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New taxa of butterflies supported by genomic analysis

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ABSTRACT. Continuing with the genomic analysis of butterflies, we present a taxonomic update. As a result of this work, 3 genera, 6 subgenera, 16 species, and 2 subspecies are described as new. New genera and subgenera are (type species in parenthesis): *Systasia* Grishin, **gen. n.** (*Hesperia zampa* W. H. Edwards, 1876) and *Asysta* Grishin, **gen. n.** (*Systasea microsticta* Dyar, 1923) in Pyrgini Burmeister, 1878 and *Alyco* Grishin, **gen. n.** (*Styriodes quota* Evans, 1955) in Moncina A. Warren, 2008; *Ocynthus* Grishin, **subgen. n.** (*Ocybadistes hypomeloma* Lower, 1911) of *Potanthus* Scudder, 1872, *Arrhona* Grishin, **subgen. n.** (*Padraona tranquilla* Swinhoe, 1905) and *Comba* Grishin, **subgen. n.** (*Hesperia wama* Plötz, 1885) of *Kobrona* Evans, 1935, *Telines* Grishin, **subgen. n.** (*Pamphila eurotas* C. Felder, 1860) of *Arrhenes* Mabille, 1904, *Kolba* Grishin, **subgen. n.** (*Telicota kolbei* Ribbe, 1899) of *Sabera* Swinhoe, 1908, and *Sarala* Grishin, **subgen. n.** (*Parnara sarala* Nicéville, 1889) of *Acerbas* Nicéville, 1895, all in Hesperiidae Latreille, 1809. New species and subspecies are (type localities in parenthesis): *Catocyclotis secuza* Grishin, **sp. n.** (Peru: Cuzco), *Catocyclotis serio* Grishin, **sp. n.** (Brazil: Rio de Janeiro), *Catocyclotis luteonaevia* Grishin, **sp. n.** (Bolivia: La Paz), *Synargis gohia* Grishin, **sp. n.** (Brazil: Bahia), and *Synargis maxidifa* Grishin, **sp. n.** (Peru: Loreto) in Riodinidae Grote, 1895 (1827); *Bungalotis corentus* Grishin, **sp. n.** (Ecuador: Pichincha), *Bungalotis amydros* Grishin, **sp. n.** (Ecuador: Pichincha), *Salatis minimaculatis* Grishin, **sp. n.** (Peru: Loreto), *Pellicia* (*Mictris*) *rio* Grishin, **sp. n.** (Brazil: Rio de Janeiro), *Clytius mattus* Grishin, **sp. n.** (USA: Hidalgo Co.), *Perus* (*Menuda*) *tinctus* Grishin, **sp. n.** (deduced as South America), *Timochares fuscifasciata* Grishin, **sp. n.** (USA: Texas, Hidalgo Co.), *Quasimellana duranga* Grishin, **sp. n.** (Mexico: Durango), *Stinga azteca* Grishin, **sp. n.** (Mexico: México), *Vistigma* (*Vistigma*) *shnoba* Grishin, **sp. n.** (Peru: Madre de Dios), *Vertica* (*Brasta*) *asta* Grishin, **sp. n.** (Colombia: Valle del Cauca) in Hesperiidae; *Synargis flavicauda cosita* Grishin, **ssp. n.** (Guyana) in Riodinidae and *Notamblyscirtes durango seaza* Grishin, **ssp. n.** (USA: Arizona, Santa Cruz Co.) in Hesperiidae, as all other taxa below. *Suniana* Evans, 1934 is a subgenus of *Potanthus* Scudder, 1872. The following species are transferred between genera to form new combinations: *Camptopleura polax* (Evans, 1953), **comb. nov.** (not *Cycloglypha* Mabille, 1903), *Potanthus hypomeloma* (Lower, 1911), **comb. nov.** (not *Ocybadistes* Heron, 1894), *Kobrona tranquilla* (Swinhoe, 1905), **comb. nov.** (not *Arrhenes* Mabille, 1904), *Arrhenes eurotas* (C. Felder, 1860), **comb. nov.** and *Arrhenes eurychlora* (Lower, 1908), **comb. nov.** (not *Telicota* Moore, 1881), *Sabera kolbei* (Ribbe, 1899), **comb. nov.** (not *Mimene* Joicey & Talbot, 1917), and *Vistigma* (*Vistigma*) *meesi* (de Jong, 1983), **comb. nov.** (not *Phlebodes* Hübner, 1819). The following are species-level taxa, not subspecies or synonyms: *Salatis pelignus* (Hewitson, 1867), **stat. rest.** (not *Salatis salatis* (Stoll, 1782)), *Pellicia* (*Mictris*) *cambyses* Hewitson, 1878, **stat. rest.** (not *Pellicia* (*Mictris*) *crispus* Herrich-Schäffer, 1870), *Clytius unifascia* (Mabille, 1889), **comb. nov.** (not *Staphylus azteca* (Scudder, 1872) or *Clytius clytius* (Godman & Salvin, 1897)), *Clytius semitincta* (Dyar, 1924), **stat. rest.** (not *Clytius clytius*), *Timochares sanda* Evans, 1953, **stat. nov.** (not *Timochares trifasciata* (Hewitson, 1868)) and *Sabera tenebricosa* (Mabille, 1904), **comb. nov., stat. rest.** (not *Sabera kolbei* (Ribbe, 1899)). The following taxa are **new** junior subjective synonyms: *Mycteris caerula* Mabille, 1877 of *Pellicia* (*Mictris*) *crispus* Herrich-Schäffer, 1870, *Timochares ruptifasciata runia* Evans, 1953 of *Timochares ruptifasciata* (Plötz, 1884). *Staphylus veytius* H. Freeman, 1969 is confirmed as a junior subjective synonym of *Staphylus tierra* Evans, 1953. *Pellicia pericles* Mabille, 1903 is a junior subjective synonym of *Pellicia* (*Mictris*) *cambyses* **stat. rest**. (not of *Pellicia* (*Mictris*) *crispus*). *Eudamus sebrus* C. Felder & R. Felder, 1867 and *Bungalotis sapucayae* Jörgensen, 1935 are junior subjective synonyms of *Salatis pelignus* **stat. rest.** (not of *Salatis salatis*). The type species of *Lintneria* W. H. Edwards & Butler, 1877 is fixed as *Thanaos potrillo* Lucas, 1857 thus making *Cabares* Godman & Salvin, 1894 a junior objective synonym of *Systasea* Butler, 1877, which is a replacement name for *Lintneria* that becomes a junior subjective synonym of *Autochton* Hübner, 1823. **Lectotypes** are designated for 6 Hesperiidae (type localities in parenthesis): *Pellicia crispus* Herrich-Schäffer, 1870 (Venezuela), *Antigonus unifascia* Mabille, 1889 (Honduras), *Leucochitonea trifasciata* Hewitson, 1868 (Bolivia), *Timochares trifasciata* form *obscurior* Draudt, 1923 (Bolivia: Rio Zongo), *Antigonus ruptifasciata* Plötz, 1884 (Jamaica; deduced by genomic sequence comparison), and *Telicota kolbei* Ribbe, 1899 (Papua New Guinea: New Britain Island). Furthermore, we show that *Timochares trifasciata* form *obscurior* Draudt, 1923 is an unavailable name; a nomen

nudum *Pholisora elis* in J. B. Smith et al., 1891 (List of the Lepidoptera of boreal America) refers to a specimen of *Clytius clytius* from USA: Arizona; a specimen in MFNB curated as a type of *Achlyodes serapion* Plötz, 1884 is a pseudotype; and *Cecropterus* (*Murgaria*) *markwalkeri* Grishin, 2023 is widely distributed in western and southern Mexico. Finally, we illustrate the genitalia of the lectotype of *Achlyodes cnidus* Plötz, 1884.

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

ZooBank registration: http://zoobank.org/4F2EC806-72C0-4BA6-9FBB-E6E6EC22A523

INTRODUCTION AND METHODS

This study expands on our research originating from the genomic sequencing of butterflies and follows the same principles and methodologies (Cong et al. 2019a, b; Li et al. 2019; Zhang et al. 2019a–d; Cong et al. 2020; Zhang et al. 2020; Cong et al. 2021; Zhang et al. 2021; Robbins et al. 2022; Zhang et al. 2022b, d; Zhang et al. 2023a, c–g; Zhang et al. 2024). Our goal is to improve butterfly classification by analyzing genomic data. This approach examines various butterfly taxa globally with specimens primarily sourced from museum and private collections (see Acknowledgments). Collected specimens vary in age, from recent to over 250 years old. When possible, we sequence DNA from primary type specimens to create an objective reference for the names (Zhang et al. 2022a). DNA is typically extracted from legs, with a non-destructive method that preserves them. After extraction, DNA is fragmented, if not already so due to age, and sequenced using the Illumina platform with 150 bp reads. Rather than amplifying specific genes, we sequence all DNA segments in the sample, making this method applicable even for specimens collected centuries ago and with short DNA fragments (30–50 bp).

Short DNA fragments from each specimen, 150 base pairs or less, are assembled into exons for protein-coding genes, using a reference genome from closely related species as a guide. These genes inform phylogenetic tree construction, with three trees generated using IQ-TREE v1.6.12 and the GTR+GAMMA model (Nguyen et al. 2015): one from autosomes, another from the predicted Z chromosome genes, and a third from the mitochondrial genome. For computational efficiency, 100,000 codons are randomly sampled (unless stated otherwise in figure legends), representing about 2% of the data, to build nuclear trees (about 300,000 base pairs). Statistical branch support is evaluated from 100 replicates, each drawing 10,000 codons at random from the original dataset. Support values (0 to 100) represent the replicates with a matching bipartition in the 100,000-codon tree (unless stated otherwise in figure legends). For further specifics, refer to our previous works (Li et al. 2019; Zhang et al. 2022b).

Phylogenetic trees were visualized, rotated, and colored with FigTree (Rambaut 2018). We mapped current taxonomy onto these trees to detect non-monophyletic taxa and identify unnamed clades. Genomic trees often reveal "levels" that represent diversification timelines where independent evolution occurred in multiple lineages (Zhang et al. 2021). These points, often triggered by geological events impacting several lineages, enable the alignment of taxonomic ranks (tribe, subtribe, genus, subgenus) with levels from genomic trees. This produces an internally consistent classification that considers genetic differentiation and paleontological history. Our classification decisions emphasize genomic trees, with morphological traits used as additional evidence to support conclusions. Genomes capture a broad array of information—life history, habitat, mating and diet preferences—beyond adult morphology traditionally used in butterfly taxonomy. Although we may not yet be able to directly link phenotypic traits to genetic sequences, we use aggregated random codons from all protein-coding genes to derive a taxonomic classification grounded in phylogeny and evolutionary theory.

Defined taxa are monophyletic and represent prominent clades, with "prominent" denoting well-supported branches with high (100%) replicate agreement and generally longer than adjacent branches. Branch length corresponds to the number of base-pair substitutions; thus, longer branches are statistically stronger and likely lead to more phenotypic differences, which may appear in adult or immature stages or other phenotypic characters. However, the correlation between genetic changes and visible phenotypic differences is non-linear (Zhang et al. 2019a). Thus, short branches can still represent visibly distinct taxa,

and each case is evaluated individually. Importantly, significant phenotypic changes, possibly caused by minimal genetic alterations like single genomic inversions, may not always justify a distinct taxon if other characters, such as caterpillar traits, remain similar to those of related lineages. Our taxonomic proposals consider existing classification, using current names and taxonomic ranks as benchmarks to define tree levels and detect new taxa.

This work addresses higher classification issues, such as new genera, subgenera, and genus transfers to restore monophyly, but it primarily focuses on species and subspecies. Species distinctions rely on Z chromosome genetic differentiation (F_{st} > 0.20 typically indicates distinct species), gene flow (G_{min} < 0.05 for different species) (Cong et al. 2019a), COI barcode differences (>2% usually suggests speciation) (Hebert et al. 2003) that are complemented by phenotypic differences (Lukhtanov et al. 2016), and well-supported, prominent species-level clades (Zhang et al. 2022d). We keep in mind that COI barcodes and mitochondria frequently introgress across species (Bachtrog et al. 2006; Cong et al. 2017a), with some distinct species sharing similar or identical barcodes (Burns et al. 2008; Zhang et al. 2023b). For further details, refer to the "Species, subspecies, and genomics" section in Zhang et al. (2022a).

Subspecies typically denote geographically distinct populations with identifiable phenotypic differences (70% recognizable without locality knowledge) yet capable of interbreeding (Mayr 1982; Monroe 1982). In practice, interbreeding is hard to assess, so subspecies delineation often relies solely on wing pattern differences among allopatric populations. It is usually unknown if wing pattern differences are genetic or environmental. Genomic sequences enable genotype-based comparisons between populations. Here, new subspecies are proposed for genetically distinct populations forming separate clades in at least one genomic tree, albeit less distinct than species. These subspecies are "incipient species": differentiated genetically, though less so than species. Once subspecies are delineated, we assess wing patterns to identify characters statistically distinguishing them. Wing pattern diagnoses may apply to ~70% of individuals. However, clade-based DNA characters in genomic trees are expected to apply broadly across specimens, so we provide DNA-based diagnoses for all newly described subspecies.

Sections of this publication are presented in taxonomic sequence derived from genome-wide phylogeny, enhanced by phenotypic insights. For newly described taxa, we provide concise phenotypic descriptions, often supplemented with references that detail and illustrate morphological characteristics more thoroughly. In addition, we include diagnostic DNA characters in the nuclear genome and, where applicable, in the COI barcode. Nuclear protein-coding regions yield DNA characters identified using our previously established method (see SI Appendix to Li et al. 2019). The rationale behind selecting these characters, as outlined in Cong et al. (2019b), is to identify robust characters that will likely remain reliable as further specimens and species undergo sequencing.

The character states are given diagnoses of new taxa as abbreviations for one of the two reference genomes: *Calephelis nemesis* (W. H. Edwards, 1871) (cne) (Cong et al. 2017b), or *Cecropterus lyciades* (Geyer, 1832) (aly, because this species was formerly in the genus *Achalarus* Scudder, 1872) (Shen et al. 2017). E.g., aly728.44.1:G672C means position 672 in exon 1 of gene 44 from scaffold 728 of the *Cecropterus lyciades* (Geyer, 1832) reference genome (Shen et al. 2017) 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). Similar abbreviations are used for the characters in the COI barcode but without a prefix ending with ':'. The sequences of exons from a corresponding reference genome with positions taken as characters highlighted in green are given in the supplemental file deposited at < https://osf.io/ad5gu/ >. This link to the DNA sequences accessible from this publication ensures that DNA characters used in the diagnoses can be confidently associated with their sequences.

Whole genome shotgun datasets we obtained and used in this work are available from the NCBI database < https://www.ncbi.nlm.nih.gov/ > as BioProject PRJNA1181280 and BioSample entries of the project contain locality and other collection data of the sequenced specimens shown in the trees. Some sequence datasets have been published previously, e.g., in Zhang et al. (2023g), and re-used in this study.

For each specimen in tree figures, the following information is listed (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, PLT, or HT, status not investigated), PT paratype, PLT paralectotype; and if a synonym name is given (in parenthesis, preceded by "="), and in addition by "‡" for unavailable names), type status refers to the synonym. COI barcode sequences reported here have been deposited in GenBank with accessions PQ489696–PQ489719. Abbreviations or acronyms for collections are listed in the Acknowledgments section.

Family Riodinidae Grote, 1895 (1827)

Catocyclotis secuza Grishin, new species

http://zoobank.org/80A7A093-35F9-4FE1-ABD2-F9475FFBFA66

(Figs. 1 part, 2–3)

Definition and diagnosis. Genomic phylogeny of *Catocyclotis* Stichel, 1911 (type species *Hesperia aemulius* Fabricius, 1793) reveals that specimens identified as *Catocyclotis sejuncta* (Stichel, 1910) (type locality in Brazil: Rio de Janeiro) are genetically differentiated from its lectotype (sequenced as NVG-21121A10) at the species level (Fig. 1), e.g., the COI barcode of a specimen from Peru differs by 3.0% (20 bp). Therefore, this specimen represents a new species. This new species is similar to *C. sejuncta* and differs from it by paler ventral forewing with more developed pearly overscaling with brown scales partly replaced with pearly scales over the entire ventral surface. According to Hall (2018), who treated it as a color variant of *C. sejuncta* not differing in genitalia, which are shown in Fig. 3 and appear to have a shorter and more stout harpe that is more gradually bent inwards compared to *C. sejuncta*. Due to the cryptic nature of this species, definitive identification is provided by DNA, and a combination of the

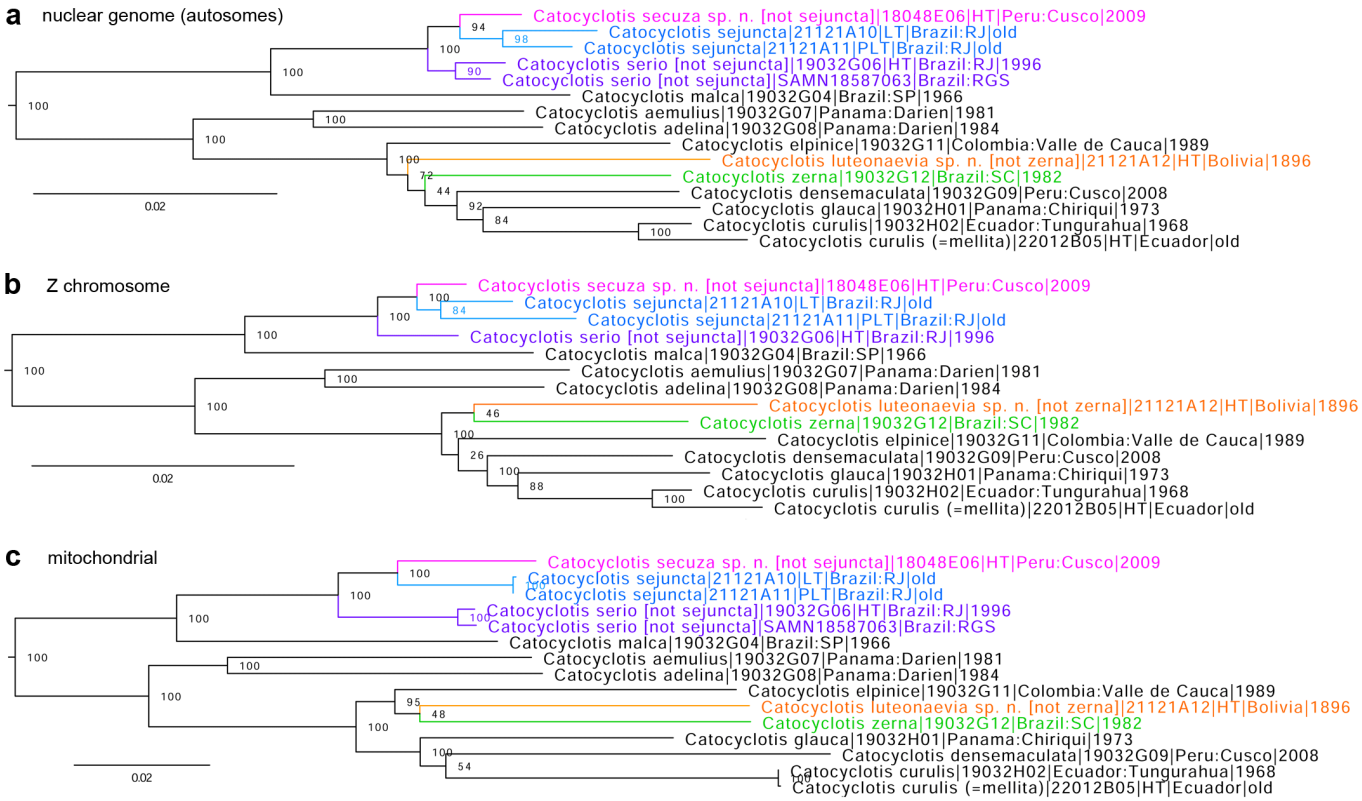

Fig. 1. Phylogenetic trees of selected *Catocyclotis* species inferred from protein-coding regions of **a)** the nuclear genome (autosomes), **b)** the Z chromosome, and **c)** the mitochondrial genome. Species discussed in the text are shown in different colors: *C. secuza* **sp. n.** (magenta), *C. sejuncta* (blue), *C. serio* **sp. n.** (purple), *C. luteonaevia* **sp. n.** (orange), *C. zerna* **sp. n.** (green). The sequence of SAMN18587063 is taken from the alignment provided in Kawahara et al. (2023).

following characters is diagnostic in the nuclear genome: cne5853.1.9:G39A, cne403.6.1:C289T, cne2935.2.13:G72T, cne9494.2.1:C33T, cne6332.2.1:G192A, cne2307.5.2:C98C (not T), cne2307.5.2:G109G (not A), cne1302.6.1:C487C (not T), cne364.20.1:G150G (not A), cne5120.2.1:C142C (not A), and COI barcode: T1C, G38A, A122G, G218A, A346C, G389A.

Barcode sequence of the holotype. Sample NVG-18048E06, GenBank PQ489696, 658 base pairs:

CACATTATATTTTATTTTTGGAATTTGAGCAGGTATAATAGGAACATCTTTAAGTCTTTTAATTCGTATAGAATTAGGAACTCCCGGATCATTAATTGGAGATGATCAAATTTATAATACT
GTTGTTACAGCTCATGCTTTTATTATAATTTTTTTTATAGTTATACCTATTATAATTGGAGGTTTTGGAAATTGATTAATTCCTTTAATATTAGGTACTCCTGATATAGCATTTCCACGAA
TAAATAATATAAGATTTTGATTATTACCCCCTTCATTATTTCTTTTAATTTCAAGAAAAATTGTAGAAAATGGTACAGGAACTGGATGAACAATTTACCCCCCCCTATCATCTAATATTGC
CCATGGAGGAGCATCAGTTGATTTAACTATTTTTTCTCTTCATTTAGCTGGTATTTCTTCAATTTTAGGAGCTATTAATTTTATTACTACTATTATTAATATACGTATTAATAATTTATCT
TTTGATCAAATACCTTTATTTGTTTGATCTGTAGGAATTACTGCATTATTATTATTATTATCTTTACCTGTATTAGCAGGTGCTATTACTATATTATTAACAGATCGAAATTTAAATACAT
CATTTTTTGACCCTGCTGGAGGAGGAGATCCAATTTTATATCAACATTTATTT

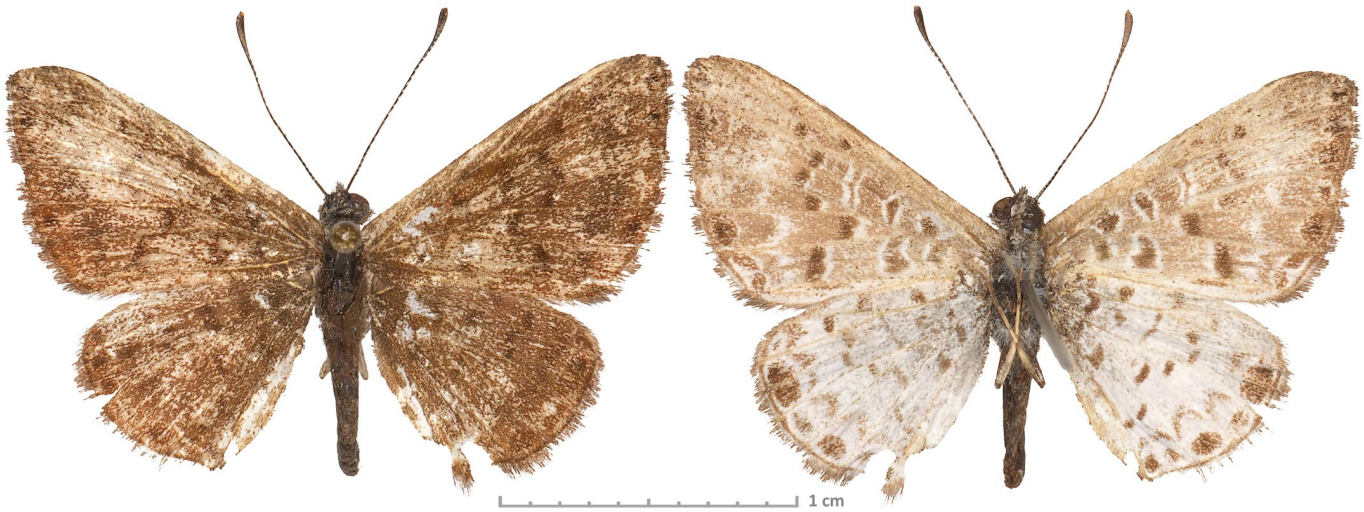

Fig. 2. Holotype of *Catocyclotis secuza* **sp. n.** in dorsal (left) and ventral (right) views, data in text.

Type material. Holotype: ♂ currently deposited in the National Museum of Natural History, Washington, DC, USA (USNM), illustrated in Fig. 2 (genitalia in Fig. 3), bears five printed (text in italics handwritten) labels: four white [PERU: Cuzco, 1050m | Quitacalzone | Cosnipata Rd *575* | 17-VIII-2009 Kinyon], [DNA sample ID: | NVG-18048E06 | c/o Nick V. Grishin], [DNA sample ID: | NVG-23115A02 | c/o Nick V. Grishin], [USNMENT | {QR Code} | 01466540], and one red [HOLOTYPE ♂ | Catocyclotis | secuza Grishin]. The first DNA sample refers to the extraction from a leg, and the second is from the abdomen prior to genitalia dissection.

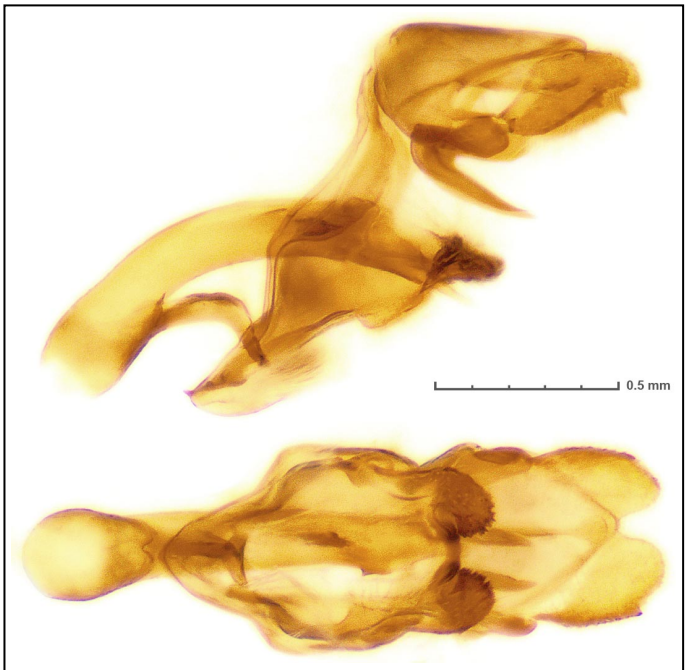

Fig. 3. Genitalia of *Catocyclotis secuza* **sp. n.** holotype in left lateral (above) and ventral (below) views.

Type locality. Peru: Cuzco Department, Cosñipata Valley, Quebrada Quitacalzón, elevation 1050 m, approx. GPS −13.0167, −71.4833.

Etymology. The name *sejuncta* likely comes from the Latin verb *sejungere*, which means to set apart, separate, or divide. Therefore, *sejuncta* can be interpreted to mean separated, set apart, divided, isolated, or secluded. We are dividing this species into several, and a segregate from Cuzco gets its name as *se*[gregate] +*Cuz*[co] + *a*. The name is treated as a feminine noun in apposition.

Distribution. Currently known only from the holotype collected in Cuzco, Peru.

Catocyclotis serio Grishin, new species

http://zoobank.org/5C003A6B-7805-4B04-B91C-C8943558CFBE

(Figs. 1 part, 4)

Definition and diagnosis. Genomic phylogeny of *Catocyclotis* Stichel, 1911 (type species *Hesperia aemulius* Fabricius, 1793) reveals that specimens identified as *Catocyclotis sejuncta* (Stichel, 1910) (type locality in Brazil: Rio de Janeiro) are genetically differentiated from its lectotype (sequenced as NVG-21121A10) at the species level (Fig. 1), e.g., the COI barcode of a specimen from Rio de Janeiro differs by 3.2% (21 bp). Therefore, this specimen represents a new species. This new species is similar to *C. sejuncta* and differs from it by darker ventral hindwing with less developed pearly overscaling and some purple overscaling on the dorsal hindwing. According to Hall (2018), who treated it as a color variant of *C. sejuncta* and detailed the differences between them, it does not differ from it in genitalia, thus best identified by its darker phenotype. Due to the cryptic nature of this species, definitive identification is provided by DNA, and a combination of the following characters is diagnostic in the nuclear genome: cne3539.9.2:T108C, cne3539.9.2:A120C, cne16860.2.5:A927G, cne1023.1.1:G87A, cne14049.3.4:C58T, cne682.1.3:T114T (not C), cne5853.1.9:G39G (not A), cne20858.1.2:C456C (not A), cne20858.1.2:T465T (not C), cne20858.1.2:A1371A (not G), and COI barcode: T34C, C85T, T106C, A160G, T259C, T547C.

Barcode sequence of the holotype. Sample NVG-19032G06, GenBank PQ489697, 658 base pairs:

TACATTATATTTTATTTTTGGAATTTGAGCAGGCATAGTAGGAACATCTTTAAGTCTTTTAATTCGTATAGAATTAGGAACTCCTGGATCATTAATTGGTGATGACCAAATTTATAATACT
ATTGTAACAGCTCATGCTTTTATTATAATTTTTTTTATGGTTATACCTATTATAATTGGAGGTTTTGGAAATTGATTAGTTCCTTTAATATTAGGTGCTCCTGATATAGCATTTCCACGAA
TAAATAATATAAGATTCTGATTACTACCCCCTTCATTATTTCTTTTAATTTCAAGAAGAATTGTAGAAAATGGTGCAGGAACTGGATGAACAGTTTACCCCCCCACTATCATCTAATATTGC
CCATGGAGGATCATCAGTTGATTTAGCTATTTTTTCTTTACATTTAGCTGGTATTTCCTCAATTTTAGGAGCTATTAATTTTATTACTACTATTATTAACATACGTATTAATAATTTATCT
TTTGATCAAATACCTTTATTTGTTTGATCTGTAGGAATTACTGCATTATTGTTATTATTATCCTTACCTGTATTAGCAGGTGCTATTACTATATTATTAACAGATCGAAATTTAAATACAT
CATTTTTTGACCCTGCTGGAGGAGGAGATCCAATTTTATATCAACATTTATTT

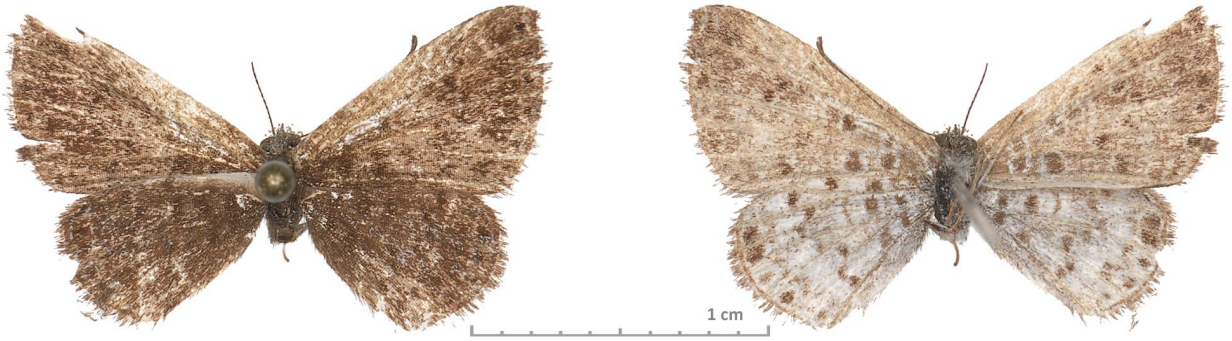

Fig. 4. Holotype of *Catocyclotis serio* **sp. n.** in dorsal (left) and ventral (right) views, data in text.

Type material. Holotype: ♂ currently deposited in the National Museum of Natural History, Washington, DC, USA (USNM), illustrated in Fig. 4, bears five printed (text in italics handwritten) labels: four white [BRAZIL, RJ, Teresopolis | 22°27'S, 42°59'W | 17 Dec 1996 1,000 m | Leg. Robbins & Caldas], [Genitalia vial | *Catocyclotis* | *sejuncta* | *USNM 344* | J. P. W. Hall], [DNA sample ID: | NVG-19032G06 | c/o Nick V. Grishin], [USNMENT | {QR Code} | 01544522], and one red [HOLOTYPE ♂ | Catocyclotis | serio Grishin].

Type locality. Brazil: Rio de Janeiro, Teresópolis, elevation 1000 m, GPS −22.450, −42.983.

Etymology. The name *sejuncta* likely comes from the Latin verb *sejungere*, which means to set apart, separate, or divide. Therefore, *sejuncta* can be interpreted to mean separated, set apart, divided, isolated, or secluded. We are dividing this species into several, and a segregate from Rio gets its name as *se*[gregate] + *Rio*. The name is treated as a feminine noun in apposition.

Distribution. Currently known only from the holotype collected in Rio de Janeiro, Brazil.

Catocyclotis luteonaevia Grishin, new species

http://zoobank.org/5B5C4D82-4ECB-49D1-8546-08AC223A0C4C

(Figs. 1 part, 5)

Definition and diagnosis. Genomic phylogeny of *Catocyclotis* Stichel, 1911 (type species *Hesperia aemulius* Fabricius, 1793) reveals that a specimen from Bolivia curated in MFNB as a type of *Echenais*

zerna f. *luteonaevia* Stichel, 1911 (sequenced as NVG-21121A12) is genetically differentiated from *Catocyclotis zerna* (Hewitson, 1872) (type locality in Brazil: Rio de Janeiro) at the species level (Fig. 1), e.g., their COI barcodes differ by 6.5% (43 bp). Furthermore, this specimen possesses a unique mitogenome (Fig. 1c), which rejects Hall's (2018) hypothesis that it is a hybrid and strongly suggests that it is a species distinct from *C. zerna* and others. The name *luteonaevia* was introduced by Stichel (1911) as "Forma ♀ luteonaevia, form. nov." thus proposed for a female form and is infrasubspecific. According to the Glossary of the ICZN Code (1999), an infrasubspecific name is "a name applied to an infrasubspecific entity." The infrasubspecific entity is defined in part as "specimen(s) within a species differing from other specimens in consequence of intrapopulational variability (e.g. opposite sexes …," which is what "Forma ♀" refers to. To further substantiate this conclusion, we note that Stichel (1911) explicitly proposed new subspecies as "subsp. nov." in this work, in contrast to the names for infrasubspecific entities. The name *luteonaevia* was proposed as infrasubspecific and was not adopted as the valid name for a species or a subspecies before 1985 (Art. 45.6.4), being treated as a "form" and in synonymy. Therefore, the name is unavailable, and its "type" specimen represents a new species. This new species is differentiated from others by the characters given in Stichel (1911:338) and elaborated by Hall (2018: 295) for *Echenais zerna* f. *luteonaevia*. In brief, a female (male unknown) differs from its relatives by an orange-brown marginal band on the dorsal forewing, similar orange overscaling over the dorsal wing surface, and three prominent stretches of white scales in the forewing fringe. Due to unexplored phenotypic variation, definitive identification is provided by DNA, and a combination of the following characters is diagnostic in the nuclear genome: cne191.3.1:A117G, cne3560.2.4:T70C, cne1941.1.6:G93C, cne21329.5.1:A372C, cne5807.3.16:A177G, cne1302.6.1:T490T (not C), cne38112.1.3:G345G (not A), cne13807.3.1:C1254C (not T), cne1425.14.2:G637G (not T), cne1425.14.2:T648T (not G), and COI barcode: A76G, T118C, G506A, T508C, T574C, T640C.

Barcode sequence of the holotype. Sample NVG-21121A12, GenBank PQ489698, 658 base pairs:

AACATTATATTTTATTTTTGGTATTTGAGCTGGTATAGTTGGAACATCATTAAGTTTATTAATTCGAATAGAATTGGGAACTCCTGGATCTTTAATTGGTGATGATCAAATTTACAACACT
ATTGTAACAGCGCATGCTTTTATTATAATTTTTTTTATAGTTATACCTATTATAATTGGAGGATTTGGTAATTGATTAGTACCTTTAATATTAGGAGCTCCCGATATAGCTTTTCCTCGAA
TAAATAATATAAGATTTTGATTACTTCCCCCATCATTATTTCTTTTAATTTCTAGAAGTATTGTAGAAAATGGAGCAGGAACAGGATGAACAGTTTATCCCCCACTTTCATCTAATATTGC
TCATGGAGGAACATCAGTTGATTTAGCTATTTTTTCTTTACATTTAGCTGGAATTTCCTCAATTTTAGGAGCTATTAATTTTATTACTACTATTATTAATATACGTATTAATAATTTATCT
TTTGATCAAATACCATTATTTATCTGATCTGTAGGTATCACTGCATTATTACTATTATTATCTTTACCTGTTTTAGCTGGTGCTATTACCATATTATTAACTGATCGAAATTTAAATACTT
CTTTTTTTGATCCTGCAGGAGGAGGAGATCCTATCTTATATCAACATTTATTT

Fig. 5. Holotype of *Catocyclotis luteonaevia* **sp. n.** in dorsal (left) and ventral (right) views, data in text.

Type material. Holotype: ♀ deposited in the Museum für Naturkunde, Berlin, Germany (MFNB), illustrated in Fig. 5, bears seven labels (3rd handwritten, others printed with handwritten text in shown italics; 1st and the last red, others white): [Type], [Rio Songo (1200 m)| Bolivia (Yungas) | 189*6*—~~6~~ Garlepp], [luteonaevia | Stich.], [Coll. | Staudinger], [DNA sample ID: | NVG-21121A12 | c/o Nick V. Grishin], [ex coll. | H. STICHEL], and [HOLOTYPE ♀ | Catocyclotis | luteonaevia Grishin]. The holotype is missing its abdomen.

Type locality. Bolivia: La Paz Department, Río Zongo, elevation 1200 m.

Etymology. For the stability of nomenclature, the infrasubspecific name proposed by Stichel (1911) is

adopted for this new species. In Latin, *luteus* means yellow, and *naevus* means birthmark or blemish. The name is given for the yellowish (actually, orange-brown) outer margin of the dorsal hindwing and is a noun in apposition.

