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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

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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 Heliconiini (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, Joycey, Kaye, Boulet and Le Cerf, and others)
    (1907-1917, 11 years) 35 names = 3.2/year
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(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, Apolinar 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 Lessé), 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. Rindge), the Carnegie Museum in Pittsburgh (CM) (H. A. Clench), and the Museu Nacional in Rio de Janeiro (MN) (A. R. do Régo 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 Agronomía 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 silvainform 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 M₃-Cu₁ and Cu₁-Cu₂. 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 *arthis* (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/besckeii* (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, pardalinus, 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). The remaining and available names

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2 I am grateful to Gerardo Lamas Müller, Museu 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 mimic 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, Espirito 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* Méndez, and *H. luciana* Lichy subspecies. a, *besckei*, male, dorsal (left) and ventral (right) wing surfaces, Itaitiaia, Rio de Janeiro, collection of the author; b, *e. elevatus* × *pseudocupidineus* Neustetter, male, dorsal, Tingo Maria, 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, Río Cuchivero, in the H. Skinner collection; h, *l. luciana*, paratype female, dorsal, same data as holotype;
i, *L. watunna* Lichy, male, dorsal, same data as (g); j, *L. watunna*, female, dorsal (left) and ventral (right) wing surfaces, Boca Aguas Negras, Guaniamo, Bolivar, in the FAM; k, *L. watunna*, male, dorsal (left) and ventral (right) wing surfaces, same data as (j). All about 0.6x life size, black, white (f, g, h) or yellow, and orange to red.

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"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.

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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 *Hyposryis*, *Callithomia*, and *Hyposcada* (some especially close pairs are illustrated in Brown and Benson, 1974). They have been found mixed with these ithomines 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](https://via.placeholder.com/150)

**Figure 5.** — Larvae of silvaniform *Heliconius*, black, white, and yellow; younger larvae dark brown (taxon, instar, locality, scale): a, ethilla nar- cœa, 1st, Rio de Janeiro, 4X; b, numata aulicus, 1st, San Esteban, Vene-

zuela, 4X; c, hecale annetta, 2nd, San Esteban, 2X; d, numata aristiona, 2nd to 3rd molt, Santa Clara, east Ecuador, 3X; e, pardalinus butleri, 3rd to 4th molt, Iquitos, Peru, 1X; f, numata silvana, 5th, Belém, Pará, Brazil, 5X; g, numata aulicus, 4th, San Esteban, 1.6X; h, numata euphone, 5th, Limoncocha, east Ecuador, 1X; i, numata silvana (ex nubifer), 5th, Km. 2 Manaus-Manacapuru road, Amazonas, Brazil, 1X; j, numata superioris X robígs hybrid, 5th, insectary, 1X; k, numata mirus, 5th, Colonia Harde-

man, north of Montero, Bolivia, 1X; l, numata ethra, 5th, Linhares, Espirito Santo, 1X; m, numata ethra, 4th, Linhares, 1.6X; n, pardalinus lucescens X radiosus, 5th, Km. 2 Manaus-Manacapuru road, 1X; o, pardalinus but-

leri, 5th, Iquitos, Peru, 1.5X; p, ethilla narcaœa, 4th to 5th molt, Petrópolis, Rio de Janeiro, 1.4X; q, ethilla metalilis, 5th, San Esteban, 1X; r, ethilla chapadensis, 5th, Buriti, Mato Grosso, 1X; s, hecale melicerta, 4th, Quibdó, Chocó, Colombia, 1.4X; t, hecale melicerta, 5th, Quibdó, 1X. 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 Cu₁, 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 M₃-Cu₁ is only very rarely elongated distally over vein M₃ 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-
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.

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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. mazaeus pothete*; l, *M. menophilus zaneka*; m, *Mechanitis polymnia caucaensis*; n, *Melinaea mazaeus messenina*; o, *M. mazaeus 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 M3-Cu1 and Cu1-Cu2) 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.

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Guianas occurs the nominate, dark-hindwing n. numata, which intergrades northwestward to the new subspecies through form "guensis," and southward to the common Amazonian n. superiors (mostly as form "maeucenas" 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. lycaeus (Inambari), n. leopardus (Yungas), n. mirus (Guaporé), n. jiparaeansis (Rondônia), and n. nubifer (Tefé). Further important mimetic morphs, such as n. isabellinus, n. idalion, n. seraphion, n. geminatus, n. spadicarius, and n. gradatus,
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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. aristolona*, 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 "macecas"). 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°07' N., 63°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...
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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 basal-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-

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**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.

