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Update to: New butterfly taxa and findings from genomic analyses

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ABSTRACT. Due to the U.S. government shutdown, GenBank services were unavailable, and accession numbers could not be obtained for the sequences reported in the original publication. This update provides the GenBank accession numbers for these sequences, together with additional taxonomic findings accumulated since the initial study. One genus, 16 species and four subspecies are proposed as new (type species or localities in parentheses): *Madaga* Grishin, **gen. n.** (*Artitropa alaotrana* Oberthür, 1916), *Udranomia eurianus* Grishin, **sp. n.** (Ecuador: Napo), *Entheus dalina* Grishin, **sp. n.** (Brazil: Pará), *Entheus ambo* Grishin, **sp. n.** (Colombia: Cauca), *Entheus pico* Grishin, **sp. n.** (Colombia: Valle del Cauca), *Entheus punyo* Grishin, **sp. n.** (Colombia: Cauca), *Porphyrogenes castana* Grishin, **sp. n.** (Brazil: Amazonas), *Porphyrogenes foxias* Grishin, **sp. n.** (Suriname), *Porphyrogenes tornus* Grishin, **sp. n.** (Brazil: Rondônia), *Porphyrogenes sepia* Grishin, **sp. n.** (Brazil: Rondônia), *Bungalotis ryta* Grishin, **sp. n.** (Panama: Chiriquí), *Pseudodrephalys gap* Grishin, **sp. n.** (Brazil: Rondônia), *Grais ecuadoricus* Grishin, **sp. n.** (Ecuador: Sucumbíos), *Grais eremitus* Grishin, **sp. n.** (USA: Texas), *Hoodus westudus* Grishin, **sp. n.** (Ecuador: Orellana), *Eutus brunninotatus* Grishin, **sp. n.** (Bolivia: Santa Cruz), *Lento mysto* Grishin, **sp. n.** (Bolivia: La Paz) and *Porphyrogenes probus curvatus* Grishin, **ssp. n.** (Costa Rica: San José) (Hesperiidae); and *Eurema ella marca* Grishin, **ssp. n.** (Peru: Cajamarca), *Eurema agave panave* Grishin, **ssp. n.** (Panama: Colón), and *Eurema agave livara* Grishin, **ssp. n.** (Ecuador: Bolívar) (Pieridae). Genomic sequencing revealed additional specimens of recently described species of *Entheus* Hübner, [1819], previously known from a single specimen. We treat the following taxa of *Lasaia* (*Lasaia*) H. Bates, 1868 (Riodinidae) as valid: *L. rosamonda* Weeks, 1900, **stat. rest.**, *L. callaina* Clench, 1972, **stat. rev.**, *L. maria anna* Clench, 1972, **stat. rest.**, *L. oaxacensis* Grishin, 2024, **stat. rest.**, and *L. cola* Grishin, 2025, **stat. rest.**; as well as *Lissia laura* (Evans, 1937) **stat. nov.** (not *Lissia luehderi* (Plötz, 1879)), and *Ephyriades brunnea electra* (Lintner, 1881), **stat. nov**. Lectotype and neotype are designated for *Antigonus fumosus* Plötz, 1884 (Brazil) and *Anastrus stigmaticus* Mabille, 1883 (Brazil), respectively, establishing these names as objective synonyms.

Key words: taxonomy, classification, genomics, phylogeny, biodiversity.

ZooBank registration: https://zoobank.org/A49DC31F-B6A7-4F9B-BFBE-DDCE2512F248

Here, we provide updates and corrections to our recently published study (Zhang et al. 2025b), resulting from the sequencing of additional specimens using the same methods within the same conceptual framework. Due to the longest government shutdown in U.S. history, NCBI services for assigning GenBank accessions were non-functional for an extended period, which prevented us from including GenBank numbers in the original work. After the shutdown ended and NCBI services resumed, we obtained these numbers, which are published here.

DNA character states are given for one of the two reference genomes: *Pieris rapae* (Linnaeus, 1758) (pra) (Shen et al. 2016), or *Cecropterus lyciades* (Geyer, 1832) (aly, because this species was formerly in the genus *Achalarus* Scudder, 1872) (Shen et al. 2017). The notation aly728.44.1:G672C means that position 672 in exon 1 of gene 44 from scaffold 728 of the *C. lyciades* reference genome (aly) is C, changed from G in the ancestor. When characters are given for the sister clade of the diagnosed taxon, the following notation is used: aly5294.20.2:A548A (not C), which means that position 548 in exon 2 of gene 20 on scaffold 5294 is occupied by the ancestral base pair A, which was changed to C in the sister clade (so it is not C in the diagnosed taxon). COI barcode characters follow the same format but

lack a prefix ending in ':' and in some cases the ancestral base pair (where unclear). Complete exon sequences from reference genomes, with diagnostic positions for new taxa highlighted in green, are provided in the supplementary file < https://osf.io/bcvxw >. By linking to this file, we ensure that the characters used in diagnoses can be traced to their actual sequences.

Whole genome shotgun datasets we generated and used in this study are available from the NCBI database < https://www.ncbi.nlm.nih.gov/ > under BioProject PRJNA1368304. Associated BioSample records include locality data and other collection information for all specimens sequenced by us and shown in the trees. Tree figures list the following information for each specimen, separated by "|": taxon name with comments in square brackets, DNA sample code, type status, general locality, and year of collection ("old" if not dated and likely collected 100–150 years ago). Type status abbreviations are: HT holotype, LT lectotype, ST syntype, NT neotype, T type (could be ST, LT, paralectotype, or HT, status not investigated), PT paratype, AT allotype, PLT paralectotype, TT topotype (not a true type, but a specimen from the general area of the type locality of a taxon); and if a synonym name is given (in parentheses, preceded by "=", and in addition by "‡" for unavailable names), type status refers to the synonym. Ultrafast bootstrap (Hoang et al. 2018) values are shown at the nodes. COI barcode sequences reported here and in Zhang et al. (2025b) have been deposited in GenBank with accessions PX501749, PX525184–PX525254, PX568478–PX568502, PX626415, PX645477, and PX660127. Abbreviations or acronyms for collections are listed in the Acknowledgments.

GenBank accessions for COI barcode sequences reported in Zhang et al. (2025b)

The names of taxa, their DNA sample IDs, and GenBank accessions are given below.

Dione (*Agraulis*) *galapagensis* (W. Holland, 1890)
non-type ♂, sample NVG-19094A07, GenBank PX525184
non-type ♂, sample NVG-19094A04, GenBank PX525185

Dione (*Agraulis*) *lamasi* Grishin, 2025
holotype ♂, sample NVG-19094A05, GenBank PX525186

Dione (*Agraulis*) *forbesi* (Michener, 1942)
holotype ♂, sample NVG-22043C08, GenBank PX525187
allotype ♀, sample NVG-22043C09, GenBank PX525188

Lasaia (*Lasaia*) *chiapis* Grishin, 2025
holotype ♂, sample NVG-24079D06, GenBank PX525189

Lasaia (*Lasaia*) *occalla* Grishin, 2025
holotype ♂, sample NVG-24081F02, GenBank PX525190

Lasaia (*Lochris*) *oilenor* Grishin, 2025
holotype ♀, sample NVG-23111F04, GenBank PX525191

Lasaia (*Lochris*) *oilepanor* Grishin, 2025
holotype ♀, sample NVG-23115C05, GenBank PX525192

Lasaia (*Lochris*) *oilemarca* Grishin, 2025
holotype ♀, sample NVG-23115C10, GenBank PX525193

Emesis (*Tenedia*) *peripore* Grishin, 2025
holotype ♂, sample NVG-24067A04, GenBank PX525194

Burara danata Grishin, 2025
holotype ♂, sample NVG-22083F05, GenBank PX525195

Burara danata himavata Grishin, 2025
holotype ♂, sample NVG-22099C09, GenBank PX525196

Burara gomata burmana Grishin, 2025
holotype ♂, sample NVG-7866, GenBank PX525197

Burara gomata namata Grishin, 2025
holotype ♀, sample NVG-22083F07, GenBank PX525198

Burara lawana Grishin, 2025
holotype ♂, sample NVG-23079F03, GenBank PX525199
Burara lorquini vichitra Grishin, 2025
holotype ♂, sample NVG-23026G10, GenBank PX525200
Bungalotis quadra Grishin, 2025
holotype ♂, sample NVG-23125H01, GenBank PX525201
Bungalotis barbalotis Grishin, 2025
holotype ♂, sample NVG-15026B06, GenBank PX525202
Cecropterus (*Murgaria*) *eryssus* Grishin, 2025
holotype ♂, sample NVG-24021B02, GenBank PX525203
Cecropterus (*Murgaria*) *chales estales* Grishin, 2025
holotype ♂, sample NVG-3610, GenBank PX525204
Urbanus (*Urbanus*) *viterboana* (Ehrmann, 1907)
holotype ♂, sample NVG-15095A01, GenBank PX525205
Urbanus (*Urbanus*) *dubius* Steinhauser, 1981
holotype ♂, sample NVG-15038B12, GenBank PX525206
Cephise panuspe Grishin, 2025
holotype ♂, sample NVG-2072, GenBank PX525207
Pholisora mejicanus yuesanus Grishin, 2025
holotype ♂, sample NVG-19013D11, GenBank PX525208
Noctuana haematoesta Grishin, 2025
holotype ♂, sample NVG-23053G12, GenBank PX525209
Noctuana statonama Grishin, 2025
holotype ♂, sample NVG-23095A01, GenBank PX525210
Celotes sabinus verdinus Grishin, 2025
holotype ♂, sample NVG-23054H06, GenBank PX525211
Diaeus piura Grishin, 2025
holotype ♀, sample NVG-23124A12, GenBank PX525212
Zopyrion (*Zopyrion*) *cruise* Grishin, 2025
holotype ♂, sample NVG-23124F05, GenBank PX525213
Ephyriades brunnea sansalva Grishin, 2025
holotype ♂, sample NVG-19031F01, GenBank PX525214
Ephyriades brunnea turcaica Grishin, 2025
holotype ♀, sample NVG-17093E04, GenBank PX525215
Ephyriades arcas norleewa Grishin, 2025
holotype ♂, sample NVG-17095D09, GenBank PX525216
Chaetocneme triton (Boisduval, 1832)
neotype ♂, sample NVG-18095F02, GenBank PX525217
Chaetocneme editus (Plötz, 1885)
lectotype ♀, sample NVG-22016C12, GenBank PX525218
Chaetocneme triuna Grishin, 2025
holotype ♀, sample NVG-17068G02, GenBank PX525219
Chaetocneme brazza Grishin, 2025
holotype ♀, sample NVG-23086B10, GenBank PX525220
Ge pina Grishin, 2025
holotype ♂, sample NVG-24026F12, GenBank PX525221
Pamphila philino Möschler, 1879 (junior subjective synonym of *Parnara mangala* (F. Moore, 1866))
holotype ♂, sample NVG-18074G07, GenBank PX525222

Hesperia kolantus Plötz, 1885 (junior subjective synonym of *Parnara mangala* (F. Moore, 1866))
lectotype ♂, sample NVG-22016H06, GenBank PX525223
Parnara daendeli (Plötz, 1885)
lectotype ♂, sample NVG-22016H08, GenBank PX525224
Parnara philotas (de Nicéville, 1895)
non-type ♂, sample NVG-24068E02, GenBank PX525225
Parnara guda Grishin, 2025
holotype ♀, sample NVG-18102F01, GenBank PX525226
Parnara sulawesa Grishin, 2025
holotype ♂, sample NVG-18097A10, GenBank PX525227
Tisias panamyna Grishin, 2025
holotype ♂, sample NVG-18112A06, GenBank PX525228
Xeniades (*Tixe*) *lora* Grishin, 2025
holotype ♂, sample NVG-24071F05, GenBank PX525229
Oligoria (*Oligoria*) *lucifer* (Hübner, [1829])
lectotype ♀, sample NVG-18113B06, GenBank PX525230
Oligoria (*Oligoria*) *pindar* (Schaus, 1913)
lectotype ♂, sample NVG-23119B09, GenBank PX525231
Oligoria (*Oligoria*) *costaria* Grishin, 2025
holotype ♂, sample NVG-21054E11, GenBank PX525232
Oligoria (*Oligoria*) *bahia* Grishin, 2025
lectotype ♀, sample NVG-23079B05, GenBank PX525233
Alychna ventanilla Grishin, 2025
holotype ♂, sample NVG-8007, GenBank PX525234
Thoon cuadius Grishin, 2025
holotype ♂, sample NVG-23056D04, GenBank PX525235
Viridina viridella Grishin, 2025
holotype ♂, sample NVG-18125E10, GenBank PX525236
Tricrista lingulata Grishin, 2025
holotype ♂, sample NVG-21048D09, GenBank PX525237
Tricrista taxolla Grishin, 2025
holotype ♂, sample NVG-18127D08, GenBank PX525238
Vettius fuscapicalis Grishin, 2025
holotype ♂, sample NVG-19022D03, GenBank PX525239
Mnasitheus oaxaceus Grishin, 2025
holotype ♂, sample NVG-23114B03, GenBank PX525240
Tarmia bolivia Grishin, 2025
holotype ♀, sample NVG-23079C05, GenBank PX525241
Artines tines Grishin, 2025
holotype ♂, sample NVG-21046H10, GenBank PX525242
Calpodes hewitsoni supernalis Grishin, 2025
holotype ♂, sample NVG-24129E05, GenBank PX525243
Calpodes salma Grishin, 2025
holotype ♀, sample NVG-25011A10, GenBank PX525244
Calpodes anabara Grishin, 2025
holotype ♂, sample NVG-25011C01, GenBank PX525245
Talides megamaca Grishin, 2025
holotype ♂, sample NVG-24071E10, GenBank PX525246

Perichares guatine Grishin, 2025
holotype ♂, sample NVG-18111G04, GenBank PX525247
Proteides hyas Mabille, 1891 (junior subjective synonym of *Perichares fulvimargo* (Butler, 1873))
lectotype ♂, sample NVG-18043B07, GenBank PX525248
Perichares luscinia (Plötz, 1882)
lectotype ♂, sample NVG-18043C01, GenBank PX525249
Perichares solamancha Grishin, 2025
holotype ♂, sample NVG-18125D09, GenBank PX525250
Perichares indivisa Grishin, 2025
holotype ♂, sample NVG-22019E10, GenBank PX525251
Perichares amaletes Grishin, 2025
holotype ♂, sample NVG-18125B10, GenBank PX525252
Perichares aura Grishin, 2025
holotype ♂, sample NVG-18125B07, GenBank PX525253
Lycas gabriel Grishin, 2025
holotype ♀, sample NVG-23122G07, GenBank PX525254

The following sequence for a specimen reported in Zhang et al. (2025b) was not published in that work, but was deposited in GenBank as a test, which revealed that GenBank accessions were not issued during the government shutdown even for species present in the NCBI Taxonomy database:

Parnara guttatus (Bremer & Grey, [1852])
non-type ♀, sample NVG-24068F05, GenBank PX501749

Species with holotypes transferred to the MUSM collection

Holotypes of the following ten species from Peru, originally in the Dempwolf collection, Austin, Texas, USA, have been transferred to the Museo de Historia Natural, Lima, Peru (MUSM), where they are now deposited. The type locality is listed for each species.

Urbanus (*Urbanus*) *alvinus* Grishin, 2025
Cuzco, Cosñipata Valley, Quebrada Quitacalzón, 1050 m, −13.0167, −71.4833
Noctuana ventrovenata Grishin, 2025
Cuzco, Cosñipata Valley, Rocotal, 1970 m, −13.100, −71.567
Xeniades (*Tixe*) *cuska* Grishin, 2025
Cuzco, Cosñipata Valley, Chontachaca, 950 m, −13.0333, −71.4667
Vacerra cuza Grishin, 2025
Cuzco, Cosñipata Valley, San Pedro, 1375 m, −13.05, −71.55
Viridina viridella Grishin, 2025
Cuzco, Cosñipata Valley, Yanamayo, 2350 m, −13.1333, −71.5833
Tricrista taxolla Grishin, 2025
Madre de Dios, Alto Madre de Dios at the Pantiacolla Lodge, 400 m, −12.6500, −71.2167
Rigga spanglata Grishin, 2025
Cuzco, Cosñipata Valley, Rocotal, 1970 m, −13.100, −71.567
Perichares solamancha Grishin, 2025
Cuzco, Cosñipata Valley, San Pedro, 1375 m, −13.05, −71.55
Perichares amaletes Grishin, 2025
Madre de Dios, Alto Madre de Dios at the Pantiacolla Lodge, 400 m, −12.6500, −71.2167
Perichares aura Grishin, 2025
Cuzco, Cosñipata Valley, San Pedro, 1375 m, −13.05, −71.55

Family Pieridae Swainson, 1820

Eurema ella marca Grishin, new subspecies

https://zoobank.org/ABF4CFEB-B65D-436D-B200-5A77D33E5770

(Figs. 1 part, 2a–b)

Definition and diagnosis. Genomic analysis reveals that specimens from the Andes in northern Peru initially identified as *Eurema ella* (Röber, 1909) (type locality in Ecuador) are genetically differentiated from it at least at the subspecies level (Fig. 1); e.g., their COI barcodes differ by 3.3% (24 bp). However, the nuclear genome divergence is not prominent (Fig. 1a, green vs. violet), even compared with that

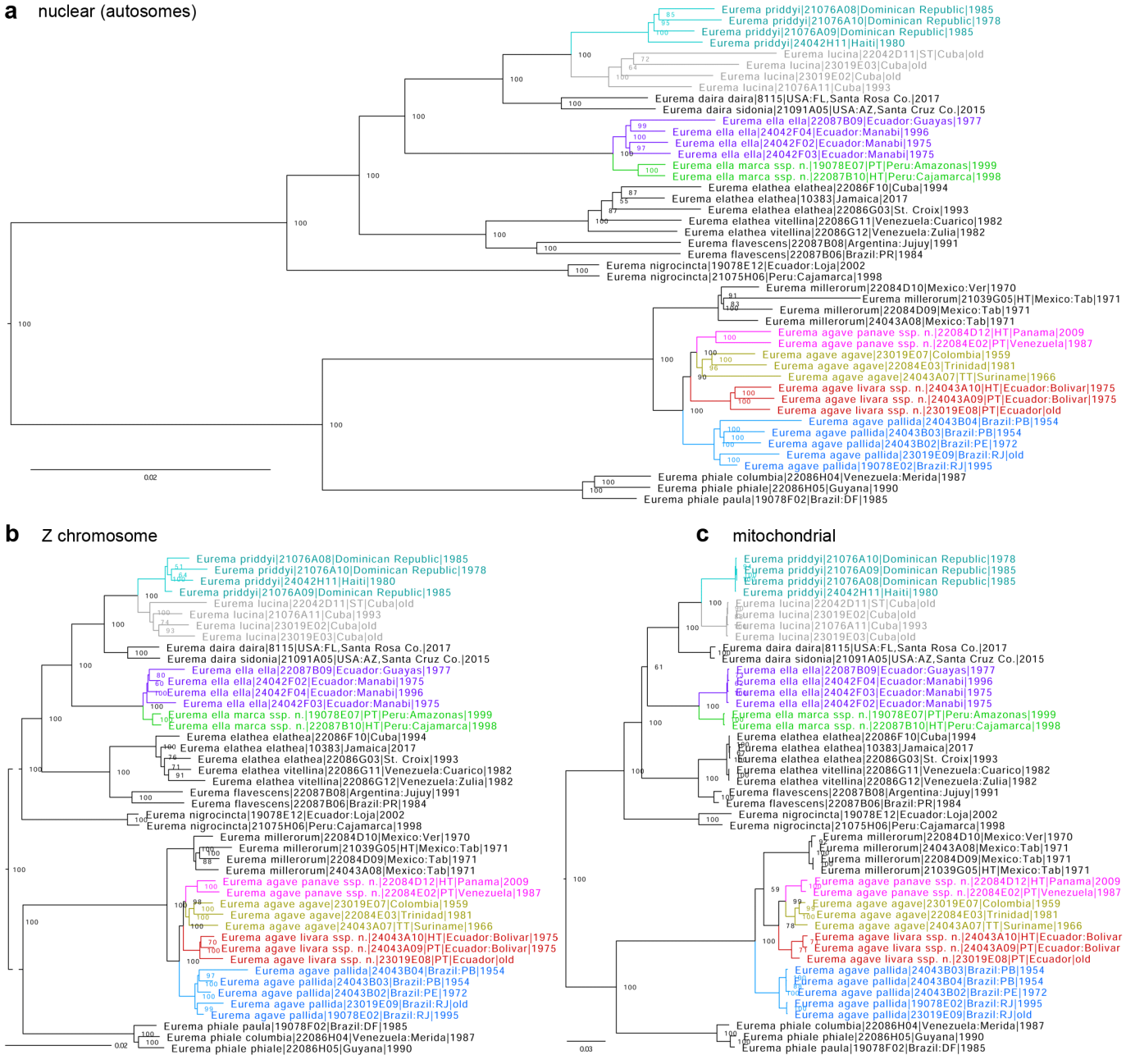

Fig. 1. Phylogenetic trees of all valid *Eurema* species constructed from protein-coding regions in: **a)** the nuclear genome (autosomes), based on 1,881,060 positions, **b)** the Z chromosome, based on 347,178 positions, and **c)** the mitochondrial genome. Taxa discussed in the text are colored: *E. priddyi* (cyan), *E. lucina* (gray), *E. ella ella* (violet), *E. ella marca* **ssp. n.** (green), *E. agave panave* **ssp. n.** (magenta), *E. agave agave* (olive), *E. agave livara* **ssp. n.** (red), and *E. agave pallida* (blue). Ultrafast bootstrap (Hoang et al. 2018) values are shown at nodes. Gaps in branches indicate where a vertical slice of the tree was removed to reduce its horizontal dimension (to allow an increase in the font size), i.e., branches with gaps are longer than shown.

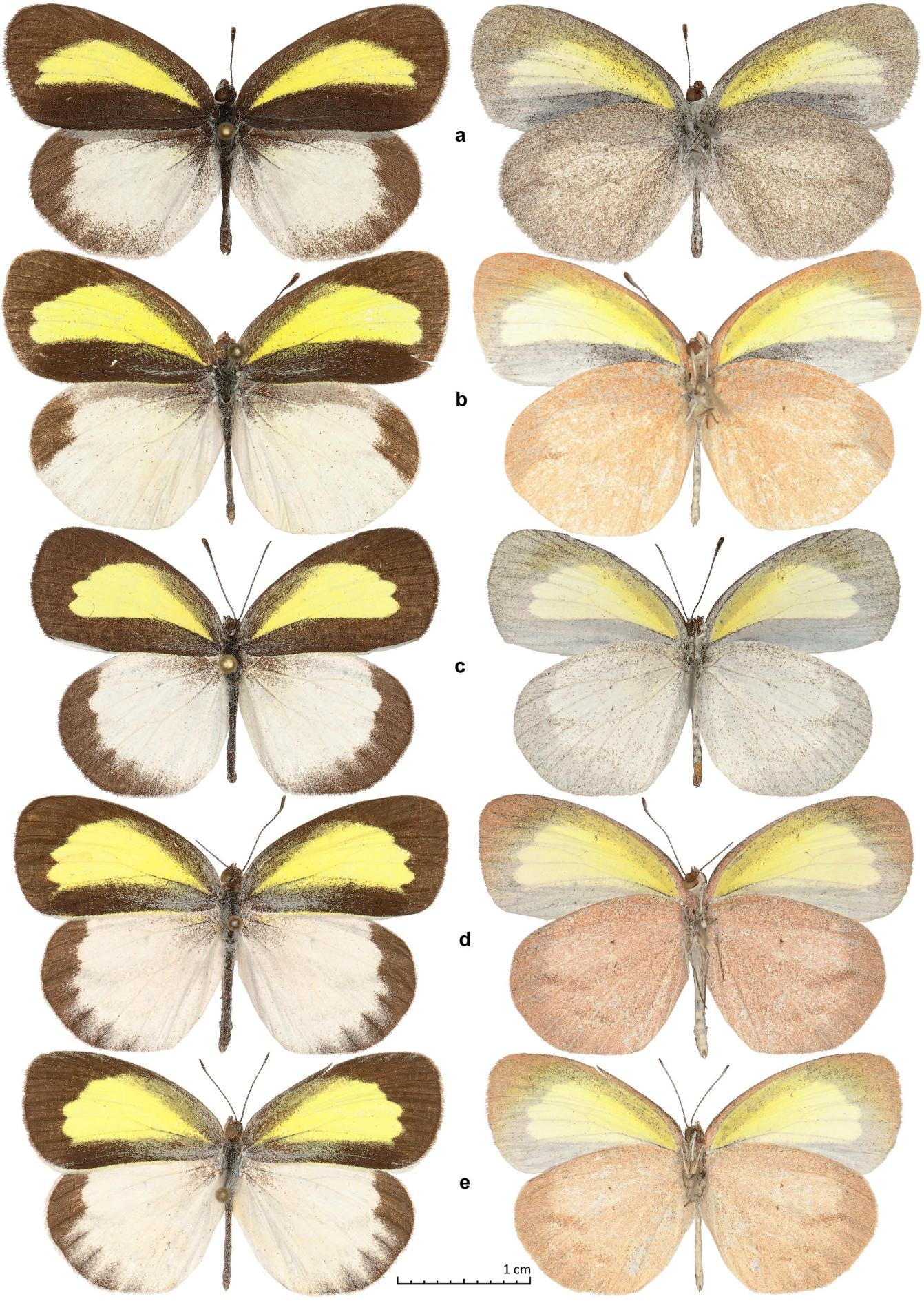
a
b
c
d
e
1 cm

Fig. 2 (see the previous page). *Eurema ella* males in dorsal (left) and ventral (right) views: **a–b)** *E. ella marca* **ssp. n.** from Peru: **a)** holotype NVG-22087B10 from Cajamarca, between Limón and St. Rosa, 1800–3000 m, Jan–Feb-1998, R. Marx leg. [MGCL] and **b)** paratype NVG-19078E07 from Amazonas, Balsas, 950 m, 18-Sep-1999, R. K. Robbins, G. Lamas, D. H. Ahrenholz leg. [USNM] and **c–e)** *E. ella ella* non-type specimens from Ecuador: **c)** NVG-22087B09 Ecuador: Guayas, 105 km W of Guayaquil on rd. to Salinas, 6-Mar-1977, G. T. Austin colln. [MGCL] and **d–e)** Manabí Province, [SMNS]: **d)** NVG-24042F02 vic. San Antonio, 39 km before Bahía de Caráquez, 15 m, 26-Dec-1975, E. E. Reissinger leg. and **e)** NVG-24042F04 10 km S of La Pila, 300 m, 29-Jul-1996, T. Racheli leg.

between the two most closely related species *Eurema lucina* (Poey, [1852]) (type locality in Cuba) (Fig. 1 gray) and *Eurema priddyi* (Lathy, 1898) (type locality in Haiti) (Fig. 1 cyan). Therefore, we conservatively regard these specimens as representing a new subspecies rather than a species. This new subspecies is most similar to *E. ella* in males having a widely dark inner margin of the dorsal forewing without a yellow or orange longitudinal stripe right along the margin, but differs from it and other relatives by the following combination of characters in males (female unknown): slightly larger in size; the dorsal forewing inner margin is more widely dark, i.e., dark scales are present anteriad of the vein CuA_2, and in the holotype, the posterior half of cell CuA_1-CuA_2 is dark [the dark inner marginal area ends sharply at the vein CuA_2 in the nominotypical subspecies (Fig. 2c), or the anterior part of cell CuA_2-1A+2A is yellow (Fig. 2d, e)]; the outer margin of the dorsal forewing is, in contrast, more narrowly dark, e.g., between veins M_3 and CuA_2 [larger portion of cell CuA_1-CuA_2 is dark from the outer margin in *E. ella ella*]; the dorsal hindwing is more heavily overscaled with dark scales from the costal margin to the vein Rs; and the proximal edge of the apical dark area by the dorsal hindwing apex is more diffuse (e.g., in cell Rs-M_1). Due to poorly explored individual and seasonal variation that is expected to be substantial, as in its relatives, this subspecies is best identified by DNA, with diagnostic base pairs in the nuclear genome: pse53.65.4:A119T, pse53.65.4:T150C, pse1526.26.3:C54T, pse1526.26.3:C84T, pse5689.5.3:G42A; and the COI barcode: T50C, T85T, G200A, A316G, T394C, T589C.

Barcode sequence of the holotype. Sample NVG-22087B10, GenBank PX568478, 658 base pairs:

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AACTTTATATTTTATTTTTGGAATTTGATCAGGTATAGTAGGAACTTCCCTAAGTTTATTAATTCGTACTGAATTAGGAAACCCTGGCTCTCTAATTGGAGATGATCAAATTTATAATACA
ATTGTTACAGCTCATGCTTTTATTATAATTTTTTTTATAGTTATACCTATTATAATTGGAGGATTTGGAAATTGATTAATTCCCTTAATATTAGGAGCACCTGATATAGCTTTTCCCCGAA
TAAATAATATAAGTTTTTGACTTCTTCCCCCATCCCTTACCTTATTAATTTCAAGAAGTATTGTTGAAAACGGGGCAGGAACAGGATGAACAGTTTACCCTCCTCTTTCATCTAATATTGC
TCATAGTGGTTCCTCTGTTGATTTAGCAATCTTTTCTCTTCATTTAGCTGGTATTTCTTCAATTTTAGGAGCAATTAATTTTATTACTACTATTATTAATATACGAATTAATAATATATCT
TTTGATCAAATACCTTTATTTGTATGAGCTGTAGGTATTACAGCTTTATTATTATTATCTTTACCTGTTTTAGCTGGAGCAATTACAATACTTCTTACTGACCGTAATTTAAATACTT
CATTTTTTGATCCTGCAGGAGGAGGAGATCCAATTTTATATCAACATTTATTT
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COI barcode sequence of the paratype (sample NVG-19078E07, GenBank PX568479) differs from that of the holotype by 1 bp.

Type material. Holotype: ♂ currently deposited in the McGuire Center for Lepidoptera and Biodiversity collection, Gainesville, FL, USA (MGCL), illustrated in Fig. 2a, bears the following five printed rectangular labels (text in italics handwritten), four white: [NORDPERU, 1800- | 3000m, Department | Cajamarca, zwischen | Limon und St. Rosa | Januar-Februar 1998 | RAINER MARX leg. | EMEM, 30.III.1998], [MGCL General Acc.], [DNA sample ID: | NVG-22087B10 | c/o Nick V. Grishin], [{QR Code} UF | FLMNH | MGCL 1034398], and one red [HOLOTYPE ♂ | Eurema ella | marca Grishin]. **Paratype:** 1♂ NVG-19078E07, USNMENT_01559878 Peru: Amazonas, Balsas, 950 m, approx. GPS 6° 51'S, 78° 02'W, 18-Sep-1999, R. K. Robbins, G. Lamas, D. H. Ahrenholz leg. [USNM] (Fig. 2b). GPS points to a locality in Cajamarca, just across the river from Amazonas, likely due to the lack of precision.

Type locality. Peru: Cajamarca Region, between Limón and Santa Rosa, elevation 1800–3000 m.

Etymology. The name is derived from the Peruvian region of the type locality [Caja]*marca*, reflects more strongly marked with black forewings of this new subspecies, and is treated as a noun in apposition.

Distribution. Currently known from the Andes in northern Peru.

Genetic differentiation in *Eurema agave* (Cramer, 1775)

Genomic analysis of specimens of *Eurema agave* (Cramer, 1775) (type locality in Suriname; topotypical specimen sequenced as NVG-24043A07 (Figs. 1, 3e)) from across the range (Figs. 3, 4) reveals substantial

genetic differentiation, and groups of specimens forming compact clades are well separated from each other both in the nuclear and mitochondrial genome (Fig. 1 magenta, olive, red, and blue). While COI barcode differences between some of these clades are substantial (around 2%, 13 bp), the differentiation in the nuclear genome is less prominent (Fig. 1a, b), even compared to that between the two most closely related species *Eurema lucina* (Poey, [1852]) (type locality in Cuba) (Fig. 1 gray) and *Eurema priddyi* (Lathy, 1898) (type locality in Haiti) (Fig. 1 cyan). Therefore, until a larger number of specimens, including those from additional localities, are analyzed, we conservatively consider these clades to represent subspecies rather than species.

The topotypical male from Suriname (Fig. 3e) is in the clade (Fig. 1 olive) with specimens from eastern Colombia (Fig. 3d) and Trinidad (Fig. 3c). This clade corresponds to the nominotypical subspecies. We identify specimens from eastern and southern parts of Brazil as *Eurema agave pallida* (Chavannes, 1850) (type locality in Brazil: São Paulo) (Figs. 1 blue, 4d, e). This Atlantic subspecies is variable in the extent of expression of the dark border on the dorsal hindwing (Fig. 4d vs. e) and differs from the nominotypical (Amazonian) subspecies by a slightly narrower apical dark area on the dorsal forewing; this area has a more toothed proximal border along the veins. Two other subspecies, one from the northwestern part of the range (Panama and western Venezuela), and the other from the Andes in Ecuador, are described as new next.

Eurema agave panave Grishin, new subspecies

https://zoobank.org/E2C68CB6-0AE7-48EA-B628-B817C657E0F2

(Figs. 1 part, 3a–b)

Definition and diagnosis. Genomic analysis reveals that two specimens (from central Panama and western Venezuela) are genetically differentiated from *Eurema agave agave* (Cramer, 1775) (type locality in Suriname; topotypical specimen sequenced as NVG-24043A07) at least at the subspecies level (Fig. 1); e.g., their COI barcodes differ by 2% (13 bp). Due to the lack of stronger genetic differentiation in the nuclear genome (Fig. 1a, b), we conservatively regard these specimens as representing a new subspecies rather than a species. This new subspecies differs from others by the following combination of characters: slightly larger in overall size; with a more contrasting marginal dark pattern (also present on the dorsal hindwing in the specimens of the type series; but individuals in other populations vary in the extent of this dark marginal border from well-developed to completely absent, and this subspecies may also be variable when more individuals are examined); the dorsal forewing dark band along the outer margin spans from the costa to the middle of cell CuA_2-1A+2A forming two prominent tooth-shaped protrusions into the pale area of the wing along veins CuA_1 and CuA_2, nearly straight from the vein R_{3+4+5} to mid-cell M_3-CuA_1, and strongly concave (i.e., roundly indented) near the costa between veins R_1 and R_{3+4+5} [this band is less indented by the costa in other subspecies; rather straight to slightly concave throughout with more weakly developed “teeth” in the nominotypical subspecies (Fig. 3c–e); and narrower, may be with “teeth”, which are usually smaller and finer and may include an additional “tooth” at veins M_2 and M_3 in *Eurema agave pallida* (Chavannes, 1850) (type locality in Brazil: São Paulo) (Fig. 4d, e)]; somewhat greener (rather than yellower) ventral side scaling especially over the areas with dark scales on the dorsal side of the wings; and only weakly expressed postdiscal brown spots on the ventral hindwing with the largest (chevron-shaped) spot in cell M_1-M_2. Due to its partly cryptic nature and poorly explored individual and seasonal variation that is expected to be substantial, as in its relatives, this subspecies is best identified by DNA, with diagnostic base pairs in the nuclear genome: pse86800.23.3:A352T, pse5590.3.1:C27T, pse5590.3.1: C69T, pse1450.3.13:C78T, pse132.4.3:C2889T; and the COI barcode: A22G, A217G, A241A, 487C, A538A, T586C.

Barcode sequence of the holotype. Sample NVG-22084D12, GenBank PX568480, 658 base pairs:

AACTTTATATTTTATTTTTGGGATTTGATCAGGAATGGTAGGAACTTCTTTAAGACTATTAATTCGGACTGAATTAGGAAACCCCGGATCTCTCATTGGAGATGATCAAATTTATAATACA
ATTGTAACCGCTCATGCTTTTATTATAATTTTTTTTATAGTTATACCTATTATAATTGGAGGATTCGGAAATTGATTAATTCCTCTTATACTAGGGGCACCAGATATAGCTTTCCCCCGAA
TAAATAATATAAGTTTTTGACTTCTTCCTCCTTCTTTAACATTACTAATTTCAAGAAGTATTGTTGAAAATGGAGCAGGTACTGGTTGAACAGTTTACCCCCCTCTTTCCTCTAATATCGC
CCATAGAGGATCATCTGTTGACCTAGCAATTTTTTCTTTACATTTAGCCGGTATTTCTTCTATTTTAGGGGCTATTAATTTTATCACCACAATTATTAATATACGTATTAATAGAATATCA
TTCGATCAAATACCTCTTTTTGTTTGAGCTGTAGGAATTACAGCCTTATTATTATTACTTTCTTTACCTGTTTTAGCTGGGGCTATTACTATATTACTTACCGACCGTAATTTAAATACTT
CATTTTTTGACCCAGCAGGAGGGGGAGACCCAATCTTATACCAACATTTATTC

Fig. 3 (legend continues on the next page). *Eurema agave* in dorsal (left) and ventral (right) views, data in text or below: **a–b)** *E. agave panave* **ssp. n.** type series: **a)** holotype ♀ NVG-22084D12 Panama and **b)** paratype ♀ NVG-22084E02 Venezuela and **c–e)** *E. agave agave* non-type specimens: **c)** NVG-22084E03 ♀ Trinidad: Wallerfield, 7-Nov-1981, J. & F. Preston leg.

[MGCL]; **d)** NVG-23019E07 ♀ Colombia: Meta, Río Guayabero, Serranía de la Macarena, 300 m, 15-Jan-1959, D. Trapp leg. [ZSMC]; and **e)** topotype ♂ NVG-24043A07 Suriname: Batavia, 2-Oct-1966, H. P. Marx leg. [SMNS].

Type material. Holotype: ♀ deposited in the McGuire Center for Lepidoptera and Biodiversity collection, Gainesville, FL, USA (MGCL), illustrated in Fig. 3a, bears the following four printed rectangular labels, three white: [PANAMA: elev. 95-105 ft. | Colon Prov., Black Tank Rd. | 5 km N Gatun Locks | San Lorenzo Nat. Park | 9' 17.51"N, 79' 56.14"W | V.30.2009; C.V. Covell Jr.], [C. V. Covell colln. | MGCL Accession | # 2009-19], [DNA sample ID: | NVG-22084D12 | c/o Nick V. Grishin], and one red [HOLOTYPE ♀ | Eurema agave | panave Grishin]. **Paratype:** 1♀ NVG-22084E02 Venezuela: Zulia, Catatumbo, 8-Jan-1987, R. F. Denno leg. [MGCL] (Fig. 3b).