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

Synargis gohia Grishin, new species

http://zoobank.org/2E0150FE-9303-4BA0-86A3-D642712A4E2C

(Figs. 6 part, 7d–f)

Definition and diagnosis. Genomic analysis of additional specimens in the *Synargis regulus* group reveals a clade from Brazil (Bahia and Goiás) (Fig. 6 red) representing a taxon most closely related to *Synargis regina* Grishin, 2024 (type locality in Peru) (Fig. 6 blue) and *Synargis reginella* Grishin, 2024 (type locality in Brazil: Pará) (Fig. 6 green), but distinct from them both at the species level (Fig. 6), e.g., its COI barcodes differ from those of *S. regina* and *S. reginella* by 2% (13 bp) and 2.4% (16 bp), respectively. This new species is most similar to *S. regina* and *S. reginella* and differs by less extensive than in *S. reginella* but more extensive than in *S. regina* yellow spotting along the outer margin of ventral hindwing, somewhat broader brown bands between yellow areas, and longer than in *S. reginella* postdiscal yellow area along the inner margin of hindwing as a result of wider separation between the brown bands towards the inner margin. Males are yellower and less orange than *S. reginella*, with abdomen brown above and pale-yellow beneath (males of *S. regina* are unknown). Females of the new species we sequenced are smaller in size than either *S. regina* or *S. reginella* (Fig. 7). However, the male is comparable to males of *S. reginella*, and, therefore, the difference in size may be individual variation. Due to unexplored phenotypic variation, most reliable identification is achieved by DNA, and a combination of the following base pairs is diagnostic in the nuclear genome: cne6558.13.3:A1623C, cne6558.13.3:C1632T, cne12987.3.24:G2562T, cne12987.3.24:T2565G, cne12987.3.24:T2568G, and COI barcode: C81C, T274T, T283C, T334T, T479C, T514C.

Barcode sequence of the holotype. Sample NVG-23103C07, GenBank PQ489699, 658 base pairs:

AACTTTATATTTTATTTTTGGAATCTGAGCAGGTATAATAGGAACATCTCTTAGTTTATTAATTCGAATAGAATTAGGAACTCCTGGTTCTTTAATTGGAAATGATCAAATTTATAATACT
ATTGTTACAGCTCATGCATTTATTATAATTTTTTTTATAGTTATACCTATTATAATTGGAGGATTTGGAAATTGATTAGTTCCATTAATATTAGGAGCTCCAGATATAGCTTTTCCTCGTA
TAAATAATATAAGATTTTGATTATTACCTCCTTCTTTATTCTTATTAATTTCTAGAAGAATTATTGAAAATGGAGCAGGAACTGGATGAACTGTGTACCCCCCACTTTCATCTAATATTGC
TCACAGAGGAGCTTCTGTTGATTTAGCTATTTTTTCTCTTCATTTAGCTGGAATTTCATCAATTTTAGGTGCAATTAATTTTATTACTACTATTATTAATATACGTATTAATAATCTATCA
TTTGATCAAATACCTTTATTTATTTGATCCGTAGGAATTACTGCTCTTCTTCTTTTATTATCTTTACCTGTTTTAGCAGGAGCTATTACTATATTACTTACAGATCGAAATTTAAATACAT
CTTTTTTTGATCCCGCAGGAGGTGGAGATCCAATTTTATATCAACATTTATTT

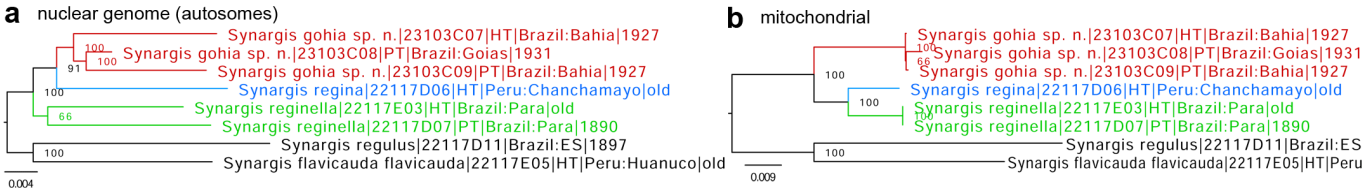

Fig. 6. Phylogenetic trees of selected *Synargis* species constructed from protein-coding regions of **a)** the nuclear (autosomes) and **b)** the mitochondrial genome: *S. gohia* **sp. n.** (red), *S. regina* (blue), and *S. reginella* (green).

Type material. Holotype: ♀ currently deposited in the Senckenberg Naturmuseum, Frankfurt, Germany (SMF), illustrated in Fig. 7e, bears the following three printed rectangular labels, two white: [Rio Preto | März 1927 | Dr. Seitz leg.], [DNA sample ID: | NVG-23103C07 | c/o Nick V. Grishin], and one red [HOLOTYPE ♀ | Synargis | gohia Grishin]. **Paratypes:** 1♂ and 1♀ from Brazil in SMF: 1♂ NVG-23103C08 Goias, Viannepolla, Nov-1921, Coll. R. Spitz and 1♀ NVG-23103C09 data as the holotype.

Type locality. Brazil: Bahia, Preto River.

Etymology. The name is a fusion of the names of states where this species has been recorded from: *Go*[iás] + [Ba]*hia*. Furthermore, goia means joy in Guaraní, fitting the appearance of this joyful species. The name is treated as a noun in apposition.

Distribution. Currently known from central and northeastern Brazil, the states of Goiás and Bahia.

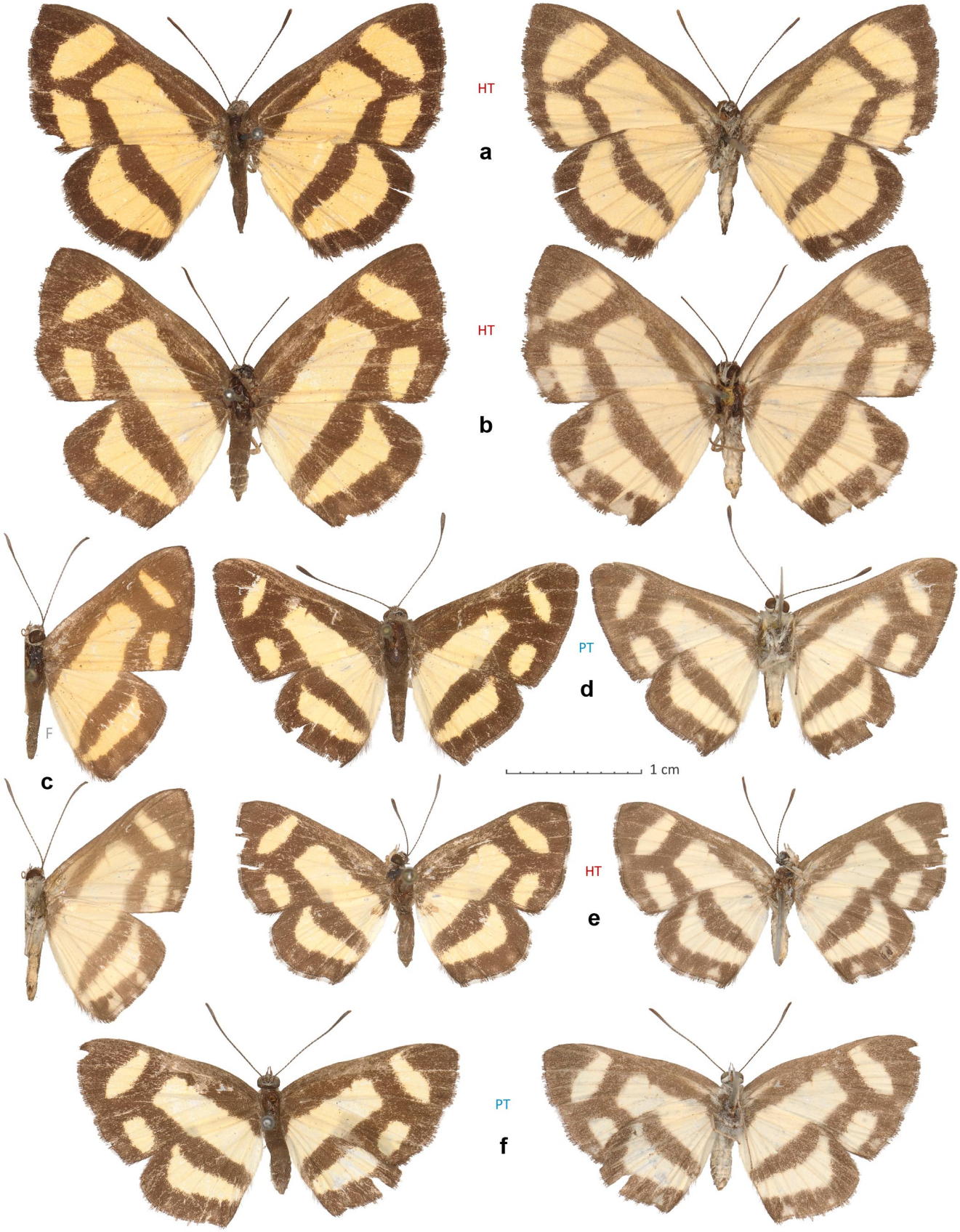

Fig. 7. *Synargis* species in dorsal (left or above the panel letter) and ventral (right or below) views, the same scale as Figs. 9 and 10 below and Figs. 16 and 17 from Zhang et al. (2024), data in text and in Zhang et al. (2024): **a)** *S. regina* holotype ♀ NVG-22117D06; **b, c)** *S. reginella*: **b)** holotype ♀ NVG-22117E03, **c)** ♂ NVG-23103C06 Brazil: Para, Tapajos, old (~1900) [SMF], F indicates flipped image (i.e. left-right inverted); **d–f)** *S. gohia* **sp. n.**: **d)** paratype ♂ NVG-23103C08, **e)** holotype ♀ NVG-23103C07, **f)** paratype ♀ NVG-23103C09.

Synargis maxidifa Grishin, new species

http://zoobank.org/5A2CCC55-4575-451F-9A5E-8CB2A1EE668E

(Figs. 8 part, 9a)

Definition and diagnosis. Genomic analysis reveals that a specimen from northern Peru unique in its wing pattern (Fig. 9a) belongs to the *Synargis regulus* group but is genetically differentiated from others at the species level (Fig. 8), e.g., its COI barcode differs from closer relatives such as *Synargis latidifa* Grishin, 2024 (type locality in French Guiana) and *Synargis tenebritorna* Grishin, 2024 (type locality in Brazil: Bahia) by 2.6% (17 bp), and, therefore, represents a new species. This new species is somewhat intermediate in appearance between typical *S. regulus* group representatives and *Synargis chaonia* (Hewitson, [1853]) (type locality in Brazil: Amazonas), and differs from its relatives by much broader (more than 5 times) discal yellow band compared to the submarginal band, mostly due to the submarginal band being narrower than in other species, and by slightly paler yellow color compared to *S. latidifa*. The new species is also similar to *Synargis sylvarum* (H. Bates, 1867) (type locality in Brazil: Pará), which we have not sequenced. However, in *S. sylvarum*, the two submarginal spots are connected into a band on the ventral forewing (separated in the new species), dorsal hindwing submarginal band is longer, nearly reaching costal and inner margins (widely separated from the costal margin in the new species), veins on the ventral side of wings are yellower (of the same brown ground color in the new species), and the forewing central spot-like band narrows anteriad, more triangular in shape (rectangular to oval in the new species). This new species is not cryptic and is recognizable by its wing pattern. In DNA, a combination of the following base pairs is diagnostic in the nuclear genome: cne14967.2.1:C384A, cne14967.2.1:C387T, cne14967.2.1:A396G, cne14967.2.1:C399T, cne14967.2.1:C405T, cne349.3.6:C84C (not T), cne349.3.6:C90C (not T), cne349.3.6:G117G (not C), cne40.6.1:T711T (not G), cne40.6.1:G717G (not T), and COI barcode: A316T, C391C, T442C, T463C, A494T, T464C.

Barcode sequence of the holotype. Sample NVG-23103C10, GenBank PQ489700, 658 base pairs:

AACTTTATATTTTATTTTTGGAATTTGAGCAGGTATAATAGGAACATCTCTTAGTTTACTAATTCGAATAGAATTAGGAACTCCTGAATCTTTAATTGGAGATGATCAAATTTATAATACT
ATTGTTACAGCTCATGCATTTATTATAATTTTTTTTATAGTTATACCTATTATAATTGGAGGATTTGGAAATTGATTAGTTCCATTAATATTAGGAGCTCCAGATATAGCTTTCCCCCGTA
TAAATAACATAAGATTTTGATTATTACCTCCTTCTTTATTTTTATTAATCTCCAGAAGAATTGTTGAAAATGGTGCAGGAACTGGATGAACAGTGTACCCCCCACTTTCATCTAATATTGC
TCATAGAGGAACTTCTGTTGATTTAGCCATTTTTTCTCTTCATTTAGCTGGAATTTCATCAATCTTAGGTGCAATTAACTTTATTACTACTATTATTAACATACGTATTAATAATTTATCA
TTTGATCAATTACCTTTATTTGTTTGATCAGTAGGAATTACTGCTCTTCTTCTTTTATTATCATTACCTGTTTTAGCGGGAGCTATTACTATATTACTTACTGATCGAAATTTAAATACAT
CTTTTTTTGATCCTGCAGGAGGTGGAGATCCAATTTTATACCAACATTTATTT

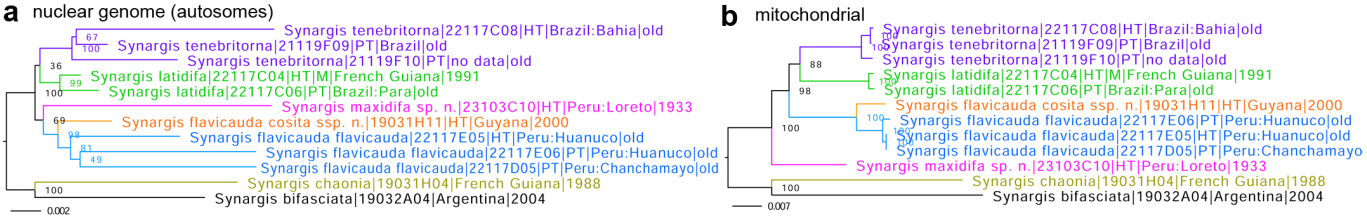

Fig. 8. Phylogenetic trees of selected *Synargis* species constructed from protein-coding regions of **a)** the nuclear (autosomes) and **b)** the mitochondrial genome: *S. tenebritorna* (purple), *S. latidifa* (green), *S. maxidifa* **sp. n.** (magenta), *S. flavicauda cosita* **ssp. n.** (orange), *S. flavicauda flavicauda* (blue), and *S. chaonia* (olive).

Type material. Holotype: ♂ currently deposited in the Senckenberg Naturmuseum, Frankfurt, Germany (SMF), illustrated in Fig. 9a, bears the following three rectangular labels (1st handwritten, others printed), two white: [Pumayacú | Sept · 1933], [DNA sample ID: | NVG-23103C10 | c/o Nick V. Grishin], and one red [HOLOTYPE ♂ | Synargis | maxidifa Grishin].

Type locality. Peru: Loreto Region, Pumayacu.

Etymology. The name is given for the large difference in widths of the discal (very broad) and submarginal (narrow) bands, compared to its relative *S. latidifa*, where the difference is notable: *maxi*[ma]+*dif*[ferenti]*a*, i.e., maximal difference in Latin. The name is treated as an adjective.

Distribution. Currently known only from the holotype collected in the Loreto Region, northeastern Peru.

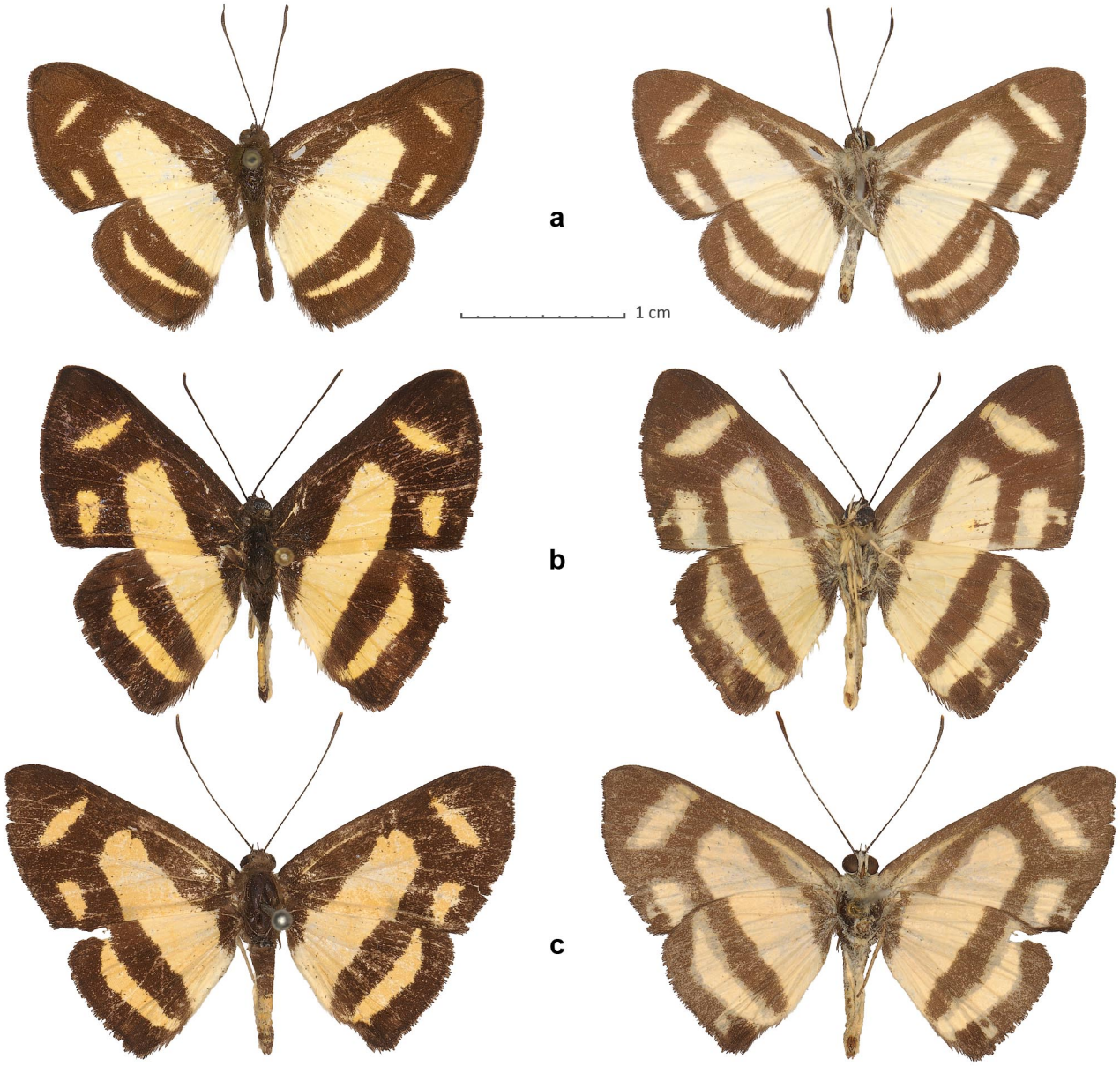

Fig. 9. *Synargis* species in dorsal (left) and ventral (right) views, same scale as in Figs. 7 and 10 above and below and in Figs. 16 and 17 from Zhang et al. (2024), data in text and in Zhang et al. (2024): **a)** *Synargis maxidifa* **sp. n.** holotype ♂ NVG-23103C10 and *Synargis latidifa* ♂♂: **b)** holotype NVG-22117C04 and **c)** paratype NVG-22117C06.

Synargis flavicauda cosita Grishin, new subspecies

http://zoobank.org/5DD01B37-C398-435A-BDC6-F726DBF1F0D6

(Figs. 8 part, 10a, 11)

Definition and diagnosis. A male from Guyana that is sister to other *Synargis flavicauda* Grishin, 2024 (type locality Peru: Rio Pachitea, Monte Alegre) shows moderate genetic differentiation from the Peruvian specimens (Fig. 8), e.g., their COI barcodes differ by 1.5% (10 bp), and therefore represents a new taxon. We conservatively regard it as a subspecies of *S. flavicauda*. This new subspecies is similar to the nominate but differs from it by being darker and smaller overall. In addition, the yellow discal bar on the dorsal forewing does not reach as far into the discal cell and is more rounded anteriad, the outer margin of the yellow discal band on the hindwing is more concave, somewhat angular, and on the ventral side extends into a small tooth along the costal margin, and the outer edge of the yellow postdiscal hindwing band is more sinuous. Due to unexplored phenotypic variation, most reliable identification is achieved by DNA, and a combination of the following base pairs is diagnostic in the nuclear genome:

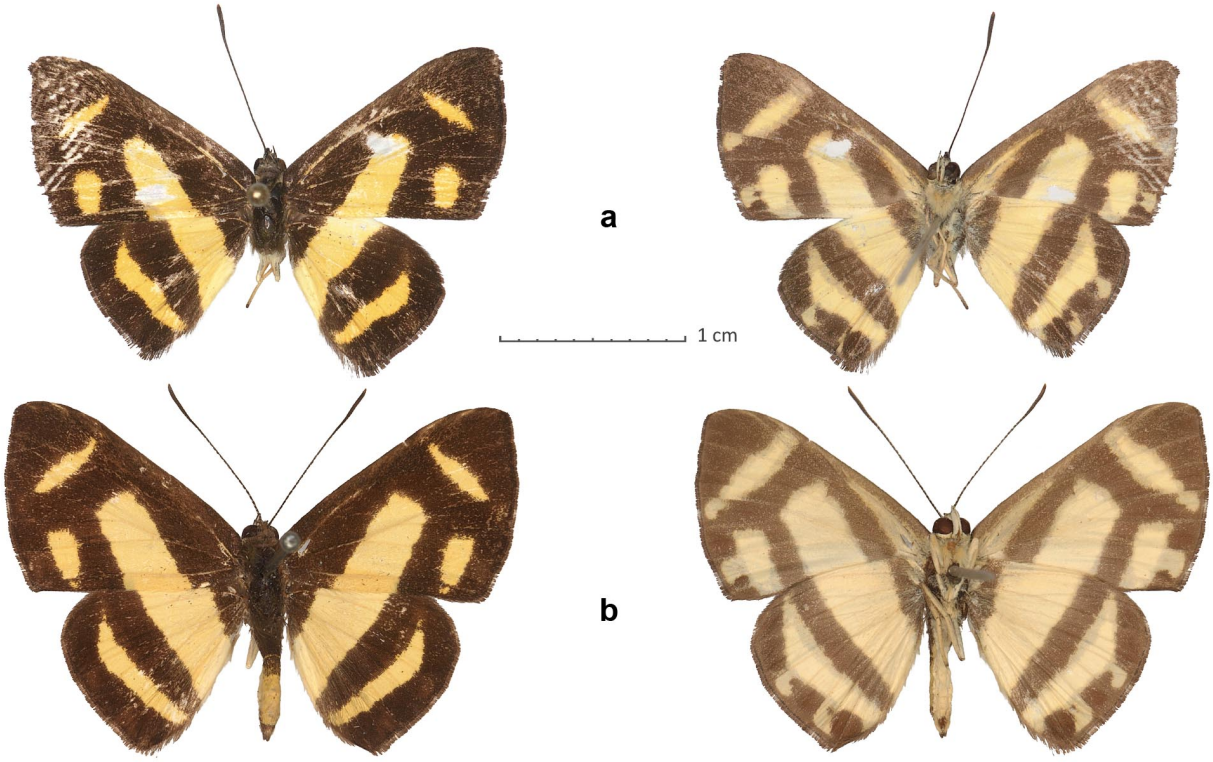

Fig. 10. *Synargis* species in dorsal (left) and ventral (right) views, same scale as in Figs. 7 and 9 above and in Figs. 16 and 17 from Zhang et al. (2024), data in text and in Zhang et al. (2024): **a)** *Synargis flavicauda cosita* **ssp. n.** holotype ♂ NVG-19031H11 and **b)** *S. flavicauda flavicauda* holotype ♂ NVG-22117E05.

cne2447.1.1:A144G, cne2447.1.1:A174T, cne12569.1.1:T2037C, cne12569.1.1:G2049C, cne3335.1.4:A629T, cne6043.2.3:T99T (not C), cne23345.4.2:A228A (not T), cne2811.4.13:A66A (not G), cne2082.8.6:T174T (not C), cne585.4.29:G87G (not A), and COI barcode: A223A, C238T, T250C, 337G, C451T, T542C.

Barcode sequence of the holotype. Sample NVG-19031H11, GenBank PQ489701, 658 base pairs:

AACTTTATATTTTATTTTTGGAATTTGAGCAGGTATAGTAGGAACATCTCTTAGTTTA
CTAATTCGAATAGAATTAGGAACTCCTGGATCTTTAATTGGAGACGATCAAATTTATA
ATACTATTGTTACAGCTCATGCATTTATTATAATTTTTTTTATAGTTATACCTATTAT
AATTGGAGGATTTGGAAACTGATTAGTTCCATTAATATTAGGAGCTCCAGATATAGCT
TTCCCTCGTATAAATAACATAAGATTTTGATTATTACCTCCTTCTTTATTTTTATTAA
TCTCCAGAAGAATTGTTGAAAATGGAGCAGGAACTGGATGAACAGTGTACCCCCCACT
TTCATCTAATATTGCTCATAGAGGAACTTCTGTTGATTTAGCTATTTTTTCTCTTCAT
TTAGCTGGAATTTCATCAATCTTAGGTGCAATTAATTTTATTACTACTATTATTAATA
TACGTATTAATAATTTATCATTTGATCAAATACCTTTATTTATTTGATCAGTAGGAAT
TACTGCTCTTCTTCTTTTACTATCATTACCTGTTTTAGCGGGAGCTATTACTATATTA
CTTACTGATCGAAATTTAAACACATCTTTTTTTGATCCTGCAGGAGGTGGAGATCCAA
TTTTATATCAACATTTATTT

Type material. Holotype: ♂ deposited in the National Museum of Natural History, Smithsonian Institution, Washington, DC, USA (USNM), illustrated in Fig. 10a, (genitalia in Fig. 11) bears the following five printed rectangular labels, 2nd green, last red and others white: [GUYANA: Two Hat Mt, | E.Kanukus, S.Rupununi, | S. Slope summit 850-1200' | 21-28.IX.2000 | 3° 6.8'N 59° 5.9'W | Leg. S.Fratello et al], [GENITALIA No. | 2012: 50♂ | DOLIBAINA], [DNA sample ID: | NVG-19031H11 | c/o Nick V. Grishin], [{QR Code} | USNM ENT 00234162], [HOLOTYPE ♂ | Synargis flavicauda | cosita Grishin].

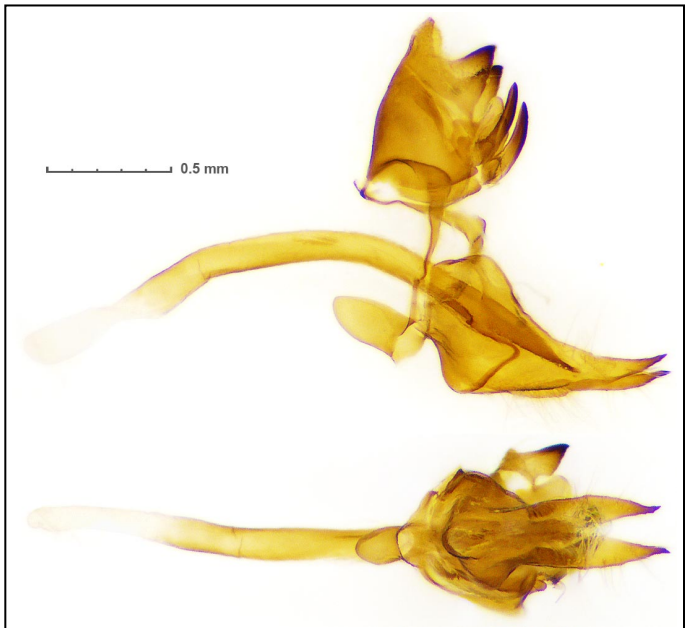

Fig. 11. Genitalia of *Synargis flavicauda cosita* **ssp. n.** holotype in left lateral (above) and ventral (below) views.

Type locality. Guyana: Eastern Kanuku Mountains, Two Hat Mountain south slope summit, elevation 850'–1200', GPS 3.1133, −59.0983.

Etymology. In Spanish, cosita means little thing or little object and refers to a smaller size of this subspecies than many other *Synargis* from the *regulus* group. The name is a noun in apposition.

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

A correction to the sample number of a smaller *Synargis regulus* (Fabricius, 1793)

In Zhang et al. (2024:18), we stated: "However, not all *S. regulus* specimens are that large, and NVG-21119F08 is smaller than an average *S. attilius*," where NVG-21119F08 was given by mistake. NVG-21119F08 refers to the "holotype" of an infrasubspecific name *Nymula regulus regulus* forma *ingens* Stichel, 1925 (from Brazil: Espirito Santo). It is a large specimen with a wingspan of about 42 mm. A smaller specimen is NVG-22117D10, also from Espirito Santo (Leopoldina) [MFNB], and its wingspan is about 34 mm. The number 21119F08 should be corrected to 22117D10. Both specimens are illustrated on the Butterflies of America website (Warren et al. 2024).

Family Hesperiidae Latreille, 1809
Subfamily Eudaminae Mabille, 1877
Tribe Phocidini Tutt, 1906

Bungalotis corentus Grishin, new species

http://zoobank.org/C2A91FBA-F127-421D-AADD-E7413CF65DFC

(Figs. 12 part, 13–14)

Definition and diagnosis. Genomic analysis of *Bungalotis* E. Watson, 1893 (type species *Papilio midas* Cramer, 1775) specimens from western Ecuador reveals that they are sister to *Bungalotis corentinus* (Plötz, 1882) (type locality in Suriname) but are genetically differentiated from it at the species level (Fig. 12), e.g., their COI barcodes differ by 1.7% (11 bp), and therefore represent a new species. This new species keys to "*Bungalotis diophorus*" (D.1.2) in Evans (1952), which is a junior objective synonym of *B. corentinus*, and differs from it by rusty-reddish color of the dorsal side, more red than yellow (is usually yellower in *B. corentinus*), larger spots on wings, discal cell spot on the dorsal hindwing is oval, with brown contour, filled with ground color; some postdiscal spots may be paler in the middle; ventral side is browner, spots are larger on the ventral hindwing and filled with more extensive whitish scaling;

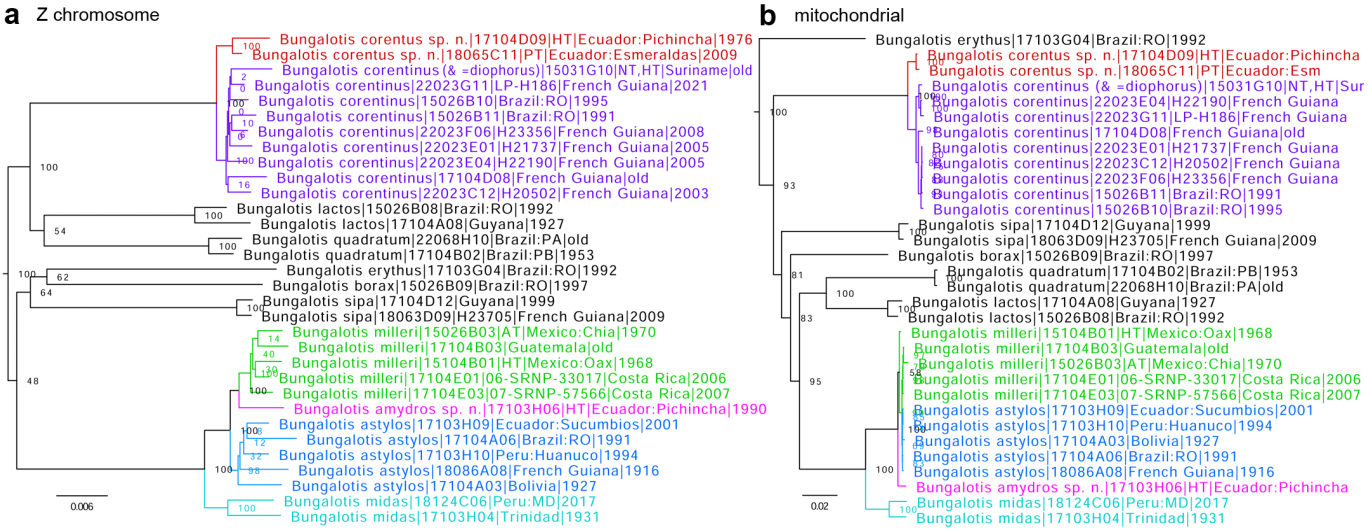

Fig. 12. Phylogenetic trees of *Bungalotis* constructed from protein-coding regions of **a)** the Z chromosome and **b)** the mitochondrial genome: *B. corentus* **sp. n.** (red), *B. corentinus* (purple), *B. milleri* (green), *B. amydros* **sp. n.** (magenta), *B. astylos* (blue), and *B. midas* (cyan).

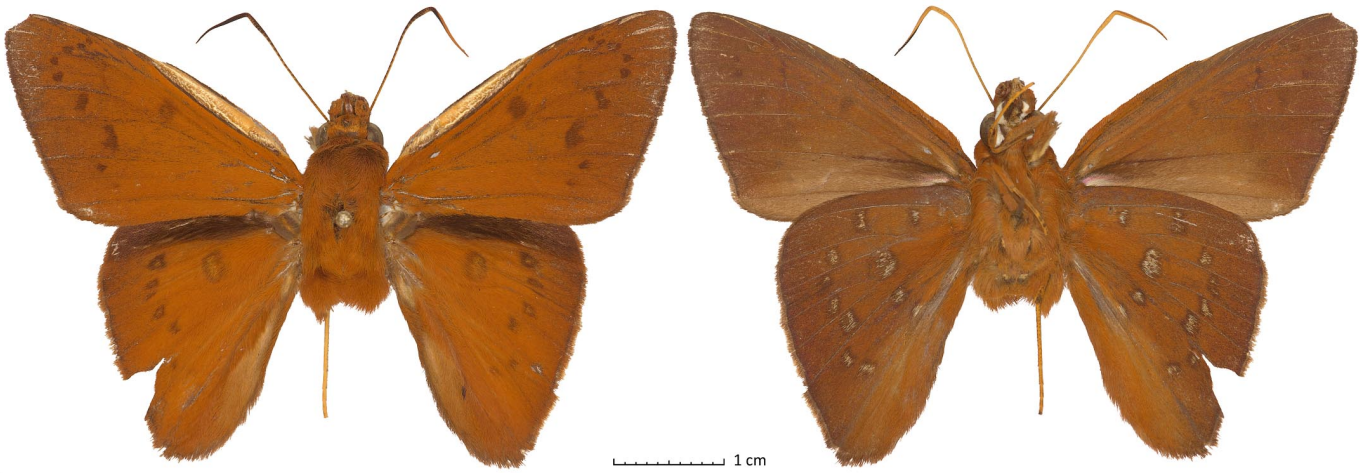

Fig. 13. *Bungalotis corentus* **sp. n.** holotype ♂ NVG-17104D09 in dorsal (left) and ventral (right) views, data in text.

Fig. 14. Male genitalia of *Bungalotis corentus* **sp. n.** holotype NVG-17104D09, vial no. X-5445 J.M.Burns 2003 (data in text) in **a)** left lateral and **b)** dorsal views. Note a bundle of cornuti by the right valva in dorsal view (near top right of the image).

harpe is much longer (1.5–2 times of *B. corentinus*) and the process of the ampulla is broader (Fig. 14). Due to unexplored phenotypic variation of this species, most reliable identification is achieved by DNA, and a combination of the following base pairs is diagnostic in the nuclear genome: aly276665.10.2:A40T, aly349.33.2:A303T, aly349.33.2:A318G, aly666.26.1:C111T, aly3177.6.10:G150A, and COI barcode: A79G, T220C, G316A, T325C, T352C.

Barcode sequence of the holotype. Sample NVG-17104D09, GenBank PQ489702, 658 base pairs:

AACCTTATATTTTATTTTTGGTATTTGAGCAGGAATAATTGGAACTTCATTAAGATTACTAATTCGAACTGAATTAGGGACCCCTGGATCTTTAATTGGAGATGATCAAATTTATAATACT
ATTGTTACTGCCCATGCTTTTATTATAATTTTTTTTATAGTTATACCTATTATAATTGGAGGATTTGGAAATTGATTAGTACCTTTAATATTAGGAGCCCCAGATATAGCATTTCCACGAA
TAAATAATATAAGATTTTGATTATTACCACCTTCATTAACTTTATTAATTTCAAGAAGAATTGTTGAAAATGGAGCTGGTACCGGATGAACAGTATATCCTCCTTTATCCTCAAATATTGC
TCACCAAGGTTCTTCTGTTGATTTAGCAATTTTTTCTCTTCATTTAGCTGGAATTTCATCTATTTTAGGAGCTATTAATTTTATTACAACAATTATTAATATACGAATTAAAAATTTATCT
TTTGATCAAATACCATTATTTGTTTGAGCTGTAGGAATTACAGCAATTTTACTATTACTTTCTTTACCTGTTTTAGCAGGAGCTATTACTATACTTTTAACAGATCGAAATCTTAATACTT
CATTTTTTGATCCTGCAGGAGGAGGAGATCCAATTTTATATCAACATTTATTT

Type material. Holotype: ♂ deposited in the National Museum of Natural History, Smithsonian Institution, Washington, DC, USA (USNM), illustrated in Fig. 13 (genitalia in Fig. 14), bears the following seven rectangular labels (4th handwritten others printed with handwritten text shown in italics), six white: [Alluriquin 700m | PICHINCHA ECUADOR | *11 Sept. '76* | S. S. Nicolay], [*Bungalotis* | *clusia* ♂ | Det. *E.* | S.S. Nicolay], [GENITALIA NO. | X-54 45 | J.M.Burns 2003], [LIKE ACG NOT- | diophorus ♂ USNM], [DNA sample ID: | NVG-17104D09 | c/o Nick V. Grishin], [USNMENT | {QR Code} | 00913870], and one red [HOLOTYPE ♂ | Bungalotis | corentus Grishin]. **Paratype:** 1♂ NVG-18065C11 Ecuador: Esmeraldas, 500-800 m, Apr-2009, ex coll. M. Büche [EBrockmann].

Type locality. Ecuador: Pichincha Province, Alluriquín, elevation 700 m.

