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Butterfly taxa discovery via genomic analysis

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ABSTRACT. Expanding a genomics-guided assessment of butterfly taxonomy, we integrate phylogenetic evidence from all protein-coding genes with morphological considerations to refine our understanding of butterfly systematics and discover new taxa. As a result, 2 subgenera, 39 species, and 5 subspecies are proposed as new (type species in original combinations or type localities are listed in parentheses): *Erebia* (*Magda*) *magdalena uintana* Grishin, **ssp. n.** (USA: Utah, Uintah Co.) in Nymphalidae Rafinesque, 1815; *Myselasia rondea* Grishin, **sp. n.** (Brazil: Rondônia), *Myselasia pseudocrinon* Grishin, **sp. n.** (Ecuador: Pastaza), *Myselasia paramatuta* Grishin, **sp. n.** (Ecuador: Morona-Santiago), *Euselasia anapellus* Grishin, **sp. n.** (Peru: Loreto), *Ectosemia lavanda* Grishin, **sp. n.** (Brazil: Amazonas), *Ectosemia dira* Grishin, **sp. n.** (Peru: Cuzco), *Ectosemia attavus cyanea* Grishin, **ssp. n.** (Ecuador: Tungurahua), *Mesosemia tinypuncta* Grishin, **sp. n.** (Panama: Chiriquí), *Mesosemia parabanda* Grishin, **sp. n.** (Peru: Cuzco), *Napaea extraperlata* Grishin, **sp. n.** (Ecuador: Morona-Santiago), *Ithomiola* (*Ithomiola*) *cuscola* Grishin, **sp. n.** (Peru: Cuzco), *Ithomiola* (*Ithomiola*) *bolitanos* Grishin, **sp. n.** (Bolivia: La Paz), *Ithomiola* (*Ithomiola*) *ecuatanos* Grishin, **sp. n.** (Ecuador: Tungurahua), *Ithomiola* (*Ithomiola*) *tanos cuscanos* Grishin, **ssp. n.** (Peru: Cuzco), *Ithomiola* (*Ithomiola*) *manchola* Grishin, **sp. n.** (Peru: Madre de Dios), *Ithomiola* (*Ithomiola*) *triola* Grishin, **sp. n.** (Bolivia: Santa Cruz), *Apodemia* (*Apodemia*) *estrellada* Grishin, **sp. n.** (Mexico: Sonora), and *Synargis corta* Grishin, **sp. n.** (French Guiana: Roura) in Riodinidae Grote, 1895 (1827); *Idiospilix* Grishin, **subgen. n.** (*Rapala subguttata* Elwes, [1893]) in Lycaenidae [Leach], [1815]; and *Drephalys* (*Paradrephalys*) *cremoreus* Grishin, **sp. n.** (Bolivia: Santa Cruz), *Dyscophellus megaporsena* Grishin, **sp. n.** (Northern Argentina), *Cecropterus* (*Murgaria*) *perichales* Grishin, **sp. n.** (Peru), *Cecropterus* (*Murgaria*) *guatemalensis* Grishin, **sp. n.** (Guatemala: Petén), *Charidia paronia* Grishin, **sp. n.** (Brazil: Rondônia), *Quadrus* (*Quadrus*) *teelatus* Grishin, **sp. n.** (Venezuela: Aragua), *Quadrus* (*Quadrus*) *truncatina* Grishin, **sp. n.** (Peru: Junín), *Gindanes vittatus* Grishin, **sp. n.** (Brazil: Rondônia), *Arteurotia artistella sinalima* Grishin, **ssp. n.** (Mexico: Sinaloa), *Bolla* (*Sebia*) *azora* Grishin, **sp. n.** (Mexico: Oaxaca), *Bolla* (*Sebia*) *brennatus* Grishin, **sp. n.** (Panama: Darién), *Bolla* (*Sebia*) *zuelisa* Grishin, **sp. n.** (Venezuela: Trujillo), *Bolla* (*Uniphylus*) *martea* Grishin, **sp. n.** (Colombia: Magdalena), *Staphylus* (*Capilla*) *lemesi* Grishin, **sp. n.** (Venezuela: La Guaira), *Anisochoria minorella hermiere* Grishin, **ssp. n.** (Argentina: Salta), *Justa* Grishin, **subgen. n.** (*Thoressa justini* Inoué & Kawazoé, 1969), *Isma bulaga* Grishin, **sp. n.** (Philippines: Mindanao), *Isma leytatus* Grishin, **sp. n.** (Philippines: Leyte), *Decinea buenia* Grishin, **sp. n.** (Bolivia: Santa Cruz), *Decinea brocki* Grishin, **sp. n.** (Peru: Cuzco), *Zenis parlatatus* Grishin, **sp. n.** (Brazil: Rondônia), *Zenis doris* Grishin, **sp. n.** (Ecuador: Morona-Santiago), *Mucia rustana* Grishin, **sp. n.** (Peru: Cuzco), *Mucia castanuzza* Grishin, **sp. n.** (Peru: Cuzco), *Alerema uniplex* Grishin, **sp. n.** (Bolivia: La Paz), and *Racta racteca* Grishin, **sp. n.** (Ecuador: Tungurahua), in HesperIIDae Latreille, 1809. *Lacturnea* Nazari & Fric, 2025, **stat. nov.**, *Huegelia* Nazari & Fric, 2025, **stat. nov.**, and *Everes* Hübner, [1819], **stat. rev.** are subgenera of *Cupido* Schrank, 1801 (not genera). The following are new combinations: *Ajenorix subguttata* (Elwes, [1893]), **comb. nov.** (not *Virachola* F. Moore, 1881) and *Halpe justini* (Inoué & Kawazoé, 1969), **comb. nov.** (not *Thoressa* Swinhoe, 1913). The following taxa are species (not subspecies or synonyms of the taxa given in parentheses): *Erebia* (*Magda*) *avinoffi* W. Holland, 1930, **stat. rest.** (not *Erebia* (*Magda*) *fasciata* Butler, 1868), *Myselasia gonzaloi* (Salazar & Henao, 2019), **stat. nov.** (not *Myselasia gradata* (Stichel, 1927)), *Ectosemia attalus* (Seitz, 1913), **stat. nov.** (not *Ectosemia eumene* (Cramer, 1776)), *Ectosemia furia* (Stichel, 1910), **stat. nov.** (not *Ectosemia erinnya* (Stichel, 1910)), *Cupido* (*Sinocupido*) *korlana* Staudinger, 1901, **stat. nov.** (not *Cupido* (*Everes*) *prosecusa duplex* (Alphéraky, 1887)), *Plebejus* (*Lycaeides*) *scudderii* (W. H. Edwards, 1861), **stat. rest.** (not *Plebejus* (*Lycaeides*) *idas* (Linnaeus, 1760); consequently, all North American subspecies formerly assigned to *P. idas* are treated here as subspecies of *P. scudderii*), *Cecropterus* (*Cecropterus*) *capys* Godman & Salvin, 1894, **stat. rest.** (not *Cecropterus* (*Cecropterus*) *longipennis* Plötz, 1882), *Cogia terranea* (Butler, 1874), **stat. rest.** (not *Cogia calchas* (Herrich-Schäffer, 1869)), *Halpe raphaeli* (Nuyda & Kitamura, 1994), **comb. et stat. nov.**

(not *Halpe justini* (Inoué & Kawazoé, 1969), **comb. nov.**), and *Potanthus* (*Potanthus*) *pavor* (De Niceville, 1894), **stat. rest.** (not *Potanthus* (*Potanthus*) *euria* (Plötz, 1883)). The following taxa are valid subspecies, not species or synonyms: *Erebia* (*Magda*) *avinoffi semo* Grum-Grshimailo, 1899, **stat. rev.**, *Satyrium californica helenae* M. Fisher, 2009, **stat. rest.**, *Cecropterus* (*Cecropterus*) *longipennis punctisignatus* Bryk, 1953, **stat. rest.**, *Bolla* (*Bolla*) *nigerrima banosa* (Bell, 1937), **stat. nov.**, *Staphylus* (*Capilla*) *azteca machuca* (Schaus, 1913), **stat. nov.**, and *Staphylus* (*Capilla*) *tyro nicoleae* Lemes, 2026, **stat. nov.** The following taxa are confirmed as valid: *Erebia* (*Magda*) *mackinleyensis* Gunder, 1932, *Satyrium californica wapiti* M. Fisher, 2006, and *Isma bipunctata* Elwes & Edwards, 1897. The following taxa are **new** junior subjective synonyms: *Lethina* Reuter, 1896 of *Parargina* Tutt, 1896, *Euselasia ella terrea* Stichel, 1924 of *Myselasia eulione* (Hewitson, 1856), *Euselasia gradata* Stichel, 1927 of *Myselasia cucuta* (Schaus, 1902), *Euselasia pseudomys* Callaghan, 1999 of *Myselasia rhodon* (Seitz, 1913), *Euselasia crotopus* form. *mutator* Seitz, 1916 of *Erythia micaela* (Schaus, 1902), *Mesosemia meyi* Brévignon, 1997 of *Ectosemia eumene* (Cramer, 1776), *Lycaena gisela* Püngeler, 1901 of *Cupido* (*Sinocupido*) *korlana* Staudinger, 1901, **stat. nov.**, and *Pamphila orfitus* Mabille, 1883 of *Potanthus* (*Potanthus*) *euria* (Plötz, 1883); and the following are revised junior subjective synonyms: *Sinocupido lokiangensis* Lee, 1963 of *Cupido* (*Sinocupido*) *korlana* Staudinger, 1901 and *Staphylus inconstans* Bell, 1932 of *Staphylus* (*Capilla*) *azteca machuca* (Schaus, 1913), **stat. nov.** A confidently resolved phylogeny suggests partitioning the tribe Satyrini Boisduval, 1833 into 13 subtribes and places *Llorenteana* Vilorio & Luis-Martínez, [2019] in Euptychiina Reuter, 1896 (not Ypthimina Reuter, 1896). The following species described from a single specimen are confirmed by genomic sequencing of additional specimens: *Phanus centralis* Grishin, 2025 (known from El Salvador), *Phanus ecutinus* Grishin, 2025 (range extended from northwestern Ecuador to Panama), *Telegonus* (*Rhabdoides*) *elorianus* Grishin, 2025 (recorded from southern Brazil and Argentina), and *Rhomba pulla* Grishin, 2023. Furthermore, we clarify the type locality of *Apodemia* (*Apodemia*) *apache* Grishin, 2026 as USA: Arizona, Apache Co., US-60, 8 mi west of Greens Peak Road, elevation 7000 ft; provide additional evidence for the distinction of *Satyrium dryope* (W. H. Edwards, 1870) as a species-level taxon that possibly does not form a monophyletic group with *Satyrium sylvinus* Boisduval, 1852, and demonstrate that both *Arteurotia artistella* Grishin, 2023 and *Arteurotia tractipennis* A. Butler & H. Druce, 1872 occur in eastern Chiapas (Mexico) and Guatemala. **Lectotypes** are designated for 18 taxa: *Erebia magdalena* Strecker, 1880 (USA: Colorado, Clear Creek Co.), *Erebia fasciata* Butler, 1868 (Canada: Nunavut, Victoria Is.), *Euselasia ella* Seitz, 1916 (Bolivia: La Paz, Río Zongo), *Euselasia ella terrea* Stichel, 1924 (Brazil: Pará, Río Moju), *Eurygona cucuta* Schaus, 1902 (Venezuela: Táchira, vic. Cúcuta), *Eurygona matuta* Schaus, 1913 (Costa Rica: Cartago, Juan Viñas), *Eurygona micaela* Schaus, 1902 (Peru), *Euselasia crotopus* form. *mutator* Seitz, 1916 (Peru), *Mesosemia eumene* form. *attalus* Seitz, 1913 (French Guiana: Nouveau Chantier), *Mesosemia albipuncta* Schaus, 1913 (Costa Rica: Limón, Guápiles, La Esperanza), *Apodemia multiplaga* Schaus, 1902 (Mexico: Veracruz, Rinconada), *Lycaena gisela* Püngeler, 1901 (China: Xinjiang, Tarim River area vic. Aksu), *Lycaena prosecusa* v. *korlana* Staudinger, 1901 (China: Xinjiang, Korla), *Eudamus calchas* Herrich-Schäffer, 1869 (Brazil: Rio de Janeiro), *Nisoniades braco* Herrich-Schäffer, 1865 (Cuba), *Bolla nigerrima* Mabille & Boulet, 1917 (Peru: Puno, Chaquimayo), *Anisochoria minorella* Mabille, 1898 (Bolivia: La Paz, Río Tanampaya), and *Hesperia euria* Plötz, 1883 (Java). **Neotypes** are designated for *Papilio eumene* Cramer, 1776 (Suriname) and *Nisoniades undulatus* Herrich-Schäffer, 1865 (Cuba: Matanzas). A full-length COI barcode sequence is provided for every designated lectotype and neotype.

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

ZooBank registration: <https://zoobank.org/F1976E0A-4266-4DC5-ABE3-796B7DE58014>

INTRODUCTION, CONCEPTS, AND METHODS

This study directly extends our previous investigations by adding newly sequenced specimens generated with the same methodologies and interpreted within the same analytical framework (Cong et al. 2019b; 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. 2023b, d, f; Zhang et al. 2024a–c; Zhang et al. 2025a–c, e; Cong et al. 2026a, b; Zhang et al. 2026). The goal of the present work is to discover previously unrecognized butterfly species and subspecies using genomic evidence. To achieve this objective, we examine a broad array of butterfly lineages from throughout the world. The specimens studied derive primarily from museum and private collections (see Acknowledgments for details) and range from recently collected material to specimens preserved for hundreds of years. Whenever possible, DNA is obtained from primary type specimens so that species names can be anchored to objective genomic references (Cong et al. 2021; Zhang et al. 2022a). DNA is usually extracted from a leg using a non-destructive protocol that maintains the morphology of the specimen for later examination. When DNA has not already been degraded by age, it is fragmented before library preparation. Sequencing is

performed on the Illumina platform and produces 150-base-pair (bp) reads. Rather than relying on targeted amplification of particular genes or fragments, the method sequences all DNA fragments recovered from the specimen. As a result, it is equally effective for historical material with highly fragmented DNA, often only 30–50 bp long.

For every specimen, all sequencing reads are utilized, including both complete 150-bp reads and shorter fragments, to reconstruct exons of protein-coding genes. Reconstruction is guided by the genome of a closely related species for which a high-quality reference assembly is available. These reconstructed genes form the basis of phylogenetic analyses. We infer three phylogenetic trees using IQ-TREE v1.6.12 under the GTR+GAMMA model (Nguyen et al. 2015): one from autosomal nuclear genes, one from genes inferred to reside on the Z chromosome, and one from mitochondrial DNA. All adequately covered codons are incorporated into an alignment generated dynamically and not retained, and the number of positions included in each nuclear-genome analysis is reported in the corresponding figure legend, ranging from hundreds of thousands to several million sites. Mitogenomes are approximately 15,000 bp in length. Statistical support is evaluated with ultrafast bootstrap values; support above 97% is regarded as reliable, whereas values below 90% are considered weak and leave relationships unresolved (Hoang et al. 2018). Additional methodological information can be found in our earlier publications (Li et al. 2019; Zhang et al. 2022b).

Phylogenetic trees are displayed, recolored, and rearranged using FigTree (Rambaut 2018). Existing classifications are then overlaid on these trees to identify taxa that are not monophyletic and to recognize clades corresponding to previously overlooked groups. Genome-scale phylogenies frequently reveal distinct evolutionary “levels,” representing intervals during which several lineages diversified at approximately the same time (Zhang et al. 2021). Such concurrent radiations are often associated with geological or climatic events affecting multiple butterfly groups simultaneously. These patterns provide a basis for matching taxonomic categories such as tribe, subtribe, genus, and subgenus to diversification levels evident in genomic data. This approach promotes a classification that is evolutionarily informative and internally coherent, being rooted in genetic divergence and informed by paleontological evidence. Applying these principles consistently should improve long-term taxonomic stability. Our taxonomic decisions rely primarily on genomic phylogenies, while morphology serves a supporting role. This preference reflects the fact that genomes contain information extending beyond adult morphology, traditionally the cornerstone of butterfly taxonomy, to include signals related to ecology, reproduction, life history, and diet. Although phenotypes cannot yet be predicted directly from DNA sequences, large datasets of protein-coding genes provide dependable genetic proxies, and well-supported phylogenies offer a robust basis for classification. Together, these considerations support a taxonomic framework aligned with both evolutionary history and genomic evidence.

