

A LITTLE-RECOGNISED SPECIES OF
HELICONIUS BUTTERFLY
(NYMPHALIDAE)^{1,2}

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THE TAXONOMY OF THE SOUTH AMERICAN butterfly genus *Heliconius* (Nymphalidae) Kluk is in confusion, not because the species are "critical" as a result of inbreeding, apomixis or other evolutionary processes incompatible with the rigid species concepts inherited from the theory of special creation, but simply because the species are polymorphic, show remarkable geographical variation, and mimic each other; thus as Fox (1956) has said of another South American group, the Ithomiidae, two apparently identical butterflies may belong to distantly related species, while two having hardly a single pattern in common may be conspecific.

While studying geographical variation and mimicry in the genus (See Turner 1963b, 1965 for preliminary summaries) I find it necessary to give a definition of *Heliconius elevatus* Nöldner, a species which has seldom been properly recognised, and to describe a new subspecies.

The species *H. elevatus* shows strong geographical variation, each form resembling very closely a form of *Heliconius melpomene* (Linnaeus), a highly variable species which shows both geographical variation and polymorphism (Turner & Crane 1962; Sheppard 1963; Turner 1965); as a result the two species are usually confused in various ways. Neustetter (1929) came near to the truth in separating several forms of *elevatus* as a species different from *melpomene*, but spoiled the result by splitting *melpomene* itself into several species, and including two of the *elevatus* subspecies with *melpomene*. Eltringham (1917) was firm about the separation of *elevatus* from *melpomene*, although he regarded *tumatumari* Kaye, here listed as a subspecies of *elevatus*, as a species in its own right. Oberthür (1916) correctly regarded *tumatumari* as a form of his own *bati* and separate from *melpomene*. In other works (e.g. Emsley 1964) and in most collections, *melpomene* and *elevatus* are confused. The latest revision

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Table 1
CONDITIONS FOR DYE-FEEDING

Brood No.	<u>Colias</u> <u>Species</u>	Dye (% of blend)	Feeding Start Length, mm	Time, day	Time Dye Fed, days	Pupation, day	Yield Pupae	Color Pupae
1	<u>eurytheme</u>	none	-	-	-	23-31	(34 from 65 1st-in- star larvae)	green
2	<u>eurytheme</u>	Nile blue A (5)	22-24	20-21	1.5-1.8	22-27	10/10	one blue (15 mm), rest sl. blue- green at most
		neutral red (5)	19-24	17-21 ¹	5	23-26	7/9	pink (esp. on abdomen) to deep red
		Nile blue A (1) and neut. red (1)	22	21 ¹	3-5	24-26	5/5	green to green with blue ab- domen
		brill. cre- syl blue (5)	18-20	21 ¹	4-5	25-26	3/3	green
3	<u>philodice</u>	Nile blue A (5)	15-23	14	0.8-1.4	18-19	4/20	blue-green ²
		Nile blue A (1)	24-27	16	2.3-4.5	20-22	2/8	greenish-blue; blue
	(1)	neutral red (5)	15-19	14 ¹	4-5	18-19	7/10	dark-red
	(2)	neutral red (5)	26-30	18	0.5	20-21	3/3	two dark-red; one green with red abdomen
		Nile blue A (1) and neut. red (1)	17-19	15	0.5	19	4/5	sl. blue tint
		brill. cre- syl blue (5)	18-19	15 ¹	3-4	18-19	4/4	sl. grayish green
4	<u>philodice</u>	neutral red (5)	28-32 (one at 24)	16-19 ¹	0-3	19-21	32/32	red to dark-red
5	<u>philodice</u>	Nile blue A (1)	27-30	16-17 ¹	2-3	18-20	4/10	blue-green

¹fed dye to pupation.²green for controls.