Etymology. The name is formed from the name of its sister species *B. corentinus*, made shorter for its new more western relative. The name is treated as a masculine noun in apposition.

Distribution. Currently known only from western Ecuador.

Bungalotis amydros Grishin, new species

http://zoobank.org/18FC50D7-3808-49C3-94B4-A165637BA641

(Figs. 12 part, 15–16)

Definition and diagnosis. Genomic analysis of a specimen from Ecuador superficially similar to *Bungalotis astylos* (Cramer, 1780) (type locality in Suriname) in having ventrally brown palpi and cheeks reveals that it is sister to *Bungalotis milleri* H. Freeman, 1977 (type locality in Mexico: Oaxaca), which is a Central American species, but is genetically differentiated from it at the species level (Fig. 12), thus representing a new species. In mitochondrial DNA, the three species (*B. milleri*, *B. astylos*, and the new one) are not strongly differentiated from each other, although in our tree, the new species is sister to both *B. milleri* and *B. astylos*. The new species keys (incompletely) to *Bungalotis astylos* (D.1.4) in Evans (1952) and is most similar to *Bungalotis milleri*, with the description by Freeman (1977) applicable to the male of the new species, except as stated below. In contrast to *B. milleri* (see Freeman 1977), the new species possesses a ray of shiny-blue scales by the costa of the dorsal hindwing (Fig. 15 bottom) characteristic of *B. astylos*, *Bungalotis midas* (Cramer, 1775) (type locality in Suriname), and *Bungalotis aureus* Austin, 2008 (type locality in Ecuador), and shares with *B. astylos* ventrally tawny-brown palpi and cheeks (except some white scales along the cheeks' posterior). The new species differs from *B. milleri* and *B. astylos* by being darker and having browner ground color; in particular, the yellow area in the posterior part of the ventral forewing is smaller, does not reach past the postdiscal spots and vein CuA_1, and is more clearly separated from brown ground color. Due to the cryptic nature of this species and unexplored phenotypic variation, most reliable identification is achieved by DNA, and a combination

Fig. 15. *Bungalotis amydros* **sp. n.** holotype ♂ NVG-17103H06 in dorsal (top left) and ventral (top right) views, data in text. Photographs at the bottom are taken at varying angles to reveal shiny blue scales along the costal margin of the hindwing.

Fig. 16. Genitalia of *Bungalotis amydros* **sp. n.** holotype ♂ NVG-17103H06 in left lateral (left) and dorsal (right) views.

of the following base pairs is diagnostic in the nuclear genome: aly6841.81.1:C454T, aly6841.81.1:G498A, aly1139.51.7:T43G, aly2284.27.1:T39A, aly2284.27.1:G44A, aly2954.3.1:A771A (not C), aly1409.11.16: C73C (not T), aly2101.22.3:C114C (not G), aly2101.22.3:C117C (not T), aly398.2.3:C66C (not T), and COI barcode: T133C, T340C, A622A, T646C (the barcode may not offer reliable identification on a larger sample of specimens).

Barcode sequence of the holotype. Sample NVG-17103H06, GenBank PQ489703, 658 base pairs:

AACATTATATTTTATTTTTGGTATTTGAGCAGGTATAATTGGAACTTCATTAAGATTACTAATTCGAACTGAATTAGGTACCCCCGGATCTTTAATTGGAGATGATCAAATTTATAATACT
ATTGTTACTGCCCATGCTTTTATTATAATTTTTTTTATAGTTATACCTATTATAATTGGAGGATTTGGAAATTGATTAGTACCATTAATATTAGGAGCTCCTGACATAGCTTTTCCTCGAA
TAAATAACATAAGATTTTGATTATTACCCCCTTCTTTAACTTTATTAATTTCAAGAAGAATTGTTGAAAATGGTGCTGGTACTGGTTGAACAGTTTACCCACCATTATCTACTAATATTGC
TCATCAAGGATCTTCTGTTGATTTAGCAATTTTTTCTTTACATTTAGCTGGTATTTCATCTATTTTAGGAGCTATTAATTTTATTACAACAATTATCAATATACGAATTAGAAATTTATCT
TTTGATCAAATACCATTATTTATTTGAGCTGTAGGAATTACAGCAATCTTATTATTATTATCATTACCTGTATTAGCAGGAGCTATTACTATACTTTTAACAGATCGAAATCTTAATACTT
CATTCTTTGATCCTGCAGGAGGAGGAGATCCAATTTTATACCAACATTTATTTT

Type material. Holotype: ♂ deposited in the National Museum of Natural History, Smithsonian Institution, Washington, DC, USA (USNM), illustrated in Fig. 15 (genitalia in Fig. 16), bears the following six rectangular labels (2nd and 3rd handwritten, others printed with handwritten text shown in italics), five white: [ECUADOR: Pichincha | Tinalandia, 600m, 16km | E Santo Domingo de los | Colorados *18–22* Apr '90 | leg. Brian Harris], [Bungalotis | midas], [Collected at | mercury | vapor light!], [DNA sample ID: | NVG-17103H06 | c/o Nick V. Grishin], [DNA sample ID: | NVG-23116D05 | c/o Nick V. Grishin], [USNMENT | {QR Code} | 00913817], and one red [HOLOTYPE ♂ | Bungalotis | amydros Grishin]. The first DNA sample refers to the extraction from a leg, and the second is from the abdomen prior to genitalia dissection.

Type locality. Ecuador: Pichincha Province, 16 km east of Santo Domingo, Tinalandia, elevation 600 m.

Etymology. In Greek, αμυδρός (amydros) means dim or faint and refers to reduced orange areas in this species compared to its relatives. The name is a noun in apposition.

Distribution. Currently known only from the holotype collected in the western slopes of the Andes in northern Ecuador.

Salatis pelignus (Hewitson, 1867) is a species distinct from *Salatis salatis* (Stoll, 1782)

Genomic analysis reveals that a specimen of *Salatis* Evans, 1952 (type species *Papilio salatis* Stoll, 1782) from Southeast Brazil, together with another specimen from an unknown locality (possibly from around Rio de Janeiro, Brazil), are genetically differentiated from others at the species level in the Z chromosome (Fig. 17a) with F_{st}/G_{min} of 0.34/0.00, although not differing significantly in the mitochondrial genome (Fig. 17b). Thus, these two specimens represent a species distinct from *Salatis salatis* (Stoll, 1782) (type locality in Suriname), and the name *Eudamus pelignus* Hewitson, 1867 (type locality in Brazil: Rio de Janeiro) applies to them judging by the locality and phenotypic similarity. Therefore, we propose that *Salatis pelignus* (Hewitson, 1867), **stat. rest.** is a species distinct from *Salatis salatis* (Stoll, 1782). Furthermore, we suggest, pending further examination of their primary type specimens, to treat two other taxa with the southern distribution, i.e., *Eudamus sebrus* C. Felder & R. Felder, 1867 (type locality in Brazil: Bahia) and *Bungalotis sapucayae* Jörgensen, 1935 (type locality in Paraguay: Sapucaí), as junior subjective synonyms of *Salatis pelignus* (Hewitson, 1867), **stat. rest.** and not of *S. salatis*.

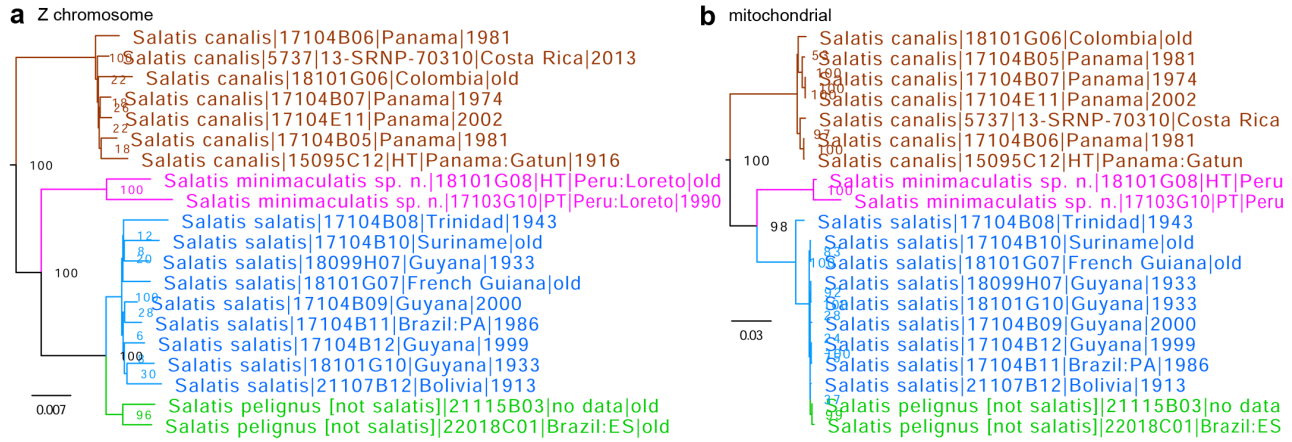

Fig. 17. Phylogenetic trees of *Salatis* species inferred from protein-coding regions of **a)** the Z chromosome and **b)** the mitochondrial genome. Different species are shown in different colors: *S. canalis* (Skinner, 1920) (brown), *S. minimaculatis* **sp. n.** (magenta), *S. salatis* (blue), and *S. pelignus* **stat. rest.** (green).

Salatis minimaculatis Grishin, new species

http://zoobank.org/8789C473-7A6E-4E19-8D3F-3D929CD940D8

(Figs. 17 part, 18–19)

Definition and diagnosis. Genomic analysis of *Salatis* Evans, 1952 (type species *Papilio salatis* Stoll, 1782) specimens from Loreto Region in Peru reveals that while being sister to *Salatis salatis* (Stoll, 1782)

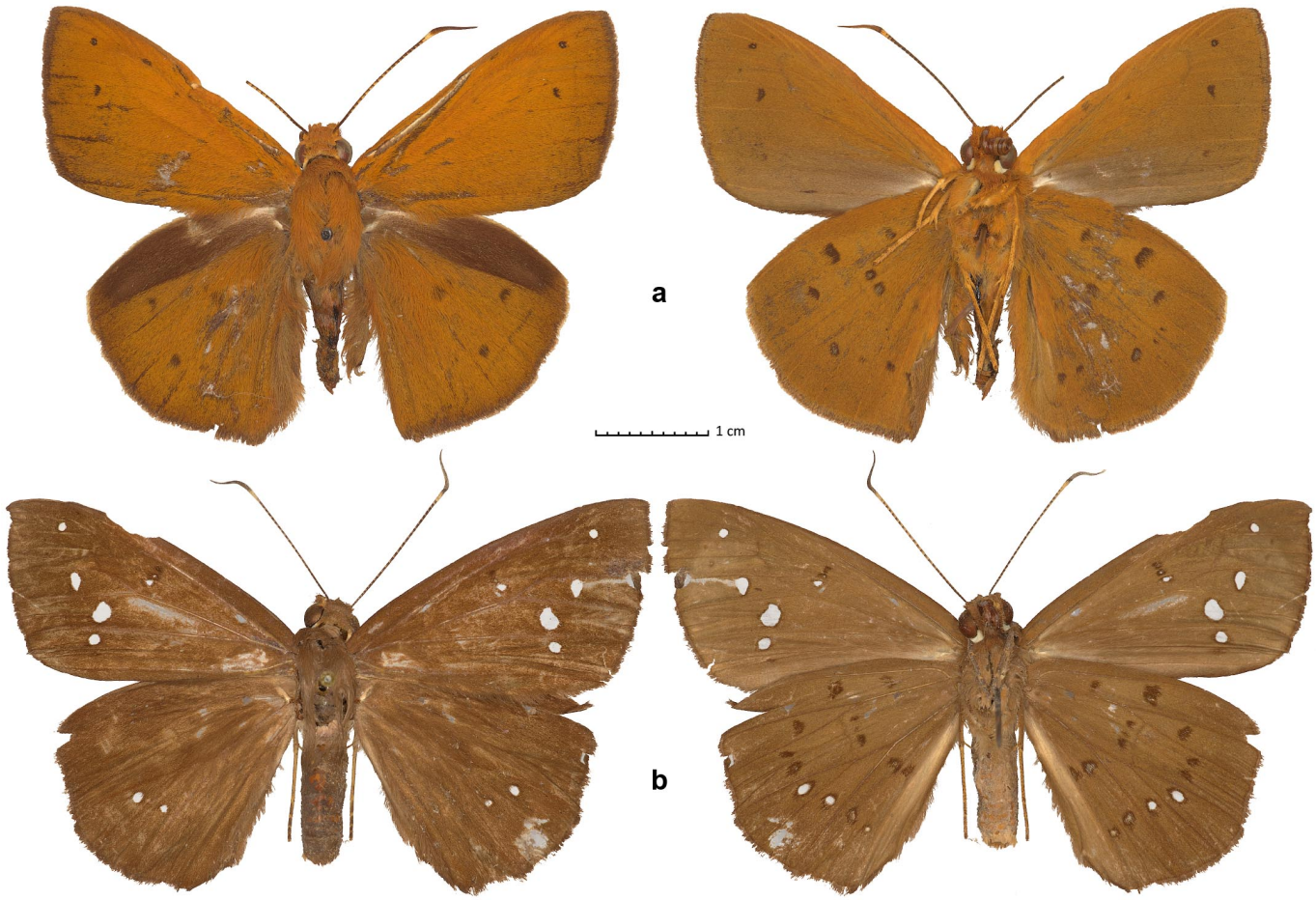

Fig. 18. *Salatis minimaculatis* **sp. n.** type series: **a)** holotype ♂ NVG-18101G08 and **b)** paratype ♀ NVG-17103G10 in dorsal (left) and ventral (right) views, data in text.

(type locality in Suriname), they are most strongly differentiated genetically from it (Fig. 17), i.e., their COI barcodes differ by 4.4% (29 bp). Therefore, these specimens represent a distinct species that is new because taxa treated as junior subjective synonyms of *S. salatis*, i.e., *Eudamus gonatas* Hewitson, 1867 (type locality in Brazil: Pará, Tapajós) and *Telegonus ophiuchus* Plötz, 1882 (type locality in Suriname) are phenotypically different from it in having larger spots in both sexes. This new species keys to *Salatis salatis* (D.2.2) in Evans (1952) and differs from it by smaller spots in both sexes: the male is mostly rusty-orange, with only small brown spots, not pupillated with pale scales (except some larger spots on the ventral hindwing), and the female is with much smaller hyaline spots, especially the spot in the forewing discal cell is much reduced and is the smallest of all forewing spots, divided into three: the upper one is brown, the central is pupillated with a tiny hyaline dot, and the lowest is larger and mostly hyaline. Due to unexplored phenotypic variation, it is unclear whether these phenotypic characters will hold in all specimens. While we expect the specimens of this species to be mostly less patterned than *S. salatis*, mainly due to consistently reduced spotting in both male and female of the type series, most reliable identification is achieved by DNA, and a combination of the following base pairs is diagnostic in the nuclear genome: aly1379.16.2:C96T, aly536.13.6:A162G, aly536.13.6:G183A, aly2178.10.1:G45A, aly2178.10.1:T109A, and COI barcode: T25C, C50T, T127C, A217G, A268G, T277C.

Fig. 19. Female genitalia of *Salatis minimaculatis* **sp. n.** paratype NVG-17103G10, NVG-23125F08 (data in text) in ventral (left) and right ventrolateral (right) views.

Barcode sequence of the holotype. Sample NVG-18101G08, GenBank PQ489704, 658 base pairs:

AACATTATATTTTATTTTTGGAATCTGAAGAGGTATATTAGGAACTTCTTTAAGATTATTAATTCGAACTGAATTAGGAACTCCTGGATCTTTAATTGGAGATGATCAAATTTATAATACA
ATTGTCACAGCTCATGCCTTTATTATAATTTTTTTTATAGTAATACCTATTATAATTGGAGGATTTGGTAATTGATTAGTTCCTTTAATATTAGGGGCCCCTGATATAGCTTTTCCACGAA
TAAATAATATAAGATTTTGATTATTGCCCCCTTCCTTAACTTTATTAATTTCAAGAAGAATCGTAGAAAATGGTGCTGGAACAGGTTGAACAGTTTATCCTCCTTTATCTGCTAATATTGC
TCACCAGGGATCTTCTGTTGATTTAGCAATTTTCTCCCTTCATTTAGCCGGAATTTCTTCTATTTTAGGAGCTATTAATTTTATTACAACAATTATTAATATACGTATTAGAAATTTATCT
TTTGACCAAATACCATTATTCATTTGAGCTGTTGGAATTACAGCAATTTTATTATTAATTTCTTTACCTGTATTAGCTGGAGCTATTACTATACTTTTAACTGATCGAAATCTTAATACTT
CATTTTTTGATCCTGCAGGAGGAGGTGATCCAATTTTATATCAACATTTATTC

Type material. Holotype: ♂ deposited in the American Museum of Natural History, New York, NY, USA (AMNH), illustrated in Fig. 18a, bears the following four rectangular labels (1st handwritten, others printed), three white: [Yurimaguas | Huallaye River | Peru], [G819] (this is its genitalia slide number), [DNA sample ID: | NVG-18101G08 | c/o Nick V. Grishin], and one red [HOLOTYPE ♂ | Salatis | minimaculatis Grishin]. The genitalia slide has not been located and will be illustrated when found. **Paratype:** 1♀: NVG-17103G10 (leg sample), NVG-23125F08 (abdomen extraction followed by genitalia dissection) Peru, Loreto Region, 50 mi E of Iquitos, Amazon River, Explorama Lodge, 200 m, 12-16-Sep-1990, Ron Leuschner leg. [USNM] (Fig. 18b, genitalia in Fig. 19).

Type locality. Peru: Loreto Region, Yurimaguas, Huallaga River.

Etymology. In Latin, *minimus* means smallest or least significant, and *maculatis* means spotted or stained. The name is given for the reduced spotting in both sexes of this species and is the perfect passive participle in the nominative singular.

Distribution. Currently known only from the Loreto Region in northeastern Peru.

Cecropterus markwalkeri Grishin, 2023 is widely distributed in western and southern Mexico

Genomic sequencing of specimens from multiple localities reveals that *Cecropterus* (*Murgaria*) *markwalkeri* Grishin, 2023 (type locality in Mexico: Sonora) is widely distributed in western and southern Mexico along Sierra Madre Occidental and Sierra Madre del Sur, while its sister *Cecropterus* (*Murgaria*) *albociliatus* (Mabille, 1877) (type locality in Colombia, Panama, and Guatemala) is an eastern and southern species (Figs. 20–21). The two species may be sympatric in Oaxaca, Mexico. Judging from the distribution of sequenced specimens (Fig. 20), it is most likely that the records of "*Achalarus albociliatus*" from south-eastern Arizona, USA, e.g., by Roever (2006), refer to *C.* (*M.*) *markwalkeri*.

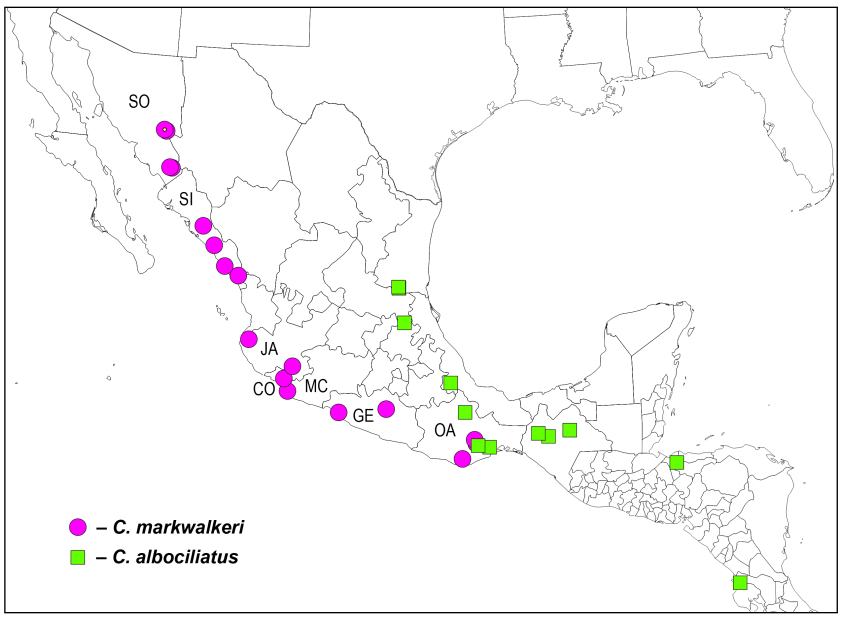

Fig. 20. A map of sequenced specimens of *C. markwalkeri* (magenta circles, the type locality is marked with a tiny white circle, Mexican states with records are labeled with two-letter codes) and *C. albociliatus albociliatus* (green squares).

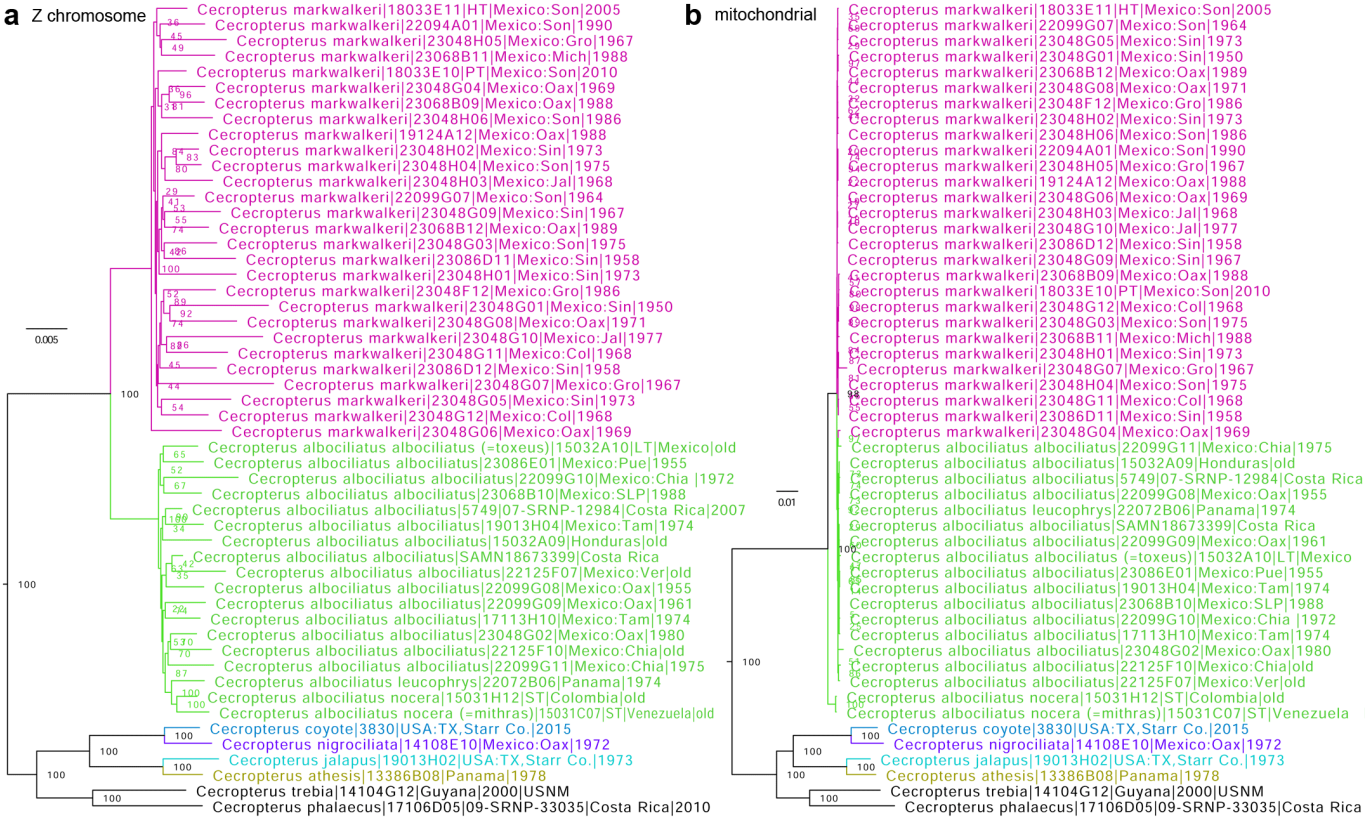

Fig. 21. Phylogenetic trees of selected *Cecropterus* (*Murgaria*) species inferred from protein-coding regions of **a)** the Z chromosome, and **b)** the mitochondrial genome: *C. markwalkeri* (magenta), *C. albociliatus* (green), *C. coyote* (Skinner, 1892) (blue), *C. nigrociliata* (Mabille & Boullet, 1912) (purple), *C. jalapus* (Plötz, 1881) (cyan), and *C. athesis* (Hewitson, 1867) (olive). The sequence of SAMN18673399 is taken from the alignment provided in Kawahara et al. (2023).

Subfamily Tagiadinae Mabille, 1878
Tribe Tagiadini Mabille, 1878

On the lectotype of *Achlyodes cnidus* Plötz, 1884

As we demonstrated recently (Zhang et al. 2024), *Achlyodes cnidus* Plötz, 1884 (type locality not specified) is a valid species of *Gerosis* Mabille, 1903 (type species *Coladenia hamiltoni* Nicéville, 1889, which is a junior subjective synonym of *Satarupa phisara* (Moore, 1884)) with its nomenclature stabilized by the lectotype designation. Here, we illustrate the genitalia of the lectotype (Fig. 22) and, before dissection, extracted DNA from its abdomen (NVG-23075D07, sequence dataset combined with NVG-21115E07 from a leg) to improve the genomic dataset that is now used in the three phylogenetic

Fig. 22. Genitalia of *Gerosis cnidus* (Plötz, 1884) lectotype ♂ in different views: **a)** left lateral, **b)** right lateral, **c)** posterior, **d)** dorsal, **e)** ventral, **f)** right posterolateral. Note slightly asymmetrical valvae, strongly asymmetrical aedeagus bent in the lateral direction, and expanded juxta shaped like a broad leaf of an *Agave* plant.

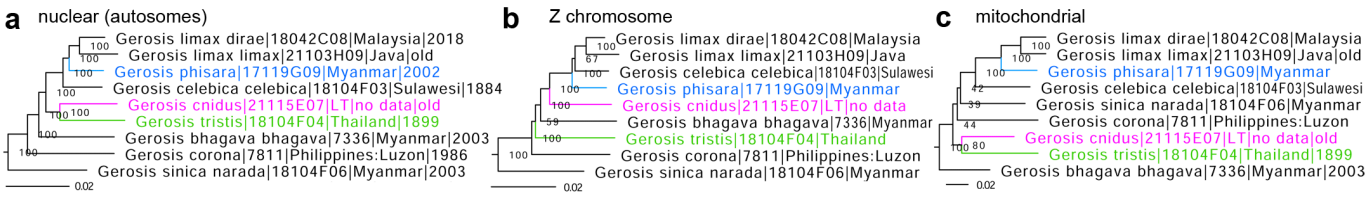

Fig. 23. Phylogenetic trees of selected *Gerosis* species inferred from protein-coding regions in **a)** the nuclear genome (autosomes), based on 7,793,238 positions, **b)** the Z chromosome, based on 217,887 positions, and **c)** the mitochondrial genome. Ultrafast bootstrap (Minh et al. 2013) values are shown at nodes, and three species are colored: *G. phisara* (blue), *G. cnidus* (magenta), and *G. tristis* (Eliot, 1959) (green).

trees of *Gerosis* shown in Fig. 23. The COI barcode sequence of the lectotype, sample NVG-21115E07, GenBank PQ489705, 658 base pairs is:

AACTCTATATTTTATTTTTGGAATTTGAGCAGGAATAGTGGGAACTTCTCTTAGTTTATTAATTCGAACTGAATTAGGAAACCCTGGATCTTTAATTGGAGATGATCAAATTTATAATACT
ATCGTAACAGCTCATGCTTTTATTATAATTTTTTTTATAGTTATACCTATTATAATTGGAGGATTTGGAAATTGACTTGTTCCATTAATATTAGGAGCACCTGATATAGCCTTCCCACGAA
TAAATAACATAAGATTTTGATTATTACCTCCATCTCTTACTCTTTTAATTTCTAGAAGTATCGTAGAAAACGGTTCAGGAACTGGTTGAACTGTTTACCCCCCTTTATCTTCTAATATTGC
TCATCAAGGAGCTTCTGTTGACTTAGCTATTTTTTCATTACATTTAGCTGGTATTTCTTCTATTTTAGGAGCAATTAATTTTATTACTACTATTATTAACATACGAATTAAAAATTTATCT
TTTGACCAAATACCTTTATTTGTTTGAGCTGTAGGAATTACAGCATTATTACTTCTTCTTTCACTTCCAGTTTTAGCAGGTGCTATTACAATATTATTAACAGATCGTAATCTTAATACAT
CATTTTTTGATCCTGCAGGAGGAGGAGATCCAATTTTATATCAACATTTATTT

Subfamily Pyrginae Burmeister, 1878
Tribe Carcharodini Verity, 1940

Mycteris caerula Mabille, 1877 is a junior subjective synonym of *Pellicia* (*Mictris*) *crispus* Herrich-Schäffer, 1870

Genomic analysis of a syntype of *Pellicia crispus* Herrich-Schäffer, 1870 (type locality in Venezuela, sequenced as NVG-15032D09) places it among specimens with metallic-blue posterior third of ventral hindwing (not pale brown with violet sheen) and therefore identified as *Pellicia* (*Mictris*) *crispus caerula* (Mabille, 1877) (type locality in Colombia) (Fig. 24). A more careful inspection of the syntype reveals the metallic-blue hindwing pattern, although both hindwings are folded inward to cover most of it. Therefore, the syntype of *P. crispus* is genetically and phenotypically similar to *P. crispus caerula* and not to specimens traditionally associated with the name *P. crispus crispus*, and thus is conspecific with the former and not with the latter.

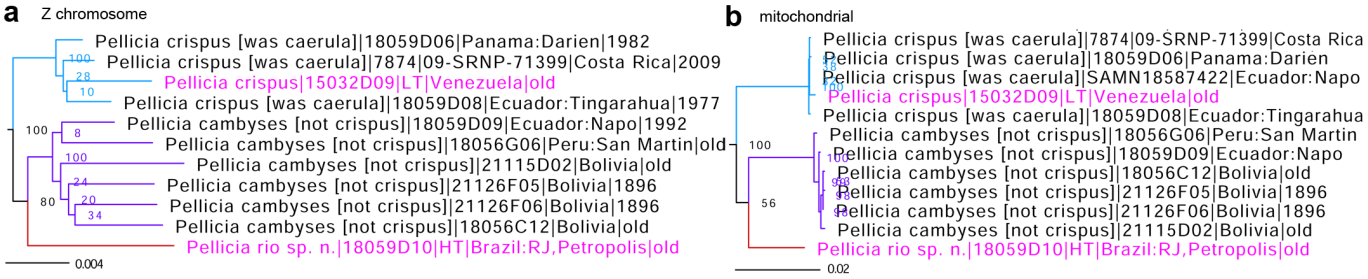

Fig. 24. Phylogenetic trees of *Pellicia* (*Mictris*) constructed from protein-coding regions in **a)** the Z chromosome and **b)** the mitochondrial genome: *P. rio* **sp. n.** (red), *P. crispus* (blue), and *P. cambyses* (purple). Primary type specimens are labeled in magenta. The mitochondrial sequence of SAMN18587422 is taken from the alignment provided in Kawahara et al. (2023).

This syntype is the only one we were able to locate, but it agrees with the original description (Herrich-Schäffer 1870), comes from Herrich-Schäffer's collection, and bears an identification label in Herrich-Schäffer's handwriting "crispus m", where 'm' stands for 'mihi' (Latin for 'of me'), placed after a species name as an attribution of the new species to the writer. This notation was common over a century ago, instead of the author's name being written directly. This 'm' corroborates that the label was written by Herrich-Schäffer and offers additional evidence that this specimen is a syntype. Furthermore, the original description of *P. crispus* specifically mentions the shiny blue colors on the ventral hindwing, translated as "beneath dark reddish brown with a violet shimmer, especially on the inner margin half of all wings." Furthermore, Godman's (1907) copy (in BMNH) of Plötz's drawing t[afel]. 204, most likely depicting Herrich-Schäffer's syntype of *P. crispus*, shows the posterior half of the ventral hindwing violet-blue, not brownish with bands and spots. Finally, the illustration of *P. crispus* in Draudt (1921–1924), which is possibly a copy of Plötz's unpublished drawing, also shows a violet-blue tornal section of the ventral hindwing, not brown. For all these reasons, we conclude that we found and sequenced a true syntype of *P. crispus* and propose that *Mycteris caerula* Mabille, 1877, **syn. nov.** is a junior subjective synonym of *Pellicia* (*Mictris*) *crispus* Herrich-Schäffer, 1870.

To stabilize nomenclature and define the name *P. crispus* objectively, N.V.G. hereby designates a syntype in the MFNB collection that bears the following seven labels (1st purple, others white; 2nd, 4th,

and 5th handwritten, others printed with handwritten text shown in italics): [Origin.], [crispus m], [Coll. H.—Sch | *Venezuela*], [Mycteris | Crispa | HS.], [Crispus | H-Sch.], [{QR Code} http://coll. mfn-berlin.de/u/ | 940b8c], [DNA sample ID: | NVG-15032D09 | c/o Nick V. Grishin] as the **lectotype** of *Pellicia crispus* Herrich-Schäffer, 1870. The 2nd and the 4th labels are in Herrich-Schäffer's and Staudinger's handwriting, respectively. The word "Venezuela" on the 3rd label is in the handwriting of the 5th label and, therefore, was probably added later during subsequent curation of the collection. The lectotype has the right hindwing with a segment at the outer margin torn away, and both hindwings are partly folded at the tornus and inner margin. Images of this specimen photographed by B. Hermier are shown on the Butterflies of America website (Warren et al. 2024). The COI barcode sequence of the lectotype, sample NVG-15032D09, GenBank PQ489706, 658 base pairs is:

AACTTTATACTTTATCTTTGGAATTTGATCAGGAATAGTAGGAACATCATTAAGATTACTTATTCGATCTGAATTAGGTACGCCTGGATCTTTAATTGGAGATGATCAAATTTATAATACT
ATTGTAACAGCTCATGCTTTTATTATAATTTTTTTTATAGTTATACCTATCATAATTGGAGGATTCGGAAATTGATTAGTGCCTCTTATGTTAGGAGCTCCTGATATAGCTTTCCCCCGAA
TAAATAATATAAGATTTTGATTATTACCCCCCTCTCTTACATTACTAATTTCAAGAAGTATTGTAGAAAATGGTGCTGGAACAGGTTGAACAGTTTATCCCCCTTTATCTGCTAATATTGC
CCATCAAGGTTCTTCAGTTGATTTAGCTATTTTCTCTTTACATTTAGCAGGTATTTCATCTATTTTAGGTGCTATTAATTTTATTACAACCATTATCAATATACGAATTAATAAATTATTA
TTTGATCAAATACCTTTATTTATTTGAGCAGTAGGAATTACAGCTTTACTTTTATTATTATCTCTTCCAGTTTTAGCTGGAGCTATTACCATACTTTTAACTGATCGTAATTTAAATACAT
CTTTTTTCGACCCTGCTGGAGGAGGTGATCCAATTTTATATCAACATTTATTT

Pellicia (*Mictris*) *cambyses* Hewitson, 1878 is a valid species distinct from of *Pellicia* (*Mictris*) *crispus* Herrich-Schäffer, 1870

Genomic analysis reveals that specimens with brownish ventral hindwing are genetically differentiated from *Pellicia* (*Mictris*) *crispus* Herrich-Schäffer, 1870 (type locality in Venezuela) characterized by metallic-blue posterior third of ventral hindwing are genetically differentiated from each other at the species level (Fig. 24), e.g., their COI barcodes differ by 2.6% (17 bp). The name *P. crispus* was previously misapplied to the species with brown hindwing, and the oldest name applicable to this species is *Arteurotia cambyses* Hewitson, 1878 (type locality in Bolivia). Therefore, we propose that *Pellicia* (*Mictris*) *cambyses* Hewitson, 1878, **stat. rest.** is a valid species distinct from *Pellicia* (*Mictris*) *crispus* Herrich-Schäffer, 1870. Due to phenotypic similarities, *Pellicia pericles* Mabille, 1903 (type locality in Bolivia) is a junior subjective synonym of *Pellicia* (*Mictris*) *cambyses* Hewitson, 1878, **stat. rest**. and not of *Pellicia* (*Mictris*) *crispus* Herrich-Schäffer, 1870.

Pellicia (*Mictris*) *rio* Grishin, new species

http://zoobank.org/83EF1B93-BD7C-4CB3-A2F3-82E783A8E1E6

(Figs. 24 part, 25, 26a–c)

Definition and diagnosis. Genomic analysis reveals that a specimen from Southeast Brazil identified as *Pellicia* (*Mictris*) *cambyses* (Hewitson, 1878) (type locality in Bolivia) is genetically differentiated from it at the species level (Fig. 24), e.g., their COI barcodes differ by 2.1% (14 bp), and therefore represents a new species. This new species keys to "*Mycteris crispus crispus*" (E.15.(b)) in Evans (1953) and was included in this taxon. It differs from its relatives by a combination of the following characters: the hindwing beneath is paler in the posterior half but without the glittering overscaling of *Pellicia crispus* Herrich-Schäffer, 1870 (type locality in Venezuela), and paler areas are broader than in a typical *P. cambyses*, including paler area right at the forewing tornus beneath; a postdiscal band of glittering spots on the dorsal hindwing is closer to the outer wing margin towards apex than in *P. cambyses*, in which the band bends stronger towards the base between the vein CuA_1 and the costal margin; harpes are less robust, shorter, and stronger curved dorsad (Fig. 26a–c) than in *P. cambyses*, in which the left harpe is distally expanded and the right harpe is narrower (Fig. 26d–f), and the spiculose expansion on the right ampulla is not curving inward dorsally at its base as in *P. cambyses* (Fig. 26c, f). Due to unexplored phenotypic variation in this species, most reliable identification is achieved by DNA, and a combination of the following base pairs is diagnostic in the nuclear genome: aly2275.10.10:C144T, aly1454.4.1:T222C, aly1454.4.1:A237T, aly1454.4.1:A267G, aly1454.4.1:A270G, aly279231.1.1:C117C (not T), aly13198.5.4: C48C (not T), aly3312.1.2:A189A (not G), aly1454.4.1:C261C (not A), aly164.12.1:T2079T (not C), and COI barcode: G82A, T124C, A127T, T145C, T407C, T499C.