In this study, we focus mostly on species- and subspecies-level taxonomy. Species limits are assessed using multiple lines of evidence, including Z-chromosome differentiation with F_{st} values greater than 0.20 (generally indicative of species-level divergence), G_{min} values below 0.05 (suggesting restricted gene flow) (Cong et al. 2019a; Cong et al. 2026a), COI barcode divergence of approximately 2% or greater (Hebert et al. 2003) together with corresponding phenotypic differences (Lukhtanov et al. 2016), and the presence of distinct, strongly supported clades in phylogenetic trees (Zhang et al. 2022d). We recognize that mitochondrial markers such as COI frequently introgress between species (Bachtrog et al. 2006; Cong et al. 2017a), meaning that otherwise distinct species may sometimes share identical barcodes (Burns et al. 2008; Zhang et al. 2023a). Additional discussion is provided in Zhang et al. (2022a), under the section “Species, subspecies, and genomics.”

Traditionally, subspecies are viewed as geographically separated populations that exhibit consistent phenotypic differences (for example, when roughly 70% of individuals can be identified by appearance alone regardless of locality) while potentially remaining capable of interbreeding (Mayr 1982; Monroe 1982). In practice, reproductive compatibility is rarely tested, and butterfly subspecies are usually diagnosed solely from wing-pattern variation. Whether such differences are genetically determined or environmentally induced is often unclear. Genomic approaches allow populations to be compared directly

at the DNA level. Here, we describe new subspecies that correspond to genomic clades, namely distinct groups recovered in at least one phylogenetic tree that are genetically differentiated and strongly supported (approximately 100% bootstrap), yet insufficiently divergent to warrant recognition as separate species. These taxa represent early stages of speciation, reflecting populations that have begun diverging but may not yet have developed substantial reproductive isolation. After identifying such clades, we evaluate wing patterns to determine diagnostic phenotypic traits. As expected for subspecies, these characters are statistical rather than absolute and show individual variation. Because our subspecies are defined by genomic clades, the associated DNA characters provide more reliable diagnostics than morphology and apply to nearly all specimens. Consequently, DNA-based diagnoses are supplied for every newly described subspecies.

The taxa treated in this work are arranged according to the genome-wide phylogeny, supplemented by morphological considerations. For each newly proposed taxon, we provide concise descriptions of diagnostic morphological characters, often accompanied by references containing identification keys, detailed treatments, and illustrations, together with diagnostic DNA characters from the nuclear genome and, where available, the COI barcode. These DNA characters were derived from protein-coding regions using our previously established protocol (see SI Appendix in Li et al. (2019)). The procedure for identifying robust diagnostic characters, described in Cong et al. (2019b), is intended to produce characters that should remain informative as additional specimens and taxa are incorporated into genomic datasets.

DNA character states are reported relative to one of four reference genomes: *Heliconius melpomene* (Linnaeus, 1758) (hm) (Davey et al. 2016), *Calephelis nemesis* (W. H. Edwards, 1871) (cne) (Cong et al. 2017b), *Calycopis cecrops* (Fabricius, 1793) (cce) (Cong et al. 2016), or *Cecropterus lyciades* (Geyer, 1832) (aly, reflecting the former placement of this species in *Achalarus* Scudder, 1872) (Shen et al. 2017). The notation used are aly728.44.1:G672C means position 672 in exon 1 of gene 44 from scaffold 728 of the *C. lyciades* reference genome (aly) is C, changed from G in the ancestor. When characters are given for the sister clade of the diagnosed taxon, the following notation is used: aly5294.20.2:A548A (not C), which means that position 548 in exon 2 of gene 20 on scaffold 5294 is occupied by the ancestral base pair A, which was changed to C in the sister clade (so it is not C in the diagnosed taxon). COI barcode characters follow the same format but lack a prefix ending in ‘:’ and in some cases ancestral base pair (where unclear). Complete exon sequences from the reference genome, with diagnostic positions for new taxa highlighted in green, are provided in the supplementary file <https://osf.io/3q72k>. This file allows all diagnostic characters to be traced directly to their underlying sequences. Links to iNaturalist (2026) observations by observation number reported in figure legends are <https://www.inaturalist.org/observations/n>, where n denotes the observation number.

The whole-genome shotgun datasets generated and analyzed in this work will be made available through the NCBI database (<https://www.ncbi.nlm.nih.gov>) under BioProject PRJNA1478341. Associated BioSample records contain locality information and other collection data for all sequenced specimens included in the phylogenetic trees. In tree figures, each specimen is annotated with the following fields separated by “|”: taxon name (with comments in square brackets where applicable), DNA sample identifier, type status, general locality, and year of collection (“old” for undated specimens likely collected approximately 100–150 years ago). Type-status abbreviations are HT (holotype), LT (lectotype), ST (syntype), NT (neotype), PT (paratype), AT (allotype), PLT (paralectotype), and TT (topotype, not a formal type but a specimen originating from the vicinity of the type locality). When a synonym is listed in parentheses and preceded by “=” (and additionally by “‡” for unavailable names), the type status refers to the synonym unless the symbol “&” indicates that it applies simultaneously to both names, as may occur with replacement names for junior homonyms or objective synonyms. COI barcode sequences reported here have been deposited in GenBank under accessions [PZ516372–PZ516446](#). Abbreviations or acronyms for collections are listed in the Acknowledgments.

Family Nymphalidae Rafinesque, 1815

Lethina Reuter, 1896 is a junior subjective synonym of Parargina Tutt, 1896

A confidently supported genomic phylogeny of the tribe Satyrini Boisduval, 1833 constructed from concatenated protein-coding regions of all autosomal genes agrees with the recognition of 13 subtribes: Ragadiina Herrich-Schäffer, 1864, Eritina L. Miller 1968, Parargina Tutt, 1896, Mycalesina Reuter, 1896, Coenonymphina Tutt, 1896, Satyrina Boisduval, 1833, Euptychiina Reuter, 1896, Pronophilina Reuter, 1896, Erebiina Tutt, 1896, Callerebiina Grishin, 2021, Ypthimina Reuter, 1896, Calistina Grishin, 2021, and Gyrocheilina Grishin, 2021 (Zhang et al. 2021) (Fig. 1).

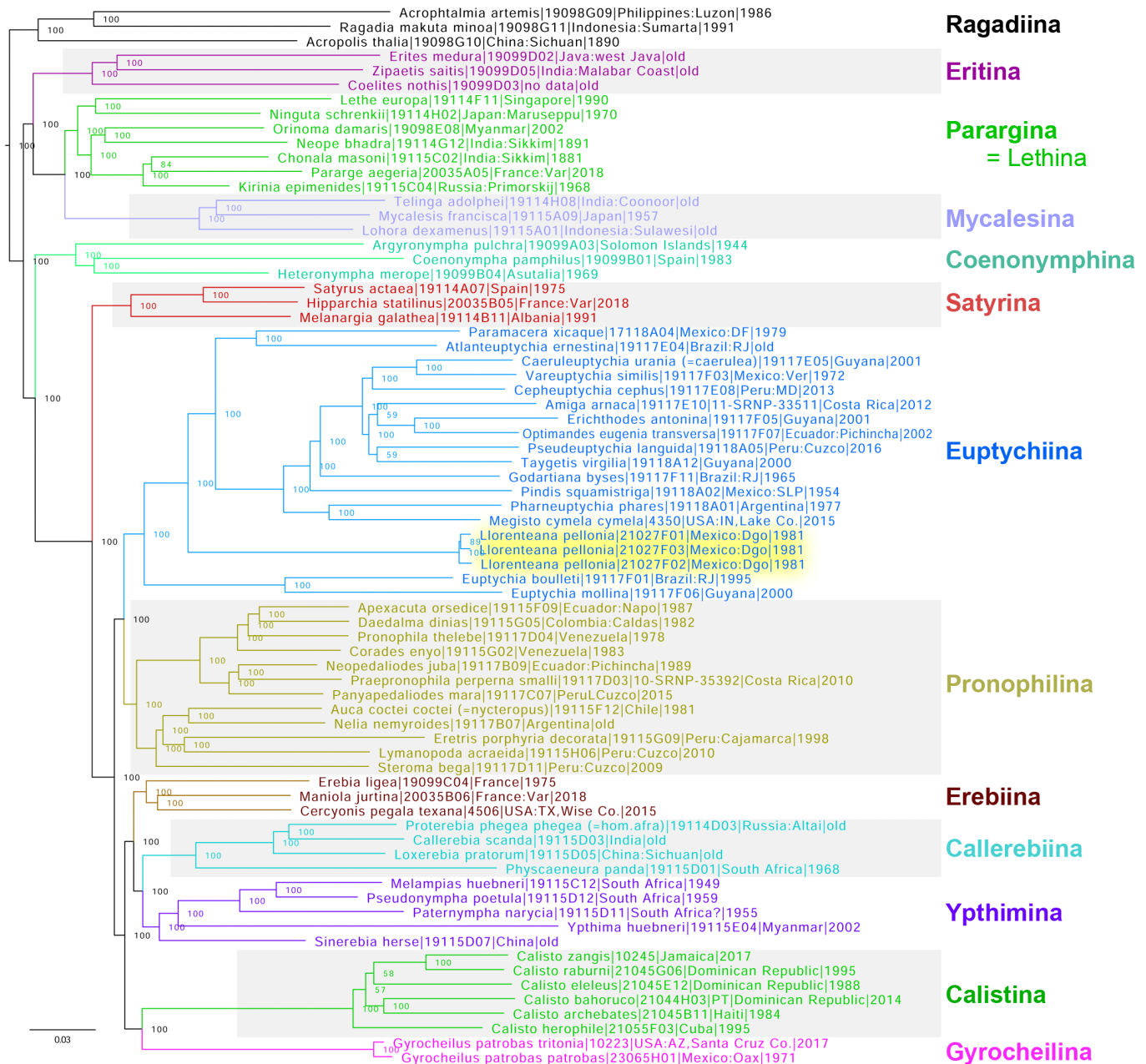


Fig. 1. Phylogenetic trees of selected Satyrini species representing all subtribes constructed from protein-coding regions in the nuclear genome (autosomes), based on 4,527,756 positions. Different subtribes are colored differently: Ragadiina (black), Eritina (purple), Parargina (green, with Lethina as its synonym), Mycalesina (lavender), Coenonymphina (aquamarine), Satyrina (red), Euptychiina (blue), Pronophilina (olive), Erebiina (brown), Callerebiina (cyan), Ypthimina (violet), Calistina (darker green), and Gyrocheilina (magenta). *Llorenteana pellowia* is highlighted in yellow. Ultrafast bootstrap (Hoang et al. 2018) values are shown at nodes.

Most of these subtribes were based on morphological considerations and correspond to recognizable phenotypes, while members of the two monotypic subtribes supported by the genomic comparison have been previously and incorrectly included in Pronophilina, rendering it polyphyletic (Zhang et al. 2021) (Fig. 1). With a more strongly supported phylogeny, we find that these two subtribes, Calistina and Gyrocheilina, may be sister taxa (Fig. 1). However, their substantial genetic differentiation and phenotypic distinction preclude unifying Calistina and Gyrocheilina into a single subtribe.

Furthermore, we find that Lethina and Parargina are both polyphyletic in the autosome-based phylogeny, e.g., *Neope* F. Moore, 1866 (type species *Lasiommata* (?) *bhadra* F. Moore, 1858) [from Lethina] and *Orinoma* G. Gray, 1846 (type species *Orinoma damaris* G. Gray, 1846) [from Parargina] are recovered as sister taxa, with their clade being sister to the rest of Parargina (Fig. 1). Genetic differentiation among the clades corresponding to genera from Lethina and Parargina is not prominent, and instead of rearranging genera between the two subtribes to restore their monophyly, we propose that Lethina Reuter, 1896, **syn. nov.** is a junior subjective synonym of Parargina Tutt, 1896. We note that Parargina Tutt, 1896 was published on April 15, 1896 (Tutt 1896), and Lethina Reuter, 1896 was published after May of the same year (Reuter 1896), thus setting the priority for the two names.

***Llorenteana* Viloría & Luis-Martínez, [2019] belongs to Euptychiina Reuter, 1896**

Genomic phylogeny places specimens of *Llorenteana pellowia* (Godman, 1901) (type locality in Mexico: Durango and Jalisco) (Fig. 2), the type and the only species of *Llorenteana* Viloría & Luis-Martínez, [2019], in the subtribe Euptychiina Reuter, 1896 with the strongest possible support (Fig. 1 blue highlighted in yellow) and away from the subtribe Ypthimina Reuter, 1896 (Fig. 1 violet), where it was originally placed (Viloría and Luis-Martínez 2019). Therefore, we propose that *Llorenteana* Viloría & Luis-Martínez, [2019] belongs to Euptychiina Reuter, 1896. Previously, Euptychiina was partitioned into

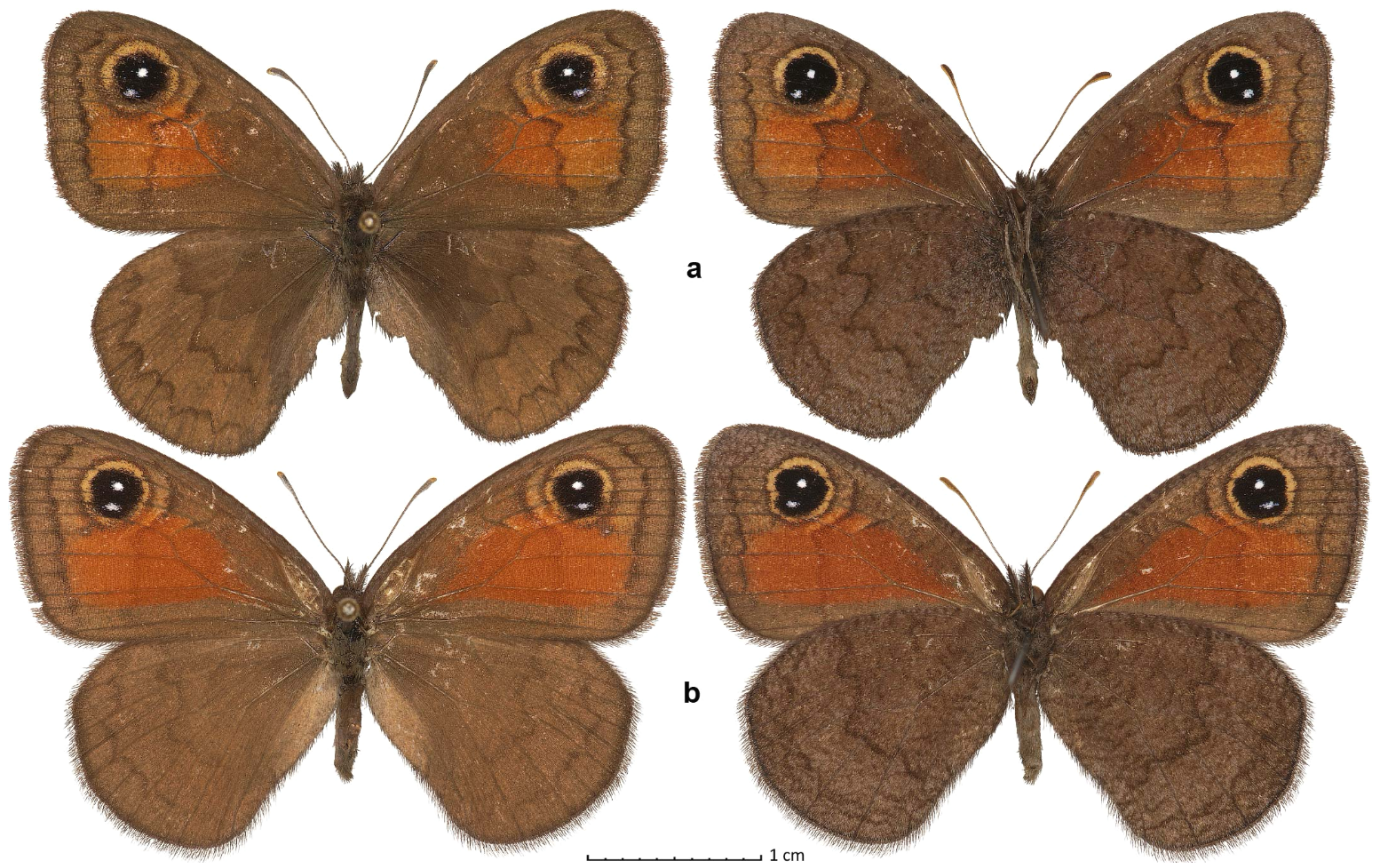


Fig. 2. *Llorenteana pellowia* from Mexico: Durango, 3 mi E of Río Mimbres, Hwy 45, 27-Jul-1981, R. E. Stanford leg. [CSUC] in dorsal (left) and ventral (right) views: **a)** ♂ NVG-21027F01 and **b)** ♀ NVG-21027F02.

two major clades with prominent genetic differentiation between them: a single genus, *Euptychia* Hübner, 1818 (type species *Oreas mollina* Hübner, [1813]) and all other genera included in the tribe (Zhang et al. 2021). *Llorenteana* fills the phylogenetic gap between the two clades, making them less prominent (Fig. 1 blue highlighted in yellow), while being sister to all other Euptychiina genera except *Euptychia*.