Fig. 1. Parallel variation of *H. elevatus* (left) and *H. melpomene* (right) Specimens of *H. elevatus* from the British Museum, (Natural History), of *H. melpomene* from the Hope Department of Entomology, Oxford (except). Colour: ground, dark brown to black; pale marks, yellow; dark marks, red. Left: A. *H. e. elevatus* ♂ Sao Paulo de Olivenca, upp. Amazons, August 1907 (M. de Mathan); B. *H. e. bari* ♂ Essequibo R., Brit. Guiana; C. *H. e. perchlorus* ♂, Mauchay, Beni R. viii 95 (Stuart); D. *H. e. tumatumari* ♀. Tiger Creek, Potaro R., Br. Guiana, May '07 (C. B. Roberts); E. *H. e. roraima* ♂, see type description; Right: F. *H. m. aglaope* ♂, "Tonantins, Amazon"; G. *H. m. thelxiope* ♂, Para, L. Amazon, iii — vi, 1915 (A. M. Moss, ex W. J. Kaye coll.); H. *H. m. vicinus* ♂, no data, ex coll. J. A. Gibbs, Keble college; I. *H. m. cybele* ♂, Guyane francse. St. Jean de Maroni (coll. le Moul).



TABLE 2. DIFFERENCES BETWEEN H. ELEVATUS AND H. MELPOMENE

<u>elevatus</u>	<u>melpomene</u>
Male genital valves with a large strong hook and a marked tuft of hairs at the tip.	Male genital valves with weak hook near the tip, not accompanied by a marked tuft of hairs.
Anterior margin of hindwing with a red stripe on the underside	Anterior margin of hindwing with a yellow or red stripe on the underside.
A yellow stripe a few millimetres behind the anterior margin of the hindwing, underside.	A few millimetres behind the anterior margin of the hindwing' underside, either no stripe or a red stripe.
No prominent red spots at the base of the hindwing, underside.	Three to five deep red spots at the base of the hindwing, underside.
Often a row of marginal white spots on the hindwing, underside.	Seldom a row of marginal white spots on hindwing, underside.
Rays on hindwing, upperside, tend to be thick.	Rays on hindwing, upperside, tend to be thin.
Apical spots on forewing often present.	Yellow apical spots on forewing hardly ever present.
Often a yellow fleck at inner angle of forewing.	Never a yellow fleck at inner angle of forewing.
Yellow mark between veins M_3 and Cu_1 often with concavely indented distal border.	Yellow mark between veins M_3 and Cu_1 usually convex at its distal border.
Spots on head and palpi often white.	Spots on head and palpi often yellow.

of *Heliconius* separates some forms of *elevatus* but places two of the subspecies as hybrids between *H. melpomene* and *H. aoede* (Hübner); this revision (Emsley 1965) appeared while the present paper was in draft, and the evidence presented here is independent of Emsley's study; the general agreement of the two studies testifies to their correctness.

TABLE 3. NUMBERS OF GENITALIA EXAMINED

species	infraspecies	number
<u>melpomene</u>	<u>aglaope</u>	7
	<u>flavotenuiata</u>	0
	<u>thelxiope</u>	2
	<u>vicinus</u>	7
	<u>meriana</u>	0
	others	6
	total	22
<u>elevatus</u>	<u>elevatus</u>	9
	<u>pseudocupidineus</u>	2°
	<u>bari</u>	2°+
	<u>perchlorus</u>	4
	<u>taracuanus</u>	1° ¹
	<u>tumatumari</u>	2
	<u>roraima</u>	4° ²
	total	24

° External only, without dissection

+ Including holotype

¹ Holotype² Holotype and male paratypes

No one looking at figure 1, which shows the main forms of *elevatus* and the parallel forms of *melpomene*, will be surprised at the confusion of the species (the space in the lower right hand corner of the plate could also have been filled with an equivalent form of *melpomene* which is so rare that I was unable to obtain a specimen to photograph); the parallel variation is further summarised in table 1.

