Lepidoptera from the Pantepui. Part XIV. A new subspecies of *Heliconius elevatus* Nöldner, 1901

(Papilionoidea Nymphalidae Heliconiinae)

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< https://zoobank.org/References/C3F9A2A5-813C-4EB9-9EB8-4849CA962085 >

Abstract

A new subspecies of Lepidoptera (Papilionoidea) is described from the Pantepui: *Heliconius elevatus jigginsi* Costa & Neild, **n. ssp.** (Nymphalidae, Heliconiinae, Heliconiini) from Auyán Tepui (Venezuela), probably strictly endemic to the Auyán Massif. A new synonymy is proposed: *Heliconius elevatus sonjae* Neukirchen, 1997, **n. syn.** of *Heliconius elevatus tumatumari* Kaye, 1906.

Resumen

Lepidoptera del Pantepui. Parte XIV. Una nueva subespecie de *Heliconius elevatus* Nöldner, 1901

Se describe una nueva subespecie de Lepidoptera (Papilionoidea) del Pantepui: *Heliconius elevatus jigginsi* Costa & Neild, **n. ssp.** (Nymphalidae, Heliconiinae, Heliconiini) del Auyán Tepui (Venezuela), tal vez estrictamente endémica del Macizo del Auyán. Se propone una nueva sinonimia: *Heliconius elevatus sonjae* Neukirchen, 1997, **n. syn.** de *Heliconius elevatus tumatumari* Kaye, 1906.

Résumé

Lepidoptera du Pantepui. Partie XIV. Une nouvelle sous-espèce d'*Heliconius elevatus* Nöldner, 1901

Lors de notre première expédition à Auyán Tepui (Venezuela, État de Bolívar) en 2012, nous avons recueilli un spécimen d'*Heliconius elevatus* Nöldner, 1901, semblable à *H. e. roraima* Turner, [1967], mais présentant quelques caractères distinctifs. Au cours des quatre expéditions suivantes (2013, 2015, 2017 et 2019), nous avons réussi à compléter une série de vingt-quatre spécimens aux caractéristiques identiques et constantes, ce qui nous a permis de reconnaître une nouvelle sous-espèce de Lépidoptères (Papilionoidea) du Pantepui, qui est décrite dans la première partie du présent travail : *Heliconius elevatus jigginsi* Costa & Neild, **n. ssp.** (Nymphalidae, Heliconiinae, Heliconiini), peut-être strictement endémique du Massif Auyán.

Il est possible que cette nouvelle sous-espèce soit endémique du massif d'Auyán uniquement, si l'on tient compte de sa connotation de sous-unité hautement endémique au sein même de la province biogéographique de Pantepui (Costa *et al.,* 2019 c). Sa condition physiographique d'isolement par rapport à la Sierra de Lema et à la Gran Sabana a permis la conservation d'un nombre important de taxa endémiques qui vivent dans ses zones les plus élevées (Costa *et al*., 2014 a, b, 2016, 2017, 2018, 2019 a, b, c ; Viloria & Costa, 2019 ; Costa *et al*., 2020, 2021 a, b, 2022, 2023).

Malgré l'existence d'un grand nombre de sous-espèces d'*Heliconius elevatus*, l'absence de rayons rouges sur les ailes postérieures d'*Heliconius elevatus jigginsi* **n. ssp.** simplifie le diagnostic, ce dernier n'étant comparable qu'avec les sous-espèces suivantes :

– *H. elevatus roraima* Turner, [1967] (TL : Guyane)

– *H. elevatus tumatumari* Kaye, 1906 (TL : Guyane)

– *H. elevatus sonjae* Neukirchen, 1997 (TL : Brésil, Pará)

L'holotype et plusieurs paratypes de la nouvelle sous-espèce sont figurés, ce qui permet de visualiser ses variations chez les mâles et les femelles ; la carte de sa répartition connue à ce jour est présentée et des notes détaillées sur son habitat et son éthologie sont consignées.

Dans la deuxième partie du présent article, deux des sous-espèces mentionnées ci-dessus, *sonjae* et *tumatumari*, sont comparées. En ce qui concerne *H. e. tumatumari*, Kaye (1906) n'a pas désigné explicitement un holotype dans sa description originale, mais a figuré un spécimen femelle, qui a ensuite été valablement désigné comme lectotype par LAMAS (1998).

Cependant, ce lectotype femelle ne semble pas être le plus représentatif de l'entité que l'on peut actuellement interpréter comme cette sous-espèce d'*H. elevatus*, mais il faut tenir compte du fait que les femelles sont généralement moins « stables » phénotypiquement que les mâles et qu'il existe toujours potentiellement un certain degré de flux génique et/ou d'introgression entre populations plus ou moins proches d'*Heliconius*.

Pour clarifier les doutes sur l'interprétation du phénotype d'*H. e. tumatumari*, le lectotype et les syntypes les plus probables de ce taxon sont figurés pour comparaison avec l'holotype et la plupart des paratypes d'*H. e. sonjae*.

Il résulte de l'analyse comparative des phénotypes des sous-espèces *tumatumari* et *sonjae* la mise en évidence d'un chevauchement morphologique dans leur plage raisonnable de variation. Nous procédons ensuite formellement à la mise en synonymie du taxon *sonjae* **n. syn.** avec *tumatumari* Kaye, 1906.

Keywords. — Akayma – Auyán Tepui – *roraima* – *sonjae* – *tumatumari* – Endemism – Tumatumari – Roraima.

Abbreviations. Worldwide institutional and private collections, containing specimens examined for the present work, are housed in the following:

AFN	Andrew F. E. Neild, Wheathampstead, UK.
MB	Mohamed Benmesbah, Toulouse, France.
MC	Mauro Costa, Caracas, Venezuela.
MGCL-FLMNH	McGuire Center for Lepidoptera & Biodiversity, Gainesville, USA.
MIZA	Museo del Instituto de Zoología Agrícola, Facultad de Agronomía, Universidad Central de Venezuela, Maracay, Venezuela.
MNHN	Muséum national d'Histoire naturelle, Paris, France.
MUSM	Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, Lima, Peru
NBC	Naturalis Biodiversity Center, Leiden, The Netherlands.
NHMUK	The Natural History Museum, London, UK.
USNM	National Museum of Natural History, Smithsonian Institution, Washington, USA.
ZMHU	Zoologisches Museum der Humboldt-Universität, Berlin, Germany

HT = Holotype, **LT** = Lectotype, **OD** = Original description, **PLT** = Paralectotype, **PT** = Paratype, **TL** = Type locality

Terminology of wing venation follows the Comstock-Needham nomenclature system (Miller, 1970).

Family **Nymphalidae** Rafinesque, 1815

Subfamily **Heliconiinae** Swainson, 1822

Tribe **Heliconiini** Swainson, 1822

Genus ***Heliconius*** Kluk, 1780

Introduction

Several pieces of evidence indicate that the Auyán Tepui Massif, located in the southeast of Venezuela, is likely to be a highly endemic subunit within the Pantepui biogeographic Province itself (Costa *et al.,* 2019 c); its physiographic condition of isolation with respect to the Sierra de Lema and to the Gran Sabana has allowed the conservation of a significant number of endemic taxa living in its highest areas (Costa *et al.*, 2014 a, b, 2016, 2017, 2018, 2019 a, b, c ; Viloria & Costa, 2019 ; Costa *et al.*, 2020, 2021 a, b, 2022, 2023).

On our first expedition to Auyán Tepui (2012) we found a specimen of *Heliconius elevatus* Nöldner, 1901, similar to *H. e. roraima* Turner, [1967], but with some distinctive characters. Over the following four expeditions (2013, 2015, 2017 and 2019) we managed to assemble a series of twenty-four specimens with near identical and constant characteristics, allowing us to recognize a new subspecies, which we describe below.