Type locality. Panama: Colón Province, San Lorenzo National Park, Black Tank Road, 5 km north of Gatún Locks, elevation 95–105 ft, GPS 9.2918, −79.9357.

Etymology. The name is given for the distribution of this subspecies, is a fusion: *Pana*[ma] + *ve*[nezuela], and is treated as a noun in apposition.

Distribution. Currently known from Panama and Venezuela.

Eurema agave livara Grishin, new subspecies

https://zoobank.org/E5272962-87B8-4085-AD7C-034D5340FD32

(Figs. 1 part, 4a–c)

Definition and diagnosis. Genomic analysis reveals that three specimens from the Andes in Ecuador are genetically differentiated from *Eurema agave agave* (Cramer, 1775) (type locality in Suriname; topotypical specimen sequenced as NVG-24043A07) at least at the subspecies level (Fig. 1); e.g., their COI barcodes differ by 2.1% (14 bp), and the barcode difference from *Eurema agave panave* **ssp. n.** is 2.5% (17 bp). Due to the lack of stronger genetic differentiation in the nuclear genome (Fig. 1a, b), we conservatively regard these specimens as representing a new subspecies rather than a species. This new subspecies differs from others by the following combination of characters: medium in overall size; with rather contrasting marginal dark pattern, browner and less black than in some relatives (may be partly expressed on the dorsal hindwing in some specimens); the dorsal forewing dark band along the outer margin spans from the costa to before the middle of cell CuA_2-1A+2A forming two nearly right-angled tooth-shaped protrusions into the pale area of the wing along veins CuA_1 and CuA_2, and a small denticle at the vein M_3, the band is slightly concave between veins M_1 and M_3, convex around the vein R_{3+4+5} and terminating at the costa near the end of the vein R_1 [not continuing along the costa as in *Eurema agave pallida* (Chavannes, 1850) (type locality in Brazil: São Paulo) (Fig. 4d, e); this band is strongly indented by the costa in *Eurema agave panave* **ssp. n.** (Fig. 3a, b) and rather straight to slightly concave throughout with more weakly developed "teeth" in the nominotypical subspecies (Fig. 3c–e)]; somewhat yellower (rather than greener) ventral side scaling; and well-defined, although diffuse, brown spots on the ventral hindwing. Due to its partly cryptic nature and poorly explored individual and seasonal variation that is expected to be substantial, as in its relatives, this subspecies is best identified by DNA, with diagnostic base pairs in the nuclear genome: pse13590.2.7:A444G, pse13590.2.7:A805G, pse165.60.3:A83T, pse13318.7.4:C96T, pse67313.1.4:C90T; and the COI barcode: A22A, A217A, A241G, T268C, 487C, A538G, T586T.

Barcode sequence of the holotype. Sample NVG-24043A10, GenBank PX568481, 658 base pairs:

AACTTTATATTTTATTTTTGGAATTTGATCAGGAATAGTAGGAACTTCTTTAAGACTATTAATTCGAACTGAATTAGGAAACCCCGGGTCTCTCATTGGAGATGATCAAATTTATAACACA
ATTGTAACCGCTCATGCTTTTATTATAATTTTTTTTATAGTTATACCTATTATAATTGGGGGATTCGGAAATTGATTAATTCCTCTTATACTAGGAGCACCAGATATAGCTTTCCCCCGGA
TAAATAATATAAGTTTTTGACTTCTCCCTCCTTCTTTAACATTACTAATTTCAAGAAGTATTGTTGAAAATGGAGCAGGTACTGGTTGAACAGTTTACCCCCCTCTTTCCTCTAATATCGC
CCATAGAGGATCATCTGTTGACCTAGCAATTTTTTCTTTACATTTAGCTGGTATTTCTTCTATTTTAGGAGCTATTAATTTTATCACCACAATTATTAATATACGTATTAATAGAATGTCA
TTCGATCAAATACCTCTTTTTGTTTGAGCTGTAGGAATTACAGCCTTATTATTGTTACTTTCTTTACCTGTTTTAGCTGGAGCTATTACTATATTACTTACTGACCGTAATTTAAATACTT
CATTTTTTGACCCAGCAGGAGGAGGAGACCCAATCTTATACCAACATTTATTT

COI barcode sequences of paratypes (sample NVG-24043A09, GenBank PX568482 and sample NVG-23019E08, GenBank PX568483) are identical to that of the holotype.


a
b
c
d
e
1 cm

Fig. 4 (see the previous page). *Eurema agave* in dorsal (left) and ventral (right) views, data in text or below: **a–c)** *E. agave livara* **ssp. n.** type series from Ecuador: **a)** holotype ♂ NVG-24043A10 and paratypes: **b)** ♂ NVG-24043A09 and **c)** ♀ NVG-23019E08 and **d–e)** *E. agave pallida* non-type ♂♂ from Brazil: Rio de Janeiro: **d)** NVG-19078E02, USNMENT_01559874 Itatiaia National Park, 800 m, 22-Feb-1995, A. Caldas & students leg. [USNM] and **e)** NVG-23019E09 Cascadura, 15-Feb-1892, ex coll. Erhardt [ZSMC].

Type material. Holotype: ♂ deposited in the Staatliches Museum für Naturkunde, Stuttgart, Germany (SMNS), illustrated in Fig. 4a, bears the following five printed rectangular labels (text in italics handwritten), four white: [ECUADOR occ. | Prov. BOLIVAR | Umg. Balzapamba | 250–400m | 29.XII. 1979], [lg. Reissinger], [Staatl. Museum | für Naturkunde | Stuttgart | XII.1979], [DNA sample ID: | NVG-24043A10 | c/o Nick V. Grishin], and one red [HOLOTYPE ♂ | Eurema agave | livara Grishin]. **Paratypes:** 1♂ and 1♀: Ecuador: 1♂ NVG-24043A09 data as the holotype (Fig. 4b) and 1♀ NVG-23019E08 no locality details, old, ex coll. Erhardt [ZSMC] (Fig. 4c).

Type locality. Ecuador: Bolívar Province, vicinity of Balzapamba, elevation 250-400 m.

Etymology. The name is derived from the Ecuadorian province of the type locality, [bo]*livar* + *a*, and is treated as a feminine noun in apposition.

Distribution. Currently known from the Andes in Ecuador.

Family Riodinidae Grote, 1895 (1827)

Lasaia rosamonda Weeks, 1900 is a valid species distinct from *Lasaia moeros* Staudinger, 1888

Lasaia rosamonda Weeks, 1900 was described from an unstated number of specimens from Colombia: Bogotá (likely only one specimen, in MCZ) (Weeks 1900) and has been treated as a junior subjective synonym of *Lasaia moeros* Staudinger, 1888 (type locality in Peru: Junín; syntype sequenced as NVG-18054F02). The genomic analysis reveals that specimens from Ecuador that we identified as *L. rosamonda* form a clade sister to both *L. moeros* and *Lasaia kennethi* Weeks, 1901 (type locality in Bolivia), and therefore this clade represents a species-level taxon, which is genetically differentiated from others (Fig. 5), e.g., their COI barcodes differ by 2.6% (17 bp) from *L. moeros* and by 2.7% (18 bp) from *L. kennethi*. Therefore, we propose that *Lasaia rosamonda* Weeks, 1900, **stat. rest.** is a valid species distinct from *L. moeros* Staudinger, 1888.

Species concepts in *Lasaia* H. Bates, 1868

Using an adult-morphological species concept (i.e., one based on morphology of imagines), Arellano-Covarrubias et al. (2025) propose taxonomic adjustments to *Lasaia* (*Lasaia*) H. Bates, 1868 (type species *Papilio meris* Stoll, 1781), largely focusing on Mexican species. While the morphospecies concept may be convenient for simplifying the curation of pinned butterfly collections, DNA-based studies have been instrumental in uncovering hidden species diversity in butterflies (Hebert et al. 2004; Núñez et al. 2022; Álvarez et al. 2025). Reducing a species to "adult morphology traits" (Arellano-Covarrubias et al. 2025) contrasts with these contemporary and more objective approaches stemming from a modified biological species concept (i.e., species are reproductively isolated groups of populations in nature, although the reproductive barrier is porous to varying degrees), most similar to the "genomic integrity species definition" of Sperling (2003), which we regard as a better representation of biological reality. Genomic sequence encodes all features of the phenotype, which, in addition to adult characters, include those of immature stages, behavior (including mating preferences), and habitat preference or tolerance, among others. Moreover, genomic analysis offers a direct way of measuring gene flow within species and gene exchange among species in nature, which are instrumental for species delimitation (Rosser et al. 2024).

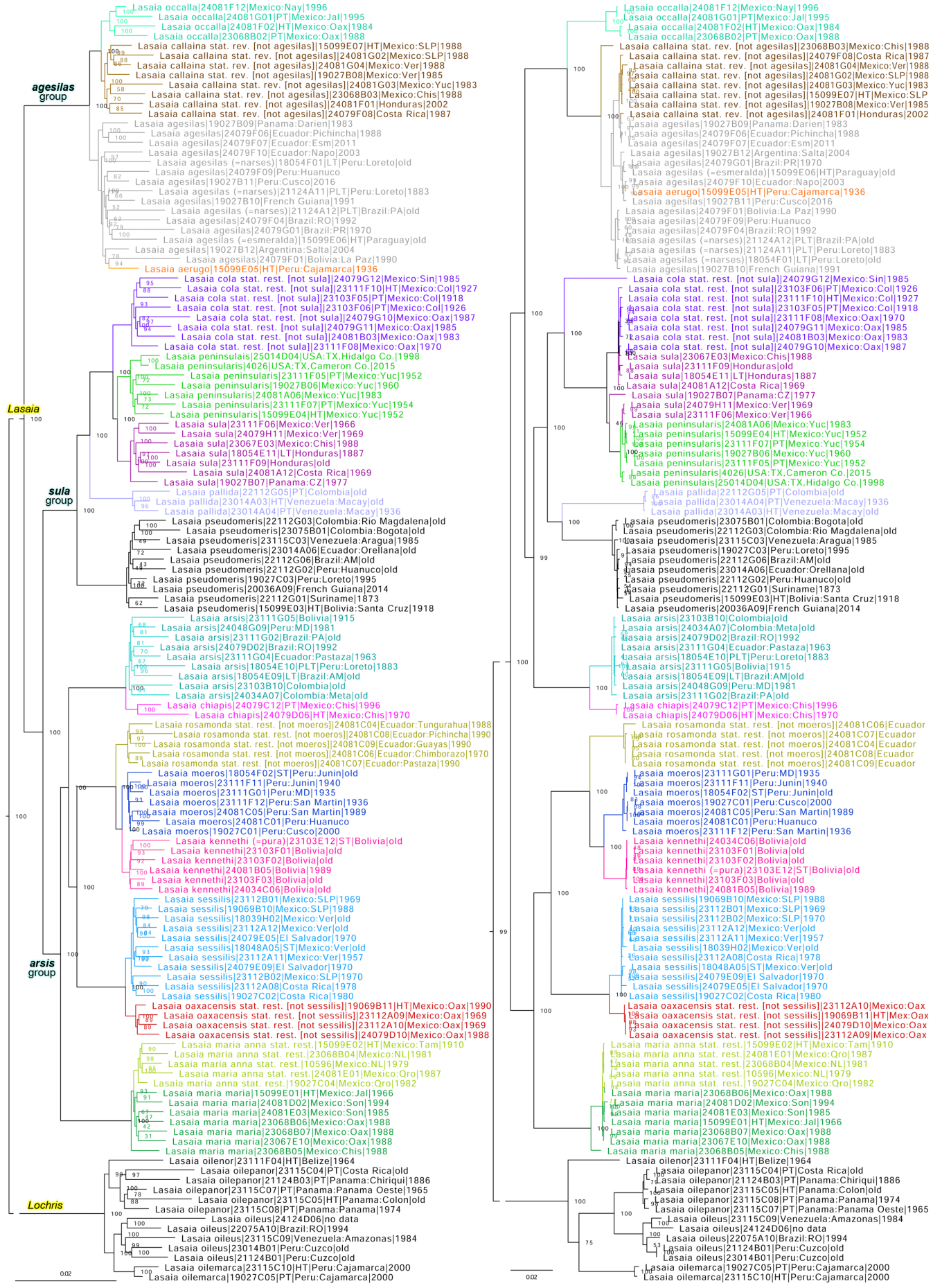

a
nuclear genome (autosomes)
b
mitochondrial genome
agesilas group
sula group
arsis group
Lasaia
Lochris
Lasaia occalla|24081F12|Mexico:Nay|1996
Lasaia occalla|24081G01|PT|Mexico:Jal|1995
Lasaia occalla|24081F02|HT|Mexico:Oax|1984
Lasaia occalla|23068B02|PT|Mexico:Oax|1988
Lasaia callaina stat. rev. [not agesilas]|15099E07|HT|Mexico:SLP|1988
Lasaia callaina stat. rev. [not agesilas]|24081G02|Mexico:SLP|1988
Lasaia callaina stat. rev. [not agesilas]|24081G04|Mexico:Ver|1988
Lasaia callaina stat. rev. [not agesilas]|19027B08|Mexico:Ver|1985
Lasaia callaina stat. rev. [not agesilas]|24081G03|Mexico:Yuc|1983
Lasaia callaina stat. rev. [not agesilas]|23068B03|Mexico:Chis|1988
Lasaia callaina stat. rev. [not agesilas]|24081F01|Honduras|2002
Lasaia callaina stat. rev. [not agesilas]|24079F08|Costa Rica|1987
Lasaia agesilas|19027B09|Panama:Darien|1983
Lasaia agesilas|24079F06|Ecuador:Pichincha|1988
Lasaia agesilas|24079F07|Ecuador:Esm|2011
Lasaia agesilas|24079F10|Ecuador:Napo|2003
Lasaia agesilas (=narses)|18054F01|LT|Peru:Loreto|old
Lasaia agesilas|24079F09|Peru:Huanuco
Lasaia agesilas|19027B11|Peru:Cusco|2016
Lasaia agesilas (=narses)|21124A11|PLT|Peru:Loreto|1883
Lasaia agesilas|19027B10|French Guiana|1991
Lasaia agesilas (=narses)|21124A12|PLT|Brazil:PA|old
Lasaia agesilas|24079F04|Brazil:RO|1992
Lasaia agesilas|24079G01|Brazil:PR|1970
Lasaia agesilas (=esmeralda)|15099E06|HT|Paraguay|old
Lasaia agesilas|19027B12|Argentina:Salta|2004
Lasaia agesilas|24079F01|Bolivia:La Paz|1990
Lasaia aerugo|15099E05|HT|Peru:Cajamarca|1936
Lasaia cola stat. rest. [not sula]|24079G12|Mexico:Sin|1985
Lasaia cola stat. rest. [not sula]|23111F10|HT|Mexico:Col|1927
Lasaia cola stat. rest. [not sula]|23103F05|PT|Mexico:Col|1918
Lasaia cola stat. rest. [not sula]|23103F06|PT|Mexico:Col|1926
Lasaia cola stat. rest. [not sula]|24079G10|Mexico:Oax|1987
Lasaia cola stat. rest. [not sula]|24079G11|Mexico:Oax|1985
Lasaia cola stat. rest. [not sula]|24081B03|Mexico:Oax|1983
Lasaia cola stat. rest. [not sula]|23111F08|Mexico:Oax|1970
Lasaia peninsularis|25014D04|USA:TX,Hidalgo Co.|1998
Lasaia peninsularis|4026|USA:TX,Cameron Co.|2015
Lasaia peninsularis|23111F05|PT|Mexico:Yuc|1952
Lasaia peninsularis|19027B06|Mexico:Yuc|1960
Lasaia peninsularis|24081A06|Mexico:Yuc|1983
Lasaia peninsularis|23111F07|PT|Mexico:Yuc|1954
Lasaia peninsularis|15099E04|HT|Mexico:Yuc|1952
Lasaia sula|23111F06|Mexico:Ver|1966
Lasaia sula|24079H11|Mexico:Ver|1969
Lasaia sula|23067E03|Mexico:Chis|1988
Lasaia sula|18054E11|LT|Honduras|1887
Lasaia sula|23111F09|Honduras|old
Lasaia sula|24081A12|Costa Rica|1969
Lasaia sula|19027B07|Panama:CZ|1977
Lasaia pallida|22112G05|PT|Colombia|old
Lasaia pallida|23014A03|HT|Venezuela:Macay|old
Lasaia pallida|23014A04|PT|Venezuela:Macay|1936
Lasaia pseudomeris|22112G03|Colombia:Rio Magdalena|old
Lasaia pseudomeris|23075B01|Colombia:Bogota|old
Lasaia pseudomeris|23115C03|Venezuela:Aragua|1985
Lasaia pseudomeris|23014A06|Ecuador:Orellana|old
Lasaia pseudomeris|22112G06|Brazil:AM|old
Lasaia pseudomeris|22112G02|Peru:Huanuco|old
Lasaia pseudomeris|19027C03|Peru:Loreto|1995
Lasaia pseudomeris|20036A09|French Guiana|2014
Lasaia pseudomeris|22112G01|Suriname|1873
Lasaia pseudomeris|15099E03|HT|Bolivia:Santa Cruz|1918
Lasaia arsis|23111G05|Bolivia|1915
Lasaia arsis|24048G09|Peru:MD|1981
Lasaia arsis|23111G02|Brazil:PA|old
Lasaia arsis|24079D02|Brazil:RO|1992
Lasaia arsis|23111G04|Ecuador:Pastaza|1963
Lasaia arsis|18054E10|PLT|Peru:Loreto|1883
Lasaia arsis|18054E09|LT|Brazil:AM|old
Lasaia arsis|23103B10|Colombia|old
Lasaia arsis|24034A07|Colombia:Meta|old
Lasaia chiapis|24079C12|PT|Mexico:Chis|1996
Lasaia chiapis|24079D06|HT|Mexico:Chis|1970
Lasaia rosamonda stat. rest. [not moeros]|24081C04|Ecuador:Tungurahua|1988
Lasaia rosamonda stat. rest. [not moeros]|24081C08|Ecuador:Pichincha|1990
Lasaia rosamonda stat. rest. [not moeros]|24081C09|Ecuador:Guayas|1990
Lasaia rosamonda stat. rest. [not moeros]|24081C06|Ecuador:Chimborazo|1970
Lasaia rosamonda stat. rest. [not moeros]|24081C07|Ecuador:Pastaza|1990
Lasaia moeros|18054F02|ST|Peru:Junin|old
Lasaia moeros|23111F11|Peru:Junin|1940
Lasaia moeros|23111G01|Peru:MD|1935
Lasaia moeros|23111F12|Peru:San Martin|1936
Lasaia moeros|24081C05|Peru:San Martin|1989
Lasaia moeros|24081C01|Peru:Huanuco
Lasaia moeros|19027C01|Peru:Cusco|2000
Lasaia kennethi (=pura)|23103E12|ST|Bolivia|old
Lasaia kennethi|23103F01|Bolivia|old
Lasaia kennethi|23103F02|Bolivia|old
Lasaia kennethi|24081B05|Bolivia|1989
Lasaia kennethi|23103F03|Bolivia|old
Lasaia kennethi|24034C06|Bolivia|old
Lasaia sessilis|23112B01|Mexico:SLP|1969
Lasaia sessilis|19069B10|Mexico:SLP|1988
Lasaia sessilis|18039H02|Mexico:Ver|old
Lasaia sessilis|23112A12|Mexico:Ver|old
Lasaia sessilis|24079E05|El Salvador|1970
Lasaia sessilis|18048A05|ST|Mexico:Ver|old
Lasaia sessilis|23112A11|Mexico:Ver|1957
Lasaia sessilis|24079E09|El Salvador|1970
Lasaia sessilis|23112B02|Mexico:SLP|1970
Lasaia sessilis|23112A08|Costa Rica|1978
Lasaia sessilis|19027C02|Costa Rica|1980
Lasaia oaxacensis stat. rest. [not sessilis]|19069B11|HT|Mexico:Oax|1990
Lasaia oaxacensis stat. rest. [not sessilis]|23112A09|Mexico:Oax|1969
Lasaia oaxacensis stat. rest. [not sessilis]|23112A10|Mexico:Oax|1969
Lasaia oaxacensis stat. rest. [not sessilis]|24079D10|Mexico:Oax|1988
Lasaia maria anna stat. rest.|15099E02|HT|Mexico:Tam|1910
Lasaia maria anna stat. rest.|23068B04|Mexico:NL|1981
Lasaia maria anna stat. rest.|10596|Mexico:NL|1979
Lasaia maria anna stat. rest.|24081E01|Mexico:Qro|1987
Lasaia maria anna stat. rest.|19027C04|Mexico:Qro|1982
Lasaia maria maria|15099E01|HT|Mexico:Jal|1966
Lasaia maria maria|24081D02|Mexico:Son|1994
Lasaia maria maria|24081E03|Mexico:Son|1985
Lasaia maria maria|23068B06|Mexico:Oax|1988
Lasaia maria maria|23068B07|Mexico:Oax|1988
Lasaia maria maria|23067E10|Mexico:Oax|1988
Lasaia maria maria|23068B05|Mexico:Chis|1988
Lasaia oilenor|23111F04|HT|Belize|1964
Lasaia oilepanor|23115C04|PT|Costa Rica|old
Lasaia oilepanor|21124B03|PT|Panama:Chiriqui|1886
Lasaia oilepanor|23115C07|PT|Panama:Panama Oeste|1965
Lasaia oilepanor|23115C05|HT|Panama:Colon|old
Lasaia oilepanor|23115C08|PT|Panama:Panama|1974
Lasaia oileus|24124D06|no data
Lasaia oileus|22075A10|Brazil:RO|1994
Lasaia oileus|23115C09|Venezuela:Amazonas|1984
Lasaia oileus|23014B01|Peru:Cuzco|old
Lasaia oileus|21124B01|Peru:Cuzco|old
Lasaia oilemarca|23115C10|HT|Peru:Cajamarca|2000
Lasaia oilemarca|19027C05|PT|Peru:Cajamarca|2000
0.02

Fig. 5 (see the previous page). Phylogenetic trees of *Lasaia* constructed from protein-coding regions in: **a)** the nuclear genome (autosomes), based on 1,069,491 positions, and **b)** the mitochondrial genome. Subgenera (*Lasaia* and *Lochris*) and species groups are labeled by their clades in the nuclear genome tree (highlighted yellow and blue, respectively), and different species in the subgenus *Lasaia* are colored: *L. occalla* (aquamarine), *L. callaina* **stat. rev.** (brown), *L. agesilas* (gray), *L. aerugo* (orange), *L. cola* **stat. rest.** (violet), *L. peninsularis* (green), *L. sula* (dark magenta), *L. pallida* (lavender), *L. pseudomeris* (black), *L. arsis* (cyan), *L. chiapis* (magenta), *L. rosamonda* (olive), *L. moeros* (dark blue), *L. kennethi* (pink), *L. sessilis* (blue), *L. oaxacensis* **stat. rest.** (red), and *L. maria* (dark green with *L. maria anna* **stat. rest.** in lime green). Ultrafast bootstrap (Hoang et al. 2018) values are shown at nodes. Gaps in branches indicate where a vertical slice of the tree was removed to reduce its horizontal dimension (to allow an increase in the font size), i.e., branches with gaps are longer than shown.

Even within their framework limited to phenotypic characters of adults, Arellano-Covarrubias et al. (2025) confirmed that *Inkana* Grishin, 2021 (type species *Charis incoides* Schaus, 1902) was distinct from *Lasaia* and that *Lasaia* (*Lasaia*) *peninsularis* Clench, 1972 (type locality Mexico: Yucatán, Pisté) was a species-level taxon. The use of "**stat. nov.**" (*status novus*, "new status") for *L. peninsularis* in their work is a *lapsus*, because they did not propose a taxonomic change, but only reaffirmed the treatment previously published in Zhang et al. (2023) and already implemented on several websites (Warren et al. 2024; iNaturalist 2025).

Opinions expressed in Arellano-Covarrubias et al. (2025) about several *Lasaia* taxa, based on visual inspection of their phenotypes, conflict with results obtained through genomic analyses. Because of the tree topology and genetic differentiation across different genomic regions, including nuclear and mitochondrial (see fig. 11 in Zhang et al. (2024), figs. 6, 9 in Zhang et al. (2025a), fig. 6 in Zhang et al. (2025b), and Fig. 5 in this work), we restore the following taxa as valid species: *Lasaia* (*Lasaia*) *callaina* Clench, 1972, **stat. rev.** (type locality in Mexico: San Luis Potosí) [not a subspecies of *Lasaia agesilas* (Latreille, [1809]) (type locality in Peru)], *Lasaia* (*Lasaia*) *oaxacensis* Grishin, 2024, **stat. rest.** (type locality in Mexico: Oaxaca) [not a synonym of *Lasaia* (*Lasaia*) *sessilis* Schaus, 1890 (type locality Mexico: Veracruz, Coatepec)], and *Lasaia* (*Lasaia*) *cola* Grishin, 2025, **stat. rest.** (type locality Mexico: Colima, Comala) [not a synonym of *Lasaia* (*Lasaia*) *sula* Staudinger, 1888 (type locality in Honduras)]. For instance, *L. cola* cannot be a synonym of *L. sula* if *L. peninsularis* is treated as a valid species, because *L. sula* is not sister to *L. cola*, but to *L. peninsularis* (fig. 6a in Zhang et al. (2025b) and Fig. 5). Hence, synonymizing *L. cola* with *L. sula* renders *L. sula* paraphyletic with respect to *L. peninsularis*. Furthermore, we restore *Lasaia* (*Lasaia*) *maria anna* Clench, 1972, **stat. rest.** (type locality in Mexico: Tamaulipas) as a valid subspecies [not a synonym of *Lasaia* (*Lasaia*) *maria* Clench, 1972 (type locality in Mexico: Jalisco)], pending further studies, because we find measurable genetic differentiation in the nuclear genome between the northeastern and southwestern populations in this species (Fig. 5a lime vs. dark green), consistent with their minor phenotypic differences and distinct biogeographical realms.

Moreover, as a result of additional specimen sequencing, we extend the range for recently described Mexican species: *Lasaia occalla* Grishin, 2025 (type locality in Oaxaca) is found in Nayarit (Fig. 6a) in addition to Jalisco and Oaxaca, and *L. cola* **stat. rest.** is present in Sinaloa (Fig. 6b) and Oaxaca (Fig. 6c–e), in addition to Colima. Future field studies involving immature stages and habitat preferences (beyond a limited set of adult phenotype characters), together with genomic sequencing of additional specimens followed by analyses of genome structure and non-coding regions (in addition to protein-coding genes that we analyzed), are expected to bring additional insight into *Lasaia* systematics. As in the case with *Pterourus* Scopoli, 1777 (Pavulaan 2024; DeRoller et al. 2025), *Celastrina* Tutt, 1906 (LaBar et al. 2022; Pavulaan 2025), and *Euphilotes* Mattoni, [1978] (Kohler and Warren 2021), such studies of *Lasaia* are more likely to reveal additional species and subspecies, rather than lump described taxa.

Incongruence between the nuclear genome and the mitochondrial genome phylogenies in *Lasaia* H. Bates, 1868, and the status of *Lasaia aerugo* Clench, 1972

While the topology reflecting relationships among some *Lasaia* species is the same in the nuclear and the mitochondrial genome trees, e.g., the *L. arsis* group species (except the position of *L. arsis* with *L. chiapis*)

Fig. 6. New records of *Lasaia* from Mexican states, ♂♂ in dorsal (above or left) and ventral (below or right) views [MGCL]: **a)** *L. occalla* NVG-24081F12 Nayarit, vic. San Francisco, 30-Sep-1996 and **b–e)** *L. cola* **stat. rest.**: **b)** NVG-24079G12 Sinaloa, Rte 40, 5 mi E Jct Rte 15, 22-Jul-1985, D. D. Mullins leg. and **c–e)** Oaxaca, Candelaria Loxicha: **c)** NVG-24079G10, 30-Jul-1987, E. C. Welling leg.; **d)** NVG-24079G11, 15-Aug-1985, E. C. Welling leg.; and **e)** NVG-24081B03, 16-Aug-1983.

(Fig. 5a vs. b), others exhibit topological differences. The most notable difference is that the subclade of *L. arsis* with *L. chiapis* is placed confidently within the *L. arsis* group clade in the nuclear genome tree (see the list below) (Fig. 5a), but this subclade is sister to the *L. sula* group in the mitochondrial genome tree (Fig. 5b). Next, mitochondrial haplotypes in the *L. agesilas* group (except for *L. occalla*) (Fig. 5b) do not correspond to the species defined by the nuclear genome tree (Fig. 5a). Finally, *L. sula* possesses mitochondrial haplotypes of both *L. cola* and *L. peninsularis*, and a specimen of *L. cola* from Mexico: Sinaloa (NVG-24079G12) has a unique haplotype. This incongruence implies that COI barcodes may be of limited value for *Lasaia* identification and suggests complexities in the evolution of this genus, such as incomplete lineage sorting and introgression. It is possible that the most divergent haplotype found in the northernmost specimen of *L. cola* that we sequenced corresponds to the original haplotype of this species, and the haplotype shared with *L. sula* is the result of introgression.

Genomic phylogenies do not reveal overall genetic differentiation of *Lasaia aerugo* Clench, 1972 known from a single specimen (the holotype) from Cajamarca, Peru, and place it within *Lasaia agesilas* (Latreille, [1809]) (type locality in Peru) (Fig. 5 orange) despite phenotypic uniqueness of this male (Clench 1972). Hence, either this specimen is an aberrant or a variation of *L. agesilas*, or the resolution of our global genomic analysis is insufficient to understand details of speciation in this group. Short of a more detailed DNA analysis or finding additional specimens of this species, we conservatively do not propose changes to the status of *L. aerugo* and keep it as a species-level taxon pending further studies.

A preliminary taxonomic list of *Lasaia* H. Bates, 1868

To aid future research, we compiled a preliminary taxonomic list of the genus *Lasaia*. The genus consists of two subgenera, and we divide the nominotypical subgenus into three species groups corresponding to the three major clades in the nuclear genome tree (Fig. 5a). *Lasaia* species are tentatively ordered to maximize phenotypic similarity and geographic proximity of the list neighbors but without disrupting phylogenetic order in the nuclear genome tree (Fig. 5a): i.e., a strongly supported clade in the tree is a continuous segment in the list. Arbitrarily, and following Clench (1972), we place the subgenus *Lochris* consisting of brown species last. Therefore, less blue, brownish species of the subgenus *Lasaia* are placed right before *Lochris*, and this decision sets the order of all major clades according to the phylogeny. Additionally, we place *L. meris* next to *L. pseudomeris*. We note that since Clench (1972), *L. meris* is effectively treated as a *nomen dubium*, without formally giving it this status. No specimens definitively identified as *L. meris* are known, but the original illustration (Stoll 1781) depicts a species most similar in facies to *L. arsis*, and *L. meris* is tentatively placed before it in the list. The category of taxonomic change is shown in red font. Comments are given following a vertical bar | after the type locality; an equal sign = precedes junior subjective synonyms given in their original genus combinations. The list covers 24 valid taxa comprising 23 species and 1 additional subspecies.

Genus ***Lasaia*** H. Bates, 1868; type species *Papilio meris* Stoll, 1781

Subgenus *Lasaia* H. Bates, 1868; type species *Papilio meris* Stoll, 1781

agesilas species group

Lasaia occalla Grishin, 2025; Mexico: Oaxaca, Candelaria Loxicha

Lasaia callaina Clench, 1972; Mexico: San Luis Potosí

Lasaia agesilas (Latreille, [1809]); Peru

= *Lasaia narses* Staudinger, 1888, syn. conf. (Fig. 5); Peru: Loreto | junior subjective synonym

= *Lasaia agesilas esmeralda* Clench, 1972, syn. conf. (Fig. 5); Paraguay | junior subjective synonym

Lasaia aerugo Clench, 1972; Peru: Cajamarca | possibly a subspecies or synonym of *L. agesilas*

Lasaia maritima J. Hall & Lamas, 2001; Peru: Piura | no genomic data yet; position in the list is tentative

sula species group

Lasaia cola Grishin, 2025, stat. rest.; Mexico: Colima, Comala | not a synonym of *L. sula*

Lasaia peninsularis Clench, 1972; Mexico: Yucatán
Lasaia sula Staudinger, 1888; Honduras
Lasaia pallida Grishin, 2024; Venezuela: Aragua, Maracay
Lasaia pseudomeris Clench, 1972; Bolivia

arsis species group

Lasaia meris (Stoll, 1781); Surinam | no specimens known; functionally, a *nomen dubium*
Lasaia arsis Staudinger, [1887]; Brazil: Amazonas, Manicoré | possibly a synonym of *L. meris*
Lasaia chiapis Grishin, 2025; Mexico: Chiapas, San Quintín
Lasaia rosamonda Weeks, 1900, stat. rest.; Colombia: Bogotá | not a synonym of *L. moeros*
Lasaia moeros Staudinger, 1888; Peru: Junín, Chanchamayo
Lasaia kennethi Weeks, 1901; Bolivia
= *Lasaia merita* Godman, 1903; Bolivia | junior subjective synonym
= *Lasaia pura* Seitz, 1917, syn. conf. (Fig. 5); Bolivia | junior subjective synonym
Lasaia sessilis Schaus, 1890; Mexico: Veracruz, Coatepec
Lasaia oaxacensis Grishin, 2024, stat. rest.; Mexico: Oaxaca | not a synonym of *L. sessilis*
Lasaia maria Clench, 1972; Mexico: Jalisco, Ajijic
Lasaia maria anna Clench, 1972, stat. rest.; Mexico: Tamaulipas | not a synonym of *L. maria*
Lasaia maria maria Clench, 1972; Mexico: Jalisco, Ajijic

Subgenus *Lochris* Grishin, 2025; type species *Lasaia oileus* Godman, 1903

Lasaia oilenor Grishin, 2025; Belize: Stann Creek, Middlesex
Lasaia oilepanor Grishin, 2025; Panama: Colón, Gatún Lake area
Lasaia oileus Godman, 1903; Paraguay
Lasaia oilemarca Grishin, 2025; Peru: Cajamarca, Chilasque

Family Hesperiidae Latreille, 1809

Udranomia eurianus Grishin, new species

https://zoobank.org/B681E3D2-37A2-4179-82A3-11BAF4F86F5C

(Figs. 7 part, 8a, 9)

Definition and diagnosis. Genomic analysis reveals that a specimen from north-central Ecuador initially identified as *Udranomia eurus* (Mabille & Boullet, 1919) (type locality in Venezuela: vic. Mérida; holotype sequenced as NVG-18086C05) (Fig. 8b–d) is genetically differentiated from it at the species level (Fig. 7); e.g., their COI barcodes differ by 4.4% (29 bp), and therefore this specimen represents a new species. This new species keys to *Udranomia eurus* (B.5.3) in Evans (1952), but differs from it and

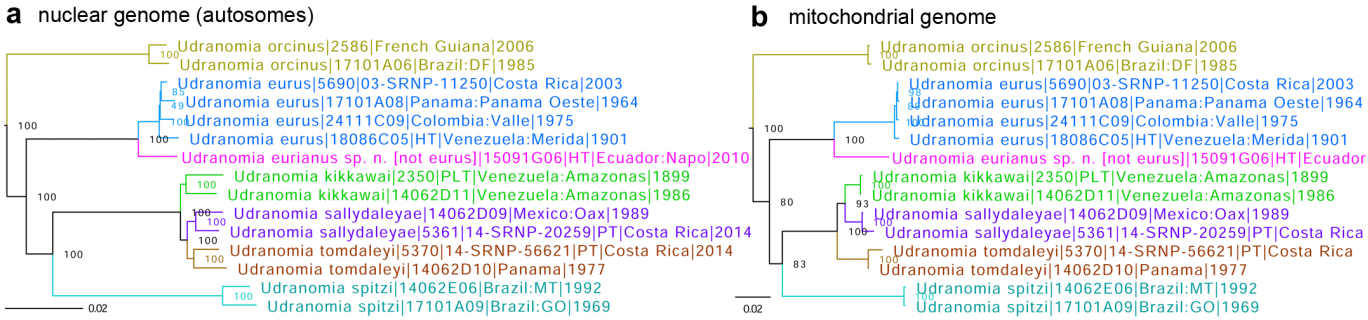


Fig. 7. Phylogenetic trees of all valid species of *Udranomia* A. Butler, 1870 constructed from protein-coding regions in: **a)** the nuclear genome (autosomes), based on 5,806,080 positions, and **b)** the mitochondrial genome. Different species are colored differently: *U. orcinus* (C. Felder & R. Felder, 1867) (olive), *U. eurus* (blue), *U. eurianus* **sp. n.** (magenta), *U. kikkawai* (Weeks, 1906) (green), *U. sallydaleyae* Burns, 2017 (violet), *U. tomdaleyi* Burns, 2017 (brown), and *U. spitzi* (Hayward, 1942) (cyan). Ultrafast bootstrap (Hoang et al. 2018) values are shown at nodes.

Fig. 8. *Udranomia* specimens in dorsal (left of the panel letter) and ventral (right of the panel letter) views: **a)** *U. eurianus* **sp. n.** holotype ♂ NVG-18086C05 from Ecuador: Napo, Tena, 650 m, Oct-2010, M. Simon leg. [MGCL] and **b–d)** *U. eurus*: **b)** non-type ♀ NVG-24111C09 from Colombia: Valle del Cauca, Río Anchicayá, 1150 m, 24-Dec-1975, S. R. & L. M. Steinhauser leg., genitalia SRS-1240 [MGCL], **c)** holotype ♂ NVG-18086C05, EL63184 from Venezuela, Mérida, 1901, Boursey leg. [MNHP]; and **d)** non-type ♂ NVG-17101A08, USNMENT_00913561 from Panama: Panamá Oeste, Cerro Campana, 2570', 19-Aug-1964, G. B. Small leg. [USNM].

other relatives by the following combination of characters in males: generally larger semihyaline spots on the hindwing, e.g., the spot in cell CuA_2-1A+2A that does not overlap the spot in cell CuA_1-CuA_2; a more prominent anterior arm of the dorsal forewing discal cell spot; more extensive olive overscaling towards the inner forewing margin on the dorsal side; more expressed green overscaling in the posterior part of the dorsal hindwing base; a rounder and more prominently serrate dorsal process of the harpe; a longer ampulla with a straighter dorsal margin; and a broader ventral tooth of the aedeagus. Due to its cryptic nature and unexplored individual variation, this species is best identified by DNA, with diagnostic base pairs in the nuclear genome: aly5294.28.7:C51T, aly281.9.5:G64C, aly1603.84.3:C1125T, aly221.13.16:C63A, aly727.21.2:C87A, aly300.3.1:A69A (not C), aly16576.6.12:T117T (not C), aly318.28.6:C130C (not T), aly1097.6.3:T46T (not C), aly1097.6.3:A75A (not G); and the COI barcode: T118C, T172C, A283C, A388G, A466A.