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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 Bolivia, 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 _Grandidilla_ (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 Chiriqui-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 Cu1), 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, 19-1-76, 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 Cu₁ 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 Óbidos, 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 Dios). 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 Huallaga 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* × *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
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. fornarina* 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. fornarina* (Mexico and Guatemala) 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. boulleti* 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. fornarina* 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 Óbidos, Pará. A most strange and isolated subspecies, *h. metelius*, is confined to the island of Taparà 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, northwestern 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 (*anetta/anderida* and *ithaca*/"vitatus"):

**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 obsolete 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 Ticoporo (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) Barinatas (8°45' N., 70°25' W.), 525 m., two males, 14/1/76, in the FA, K. Brown leg.; two males and one female, 14/1/76, 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 "Encyclopedie 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
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 M₃-Cu₁ in Amazonian *ethilla* not of the *eucoma* phenotype is teardrop-shaped, projecting distally over vein M₃, 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. eucom/a numismaticus, Guianan e. thielei, and Trinidadian e. ethilla. E. thielei grades southward through e. hyalina in Roraima to e. eucom/a in the Amazon Basin, which intergrades with e. narcae/a and e. flavomaculatus in eastern Brazil, e. chapadensis 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. adel/a in northeastern Peru shows intermediates eastward to eucom/a types.

A new subspecies of ethilla, very near to e. eucom/a, has recently been studied in southwestern Brazil:

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

FW 35-40 mm. Sexes similar. Readily distinguishable from the otherwise very similar e. eucom/a 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°27' S., 62°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°45' S., 63°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°03' S., 62°52' W.), one female in the BM (W. Hoffmans; Rothschild Bequest, acc. 1939-1); from Jaru, one male, 30-IX-75, donated to
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, Espirito Santo), from the Rifforth collection, now in the BM; d, Heliconius seraphini Talbot, dorsal, Guyane, St. Laurent, apparently a hybrid between H. numata numata and H. melpomene thelioteola, 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.

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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 Cu₁-Cu₂, or else lying over vein Cu₁ and filling most of the two adjacent spaces, leaving elongated spots along the central parts of veins M₃ and Cu₂; 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 Panama, 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 Cu₂-₁A of the ventral hindwing, usually poorly separated from the adjacent orange or red-brown by black; Amazon Basin from Obidos 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 Cu₁-Cu₂ either absent, or else in the form of an arrowhead with one arm along Cu₁, or a recurved paraboloid spot in the middle of the space, always cutting off a submarginal spot which extends into the upper (Cu₁) 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 Panama, Colombia, western Ecuador and Ven-
ezuela 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 obsolete, 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 Cu₁-1A 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 Bolivia, 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, pm ed. = 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 Cu i-Cu 2 obsolescent 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 pm ed. yellow band broad and continuous .......

............................................................... *ithaca*  

(= f. "sulphureofasciata")

cc. Spots in inner angles of FW spaces M 3-Cu 1 and Cu 1-Cu 2 enlarged, the upper of these fused with the ap. area along veins M 2 and Cu 1, breaking yellow pm ed. band ................................................. f. "cajetani"

* 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 Cu i-Cu 2.

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 sepa-
      rated by orange .......................  f. "hero"
   ee. Dark med. and marg. bands on HW well sepa-
      rated by orange.
   f. HW med. band heavy and continuous ........
      ........................................  f. "vittatus"
      (= f. "nigroapicalis")
   ff. HW med. band broken into a series of sep-
      arated 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, arrow-
      head, 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 Cu4+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 $\frac{1}{2}$ wing
      length; HW with a diffuse but continuous non-dentate med.
      bar, and either very reduced marg. black or else teeth extend-
      ing distad between the veins; a large diffuse red basal spot on
      the HW between veins Cu2 and 1A (Tarapoto area south-
      ward, in C Peru) ................................ pardalinus 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,) part of the space (H. hecale, H. par-
dalinus) ............................................................................ 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, (H. ismenius, H.
umata, and H. ethilla) .............................................................................. 42

* Some numata from Ecuador and Peru have the comma-mark under vein Cu, obsolete marginally, with space Cu,-Cu 3 completely orange sub-
marginally. 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 fornarina
b. FW med. band and subap. spots yellow ........ fornarina
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 (ext-
treme NW Guyana and extreme E Venezuela, coastally)
........................................................................................................... hecale clearei
aa. White band narrowed costally, not entering the discal cell
(Paria Peninsula of NE Venezuela, strays to Trinidad) ........
........................................................................................................... hecale barcanti

10( 6) a. A large yellow subap. patch, surrounded by black, on the
FW (Iquitos area of NE Peru to extreme NW Brazil) ....

b. Med. and marg. areas on HW fused to form a single large black patch covering lower 1/ of wing .... *hecale 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 basocostal 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) .......

h. Same intermediate forms may have the HW 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) .......

aa. HW pmed. band with strong yellow lunules (lower R. Perene, Peru) ............................................................ *hecale sulphureus*

b. HW pmed. band with extremely extensive and continuous, across the outer part of the FW discal cell and in space Cu1-

* 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: 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

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

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 (Nicaragua to Costa Rica and W Panama)

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 zuleika

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 chrysantis

ee. HW with no yellow stripe in discal cell discomaculatus

bb. FW spots white 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 australis

17( 16) a. Dorsal HW black border much narrower than orange basal area, no med. band dorsally or ventrally (W Ecuador, rare)

b. FW yellow med. band wide and continuous.

c. One series of FW subap. spots melicerta

cc. Two series of FW subap. spots 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( 19) a. A partial dorsal HW med. band, not entering cubital region

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"

c. 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 obsolete hindmargin bar on FW .......................... *anderida

bb. Strong hindmargin bar on FW ........................................ f. "rebeli"

aa. FW comma-mark closing to margin on vein Cu_q; anal angle dark, completely enclosing a light spot (W Colombia) ................................................................. *hecale holcophorus

c. A full hindmargin bar on FW ........................................ *holcophorus

c. A weak to obsolete hindmargin bar on FW ..........................

f. "eucherius"

24(22) a. A strong, hindmargin bar on FW (Guatemala) ......................