The chief differences between *melpomene* and *elevatus* are summarised in table 2 and illustrated in figure 2, in many specimens of *elevatus* the hook on the genital valve can be seen without dissection; the characters used, the male genitalia and the basal markings of the hindwings, appear to be "good" specific characters in the genus *Heliconius*, showing much less variation than the major wing markings, although they do vary between localities and a little between individuals; the range of variation of both characters in *melpomene* and *elevatus* is distinct and shows no overlap. Table 2 is based on the examination of thousands of *H. melpomene*, between fifty and a hundred of *H.e.elevatus*, perhaps two dozen of *H.e.tumatumari*, the five type specimens of the new subspecies, and not more than a dozen of

each of the other subspecies; table 3 shows the numbers of male genitalia examined. It could be argued that the apparent species are no more than genetic polymorphs. The basal markings are not known to be polymorphic in any other *Heliconius*. Polymorphic genitalia are likewise not known in the genus, although not many specimens of each species have been examined; taxonomists usually underestimate the variability of these organs (Ford 1955) despite the finding of Kerkis (1931) that the genital apodemes of a hemipteron have higher coefficients of variation than other parts of the body; a thorough survey of the African butterfly *Papilio dardanus* Brown showed strong variation and even polymorphism in the male genitalia (Turner 1963a). But if it can be established that the basal markings and genital characters are correlated, so that we do not find *melpomene* markings with *elevatus* genitalia or vice versa, then it becomes highly unlikely that the forms are merely polymorphs, as it would be too great a coincidence for two characters "good" in the rest of the genus to become in one species not simply polymorphic, but controlled by the same genetic switch mechanism.

To check on this I selected from the Tring collection 14 males of *H. melpomene* (7 of the *aglaope* pattern and 7 of the *vicinus* pattern) and 8 of *H. elevatus* (5 of the *elevatus* pattern and 3 of the *perchlorus* pattern) all from the upper Amazon basin; the identification being made by means of the basal marks. The genitalia were prepared by Miss Susan May, an assistant in the Museum, and I then sorted them into *melpomene* and *elevatus* types, without knowing which butterfly they belonged to (all preparations were of course numbered). The result was:

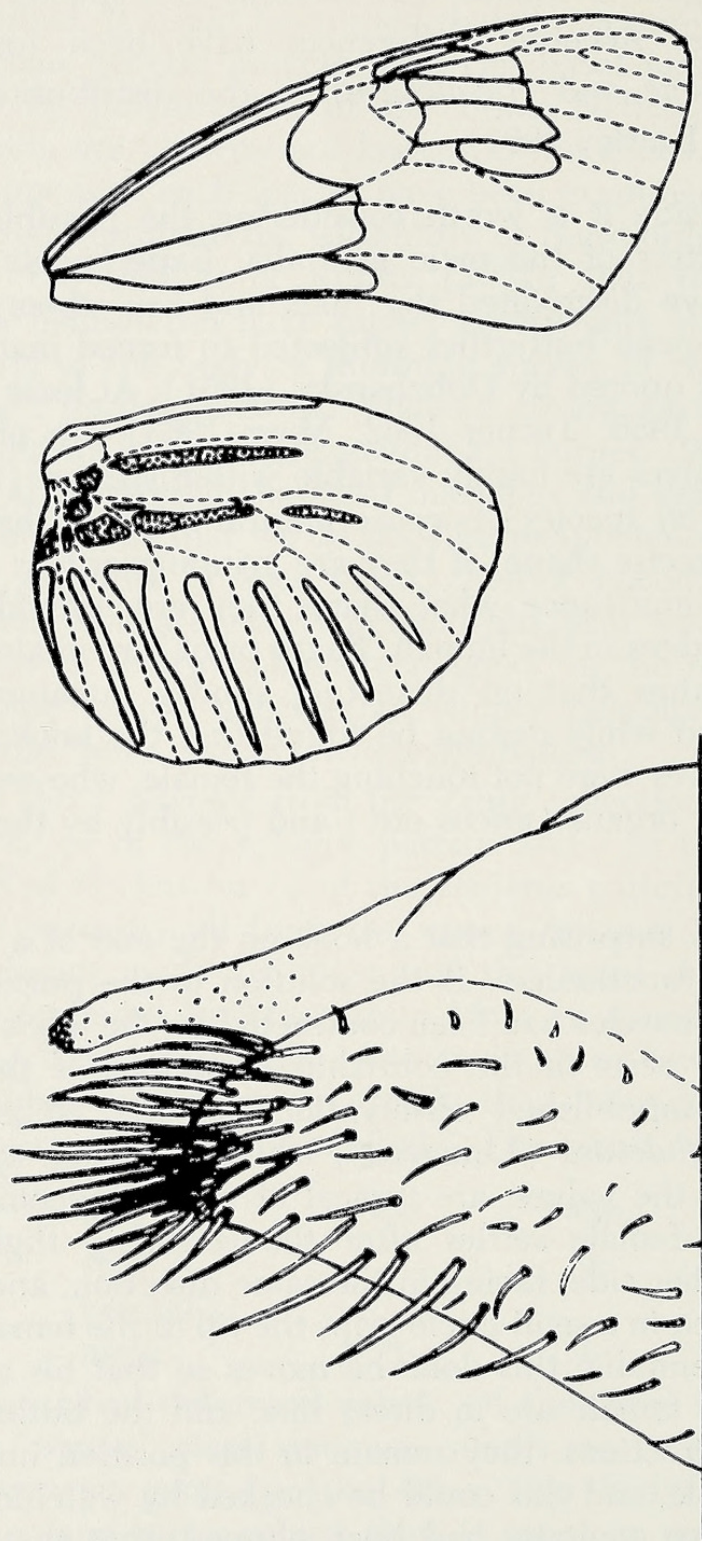
pattern:	<i>elev.</i>	<i>melp.</i>
<i>elev.</i>	7	0
genitalia:		
<i>melp.</i>	3	11