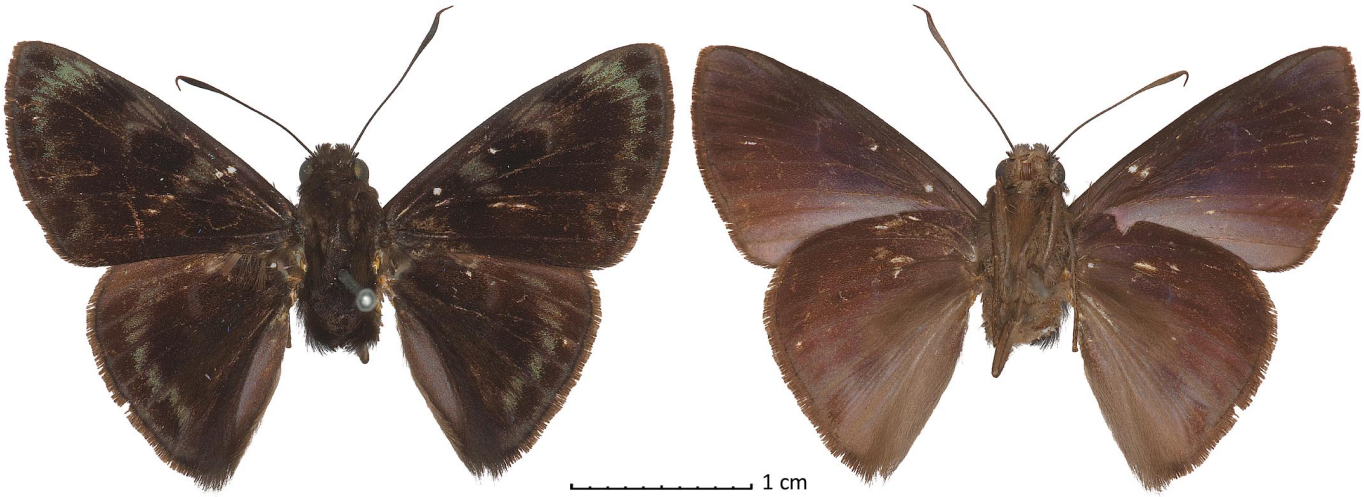

Fig. 25. *Pellicia* (*Mictris*) *rio* **sp. n.** holotype ♂ NVG-18059D10 in dorsal (left) and ventral (right) views, data in text.

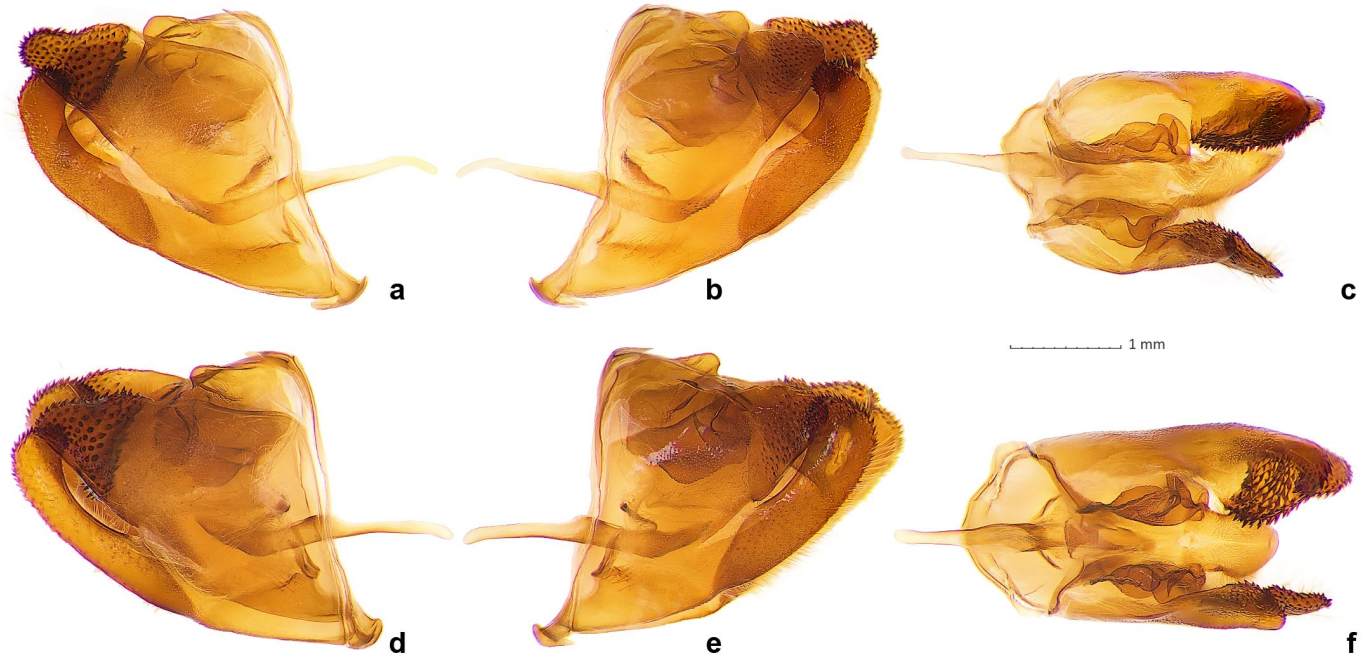

Fig. 26. Male genitalia of *Pellicia* (*Mictris*): **a–c)** *P.* (*M.*) *rio* **sp. n.** holotype NVG-18059D10, vial no. X-5777 J.M.Burns 2004 (data in text) and **b–f)** *P.* (*M.*) *cambyses* **stat. rest.** NVG-18059D09, vial no. X-5776 J.M.Burns 2004, Ecuador, Napo, Jatun Sacha Biological Station, 12-Nov-1992, S. S. Nicolay leg. [USNM] in different views: **a**, **d)** right lateral, **b**, **e)** left lateral, and **c**, **f)** dorsal.

Barcode sequence of the holotype. Sample NVG-18059D10, GenBank PQ489707, 658 base pairs:

AACTTTATACTTTATTTTTGGAATTTGATCAGGAATAGTAGGAACATCATTAAGATTACTTATTCGATCTGAATTAGGTACACCTGGATCTTTAATTGGAGATGATCAAATTTATAATACT
ATCGTTACAGCTCATGCTTTTATCATAATTTTTTTTATAGTTATACCTATCATAATTGGAGGATTCGGAAATTGATTAGTACCCCTTATATTAGGAGCCCCTGATATAGCTTTTCCCCGAA
TAAATAACATAAGATTTTGATTATTACCCCCCTCTCTTACATTATTAATTTCAAGAAGTATTGTAGAAAATGGTGTTGGAACAGGTTGAACAGTTTATCCCCCTTTATCTGCTAATATTGC
TCACCAAGGTTCTTCAGTTGATTTAGCTATTTTCTCTTTACATCTAGCAGGTATTTCATCTATTTTAGGTGCTATTAATTTTATTACAACCATTATTAATATACGAATTAATAATTTATTA
TTTGATCAAATACCCTTATTCATTTGAGCAGTAGGAATTACAGCTTTACTTCTATTATTATCCCTTCCAGTTTTAGCTGGAGCTATTACCATACTTTTAACTGATCGTAATTTAAATACAT
CTTTTTTTGACCCTGCTGGAGGAGGTGATCCAATTTTATATCAACATTTATTT

Type material. Holotype: ♂ currently deposited in the National Museum of Natural History, Smithsonian Institution, Washington, DC, USA (USNM), illustrated in Fig. 25 (genitalia in Fig. 26a–c), bears the following seven rectangular labels (2nd handwritten, others printed), six white: [Petropolis, | Brazil.], [Mycteris | cambyses | Hew | fide Godm], [Collection | W.Schaus], [GENITALIA NO. | X-57 77 | J.M.Burns 2004], [DNA sample ID: | NVG-18059D10 | c/o Nick V. Grishin], [USNMENT | {QR Code} | 01466804], and one red [HOLOTYPE ♂ | Pellicia (Mictris) | rio Grishin].

Type locality. Brazil: Rio de Janeiro, Petropolis.

Etymology. The name is taken from the name of the Brazilian state with the type locality and is treated as a noun in apposition.

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

Clytius unifascia (Mabille, 1889), comb. nov. is a valid species distinct from *Staphylus azteca* (Scudder, 1872) and *Clytius clytius* (Godman & Salvin, 1897)

Genomic sequencing of a syntype of *Antigonus unifascia* Mabille, 1889 (type locality in Honduras, sequenced as NVG-15033G05) that since Evans (1953) is treated as a junior subjective synonym of *Staphylus azteca* (Scudder, 1872) (type locality in Mexico: Oaxaca, Tehuantepec), reveals that it is not monophyletic with it and does not even belong to *Staphylus* Godman and Salvin, 1896 (type species *Helias ascalaphus* Staudinger, 1875) but instead is placed in the genus *Clytius* Grishin, 2019 (type species *Pholisora clytius* Godman & Salvin, 1897), together with the sequenced primary type specimens of *P clytius* (type locality in Mexico: Nayarit, Tres Marias Island) and *Bolla semitincta* Dyar, 1924 (type locality in Colima); the latter is currently treated as a junior subjective synonym of the former (Fig. 27). Moreover, *A. unifascia* is genetically differentiated from both *C. clytius* and *B. semitincta* at the species level (Fig. 27), e.g., their COI barcode differences are 2.6% (17 bp) and 1.4% (9 bp), respectively. The latter COI difference is smaller, but *A. unifascia* is not monophyletic with *B. semitincta* in the Z chromosome tree (Fig. 27b). Therefore, we propose that *Clytius unifascia* (Mabille, 1889), **comb. nov.**, **stat. rest.** is a species-level taxon distinct from both *Staphylus azteca* (Scudder, 1872) and *Clytius clytius* (Godman & Salvin, 1897).

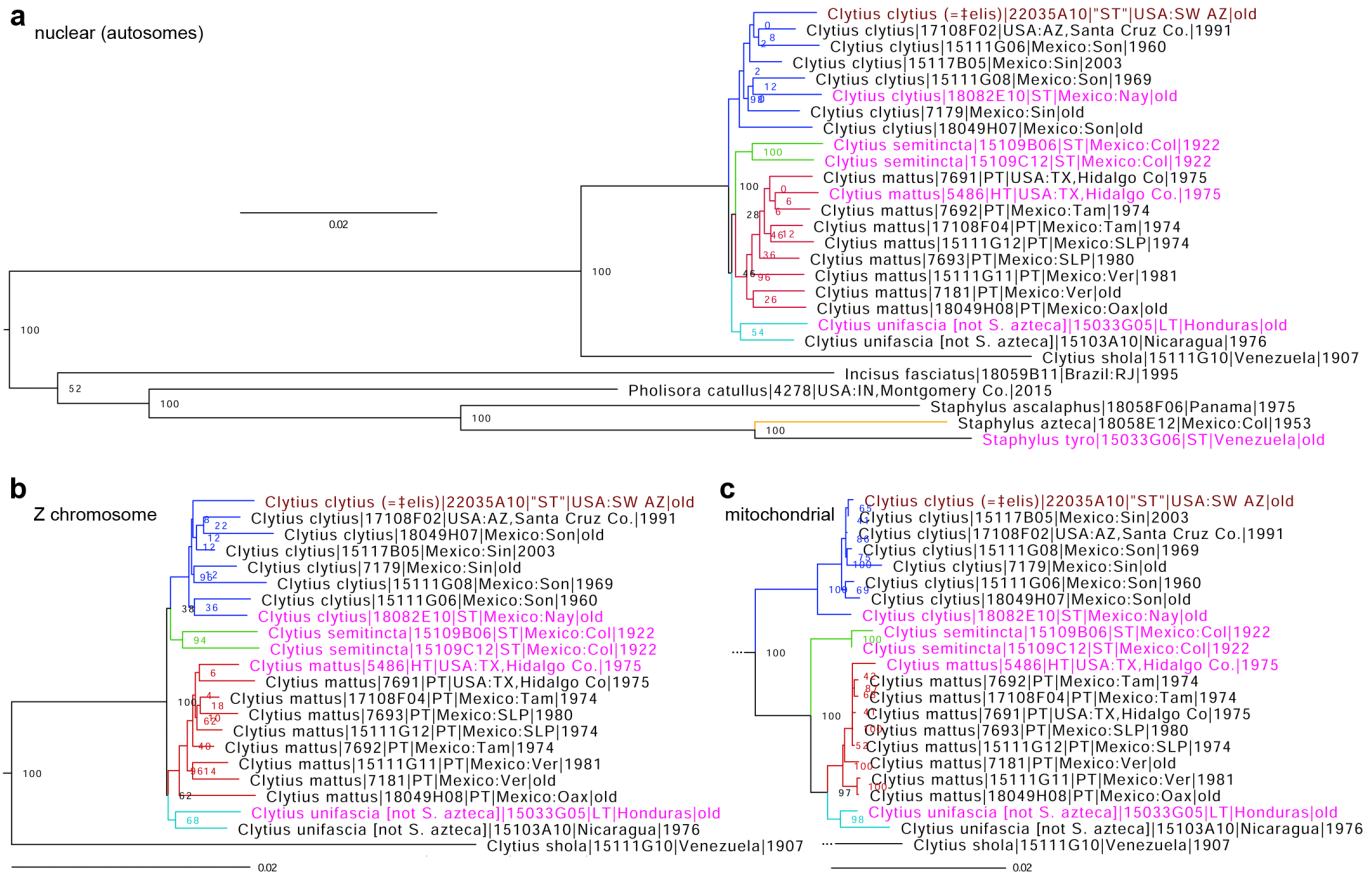

Fig. 27. Phylogenetic trees of *Clytius* species and relatives inferred from protein-coding regions of **a)** the nuclear genome (autosomes), **b)** the Z chromosome, and **c)** the mitochondrial genome. Only *Clytius* is shown in **b)** and **c)**, with the long branch redacted in the latter, as indicated by dots. Primary type specimens are labeled in magenta, and a specimen deemed as a "type" of a nomen nudum *Pholisora elis* is labeled in brown color. Different species are shown in different colors: *C. clytius* (dark blue), *C. semitincta* (green), *C. mattus* (red), *C. unifascia* (cyan), and *Staphylus azteca* (orange).

To stabilize nomenclature and define the name *A. unifascia* objectively, N.V.G. hereby designates a syntype in the MFNB collection that bears the following six labels (1st and 3rd shades of purple, others white; 3rd and 4th handwritten, others printed): [Origin. | ♀], [Hond. | Wittk.], [nis. uni- | fascia Mab.], [Unifascia | Mab.], [{QR Code} http://coll.mfn-berlin.de/u/ | 80a64f], [DNA sample ID: | NVG-15033G05 | c/o Nick V. Grishin] as the **lectotype** of *Antigonus unifascia* Mabille, 1889. According to its label, the lectotype was collected in Honduras by Wittkugel. The 3rd and the 4th labels are in Mabille's and Staudinger's handwriting, respectively. The lectotype has costal folds open on both wings, its abdomen and the tornus of the right hindwing are missing. Images of this specimen photographed by B. Hermier are shown on the Butterflies of America website (Warren et al. 2024).

Clytius semitincta (Dyar, 1924) is a valid species distinct from *Clytius clytius* (Godman & Salvin, 1897)

Genomic analysis of two syntypes of *Bolla semitincta* Dyar, 1924 (type locality in Colima, sequenced as ♂ NVG-15109B06 and ♀ NVG-15109C12) currently regarded as a junior subjective synonym of *Clytius clytius* (Godman & Salvin, 1897) (type locality in Mexico: Nayarit, Tres Marias Island) reveals that the two taxa are genetically differentiated at the species level (Fig. 27), e.g., their F_{st}/G_{min}/COI barcode differences are 0.22/0.004/2.1% (14 bp). Hence, we propose that *Clytius semitincta* (Dyar, 1924), **stat. rest.** is a species distinct from *Clytius clytius* (Godman & Salvin, 1897). Furthermore, in addition to *C. clytius*, *C. semitincta* (Dyar, 1924), and *Clytius unifascia* (Mabille, 1889), **comb. nov.**, **stat. rest.** (type locality in Honduras), we observe a clade corresponding to a fourth species in the group, from eastern and southern Mexico, that enters the USA in the lower Rio Grande Valley of Texas. This species does not have a name and is described as new below.

Clytius mattus Grishin, new species

http://zoobank.org/DD29A886-8DAF-4083-AA50-0BD745320AFC

(Figs. 27 part, 28–29, 30 part)

Definition and diagnosis. Genomic analysis of *Clytius* Grishin, 2019 (type species *Pholisora clytius* Godman & Salvin, 1897) reveals a clade that does not have an available name associated with it (Fig. 27). These specimens are genetically differentiated from others at the species level, e.g., F_{st}/G_{min}/COI barcode differences are 0.27/0.00/0.5% (3 bp) (from *Clytius unifascia* (Mabille, 1889), **comb. nov.**, **stat. rest.**), 0.40/0.009/2.1% (14 bp) (from *Clytius clytius* (Godman & Salvin, 1897)), and 0.36/0.005/0.9% (6 bp) (from *Clytius semitincta* (Dyar, 1924), **stat. rest.**). Therefore, they represent a new species. Although COI barcodes are only weakly different between some of these species, nuclear genome trees (Fig. 27a, b) and statistics substantiate their species status. This new species keys to "*Bolla clytius*" (E.31.22) in Evans (1953) and was included in this species. The new species differs from its relatives by the following

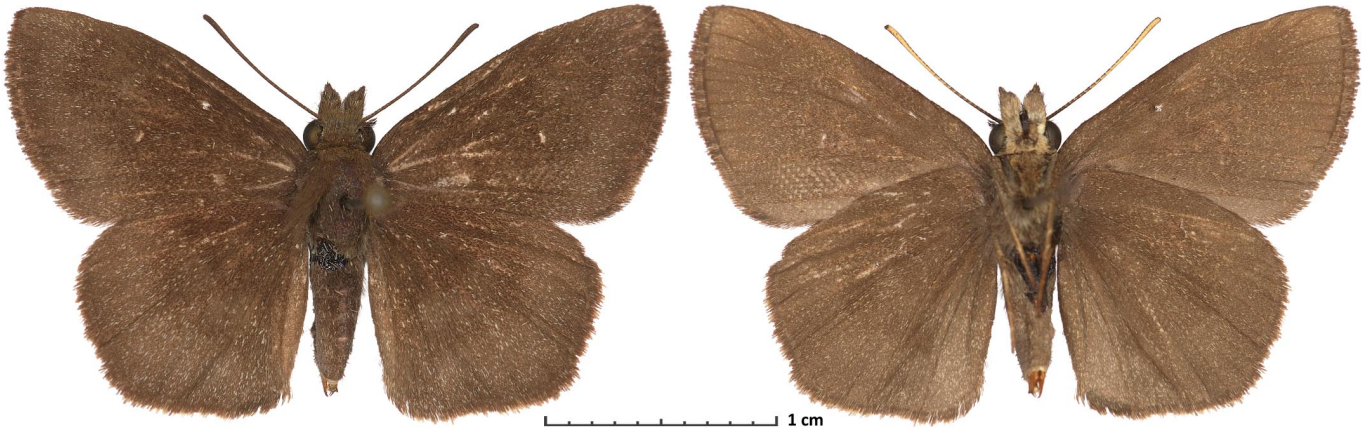

Fig. 28. *Clytius mattus* **sp. n.** holotype ♂ NVG-5486 in dorsal (left) and ventral (right) views, data in text.

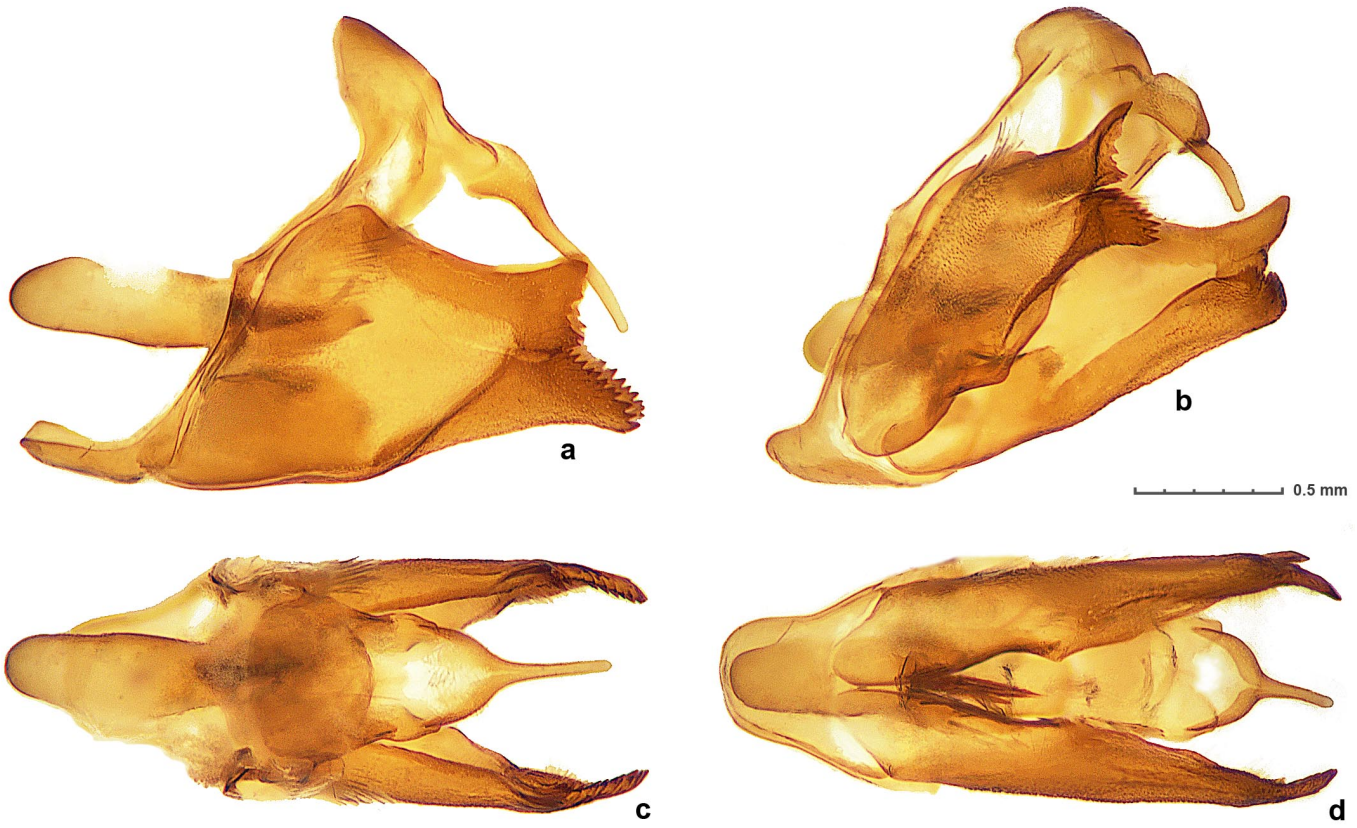

Fig. 29. Genitalia of *Clytius mattus* **sp. n.** holotype NVG-5486 vial NVG160110-27 (data in text) in different views: **a)** left lateral, **b)** left posterolateral, **c)** dorsal, **d)** ventral.

combination of characters: more uniform coloration, frequently without defined bands and only somewhat darker in the basal half of wings, usually one or two forewing subapical spots and maybe a small spot by the base of the cell CuA_1-CuA_2, and narrower male genitalic valva with longer harper and more expanded, less concave ampulla (Figs. 29, 30). Due to the relatively cryptic nature of this species, most reliable identification is achieved by DNA, and a combination of the following base pairs is diagnostic in the nuclear genome: aly536.132.2:A330G, aly444.7.11:C138T, aly2879.4.2:C58T, aly1118.1.4:C60T, aly1118.1.4:C94T, and COI barcode: A28G, T49C, T74T, T640T, T641C (the barcode may not differ from *C. unifascia*).

Barcode sequence of the holotype. Sample NVG-5486, GenBank PQ489708, 658 base pairs:

AACTTTATACTTTATTTTTGGTATTTGGTCTGGTATAGTAGGAACTTCCTTAAGTATA
TTAATTCGTTCTGAACTAGGAACCCCTGGATCTTTAATTGGAGATGATCAAATTTATA
ATACTATTGTAACAGCTCATGCTTTTATTATAATTTTTTTTATAGTTATACCCATTAT
AATTGGAGGATTCGGAAATTGATTAGTACCCCTTATATTAGGAGCCCCTGATATAGCT
TTTCCCCGAATAAATAATATAAGATTTTGACTTTTACCTCCTTCTTTAATATTATTAA
TTTCAAGAAGAATTGTAGAAAATGGAGCTGGAACAGGATGAACTGTTTATCCCCCTTT
ATCAGCTAATATTGCTCATCAAGGTTCTTCTGTAGATTTAGCCATTTTTTCTTTACAT
TTAGCTGGAATTTCCTCTATTTTAGGTGCTATTAATTTTATTACAACTATTATTAATA
TGCGAATTAATAATTTATCTTTCGATCAAATACCTTTATTTGTATGAGCTGTGGGAAT
CACAGCTTTACTTTTACTTTTATCTCTACCAGTTTTAGCTGGAGCTATTACAATACTT
TTAACTGATCGAAATCTTAACACGTCTTTTTTTGACCCTGCTGGTGGAGGAGATCCTA
TTCTATATCAACATTTATTT

Type material. Holotype: ♂ deposited in the Texas A&M University Insect Collection, College Station, TX, USA (TAMU), illustrated in Fig. 28 (genitalia in Fig. 29), bears the following six printed (text in italics handwritten) rectangular labels, five white: [TEXAS: | Hidalgo County | Bentsen-Rio Grande | Valley State Park | south of Mission], [coll. | *18 Oct* 1975 | Edward C. Knudson], [HESPERIIDAE, | Pyrginae: | Bolla

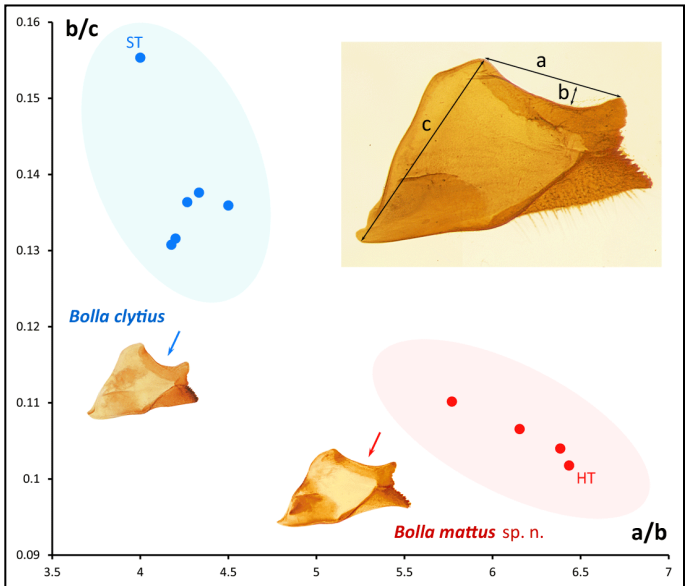

Fig. 30. Geometric morphometrics of genitalic valvae to distinguish between *C. clytius* and *C. mattus* **sp. n.**

clytius (God. & Salvin, 1897, | ♂ det. R.O. Kendall | M. & B. No. 66], [DNA sample ID: | NVG-5486 | c/o Nick V. Grishin], [genitalia | NVG160110-27 | Nick V. Grishin], and one red [HOLOTYPE ♂ | Clytius mattus | Grishin]. **Paratypes:** 18♂♂ and 15♀♀: 1♀ NVG-7691 the same data as the holotype, genitalia vial NVG170108-22; USA: Texas, Hidalgo Co, W. W. McGuire leg., first US record [TAMU]: 1♀ Santa Ana National Wildlife Refuge, 17-Oct-1973, 1♂ and 1♀ Abrams, 18-Oct-1973, and 1♀ Relampago at USH281 21-Oct-1973; and Mexico: Tamaulipas: 1♂ NVG-17108F04 40 mi E of Ciudad Victoria, 21-Oct-1974, W. W. McGuire leg. [LACM] and Roy O. Kendall & C. A. Kendall leg., [TAMU]: El Nacimiento, Rio Mante: 1♂ NVG-7692 21-Jan-1974, genitalia vial NVG170108-23, 3♂♂ 18-Feb-1974, and 1♀ 10-Nov-1974; 1♂ and 3♀♀ 28 km S of San Fernando, 16-Dec-1973; Sierra Cuchara, near rock quarry: 2♂♂ 17-Feb-1974 and 2♂♂ 24-Feb-1974; and 2♂♂ and 1♀ Rancho Pico de Oro, vicinity of Los Kikos, 22-Feb-1974; San Luis Potosi: 1♂ NVG-15111G12 Ciudad Valles, 18-Jun-1974, H. A. Freeman leg. [AMNH] and ca. 16 km E of Ciudad Valles, Hotel Taninul, Roy O. Kendall & C. A. Kendall leg. [TAMU]: 1♂ 4-Feb-1980 and 1♀ NVG-7693 30-Jan-1980, genitalia vial NVG170108-24; Veracruz: 1♂ NVG-15111G11 near Paraje Nuevo, Hacienda Potrero Viejo, 5-Jun-1981, J. & R. Potts leg., genitalia slide G1705 [AMNH] and all the rest in USNM, no dates known unless specified: 1♂ Xalapa; 1♀ La Gloria, Cardel, J. Camelo G. leg.; 1♀ Tlacotalpan, 29-Jul-1897; and W. Schaus collection: 1♂ Paso San Juan, 1♀ Coatepec, and 1♀ NVG-7181, USNMENT_01321029 Orizaba, genitalia vial NVG161005-08; and 1♀ NVG-18049H08, USNMENT_01466670 Oaxaca, Tuxtepec, Camelo leg.

Type locality. USA: Hidalgo Co., Bentsen-Rio Grande Valley State Park.

Etymology. The name is formed from the word matte and is given for the dull, matte colors of this species. The name is a Latinized masculine adjective.

Distribution. From the lower Rio Grande Valley in South Texas, USA, to Veracruz and Oaxaca, Mexico. The southern limits of the range remain to be investigated.

Suggested English name. Matte Sootywing.

Comment. We note that two species of *Clytius* have been recorded in the USA: *C. clytius* in Arizona and *C. mattus* **sp. n.** in Texas, confirmed by genomic sequencing (Fig. 27).

A nomen nudum *Pholisora elis* in J. B. Smith et al., 1891 refers to a specimen of *Clytius clytius* (Godman & Salvin, 1897) from USA: Arizona

The name *Pholisora elis* in Smith et al. (1891) is a nomen nudum (no description or indication published, just the name listed) of currently unknown attribution (Mielke 2005). A specimen labeled as a type of "Pholisora Elis Edw." collected in "S. W. Arizona" was found in the USNM collection (Fig. 31). It bears the label "Pho. Elis ♀ | Ariz[a]" in Edward's handwriting, which supports the authenticity of this specimen as a reference for the name. Genomic sequencing of this specimen places it among *Clytius clytius* Godman & Salvin, 1897 (type locality in Mexico: Nayarit, Tres Marias Island), closest to another specimen collected in Arizona and a specimen from Mexico: Sonora (Fig. 27), thus supporting its collecting locality in the USA. Therefore, we propose to list *Pholisora elis* of J. B. Smith et al., 1891, **nom. nud.** in synonymy with *Clytius clytius* Godman & Salvin, 1897. Because the name *P. elis* is unavailable, it does not formally have type specimens, and the specimen labeled as "Type" is not a syntype but a regular specimen, a male, that helps us refine the synonymic placement of this name. The COI barcode sequence of this specimen, sample NVG-22035A10, GenBank PQ489709, 658 base pairs is:

AACTTTATACTTTATTTTTGGTATTTGATCTGGTATAGTAGGAACTTCTTTAAGTATATTAATTCGCTCTGAACTAGGAACCCCTGGATCTTTAATTGGAGATGATCAAATTTATAATACT
ATTGTAACAGCTCATGCTTTTATTATAATTTTTTTTATAGTTATACCCATTATAATTGGAGGATTTGGAAATTGATTAGTACCCCTTATATTAGGAGCCCCTGATATAGCTTTTCCCCGAA
TAAATAATATAAGATTTTGACTTTTACCTCCTTCTTTAATATTACTAATTTCAAGAAGAATTGTAGAAAATGGAGCTGGAACAGGATGAACTGTTTATCCCCCTTTATCAGCTAATATTGC
TCACCAAGGTTCTTCTGTAGATTTAGCCATTTTTTCATTACATTTAGCTGGAATTTCTTCTATTTTAGGTGCTATTAATTTTATTACAACTATTATTAATATACGAATTAATAATTTATCT
TTCGATCAAATACCTTTATTCGTATGAGCTGTAGGAATCACAGCTTTACTTTTACTTTTATCTCTGCCAGTTTTAGCTGGAGCTATTACAATACTTTTAACTGACCGAAATCTTAATACAT
CTTTTTTTGATCCTGCTGGTGGAGGAGATCCTATTTTATATCAACATTTATTT

Fig. 31. A specimen labeled as a "type" of *Pholisora elis* (it is ♂, not ♀) in dorsal (left) and ventral (right) views with its original labels below (reduced to half the scale of the specimen). The larger scale bar refers to the specimen, and the smaller one refers to labels.

Perus (*Menuda*) *tinctus* Grishin, new species

http://zoobank.org/B3612B03-2C13-467B-A3D5-EBBCFBD2180F

(Figs. 32 part, 33)

Definition and diagnosis. Genomic sequencing of a specimen curated in MFNB as "Origin." of the name "Antigonus vulgata HS" (either unpublished or published with misattributed authorship and misidentified, see comment below) reveals that it is related to *Perus menuda* (Weeks, 1902) (type locality in Bolivia, syntypes sequenced as NVG-19055F05, 06, and 07), but is genetically differentiated from it at the species level (Fig. 32), e.g., their COI barcodes differ by 5.4% (35 bp). Therefore, this specimen represents a new species. This new species keys to "*Staphylus menuda*" (E.32.16) in Evans (1953), and might have been included in it (Evans' female from Rio de Janeiro, Brazil: "unh tornally with whitish scaling"), but differs from true *P. menuda* by the tornal area of the ventral hindwing overscaled with cream-colored scales and more prominent cream spots overall. Differs from other relatives by a combination of rounded (not scalloped) at margin wings with brown fringes, brown head above (with some cream overscaling, but not orange or green), costal fold in males, the lack of forewing apical spots, a well-defined row of pale spots in the submarginal area of all wings above (weakly expressed on the ventral hindwing as well), diffuse paler spot at the end of the discal cell of the dorsal forewing, a pale bar at the end of the discal cell, and oval discal spots in cells CuA_1-CuA_2 and CuA_2-1A+2A (the latter being the largest) on both sides of hindwings. The holotype (the only known specimen) lacks an abdomen; thus, the most reliable identification is achieved by DNA, and a combination of the following base pairs is diagnostic in the nuclear genome: aly10226.6.1:C228T, aly3109.11.2:A177G, aly2844.9.2:A54G, aly1313.29.3:A60T, aly1139.2.13:A69C, aly3109.11.2:T171T (not C), aly536.39.4:G207G (not A), aly490.12.1:A3342A (not G), aly5021.7.12:T843T (not C), aly5021.7.12:C902C (not T), and COI barcode: T10T, T142C, T157C, A217G, T421C, T478C.

Barcode sequence of the holotype. Sample NVG-21117C03, GenBank PQ489710, 658 base pairs:

AACTTTATATTTTATTTTCGGTATTTGATCAGGTATAGTAGGTACTTCTTTAAGTATTCTTATTCGATCAGAATTAGGAATCCCAGGATCTTTAATTGGAGATGATCAAATTTATAATACT
ATTGTAACAGCTCATGCTTTCATTATAATTTTTTTCATAGTAATACCTATTATAATTGGGGGATTTGGAAATTGATTAGTACCTCTTATATTAGGGGCCCCTGATATAGCTTTCCCACGAA
TAAATAATATAAGATTTTGACTTTTACCCCCTTCTCTCATACTTTTAATTTCAAGAAGTATTGTAGAAAATGGAGCAGGTACTGGATGAACTGTCTATCCCCCTCTTTCAGCCAATATTGC
CCATCAAGGTTCATCTGTAGATTTAGCTATTTTTTCCCTTCATTTAGCTGGAATTTCCTCAATTTTAGGAGCAATTAATTTTATTACAACTATTATTAATATACGAATTAATAACTTATCT
TTTGATCAAATACCTTTATTTGTATGAGCTGTTGGAATTACAGCTTTACTTTTATTACTATCTTTACCAGTTTTAGCTGGGGCCATTACCATACTCCTAACAGATCGAAATCTTAATACTT
CTTTTTTTGATCCAGCAGGTGGAGGAGATCCTATTTTATACCAACATTTATTT

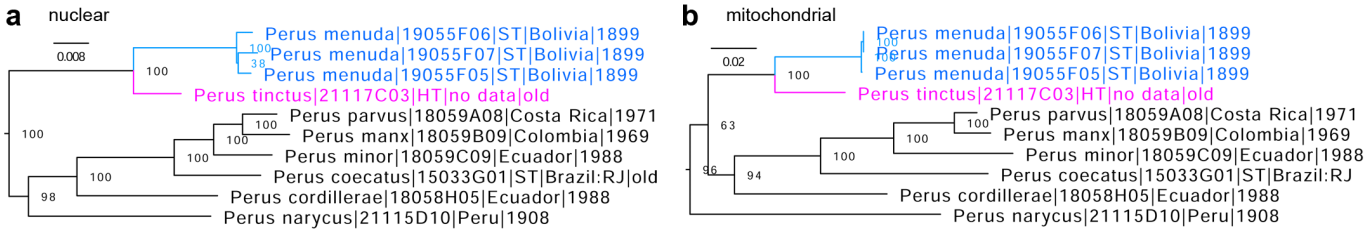

Fig. 32. Phylogenetic trees of *Perus* species constructed from protein-coding regions in **a)** the nuclear genome (autosomes) and **b)** the mitochondrial genome: *P. menuda* (blue) and *P. tinctus* **sp. n.** (magenta).

Fig. 33. *Perus* (*Menuda*) *tinctus* **sp. n.** holotype ♂ NVG-21117C03 in dorsal (left) and ventral (right) views with its labels below (reduced to half the scale of the specimen, the "holotype" label not shown). The larger scale bar refers to the specimen, and the smaller one refers to labels.