......................................................... *hecale fornarina, f. "bouvieri"

aa. No hindmargin bar on FW (Panama) ........................................

......................................................... transitions, *h. melicerta x 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.

b. 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 X boulleti*) (64a, 65a).

The form of the comma-mark in FW space Cu_q-Cu, permits separation; *hecale* forms have a light submarginal spot essentially always lacking in *ismenius* forms.

25(15) a. Basal part of space Cu_q-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 Cu_q-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, obsolete anally; much yellow in FW space Cu_q-Cu (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 Cu_q-Cu .......................... 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 narrower 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
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[Images of various butterfly specimens]
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<sub>2</sub>-Cu<sub>1</sub> and Cu<sub>1</sub>-Cu<sub>2</sub> obsolescent, the yellow pm. band broad, and four subap. spots present (upper middle Amazon near Tefé) ........................................ hecale ennius

bb. HW med. spots light, HW also lightly marked, pm. band on FW mostly orange, and/or FW apex dark ............................... 34

34( 33) a. A wide, clear yellow pm. band on FW (N Bolivia to C Peru, polymorphic northwards) ......................... hecale felix

bb. FW apex with reduced or no orange color ................ felix

cc. FW with yellow subap. dots, sometimes with yellow in pm. band, especially costally.

d. Ground color uniform bright orange ...... sisyphus
der. Ground color uniform dull orange-brown ..............

cc. Small yellow subap. dots, pm. band yellow-dusted

ee. Small yellow subap. dots, pm. band yellow-dusted

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 (14a).

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 .......................... pardalinus maeon

bb. FW med. band broken into small spots, tending towards obsolescence; FW orange, with apex mostly dark (SE Peru E to extreme SW Brazil) .................. pardalinus tithoreides

cc. HW med. band continuous, FW with yellow subap. spots

cc. HW med. band broad, often strongly dentate; well-developed marg. teeth over HW veins (C and S Peru, N Bolivia) ....

37( 36) a. HW med. band broad, often strongly dentate; well-developed marg. teeth over HW veins (C and S Peru, N Bolivia) ......
b. FW with much yellow in med. area .................. tintoreides
   bb. Yellow color restricted to FW subap. dots f. "garleppi"
   aa. HW med. bar narrow, smooth; marg. teeth much reduced

38(a)  a. FW heavily suffused with yellow scaling, suppressing almost
      all orange color (S-C Colombia, perhaps E Ecuador) ..... pardinus orteguaza
      aa. FW with orange pigment in basal and med. areas (N and C
      Peru to SW Brazil) .................................. pardinus dilatus
      b. FW yellow color confined to subap. area .......... dilatus
      bb. FW with yellow pmed. band, sometimes yellow basally
          ........................................................................ f. "colorata"

39(a)  a. Yellow on FW restricted to ap. region, HW very dark (Upper
      Amazon Basin from extreme W Brazil to C Peru) ........ pardinus butleri
      aa. FW with a well-developed yellow pmed. band ........ 40

40(a)  a. Color orange-brown (lower middle Amazon) ........ pardinus radiosus
      aa. Color reddish to mahogany-brown ..................... 41

41(a)  a. No yellow in FW discal area; HW heavily marked with black
      (upper Amazon area along the Rio Solimões, near Tefé) ... pardinus pardalinus
      aa. Yellow across FW cell and space Cu1-Cu2; HW lightly
      marked with black, suffused with mahogany (R. Madeira)
          ........................................................................ pardinus lucensens

42(a)  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 hind-
      marg. 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
  M2-Cu1 of the FW.

aa. Not as in descriptor a ..................................... 43

43(a)  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(a)  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.
SILVANIFORM HELICONIUS
ethilla) ........................................................................ 45
aa. No red basal dot on the ventral HW; inner angle of FW not
usually having black (if present) diamond-shaped or appreci-
cably wider than anal bar, except in some Bolivian speci-
cmens which have yellow in the cell and space Cu_1-Cu_2 (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, espe-
cially the anal bar terminating in a diamond-shaped expansion, and the
spots in the inner angles of spaces M_1-Cu and Cu_1-Cu_2 (upper dot ex-
tending distad over M_2).