A further *elevatus* had deformed valves. Of the three specimens placed in the "wrong" class, one was simply an error, having ordinary *melpomene* genitalia; the other two had the apical extension longer and more robust than is usual in *melpomene*, but on re-examining them I found that the extensions were still much weaker than those found in *elevatus*. The probability of finding such an association between the wing and genital characters in a sample if there was in fact no association in the total population is less than one in one hundred (Fisher's exact test, two tails).

This is good evidence that *elevatus* is a species distinct from *melpomene*. Recently differences have been found between *H.melpomene* and *H.e.elevatus* in the distribution of the androconia (Emsley 1965).

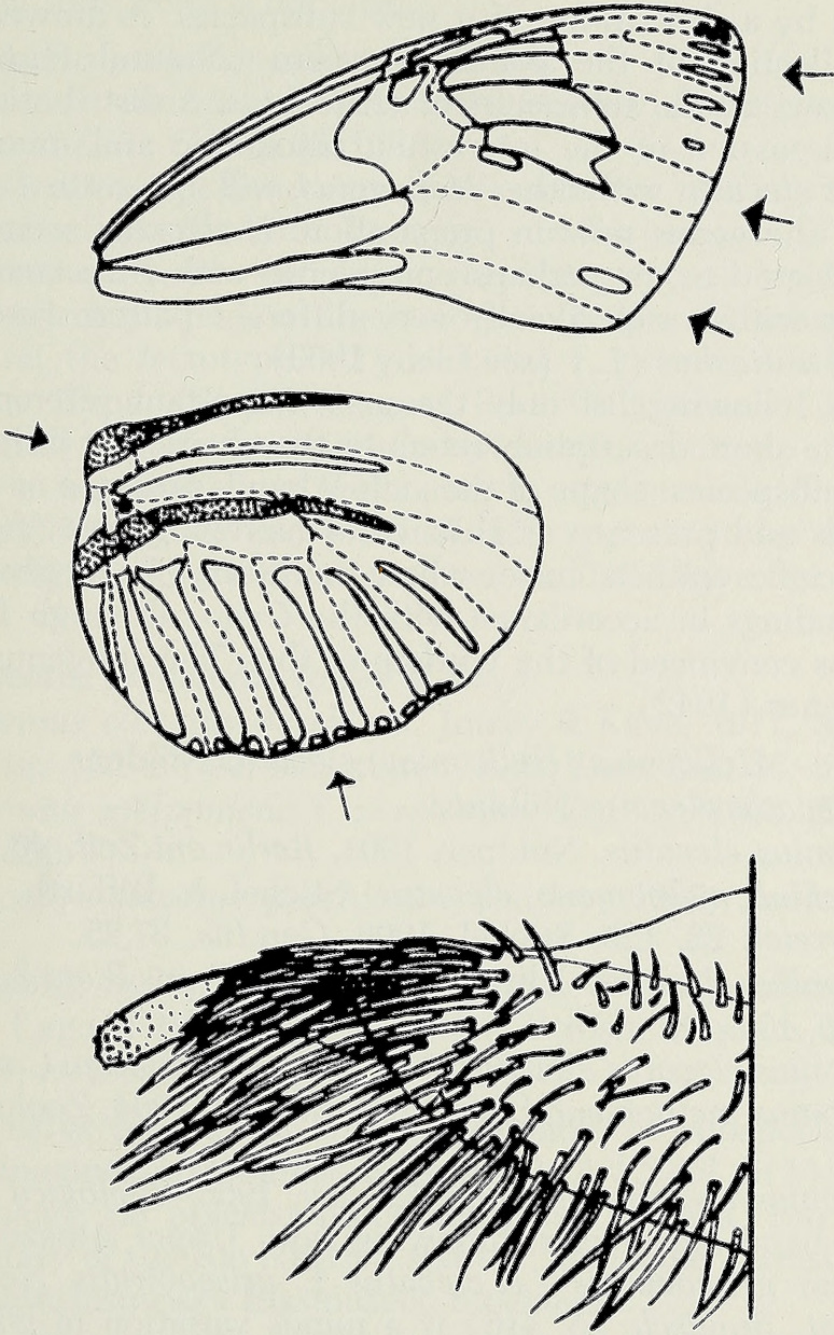
As an aside it is worth considering the possible function of the characters of the male genitalia. Experiments by Lorkovic (1953) have discredited the "lock and key" theory at least for some European butterflies subjected to forced mating (see also other work quoted by Dobzhansky (1951)). At least three authors (Lorkovic 1956, Turner 1962, Mayr 1963) are of the opinion that the valves are highly variable within species (and therefore also between species) because natural selection has little effect on their precise shape: if they are gripping organs then it is not of great significance what shape they are, provided that they grip; the ridges in the human "finger print" are analogous. Emsley (1963) claims that on dissecting sundry unnamed *Heliconids* electrocuted while mating he found that the hooked tips of the genital valves were not touching the female, who was gripped by the median organs (uncus etc.) and possibly by the bases of the valves.

It is very surprising that a hook on the end of a genital valve should be functionless. If the solution to the puzzle is not that the male's muscles had been contracted by the electrocution, then it probably rests in the courtship behaviour of the butterflies; my own unpublished observations of the *Heliconid* species *Dryadula phaetusa* (Linnaeus), which has large appendages at the tips of the valves, are typical of most *Heliconid* courtships. When the female settles after the courtship flight, the male alights by her side, facing in the same direction, and by bending his abdomen in a semi-circle grips the tip of the female's abdomen with his genitalia; this done he moves so that his abdomen and that of the female are in direct line, and the butterflies face in opposite directions; they remain in this position until they part. It is possible, and this could be checked by watching matings of males whose genitalia had been clipped, that the hooks at the tips of the valves grip the female during the first phase of copulation when the couple are facing in the same direction, and that on moving his position the male changes his grip on the female, holding her from then on with median organs and the bases of the valves. The small hooks of *H.melpomene* and some other species may be vestigial.



melpomene

Fig. 2. Differences between *H. elevatus* and *melpomene*, as shown by the forewing upperside, hindwing underside, and the tip of the male genital



elevatus

valve. Basal marks on the hindwing are shaded if red, unshaded if yellow; no other marks are shaded.

