

Species delimitation in Neotropical *Hypochroma* moths (Geometridae: Ennominae): what to do when data are not congruent?

Delimitación de especies del género Neotropical de polillas *Hypochroma* (Geometridae: Ennominae): ¿Qué hacer cuando los datos no son congruentes?

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- Received: 26/08/2025
- Accepted: 19/04/2026
- Online Publishing: 26/08/2026

Citation: Murillo-Ramos, L. & Sihvonen, P. (2026). Species delimitation in Neotropical *Hypochroma* moths (Geometridae: Ennominae): what to do when data are not congruent? *Caldasia*, 48, e121794. <https://doi.org/10.15446/caldasia.v48.121794>

ABSTRACT

The current classification of the Neotropical moth genus *Hypochroma* (Lepidoptera: Geometridae) is problematic because it is based solely on wing patterns and colours, which do not allow unambiguous grouping of taxa. We sequenced historical DNA from type specimens of the three recognised species and examined both external and internal morphological traits to clarify species boundaries. Our species delimitation analysis results indicate that *Hypochroma* comprises two putative species, *H. marginata* and *H. brepharia*, which shows genetic overlap with *H. flavinigra* showing genetic overlap. Although mitochondrial genetic data support the existence of two species, the structures of the male and female genitalia showed no noticeable differences. We discuss the morphological traits that define species of *Hypochroma*. Based on our analyses, emphasizing molecular data, we synonymize *Hypochroma flavinigra* syn. nov. with *H. brepharia*. We highlight that additional natural history data and further analyses are necessary to confidently determine the sister group of *Hypochroma*.

Keywords: Colombia, Tropical dry forest, Ennominae, Insects

RESUMEN

Secuenciamos ADN antiguo de ejemplares tipo del género Neotropical *Hypochroma* (Lepidoptera: Geometridae) y examinamos rasgos morfológicos para clarificar los límites entre especies. Analizamos códigos de barras de ADN junto con un amplio conjunto de datos publicados sobre polillas geometridas y realizamos análisis de delimitación de especies. Nuestros resultados indican que *Hypochroma* comprende dos especies putativas, con *H. brepharia* y *H. flavinigra* mostrando solapamiento genético.

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Aunque los datos genéticos mitocondriales respaldan la existencia de dos especies, la disección de las estructuras genitales no reveló diferencias notables. Discutimos los caracteres morfológicos que definen las especies de *Hypochroma*. Con base en nuestra clasificación, sinonimizamos *Hypochroma flavinigra* syn. nov. con *H. brepharia*, reconociendo que se necesitan más datos de historia natural y análisis adicionales para determinar con certeza el grupo hermano de *Hypochroma*.

Palabras clave: Bosque Seco Tropical, Colombia, Ennominae, Insectos

INTRODUCTION

Studies on the systematics and taxonomy of Neotropical Geometridae moths using molecular and morphological data have increased in recent years (Bodner et al., 2012; Brehm et al., 2011; Brehm et al., 2013; Brehm et al., 2019; Joele et al., 2024; Murillo-Ramos et al., 2021; Strutzenberger et al., 2011, 2012; Strutzenberger et al., 2017), providing us with a better understanding of the phylogenetic relationships of diverse geometrid genera. Despite significant taxonomic progress, many genera remain poorly delimited, and their classifications are uncertain, with several unnamed clades (Brehm et al., 2019). At the species level, molecular data, specifically DNA barcodes, have opened up the possibility of unravelling hidden diversity (Hebert et al., 2003). When DNA barcodes are analysed in platforms such as BOLD Systems (Ratnasingham & Hebert, 2007), they have helped to speed up species inventories in poorly sampled Neotropical countries (Murillo-Ramos et al., 2021). Thus, DNA barcodes have become essential in the estimation of preliminary species diversity, species descriptions and taxonomy, especially in taxonomically long-neglected taxonomical insect groups.

The Neotropics are well known as a biodiversity hotspot (Meseguer et al., 2022), and geometrid moths are a species-rich insect group particularly diverse in this bioregion (Brehm et al., 2019). Within the geometrid subfamilies, the Ennominae are considered the most species-rich (Pitkin, 2002; Rajaei et al., 2022), which have been the focus of taxonomic studies in the last 20 years, e.g. (Joele et al., 2024; Parra & Hernandez, 2010; Ramos-Gonzalez et al., 2018; Scoble, 1995; Sepúlveda-Zuniga et al., 2016).