Heliconius elevatus jigginsi Costa & Neild, **n. ssp.**

< https://zoobank.org/NomenclaturalActs/DBEABB54-CB76-408E-BB0A-DAB339564109 >

Holotype ♂ (fig. 1 a, b). VENEZUELA, Bolívar, Auyán Tepui, entre Guayaraca y El Danto, 1400 m, 12-I-2017. M. Costa & M. Benmesbah *leg. In* MIZA. (DNA # 22066B11, N. Grishin)

Paratypes (14 ♂, 9 ♀). Same data as the holotype, except:

1 ♂, 1300 m, 27-XII-2012. M. Costa *leg. In* MIZA; 1 ♂, 1400 m, 3-IV-2015. M. Costa *leg. In* MB (gen. prep. # MB-0404); 2 ♂, 4-IV-2015. M. Costa *leg. In* MC; 1 ♂, 1300 m, 11-I-2017. M. Costa & M. Benmesbah *leg. In* NHMUK (DNA # NE20-14, N. Rosser); 1 ♂, 1400 m, 15-I-2017. M. Costa & M. Benmesbah *leg. In* MC; 1 ♂, 1300 m, 20-I-2017. M. Costa & M. Benmesbah *leg. In* NHMUK (DNA # NE20-15, N. Rosser); 1 ♂, 1100 m, 21-I-2017. M. Costa & M. Benmesbah *leg. In* MC; 1 ♂, 1300 m, 28-I-2017. M. Costa & M. Benmesbah *leg. In* NHMUK (DNA # NE20-16, N. Rosser); 3 ♂, 1400 m, 27-I-2019. M. Costa & M. Benmesbah *leg. In* AFN, MC and MIZA; 2 ♂, 1400 m, 28-I-2019. M. Costa & M. Benmesbah *leg. In* MB and MIZA; 3 ♀, 1350 m, 22-III-2013. M. Costa *leg. In* MIZA (2) and AFN (1); 1 ♀, 1400 m, 4-IV-2015. M. Costa *leg. In* MC; 1 ♀, 1400 m, 12-I-2017. M. Costa & M. Benmesbah *leg. In* MC; 1 ♀, 1400 m, 13-I-2017. M. Costa & M. Benmesbah *leg. In* MB; 1 ♀, 1400 m, 20-I-2017. M. Costa & M. Benmesbah *leg. In* MB, (gen. prep. # MB-0405); 1 ♀, 1400 m, 27-I-2019. M. Costa *leg. In* MC; 1 ♀, 1400 m, 28-I-2019. M. Costa & M. Benmesbah *leg. In* MIZA.

Diagnosis. The ventral side of the hindwings of the new subspecies, with a red costal stripe and a yellow stripe (just below Sc+R_1), confirms conspecifity with *H. elevatus*. Despite the large number of subspecies in this taxon, the absence of red hindwing rays in *Heliconius elevatus jigginsi* **n. ssp.** simplifies the diagnosis, being comparable only with the following subspecies:

– *H. elevatus roraima* Turner, [1967] (TL: Guyana)
– *H. elevatus tumatumari* Kaye, 1906 (TL: Guyana)
– *H. elevatus sonjae* Neukirchen, 1997 (TL: Brazil, Pará)

The new subspecies (fig. 1, 2 a) differs from *H. e. roraima* (fig. 2 b) in the reduction of the yellow spot in Cu_1-Cu_2 on the forewings and

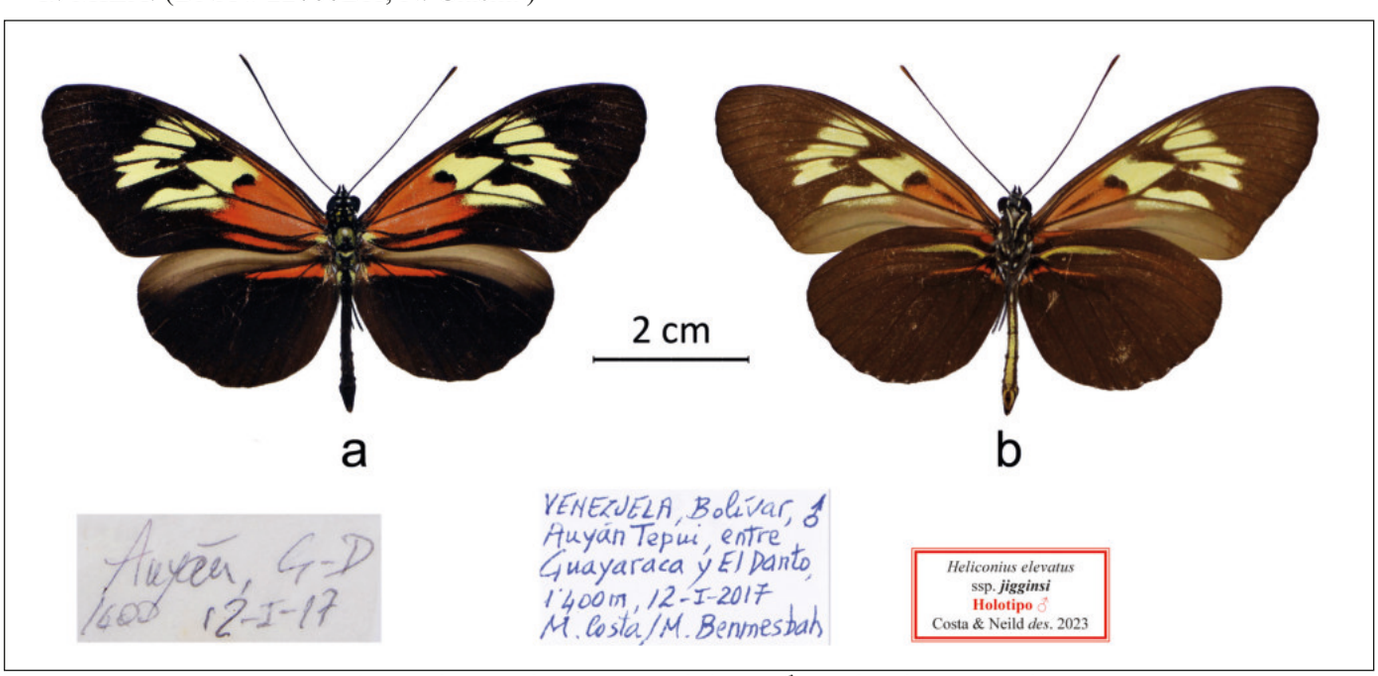

Fig. 1. — *Heliconius elevatus jigginsi,* holotype ♂. – **a**, dorsal. – **b**, ventral.

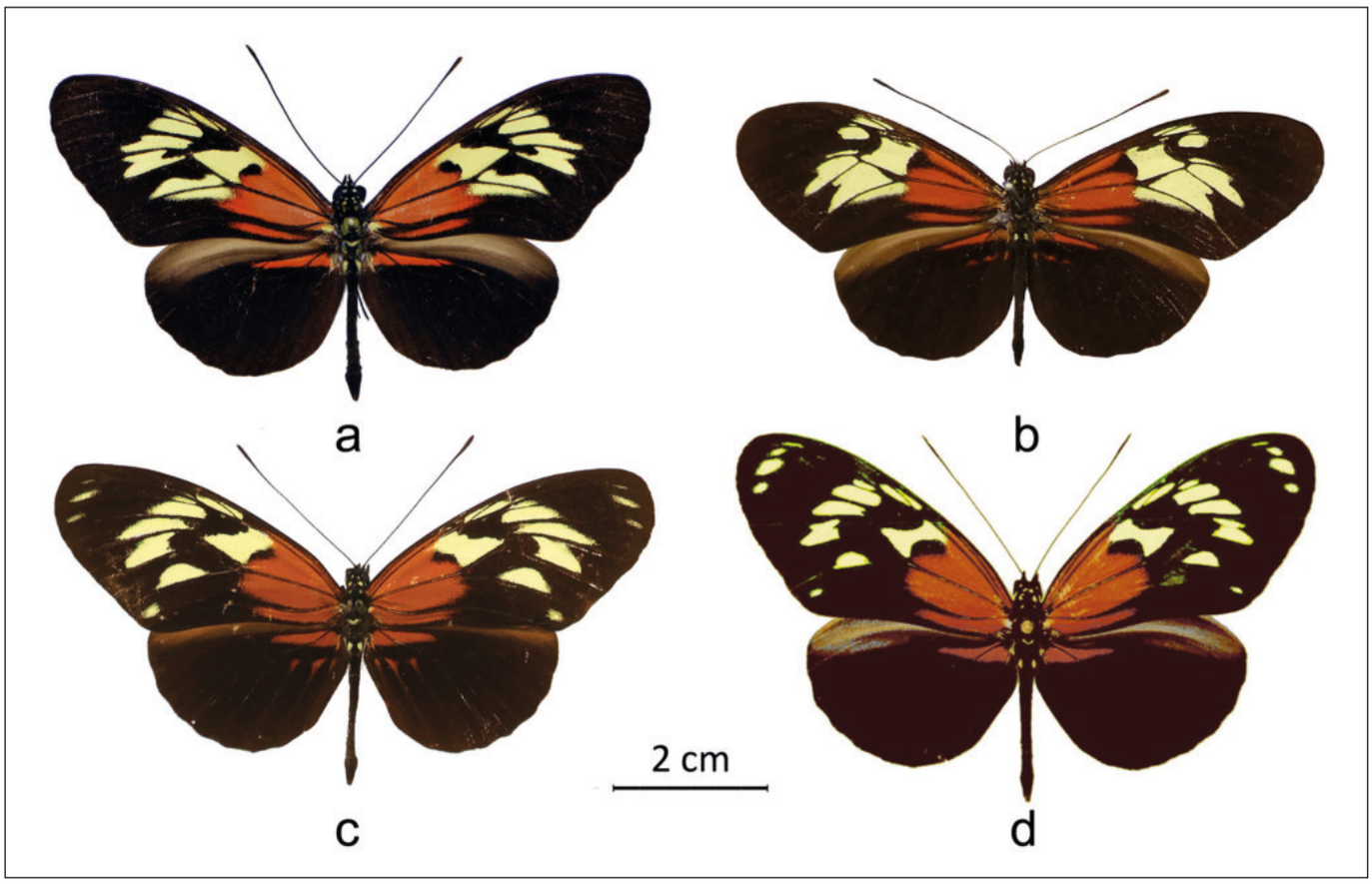

Fig. 2. — Comparison between males of subspecies of *Heliconius elevatus*. – **a**, *H. elevatus jigginsi* n. ssp. HT ♂. – **b**, *H. elevatus roraima* HT ♂, Roraima, B. Guyana, H. Whitely (NHMUK). © Trustees of the NHMUK. – **c**, *H. elevatus tumatumari* PLT ♂, Br. Guiana, Parish // Det. W. J. Kaye // Ex. Grose Smith, 1910 // BMNH (E) # 787070 (NHMUK). © Trustees of the NHMUK. – **d**, *H. elevatus sonjae* HT ♂, Óbidos, Pará, Brazil, III-1993 (ZMHU).