Lectotype designation for *Erebia magdalena* Strecker, 1880

Erebia (Magda) magdalena was described by Strecker (1880) from three males in his collection, now in FMNH. These syntypes were “taken by Prof. E. T. Owen in the summer of 1879 in some almost inaccessible place on the mountains near Georgetown, Colorado” (Strecker 1880). We sequenced one syntype as NVG-18041C02. This specimen already bears a lectotype label, but we were not able to find where the designation was published. To stabilize nomenclature and define the name *E. magdalena* objectively, N.V.G. hereby designates this syntype in the FMNH collection, a male illustrated in Fig. 3a that bears the following eight rectangular labels (5th red, 7th blue, others white, 3rd red-framed; first three handwritten, others printed with handwritten text shown in *italics*): [Georgetown], [Col.], [E. Magdalena | Streck. | Georgetown Col. | orig. | Type. E. T. Owen | 1879], [Lepidoptera Type | Photograph No. 130 | Field Museum], [*LectoType* ♂ | CNHM | *EREBIA MAGDALENA* | *STRECKER* | *P. R. EHRLICH, VI-58*], [FMNH-INS | 0000 095 299], [PHOTOGRAPHED | Allie Stone 2012 | KE Emu catalog], and [DNA sample ID: | NVG-18041C02 | c/o Nick V. Grishin], as the **lectotype** of *Erebia magdalena* Strecker, 1880. The lectotype is a specimen in good condition, missing the distal third of the right antenna and with some damage to the right forewing fringe near the apex. The type locality of *E. magdalena* remains USA: Colorado, Clear Creek Co., mountains near Georgetown. The COI barcode sequence of the lectotype, sample NVG-18041C02, GenBank [PPZ516372](https://www.ncbi.nlm.nih.gov/nuclseq/PPZ516372), 658 base pairs, is:

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AACTTTATATTTTATTTTGGTATTTGAGCAGGTATAGTAGGGACATCTCTTAGTCTCATTATTCGAACAGAATTAGGTAACCCAGGATTTTAAATGGAGATGATCAAATTTATAATACT
ATTGTTACAGCTCATGCTTTTATTATAATTTTATAGTTATGCCAATTATAAATGGAGGGTTTGGTAACAGTACTGTCCCTTATATTAGGAGCTCCTGATATAGCTTTCCCGCGAA
TAAATAATATAAGATTTTGATTACTTCCCTCTCTTAATTTTATTAATTTCAAGCAGTATTGTAGAAAATGGTGCTGGCACAGGATGAACCGTTTACCTCTCTTTTCAGCTAATATTGC
TCATAGCGGATCCTCTGTTGACTTAGCAATCTTTTACATTTAGCTGGAATTTCCCTCTATTCTCGGAGCTATTAAATTTATTACCACAATTATCAATATACGAATTAATAAATATCA
TATGATCAAATACCTTATTGTTGAGCTGTTGGAATTACAGCATTATTATTACTTTTCATTACCAGTATTAGTGGAGCTATCACTATACTTCTTACAGATCGAAATTTAAATACCT
CTTTTTTGTATCTGCTGGAGGAGGAGATCTATTTTATACCAACACTTATTT
```

Erebia (Magda) mackinleyensis Gunder, 1932 is confirmed as a species-level taxon

Genomic analysis of the *Erebia (Magda) magdalena* clade reveals substantial genetic differentiation in the nuclear genome between *Erebia (Magda) magdalena* Strecker, 1880 (type locality in USA: Colorado, Clear Creek Co.) and *Erebia (Magda) mackinleyensis* Gunder, 1932 (type locality in USA: Alaska, Denali National Park) (Fig. 4a, b), e.g., the F_{st} between them is 0.52. Furthermore, the 1.8–2.1% (12–14 bp) COI barcode divergence between these taxa is consistent with their species-level distinction, supporting the conclusion of Hilchie (1990) over the reservations expressed by Layberry et al. (1998). Moreover, the nuclear genome genetic differentiation between *E. magdalena* and *E. mackinleyensis* is larger than that between *Erebia (Magda) discoidalis* (W. Kirby, 1837) (type locality in Canada: Saskatchewan) and *Erebia (Magda) lena* Christoph, 1889 (type locality in Russia: Irkutsk Region), currently treated as distinct species following Belik (2019) (Fig. 4a, b lavender vs. brown) in agreement with our analysis (F_{st} of 0.35). Therefore, we confirm that *E. mackinleyensis* is best treated as a species-level taxon.

Genomic analysis of *Erebia (Magda) magdalena* Strecker, 1880

Erebia (Magda) magdalena Strecker, 1880 (type locality in USA: Colorado, Clear Creek Co.; lectotype sequenced as NVG-18041C02) occurs from British Columbia and Alberta in Canada through Wyoming and northeastern Utah to central Colorado and northern New Mexico in the USA, being confined to montane habitats at higher elevations (Hilchie 1990). In addition to the nominotypical subspecies, *Erebia (Magda) magdalena hilchie* Kemal & Koçak, 2007 (type locality in Canada: Alberta; holotype sequenced as NVG-23127C10), which is a substitute name for the junior homonym *Erebia magdalena saxicola* Hilchie, 1990, is currently treated as valid. Nuclear genomic analysis of *E. magdalena* populations from across the range partitions them into two major clades (Fig. 4a, b violet vs. red with cyan).

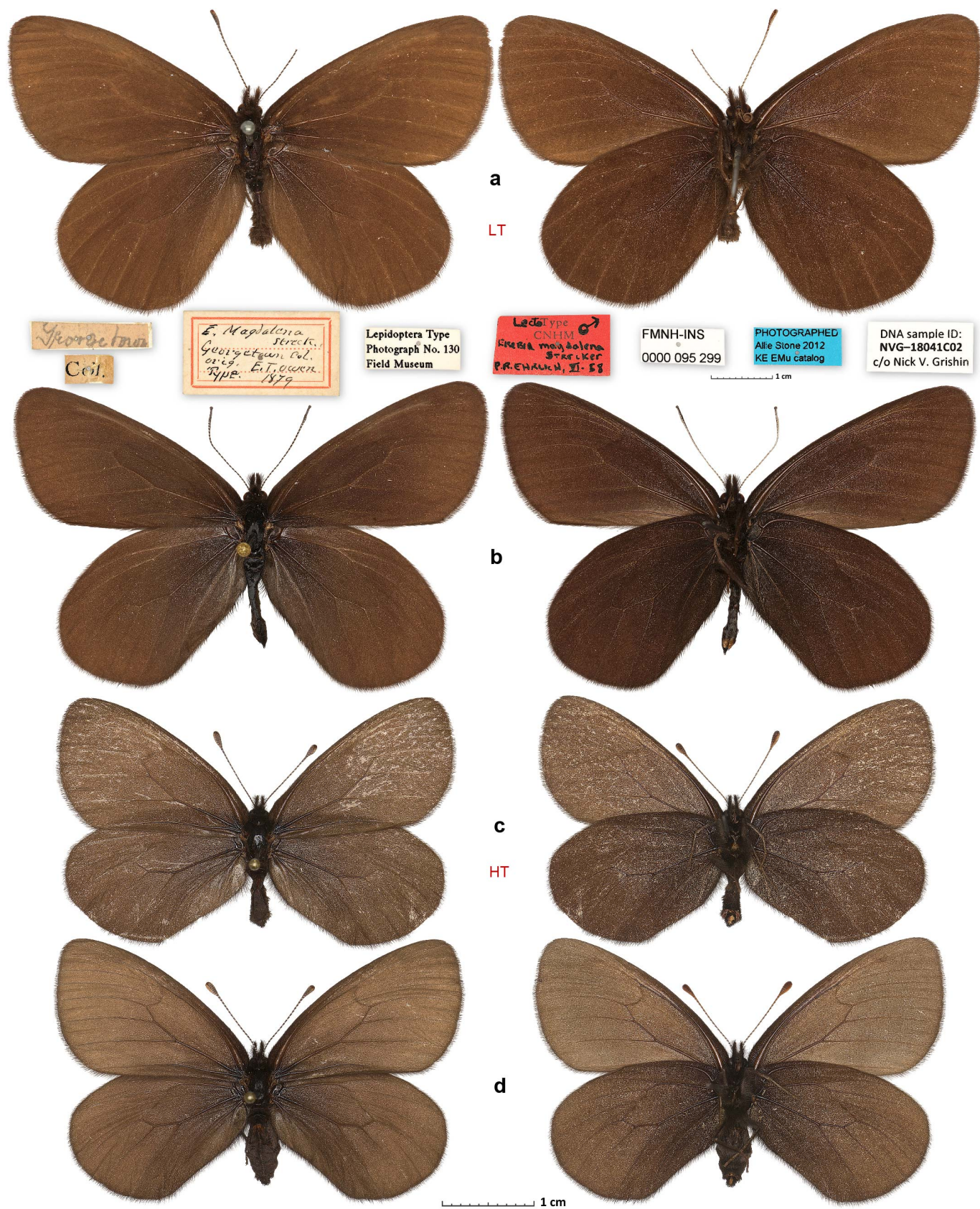
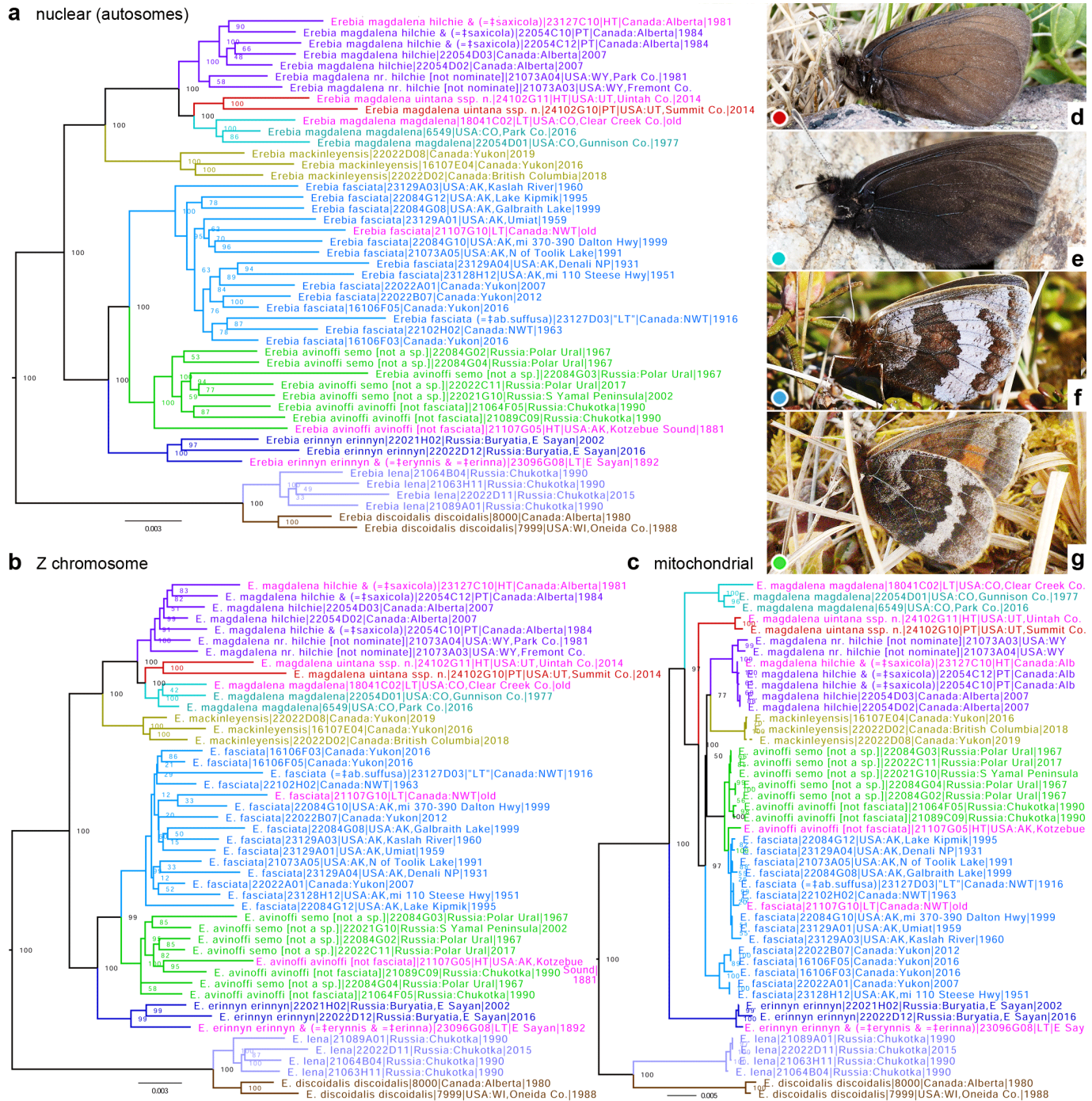


Fig. 3. *Erebia magdalena* specimens from USA in dorsal (left) and ventral (right) views, detailed data in text: **a)** lectotype (designated herein) ♂ NVG-18041C02 from CO, Clear Creek Co., mts. nr. Georgetown [FMNH] with its labels shown below; **b)** *E. magdalena* nr. *hilchie* non-type ♂ NVG-21073A03 from WY, Fremont Co. [MGCL]; **c–d)** *E. magdalena uintana* **ssp. n.** type series from UT, Uinta Mts.: **c)** holotype ♂ NVG-24102G11 and **d)** paratype ♀ NVG-24102G10. Labels are reduced by a third compared to specimens; the smaller scale below the labels refers to labels and the larger scale at the bottom refers to specimens.



The northern clade includes specimens from Canada: Alberta and USA: Wyoming and contains the holotype of *E. magdalena hilchie* (Fig. 4a, b violet), while the lectotype of the nominotypical subspecies belongs to the southern clade (Fig. 4a, b red with cyan). Therefore, Wyoming populations (Fig. 3b) do not belong to the nominotypical *E. magdalena* (Fig. 3a, 4e), where they have been previously assigned (Hilchie 1990), because they are not in the same clade as the lectotype and other specimens from Colorado. These Wyoming populations typically lack the white scales on the ventral side of the wings characteristic of *E. magdalena hilchie*, and we tentatively term them *E. magdalena* near *hilchie*. They are only weakly differentiated genetically from the true *E. magdalena hilchie* in both nuclear and mitochondrial genomes (Fig. 4a–c violet).

The southern clade is less homogeneous and partitions into two subclades genetically differentiated at the subspecies level in the nuclear genome (Fig. 4a, b red vs. cyan, F_{st} of 0.16) but form non-sister clades in the mitochondrial genome (Fig. 4c red and cyan), differing by 2% (13 bp) in the COI barcode. Therefore, these two subclades represent two distinct taxa. The subclade with the lectotype of *E. magdalena* and specimens from Colorado represents the nominotypical subspecies. The second subclade, from the Uinta Mountains in northeastern Utah, USA, is not associated with any available name and represents a new subspecies described next.

***Erebia (Magda) magdalena uintana* Grishin, new subspecies**

<https://zoobank.org/95D84FD9-B1C5-4591-AEEE-8CECACB55CC5>

(Figs. 3c–d, 4a–c part, 4d)

Definition and diagnosis. Genomic analysis reveals that specimens from the Uinta Mountains in northeastern Utah, USA, initially identified as *Erebia (Magda) magdalena* Strecker, 1880 (type locality in USA: Colorado, Clear Creek Co.; lectotype sequenced as NVG-18041C02) are genetically differentiated from it at least at the subspecies level (Fig. 4a–c red vs. cyan); e.g., their COI barcodes differ by 2% (13 bp), and therefore these specimens represent a new subspecies. This new subspecies is similar to the nominotypical subspecies in the absence of white scales on the ventral side of the wings characteristic of *Erebia (Magda) magdalena hilchie* Kemal & Koçak, 2007 (type locality in Canada: Alberta; holotype sequenced as NVG-23127C10) and differs from both of them by typically being smaller in size, having more translucent and browner (rather than blacker) wings, and having more rounded forewings in males. Due to its cryptic nature and poorly explored individual variation, this subspecies is best identified by DNA, with diagnostic base pairs in the nuclear genome: hm2005838-RA.2:C39T, hm2005838-RA.2:G48A, hm2001031-RA.2:C186T, hm2001031-RA.2:T252G, hm2013316-RA.2:T54C; and the COI barcode: C43A, G84G, A217A, C370T, T406T.

Barcode sequence of the holotype. Sample NVG-24102G11, GenBank PZ516373, 658 base pairs:

```
AACTTTATATTTTATTTTGGTATTTGAGCAGGTATAGTAGAACATCTCTAGTCTCATTATTCGAACAGAATTAGGTAACCCAGGATCTTTAATTGGAGATGATCAAAATTTATAATACC
ATTGTTACAGCTCATGCTTTTATTATAATTTTATAGTTATACCTATTATAATTGGAGGGTTTGGTAATTGACTTGTCCCCCTTATATTAGGAGCTCCTGATATAGCTTTCCCCCGAA
TAAATAATATAAGATTTTGATTACTCCCCCCTCTTAATTTTATTAATTTCAAGCAGTATTGTAGAAAATGGTGCTGGCAGGATGAACCGTTTACCCTCCTCTTTCATCTAATATTGC
TCATGGTGGATCCTCTGTTGACTTAGCAATCTTTCTTACATTAGCTGGAATTTCCCTCTATTCTTGGAGCTATTAAATTTATTACCACAATTATCAATATACGAATTAATAGAATATCA
TATGATCAAAATACCCCTATTGTTTGGAGCTGTTGGAATTACAGCATTATTATTACTTTTACCTACCGGTATTAGCTGGAGCTATCACTATATCTTTACAGATCGAAATTTAAATACCT
CTTTTTTGATCCTGCTGGAGGAGGAGATCTATTTTATACCAACACTTATTT
```

Type material. Holotype: ♂ currently in the Dempwolf collection (Austin, Texas, USA), to be deposited in the McGuire Center for Lepidoptera and Biodiversity collection, Gainesville, FL, USA (MGCL), illustrated in Fig. 3c, bears the following five printed rectangular labels, four white: [UT: Uintah Co. 10,935+' | Leidy Pk, 40° 46' | 39.1°N, 109° 48' 54.1" W | July 16, 2014 | Leg: W. Dempwolf], [*Erebia magdalena* | ♂ | Coll of: W R Dempwolf], [DNA sample ID: | NVG-24102G11 | c/o Nick V. Grishin], [WRD 8868], and one red [HOLOTYPE ♂ | *Erebia (Magda) | magdalena uintana* | Grishin]. **Paratype:** 1♀ NVG-24102G10 USA: Utah, Summit Co., Bald Mountain, 10,500 ft, GPS 40.6891, -110.9039, 14-July-2014, W. Dempwolf leg. [WRDC] (Fig. 3d).

Type locality. USA: Utah, Uintah Co., Leidy Peak, >10,935 ft, GPS 40.7775, -109.8150.

Etymology. The name is derived from the range of this subspecies being in the Uinta Mountains and is an adjective.

Distribution. The Uinta Mountains in northeastern Utah, USA.

Remarks. Because subspecies are traditionally defined by wing pattern differences, one may find it odd that several subspecies have been proposed for a non-patterned, essentially all brown-black butterfly. Recently, subspecies have been viewed as potential conservation units. Because it is sensible to conserve genetically distinct segments of a population, such segments may be defined as subspecies: each one possessing unique genes and, consequently, possibly yet undiscovered, unique phenotypic traits encoded by those genes. The three groups of *E. magdalena* populations defined as three subspecies (nominotypical, *E. magdalena hilchie*, and the new one) are genetically distinct from each other, and even their COI barcodes differ at the species level (around 2%). Therefore, these subspecies represent three potential conservation units, each possessing unique genetic properties. We note that currently all subspecies are common where they occur, occupy largely inaccessible habitat, and are not of conservation concern.

Lectotype designation for *Erebia fasciata* Butler, 1868

Erebia (Magda) fasciata was described by Butler (1868) from nine specimens collected in “Arctic America” at a single locality detailed by Elwes (1898) as “Winter Cove in Cambridge Bay, Victoria Land, about 69° N, 107° W.” According to Holland (1930), a pair of syntypes was presented to W. H. Edwards and currently is housed in the CMNH (Fig. 5a, b). We sequenced a female syntype as NVG-21107G10. To stabilize nomenclature and define the name *E. fasciata* objectively, N.V.G. hereby designates the syntype in the CMNH collection, a female illustrated in Fig. 5b, that bears the following three rectangular labels (1st handwritten, others printed with handwritten text shown in *italics*): [*Fasciata* ♀ | Arctic Am.], [Butterfly Book | Pl. 61 Fig. 6], and [DNA sample ID: | NVG-21107G10 | c/o Nick V. Grishin], as the **lectotype** of *Erebia fasciata* Butler, 1868. The first label is in W. H. Edwards’s handwriting. The second label states that this specimen was illustrated in Holland (1931) and was likely added by him. The lectotype is generally well-preserved, though it exhibits localized descaling on the wings and minor tears at both hindwing torni. A female specimen is chosen as the lectotype, because the holotype of the closest taxon, *Erebia avinoffi* W. Holland, 1930, is a female (Fig. 5c). The type locality of *E. fasciata* remains “Arctic America,” most likely Canada: Nunavut, Victoria Island, Cambridge Bay, Winter Cove, approx. GPS 69.0, -107.0. The COI barcode sequence of the lectotype, sample NVG-21107G10, GenBank [PP516374](https://www.ncbi.nlm.nih.gov/nuclseq/PP516374), 658 base pairs, is:

```
AACTTTATATTTTATTTTGGTATTTGAGCAGGTATAGTAGGGACATCCCTTAGTCTCATTATTCGAACAGAATTAGGTAACCCAGGATCTTTAATTGGAGATGATCAAATTTATAATACC  
ATTGTTACAGCTCATGCTTTTATTATAATTTTATAGTTATACCTATTATAATTGGAGGGTTTGGTAAGTACTGTCCCTTATATTAGGAGCTCCTGATATAGCTTTCCCCCGAA  
TAAATAATAAGATTTTGATTACTCCCCCTCTTAATTTTATTAATTTCAAGCAGTATCGTAGAAAATGGTGCTGGCACAGGATGAACCGTTTACCTCCTCTTCATCTAATATTGC  
TCATGGCGGATCCTCTGTTGACTTAGCAATCTTTTACATTTAGCTGGAATTTCTCTATTCTTGGAGCTATTAATTTTATTACCACAATTATCAATATACGAATTAATAGAATATCA  
TATGATCAAATACCCTTATTGTTTGGAGCTGTTGGAATTACAGCATTATTATTACTTTTACCTTACCTGAGCTATCACTATACTTCTTACAGATCGAAATTTAAATACCT  
CTTTTGTGATCCTGCTGGAGGAGGAGATCTTATTTATACCAACCTTATTT
```

***Erebia (Magda) avinoffi* W. Holland, 1930, stat. rest.
is a species distinct from *Erebia (Magda) fasciata* Butler, 1868 and
Erebia (Magda) avinoffi semo Grum-Grshimailo, 1899, stat. rev. is its subspecies**

Genomic analysis of the *Erebia (Magda) magdalena* clade reveals prominent genetic differentiation in the nuclear genome between *Erebia (Magda) fasciata fasciata* Butler, 1868 (type locality in Canada: Nunavut, Victoria Island; lectotype sequenced as NVG-21107G10) and a clade composed of two other taxa *Erebia (Magda) fasciata avinoffi* W. Holland, 1930 (type locality in USA: Alaska, Kotzebue Sound; holotype sequenced as NVG-21107G05) and *Erebia semo* Grum-Grshimailo, 1899 (type locality in Russia: Siberia, mts. between the Olenek and Khatanga rivers, and the Kolyma River valley) (Fig. 4a, b), e.g., F_{st}/G_{min} between the two clades are 0.37/1.5% (mitochondrial genomes experience introgression, and some *E. fasciata fasciata* have a mitochondrial haplotype similar to that of *E. fasciata avinoffi* (Fig. 4c)). Therefore, the two clades represent two species. While *E. semo* (Fig. 5d), originally described as a subspecies (“var.”) of *E. fasciata*, is currently regarded as a species-level taxon, *E. fasciata avinoffi*, originally described as a species, is treated as a subspecies. Our analysis suggests that these two taxa are

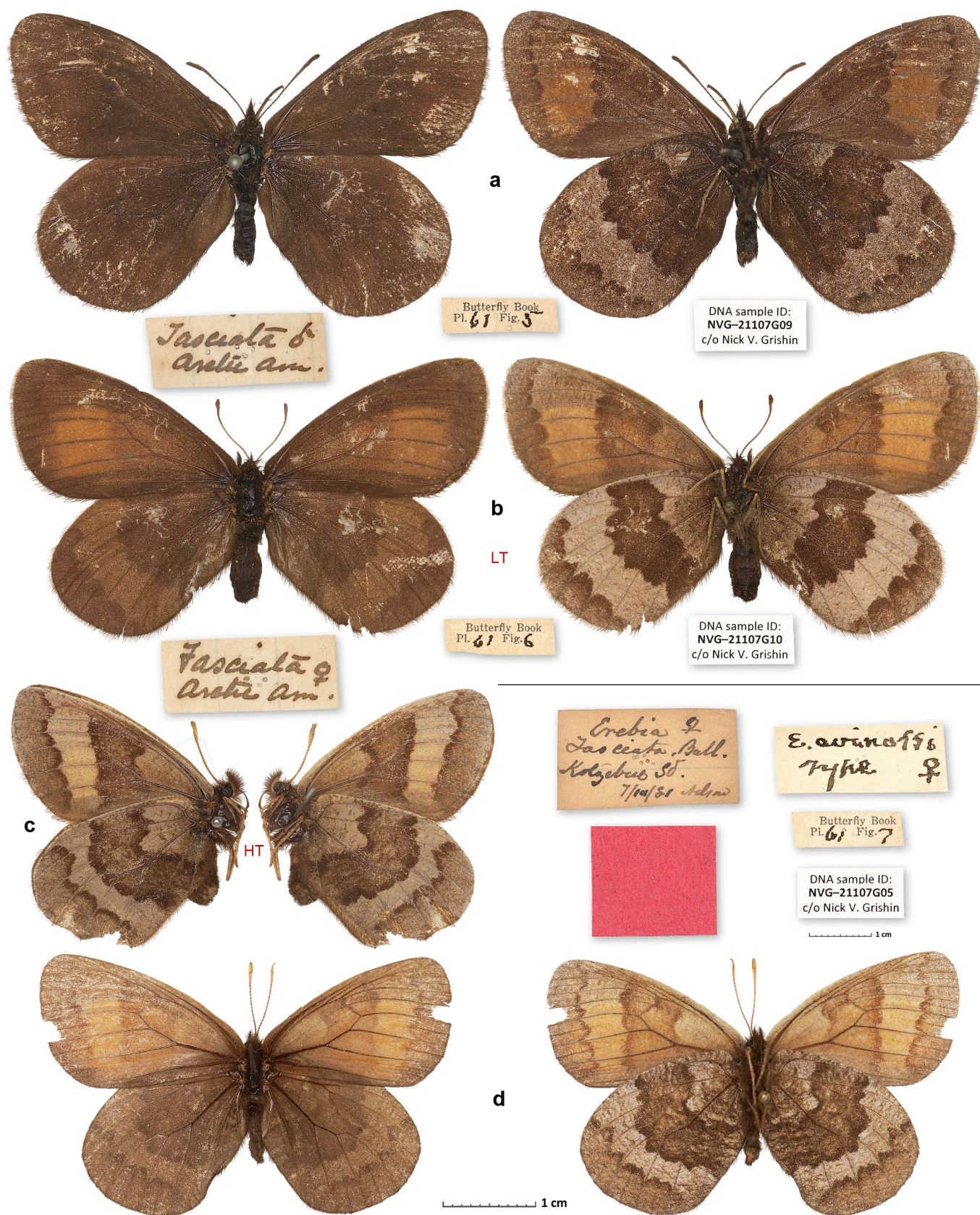


Fig. 5. *Erebia* specimens in dorsal (left of the panel letter) and ventral (right) views with labels for (a–c) (below or to the right of each specimen; the horizontal line on the right separates labels of (b) and (c)) in CMNH (unless indicated), detailed data in text: **a–b)** *E. fasciata* from “Arctic Am[erica].”: **a)** paralectotype ♂ NVG-21107G09 and **b)** lectotype (designated herein) ♀ NVG-21107G10, and **c–d)** *E. avinoffi* **stat. rest.**: **c)** holotype ♀ NVG-21107G05 from USA: Alaska, Kotzebue Sound and **d)** *E. avinoffi* **semo** **stat. rev.** ♀ NVG-22084G04 from Russia: Polar Ural [MGCL]. Labels are reduced by a third compared to specimens; the smaller scale below one of the labels refers to labels and the larger scale at the bottom refers to specimens.

closely related to each other, especially in the Z chromosome (Fig. 4b), but differ from *E. fasciata* *fasciata* at the species level. Therefore, we propose that *Erebia (Magda) avinoffi* W. Holland, 1930, **stat. rest.** is a species distinct from *Erebia (Magda) fasciata* Butler, 1868 and *Erebia (Magda) avinoffi semo* Grum-Grshimailo, 1899, **stat. rev.** is its subspecies. The COI barcode sequence of the *E. avinoffi* holotype, sample NVG-21107G05, GenBank [PZ516375](#), 658 base pairs, is:

```
AACCTTATATTTTATTTTGGTATTTGAGCAGGTATAGTAGGGACATCCCTTAGTCTCATTATTCGAACAGAATTAGGTAACCCAGGATCTTTAATTTGGAGATGATCAAATTTATAATACC
ATTGTTACAGCTCATGCTTTTATTATAATTTTATAGTTATACCTATTATAATTGGAGGGTTTGGTAAGTACTGACTGTCCCTTATATTAGGAGCTCCTGATATAGCTTTCCCGGAA
TAAATAATATAAGATTTTGATTACTCCCCCTCTTAATTTTATTAATTTCAAGCAGTATTGTAGAAAATGGTGTGGACAGGATGAACCGTTTACCTCCTCTTTCATCTAATATTGC
TCATGGCGGATCCTCTGTTGACTTAGCAATCTTTCTTTACATTTAGCTGGAATTTCTCTATTCTTGGAGCTATTAAATTTATTACCACAATTATCAATATACGAATTATAGAAATATCA
TATGATCAAATACCTTATTGTTGAGCTGTTGGAATTACAGCATTATTATTACTTTCATTACCGGTATTAGCTGGAGCTATCACTATACCTTCTTACAGATCGAAATTTAAATACCT
CTTTTTTGTATCCTGCTGGAGGAGGAGATCTATTTTATACCAACACTTATTT
```

Family Riodinidae Grote, 1895 (1827)

Lectotype designation for *Euselasia ella* Seitz, 1916

Euselasia ella Seitz, 1916 (currently *Myselasia ella ella*) was described from an unspecified number of specimens from Bolivia, with the name attributed to Staudinger: “*E. ella* *Stgr.* i. l.” (Seitz 1916). In the Staudinger collection, now in MFNB, we found a specimen from Bolivia labeled “Ella | Stgr” in Staudinger’s handwriting. A red label “Type” is affixed to this specimen, probably added at a later time by an English-speaking worker. This specimen, sequenced as NVG-21122C06, agrees with the original description and is similar to the illustration, and, because Seitz referred to Staudinger in the description, is likely a syntype of *E. ella*. To define the taxonomic identity of the name *E. ella* objectively, N.V.G. hereby designates the syntype in the MFNB collection, a male illustrated in Fig. 6a bearing the following five rectangular labels (3rd handwritten, others printed; 1st red, others white): [Type], [Rio Songo (1200 m) | Bolivia (Yungas) | 1895—6. Garlepp], [Ella | Stgr], [ex Coll. | Staudinger], and [DNA sample ID: | NVG-21122C06 | c/o Nick V. Grishin], as the **lectotype** of *Euselasia ella* Seitz, 1916. The 4th label is a header identification label for the series, now on the specimen pin. The lectotype is missing half of the club on the right antenna, and nearly the entire left forewing (except the anterior quarter) and the left hindwing (except the anal fold) have been glued on. The type locality of *E. ella* according to the lectotype label is Bolivia: La Paz, Río Zongo, 1200 m. The COI barcode sequence of the lectotype, sample NVG-21122C06, GenBank [PZ516376](#), 658 base pairs, is:

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AACATTACTTTTATTTTGGAAATTTGAGCTGGAATAATTGGAACATCATTAGTATATTAATTCGAATAGAATTAGGAACCTTCAGGTTCTTATATTGGAGATGACCAAATTTATAATACT
ATTGTAAGTCTCATGCTTTTATTATAATTTTATAGTTATACCCATTATAATTGGAGGATTTGGAAATTTGATTAGTACCTTTAATACTAGGGGCCCTGATATAGCTTTCCACGAA
TAAATAATATAAGATTTTGACTTTTACCCCTCACTAATTTCTATTAAATTTCAAGAAGAATTGTAGAAAATGGTGTGGAACCTGGATGAACAGTATACCCCTTCTCATCTAATATTGC
TCATAGAGGATCATGATTGATTTAGCTATTTTCTTTACATTTAGCAGGAATTTCTTCTATTTTAGGAGCTATTAAATTTATTACAACAATTATTAACATACGTATTAATAATAATA
CTTGATCAAATACCTCTATTGTTGTGATCAATTTGGAATTACAGCTTTATTGTTATTACTATCATTACCAGTATTAGCAGGAGCTATCACTATATTACTCACAGATCGTAATTTAAACACTT
CCTTTTTGTATCCTGCTGGAGGGGAGATCCTATTTCTTTATCAACATCTATTT
```