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 (Paraiba to Bahia, E Brazil) ......
   ethilla flavomaculatus
   aa. FW subap. spot white (C and S Brazil) ........... ethilla narcaea
   b. FW with as much orange as yellow pigment.
      c. FW pméd. band and HW median bar yellow ........
         ........................................................................ narcaea
   cc. HW med. bar orange.
      d. FW yellow pméd. band widened costally, white
         subap. spot reduced, indistinct .................. f. “satis”
      dd. FW pméd. band narrow, orange-suffused ........
         ........................................................................ f. “brunnescens”
   bb. FW mostly yellow, with little orange pigment.
      c. 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 cephallenia
   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 pméd. band yellow ......................... thielei
      cc. FW pméd. band wide, suffused with orange ..........
         ........................................................................ f. “fusca”

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

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<table>
<thead>
<tr>
<th>Rule</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>49(47)</td>
<td>a. FW light areas all hyaline (translucent), yellow, HW with a yellow median bar (S Guyana and extreme N Brazil) \ethilla hyalina\</td>
</tr>
<tr>
<td></td>
<td>aa. FW yellow areas not hyaline \ethilla hyalina\</td>
</tr>
<tr>
<td>50(49)</td>
<td>a. Both FW and HW with much more yellow than orange pigment (Trinidad and extreme NE Venezuela) \ethilla ethilla\</td>
</tr>
<tr>
<td></td>
<td>* Occasional extremely yellow-washed specimens of other subspecies may key out here; separate by locality and pattern.</td>
</tr>
<tr>
<td></td>
<td>aa. Orange pigment equal to or more than yellow, at least on HW \ethilla ethilla\</td>
</tr>
<tr>
<td>51(50)</td>
<td>a. Comma-mark a triangle filling the entire margin of FW space Cu₁-Cu₂; a broad yellow med.-pmed. band on the FW ... \ethilla metalis, form “mentor”</td>
</tr>
<tr>
<td></td>
<td>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 pmed. and ap. areas \ethilla semiflavidus\</td>
</tr>
<tr>
<td>52(51)</td>
<td>a. FW hindmarg. bar absent, but inner angle filled with black (NW Colombia) \ethilla adela\</td>
</tr>
<tr>
<td></td>
<td>aa. If FW hindmarg. bar light, comma-mark also light, not closing back to vein Cu₂ at margin \ethilla tyndarus\</td>
</tr>
<tr>
<td>53(51)</td>
<td>a. FW hindmarg. bar present and strong, ending in an arrow-head near the anal angle (Cauca Valley, Colombia) \ethilla semiflavidus\</td>
</tr>
<tr>
<td></td>
<td>bb. FW apex with three yellow spots \ethilla semiflavidus\</td>
</tr>
<tr>
<td></td>
<td>bb. FW apex completely dark \ethilla semiflavidus\</td>
</tr>
<tr>
<td>54(53)</td>
<td>a. FW yellow subap. spots large; dark spot in the inner corner of FW space M₂-Cu₁, obsolescent; HW med. band smooth and complete (Iquitos region of NE Peru) \ethilla adela\</td>
</tr>
<tr>
<td></td>
<td>aa. FW yellow subap. spots small; dark spot in inner angle of FW space M₁-Cu₁ present; HW median band, formed of a series of discrete spots, obsolescent anally (N Bolivia) \ethilla tyndarus\</td>
</tr>
<tr>
<td>55(53)</td>
<td>a. FW pmed. band (almost always yellow) broad and continuous, with FW dark markings and anal bar relatively weakly represented; subap. spots usually small \ethilla tyndarus\</td>
</tr>
<tr>
<td></td>
<td>aa. FW pmed. band narrower, often broken into two distinct parts by a black line over vein M₃; subap. spots usually larger \ethilla tyndarus\</td>
</tr>
<tr>
<td>56(55)</td>
<td>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\</td>
</tr>
<tr>
<td></td>
<td>b. HW discal area orange to orange-brown \ethilla eucoma\</td>
</tr>
</tbody>
</table>
bb. HW discal area strongly yellowed ...... f. "flavofasciatus"
aa. FW antepical 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 M3-Cu1 squarish, generally smaller than that below it, not extending outward over vein M4 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 M3-Cu1 teardrop- or comma-shaped, larger than that below it in Cu1-Cu2, extending out along vein M3 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 M3; 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. "orchamus"

* 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 HW med. region.

aa. FW pmed. band wider, barely severed by the black scaling over vein M3, 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 analy (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 unimpeded, filling all the anal margin from base to inner angle; FW pmmed. band yellow; HW with narrow, smooth black med. and marg. bars (Mexico to W Panama, 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 Panama) .................................................... *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 pmmed. 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 pmmed. region, or appreciable med. or ap. black on HW ........................................................................................................ 63

63(62) a. FW with a spotted yellow pmmed. band but no yellow in med. area, HW with a full black med. band (W Colombia) ............................................................... *ismenius occidentalis*

   aa. *FW with white or yellow in med. region or a white pmmed. 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 Panama through C and W Colombia to upper Putumayo and Villavicencio) ................................................................. *ismenius ismenius*

   b. Cells M₃-Cu₄ and Cu₁-Cu₆ of FW nearly filled with an hourglass-shaped black mark, leaving elongate white or yellow spots in the upper outer part of M₃-Cu₄ (sometimes obsolete) and the lower middle part of Cu₁-Cu₆, bounded by vein Cu₂, and dividing the light med./pmmed. band into two spot-bands.

   c. FW light med./pmmed. spots and subap. spots white, well developed.