Type material. Holotype: ♂ deposited in the Museum für Naturkunde, Berlin, Germany (MFNB), illustrated in Fig. 33, bears the following nine rectangular labels (1st purple, last red, others white; 2nd, 4th, and 6th handwritten, others printed): [Origin.], [Ant. vulgata | ĉ HS], [Coll. H.—Sch.], [Antig. | vulgata | HS.], [Coll. | Staudinger], [type | von ?], [{QR Code} http://coll.mfn-berlin.de/u/ | 908615], [DNA sample ID: | NVG-21117C03 | c/o Nick V. Grishin], and [HOLOTYPE ♂ | Perus (Menuda) | tinctus Grishin]. The abdomen is missing in the holotype.

Type locality. South America, as deduced by the range of related species, otherwise unknown, possibly Southeast Brazil.

Etymology. In Latin, *tinctus* means stained, dyed, tinged, tinted, or colored. The name is given for the cream overscaling towards the tornus of the ventral hindwing, which is not expressed in its sister species. The name is a participle.

Distribution. Currently known only from the holotype likely collected in South America, possibly in Southeast Brazil.

Comments. The holotype of this new species, a specimen originally from Herrich-Schäffer's collection, is most probably a specimen that Plötz intended to use in his description of a species he planned to name "*vulgata*." Plötz effectively published this name in 1884 (Plötz 1884), but after Möschler had already described *Achlyodes vulgata* Möschler, 1878 (type locality in Colombia), currently a valid species of *Staphylus* Godman & Salvin, 1896 (type species *Helias ascalaphus* Staudinger, 1875). Plötz explicitly referenced *A. vulgata* Möschler in his 1884 description of *vulgata*. Therefore, *vulgata*, as published by Plötz in 1884, is not a new species (or a replacement name—the name is the same), even if it was Plötz's original intention, and the specimens he used for this description, other than Möschler's two syntypes of

vulgata, are not types. This Herrich-Schäffer's specimen might have been illustrated in Plötz's unpublished t[afel]. 958 because it agrees with his description of *A. vulgata* and is curated as a type of "vulgata" but is not a syntype of *A. vulgata* Möschler, 1879. Both syntypes (male and female) of *A. vulgata* Möschler, 1879 are extant, and this is a third specimen. The locality "Colombia" in the original description likely referred to Möschler's publication (1879) referenced by Plötz after his name "vulgata Pl" (Plötz 1884) because Herrich-Schäffer's "vulgata" specimen lacks a locality label. We consider Plötz's *Achlyodes vulgata* a misattribution and misidentification of *Achlyodes vulgata* Möschler, 1879, assuming that "Pl" after the name resulted from some mistake. "Pl" might have been "inherited" from an earlier version of the manuscript prepared before the availability of Möschler's *vulgata*, and it should have been "Mösch" instead. In any interpretation of "vulgata Pl", the name *vulgata* cannot be used as valid for this specimen.

A specimen in MFNB curated as a type of *Achlyodes serapion* Plötz, 1884 is a pseudotype

A single specimen that, according to its label, was identified by Plötz as "serapion" ("best[immt]. v[on]. Plötz") is placed under the handwritten on blue-green paper header label "serapion | Plötz" with a red handwritten label "Typus" pinned next to it. This specimen was photographed by Bernard Hermier; photographs shown on the Butterflies of America website (Warren et al. 2024). It is a worn specimen, which, judging from its labels, was originally from the Weymer collection, collected in Central America in 1876. Its phenotype and locality do not agree with the original description of *Achlyodes serapion* Plötz, 1884 (type locality Brazil: Rio de Janeiro, Nova Friburgo). Moreover, no "i. l." (for *in litteris*, referring to unpublished names) was added to the name on the identification label of this specimen. The "i. l." is typical of Plötz's type specimens in the Weymer collection that Plötz identified before his publication. For instance, lectotypes of *Pyrgus* (*Pyrgus*) *albescens* Plötz, 1884 (type locality in Mexico), currently *Burnsius communis albescens*, and *Hesperia erratica* Plötz, 1883 (type locality in the USA as deduced by genomic sequencing, not Guatemala as on the specimen label and in the publication), currently a junior subjective synonym of *Lon zabulon* (Boisduval & Le Conte, [1837]), have "i. l." on their labels. Another label includes the number of Plötz's unpublished drawing, e.g., "taf. 889" for *P. albescens* and "taf. 656" for *H. erratica*. No mention of Plotz's taf[el]. number was on the labels of the "serapion" specimen. Moreover, its identification label has both localities: "N Freyburg." and "Amer centr." The latter was possibly added later and agrees with the same statement on the locality/date/collector label, and the former likely refers to the locality given in the publication (Plötz 1884).

To learn more about this putative "serapion" specimen, it was sampled for DNA and sequenced as NVG-15032H01. The genomic analysis identified it as *Staphylus* (*Scantilla*) *opites* Godman & Salvin, 1896 (type locality in Guatemala) (Fig. 34 magenta within green), a species known only from Mexico and Central America. Therefore, the "Amer centr." locality given on the locality/date/collector label should be correct, but "N Freyburg." on the identification label simply states the type locality of *A. serapion*. We conclude that the specimen NVG-15032H01 is not a syntype of *Achlyodes serapion* Plötz, 1884, because it does not closely agree with the original description and is from Central America, instead of being from the type locality in Brazil. It was probably identified by Plötz as *A. serapion* after this name was

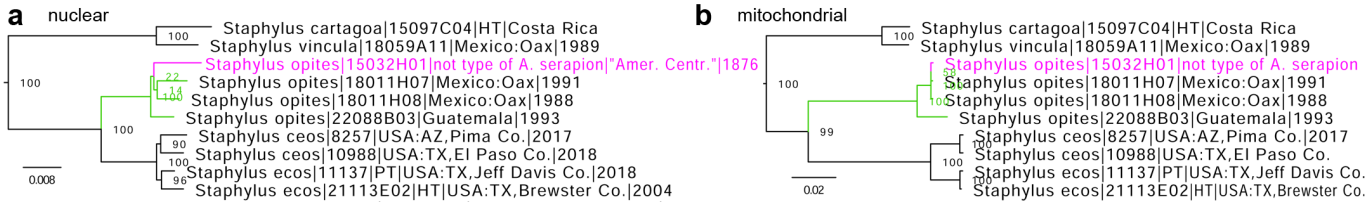

Fig. 34. Phylogenetic trees of *Staphylus* (*Scantilla*) species inferred from protein-coding regions of **a)** the nuclear genome (autosomes), **b)** the mitochondrial genome showing the placement of *Achlyodes serapion* pseudotype (magenta) within *S. opites* (green).

published. Because *S. opites* is unlikely to occur in Southeast Brazil and, having almost uniformly dark dorsal hindwing, this species does not agree with the original description of *A. serapion*, the specimen NVG-15032H01 was misidentified by Plötz, possibly after the description of *A. serapion*.

Future studies will shed light on the true identity of *A. serapion*. It is possible that Evans (1953) was correct, and the discovery of a male conspecific with the specimens Evans identified as *A. serapion* should be able to address this question. Another twist to this puzzle is offered by a specimen in MFNB (sequenced as NVG-15032E04) curated as a syntype of *Pellicia licisca* Plötz, 1882 (type locality in Nicaragua). Although, according to its label, it was identified as *P. licisca* by Plötz, this specimen agrees neither with the original description nor the type locality (labeled from Brazil, not Nicaragua) of *P. licisca*. This specimen, identified by us as *Viola minor* (Hayward, 1933) (type locality in Argentina, also known from SE and S Brazil), agrees reasonably well with Godman's copy of the unpublished drawing of *A. serapion*. What if, due to some label mix-up, this specimen is a syntype of *A. serapion*? If this was not for Evans' choice, which may be fitting Plötz's illustration better (if a male of that species has mostly brown ventral hindwing darker towards the base), out of all Hesperiidae known to us, *V. minor* may indeed be in the best agreement with all information we have about *A. serapion*.

Staphylus veytius H. Freeman, 1969 is confirmed a junior subjective synonym of *Staphylus tierra* Evans, 1953

Genomic sequencing of the holotype of *Staphylus veytius* H. Freeman, 1969 (type locality in Mexico: Chiapas, sequenced as NVG-18025C06) regarded by Mielke (2005) as a valid species, places it within specimens of *Staphylus tierra* Evans, 1953 (type locality in Mexico: Guerrero) (Fig. 35 red within blue), as already suggested by Warren (2000). Therefore, our results support Warren's hypothesis, and we agree with the treatment of *Staphylus veytius* H. Freeman, 1969, **syn. conf.** as a junior subjective synonym of *Staphylus tierra* Evans, 1953.

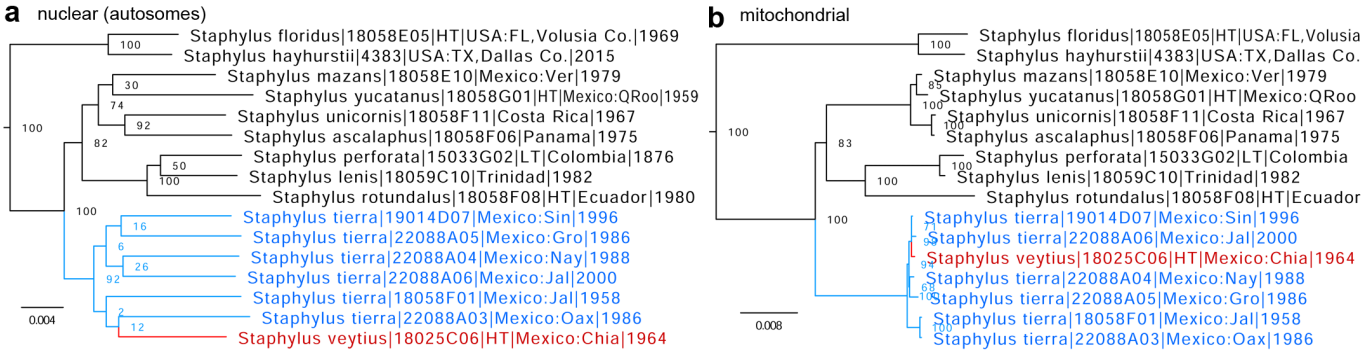

Fig. 35. Phylogenetic trees of selected *Staphylus* (*Staphylus*) species constructed from protein-coding regions in **a)** the nuclear genome (autosomes) and **b)** the mitochondrial genome: *S. tierra* is colored blue with the holotype of *S. veytius* in red.

Tribe Pyrgini Burmeister, 1878

Cabares Godman & Salvin, 1894 is a junior objective synonym of *Systasea* Butler, 1877, which is a junior subjective synonym of *Autochton* Hübner, 1823

The genus *Lintneria* W. H. Edwards & Butler, 1877 was proposed in a publication by Edwards, who provided a description of this genus that mentions two species (*Papilio daunus* Cramer, 1777 and *Hesperia zampa* W. H. Edwards, 1876) and cited verbatim a segment of a letter from A. G. Butler, who, in addition to these two species, listed two others and designated *P. daunus* to be the type species. Butler and Edwards misidentified *P. daunus*: they listed it from St. Domingo and described the outline of the hindwing as "angulated" (rounded in *P. daunus*). The only species from Hispaniola (referred to as "St.

Domingo") with "angulated" hindwing that otherwise resembles *P. daunus* (and other three species placed in *Lintneria*) is *Autochton potrillo* (Lucas, 1857) (type locality in Cuba). Calhoun (2007) reached the same conclusion. To secure the applicability of the description by Edwards & Butler and ensure the stability of nomenclature that may be threatened by the uncertain identity of *P. daunus*, a *nomen dubium*, we fix (under Article 70.3.2 of the ICZN Code) the type species of *Lintneria* as *Thanaos potrillo* Lucas, 1857 (the taxonomic species actually involved in the misidentification), misidentified as *Papilio daunus* Cramer, 1777 (the name previously cited as the type species) in the original description of *Lintneria* by W. H. Edwards and Butler in Edwards (1877a).

Lintneria W. H. Edwards & Butler, 1877 (type species *Thanaos potrillo* Lucas, 1857) is a junior homonym of *Lintneria* Butler, 1876 (Sphingidae). A new replacement name, *Systasea*, was proposed by Butler and published by Edwards (1877b) as "Mr. Butler proposes the name *Systasea* for the genus of Hesperidae [sic!] spoken of, which therefore should stand *Systasea* Butl" (Edwards 1877b). Although this work was authored by Edwards, using Article 50.1.1 of the ICZN Code, we determine that the sole author of the replacement name *Systasea* is Butler because "it is clear from the contents that some person other than an author of the work is alone responsible both for the name … and for satisfying the criteria of availability other than actual publication" (ICZN 1999), as quoted above. The name was published before 1931. Therefore, an indication (Art. 12.2.3: "the proposal of a new replacement name (nomen novum) for an available name") is sufficient for "satisfying the criteria of availability other than actual publication."

Because this is a replacement name, according to Art. 67.8, the type species of *Systasea* is the same as of *Lintneria*, which is *Thanaos potrillo* Lucas, 1857. Because *Thanaos potrillo* Lucas, 1857 is also the type species of *Cabares* Godman & Salvin, 1894, according to Art. 61.3.3, *Cabares* Godman & Salvin, 1894 is a **junior objective synonym** of *Systasea* Butler, 1877. And because *Thanaos potrillo* Lucas, 1857 is currently attributed to the nominate subgenus of *Autochton* Hübner, 1823, *Systasea* Butler, 1877 is a **junior subjective synonym** of *Autochton*.

Being a junior synonym, the name *Systasea* cannot be used as valid for the three species currently placed in this genus: *Leucochitonea pulverulenta* R. Felder, 1869 (type locality in Mexico: Veracruz), *Hesperia zampa* W. H. Edwards, 1876 (type locality in USA: Arizona), and *Systasea microsticta* Dyar, 1923 (type locality in Mexico: Guerrero). Moreover, these three species are not monophyletic with the type species of *Systasea*. To maintain the traditional usage of *Systasea*, we have considered referring the matter to ICZN so that the type species of *Systasea* is reassigned as *H. zampa*. However, previously, the Commission has not favored reassignment of the type species even for the genus *Drosophila* Fallén, 1823 (type species *Musca funebris* Fabricius, 1787, not *Drosophila melanogaster* Meigen, 1830) (ICZN 2010), probably the most widely used name of an insect. Therefore, we opted for a more straightforward solution within our means to ensure the preservation, albeit phonetic, of this name.

Systasia Grishin, new genus

http://zoobank.org/68FC6FF0-2CDB-479F-BD98-ED1BC6D17C5A

Type species. *Hesperia zampa* W. H. Edwards, 1876.

Definition. Genomic analysis of Pyrgini Burmeister, 1878 reveals that a phylogenetic lineage consisting of two known species (*Hesperia zampa* W. H. Edwards, 1876 and *Leucochitonea pulverulenta* R. Felder, 1869) is confidently placed in the clade with *Diaeus* Godman & Salvin, 1895 (type species *Leucochitonea lacaena* Hewitson, 1869) and *Zobera* Freeman, 1970 (type species *Zobera albopunctata* Freeman, 1970), and is sister to *Onenses* Godman & Salvin, 1895 (type species *Leucochitonea hyalophora* R. Felder, 1869) in the Z chromosome tree (Fig. 36b). This lineage is genetically differentiated from its closest relatives at the genus level (Fig. 36): e.g., *O. hyalophora* COI barcode differs by 11.2% (74 bp) from *H. zampa* and by 10.5% (69 bp) from *L. pulverulenta*. For comparison, the human (*Homo sapiens* Linnaeus, 1758) and chimp (*Pan troglodytes* (Blumenbach, 1775)) COI barcode difference is 9.6% (63 bp). As discussed above, the genus-group name *Systasea* Butler, 1877 (type species *Thanaos potrillo* Lucas,

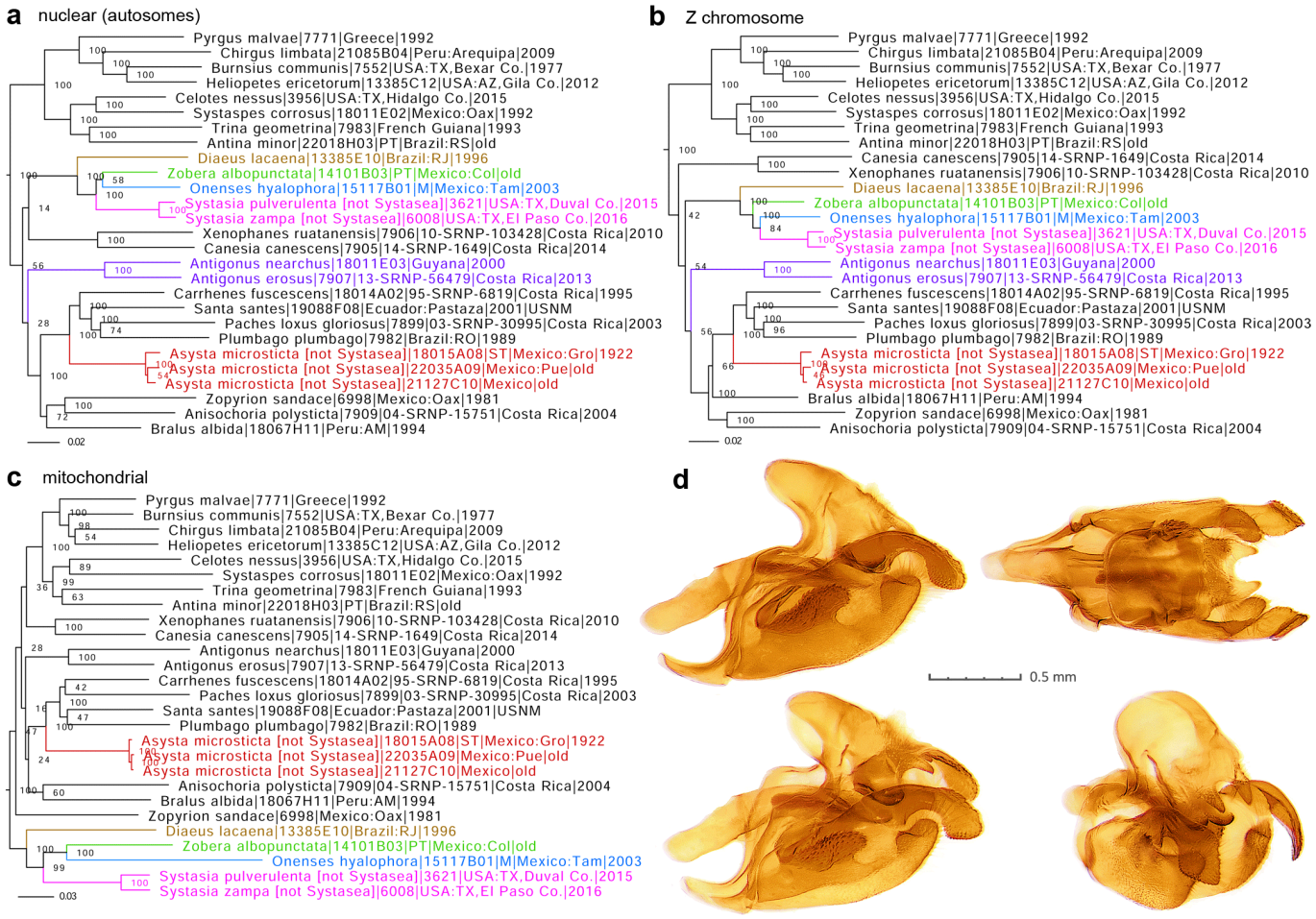

Fig. 36. Phylogenetic trees of Pyrgini, including species previously placed in *Systasea* constructed from protein-coding regions of **a)** the nuclear genome (autosomes), **b)** the Z chromosome, and **c)** the mitochondrial genome: *Systasia* **gen. nov.** (magenta), *Onenses* (blue), *Zobera* (green), *Diaeus* (brown), *Antigonus* Hübner, [1819] (purple), and *Asysta* **gen. nov.** (red). **d)** Male genitalia of *Asysta microsticta* **comb. nov.** syntype from Mexico: Guerrero, May-1922, R. Muller leg., genitalia no. X-2321 J. M. Burns 1987 [USNM], in several views: left lateral (top left), left dorsolateral (bottom left), dorsal (top right), and posterior slightly from the left (bottom right); ejaculatory duct is digitally removed.

1857) traditionally applied to *H. zampa* and *L. pulverulenta* cannot be used for them because they are not monophyletic with the type species of *Systasea* and even belong to different subfamilies (Mielke 2005; Li et al. 2019). Therefore, because no other available genus name applies to the lineage with *H. zampa* and *L. pulverulenta*, it represents a new genus. This new genus keys to E.56 in Evans (1953) and differs from its relatives by a combination of the following characters: apiculus is blunt; forewing apex is not truncate and the inner margin is concave, forewing is not excavate along the margin in cell CuA_2-1A+2A and hindwing in cell Sc+R_1-RS; the hindwing outer margin is irregular; males have a costal fold, hindtibial tuft, and thoracic pouch; uncus is narrower in dorsal view than in relatives, undivided; harpe is terminally rounded or expanded, not narrowing; costa of valva is armed with a terminally rounded curved process not shorter and only slightly narrower than harpe at its base. In DNA, a combination of the following characters is diagnostic in the nuclear genome: aly276665.11.11:T52C, aly4456.14.6:T109G, aly1041.8.11:C48T, aly3824.3.5:A192G, aly2250.3.1:A152G, and COI barcode: A214T, T364A, A421T, 547C, T581C.

Etymology. For the stability of nomenclature, the name is chosen to be as close as conceivable to *Systasea*. The name is a feminine noun in the nominative singular.

Species included. The type species (i.e., *Hesperia zampa* W. H. Edwards, 1876) and *Leucochitonea pulverulenta* R. Felder, 1869.

Parent taxon. Tribe Pyrgini Burmeister, 1878.

Asysta Grishin, new genus

http://zoobank.org/74B2BC62-F359-4945-91DA-B3D93FC9F53D

Type species. *Systasea microsticta* Dyar, 1923.

Definition. Genomic phylogeny of Pyrgini Burmeister, 1878 reveals that *Systasea microsticta* Dyar, 1923 (type locality in Mexico: Guerrero) is not monophyletic with *Hesperia zampa* W. H. Edwards, 1876 (type locality in USA: Arizona) and *Leucochitonea pulverulenta* R. Felder, 1869 (type locality Mexico: Veracruz, Orizaba) formerly in *Systasea* Butler, 1877 (type species *Thanaos potrillo* Lucas, 1857) and placed in *Systasia* **gen. nov.** above, but forms a lineage in deeper radiation of the tribe not closely related to any other single genus (Fig. 36). Therefore, this lineage represents a new genus that keys to E.56.3 in Evans (1953) and differs from its relatives by a combination of the following characters: apiculus is blunt; forewing apex is not truncate and inner margin is concave, forewing is not excavate along the margin in cell CuA2-1A+2A but the hindwing margin is concave in cell Sc+R_1-RS; hindwing outer margin is irregular but less so than in *Systasia* **gen. nov.**; males have costal fold, hindtibial tuft, and thoracic pouch; the 1st segment of palpi is narrower and the 3rd segment is directed somewhat outwards, tilted stronger than in relatives; forewing discal band is relatively straight, composed of several smaller semihyaline pale spots including two separate spots anteriad of the discal cell (better seen ventrally), forewing is prominently paler by the inner margin beneath (Fig. 37); uncus is divided and broader than long, arms are slightly longer than wide; sacculus is massively expanded into a spiculose process about the same size as harpe; harpe is terminally narrower, rounded, inwardly curved towards the other harpe; process from the ampulla is curved ventrad and more than twice as long as harpe, terminally semi-rhomboidal (Fig. 36d). In DNA, a combination of the following characters is diagnostic in the nuclear genome: aly2163.3.10: G144A, aly216.30.8:T72A, aly5715.3.24:G78A, aly214.16.5:C43T, aly1859.1.1:C826A, and COI barcode: A34T, G38A, T133C, A190T, A334G.

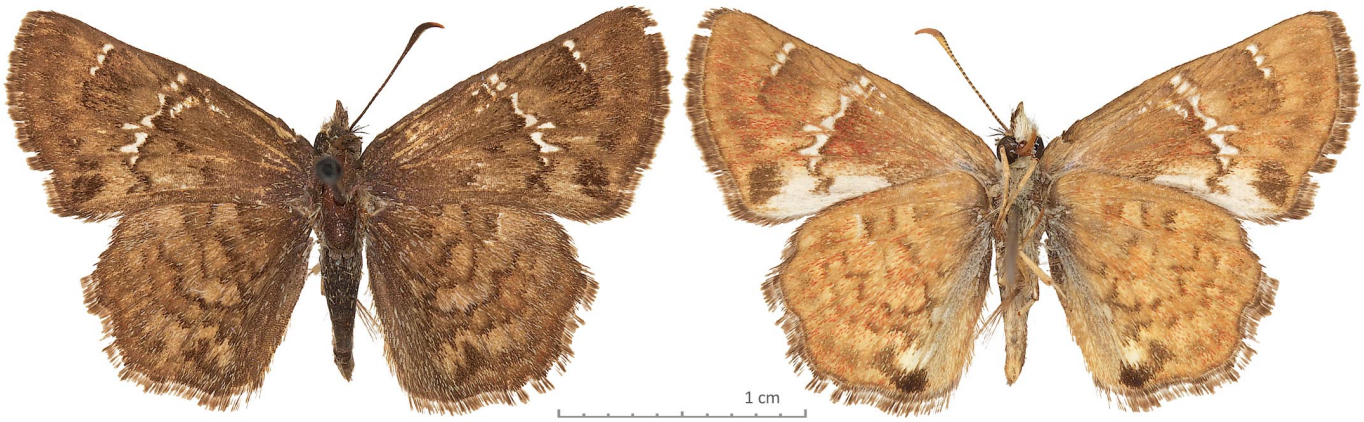

Fig. 37. *Asysta microsticta* **comb. nov.** ♂ NVG-22035A09 Mexico: Puebla, Tehuacán, R. Müller leg. [USNM]. This specimen is curated as a "type" of an unpublished name "Systasea subcumulans Dyar."

Etymology. The name is formed from the original genus name of the type species by shortening it and adding a negating a- (i.e., not *Systasea*). The name is a feminine noun in the nominative singular.

Species included. Only the type species (i.e., *Systasea microsticta* Dyar, 1923).

Parent taxon. Tribe Pyrgini Burmeister, 1878.

Tribe Erynnini Brues & F. Carpenter, 1932

Cycloglypha polax Evans, 1953 belongs to the genus *Camptopleura* Mabille, 1877 and not *Cycloglypha* Mabille, 1903

Genomic analysis of Erynnini Brues & F. Carpenter, 1932 reveals that *Cycloglypha polax* Evans, 1953 (type locality in Brazil: Mato Grosso) is not placed within *Cycloglypha* Mabille, 1903 (type species

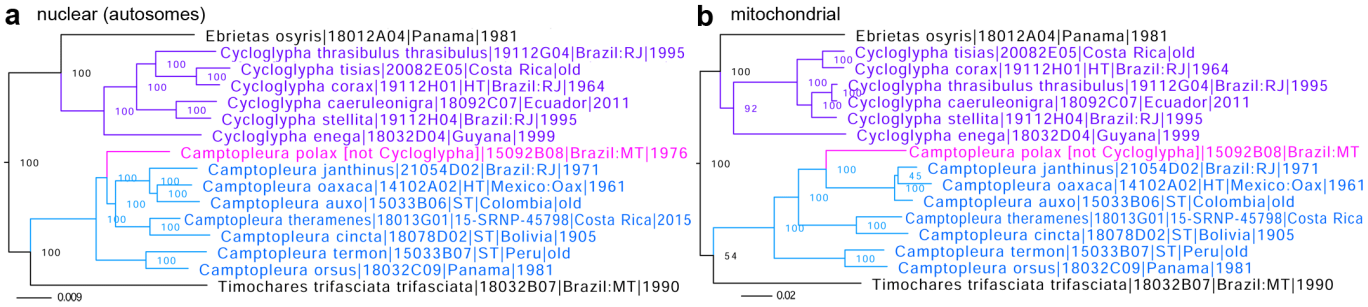

Fig. 38. Phylogenetic trees of *Cycloglypha*, *Camptopleura*, and relatives inferred from protein-coding regions of **a)** the nuclear genome (autosomes) and **b)** the mitochondrial genome: *Cycloglypha* (purple) and *Camptopleura* (blue) with *Camptopleura polax* **comb. nov.** (magenta).

Hesperia thrasibulus Fabricius, 1793) but instead originates within *Camptopleura* Mabille, 1877 (type species *Camptopleura theramenes* Mabille, 1877) (Fig. 38). Therefore, we propose to place it in the latter genus as *Camptopleura polax* (Evans, 1953), **comb. nov.**

Lectotype designation for *Leucochitonea trifasciata* Hewitson, 1868

To stabilize nomenclature, define the name *L. trifasciata* objectively, and clarify its type locality that was not specified in the original description, N.V.G. hereby designates a female syntype in the BMNH collection that bears the following four labels (1st and 2nd round, others rectangular; 1st with a red circle above, 2nd yellow above, others white; 2nd handwritten, others printed with handwritten text shown in italics): (Type) above and (H | 831) beneath, (1067), [*Bolivia.* | Hewitson Coll. | 79-69. | Leucochitonea | *trifasciata. 3.*], [BMNH(E) #810335] as the **lectotype** of *Leucochitonea trifasciata* Hewitson, 1868. The lectotype lacks antennae, and its wings are angled down and secured by glue beneath. Images of the lectotype photographed by N.V.G. are shown on the Butterflies of America website (Warren et al. 2024). The type locality of *T. trifasciata* becomes Bolivia, according to the label of the lectotype.

Lectotype designation for *Timochares trifasciata* form *obscurior* Draudt, 1923

Mielke (1993) designated a lectotype of *Timochares trifasciata* form *obscurior* Draudt, 1923 (type locality not specified) (Fig. 39a). However, this specimen does not agree with the original description and the original illustration (Draudt 1923) (Fig. 39e) and therefore is not a syntype. Syntypes of *T. trifasciata* f. *obscurior* were described as darker, but the "lectotype" is a paler specimen. The dark bands in the illustration are entire (Fig. 39a), but they are separated into spots in the "lectotype" (Fig. 39a). Austin and Warren (2002) who, per the identity of Mielke's lectotype, placed *T. trifasciata* form *obscurior* as a synonym of *Timochares ruptifasciata* (Plötz, 1884) (type locality in "South America," a mistake) instead of *Timochares trifasciata* (Hewitson, 1868) (type locality in Bolivia as indicated on the label of the lectotype), noted that additional investigations are warranted.

We carried out additional investigations and found a specimen in ZfBS with the identification label "obscurior" in Draudt's handwriting and typical of specimens illustrated in Draudt (1921–1924) (Fig. 39f). This specimen is in the drawer of specimens that were likely illustrated in Draudt (1921–1924), agrees with the original description and illustration (Fig. 39e) of *T. trifasciata* form *obscurior*, and is confidently a syntype. Invalid paralectotypes in SMF, Seitz specimens with numbers 6316 (Fig. 39c) and 6317 (Fig 39b) may not be syntypes of *T. trifasciata* form *obscurior*, but specimens Draudt considered to be regular *T. trifasciata* (Fig. 39d).

To stabilize nomenclature and define the name *T. trifasciata* form *obscurior* objectively, N.V.G. hereby designates a male syntype in the ZfBS collection (Fig. 39f) that bears the following four rectangular labels (2nd and 3rd handwritten, others printed): [Rio Songo | Bolivia | 750 m | Coll. Fassl],

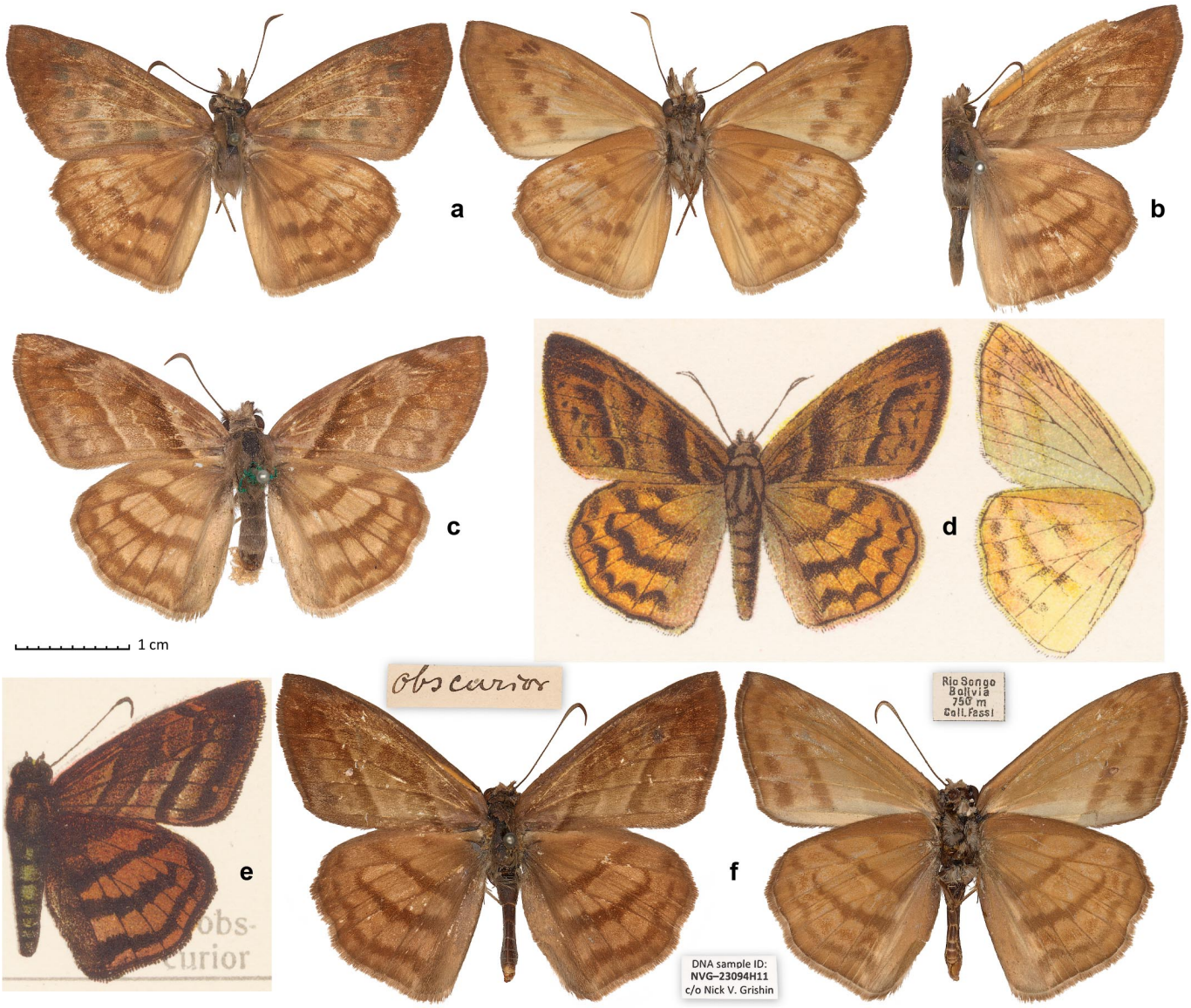

Fig. 39. Investigation of *Timochares trifasciata* form *obscurior* Draudt, 1923: **a)** invalid lectotype, which is not a syntype, but a specimen (paratype) of *T. fuscifasciata* **sp. n.**; **b)** and **c)** invalid paralectotypes, specimens 6317 and 6316, respectively, possibly considered typical *trifasciata* by Draudt (1923) with **c)** similar to **d)** illustration by Draudt (1923); **e)** illustration of *T. trifasciata* form *obscurior* from Draudt (1923), and **f)** the lectotype of *T. trifasciata* form *obscurior* designated herein, with its labels (labels reduced two times compared to specimens, and a folded incorrect identification label on a piece of newspaper is not shown). Dorsal and ventral views are shown on the left and right of the figure panel letter.

[obscurior], [Timochares ruptifasciata Plötz | (Antigonus))] (label folded, written on a piece of newspaper), and [DNA sample ID: | NVG-23094H11 | c/o Nick V. Grishin] as the **lectotype** of *Timochares trifasciata* form *obscurior* Draudt, 1923. The lectotype lacks its left antenna, has nearly no damage to fringes, its right costal fold is closed, and its left fold is partly open from the base. Images of the lectotype photographed by Ernst Brockmann are shown on the Butterflies of America website (Warren et al. 2024). The type locality of *T. trifasciata* form *obscurior* becomes Bolivia: Rio Zongo, elevation 750 m, and the name returns to the synonymy with *Timochares trifasciata* (Hewitson, 1868) as originally proposed.

Timochares sanda Evans, 1953, stat. nov. is a species distinct from *Timochares trifasciata* (Hewitson, 1868)

Genomic analysis reveals that *Timochares trifasciata sanda* Evans, 1953 (type locality in Argentina) is genetically differentiated from *Timochares trifasciata trifasciata* (Hewitson, 1868) (type locality in

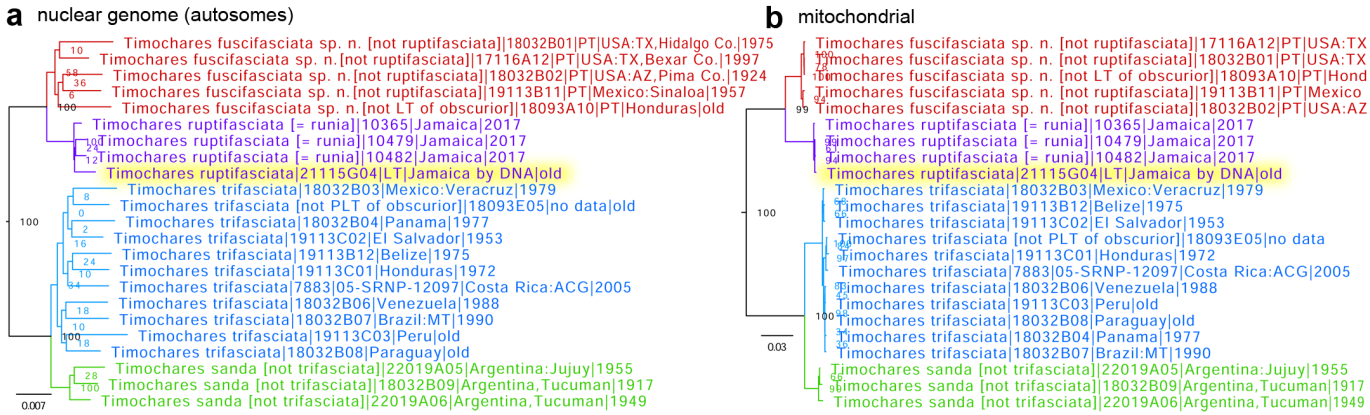

Fig. 40. Phylogenetic trees of *Timochares* species inferred from protein-coding regions of **a)** the nuclear (autosomes) and **b)** the mitochondrial genome. Different species are shown in different colors: *T. fuscifasciata* **sp. n.** (red), *T. ruptifasciata* (purple, the lectotype highlighted in yellow), *T. trifasciata* (blue), and *T. sandia* **stat. n.** (green).