The Ennominae genus *Hypochroma* Herrich-Schäffer, 1855 was a monotypic genus, including the type species *H. brepharia* Herrich-Schäffer, 1855, until Pitkin (2002) transferred two species from “*Xanthoprepes*” Warren

[never validated by formal publication] to *Hypochroma* (see Scoble, 1999). Currently, it represents a small clade of Neotropical Ennominae with three valid species: *H. brepharia* Herrich-Schäffer, 1855, *H. flavinigra* (Warren, 1897) and *H. marginata* (Warren, 1900) (Rajaei et al., 2022; Scoble, 1999). This genus is narrowly distributed in the Neotropics, with the species found in Colombia and Venezuela (Pitkin, 2002). These moths are medium-sized, wingspan being between 25–30 mm, and they have a characteristic colouration of yellow with dark brown borders, without medial lines. Apomorphic characters defining the genus are found in the genitalia as follows: “the gnathos not expanded medially but with long rows of spines, the process of the aedeagus narrowest basally, and the vesica with a narrow-wrinkled strip; in the female: the signum small with partial dentate edge” (Pitkin, 2002). *Hypochroma* has been classified in Ourapterygini earlier, with a close relationship to *Eusarca* Hübner, 1813 (Pitkin, 2002). In a molecular phylogenetic analysis, it was recovered as part of the tribe Ennomini (which also included Ourapterygini, as suggested earlier by Beljaev (2008)), with an undescribed genus from Colombia to be the closest relative (Murillo-Ramos et al., 2019).

Here, we used morphological characters and molecular data to test the taxonomic status of the species currently assigned to *Hypochroma*. We analyzed type specimens and sequenced tissues from historical and fresh specimens using next-generation and Sanger sequencing to provide insights into the species boundaries and phylogenetic relationships. We use this data to propose taxonomic changes accordingly.

MATERIALS AND METHODS

Specimens and DNA barcoding

Tissue samples were obtained from six historical specimens of *Hypochroma* deposited at the Natural History

Museum in London (NHMUK, five specimens, all collected before 1939), one specimen in Zoologische Staatssammlung München in Munich (SNSB, collected in 1989), and one specimen in Universidad de Sucre, Colombia (MZUSU, collected in 2016), see [Table 1](#).

DNA from historical museum samples was extracted and sequenced using Single Molecule Real Time (SMRT) sequencing protocols to obtain barcodes from short reads generated by the Sequel platform from Pacific Biosciences (Hebert et al., 2018). DNA extracts were generated using membrane-based protocols from a single leg of the specimens. PCR protocols targeted a 658bp segment of the mitochondrial marker Cytochrome Oxidase I (COI), and amplicons were generated for SMRT sequencing. Samples were processed at the Canadian Centre for DNA Barcoding (CCDB). To check for potential contamination from DNA extracts and sequences, we retrieved DNA barcode sequences (COI) from BOLD SYSTEM and compared them to those obtained during the SMRT sequencing (Hebert et al., 2018). BOLD stores references of more than 21 000 geometrid species which are available, some 10 000 of them properly curated and identified to Linnaean species names. GenBank accession numbers for new sequences used in this study are provided in [Table 1](#).

The Barcode Index Numbers (BIN) (Ratnasingham & Hebert, 2007) are given for all species. All DNA barcode

sequences and metadata are accessible on BOLD (dx.doi.org/10.5883/DS-HYPO).

DATA ANALYSES

Phylogenetic inference

To analyse the data, we added the *Hypocroma* barcodes to a multigene dataset that included up to four genes (one mitochondrial gene, COI, and three coding genes, ArgK, EF1a, and Wingless) from geometrid data analysed by Murillo-Ramos et al. (2019). The dataset included one *Hypochroma marginata* and representative taxa of potential sisters of *Hypochroma* from the tribe Ennomini: *Somatolophia haydenata* (Packard, 1876), *Eusarca nemo* (Druce, 1892) and *Tmetomorpha bitias* (Druce, 1892) according to Murillo-Ramos et al. (2019).