Lectotype designation for *Euselasia ella terrea* Stichel, 1924

Euselasia ella terrea Stichel, 1924 (currently *Myselasia ella terrea*) was described from two specimens: one from “Mu” (i.e., Río Moju vic. Santarém), No. 374 in the Stichel collection, now in MFNB; and the second, without locality, in the ZSMC (Stichel 1924). We found and sequenced syntype No. 374 as NVG-21123B07. To define the taxonomic identity of the name *E. ella terrea* objectively, N.V.G. hereby designates the syntype in the MFNB collection, a male illustrated in Fig. 6b bearing the following six rectangular labels (4th handwritten, others printed with handwritten text shown in *italics*; 1st red, others white; 4th black-framed): [Co-Typus], [Amazonas *IX* | *Moju* (Santarém) | e.c.H.Stichel], [374 |], [*terrea* Stich.], [ex coll. | H. STICHEL], and [DNA sample ID: | NVG-21123B07 | c/o Nick V. Grishin], as the **lectotype** of *Euselasia ella terrea* Stichel, 1924. The number 374 is the Stichel collection number of this specimen mentioned in the original description. The 4th label is a header identification label for the series, now on the specimen pin. The lectotype is missing the right antenna, its head is tilted to the left, and the right wings are glued on. The type locality of *E. ella terrea* according to the lectotype label is Brazil: Pará, Río Moju, vic. Santarém. The COI barcode sequence of the lectotype, sample NVG-21123B07, GenBank [PZ516377](#), 658 base pairs, is:

AACATTATATTTATTTTGAATTTGAGCCGGAATAATTGGGACATCATTAAAGTATATTAATTCGAATAGAATTGGGAACCTCAGGTCTTATATGGTGATGATCAAATTTATAATACT
ATTGTAACGCTCATGCTTTTATTATAATTTTATAGTTATACCTATTATAATTGGAGGTTTGGAAATTGATTAGTACCTTTAATATTAGGAGCCCCGACATAGCTTTCCCGCGAA
TAAATAATATAAGATTTTGACTTTTACCCCCCTCATTAAATTTTATTAATCTCAAGAAGAATTGTAGAAAATGGTGCTGGAACAGGATGAACAGTGTAACCCCCACTTTTCATCTAACATTGC
TCATAGAGGATCATCAGTTGATTAGCTATTTTCTTTACACTTAGCAGGAATTTCTTCTATTTTAGGAGCTATTAATTTTATTACAACAATTATTAACATACGAATCAATAATAATA
TTTGATCAGATACCCCTATTCTGATGATCTGTTGGAATTACAGCTTTATTATTATTATTATCATTACCAGTATTAGCGGGAGCTATCACCATGTTACTTACAGATCGTAATTTAAATACTT
CATTTTGTATCCTGCTGGAGGAGGAGATCCTATTCTTTATCAACACTTTT



Fig. 6. *Myselasia ella* and *M. eulione* in dorsal (left) and ventral (right) views: **a)** *M. ella* lectotype (designated herein) ♂ NVG-21122C06 Bolivia: La Paz, Río Zongo, 1200 m, 1895–1896, Garlepp leg. [MFNB] and **b–d)** *M. eulione*: **b)** lectotype (designated herein) ♂ of *Euselasia ella terrestra* NVG-21123B07 Brazil: Pará, Río Moju, vic. Santarém [MFNB]; **c)** non-type ♂ NVG-23103H01 Brazil: Pará, Río Tapajóz, old [SMF] and **d)** non-type ♀ NVG-22074A10 Colombia: Vaupés, Mitú, 3-Nov-1981 [MGCL].

Euselasia ella terrea Stichel, 1924 is a new junior subjective synonym of *Myselesia eulione* (Hewitson, 1856)

Visual comparison of the lectotype of *Myselesia ella terrea* Stichel, 1924 (type locality Brazil: Pará, Río Moju, vic. Santarém) with a syntype No.Rh.1153 of *Myselesia eulione* (Hewitson, 1856) (type locality in “Amazon”) reveals unique similarities in wing patterns that set these two taxa apart from other species. For instance, the black submarginal spot in cell M₃-CuA₁ of the ventral hindwing is placed away from the outer margin and is nearly touching the postdiscal band, which is well-developed and broader than in most other species. Even Hewitson’s description of *M. eulione* emphasizes the former character: “central black spot ... at a distance from the outer margin” and again “black spot ... is further from the outer margin” (Hewitson 1867–1871). Similar specimens are found throughout the Amazonian region, from its upper reaches in eastern Colombia (Fig. 6d) to the lower reaches in Pará, Brazil (Fig. 6b, c), and genomic analysis is consistent with all these specimens being conspecific (Fig. 7). Therefore, we propose that *Euselasia ella terrea* Stichel, 1924, **syn. n.** is a junior subjective synonym of *Myselesia eulione* (Hewitson, 1856).

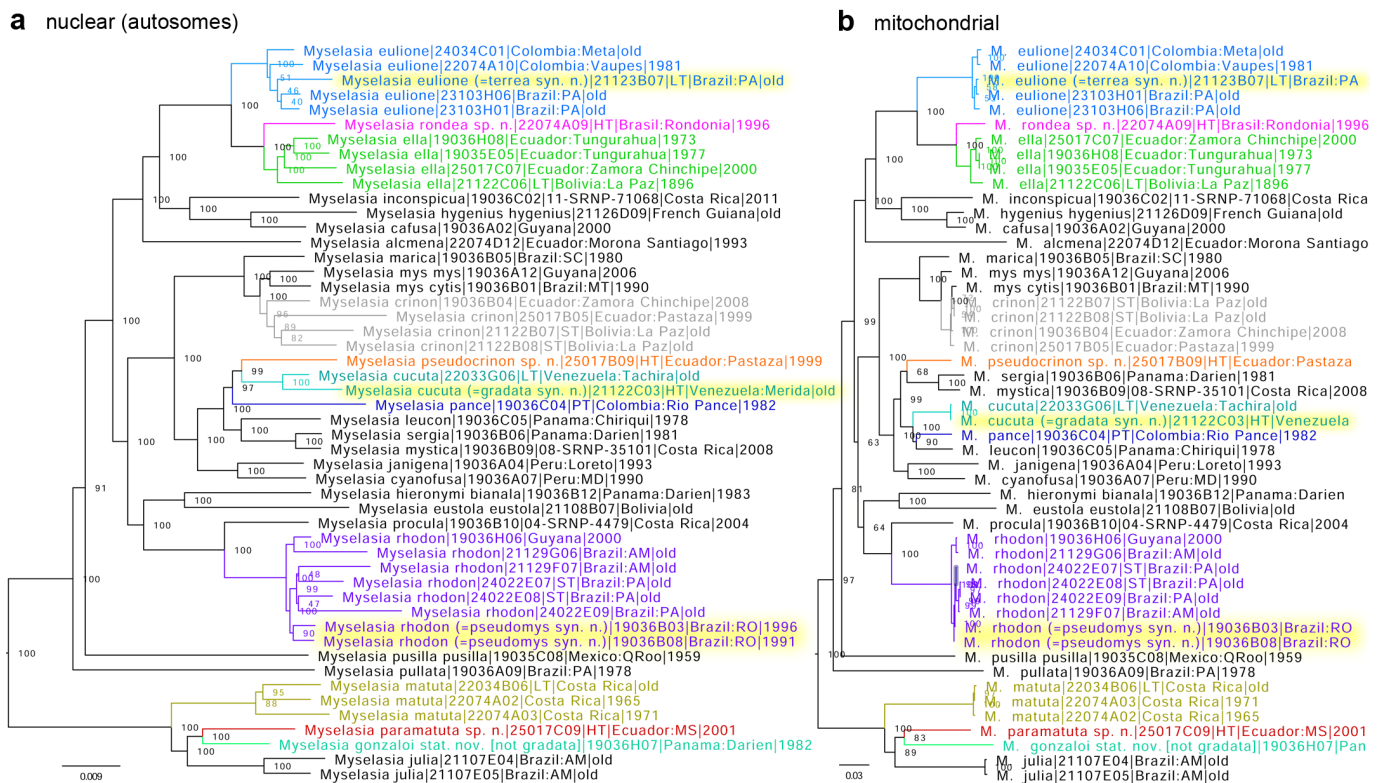


Fig. 7. Phylogenetic trees of selected *Myselesia* Grishin, 2021 species constructed from protein-coding regions in: **a)** the nuclear genome (autosomes), based on 441,264 positions, and **b)** the mitochondrial genome. Different species mentioned in the text are colored differently: *M. eulione* (blue), *M. rondea* sp. n. (magenta), *M. ella* (green), *M. crinon* (gray), *M. pseudocrinon* sp. n. (orange), *M. cucuta* (cyan), *M. pance* (dark blue), *M. rhodon* (violet), *M. matuta* (olive), *M. paramatuta* sp. n. (red), and *M. gonzaloi* stat. nov. (aquamarine). Labels of new junior subjective synonyms proposed herein are highlighted in yellow. Ultrafast bootstrap (Hoang et al. 2018) values are shown at nodes.

Myselesia rondea Grishin, new species

<https://zoobank.org/2DBDD699-303D-4BAE-B382-CC9F0489A23A>

(Figs. 7 part, 8–9)

Definition and diagnosis. Genomic analysis reveals that a specimen from Rondônia, Brazil, initially identified as *Myselesia ella terrea* (Stichel, 1924) (type locality Brazil: Pará, Río Moju, vic. Santarém) is not monophyletic with its lectotype (NVG-21123B07) and instead is sister to specimens of *Myselesia ella* (Seitz, 1916) (type locality in Bolivia: La Paz, Río Zongo, 1200 m) including its lectotype (NVG-

21122C06), but is genetically differentiated from them at the species level (Fig. 7); e.g., their COI barcodes differ by 3.3% (22 bp), and therefore this specimen represents a new species. This new species is similar to both *Myselasia eulione* (Hewitson, 1856) (type locality in “Amazon”; *Euselasia ella terrea* is its junior subjective synonym) and *M. ella* in having the submarginal row of black spots on the ventral hindwing being placed farther from the outer margin than in other species with brown dorsal side, but differs from them and other relatives by nearly vestigial postdiscal brown band on ventral hindwing [prominent in *M. eulione*], thus being more similar to *M. ella*, from which it differs by having smaller submarginal black spots, especially the spot in cell M_3 -CuA₁ of the ventral hindwing is weakly developed and only about twice as large as the spot in cell Sc+R₁-Rs [many times larger in both *M. eulione* and *M. ella*]. Due to poorly explored variation of this new species currently known only from a single locality, it is best identified by DNA, with diagnostic base pairs in the nuclear genome: cne4378.7.7:A381G, cne4378.7.7:A402G, cne22301.1.2:T2443C, cne11199.3.3:T192C, cne2170.2.1:A3777G, cne458.3.5:A951A (not G), cne520.2.1:T837T (not G), cne21689.3.10:C90C (not T), cne21689.3.10:T123T (not C), cne644.7.3:G81G (not A); and the COI barcode: A38G, A43G, T169T, A424T, A520T.