in the set of postdiscal yellow spots that form a wider and more uniform band compared to that of *H. e. roraima*. It differs from *H. e. tumatumari* (fig. 2 c) and *H. e. sonjae* (fig. 2 d) in the presence of a yellow streak below Cu_2 (absent in *tumatumari* and *sonjae*) and by the absence of the subapical and tornal forewings spots in the males (see discussion for details). The females of the new subspecies are variable in this last character (see "variations" section), denoting certain sexual dimorphism, something unusual in all subspecies of *H. elevatus.*

Description

Male (HT, fig. 1, fig. 2 a; PTs, fig. 3 a-c). Forewing length: HT = 41.5 mm (type series 36.0-42.0 mm, average = 39.5 mm, n = 15). Males similar in most respects to *H. elevatus roraima*, as described by Turner ([1967]), except the forewings habitus, which differs as follows:

– the yellow post-discal band is wider and more uniform in the new ssp. (narrow and irregular in *roraima*);

– the yellow patch in Cu_1-Cu_2 occupies only the lower half of the space, resting on Cu_2 and touching the cell (complete and delimited by both veins in *roraima*).

Female (PTs, fig. 3 d-f). Forewing length: type series 34.5-42.0 mm, average = 39.0 mm, n = 9). Similar to males, but with apical and tornal spots of variable size, rarely absent (see "variations" section).

Variations in *Heliconius elevatus jigginsi* n. ssp.

Males (fig. 3 a-c) are relatively stable. Some variation has been noted in the yellow patch in space Cu_1-Cu_2: in one male of 24 paratypes (fig. 3 b) this spot is almost complete. In about 50 % of the male paratypes the lower yellow patch in Cu1-Cu_2 is accompanied in the upper part of the cell by a tiny stripe just below Cu_1 (fig. 3 a). Some male paratypes (2 of 15, fig. 3 c) display some scattered subapical yellow scales, a character absent in the other 13 males of *H. e. jigginsi* **n. ssp.**

Females (fig. 3 d-f) are variable in the forewing subapical and tornal spots: these spots can be completely absent (as in the males), barely marked (fig. 3 d), evident (fig. 3 e) or even strongly marked (fig. 3 f). The broad, fuzzy shape of the subapical spots (when present) are distinct from those of *H. e. tumatumari* and *H. e. sonjae* that are rather slender, elongated and well defined (fig. 4).

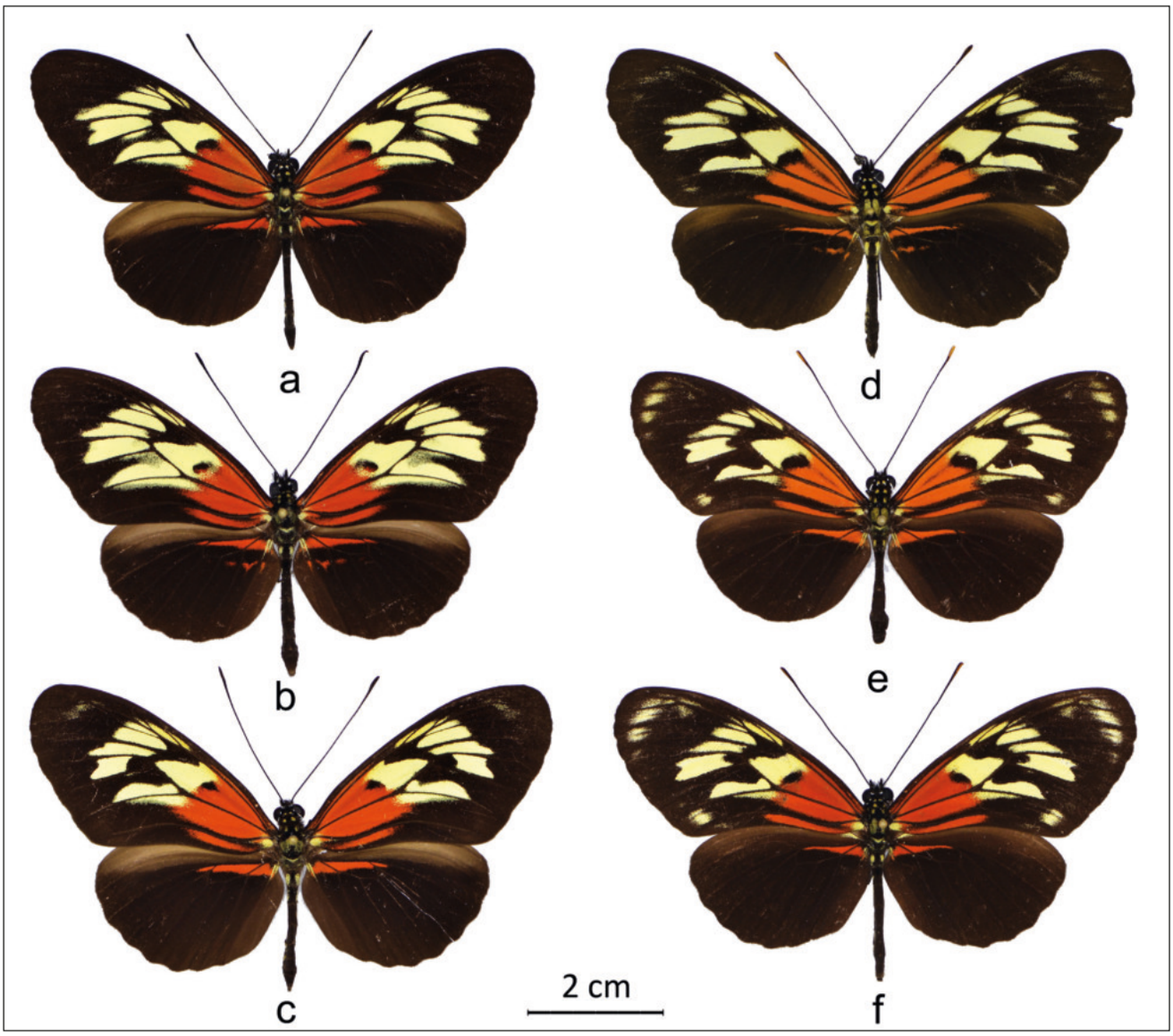

Fig. 3. — *Heliconius elevatus jigginsi* **n. ssp.**: variations in males and females (all paratypes from Venezuela, Bolívar, Auyán Tepui, entre Guayaraca y El Danto, 1,400 m). – **a**, PT ♂, 15-I-2017. M. Costa & M. Benmesbah *leg. In* MC. – **b**, PT ♂, 27-I-2019. M. Costa & M. Benmesbah *leg. In* MC.– **c**, PT ♂, 4-IV-2015. M. Costa *leg. In* MC. – **d**, PT ♀, 28-I-2019. M. Costa & M. Benmesbah *leg. In* MIZA. – **e**, PT ♀, 28-I-2019. M. Costa & M. Benmesbah *leg. In* MC. – **f**, PT ♀, 27-I-2019. M. Costa & M. Benmesbah *leg. In* MC.

Fig. 4. — Differences in the shape and definition of the apical and tornal forewing spots in *H. e. tumatumari/sonjae* and *H. e. jigginsi* **n. ssp.**: left, typical forewings of *H. e. tumatumari/sonjae* (males and females); right, a spotted female of *H. e. jigginsi* **n. ssp.** (typical males lack spots).