We conducted a phylogenetic analysis under a Maximum-likelihood (ML) approach in IQ-TREE2 V2.0.7 (Nguyen et al., 2015). The dataset was partitioned by genes. The best substitution models that fit our data were selected with ModelFinder (Kalyanamoorthy et al., 2017). Support for nodes was evaluated with 1000 ultrafast bootstrap (UFBoot2) approximations (Hoang et al., 2018) and the SH-like approximate likelihood ratio test (Guindon et al., 2010). Branch support was evaluated with the UFBoot2 test. We visualised and edited the trees in FigTree v1.4.3 and CorelDraw v. 24 (2023).

Table 1. Metadata of *Hypochroma* voucher specimens used in the DNA barcode analysis.

Linnaean name	Sex	Voucher code	bases [Am-big]	Collection	GenBank code	BIN	Metadata
<i>H. marginata</i>	male	LMR_Geo164	656[0]	MZUSU	MK739597	BOLD:AEA7619	Colombia: Chalán, Sucre, January 2016
<i>H. marginata</i>	male	Sihvonen_382	658[200]	NHMUK	PX068088	No BIN	Venezuela: La Vuelta, April 1903
<i>H. marginata</i>	female	Sihvonen_383	658[139]	NHMUK	PX068087	BOLD:AEA7619	Venezuela: Ciud. Bolivar
<i>H. brepharia</i>	female	BC_ZSM_Lep_73060	658[0]	SNSB	PX068090	BOLD:ACU1063	Venezuela: Maracay, 31.7.1989, 1190 m
<i>H. brepharia</i>	female	Sihvonen_379	658[0]	NHMUK	PX068091	BOLD:ACU1063	Colombia: East Colombia, 800 m
<i>H. brepharia</i>	male	Sihvonen_378	658[145]	NHMUK	PX068089	No BIN	Venezuela
<i>H. flavinigra</i>	female	Sihvonen_381	658[200]	NHMUK	PX068086	No BIN	Colombia: Bogota, December 1917
<i>H. flavinigra</i>	male	Sihvonen_380	658[89]	NHMUK	PX068085	BOLD:ACU1063	Venezuela: Las Quiguas

Species delimitation

For our species delimitation, we used an integrative approach emphasising congruence, i.e., the validity of a species is more likely if supported by several independent character sets (Padial et al., 2010). We emphasised this research on character sets that are widely used in geometrid taxonomy (see e.g., Hausmann, 2004; Müller et al., 2019; Sihvonen, 2005) as follow: 1) external morphology, 2) genitalia morphology, 3) mitochondrial DNA barcode, 4) ecology and distribution.

We analysed our barcode data with the Assemble Species by Automatic Partitioning (ASAP) method (Puillandre et al., 2021). This species delimitation method builds species partitions from single-locus sequence alignments and assigns the sequences into putative species. We uploaded a fasta file with sequences to the web server (ASAP) and used Jukes-Cantor (JC69) as a substitution model to compute genetic distances.

Morphological examination

Specimens prepared by us for this study were first photographed, and the abdomens of both sexes were removed, and the genitalia were dissected following established preparation protocols (e.g., Hardwick, 1950; Sihvonen, 2001; Sihvonen & Kaila, 2003, described in detail in Sihvonen, 2005). Some structures were photographed *in situ* during dissection to allow an optimal angle for observing and illustrating certain structures (Fig. 4). All structures were stained with Chlorazol black. Preparations of genital and abdominal structures were eventually mounted in Euparal. The preparation method of the dissections examined from the NHMUK is unknown. Potentially, they have been stained with Eosin, because the structures are red. Structural characters were examined and photographed using a Leica S9D stereomicroscope, Leica DM1000 LED microscope and Canon EOS 5D digital camera with MP-E 65 mm EF 100 mm macro lenses. Photos were taken with StackShot automated macro rail and focus stacked in Zerene Stacker or in Adobe Photoshop v. 24 (2023). Image files were edited in Photoshop v. 24 (2023) and the final plates were arranged using CorelDraw v. 24 (2023).

Genital terminology follows Klots (1970) and Sibatini (1972), and wing venation terminology follows McGuffin (1977). In ambiguous cases, descriptive terms were used and were accompanied by illustrations.