Barcode sequence of the holotype. Sample NVG-22074A09, GenBank [PZ516378](https://www.ncbi.nlm.nih.gov/nuccore/PZ516378), 658 base pairs:

```
AACATTATACTTTATTTTGGAAATTTGAGCTGGAATAGTTGGGACATCATTAAAGTATATTAATTCGAATAGAATTAGGAACCTCAGGTTCTTATATTGGAGATGATCAAATTTATAATACT
ATTGTAACGCTCATGCTTTTATTATAATTTTTTTATAGTTATACCTATTATAATTTGGAGGATTTGGAAATTTGATTAGTACCTTTGATACTAGGAGCCCTGATATAGCTTTTCCACGAA
TAAATAATATAAGATTTTGACTTTTACCCCTCACTAATCTATTAAATTTCAAGAAGAAATTTAGAAAAATGGTGCTGGAACCTGGATGAACAGTATACCCCTTTCATCTAATATTGC
TCATAGAGGATCATCGGTTGATTAACTATTTTCTTACATTTAGCAGGAATTTCTTCTATTTTAGGGGCTATTAAATTTTATTACAACAATTATTAACATACGTATTAAATAATAATA
CTTGATCAAAATACCTTTATTTGTGTGATCAGTTGGTATTACAGCTTTTGTGTACTATTATCATTACCAGTATTAGCAGGAGCTATCACCATTACTTACAGATCGTAATTTAAACACTT
CTTTTTTTGACCCCTGCAGGAGGAGAGATCTATTCTTTATCAACACCTATT
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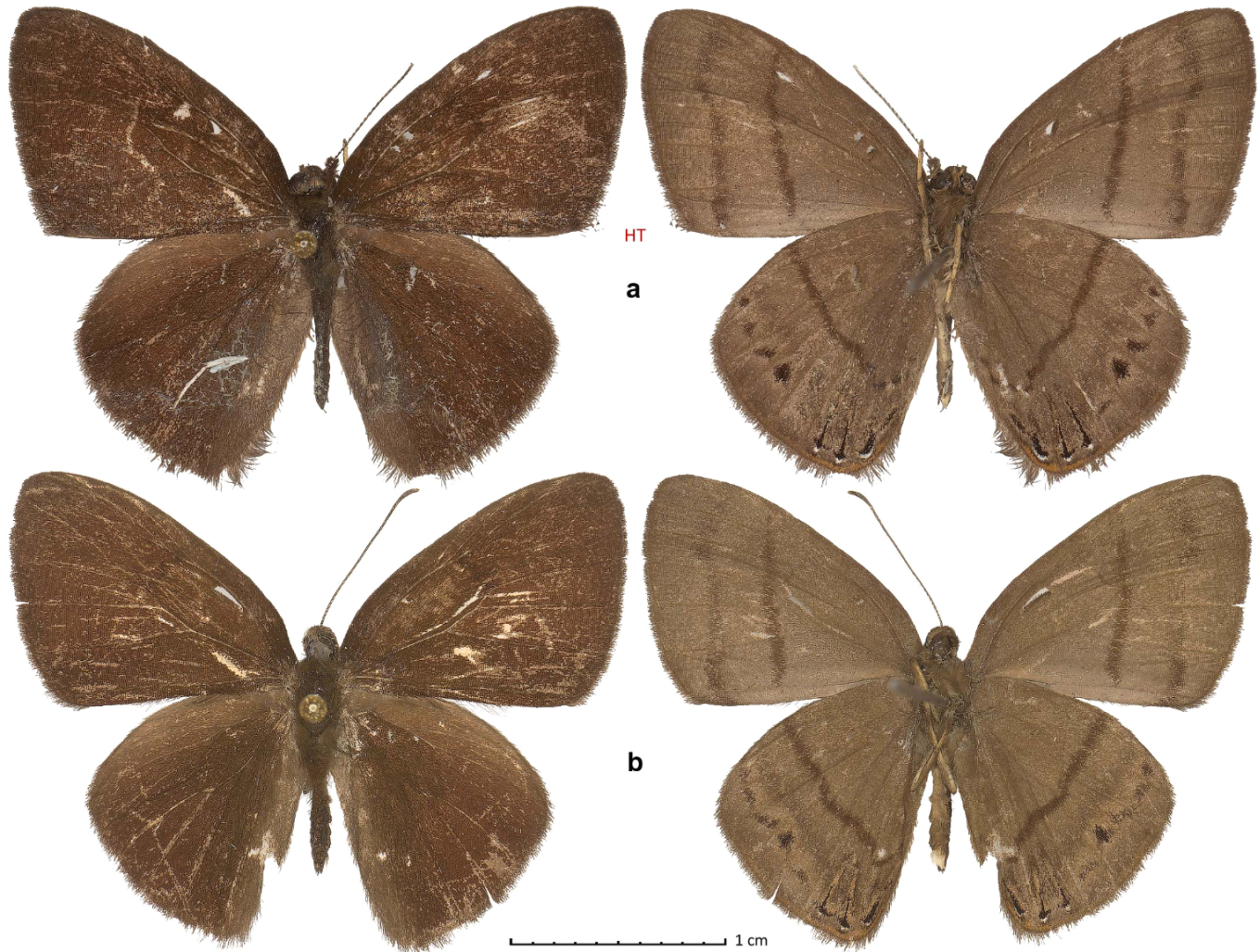


Fig. 8. *Myselasia rondea* sp. n. males, Brazil: Rondônia, 62 km S of Ariquemes, Linha C-10, 5 km S of Cacaulândia, O. Gomes leg. [MGCL], in dorsal (left) and ventral (right) views: **a)** holotype NVG-22074A09, 22-Sep-1996 and **b)** paratype NVG-25068E01, 14-Jun-1995.

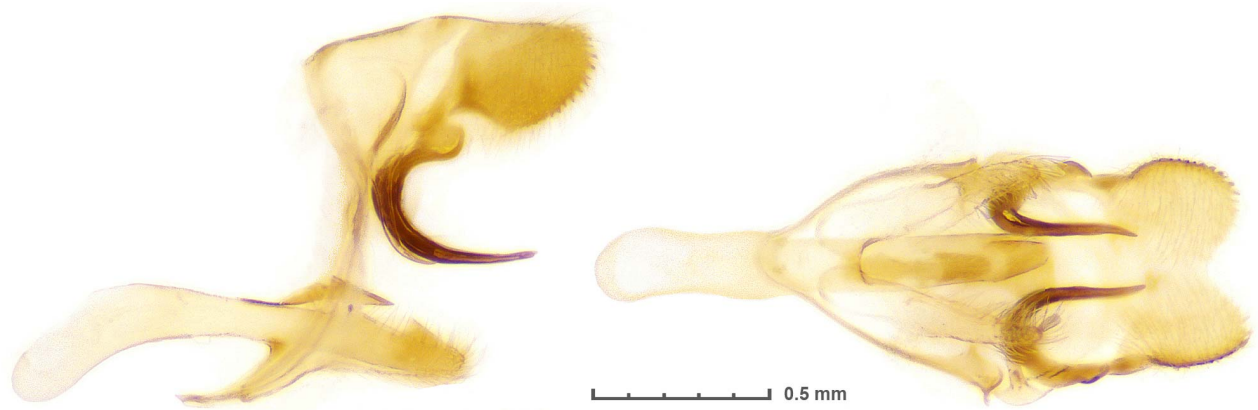


Fig. 9. Male genitalia of *Myselasia rondea* sp. n. holotype NVG-22074A09 in left lateral (left) and ventral (right) views.

Type material. Holotype: ♂ currently deposited in the McGuire Center for Lepidoptera and Biodiversity collection, Gainesville, FL, USA (MGCL), illustrated in Fig. 8a (genitalia Fig. 9), bears the following seven printed rectangular labels (text in *italics* handwritten), six white: [BRASIL: Rondônia; | 62 km S Ariquemes | linha C-10, 5 km S | of Cacaupônia | 22 SEP 1996 | leg. O. Gomes], [TRAP # 16 | forest], [G T Austin colln | MGCL Acc. | 2004-5], [DNA sample ID: | NVG-22074A09 | c/o Nick V. Grishin], [DNA sample ID: | NVG-25068D11 | c/o Nick V. Grishin], [genitalia: | NVG260613-01 | c/o Nick V. Grishin], and one red [HOLOTYPE ♂ | Myselasia | rondea Grishin]. The first DNA sample ID refers to the extraction from a leg (sequenced), and the second from the abdomen (stored) prior to genitalia dissection. A leg that is attached to the moldy dorsal surface of the left hindwing is excluded from the holotype. **Paratypes:** 4♂♂ with the same data as the holotype, except as indicated: 1♂ NVG-25068E01, 14-Jun-1995 (Fig. 8b); 1♂ NVG-25068E03 at Rio Pardo off B-65, 15-Nov-1995; 1♂ NVG-25068E02, 16-Sep-1996; and 1♂ NVG-25068D12, 4-Oct-1997, G. T. Austin leg.

Type locality. Brazil: Rondônia, 62 km south of Ariquemes, Linha C-10, 5 km south of Cacaupônia.

Etymology. The name is derived from the type locality in Rondônia to rhyme with *terrea* and treated as a noun in apposition.

Distribution. Currently known only from the type locality in Rondônia, Brazil.

***Myselasia gonzaloi* (Salazar & Henao, 2019), stat. nov. is a species distinct from *Myselasia gradata* (Stichel, 1927)**

Genomic sequencing of a specimen NVG-19036H07 from Panama: Darién that we identified as *Myselasia gradata gonzaloi* (Salazar & Henao, 2019) (Fig. 10) and of the holotype of *Myselasia gradata*



Fig. 10. *Myselasia gonzaloi* stat. nov. non-type ♂ NVG-19036H07, USNMENT_01544856 from Panama: Darién, Serranía de Pirre, Cana, 1200 m, 5-Sep-1982, G. B. Small leg. [USNM] in dorsal (left) and ventral (right) views.

(Stichel, 1927) (type locality in Venezuela: Mérida; sequenced as NVG-21122C03; holotype by monotypy, No. 1113, because the Stichel collection specimen number, which is unique to each specimen, was given in the original description (Stichel 1927)) reveals that they are not closely related to each other and belong to different clades (Fig. 7). Each taxon is associated with different closely related species; thus, the two taxa are not monophyletic. Therefore, we propose that *Myselasia gonzaloi* (Salazar & Henao, 2019), **stat. nov.** is a species distinct from *Myselasia gradata* (Stichel, 1927).

Lectotype designation for *Eurygona cucuta* Schaus, 1902

Eurygona cucuta Schaus, 1902 (currently *Myselasia cucuta*) was described from an unspecified number of specimens (No. 5893) from “Cucuta, Venezuela” (Schaus 1902). We found a syntype in USNM, originally from the W. Schaus collection, with No. 5893 and the word “type” written in the bottom left corner of its identification label. Schaus labeled specimens he considered “types” (one per sex) with the handwritten word “type” but did not write this word on identification labels of other specimens in his series. Therefore, even if there were other syntypes, this specimen was considered a name-bearing specimen by Schaus. To define the taxonomic identity of the name *E. cucuta* objectively, N.V.G. hereby designates the syntype in the USNM collection, a male bearing the following four rectangular labels (3rd handwritten, others printed with handwritten text shown in *italics*; last red, others white): [Cucuta, | Venezuela], [Eurygona | cucuta | type Schs], [Collection | W.Schaus], [Type | No. 5893 | U.S.N.M.], as the **lectotype** of *Eurygona cucuta* Schaus, 1902. The lectotype’s abdomen is in a gelatine capsule pinned next to it, the left pair of wings are closer together, and the right forewing has some scales rubbed off distad of the discal cell. Images of this specimen, photographed by G. Lamas, are shown on the Butterflies of America website (Warren et al. 2024). The city of Cúcuta is the capital of Norte de Santander Department in Colombia, at the border with the Venezuelan state of Táchira. However, the label of the type states “Cucuta | Venezuela”, so we keep Venezuela as the country of the type locality short of dedicated investigation into this matter, and list the type locality as Venezuela: Táchira, vic. Cúcuta. The COI barcode sequence of the lectotype, sample NVG-22033G06, GenBank [PZ516379](#), 658 base pairs, is:

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AACATTATATTTTATTTTGAATCTGAGCTGGAATAATTGGAACATCTTTAAGTATATTAATTCGAATAGAATTAGGAACCTTCAGGTTTCATTATCGGAGATGATCAAATTTATAATACT
ATAGTAACTGCTCATGCTTTTATTATAATTTTATAGTTATACCTATTATAATTTGGAGGATTTGGAAATTGATTAGTACCATTAAATATTAGGAGCCCTGATATAGCTTTCCACGAA
TAAATAATATAAGATTTTGATTATTACCCCTCTCTTTATTTCTTTTAAATTTCAAGAAGAATTGTAGAAAATGGTGCTGGAACAGGATGAACAGTATACCCCCCTTTTCATCTAACATTGC
TCATAGAGGATCTTCTGTTGATTAGCTATTTTCTTTACATTTAGCAGGAATCTCATCAATTTAGGAGCTATTAATTTTATTACAACAATTATCAATATACGAATTAATAATAATA
TTTGATCAAATACCTTTATTGTATGAGCTGTAGGAATTACAGCATTATTATTGTTATTGTCATTACCTGTTTGTAGCTGGAGCTATTACTATATTACTTACAGATCGTAATTTAAATACTT
CATTTTTTGATCTGCTGGAGGAGGAGACCCCATCTTTATCAACATTTATT
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Euselasia gradata Stichel, 1927 is a new junior subjective synonym of *Myselasia cucuta* (Schaus, 1902)

Genomic analysis reveals that the holotype ♀ of *Myselasia gradata* (Stichel, 1927) (type locality in Venezuela: Mérida; sequenced as NVG-21122C03; holotype by monotypy, No. 1113, because the Stichel collection specimen number, which is unique to each specimen, was given in the original description (Stichel 1927)) and the lectotype ♂ of *Myselasia cucuta* (Schaus, 1902) (type locality in Venezuela: Táchira, nr. Cúcuta, sequenced as NVG-22033G06) are genetically similar (Fig. 7), e.g., their COI barcodes are identical. Both being from nearby localities in Venezuela (Táchira and Mérida), the two taxa are most likely conspecific, representing the male and female of the same species. Therefore, we propose that *Euselasia gradata* Stichel, 1927, **syn. n.** is a junior subjective synonym of *Myselasia cucuta* (Schaus, 1902). The COI barcode sequence of the holotype of *Euselasia gradata*, sample NVG-21122C03, GenBank [PZ516380](#), 658 base pairs, is:

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AACATTATATTTTATTTTGAATCTGAGCTGGAATAATTGGAACATCTTTAAGTATATTAATTCGAATAGAATTAGGAACCTTCAGGTTTCATTATCGGAGATGATCAAATTTATAATACT
ATAGTAACTGCTCATGCTTTTATTATAATTTTATAGTTATACCTATTATAATTTGGAGGATTTGGAAATTGATTAGTACCATTAAATATTAGGAGCCCTGATATAGCTTTCCACGAA
TAAATAATATAAGATTTTGATTATTACCCCTCTCTTTATTTCTTTTAAATTTCAAGAAGAATTGTAGAAAATGGTGCTGGAACAGGATGAACAGTATACCCCCCTTTTCATCTAACATTGC
TCATAGAGGATCTTCTGTTGATTAGCTATTTTCTTTACATTTAGCAGGAATCTCATCAATTTAGGAGCTATTAATTTTATTACAACAATTATCAATATACGAATTAATAATAATA
TTTGATCAAATACCTTTATTGTATGAGCTGTAGGAATTACAGCATTATTATTGTTATTGTCATTACCTGTTTGTAGCTGGAGCTATTACTATATTACTTACAGATCGTAATTTAAATACTT
CATTTTTTGATCTGCTGGAGGAGGAGACCCCATCTTTATCAACATTTATT
```

Myselasia pseudocrinon Grishin, new species

<https://zoobank.org/DBB8B250-1D2A-447A-BBDA-0C1768495EE5>

(Figs. 7 part, 11a–b, 12a)

Definition and diagnosis. Genomic analysis reveals that a specimen from eastern Ecuador that is similar in appearance to *Myselasia crinon* (Stichel, 1919) (type locality in Bolivia and Peru; syntypes sequenced as NVG-21122B07 and NVG-21122B08) is in a different clade from it, and instead is more closely related to *Myselasia leucon* (Schaus, 1913) (type locality in Costa Rica), *Myselasia pance* (Callaghan, 1999) (type locality in Colombia), and *Myselasia cucuta* (Schaus, 1902) (type locality in Venezuela: Táchira, nr. Cúcuta), among others, while being genetically differentiated from them at the species level (Fig. 7); e.g., their COI barcodes differ by 3.6%–5.2% (24–34 bp), and therefore this specimen represents a new species. This new species is most similar to *M. crinon* and *M. pance*, but differs from them and other relatives by the following combination of characters in males: the orange patch on the dorsal forewing is sharply bordered by the discal cell and does not enter it [there is some orange, either a spot or a continuation of the orange patch, in similar species such as *M. crinon* and *M. pance*]; the orange color is darker, with brown shades rather than the brighter orange seen in relatives; the orange patch on the dorsal forewing is two-toned: paler in the middle of the wing and browner towards the base; the dorsal hindwing is mostly orange with the anterior portion being dark brown through part of the discal cell, with stronger brown overscaling along the basal part of vein M_1 and other veins around the discal cell, cell $Rs-M_1$ is mostly orange in the middle (but the outer margin is brown), and the outer margin is orange posteriad of vein M_1 [different pattern of brown on the hindwing occur in other species, e.g., dark brown may cover the entire anterior part of the wing to vein M_1 , and there is no prominent brown overscaling along the veins]; more prominent postdiscal brown bands on the ventral forewing, similar to those in *M. pance* [weakly developed in *M. crinon*]; and a more sharply outlined lunular postdiscal band on the ventral hindwing [typically more diffuse in relatives]. In male genitalia, compared to *M. crinon* (Fig. 12b), the valva and transtilla are both longer in lateral view and the uncus is narrower; the aedeagus is thicker, particularly caudad; and the saccus is better developed, slightly longer and broader (Fig. 12a). This species is not cryptic, but due to relatively unexplored individual variation, it is best identified by DNA, with diagnostic base pairs in the nuclear genome: cne2178.3.3:T39A, cne2068.2.1:A558G, cne2068.2.1:C1284T, cne3615.3.2:A75G, cne3615.3.2:A96G, cne482.2.4:C39C (not G), cne5285.4.7:C117C (not T); and the COI barcode: G38A, T91A, T448C, A477G, T505C.