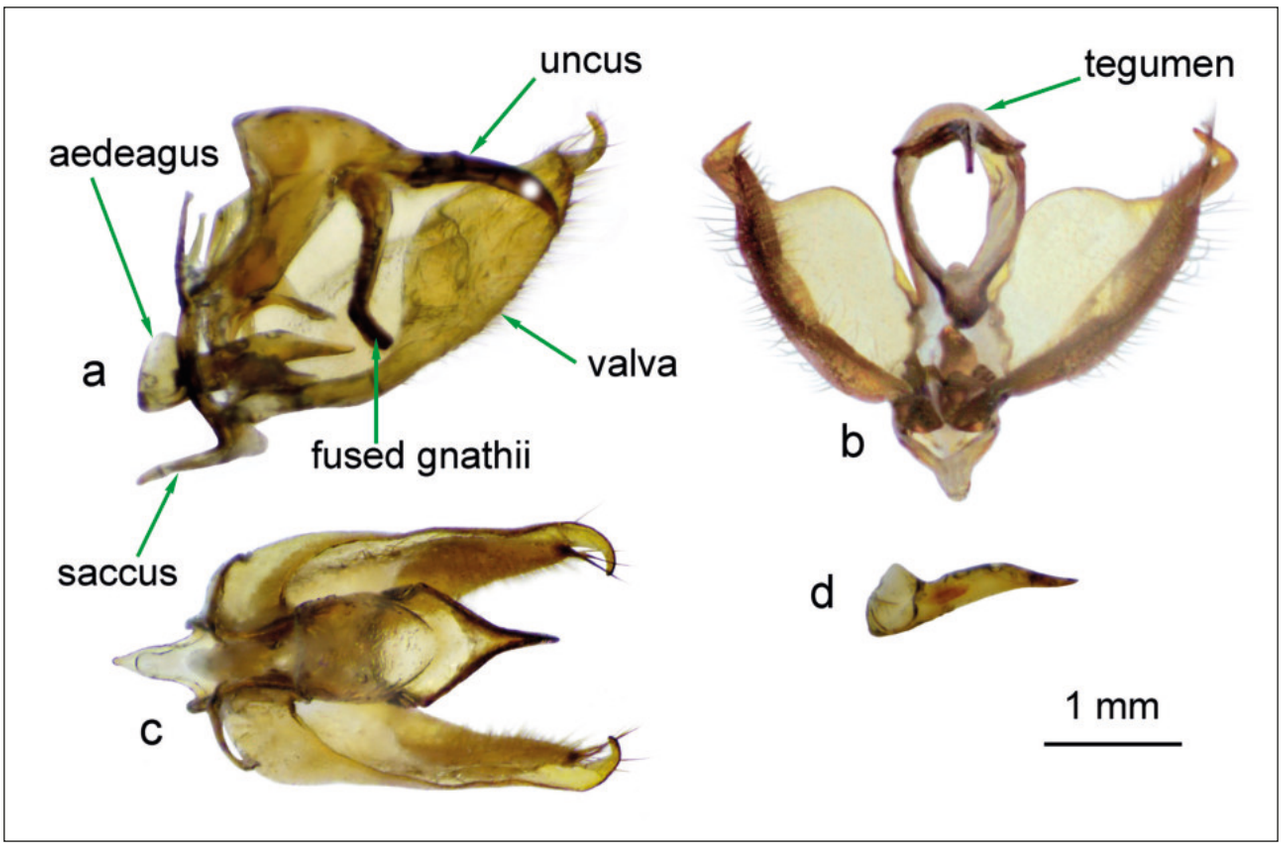

Fig. 5. — Male genitalia of *Heliconius elevatus jigginsi* **n. ssp.** – **a**, lateral view (left valva removed). – **b**, posterior view (valvae slightly separated). – **c**, dorsal view. – **d**, lateral view of aedeagus (photographs by M. Benmesbah).

Genitalia. Male genitalia of *Heliconius elevatus jigginsi* **n. ssp.** are illustrated in fig. 5. Previous works depicting the genitalia of *H. elevatus* and related species include Holzinger & Holzinger, 1994; Eltringham, 1916; Emsley, 1963, 1965; Turner, [1967].

Distribution, habitat and ethology of *Heliconius elevatus jigginsi* n. ssp.

Heliconius elevatus jigginsi **n. ssp.** is known only from the southern slopes of Auyán Tepui, where the type series comes from elevations between 1,100 and 1,400 m (figs. 6, 7 and 11). Some specimens have been observed up to 1,500 m, the upper limit of the local cloud forest, which is composed by trees of considerable height. From this point upwards the tepuian vegetation begins, comprising mainly shrubs and low plants, and in this very different habitat *H. e. jigginsi* **n. ssp.** has never been observed. Like *H. e. roraima*, whose great affinity is also confirmed by the DNA sequence clustering of both taxa, it is adapted to premontane and montane habitat, while all the other subspecies of *H. elevatus* from northeastern South America (*tumatumari, sonjae* and *bari* Oberthür, 1902) are distributed in the lowlands.

Brown & Fernandez (1985 : 54) had predicted the presence of *H. e. roraima* in the nearby Sierra de Lema (north of the Gran Sabana), despite not having any reports from that area at the time. Indeed, during our recent expeditions to the Sierra de Lema we finally confirmed this prediction, encountering specimens on the slopes of Ptarí and Sororopán Tepuis. One of them, with an incipient reduction of the yellow patch in Cu_1-Cu_2, suggests some genetic influence from *H. e. jigginsi* **n. ssp**. It is not surprising that the new subspecies differentiated in the Auyán Massif due to its relatively more pronounced isolation within the Pantepui Province itself (Costa *et al.,* 2019 c). One would also expect to find *H. e. roraima* (or perhaps an undescribed subspecies) in the almost unexplored Chimantá Massif (western Gran Sabana) and, maybe, on the heights of the extensive Cerro Guaiquinima to the east of Auyán Tepui.

On the ascent to Auyán Tepui, from Guayaraca (1,000 m, fig. 7) towards El Danto (1,500 m), the trail crosses the cloud forest of the southern slopes, and the new subspecies begins to appear more frequently above 1,300 m. It is not uncommon along stream edges and near flowering plants, and individuals can be attracted to lures of red cloth ; over the five expeditions made to Auyán Tepui,

FIG. 6. — Southwestern slopes of Auyán Tepui, habitat of *Heliconius elevatus jigginsi* **n. ssp.** at elevations between 1,100 and 1,500 m (photograph by M. COSTA).

this forest was crossed ten times and, even though collecting for only a few hours each time (and not always with good weather), a total of 24 specimens was obtained. When lures are used to attract it, this butterfly may appear unexpectedly and the collector has to be very well prepared to catch it in flight on their first (and probably only) attempt, since the insect can very quickly become aware of the deception and rapidly flies to the tree canopy. However, if flowers are found in some of the streams that the path crosses, the capture is much easier. We suspect *H. e. jigginsi* **n. ssp.** flies mostly in the upper forest strata and only occasionally comes down when attracted to flowers or other lures. For logistical reasons this slope is normally crossed between 11 am and 2 pm when ascending or descending the massif. These are the hottest hours of the day and, on sunny days, we have almost always found this butterfly. Under normal conditions *Heliconius elevatus jigginsi* **n. ssp.** flies

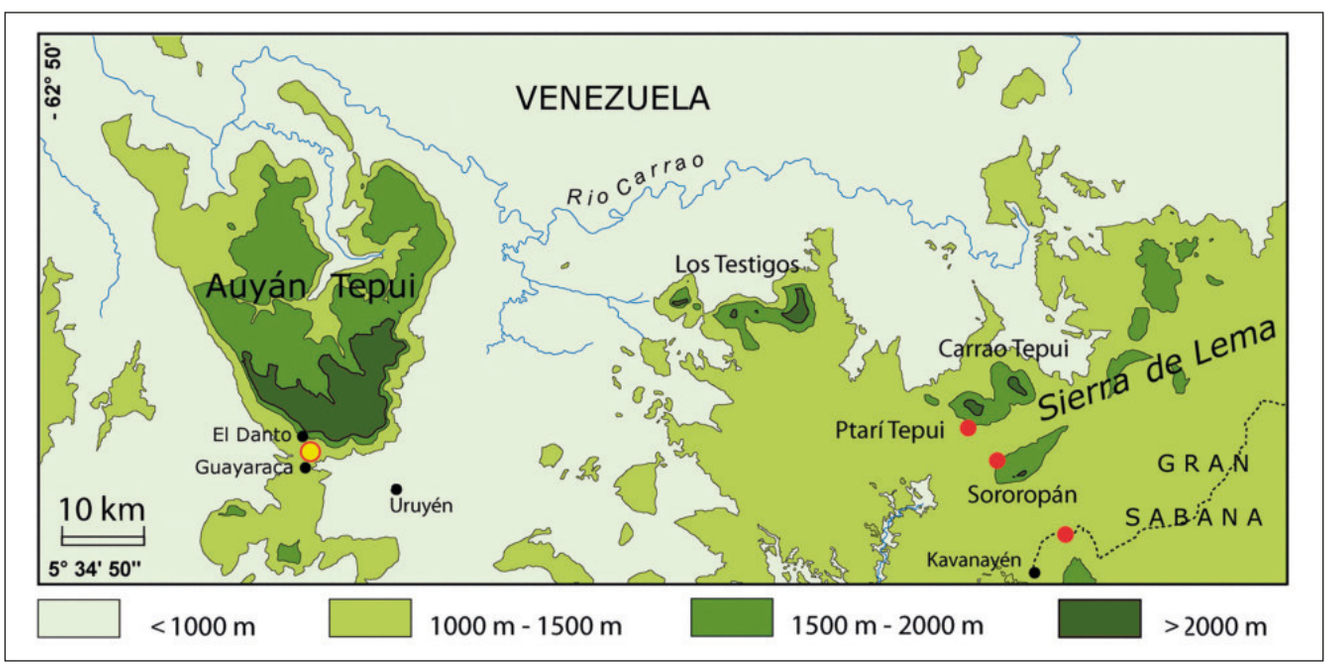

FIG. 7. — Auyán Tepui, type locality of *Heliconius elevatus jigginsi* **n. ssp.** (yellow circle outlined in red). The red circles on the Sierra de Lema correspond to collecting sites for *H. e. roraima* (map by Gilles SÉRAPHIN).

slowly and with pauses (for example, near flowers), but it becomes very fast and erratic if disturbed.