RESULTS

DNA barcodes from historical specimens were successfully amplified, yet with some missing nucleotides, between 89–200 bp (see Table 1). Our phylogenetic inference suggested a monophyletic genus with two well-defined species (UFBoot = 100, SH-like = 99.9) (Fig. 1). *Hypochroma brepharia* and *H. flavinigra* mixed together, suggesting that these species belong to the same taxa, sister to *H. marginata*. The sister taxa of *Hypochroma* are unclear because of limited taxon sampling and we would need further analyses.

Species delimitation analyses based on DNA barcodes also suggested that *Hypochroma brepharia* and *H. flavinigra* are conspecific. Meanwhile, specimens identified as *H. marginata* were delimited as either two putative species (asap score = 1.5), potentially including one undescribed taxon or a single species (asap = 2.0) (Fig. 1).

Morphological traits between the studied specimens are similar, without qualitative differences that would be useful to diagnose the taxa on species level. The extent of brown areas on wings varies from almost absent to that covering the majority of the wings, while there appear to be small quantitative differences in the presence or absence of the brown markings on the forewing costa. Also, the inner margin of the brown area undulates slightly differently between taxa (see Taxonomy below). No difference in the wing patterns was observed between sexes. In the male genitalia, the most variable structure is the vesica, which opens in a variable position between 90–135 degrees relative to the aedeagus. The female genitalia are also homogeneous, with rather small quantitative differences in the shape of the signum and the corpus bursae.

TAXONOMY

Based on our results, we propose an update to the *Hypochroma* taxonomy.

Hypochroma Herrich-Schäffer, 1855

Hypochroma Herrich-Schäffer 1855 1850–1858, Samml. neuer oder wenig bekannter aussereur. Schmett. 1 (1): wrapper, pl. 60, fig. 335. Type species: *Hypochroma brepharia* Herrich-Schäffer 1855.

“*Xanthoprepes*” Warren, unpublished. Unavailable.