Barcode sequence of the holotype. Sample NVG-15091G06, GenBank PX568484, 658 base pairs:

AACATTATATTTTATTTTTGGAATTTGAGCAGGAATAGTAGGAACATCTCTTAGTCTTCTAATTCGAACTGAATTAGGAACCCCAGGATCTTTAATTGGAGATGATCAAATTTATAACACT
ATTGTTACAGCTCATGCTTTTATTATAATTTTTTTTATAGTTATACCTATCATAATTGGAGGATTTGGAAATTGATTAGTACCATTAATATTAGGAGCTCCTGATATAGCTTTCCCCCGAA
TAAATAATATAAGATTCTGATTATTACCCCCTTCATTAACCCTTTTAATTTCAAGAAGAATCGTAGAAAATGGAGCTGGAACTGGATGAACAGTTTACCCCCCACTTTCATCTAATATTGC
ACACCAAGGATCATCAGTAGATTTGGCAATTTTTTCACTTCATTTAGCAGGAATTTCTTCAATCTTAGGAGCTATTAATTTTATTACAACAATTATTAATATACGAGTTAGAAATTTATCA
TTTGATCAACTTCCACTTTTTATTTGAGCTGTAGGAATTACTGCATTATTATTATTACTTTCTTTACCTGTATTAGCAGGAGCTATTACTATACTTTTAACAGATCGAAATTTAAATACAT
CATTTTTCGATCCTGCTGGAGGAGGAGATCCAATTCTTTATCAACATTTATTT

Type material. Holotype: ♂ deposited in the McGuire Center for Lepidoptera and Biodiversity collection, Gainesville, FL, USA (MGCL), illustrated in Fig. 8a (genitalia Fig. 9), bears the following six rectangular labels (1st handprinted, others printed), five white: [ECUADOR-NAPO | TENA 650 M | X-10], [M. Simon | MGCL Accession | #2011-8], [DNA sample ID: | NVG-15091G06 | c/o Nick V. Grishin], [DNA sample ID: | NVG-24111C08 | c/o Nick V. Grishin], [genitalia | NVG250720-14 | c/o Nick V. Grishin], and one red [HOLOTYPE ♂ | Udranomia | eurianus Grishin]. The first label is in Mark Simon's handwriting, and he must have collected this specimen. The first DNA sample ID refers to the extraction from a leg (sequenced), and the second from the abdomen (stored) prior to genitalia dissection.

Type locality. Ecuador: Napo, Tena, elevation 650 m.

Etymology. The name is derived from the name of its sister species *U. eurus* and is treated as a noun in apposition.

Distribution. Currently known from the holotype collected in north-central Ecuador at the eastern foothills of the Andes.

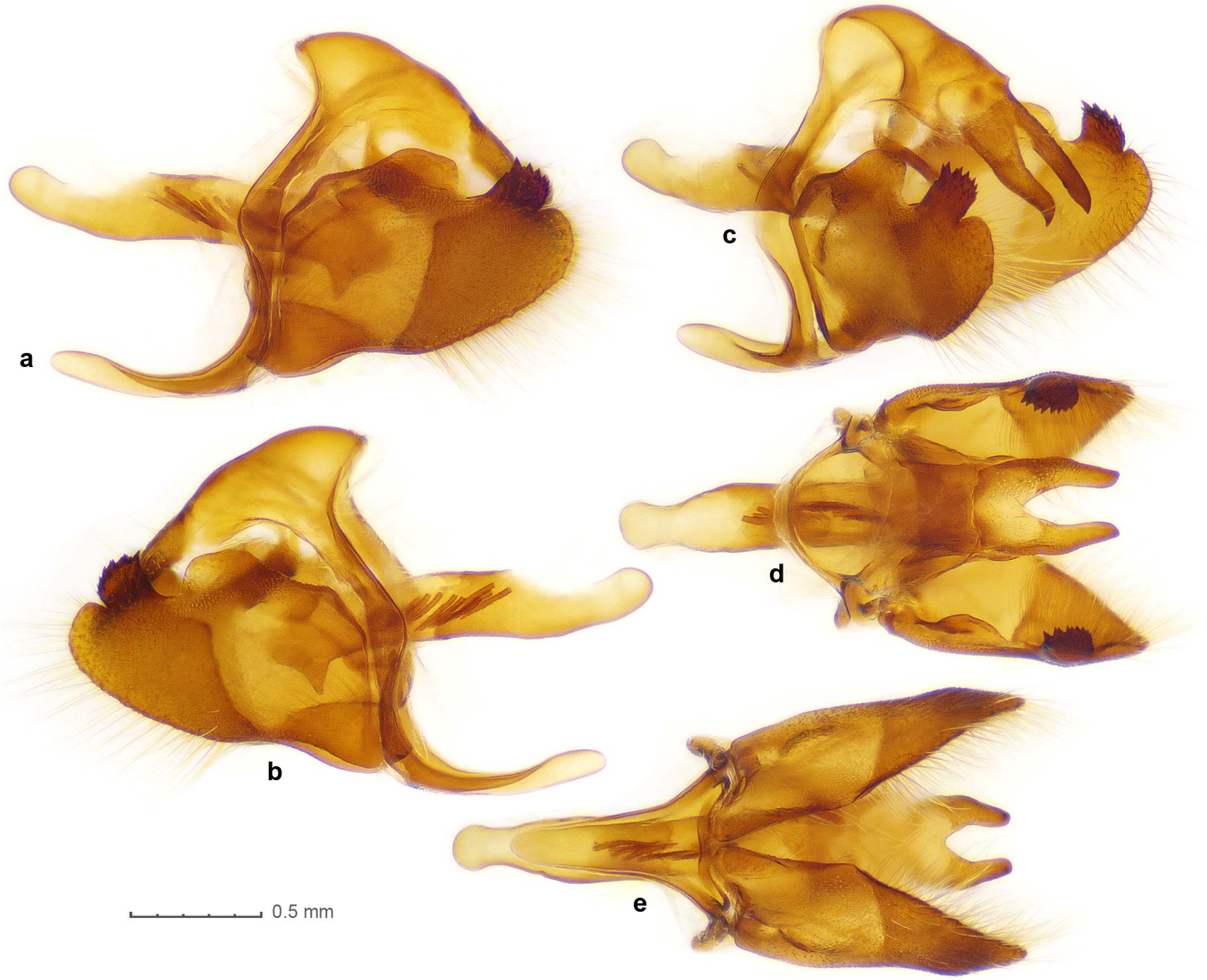


Fig. 9. Male genitalia of *Udranomia eurianus* **sp. n.** holotype NVG-18086C05 in different views: **a)** left lateral, **b)** right lateral, **c)** left posterolateral, **d)** dorsal, and **e)** ventral.

Additional specimens of recently described *Entheus* Hübner, [1819] species found by genomic sequencing

Genomic sequencing revealed additional specimens of several species of *Entheus* Hübner, [1819] (type species *Papilio peleus* Linnaeus, 1763, a junior subjective synonym of *P. priassus* Linnaeus, 1758) originally described from a single specimen, thus confirming them as species-level taxa and discovering specimens of the opposite sex to the holotype—a challenge given the strong sexual dimorphism in this genus (Fig. 10).

Entheus proxemus Grishin, 2025 was described from the male holotype NVG-23064B05 collected by Dan L. Lindsley in Brazil: Pará, Belém on 11-Jan-1961 [MGCL] (Zhang et al. 2025a) (Fig. 11a). Now, we found a pair collected by Samuel M. Klages in Brazil: Pará, Benevides during Oct-1918 [CMNH]: the second male NVG-23112H01 and the first female NVG-23112G12 illustrated here in Fig. 11b, c. The male is noticeably larger than the holotype, but otherwise similar in appearance, except for the somewhat broader forewing discal orange band. The female is similar to *Entheus telemus* Mabille, 1898 (type locality in Brazil), but differs by a smaller white hindwing discal patch not invading the anal fold on the dorsal side (the anal fold is paler brown than the ground color, especially next to the white patch) and ventrally with some brown (except at the base) along the inner margin, and more closely aligned semihyaline spots in the apical band (the submarginal doublet touches or overlaps the subcostal quadruplet).

Entheus hyponota Grishin, 2025 was described from the female holotype NVG-22091B03 collected by Paul Hahnel in Brazil: Amazonas, Massauari [MFNB] (Zhang et al. 2025a) (Fig. 12b). Now, we found two males: NVG-23128B11 from "Amaz.", old specimen [CNC], illustrated here in Fig. 12a and NVG-24054C03 from Brazil: Amazonas, Maués, Dec-1922, H. C. Baz leg. [ZMUC]. The male is rather similar to *Entheus priassus* (Linnaeus, 1758) (type locality in Suriname; neotype sequenced as NVG-18095F12), while not being phylogenetically close to it. Both species have extensive hyalinity in the forewing orange

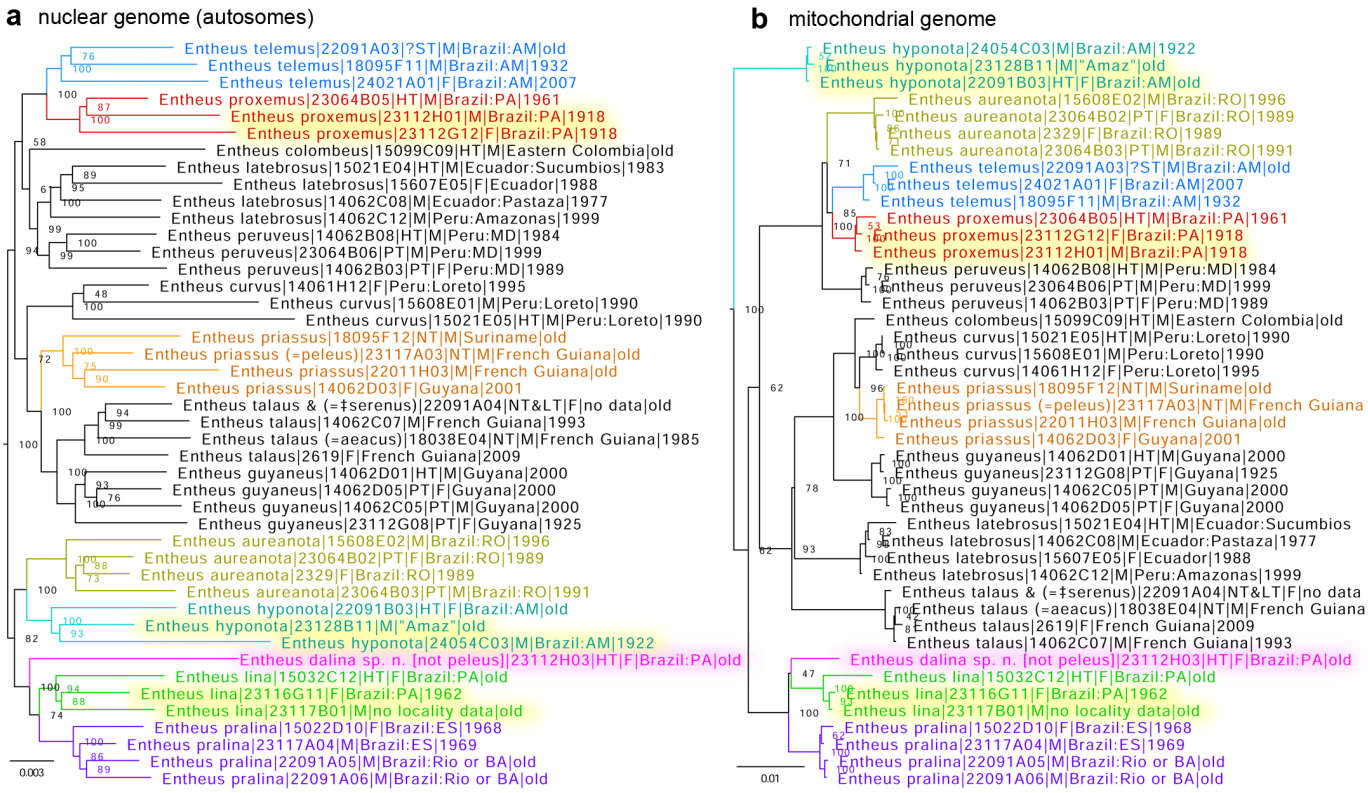


Fig. 10. Phylogenetic trees of all valid species from the *Entheus priassus* group constructed from protein-coding regions in **a)** the nuclear genome (autosomes), based on 590,538 positions, and **b)** the mitochondrial genome. Species mentioned in the text are colored: *E. telemus* (blue), *E. proxemus* (red), *E. priassus* (orange), *E. aureanota* (olive), *E. hyponota* (cyan), *E. dalina* **sp. n.** (magenta), *E. lina* (green), and *E. pralina* (violet). Newly discovered specimens of species previously known from a single specimen are highlighted in yellow, and the new species is highlighted in magenta. Ultrafast bootstrap (Hoang et al. 2018) values are shown at nodes.

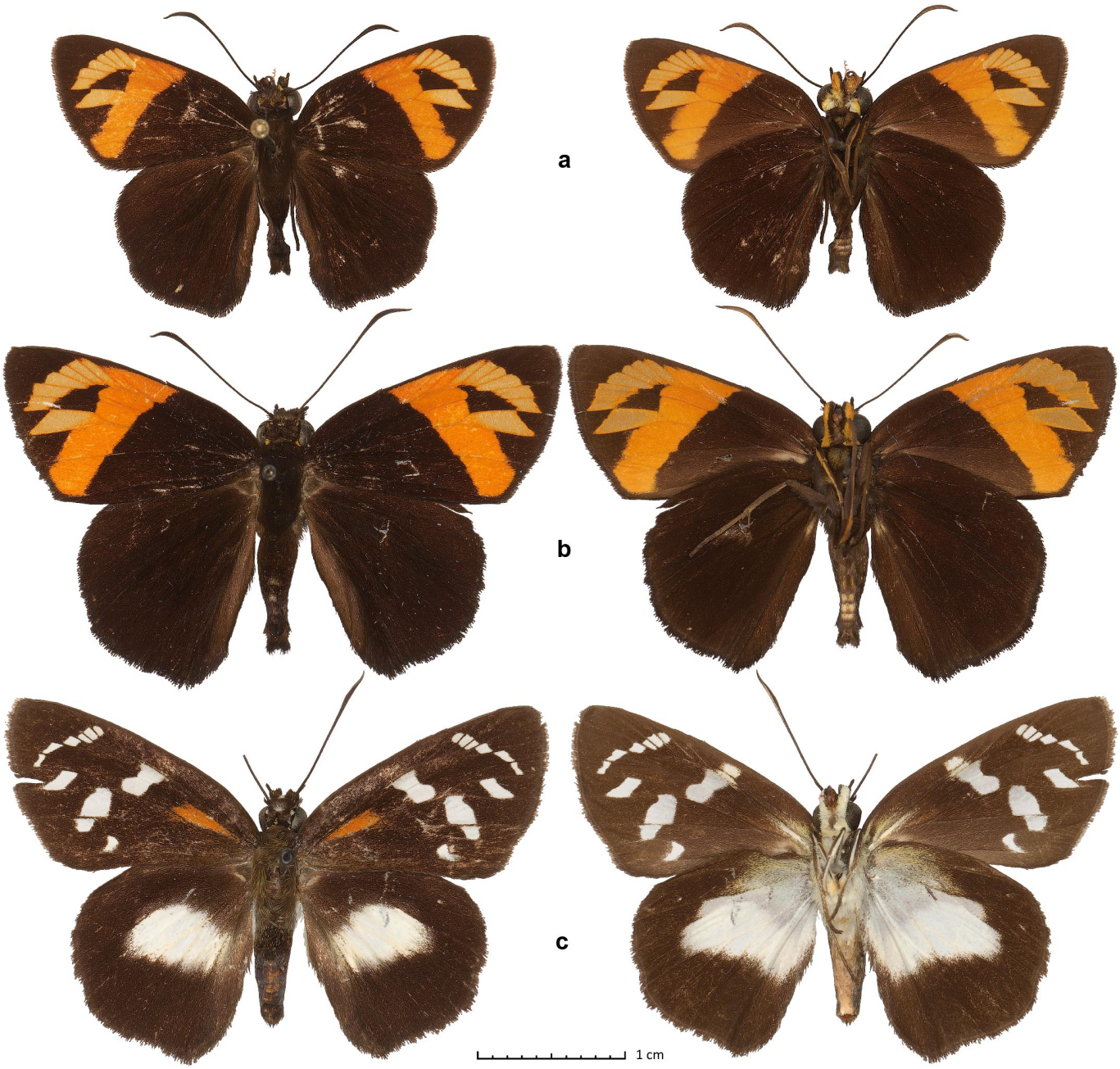


Fig. 11. *Entheus proxemus* in dorsal (left) and ventral (right) views: **a)** holotype ♂ NVG-23064B05 Brazil: Pará, Belém, 11-Jan-1961, D. L. Lindsley leg. [MGCL] and **b–c)** non-types from Brazil: Pará, Benevides, Oct-1918, S, M. Klages leg. [CMNH]: **b)** ♂ NVG-23112H01 and **c)** ♀ NVG-23112G12.

bands, but *E. hyponota* differs by having a broader forewing discal band and a brown (not yellow) hindtibial tuft.

Entheus lina Grishin, 2025 was described from the female holotype NVG-15032C12 collected by Friedrich Wilhelm Sieber in Brazil: Pará [MFNB] (Zhang et al. 2025a) (Fig. 13b). Now, we found a male, NVG-23117B01 from an unstated locality, labeled as "Lot 147, Sub. 8 23 July", old specimen [CUIC], illustrated here in Fig. 13a and a female, NVG-23116G11 Brazil: Pará, Belem, Sep-1962 [USNM]. The male is somewhat similar to *Entheus priassus* (Linnaeus, 1758) (type locality in Suriname; neotype sequenced as NVG-18095F12) while not being phylogenetically close to it. Both species have extensive hyalinity in the forewing orange bands, but *E. lina* differs by a broader subapical band with spots more closely aligned at their margins and nearly connected to the discal band near the costa.

With the continuing accumulation of genomic data, we hope to build a collection of genetically identified *Entheus* specimens and identify more reliable phenotypic characters to distinguish them.

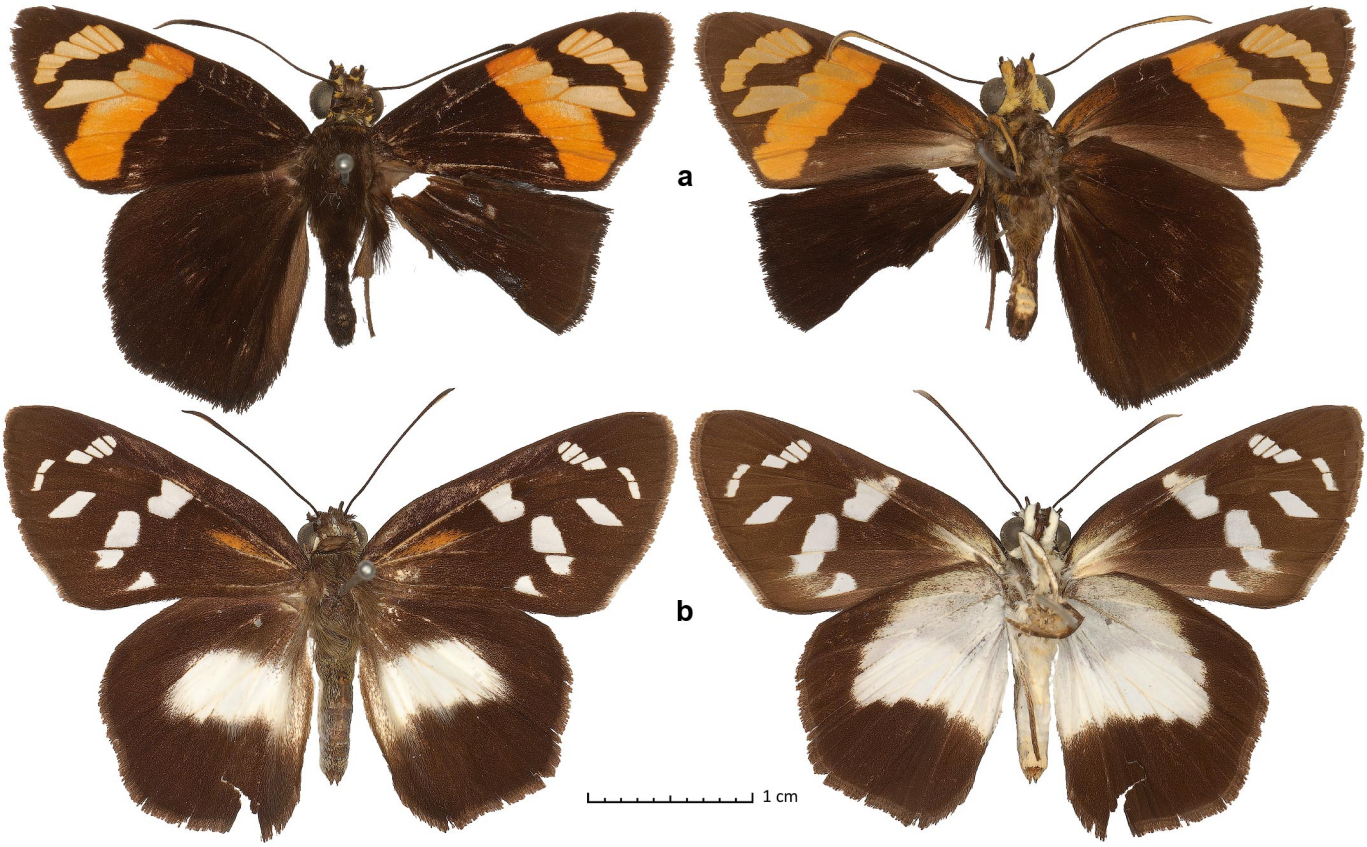


Fig. 12. *Entheus hyponota* in dorsal (left) and ventral (right) views: **a)** non-type ♂ NVG-23128B11 from "Amaz.", old [CNC]; **b)** holotype ♀ NVG-22091B03 from Brazil: Amazonas, Massauari, old, P. Hahnel leg. [MFNB].

Entheus dalina Grishin, new species

https://zoobank.org/9CCB93A4-1F3C-4A5A-B29B-E32A1E110185

(Figs. 10 part, 13c)

Definition and diagnosis. Genomic analysis reveals that a female from the Lower Amazon region identified by F. D. Godman as *Entheus peleus* (Linnaeus, 1763) (type locality in French Guiana; neotype sequenced as NVG-23117A03), which is a junior subjective synonym of *Entheus priassus* (Linnaeus, 1758) (type locality in Suriname; neotype sequenced as NVG-18095F12), is phylogenetically distant from it and instead is closely related to *Entheus pralina* Evans, 1952 (type locality in Brazil: Espirito Santo) and *Entheus lina* Grishin, 2025 (type locality in Brazil: Pará), being genetically differentiated from them at the species level (Fig. 10); e.g., their COI barcodes differ by 0.9% (6 bp) from either of these species (barcode differences tend to be small in this genus), and therefore this female represents a new species. This new species keys to "*Entheus priassus telemus*" (B.10.4(b)) in Evans (1952), but differs from it and other relatives by the following combination of characters in females: the subapical hyaline forewing band is broken and the two posterior spots (submarginal doublet) are offset distad from the rest (all spots are aligned in *E. pralina*); the hindwing white area is larger than in most relatives, but smaller than in *E. lina*, not reaching the inner margin on the dorsal side, with a straight and somewhat sinuous distal margin (brown scales reach into the white area along veins), and the boundary between the white area and brown postdiscal part of the wing is blurred towards the inner wing margin; the anal fold is beige, strongly overscaled with dark-brown scales; extensive pale to olive scaling at the base of the ventral forewing (mostly missing in *E. lina*); more extensive olivaceous overscaling in the basal half of the anterior part of the ventral hindwing; and the white spot by the forewing vein 1A+2A is approximately three times smaller than the spot posterior to the vein CuA_2. Due to its cryptic nature and unexplored individual variation, this species is best identified by DNA, with diagnostic base pairs in the nuclear genome:

aly3967.1.6:A49T, aly3967.1.6:C51T, aly1041.9.2:G48A, aly1041.9.2:T54A, aly2487.36.5:A45T, aly814.7.5:T219T (not A), aly594.12.18:A207A (not G), aly806.13.25:C223C (not T), aly1018.14.2:G33G (not A), aly1018.14.2:G42G (not A); and the COI barcode: A133G, A214A, 499C, T530T, A628A, T643C.

Barcode sequence of the holotype. Sample NVG-23112H03, GenBank PX568485, 658 base pairs:

AACTTTATATTTTATTTTCGGAATTTGAGCAGGAATAGTAGGAACTTCCTTAAGATTATTAATTCGAACTGAATTAGGAACTCCTGGATCATTAATTGGAGATGATCAAATTTATAATACT
ATCGTTACTGCGCATGCTTTTATTATAATTTTTTTTATAGTTATACCAATTATAATTGGAGGATTTGGAAATTGATTAGTACCTTTAATATTAGGAGCCCCTGACATAGCTTTTCCTCGAA
TAAATAATATAAGTTTTTGACTCTTACCCCCATCATTAACATTATTAATTTCTAGAAGAATTGTTGAAAATGGAGCTGGAACAGGATGAACTGTTTACCCCCCTTTATCTGCTAATATTGC
CCACCAAGGATCTTCTGTAGATTTAGCCATTTTTTCCCTTCATTTAGCTGGAATTTCATCAATTTTAGGAGCTATTAATTTTATTACAACAATTATTAATATACGTATTAGAAATTTATCA
TTTGATCAAATACCCCTATTTGTTTGAGCAGTAGGTATTACTGCATTACTTTTATTATTATCTTTACCTGTATTAGCAGGTGCTATTACTATACTTTTAACAGATCGAAATTTAAATACAT
CATTTTTTGATCCTGCGGGAGGAGGAGATCCTATTCTCTATCAACACTTATTT

Type material. Holotype: ♀ currently deposited in the Carnegie Museum of Natural History, Pittsburgh, PA, USA (CMNH), illustrated in Fig. 13c, bears the following five printed rectangular labels, four white: [Santarem, | Amazons. | H. H. Smith.], [♀], [B.C.A.Lep.Rhop. | Entheus | peleus, | Linn.], [DNA sample ID: | NVG-23112H03 | c/o Nick V. Grishin], and one red [HOLOTYPE ♀ | Entheus | dalina Grishin].

Fig. 13. *Entheus* specimens in dorsal (left) and ventral (right) views: **a–b)** *Entheus lina*: **a)** non-type ♂ NVG-23117B01 without locality data, only "Lot 147, Sub. 8 23 July", old [CUIC]; **b)** holotype ♀ NVG-15032C12 from Brazil: Pará, old [MFNB]; and **c)** *Entheus dalina* **sp. n.** holotype ♀ NVG-23112H03 from Brazil: Pará, Santarém, old, H. H. Smith leg. [CMNH].

Type locality. Brazil: Pará, Santarém.

Etymology. The name reflects the *da*[rker anal fold of this relative of E.]*lina* and is treated as a noun in apposition. Thus, *li-* in *lina* is for lighter, and *da-* in *dalina* stands for darker.

Distribution. Currently known only from the holotype collected in the Lower Amazon region.

Entheus ambo Grishin, new species

https://zoobank.org/6311D2EE-0966-4C5D-A603-79E8D0CAA5BE

(Figs. 14 part, 15a–c)

Definition and diagnosis. Genomic analysis reveals that males from the western Andes in Colombia identified in the CEPUJ collection as *Entheus latifascius* M. Hering, 1925 (type locality Colombia, Chocó, Rio Micay) are phylogenetically distant from and not monophyletic with it, and instead are more closely related to *Entheus bogoteus* Grishin, 2025 (type locality Colombia: Bogotá) (Fig. 15d) and *Entheus warreni* Grishin, 2012 (type locality in Ecuador: Esmeraldas), being genetically differentiated from them at the species level (Fig. 14); e.g., their COI barcodes differ by 2.1% (14 bp) and 2.3% (15 bp), respectively, and therefore these males represent a new species. This new species keys to "*Entheus matho latifascius*" (B.10.5(b)) in Evans (1952), males of which he misidentified and incorrectly associated with females, and differs from it and other relatives by the following combination of characters in males: the forewing discal band is orange, narrower than in *E. bogoteus*, partly hyaline towards its outer margin, where it is yellower (the hyalinity is more developed than in *E. bogoteus*, e.g., in the discal cell), lacking an orange streak between the costa and the discal cell reaching towards the wing base, but usually thicker towards the costa, and the two posterior semi-hyaline spots of the subapical band are strongly (by more than half of their width) offset distad from the rest along the distal edge of the band, while the anterior part of the proximal edge of the spot in cell M_1-M_2 is more aligned with the posterior part of the spot in R_5-M_1 or halfway between it and the anterior part of the spot in M_2-M_3 (proximal edges of the spots in cells M_1-M_2 and M_2-M_3 are nearly aligned with each other in *E. bogoteus*); the anal fold is creamy-white, slightly yellower towards its sides; the hindtibial tuft is tawny with a yellower tint than a more reddish tuft of *E. bogoteus*. Due to its cryptic nature and poorly explored individual variation, this species is best identified by DNA, with diagnostic base pairs in the nuclear genome: aly1134.3.1:C231T, aly1134.3.1:C243T, aly3555.6.3:A114G, aly3555.6.3:A120G, aly44898.1.2:C135G; and the COI barcode: T157C, T284C, A421G, T428C, A622G, A631G.

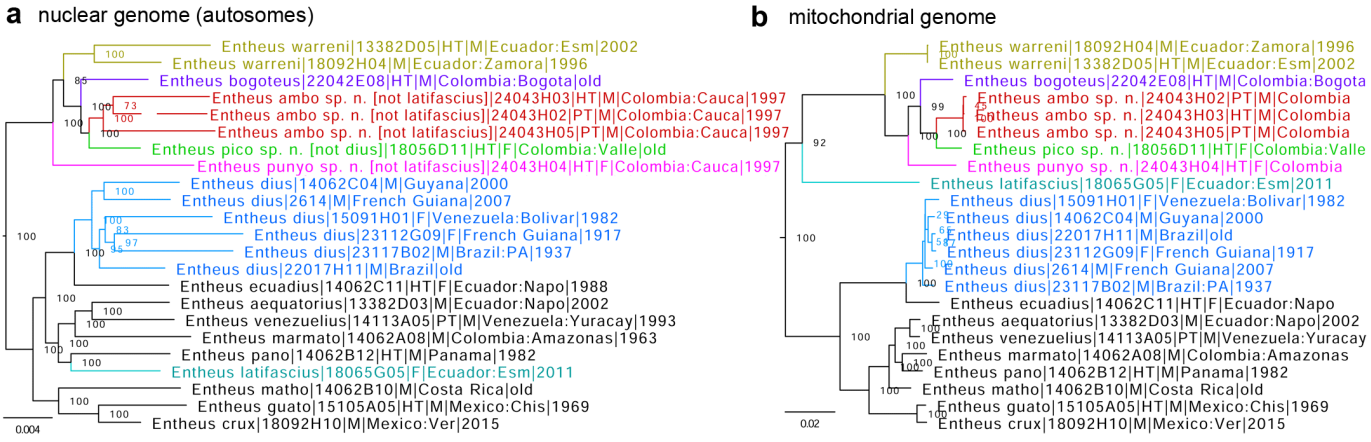


Fig. 14. Phylogenetic trees of all valid species from the *Entheus warreni* and *E. matho* groups constructed from protein-coding regions in: **a)** the nuclear genome (autosomes), based on 4,150,500 positions, and **b)** the mitochondrial genome. Species mentioned in the text are colored: *E. warreni* (olive), *E. bogoteus* (violet), *E. ambo* **sp. n.** (red), *E. pico* **sp. n.** (green), *E. punyo* **sp. n.** (magenta), *E. dius* (blue), and *E. latifascius* (cyan). A gap in a terminal branch indicates that a segment of the branch was cut out to reduce its length (to allow an increase in the font size), i.e., the branch with the gap is longer than shown. Ultrafast bootstrap (Hoang et al. 2018) values are shown at nodes.

Fig. 15. *Entheus* ♂♂ from Colombia in dorsal (left) and ventral (right) views, data in text: **a–c)** *E. ambo* **sp. n.**: **a)** holotype NVG-24043H03 and paratypes: **b)** NVG-24043H02 and **c)** NVG-24043H05; and **d)** *E. bogoteus* holotype NVG-22042E08. The inset shows the hindtibial tuft enlarged two times compared to the specimen (scale not given).

Barcode sequence of the holotype. Sample NVG-24043H03, GenBank PX568486, 658 base pairs:

AACTTTATATTTTATTTTCGGAATTTGAGCAGGAATAGTAGGTACTTCTTTAAGATTATTAATTCGAACTGAATTAGGAACTCCAGGATCATTAATTGGAGATGATCAAATTTATAATACT
ATTGTTACTGCTCATGCTTTTATTATAATTTTTTTCATAGTTATACCAATTATAATTGGAGGATTTGGAAATTGATTAGTACCTTTAATATTAGGAGCCCCTGATATAGCTTTTCCTCGAA
TAAATAATATAAGTTTTTGACTTCTACCCCCATCATTAACACTATTAATTTCTAGAAGAATTGTTGAAAATGGAGCTGGAACAGGATGAACTGTTTATCCCCCTTTATCTGCTAATATTGC
CCATCAAGGATCTTCAGTAGATTTAGCTATTTTTTCCCTTCACTTAGCTGGTATTTCGTCAATCCTAGGAGCTATTAATTTTATTACAACAATTATTAATATACGTATTAGAAATTTATCA
TTTGATCAAATACCTTTATTTGTTTGAGCAGTAGGTATTACCGCATTACTTTTATTATTATCATTACCTGTATTAGCTGGTGCTATTACTATACTTTTAACAGATCGAAACTTAAATACAT
CATTTTTTGATCCTGCGGGAGGTGGGGATCCAATTCTCTATCAACATTTATTT

Type material. Holotype: ♂ deposited in the Nature Education Centre of the Jagiellonian University, Kraków, Poland (CEPUJ), illustrated in Fig. 15a, bears the following four printed rectangular labels (2nd green, 4th red, others white): [COLOMBIA | Western Cordillera | Tambito Forest Res. | 1500 m | 4.III.1997 | Leg. Wojtusiak & Pyrcz], [CEP-DNA | 7181 | tissue sample], [DNA sample ID: | NVG-24043H03 | c/o Nick V. Grishin], and [HOLOTYPE ♂ | Entheus | ambo Grishin]. **Paratypes:** 2♂♂ with the same data as the holotype except as indicated: 1♂ NVG-24043H02, CEP-DNA 7180 (Fig. 15b) and 1♂ NVG-24043H05, CEP 7183, 28-Feb–6-Mar-1997, Wojtusiak leg. (Fig. 15c).

Type locality. Colombia: Cauca Department, El Tambo Municipality, Reserva Natural Tambito, elevation 1500 m.

Etymology. In Latin, *ambo* means both (like in a pair) and *ambo-* is a Greek-derived prefix that means on both sides or around. The name refers to the forewing orange spot in cell M_1-M_2 that tends to belong to both the subapical and submarginal segments of the band. The name is treated as a noun in apposition.

Distribution. Currently known only from the western Andes in Colombia.

Entheus pico Grishin, new species

https://zoobank.org/78D71635-77C5-43EF-8643-1CCBF553497B

(Figs. 14 part, 16a)

Definition and diagnosis. Genomic analysis reveals that a female from the western Colombia identified in the ZfBS collection as *Entheus dius* Mabille, 1898 (type locality in Brazil) is phylogenetically distant from and not monophyletic with it, and instead is more closely related to *Entheus bogoteus* Grishin, 2025 (type locality Colombia: Bogotá) and *Entheus warreni* Grishin, 2012 (type locality in Ecuador: Esmeraldas), being sister to the new species described above as *Entheus ambo* **sp. n.** and genetically differentiated from it at the species level (Fig. 14); e.g., their COI barcodes differ by 1.8% (12 bp), therefore this female represents a new species. This new species keys to "*Entheus matho dius*" (B.10.5(d)) in Evans (1952), but differs from it and other relatives by the following combination of characters in females: the white area on the hindwing is larger and is extended into a "beak" along the vein M_3, and does not reach the inner margin on the dorsal side; the anal fold is dorsally overscaled with white; the orange streak in the forewing discal cell is prominently expressed; a white smudge at the mid-costa; the semihyaline spot in the cell CuA_1-CuA_2 is shifted distad from the discal cell spot; the spot in the posterior part of cell CuA_2-1A+2A is well-developed, crescent-shaped; the submarginal doublet of semihyaline spots is strongly offset distad from the quadruplet of subapical spots, which are mostly aligned with each other. Due to its cryptic nature, unknown males, and unexplored individual variation, this species is best identified by DNA, with diagnostic base pairs in the nuclear genome: aly18312.9.16:T273A, aly18312.9.16:T291C, aly2124.1.12:T93C, aly1456.9.2:G93A, aly1456.9.2:C96T, aly36374.1.1:A167A (not T), aly1432.15.1:T153T (not G), aly945.3.1:C6C (not T), aly887.11.3:C111C (not A), aly420.45.9:A18A (not G); and the COI barcode: T59C, A214G, T284C, T313C, A466G, T490C, A631A.