Bolivia per the label of the lectotype) at the species level (Fig. 40), e.g., their COI barcodes differ by 2.3% (15 bp). Therefore, we propose that *Timochares sanda* Evans, 1953, **stat. nov.** is a species distinct from *Timochares trifasciata* (Hewitson, 1868).

Timochares trifasciata form *obscurior* Draudt, 1923 is an unavailable name

The original description of *Timochares trifasciata* form *obscurior* Draudt, 1923 (type locality in Bolivia: Rio Zongo) states: "The ground-colour is variable, and dark (= obscurior form. nov.) … and light forms fly together at the same places" (Draudt 1923). According to the Glossary of the ICZN Code (1999), an infrasubspecific name is "a name applied to an infrasubspecific entity." The infrasubspecific entity is defined in part as "specimen(s) within a species differing from other specimens in consequence of intra-populational variability (e.g. … variants of … polymorphism)." Because the statement "dark … and light forms fly together at the same places" as a qualification of variable ground color refers to "variants of … polymorphism" if these "forms" are conspecific, and in this case, both are *Timochares trifasciata* according to Draudt (1923), *Timochares trifasciata* form *obscurior* is an infrasubspecific entity, and the name applied to it is infrasubspecific. The name *obscurior* was proposed as infrasubspecific and was not adopted (per ICZN Code glossary: "adopt, v. To use an unavailable name as the valid name of a taxon in a way which establishes it as a new name with its own authorship and date") as the valid name for a species or a subspecies before 1985 (Art. 45.6.4) (Evans 1953). Therefore, we conclude that the name *Timochares trifasciata* form *obscurior* Draudt, 1923 is unavailable according to the ICZN Code article 45.6. For those who accept this conclusion, this name does not have formal type specimens, and its "lectotype" is designated above instead of the invalid "lectotype" (not a syntype) designated by Mielke (1993).

Lectotype designation for *Antigonus ruptifasciata* Plötz, 1884

Antigonus ruptifasciata Plötz, 1884 was described from an unstated number of specimens from "South America" (Plötz 1884) and is currently treated as a valid species of the genus *Timochares* Godman & Salvin, 1896 (type species *Leucochitonea trifasciata* Hewitson, 1868) (Mielke 2005). In Latin, *ruptus* means broken, torn, or severed, and *fascia* means band or stripe. The original description and the name indicate that *A. ruptifasciata* has bands broken into spots in contrast to *Timochares trifasciata* (Hewitson, 1868) (type locality in Bolivia, as indicated on the label of the lectotype).

To our knowledge, this species has not been recorded from South America (Evans 1953), and therefore the type locality is questionable. To deduce its possible type locality by genomic comparison, we searched for syntypes of *A. ruptifasciata*. One syntype, from the Weymer collection, now in MFNB, was found (Fig. 41a). According to its labels, it was identified by Plötz as *ruptifasciata* before publication

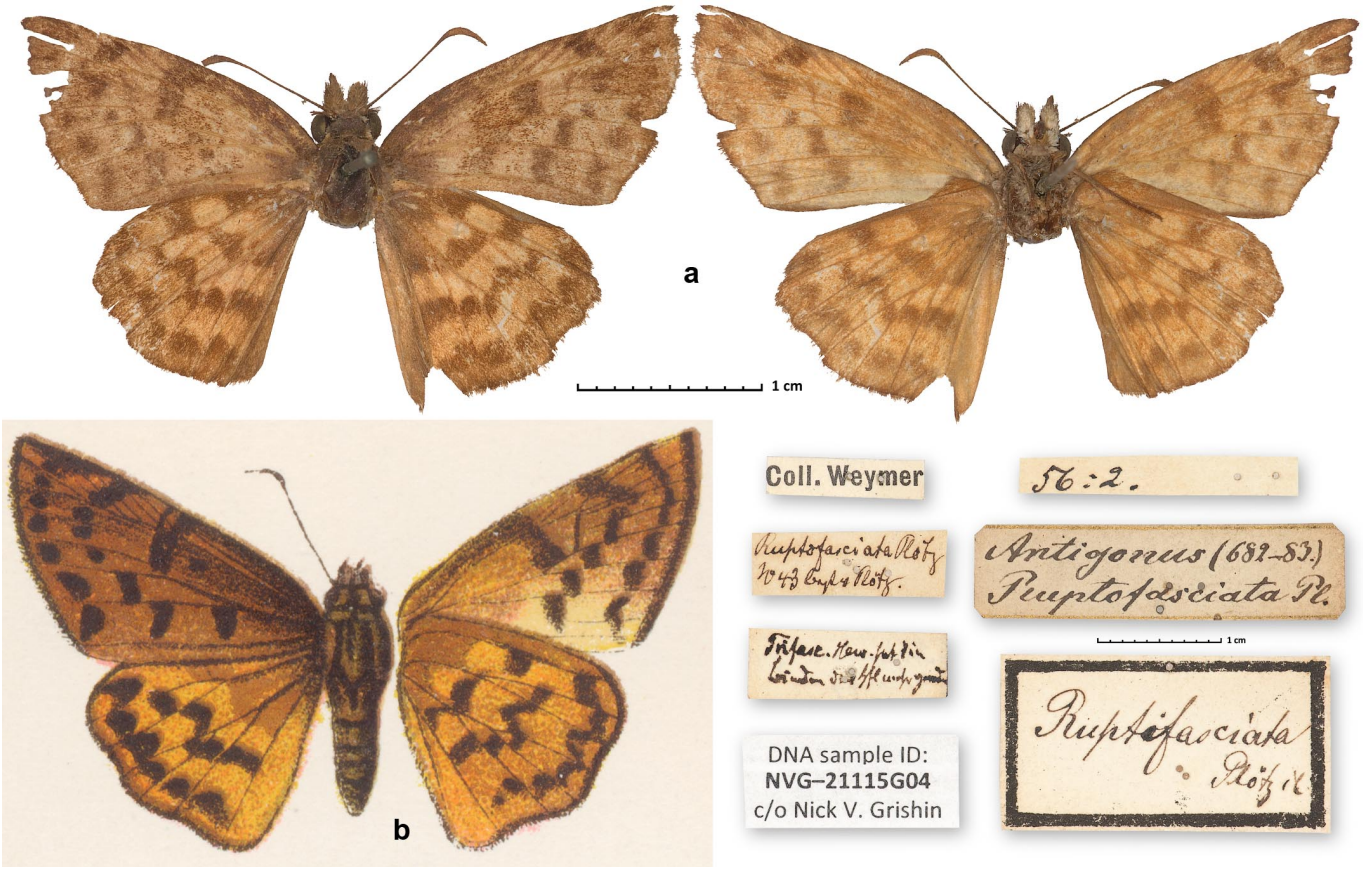

Fig. 41. *Antigonus ruptifasciata* **a)** lectotype with its labels (reduced by a third compared to the specimen, scale among them), and **b)** illustration from Draudt, likely a copy of the unpublished Plötz drawing t. 1019. Dorsal and ventral views are shown on the left and right of the figure panel letter.

of the name (the name was given as "i l" for "in litteris"), and one of the identification labels is in Plötz's handwriting. The specimen lacks any indication of its provenance, which may explain a vague "South America" as the type locality, possibly Plötz's or Weymer's guess. Although this specimen does not bear a label to explicitly indicate that it is a type specimen, it agrees with the original description and was studied and identified by Plötz before publication, and, therefore, it is a syntype. Moreover, the syntype also agrees with the illustration of *A. ruptifasciata* in Draudt (1923), which shows a pale specimen with large and distinct brown spots arranged into irregular bands (reproduced here as Fig. 41b). This illustration is a likely copy of Plötz's unpublished and presumably lost drawing t.[afel] 1019 (Plötz 1884). We have not found any other credible syntypes of *A. ruptifasciata* and it is possible that no others existed. Nevertheless, we follow the ICZN Code Recommendation 73F (ICZN 1999) avoiding the assumption of the holotype and considering any type specimens of *A. ruptifasciata* to be syntypes.

To stabilize nomenclature and define the name *A. ruptifasciata* objectively, N.V.G. hereby designates the sequenced syntype, a female in the MFNB collection that bears the following seven white rectangular labels (1st and last printed, others handwritten): [Coll. Weymer], [Ruptofasciata Plötz | nº 43 best. v. Plötz], [Trifasc.Hew.ist die | binden im Hfl mehr gerade], [Antigonus (682-83.) | Ruptofasciata Pl.], [Ruptifasciata | Plötz i l], [56:2.], and [DNA sample ID: | NVG-21115G04 | c/o Nick V. Grishin] as the **lectotype** of *Antigonus ruptifasciata* Plötz, 1884. The number 43 possibly refers to some specimen number in Weymer's collection, maybe a sequential number of each specimen identified by Plötz in all Plötz's identifications of Weymer's specimens, like "43rd specimen identified by Plötz"; best[immt]. v[on]. is for identified by; the 2nd and 5th labels are in Weymer's handwriting, and the 4th label is in Plötz's handwriting; the label 56:2 gives a genus number (56 - *Timochares*) and a species number (2 - *ruptifasciatus*) in the Mabille catalog (1903) that was used as a guide for arranging the Hesperiidae

collection in Berlin. The lectotype lacks its abdomen and has chipped at the outer margin: left forewing near the apex, right forewing in the middle, and right hindwing near the tornus. The COI barcode sequence of the lectotype, sample NVG-21115G04, GenBank PQ489711, 658 base pairs is:

AACTTTATATTTTATTTTTGGAATTTGAGCAGGAATAGTTGGAACTTCTCTAAGCCTTCTTATTCGAACTGAATTAGGAAATCCCGGATCATTAATTGGAGATGATCAAATTTATAATACA
ATTGTTACAGCTCATGCCTTCATTATAATTTTTTTTATGGTTATACCAATTATAATTGGAGGATTTGGAAATTGATTAGTACCATTAATATTAGGAGCTCCAGATATAGCATTTCCACGAA
TAAATAATATAAGATTTTGACTTTTACCCCCCTCTTTAATATTATTAATTTCTAGAAGAATCGTAGAAAATGGAGCCGGAACAGGATGAACAGTTTACCCCCCCCTCTCAGCTAATATTGC
ACACCAAGGTTCTTCTGTGGACTTAGCTATTTTTTCCCTACATTTAGCAGGTATCTCCTCAATTCTTGGAGCAATTAATTTTATTACAACAATTATTAATATACGAATTAGAAATTTATCC
TTTGATCAAATACCCCTATTTGTCTGAGCTGTTGGTATTACAGCATTACTTTTATTATTATCTTTACCAGTTTTAGCTGGAGCTATTACTATACTTCTAACTGATCGAAATCTTAATACAT
CATTTTTTGATCCTGCAGGAGGGGGAGATCCAATTTTATATCAACATTTATTT

Genomic comparison places the lectotype with specimens from Jamaica and not with those from continental America (Fig. 40). Wing patterns (Fig. 41) agree with this conclusion: brown spots are larger and darker and stand out with more contrast from the pale ground color in the lectotype, more similar to Jamaican specimens. Therefore, the type locality of *A. ruptifasciata* becomes Jamaica.

Timochares ruptifasciata runia Evans, 1953 is a new junior subjective synonym of *Timochares ruptifasciata* (Plötz, 1884)

Before Evans (1953), all populations of *Timochares ruptifasciata* (Plötz, 1884) (type locality in Jamaica, see above) were treated under this name. Evans (1953) was the first to divide *T. ruptifasciata* into subspecies. However, he did not have access to the type material and apparently overlooked the illustration of *T. ruptifasciata* in Draudt (1923) (reproduced here as Fig. 41b), which agrees better with the Jamaican populations than continental populations. Due to these oversights, instead of proposing a new name for the continental populations, Evans described Jamaican specimens as a new subspecies, thus misidentifying *Timochares ruptifasciata* because he assumed that this name referred to the continental subspecies. Both wing pattern and genomic analysis of the *T. ruptifasciata* lectotype designated above place it with Jamaican specimens. Therefore, we propose that *Timochares ruptifasciata runia* Evans, 1953, **syn. nov.** is a junior subjective synonym of *Timochares ruptifasciata* (Plötz, 1884). As a result, continental populations remain without an available name. Moreover, Austin and Warren (2002) argued that Jamaican populations (referred to by the name *T. runia*) and continental populations (referred to by the name *T. ruptifasciata*) are distinct at the species level, and our genomic analysis agrees with this conclusion (Fig. 40), e.g., their COI barcodes differ by 3.6% (24 bp). For all these reasons, continental populations of *T. ruptifasciata* constitute a new species described below.

Timochares fuscifasciata Grishin, new species

http://zoobank.org/77C3A246-2F3A-465B-8091-42AB7491A0C5

(Figs. 39a, 40 part, 42–43)

Definition and diagnosis. As discussed above, Evans (1953) misidentified *Timochares ruptifasciata* (Plötz, 1884) (type locality in Jamaica) and misapplied this name to continental populations related to Jamaican *T. ruptifasciata*. These continental populations are genetically differentiated from *T. ruptifasciata* at the species level (Fig. 40), e.g., their COI barcodes differ by 3.6% (24 bp), thus confirming phenotypic assessment of Austin and Warren (2002). Because no available name applies to this species, it is new. This new species keys to "*Timochares ruptifasciata ruptifasciata*" (F.5.2(a)) in Evans (1953) and was regarded as this taxon by him due to misidentification. Therefore, Evans' key directly applies to this species, with additional comments on the identification by Austin and Warren (2002) (under the name *T. ruptifasciata*) who illustrated its genitalia. In summary, the new species differs from its relatives by the following combination of characters: pale yellowish-brown (frequently tan) wings with irregular brown bands separated into spots (bands are less irregular than in *T. ruptifasciata*); compared to *T. ruptifasciata*, the spots are more interconnected and less contrasting with the ground color, dorsal hindwing is usually with a yellower than redder tint, and ventral side of wings is yellow-tan rather than red-tan. In DNA, a combination of the following base pairs is diagnostic in the nuclear genome: aly5196.11.5:A1762T, aly5196.11.5:G1789A, aly5196.11.5:T1848C, aly16.16.5:C72G, aly16.16.5:A99T, and COI barcode: A91C, C340T, A466G, T490C, T589C, A622G.

Fig. 42. *Timochares fuscifasciata* **sp. n.** holotype ♀ in dorsal (left) and ventral (right) views, data in text.

Barcode sequence of a paratype. Sample NVG-17116A12, GenBank PQ489712, 658 base pairs:

AACTTTATACTTTATTTTTGGAATTTGGGCAGGAATAGTTGGAACTTCTCTAAGTCTTCTTATTCGAACTGAATTAGGAAATCCCGGATCCTTAATTGGAGATGATCAAATTTATAATACA
ATTGTTACAGCTCATGCCTTCATTATAATTTTTTTTATAGTTATACCAATTATAATTGGAGGATTTGGAAATTGATTAGTACCATTAATATTAGGAGCCCCAGATATAGCATTTCCACGAA
TAAATAATATAAGATTTTGACTTTTACCCCCCTCTTTAATATTATTAATTTCTAGAAGAATCGTAGAAAATGGAGCCGGAACAGGATGAACAGTTTATCCCCCCCTTTCAGCTAATATTGC
ACATCAAGGTTCTTCTGTAGACTTAGCTATTTTTTCCCTACATTTAGCAGGTATTTCCTCAATTCTTGGAGCAATTAACTTTATTACAACAATTATTAATATGCGAATTAGAAATTTATCT
TTTGACCAAATACCTTTATTTGTTTGAGCTGTTGGTATTACAGCATTACTTTTGTTATTATCTTTACCAGTTTTAGCTGGAGCTATTACTATACTTTTAACTGACCGAAATCTTAATACAT
CATTTTTTGACCCTGCGGGAGGAGGAGATCCAATTTTATATCAACATTTATTT

Type material. Holotype: ♀ deposited in the Texas A&M University Insect Collection, College Station, TX, USA (TAMU), illustrated in Fig. 42, bears the following five printed (text in italics handwritten) rectangular labels, four white: [TEXAS: | HIDALGO COUNTY, | Santa Ana National | Wildlife Refuge], [ex larva | *7 FEB 1972* | Roy O. Kendall | & C. A. Kendall], [Larval foodplant: | MALPIGHIACEAE | Malpighia glabra | Linnaeus | (~~Juvenile~~ fol./~~b. buds~~)], [HESPERIIDAE, | Pyrginae: | Timochares ruptifas- | ciatus ruptifasciatus | (Plotz, 1884) | ♀ det. R.O. Kendall | [M. & B. No. 79]], and one red [HOLOTYPE ♀ | Timochares | fuscifasciata Grishin]. A female is chosen as the holotype, the same sex as the lectotypes of *T. trifasciata* and *T. ruptifasciata*. **Paratypes:** 6♂♂ and 6♀♀: USA: 1♀ NVG-18032B02, USNMENT_01201760 Arizona, Pima Co., Baboquivari Mts., 1924, O. C. Poling leg. [USNM] and Texas: 1♀ NVG-17116A12 Bexar Co., San Antonio, 17-Jul-1997, Roy O. Kendall leg., ex larva on *Malpighia glabra* [TAMU]; Hidalgo Co.: 1♀ NVG-23074A11, Peñitas, 4-Nov-2004, N. V. Grishin leg. [NVG]; 1♂ NVG-18032B01, USNMENT_01201758 Bentsen-Rio Grande Valley State Park, 18-Oct-1975 E. C. Knudson leg. [USNM]; Mission, 10th Street at irrigation ditch, Roy O. Kendall & C. A. Kendall leg. [TAMU]: 1♂ 9-Sep-1972 and 1♀ 8-Sep-1972, genitalia vials NVG130104-15 and NVG130104-14, respectively; and 1♀ McAllen, Vanecia Motel, 22-Oct-1972, Roy O. Kendall & C. A. Kendall leg., ex larva on *Malpighia glabra* [TAMU] and Cameron Co., Brownsville: 1♂ NVG-23124H07, USNMENT_01201759 13-May-1945, H. A. Freeman leg.

Fig. 43. Male genitalia of *Timochares fuscifasciata* **sp. n.** paratype NVG-23124H07 (data in text): **a)** left and **b)** right lateral and **c)** dorsal views.

[USNM] and 1♀ 11-Jan-1970, Roy O. Kendall & C. A. Kendall leg., ex larva on *Malpighia glabra* [TAMU]; Mexico: 1♀ Tamaulipas, Paso del Abra, near El Abra, 1-Apr-1974, Roy O. Kendall & C. A. Kendall leg., ex larva on *Malpighia glabra* [TAMU] and 1♂ NVG-19113B11, USNMENT_01602123 Sinaloa, Culiacán, 8-Jul-1957, G. W. Rawson leg. [USNM]; and 1♂ NVG-18093A10 Honduras: San Pedro Sula, ex. coll. Fruhstorfer, invalid lectotype of *Timochares trifasciata* form *obscurior* Draudt, 1923 [SMF].

Type locality. USA: Texas, Hidalgo Co., Santa Ana National Wildlife Refuge.

Etymology. In Latin, *fuscus* is brown, and *fascia* is a band. The name is a Latin equivalent of "Brown-banded," the English name of the species found in the USA, present in the lower Rio Grande Valley of Texas in most years and straying to Arizona and New Mexico. The name is an adjective. Spots on wings are more discrete and irregular in the Jamaican species. Therefore, *rupti-* is in better agreement with Jamaican populations.

Suggested English name. Brown-banded Skipper is the current name for this species, which is misidentified by the Latin name.

Distribution. From southern USA (SE Arizona, SW New Mexico, S Texas) through Mexico to Honduras.

Comments. Primary types are the name bearers and specimens conspecific with the type bear its name. This is one of the basic principles of the ICZN Code (ICZN 1999). As in other similar cases, e.g., *Hesperia colorado* (Scudder, 1874) (Cong et al. 2021), *Burnsius communis albescens* (Plötz, 1884) (Zhang et al. 2022a), and *Nastra fusca* (Grote & Robinson, 1867) (Zhang et al. 2022c), we accept the type specimen of *T. ruptifasciata* as the name bearer instead of attempting to set it aside. Notably, before 2002, when Austin and Warren (2002) proposed to treat Jamaican populations of *T. ruptifasciata* as a distinct species *Timochares runia* Evans, 1953, they were considered conspecific with continental populations.

Subfamily Hesperiinae Latreille, 1809
Tribe Taractrocerini Voss, 1952

Suniana Evans, 1934 is a subgenus of *Potanthus* Scudder, 1872

Genomic phylogeny of the tribe Taractrocerini Voss, 1952 highlights genetic closeness of three genera: *Potanthus* Scudder, 1872 (type species *Hesperia omaha* Edwards, 1863), *Ocybadistes* Heron, 1894 (type species *Ocybadistes walkeri* Heron, 1894), and *Suniana* Evans, 1934 (type species *Pamphila lascivia* Rosenstock, 1885) (Fig. 44 green, blue, and olive), e.g., COI barcodes of *Potanthus* and *Suniana* differ by 5.9–6.2% (39–41 bp). Genetic differentiation between *Potanthus* and *Suniana* is smaller than that for most genera. Furthermore, they are close in appearance and are not immediately recognizable in the field. Therefore, we proposed to treat *Suniana* Evans, 1934, **stat. nov.** as a subgenus of *Potanthus* Scudder, 1872. Presently, we retain *Ocybadistes* as a genus because it is stronger separated genetically from *Potanthus* than *Suniana*, but it may be that the former is also a subgenus of the latter, a question to be addressed with a comprehensive species-level phylogeny of the group. *Suniana* was morphologically differentiated from *Potanthus* mainly by the flattened antennal club (a character shared with *Ocybadistes*, which is not its closest relative) and divided uncus (in *Potanthus*, the shape of uncus is variable, and some species currently placed in this genus have bifid uncus) (Evans 1949). Thus, although *Suniana* is a morphologically compact group of currently three species, it falls among other such groups in *Potanthus* and *Ocybadistes*. *Potanthus* encompasses about 40 species, some of which are phenotypically more different from others than *Suniana*. Therefore, including three *Suniana* species in *Potanthus* to achieve a more internally consistent classification into genera seems advantageous.

Ocybadistes hypomeloma Lower, 1911 belongs to the genus *Potanthus* Scudder, 1872 and not *Ocybadistes* Heron, 1894

Genomic analysis reveals that *Ocybadistes hypomeloma* Lower, 1911 (type locality in Australia: Sydney, the sequenced specimen shown in Fig. 45a) since its description placed in *Ocybadistes* Heron, 1894 (type

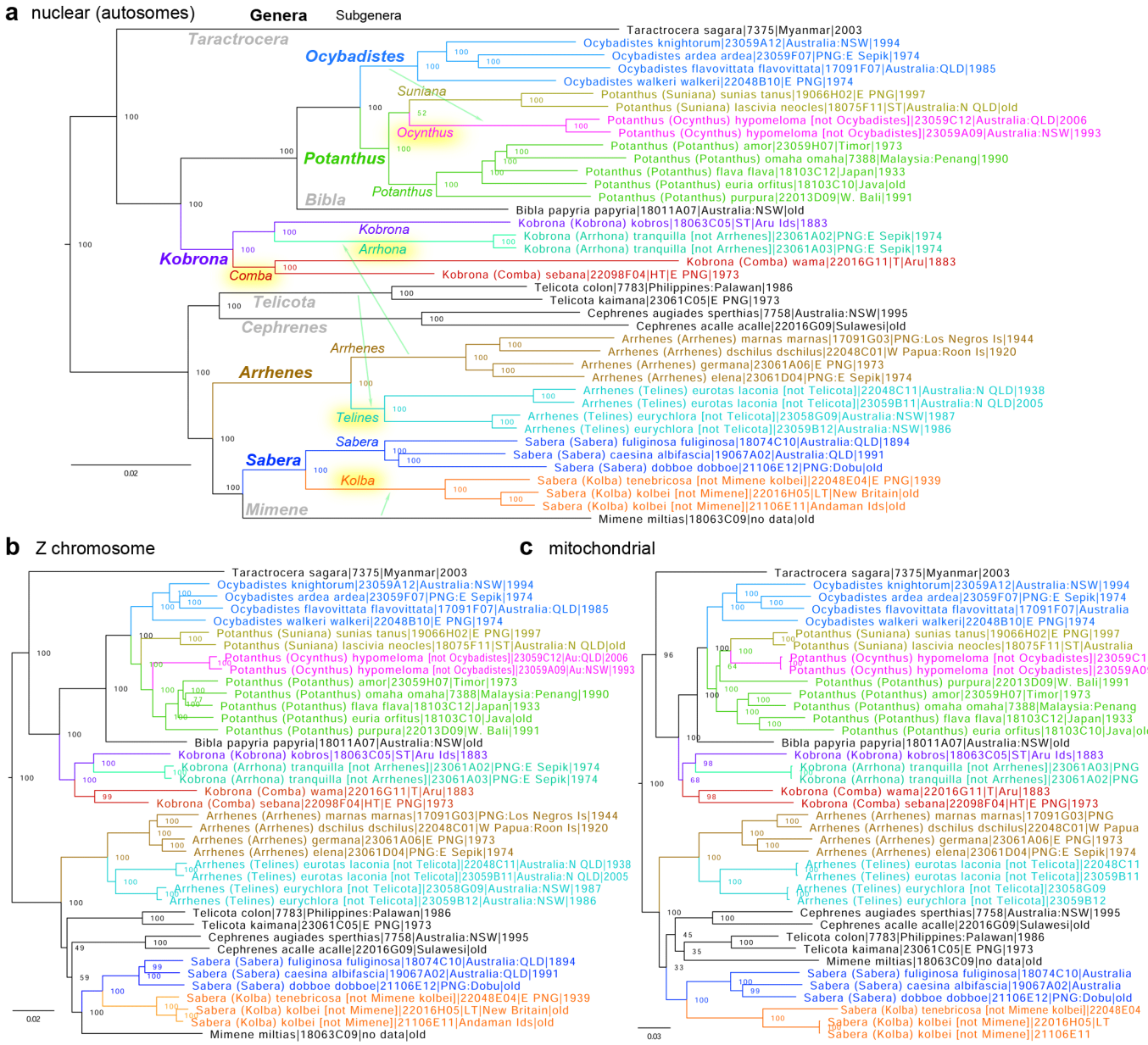

Fig. 44. Phylogenetic trees of selected Taractrocerini inferred from protein-coding regions in **a)** the nuclear genome (autosomes), based on 2,613,594 positions, **b)** the Z chromosome, based on 187,662 positions, and **c)** the mitochondrial genome (ultrafast bootstrap): *Ocybadistes* (blue), *Potanthus* (green, with subgenera *Suniana* in olive and *Ocynthus* **subgen. n.** in magenta), *Kobrona* (purple with subgenera *Arrhona* **subgen. n.** in aquamarine and *Comba* **subgen. n.** in red), *Arrhenes* (brown with subgenus *Telines* **subgen. n.** in cyan), and *Sabera* (dark blue with subgenus *Kolba* **subgen. n.** in orange). In **a)**, names of genera and subgenera are given near corresponding branches, names of subgenera described in this work are highlighted in yellow. Green arrows point from the clade of the genus where one or several species were placed previously (name after "not" in square brackets) to the clade of this species/several species that is/are being transferred between genera.

species *Ocybadistes walkeri* Heron, 1894) is not monophyletic with it and instead originates within *Potanthus* Scudder, 1872 (type species *Hesperia omaha* Edwards, 1863) that includes *Suniana* Evans, 1934 (type species *Pamphila lascivia* Rosenstock, 1885) as a subgenus, see above (Fig. 44). Therefore, we propose that *O. hypomeloma* belongs to the genus *Potanthus* Scudder, 1872 and not *Ocybadistes* Heron, 1894, as *Potanthus hypomeloma* (Lower, 1911), **comb. nov**. *Potanthus hypomeloma* is confidently placed as sister to sequenced specimens of the subgenus *Potanthus* in the Z chromosome tree (Fig. 44b), is a confident sister to the subgenus *Suniana* in the mitochondrial genome tree (Fig. 44c), and its affinity within the genus *Potanthus* is not strongly supported in the autosome tree (Fig. 44a). Therefore, *P. hypomeloma* is from a lineage equivalent to the subgenera *Potanthus* and *Suniana*, hence representing a separate subgenus, which is new, because there are no available genus-group names associated with it.

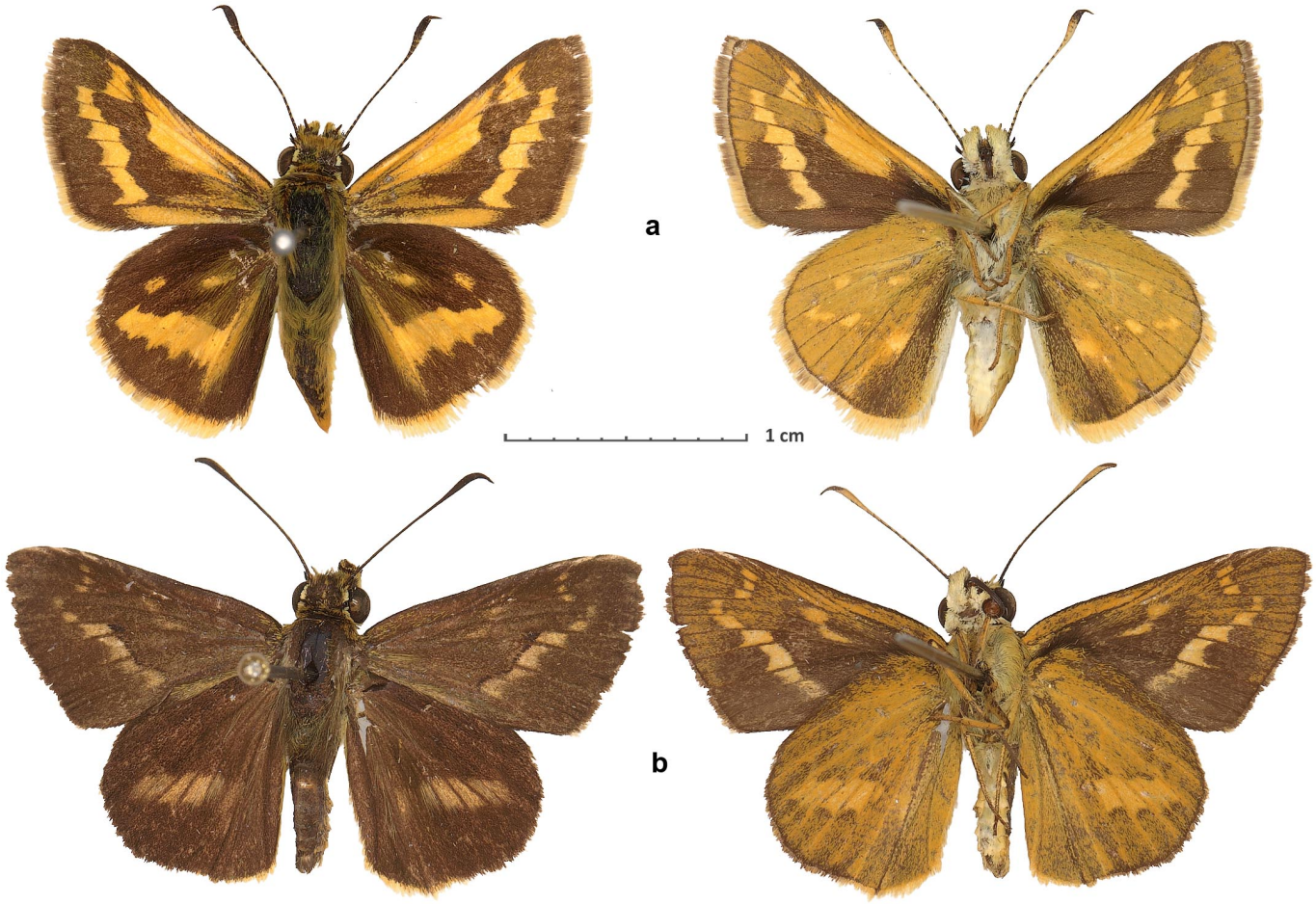

Fig. 45. Sequenced specimens of Taractrocerini in dorsal (left) and ventral (right) views [MGCL]: **a)** *Potanthus* (*Ocynthus*) *hypomeloma* **comb. nov.** ♂ NVG-23059A09 Australia, New South Wales, 10 km W of Mt. Sugarloaf, 3-Feb-1993, A. Atkins leg.; **b)** *Kobrona* (*Arrhona*) *tranquilla* **comb. nov.** ♂ NVG-23061A03 Papua New Guinea, Eastern Sepik District, 10 mi S of Maprik, 31-May-1974, D. L. Lindsley leg.

Ocynthus Grishin, new subgenus

http://zoobank.org/82DE2305-BD50-4DCC-A3A4-3E886EDD0124

Type species. *Ocybadistes hypomeloma* Lower, 1911.

Definition. Genomic phylogeny of the tribe Taractrocerini Voss, 1952 reveals that *Potanthus hypomeloma* (Lower, 1911), **comb. nov.** cannot be reliably assigned to existing subgenera in *Potanthus* Scudder, 1872 (type species *Hesperia omaha* Edwards, 1863) (see above) and thus represents a new subgenus. This new subgenus keys to L.2.3 in Evans (1949) and differs from its relatives by a combination of the following characters: flattened antennal club; notched at the tip uncus not narrowing to a single point; rounded valva with a terminal small knob; narrow and irregular black discal forewing stigma in males between the veins M_3 and 1A+2A; whitish inner margin of ventral hindwing; and orange-yellow spot in the cell RS-M_1 of the dorsal hindwing separated from the postdiscal band (Fig. 45a). In DNA, a combination of the following characters is diagnostic in the nuclear genome: aly956.3.2:T502C, aly956.3.2:G2082A, aly1264.8.3:G292C, aly4305.13.5:G141A, aly517.17.2:G534A, and COI barcode: T13C, T52C, T256C, T358C, A484T.

Etymology. This name combines the previous and current genus names of these species: *Ocy*[badistes] + [Pota]*nthus* and is a masculine noun in the nominative singular.

Species included. Only the type species (i.e., *Ocybadistes hypomeloma* Lower, 1911).

Parent taxon. Genus *Potanthus* Scudder, 1872.

Padraona tranquilla Swinhoe, 1905 belongs to the genus *Kobrona* Evans, 1935 and not *Arrhenes* Mabille, 1904

Genomic phylogeny of the tribe Taractrocerini Voss, 1952 that includes a pair of *Padraona tranquilla* Swinhoe, 1905 (type locality in Papua New Guinea: Milne Bay, a male shown in Fig. 45b), currently in the genus *Arrhenes* Mabille, 1904 (type species *Pamphila marnas* Felder, 1860) reveals that it is not monophyletic with this genus and instead originates within *Kobrona* Evans, 1935 (type species *Plastingia kobros* Plötz, 1885). Therefore, *Padraona tranquilla* Swinhoe, 1905 belongs to the genus *Kobrona* Evans, 1935 and not *Arrhenes* Mabille, 1904, and we propose *Kobrona tranquilla* (Swinhoe, 1905), **comb. nov**.

Arrhona Grishin, new subgenus

http://zoobank.org/08BDABFE-9AB9-4952-9D26-9D2995D5419A

Type species. *Padraona tranquilla* Swinhoe, 1905.

Definition. The lineage with *Kobrona tranquilla* (Swinhoe, 1905), **comb. nov.** represents a new subgenus due to its phenotypic distinction that caused its former misclassification as *Arrhenes* Mabille, 1904 (type species *Pamphila marnas* Felder, 1860) (see above) and notable genetic differentiation (Fig. 44), e.g., COI barcodes of the type species of *Kobrona* Evans, 1935, *K. kobros* (Plötz, 1885) (type locality in Aru), and *K. tranquilla* differ by 7% (46 bp). This new subgenus keys to L.6.6 in Evans (1949) and differs from its relatives by a combination of the following characters: not flattened antennal club; relatively long antennae, about ½ of the costal margin; rather thin 3rd segment of palpi, not as narrow as in *Ocybadistes* Heron, 1894 (type species *Ocybadistes walkeri* Heron, 1894) but not a stout as in other *Kobrona*; undivided (but with side points) uncus, terminally rectangular and flat, with lateral margins nearly parallel in dorsal view and flat; expanded dorsad ampulla of the valva, with concave dorsal margin posteriad, weakly developed, knob-like harpe armed with small spines; narrow and irregular stigma in males between veins M_3 and 1A+2A in the middle of the forewing; and pale-brown (not orange) and narrow spots on wings (Fig. 45b). In DNA, a combination of the following characters is diagnostic in the nuclear genome: aly814.12.10:G51A, aly1313.18.2:T943C, aly1313.18.2:T972C, aly1313.18.2:A978C, aly235.6.3:T141C, and COI barcode: T133C, T287C, T382A, T418C, A474G, A526T.

Etymology. This name combines the previous and current genus names of these species: *Arrh*[enes] + [Kobr]*ona* and is a feminine noun in the nominative singular.

Species included. Only the type species (i.e., *Padraona tranquilla* Swinhoe, 1905).

Parent taxon. Genus *Kobrona* Evans, 1935.

Comba Grishin, new subgenus

http://zoobank.org/619BDB9D-5E50-4F5E-88FA-30AF030EF1CF

Type species. *Hesperia wama* Plötz, 1885.

Definition. Genomic analysis reveals that *Kobrona* Evans, 1935 (type species *Plastingia kobros* Plötz, 1885) is a genetically diverse genus (Fig. 44), e.g., COI barcodes of the type species and *Kobrona sebana* M. Parsons, 1986 (type locality in Papua New Guinea: Morobe District) differ by 8.1% (53 bp). Moreover, the newly described subgenus *Arrhona* **subgen. n.**, renders the rest of *Kobrona* paraphyletic, consisting of two other clades that represent other subgenera: the nominate subgenus sister to *Arrhona* and an unnamed one that includes *K. sebana*. For these two reasons, a morphologically distinct group of species that includes *K. sebana* constitutes an unnamed subgenus distinct from the nominate and *Arrhona*. This new subgenus keys to L.12.1 in Evans (1949) and differs from its relatives by a combination of the following characters: terminally concave harpe densely decorated with bristles that give the distal margin appearance of a comb (as illustrated by Evans (1949) and Parsons (1986)); tapered, weakly divided uncus with knob- or tooth-like arms; long antennae, longer than ½ of the costal margin; shorter and stouter 3rd segment of palpi; and rather produced, not rounded, forewings. In DNA, a combination of the following

characters is diagnostic in the nuclear genome: aly528.40.1:C1030T, aly10226.43.1:T54C, aly363.24.2:T18C, aly84.12.3:A69T, aly349.41.4:G834A, and COI barcode: A25T, 38T, A88T, T187C, T190A, C328C.