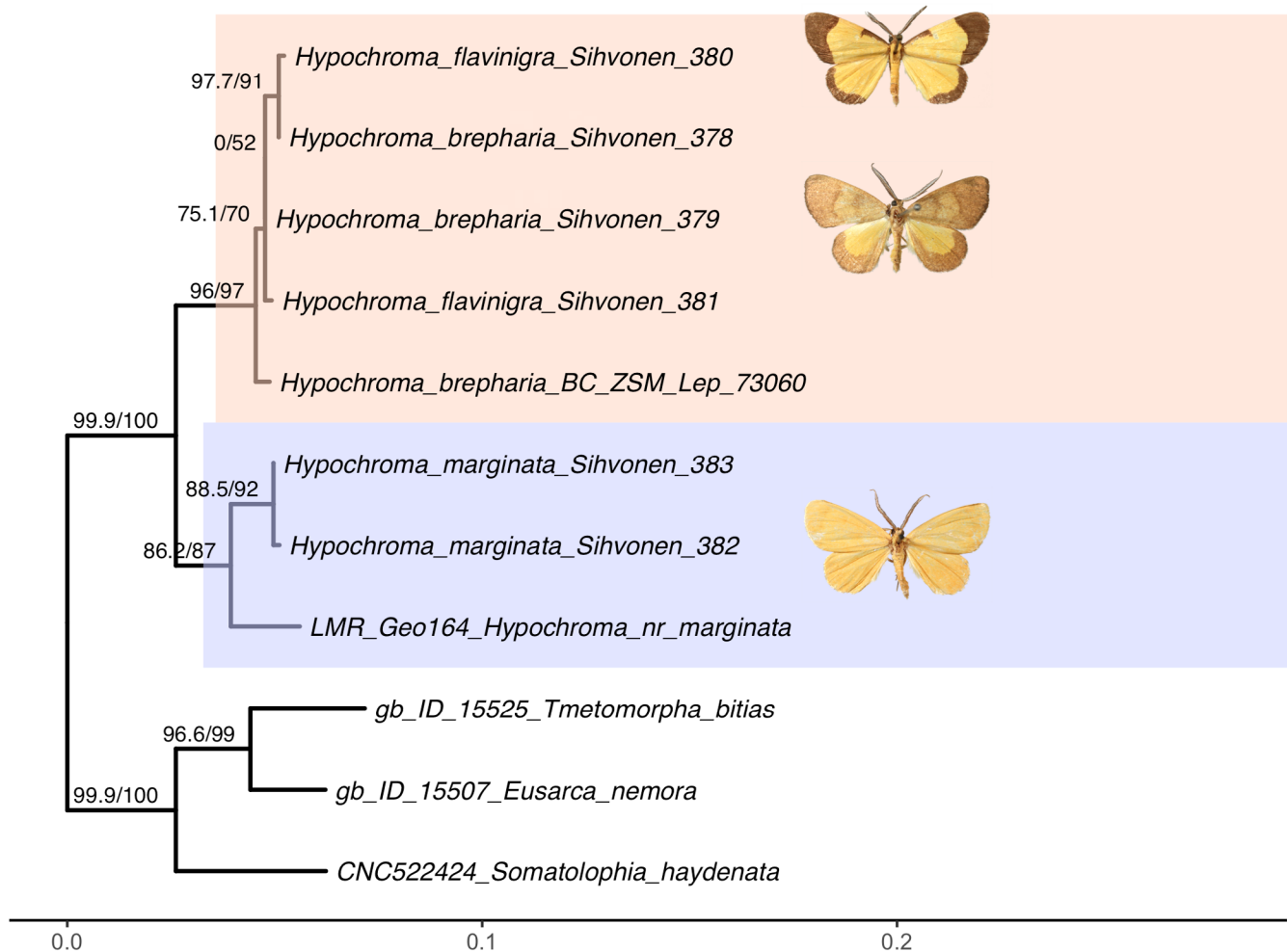


Figure 1. Phylogenetic inference and species delimitation of *Hypochroma* (Ennominae). We represent the best combination of primary species hypotheses by ASAP Web results. Numbers are SH-aLRT support (%) / ultrafast bootstrap support (%) from IQTREE2 analyses. The results from ASAP are reported in the supplementary material (Fig. S3). Specimens correspond to males of *Hypochroma*.

Diversity and distribution: Two species in northern South America, currently only known from Venezuela and Colombia.

External characters and abdomen: Wingspan 25–30 mm in both sexes (Fig. 2–4). Upperside of wings dark yellow, margins typically broadly dark brown, wider on forewings. Medial lines typically not visible. Underside similar, colours paler. Forewing without an accessory cell. Male antennae bipectinate, female antennae filiform. Hindlegs of both sexes with 2 + 2 spurs, male hindleg with small hair pencil. Tympanal organs medium-sized, not touching each other, medial part with distinct pouch. Male 3rd ster-

nite with row of setae. Abdominal segments 3–8 in both sexes undifferentiated.

Male genitalia: Uncus long, evenly curved ventrally. Socii small, setose bulb. Gnathos apex with short spines (Fig. 2). Valva evenly curved, apex blunt, costa weakly sclerotized, without processes. Juxta asymmetrical, right arm long, sclerotized, apex densely setose (spinulose). Saccus short, weakly elongated, with upwards pointing tiny projection medially, Aedeagus narrow, caecum short, apex with narrow but distinct process. Vesica basally swollen, opening laterally between 90–135 degrees, cornuti absent.