Barcode sequence of the holotype. Sample NVG-18056D11, GenBank PX568487, 658 base pairs:

AACTTTATATTTTATTTTCGGAATTTGAGCAGGAATAGTAGGTACTTCTTTAAGATTACTAATTCGAACTGAATTAGGAACTCCAGGATCATTAATTGGAGATGATCAAATTTATAATACT
ATTGTTACTGCTCATGCTTTTATTATAATTTTTTTTATAGTTATACCAATTATAATTGGGGGATTTGGAAATTGATTAGTACCCTTAATATTGGGAGCCCCTGATATAGCTTTTCCTCGAA
TAAATAATATAAGTTTTTGACTTCTACCCCCATCATTAACACTATTAATTTCTAGAAGAATTGTTGAAAACGGAGCTGGAACAGGGTGAACTGTTTATCCCCCTTTATCTGCTAATATTGC
CCATCAAGGATCTTCAGTAGATTTAGCTATTTTTTCCCTTCACTTAGCTGGTATTTCATCAATCCTAGGAGCTATTAATTTTATTACAACAATTATTAATATGCGTATTAGAAATTTATCA
TTTGACCAAATACCTTTATTTGTTTGAGCAGTAGGTATTACCGCATTACTTTTATTATTATCATTACCTGTATTAGCTGGTGCTATTACTATACTTTTAACAGATCGAAACTTAAATACAT
CATTTTTTGATCCTGCAGGAGGTGGAGATCCAATTCTCTATCAACATTTATTT

Type material. Holotype: ♀ deposited in the collection of the Zentrum für Biodokumentation des Saarlandes, Schiffweiler, Germany (ZfBS), illustrated in Fig. 16a, bears the following four rectangular labels (2nd handwritten, others printed), three white: [Rio Aguacatal | Colomb. W.Codr. | 2000 m | Coll.

Fassl], [dius ♀], [DNA sample ID: | NVG-18056D11 | c/o Nick V. Grishin], and one red [HOLOTYPE ♀ | Entheus | pico Grishin]. Judging from its handwritten label, the dorsal side of this specimen was illustrated as a female of *E. dius* in Draudt (1921–1924). The illustration (plate 172, row f, image [1]) bears good resemblance to this specimen, which is not *E. dius*. The outer marginal area of the right hindwing and the tornus of the left hindwing of the holotype were repaired by attaching wing parts of different specimen(s). These wing pieces are excluded from the holotype.

Type locality. Colombia: Valle del Cauca, Río Aguacatal, elevation ca. 2000 m.

Etymology. In Spanish, el pico means peak, beak, or bill and reflects the beak-like pointed extension of the large white patch in the middle of the dorsal hindwing of this species. The name is a noun in apposition.

Distribution. Currently known only from the holotype collected in western Colombia.

Entheus punyo Grishin, new species

https://zoobank.org/57D72D46-5D4A-42CF-ADB8-D1E830510C78

(Figs. 14 part, 16b)

Definition and diagnosis. Genomic analysis reveals that a female from the western Colombia identified in the CEPUJ collection as *Entheus latifascius* M. Hering, 1925 (type locality Colombia, Chocó, Rio Micay) is phylogenetically distant from and not monophyletic with it, and instead is more closely related to *Entheus warreni* Grishin, 2012 (type locality in Ecuador: Esmeraldas), being sister to the clade consisting of three Colombian species: *Entheus bogoteus* Grishin, 2025 (type locality Colombia: Bogotá), *Entheus ambo* **sp. n.**, and *Entheus pico* **sp. n.** (Fig. 14), and therefore this female represents a new species. This new species keys to "*Entheus matho dius*" (B.10.5(d)) in Evans (1952), but differs from it and other relatives

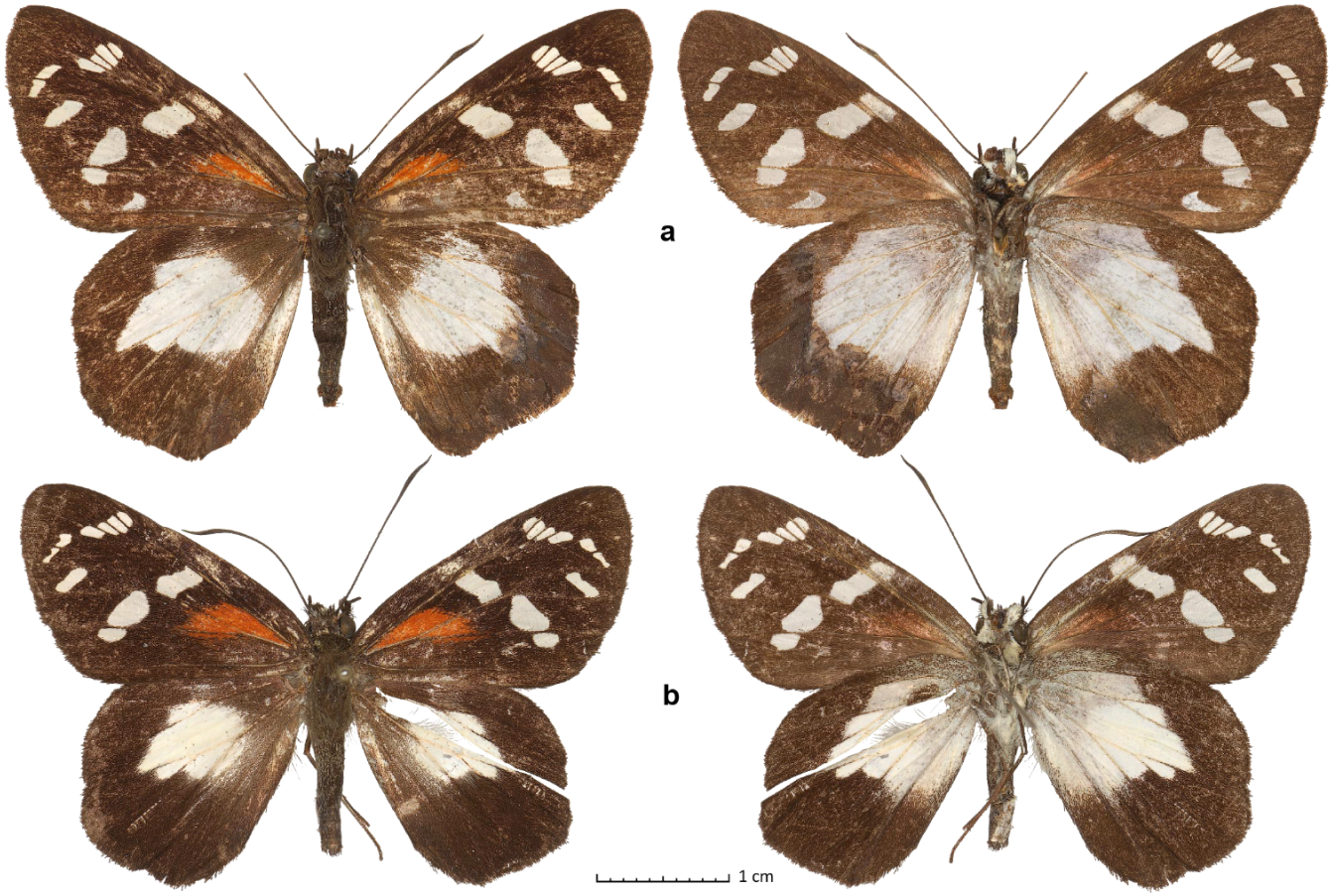


Fig. 16. *Entheus* holotypes ♀♀ from Colombia in dorsal (left) and ventral (right) views, data in text: **a)** *E. pico* **sp. n.** NVG-18056D11 and **b)** *E. punyo* **sp. n.** NVG-24043H04.

by the following combination of characters in females: the white area on the hindwing is smaller, fist-shaped, and confined to the middle of the wing, only slightly extending along the vein M_3 on the dorsal side (but more strongly on the ventral side, where it ends in a sharp point), and barely reaches the middle of cell CuA_2-1A+2A on the dorsal side; the anal fold is dorsally brown; the orange streak in the forewing discal cell is prominently expressed; a white smudge at the mid-costa; the semihyaline spot in cell CuA_1-CuA_2 is more closely aligned with the discal cell spot than in *E. pico* **sp. n.**, but less than in *E. dius*; the spot in the posterior part of cell CuA_2-1A+2A is lacking; the submarginal doublet of semihyaline spots is slightly offset distad from the quadruplet of subapical spots, which are concave outward, and the spot in R_5-M_1 is shifted distad, thus being closer to the submarginal doublet than in *E. pico* **sp. n**. Due to its cryptic nature, unknown males, and unexplored individual variation, this species is best identified by DNA, with diagnostic base pairs in the nuclear genome: aly2627.8.4:G117A, aly2627.8.4:C120T, aly1489.12.1:C2106T, aly1489.12.1:T2133C, aly1489.12.1:A2178T, aly935.2.13:C46C (not A), aly3561.7.2:T663T (not C), aly89517.1.2:T30T (not C), aly89517.1.2:T57T (not C), aly5715.3.15:G51G (not A); and the COI barcode: A40G, A85G, T284T, A328G, T407C, T428T.

Barcode sequence of the holotype. Sample NVG-24043H04, GenBank PX568488, 658 base pairs:

AACTTTATATTTTATTTTTGGAATTTGAGCAGGAATAGTGGGTACTTCTTTAAGATTATTAATTCGAACTGAATTAGGAACTCCGGGATCATTAATTGGAGATGATCAAATTTATAATACT
ATTGTTACTGCTCATGCTTTTATTATAATTTTTTTTATAGTTATACCAATTATAATTGGGGGATTTGGAAATTGATTAGTACCATTAATACTAGGAGCCCCTGATATAGCTTTTCCTCGAA
TAAATAATATAAGTTTTTGACTTCTACCCCCATCATTAACATTATTAATTTCTAGAAGAATTGTTGAAAATGGAGCTGGAACAGGGTGAACTGTTTACCCCCCTTTATCTGCTAATATTGC
CCATCAAGGATCTTCAGTAGATTTAGCTATTTTTTCCCTTCACCTAGCTGGTATTTCATCAATTTTAGGAGCTATTAATTTTATTACAACAATTATTAATATACGTATTAGAAATTTATCA
TTTGATCAAATACCTTTATTTGTTTGAGCAGTAGGTATTACTGCATTACTTTTATTGTTATCATTACCTGTATTAGCTGGTGCTATTACTATACTTTTAACAGATCGAAACTTAAATACAT
CATTTTTTGATCCTGCAGGGGGTGGAGATCCAATTCTTTACCAACATTTATTT

Type material. Holotype: ♀ deposited in the Nature Education Centre of the Jagiellonian University, Kraków, Poland (CEPUJ), illustrated in Fig. 16b, bears the following four printed rectangular labels (2nd green, 4th red, others white): [Entheus | latifascius | ♀], [CEP-DNA | 7182 | tissue sample], [DNA sample ID: | NVG-24043H04 | c/o Nick V. Grishin], and [HOLOTYPE ♀ | Entheus | punyo Grishin]. The holotype is from the same series as the type specimens of *Entheus ambo* **sp. n**.

Type locality. Colombia: Cauca Department, El Tambo Municipality, Reserva Natural Tambito, elevation 1500 m.

Etymology. In Spanish, el puño means fist. The name reflects a fist-shaped white spot on the dorsal hindwing and is a noun in apposition.

Distribution. Currently known only from the holotype collected in the western Andes of Colombia.

New taxa of *Porphyrogenes* Watson, 1893

A preliminary genomic analysis of *Porphyrogenes* Watson, 1893 (type species *Telegonus omphale* Butler, 1871) reveals several prominent clades genetically differentiated from described species, thus representing new taxa (Fig. 17). Three of them correspond to recognizable phenotypes, and two new species are among paratypes of *Porphyrogenes spadix* Austin & O. Mielke, 2008 (type locality in Brazil: Rondônia), and therefore are cryptic, but strongly differentiated genetically from the *P. spadix* holotype. These five new taxa are described below.

Porphyrogenes castana Grishin, new species

https://zoobank.org/CE0112F5-F41F-41D6-BA6D-8BBA3AF10E0D

(Figs. 17 part, 18a–b)

Definition and diagnosis. Genomic analysis reveals that two males from the Amazon region identified in the ZSMC collection as *Porphyrogenes spanda* Evans, 1952 (type locality in Brazil: Pará) form a clade sister to both *Porphyrogenes despecta* (Butler, 1870) (type locality in Brazil: Pará) (Fig. 18c) and *Porphyrogenes ferruginea* (Plötz, 1883) (type locality in Brazil: Bahia) (Fig. 18d, e), but are genetically differentiated from them at the species level (Fig. 17); e.g., their COI barcodes differ by 4.6% (30 bp). These two specimens phenotypically differ from all described species of *Porphyrogenes* Watson, 1893 (type species *Telegonus omphale* Butler, 1871) and therefore they represent a new species. This new

species keys (incompletely) to *P. spanda* (D.7.12) in Evans (1952), but differs from it and other relatives by the following combination of characters in males: the dorsal side is not overscaled with orangish or tawny scales [overscaled, especially on the hindwing, in many congeners, such as *P. spanda*, *P. despecta* (Fig. 18c), and *P. ferruginea* (Fig. 18d, e)], unspotted, and of a monochrome chestnut color with a unique tint: darker and redder than in congeners; the ventral side is similar and with a prominent "speculum" (an oval area covered with pale shiny scales) at the base of the forewing vein 1A+2A [similar in *P. despecta* (Fig. 18c)]; the anal fold tuft is well developed and dark [pale and weak in *P. spanda*]; the hindwing

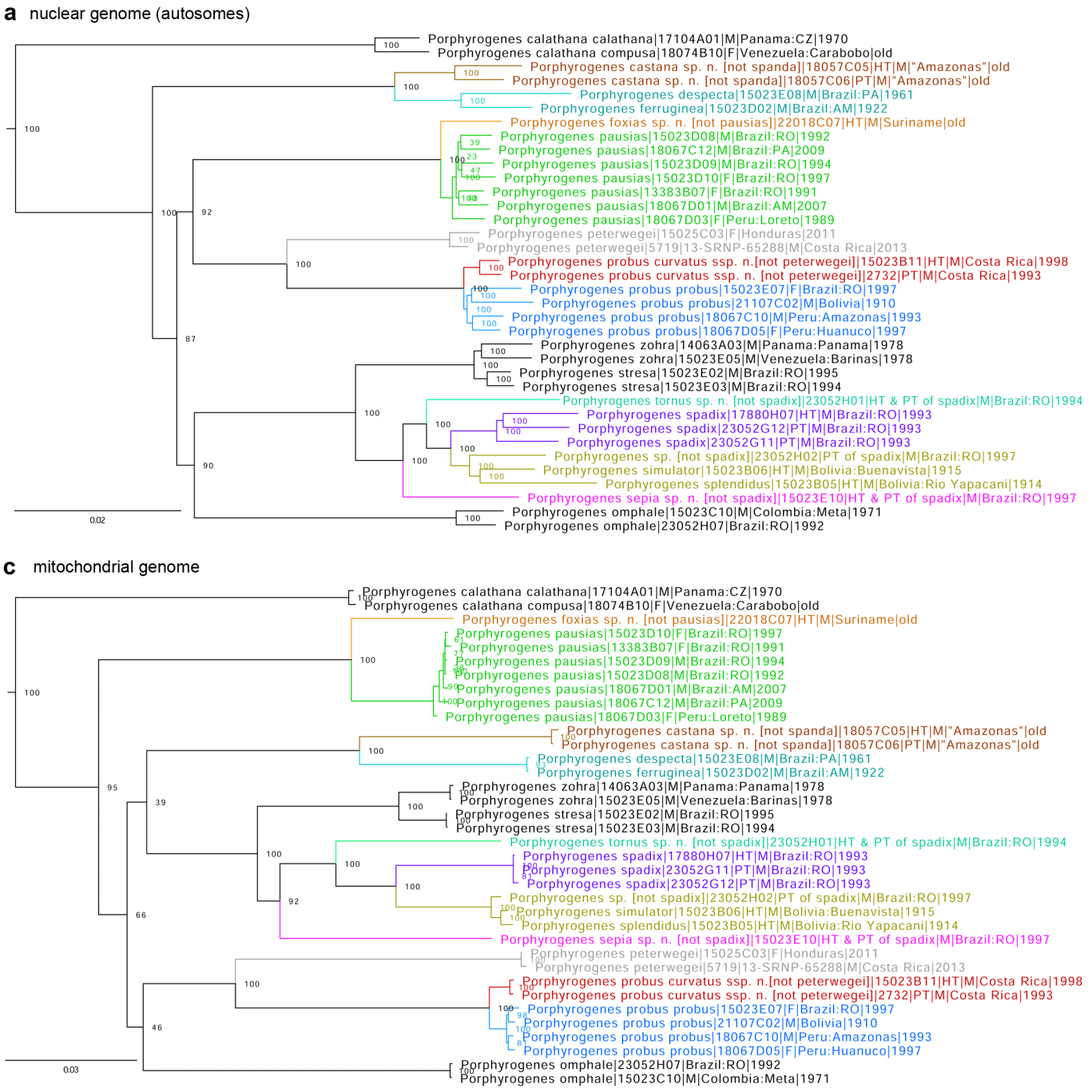


Fig. 17. Phylogenetic trees of selected *Porphyrogenes* species constructed from protein-coding regions in: **a)** the nuclear genome (autosomes), based on 1,507,707 positions, and **b)** the mitochondrial genome. Taxa discussed in the text are colored: *P. castana* **sp. n.** (brown), *P. despecta* with *P. ferruginea* (cyan), *P. foxias* **sp. n.** (orange), *P. pausias* (green), *P. peterwegei* (gray), *P. probus curvatus* **ssp. n.** (red), *P. probus probus* (blue), *P. tornus* **sp. n.** (aquamarine), *P. spadix* (violet), *P. simulator* with *P. splendidus* and an unidentified specimen (see text) (olive), *P. sepia* **sp. n.** (magenta). Ultrafast bootstrap (Hoang et al. 2018) values are shown at nodes.

Fig. 18. *Porphyrogenes* males in dorsal (left) and ventral (right) views: **a–b)** *P. castana* **sp. n.** from Brazil: Amazonas, old [ZSMC]: **a)** holotype NVG-18057C05 and **b)** paratype NVG-18057C06; **c)** *P. despecta* NVG-15023E08 Brazil: Pará, Belém, 1-Jul-1961, D. L. Lindsley leg., genitalia GTA-7587 [MGCL]; and **d–e)** *P. ferruginea*: **d)** NVG-18067D02 Peru: Loreto, vic. Iquitos, Rio Tigre, Sep-2003, ex coll. M. Büche [EBC] and **e)** NVG-15023D02 Brazil: Amazonas, Rio Purus, Huitanaã, Mar-1922, S. M. Klages, genitalia GTA-4184 [CMNH].

tornus is more strongly lobed than in *P. spanda* and many other smaller species, except *Porphyrogenes sparta* Evans, 1952 (type locality in Brazil: Pará); and the dorsal hindwing is unspotted [with two or three postdiscal spots in *P. spanda*]. This species is not cryptic, but because individual variation is poorly

documented, and females remain unknown, it is best identified by DNA, with diagnostic base pairs in the nuclear genome: aly208.42.3:C132T, aly1603.73.2:G39A, aly1603.73.2:A42G, aly1097.9.1:G75A, aly1146.47.6:T99C; and the COI barcode: A4T, A76G, C284T, A469T, A553G, T619A.

Barcode sequence of the holotype. Sample NVG-18057C05, GenBank PX568489, 658 base pairs:

AACTTTATATTTTATTTTTGGAATTTGAGCAGGAATAGTAGGTACTTCATTAAGATTACTAATTCGAACTGAATTGGGCACCCCTGGATCTTTAATTGGAGATGATCAAATTTATAATACT
ATTGTAACAGCTCATGCTTTTATTATAATTTTTTTTATAGTTATACCCATTATAATTGGAGGATTTGGAAATTGATTAATTCCTTTAATATTAGGAGCACCAGATATAGCATTTCCTCGTA
TAAATAATATAAGATTTTGATTATTACCTCCTTCTTTAACTTTATTAATTTCAAGAAGTATTGTTGAAAATGGTGCAGGTACAGGTTGAACTGTTTACCCTCCTTTATCATCAAATATTGC
TCATCAAGGATCTTCAGTTGATTTAGCAATTTTTTCTTTACATCTTGCAGGAATTTCTTCAATTTTAGGAGCTATCAATTTTATTACTACAATTATTAATATACGTATTAATAATTTATCA
TTTGATCAAATACCTTTATTTATTTGAGCAGTAGGAATTACAGCTTTATTATTATTATTATCTTTACCGGTATTAGCTGGAGCAATTACTATACTTTTAACTGATCGAAATTTAAATACTT
CATTTTTTGATCCAGCAGGTGGAGGTGACCCTATTTTATATCAACATTTATTT

Type material. Holotype: ♂ currently deposited in the Zoologische Staatssammlung München, Germany (ZSMC), illustrated in Fig. 18a, bears the following three printed rectangular labels, two white: [Amazonas | Coll. Fassl | in Coll. Arp], [DNA sample ID: | NVG-18057C05 | c/o Nick V. Grishin], and one red [HOLOTYPE ♂ | Porphyrogenes | castana Grishin]. **Paratype:** 1♂ NVG-18057C06 with the same data as the holotype (Fig. 18b).

Type locality. Brazil: Amazonas.

Etymology. In Latin, *castanea* is chestnut. The name reflects a unique chestnut color of the dorsal side of this species and is treated as a noun in apposition.

Distribution. Currently known only from the type locality in Amazonas (Brazil).

Porphyrogenes foxias Grishin, new species

https://zoobank.org/0BD056FC-0B3C-47F9-AA83-7707A39849DE

(Figs. 17 part, 19a)

Definition and diagnosis. Genomic analysis reveals that a male from Suriname initially identified as *Porphyrogenes pausias* (Hewitson, 1867) (type locality in Brazil: Amazonas) (Fig. 19b–e) is genetically differentiated from it at the species level (Fig. 17); e.g., their COI barcodes differ by 4.6% (30 bp), and therefore this specimen represents a new species. This new species keys to *P. pausias* (D.7.11) in Evans (1952), but differs from it and other relatives by the following combination of characters in males: larger in size, with yellower tawny dorsal overscaling [redder in *P. pausias* (Fig. 19b–e)], more strongly lobed hindwing tornus, a prominent tuft of dark scales, paler at the base, along the anal fold, and a darker, grayish "speculum" (an area of distinct scales near the base of the ventral forewing vein 1A+2A). This species is not cryptic, but due to unexplored individual variation, it is best identified by DNA, with diagnostic base pairs in the nuclear genome: aly2012.31.22:T1761C, aly2012.31.22:A1773G, aly1091.9.5:G714A, aly1091.9.5:C900T, aly1091.9.5:T1404C, aly349.24.4:G564G (not T), aly349.24.4:T591T (not C), aly256.13.4:G861G (not A), aly256.13.4:C1746C (not T), aly2790.8.4:A186A (not G); and the COI barcode: A145C, A157C, T283C, T478C, T485C, T533T.

Barcode sequence of the holotype. Sample NVG-22018C07, GenBank PX568490, 658 base pairs:

AACATTATACTTTATTTTTGGAATTTGAGCAGGAATATTAGGTACTTCTTTAAGATTATTAATTCGAACAGAATTAGGTACTCCTGGATCTTTAATTGGAGATGACCAAATCTATAATACT
ATTGTTACAGCTCATGCTTTTATCATAATTTTTTTCATAGTTATACCTATTATAATTGGAGGTTTTGGAAATTGATTAATTCCTCTAATATTAGGAGCCCCCGATATAGCATTCCCTCGAA
TAAATAATATAAGATTTTGATTATTACCTCCATCTTTAACCCTTTTAATTTCAAGAAGAATTGTAGAAAATGGTGCAGGAACAGGTTGAACTGTTTATCCTCCTTTATCCTCTAATATTGC
TCATCAAGGATCTTCAGTTGATTTAGCAATTTTTTCATTACATCTTGCAGGTATTTCATCTATTTTAGGGGCTATTAACTTTATCACTACAATTATTAATATACGAATCAATAACTTATCA
CTTGATCAAATACCCTTATTTGTTTGAGCAGTAGGAATCACAGCTTTATTATTATTACTATCTCTACCTGTATTAGCAGGTGCAATTACTATACTTTTAACTGATCGAAATTTAAATACTT
CATTTTTTGATCCTGCAGGAGGAGGAGATCCTATTTTATATCAACATTTATTT

Type material. Holotype: ♂ deposited in the Zoologische Staatssammlung München, Germany (ZSMC), illustrated in Fig. 19a, bears the following three printed rectangular labels (1st tan, 2nd, 3rd red): [Surinam | V. – IX. | Fruhstorfer], [DNA sample ID: | NVG-22018C07 | c/o Nick V. Grishin], and [HOLOTYPE ♂ | Porphyrogenes | foxias Grishin].

Type locality. Suriname.

Etymology. The name reflects the more orange, *fox*[-like color of this sister to P. paus]*ias* and is treated as a noun in apposition.

Distribution. Currently known only from the holotype collected in Suriname.

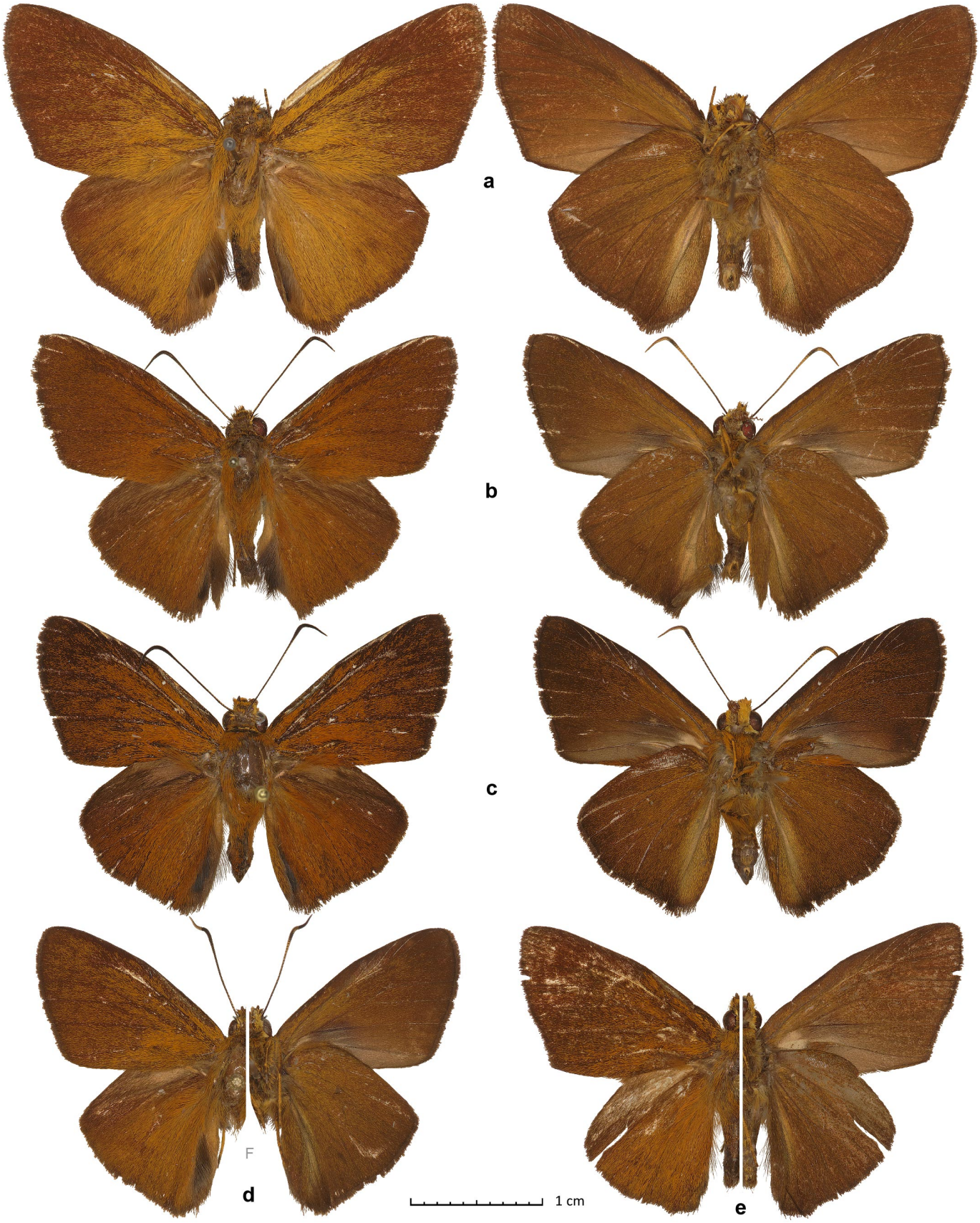


Fig. 19. *Porphyrogenes* males in dorsal (left) and ventral (right) views: **a)** *P. foxias* **sp. n.** holotype NVG-22018C07 from Suriname, old [ZSMC] and **b–e)** *P. pausias* from Brazil: **b)** NVG-18067D01 Amazonas, Maués, Rio Preto, 15–25-Nov-2007 [EBC]; **c)** NVG-18067C12 Pará, ca. 50 km ENE from Belém, Santo Antônio do Tauá, 7-Aug-2009, P. Jauffret leg. [EBC]; **d–e)** Rondônia, 62 km S of Ariquemes, linha C-10, 5 km E of Cacaulândia, O. Gomes leg. [MGCL]: **d)** NVG-15023D09, 13-Nov-1994, genitalia GTA-5339 and **e)** NVG-15023D08, 19-Jul-1992. F indicates flipped (left-right inverted) images.

Genomic analysis of paratypes of *Porphyrogenes spadix* Austin & O. Mielke, 2008

Genomic analysis of all five paratypes of *Porphyrogenes spadix* Austin & O. Mielke, 2008 (type locality in Brazil: Rondônia) (Fig. 17), from approximately the same locality, reveals that they represent four distinct sympatric species (two new) that are apparently rather cryptic and do not differ strongly in genitalia — all dissected by George T. Austin, who concluded that all five were conspecific. According to our analysis, only two paratypes (NVG-23052G11 and NVG-23052G12, Fig. 20c, d) are conspecific with the holotype and therefore are *P. spadix*. One paratype (NVG-23052H02, Fig. 20e) is genetically close to *Porphyrogenes simulator* Austin & O. Mielke, 2008 (sequenced as NVG-15023B06) and *Porphyrogenes splendidus* Austin & O. Mielke, 2008 (sequenced as NVG-15023B05), both known only from a single specimen, from Bolivia, and genetically close to each other (Fig. 17). It is possible that all three specimens (the holotypes of *P. splendidus* and *P. simulator* and the paratype of *P. spadix*) are conspecific; however, we refrain from formally proposing synonymy pending genomic sequencing of additional specimens. Two remaining paratypes of *P. spadix* represent two new species that are strongly differentiated from *P. spadix* genetically and are described next.

Porphyrogenes tornus Grishin, new species

https://zoobank.org/D38E04C4-8E27-480E-8151-C8651D234DB1

(Figs. 17 part, 20a)

Definition and diagnosis. Genomic analysis reveals that a paratype of *Porphyrogenes spadix* Austin & O. Mielke, 2008 (type locality in Brazil: Rondônia) sequenced as NVG-23052H01 is genetically differentiated from it at the species level (Fig. 17); e.g., their COI barcodes differ by 4.3% (28 bp), and therefore this specimen represents a new species. This new species keys to *P. spadix* in Austin and Mielke (2008), but differs from it and other relatives by the following combination of characters in males: the hindwing tornus is not as strongly lobed and the outer margin is straighter, not as concave before it, the color of the reddish dorsal overscaling is slightly browner, not as orange as in *P. spadix* (i.e., redder rather than yellower in hue); and the area of the ventral forewing by the inner margin is darker. Due to its cryptic nature and unexplored individual variation, this species is best identified by DNA, with diagnostic base pairs in the nuclear genome: aly2202.11.1:C235T, aly2202.11.1:T225C, aly216.33.13:G393A, aly276665.19.5:A932G, aly276665.19.5:G951A, aly144.32.1:T237T (not C), aly144.32.1:C253C (not T), aly171.4.1:T573T (not C), aly2976.3.2:C214C (not T), aly2976.3.2:A478A (not G); and the COI barcode: T16C, T250C, A403T, T457C, T529T (not C), T595C.

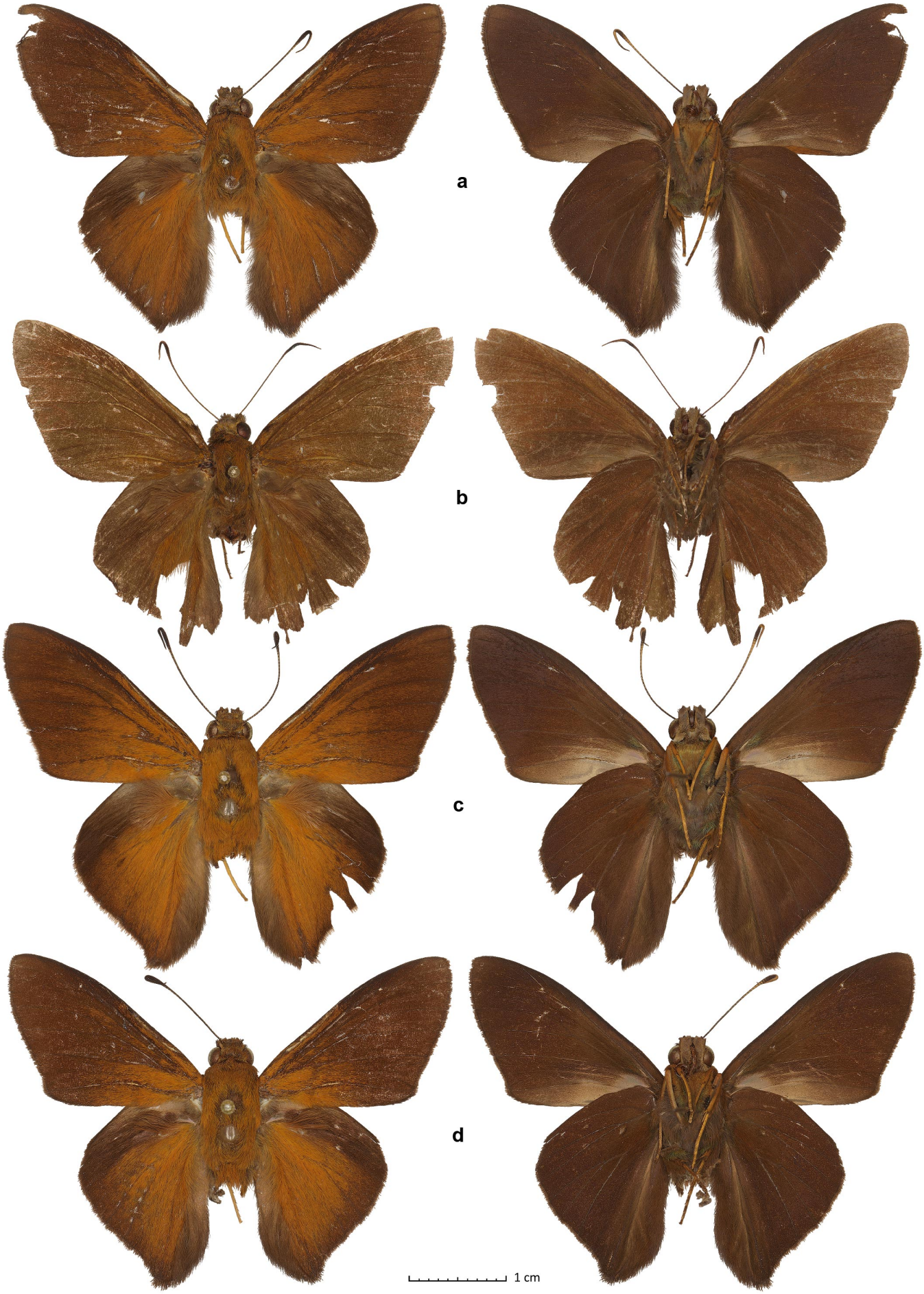
Barcode sequence of the holotype. Sample NVG-23052H01, GenBank PX568491, 658 base pairs:

AACATTATATTTTATCTTTGGAATTTGAGCAGGAATAGTAGGAACTTCACTAAGATTATTAATTCGAACCGAATTAGGTACCCCCGGATCTTTAATTGGAGATGATCAAATTTATAATACT
ATTGTCACAGCTCATGCTTTTATCATAATTTTTTTTATAGTTATACCTATTATAATTGGAGGTTTTGGAAATTGACTAATTCCCTTAATATTAGGAGCTCCCGATATAGCATTCCCCCGAA
TAAATAACATAAGATTTTGATTATTACCTCCTTCATTAACTCTTTTAATTTCGAGAAGAATTGTAGAAAATGGTGCAGGTACAGGTTGAACTGTTTATCCCCCTTTGTCTTCTAATATTGC
CCACCAAGGATCTTCTGTCGATTTAGCAATCTTTTCTCTTCATTTAGCAGGTATCTCTTCAATTTTAGGAGCAATTAATTTTATTACTACAATCATTAATATACGAATTAGAAATTTATCT
TTTGATCAAATACCTTTATTTGTTTGAGCAGTAGGAATTACAGCTTTATTATTATTATTATCATTACCAGTATTAGCAGGTGCTATTACTATACTTTTAACTGATCGAAACTTAAATACTT
CATTTTTTGATCCTGCAGGTGGAGGTGACCCAATTTTATATCAACATTTATTT

Type material. Holotype: ♂ currently deposited in the McGuire Center for Lepidoptera and Biodiversity collection, Gainesville, FL, USA (MGCL), illustrated in Fig. 20a, bears the following six printed rectangular labels (text in italics handwritten; 3rd blue, 6th red, others white): [BRASIL:Rondônia; | 62 km S Ariquemes | linha C-20, 7 km E | B-65, Fazenda | Rancho Grande | 11 August 1994 | leg. G. T. Austin | at paper lures | 1800-1830], [Genetalic Vial | GTA - *8875*], [PARATYPE | Porphyrogenes spadix | Austin & Mielke 2008], [G.T. Austin colln. | MGCL Accession | # 2004-5], [DNA sample ID: | NVG-23052H01 | c/o Nick V. Grishin], and [HOLOTYPE ♂ | Porphyrogenes | tornus Grishin]. The holotype of the new species is also a paratype of *Porphyrogenes spadix* Austin & O. Mielke, 2008 that is not conspecific with the holotype of the latter species.

Type locality. Brazil: Rondônia, 62 km south of Ariquemes, linha C-20, 7 km east of B-65, Fazenda Rancho Grande.