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

   aa. *FW with white or yellow in med. region or a white pmmed. band, or HW lacking a full and separate med. band ........ 64

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d. HW with a narrow black margin, med. band well represented.

e. Med. band on HW absent anally ..........

........................................... ismenius

eee. 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"

c. 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. "hermannii"

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).

I. More than four black spots in HW median band (NE Colombia) ..............

........................................... f. "ocanna"

II. 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
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to near margin.

\hspace{0.5em} o. FW med./pmed. band yellow ... f. “hoppi”
\hspace{0.5em} oo. FW med./pmed. band white ......................
\hspace{1.5em} .................. f. “albofasciatus”
\hspace{0.5em} nn. FW med./pmed. band smooth distally, white ...
\hspace{1.5em} .............................................................. 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 mon-
omorphic 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; color deep orange (Darién, Pan-
amá 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; color bright orange (extreme W Venezuela) .... *ismenius tilletti*

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\(_2\) and the ra-
dial); 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, inter-
rupted at most at vein M\(_2\) (*numata, superioris-morph group*)

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

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area narrow, frayed inward, or absent (SW Venezuela) ...... ................................. 70
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) .................................................. 71

* 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) ...... 72
.......................................................................................................................... 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) ...... 72
.......................................................................................................................... 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) ............. 72
.......................................................................................................................... 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 ......
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

numata leopardus, f. "artemis" (93cc)

aa. FW ap. area solid black; ground color bright orange

76 (75) a. FW pmcd. band yellow (principally E Ecuador, also in polymorphic populations in Colombia, Peru, and SW Brazil)

numata lenaeus

aa. HW med. black band present, well-developed, or if narrow and broken, black border well represented

numata timaeus, f. "aristeus"

aa. HW pmed. band orange

77 (76) a. FW very lightly marked with black, the med. spots and comma-mark nearly obsolete; pmed. band narrow (C Peru)

numata lycaeus

aa. FW heavily marked with black, pmed. band wider (SE Peru to W Brazil)

numata aulicus

aa. Not exactly as in descriptor a

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

numata peeblesi (69a)

aa. Not exactly as in descriptor a

81 (80) a. HW with med. and marg. black areas dorsally separated, 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)
SILVANIFORM HELICONIUS
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

b. Entire basal area of HW black, leaving only limited orange in apex; base of FW black, dark brown, or rarely orange-brown ........................................ 84

bb. Outer quarter of HW mostly orange ........................................ f. “euphrasinus”

cc. Base of FW not wholly black in color (commoner southward).

d. Black spots in med. area of FW not fused ..........

tending to fuse into a transverse band .......... 85

cc. Black markings in med. area of FW very light, with comma-mark and spot in M₃-Cu₁ obsolescent .......... 84( 83) a. FW with a broad yellow pm1. band (E Colombian Andes, also as a recombinant in Ecuador and Peru) .................................

................................. numata messene

dd. Black spots in med. area of FW large and heavy, tending to fuse into a transverse band .......... f. “colombiana”

dd. Black spots in med. area of FW not obsolescent.

dd. Black spots in med. area of FW not fused

c. Black markings in med. area of FW not obsolescent.

c. Black markings in med. area of FW not obsolescent.

c. Black markings in med. area of FW very light, with comma-mark and spot in M₃-Cu₁ obsolescent .......... f. “juncta”

................................. numata aristiona

dd. Black spots in med. area of FW large and heavy, tending to fuse into a transverse band .......... f. “splendidus”

dd. Black spots in med. area of FW not obsolescent.

eye. Base of FW almost wholly black in color (commoner northward).

e. Base of FW not wholly black in color (commoner southward).

................................. 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) ...........

ff. FW base chocolate to russet in color (Bolivia) ...........

f. “splendidus”

gg. Black spots in med. area of FW normally represented, not tending to fuse .......... f. “bicoloratus”

* 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) .................................
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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 Cu$_1$-Cu$_2$ .......................... f. "melanops"
               dd. FW with no spot, or a streak connected to the comma-bar, in inner angle of space Cu$_1$-Cu$_2$ (NW Brazil) ................................................................. unnamed form
   bb. FW pmed. band orange-suffused.
      e. HW med. and marg. bands incompletely fused ........................................... "intermedia"
         ee. HW med. and marg. bands completely fused ........................................... "melanopora"
   aa. Dark patch more limited distally on HW, leaving large orange subap. spots or a continuous orange area to about the end of vein M$_3$ ......................................................................................................................... 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
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barely confluent, with orange lunules between them ......