Appended is a synopsis of the infra-specific forms of *H.elevatus*, followed by a description of a new subspecies. A drawer in the main collection of the British Museum (Natural History) at Tring shows all the subspecies of *H.elevatus*. A distribution map, and a discussion of the interesting taxonomic and mimetic relations of *elevatus* with other *Heliconius*, will appear in a detailed study of the genus now in preparation. *H.elevatus* seems to be closely related to, or perhaps conspecific with *H.luciana* Lichy, a species with a superficially very different pattern resembling that of *H.antiochus* (L.) (see Lichy 1960).

In the following list only the most important references are given; the short description refers to the characters differentiating the subspecies: shape of the yellow band, presence or absence of apicals and presence or absence of hindwing rays (fig. 2).

Subspecific epithets have, where necessary, been given masculine endings in accordance with the *Code*, although I am by no means convinced of the wisdom of this. The subgenus is that of Michener (1942).

Heliconius (Heliconius) elevatus Nöldner

1. *H. elevatus elevatus* Nöldner

Heliconius elevatus. Nöldner, 1901, *Berlin.ent.Zeit.* 46, 5.

Heliconius melpomene elevatus. Stichel & Riffarth, 1905, *Tierreich* 22, 120; Stichel, 1906, *Gen.Ins.* 37, 25.

Heliconius elevatus. Eltringham, 1917, *Trans.R.ent.Soc.Lond.* 1916, 134.

Heliconius elevatus elevatus. Neustetter, 1929, *Lep. Cat.* 36, 52.

Heliconius melpomene f. *elevatus*. Emsley, 1964, *Zoologica* 49, 262.

Heliconius elevatus elevatus. Emsley, 1965, *Zoologica* 50, 210. Narrow band; no apicals; hindwing rays. Upper Amazon basin. The form *griseoviridis* (*H.elevatus* f. *griseoviridis* Neustetter, 1938, *Ent. Rundsch.* 55, 416) is a minor variation in which the band is extended posteriorly and proximally by an area of mixed black and yellow scales.

Form *noeldneri* (*H.elevatus* f. *nöldneri* Neustetter, 1938, *Ent. Rundsch.* 55, 415) has abnormally strong development of red marks, having red proximal to the band, a hammer-headed red band extending from the basal red along Cu₂ to the margin of the forewing, two rows of red subapical spots on the forewing, and abnormally wide heads to the rays on the hindwing. It gives the impression of reverting toward the "Tiger" pattern of those *Heliconii* which mimic *Ithomiids*.

The types of both these varieties, in the Naturhistorisches Mu-

seum, Wien, come from Yurimaguas, Peru; their relation with the following subspecies is not clear.

2. *H. elevatus pseudocupidineus* stat. nov.

Heliconius elevatus f. *pseudocupidineus*. Neustetter, 1931, *Int. ent. Zeit.*, Guben 25, 169.

As *H. e. elevatus*, but band very much narrower. Perhaps only just worthy of subspecific rank. Tarapoto and Yurimaguas, N.E. Peru. Types (one male, one female) in the Naturhistorisches Museum, Wien. I select the male as the lectotype of the new subspecies.

Labels on the lectotype: (1) *elevatus* f. *pseudo*=/*cupidineus* Neust./ ♂ Type. (2) Yurimaguas/Peru/O. Michael. (3) Coll./Neustetter. (4) *H. elevatus pseudocupidineus*, /lectotype (Turner). The form *nigromacula* (*H. elevatus* f. *nigromacula* Neustetter, 1932, *Zeit. österr. Ent. Ver.*, Wien 17, 15) appears to be similar to form *noeldneri* (but with a narrower band). I have not seen the type.

3. *H. elevatus perchlorus* Joicey & Kaye

Heliconius elevatus perchlora. Joicey & Kaye, 1917, *Ann. Mag. nat. Hist.* (8) 20, 94; Neustetter, 1929, *Lep. Cat.* 36, 52.

Heliconius melpomene f. *perchlorus*. Emsley, 1964, *Zoologica* 49, 262.

Heliconius elevatus perchlorus. Emsley, 1965, *Zoologica* 50, 210.

Broad band; no apicals; hindwing rays. Bolivia, valleys north-east of Lago Titicaca. Type in the British Museum (Natural History); no locality data.

