₁-Cu₂ (*H. ismenius* and *H. numata*) 59
 * Some Amazonian and Guianan *ethilla* have the red basal dot obsolete, but this character is the most consistent for separation of *ethilla* from near-identical sympatric forms of *numata*. The few exceptions almost always stand out from *numata* through the FW pattern elements, especially the anal bar terminating in a diamond-shaped expansion, and the spots in the inner angles of spaces M₃-Cu₁ and Cu₁-Cu₂ (upper dot extending distad over M₃).
 45(44) a. FW with only a single, centrally placed subap. spot 46
 aa. FW with three or no subap. spots 47
 46(45) a. FW subap. spot yellow (Paraíba to Bahia, E Brazil)
 *ethilla flavomaculatus*
 aa. FW subap. spot white (C and S Brazil) *ethilla narcea*
 b. FW with as much orange as yellow pigment.
 c. FW pmed. band and HW median bar yellow
 *narcea*
 cc. HW med. bar orange.
 d. FW yellow pmed. band widened costally, white
 subap. spot reduced, indistinct f. "satis"
 dd. FW pmed. band narrow, orange-suffused
 f. "brunnescens"
 bb. FW mostly yellow, with little orange pigment.
 e. Comma-mark heavy and extended, nearly touching
 or confluent with med. black spots (mostly females)
 f. "polychrous"
 ee. Comma-mark restricted to near margin
 f. "physcoa"
 47(45) a. HW mostly black, with enlarged med. and marg. bands fused
 or at most poorly separated by orange lunules 48
 aa. HW with med. and marg. black bands well separated 49
 48(47) a. HW very dark, med. and marg. bands completely fused
 mostly in the eastern Guianas, especially Guyane)
 *ethilla cephalenia*
 b. Strong yellow submarg. streaks on HW *cephalenia*
 bb. No yellow streaks on HW unnamed (and usual) form
 aa. HW with narrow orange lunules separating med. and marg.
 black bands (SE Venezuela through Guianas) .. *ethilla thielei*
 c. FW pmed. band yellow *thielei*
 cc. FW pmed. band wide, suffused with orange
 f. "fusca"

* Many additional forms are known (some illustrated), resulting in part from mixture with *cephalenia* and *e. hyalina*.

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- 49(47) a. FW light areas all hyaline (translucent), yellow, HW with a yellow median bar (S Guyana and extreme N Brazil)
..... *ethilla hyalina*
aa. FW yellow areas not hyaline 50
- 50(49) a. Both FW and HW with much more yellow than orange pigment (Trinidad and extreme NE Venezuela) *ethilla ethilla*
- * Occasional extremely yellow-washed specimens of other subspecies may key out here; separate by locality and pattern.
- aa. Orange pigment equal to or more than yellow, at least on HW 51
- 51(50) a. Comma-mark a triangle filling the entire margin of FW space Cu₁-Cu₂; a broad yellow med.-pmmed. band on the FW 52
aa. Comma-mark usually a bar under Cu₁ with a streak from its inner end back towards the junction of Cu₂ and the margin, but not always reaching the margin; yellow on FW only in pmmed. and ap. areas 53
- 52(51) a. FW hindmarg. bar absent, but inner angle filled with black (NW Colombia) *ethilla metalilis*, form "mentor"
aa. FW hindmarg. bar present and strong, ending in an arrowhead near the anal angle (Cauca Valley, Colombia)
..... *ethilla semiflavidus*
b. FW apex with three yellow spots *semiflavidus*
bb. FW apex completely dark f. "juntana"
- 53(51) a. FW hindmarg. bar essentially absent; comma-mark heavy, closing back fully to vein Cu₂ at margin 54
aa. If FW hindmarg. bar light, comma-mark also light, not closing back to vein Cu₂ at margin 55
- 54(53) a. FW yellow subap. spots large; dark spot in the inner corner of FW space M₃-Cu₁ obsolescent; HW med. band smooth and complete (Iquitos region of NE Peru) *ethilla adela*
aa. FW yellow subap. spots small; dark spot in inner angle of FW space M₃-Cu₁ present; HW median band, formed of a series of discrete spots, obsolescent anally (N Bolivia)
..... *ethilla tyndarus*
- 55(53) a. FW pmmed. band (almost always yellow) broad and continuous, with FW dark markings and anal bar relatively weakly represented; subap. spots usually small 56
aa. FW pmmed. band narrower, often broken into two distinct parts by a black line over vein M₃; subap. spots usually larger 57
- 56(55) a. No orange in FW subap. region, dorsally or ventrally (Amazon and Orinoco Basins from E Venezuela to Goiás and Rondônia, Brazil, most common around peripheries of region) *ethilla eucoma*
b. HW discal area orange to orange-brown *eucoma*

- bb. HW discal area strongly yellowed f. "flavofasciatus"
- aa. FW anteapical region with orange streaks at least ventrally, usually dorsally and occasionally fused into a large patch (Rondônia, SW Brazil) *ethilla jaruensis* n.
- 57(55) a. Dark spot in inner angle of FW space M_3 - Cu_1 squarish, generally smaller than that below it, not extending out over vein M_3 in a heavy line; HW med. bar with some basal tapering, strongly dentate distally (C Mato Grosso, Brazil) *ethilla chapadensis*
- aa. Dark spot in inner angle of FW space M_3 - Cu_1 teardrop- or comma-shaped, larger than that below it in Cu_1 - Cu_2 , extending out along vein M_3 to sever the yellow pmed. band in two 58
- 58(57) a. FW pmed. band either strongly overlaid with orange scaling, or narrow, fully and heavily severed by a black line over vein M_3 ; HW med. bar with nearly parallel margins, moderately dentate (N and W Venezuela, C and E Colombia) *ethilla metalilis*
- b. Subap. spots well developed on FW.
 - c. FW anal bar terminating in an enlarged arrowhead *metalilis*
 - cc. FW anal bar strong, but barely enlarged in the inner angle of wing (Trinidad only) *ethilla ethilla*, form "depuncta"
- bb. No subap. spots on FW f. "orcharmus"
- * Additional unnamed forms show orange suffusion in the pmed. band or apex of the FW, an abbreviated med. band on the HW, a yellow disk on the HW, or a white pmed. band on the FW (see Illustrations).
- ** Occasional hybrids between *hecale quitalena* and *h. ithaca* in the S part of Meta, Colombia, are almost indistinguishable from sympatric *metalilis*; the comma-marks differ slightly, and *hecale* usually has yellow scaling in the FW med. region.
 - aa. FW pmed. band wider, barely severed by the black scaling over vein M_3 , not overlaid with orange; HW med. bar more club-shaped, narrowed towards anal margin, weakly dentate on distal side (Amazon Basin, principally in N Brazil) *ethilla numismaticus*
- * Not a very well-separated subspecies, often flying with *eucoma*.
- 59(44) a. Four subap. spots on FW in two widely separated pairs, the second and third essentially never sharing a boundary; HW med. band, if present, continuous, at most fragmented anally (*H. ismenius*) 60
- aa. No to three subap. spots on FW; or if four, middle two always sharing a boundary, not widely separated; or in the few specimens where separated, HW med. band broken or truncate apically (*H. numata*) 66

* *Ismenius* subspecies (couplets 60-65) can also be separated from other silvaniforms by the much reduced dorsal process at the tip of the male genital valve (Figure 10), usually visible without dissection; in *numata*, this process is always longer.

- 60(59) a. A broad orange bar from base to outer margin of FW, completely filling the lower part of space Cu₁-Cu₂; a full cuneiform midcell mark from base of FW; anal bar of FW long, smooth, and untapered, filling all the anal margin from base to inner angle; FW pmed. band yellow; HW with narrow, smooth black med. and marg. bars (México to W Panamá, rarer southward) *ismenius telchinia*
 aa. Not as in descriptor a 61
- 61(60) a. HW essentially completely orange, except for a very narrow dark margin; at most traces of a median band, apically; FW similar to that of *telchinia* (60a) (SE Costa Rica, W Panamá) *ismenius clarescens*
 aa. HW with either a broad dark margin, or at least a partial median band (stronger apically) 62
- 62(61) a. FW bearing a broad smooth yellow bar, not including dark spots or intrusions of the black distal border, across the outer half of the discal cell and the inner two-thirds of space Cu₁-Cu₂; very little if any yellow in the black pmed. area; HW with med. band obsolete, leaving at most a few spots in the apical third of the wing, confluent with the black border (SW Colombia to NW Peru) *ismenius metaphorus*
 aa. If a smooth yellow med. band present on FW, either also much yellow in pmed. region, or appreciable med. or ap. black on HW 63
- 63(62) a. FW with a spotted yellow pmed. band but no yellow in med. area, HW with a full black med. band (W Colombia) *ismenius occidentalis*

* Most populations are mixed with forms of *i. ismenius*.