Etymology. The name is given for the comb-like array of bristles at the distal and somewhat excavate margin of the valva. The name is a feminine noun in the nominative singular.

Species included. The type species (i.e., *Hesperia wama* Plötz, 1885), *Kobrona croma* Evans, 1949, *Kobrona denva* Evans, 1949, *Kobrona edina* Evans, 1949, *Kobrona idea* Evans, 1949, *Kobrona pansa* Evans, 1935, *Kobrona sebana* M. Parsons, 1986, and *Kobrona vanda* Evans, 1949.

Parent taxon. Genus *Kobrona* Evans, 1935.

Pamphila eurotas C. Felder, 1860 and *Telicota eurychlora* Lower, 1908 belong to the genus *Arrhenes* Mabille, 1904 and not *Telicota* Moore, 1881

Genomic phylogeny of the tribe Taractrocerini Voss, 1952 reveals that *Pamphila eurotas* C. Felder, 1860 (type locality in Ambon) and *Telicota eurychlora* Lower, 1908 (type locality Australia: New South Wales, Ballina) (two sequenced specimens shown in Fig. 46) currently placed in *Telicota* F. Moore, 1881 (type species *Papilio colon* Fabricius, 1775) are not monophyletic with it and form a clade sister to *Arrhenes* Mabille, 1904 (type species *Pamphila marnas* Felder, 1860) (Fig. 44). Therefore, these two species do not belong in *Telicota*, and we place them in *Arrhenes* as *Arrhenes eurotas* (C. Felder, 1860), **comb. nov.** and *Arrhenes eurychlora* (Lower, 1908), **comb. nov**.

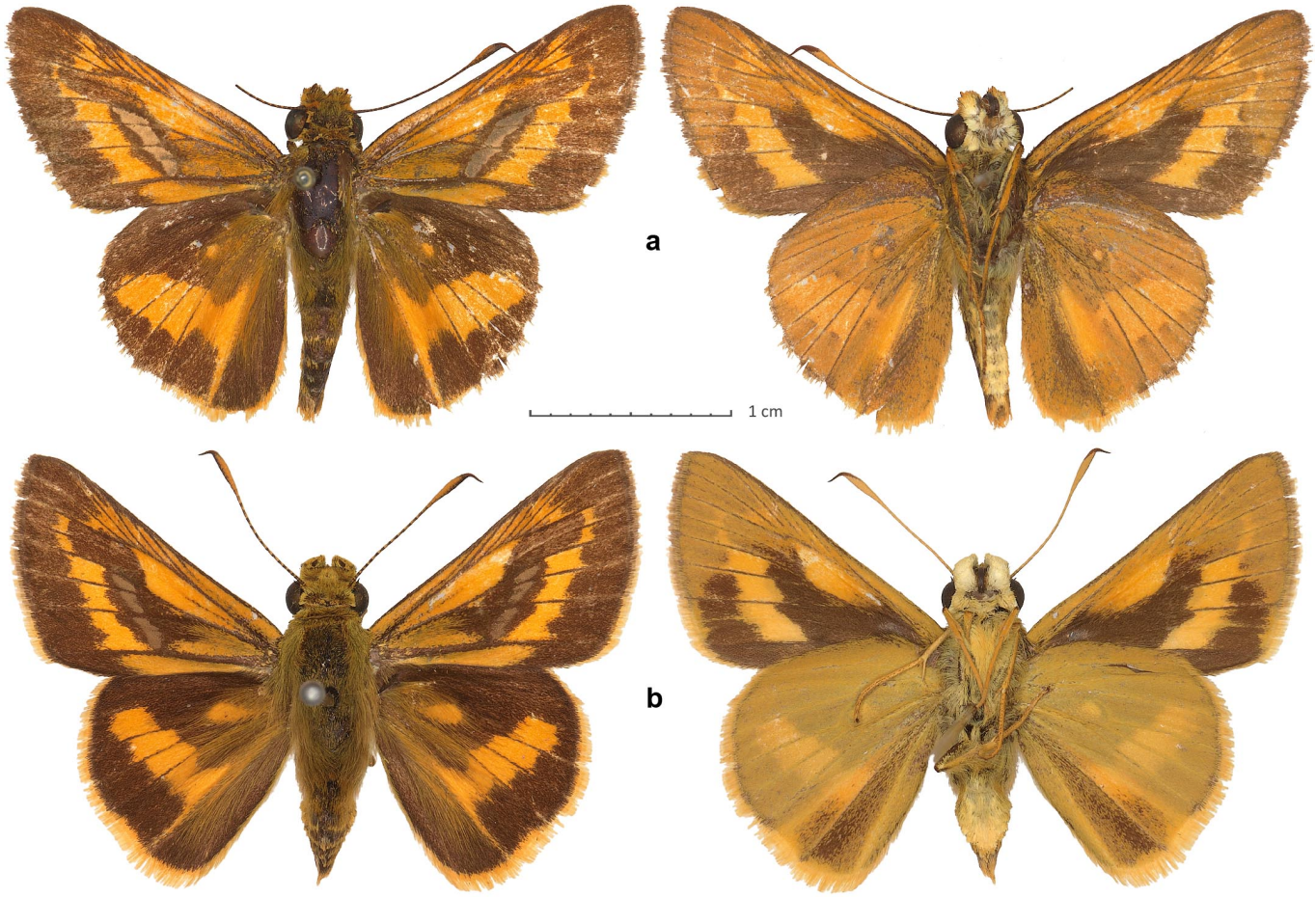

Fig. 46. Sequenced specimens of *Arrhenes* (*Telines* **subgen. n.**) from Australia in dorsal (left) and ventral (right) views: **a)** *A.* (*T.*) *eurotas laconia* (Waterhouse, 1937) **comb. nov.** ♂ NVG-22048C11 North Queensland, Edge Hill, 22-Aug-1938, R. G. Wind leg. [CUIC]; **b)** *A.* (*T.*) *eurychlora* **comb. nov.** ♂ NVG-23058G09 New South Wales, Dudley, 8-Nov-1987, A. Atkins leg. [MGCL].

Telines Grishin, new subgenus

http://zoobank.org/BF70767A-6DDF-43FB-B665-EC721E59A79E

Type species. *Pamphila eurotas* C. Felder, 1860.

Definition. Genomic phylogeny of the tribe Taractrocerini Voss, 1952 shows a notable genetic differentiation between the clade with *Arrhenes eurotas* (C. Felder, 1860), **comb. nov.** (type locality in Ambon) and *Arrhenes eurychlora* (Lower, 1908), **comb. nov.** (type locality Australia: New South Wales, Ballina) that we placed in *Arrhenes* Mabille, 1904 (type species *Pamphila marnas* Felder, 1860) above, and other species of *Arrhenes*, including the type (Fig. 44), e.g., their COI barcodes differ by 7.6–8.7% (50–57 bp). Therefore, this clade represents a new subgenus. This new subgenus keys to L.7.1 in Evans (1949) and differs from its relatives by a combination of the following characters: undivided uncus, terminally narrow and flat; rounded valva without prominently concave dorsal margin at ampulla-harpe, without spines; long antennae, longer than ½ of the costal margin; shorter and stouter 3rd segment of palpi; broad and straight stigma; rather narrow wings (Fig. 46) as in most species of *Telicota* F. Moore, 1881 (type species *Papilio colon* Fabricius, 1775) and not as rounded as in a typical *Arrhenes* Mabille, 1904. In DNA, a combination of the following characters is diagnostic in the nuclear genome: aly1841.5.20:A237T, aly1841.5.20:G259A, aly600.14.1:C84T, aly600.14.1:G87A, aly4645.10.1:A490C, and COI barcode: T70A, A181T, T376C, T530C, T547A.

Etymology. This name combines the previous and current genus names of these species: *Teli*[cota] + [Arrhe]*nes* and is a masculine noun in the nominative singular.

Species included. The type species (i.e., *Pamphila eurotas* C. Felder, 1860) and *Telicota eurychlora* Lower, 1908.

Parent taxon. Genus *Arrhenes* Mabille, 1904.

Telicota kolbei Ribbe, 1899 belongs to the genus *Sabera* Swinhoe, 1908 and not *Mimene* Joicey & Talbot, 1917

Genomic analysis of a syntype of *Telicota kolbei* Ribbe, 1899 (type locality in New Britain, sequenced as NVG-22016H05) reveals that it is not monophyletic with *Mimene* Joicey & Talbot, 1917 (type species *Ismene miltias* Kirsch, 1877), the genus of its current placement, but instead is sister to *Sabera* Swinhoe, 1908 (type species *Hesperia caesina* Hewitson, 1866), which is a sister genus of *Mimene* (Fig. 44). Therefore, *T. kolbei* does not belong to *Mimene*, and we transfer it to *Sabera* forming *Sabera kolbei* (Ribbe, 1899), **comb. nov**.

Furthermore, to stabilize nomenclature and define the name *T. kolbei* objectively, N.V.G. hereby designates a sequenced syntype in ZSMC (Fig. 47a), female that, according to its label, was illustrated in the original description by Ribbe (1899) and bears the following six rectangular labels (2nd, 3rd, and 5th handwritten, others printed; 2nd green, 4th purple, others white): [Neu Pommern | Kinigunang | C. Ribbe], [abgebildet], [Kolbei | Ribbe | abgebild.], [Original], [♀ Cerone Kolbei Rib. | typ. | N. Pommern], [DNA sample ID: | NVG-22016H05 | c/o Nick V. Grishin] as the **lectotype** of *Telicota kolbei* Ribbe, 1899. The lectotype has a tear near the base of the forewing costa, is missing the right antenna, and its left antenna is wide-S shaped. The COI barcode sequence of the lectotype, sample NVG-22016H05, GenBank PQ489713, 658 base pairs is:

```
AACTTTATATTTTATTTTTGGTATTTGATCAGGAATATTAGGAACTTCCTTAAGTCTATTAATTCGTACCGAATTGGGTAACCCAGGATCTTTAATTGGAGATGATCAAATTTATAATACT
ATCGTAACTGCTCATGCTTTTATTATAATTTTTTTTATAGTTATACCTATTATAATTGGAGGATTTGGAAATTGATTAATTCCCTTAATACTAGGAGCCCCTGATATAGCTTTCCCACGAA
TAAATAATATAAGATTTTGAATATTACCCCCTTCTTTAACACTTTTAATTTCTAGAAGAATTGTAGAAAACGGTGCCGGAACTGGTTGAACTGTTTACCCCCCTCTTTCTTCTAATATTGC
TCATCAAGGTTCCTCTGTTGATTTAGCAATCTTTTCTTTACATTTAGCTGGAATTTCATCAATTTTAGGAGCTATTAATTTTATTACCACAATTATTAATATACGAATTAACAATTTATCA
TTTGATCAAATACCTCTATTTATTTGATCTGTAGGAATTACAGCATTATTATTATTAATTTCATTACCAGTCTTAGCAGGAGCTATTACCATATTATTAACTGATCGAAATTTAAATACTT
CATTTTTCGACCCTGCAGGAGGAGGTGATCCTATTTTATATCAACATTTATTT
```

Sabera tenebricosa (Mabille, 1904) is a species distinct from *Sabera kolbei* (Ribbe, 1899)

Telicota tenebricosa Mabille, 1904 (type locality in New Guinea) (Fig. 47b) is currently treated as a subspecies of *Sabera kolbei* (Ribbe, 1899), **comb. nov.** (type locality in New Britain) (Fig. 47a), formerly

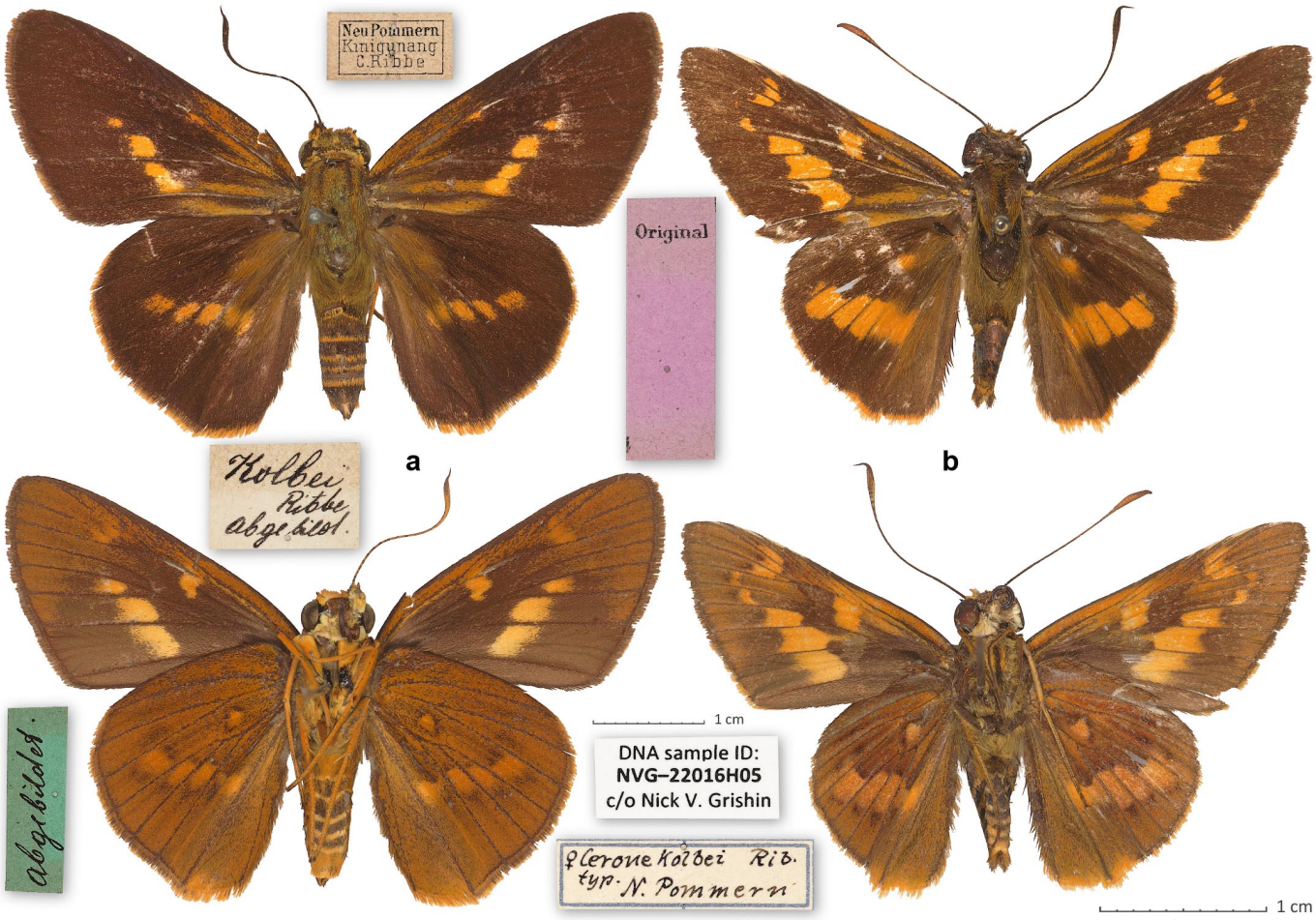

Fig. 47. Sequenced specimens of *Sabera* (*Kolba* **subgen. n.**) in dorsal (top) and ventral (bottom) views: **a)** *S.* (*K.*) *kolbei* **comb. nov.** lectotype ♀ NVG-22016H05 with its labels (reduced by a third compared to specimens), data in text; **b)** *S.* (*K.*) *tenebricosa*, **comb. nov., stat. rest.** ♂ NVG-22048E04 Papua New Guinea, Port Moresby, 20-May-1939, R. G. Wind leg. [CUIC]. The larger scale bar refers to specimens, and the smaller one to labels. All labels are of the lectotype shown in **a)**, no labels are shown for the specimen in **b)**.

in the genus *Mimene* Joicey & Talbot, 1917 (type species *Ismene miltias* Kirsch, 1877) (Evans 1949). Genomic analysis reveals that while *T. tenebricosa* is indeed sister to *S. kolbei* and thus belongs to the same genus *Sabera* Swinhoe, 1908 (type species *Hesperia caesina* Hewitson, 1866), the two taxa are genetically differentiated at the species level (Fig. 44), e.g., their COI barcodes differ by 6.4% (42 bp). Therefore, we propose that *Sabera tenebricosa* (Mabille, 1904), **comb. nov.**, **stat. rest.** is a species distinct from *Sabera kolbei* (Ribbe, 1899), **stat. nov**.

Kolba Grishin, new subgenus

http://zoobank.org/91DE51B4-EA9A-44F1-9BEC-637E5268E303

Type species. *Telicota kolbei* Ribbe, 1899.

Definition. Genomic analysis shows that the lineage with *Sabera kolbei* (Ribbe, 1899), **comb. nov.** (type locality in New Britain), is genetically differentiated from the type species of *Sabera* Swinhoe, 1908, *S. caesina* Hewitson, 1866) (type locality in Aru) at the subgenus level (Fig. 44), e.g., their COI barcodes differ by 8.1% (53 bp). Therefore, this lineage represents a new subgenus. This new subgenus keys to L.14.2 in Evans (1949) and differs from its relatives by a combination of the following characters: undivided, terminally pointed uncus, enlarged in the middle and narrowing near tegumen in dorsal view,

concave towards the distal end and swollen in the middle in lateral view; tapering to a point harpe with somewhat wavy dorsal margin; long antennae, longer than ½ of the costal margin; shorter and stouter 3rd segment of palpi; rather produced forewings; apical spots on dorsal forewing but not beyond (towards costa) vein R_3; no strong sexual dimorphism in wing pattern (Fig. 47). In DNA, a combination of the following characters is diagnostic in the nuclear genome: aly490.12.1:A1635G, aly490.12.1:T1662C, aly490.12.1:A4152G, aly430.8.1:T51A, aly430.8.1:C86G, and COI barcode: G29T, T127A, A130T, A286T, T553A.

Etymology. The name is inspired by the type species name. Moreover, in several Slavic languages, the word kolba means a flask with an expanded bottom, and Kolben in German may mean a bulb. The name refers to the bulbous enlargement of uncus in the middle (in dorsal view) that is characteristic of these species and is a feminine noun in the nominative singular.

Species included. The type species (i.e., *Telicota kolbei* Ribbe, 1899) and *Telicota tenebricosa* Mabille, 1904, **stat. rest**.

Parent taxon. Genus *Sabera* Swinhoe, 1908.

Tribe Erionotini Distant, 1886

Sarala Grishin, new subgenus

http://zoobank.org/5063C1BE-31F4-4367-923F-12FF8DEF1BB2

Type species. *Parnara sarala* Nicéville, 1889.

Definition. Genomic phylogeny of *Acerbas* Nicéville, 1895 (type species *Hesperia anthea* Hewitson, 1868) and relatives reveals that the genus partitions into two prominent clades with genetic differentiation that correspond to at least subgenera (Fig. 44), e.g., their COI barcodes differ by about 11.2% (74 bp). The first clade consists of the type species of *Acerbas*. Because no type species of available genus-group names belongs to the second clade, it represents a new genus-group taxon that we conservatively propose as a subgenus. This new subgenus keys to J.22.2b in (Evans 1949) and differs from its relatives by a combination of the following characters: forewing vein 2 originates closer to the base than to the origin of vein 3; forewing discal cell with pale spots; gnathos is usually less developed than in the nominate subgenus, aedeagus is less expanded terminally, and the valva is more elongated. In DNA, a combination of the following characters is diagnostic in the nuclear genome: aly499.8.4:C57T, aly171.12.1:G39C, aly171.12.1:T42C, aly577.55.7:C97A, aly3616.1.1:A465G, and COI barcode: T316A, T424A, A484T, C641C, T643T.

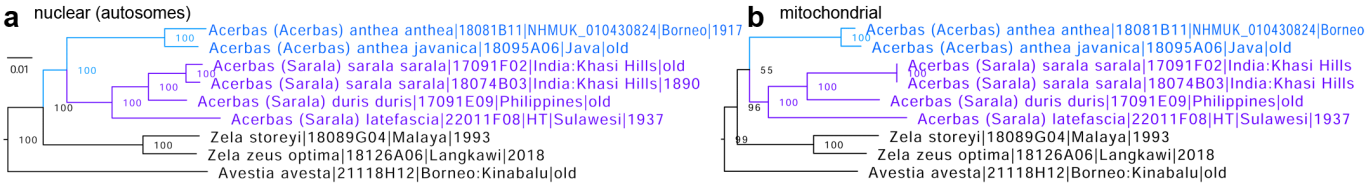

Fig. 48. Phylogenetic trees of *Acerbas* and relatives constructed from protein-coding regions in **a)** the nuclear genome (autosomes) and **b)** the mitochondrial genome: subgenus *Sarala* **subgen. n.** is shown in purple.

Etymology. The name is tautonymous with the type species name and is a feminine noun in the nominative singular.

Species included. The type species (i.e., *Parnara sarala* Nicéville, 1889), *Carystus duris* Mabille, 1883, *Acerbas selta* Evans, 1949, *Acerbas latefascia* de Jong, 1982, and *Acerbas suttoni* Russell, 1984.

Parent taxon. Genus *Acerbas* Nicéville, 1895.

Tribe Hesperiini Latreille, 1809
Subtribe Hesperiina Latreille, 1809

Notamblyscirtes durango seaza Grishin, new subspecies

http://zoobank.org/44D73157-48E8-411C-B5D3-E53D8CBD049A

(Figs. 49 part, 50)

Definition and diagnosis. Genomic analysis of additional *Notamblyscirtes* J. Scott, 2006 (type species *Amblyscirtes simius* W. H. Edwards, 1881) specimens from across its range reveals that populations of *Notamblyscirtes durango* J. Scott, 2017 (type locality in Mexico: Durango) partition into two clades by their nuclear genome (Fig. 49a, b, red and purple), thus being genetically differentiated from each other, albeit with moderate statistical support (minimal of four clades over two trees is 60% replications). Therefore, these groups of populations represent major genomic groups of *N. durango* below the species level, and thus correspond to subspecies. These subspecies do not consistently differ in mitochondrial DNA (Fig. 49c). The nominate subspecies, as the trees demonstrate (Fig. 49 purple), is known only from Mexico: states of Nuevo Leon, Coahuila, and Durango. The second subspecies inhabits southeastern Arizona and southwestern New Mexico (Fig. 49 red), does not have a name associated with it, and hence is new. The new subspecies possesses the characters given for *N. durango* in the original description (Scott et al. 2017) and is most similar to the nominate subspecies from Mexico in its darker aspect compared to its sister species *Notamblyscirtes simius* (W. H. Edwards, 1881) (type locality in USA: Colorado, Pueblo Co,), but differs in being somewhat paler (e.g., towards the base and inner margin of and typically brighter orangish postdiscal area on ventral forewing), and with sharper-defined pale spots on ventral hindwing, especially in females. Due to phenotypic variation, most reliable identification is achieved by DNA, and a combination of the following base pairs is diagnostic in the nuclear genome: aly331.20.14:C144T, aly331.20.14:G180A, aly4237.1.2:C21T, aly164.66.3:A39G, aly164. 66.3:C57T. There are no differences in the COI barcode.

Barcode sequence of the holotype. Sample NVG-22094G07, GenBank PQ489714, 658 base pairs:

AACTTTATATTTTATTTTTGGTATTTGAGCAGGAATATTAGGAACTTCATTAAGTTTATTAATTCGTACAGAATTAGGAAATCCAGGATCATTAATTGGAGATGATCAAATTTATAATACT
ATTGTCACAGCTCATGCTTTTATTATAATTTTTTTTATAGTTATACCTATTATAATTGGAGGATTTGGAAATTGATTAGTTCCTTTAATATTAGGAGCCCCTGATATAGCTTTCCCCCGAA
TAAATAATATAAGATTTTGAATATTACCCCCTTCTTTAACACTTTAATCTCAAGAAGAATTGTAGAAAATGGAGCAGGAACTGGATGAACAGTTTATCCCCCACTATCATCTAATATTGC
CCATCAAGGATCTTCTGTTGATATAGCAATTTTCTCCCTTCATCTAGCTGGAATTTCATCTATCTTAGGAGCTATTAATTTTATTACAACAATTATTAATATACGAATTAAAAATTTATCA
TTTGATCAAATACCCTTATTTGTTTGATCTGTAGGAATTACAGCATTATTATTATTATTATCTTTACCTGTTTTAGCTGGAGCTATTACAATATTATTAACAGATCGTAATTTAAATACCT
CTTTTTTTGACCCCGCAGGAGGAGGAGATCCAATTTTATATCAACATTTATTT

Type material. Holotype: ♂ deposited in the Los Angeles County Museum of Natural History, Los Angeles, CA, USA (LACM), illustrated in Fig. 50, bears the following five rectangular labels (2nd handwritten, others printed with handwritten text shown in italics), four white: [Research Ranch *RAB* | 6 mi. S.E. Elgin, AZ. | Santa Cruz Co. | Col. *27-Jul-1983*], [A. simius], [Amblyscirtes simius | Edwards |

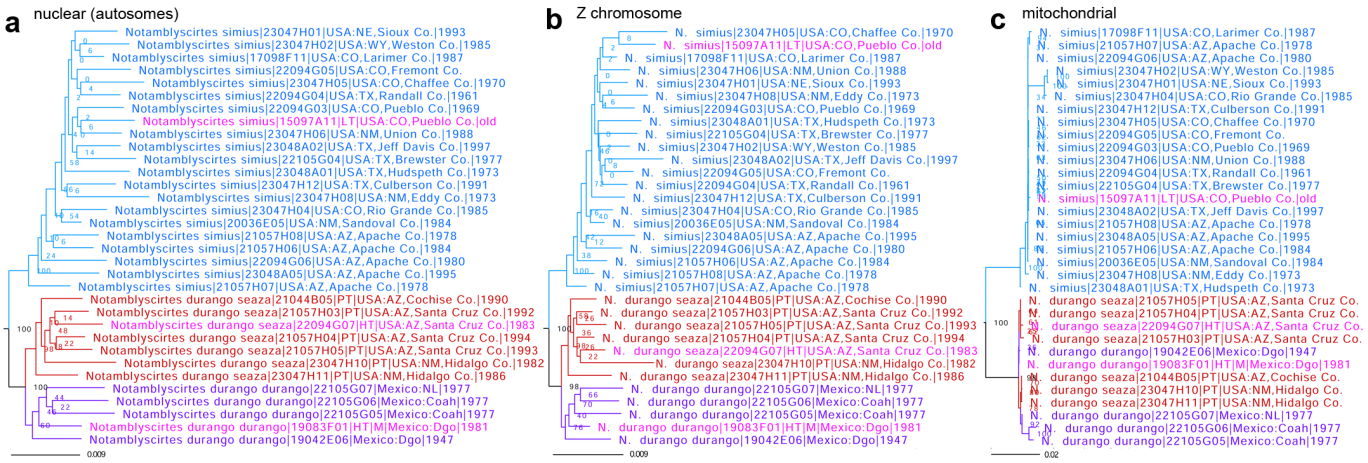

Fig. 49. Phylogenetic trees of *Notamblyscirtes* constructed from protein-coding regions in **a)** the nuclear genome (autosomes), **b)** the Z chromosome, and **c)** the mitochondrial genome: *N. simius* (blue); *N. durango seaza* **ssp. n.** (red), *N. durango durango* (purple). Primary type specimens are labeled in magenta.

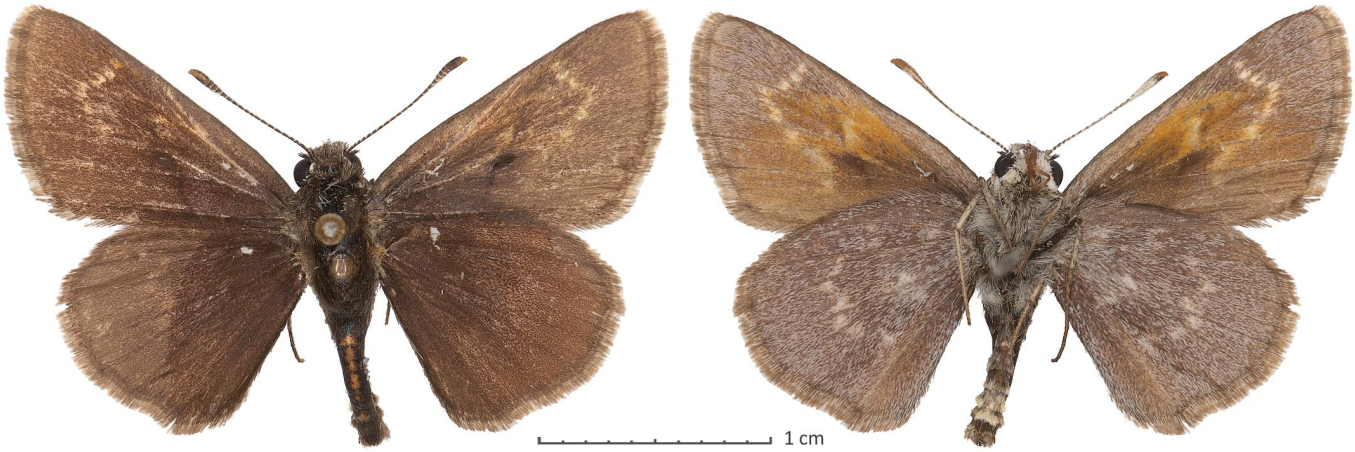

Fig. 50. *Notamblyscirtes durango seaza* **ssp. n.** holotype ♂ NVG-22094G07 in dorsal (left) and ventral (right) views, data in text.

det.Richard Bailowitz], [DNA sample ID: | NVG-22094G07 | c/o Nick V. Grishin], and one red [HOLOTYPE ♂ | Notamblyscirtes durango | seaza Grishin]. **Paratypes:** 2♂♂ and 4♀♀ USA: Arizona: Santa Cruz Co., San Rafael Valley, Bog Hole, J. P. Brock leg. [JPBrock]: 1♂ NVG-21057H03 9-Aug-1992, 1♂ NVG-21057H04 20-Aug-1994, 1♀ NVG-21057H05 7-Aug-1993; 1♀ NVG-21044B05 Cochise Co., Peloncillo Mts., Cottonwood Canyon, 16-Aug-1990, J. B. Walsh leg. [MGCL]; New Mexico, Hidalgo Co., Clanton Draw, 4 mi E of AZ state line, K. Roever leg. [MGCL]: 1♀ NVG-23047H10 8-Aug-1982 and 1♀ NVG-23047H11 1-Aug-1986.

Type locality. USA: Arizona, Santa Cruz Co., 6 mi SE of Elgin, Research Ranch.

Etymology. The name is formed from SE AZ (southeastern Arizona) for the type locality of this subspecies and is treated as a feminine noun in apposition.

Distribution. Southeastern Arizona (Cochise and Santa Cruz Cos.) and southwestern New Mexico (Hidalgo Co.), USA.

Comment. Traditionally, subspecies in butterflies have been defined by the differences in wing patterns between groups of populations that account for approximately 70% of specimens. We propose a more comprehensive definition of subspecies as major genetic groups of populations within a species and apply this definition to *N. durango*. This definition is all-encompassing because it does not rely on a single feature of an organism, such as the coloration of adults, but is an integral characteristic of the genome and is expected to reflect genetic differences between other life stages, such as caterpillars and pupae, behavior, and foodplant preferences. Subspecies, defined as major genomic clusters, represent genetically unique divisions of a species and thus may be more relevant as units considered for conservation.

Quasimellana duranga Grishin, new species

http://zoobank.org/513B0D2D-9275-4954-BE64-4E38660698AA

(Figs. 51 part, 52–53)

Definition and diagnosis. Genomic analysis reveals that a specimen from Durango, Mexico, identified as *Quasimellana mulleri* (E. Bell, 1942) (type locality in Mexico: Guerrero) is genetically differentiated from it at the species level (Fig. 51), e.g., their COI barcodes differ by 5.3% (35 bp) and therefore represents a new species. This species differs from its relatives by being darker: dorsally, two subapical orange spots are separated from the costal orange area and not connected to it through additional orange spots; ventrally, forewing dark scaling is more extensive, and the hindwing has darker marginal and basal areas giving an appearance of a faint wide central paler band (not uniformly yellow) (Fig. 52); the cornutus has a more triangular keel, rather than terminally rounded or trapezoidal, the body of cornutus is narrower; dorsodistal end of harpe is rounded and projects dorsad from the costa of the valva being separated from it by a rounded concavity (Fig. 53). Due to the cryptic nature of this species and

unexplored phenotypic variation, most reliable identification is achieved by DNA, and a combination of the following base pairs is diagnostic in the nuclear genome: aly2631.8.5:T297C, aly668.9.2:A372G, aly668.9.2:A384T, aly668.9.2:T393G, aly82.25.3:C63T, aly1603.75.15:T111T (not G), aly361.11.2:A321A (not T), aly361.25.3:A102A (not G), aly3824.6.7:C69C (not A), aly3824.6.7:C72C (not T), and COI barcode: T38T, T46C, 79T, A286T, T304C, T500C.

Barcode sequence of the holotype. Sample NVG-18117G05, GenBank PQ489715, 658 base pairs:

TACTTTATATTTTATTTTTGGTATTTGAGCAGGAATATTAGGTACCTCCTTAAGTCTTCTAATTCGAACTGAATTAGGTAATCCTGGATCTTTAATTGGAGATGATCAAATTTATAATACT
ATTGTTACAGCTCATGCTTTTATTATAATTTTTTTTATAGTTATACCTATTATAATTGGAGGATTTGGAAATTGATTAGTACCCTTAATATTAGGAGCCCCTGATATAGCTTTCCCCCGAA
TAAATAACATAAGATTTTGAATGCTACCCCCATCATTAACCCTTCTAATTTCAAGAAGTATCGTAGAAAATGGTGCAGGAACTGGATGAACAGTTTACCCCCCCCTATCTTCTAATATCGC
TCATCAAGGATCTTCTGTAGATTTAGCAATTTTTTCACTTCACTTAGCTGGAATTTCTTCTATTTTAGGAGCTATTAATTTTATTACTACAATTATTAATATACGAATTAAAAACTTATCA
TTTGATCAAATATCTCTATTTATTTGATCAGTAGGAATTACAGCATTATTATTATTATTATCTTTACCAGTTTTAGCTGGAGCTATTACCATATTACTTACAGACCGAAATTTAAACACAT
CATTCTTCGATCCAGCAGGAGGGGGGGATCCCATTCTATACCAACACTTATTT

Type material. Holotype: ♂ deposited in the National Museum of Natural History, Smithsonian Institution, Washington, DC, USA (USNM), illustrated in Fig. 52 (genitalia in Fig. 53), bears the following seven rectangular labels (1st, 2nd, and 6th handwritten, others printed with handwritten text shown in italics), five white: [Dgo, rte 40 | Mimbres Gor | ge 28 Aug 85 | DDM], [Mellana ♂ | mulleri | Bell | det.H.A.Freeman], [GENITALIA NO. | X- *31 78* | J.M.Burns 1991], [Quasimellana mulleri | (Bell) | ♂ | det. J. M. Burns 1994], [DNA sample ID: | NVG-18117G05 | c/o Nick V. Grishin], and two red [LENT BY | DOUG MULLINS | VII-91], [HOLOTYPE ♂ | Quasimellana | duranga Grishin]. The holotype was collected by Doug Mullins.

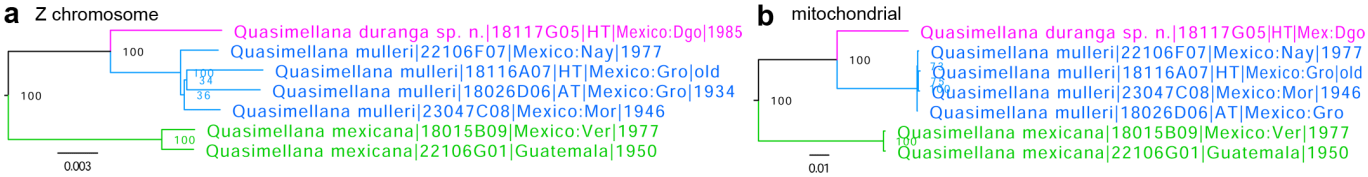

Fig. 51. Phylogenetic trees of selected *Quasimellana* species constructed from protein-coding regions in **a)** the Z chromosome and **b)** the mitochondrial genome: *Q. duranga* **sp. n.** (magenta), *Q. mulleri* (blue), and *Q. mexicana* (green).

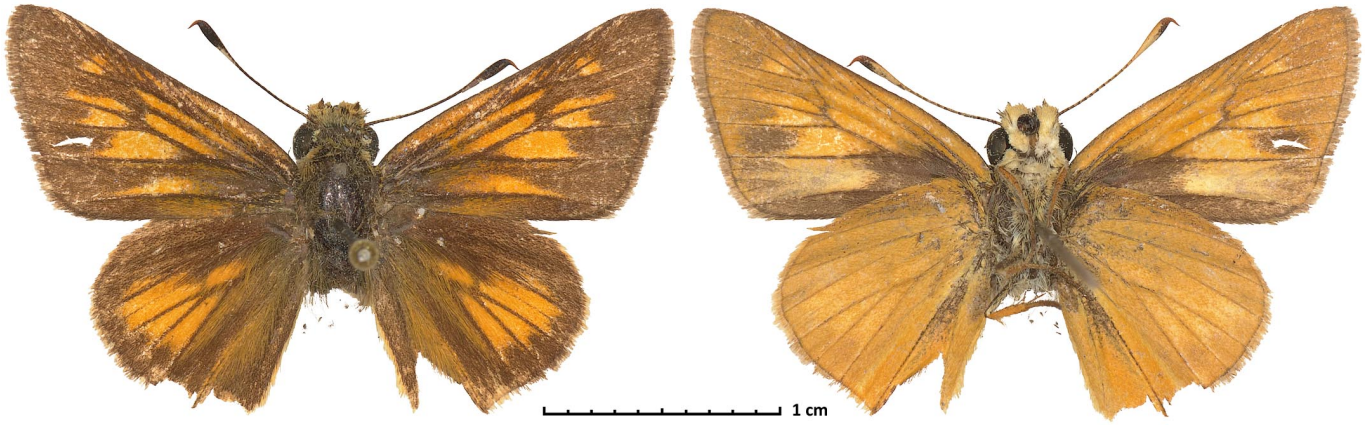

Fig. 52. *Quasimellana duranga* **sp. n.** holotype ♂ NVG-18117G05 in dorsal (left) and ventral (right) views, data in text.