Etymology. The name refers to the hindwing tornus that is not strongly lobed in this new species and is a noun in apposition.


a
b
c
d
1 cm

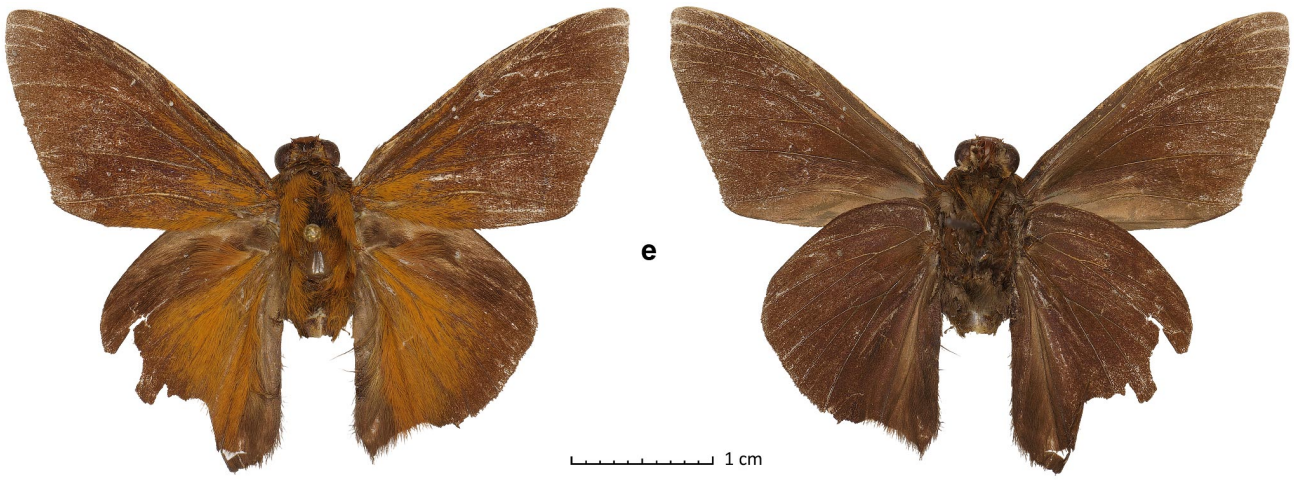


Fig. 20 (above and the previous page). Paratypes of *Porphyrogenes spadix*, males from Brazil: Rondônia, 62 km S of Ariquemes, linha C-20, 7 km E of B-65, Fazenda Rancho Grande, G. T. Austin leg. (unless indicated otherwise) [MGCL] in dorsal (left) and ventral (right) views: **a–b)** new species, not conspecific with the holotype of *P. spadix* (misidentifications): **a)** *P. tornus* **sp. n.** holotype NVG-23052H01, 11-Aug-1994, genitalia GTA-8875; **b)** *P. sepia* **sp. n.** holotype NVG-15023E10, 24-Oct-1997, genitalia GTA-9168; **c–d)** true *P. spadix* (i.e., identified correctly): **c)** NVG-23052G11, 14-Jun-1993, genitalia GTA-3587 and **d)** NVG-23052G12, 16-Jun-1993, genitalia GTA-3489; and **e)** *Porphyrogenes* sp. not conspecific with *P. spadix* (misidentification) but closely related to or conspecific with *P. simulator* and/or *P. splendidus*, NVG-23052H02 vic. Fazenda Rancho Grande, 4–16-Nov-1997, J. E. Eger leg., genitalia GTA-8878.

Distribution. Currently known only from the holotype collected in western Brazil.

Comment. To facilitate further comparisons, here we report the COI barcode sequence of *P. spadix* holotype ♂, sample NVG-17880H07, GenBank PX568492, 658 base pairs:

AACATTATATTTTATTTTTGGAATTTGAGCAGGAATAGTAGGAACTTCATTAAGATTACTAATTCGAACTGAATTAGGTACCCCCGGATCTTTAATTGGAGATGATCAAATTTATAATACT
ATTGTCACAGCTCACGCTTTTATTATAATTTTTTTTATAGTTATACCTATTATAATTGGAGGTTTTGGAAATTGATTAATTCCCTTAATATTAGGAGCCCCAGATATAGCATTCCCACGAA
TAAATAATATAAGATTTTGATTATTACCTCCTTCATTAACTCTTTTAATTTCAAGAAGAATTGTAGAAAATGGTGCAGGCACAGGTTGAACTGTTTATCCCCCTTTATCCTCAAATATTGC
TCACCAAGGATCTTCTGTCGATTTAGCAATCTTTTCATTACATTTAGCAGGTATTTCTTCAATTTTAGGAGCAATTAATTTTATTACCACAATTATTAATATACGAATTAGAAATTTATCT
TTTGATCAAATACCTTTATTTGTTTGAGCAGTAGGAATTACAGCCTTATTATTATTATTATCATTACCAGTATTAGCAGGTGCTATTACTATACTTTTAACTGATCGAAATTTAAATACTT
CATTTTTTGATCCTGCAGGTGGAGGAGATCCAATTTTATACCAACATTTATTT

Barcode sequences of two conspecific paratypes, males, sample NVG-23052G11, GenBank PX568493, and sample NVG-23052G12, GenBank PX568494, are identical.

Porphyrogenes sepia Grishin, new species

https://zoobank.org/CF8C5DF8-7A33-49F4-8E32-B192BE47C032

(Figs. 17 part, 20b)

Definition and diagnosis. Genomic analysis reveals that a paratype of *Porphyrogenes spadix* Austin & O. Mielke, 2008 (type locality in Brazil: Rondônia) sequenced as NVG-15023E10 is genetically differentiated from it at the species level (Fig. 17); e.g., their COI barcodes differ by 4.7% (31 bp), and therefore this specimen represents a new species. This new species keys to *P. spadix* in Austin and Mielke (2008), but differs from it and other relatives by the following combination of characters in males: the forewing tornus is less prominent and the outer margin is straight, not slightly concave before it, the color of the reddish dorsal overscaling is darker and the overscaling is more weakly developed, especially on the forewing; the area of the ventral forewing by the inner margin is dark, including the "speculum" area at the base, which is only slightly paler; and the legs are brown, not orange. Due to its cryptic nature and unexplored individual variation, this species is best identified by DNA, with diagnostic base pairs in the nuclear genome: aly235.20.1:T921C, aly235.20.1:T999C, aly37338.48.1:T318G, aly37338.48.1:T319C, aly50.32.4:A54G, aly2202.11.1:C235C (not T), aly2202.11.1:T225T (not C), aly536.174.1:G1878G (not A), aly536.174.1:T1848T (not C), aly536.174.1:A1038A (not T); and the COI barcode: T5C, C282T, T374C, A433G, T484C, T529C, T580A.

Barcode sequence of the holotype. Sample NVG-15023E10, GenBank PX568495, 658 base pairs:

AACACTATATTTTATTTTTGGAATTTGAGCAGGAATAGTAGGAACTTCATTAAGATTACTAATTCGAACTGAATTAGGTACCCCCGGATCTTTAATTGGAGATGATCAAATTTATAATACT
ATTGTTACAGCTCATGCTTTTATTATAATTTTTTTTTATAGTTATACCTATTATAATTGGAGGTTTTGGAAATTGATTAGTTCCTCTAATACTAGGAGCTCCTGATATAGCATTCCCACGAA
TAAATAATATAAGATTTTGATTATTACCCCCTTCTTTAATTCTTTTAATTTCAAGAAGAATTGTAGAAAATGGTGCAGGTACAGGCTGAACTGTTTATCCTCCTTTATCCTCAAACATTGC
TCATCAAGGACCCTCTGTTGATTTAGCAATTTTTTCATTACATTTAGCAGGTATCTCATCAATTTTAGGGGCAATTAATTTTATTACTACAATTATTAATATACGAATTAGAAATTTATCC
TTTGATCAAATACCTTTATTTGTTTGAGCAGTAGGAATTACAGCCTTATTATTATTATTATCATTACCAGTATTAGCAGGTGCTATTACTATACTATTAACTGATCGAAATTTAAATACTT
CATTTTTTGATCCTGCTGGTGGAGGTGATCCAATTTTATATCAACACTTATTT

Type material. Holotype: ♂ currently deposited in the McGuire Center for Lepidoptera and Biodiversity collection, Gainesville, FL, USA (MGCL), illustrated in Fig. 20b, bears the following six printed rectangular labels (text in italics handwritten; 3rd blue, 6th red, others white): [BRASIL:Rondônia; | 62 km S Ariquemes | linha C-20, 7 km E | B-65, Fazenda | Rancho Grande | 24 October 1997 | leg. G. T. Austin | (at paper lures | 1700-1730)], [Genetalic Vial | GTA - *9168*], [PARATYPE | Porphyrogenes spadix | Austin & Mielke 2008], [G.T. Austin colln. | MGCL Accession | # 2004-5], [DNA sample ID: | NVG-15023E10 | c/o Nick V. Grishin], and [HOLOTYPE ♂ | Porphyrogenes | sepia Grishin]. The holotype of the new species is also a paratype of *P. spadix* that is not conspecific with the holotype of the latter species.

Type locality. Brazil: Rondônia, 62 km south of Ariquemes, linha C-20, 7 km east of B-65, Fazenda Rancho Grande.

Etymology. The name reflects the darker, muted, less saturated color of this species and is treated as a noun in apposition.

Distribution. Currently known only from the holotype collected in western Brazil.

Porphyrogenes probus curvatus Grishin, new subspecies

https://zoobank.org/A0E63445-8D37-4AC9-BA91-781EAB45DA03

(Figs. 17 part, 21a–b)

Definition and diagnosis. Genomic analysis of a male from Costa Rica, sampled as NVG-15023B11, identified by Austin and Mielke (2008) as a new species later named *Porphyrogenes peterwegei* Burns, 2010 (type locality in Costa Rica) (Fig. 21a), together with another Costa Rican male (Fig. 21b) labeled by J. M. Burns as "Like Fig. 152 in Austin & Mielke 2008" (fig. 152 depicts genitalia of NVG-15023B11), reveals that they are indeed conspecific (Fig. 17 red), but not closely related to *P. peterwegei* (Fig. 17 gray). Instead, these two specimens form a clade sister to *Porphyrogenes probus* (Möschler, 1876) (type locality in Suriname) (Figs. 17 blue, 21c, d) that is not strongly differentiated genetically in both the nuclear (Fig. 17a) and mitochondrial (Fig. 17b) genomes, e.g., their COI barcodes differ by 0.8% (5 bp). This was a surprise, because the two males differ in facies and genitalia from *P. probus* (although they are similar in having a paler ventral forewing apex), and therefore represent a new taxon. Due to the lack of genetic differentiation typical for distinct species, this taxon is conservatively proposed as a subspecies. Curiously, this new subspecies indeed keys to *P. probus* in Austin and Mielke (2008), but differs from it and other relatives by the following combination of characters in males: narrower and more curved harpe; unspotted dorsal side of wings [brown spots at least on the hindwing in *P. probus probus*] with tawny overscaling [brighter than in *P. probus probus*] and tawny [not whitish as in *P. peterwegei*] fringes; and a more elongated hindwing. This subspecies is not cryptic, but because individual variation is poorly documented and females remain unknown, it is best identified by DNA, with diagnostic base pairs in the nuclear genome: aly420.49.1:G339A, aly1432.13.2:A156G, aly276791.2.3:C121T, aly824.16.2:G94A, aly824.16.2:C102T; and the COI barcode: T127A, A253A (not G), T361C, T428C, T616T.

Barcode sequence of the holotype. Sample NVG-15023B11, GenBank PX568496, 658 base pairs:

AACATTATATTTTATTTTTGGAATTTGAGCAGGAATAGTAGGAACTTCTTTAAGATTACTAATTCGAACTGAATTAGGTACCCCTGGATCTTTAATTGGAGATGATCAAATTTATAATACT
ATTGTAACAGCTCATGCTTTTATTATAATTTTTTTTATAGTTATACCTATTATAATTGGAGGTTTTGGAAATTGATTAATCCCTTTAATGTTAGGAGCTCCCGATATAGCATTCCCCCGAA
TAAATAATATAAGATTTTGATTATTACCCCCTTCTTTAACTCTTTTAATTTCAAGAAGAATTGTTGAAAATGGTGCAGGAACAGGATGAACTGTTTACCCCCCTTTATCATCTAATATCGC
CCATCAAGGATCTTCAGTTGATTTAGCAATTTTTTCATTACATCTTGCAGGTATTTCCTCAATTCTAGGAGCTATTAATTTTATTACTACAATTATTAATATACGAATTAATAATTTATCT
TTTGATCAAATACCTTTATTTGTTTGAGCAGTAGGAATTACAGCTTTATTATTATTATTATCATTACCTGTATTAGCAGGAGCAATTACTATACTTTTAACTGATCGAAATTTAAATACTT
CATTTTTTGATCCTGCAGGAGGAGGAGATCCTATTTTATATCAACATTTATTT

Type material. Holotype: ♂ currently deposited in the McGuire Center for Lepidoptera and Biodiversity collection, Gainesville, FL, USA (MGCL, originally from the Museo Nacional de Costa Rica collection),

Fig. 21. *Porphyrogenes* in dorsal (left) and ventral (right) views: **a–b)** *P. probus curvatus* **sp. n.** from Costa Rica: **a)** holotype NVG-15023B11 San José Province, Ciudad Colón, 900 m, 9°54'N, 84°17.5'W, 15-Sep-1998, P. Gloor leg., genitalia GTA-13917; **b)** paratype NVG-2732 Limón, Estación Hitoy Cerere, Río Cerere, Reserva Biológica Hitoy Cerere, 100 m, Apr-1993, G. Carballo leg., genitalia X-5033 J.M.Burns 2001; and **c–d)** *P. probus probus*: **c)** NVG-21107C02, Bolivia: Santa Cruz Department, Sara or Ichilo Province, 450 m, Mar-1910, J. Steinbach leg. [CMNH] and **d)** NVG-18067C10, Peru: Amazonas, Rodríguez de Mendoza, 28-Sep-1993 [EBC].

illustrated in Fig. 21a, bears the following six rectangular labels (4th handwritten, others printed with handwritten text shown in italics; 4th yellow, 6th red, others white): [Finca Hamàdryas | Ciudad Colon CR | 900 m/M 9°54'N/84°17,5'W | 15. 09. 98 | leg P.Gloor], [Genitalic Vial | GTA-*13917*], [Porphyrogenes | undescribed sp.; see | Janzen & Hallwachs 2008 | det. G. T. Austin 2008], [MNCR], [DNA sample ID: | NVG-15023B11 | c/o Nick V. Grishin], and [HOLOTYPE ♂ | Porphyrogenes probus | curvatus Grishin]. **Paratype:** 1♂ NVG-2732 Costa Rica, Limón, Estación Hitoy Cerere, Río Cerere, Reserva Biológica Hitoy Cerere, 100 m, GPS 9.67, −83.05, Apr-1993, G. Carballo leg., genitalia X-5033 J. M. Burns 2001, currently in USNM (Fig. 21b).

Type locality. Costa Rica: San José Province, Ciudad Colón, Finca Hamàdryas, elevation 900m, approx. GPS 9.9000, −84.2917.

Etymology. The name reflects the shape of the genitalic harpe, more curved and narrower than in the nominotypical subspecies and is an adjective.

Distribution. Currently known only from two males collected in Costa Rica.

Bungalotis ryta Grishin, new species

https://zoobank.org/BE5DED11-74F3-4CA9-BA9B-A75645FF101B

(Figs. 22 part, 23a)

Definition and diagnosis. Genomic analysis reveals that a male from western Panama identified as *Bungalotis erythus* (Cramer, 1775) (type locality in Suriname) (Fig. 23b–d) is genetically differentiated from it at the species level (Fig. 22); e.g., their COI barcodes differ by 3.0% (20 bp), and therefore this specimen represents a new species. This new species keys to *B. erythus* (D.1.1) in Evans (1952), but differs from it and other relatives by the following combination of characters in males: the discal cell hyaline spot is narrower on all wings; the two tornal-most hyaline spots on the hindwing are smaller, dot-like in the holotype (enclaved by larger white spots on the ventral side); the posterior subapical hyaline spot is more strongly offset distad from the other two, and all three spots are smaller; overall smaller in size; and the harpe is broader at the base. Due to its cryptic nature and unexplored individual variation, this species is best identified by DNA, with diagnostic base pairs in the nuclear genome: aly2487.1.4:A466G, aly2487.1.4:C474T, aly3268.9.3:A69T, aly3268.9.3:T111C, aly1249.9.24:A144C, aly203.15.3:A1695A (not T), aly536.148.3:T138T (not A), aly19461.2.3:G690G (not A), aly2694.22.1:C602C (not T), aly4966.12.11:C137C (not T); and the COI barcode: T19C, A88G, T355C, A470G, T589C, T601T (not C).

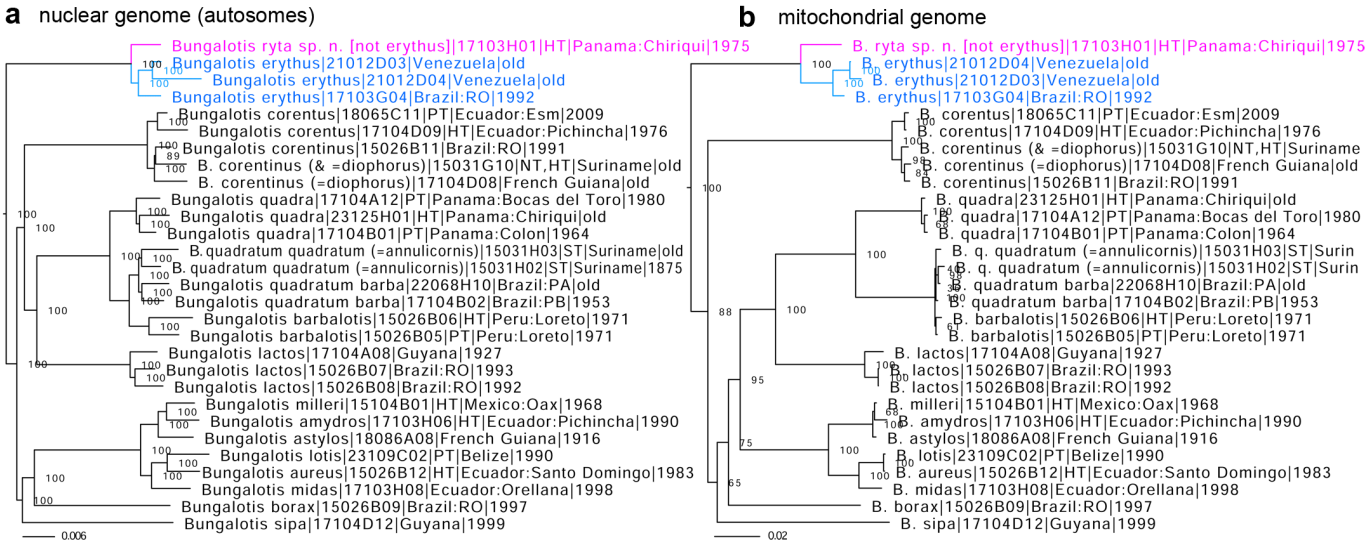


Fig. 22. Phylogenetic trees of selected *Bungalotis* E. Watson, 1893 species constructed from protein-coding regions in: **a)** the nuclear genome (autosomes), based on 2,094,021 positions, and **b)** the mitochondrial genome. Species discussed in the text are colored: *B. ryta* **sp. n.** (magenta) and *B. erythus* (blue). Ultrafast bootstrap (Hoang et al. 2018) values are shown at nodes.

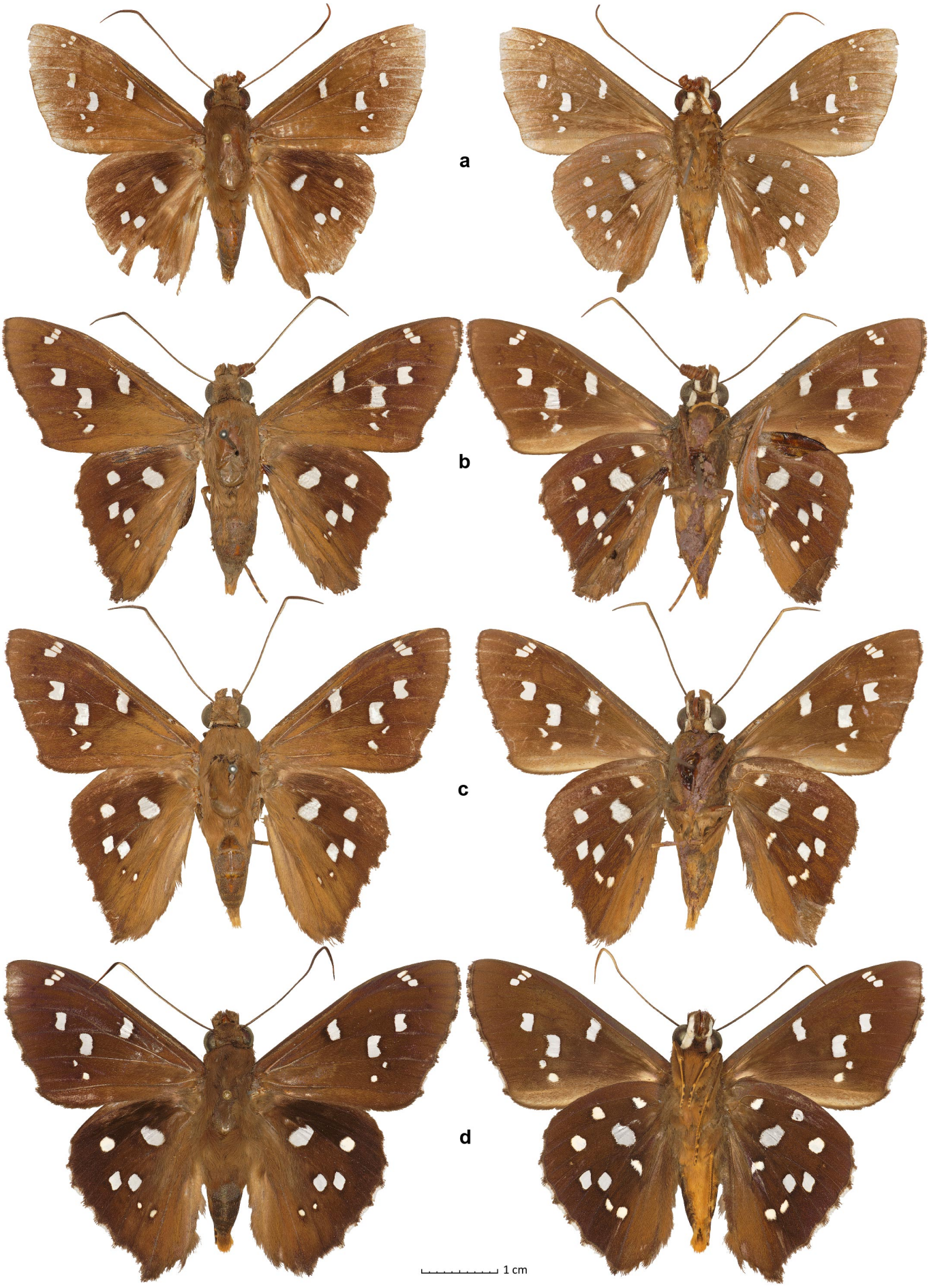

a
b
c
d
1 cm

Fig. 23 (see the previous page). Males of *Bungalotis* in dorsal (left) and ventral (right) views: **a)** *B. ryta* **sp. n.** holotype NVG-17103H01 Panama: Chiriquí, Santa Cruz, 2-Aug-1975, G. B. Small leg. [USNM] and **b–d)** *B. erythus*: **b–c)** Venezuela, old, Holland collection [CMNH]: **b)** NVG-21012D04 and **c)** NVG-21012D03; and **d)** NVG-17103G04, USNMENT_00913803 Brazil: Rondônia, 62 km S of Ariquemes, Fazenda Rancho Grande, 165 m, 10°32'S, 63°48'W, 29-Sep–10-Oct-1992, B. P. Harris leg. [USNM].

Barcode sequence of the holotype. Sample NVG-17103H01, GenBank PX568497, 658 base pairs:

AACTTTATATTTTATTTTCGGAATTTGAGCAGGTATAATTGGAACTTCATTAAGATTACTAATTCGAACTGAATTAGGAACCCCCGGGTCTTTAATTGGAGATGATCAAATTTATAATACT
ATTGTTACTGCTCATGCTTTTATTATAATTTTTTTTATAGTTATACCTATTATAATTGGAGGCTTTGGAAATTGATTAGTACCTTTAATACTTGGAGCTCCTGATATAGCATTCCCTCGAA
TAAATAATATAAGATTTTGATTATTACCTCCTTCCTTAACTCTTTTAATCTCAAGAAGAATTGTAGAAAATGGAGCTGGAACTGGTTGAACAGTTTATCCTCCTTTATCCGCCAATATTGC
TCACCAAGGATCTTCTGTTGATTTAGCAATTTTTTCTCTTCATTTAGCTGGGATTTCTTCTATTCTAGGAGCTATTAATTTTATTACAACAATTATTAATATACGAGTTAGAAATTTATCT
TTTGATCAAATACCTTTATTTGTTTGAGCTGTAGGAATTACAGCCCTTTTATTATTATTATCATTACCTGTTTTAGCTGGAGCTATTACTATACTTTTAACAGACCGAAATCTTAATACTT
CTTTTTTTGATCCAGCAGGAGGAGGAGATCCAATTTTATATCAACATTTATTT

Type material. Holotype: ♂ deposited in the National Museum of Natural History, Smithsonian Institution, Washington, DC, USA (USNM), illustrated in Fig. 23a, bears the following four printed rectangular labels (text in italics handwritten), three white: [PANAMA: Chiriqui | Santa Cruz | 8°40'N 82°46'W | 2 August 1975 | leg. G.B.Small], [DNA sample ID: | NVG-17103H01 | c/o Nick V. Grishin], [USNMENT | {QR Code} | 00913812], and one red [HOLOTYPE ♂ | Bungalotis | ryta Grishin].

Type locality. Panama: Chiriquí Province, Santa Cruz, GPS 8.6667, −82.7667.

Etymology. The name is derived from its sister species, *B. erythus*, made shorter for its more northern relative and is treated as a noun in apposition.

Distribution. Currently known only from the holotype collected in western Panama.

Pseudodrephalys gap Grishin, new species

https://zoobank.org/E3A26B27-9CBD-4AB5-8B7F-6033788A8ECB

(Figs. 24 part, 25–26)

Definition and diagnosis. Genomic analysis reveals that a specimen from Rondônia, Brazil, initially identified as *Pseudodrephalys atinas* (Mabille, 1888) (type locality Peru: Loreto, Pebas) is genetically differentiated from it at the species level (Fig. 24); e.g., their COI barcodes differ by 4.0% (26 bp), and is more closely related to *Pseudodrephalys sohni* Burns, 1999 (type locality Brazil: Amazonas, Manaus) and *Pseudodrephalys tinas* Grishin, 2023 (type locality Peru: Loreto, Iquitos), but differs from them as well, e.g., in COI barcodes by 1.7% (11 bp) and 1.5% (10 bp), respectively, and therefore this specimen represents a new species. This new species keys to "*Drephalys atinas*" (B.6.7) in Evans (1952), but differs from it and other relatives by the following combination of characters in males: a narrower valva with a nearly absent cleft between the harpe and ampulla dorsally in lateral view (i.e., an expanded posteriad ampulla nearly or narrowly overlaps the harpe), similar to that in *P. sohni* [different from a larger cleft in *P. tinas* and a deep and narrowing cleft in *P. atinas*], but due to a narrower ampulla, there is a teardrop-shape gap between the ventral margin of the ampulla and the dorsal margin of the harpe near its base in lateral view [somewhat similar but narrower gap (the ampulla is shallower and broader) is observed in a more distant relative, *Pseudodrephalys hypargus* (Mabille, 1891) (type locality Brazil: Amazonas, Manaus)]; much narrower harpe compared with *P. atinas*; a convex costa-ampulla [nearly flat in *P. sohni*]; the ventral hindwing white band is broader than in other species, narrows towards the Sc+R_1 vein, reaching it [the same width at the vein in *P. sohni*], otherwise more uniform in width, not constricted or broken in the middle of cell CuA_2-1A+2A but is the broadest near the vein 1A+2A; the white longitudinally elongated spot by the inner margin of the ventral hindwing is well developed; both semihyaline forewing discal cell spots are elongated; the semihyaline apical spots are better aligned than in other species; and the violaceous postdiscal band on the ventral hindwing underside is only weakly developed. Due to unexplored individual variation, this species is best identified by DNA, with diagnostic base pairs in the nuclear genome: aly29.10.1:G191C, aly691.3.5:C67T, aly378.23.8:A84G, aly171.3.18: G129A, aly2336.9.1:G627A, aly1063.2.1:G225G (not A), aly2548.22.2:A33A (not G), aly276665.18.3:C198C (not T), aly1033. 2.17:C129C (not T), aly1340.1.1:T2175T (not C); and the COI barcode: T10C, A100C, T193C, T274C, A403G, T523T (not C), T571T (not C).

Barcode sequence of the holotype. Sample NVG-24111A04, GenBank PX568498, 658 base pairs:

AACTTTATACTTTATTTTTGGAATTTGGGCAGGAATAGTAGGTACTTCTTTAAGATTATTAATTCGTACTGAATTAGGAAATCCAGGATCTTTAATTGGCGATGATCAAATTTATAATACT
ATTGTTACAGCTCACGCTTTTATTATAATTTTTTTTATAGTTATGCCAATTATAATTGGAGGATTTGGAAACTGATTAGTACCTCTGATACTAGGAGCTCCTGATATAGCATTCCCACGAA
TAAATAATATAAGATTTTGACTACTTCCCCCCTCTTTATTATTATTAATTTCAAGAAGTATTGTAGAAAATGGTGCTGGAACTGGATGAACTGTATACCCTCCTCTTTCTTCTAATATTGC
CCATCAAGGAGCATCAGTAGATTTAGCAATTTTTTCATTGCATTTAGCAGGAATTTCATCTATTTTAGGAGCTATTAATTTTATTACAACAATTATTAATATACGAATTAATAATCTTTCC
TTTGATCAATTACCTTTATTCGTATGAGCTGTTGGTATTACAGCTTTACTCTTATTACTCTCTTTACCAGTATTAGCTGGAGCTATTACTATATTATTAACTGATCGAAATTTAAATACAT
CTTTTTTTGATCCTGCGGGAGGAGGAGATCCAATCTTATATCAACATTTATTT

Type material. Holotype: ♂ currently deposited in the McGuire Center for Lepidoptera and Biodiversity collection, Gainesville, FL, USA (MGCL), illustrated in Fig. 25 (genitalia Fig. 26), bears the following five printed rectangular labels (text in italics handwritten), four white: [BRASIL: Rondônia | 62 km S Ariquemes | linha C-20, 7 km E | B-65, Fazenda | Rancho Grande | 23 October 1997 | leg. G. T. Austin | (associated with Eciton | burchelli, 1230–1300)], [Genetalic Vial | GTA - *10386*], [G T Austin colln. | MGCL Acc. | 2004-5], [DNA sample ID: | NVG-24111A04 | c/o Nick V. Grishin], and one red [HOLOTYPE ♂ | Pseudodrephalys | gap Grishin].

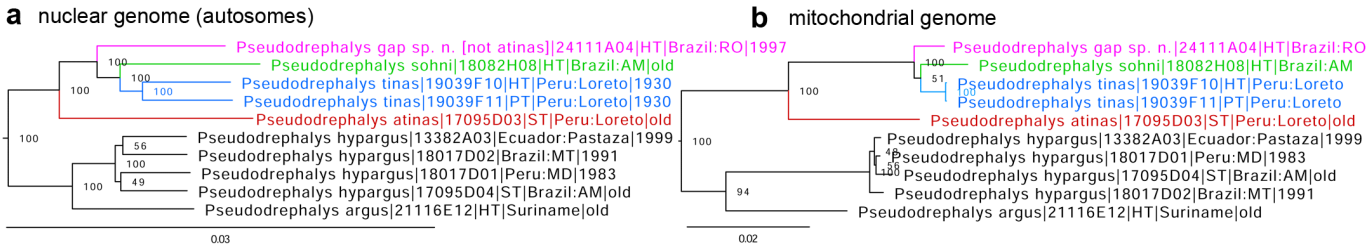


Fig. 24. Phylogenetic trees of all described *Pseudodrephalys* Burns, 1999 species constructed from protein-coding regions in: **a)** the nuclear genome (autosomes), based on 10,922,433 positions, and **b)** the mitochondrial genome. Species mentioned in the text are colored: *P. gap* **sp. n.** (magenta), *P. sohni* (green), *P. tinas* (blue), and *P. atinas* (red). Ultrafast bootstrap (Hoang et al. 2018) values are shown at nodes.

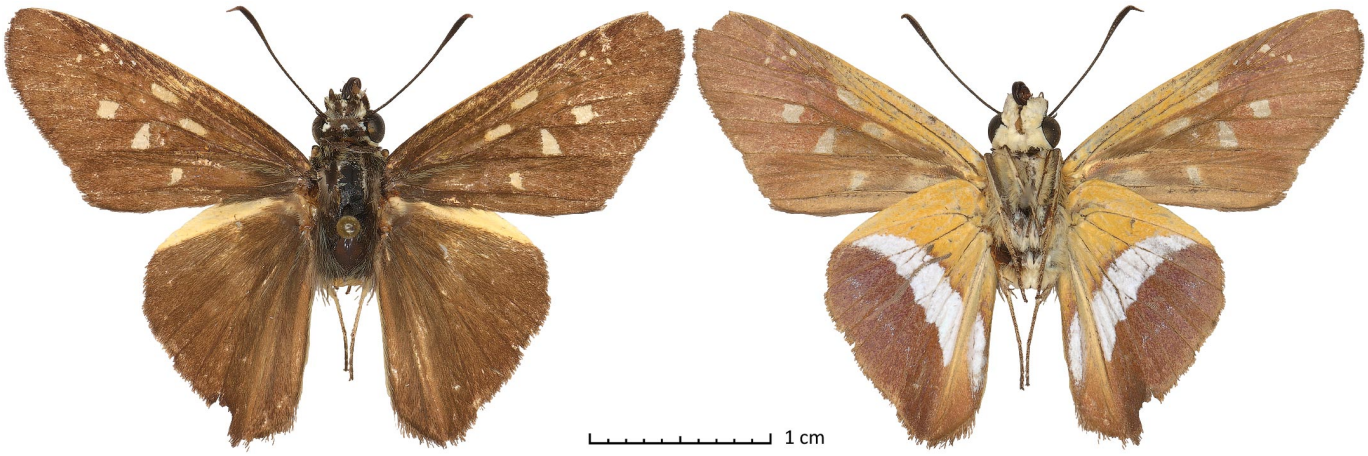


Fig. 25. *Pseudodrephalys gap* **sp. n.** holotype ♂ NVG-24111A04 in dorsal (left) and ventral (right) views, data in text.

Fig. 26. Male genitalia of *Pseudodrephalys gap* **sp. n.** holotype NVG-24111A04 in **a)** left lateral, and **b)** dorsal views.

Type locality. Brazil: Rondônia, 62 km south of Ariquemes, linha C-20, 7 km east of B-65, Fazenda Rancho Grande.

Etymology. The name refers to the teardrop-shaped gap between the ampulla and the basal portion of the harpe that characterizes this species and is treated as a noun in apposition.

Distribution. Currently known only from the holotype collected in western Brazil.

Lectotype designation for *Antigonus fumosus* Plötz, 1884

Antigonus fumosus Plötz, 1884, currently regarded as a junior subjective synonym of *Grais stigmaticus* (Mabille, 1883) (type locality in Brazil), was described from an unstated number of specimens from Brazil (Plötz 1884). The description was incorporated in identification keys, and we assemble and literally translate from German the relevant part of the key as: “Upper side reddish brown, smoky gray-brown, or

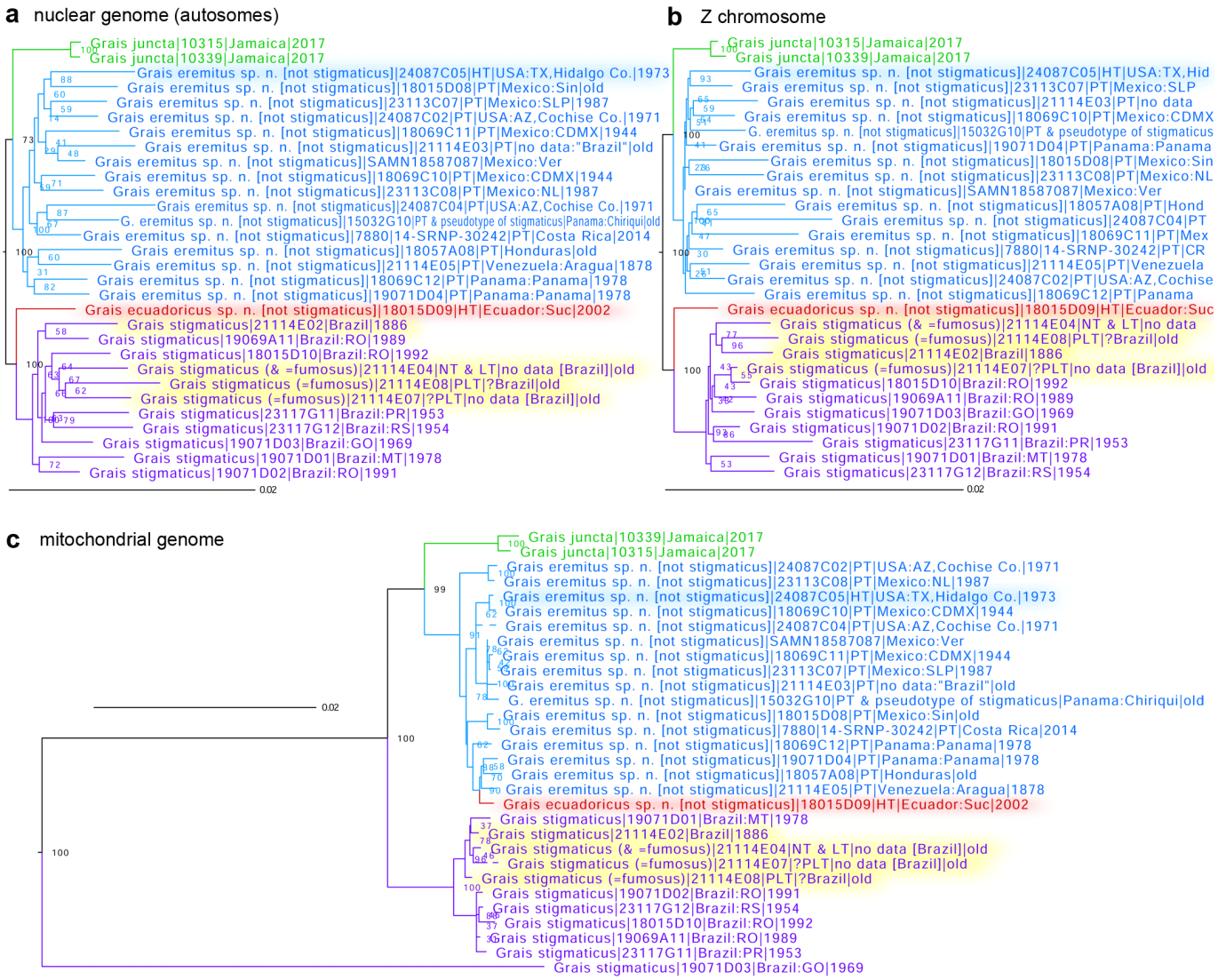


Fig. 27. Phylogenetic trees of all described *Grais* species constructed from protein-coding regions in: **a)** the nuclear genome (autosomes), based on 737,415 positions, **b)** the Z chromosome, based on 269,580 positions, and **c)** the mitochondrial genome. Different species are colored differently: *G. juncta* (green), *G. eremitus* **sp. n.** (blue), *G. ecuadoricus* **sp. n.** (red), and *G. stigmaticus* (violet). The four historical specimens of *Antigonus fumosus* discussed in the text (including the lectotype designated herein) are highlighted in yellow; the holotypes of *G. eremitus* **sp. n.** and *G. ecuadoricus* **sp. n.** are highlighted in blue and red, respectively. Gaps in terminal branches indicate that a segment of a branch was cut out to reduce its length, i.e., a branch with a gap is longer than shown. The sequence of SAMN18587087 is taken from the alignment provided in Kawahara et al. (2023). Ultrafast bootstrap (Hoang et al. 2018) values are shown at nodes.