................................................................. f. "michaeli"

89( 87) a. HW black area united into a single continuous disk (E Co-
lombia 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

c. 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 Colom-
bia) ................................................................. n. euphonic, 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 medio-costal 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 Maraj6,
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)
bb. Ground color a lighter mahogany ............ f. "obscurior"

94( 91) a. FW with an orange pmed. band, yellow absent or only in ap. area

aa. FW yellow apicals closer to wide yellow pmed. band; HW med. band crossing end of discal cell (middle to upper Amazon) .................................................. numata nubifer

95( 94) a. FW with a clear yellow pmed. band

aa. 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( 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)

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SILVANIFORM HELICONIUS
aa. Subap. spots on FW larger, the first two with a common border on vein R₅ (Amazon Basin, local, principally large rivers) ............................... *numata mavors*
c. Comma-mark separated from spot in inner angle of FW space Cu₁-Cu₂, 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. isabel-linus*, 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 M₃; 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 M₂ .... f. “tarapotensis”
   bb. HW med. bar fused, or with spots confluent with marg. black area.
      d. HW med. bar fused, limited to anal ⅓ 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 M₂; HW med. black bar extending well beyond vein M₂ ...

103(102) a. HW marg. black broken and much reduced beyond vein M₂, 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 to-
tally 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 con-
tinuous.

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 pm. band narrowed distally; comma-mark triangular, filling margin of space Cu₁-Cu₂ (E Colombia to E Peru) ........................................ numata aurora, f. "laura"

aa. FW yellow pm. 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 separated into discrete intervinal 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 pm. and subap. areas to be poorly separated (middle and upper Amazon) ............................................................... 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 

.............................................................. numata isabellinus

c. 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 pm. band on FW bordered distally 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 pm. band.

e. FW with a back transverse band across wing ........

.............................................................. superioris
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  abadiae Apolinar, 1926 — od/fh: form of ismenius ismenius with i. boulleti infusion

54a * adelae Neustetter, 1912 — I-od/d/fh: ethilla (Loreto).

3a * aerotome C. & R. Felder, 1862 — T(BM)-od/dE/bfh: ethilla (Huallaga).

16bb alibipunctata Riffarth, 1900 — T(BM, VM)-od/h: form of hecale zuleika.
albofasciatus Neustetter, 1907 — t(VM)-od/fh: form of ismenius ismenius with i. boulleti 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.


21b (*)annetta Riffarth, 1900 — i-od/bfh: hecale (Catatumbo).

64ill antioquensis Staudinger, 1885 — od/h: form of ismenius ismenius with i. boulleti infusion.

(*) arcuatus (Goeze, 1779) — indeterminable, declared non-men 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 * aristonina 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).


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(AM)-d/d/bfh: form of numata aristiona (mostly Ecuador and Peru).

65a * boulleti Neustetter, 1928 — T(PM)-od/bfh: ismenius (Darién); originally applied to a mislabeled or transplanted specimen from French Guyane.

24a bouvieri Boulet & LeCerf, 1909 — t(PM)-od/h: form of hecale fornarina 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 brunnecens Neustetter, 1907 — t(VM)-od/bfh: form of ethilla narcaea.

cajetani Neustetter, 1908 — t(VM)-od/fh: form of hecale ithaca with h. roalesi infusion.

cephallenia C. & R. Felder, 1865 — t(BM)-od/h: ethilla (Oyapock); type is an extreme yellow-streaked variant.


chrysanthis 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.)

clarescens Butler, 1875 — T(BM)-od/E/h: ismenius (Chiriqui).

clarus Michael, 1926 — i-od/h: ethilla (Ucayali).

claudia Godman & Salvin, 1881 — T(BM)-od/E/bfh: ethilla (Darién).

clearei Hall, 1930 — T(BM, AA)-od/h: hecale (Imataca).

colombiana Apolinar, 1927 — od/fh: heavily marked form of numata messene.


concors Weymer, 1894 — I-od/d/h: form of hecale sisyphus with h. felix infusion.

confluens Neustetter, 1912 — t(VM)-od/bfh: form of numata idalion with n. euphrasius infusion.

confluens Neustetter, 1931 — t(VM)-od/bfh: form of numata leopardus with n. aristiona infusion.

(connexa Seitz, 1913 — od: heavily marked, normal female form, synonym of ethilla narcaea.)

daguanus Staudinger, 1896 — od: synonym of ethilla semiavridus.)

defasciatus Neustetter, 1908 — t(VM)-od/bfh: form of ismenius ismenius.

deflavata Neustetter, 1932 — t(VM)-od/h: form of numata aurora with n. arcuella infusion.

dentata Neustetter, 1907 — t(VM)-od/h: form of hecale zuleika.

depuncta Boulet & LeCerf, 1909 — t(PM)-od/bfh: brown form of ethilla ethilla.

diflusus Butler, 1873 — T(BM)-od/d/bfh: form of numata silvana with n. superioris infusion.
38b  * dilatus Weymer, 1894 — I-od/h: pardalus (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  * ennus 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 nar- caea.)
(102dd s) euphorbus Stichel, 1923 — od: synonym of numata eu- phone, form "nephele.”)
84bb euphrasius 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 (Pernambuco).
floridus Weymer, 1894 — I-od/dE/h: form of numata isabellinus.