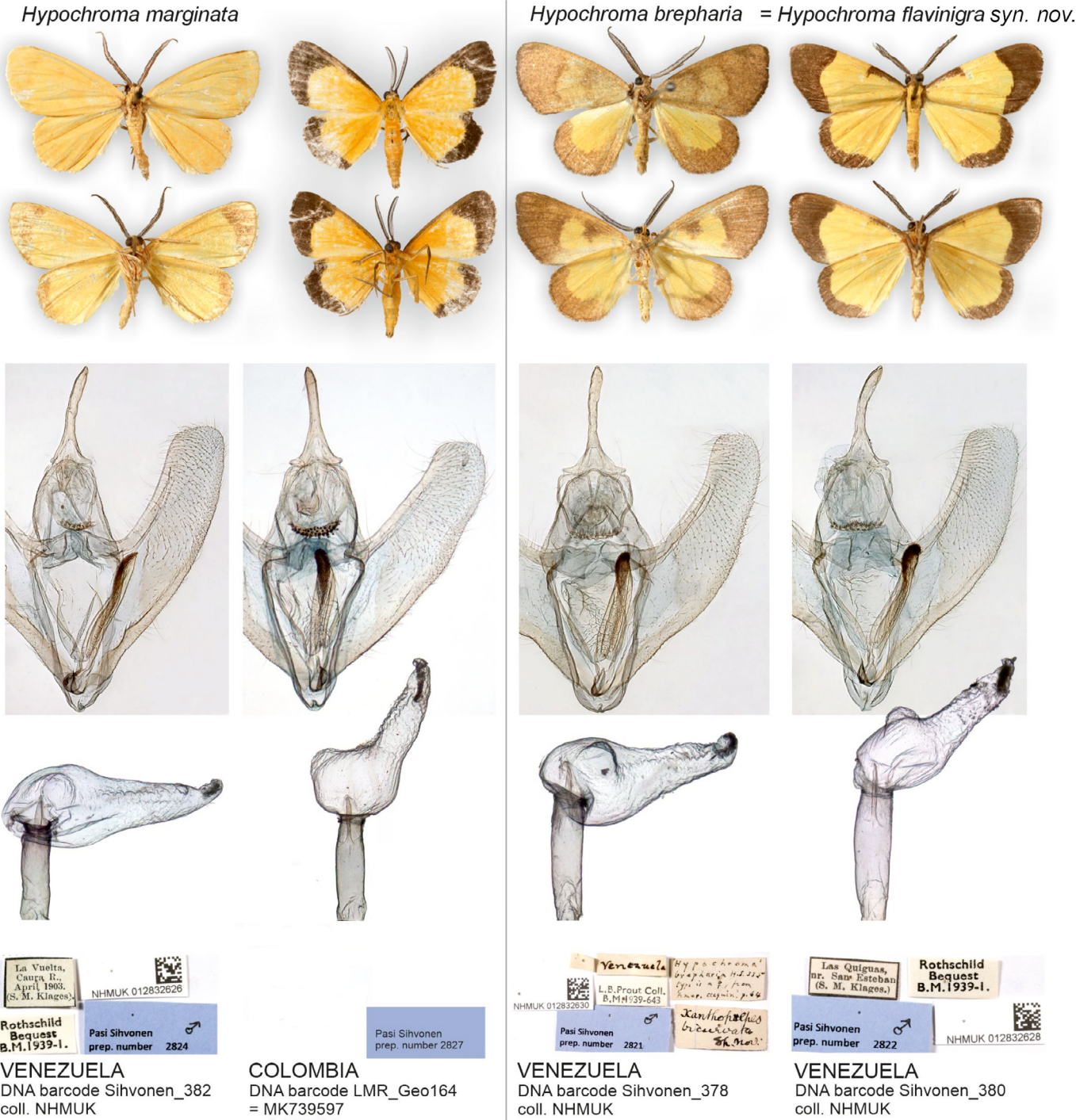


Figure 2. Male adults (top), genitalia (middle) and aedeagus with everted vesica (bottom) of *Hypochroma* species. We propose a new synonymy: *H. brepharia* Herrich-Schäffer 1855 = *H. flavinigra* Warren 1897 syn. nov.



Figure 3. Female adults (top), genitalia and enlarged signum (bottom) of *Hypochroma* species. We propose a new synonymy: *H. brepharia* Herrich-Schäffer 1855 = *H. flavinigra* Warren 1897 syn. nov. Arrow indicates position of signum, white circle indicates position of ductus seminalis.