4. *H. elevatus taracuanus* Bryk. Comb. nov. et subspecies dubia

H. melpomene taracuanus. Bryk, 1953, *Ark. Zool.* 5(1), 76.

Broad band; no apicals; hindwing rays. Taracua, Rio Uaupés (a tributary of the Rio Negro), state of Amazonas (Brasil). Type in the Naturhistoriska Riksmuseet, Stockholm.

This specimen is undoubtedly an *elevatus*, not a *melpomene*, and is very similar to *perchlorus*; individuals of this phenotype occur among the *e. elevatus* on the upper Amazonas, so it is not clear whether *taracuanus* is simply an intrapopulation variety or whether there are monomorphic populations of this phenotype in the basin of the Rio Negro which grade into the populations on the Amazonas.

5. *H. elevatus bari* (Oberthür). Comb. nov.

Heliconia bari. Oberthür, 1902, *Etudes d'entomologie* 21, 23.

Heliconius melpomene bari. Stichel & Riffarth, 1905, *Tierreich* 22, 120; Stichel, 1906, *Gen. Ins.* 37, 25.

Heliconius melpomene thelxiope forma *aquilina*. Neustetter, 1925, *Zeit.österr.Ent.Ver.*, Wien 10,12. Syn.nov.

Heliconius elevatus schmassmanni. Joicey & Talbot, 1925, *Ann.Mag.nat.Hist.* (9) 16, 647. Syn.nov.

Heliconius melpomene melpomene forma *bari*. Neustetter, 1929, *Lep. Cat.* 36, 51.

Heliconius elevatus aquilina. Neustetter, 1929, *Lep. Cat.* 36, 52.

Heliconius elevatus aquilina forma *schmassmanni*. Neustetter, 1929, *Lep.Cat.* 36, 52.

Heliconius melpomene X *Heliconius aoede*. Emsley, 1965, *Zoologica* 50, 210.

Broken band; apicals present or absent; hindwing rays. Mato Grosso and north Bolivia (*schmassmanni*), Rio Tapajos (state of Pará) and Guianas (*bari*). Types of *bari* and *schmassmanni* in the British Museum (Natural History), the first in the Levick Collection; localities "Guyane française" and "River System, Cuyaba-Corumba, Mato Grosso, Brasil" respectively. Types of *aquilina* (one male, one female) in the Naturhistorisches Museum, Wien; locality "Rio Machados, Mato Grosso." Clearly the male is the lectotype, and I have labelled it as such. The type of *bari* has apical spots, those of *schmassmanni* and of *aquilina* lack them, so one could regard *bari* and *schmassmanni* as separate subspecies, the one in the north and the other in the south, but the difference is small and based upon too few specimens.

6. *H.elevatus tumatumari* Kaye. Comb. et stat. nov.

Heliconius tumatumari. Kaye, 1906, *Entomologist* 39, 53; Eltringham, 1917, *Trans.ent.Soc.Lond.* 1916, 134.

Heliconius melpomene melpomene forma *tumatumari*. Neustetter, 1929, *Lep.Cat.* 36, 44.

Heliconius melpomene X *Heliconius aoede*. Emsley, 1965, *Zoologica* 50, 212.

Broken band; apicals; no hindwing rays. Potaro River, Guyana (=British Guiana).

7. *H.elevatus roraima* subsp.nov.

Heliconius melpomene, form near to *eulalia*. Hall, 1939, *Agric.J.Brit.Guiana* 10, 39; 1940, *Brit.Guiana Dept.Agric. Ent.Bull.* 3, 15.

Heliconius elevatus, form. Emsley, 1965, *Zoologica* 50, 212.

Broad band; no apicals; no hindwing rays. Region of Mount Roraima, Guyana. Types in the British Museum (Natural History). Emsley (1965) reports a long series in the American Museum of Natural History.

Heliconius (Heliconius) elevatus roraima subsp.nov.