- aa. FW with white or yellow in med. region or a white pmed. band, or HW lacking a full and separate med. band 64
- 64(63) a. If FW band wide and with a smooth distal border, either white, or else HW without a very broad black border (C Panamá through C and W Colombia to upper Putumayo and Villavicencio) *ismenius ismenius*
 b. Cells M₃-Cu₁ and Cu₁-Cu₂ of FW nearly filled with an hourglass-shaped black mark, leaving elongate white or yellow spots in the upper outer part of M₃-Cu₁ (sometimes obsolete) and the lower middle part of Cu₁-Cu₂, bounded by vein Cu₂, and dividing the light med./pmed. band into two spot-bands.
 c. FW light med./pmed. spots and subap. spots white, well developed.



- d. HW with a narrow black margin, med. band well represented.
 - e. Med. band on HW absent anally *ismenius*
 - ee. Med. band on HW complete to anal margin f. "fasciatus"
- dd. HW with no well-defined black med. band.
 - f. HW with a narrow black margin f. "defasciatus"
 - ff. HW with med. and marg. bands fused to give a single very broad black margin f. "immoderata"
- cc. No well-developed white med./pmed. spots on FW.
 - g. FW apex heavily marked, essentially obliterating the pmed. white spots; HW with much apical black f. "hermanni"
 - gg. FW with spotted yellow med./pmed. bands.
 - h. HW with med. and marg. bands fused to give a single very broad black margin f. "abadiæ"
 - hh. HW with a partial black med. band, truncate anally, as in *ismenius* unnamed (and common) form
- bb. A broad, continuous white or yellow band across the cell and the inner part of space Cu₁-Cu₂ on the FW, usually fused to a continuous pmed. band, and usually with no dark spot in the inner angle of space M₃-Cu₁.
 - i. Very reduced light markings in FW pmed. area.
 - j. FW med. band continuously broad.
 - k. FW med. band yellow (= *i. metaphorus*).
l. More than four black spots in HW median band (NE Colombia) f. "ocanna"
 - ll. Four or fewer black spots in HW med. band (NW and W Colombia) f. "antioquensis"
 - kk. FW med. band white unnamed forms
 - jj. FW med. band partly broken by a spot in the inner angle of space Cu₁-Cu₂, which does not however separate completely the light band.
m. FW med. band yellow f. "faunus"
 - mm. FW med. band white unnamed forms
 - ii. FW pmed. area with well-developed light markings, fused to those in the continuous med. band.
n. FW med./pmed. band jagged distally, extending



to near margin.

- o. FW med./pmed. band yellow f. "hoppi"
- oo. FW med./pmed. band white f. "albofasciatus"

nn. FW med./pmed. band smooth distally, white unnamed form

* At least ten additional unnamed forms of *i. ismenius* have been seen (some are obvious recombinants of the above traits in the FW band shape and color, and the HW med. bar); some are illustrated. No monomorphic populations of the subspecies are known, but most populations show a predominance of a given form at a given time.

aa. FW with a wide but distally smooth yellow med./pmed. band, HW med. and marg. bands fused to give a very broad black border 65

65(64) a. Outer border of FW yellow med. band smoothly curved, not sharply angled at vein Cu_1 ; color deep orange (Darién, Panamá south into western Colombia) *ismenius boulleti*

* Originally applied to a unique mislabelled or transplanted specimen from French Guyana; best separated from following subspecies by locality.

aa. Outer border of FW yellow med. band fairly sharply angled ($\sim 120^\circ$) at vein Cu_1 , at times extending marginad in space M_3-Cu_1 ; color bright orange (extreme W Venezuela) *ismenius tilletti* n.

66(59) a. Usually much yellow across cell and space Cu_1-Cu_2 of FW; no continuous pmed. band on FW (but sometimes a discrete series of spots, interrupted at least at vein M_3 and the radial); comma-mark usually triangular to trapezoidal, filling the entire margin of FW space Cu_1-Cu_2 (*numata*, *silvana*-morph group) 67

aa. Usually little or no yellow in cell or space Cu_1-Cu_2 of FW; a continuous yellow or orange pmed. band on FW, interrupted at most at vein M_3 (*numata*, *superioris*-morph group) 74

67(66) a. FW with a generalized black suffusion from apex inward nearly to cell, sometimes obliterating the subap. spots, erasing the pmed. band; no yellow in med. area (SE Peru, SW Brazil) unnamed forms

* A few *numata timaeus* (97b) may key out here.

** See also *ethilla nebulosa* (43a), with a lightly marked HW.

aa. FW without heavy black suffusion, and if no spots present in pmed. area, med. band with yellow coloration 68

68(67) a. A large black spot in the inner corner of FW space Cu_1-Cu_2 69

aa. A small or no black spot in inner corner of FW space Cu_1-Cu_2 72

69(68) a. FW subap. spots very reduced or absent; HW marg. black



- area narrow, frayed inward, or absent (SW Venezuela) *numata peeblesi*
- aa. FW subap. spots present, large; HW usually with broad margin 70
- 70(69) a. FW subap. spots very diffuse apically; much yellow scaling on ventral surface of HW, especially in cell (Upper Marañón in NW Peru) *numata talboti*
- * A supergene-morph of *n. ignotus* (104a).
- aa. FW subapicals clear; little or no yellow on ventral HW .. 71
- 71(70) a. No or reduced black dagger in basal part of FW discal cell, no scaling on distal parts of FW anal and radial veins, or if these present, HW border broken or streaked with white (C. Peru) *numata illustris*
- b. Appreciable yellow scaling in FW cell and space Cu₁-Cu₂; HW black border complete; color bright orange
- *illustris*
(= f. "mirificus")
- bb. Yellow scaling in FW med. area nearly obsolete; HW usually with a broken dark border; color orange to brown f. "subnubilis"
- aa. Black dagger in FW cell, and scaling on distal parts of FW radial and anal veins, present; HW border complete, without white streaks (N Bolivia to W Mato Grosso, Brazil)
- *numata mirus*
- 72(68) a. HW med. band concave distally, usually connected to marg. black by a dark patch (Amazon Basin of SE Colombia and NE Peru through Brazil to Guianas and S Venezuela)
- *numata silvana*
- b. HW with squarish black area connecting med. and marg. bands *silvana*
- bb. HW with med. and marg. bands poorly or not connected by black.
- c. FW end-cell spot diffuse, shadowy f. "diffusus"
- cc. FW end-cell spot clear f. "divisus"
- * These two forms represent supergene crossovers.
- aa. HW med. band straight or convex distally, paralleling margin
- 73
- 73(72) a. FW hindmarg. black bar heavy, cell dagger present; HW med. black bar continuous (E Coast of Brazil)
- *numata ethra*
- b. FW pmed. spots present, med. band yellow.
- c. HW med. band yellow, stronger ventrally *ethra*
- cc. HW med. band orange dorsally and ventrally
- f. "brasiliensis"
- bb. FW pmed. spots absent, med. band orange-suffused



- f. "hopfferi"
 aa. FW hindmarg. black bar light or absent, cell dagger absent;
 HW med. black bar tending to dissolve into separated spots
 (SE Brazil from Espírito Santo to Santa Catarina)
 *numata robigus*
- * Intermediates between *ethra* and *robigus* are frequent.
- 74(66) a. HW med. band obsolescent, or at most a series of widely separated small black dots; HW black border very narrow or obsolete 75
 aa. HW med. black band present, well-developed, or if narrow and broken, black border well represented 78
- 75(74) a. FW with 3 or 4 yellow subap. spots; ground color dark orange to mahogany-brown (Bolivia only)
 *numata leopardus*, f. "artemis" (93cc)
 aa. FW ap. area solid black; ground color bright orange 76
- 76(75) a. FW pmed. band yellow (principally E Ecuador, also in polymorphic populations in Colombia, Peru, and SW Brazil)
 *numata lenaeus*
 aa. FW pmed. band orange 77
- 77(76) a. FW very lightly marked with black, the med. spots and comma-mark nearly obsolete; pmed. band narrow (C Peru)
 *numata timaeus*, f. "aristeus"
 aa. FW heavily marked with black, pmed. band wider (SE Peru to W Brazil) *numata lyrcaeus*
- 78(74) a. Comma-mark in FW space Cu₁-Cu₂ heavy, triangular, filling entire margin of space; much yellow in FW med. and pmed. areas, but no subap. spots; HW med. black almost disjunctly dentate, marg. black border very narrow and smooth (N Venezuela) *numata aulicus*
 aa. Not exactly as in descriptor a 79
- 79(78) a. HW black border obsolescent, med. band narrow and strongly dentate distally; FW with very heavy markings in med. area, forming a complete transverse band, bordered both distally and distally by yellow (SW Venezuela)
 *numata peeblesi* (69a)
 aa. Not exactly as in descriptor a 80
- 80(79) a. HW with med. black bar strongly club-shaped, wide apically and very narrow anally, causing the orange area above it to be strongly triangular and absent distally 81
 aa. HW with med. bar not closing to costal margin near apex, not isolating a basocostal triangle of orange 82
- 81(80) a. HW with med. and marg. black areas dorsally fused, or at most separated by small orange lunules (Guyana to SE Venezuela) *numata numata*, f. "guiensis"
 aa. HW med. and marg. areas separated (NE Venezuela)