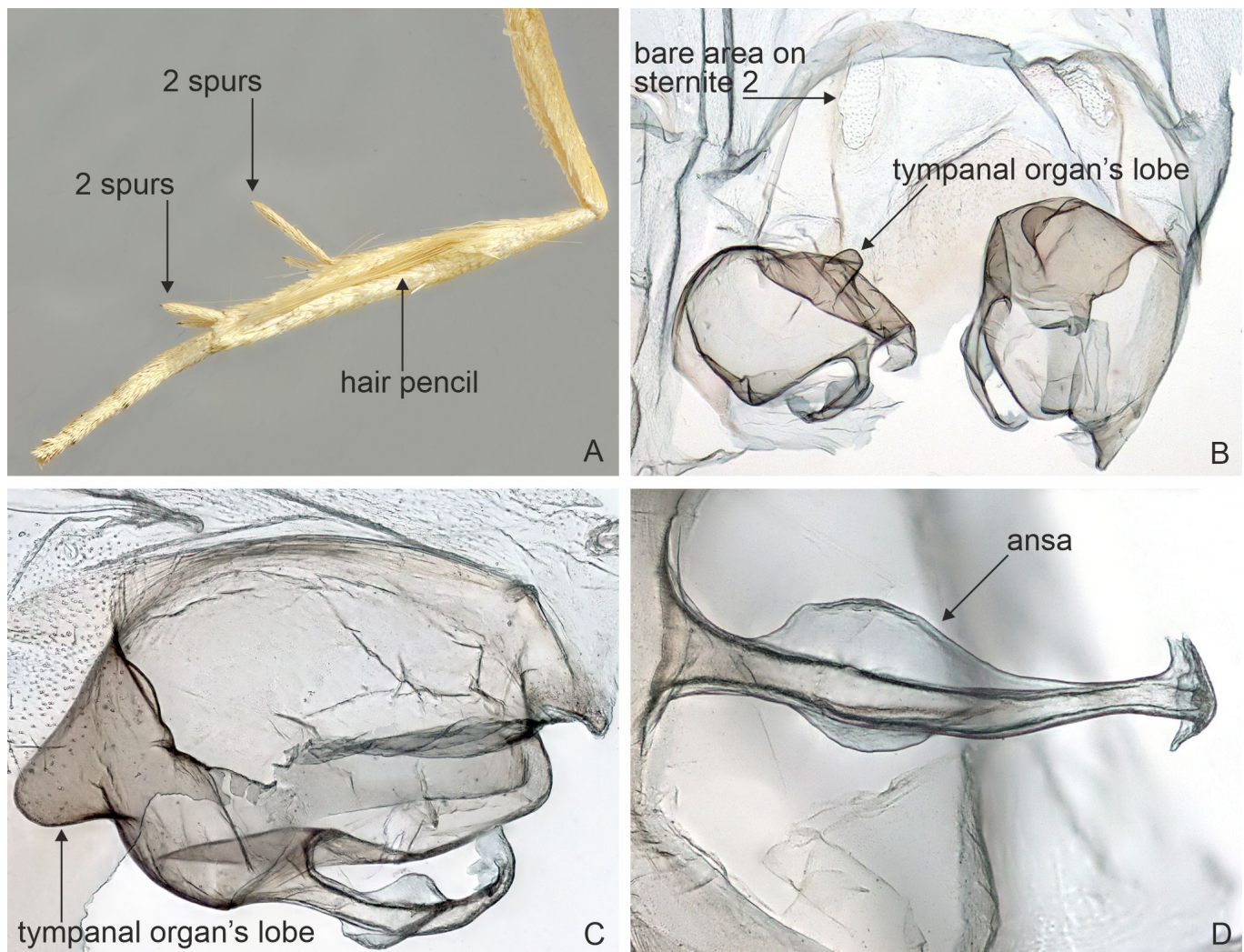


Figure 4. Selected structures of *Hypochroma* species. **A.** Male hair pencil with 2 + 2 spurs (*H. brepharia*); **B.** male tympanal organs with diagnostic lobe on medial side and paired bare area on sternite 2 (*H. marginata*); **C.** male tympanal organ's lobe enlarged (*H. marginata*); **D.** tympanal organ's ansa enlarged (*H. marginata*).

Female genitalia: Papillae anales weakly elongated, setose (Fig. 3). Apophyses anteriores about 1/3 length of posterior apophyses. Lamella antevaginalis narrow sclerotized ridge. Ductus bursae short, laterally sclerotized. Corpus bursae very long, narrow, membranous, anterior part slightly variable in shape. Signum tiny, stellate.

Biology, phenology, habitat. One recently collected specimen (MZUSU-E000326) was found in a dry tropical forest in Northern Colombia at 216 m above sea level. Other specimens in collections do not have information on habitat, however *H. brepharia* was collected at 800 m above sea level which suggest that *Hypochroma* species may prefer hilly or mountainous tropical areas. Most specimens in collections lack phenology information, but dates include April, July, September and November.

Immature stages: Unknown.