Fig. 28. Type specimens of *Grais* ♂♂ in dorsal (left) and ventral (right) views, data in text: **a)** *G. eremitus* **sp. n.** paratype (and *Anastrus stigmaticus* pseudotype) NVG-15032G10 from Panama: Chiriquí [MFNB]; **b)** *G. stigmaticus* (*Antigonus fumosus* lectotype and *Anastrus stigmaticus* neotype, both designated herein) NVG-21114E04 from Brazil [MFNB], and **c)** *G. ecuadoricus* **sp. n.** holotype NVG-18015D09 from Ecuador: Sucumbíos, Cerro Lumbaqui Norte [USNM]. Labels are shown below the two historical specimens [except two most recently added labels in (b)], and specimens are separated by black lines.

dull yellowish brown; forewings usually with distinct dark spots near the base, a dark median spot, and two bands composed of cap-shaped spots toward the margin. Hindwings likewise with spots and bands. The lighter underside shows the same pattern, but usually more sharply than above. Upper side smoky gray-brown, without, or with only indistinct, markings. Underside dirty clay-yellow, with faint dusty bands, with a brown spot at the anal angle of the hindwing. Forewing elongated, blunt. 31. Fumosus Pl. Hesp. t. 1017. 23—25 mm. Brasilien" (Plötz 1884). Because the word "usually" was used in the description, and the range for the forewing length was given instead of a fixed number, the description was based on more than one specimen.

To learn more about this taxon, we searched for its syntypes. In MFNB, we found a specimen (sequenced as NVG-21114E02, Fig. 27) with the red "Typus" label identified as "Antigonus fumanus HS" (HS is for Herrich-Schäffer) and "Antigonus fumosus Pl" (Pl is for Plötz), but according to its other label it was collected in 1886 (by Donckier), which is after the description of *A. fumosus* in 1884. Therefore, this specimen is not a syntype. Another old specimen bears an identification label "Fumosus Plötz" with the "Origin." (i.e., syntype) label (Fig. 28a, see discussion of this specimen below), but it is from Panama, not Brazil (confirmed by genomic sequencing as NVG-15032G10, Fig. 27), and hence is not a syntype of *A. fumosus* either. In addition, we found three plausible syntypes. One specimen is from the Herrich-Schäffer collection (sequenced as NVG-21114E07) with two original labels: handwritten "Antigonus | fumanus | Pl." (might be by Herrich-Schäffer) and printed "Coll. H.—Sch." (characteristic of all Herrich-Schäffer specimens). Two others (sequenced as NVG-21114E08 and NVG-21114E04) are from the Weymer collection, both with a label stating that they were identified by Plötz as "Fumosus" and also bearing identification labels with "Fumanus HS." The specimen NVG-21114E08 is labeled as "Antigonus | Fumanus HS | Brasilien." offering a link to the type locality exactly as it was listed in the original description. Genomic sequencing suggests that the three specimens (NVG-21114E04, NVG-21114E07, NVG-21114E08) are conspecific and they form a clade in the nuclear genome tree (Fig. 27a), implying that they were collected in generally nearby localities (i.e., the same province, state, or a smaller country) (Cong et al. 2021), and if the "Brasilien" locality label on one of them is accurate, it would be in Brazil. For lectotype designation, the specimen most directly linked to Plötz, i.e., the one bearing an identification label in Plötz's handwriting, was chosen (see below).

In addition, we found a specimen in MFNB (sequenced as NVG-21114E03) with a handwritten label "Fumosus Plötz | Bras." in Maassen's handwriting and a printed label "Mssn. | G." characteristic of Maassen collection specimens. While it is possible that this specimen might have been a syntype, because it was possibly collected before the description (J. Peter Maassen died in 1890), genomic analysis reveals that it is not conspecific with syntypes discussed above, and is likely from Central America, not Brazil. The word "Bras." on its identification label may refer not to the collecting locality of this particular specimen, but simply indicate the locality stated in the description of this species.

To stabilize nomenclature and define the name *A. fumosus* objectively, N.V.G. hereby designates the syntype in the MFNB collection, a male shown in Fig. 28b (genitalia Fig. 29) that bears the following seven white labels (1st–3rd handwritten, others printed): [! Obscurus ♀ | nº 53 best. v. HS. | ! Fumanus HS ♂ | nº 60 best. v. Plötz], [Antigonus (686.) | Fumanus HS.], [Ant. Fumosus Pl ♂ | Plötz taf 1070], [Coll. | Weymer], [DNA sample ID: | NVG-21114E04 | c/o Nick V. Grishin], [DNA sample ID: | NVG-23082A09 | c/o Nick V. Grishin], and [genitalia | NVG240912-11 | c/o Nick V. Grishin], as the **lectotype** of *Antigonus fumosus* Plötz, 1884. The 2nd label is in Plötz's handwriting and is the strongest evidence connecting this specimen to Plötz prior to the description of *A. fumosus*, with "fumanus" likely being an early variant of the name, possibly suggested by Herrich-Schäffer and changed to *fumosus* in the publication by Plötz. The 1st and 3rd labels are in Weymer's handwriting and "best. v." stands for "bestimmt von" (identified by), HS means Herrich-Schäffer, the numbers 53 and 60 refer to some internal and unpublished numbers in the Weymer collection, and taf[el] 1070 specifies Plötz's original drawing number for *A. fumosus*, although we are not certain that this exact specimen was illustrated. It remains unclear why this number is not 1017 as in the original description ("Pl. Hesp. t. 1017"), this could be a lapsus. The first DNA sample ID refers to the extraction from a leg (sequenced), and the second from the abdomen (also sequenced to improve the quality of the DNA dataset) prior to genitalia dissection. The

Fig. 29. Genitalia of *A. fumosus* lectotype (and *A. stigmaticus* neotype) ♂ NVG-21114E04 in **a)** left lateral and **b)** dorsal views.

genitalia vial is pinned next to the specimen. The lectotype is missing the right antenna, all wings are chipped at the outer margin and damaged at the tornus of both hindwings. The type locality of *A. fumosus* remains in Brazil, as stated in the original description, and will be further delimited based on DNA sequence comparison. The COI barcode sequence of the lectotype, sample NVG-21114E04, GenBank PX568500, 658 base pairs is:

AACTTTATATTTTATTTTTGGAATTTGAGCAGGTATAGTAGGAACATCTTTAAGTTTACTTATTCGAACTGAATTAGGTAACCCCGGTTCTTTAATTGGAGATGATCAAATTTATAATACT
ATTGTTACAGCTCATGCTTTTATTATAATTTTTTTTATAGTTATACCAATTATAATTGGTGGATTCGGTAATTGATTAGTTCCTTTAATACTAGGAGCTCCAGATATAGCTTTCCCCCGAA
TAAATAATATAAGATTTTGATTACTACCCCCATCACTAATATTATTAATTTCAAGAAGTATCGTAGAAAATGGAGCAGGTACAGGTTGAACAGTTTATCCCCCTTTATCCTCTAATATTGC
CCATCAAGGATCTTCAGTTGATTTAGCTATTTTTTCATTACATCTAGCTGGAATTTCTTCTATTTTAGGAGCTATTAATTTTATTACAACAATTATTAATATACGAATTAAAAATCTTTCC
TTTGATCAAATACCTTTATTTGTTTGAGCAGTAGGAATTACTGCTTTACTTTTACTTTTATCTCTTCCTGTTTTAGCTGGGGCTATTACTATACTTTTAACAGATCGAAATTTAAATACAT
CTTTTTTTGATCCAGCTGGTGGTGGTGATCCTATTCTTTATCAACATTTATTT

Neotype designation for *Anastrus stigmaticus* Mabille, 1883

Anastrus stigmaticus Mabille, 1883, currently a valid—and the type—species of *Grais* Godman & Salvin, 1894 was described from an unstated number of specimens from "Brasilia" (Mabille 1883). A literal translation of the entire description (from Latin and French) is: "Dusky-olivaceous; on the forewings a line, or rather a small submarginal stripe, somewhat blackish, sinuate and formed of separated spots. In the cell there are two brown spots. The outer margin of the wings is sinuate. The hindwings show three obscure, interrupted lines. The underside is dark ochraceous brown, showing the same lines, formed more distinctly by black dots. Body brown, paler beneath; the thorax is covered with white hairs; the legs and palpi are ochraceous. Brazil. This species is of a pale olive-brown; and the dark lines that run fully across all four wings are weakly marked and seem as if absorbed into the ground color. The palpi are of an ochraceous yellow, and this color extends onto the thorax" (Mabille 1883). The description is rather general, somewhat imprecise, and loosely applies to most populations of *Grais*, but strictly to none. For instance, the spots (which are not true "dots" [*punctis*] or "small spots") on the ventral side are brown, not "black" or "very dark" [*nigris*]; and the outer margin of the wings is not strictly speaking "sinuate" [*sinuatus*]. The only specific detail provided is that the type locality is in Brazil.

In contrast, Godman and Salvin (1894) stated that *G. stigmaticus* was "described by M. Mabille from Chiriqui specimens, one of which is before us." This lack of consistency about the type locality (Brazil vs. Panama) creates a problem, because our genomic analysis suggests that *Grais* from Panama and *Grais* from Brazil belong to different species (Fig. 27 blue vs. violet). Therefore, it is essential to clarify the type locality of *G. stigmaticus* and objectively define this taxon by the name-bearing type that is a single specimen. In MFNB, we located the specimen Godman and Salvin inspected and referred to by "one of" the syntypes (Fig. 28a). To support this claim, the specimen bears a label in Godman's handwriting: "Grais | stigmaticus | B.C.A.Ph. | ii.p.381" referring to the exact page 381 of the 2nd volume

of the book this specimen was mentioned (Godman and Salvin 1894). According to another label, this specimen is from Panama: Chiriquí, collected by F. Trösch (frequently abbreviated as "Tr."), and genomic sequencing (NVG-15032G10) indeed places it in the Central American clade with Panamanian specimens, and not with Brazilian specimens, supporting the locality label. This locality/collector label also shows a year "97" handwritten, meaning 1897. If the year were accurate, it would immediately disqualify this specimen from being a syntype, because 1897 is later than the species description in 1883. However, the year is crossed out, thus it is unclear when the specimen was collected. Nevertheless, a span of about 15 years needed for this specimen to be considered a syntype seems long for the inaccurate year written on the label. This specimen is labeled as "Origin." meaning a syntype, most likely due to the identification label in Mabille's handwriting "an. stigma | tica, Mab." This "Origin." label was probably added by Staudinger and is characteristic of labels he placed on syntypes of taxa he described. The final historical label states "Fumosus | Plötz" in the handwriting we do not recognize (but such large rectangular framed identification labels are frequent in the MFNB collection), with "Stigmaticus | Mab." written above and "in. l.?" written below by Staudinger. It is not clear whether "in l[*itteris*]." refers to "fumosus" or to "stigmaticus," and if the latter, it might suggest that this specimen was collected before the description, referring to a yet unpublished name. However, "in. l." is followed by a question mark and is placed under "Plötz", more likely referring to the name "fumosus" and treating "stigmaticus Mab." as an already published name. Therefore, we cannot use "in. l." as evidence that the specimen was labeled with a yet unpublished name "stigmaticus Mab." Although this specimen lacks an explicit label stating that it was from the Staudinger collection (such label might have been lost), Staudinger's most distinctive handwriting on the label and the style of this label, together with the style of others ("Origin.", "Chiriqui"), offer strong evidence to suggest it. In summary, we were not able to find evidence that this Staudinger's specimen from Panama mailed to Godman as "one of" the syntypes was identified by Mabille before the description of *Anastrus stigmaticus*.

Another complication is that the comprehensive American Hesperiidae Catalogue by Mielke (2005) gives "collection Mabille" as the source of *G. stigmaticus* syntypes, but a possible syntype discussed by Godman and Salvin (1894) was from the Staudinger collection, not likely originating from the Mabille collection. Most specimens from the Mabille collection have been deposited in BMNH, but neither Evans (1953), who consistently mentioned for each species the Mabille types that were in BMNH, nor us were able to find syntypes of *G. stigmaticus* from the Mabille collection there. If true, Mielke's statement "collection Mabille" would disqualify the specimen from the Staudinger collection as a possible syntype of *G. stigmaticus*. We turned to the original publication (Mabille 1883) and translate from French the introduction to it as follows: "We provide here the description of a large number of Hesperiids that we have been led to regard as undescribed or confused with closely related species. Having distinguished them in our collection, we have communicated their names to all those who were willing to consult us, and today we give their diagnoses, so that these names may not become an inconvenience, like all mere collection names." While indeed, according to our understanding of this text, Mabille decided that species described in this work were new on the basis of specimens in his collection ("notre collection"), he identified specimens as belonging to these new species in other collections ("en avons donné les noms à tous ceux … comme tous les noms de collection"). We interpret the meaning of this as Mabille placing labels with these yet unpublished names on specimens in other collections, and his publication meant to formalize these names. The label "an. stigma | tica, Mab." written by Mabille on the Staudinger's specimen could be an indication of that, but only if it was added before the description of *Anastrus stigmaticus*.

According to Art. 72.4.1 of the ICZN Code (ICZN 1999), "The type series of a nominal species-group taxon consists of all the specimens included by the author in the new nominal taxon …." Therefore, syntypes are not only specimens in the Mabille collection, but also specimens in other collections identified by Mabille as these species prior to publication, as he mentioned in the introduction (Mabille 1883). Further, we apply Art. 72.4.1.1: "For a nominal species or subspecies established before 2000, any evidence, published or unpublished, may be taken into account to determine what specimens constitute the type series." Synthesizing all the evidence presented above, mostly from the specimen labels, we

agree that the Staudinger's specimen from Panama was indeed identified by Mabille as *A. stigmaticus*. However, we were not able to find evidence that this specimen was identified by Mabille before the description of *Anastrus stigmaticus* in 1883. If anything, the evidence suggests the opposite: a collection year originally written on the specimen was 1897 (although later crossed out), and Staudinger labeled it with the name "Stigmaticus | Mab." without definitively adding *in litteris* after the name. And most importantly, the original type locality is given by Mabille (1883) as "Brasilia" and not "Panama." Therefore, this specimen from Panama is not a syntype, but a pseudotype of *A. stigmaticus*, which Staudinger considered a type (or a "typical specimen": the concept of the type was not fully formed a century ago) and loaned to Godman as such.

It is nevertheless unsettling that the type locality for *G. stigmaticus* was given as "Brasilia" and the only possible syntype we located was from Panama. We were not able to figure out definitively whether there was indeed a Brazilian syntype in the Mabille's collection, or whether "Brasilia" was simply a lapsus. There is no evidence that the type locality given as "Brasilia" was erroneous. Moreover, nearly all type localities given by Mabille correspond to those stated on specimen labels (for definitive syntypes) and errors were not common. Furthermore, *Grais* specimens from Brazil (see *A. fumosus* discussion above) were frequent in collections prior to 1883 (e.g., the oldest being Herrich-Schäffer's specimen), and specimens from Panama were rare (if available at all). After consulting with ICZN Commissioners and the reviewer, we decided to follow the original description and the original type locality stated therein to clarify the identity of *A. stigmaticus*. This treatment also promotes the stability of nomenclature, because *A. fumosus* is currently regarded as a junior subjective synonym of *G. stigmaticus*, both being from Brazil. Because, as we found, Brazilian and Panamanian specimens belong to two different species (Fig. 27 blue vs. violet) and taking into account additional cryptic species present among their relatives, there is an exceptional need to establish the type locality of *G. stigmaticus* objectively.

Failing to find credible syntypes, we proceeded with the neotype designation because there is an exceptional need to clarify both the taxonomic identity and the type locality of *A. stigmaticus*. Hereby, N.V.G. designates the lectotype of *Antigonus fumosus* Plötz, 1884 in MFNB, a male shown in Fig. 28b (genitalia Fig. 29, DNA sample NVG-18095F02), as the **neotype** of *Anastrus stigmaticus* Mabille, 1883. We selected this specimen as the neotype to stabilize the current treatment of *A. fumosus* as a synonym of *A. stigmaticus*. This neotype is from the old stock of Brazilian specimens that existed before 1884, and it is possible that syntypes were from the same stock.

The neotype satisfies all requirements set forth by the ICZN Article 75.3, namely: **75.3.1.** It is designated to clarify the taxonomic identity of *A. stigmaticus*, which is necessary because new species are present among its close relatives and the original description was too incomplete to differentiate between them, and to objectively define the type locality, which was stated in the original description as "Brasilia", but a pseudotype collected in Panama exists; **75.3.2.** The characters to differentiate this taxon from others, as stated in the original description (translated above), are: pale olive-brown with diffuse sinuate bands of darker brown spots: a submarginal one on the forewing, which is with two brown spots in the discal area, and three bands on the hindwing; the ventral side is brown-ochraceous with the same bands being more distinct; palpi beneath are ochraceous yellow, with this color extending onto the thorax; **75.3.3.** The neotype specimen is a male bearing seven white labels (1st–3rd handwritten, others printed): [! Obscurus ♀ | nº 53 best. v. HS. | ! Fumanus HS ♂ | nº 60 best. v. Plötz], [Antigonus (686.) | Fumanus HS.], [Ant. Fumosus Pl ♂ | Plötz taf 1070], [Coll. | Weymer], [DNA sample ID: | NVG-21114E04 | c/o Nick V. Grishin], [DNA sample ID: | NVG-23082A09 | c/o Nick V. Grishin], and [genitalia | NVG240912-11 | c/o Nick V. Grishin], and shown in Fig. 28b; the neotype is missing the right antenna, all wings are chipped at the outer margin and damaged at the tornus of both hindwings; **75.3.4.** We searched and failed to find syntypes of *A. stigmaticus* among Hesperiidae holdings in all collections we examined (see Acknowledgments for their list), in particular in BMNH, where a significant portion of specimens from Mabille's collection currently resides, and the Royal Belgian Institute of Natural Sciences, Brussels, Belgium (RBINS) that houses primary types of several names proposed by Mabille, as well as in MFNB and ZSMC, and therefore believe that they were lost; **75.3.5.** The neotype generally agrees with the

original description of *A. stigmaticus* in all characters, as evidenced by finding these characters (listed in 75.3.2 above) in the neotype photographs shown in Fig. 28b; **75.3.6.** The neotype is from Brazil, as determined by genomic comparison (Fig. 27) and it agrees with the original type locality stated as "Brasilia"; **75.3.7.** The neotype is in the collection of the Museum für Naturkunde, Berlin, Germany (MFNB). As a result of the neotype designation, the type locality of *A. stigmaticus* remains in Brazil as originally stated, to be narrowed down by genomic comparison. The COI barcode sequence of the neotype, sample NVG-21114E04, GenBank PX568500, is given above. By the neotype designation, *Antigonus fumosus* Plötz, 1884, previously treated as a junior subjective synonym, becomes a junior objective synonym of *Anastrus stigmaticus* Mabille, 1883.

Grais Godman & Salvin, 1894 includes four distinct species

Genomic analysis of specimens of *Grais* Godman & Salvin, 1894 (type species *Anastrus stigmaticus* Mabille, 1883) from across the range reveals their partitioning into four species. In addition to *Grais juncta* Evans, 1953 (type locality in Jamaica), which was given species status by Turner and Turland (2017) (Fig. 27 green), and *Grais stigmaticus* (Mabille, 1883) (type locality in Brazil; neotype sequenced as NVG-21114E04) (Fig. 27 violet), we find two other species-level lineages (Fig. 27 red and blue), which in the nuclear genome trees are sister to *G. stigmaticus* and to *G. juncta*, respectively (Fig. 27a, b, violet and green). No available names exist for these two lineages, and therefore they correspond to two new species that are described next. The mitochondrial genome tree (Fig. 27 c) is incongruent with the nuclear genome trees: one specimen of *G. stigmaticus* from Brazil: Goiás (NVG-19071D03) possesses a highly divergent mitochondrial haplotype (while not being strongly different from other specimens in the nuclear genome), but specimens of different species are more similar to each other, although COI barcode divergence reaches 1.5% (10 bp) among them. The new species from Ecuador shares its mitochondrial haplotype with the new species from North and Central America, while not being its sister in the nuclear genome trees. Therefore, mitochondrial evolution in *Grais* is obscured by introgression or possibly incomplete lineage sorting.

Grais ecuadoricus Grishin, new species

https://zoobank.org/950DDDE3-FFF8-4522-9D91-B57696EA830C

(Figs. 27 part, 28c, 30)

Definition and diagnosis. Genomic analysis reveals that a male of *Grais* Godman & Salvin, 1894 (type species *Anastrus stigmaticus* Mabille, 1883) from north-central Ecuador initially identified as *G. stigmaticus* (type locality in Brazil) is genetically differentiated from it at the species level in the nuclear genome (Fig. 27a, b red vs. violet), although their COI barcodes do not differ strongly due to introgression (0.8%, 5 bp), and this male shares the mitogenomic haplotype with the new species described next (Fig. 27c red and blue). Due to nuclear genomic and phenotypic differences, this male represents a new species. This new species keys to *G. stigmaticus* (F.3(a)) in Evans (1953), but differs from it and other relatives by the following combination of characters in males: three subapical semihyaline spots on the forewing, although small but present, thus similar to *Grais juncta* Evans, 1953 (type locality in Jamaica), but in the new species, the two costal-most spots are approximately the same size, and in *G. juncta*, the costal-most spot is the smallest or absent; slightly narrower forewing; two strongly expressed dark spots by the hindwing tornus (a variable character in other species); the hump at the base of the uncus is more prominent; the expansion of the ampulla is broader but more shallowly sclerotized, with a weaker basal inner ridge, and the basal broad prong of this expansion is more rounded; and the inward-directed process of the harpe is narrower and with a smaller number of serrations that are mostly confined to its base, where they are larger. Due to its cryptic nature and unexplored individual variation, this species is best identified by DNA, with diagnostic base pairs in the nuclear genome: aly1916.7.3:T93C, aly1916.7.3:C102T, aly272.20.2:A213G, aly272.20.2:G237A, aly6841.82.16:T51C, aly527.18.2:C189C (not T), aly527.18.2:

T240T (not C), aly85.28.2:T66T (not A), aly85.28.2:T120T (not C), aly798.12.9:A33A (not C); and the COI barcode does not reliably distinguish this species from others.

Barcode sequence of the holotype. Sample NVG-18015D09, GenBank PX568501, 658 base pairs:

AACTTTATATTTTATTTTTGGAATTTGAGCAGGTATAGTAGGAACATCTTTAAGTTTACTTATTCGAACTGAATTAGGTAACCCCGGTTCTTTAATTGGAGATGATCAAATTTATAATACT
ATTGTTACAGCTCATGCTTTTATTATAATTTTTTTTATAGTTATGCCAATTATAATTGGTGGATTTGGTAATTGATTAGTTCCTTTAATACTAGGAGCTCCAGATATAGCTTTCCCCCGAA
TAAATAATATAAGATTTTGATTACTACCCCCATCATTAATATTATTAATTTCAAGAAGTATCGTAGAAAATGGAGCAGGTACAGGTTGAACAGTTTATCCCCCCTTATCCTCTAATATTGC
CCATCAAGGATCTTCAGTTGATTTAGCTATTTTTTCATTACATCTAGCTGGAATTTCTTCTATTTTAGGAGCTATTAATTTTATTACAACAATTATTAATATGCGAATTAAAAATCTTTCC
TTTGATCAAATACCTTTATTTGTTTGAGCAGTAGGAATTACTGCTTTACTTTTACTTTTATCTCTTCCTGTTTTAGCTGGGGCTATTACTATACTTTTAACAGATCGAAATTTAAATACAT
CTTTTTTTGATCCAGCTGGTGGTGGTGATCCTATTCTTTATCAACATTTATTT

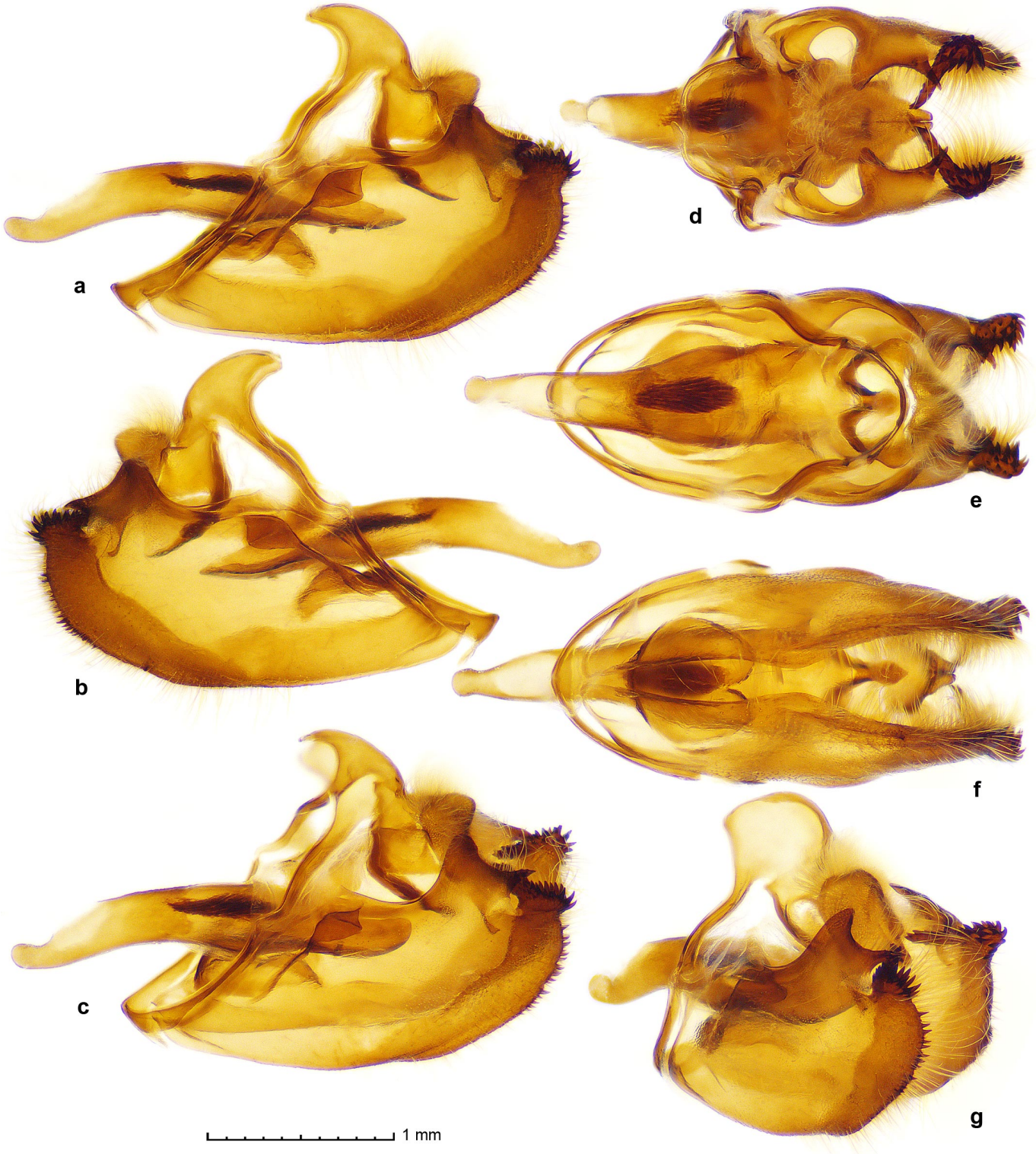


Fig. 30. Male genitalia of *Grais ecuadoricus* **sp. n.** holotype NVG-18015D09 in different views: **a)** left lateral, **b)** right lateral, **c)** left dorsolateral, **d)** dorsal, **e)** anterodorsal, **f)** ventral, and **g)** left posterolateral.

Type material. Holotype: ♂ deposited in the National Museum of Natural History, Smithsonian Institution, Washington, DC, USA (USNM), illustrated in Fig. 28c (genitalia Fig. 30), bears the following six printed rectangular labels (text in italics handwritten), five white: [ECUADOR: Sucumbíos, | Cerro Lumbaqui Norte | 0° 01.70' N, 77° 19.22' W | 950 m, 1-3 Jan 2002 | J.P.W. Hall & M.A. Solis], [DNA sample ID: | NVG-18015D09 | c/o Nick V. Grishin], [DNA sample ID: | NVG-23121C09 | c/o Nick V. Grishin], [genitalia | NVG251025-10 | c/o Nick V. Grishin], [USNMENT | {QR Code} | 01450728], and one red [HOLOTYPE ♂ | Grais ecuadoricus | Grishin]. The first DNA sample ID refers to the extraction from a leg (sequenced), and the second from the abdomen (stored) prior to genitalia dissection.

Type locality. Ecuador: Sucumbíos, Cerro Lumbaqui Norte, elevation 950 m, GPS 0.0283, −77.3203.

Etymology. The name is derived from the country of the type locality and is treated as a noun in apposition.

Distribution. Currently known from the holotype collected in north-central Ecuador at the eastern foothills of the Andes.

Grais eremitus Grishin, new species

https://zoobank.org/DE8FEF62-5A62-4B9E-8B68-704A937391EE

(Figs. 27 part, 28a, 31–32)

Definition and diagnosis. Genomic analysis reveals that North and Central American specimens traditionally identified as *G. stigmaticus* (type locality in Brazil; neotype sequenced as NVG-21114E04) are not monophyletic with it and instead form a clade sister to *Grais juncta* Evans, 1953 (type locality in Jamaica), genetically differentiated from both taxa at the species level (Fig. 27); e.g., their COI barcodes differ by 1.5% (10 bp) from *G. stigmaticus* and by 1.8% (12 bp) from *G. juncta* (COI barcodes do not differ strongly in this genus, and its mitogenome evolution is complex, see above), and therefore these specimens represent a new species. This new species keys to *G. stigmaticus* (F.3(a)) in Evans (1953) and was included by him in this species, but differs from it and other relatives by the following combination of characters: the forewing of a male without subapical hyaline spots, and the female with three or more spots; darker spots on the wings are usually better developed and more contrasting; the ventral hindwing typically without a prominent tornal dark spot (but the expression of this spot is variable, and it may be better developed in some specimens) and with more weakly checkered or uniformly colored fringes; the hump at the base of the uncus is moderately prominent; the expansion of the ampulla is narrower, weakly sclerotized, with a poorly developed basal inner ridge, and the basal prong of this expansion is narrower and longer, but less pointed terminally; the inward-directed process of the harpe is broader than in the new species described above and similar to that in *G. stigmaticus* but slightly shorter, strongly serrated throughout; the serrations are larger; the ventroposterior margin of the harpe with three patches of several (about 3–5) small and sharp teeth (instead of being serrated over the entire length), which are approximately

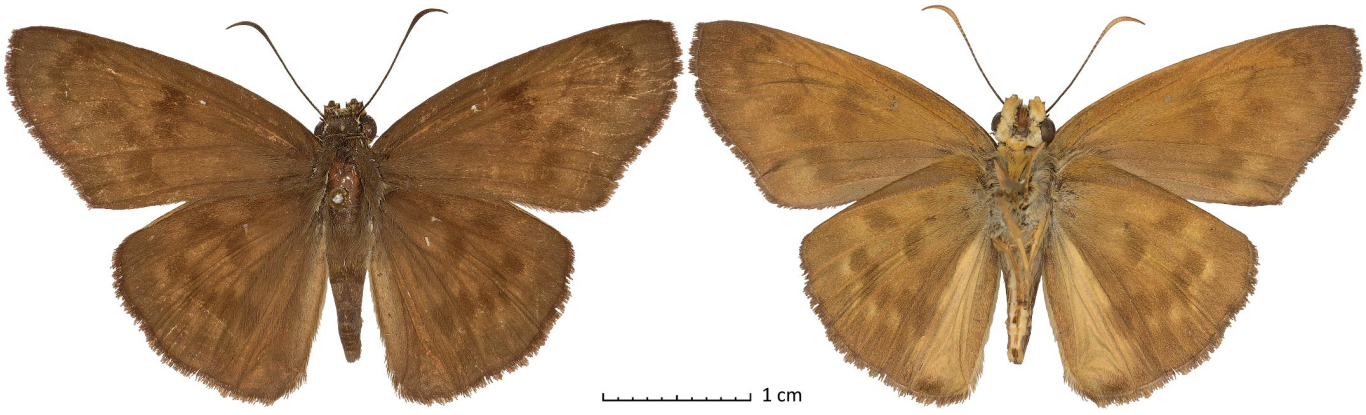


Fig. 31. *Grais eremitus* **sp. n.** holotype ♂ NVG-24087C05 in dorsal (left) and ventral (right) views, data in text.

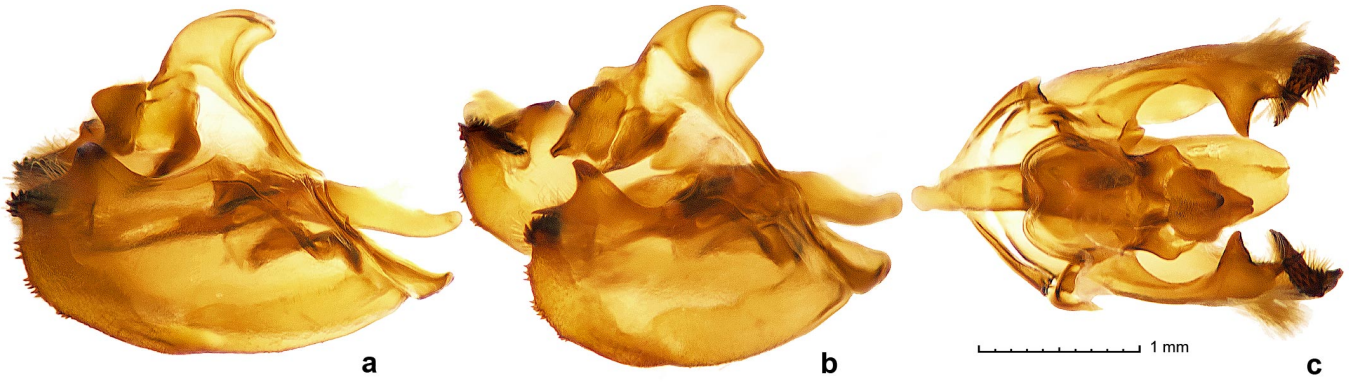


Fig. 32. Male genitalia of *Grais eremitus* **sp. n.** paratype NVG-1939 from USA: Texas, Comal Co. in different views: **a)** right lateral, **b)** right posterolateral tilted to the right, and **c)** dorsal.

the same size as the serrations at the base of the inward-directed process; and the tegumen is more convex in lateral view, rounder, and with a more prominent notch at its anterior margin. Due to its cryptic nature, this species is best identified by DNA, with diagnostic base pairs in the nuclear genome: aly2379.8.3: A57G, aly2379.8.3:T100C, aly798.33.15:G24A, aly798.33.15:C34T, aly1841.5.17:G264T; and the COI barcode does not reliably distinguish this species from others.