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- numata holzingeri* n.
- 82(80) a. HW med. and marg. areas broadened, at least partly fused, causing much of the wing to be an essentially contiguous black patch 83
 aa. Much of HW orange or orange-brown, with med. and marg. bands separate (except sometimes for black over the veins) 91
- 83(82) a. Entire basal area of HW black, leaving only limited orange in apex; base of FW black, dark brown, or rarely orange-brown 84
 aa. HW with an orange subcostal stripe which always extends to the base; base of FW mostly orange 85
- 84(83) a. FW with a broad yellow pmed. band (E Colombian Andes, also as a recombinant in Ecuador and Peru)
 *numata messene*
- b. HW almost completely black, with 2 small subap. orange spots.
 c. Black markings in med. area of FW not obsolescent.
 d. Black spots in med. area of FW not fused
 *messene*
 dd. Black spots in med. area of FW large and heavy, tending to fuse into a transverse band f. "colombiana"
 cc. Black markings in med. area of FW very light, with comma-mark and spot in M_3-Cu_1 obsolescent f. "juncta"
- * See also *hecale ithaca*, especially f. "cajetani" (lcc).
 bb. Outer quarter of HW mostly orange f. "euphrasinus"
 aa. No or very restricted yellow color in FW med. band (E slopes of Andes from Ecuador to Bolivia, 400-1800 m)
 *numata aristiona*
 e. Base of FW not wholly black in color (commoner southward).
 f. FW base invaded, sometimes perfused by orange color, black spots in med. area reduced to obsolescent
 *aristiona*
 ff. FW base chocolate to russet in color (Bolivia) f. "splendidus"
 ee. Base of FW almost wholly black in color (commoner northward).
 g. Black spots in med. area of FW large, nearly fused, strongly reducing orange pigment in area (mostly N Peru) f. "pratti"
 gg. Black spots in med. area of FW normally represented, not tending to fuse f. "bicoloratus"



- 85(83) a. A dark patch joining central parts of med. and marg. black bands on HW, leaving orange or yellow submarg. spots near apex and an orange patch anally; bowed inward, but not entering the discal cell, the wing resembling that of *n. silvana* (lower Amazon, Guianas, and S. Venezuela)
..... *numata superioris*, f. "silvaniformis"
aa. Dark patch on HW more extensive, usually entering discal cell 86
- 86(85) a. Dark patch on HW extending to the outer margin near apex, covering most of the wing except for a well-defined orange subcostal stripe, small (usually yellow) ap. dots, and/or small streaks or lunules between the med. and marg. bands (Guianas, N Brazil) *numata numata*
b. FW pmed. band yellow.
c. HW med. and marg. bands incompletely fused
..... *numata*
cc. HW med. and marg. bands totally fused.
d. FW with a well-developed spot in inner angle of space Cu₁-Cu₂ f. "melanops"
dd. FW with no spot, or a streak connected to the comma-bar, in inner angle of space Cu₁-Cu₂ (NW Brazil) unnamed form
bb. FW pmed. band orange-suffused.
e. HW med. and marg. bands incompletely fused f. "intermedia"
ee. HW med. and marg. bands completely fused f. "melanopors"
aa. Dark patch more limited distally on HW, leaving large orange subap. spots or a continuous orange area to about the end of vein M₃ 87
- 87(86) a. FW subap. spots present, large 88
aa. FW subap. spots very small or absent 89
- 88(87) a. FW pmed. yellow band broad; FW subap. spots three or four (SE Colombia) *numata idalion*, f. "confluens"
aa. FW pmed. band orange, or if yellow, narrow; subap. spots four, usually fused into a large patch (W Brazil, NE Peru)
..... *numata aurora*
b. No yellow present in FW pmed. band.
c. A large yellow subap. patch on FW *aurora*
cc. FW subap. patch orange.
d. FW heavily marked, the cell and anal black areas at least partly fused f. "phalaris"
dd. FW lightly marked, with much orange basally f. "deflavata"
bb. A narrow yellow pmed. band, HW med. and marg. areas



- barely confluent, with orange lunules between them f. "michaeli"
- 89(87) a. HW black area united into a single continuous disk (E Colombia to E Peru, often in polymorphic populations) *numata euphrasius*
- b. FW apex totally black.
- c. HW black patch passing distally of vein M_3 .
- d. FW pmed. band yellow *euphrasius*
- dd. FW pmed. band orange (Pebas, Peru) unnamed form
- cc. HW black patch limited anally of vein M_3 unnamed form
- bb. FW with very small subap. spots; black spot at inner angle of FW space Cu_1-Cu_2 usually obsolescent f. "excelsa"
- aa. HW med. and marg. black areas barely confluent, with orange lunules between them 90
- 90(89) a. Spots in inner corners of FW spaces M_3-Cu_1 and Cu_1-Cu_2 well developed; HW black area limited apically (E Colombia) *n. euphone*, f. "nephele"
- aa. Spots in inner corners of FW spaces M_3-Cu_1 and Cu_1-Cu_2 obsolescent; HW black extends to near apex (Pebas, Peru) *numata gradatus*
- 91(82) a. A large anvil-shaped yellow mediocostal patch on the ventral HW; FW subapical yellow spots small to absent, med. black elements strong, tending to fuse into a transverse band, with the spot in the inner corner of Cu_1-Cu_2 a basad projection of this; males orange dorsally, orange-brown ventrally, females chocolate-colored dorsally and ventrally (Ilha do Marajó, Pará, Brazil) *numata sourensis* n.
- aa. Not exactly as in descriptor a 92
- 92(91) a. Ground color dark chocolate brown or mahogany 93
- aa. Ground color orange to orange-brown 94
- 93(92) a. FW subap. spots well separated by black from yellow pmed. band; hindmarg. black bar on FW obsolescent; HW black med. spot-band not crossing discal cell (N Bolivia) *numata leopardus*
- b. Ground color dark chocolate-brown.
- c. HW med. band not broken into small spots.
- d. HW med. band not fused apically with marg. black *leopardus*
- dd. HW med. band heavy, confluent distally with marg. black area f. "confluens"
- cc. HW med. band broken into small spots f. "artemis" (75a)

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- bb. Ground color a lighter mahogany f. "obscurior"
- aa. FW yellow apicals closer to wide yellow pmed. band; HW med. band crossing end of discal cell (middle to upper Amazon) *numata nubifer*
- 94(91) a. FW with an orange pmed. band, yellow absent or only in ap. area 95
- aa. FW with a clear yellow pmed. band 101
- 95(94) a. A broad orange subap. patch on FW, almost obliterating black in apex and sometimes fused with pmed. orange band, no yellow color (E Peru to SW Brazil and Bolivia) *numata arcuella*
- b. Spots across discal cell and space Cu₁-Cu₂ of FW separate (usually males) *arcuella*
- bb. Spots in FW pmed. area fused into a nearly complete black transverse band, dividing wing (usually females) f. "praelautus"
- aa. No large subap. orange patch, or else yellow apicals present 96
- 96(95) a. FW apex uniformly black, or at most with one or two small and diffuse orange subap. spots 97
- aa. FW with three well-defined yellow or orange subap. spots 98
- 97(96) a. FW hindmarg. bar heavy; large black spot in inner angle of Cu₁-Cu₂; HW med. band heavy, unbroken (upper Amazon Basin) *numata seraphion*
- * Probably best treated as a gene-morph or recombinant, not subsp.
- aa. FW hindmarg. bar light to obsolescent; black spot in inner angle of space Cu₁-Cu₂ obsolescent; HW med. bar broken up into discrete spots (lowland Peru to SW Brazil) *numata timaeus*
- b. FW med. black spots and comma-mark well developed *timaeus*
- bb. FW med. black spots and comma-bar faint f. "aristeus" (77a)
- 98(96) a. FW subap. spots small, well separated from pmed. band by black 99
- aa. FW subap. spots large, partly joined to pmed. area by orange 100
- 99(98) a. FW subap. spots very small, well separated; black med. band on HW poorly separated from marginal black (Guianas).
- b. Wide orange pmed. band on FW, black spot in anal angle *ethilla thielei*, form "fusca" (48cc)
- bb. Narrow orange pmed. band on FW, broken by black scaling along the veins; no black spot in anal angle *n. numata*, f. "intermedia" (86e)