Hypochroma marginata (Warren, 1900)

marginata Warren 1900, Novit. zool. 7: 199 (*Fidonia*). Syntypes 5 males, 4 females (NHMUK), Venezuela: Ciudad Bolivar. Examined, including genitalia (dissection_PMS2825) and DNA barcode (DNA_PMS383). Examined non-type material is shown as a photograph in supplementary material (Fig. S1).

Diagnosis: Forewing costa typically without brown marking near wing base (Fig. 2-3). Inner margin of brown area evenly curved, without undulations. No diagnostic characters have been found in the male and female genitalia so far. DNA barcodes are diagnostic (BIN BOLD:AEA7619).

***Hypochroma brepharia* Herrich-Schäffer, 1855**

brepharia Herrich-Schäffer 1855, Samml. neuer oder wenig bekannter aussereur. Schmett. (1) 1 (13–17): wrapper, pl. 60, fig. 355, (*Hypochroma*). Syntype(s) female(s), Am. mer. [South Africa]. Examined based on original illustration. Examined non-type material is shown as a photograph in supplementary material (Fig. S2).

flavinigra Warren 1897, Novit. zool. 4: 475 (*Fidonia*), Syn-types 2 males (NHMUK), Venezuela: Cucuta. Examined, including genitalia (BMNH Geometridae genitalia slide 19307). **NEW SYNONYMY.** Examined non-type material is shown as a photograph in supplementary material (Fig. S2).

Diagnosis: Forewing costa typically with narrow brown marking near wing base (Fig. 2-3). Inner margin of brown area with small undulation in mid-wing. No diagnostic characters have been found in the male and female genitalia so far. DNA barcodes are diagnostic (BIN BOLD:ACU1063).

DISCUSSION

DNA barcodes clearly separate the two recognised taxa. However, wing morphology allows identification of most specimens, and the genitalia show no noticeable differences, thus suggesting the presence of a single species. Therefore, different character sets suggest different taxon delimitations, and the data are incongruent. Given that natural history data are incomplete, we prefer a conservative approach to maintain taxonomic stability.

The proposed synonymy of *H. brepharia* and *H. flavinigra* is supported by DNA barcodes and nuclear markers, which strongly support these species as a single lineage, thus conforming to a distinct genetic cluster from *H. marginata*. In our chosen classification, *H. brepharia* includes specimens with extensively brown wings, as well as specimens with brown margins only. The male genitalia of all specimens are uniform, except the vesica that opens at a slightly different angle in different specimens, but the structure did not correlate with DNA barcodes or wing patterns. Unfortunately, we do not have information on life histories, including caterpillar host plants, caterpillar morphology, pupal structures, etc., so the current taxonomic conclusions are based on DNA barcodes, nuclear

markers, and adult morphology. How can this mismatch of characters be explained? Potentially, the wing patterns have been misinterpreted. In Lepidoptera, wing morphological patterns can be highly variable and convergent, and can mislead species taxonomy. Therefore, the specimens in collections could have been arranged erroneously, or maybe external variation within species is higher than earlier acknowledged. We followed an integrative approach and considered all available evidence. In addition to the lack of genitalia differentiation, molecular data support the synonymizing of these species. We acknowledge that barcodes are not sufficient for species delimitation; however, incongruence can be resolved when analyses include nuclear markers, as we did, thereby showing a clear phylogenetic structure.

We emphasise that the proposed classification is a hypothesis awaiting testing with additional data. It has been shown repeatedly that DNA barcodes have the ability to identify cryptic species that look identical to the human eye, or the barcodes can identify synonyms overlooked by earlier taxonomic studies (for Geometridae examples, see e.g. (Hausmann et al., 2013; Hausmann et al., 2016; Müller et al., 2019)). In our case, DNA barcoding is used to flag species delimitations, which will hopefully be followed by morphological and ecological confirmation of life histories, immature-stage morphology, phenology, caterpillar host plants, or image analysis of wing patterns.

ACKNOWLEDGEMENTS

We thank Geoff Martin (NHMUK) for allowing access and loan of material for the study.

AUTHORS CONTRIBUTION

LM-R: Conception, fieldwork, laboratory, data analyses and writing; PS: Conception, photographic material, dissections of specimens and preparations and writing. The authors have no conflict of interest.

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