Etymology. Dedicated to Chris Jiggins in recognition of his enormous contribution to the study of *Heliconius* butterflies (see Jiggins, 2017, and references in Lamas, 2023).

Discussion

At first sight the habitus of *Heliconius elevatus jigginsi* **n. ssp.** resembles that of *H. e. roraima*, *H. e. tumatumari* and *H. e. sonjae*, from which it differs, however, by the particular characters described in the diagnosis. Upon obtaining the first specimen in 2012, we initially thought that it was a variety of *H. e. tumatumari* itself. However, if so, the distribution of *tumatumari* would seem unusual, being discontinuous not only regarding the area occupied but also its elevation. In fact, no subspecies of *H. elevatus* has ever been found in the lowlands of southeastern Venezuela from the Caura river eastwards, including the Orinoco River, to the lower slopes of the Sierra de Lema).

Only the subsequent collection of a series of 24 specimens on Auyán Tepui and the discovery of the presence of *H. e. roraima* in elevated areas of the Sierra de Lema motivated us to conduct a detailed study of the *tumatumari* and *sonjae* phenotypes. This allowed us to define the characters that differentiate the new subspecies. To this end we searched for all available information on the phenotypes and the distributions of the subspecies *roraima, sonjae* and *tumatumari.*

Heliconius elevatus roraima (HT fig. 2 b). Described from Mt. Roraima, its distribution extends westwards across much of the Gran Sabana plateau, where it is relatively common and stable in its phenotype. Unlike the other eastern subspecies of *H. elevatus* such as *tumatumari, bari* and *sonjae*, which inhabit areas of very low elevation, *H. e. roraima* is adapted to montane areas between 900 and 1,600 m elevation. To the southwest of Roraima it is not uncommon to find it in San Francisco de Yuruaní, Quebrada de Jaspe, Santa Elena de Uairén and along the forested road that leads to the mining town of Icabarú, where the high plateau of the Gran Sabana ends in its southwestern extremity. It also extends to the north of the Gran Sabana reaching the Sierra de Lema (see above, distribution section), and likely reaches other unexplored areas of the plateau. Males are similar to the females and both lack the forewing apical and tornal yellow spots.

Heliconius elevatus sonjae (Holotype fig. 2 a and 9 b; PTs fig. 8 a-l). Described from Óbidos, Brazil, this subspecies is widely distributed in Pará state, between the lower Amazon River and the Guianas. Its phenotype shows some variations and considering the remarkable number of specimens in collections, it is not a rare taxon. According to the OD, Neukirchen (1997) presented the following diagnosis to differentiate *sonjae* from *tumatumari*:

Whereas the sulfur-yellow outer spots of the discal band in tumatumari *cluster very densely around the distal end of the discoidal cell, in* sonjae *n. ssp., they form a loose annular band, shortened proximally by a half. The dark background color always clearly separates this annular band from the yellow patch inside the cell, which also appe ars halved. As with* tumatumari*, the yellow apical spots are quite variable in terms of number and size… The female of the new subspecies does not present differences with respect to the characteristics of the male.*(*)

(*) Neukirchen, 1997: *Während die äußeren schwefelgelben Flecken der Diskalbinde bei* tumatumari *sehr dicht um das distale Ende der Diskoidalzelle gruppiert sind, bilden sie bei* sonjae*, n. subsp. proximal um die Hälfte verkürtz, eine aufgelockerte Ringbinde. Die dunkle Grundfarbe trennt diesen Ring stets deutlich vom gelben Makel innerhalb der Zelle, der ebenfalls um die Hälfte verschmälert in Erscheinung tritt. Wie bei* tumatumari *sind die gelben Apikalfleckchen recht variabel bezüglich ihrer Anzahl und Größe… Das Weibchen der neuen Subspecies weist keine Unterschiede im Vergleich zur Merkmalsausprägung des Männchens auf.*

Neukirchen (1997) does not mention anything about the reduced "crescent" shaped yellow spot in space Cu_1-Cu_2, which seems to be another important distinctive character compared with the corresponding elongated spot of the *tumatumari* LT (fig. 9 a); however, as explained later, the *tumatumari* female lectotype is the only specimen, among those examined by Kaye for the OD, with such a kind of spot. Neukirchen probably also noticed this and therefore did not want to recognize it as a valid character. Both males and females of *tumatumari* and *sonjae* have yellow elongated and well-defined yellow apical and tornal forewing spots, variable in number and size.

Fig. 8. — *Heliconius elevatus sonjae* paratypes: all from Brazil, Pará, Óbidos (in MGCL-FLMNH, ex Neukirchen coll.). – **a**, ♂, III-1993 (voucher code: vc 9641-Z96). – **b**, ♂, 1985 (vc 0753-Z86). – **c**, ♂, III-1993, (vc 9641-Z96). – **d**, ♂, II-1986 (vc 0754-Z88). – **e**, ♂, IX-1988 (vc 5830-Z92). – **f**, ♂, III, 1994 (vc 7743-Z94). – **g**, ♂, II-1986 (vc 0745-Z88). – **h**, ♀, III-1993 (vc 9640-Z96). – **i**, ♀, 1986 (vc 5829-Z92). – **j**, ♀, II-1986 (vc 0752-Z89). – **k**, ♀, 1986 (vc 0755-Z88). – **l**, ♀, III-1993 (vc 9642-Z96) (photographs by K. Willmott).

In addition to Óbidos, this taxon has also been reported from Santarém (Neil Rosser and Fabio Vitale, pers. comms.). Its presence on the south bank of the Amazon river seems most improbable, and we suspect that these records are based on specimens collected close to the city but on the north bank.

Heliconius elevatus tumatumari (Lectotype fig. 9 a; probable syntypes, now paralectotypes, fig. 9 c-n). Kaye (1906) did not explicitly designate a holotype for *tumatumari* in his original description, but illustrated a female specimen from "Fort Akayma, Demerara River" (Guyana). It has not been easy to find the location of Fort Akayma, a locality referred to on other butterfly specimens labels collected in Guyana at the beginning of last century; however, in Harrison (1908), the two names "*Akaima* (= *Akyma*)" appear on p. 308 (Index and synonyms of names of places, British Guiana), and in Cole *et al.* (2013) this toponym (Akaima) is precisely located at 05°53'N – 59°18'W. Currently, on this site there is a bauxite mine called Akyma, which is located south of Christianburg on the left bank of the Demerara River. When Europeans settled in Guyana in the 16th and 17th centuries, they built riverside forts to protect their settlements from intruders and we surmise there was an old fort nearby, hence the name Fort Akayma.

Lamas (1998 : 118) designated the specimen pictured in Kaye (1906) as the lectotype of *H. elevatus tumatumari* (currently conserved in MGCL). This lectotype is valid for the following reasons:

1. The new taxon (species) was described by Kaye from "British Guiana", without further locality data, no indication of sex, and obviously based on examination of more than one individual ("*very few specimens seen*").

2. The written description was accompanied by an unnumbered photograph of the upperside of an unsexed individual, reproduced on pl. II of *The Entomologist* 39 (514), published in March 1906. In the text (p. 53) that image was cited as "fig. 2").

3. A female specimen exactly matching the individual illustrated on the above-mentioned pl. II, [fig. 2] was eventually found by Lamas in the MGCL collection and identified as the specimen of the taxon described and illustrated by Kaye as *H. tumatumari*. That specimen carried four labels, as follows: (1) "BRIT. GUIANA."; (2) "Fort Akayma / Rio Demerara"; (3) "Type"; and (4) "*H. tumatumari* / (type)".

4. That specimen was the most logical choice for its designation as a lectotype, since it was undoubtedly a syntype, had more precise locality data, and was accurately illustrated in a photograph and captioned from "British Guiana" (albeit without further locality data).