* fornarina Hewitson, 1853 — T(BM)-od/E/h: hecale (Guatemala).

* fortunatus Weymer, 1884 — I-od/dE/fh: hecale (south-east of Manaus).

fruitschei Möschler, 1872 — od: synonym of ismenius ismenius.

fulvescens Lathy, 1906 — T(BM): form of hecale hecale with h. vetustus infusion.

fusca Boullet & LeCerf, 1909 — t(PM)/h: form of ethilla thielei.

garleppi Neustetter, 1928 — t(VM)-od/h: form of pardalinus tithoreides with p. maeon infusion.

geminatus Weymer, 1894 — I-od/d/bfh: numata (Belem; west Brazil).

gordius Weymer, 1894 — I-od/h: form of numata isabellinus with n. superioris infusion.

grocilius Riffarth, 1907 — T(BM)-od/h: form of numata euphone with n. isabellinus infusion.

gradatus Weymer, 1894 — I-od/E/h: numata (north of Iquitos).

guensis Riffarth, 1900 — T(BM)-od/E/h: form of numata numata with n. holzingeri infusion.

hecale (Fabricius, 1775) — i-od/dE/bfh: hecale (coastal Guyana).

hermanni Riffarth, 1899 — T(BM)-od/h: form of ismenius ismenius with i. boulleti infusion.

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.

holcophorus Staudinger, 1896 — I-od/E/h: hecale (Choco?).

holzingeri Brown & Fernández Yépez, 1976 — T(AM, FA)/h: numata (Sucre/Trinidad).

hopfferi Neustetter, 1907 — t(VM)-od/d/bfh: form of numata ethra.

hoppi Neustetter, 1928 — od/bfh: form of ismenius ismenius with i. boulleti infusion.

humboldti Neustetter, 1928 — T(VM, BM)-od/h: hecale (Loreto).

hyalina Neustetter, 1928 — od/h: ethilla (Roraima).
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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  indecta Joicey & Kaye, 1917 — T(BM)-od/fh: form of hecale lthaca with h. rosalest infusion.

(46d s  infuscata Staudinger, 1885 — od: synonym of ethilla narenea, form “satis.”)

112bb  insolitus Avinoff, 1926 — T(CM)/h: form of numata spadiciarius with n. arcuella infusion.

86e, 99bb  intermedia Boulet & 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/E/bfh: ismenius (Nechi).


103b  * jiparanaensis Neustetter, 1931 — t(VM)-od/d/bfh: numata (Rondônia).

34ee  jonar 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/h: hecale (Tapajós).

110a  laura Neustetter, 1932 — I-od/h: form of numata aurora with n. silvana infusion.

76a  * lenaesus Weymer, 1890 — i-od/E/bfh: numata (Abitaguay).

93d  * leopardus Weymer, 1894 — I-od/E/bfh: numata (Yungas).

102d  lepidus Riffarth, 1907 — T(AA, BM)-od/bfh: form of numata euphone.
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41aa  * lucescens Weymer, 1894 — od/bfh: pardalinus (Madeira).

109bb  lutes Neustetter, 1931 — od/h: form of numata stau-

77aa  * lyraeus Weymer, 1890 — T(HM)-od/h: numata (In-

113ee  maecenas Weymer, 1894 — od/d/bfh: form of numata superi
oris with n. numata infusion.

36a  (*)maeon Weymer, 1890 — od/h: pardalinus (Inambari).

1ff  marius Weymer, 1890 — I-od/bfh: form of hecale ith-

99c  (*)mavors Weymer, 1894 — i-od/bfh: numata (central

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 (Ne-

52a  mentor Weymer, 1884 — T(HM)-od/h: form of ethilla metalilis with e. claudia infusion.


58c  * metalilis Butler, 1873 — T(BM)-od/E/bfh: ethilla (Rancho Grande).

62a  * metaphorus Weymer, 1884 — I-od/dE/bfh: ismenius (Chimborazo).

12b  * metellus Weymer, 1894 — I-od/h: hecale (Ilha de Ta-

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/d/E/bfh: numata (Gua-

105bb  mixta Apolinar, 1927 — od/fh: form of numata euphone

18cc  mucoensis Neustetter, 1908 — t(VM)-od/bfh: form of hecale melicerta.

46c  * narcaea (Godart, 1819) — i-od/d/E/bfh: ethilla (Rio de Janeiro).

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90a, 102dd  neplehe 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 sergestus with n. butleri infusion.

26a  * novatus Bates, 1867 — T(BM)-od/dE/bfh: hecale (Be-lém).

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 (Tapa-jós).

93bb  obscurior Stichel, 1906 — T(BM)-od/h: form of numata leopardus with n. spadicarius infusion.