- aa. Subap. spots on FW larger, the first two with a common border on vein R_5 (Amazon Basin, local, principally large rivers) *numata mavors*
- c. Comma-mark separated from spot in inner angle of FW space Cu_1 - Cu_2 , which is separate from spot above it and endcell spot *mavors*
- cc. These spots fused to a single black transverse band f. "translata"
- * Very variable; upper-Amazon females are often placed with *n. isabellinus*, which however has much yellow in the FW pmed. band.
- 100(98) a. FW subap. yellow fused to a single band, hardly separated from the broad pmed. orange band (near Iquitos) *numata aurora*, f. "elegans"
- aa. Subap. yellow on FW broken into three or four separate spots, well separated from the narrow orange pmed. band by orange or black scaling (Pucallpa, Peru and northwards) unnamed form near "floridus"
- 101(94) a. FW apex completely black beyond yellow pmed. band ... 102
- aa. FW bears yellow subap. spots 108
- 102(101) a. HW marg. black area tending to disintegrate into submarg. and marg. series, and not usually passing beyond the end of vein M_3 ; HW med. bar shortened distally, not reaching the ap. region (E Colombia S to E Peru and SW Brazil) *numata euphone*
- b. HW med. bar broken up into separate spots, and not confluent with the marg. black area.
- c. HW med. bar consisting of 4 to 7 spots *euphone*
- cc. HW med. bar consisting of three spots only, not extending apically of vein M_3 f. "tarapotensis"
- bb. HW med. bar fused, or with spots confluent with marg. black area.
- d. HW med. bar fused, limited to anal $\frac{2}{3}$ of wing f. "lepidus"
- dd. HW broken med. band confluent with marg. black through dark scaling between the veins f. "nephele" (90a)
 (= f. "euphorbus")
- aa. HW marg. black area complete, or passing well apically of vein M_3 ; HW med. black bar extending well beyond vein M_2 103
- 103(102) a. HW marg. black broken and much reduced beyond vein M_3 , not continuing to fuse with med. band at apex (SW Brazil) *numata jiparanaensis*
- b. FW with heavy black med. spots and wide pmed. band *jiparanaensis*



- bb. FW with light black med. spots and narrow pmed. band f. "mediatrix"
- aa. HW marg. black not broken into streaks, continuing nearly to apex 104
- 104(103) a. Comma-mark in FW space Cu₁-Cu₂ full, triangular, filling margin of space; HW med. band very deeply dentate or totally broken up into spots (upper R. Marañón, N Peru) *numata ignotus*
- * A supergene-morph of *n. talboti* (70a).
 - aa. Comma-mark on FW not heavily triangular; HW med. bar complete 105
 - 105(104) a. HW black marg. bar not fused to med. band at apex, though not broken and extending beyond vein M₃ forms of *numata euphone*
 - b. HW med. and marg. bars well separated by orange f. "gracilis"
 - bb. HW med. and marg. bars tending to confluence f. "mixta"
 - aa. HW marg. band extends to fuse with black med. bar near apex 106
 - 106(105) a. HW med. bar straight on upper (costal) border, terminating by enclosing a single yellow subap. spot, separated from marg. black area by an equally wide orange bar (E Mato Grosso, Brazil) *numata zobrysi*
 - aa. HW med. bar curved costally on upper edge, and/or poorly separated from marg. black, or terminating in several yellow subap. spots 107
- 107(106) a. Black spots in FW med. area obsolete (Pebas) *numata gradatus* (90aa)
 - aa. Black spots in FW med. area not obsolescent (Amazon Basin, commoner towards peripheries) *numata superioris*, f. "sincerus"
- 108(101) a. HW med. and marg. bands restricted to the base of the wing, leaving the ap. area fully orange or with only a few black dots 109
 - aa. HW med. and marg. bands complete to near apex of wing 111
- 109(108) a. FW apex heavily suffused with orange, in addition to the yellow subap. dots (mostly Huallaga Valley of Peru) *numata staudingeri*
 - b. Appreciable black in FW apex, HW med. band continuous.
 - c. More lightly marked, FW apex with much orange, HW med. band not extending heavily to near apex *staudingeri*

- cc. More heavily marked, with much black in FW apex,
HW med. band extending heavily outward to near
apex f. "pretiosus"
- bb. FW apex strongly washed with orange, reducing black to
the margin, and HW med. band broken into separate
spots f. "lutea"
 - aa. FW apex without any orange coloration 110
- 110(109) a. FW yellow pmed. band narrowed distally; comma-mark tri-
angular, filling margin of space Cu₁-Cu₂ (E Colombia to E
Peru) *numata aurora*, f. "laura"
 - aa. FW yellow pmed. band broad, comma-mark a normal bar
under Cu₁ (E Colombia to E Peru, rarer southward)
..... *numata idalion*
- 111(108) a. HW med. band narrowed or deeply dentate, essentially sep-
arated into discrete intervenal spots (peripheries of Amazon
Basin) 112
 - aa. HW med. band broad, complete and unbroken 113
- 112(111) a. FW hindmarg. bar well developed, at least distally (Amazon
Basin, especially edges: Maranhão, Mato Grosso)
..... *numata geminatus*
 - aa. FW hindmarg. bar absent or reduced to black scaling over
the anal vein (N Bolivia to W Brazil) *numata spadicarius*
 - b. Very little or no orange in FW apex *spadicarius*
 - bb. Much orange suffusion in FW apex f. "insolitus"
- * Quite variable; usually called "novatus" in the literature.
- 113(111) a. FW apex with orange suffusion, causing yellow pmed. and
subap. areas to be poorly separated (middle and upper Ama-
zon) *numata isabellinus*
 - b. HW med. and marg. black well separated by orange,
much orange in FW apex.
 - c. Ground color orange-brown, HW heavily marked
..... *isabellinus*
 - cc. Ground color orange, HW more lightly marked
..... f. "floridus"
 - bb. HW med. and marg. black narrowly separated by orange;
orange in FW apex restricted to inner border of subap.
spots; yellow pmed. band on FW bordered discally by a
black transverse band f. "gordius"
 - aa. No or minimal orange pigment in FW ap. area (Guianas,
Venezuela, and Amazon Basin to W. limits of Brazil)
..... *numata superioris*
 - d. Yellow subap. spots on FW reduced, separated, smaller
than elements of the yellow pmed. band.
 - e. FW with a back transverse band across wing
..... *superioris*

- ee. FW med. black spots separated f. "maecenas"
- dd. Yellow subap. spots on FW as broad as elements of yellow pmad. band; HW with 2-4 yellow submarg. spots near apex f. "atakama"

**ANNOTATED AND ALPHABETICAL INDEX TO
PUBLISHED TAXA OF SILVANIFORMS**

Each entry is organized in the following fashion: position in the key; status (* = subspecies, (*) = "weak subspecies", otherwise infrasubspecific), name, author, year, code letters (see below) for taxonomic, morphological, and biological work on this entity, and assignment to species or subspecies, with comments.

Code for degree of study:

first bracket = taxonomic study:

- T = type specimen(s) examined by author (location in parentheses);
- t = recent photograph of type specimen examined;
- I = original illustration of the type examined;
- i = reliable illustration examined;
- od = non-type specimens examined and compared with original description.

second bracket = morphological study:

- d = dissected by the author;
- E = genital valve figured in Eltringham (1917).

third bracket = biosystematic study:

- b = biological data available on laboratory behavior and early stages, from rearing in nature or in captivity;
- f = studied in the field by author;
- h = intergrading (hybrid) forms with other phenotypes in the same species seen.

Names in parentheses are subjectively (s) or objectively (o) judged to be without nomenclatural validity, as synonyms or homonyms.