According to Kaye (1907, 1916) and Turner ([1967]), *H. e. tumatumari* is not a common taxon (only six specimens were obtained in a six year span (Kaye, 1907) by its collector C. B. Roberts and it is certainly present in the Potaro river basin of Guyana (Kaye, 1916). Due to its scarcity, highlighted by the presence of only a single live photo on the internet (from Atta Rainforest Lodge, see front cover for details), we have searched for more specimens and we found only 23: 12 in NHMUK, 9 in MGCL, 1 in USNM and 1 (location unknown) represented in Turner, ([1967]). Except for the USNM specimen (Kanuku Mts., fig. 10 a), the great majority of the others were collected in the first decade of last century (or earlier) and among them there are probably several of the syntypes examined by Kaye. We deduce this from the following considerations, despite the fact that most specimens have no date of capture, and only a few labels indicate their collection site:

MGCL. Of the nine existing specimens from the Kaye collection, five are labeled "Tiger Creek, Potaro River, B. Guiana (C. B. Roberts)" [5°17'32"N 59° 2'25"W] and another one "Tumatumari, Potaro R., Guiana"; two specimens do not have data except the locality (Guiana) and the collector (H. Parish). The final one is the lectotype mentioned above (Fort Akayma, Demerara River). Roberts collected butterflies for Kaye mostly along the Potaro road, near Tumatumari (Kaye, 1907 : 411, "*… a forest road stretching for 16 miles back from the Potaro river about 30 miles above its confluence with the Essequibo*").

NHMUK. Of the twelve specimens, five are from Grose-Smith's collection and were collected by Herbert Simpson Parish (°1870 – † 1957), a Canadian entomologist who made several expeditions to South America. The collection of Henley Grose-Smith (°1833 – † 1911) was acquired in 1910 by John James Joicey's "Hill Museum" and later (in 1934) transferred to the NHMUK. All five specimens bear the label "Det. W. J. Kaye", which indicates that they were examined and personally identified by this author. They were certainly collected before 1910 and likely, some or all of them, prior to 1906. In Alexander (1959) there is a chronological account of Parish's collecting trips, and it turns out that he collected in British Guiana only twice before 1910: in 1899 and in 1908-1909. Grose-Smith passed away on January 15, 1911, and if Parish had collected all those *tumatumari* specimens on his second expedition, it seems unlikely that they would have been added to the Grose-Smith collection between 1909 and 1910. At that time, the shipment of specimens to Europe by sea usually took several months from the date of collection. In addition, as the collection was acquired in 1910 (before Grose-Smith's death), this suggest he may have already been in poor health and could no longer care for his collection. Therefore, we consider that it is highly probable that the five specimens are from Parisch's first expedition to Guyana, that is, they could be dated 1899 and Kaye was probably able to examine them prior to description of the new taxon, in which case all five are probably syntypes (now paralectotypes). It should be noted that Kaye visited the most important British museums (firstly the British Museum, now NHMUK) and private collections (including Godman's one) as indicated regularly in his writings (*e. g.*, Kaye, 1904). A further two specimens were donated to the British Museum by Herbert Jordan Adams (°1838 – † 1912) in 1912. At least one (but probably both) is certainly a syntype of *H. e. tumatumari*, taking into account what Kaye (1906) reports on the first page of his OD referring to the new taxon ("*The* Heliconius *of the* cybele *group* [= tumatumari] *has remained undescribed for years. It is obviously a rare species. Mr. H. J. Adams has the insect also without a name*"). Of the five remaining NHMUK specimens, two were examined by Kaye, and might

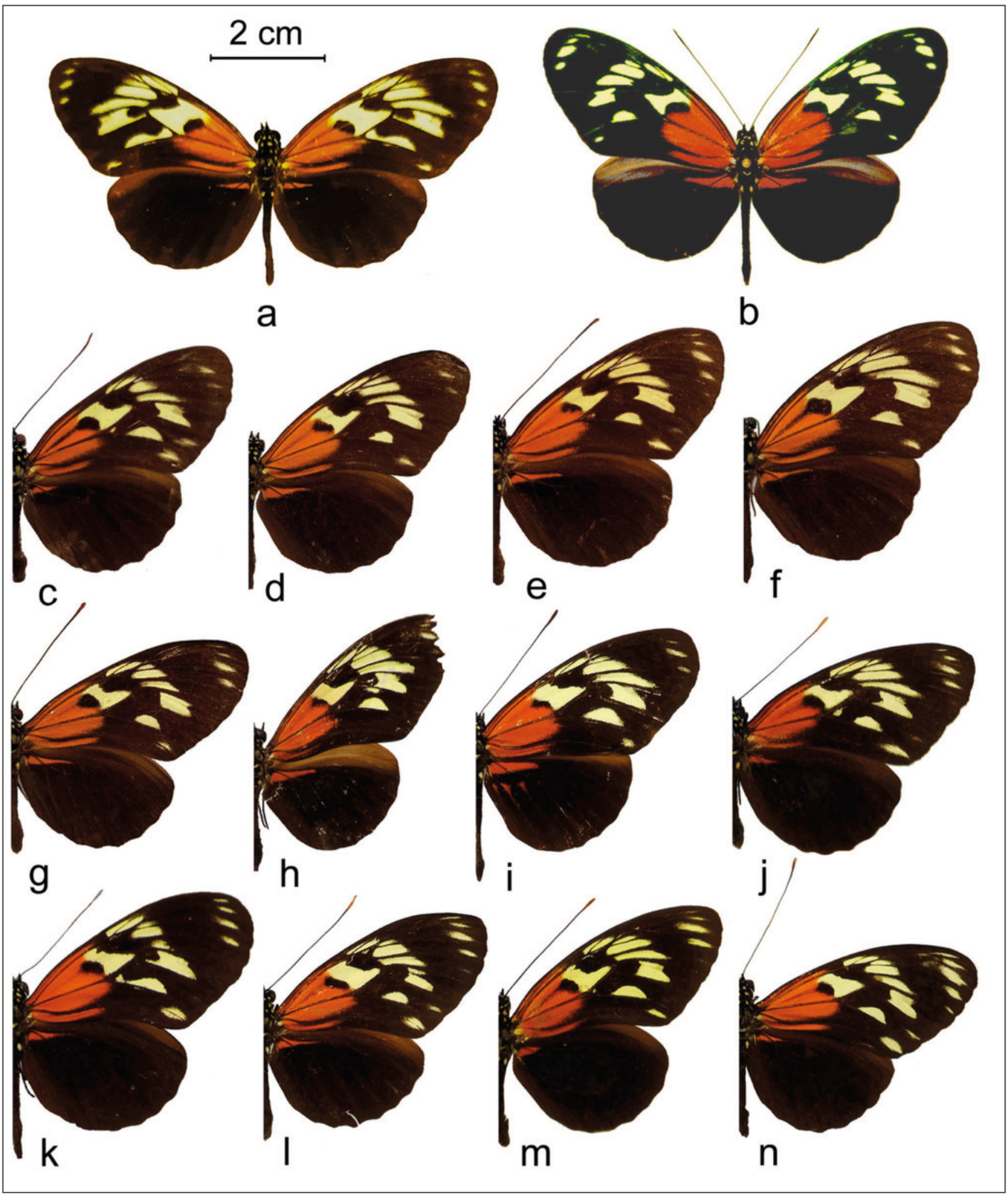

Fig. 9. — Lectotype of *H. elevatus tumatumari* Kaye, 1906, and holotype of *H. elevatus sonjae* Neukirchen, 1997, compared with probable syntypes and specimens subsequently examined by Kaye of *H. e. tumatumari* from British Guiana. – **a**, ♀, LT of *H. e. tumatumari*, Fort Akayma, Rio Demerara // Brit. Guyana (MGCL). – **b**, ♂, HT of *H. e. sonjae*, Óbidos, Pará, Brasilien, III.1993 (MGCL). – **c**, ♀, Tiger Creek, Tumatumari, 10-IX-(19)07, Brit. Guiana, C. B. Roberts (MGCL, specimen no. 140755). – **d**, ♀, same as (**c**), 3-X-(19)07 (MGCL, specimen no. 140757). – **e**, ♀, same as (**c**), (MGCL, specimen no. 140760). – **f**, ♀, same as (**c**), 25-VIII-(19)07 (MGCL, specimen no. 140759). – **g**, ♀, Br. Guiana, Parish // Ex. Grose-Smith, 1910 (MGCL, specimen no. 140758). – **h**, ♂, B. Guiana // Det. W. J. Kaye [BMNH(E) # 787069]. – **i**, ♂, B. Guiana, Parish // Det. W. J. Kaye // Ex. Grose-Smith, 1910 [BMNH(E) # 787070]. – **j**, ♀, same as (**i**) // Joicey Bequest. Brit. Mus. 1934-120 [BMNH(E) # 787079]. – **k**, ♀, same as (**i**) // Photographed by B. D'Abrera 77/78 [BMNH(E) # 787071]. – **l**, ♀, same as (**i**) // Joicey Bequest. Brit. Mus. 1934-120 [BMNH(E) # 787074]. **m**, ♀, same as (**i**) // Joicey Bequest. Brit. Mus. 1934-120 [BMNH(E) # 787077]. **n**, ♀, Demerara, Castell // 88 //Adams Bequest. B. M. 1912-399 [BMNH(E) # 787073]. All "BMNH" specimens (**h** – **n**)