64l  ocanna Buchecker, 1880 — I/bfh: form of ismenius ismenius with i. tilletti infusion.

63a  (**) occidentalis Neustetter, 1928 — T(BM)-od/bfh: ismenius (Chocó).

58bb  orchamus Weymer, 1912 — od/h: form of ethilla meta-llis.


31a  * paraensis Riffarth, 1900 — T(BM)-od/dE/h: hecale (southwest of Be-lém).

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).

(84g  s  peruanu Hopffer, 1879 — od: synonym of numata arsiti-ona, form “bicoloratus.

88d  phalaris Weymer, 1894 — I/h: form of numata aurora with n. arcuella infusion.

46ee  physcon Seitz, 1913 — I-od/bfh: form of ethilla narcae, near “polychrous.

(86c  s  pione Hübner, 1816 — od: synonym of numata numata.)


95bb  praelautus Stichel, 1906 — T(BM)-od/h: form of numata arcuella with n. isabellinus infusion.
pretiosus Weymer, 1894 — od/h: form of numata staudingeri with n. isabellinus infusion.
* radialis Butler, 1873 — T(BM)-od/bfh: pardalinus (Tapajós).
rebeli Neustetter, 1907 — t(VM)-od/bfh: form of hecale anderida with h. anetta infusion.
* robigus Weymer, 1875 — I-od/dE/bfh: numata (Rio de Janeiro).
satis Weymer, 1875 — I-od/dE/bfh: brown form of ethilla narcea.
(26a) s schulzi Riffarth, 1899 — T(BM): synonym of hecale novatus.)
* semiflavidus Weymer, 1894 — od/d/bfh: ethilla (Cauca).
seraphini Talbot, 1932 — T(BM): interspecific hybrid between numata numata and melpomene thrixiopeia.
91a (*seraphion Weymer, 1894 — I-od/d/h: numata (Inambari?).
* sergestus Weymer, 1894 — i-od/E/h: pardalinus (Huallaga).
* silvana (Stoll, 1781) — T(BM)-od/dE/bfh: numata (Belém).
silvaniformis Joicey & Kaye, 1917 — T(BM)-od/bfh: form of numata superioris with n. silvana infusion.
sincerus Riffarth, 1907 — T(BM)-od/bfh: form of numata superioris.
* steyphus Salvin, 1871 — T(BM)-od/d/h: hecale (Ucayali, Inambari).
* sourensis K. Brown, 1976 — T(MN)/bfh: numata (Ilha do Marajó, Brazil).
(*spadicarius Weeks, 1901 — I-od/bfh: numata (Yungas?).
* splendidus Weymer, 1894 — I-od/bfh: form of numata aristiona with n. leopardus infusion.
spurius Weymer, 1894 — T(HM)-od/bfh: form of hecale fortunatus with h. latus infusion.
(*)staudingeri Weymer, 1894 — I-od/h: numata (Huallaga).

(65a) o

sticheli Boulet & 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


14a *

sulphureus Weymer, 1894 — I-od/d/bfh: hecale (Imeri).

113e *

superiors 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 (Mau- naus/Guiana).

65aa *


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 *


34dd

umbrina Neustetter, 1931 — t(VM)-od/h: form of hecale sisyphus.

(8b) o

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

NAMES WHICH HAVE BEEN PUBLISHED ONLY IN SYNONMY

(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.)
(ileson, 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 (Protosilvaniform) — 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).

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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  n. idalion (E Colombia).
110aa 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  n. timaeus (E Peru to SW Brazil).
97aa form “aristeus.”
97a  n. seraphion (W Brazil and E Peru).
95a  n. arcuelia (E Peru to SW Brazil).
    form “praelautus.”
77aa n. lycaeus (SE Peru to SW Brazil).
75a  n. leopardus (N Bolivia).
93a 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. superiortis* (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. boulleti* (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).
V. Heliconius hecale

A. hecale-group

7a  h. fornarina (Mexico to Costa Rica).
24a  forms "styx" and "bouvieri."
16a  h. zuleika (Guatemala to W Panamá).
     forms "dentata," "chrysantis," "discomaculatus," and "albipunctata."
18a  h. melicerta (W Panamá, C and W Colombia to NW Venezuela).
23aa  h. holcophorus (W Colombia).
     form "eucherius."
17a  h. australis (W Ecuador).
21a  h. annetta (W Panamá to C Venezuela).
     form "estebana."
23a  h. anderida (NC Venezuela).
     form "rebeli."
19a  h. rosalesi (nov.) (SW Venezuela).
9aa  h. barcanti (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).
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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  *e. metalilis* (Colombia and Venezuela).
58a  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. cephallenia* (Eastern Guianas).
    1 unnamed form.
48aa *e. thielei* (Guianas to E Venezuela).
    form "fusca."
50a  *e. ethilla* (Trinidad to NE Venezuela).
    form "depuncta."

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46a  e. flavomaculatus (NE Brazil, mostly in Pernambuco).
46aa  e. narcaea (C, E and S Brazil into N Argentina).
                   forms “satin,” “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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