- | | |
|------|---|
| 64h | <i>abadiæ</i> Apolinar, 1926 — od/fh: form of <i>ismenius ismenius</i> with <i>i. bouletti</i> infusion |
| 54a | * <i>adela</i> Neustetter, 1912 — I-od/d/fh: <i>ethilla</i> (Loreto). |
| 3a | * <i>aerotome</i> C. & R. Felder, 1862 — T(BM)-od/dE/bfh: <i>ethilla</i> (Huallaga). |
| 16bb | <i>albipunctata</i> Riffarth, 1900 — T(BM, VM)-od/h: form of <i>hecale zuleika</i> . |

- 64oo *albofasciatus* Neustetter, 1907 — t(VM)-od/fh: form of *ismenius ismenius* with *i. bouletti* infusion.
- 24b *albucilla* Bates, 1866 — T(BM)-od/E/h: form of *hecale melicerta* with *h. zuleika* infusion.
- 10bb *alexander* Neustetter, 1928 — T(BM, VM)-od/h: form of *hecale humboldti* with *h. sisyphus* infusion.
- 23b * *anderida* Hewitson, 1853 — T(BM)-od/E/fh: *hecale* (Rancho Grande).
- 21b (**annetta* Riffarth, 1900 — i-od/bfh: *hecale* (Catatumbo).
- 64ll *antioquensis* Staudinger, 1885 — od/h: form of *ismenius ismenius* with *i. bouletti* infusion.
- (— s *arcuatus* (Goeze, 1779) — indeterminable, declared *nomen oblitum*. See also Turner & Holzinger, 1976).
- 95b * *arcuella* Druce, 1874 — T(BM)-od/E/fh: *numata* (Ucayali).
- 77a, 97bb *aristeus* Neustetter, 1931 — t(VM)-od/h: form of *numata timaeus* with *n. mirus* infusion.
- 84f * *aristiona* Hewitson, 1853 — T(BM)-od/dE/bfh: *numata* (general Andes).
- 75a, 93cc *artemis* Riffarth, 1907 — T(BM)-od/fh: form of *numata leopardus* with *n. spadicarius* infusion.
- 113dd *atakama* Neustetter, 1931 — I-od/bfh: form of *numata superioris* with *n. silvana* infusion.
- 78a * *aulicus* Weymer, 1884 — I-od/E/bfh: *numata* (Rancho Grande).
- 88c * *aurora* Bates, 1862 — T(BM)-od/dE/fh: *numata* (Lo- reto).
- 17a * *australis* K. Brown, 1976 — T(AM)/h: *hecale* (Chimborazo).
- 9aa * *barcanti* K. Brown, 1976 — T(BM, AM): *hecale* (Sucre /Trinidad).
- 84gg *bicoloratus* Butler, 1873 — T(BM)-od/d/bfh: form of *numata aristiona* (mostly Ecuador and Peru).
- 65a * *bouletti* Neustetter, 1928 — T(PM)-od/bfh: *ismenius* (Darién); originally applied to a mislabeled or transplanted specimen from French Guyane.
- 24a *bouvieri* Boullet & LeCerf, 1909 — t(PM)-od/h: form of *hecale fornaria* with *h. zuleika* infusion.
- 12bb *boyi* Röber, 1923 — i-od/d/h: normal or usual form of *hecale metellus*.
- 73cc *brasiliensis* Neustetter, 1907 — t(VM)-od/d/bfh: form of *numata ethra*.
- 46dd *brunnescens* Neustetter, 1907 — t(VM)-od/bfh: form of *ethilla narcea*.

- 39a * *butleri* K. Brown, 1976 — T(BM)-od/d/bfh: *pardalinus* (Loreto).
- 1cc *cajetani* Neustetter, 1908 — t(VM)-od/fh: form of *hecale ithaca* with *h. rosalesi* infusion.
- 48b * *cephallenia* C. & R. Felder, 1865 — t(BM)-od/h: *ethilla* (Oyapock); type is an extreme yellow-streaked variant.
- 57a * *chapadensis* K. Brown, 1973 — T(MN)-od/d/bfh: *ethilla* (central Mato Grosso).
- 16e *chrysantis* Godman & Salvin, 1881 — T(BM)/h: form of *hecale zuleika* with *h. fornarina* infusion.
- (18c) o *clara* (Fabricius, 1793) — invalid homonym, now called *hecale melicerta*.)
- (72b) s *clara* (Hübner, 1816) — od: synonym of *numata silvana*.)
- 61a * *clarescens* Butler, 1875 — T(BM)-od/E/h: *ismenius* (Chiriquí).
- 3aa * *clarus* Michael, 1926 — i-od/h: *ethilla* (Ucayali).
- 42a * *claudia* Godman & Salvin, 1881 — T(BM)-od/E/bfh: *ethilla* (Darién).
- 9a * *clearei* Hall, 1930 — T(BM, AA)-od/h: *hecale* (Imataca).
- 84dd *colombiana* Apolinar, 1927 — od/fh: heavily marked form of *numata messene*.
- 38bb *colorata* Stichel, 1919 — od/h: form of *pardalinus dilatus* with *p. orteguaza* infusion.
- 34e *concors* Weymer, 1894 — I-od/d/h: form of *hecale sisyphus* with *h. felix* infusion.
- 88a *confluens* Neustetter, 1912 — t(VM)-od/bfh: form of *numata idalion* with *n. euphrasius* infusion.
- 93dd *confluens* Neustetter, 1931 — t(VM)-od/bfh: form of *numata leopardus* with *n. aristiona* infusion.
- (46c) s *connexa* Seitz, 1913 — od: heavily marked, normal female form, synonym of *ethilla narcea*.)
- (52b) s *daguanus* Staudinger, 1896 — od: synonym of *ethilla semiflavidus*.)
- 64f *defasciatus* Neustetter, 1908 — t(VM)-od/bfh: form of *ismenius ismenius*.
- 88dd *deflavata* Neustetter, 1932 — t(VM)-od/h: form of *numata aurora* with *n. arcuella* infusion.
- 16dd *dentata* Neustetter, 1907 — t(VM)-od/h: form of *hecale zuleika*.
- 58cc *depuncta* Boullet & LeCerf, 1909 — t(PM)-od/bfh: brown form of *ethilla ethilla*.
- 72c *diffusus* Butler, 1873 — T(BM)-od/d/bfh: form of *numata silvana* with *n. superioris* infusion.

- 38b * *dilatus* Weymer, 1894 — I-od/h: *pardalinus* (Ucayali).
- 16ee *discomaculatus* Weymer, 1890 — od/h: form of *hecale zuleika* with *h. fornarina* infusion.
- 72cc *divisus* Kaye, 1906 — T(AA)-od/bfh: form of *numata silvana* with *n. superioris* infusion.
- (73c) s *dryalus* Hopffer, 1869 — od: synonym of *numata ethra*.)
- 100a *elegans* Weymer, 1894 — I-od/h: form of *numata aurora* with *n. arcuella* infusion.
- 33a * *ennius* Weymer, 1890 — I od/d/h: *hecale* (Tefé).
- 21bb *estebana* Kaye, 1913 — T(AA)-od/bfh: form of *hecale annetta*.
- 50a * *ethilla* (Godart, 1819) — i-od/E/bfh: *ethilla* (Sucre/Trinidad).
- 73c * *ethra* (Hübner, 1827-31) — I-od/dE/bfh: *numata* (Bahia).
- 23cc *eucherius* Weymer, 1906 — T(BM)-od/h: form of *hecale holcophorus*.
- 56b * *eucoma* (Hübner, 1827-31) — I(T(MN)?)-od/d/bfh: *ethilla* (Belém).
- (46c) s *eucrate* (Hübner, 1823) — I: synonym of *ethilla narcaea*.)
- 102c * *euphone* C. & R. Felder, 1862 — T(VM, BM)-od/d/bfh: *numata* (Napo).
- (102dd) s *euphorbus* Stichel, 1923 — od: synonym of *numata euphone*, form “nephele.”)
- 84bb *euphrasinus* Neustetter, 1928 — t(VM)-od/bfh: form of *numata messene* with *n. euphrasius* infusion.
- 89d * *euphrasius* Weymer, 1890 — I-od/bfh: *numata* (Putumayo).
- 89bb *excelsa* Neustetter, 1932 — I-od/fh: form of *numata euphrasius* with *n. aurora* infusion.
- 64ee *fasciatus* Godman & Salvin, 1877 — T(BM)-od/fh: form of *ismenius ismenius*, or of *ismenius boulleti* with *i. telchinia* infusion.
- 64m *faunus* Staudinger, 1885 — I-od/E/bfh: form of *ismenius ismenius* with *i. boulleti* or *i. metaphorus* infusion.
- 34b * *felix* Weymer, 1894 — I-od/dE/bfh: *hecale* (Yungas, Huallaga).
- (50a) s *flavidus* Weymer, 1894 — od: synonym of *ethilla ethilla*.)
- 56bb *flavofasciatus* Weymer, 1894 — od/bfh: yellow form of *ethilla eucoma*.
- 46a * *flavomaculatus* Weymer, 1894 — i-od/bfh: *ethilla* (Per-nambuco).