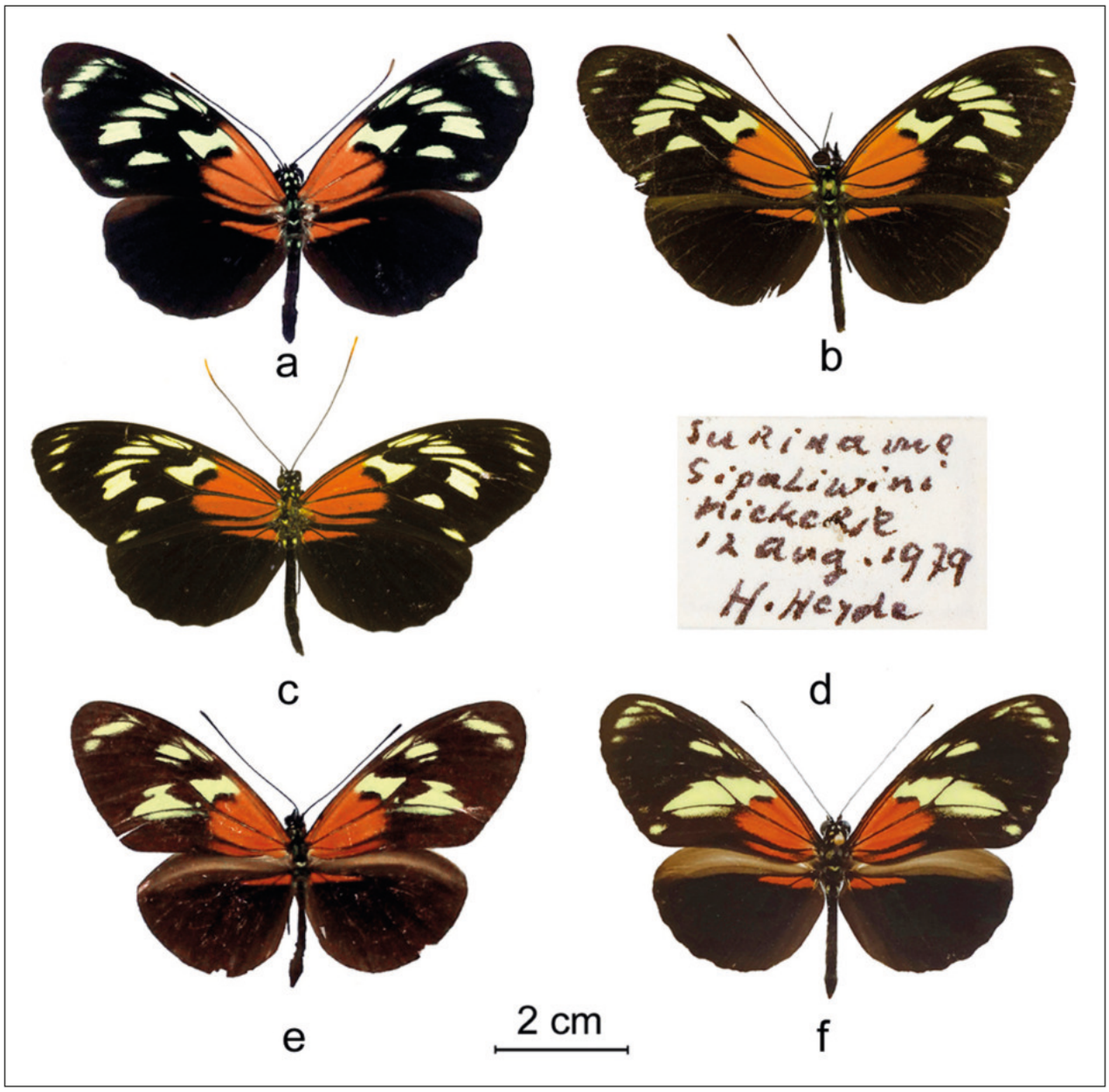

Fig. 10. — *Heliconius elevatus tumatumari* from Guyana and Suriname and two hybrids of *H. e. roraima*: – **a**, ♀, Guyana, Kanuku Mts., S. Rupununi, 20–28-IX-2000, 850-1,200 m. S. Fratello *leg. In* USNM. – **b**, ♂, Suriname, Blanche Marie Falls, 19-VIII-2001 (in coll. H.B.P.E. Gernaat). – **c**, ♀, Suriname, Sipaliwini, Nickerie, 12 Aug. 1979. H. Heyde (DB7770, NBC). – **d**, original label of the previous specimen. – **e**, ♂, hybrid (*roraima* × *tumatumari*) from Guyana, Kanuku Mts., S. Rupununi, 20–28-IX-2000, 850-1,200 m. S. Fratello *leg. In* USNM – **f**, ♂, hybrid (*roraima* × *luciana*) from Venezuela, Bolívar, Icabarú, X-1988. N. Flauger *leg. In* MGCL (ex coll. Neukirchen).

be considered syntypic, depending on when they were inspected: two were donated by J. J. Joicey (°1871 – † 1932) in 1934 (one of them bears the label "Det. W. J. Kaye"), one was donated by John Levick (°1864 – † 1941) in 1941, and the final two do not bear any data except "B. Guiana" (although one is also labelled "Det. W. J. Kaye").

USNM. Only two specimens exist, collected in recent times in southern Guyana (IX-2000) by Steve Fratello in the Kanuku Mountains, south of Potaro. One of these is *H. e. tumatumari* (fig. 10 a), while the other is probably an intergrade between *H. e. roraima* and *H. e. tumatumari* (fig. 10 e).

We have examined additional *tumatumari* material from Suriname: 1 ♂, Blanche Marie Falls (H. Gernaat coll., fig. 10 b); 10 specimens from Bakhuis Mountains (University of York, N. Rosser); four specimens from Sipaliwini savanna, 16–26-II-1975 (3 specimens) and 12–16-VIII-1979 (1 specimen), H. Heyde (NBC, ex-H. J. L. T. Stammeshaus coll.). Regarding this last specimen (fig. 10 c), it should be noted that its label (fig. 10 d) includes the name Nickerie. As Hajo Gernaat asserts (pers. comm.), "the locality labels state "Nickerie, Sipaliwini Savanna"; this is slightly ambiguous, as Nickerie, also called Nieuw

Nickerie, is a town in the northeast of Suriname close to the Atlantic Ocean. However, *H. elevatus* definitely does not occur there and there is only one place named Sipaliwini savanna, on the southern border with Brazil. Possibly, Nickerie was the name of a camping place there. So, personally I have no doubt about the locality as it is consistent with things we know already".

In summary, the evidence found indicates that:

1. The female lectotype of *H. e. tumatumari* (fig. 9 a) designated by Lamas (1988), even though it is the same specimen chosen for illustration by Kaye in the OD, is not the most representative of the typical phenotype of the specimens we have examined, which undoubtedly include several inspected by Kaye during his research. In fact, Kaye's OD stated that on the forewings ... *between veins 2, 3 there is a break with the ground colour, and just above vein 2 there is another yellow mark, sometimes elongated, and joining the yellow area with the cell*. It is worth emphasizing that, with reference to the shape of this yellow patch in Cu_1-Cu_2 (= space between veins 2 and 3), Kaye specified that it occasionally reaches the cell. In other words, Kaye surely examined specimens with a reduced patch, and these must have been the majority since he wrote that specimens with an elongated patch were only *sometimes* observed. From this also follows the implicit variability of this character and the possible reason why Neukirchen did not take it into account in his diagnosis of *sonjae.* We did not find any other *tumatumari* specimen with the patch in Cu_1-Cu_2 compact and elongated in such a way, except the female in fig. 9 k (also represented in D'Abrera, 1984, which, however, has this elongation almost broken into two patches connected only by a thin streak of yellow). Furthermore, the yellow patch in the forewing cell of the *tumatumari* lectotype is the widest among all the specimens examined, being comparable to that of *H. e. roraima*. For the reasons above, we consider that the type specimen of Kaye's *tumatumari* represents a rare case of individual variation, an aberration or an intergrade individual. In fact, it is the least representative specimen of the taxon *tumatumari* we have seen.

2. Examining the 23 specimens of *H. e. tumatumari* mentioned, it is clear that the average phenotype of the specimens from the NHMUK and those from the MGCL (ex coll. Kaye) is more similar to that of the holotype of *sonjae* (fig. 9 b) than to that of the *tumatumari* lectotype (fig. 9 a); the reduced width of the forewing postdiscal band and the length of the yellow patch inside the cell shortened by a half are characters also present in most specimens (including several probable syntypes) detected by Kaye, although with some slight variation (fig. 9). Likewise, examining the type series of *H. elevatus sonjae* (mostly represented in fig. 8) from the Neukirchen collection (now in MGCL), it becomes clear that it is impossible to differentiate them from most of the above-mentioned specimens of *H. e. tumatumari*.