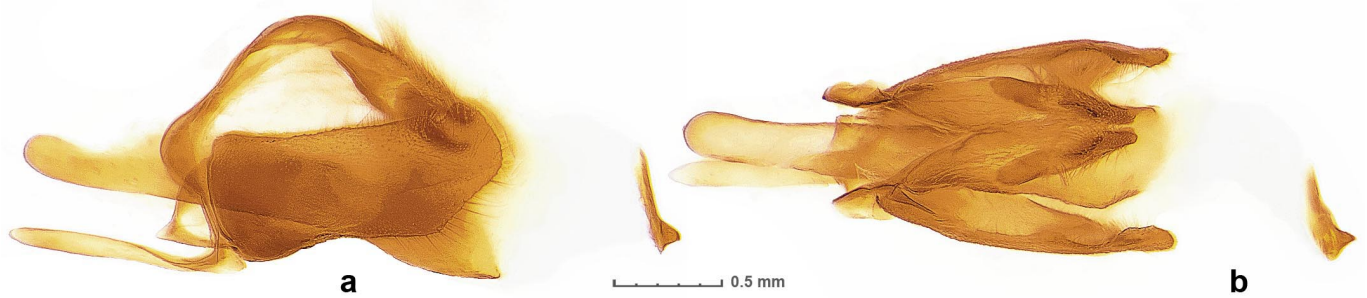

Fig. 53. Genitalia of *Quasimellana duranga* **sp. n.** holotype ♂ NVG-18117G05 in **a)** left lateral and **b)** dorsal views. The cornutus is on the right, connected to the aedeagus by (nearly transparent) vesica.

Type locality. Mexico: Durango, Mexican Highway 40, 30 mi east of El Salto, Los Mimbres Gorge.

Etymology. The name is formed from the name of the Mexican state with the type locality and is treated as a feminine noun in apposition.

Distribution. Currently known only from the holotype collected in Durango, Mexico.

Stinga azteca Grishin, new species

http://zoobank.org/C6F5C6FC-A5D2-4654-BF07-11C3D05F694B

(Figs. 54 part, 55–56)

Definition and diagnosis. Genomic phylogeny of *Stinga* Evans, 1955 (type species *Pamphila morrisoni* W. H. Edwards, 1878) reveals that specimens from southern Mexico identified as *Stinga morrisoni* (W. H. Edwards, 1878) (type locality USA: Colorado, likely in Custer Co.) are genetically differentiated from it at the species level (Fig. 54) and represent a new species. The COI barcodes are 2.3% (15 bp) different between the holotype of the new species and the lectotype of *S. morrisoni*. This new species keys to M.9. in Evans (1955) and differs from *S. morrisoni* by characters described in Warren and Austin (2009) for the phenotype "in the states of México, Tlaxcala, Guerrero and Oaxaca." In brief, specimens of the new species are smaller than *S. morrisoni* in the southern parts of its range and prominently darker, with a deeper orange color, smaller spots, and reduced pale overscaling. In male genitalia (Fig. 5c in Warren and Austin 2009), the harpe is better separated from the ampulla than in *S. morrisoni*, and the valva is somewhat narrower. In female genitalia (Fig. 6c in Warren and Austin 2009), lamella postvaginalis narrows towards ductus bursae stronger than in *S. morrisoni*. Due to unexplored phenotypic variation in other populations, definitive identification is provided by DNA, and a combination of the following characters is diagnostic in the nuclear genome: aly2874.23.3:C1218T, aly2874.23.3:C1296T, aly11945.4.2:C573T, aly11945.4.2:A1341C, aly1838.49.7:A939G, and COI barcode: A199A, C235T, A307G, T361C, T553C.

Barcode sequence of the holotype. Sample NVG-23046D06, GenBank PQ489716, 658 base pairs:

AACCTTATATTTTATTTTTGGTATTTGAGCAGGAATATTAGGAACTTCTTTAAGTTTATTAATTCGTACAGAATTAGGTAATCCAGGATCTTTAATTGGAGATGATCAAATTTATAATACC
ATTGTTACAGCTCATGCATTTATTATAATTTTTTTTATAGTTATACCCATTATAATTGGAGGATTTGGAAATTGATTAGTTCCTTTAATATTAGGAGCACCAGATATAGCTTTTCCTCGAA
TAAATAATATAAGTTTTTGAATACTACCCCCTTCATTAACATTATTAATTTCAAGAAGAATTGTGGAAAATGGTGCAGGAACAGGATGAACAGTTTACCCCCCTTTATCCTCAAATATCGC
TCATCAAGGATCCTCTGTTGATTTAGCAATTTTTTCTCTTCATTTGGCTGGAATTTCATCTATTTTAGGAGCTATTAATTTTATTACAACAATTATTAATATACGAATTAAAAATTTATCA
TTTGATCAAATACCTTTATTTGTATGATCTGTAGGTATTACAGCTTTATTATTACTTTTATCTTTACCCGTTTTAGCAGGTGCTATTACTATATTACTTACTGATCGAAATTTAAATACTT
CTTTTTTTGATCCAGCAGGAGGAGGAGATCCAATTTTATATCAACATTTATTT

Type material. Holotype: ♂ deposited in the McGuire Center for Lepidoptera and Biodiversity Collection, Gainesville, FL, USA (MGCL), illustrated in Fig. 55, bears five printed (text in italics handwritten) labels: four white [MEXICO: MÉXICO: | Mpio. Amecameca: | S slope Iztaccihuatl: | grassy slopes above | Paso de Cortes, 3400- | 3900m, 18-III-2000 | Andrew D. Warren | with MZFC crew], [Genitalic Vial | GTA-*14079*], [A. D. Warren colln. | MGCL Accession | #2009-7], [DNA sample ID: | NVG-23046D06 | c/o Nick V. Grishin], and one red [HOLOTYPE ♂ | Stinga azteca | Grishin]. **Paratype:** 1♀ NVG-23046D07 the same data as the holotype, genitalic vial GTA-14078.

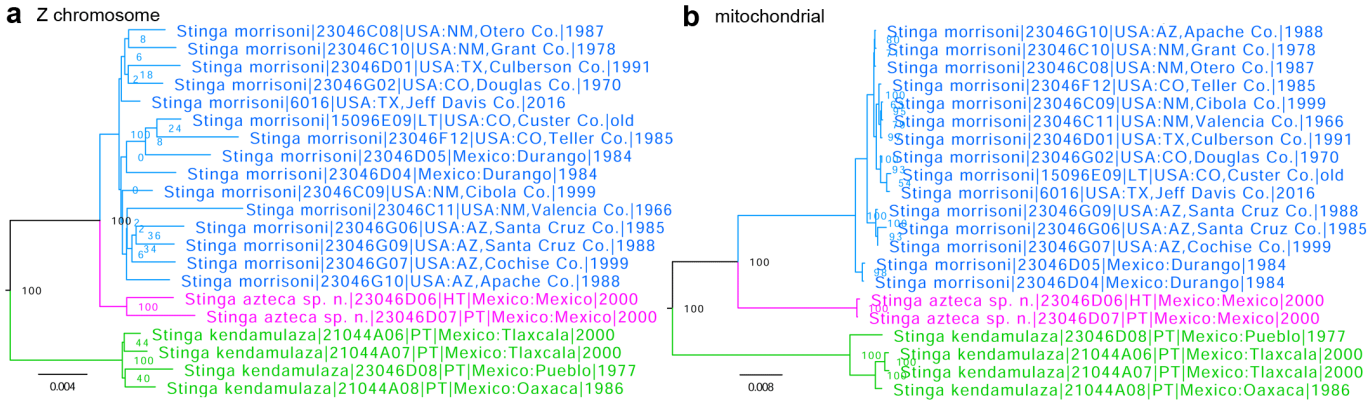

Fig. 54. Phylogenetic trees of *Stinga* constructed from protein-coding regions in **a)** the Z chromosome and **b)** the mitochondrial genome: *S. morrisoni* **sp. n.** (blue), *S. azteca* **sp. n.** (magenta), and *S. kendamulaza* A. Warren & Austin, 2009 (green).

Fig. 55. *Stinga azteca* **sp. n.** holotype ♂ NVG-23046D06 in dorsal (left) and ventral (right) views, data in text.

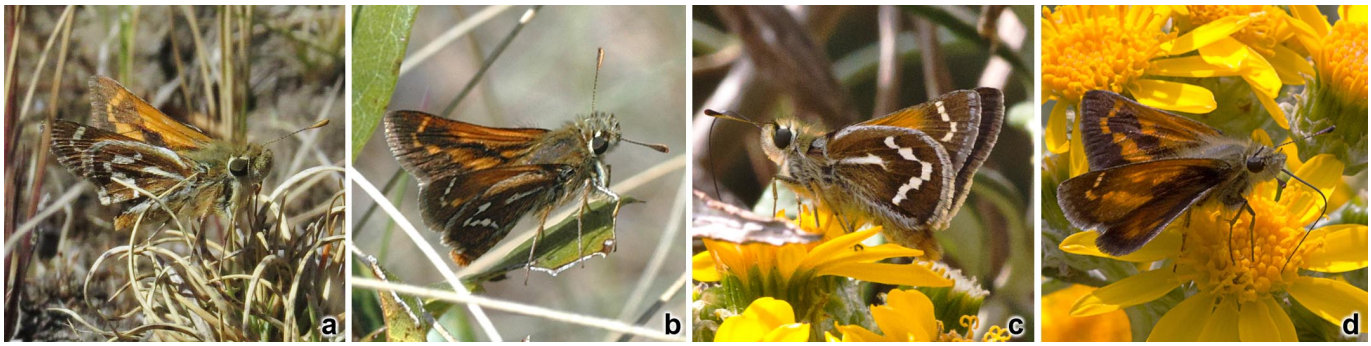

Fig. 56. *Stinga azteca* **sp. n.** iNaturalist observations from Mexico: **a)** 5191512 Distrito Federal¸ Tlalpan, Cdad. de México, 26-Feb-2017 © Mario Castañeda; **b)** 121949290 Oaxaca, Concepción Pápalo, 28-Mar-2012 © John Kemner; **c**, **d)** 91510 México, Amecameca, Paso de Cortés (the type locality), 17-Mar-2012 © Anne (annemirdl). Images are color-corrected, brightened, and cropped. CC BY-NC 4.0 https://creativecommons.org/licenses/by-nc/4.0/.

Type locality. Mexico: México, Mpio. Amecameca, south slope of Iztaccihuatl, grassy slopes above Paso de Cortés, 3400–3900 m.

Etymology. The Aztec Empire flourished in central Mexico, with their capital city, Tenochtitlan, built on an island in Lake Texcoco, which is now largely filled in and forms the base of modern-day Mexico City. This species is known from central Mexico, hence the name. The name is a feminine noun in apposition.

Distribution. Southern Mexico (México, Tlaxcala, Puebla, Guerrero, and Oaxaca).

Subtribe Moncina A. Warren, 2008

Phlebodes meesi de Jong, 1983 belongs to the nominal subgenus of *Vistigma* Hayward, 1939 and not to *Phlebodes* Hübner, 1819

Genomic analysis reveals that *Phlebodes meesi* de Jong, 1983 (type locality in Suriname) is not monophyletic with *Phlebodes* Hübner, [1819] (type species *Papilio pertinax* Stoll, 1781) but instead originates within the nominal subgenus of *Vistigma* Hayward, 1939 (type species *Vistigma xanthobasis* Hayward, 1939) being a close sister to *Vistigma* (*Vistigma*) *vira* (Butler, 1870) (type locality in Brazil: Pará) (Fig. 57). Therefore, we transfer it to this genus as *Vistigma* (*Vistigma*) *meesi* (de Jong, 1983), **comb. nov**.

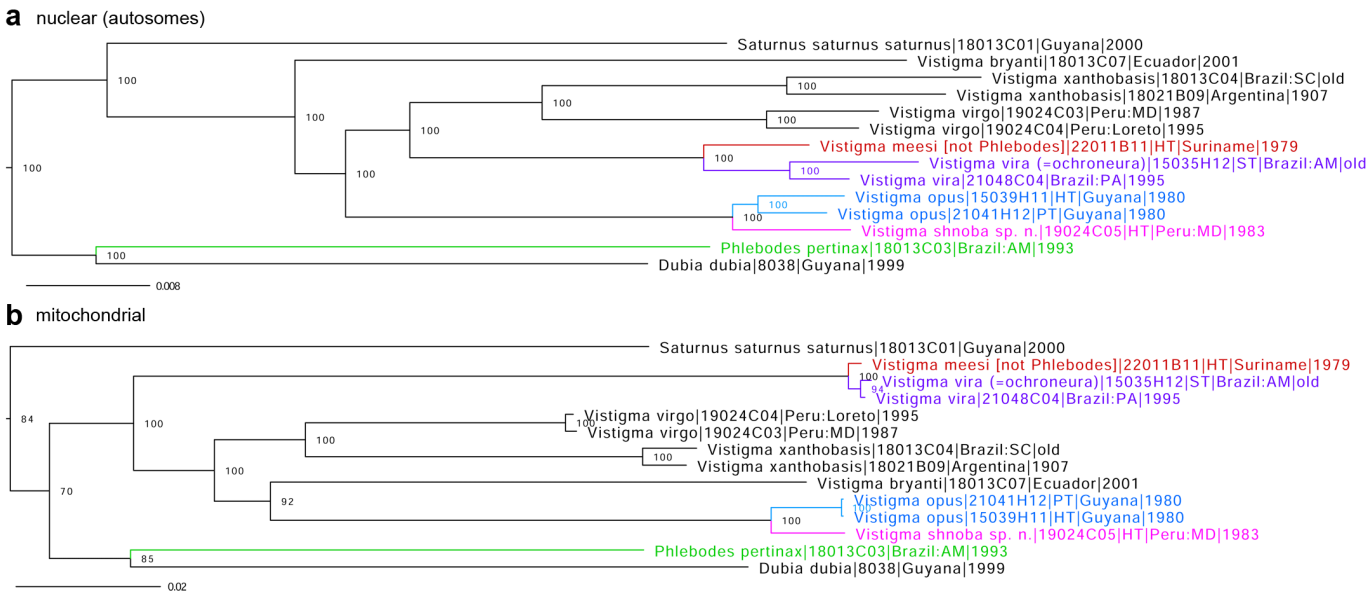

Fig. 57. Phylogenetic trees of *Vistigma* and relatives constructed from protein-coding regions in **a)** the nuclear genome (autosomes), based on 6,799,005 positions and **b)** the mitochondrial genome: *Phlebodes pertinax*, the type species of *Phlebodes* (green), *V. meesi* **comb. nov.** (red), *V. vira* (purple), *V. opus* (blue), and *V. shnoba* **sp. n.** (magenta). Ultrafast bootstrap (Minh et al. 2013) values are shown at nodes.

Vistigma (*Vistigma*) *shnoba* Grishin, new species

http://zoobank.org/112EE07F-ADEB-429B-9129-363978D56578

(Figs. 57 part, 58–59)

Definition and diagnosis. Genomic sequencing of a specimen initially identified as *Vistigma* (*Vistigma*) *opus* (Steinhauser, 2008) (type locality in Guiana) reveals that while being sister to it, it is genetically differentiated from *V. opus* at the species level (Fig. 57), e.g., their COI barcodes differ by 1.6% (11 bp), and therefore represents a new species. The description of *Thoon opus* given by Steinhauser (2008) applies to this new species, except that the forewing discal cell spot is smaller, and there is a dot-like semihyaline spot in R_4-R_5 cell on the dorsal side, not only ventrally, where the forewing lacks an ocherous streak in Cu_2-2A cell, and the hindwing has weaker ocherous overscaling, in particular, in the discal cell and along the vestigial vein 1A (but with streaks and overscaling along the veins as in *V. opus*). Due to the cryptic nature of this species and unexplored phenotypic variation, most reliable identification is achieved by DNA, and a combination of the following base pairs is diagnostic in the nuclear genome: aly728.7.2:C279T, aly1259.4.2:C180T, aly731.4.9:G51A, aly423.15.6:A132G, aly216.78.1:A528G, aly925.

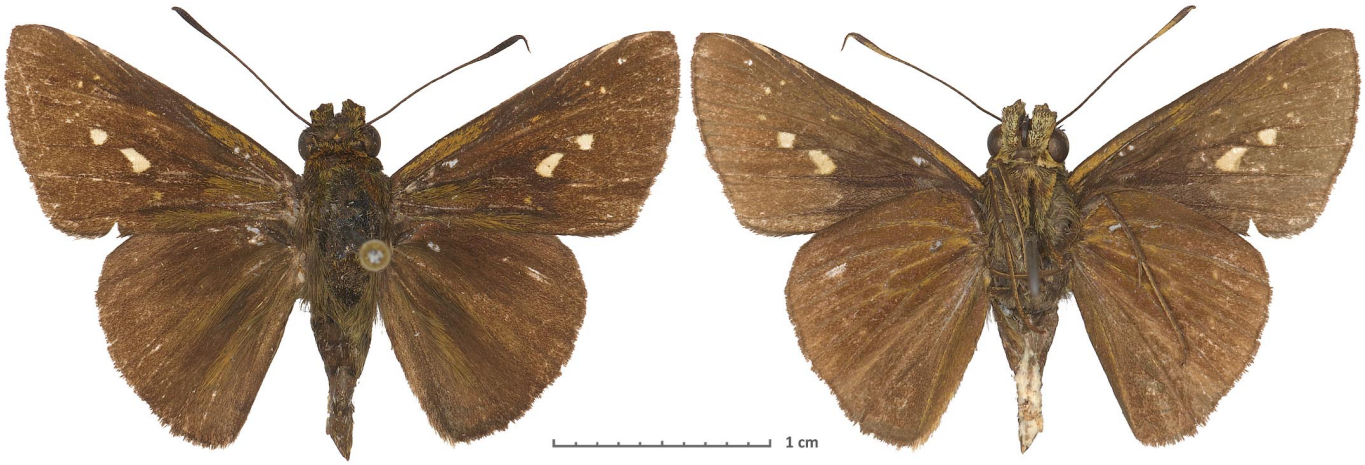

Fig. 58. *Vistigma (Vistigma) shnoba* **sp. n.** holotype ♂ NVG-19024C05 in dorsal (left) and ventral (right) views, data in text.

Fig. 59. Genitalia of *Vistigma shnoba* **sp. n.** holotype ♂ NVG-19024C05 (data in text): **a)** left lateral and **b)** dorsal view, left valva removed, **c)** left valva in inner lateral view.

44.2:C75C (not T), aly728.13.6:A72A (not G), aly1283.20.2:C159C (not T), aly736.5.4:A54A (not G), aly506.10.2:T252T (not C), and COI barcode: T38T, 100G, A211G, T304C, T541T, 607C.

Barcode sequence of the holotype. Sample NVG-19024C05, GenBank PQ489717, 658 base pairs:

AACTTTATATTTTATTTTTGGAATTTGAGCAGGAATATTAGGAACCTCTTTAAGACTATTAATCCGCACTGAATTAGGAGCTCCAGGATCATTAATTGGGGATGATCAAATTTACAACACT
ATCGTAACAGCTCATGCATTTATTATAATTTTTTTTATAGTTATACCAATTATAATCGGAGGATTTGGAAATTGATTAGTACCATTAATGCTAGGAGCTCCAGATATAGCTTTCCCTCGAA
TAAATAATATAAGATTCTGAATATTGCCCCCTTCTTTAATATTATTAATTTCAAGAAGAATCGTAGAAAATGGTGCAGGTACTGGTTGAACTGTTTATCCCCCTCTTTCATCTAATATTGC
TCATCAAGGAGCATCTGTTGACTTAGCAATTTTTTCTTTACATTTAGCAGGTATTTCTTCTATTTTAGGTGCTATTAATTTTATTACTACAATTATTAATATACGAATTAGAAATTTATCA
TTTGATCAAATACCTTTATTTGTTTGATCAGTAGGTATTACCGCATTATTATTACTTTTATCCTTACCTGTATTAGCTGGAGCTATTACTATACTTTTAACTGATCGAAATTTAAATACAT
CCTTTTTTGACCCTGCTGGTGGAGGAGATCCTATTTTATATCAACATCTATTT

Type material. Holotype: ♂ currently deposited in the National Museum of Natural History, Smithsonian Institution, Washington, DC, USA (USNM), illustrated in Fig. 58 (genitalia in Fig. 59), bears the following five printed (text in italics handwritten) rectangular labels, four white: [PERU 300m | 30 Km S.W. | Pto. Maldonado | *24 Oct. '83* | S. S. Nicolay], [genitalia | ♂ slide/vial # | *H882* | Prep. S.S. Nicolay] [DNA sample ID: | NVG-19024C05 | c/o Nick V. Grishin], [USNMENT | {QR Code} | 01532913], and one red [HOLOTYPE ♂ | Vistigma (Vistigma) | shnoba Grishin].

Type locality. Peru: Madre de Dios Region, 30 km southwest of Puerto Maldonado, elevation 300 m.

Etymology. The name is formed from Yiddish שנאָבל (shnobl) or German Schnabel for beak or nose, given for the shape of uncus that inspired the name *opus* for its sister species: "because of the resemblance of the lateral view of the uncus and gnathos to the character Opus, the penguin, in the old comic strip" (Steinhauser 2008). The name is treated as a feminine noun in apposition.

Distribution. Currently known only from the holotype collected in southeastern Peru.

Alyco Grishin, new genus

http://zoobank.org/25B2623E-097A-45C7-8D2D-90D0DB7A9D0E

Type species. *Styriodes quota* Evans, 1955.

Definition. Genomic phylogeny of Moncina A. Warren, 2008 reveals that a female from Guyana we identified as *Styriodes quota* Evans, 1955 (type locality in Guyana) (Fig. 61, genitalia in Fig. 62) is in a different clade from *Styriodes* Schaus, 1913 (type species *Styriodes lyco* Schaus, 1913), currently a subgenus of *Mnasicles* Godman, 1901 (type species *Mnasicles geta* Godman, 1901), and originates in deep radiation among genera such as *Eprius* Godman, 1901 (type species *Epeus veleda* Godman, 1901), *Lychnuchus* Hübner, [1829] (type species *Lychnuchus olenus* Hübner, [1829], which is a junior subjective synonym of *Hesperia celsus* Fabricius, 1793), and *Mit* Grishin, 2022 (type species *Mnasitheus badius* Bell, 1930), while not being particularly close to any of them (Fig. 60) and in a different clade from *Mnasicles* (see Fig. 6 in Zhang et al. (2023g)). Therefore, the lineage with *S. quota* represents a new genus. This genus differs from its relatives by a combination of the following characters: males with a short rhomboidal brand of two segments, separated by the vein CuA_2; aedeagus with two long (slightly

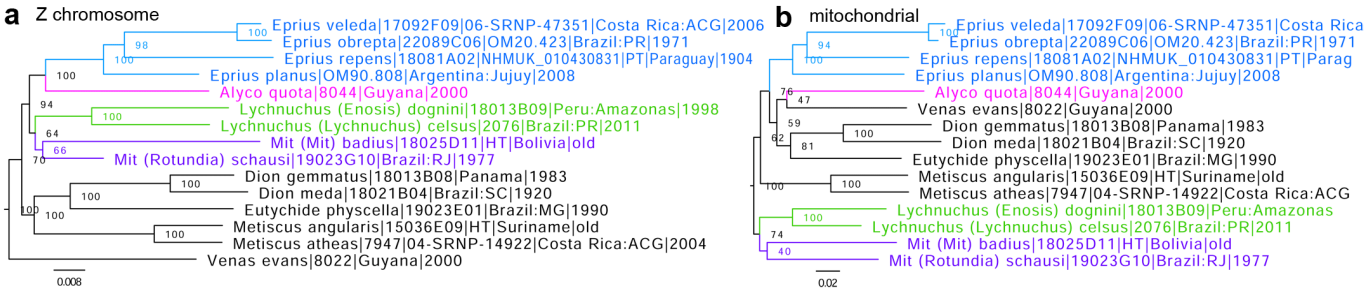

Fig. 60. Phylogenetic trees of *Alyco* **gen. n.** relatives constructed from protein-coding regions in **a)** the Z chromosome and **b)** the mitochondrial genome: *Eprius* (blue), *Alyco* **gen. n.** (magenta), *Lychnuchus* (green), and *Mit* (purple).

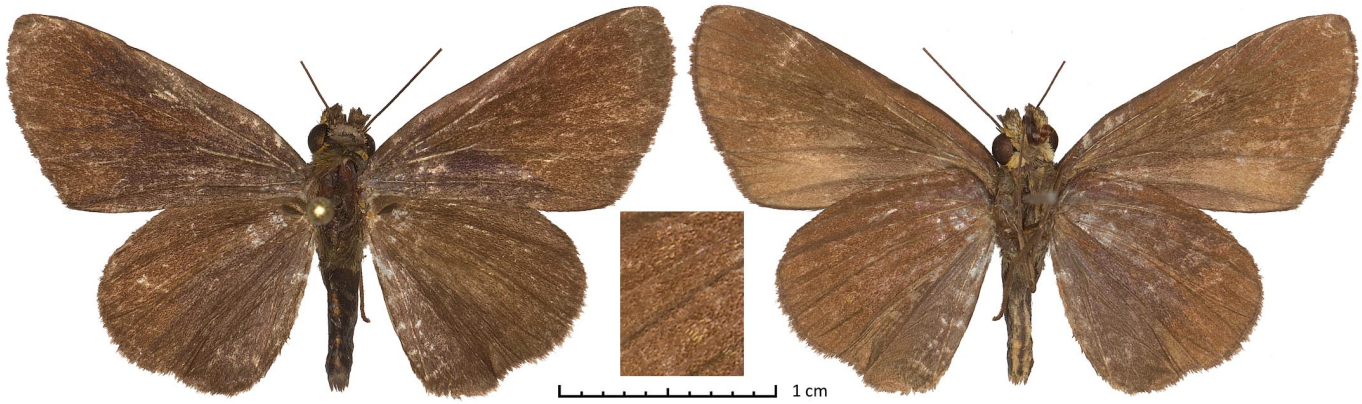

Fig. 61. *Alyco quota* **comb. nov.** ♀ NVG-8044 USNMENT 00177809 from Guyana: Cuyuni-Mazaruni Region, Cuyuni River, Kamaria Falls, 100', approx. GPS 6.40, −58.77, 30-Nov-5-Dec-2000, S. Fratello et al. leg. [USNM] in dorsal (left) and ventral (right) views. The inset displays a magnified postdiscal portion of the right hindwing ventral side, showing traces of three pale spots composed of a few scales (just three scales in one).

shorter than uncus) and arched symmetrical terminal processes; uncus is undivided, triangular in dorsal view and rather straight and narrow in lateral view; valva is elongated and rounded, with a Γ-shaped process directed dorsad (bending posteriad) from the middle of its ventral margin. In DNA, a combination of the following characters is diagnostic in the nuclear genome: aly10672.9.2:G159A, aly1456.2.1:C129T, aly525.128.1:C631A, aly824.26.7:C69T, aly887.25.3:T111C, aly1656.17.1:T189T (not C), aly240.31.3:G63G (not C), aly451.7.7:C47C (not G), aly50.27.3:C79C (not T), aly208.49.1:C148C (not A), and COI barcode: 79C, T202G, T232C, A328T, A415T, T457C.

Barcode sequence of the type species. Sample NVG-8044, GenBank PQ489718, 658 base pairs:

AACTTTATATTTTATTTTTGGTATTTGAGCAGGAATACTAGGAACTTCTTTAAGTTTA
CTAATTCGAACAGAATTAGGCAATCCTGGTTCTTTAATTGGAGATGATCAAATTTATA
ATACTATTGTAACAGCTCATGCTTTTATTATAATTTTTTTTATAGTAATACCTATTAT
AATTGGAGGATTTGGAAATTGATTAGTGCCTTTAATATTAGGAGCCCCAGATATAGCC
TTTCCACGAATAAATAATATAAGATTTTGAATATTACCCCCCTCACTATTATTACTAA
TTTCAAGAAGAATTGTTGAAAATGGTGCAGGAACTGGTTGAACTGTTTATCCCCCTTT
ATCTTCTAATATTGCTCATCAAGGTTCATCAGTTGACTTAGCAATCTTTTCTTTACAT
TTAGCTGGTATTTCCTCTATTTTAGGAGCTATTAATTTCATTACTACAATCATTAATA
TACGAATCAAAAACATATCATTTGATCAAATACCCTTATTTGTTTGATCAGTAGGAAT
TACAGCTTTATTATTATTATTATCTTTACCTGTATTAGCAGGAGCTATTACAATACTT
CTCACTGATCGAAATTTAAATACTTCTTTTTTTGATCCTGCCGGAGGAGGAGATCCTA
TTTTATATCAACATTTATTT

Etymology. The name stems from a misidentification we spotted in the USNM collection: a specimen of the type species was identified as "*Styriodes lyco*". Negating a- was added to *lyco* to form the genus name, which is treated as a feminine noun in the nominative singular.

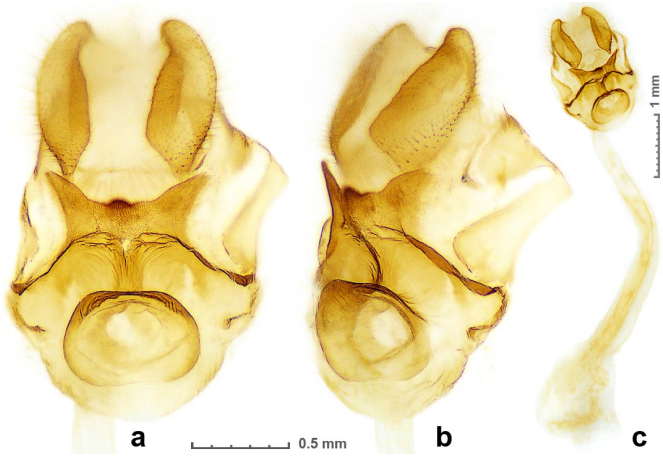

Fig. 62. Genitalia of *Alyco quota* **comb. nov.** ♀ NVG-8044, vial NVG170208-29, data in Fig. 61 legend: **a)** ventral and **b)** right ventrolateral views of sterigma (scale below), **c)** complete genitalia in ventral view (scale on the right).

Species included. Only the type species (i.e., *Styriodes quota* Evans, 1955).

Parent taxon. Subtribe Moncina A. Warren, 2008.

Comment. As far as we know, females of *Alyco quota* **comb. nov.** have not been reported. We take this opportunity to illustrate the female genitalia of this rarely encountered species (Fig. 62). An unusual feature of the female genitalia is lamella antevaginalis, which is ventrally expanded into a structure resembling an octopus sucker on a tentacle.

Subtribe Carystina Mabille 1878

Vertica (*Brasta*) *asta* Grishin, new species

http://zoobank.org/055F4CF8-5498-47F7-B800-D17EE25F3A36

(Figs. 63 part, 64)

Definition and diagnosis. Genomic analysis reveals that a specimen from Colombia identified as belonging to the subgenus *Brasta* Grishin, 2022 (type species *Lychnuchus brasta* Evans, 1955) of the genus *Vertica* Evans, 1955 (type species *Hesperia verticalis* Plötz, 1882) is genetically differentiated from the only known species in the subgenus *Vertica* (*Brasta*) *brasta* (type locality in Peru: Chanchamayo) at the species level (Fig. 63): e.g., their COI barcodes differ by 6.1% (40 bp). In the presence of phenotypic

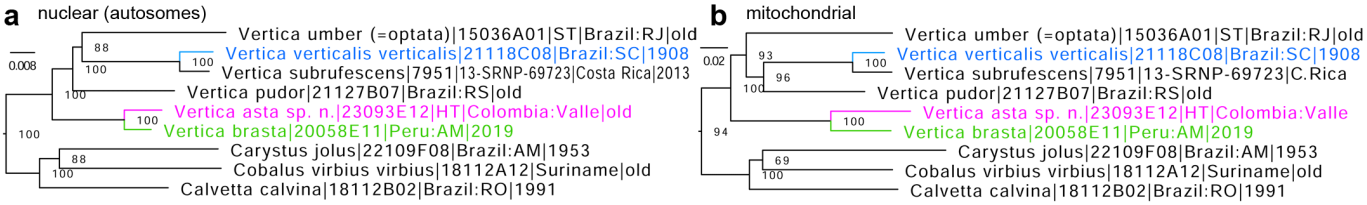

Fig. 63. Phylogenetic trees of selected species of *Vertica* constructed from protein-coding regions in **a)** the nuclear genome (autosomes) and **b)** the mitochondrial genome: *V. asta* **sp. n.** (magenta), *V. brasta* (green) and *V. verticalis* (blue).

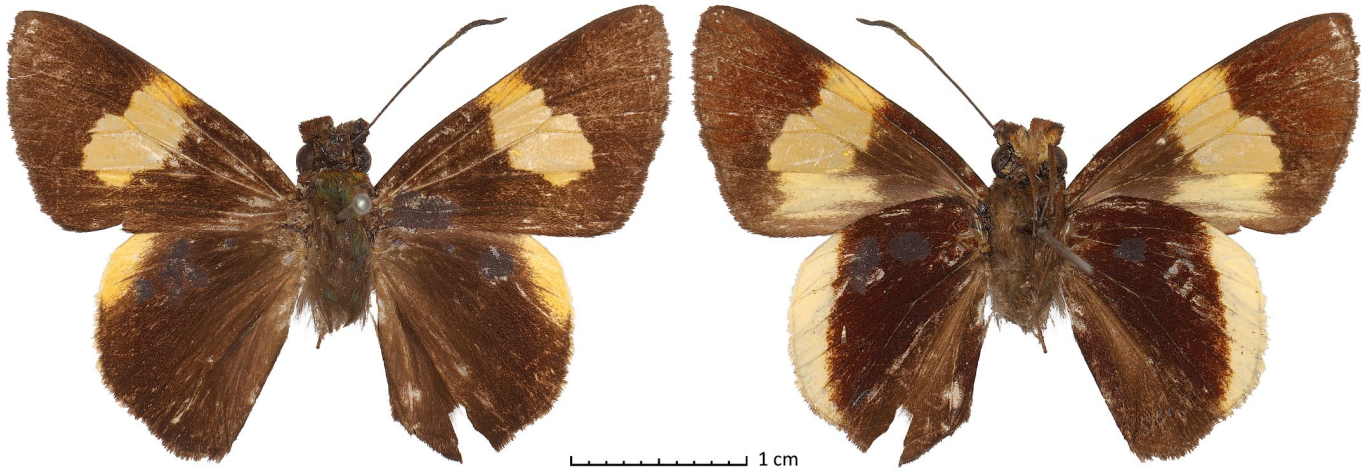

Fig. 64. *Vertica* (*Brasta*) *asta* **sp. n.** holotype ♂ NVG-23093E12 in dorsal (left) and ventral (right) views, data in text.

differences, this specimen represents a new species. This new species is closest to "*Lychnuchus brasta*" (K.12.3) and keys to it in Evans (1955) but differs by wider pale (cream-yellow) markings: broader central band (partly hyaline) on the forewing that is nearly oval rather than narrow-rectangular, beneath extending to the inner margin with a wide (nearly 2/5 of the wing length) pale spot; a wider pale spot at the hindwing apex, as well as the marginal pale stripe on ventral hindwing, the inner margin of the stripe is close to straight, not curving along the outer wing margin. Due to unexplored phenotypic variation in this species, most reliable identification is achieved by DNA, and a combination of the following base pairs is diagnostic in the nuclear genome: aly116.29.8:C117T, aly905.4.1:A801G, aly2700.2.4:C45T,

aly2700.2.4:C57T, aly128.13.1:C282T, aly725.17.2:T60T (not C), aly525.71.1:G69G (not A), aly18826.6.1: C42C (not T), aly1038.16.2:C198C (not A), aly182.2.2:C99C (not T), and COI barcode: T16C, A40C, T193C, A412G, T421C, T589C.

Barcode sequence of the holotype. Sample NVG-23093E12, GenBank PQ489719, 658 base pairs:

AACTTTATATTTTATCTTTGGTATCTGAGCAGGTATAGTCGGAACTTCTCTCAGAATATTAATTCGAACAGAATTAGGTAATCCCGGATCTTTAATCGGAGATGATCAAATTTATAACACT
ATCGTTACTGCTCACGCTTTTATTATAATTTTTTTTATAGTAATACCTATTATAATTGGAGGTTTTGGAAACTGATTAGTACCTTTAATATTAGGAGCCCCAGATATAGCTTTCCCCCGTA
TAAATAATATAAGATTTTGAATGTTGCCCCCCTCTTTAACCCTTTTAATTTCAAGAAGAATCGTAGAAAATGGAGCAGGAACAGGATGAACAGTATACCCCCCACTTTCATCTAATATTGC
TCATCAAGGATCTTCTGTTGATTTAGCAATTTTTTCATTACACTTAGCGGGAATTTCCTCAATTTTAGGAGCAATTAATTTTATTACCACAATTATTAATATACGAATTAAAAATATATCA
TTTGATCAAATACCCCTATTTATTTGATCAGTTGGAATTACAGCTTTATTATTAATTTTATCTTTACCAGTATTAGCTGGAGCTATTACAATACTTCTTACTGACCGAAATTTAAATACCT
CCTTTTTTGATCCTGCAGGAGGAGGAGATCCAATCCTATATCAACATTTATTT

Type material. Holotype: ♂ deposited in the collection of the Zentrum für Biodokumentation des Saarlandes, Schiffweiler, Germany (ZfBS), illustrated in Fig. 64, bears the following five rectangular labels (2nd handwritten, 3rd without text, others printed; 3rd and the last red, others white): [Rio Aguacatal | Colomb. W.Codr. | 2000 m | Coll. Fassl], [?], [ ] no text on this red label, [DNA sample ID: | NVG-23093E12 | c/o Nick V. Grishin], [HOLOTYPE ♂ | Vertica (Brasta) | asta Grishin].

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

Etymology. The name is formed from its sister species name, which is made shorter to indicate a more northern distribution of this species. The name is treated as a noun in apposition.

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

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