- 113cc *floridus* Weymer, 1894 — I-od/dE/h: form of *numata isabellinus*.
 7b * *fornarina* Hewitson, 1853 — T(BM)-od/E/h: *hecale* (Guatemala).
 29b * *fortunatus* Weymer, 1884 — I-od/dE/fh: *hecale* (south-east of Manaus).
 (64e s *fritschei* Möschler, 1872 — od: synonym of *ismenius ismenius*.)
 8bb *fulvescens* Lathy, 1906 — T(BM): form of *hecale hecale* with *h. vetustus* infusion.
 48cc, 99b *fusca* Boullet & LeCerf, 1909 — t(PM)/h: form of *ethilla thielei*.
 37bb *garleppi* Neustetter, 1928 — t(VM)-od/h: form of *par dalinus tithoreides* with *p. maeon* infusion.
 112a (*)*geminatus* Weymer, 1894 — I-od/d/bfh: *numata* (Belém; west Brazil).
 113bb *gordius* Weymer, 1894 — I-od/h: form of *numata isabellinus* with *n. superioris* infusion.
 105b *gracilis* Riffarth, 1907 — T(BM)-od/h: form of *numata euphone* with *n. isabellinus* infusion.
 90aa, 107a (*)*gradatus* Weymer, 1894 — I-od/E/h: *numata* (north of Iquitos).
 81a *guiensis* Riffarth, 1900 — T(BM)-od/E/h: form of *numata numata* with *n. holzingeri* infusion.
 8b * *hecale* (Fabricius, 1775) — i-od/dE/bfh: *hecale* (coastal Guyana).
 64g *hermanni* Riffarth, 1899 — T(BM)-od/h: form of *ismenius ismenius* with *i. boulleti* infusion.
 1e *hero* Weymer, 1912 — od/bfh: form of *hecale ithaca*, transition to "vittatus."
 — *hippola* Hewitson, 1867 — T(BM)-od: interspecific hybrid between *ethilla metalilis* and *H. melpomene melpomene*.
 23c (*)*holcophorus* Staudinger, 1896 — I-od/E/fh: *hecale* (Chocó?).
 81aa * *holzingeri* Brown & Fernández Yépez, 1976 — T(AM, FA)/h: *numata* (Sucre/Trinidad).
 73bb *hopfferi* Neustetter, 1907 — t(VM)-od/d/bfh: form of *numata ethra*.
 64o *hoppi* Neustetter, 1928 — od/bfh: form of *ismenius ismenius* with *i. boulleti* infusion.
 10b (*)*humboldti* Neustetter, 1928 — T(VM, BM)-od/h: *hecale* (Loreto).
 49a * *hyalina* Neustetter, 1928 — od/h: *ethilla* (Roraima).

- 110aa (*)*idalion* Weymer, 1894 — od/bfh: *numata* (southeastern Colombia).
- 104a (*)*ignotus* Joicey & Kaye, 1917 — T(BM)-od/fh: *numata* (Marañón), supergene-morph of *n. talboti*.
- 71b * *illustris* Weymer, 1894 — T(HM)-od/h: *numata* (Ucayali?).
- 64ff *immoderata* Stichel, 1906 — T(BM)-od/h: form of *ismenius ismenius*.
- 1d *indecisa* Joicey & Kaye, 1917 — T(BM)-od/fh: form of *hecale ithaca* with *h. rosalesi* infusion.
- (46d s) *infuscata* Staudinger, 1885 — od: synonym of *ethilla narcea*, form "satis.")
- 112bb *insolitus* Avinoff, 1926 — T(CM)/h: form of *numata spadicarius* with *n. arcuella* infusion.
- 86e, 99bb *intermedia* Boullet & LeCerf, 1909 — T(PM)-od/h: form of *numata numata* with *n. mavors* infusion.
- 113c (*)*isabellinus* Bates, 1862 — T(BM)-od/bfh: *numata* (west Brazil).
- 64e * *ismenius* Latreille, 1817 — i-od/dE/bfh: *ismenius* (Nechí).
- 1c * *ithaca* C. & R. Felder, 1862 — T(BM)-od/dE/bfh: *hecale* (Villavicencio).
- 56aa * *jaruensis* K. Brown, 1976 — T(MN)-od/bfh: *ethilla* (Rondônia).
- 103b * *jiparanaensis* Neustetter, 1931 — t(VM)-od/d/bfh: *numata* (Rondônia).
- 34ee *jonas* Weymer, 1894 — I-od/d/h: form of *hecale sisyphus* with *h. felix* infusion.
- 21d, 24c *jucundus* Bates, 1864 — T(BM)-od/bfh: form of *hecale melicerta* with *h. zuleika* infusion.
- 84cc *juncta* Neustetter, 1925 — t(VM)-od/bfh: lightly marked form of *numata messene*.
- 52bb *juntana* Riffarth, 1900 — i-od/bfh: brown form of *ethilla semiflavidus*.
- 31aa * *latus* Riffarth, 1900 — T(HM, BM)-od/d/fh: *hecale* (Tapajós).
- 110a *laura* Neustetter, 1932 — I-od/h: form of *numata aurora* with *n. silvana* infusion.
- 76a * *lenaeus* Weymer, 1890 — i-od/E/bfh: *numata* (Abitagua).
- 93d * *leopardus* Weymer, 1894 — I-od/dE/bfh: *numata* (Yungas).
- 102d *lepidus* Riffarth, 1907 — T(AA, BM)-od/bfh: form of *numata euphone*.

- 41aa * *lucescens* Weymer, 1894 — od/bfh: *pardalinus* (Madeira).
- 109bb *lutea* Neustetter, 1931 — od/h: form of *numata staudingeri* with *n. arcuella* infusion.
- 77aa * *lyrcaeus* Weymer, 1890 — T(HM)-od/h: *numata* (Inambari).
- 113ee *maecenas* Weymer, 1894 — od/d/bfh: form of *numata superioris* with *n. numata* infusion.
- 36a (*) *maeon* Weymer, 1890 — od/h: *pardalinus* (Inambari).
- 1ff *marius* Weymer, 1890 — I-od/bfh: form of *hecale ithaca*, near "vittatus."
- 99c (*) *mavors* Weymer, 1894 — i-od/bfh: *numata* (central Amazon).
- 103bb *mediatrix* Neustetter, 1931 — t(VM)-od/bfh: form of *numata jiparanaensis* with *n. silvana* infusion.
- 86ee *melanopors* Joicey & Kaye, 1917 — T(BM)-od/h: form of *numata numata* with *n. mavors* infusion.
- 86d *melanops* Weymer, 1894 — od/bfh: dark form of *numata numata*.
- 18c * *melicerta* Bates, 1866 — T(BM)-od/dE/bfh: *hecale* (Nechí).
- 52a *mentor* Weymer, 1884 — T(HM)-od/h: form of *ethilla metalilis* with *e. claudia* infusion.
- 84d * *messene* C. & R. Felder, 1862 — T(BM)-od/E/bfh: *numata* (Villavicencio).
- 58c * *metalilis* Butler, 1873 — T(BM)-od/dE/bfh: *ethilla* (Rancho Grande).
- 62a * *metaphorus* Weymer, 1884 — I-od/dE/bfh: *ismenius* (Chimborazo).
- 12b * *metellus* Weymer, 1894 — I-od/h: *hecale* (Ilha de Tapá, Brazil).
- 88bb *michaeli* Neustetter, 1931 — t(VM)-od/h: form of *numata aurora* with *n. isabellinus* infusion.
- (71b) s *mirificus* Stichel, 1906 — T(BM): synonym of *numata illustris*.)
- 71aa * *mirus* Weymer, 1894 — I-od/dE/bfh: *numata* (Guaporé).
- 105bb *mixta* Apolinar, 1927 — od/fh: form of *numata euphone* with *n. messene* infusion.
- 18cc *muzoensis* Neustetter, 1908 — t(VM)-od/bfh: form of *hecale melicerta*.
- 46c * *narcaea* (Godart, 1819) — i-od/dE/bfh: *ethilla* (Rio de Janeiro).
- 43a * *nebulosa* Kaye, 1916 — T(AA)-od/h: *ethilla* (Inambari).

- 90a, 102dd *nephele* Seitz, 1916 — t(VM)-od/bfh: form of *numata euphone* with *n. messene* infusion.
- (1f s *nigroapicalis* Neustetter, 1925 — t(VM)-od: synonym of *hecale ithaca*, form "vittatus.")
- 32a *nigrofasciatus* Weymer, 1894 — I-od/d/bfh: *hecale* (Rondônia).
- 4bb *ninacura* Michael, 1926 — od/h: form of *pardalinus segregatus* with *p. butleri* infusion.
- 26a * *novatus* Bates, 1867 — T(BM)-od/dE/bfh: *hecale* (Belém).
- 93aa (**)nubifer* Butler, 1875 — T(BM)-od/bfh: *numata* (Tefé).
- 86c * *numata* (Cramer, 1780) — T(BM)-od/dE/bfh: *numata* (Manaus/Guiana).
- 58aa (**)numismaticus* Weymer, 1894 — I-od/d/bfh: *ethilla* (Ta-pajós).
- 93bb *obscurior* Stichel, 1906 — T(BM)-od/h: form of *numata leopardus* with *n. spadicarius* infusion.
- 641 *ocanna* Buchacker, 1880 — I/bfh: form of *ismenius ismenius* with *i. tilletti* infusion.
- 63a (**)occidentalis* Neustetter, 1928 — T(BM)-od/bfh: *ismenius* (Chocó).
- 58bb *orcharamus* Weymer, 1912 — od/h: form of *ethilla metallilis*.
- 38a * *orteguaza* Brown, 1976 — T(AM)-od/h: *pardalinus* (Napo).
- 31a * *paraensis* Riffarth, 1900 — T(BM)-od/dE/h: *hecale* (southwest of Belém).
- 41a * *pardalinus* Bates, 1862 — T(BM)-od/dE/h: *pardalinus* (Tefé).
- (8b o *pasithoe* (Cramer, 1775) — T(BM): invalid homonym, now *hecale hecale*.)
- 69a, 79a * *peeblesi* Joicey & Talbot, 1925 — T(BM)-od/bfh: *numata* (Apure).
- (84gg s *peruana* Hopffer, 1879 — od: synonym of *numata aristiona*, form "bicoloratus.")
- 88d *phalaris* Weymer, 1894 — I/h: form of *numata aurora* with *n. arcuella* infusion.
- 46ee *physcoa* Seitz, 1913 — I-od/bfh: form of *ethilla narcaea*, near "polychrous."
- (86c s *pione* Hübner, 1816 — od: synonym of *numata numata*.)
- 46e *polychrous* C. & R. Felder, 1865 — I-od/E/bfh: form of *ethilla narcaea*.
- 95bb *praelautus* Stichel, 1906 — T(BM)-od/h: form of *numata arcuella* with *n. isabellinus* infusion.