Holotype male (fig. 2, E). Upperside: Forewing black-brown, the proximal third extensively marked with red posteriorly from vein Sc to just anterior to the posterior margin; the red being traversed by black-brown along the veins, along a line running longitudinally down the centre of the cell, and a line which runs posterior to vein 1A for 3 mms. from the proximal edge of the wings (venation is after Michener 1942), becoming coincident with the vein distally. At the base of this dark line, a yellow spot. The distal third of the cell, and portions of the wing between Sc, R₁, R₂, M₁, M₂, M₃, Cu₁, Cu₂, and posterior to Cu₃ occupied by yellow areas giving the effect of a large yellow mark invaded by black along the veins. The yellow marks between M₃ and Cu₁ and between Cu₁ and Cu₂ have V-shaped indentations distally.

Hindwing black-brown, a sub-triangular area about 1 cm. long and 2 mms. deep near the base being red, traversed by black-brown veins; posterior to the edge of this red mark three diffuse red markings lying between the veins. Anterior to the red triangle a silver-brown area extending right across the anterior margin of the wing.

Underside: forewing as upperside, except that the black line in the cell is broader, that all the wing posterior to the cell and Cu₁ is silver-brown, without markings, and that there is a basal red mark 5 mms. long between the anterior margin and vein Sc.

Hindwing black-brown, a red line 4 mms. long extending from the base along the anterior margin; 2 mms. posterior to this, and lying just posterior to vein R₁ + Sc a yellow line 10 mms. long. A red line extending across the cell and proximally in a slight curve, following chiefly the position of the posterior edge of the red triangle on the upperside; posterior to this a row of four red marks, the three distal ones occupying the same position as the three red marks on the upperside.

Antennae black-brown, slightly red-brown along one edge. Head black-brown, with white marks above and below the insertion of the antennae and on the ventral side of the palpal segments. Thorax with dorso-lateral yellow markings, but with too many scales missing for a detailed description. Abdomen black-brown, the first segment with two dorso-lateral spots. Genital valves (as seen in hand lens, without dissection) with strong hook at tip.

Labels: (1) Type/HT

(2) Roraima,/B. Guiana./H. Whitely.

(3) ♂

(4) Godman-Salvin/ Coll. 1913-2

(5) *Heliconius elevatus/ roraima* Turner 1967/Holotype

Dimensions — forewing: 3.8 cms.; antenna: 2 cms.; body from head to tip of abdomen: 2.6 cms.

Paratype male, labelled as the holotype except that (1) and (5) read "Paratype": similar except that some of the small underside marks on the hindwing are obscure or missing.

Paratype male, labelled (in manuscript ink) Roraima./Bt. Guiana/ (printed) Crowley/Bequest./1901 — 78 and with paratype label as above. Similar to type except for obscurity of some small underside hindwing markings.

Paratype male, labelled (in pencil)? Roraima/ (printed) Crowley/Bequest./1901 — 78 and with paratype labels as above. Similar to the holotype, except that the row of red dots on the upper and underside of the hindwings is absent.

Paratype female, labelled as the holotype, except that (3) is "♀" and (1) and (4) are paratype labels. Differs from the holotype in that the silver-brown areas of both wings are less extensive and less obviously differentiated in colour from the rest of the wing (a characteristic expression of sexual dimorphism in the genus *Heliconius*); the diffuse red marks on the hindwing are missing on the upperside and obscure on the underside; on the forewing the yellow mark posterior to Cu_2 is absent; and the yellow mark between M_3 and Cu_1 has a slightly curved edge instead of the V indentation; and the tips of the antennae are obviously rufous.

Holotype and paratypes in British Museum (Natural History).

The "red" of the above descriptions refers to a pigment which changes colour over the years; it is now an orange red, but was probably a brilliant carmine red when fresh; similarly the "black-brown" was probably almost black.

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SUMMARY

The South American butterfly *Heliconius elevatus* has seven subspecies, all resembling closely various forms of *H. melpomene*; the two species differ in the male genitalia and the detailed marks on the underside of the hindwings. Correlation between the characters of the wings and genitalia show that *elevatus* is a distinct species and not a form of *melpomene*, with which it is usually confused. The nomenclature of *H. elevatus* is summarised, and a new subspecies described.

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