Barcode sequence of the holotype. Sample NVG-24087C05, GenBank PX568499, 658 base pairs:

AACTTTATATTTTATTTTTGGAATTTGAGCAGGTATAGTAGGAACATCTTTAAGTTTACTTATTCGAACTGAATTAGGTAACCCTGGTTCTTTAATTGGAGACGATCAAATTTATAATACT
ATTGTTACAGCTCATGCTTTTATTATAATTTTTTTTATAGTTATGCCAATTATAATTGGTGGATTCGGTAATTGATTAGTTCCTTTAATACTAGGAGCTCCAGATATAGCTTTCCCCCGAA
TAAATAATATAAGATTTTGATTACTACCTCCATCATTAATATTATTAATTTCAAGAAGTATCGTAGAAAATGGAGCAGGTACAGGTTGAACAGTTTATCCCCCCTTATCTTCTAATATTGC
CCATCAAGGATCTTCAGTTGATTTAGCTATTTTTTCATTACATTTAGCTGGAATTTCTTCTATTTTAGGAGCTATTAATTTTATTACAACAATTATTAATATGCGAATTAAAAATCTTTCC
TTTGATCAAATACCTTTATTTGTTTGAGCAGTAGGAATTACTGCTTTACTTTTACTTTTATCTCTTCCTGTTTTAGCTGGGGCTATTACTATACTTTTAACAGATCGAAATTTAAATACAT
CTTTTTTTGATCCAGCTGGTGGGGGTGATCCTATTCTTTATCAACATTTATTT

Type material. Holotype: ♂ deposited in the McGuire Center for Lepidoptera and Biodiversity collection, Gainesville, FL, USA (MGCL), illustrated in Fig. 31, bears the following four printed rectangular labels (text in italics handwritten), three white: [*1 mi. S. of Mission* | *Hidalgo* Co., Texas | *18.X.* 1973 | leg. W.W.&N.M.McGuire], [MGCL collection | W. McGuire coll. | Ex K. Roever], [DNA sample ID: | NVG-24087C05 | c/o Nick V. Grishin], and one red [HOLOTYPE ♂ | Grais eremitus | Grishin]. **Paratypes:** 6♂♂ and 17♀♀: USA: Arizona, Cochise Co., Guadalupe Mts., Guadalupe Canyon, Kilian Roever leg. [MGCL]: 1♀ NVG-24087C02 22-Aug-1971, 1♀ NVG-24087C04 23-Aug-1971, and 1♀ NVG-24087C06 23-Aug-1971; and Texas: 1♂ NVG-1939 Comal Co., NW of New Braunfels at 1st crossing of Guadalupe River, 9-Aug-1959, R. O. Kendall & C. A. Kendall, genitalia NVG130104-12 (Fig. 32) [TAMU] and Hidalgo Co., Mission, 4-Sep-1972, W. W. McGuire leg: 1♀ NVG-1938 10th Street at irrigation ditch, genitalia NVG140104-75 [TAMU] and 1♀ 11-BOA-13383BrockA08 [JPB]; Mexico: Nuevo León: 1♀ NVG-23113C08 Raíces, 7-Nov-1987, J. Kemner [CMNH] and Cola de Caballo, Roy O. Kendall & C. A. Kendall leg. [TAMU]: 1♀ TAMUICEGR-0094 23-Oct-1979, 1♀ TAMUICEGR-0095 23-Oct-1979, and 1♀ TAMUICEGR-0093 27-Oct-1979, genitalia NVG130104-13; Tamaulipas, Roy O. Kendall & C. A. Kendall leg. [TAMU]: 1♀ NVG-19014G03 Villa Gomez Farias, 500 m, 19-Nov-1974 and 1♀ NVG-19014G04 Paso del Abra nr. El Abra, 18-Dec-1973; 1♂ NVG-23113C07 San Luis Potosí, hotel Covadonga, 4-Aug-1987, J. Kemner leg. [CMNH]; 1♀ NVG-18015D08, USNMENT_01450727 Sinaloa, Mazatlán, old, J. A. Kusche leg. [USNM]; Mexico City, G. W. Rawson colln. [USNM]:1♂ NVG-18069C10 30-Aug-1944 and 1♀ NVG-18069C11 17-Aug-1944; and 1♂ NVG-21114E03 no data, likely Mexico by DNA, "Brazil" on the identification label, before 1890, J. P. Maassen colln. [MFNB]; 1♀ NVG-18057A08 Honduras, old, Staudinger colln. [ZSMC]; 1♀ NVG-7880, USNMENT_01321720, 14-SRNP-30242 Costa Rica, Guanacaste Prov., Área de Conservación Guanacaste, Sector Pitilla, 390 m, GPS 11.04249, −85.40339, eclosed on 16-Mar-2014, M. Rios leg., genitalia NVG170206-65 [USNM]; Panama: 1♂ NVG-15032G10 (pseudotype of *A. stigmaticus*) Chiriquí, old, F. Trösch leg. [MFNB] (Fig. 28a) and Panamá, 5 mi N of El Llano, 330 m, 9.283, −79.000, 4-Jun-1978, G. B. Small leg. [USNM]: 1♂ NVG-19071D04, USNMENT_01588485 and 1♀ NVG-18069C12; and 1♀ NVG-21114E05 Venezuela, Aragua, Tovar, 1878, Weymer colln. [MFNB].

Type locality. USA: Texas, Hidalgo Co., 1 mi south of Mission.

Etymology. The name is the Latin translation of the English vernacular name used for this species in North America, 'Hermit Skipper', and it is an adjective.

English name. We propose retaining Hermit Skipper as the name for this new species, while the largely Brazilian *G. stigmaticus* can be called Brazilian Hermit, the Jamaican *G. juncta* is Jamaican Hermit, and *G. ecuadoricus* **sp. n.** is Ecuadorian Hermit.

Distribution. Currently known from North and Central America. In the U.S., recorded from central to southern Texas (strays north and into Oklahoma), extreme southwestern New Mexico, and southeastern Arizona. In addition, an old specimen labeled from "Tovar" (Venezuela) (NVG-21114E05) belongs to this species, but it might have been mislabeled.

Clito congruens Grishin, 2023 is recorded from northwestern Ecuador

Genomic analysis of additional *Clito* Evans, 1953 (type species *Hydraenomia aberrans* Draudt, 1924) specimens reveals a male from northern coastal Ecuador in the clade with North and Central American specimens corresponding to *Clito congruens* Grishin, 2023 (type locality Panama: Colón, Gatún; holotype sequenced as NVG-14064A06) (Fig. 33). Unless this specimen is mislabeled, it represents the first record of *C. congruens* from South America, previously known from eastern and southern Mexico (Yucatán, Oaxaca), Guatemala, Costa Rica, and Panama. Other South American specimens of similar appearance are *Clito aberrans* (Draudt, 1924) (type locality Brazil: Amazonas, Tefé; holotype sequenced as NVG-18093A08), a species we sequenced from Colombia (Caquetá), Venezuela (Mérida), Peru (Loreto), Bolivia, and Brazil (Paraiba, Amazonas, Rondônia, and Rio de Janeiro). This male (NVG-24112B02, LEP-61304) was collected by Mark Simon in Ecuador: Esmeraldas Province, San Lorenzo, 100 m, Jul-2009 [MGCL], and we are not aware of any Simon's specimens being mislabeled. Inspection of wing patterns (Fig. 34) and genitalia (Fig. 35a) did not reveal appreciable differences from *C. congruens* (Fig. 35b, c) (except that the valva is slightly narrower and the process of the ampulla is shorter in lateral view; to be investigated when additional specimens are found), in agreement with the genomic phylogeny (Fig. 33) placing it among specimens of *C. congruens*. The COI barcode sequence of this Ecuadorian specimen, sample NVG-24112B02, GenBank PX568502, 658 base pairs is:

AACTTTATATTTTATTTTTGGAATTTGATCAGGAATAGTGGGAACTTCCTTAAGTATATTAATTCGAACTGAATTAGGAAATCCTGGATCTTTAATTGGGGATGACCAAATTTATAATACT
ATTGTTACAGCTCATGCTTTCATTATAATTTTCTTTATAGTAATACCAATTATAATCGGAGGATTTGGAAATTGATTAGTTCCTTTAATATTAGGAGCCCCTGATATAGCTTTCCCTCGAA
TAAATAATATAAGATTTTGATTATTACCCCCTTCTTTAATATTATTAATTTCAAGTAGTATTGTAGAAAATGGTGCAGGAACAGGATGAACTGTTTACCCCCCTTTATCTGCTAATATTGC
CCATCAAGGATCTTCTGTAGATTTAGCTATTTTCTCATTACACTTAGCTGGAATTTCTTCAATTTTAGGAGCTATTAATTTTATTACTACTATTATTAATATACGTGTTAGAAATTTATCA
TTTGATCAAATACCTTTATTTGTGTGAGCAGTAGGTATTACTGCACTATTATTATTATCATTACCTGTTTTAGCTGGAGCTATTACAATACTTTTAACAGATCGAAATTTAAATACAT
CTTTTTTTGATCCAGCAGGAGGAGGAGATCCTATTTTATATCAACATCTATTT

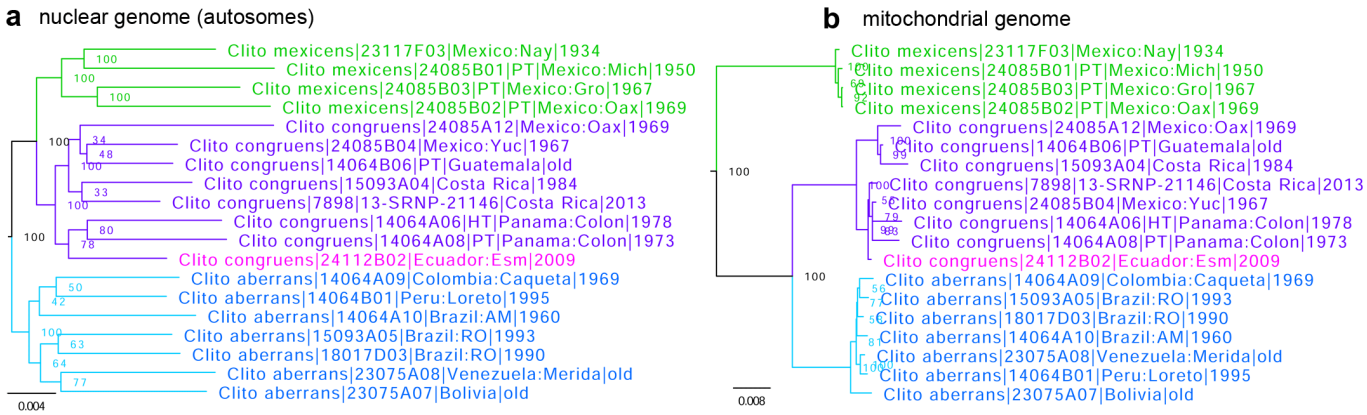


Fig. 33. Phylogenetic trees of three species of *Clito* constructed from protein-coding regions in: **a)** the nuclear genome (autosomes), based on 2,645,859 positions, and **b)** the mitochondrial genome. Different species are colored differently: *C. mexicens* (green), *C. congruens* (violet with the specimen from Ecuador discussed in the text labeled in magenta), and *C. aberrans* (blue). Ultrafast bootstrap (Hoang et al. 2018) values are shown at nodes.

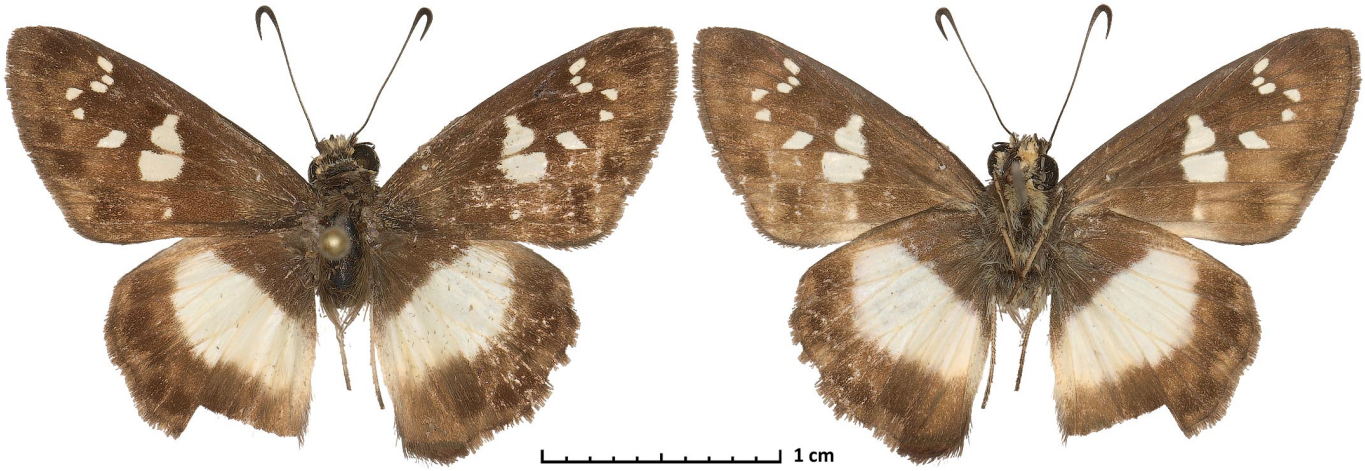


Fig. 34. *Clito congruens* ♂ NVG-24112B02 from northwestern Ecuador in dorsal (left) and ventral (right) views, data in text.

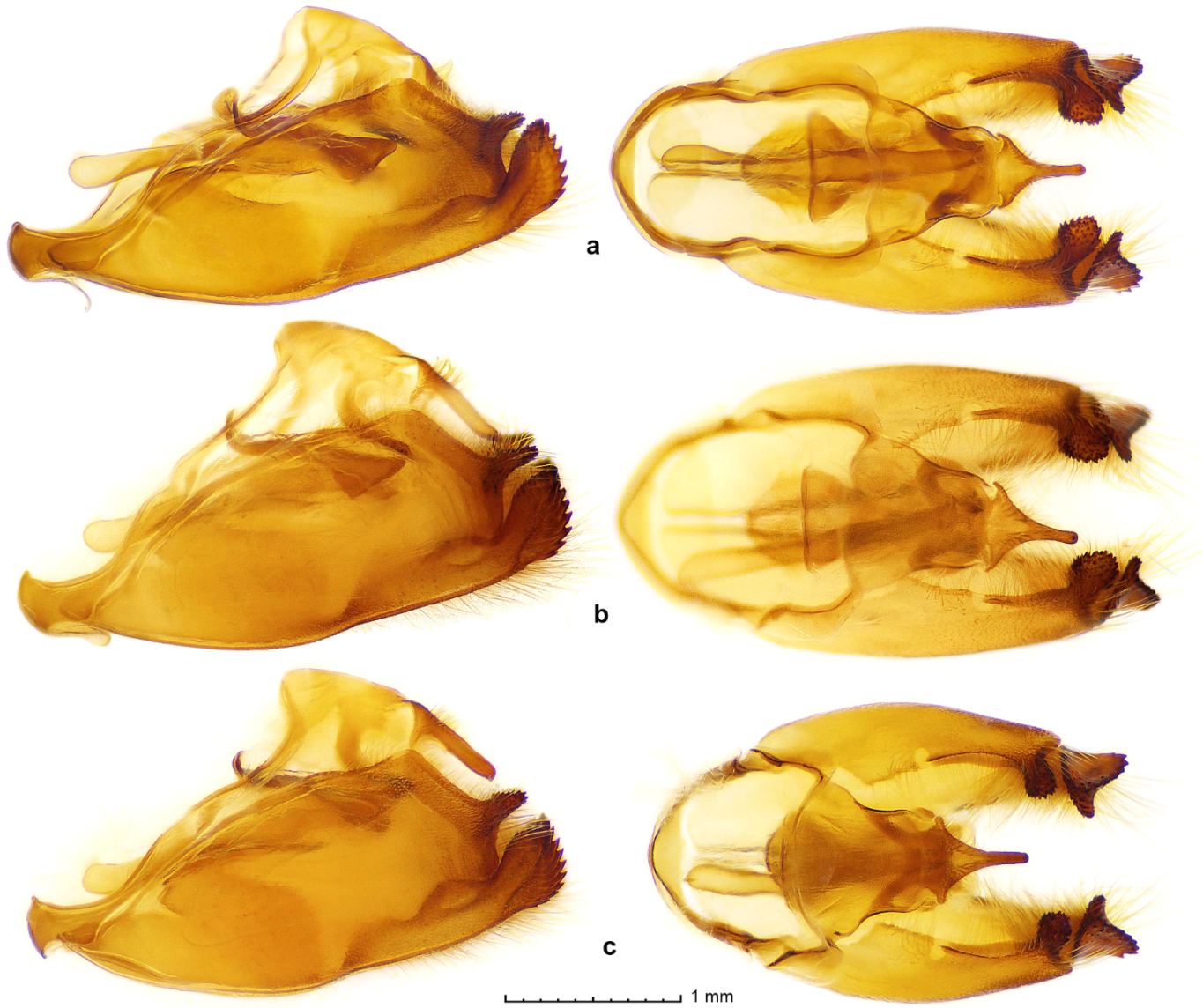


Fig. 35. Male genitalia of *Clito congruens* in left lateral (left) and dorsal (right) views: **a)** non-type NVG-24112B02 from Ecuador: Esmeraldas Province, San Lorenzo, 100 m, Jul-2009, M. Simon leg., genitalia LEP-61304 [MGCL]; **b)** holotype NVG-14064A06 (leg), NVG-22032E12 (abdomen) from Panama: Colón Province, Gatún, GPS 9.2833, −79.9500, 10-Dec-1978, G. B. Small leg., genitalia NVG230216-36 [USNM], and **c)** non-type NVG-24085A11 from Mexico: Oaxaca, 3 mi SE of Tapanatepec, 150 m, 5-Feb-1969, L. D. and J. Y. Miller leg., genitalia NVG241220-24 [MGCL].

Taxonomic challenges in *Hoodus* Grishin, 2019

We inferred the phylogeny of all described species of *Hoodus* Grishin, 2019 (Fig. 36). The genus *Hoodus* was proposed for the "*pelopidas*" group of Austin (2000) and currently consists of six species (Cong et al. 2019). The type species, *Hoodus pelopidas* (Fabricius, 1793) (type locality in Indiis), is most different from the rest and has a slender, drawn-out harpe; while other species have a short, rounded, and upturned harpe and are more difficult to tell apart from each other, thus being partly cryptic. *Hoodus cristata* (Austin, 2000) (type locality in Guatemala: Petén) (Fig. 37a) and *Hoodus jason* (Ehrmann, 1907) (type locality Venezuela: Suapure) (Fig. 37b) are characterized by more strongly mottled wings on the dorsal side, a rounder forewing apex, and a more robust harpe, while *Hoodus exstincta* (Mabille & Boullet, 1917) (type locality in Upper Amazons, likely in Peru) (Fig. 37c), *Hoodus simplex* Austin, 2000 (type locality in Brazil: Rondônia) (Fig. 37d), and *Hoodus argonautarum* Austin, 2000 (type locality in Brazil: Rondônia) (Fig. 37e) have more uniformly colored wings, a truncate and more pointed forewing apex, and a thinner harpe (best seen in dorsal view). Austin (2000) characterized *H. cristata* and *H. argonautarum* as having caudal bristles on the harpe, which other species lack.

The genomic phylogeny we obtained for *Hoodus* is generally consistent with these morphological considerations (Fig. 36). Indeed, *H. pelopidas* (Fig. 36 cyan) is sister to other species, which partition into two clades: *H. cristata* (Fig. 36 violet) with *H. jason* (Fig. 36 green) and the rest, among which we found a new species to be described next (Fig. 36 red). However, within these clades, genetic differentiation is low, except for the new species, which prominently differs from the blue subclade of three species (e.g., Fig. 36b red vs. blue clade). We do not find strong overall genetic differences associated with the presence of caudal bristles on the harpe. Moreover, the two specimens from Guatemala, which Austin (2000) identified as *H. jason* (Fig. 36 labeled in dark cyan)—likely because they lacked the bristles, are in the clade with *H. cristata* specimens, including the holotype and others from Guatemala. Therefore, we

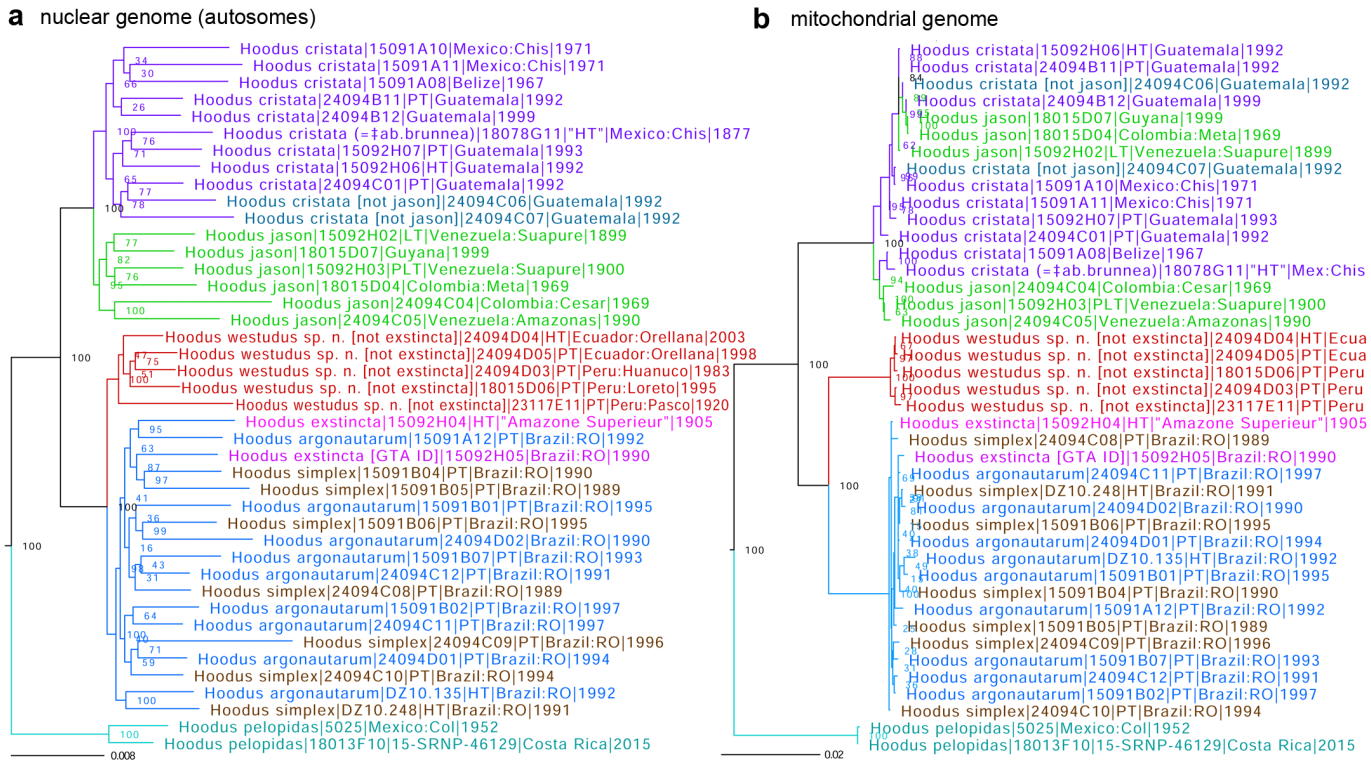


Fig. 36. Phylogenetic trees of all described *Hoodus* species constructed from protein-coding regions in: **a)** the nuclear genome (autosomes), based on 2,988,153 positions, and **b)** the mitochondrial genome. Different species are colored differently: *H. cristata* (violet, with specimens identified by G. T. Austin as "*jason*" labeled in dark cyan); *H. jason* (green), *H. westudus* **sp. n.** (red), *H. exstincta* together with *H. simplex* and *H. argonautarum* (blue, the holotype of *H. exstincta* is labeled in magenta, the specimen identified as G. T. Austin as *H. exstincta* [GTA ID] in purple, and *H. simplex* in brown), and *H. pelopidas* (cyan). Ultrafast bootstrap (Hoang et al. 2018) values are shown at nodes.

identify them as *H. cristata* and not *H. jason*. Although *H. cristata* and *H. jason* separate into two clades in the nuclear genome tree, genetic differentiation between the two taxa is low (Fig. 36a). Furthermore, despite having the bristles, *H. argonautarum* specimens do not form a clade in either tree (Fig. 36 labeled in blue) and are intermixed with specimens of *H. exstincta* (Fig. 36 labeled in magenta)—including the holotype and a specimen from Rondônia, Brazil, which Austin (2000) identified as this species—and of *H. simplex* (Fig. 36 labeled in brown), which do not separate into clades either. It is uncommon for distinct species not to form distinct clades in genomic trees, and such cases require more detailed analysis.

A hypothesis to reconcile the disagreement between genomics and morphology is that the caudal bristles on the harpe are easily broken off, thus leading to misidentifications, or their expression is variable within these species. Alternatively, the species described by Austin (2000) might have diverged very recently and have not yet acquired genetic differentiation in most genomic regions, differing only in several. It is also possible that at least some of the names proposed by Austin are best treated as synonyms, e.g., *H. simplex* and *H. argonautarum* might be conspecific. However, without a more detailed analysis, we refrain from proposing synonymies and simply present our findings as open questions.

Finally, we find that a specimen curated as the "holotype" of an infrasubspecific name *Mylon ozema* ab. *brunnea* Mabille & Boullet, 1917 collected in Mexico: Chiapas (unavailable names do not have formal holotypes or type localities and are not regulated by the ICZN Code) and currently identified as a specimen of *H. pelopidas*, is not this species and instead is a specimen of *H. cristata*. Therefore, *Mylon ozema* ab. *brunnea* Mabille & Boullet, 1917 should be placed in synonymy with *Hoodus cristata* (Austin, 2000) in catalogues that include unavailable names.

Hoodus westudus Grishin, new species

https://zoobank.org/CE47050B-EEB4-4EE6-85F4-F6DC4DF470CB

(Figs. 36 part, 38, 39)

Definition and diagnosis. Genomic analysis reveals that specimens from Ecuador and Peru (Fig. 38) that are related to *Hoodus jason* (Ehrmann, 1907) (type locality Venezuela: Suapure) (Fig. 37b) form a clade sister to the clade of three species: *Hoodus exstincta* (Mabille & Boullet, 1917) (type locality in Upper Amazons, likely in Peru) (Fig. 37c), *Hoodus simplex* Austin, 2000 (type locality in Brazil: Rondônia) (Fig. 37d), and *Hoodus argonautarum* Austin, 2000 (type locality in Brazil: Rondônia) (Fig. 37e), being genetically differentiated from them at the species level (Fig. 36); e.g., their COI barcodes differ by 2.3% (15 bp), and therefore these specimens represent a new species. This new species keys to "*Mylon jason*" (E.50.11) in Evans (1953) and to "*Mylon exstincta*" in Austin (2000), but differs from them and other relatives by the following combination of characters: the forewing apex is more prominently truncate with the apical point sharper [rounder in *Hoodus cristata* (Austin, 2000) (type locality in Guatemala: Petén) (Fig. 37a) and *H. jason*], overall darker with a better defined brown pattern, especially on the dorsal side of the wings [paler and more uniformly patterned wings in *H. exstincta*, *H. simplex*, and *H. argonautarum*], and has a broader and more irregular, blotchy postdiscal dark band on the ventral hindwing [a narrow and regular line in *H. jason* and *H. cristata*, a vestigial band may remain towards the inner margin in other species]; lacks bristles at the distal end of the harpe [with bristles in *H. cristata* and *H. argonautarum*], and the harpe is dorsally rounded [more angled near the process of the ampulla in both *H. argonautarum* and *H. simplex* and rather straight at the dorsoposterior margin in *H. exstincta*], with larger and more regular serrations. Due to its cryptic nature and unexplored individual variation, this species is best identified by DNA, with diagnostic base pairs in the nuclear genome: aly536.120.2:A199C, aly1689.9.7:C69T, aly1689.9.7:C81T, aly2363.6.13:T67G, aly2363.6.13:C84A; and the COI barcode: T212C, A316G, T367C, A451G, A565G.

Barcode sequence of the holotype. Sample NVG-24094D04, GenBank PX645477, 658 base pairs:

AACTTTATATTTTATTTTTGGAATTTGAGCAGGAATAGTAGGAACTTCATTAAGTTTATTAATTCGAACTGAATTAGGAAACCCAGGATTTTTAATTGGAGATGATCAAATTTATAATACT
ATTGTTACAGCTCATGCTTTTATTATAATTTTTTTTATAGTTATACCAATTATAATTGGAGGATTTGGTAATTGATTAGTTCCTTTAATACTAGGAGCCCCTGACATAGCATTCCCACGAA
TAAATAATATAAGATTTTGACTTTTACCTCCTTCATTAATATTATTAATTTCTAGAAGAATTGTAGAAAATGGGGCAGGAACAGGTTGAACTGTTTATCCCCCTCTTTCAGCAAATATTGC
TCACCAAGGTTCATCTGTAGATTTAGCAATTTTTTCTTTACACTTAGCAGGAATTTCTTCTATTCTTGGAGCTATTAATTTTATTACGACAATTATTAATATACGAATTAGAAATTTATCA
TTTGATCAAATACCTTTATTTGTTTGAGCAGTAGGTATTACTGCTCTATTATTATTACTTTCATTACCAGTATTAGCTGGGGCTATTACTATATTATTAACAGATCGAAATTTAAATACAT
CTTTTTTTGATCCTGCTGGAGGAGGAGATCCTATTTTATATCAACATTTATTT

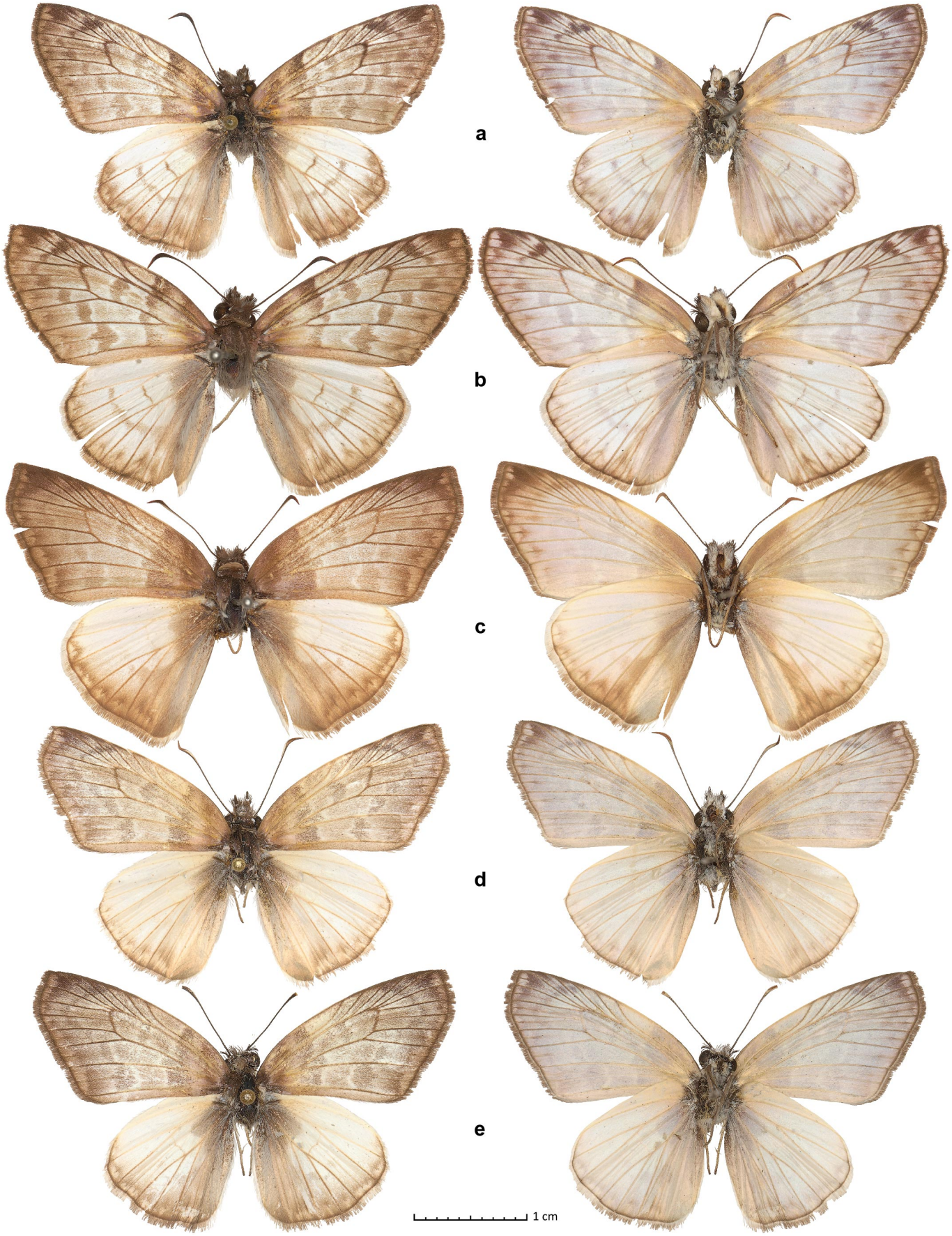


Fig. 37. Type specimens of *Hoodus* in dorsal (left) and ventral (right) views, detailed data in Austin (2000): **a)** *H. cristata* holotype ♂ NVG-15092H06 from Guatemala; **b)** *H. jason* lectotype ♂ NVG-15092H02 from Venezuela; **c)** *H. exstincta* holotype ♀ NVG-15092H04 from "Amazone Supérieur"; and **d–e)** paratypes ♂♂ from Brazil, Rondônia: **d)** *H. simplex* NVG-24094C08, genitalia GTA-459 and **e)** *H. argonautarum* NVG-24094D01, genitalia GTA-7321.

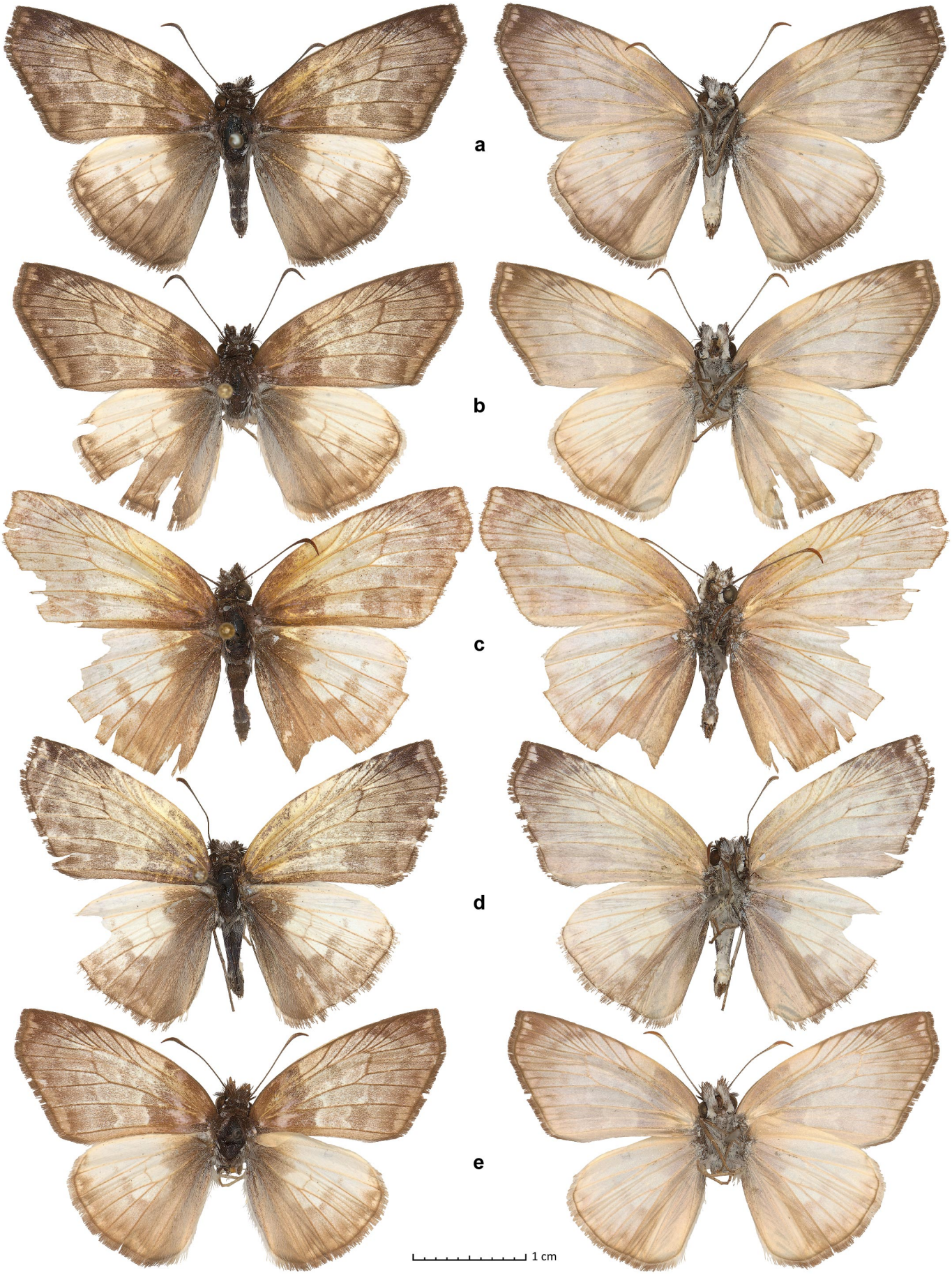


Fig. 38. *Hoodus westudus* **sp. n.** type series, ♂♂ in dorsal (left) and ventral (right) views, data in text: **a)** holotype NVG-24094D04 and **b–e)** paratypes: **b)** NVG-24094D05; **c)** NVG-18015D06; **d)** NVG-24094D03; and **e)** NVG-23117E11.

Type material. Holotype: ♂ deposited in the McGuire Center for Lepidoptera and Biodiversity collection, Gainesville, FL, USA (MGCL), illustrated in Fig. 38a, bears the following six rectangular labels (2nd handwritten, others printed with handwritten text shown in italics), five white: [Ecuador: Napo | Yasuni Nat. Pk. | 20-IX–4-X–03 | B/K-TLS coll.], [21], [*Mylon* | *pelopidas* | *gp.* det. E. Knudson], [MGCL Accession | #2016-40 | E.C.Knudson | Knudson/Bordelon], [DNA sample ID: | NVG-24094D04 | c/o Nick V. Grishin], and one red [HOLOTYPE ♂ | Hoodus westudus Grishin]. B/K stands for Bordelon/ Knudson and TLS stands for Texas Lepidoptera Survey. **Paratypes:** 4♂♂: 1♂ NVG-24094D05 Ecuador: Orellana Province, Yasuní Research Station, Ríos Tivacuno & Tiputini, 250 m, GPS −0.633, −76.600, 21-Oct-1998, D. & J. Lindsley leg. [MGCL] (Fig. 38b) and Peru: 1♂ NVG-18015D06, USNMENT_01450726 Loreto Region, Rio Sucusari, Explornapo-ACEER, 140 m, GPS −3.233, −72.917, 9-Sep-1995, G. Lamas leg. [USNM] (Fig. 38c); 1♂ NVG-24094D03 Huánuco Region, 13 km S of Tingo Maria, Tambello Grande Canyon, 19-Jun-1983, T. C. Emmel, P. Eliazar, J. L. Nation, and J. Avitabile [MGCL] (Fig. 38d); and 1♂ NVG-23117E11 Pasco Region, Río Pichis, Puerto Bermúdez, 14-Jul-1920, genitalia slide 9 A.W.L. by Lindsey [CUIC] (Figs. 38e, 39).