3. The vast majority of these 23 specimens examined come from the lowlands of the "Potaro district" (Potaro-Siparuni Region), British Guiana (Kaye, 1907, 1916, and Turner [1967]) with a single additional record from the upper Demerara River (Fort Akayma); the others have no data. The "Potaro district" mentioned by Kaye lies near the eastern distribution limit of *H. e. roraima*, a subspecies that, although adapted to premontane and montane areas, can occasionally drop below 1,000 m elevation and may have genetic exchange with other taxa from the surrounding lowlands, in this case *H. e. tumatumari*. It is understandable then how phenotypically variable individuals can appear in the Potaro-Siparuni Region and more variable individuals can be found. We do have evidence of intergrade individuals in areas contiguous with the distribution limits of *H. e. roraima* (fig. 11): a supposed hybrid of *roraima* × *tumatumari* (fig. 10 e) collected by Steve Fratello in the Kanuku Mountains (south of the eastern distribution limit of *H. e. roraima*) is found in the USNM and another (*roraima* × *luciana* Lichy, 1960) is found in the MGCL (coll. Neukirchen, fig. 10 f) from Icabarú, a locality that represents the southwestern limit of the distribution of *H. e. roraima*.). This might be an interspecific hybrid, if *luciana* is truly a separate species (*Heliconius luciana* is distributed in the lowlands of Bolívar, in the eastern half of Venezuelan Amazonas state, and in central-northern Brazil, fitting perfectly into the range of other "*elevatus*" taxa, therefore possibly it could be a subspecies of *elevatus*). Likewise, we have a record of a *tumatumari* × *bari* hybrid collected by Neil Rosser in western Suriname (Bakhuis Mountains, 2014), a unique specimen with well-developed hindwing rays among 10 individuals of *H. e. tumatumari* collected in the same area.

Heliconius elevatus sonjae, n. syn.

In conclusion, after examining and illustrating herein a representative sample of the old and modern specimens of *H. e. tumatumari* from Guyana and Suriname, we have presented a clearer view of the average phenotype and variations of this taxon. Our comparative analyses of the facies of subspecies *sonjae* and *tumatumari* demonstrate an almost total overlap of phenotypical variation across most of their shared distribution range. The remarkable resemblance between specimens of the type series of *sonjae* and most of the probable *tumatumari* syntypes, as well as additional non-type material, all cast doubt on whether the (now lectotype) specimen illustrated in KAYE's description was the one that best represented his taxon *tumatumari*. The author himself stated that few specimens were known to him (KAYE, 1906), and of these, subsequent comments (KAYE, 1907, 1916) indicate most came from the "Potaro district" where occasional intermediate forms of this lowland taxon are found, due to its proximity to the type locality of *H. e. roraima*. As a result, KAYE (1906) was unable to make an informed decision regarding the most representative specimen

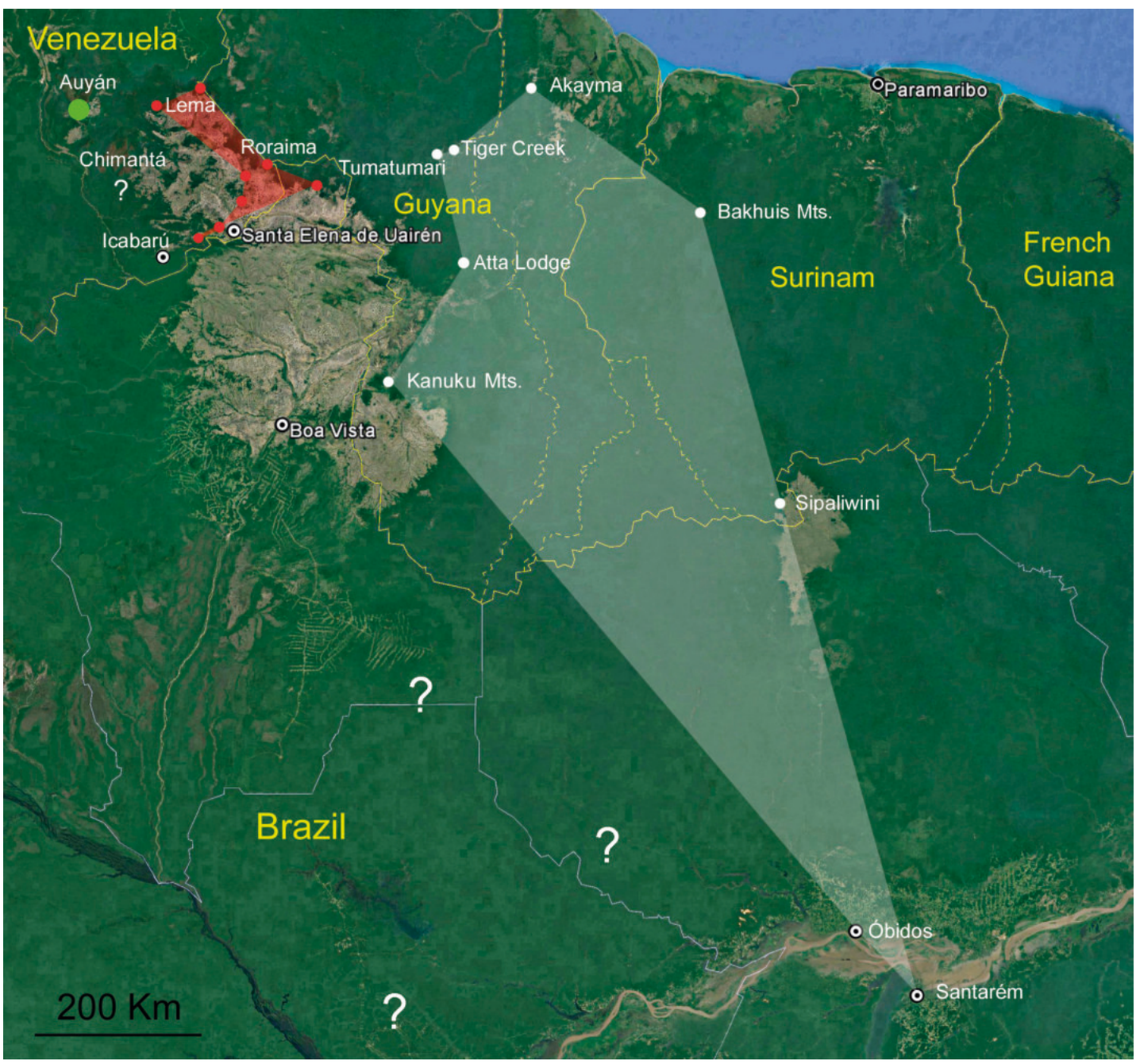

FIG. 11. — Known distribution of *Heliconius elevatus tumatumari* (white spots), *H. e. roraima* (red spots) and *H. e. jigginsi* **n. ssp.** (solid green circle).

for his new discovery. This unrepresentative lectotype, figured in the original description, resulted in confusion for subsequent investigators, and encouraged Neukirchen (1997) to describe *H. e. sonjae*. It is unlikely that this would have happened if Kaye (1906) had figured a more typical Guyanan specimen.

For all the reasons expounded in our treatise above, we consider it appropriate to formally synonymize *Heliconius elevatus sonjae*, **n. syn.** with *Heliconius elevatus tumatumari* Kaye, 1906, as was already proposed informally by Rosser *et al*. (2012) in their Appendix S1.

Conclusion

Following our synonymization of the taxon *sonjae* **n. syn**., we present the known distribution (fig. 11) of the three-remaining subspecies of *Heliconius elevatus* treated in this work: *H. e. tumatumari, H. e. roraima* and *H. e. jigginsi* **n. ssp**. Among all the subspecies of *H. elevatus* these are the only three that are devoid of orange/red hindwing rays and their distribution is contiguous. *H. e. tumatumari* is distributed in a very large lowlands area, while the other two (*roraima* and *jigginsi* **n. ssp.**) are adapted to montane habitats with much smaller distribution areas, especially the latter, for now known only from the Auyán Massif. The distribution map is based exclusively on records supported by photos and precise data (the putative hybrids are excluded). Despite the existence of a single imprecise record of *H. e. tumatumari* (Brown, 1979) from an unspecified site to the north of Manaus (Brazil), we have not found any other evidence from this region to date. Although we consider that in this large area (of more than 300.000 km^2) *H. e. tumatumari* may actually occur, we believe it best to recognize this range extension only when its presence is confirmed by factual reports.

Heliconius elevatus jigginsi **n. ssp.** increases the list of taxa that, until now, are considered endemic to Auyán Tepui, since none have yet been found in any other part of the Pantepui nor elsewhere:

– *Protopedaliodes profauna* Viloria & Pyrcz, 2000

– *Pedaliodes terramaris* Viloria & Pyrcz, 2000

– *Perisama tepuiensis* Attal & De Marmels, 2012

– *Archaeogramma claritae* Costa, 2014

– *Strymon auyana* Bálint, Benmesbah & Viloria, 2018

– *Memphis paulus clarae* Attal & Costa, 2019

– *Damas cervelina* (Orellana & Costa, 2019) (previously *Megaleas cervelina*, see Zhang *et al*., 2023)

– *Symmachia virgaurea souadae* Benmesbah & Costa, 2020

– *Dismorphia zathoe blanca* Costa & Attal, 2021

– *Dismorphia crisia eburnea* Benmesbah & Costa, 2021

– *Pyrrhopyge steyermarki* Orellana, Costa & Grishin, 2021

– *Emesis malik* Callaghan, Costa, Trujano-Ortega & Benmesbah, 2022

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