- 84g *pratti* Joicey & Kaye, 1917 — T(BM)-od/fh: form of *numata aristiona* (mostly upper Marañón, N Peru).
- 109cc *pretiosus* Weymer, 1894 — od/h: form of *numata staudingeri* with *n. isabellinus* infusion.
- 27b * *quitalena* Hewitson, 1853 — T(BM)-od/E/bfh: *hecale* (Abitagua).
- 29a, 40a * *radiosus* Butler, 1873 — T(BM)-od/bfh: *pardalinus* (Tapajós).
- 23bb *rebeli* Neustetter, 1907 — t(VM)-od/bfh: form of *hecale anderida* with *h. annetta* infusion.
- 73aa * *robigus* Weymer, 1875 — I-od/dE/bfh: *numata* (Rio de Janeiro).
- 19a * *rosalesi* K. Brown & Fernández Yépez, 1976 — T(FA)-od/bfh: *hecale* (Apure).
- 46d *satis* Weymer, 1875 — I-od/dE/bfh: brown form of *ethilla narcea*.
- (26a s *schulzi* Riffarth, 1899 — T(BM): synonym of *hecale novatus*.)
- 52b * *semiflavidus* Weymer, 1894 — od/d/bfh: *ethilla* (Cauca).
- 21c *semiphorus* Staudinger, 1896 — T(BM)-od/bfh: form of *hecale melicerta* with *h. holcophorus* infusion.
- *seraphini* Talbot, 1932 — T(BM): interspecific hybrid between *numata numata* and *melpomene thelxiopeia*.
- 97a (*)*seraphion* Weymer, 1894 — I-od/d/h: *numata* (Inambari?).
- 4b * *sergestius* Weymer, 1894 — i-od/E/h: *pardalinus* (Hualalaga).
- 14aa * *shanki* Lamas & K. Brown, 1976 — T(JP)/h: *hecale* (Chanchamayo).
- 72b * *silvana* (Stoll, 1781) — T(BM)-od/dE/bfh: *numata* (Belém).
- 85a *silvaniformis* Joicey & Kaye, 1917 — T(BM)-od/bfh: form of *numata superioris* with *n. silvana* infusion.
- 107aa *sincerus* Riffarth, 1907 — T(BM)-od/bfh: form of *numata superioris*.
- 34d * *sisyphus* Salvin, 1871 — T(BM)-od/d/h: *hecale* (Ucayali, Inambari).
- 91a * *sourensis* K. Brown, 1976 — T(MN)/bfh: *numata* (Ilha do Marajó, Brazil).
- 112b (*)*spadicarius* Weeks, 1901 — I-od/bfh: *numata* (Yungas?).
- 84ff *splendidus* Weymer, 1894 — I-od/bfh: form of *numata aristiona* with *n. leopardus* infusion.
- 29bb *spurius* Weymer, 1894 — T(HM)-od/bfh: form of *hecale fortunatus* with *h. latus* infusion.

- 109c (*) *staudingeri* Weymer, 1894 — I-od/h: *numata* (Huallaga).
- (65a o) *sticheli* Bouillet & LeCerf, 1909 — T(PM): invalid homonym, now *ismenius bouletti*.)
- 7bb *styx* Niepelt, 1921 — T(BM): aberrant form of *hecale fornarina*.
- 71bb *subnubilis* Stichel, 1906 — T(BM)-od/h: form of *numata illustris*.
- (1c s) *sulphureofasciata* Neustetter, 1925 — t(VM): synonym of *hecale ithaca*.)
- 14a * *sulphureus* Weymer, 1894 — I-od/d/bfh: *hecale* (Imeri).
- 113e * *superioris* Butler, 1875 — T(BM)-od/dE/bfh: *numata* (Tapajós).
- 70a * *talboti* Joicey & Kaye, 1917 — T(BM)-od/bfh: *numata* (Marañón).
- 102cc *tarapotensis* Riffarth, 1901 — T(BM)-od/E/h: form of *numata euphone*.
- 60a * *telchinia* Doubleday, 1847 — T(BM)-od/dE/h: *ismenius* (Guatemala).
- 48c * *thielei* Riffarth, 1900 — T(MN)-od/d/bfh: *ethilla* (Manaus/Guiana).
- 65aa * *tilletti* K. Brown & Fernández Yépez, 1976 — T(FA)-od/bfh: *ismenius* (Catatumbo).
- 97b (*) *timaeus* Weymer, 1894 — I-od/bfh: *numata* (Ucayali?).
- 37b * *tithoreides* Staudinger, 1900 — T(HM)-od/h: *pardalinus* (Yungas).
- 99cc *translata* Joicey & Kaye, 1917 — T(BM)-od/bfh: form of *numata mavors* with *n. superioris* infusion.
- 54aa * *tyndarus* Weymer, 1896 — I-od/E/bfh: *ethilla* (Yungas).
- 34dd *umbrina* Neustetter, 1931 — t(VM)-od/h: form of *hecale sisyphus*.
- (8b o) *urania* (Müller, 1774) — od: invalid homonym, now called *hecale hecale*.)
- 34bb *versicolor* Weymer, 1894 — I-od/h: form of *hecale felix* (mostly Huallaga).
- 12aa * *vetustus* Butler, 1873 — T(BM)-od/E/bfh: *hecale* (Manaus/Guiana).
- 1f *vittatus* Butler, 1873 — T(BM)-od/d/bfh: light form of *hecale ithaca* (Napo?).
- 21dd, 24cc *xanthicus* Bates, 1864 — T(BM)-od/bfh: form of *hecale melicerta* with *h. zuleika* infusion.
- (31aa s) *xinguensis* Neustetter, 1925 — t(VM): synonym of *hecale latus*.)

- 106a * *zobrysi* Fruhstorfer, 1910 — T(BM)-od/bfh: *numata* (Araguaia).
 16d * *zuleika* Hewitson, 1853 — T(BM)-od/dE/h: *hecale* (Chiriquí).
 18bb *zygia* Riffarth, 1907 — T(BM)-od/bfh: form of *hecale melicerta*.

NAMES WHICH HAVE BEEN PUBLISHED ONLY IN SYNONYMY

(See Riffarth 1901, Berl. ent. Zeit. 46:25-183)

From Plotz's unpublished icones, 1879:

(*aganippe*, no. 488: synonym of *numata idalion*.)
(*arethusa*, no. 491: synonym of *numata spadicarius*.)
(*catilina*, no. 496: synonym of *ismenius metaphorus*.)
(*distincta*, no. 237: synonym of *ismenius ismenius*.)
(*etholea*, no. 248: synonym of *hecale melicerta*.)
(*sikinos*, no. 251: synonym of *numata messene*.)
(*tleson*, no. 250: synonym of *numata euphone*.)
(*zagora*, no. 487: synonym of *hecale anderida*.)

From notes on the specimens in Plotz's collection:
(colepta: synonym of *hecale lenaeus*.)

From notes on the specimens in Maassen's collection:
(*clarissa*: synonym of *hecale vetustus*.)

CHECK LIST

[new synonymies are indicated by (= "name")]

I. Heliconius nattereri (Protosilyvaniform) — E. Brazil, near extinction.

II. *Heliconius numata*

A. *silvana*-group

- 72a *n. silvana* (Guianas and S Venezuela, E Colombia and Ecuador through Amazonian Brazil).
forms "diffusus" and "divisus."

70a *n. talboti* (NW Peru in upper Marañón valley).

71a *n. illustris* (C Peru). (= "mirificus")
form "subnubilis."