Fig. 39. Male genitalia of *H. westudus* **sp. n.** paratype NVG-23117E11, slide 9 A.W.L., in left lateral view, left valva removed and shown below (partly broken).

Type locality. Ecuador: Orellana Province, Yasuní National Park.

Etymology. The name reflects a more western distribution of this species of *Hoodus* compared to its relatives and is treated as a noun in apposition.

Distribution. Currently recorded from the eastern slopes and to the east of the Andes in Ecuador and Peru.

Ephyriades brunnea electra (Lintner, 1881), stat. nov. is a valid subspecies

Genomic analysis of *Eudamus electra* Lintner, 1881 holotype (likely mislabeled from Canada: Ontario, Hamilton; sequenced as NVG-15096A09) reveals a non-trivial level of genetic differentiation from three tightly clustered specimens of *Ephyriades brunnea floridensis* E. Bell & W. P. Comstock, 1948 (type locality in USA: Florida, Monroe Co., Key Largo) (Fig. 40). Previously (Zhang et al. 2025b), we incorrectly synonymized *Eudamus electra* Lintner, 1881 with *Ephyriades brunnea floridensis*. Here, we conservatively propose that *Ephyriades brunnea electra* (Lintner, 1881), **stat. nov.** is a valid subspecies distinct from *E. brunnea floridensis* due to this genetic differentiation. The provenance of the holotype remains unknown, but due to nuclear genome differences from the U.S. populations, it might have been from the Bahamas, and genomic sequencing of additional specimens will be carried out to address this question.

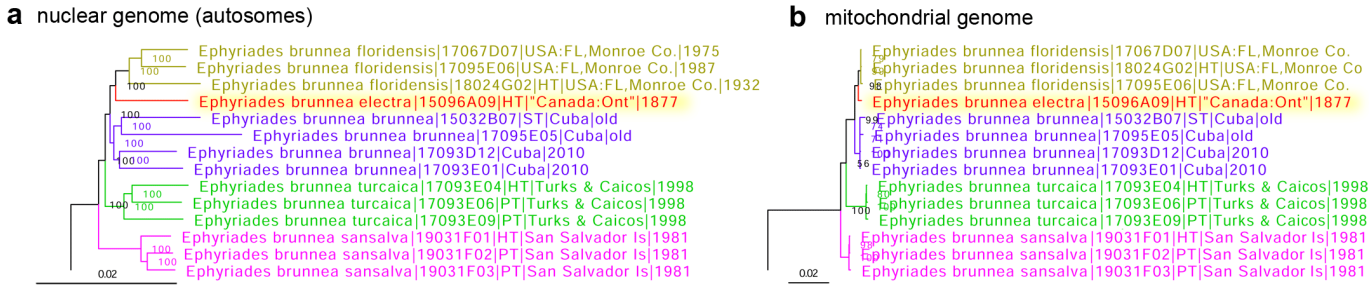


Fig. 40. Phylogenetic tree segment showing all described *Ephyriades brunnea* subspecies constructed from protein-coding regions in: **a)** the nuclear genome (autosomes), based on 9,520,194 positions, and **b)** the mitochondrial genome. Different subspecies are colored differently: *E. brunnea floridensis* (olive), *E. brunnea electra* **stat. nov.** (red), *E. brunnea brunnea* (purple), *E. brunnea turcaica* Grishin, 2025 (green), and *E. brunnea sansalva* Grishin, 2025 (magenta). The holotype of *Eudamus electra* is highlighted in yellow. Ultrafast bootstrap (Hoang et al. 2018) values are shown at nodes.

Lissia laura (Evans, 1937) is a species distinct from *Lissia luehderi* (Plötz, 1879)

Genomic analysis reveals that *Leona luehderi laura* Evans, 1937 (type locality Uganda: Mabira Forest), originally described and currently treated as a valid subspecies of *Lissia luehderi* (Plötz, 1879) (type locality Ghana: Aburi) in the genus *Lissia* Grishin, 2019 (type species *Leona lissa* Evans, 1937), is genetically differentiated from the nominotypical subspecies at the species level (Fig. 41), e.g., their COI barcodes differ by 5.6% (37 bp). Therefore, we propose that *Lissia laura* (Evans, 1937), **stat. nov.** is a species distinct from *Lissia luehderi* (Plötz, 1879). Phenotypically, *L. laura* **stat. nov.** is paler, the ventral forewing apex is yellower (not tawny as in *L. luehderi*), and the ventral hindwing is mostly yellow with a discal tawny band and markings (tawny with a yellow basal third and postdiscal spots in *L. luehderi*).

Madaga Grishin, new genus

https://zoobank.org/D13EA50C-6613-417A-A141-0EDAADEBDF34

Type species. *Artitropa alaotrana* Oberthür, 1916.

Definition. Genomic phylogeny places a female of *Artitropa alaotrana* Oberthür, 1916 (type locality in Madagascar: Lake Alaotra) (Fig. 42) as sister to both *Artitropa* Holland, 1896 (type species *Pamphila erinnys* Trimen, 1862) and *Gamia* Holland, 1896 (type species *Proteides galua* Holland, 1891), rendering *Artitropa* paraphyletic with respect to *Gamia* (Fig. 41). To restore monophyly, we propose to treat the lineage with *A. alaotrana* as a distinct genus, which is new. This new genus generally keys to *Artitropa* (VIII *Ploetzia* group, genus 55) as it was circumscribed by Evans (1937), sharing all the characters given for the genus, and more specifically to (55.B), thus differing from the true *Artitropa* by the following combination of characters: the forewing discal cell has a semihyaline bar crossing it (not merely a spot restricted to the anterior part of the cell); semihyaline spots in forewing cells M_3-CuA_1 and CuA_1-CuA_2 are squarish, broader than the narrow streak-like and sometimes bent spots in *Artitropa*; subapical semihyaline forewing spots are usually larger; and the ventral hindwing cell CuA_2-1A+2A has a longer dark-brown to black central area demarcated by paler scales basad and distad (this area is smaller in *Artitropa*, and frequently reduced to a spot, dot, or even absent). In DNA, a combination of the following characters is diagnostic in the nuclear genome: aly1603.65.6:G81A, aly1603.65.6:G252A, aly1603.65.6:A306G, aly276665.25.1:A258G, aly276665.25.1:G264A, aly528.27.1:G387G (not A), aly361.8.4:G162G (not A), aly2334.7.2:A183A (not T), aly587.21.2:G222G (not A), aly420.35.1:G183G (not A); and the COI barcode: C56C, T58T, T88A, T212T, T379A, A391A, T418T, T619T.

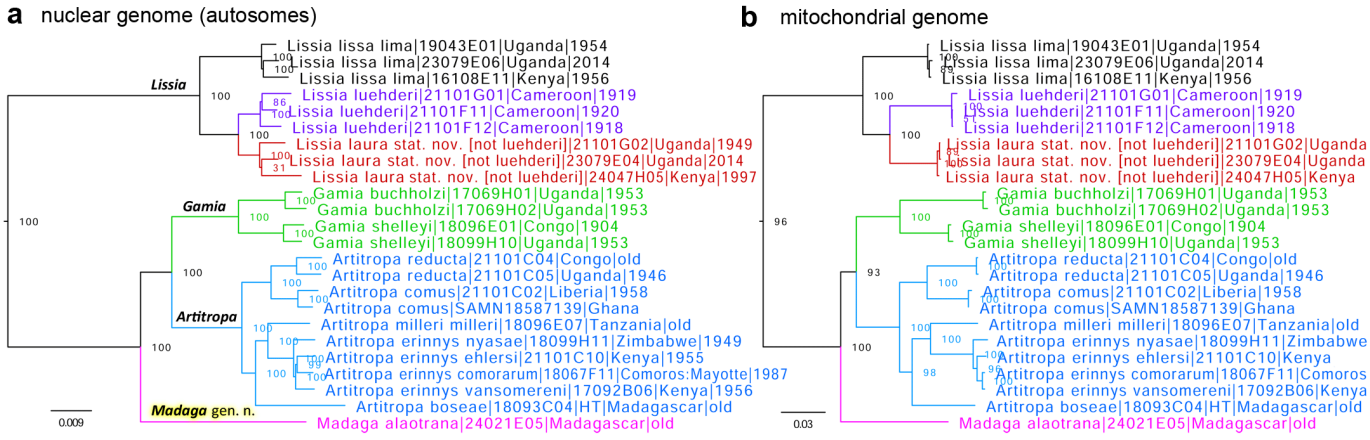


Fig. 41. Phylogenetic trees of the Astictopterina clade with *Artitropa* constructed from protein-coding regions in: **a)** the nuclear genome (autosomes), based on 3,156,756 positions, and **b)** the mitochondrial genome. Genera are labeled in the nuclear genome tree above their clades, and the new genus is highlighted in yellow. Taxa discussed in the text are colored: *Lissia luehderi* (violet), *Lissia laura* **stat. nov.** (red), *Gamia* (green), *Artitropa* (blue), and *Madaga* **gen. n.** (magenta). The sequence of SAMN18587139 is taken from the alignment provided in Kawahara et al. (2023). Ultrafast bootstrap (Hoang et al. 2018) values are shown at nodes.

Fig. 42. *Madaga alaotrana* ♀ NVG-24021E05 from Madagascar: S. Betsileo, old, Hildebrandt leg., A. Seitz collection [SMF] in dorsal (left) and ventral (right) views.

Etymology. The name is derived from the country where species of this genus are found, *Madaga*[scar], and is a feminine noun in the nominative singular.

Species included. The type species (i.e., *Artitropa alaotrana* Oberthür, 1916) and *Artitropa hollandi* Oberthür, 1916.

Parent taxon. Subtribe Astictopterina Swinhoe, 1912.

Comment. The third Malagasy species, *Artitropa boseae* (Saalmüller, 1880), belongs to *Artitropa*, not the new genus (Fig. 41). Although mostly unspotted on the dorsal side of wings, its ventral forewing lacks the pale discal cell bar, but has a pale spot in the anterior part of the discal cell and similar narrow spots in cells M_3-CuA_1 and CuA_1-CuA_2 in place of the semihyaline spots of other *Artitropa* species.

A female of *Thespieus grandosul* Grishin, 2025

Genomic analysis of additional specimens yielded a female of *Thespieus grandosul* Grishin, 2025 (type locality in Brazil: Rio Grande do Sul), previously known from a single male, the holotype (Figs. 43, 44a). This female, NVG-24046C12, CEP-7418 from Brazil: Paraná, São Mateus do Sul–Joinville, Serra Dona

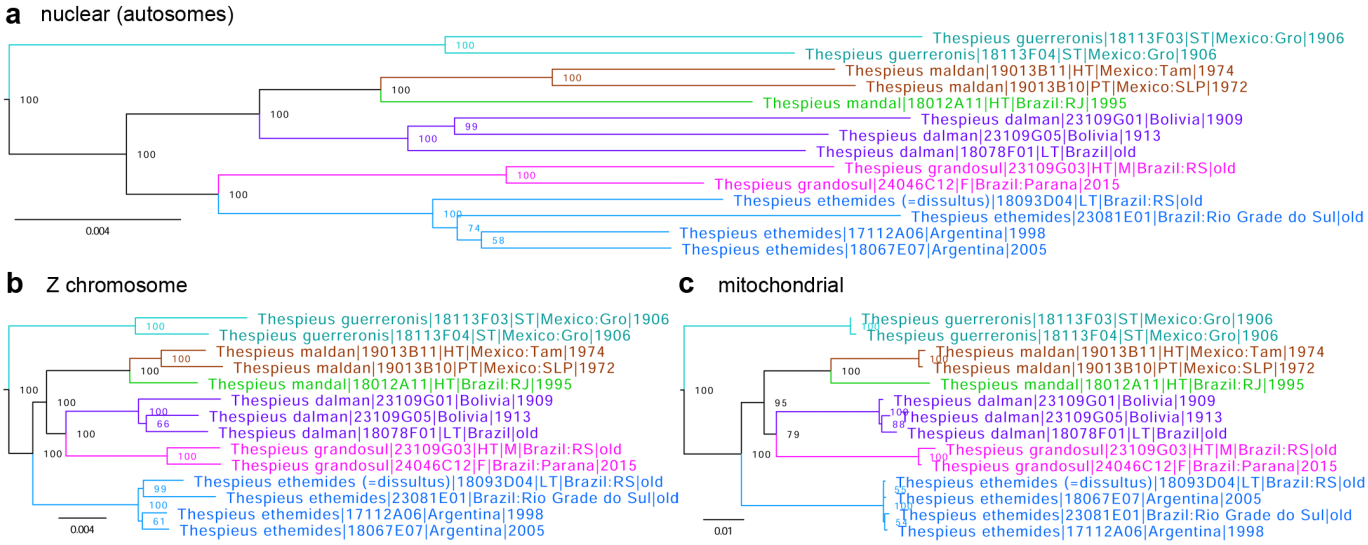


Fig. 43. Phylogenetic trees of *Thespieus dalman* relatives constructed from protein-coding regions in: **a)** the nuclear genome (autosomes), based on 9,842,022 positions, **b)** the Z chromosome, based on 369,405 positions, and **c)** the mitochondrial genome. Different species are colored differently: *T. guerreronis* Dyar, 1913 (cyan), *T. maldan* (brown), *T. mandal* (green), *T. dalman* (purple), *T. grandosul* **sp. n.** (magenta), and *T. ethemides* (blue). Ultrafast bootstrap (Hoang et al. 2018) values are shown at nodes.

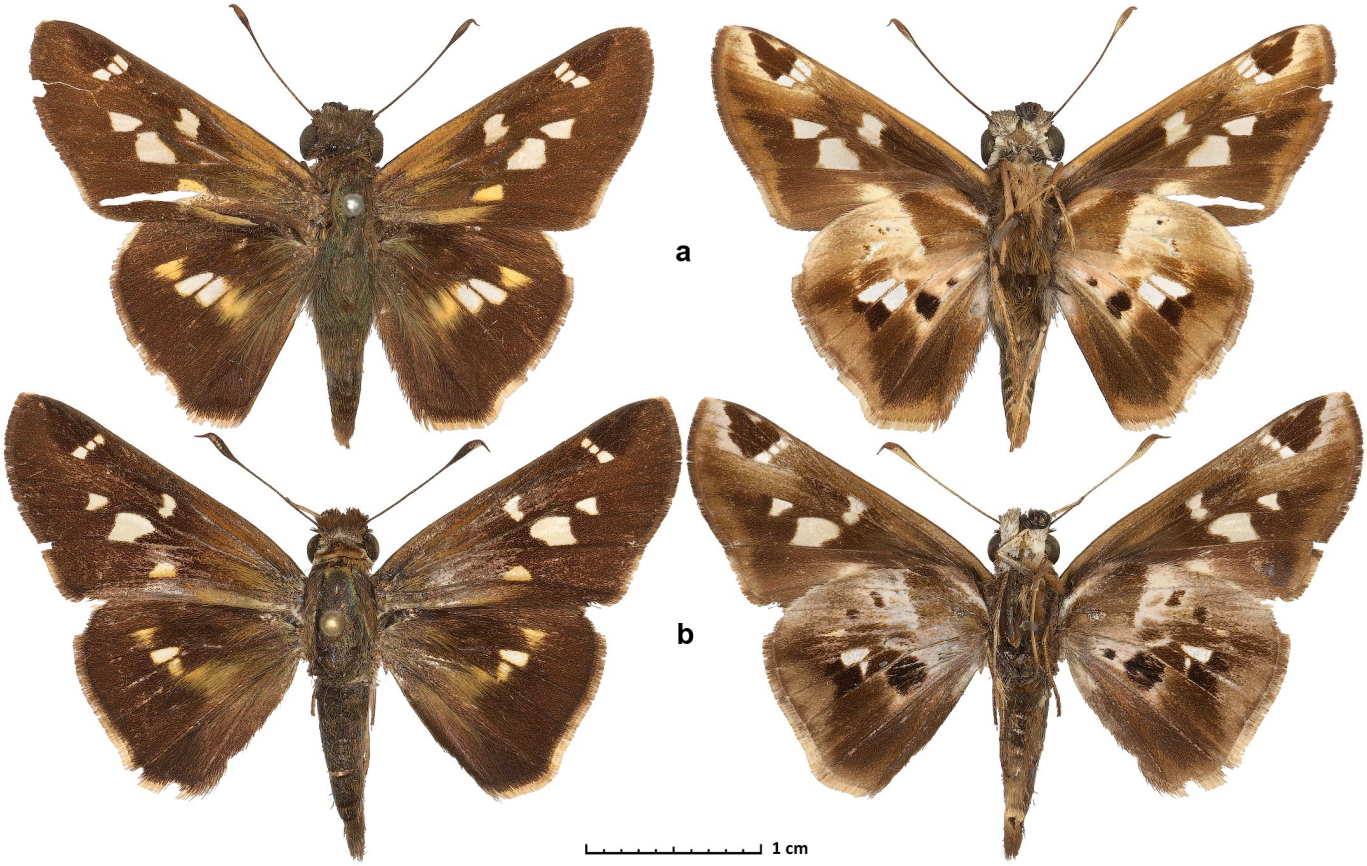


Fig. 44. *Thespieus grandosul* specimens in dorsal (left) and ventral (right) views: **a)** holotype ♂ NVG-23109G03 Brazil: Rio Grande do Sul, old [CMNH] and **b)** ♀ NVG-24046C12, CEP-7418 Brazil: Paraná, São Mateus do Sul–Joinville, Serra Dona Francisca, 770–800 m, 19-Feb-2015, T. Pyrcz leg. [CEPUJ]. The color difference (warmer, yellower in the male) is, at least in part, due to color change with the specimen age.

Francisca, 770–800 m, 19-Feb-2015, T. Pyrcz leg. [CEPUJ] (Fig. 44b), confirms *T. grandosul* as a valid species and is similar to the male, but lacks the stigma on the forewing; the semihyaline spot in cell CuA_1-CuA_2 is nearly pentagonal instead of trapezoidal; its hindwing tornus is less produced; semihyaline and yellowish spots are smaller, in particular, on the hindwing, where the spot in cell CuA_1-CuA_2 is reduced to a small triangle; and the dark pattern is expanded on the ventral hindwing, with two prominent dark-brown spots inside the beige area in cells Sc+R_1-Rs and Rs-M_1, and a larger, nearly square (with rounded angles) spot in cell CuA_2-1A+2A.

Eutus brunninotatus Grishin, new species

https://zoobank.org/85468DB3-609A-4498-AD59-AC7F8F3AF8BC

(Figs. 45 part, 46)

Definition and diagnosis. Wing pattern inspection and genomic analysis reveal that a male from Bolivia identified in the ZMUC collection as *Carystus* (*Argon*) *argus* Möschler, 1878 (type locality in Colombia) is both phenotypically and genetically different from it and instead belongs to the genus *Eutus* Grishin, 2022 (type species *Cobalus rastaca* Schaus, 1902), being a distant sister to *Eutus septemaculatus* Grishin, 2023 (type locality in Brazil: Mato Grosso) genetically differentiated from it at the species level (Fig. 45); e.g., their COI barcodes differ by 7.1% (47 bp), and therefore this specimen represents a new species. This new species keys (incompletely) to "*Argon argus*" (K.8) in Evans (1955), who treated *C. rastaca* as its junior subjective synonym, and possibly to "*Decinea mubevensis*" (L.11.9), currently *Eutus mubevensis* (Bell, 1932) (type locality Paraguay: Mubevo), but differs from it and other relatives by the following combination of characters in males: wing shape and forewing maculation are similar to *E. septemaculatus*, but the subapical semihyaline spots may be smaller or vestigial (only one is fully

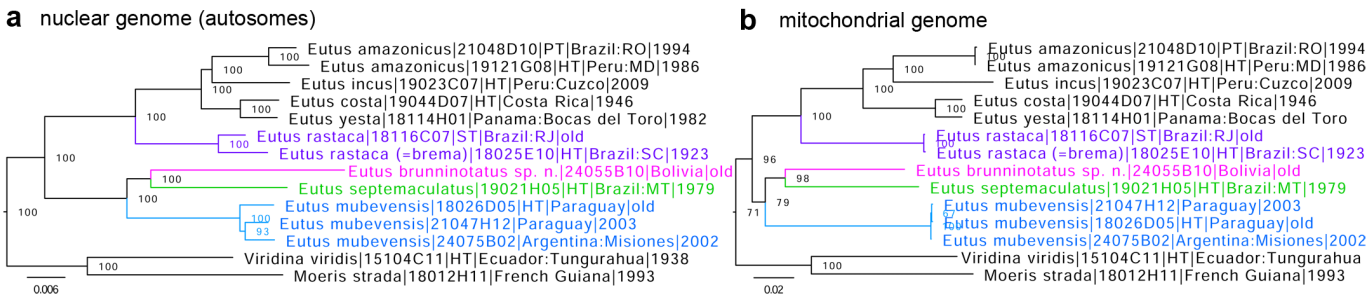


Fig. 45. Phylogenetic trees of all valid *Eutus* species constructed from protein-coding regions in: **a)** the nuclear genome (autosomes), based on 3,497,142 positions, and **b)** the mitochondrial genome. Species discussed in the text are colored: *E. rastaca* (violet), *E. brunninotatus* **sp. n.** (magenta), *E. septemaculatus* (green), and *E. mubevensis* (blue). Ultrafast bootstrap (Hoang et al. 2018) values are shown at nodes.

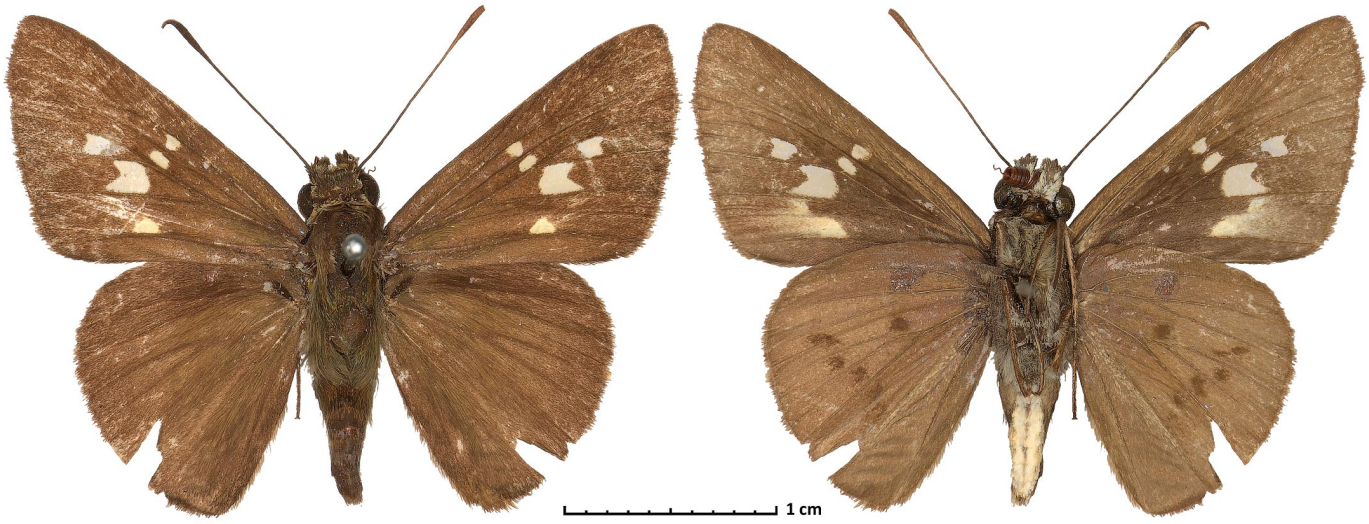


Fig. 46. *Eutus brunninotatus* **sp. n.** holotype ♂ NVG-24055B10 in dorsal (left) and ventral (right) views, data in text.

expressed on the right forewing in the holotype) and the other five spots are larger, e.g., the two discal cell spots are separated by a narrower brown space, and the ventral forewing pattern in the distal half of cell CuA_2-1A+2A consists of two connected spots (the anterior one is strongly offset distad and its distal border is aligned with the distal border of the spot in CuA_1-CuA_2; the proximal border of the posterior one is aligned with the proximal border of the spot in CuA_1-CuA_2), the ventral hindwing has prominent dark-brown partly diffuse spots: at the end of the discal cell and five or six postdiscal spots between veins M_1 and 1A+2A (two in cell CuA_2-1A+2A), these spots lack white centers and there are no pale spots on the hindwing that are present in other species of *Eutus* (sometimes vestigial). This species is not cryptic, but due to unexplored individual variation and females being unknown, it is best identified by DNA, with diagnostic base pairs in the nuclear genome: aly4778.13.2:C21T, aly4778.13.2:T36C, aly594.6.2:G69A, aly594.6.2:T81C, aly85.33.2:T768G, aly84.40.3:A108A (not C), aly3561.6.1:G132G (not A), aly430.8.2: T72T (not C), aly853.3.3:C36C (not T), aly853.3.3:C39C (not T); and the COI barcode: T19C, A34T, T136C, A319T, T382A, T407C, T553A, A559G.

Barcode sequence of the holotype. Sample NVG-24055B10, GenBank PX626415, 658 base pairs:

AACTTTATATTTTATTTTCGGAATTTGAGCAGGTATATTAGGAACTTCCTTAAGTTTATTAATTCGTACAGAATTAGGAAATCCTGGATCTTTAATTGGAGATGATCAAATTTATAATACT
ATTGTTACAGCTCACGCTTTTATTATAATTTTTTTTATAGTTATACCCATTATAATTGGAGGATTTGGAAATTGATTAGTACCCCTAATATTAGGGGCACCTGATATAGCTTTCCCACGAA
TAAATAATATAAGATTTTGAATACTTCCCCCCTCTTTATTACTACTAATTTCAAGAAGAATTGTAGAAAATGGTGCTGGAACAGGATGAACAGTTTACCCTCCACTTTCTTCTAATATTGC
TCATCAAGGATCTTCTGTAGATTTAGCAATTTTCTCTCTTCATCTAGCAGGAATTTCATCAATTTTAGGAGCTATTAATTTTATTACTACAATTATTAATATACGAATTAGAAATATATCT
TTTGATCAAATACCATTATTTGTATGATCTGTAGGAATTACTGCTCTTTTATTACTTTTATCTTTACCAGTACTGGCAGGAGCTATCACTATATTATTAACAGATCGAAACTTAAATACTT
CTTTTTTTGATCCTGCTGGAGGAGGAGATCCTATTTTATACCAACATTTATTT

Type material. Holotype: ♂ deposited in the Natural History Museum of Denmark, University of Copenhagen, Copenhagen, Denmark (ZMUC), illustrated in Fig. 46, bears the following four rectangular labels (2nd handwritten, others printed with handwritten text shown in italics), three white: [*Buenavista 450 m* | *Bolivia Steinbach.* | Modt. *11/11 1925* af | *José Steinbach. Bolivia.* | Coll.C.S.Larsen, Faaborg],

[Cobalus argus | Mschl.], [DNA sample ID: | NVG-24055B10 | c/o Nick V. Grishin], and one red [HOLOTYPE ♂ | Eutus brunninotatus | Grishin]. The date on the specimen label indicates when this specimen was received by Larsen, not collected by Steinbach (Danish: Modt[aget]. = received; af = from).

Type locality. Bolivia: Santa Cruz Department, 75 km northwest of Santa Cruz, Buena Vista, elevation 450 m, approx. GPS −17.47, −63.62.

Etymology. In Latin, *brunneus* means brown and *notatus* means marked or spotted. The name reflects brown spots (without white dots) on the ventral hindwing in this new species and is an adjective.

Distribution. Currently known only from the holotype collected in central Bolivia.

Lento mysto Grishin, new species

https://zoobank.org/9FBFCA34-FA1A-4B06-80BF-3FDD0017C3E3

(Figs. 47 part, 48b)

Definition and diagnosis. Genomic analysis reveals that a male from Bolivia misidentified in the collection as *Pamphila epictetus* (Fabricius, 1793) (currently in the genus *Anthoptus* E. Bell, 1942, *Hesperia epictetus* being its type species) is placed within *Lento* Evans, 1955 (type species *Pamphila lento* Mabille, 1878) (Fig. 47) as a distant sister to *Lento xanthina* (Mabille, 1891) (type locality Venezuela: Trujillo, Valera; syntype sequenced as NVG-18043H04) (Fig. 48a), with *Lento imerius* (Plötz, 1884) (type locality in Brazil; neotype sequenced as NVG-22014H01) (Fig. 48c, d) being sister to both. This male is genetically differentiated from *L. xanthina* at the species level, e.g., their COI barcodes differ by 8.5% (56 bp), and is more similar in appearance to *Lento longa* Evans, 1955 (type locality in Peru: Loreto), which we have not sequenced, but differs from it by a mostly orange forewing discal cell and the basal three-fifths of the forewing inner margin; a much narrower dark-brown margin on the dorsal hindwing and a much larger orange area, which occupies most of the hindwing; and the very prominent brands of *L. longa* near the base of the forewing vein CuA_2 are not apparent in the Bolivian male (Fig. 48b). Therefore, this male represents a new species. This new species keys (incompletely) to *L. longa* (L.3.3) in Evans (1955), but differs from it and other relatives by the following combination of characters in males (females are unknown): largely orange-colored on both sides of the wings with about one-fifth of the dorsal forewing being brown at the margin with a dull arrowhead (directed basad) brown area from the discal cell toward the apex and the outer margin, merging with the brown marginal area and enclosing a semi-triangular orange spot; the arrowhead area is disconnected from the brown ray running along the posterior side of the discal cell (which is orange, not brown) from the base of the wing through the area with brands and

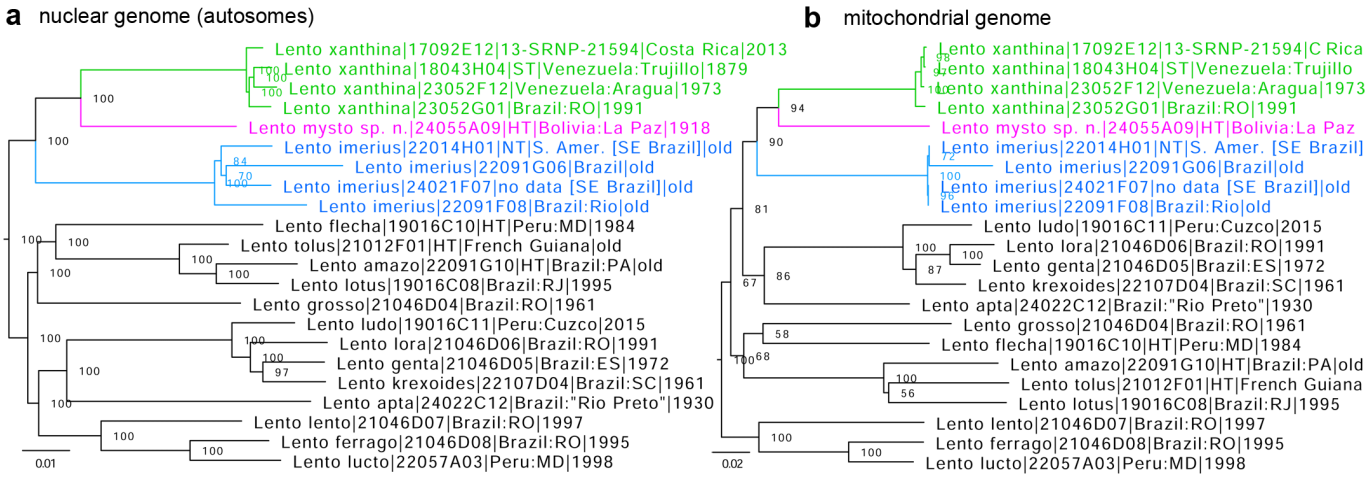


Fig. 47. Phylogenetic trees of selected *Lento* species constructed from protein-coding regions in: **a)** the nuclear genome (autosomes), based on 1,114,386 positions, and **b)** the mitochondrial genome. Species discussed in the text are colored: *L. xanthina* (green), *L. mysto* **sp. n.** (magenta), and *L. imerius* (blue). Ultrafast bootstrap (Hoang et al. 2018) values are shown at nodes.

Fig. 48. Males of *Lento* in dorsal (left) and ventral (right) views, data in text or below: **a)** *L. xanthina* non-type NVG-23052G01 from Brazil: Rondônia, ca. 70 km S of Ariquemes, B-80 between linhas C-10 & C-15, 19-Nov-1991, G. T. Austin leg. [MGCL]; **b)** *L. mysto* **sp. n.** holotype ♂ NVG-24055A09 from Bolivia; and **c–d)** *L. imerius* non-types: **c)** NVG-22091F08 from Brazil: Rio de Janeiro, pre-1852, G. von Langsdorff leg., a specimen from a lot No. 5416 [MFNB], and **d)** NVG-24021F07 no locality data [SMF], with its historical labels reduced five times compared to the specimens. The smaller scale between the labels refers to the labels, and the larger scale at the bottom refers to all the specimens.

ending within the base of cell CuA_1-CuA_2; the dorsal hindwing has a narrow dark-brown outer margin (narrower than the orange fringe between veins M_1 and M_2), and is mostly brown anteriad of the discal cell and in the anal fold; the ventral forewing has brown patches at the base, tornus, and a more weakly defined and diffuse one past the end of the discal cell; the ventral hindwing lacks any trace of yellower scaling along the veins (or darker areas between the veins) [present in most other relatives], is weakly overscaled with brown in cell 1A+2A-3A from the base to the outer margin [lacking in *L. longa*], and lacks brown outer-marginal spots at the ends of veins characteristic of *L. longa*. This species is not cryptic, and its males are confidently identifiable by wing patterns. However, because no females are known and individual variation is unexplored, this species is best identified by DNA, with diagnostic base pairs in the nuclear genome: aly141.3.3:C90T, aly141.3.3:A129G, aly2532.2.1:T429C, aly3367.11.4:A81G, aly3367.11.4:C100T, aly159.16.2:G867G (not A), aly159.16.2:T873T (not C), aly3241.4.3:T57T (not C), aly1603.14.1:T72T (not G), aly2532.2.1:A345A (not T); and the COI barcode: T457C, A466G, T556G, T596C, A607T, T646C.

Barcode sequence of the holotype. Sample NVG-24055A09, GenBank PX660127, 658 base pairs:

AACATTATATTTTATTTTTGGTATTTGAGCAGGTATATTAGGAACTTCTCTAAGATTATTAATTCGTACTGAATTAGGAAATCCAGGATCTTTAATTGGAGATGATCAAATTTATAATACT
ATTGTAACAGCTCATGCTTTTATTATAATTTTTTTTATAGTAATACCTATTATAATTGGAGGATTTGGAAATTGATTAGTTCCTTTAATATTAGGAGCTCCTGATATAGCTTTCCCCCGTA
TAAATAATATAAGATTTTGAATGCTGCCCCCTTCATTAACTCTTTTAATTTCAAGAAGAATTGTAGAAAATGGTGCAGGAACAGGATGAACAGTTTACCCCCCACTTTCATCAAATATTGC
TCATCAAGGATCATCTGTTGATTTAGCAATTTTTTCCTTACATTTAGCAGGAATTTCTTCAATCTTAGGAGCTATTAATTTTATTACTACAATCATTAATATGCGAATCTCAAACTTATCA
TTTGATCAAATACCACTATTTGTATGATCTGTAGGAATTACTGCATTATTATTACTTTTATCTTTACCTGTGTTAGCAGGAGCTATTACTATACTTTTAACTGACCGAAATCTAAATACTT
CTTTTTTTGATCCAGCAGGAGGAGGAGATCCAATTTTATACCAACATTTATTT

Type material. Holotype: ♂ deposited in the Natural History Museum of Denmark, University of Copenhagen, Copenhagen, Denmark (ZMUC), illustrated in Fig. 48b, bears the following five rectangular labels (first two handwritten, others printed), four white: [Mapiri], [Pamphila | epictetus | Mapiri | 29-5-1918], [Coll. | E. C. Barfoed], [DNA sample ID: | NVG-24055A09 | c/o Nick V. Grishin], and one red [HOLOTYPE ♂ | Lento mysto | Grishin].

Type locality. Bolivia: La Paz Department, Mapiri.

Etymology. This new species superficially resembles *Zariaspes mys* (Hübner, [1808]) but belongs to *Lento*: *mys* + [Len]*to*. Moreover, this species is somewhat *myst*eri*o*us due to its unique appearance, yet it has remained undiscovered until now. The name is treated as a noun in apposition.

Distribution. Currently known only from the holotype collected in western Bolivia.

Historical specimens of *Lento imerius* (Plötz, 1884)

We found several historical specimens of *Lento imerius* (Plötz, 1884) (type locality in Brazil; neotype sequenced as NVG-22014H01) and confirmed their identification using genomic analysis (Fig. 47 blue). First, we located four specimens (out of five in the lot No. 5416) in the MFNB collection from “Rio” collected by G. von Langsdorff (1774–1852) according to the label on one of these specimens and the entry in the historical collection catalog handwritten by C. H. Hopffer (1810–1876) who identified them as “*Hesperia* sp.”, the best specimen shown in Fig. 48c; five specimens are listed under the entry 5416. This finding is consistent with the hypothesis that the type locality of *Lento imerius* is in Southeast or South Brazil. We did not find a connection between these specimens and the name *imerius*, and therefore it is not likely that they were syntypes, although their existence suggests that specimens of this species were probably not uncommon in collections. Second, we sequenced a specimen (Fig. 48d) in the SMF collection that according to its label “imerius | Pl. 765” was illustrated on the Plate 183, row e, image [7] in Draudt (1921–1924). Similarly styled labels appear on specimens that served as models for Draudt’s illustrations, sometimes with the letter “U” added if the illustration showed the ventral side. Although the label specifically mentions Plötz’s unpublished drawing number 765 referring to *Apaustus imerius*, it is unlikely that this specimen was illustrated or even known to Plötz. Such labels for many specimens in SMF illustrated in Draudt mention Plötz’s illustration numbers, but no Plötz’s types are known from this collection. It is more likely that when specimens were selected for illustrations, they were compared with the original Plötz’s drawings, and the agreement was noted on their labels. However, this specimen further supports the historical accuracy of the *Apaustus imerius* neotype being a specimen of this species.

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