71aa *n. mirus* (S Peru and N Bolivia to SW Brazil).

73a *n. ethra* (E Brazil coast).
forms "brasiliensis" and "hopfferi."

73aa *n. robigus* (SE Brazil coast).

B. aristiona-group

- 78a *n. aulicus* (NC Venezuela).
 69a *n. peeblesi* (SW Venezuela).
 79a
 84a *n. messene* (EC to SC Colombia, Andean slopes).
 forms "colombiana," "juncta," and "euphrasinus."
 89a *n. euphrasius* (E Colombia to E Ecuador and N Peru).
 form "excelsa" and 2 unnamed forms.
 88a
 110aa *n. idalion* (E Colombia).
 form "confluens."
 84aa *n. aristiona* (Ecuador to Bolivia, middle Andean slopes).
 forms "splendidus," "pratti," "bicoloratus."
 88aa
 100a *n. aurora* (W Brazil, SE Colombia and NE Peru).
 110a forms "phalaris," "deflavata," "michaeli," "elegans," and "laura."
 90a
 102a *n. euphone* (E Colombia to SW Brazil).
 105a forms "nephele" (= "euphorbus"), "tarapotensis," "lepidus,"
 "gracilis," and "mixta."
 76a *n. lenaeus* (E Colombia and E Ecuador to SW Brazil).
 104a *n. ignotus* (NW Peru in upper Marañón valley).
 109a *n. staudingeri* (C Peru, mostly Huallaga Valley).
 forms "pretiosus" and "lutea."
 77a
 97aa *n. timaeus* (E Peru to SW Brazil).
 form "aristeus."
 97a *n. seraphion* (W Brazil and E Peru).
 95a *n. arcuela* (E Peru to SW Brazil).
 form "praelautus."
 77aa *n. lyrcaeus* (SE Peru to SW Brazil).
 75a
 93a *n. leopardus* (N Bolivia).
 forms "confluens," "artemis," and "obscurior."

C. numata-group

- 81aa *n. holzingeri* (nov.) (NE Venezuela).
 81a
 86a *n. numata* (S Venezuela, Guianas and N Brazil).
 99bb forms "guiensis," "melanopors," "intermedia," "melanops," and
 1 unnamed form.
 99aa *n. mavors* (Guianas and N Brazil).
 form "translata."

- 91a *n. sourensis* (nov.) (Marajó island, NE Brazil).
 85a
 107aa *n. superioris* (Guianas and S Venezuela to N and SW Brazil).
 113aa forms "silvaniformis," "sincerus," "maecenas," and "atakama."
 93aa *n. nubifer* (W Brazil to E Peru).
 112a *n. geminatus* (NE and SW Brazil).
 100aa *n. isabellinus* (W Brazil and E Peru).
 113a forms "floridus" and "gordius," 1 unnamed form.
 90aa *n. gradatus* (NE Peru).
 107a
 103a *n. jiparanaensis* (SW Brazil).
 form "mediatrix."
 106a *n. zobrysi* (C Brazil).
 112aa *n. spadicarius* (SW Brazil to N Bolivia).
 form "insolitus."
 34 subspecies and 47 additional forms.

III. *Heliconius ismenius*

- 60a *i. telchinia* (Mexico to W Panamá).
 61a *i. clarescens* (SE Costa Rica and W Panamá).
 65a *i. bouletti* (E Panamá to W Colombia).
 64a *i. ismenius* (C Panamá to C and W Colombia).
 forms "fasciatus," "defasciatus," "immoderata," "hermanni,"
 "abadiæ," "ocanna," "antioquensis," "faunus," "hoppi," and
 "albofasciatus," 14 or more unnamed forms.
 65aa *i. tilletti* (nov.) (W Venezuela to extreme NE Colombia).
 63a *i. occidentalis* (W Colombia).
 62a *i. metaphorus* (W Colombia to W Ecuador and NW Peru).
 7 subspecies and 24 or more additional forms.

IV. *Heliconius pardalinus*

- 38a *p. orteguaza* (SC Colombia).
 4a *p. sergestus* (C Peru in northern Huallaga Valley).
 form "ninacura."
 38aa *p. dilatus* (N and C Peru to SW Brazil).
 form "colorata."
 36a *p. maeon* (S Peru to SW Brazil).
 37a *p. tithoreides* (C and S Peru to N Bolivia).
 form "garleppi."
 39a *p. butleri* (W Brazil to NE Peru).

- 41a *p. pardalinus* (W Brazil near Tefé).
 41aa *p. lucescens* (WC Brazil along Rio Madeira).
 29a *p. radiosus* (NC Brazil along Amazon River).
 40a 9 subspecies and 3 additional forms.

V. *Heliconius hecale*

A. *hecale*-group

- 7a
 24a *h. fornaria* (Mexico to Costa Rica).
 forms "styx" and "bouvieri."
 16a *h. zuleika* (Guatemala to W Panamá).
 forms "dentata," "chrysantis," "discomaculatus," and "albipunctata."
 18a
 21aa *h. melicerta* (W Panamá, C and W Colombia to NW Venezuela).
 24aa forms "muzoensis," "zygia," "semiphorus," "jucundus," "xanthicus," and "albucilla."
 23aa *h. holcophorus* (W Colombia).
 form "eucherius."
 17a *h. australis* (W Ecuador).
 21a *h. annetta* (W Panamá to C Venezuela).
 form "estebana."
 23a *h. andrida* (NC Venezuela).
 form "rebeli."
 19a *h. rosalesi* (nov.) (SW Venezuela).
 9aa *h. barcantii* (NE Venezuela).
 9a *h. clearei* (E Venezuela to NW Guyana).
 8a *h. hecale* (NC Guyana).
 form "fulvescens."
 12aa *h. vetustus* (SE Venezuela and Guianas to N Brazil).
 26a *h. novatus* (NE Brazil). (= "schulzi")
 12a *h. metellus* (Tapará Island, N Brazil).
 form "boyi."

B. *quitalena*-group

- 1a *h. ithaca* (EC Colombia). (= "sulphureofasciata")
 forms "cajetani," "indecisa," "hero," "vittatus" (= "nigroapicalis"), and "marius."
 27a *h. quitalena* (S Colombia to E Ecuador).
 14a *h. sulphureus* (NW Brazil).

- 10a *h. humboldti* (W Brazil to NE Peru).
 form "alexander."
 34a *h. felix* (W Brazil and E Peru to N Bolivia).
 form "versicolor" (mostly Huallaga Valley, Peru).
 34aa *h. sisyphus* (W Brazil and E Peru).
 forms "umbrina," "concors," and "jonas."
 14aa *h. shanki* (nov.) (C Peru).
 33a *h. ennius* (NW Brazil near Tefé).
 32a *h. nigrofasciatus* (SW Brazil).
 29aa *h. fortunatus* (NC Brazil along the Amazon River).
 form "spurius."
 31aa *h. latus* (C Brazil along the Rios Tapajós and Xingu). (= "xinguensis")
 31a *h. paraensis* (NC Brazil near the lower Amazon River).
 26 subspecies and 28 additional forms.

VI. *Heliconius ethilla*

- 42a *e. claudia* (C and E Panamá on Pacific side).
 52aa *e. semiflavidus* (W Colombia in the Cauca Valley).
 form "juntana."
 52a
 58a *e. metalilis* (Colombia and Venezuela).
 forms "mentor" and "orchamus."
 54a *e. adela* (NE Peru).
 3a *e. aerotome* (NC Peru in the middle Huallaga Valley).
 3aa *e. clarus* (EC Peru in the Ucayali Valley).
 43a *e. nebulosa* (SE Peru to SW Brazil).
 54aa *e. tyndarus* (N Bolivia).
 56aa *e. jaruensis* (nov.) (SW Brazil).
 57a *e. chapadensis* (C Brazil in the Cuiabá area).
 56a *e. eucoma* (C and N Brazil into Guianas and S Venezuela).
 form "flavofasciatus."
 58aa *e. numismaticus* (N Brazil).
 49a *e. hyalina* (Roraima, N Brazil).
 48a *e. cephalenia* (Eastern Guianas).
 1 unnamed form.
 48aa *e. thielei* (Guianas to E Venezuela).
 99b
 form "fusca."
 50a *e. ethilla* (Trinidad to NE Venezuela).
 form "depuncta."

46a *e. flavomaculatus* (NE Brazil, mostly in Pernambuco).

46aa *e. narcaea* (C, E and S Brazil into N Argentina).

forms "satis," "brunnescens," "polychrous," and "physcoa."

18 subspecies and 11 additional forms.

VII. *Heliconius atthis* (Post-silvaniform) — SW Colombia to W Ecuador.

Seven species (five principal differentiated species)

Ninety-four recognized subspecies and one hundred and thirteen or more additional forms.

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