Barcode sequence of the holotype. Sample NVG-25017B09, GenBank [PZ516381](https://www.ncbi.nlm.nih.gov/GenBank/entry/viewer?accession=PZ516381), 658 base pairs:

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AACATTATATTTTATCTTTGGAATCTGAGCTGGAATAATTGGAACATCTTTAAGTATATTAATTCGAATAGAAATTAGGAACCTTCAGGTTTCATTTATGGAGATGATCAAAATTTATAATACT
ATTGTAACCTGCTCATGCTTTTATTATAATTTTTTTTATAGTTATACCTATTATAATTTGGTGGATTGGAAATGATTAGTGCCATTAATATTAGGAGCTCCAGATATAGCTTTCCACAGAA
TAAATAATATAAGATTTTGATTATTACCCCTTCTTTAATCTTTTAAATTTCAAGAGAATTGTAGAAAATGGTGTGGAACAGGATGAACAGTGTACCCCCACTTTCATCTAATATTGC
TCATAGAGGATCTTCAGTTGATTTAGCTATTTTCTTTACATTTAGCAGGAATCTCATCAATTTTAGGAGCTATCAATTTTATCACAACAATTATTAATATACGAATTAATAGTATAATA
TTTGATCAAAATACCTTTATTCGTATGAGCTGTAGGAATTACAGCATTATTATTATTATTATCATTACCTGTTTGTAGCTGAGCTATTACTATATTACTTACAGATCGTAATTTAAATACCT
CATTTTTTGATCCTGCTGGTGGAGGAGATCCTATTCTTTATCAACATTTATT
```

Type material. Holotype: ♂ deposited in the McGuire Center for Lepidoptera and Biodiversity collection, Gainesville, FL, USA (MGCL), illustrated in Fig. 11a (genitalia Fig. 12a), bears the following five printed rectangular labels, four white: [ECUADOR | Pastaza Province | 51 km. S. of Puyo (800m) | 7. ix. 1999 Pitirishca | leg. Robert C. Busby], [DNA sample ID: | NVG-25017B09 | c/o Nick V. Grishin], [DNA sample ID: | NVG-25058B03 | c/o Nick V. Grishin], [genitalia: | NVG260613-02 | c/o Nick V. Grishin], and one red [HOLOTYPE ♂ | Myselasia | pseudocrinon Grishin]. The first DNA sample ID refers to the extraction from a leg (sequenced), and the second from the abdomen (stored) prior to genitalia dissection. **Paratypes:** 3♂♂ with the same data as the holotype except as indicated: 1♂ NVG-25058B04 (Fig. 11b); 1♂ NVG-25058B06, 13-Sep-1999; and 1♂ NVG-25058B05, 24-Sep-1999.

Type locality. Ecuador: Pastaza Province, 51 km south of Puyo, Pitirishka, elevation 800 m.

Etymology. The name is derived from the name of the most similar species, *M. crinon*, that is not closely related, therefore *pseudo*-. The name is in noun in apposition.

Distribution. Currently known only from the type locality in the Andean foothills of the Amazon Basin in central Ecuador.

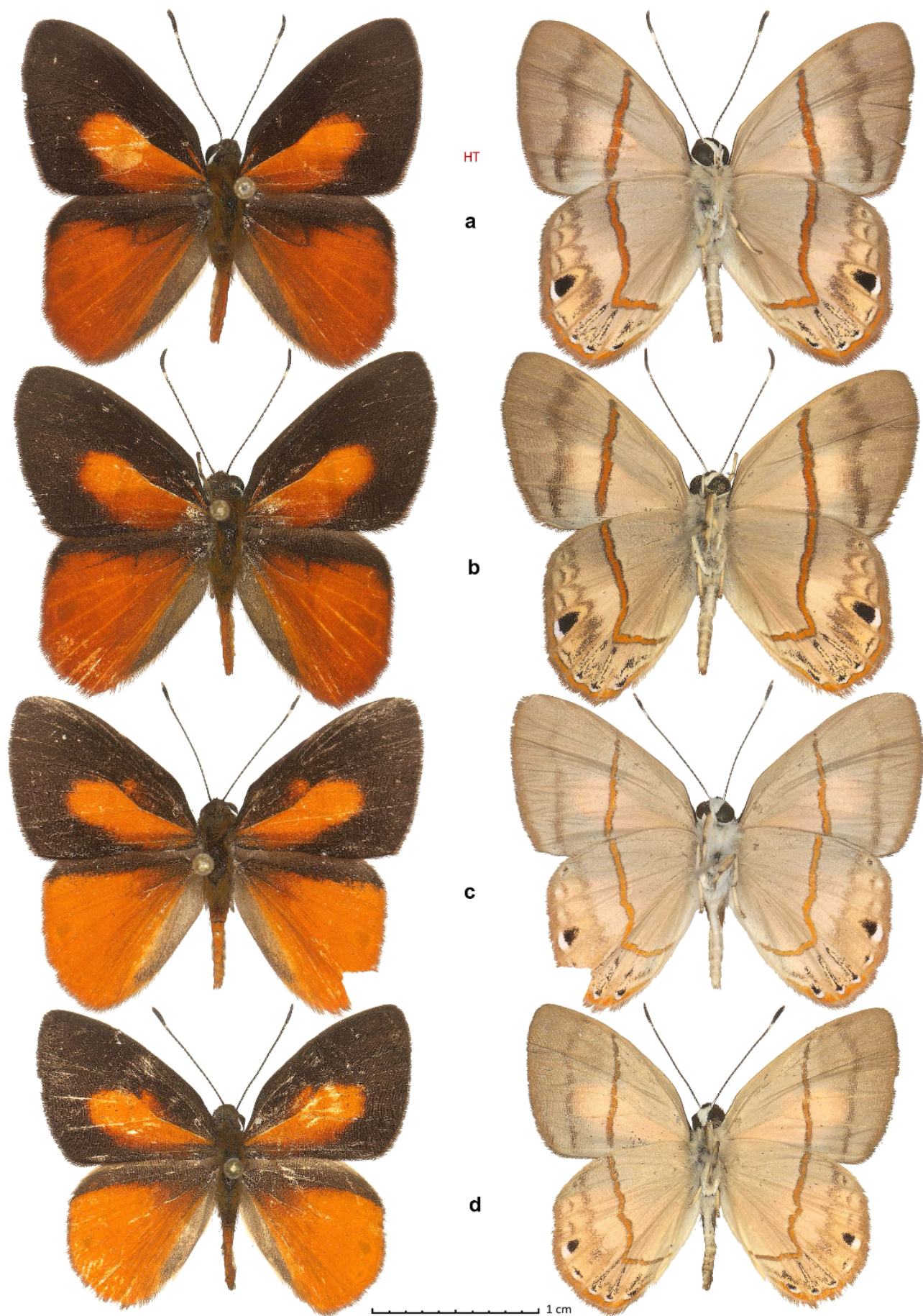


Fig. 11 (legend continues on the next page). *Myselasia* males from Ecuador, Robert C. Busby leg. [MGCL] in dorsal (left) and ventral (right) views: **a-b)** *M. pseudocrinon* **sp. n.**, Pastaza, 51 km S of Puyo, Pitirishka, 800 m, 7-Sep-1999: **a)** holotype



Fig. 12. Male genitalia of *Myselasia* from Ecuador, Robert C. Busby leg. [MGCL], in left lateral (left) and ventral (right) views: **a)** *M. pseudocrinon* sp. n. holotype NVG-25017B09 Pastaza, 51 km S of Puyo, Pitarishka, 800 m, 7-Sep-1999; and **b)** *M. crinon* NVG-25017B05 Pastaza, 45 km along the Puyo-Arajuno Rd., 1000 m, 15-Sep-1999, genitalia NVG260613-03.

Lectotype designation for *Eurygona matuta* Schaus, 1913

Eurygona matuta Schaus, 1913 (currently *Myselasia matuta*) was described from an unspecified number of specimens from “Juan Vinas”, Costa Rica (Schaus 1913). We found a syntype in USNM, originally from the Wm. Schaus collection, with the word “type” written in the bottom left corner of its identification label. Schaus labeled specimens he considered “types” (one per sex) with the handwritten word “type” but did not write this word on identification labels of other specimens in his series. Therefore, even if there were other syntypes, this specimen was considered a name-bearing specimen by Schaus. To define the taxonomic identity of the name *E. matuta* objectively, N.V.G. hereby designates the syntype in the USNM collection, a male bearing the following six rectangular labels (3rd handwritten, others printed with handwritten text shown in *italics*; 5th red, others white): [Jaun Vinas | CR], [2500–3500 | feet alt], [*Eurygona* | *matuta* | type Schs], [Collection | Wm Schaus], [Type | No. 16792 | U.S.N.M.], and [This specimen used | for illustration in | Butterflies of Costa Rica: | Riodinidae by P.J.DeVries], as the **lectotype** of *Eurygona matuta* Schaus, 1913. The lectotype’s abdomen is in a gelatine capsule affixed to the specimen pin. The lectotype is missing its left antenna, has a long scratch in the postdiscal area on the dorsal side of the left hindwing, and has some damage near the tornus of all wings, except the right forewing. Images of this specimen, photographed by G. Lamas, are shown on the Butterflies of America website (Warren et al. 2024). The type locality of *E. matuta* remains Costa Rica: Cartago, Juan Viñas, 2500–3500 ft. The COI barcode sequence of the lectotype, sample NVG-22034B06, GenBank [PZ516382](https://www.ncbi.nlm.nih.gov/nuclot/PZ516382), 658 base pairs, is:

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AACACTATACTTTATTTTCGGAATTTGAGCTGGAATAGTTGGTACATCATTAAAGTATATTAATTCGAATAGAACTAGGTACTTCAGGCTCTTATATTGGAGACGATCAAATTTATAACACT
ATTGTAACCGCTCATGCTTTTATCATAAATTTTTTATAGTAATACCTATTATAATTGGAGGATTCGGTAATTGATTGGTACCCCTAATATTAGGGGCTCCTGATATAGCTTTCCACGAA
TAAACAATATAAGATTTTGACTTTTACCCCATCATTAATTTTATTAAATTTCAAGAAGAATTGTAGAAAATGGAGCAGGAACCGGATGAACAGTATACCCCTCTTTTCATCTAATATTGC
TCACAGAGGATCATCTGTTGATTAGCTATTTTTTTCATTACATTTGGCCGGAATTTTCATCAATTTTAGGAGCTATCAATTTTATCACACAATCATTAAATATACGGGTTAATAATATAATA
TTTGATCAAAATACCATTATTTGTATGAGCTGTAGGAATCACAGCATTATTATTATTATCTTTACCAGTTTTAGCTGGAGCTATTACAATATTACTCACAGATCGTAATCTTAATACCT
CATCTTTTGACCCAGCTGGAGGAGGAGACCTATTCTTTATCAACATTTATTT
```


Myselasia paramatuta Grishin, new species

<https://zoobank.org/AC753643-F483-464F-A99C-62BEBA54FC28>

(Figs. 7 part, 13a–b, 14)

Definition and diagnosis. Genomic analysis reveals that a specimen from the Andes in southeastern Ecuador initially identified as *Myselasia matuta* (Schaus, 1913) (type locality Costa Rica: Cartago, Juan Viñas) is not monophyletic with it and is genetically differentiated from it at the species level (Fig. 7); e.g., their COI barcodes differ by 8.5% (56 bp), and therefore this specimen represents a new species. This new species is similar to *M. matuta*, but differs from it and other relatives by the following combination of characters in males: a larger orange patch in the center of the forewing that enters the discal cell (at least as orange-brown scaling) [the patch typically does not invade the discal cell in *M. matuta*]; orange-brown overscaling from the base of the dorsal forewing reaching the tornus along the inner margin [mostly restricted to the basal half of the wing in *M. matuta*]; and the brown postdiscal line on the ventral forewing being more pointed at the turn near the tornus [rounder in *M. matuta*, and may be weakly developed in some specimens]. Due to its cryptic nature and poorly explored individual variation, this species is best identified by DNA, with diagnostic base pairs in the nuclear genome: cne1684.4.3: A189G, cne1957.9.11:G57A, cne1957.9.11:T96C, cne2803.9.1:G9A, cne5629.4.3:G132A, cne300.2.1:A46A (not T), cne4228.2.4:C54C (not T), cne4228.2.4:G66G (not A), cne3355.7.1:C57C (not T), cne1957.9.11: C78C (not G); and the COI barcode: T163A, G218T, T346C, A382C, T529C.

Barcode sequence of the holotype. Sample NVG-25017C09, GenBank [PZ516383](https://www.ncbi.nlm.nih.gov/nuclot/PZ516383), 658 base pairs:

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AACTTTATATTTTATTTTCGGAATTTGAGCTGGAATAGTTGGTACATCCCTAAGTATATTAATTCGAATAGAATTAGGTACTTCGGCTCTTATATTGGAGACGATCAAATTTATAATACT
ATTGTAAGTCTCATGCCTTTATATAATTTTTCATAGTAATACCTATTATAATTTGGAGGATTTGGTAAGTATTAGTCCATTAATGTTAGGATCTCCTGATATAGCTTTCCACGAA
TAAATAATATAAGATTTTGACTTCTACCTCCATCATTAACTTTATTAATTTCAAGAAGAGTTGTAGAAAATGGAGCAGGAAGTGGATGAACAGTTTATCCCCCTCTCATCTAATATTGC
TCATAGAGGATCTTCTGTCGATTTAGCTATTTTTCATTACATCTAGCAGGAATCTCATCAATTTTAGGGGCTATTAATTTTATTACAACAATTATTAATATACGAGTCAATAATATAATA
TTTGATCAAATACCTTATTCGTATGAGCTGTAGGAATTACAGCCTTATTACTATTATTCTTTACCTGTATTAGCTGGAGCTATTACAATATTACTTACAGATCGTAATCTTAACACCT
CATTTTTTGACCCAGCTGGGGTGGAGACCTATTCTTTATCAACATTTATTT
```

Type material. **Holotype:** ♂ deposited in the McGuire Center for Lepidoptera and Biodiversity collection, Gainesville, FL, USA (MGCL), illustrated in Fig. 13a (genitalia Fig. 14), bears the following five printed rectangular labels, four white: [ECUADOR: Morona-Santiago | Nueve de Octubre, 1800 m | 2° 12.2' S, 78° 13.1' W | 29 September 2001 | Robert C. Busby, leg.], [DNA sample ID: | NVG-25017C09 | c/o Nick V. Grishin], [DNA sample ID: | NVG-25058A08 | c/o Nick V. Grishin], [genitalia: | NVG260613-04 | c/o Nick V. Grishin], and one red [HOLOTYPE ♂ | Myselasia | paramatuta Grishin]. The first DNA sample ID refers to the extraction from a leg (sequenced), and the second from the abdomen (stored) prior to genitalia dissection. **Paratypes:** 5♂♂ Ecuador, R. C. Busby leg. [MGCL]: the same data as the holotype except as indicated: 1♂ NVG-25058B01, 11-Sep-1999 and 1♂ NVG-25058A11, 28-Sep-2001; 1♂ NVG-25058A09 Morona-Santiago, 1 km E of Río Abanico, 1600 m, GPS -2.257, -78.195, 30-Sep-2001 (Fig. 13b); and Zamora-Chinchipe, Zamora (ridge W of town), 1450 m: 1♂ NVG-25058A10, 20-May-2000 and 1♂ NVG-25058A12, 24-Sep-2001.

Type locality. Ecuador: Morona-Santiago Province, ca. 20 km W of Macas, Nueve de Octubre, elevation 1800 m, GPS -2.2033, -78.2183.

Etymology. This new species *para*[llels its superficially similar relative *M.]matuta*. The name is treated as a noun in apposition.

Distribution. Currently known from the eastern slopes of the Andes in southeastern and southern Ecuador.

Euselasia pseudomys Callaghan, 1999 is a new junior subjective synonym of *Myselasia rhodon* (Seitz, 1913)

Genomic analysis reveals that topotypical specimens identified as *Myselasia pseudomys* (Callaghan, 1999) (type locality in Brazil, Rondônia) and *Myselasia rhodon* (Seitz, 1913) (type locality in Brazil: Pará, Rio Tapajóz as deduced from the labels of syntypes) including two syntypes of the latter taxon (one labeled as “lectotype” but the designation has not yet been published) are genetically close in both the



Fig. 13. *Myselasia* males in dorsal (left) and ventral (right) views: **a–b)** *M. paramatuta* **sp. n.** from Ecuador: Morona-Santiago, Robert C. Busby leg. [MGCL]: **a)** holotype NVG-25017C09 ca. 20 km W of Macas, Nueve de Octubre, elevation 1800 m, GPS –2.2033, –78.2183, and **b)** paratype NVG-25058A09 1 km E of Río Abanico, 1600 m, GPS –2.257, –78.195, 30-Sep-2001; **c–d)** *M. matuta* from Costa Rica: Cartago, Turrialba: **c)** NVG-22096D05 CATIE, 31-May-1988, Brian Harris leg. [LACM], and **d)** NVG-22074A02, John P. Miles & John C. Downey leg. 16-30-Jul-1965 [MGCL].

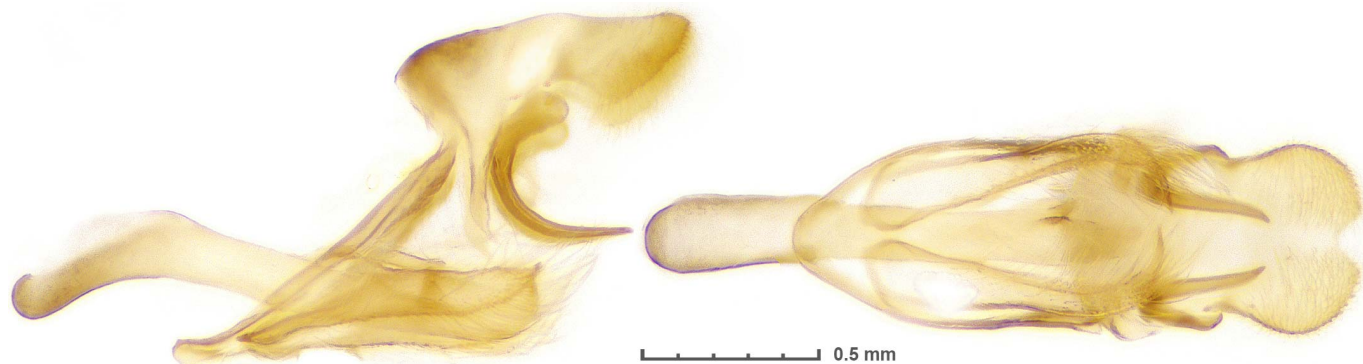


Fig. 14. Male genitalia of *Myselasia paramatuta* sp. n. holotype NVG-25017C09 in left lateral (left) and ventral (right) views.

nuclear and mitochondrial genome (Fig. 7). These two taxa are also similar in appearance, e.g., both have the tawny sector of the hindwing and weakly developed tornal dark streaks on the ventral hindwing, and we propose that *Euselasia pseudomys* Callaghan, 1999, **syn. nov.** is a junior subjective synonym of *Myselasia rhodon* (Seitz, 1913).

Lectotype designation for *Eurygona micaela* Schaus, 1902

Eurygona micaela Schaus, 1902 (currently *Erythia micaela*) was described from an unspecified number of specimens (No. 5894) from “Peru” (Schaus 1902). We found a syntype in USNM, originally from the W. Schaus collection, with No. 5894 and the word “type” written in the bottom left corner of its identification label. Schaus labeled specimens he considered “types” (one per sex) with the handwritten word “type” but did not write this word on identification labels of other specimens in his series. Therefore, even if there were other syntypes, this specimen was considered a name-bearing specimen by Schaus. To define the taxonomic identity of the name *E. micaela* objectively, N.V.G. hereby designates the syntype in the USNM collection, a male bearing the following four rectangular labels (3rd handwritten, others printed with handwritten text shown in *italics*; last red, others white): [Peru], [*Eurygona | micaela | type Schs*], [Collection | W.Schaus], [Type | No. 5894 | U.S.N.M.], as the **lectotype** of *Eurygona micaela* Schaus, 1902. The lectotype is missing both antennae (only the stub of the left one remains), its head is tilted to the right, scales are rubbed off near the tornus of the left hindwing, and the outer margin of the left forewing is notched at vein M₃. Images of this specimen, photographed by G. Lamas, are shown on the Butterflies of America website (Warren et al. 2024). The type locality of *E. micaela* remains Peru and will be refined by genomic sequence comparison. The COI barcode sequence of the lectotype, sample NVG-22034B12, GenBank [PZ516384](https://www.ncbi.nlm.nih.gov/nuclot/PZ516384), 658 base pairs, is:

```
AACTTTATATTTATTTTGGAAATTTGAGCAGGTATAGTAGGAACATCTTTAAGTTTAATAATTCGAATAGAATTAGGAACCTCAGGTTCTTATATTTGGTGACGATCAAATTTATAATACT
ATTGTAACCTGCTCATGCTTTTATTATAATTTTTTTTATAGTAATACCTATTATAATTTGGAGGATTGGAAATTTGATTAGTTCCATTAACTAGGAGCCCCAGACATAGCTTTCCCTCGAA
TAAATAATATAAGATTTTGATTATTACCTCCTTAAATCTTCTAATTTCAAGAAGAATTGTAGAAAAATGGAGCAGGAACCGGATGAACAGTGTACCCCCGCTATCATCTAATATTGC
TCATAGAGGATCCTCCGTTGATTAGCTATTTTTTCATTACATTAGCAGGAATTTTCATCAATTTAGGAGCTATTAAATTTATTACAACAATTATTAATATACGTGTTAATAATATAATA
TTTGATCAAAATACCCCTATTGTATGAGCAGTAGGTATTACAGCTTTATTACTCTTACTTTCCTCCAGTTTTCAGGAGCTATTACTATATTATTAAACAGATCGAAATTTAAATACAT
CATTTTTTGATCCCGCAGGAGGGGGAGACCTATCTTTTATCAACATTTATT
```

Lectotype designation for *Euselasia crotopus* form. *mutator* Seitz, 1916

Euselasia crotopus form. *mutator* Seitz, 1916 (currently *Erythia mutator mutator*) was described from an unspecified number of specimens and localities; the entire original description translated from German is: “The following forms occur in the ♂ ... Forewing with a dull, indistinct orange spot, hindwing with a magnificent bluish-violet reflection: **mutator** form. nov.” (Seitz 1916). Although proposed as an infrasubspecific name (male form), it was “before 1985 ... adopted as the valid name of a species” (ICZN Code Art. 45.6.4.1) by Stichel (1919), making it available “from its original publication” (ICZN 1999). In the SMF collection, we found a specimen identified as a syntype of *E. crotopus* form. *mutator* by Gerardo Lamas. According to its labels, this specimen is originally from the Seitz collection. It agrees with the

original description, and we agree with G. Lamas that this specimen is a syntype. Genomic analysis reveals that this specimen is likely conspecific with a “syntype” of *Euselasia aedina* (from Bolivia: La Paz, San Antonio, 1800 m; sequenced as NVG-21123A11), an unavailable name proposed by Stichel (1919) in synonymy (Art. 11.6) with *Euselasia mutator*, thus indirectly suggesting that it is a syntype. To define the taxonomic identity of the name *E. crotopus* form. *mutator* objectively, N.V.G. hereby designates the syntype in the SMF collection, a male bearing the following four white rectangular labels (2nd printed, others handwritten): [Peru | Rolle], [Coll. | A. Seitz], [SYNTYPE ♂ | Euselasia crotopus | f. mutator | Seitz, 1916], and [DNA sample ID: | NVG-24022D02 | c/o Nick V. Grishin], as the **lectotype** of *Euselasia crotopus* form. *mutator* Seitz, 1916. According to its label, Seitz obtained the specimen from the dealer Franz Hermann Rolle (1864–1929), but the collector remains unknown. The “syntype” label was written by Gerardo Lamas, who identified this specimen in the collection. The lectotype is missing a section of the left hindwing with the anal fold (except for the base) and is chipped at the outer margin of the left forewing in the middle, the left hindwing near the tornus, and the right hindwing from the middle toward the tornus. Images of this specimen, photographed by G. Lamas, are shown on the Butterflies of America website (Warren et al. 2024). The type locality of *E. crotopus* form. *mutator* according to the lectotype label is Peru and will be refined by genomic sequence comparison. The COI barcode sequence of the lectotype, sample NVG-24022D02, GenBank [PZ516385](#), 658 base pairs, is:

```
AACTTTATATTTTATTTTGGAAATTTGAGCAGGTATAGTAGGAACATCTTTAAGTTTAATAATTCGAATAGAACTTACAGTTCTTATATTGGTGACGATCAAATTTATAATACT
ATTGTAAGTCTCATGCTTTTATATAATTTTATAGTAATACCTATTATAATTTGGAGGATTTGGAAATTTGATTAGTTCCATTAACTAGGAGCCCGACATAGCTTTCCCTCGAA
TAAATAATATAAGATTTTGATTATACCTCTCTTCAATCTTCTAATTTCAAGAGAATTGTAGAAAATGGAGCAGGAACCGGATGAACAGTGTACCCCGCTATCATCTAATATTGC
TCATAGAGGATCCTCCGTTGATTAGCTATTTTTCATTACATTTAGCAGGAATTTTCATCAATTTTAGGAGCTATTAATTTTATTACAACAATTATTAATATACGTGTTAATAATATAATA
TTTGATCAAATACCCCTTATTGTATGAGCAGTAGGTATTACAGCTTTATTACTCTTACTCCAGTTTATAGCAGGAGCTATTACTATATTATTAACAGATCGAAATTTAAATACAT
CATTTTGTATCCCGCAGGAGGGGAGACCTATCTTTATCAACATTTATT
```

***Euselasia crotopus* form. *mutator* Seitz, 1916 is a new junior subjective synonym of *Erythia micaela* (Schaus, 1902)**

Genomic analysis reveals that lectotypes of two taxa currently regarded as species, *Erythia mutator* (Seitz, 1916) (type locality in Peru; sequenced as NVG-24022D02) and *Erythia micaela* (Schaus, 1902) (type locality in Peru; sequenced as NVG-22034B12), are close to each other genetically, e.g., their COI barcodes are identical, and they form a tight clade together with specimens from Bolivia, including a “syntype” of *Euselasia aedina* (from La Paz, San Antonio, 1800 m; sequenced as NVG-21123A11), an unavailable name proposed by Stichel (1919) in synonymy with his *Euselasia mutator*, although a description was provided (Fig. 15). Thus, all these specimens are likely conspecific. Curiously, Seitz (1916) who described *Euselasia crotopus* form. *mutator*, placed *Euselasia micaela*, as the next species, stating “The species is unknown to me.” Lectotypes of both taxa are from Peru and are phenotypically similar. Therefore, we propose that *Euselasia crotopus* form. *mutator* Seitz, 1916, **syn. nov.** is a junior subjective synonym of *Erythia micaela* (Schaus, 1902).

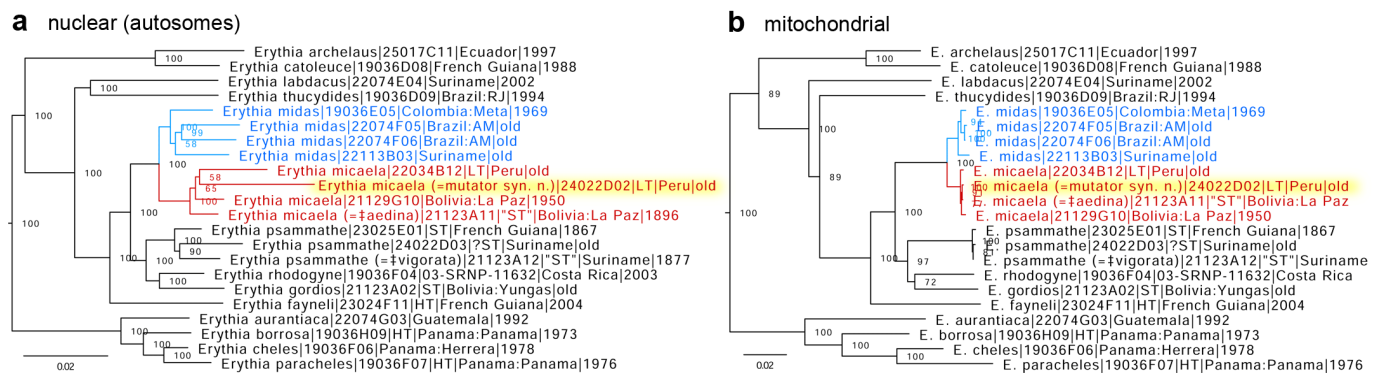


Fig. 15. Phylogenetic trees of selected *Erythia* Hübner, [1819] species constructed from protein-coding regions in: **a)** the nuclear genome (autosomes), based on 1,560,084 positions, and **b)** the mitochondrial genome: *E. midas* (blue) and *E. micaela* (red, with its junior subjective synonym *Euselasia crotopus* form. *mutator* Seitz, 1916, **syn. n.** highlighted in yellow). Ultrafast bootstrap (Hoang et al. 2018) values are shown at nodes.

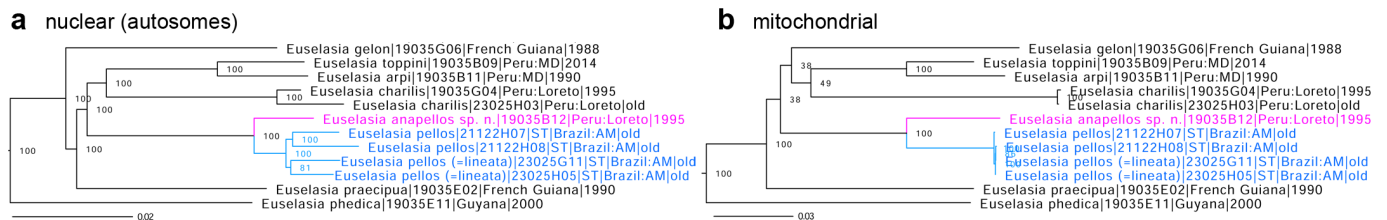


Fig. 16. Phylogenetic trees of selected *Euselasia* Hübner, [1819] species constructed from protein-coding regions in: **a)** the nuclear genome (autosomes), based on 10,068,450 positions, and **b)** the mitochondrial genome: *E. anapellos* sp. n. (magenta), and *E. pellos* (blue). Ultrafast bootstrap (Hoang et al. 2018) values are shown at nodes.



Fig. 17. *Euselasia* males in dorsal (left) and ventral (right) views, data in text or below: **a)** *E. anapellos* sp. n. holotype NVG-19035B12 from Peru: Loreto and **b–c)** *E. pellos* syntypes from Brazil: Amazonas, Tefé, P. Hahnel leg. [MFNB]: **b)** NVG-21122H07 and **c)** NVG-21122H08.

Euselasia anapellos Grishin, new species

<https://zoobank.org/54713FC7-B94E-49DD-B8E1-71DACE9191C9>

(Figs. 16 part, 17a)

Definition and diagnosis. Genomic analysis reveals that a specimen from northeastern lowland Peru, initially identified as *Euselasia pellos* Stichel, 1919 (type locality Brazil: Amazonas, Tefé; syntypes sequenced as NVG-21122H07 and NVG-21122H08) is genetically differentiated from it and syntypes of its junior subjective synonym *Euselasia pellos lineata* Rebillard, 1958 (type locality in Brazil: Amazonas, Maués, syntypes sequenced as NVG-23025G11 and NVG-23025H05) at the species level (Fig. 16); e.g., their COI barcodes differ by 5.8% (38 bp), and therefore this specimen represents a new species. This new species is most similar to its sister *E. pellos* (Fig. 17b, c), but differs from it and other relatives by the following combination of characters: wider orange submarginal band on the ventral hindwing, especially near the middle of the outer margin; less convex whitish submarginal band; the whitish postdiscal band on the ventral hindwing is approximately midway between the discal yellow band and the postdiscal orange band (not closer to the orange band); and possibly larger size. Due to its cryptic nature and unexplored individual variation, this species is best identified by DNA, with diagnostic base pairs in the nuclear genome: cne2972.4.5:C48T, cne4738.7.1:A315G, cne721.4.2:T78C, cne12236.1.26:T339C, cne36.5.2:C132A, cne2359.1.1:T87T (not C), cne7977.2.2:C66C (not A), cne2258.4.3:A78A (not C), cne2258.4.3:T85T (not C), cne5064.7.4:T97T (not C); and the COI barcode: C90A, A238C, T337T, T472T, G517A, A619C.

Barcode sequence of the holotype. Sample NVG-19035B12, GenBank [PZ516386](https://www.ncbi.nlm.nih.gov/nuclot/PZ516386), 658 base pairs:

```
AACATTATATTTTATTTTGGAAATTTGAGCTGGAATAATAGGAACCTTCATTAGTCTATTAATTCGTATAGAATTAAGAGTACCAGGTAATTTATTTGGTGATGATCAAATTTATAATACT
ATTGTAACCGCTCATGCTTTTATTATAATTTTATGTTATACCTATTATAATGGTGGATTGGAAATTGATTAGTTCCTTTAATATTAGGTGCTCCTGATATAGCTTTCCCGGAA
TAAATAATATAAGATTTTGATTACTTCCACCTTCATTATTCTTTTAAATTTCAAGAAGAATTGTAGAAAATGGAGCAGGAACAGGATGAACAGTTTACCCCCACTTTCATCCAATATTGC
TCATAGAGGATCTTCAGTTGATTAGCTATTTTCTCTTCATTAGCTGGTATTTTCATCAATTTTAGGAGCTATTAAATTTATTACAACAATTATAATATACGAATTAATAATAATA
TTTGATCAAAATACCTTTATTTGTATGATCTGTAGGTATTACAGCTTTATTACTTTTATTATCTTTACCAGTTTGTAGCTGGAGCTATTACTATACTTCTTACAGATCGAAATTTAAATACAT
CATTTTGTATCCCGCAGGAGGAGGTGATCCAATTTCTTTCAACATTTATTT
```

Type material. Holotype: ♂ deposited in the National Museum of Natural History, Smithsonian Institution, Washington, DC, USA (USNM), illustrated in Fig. 17a, bears the following five printed rectangular labels, four white: [PERU, Loreto, Rio | Sucusari, 140m | Explornapo-ACEER | 03°14'S, 72°55'W | 9 Sept 1995 | Leg. A. Caldas], [576], [DNA sample ID: | NVG-19035B12 | c/o Nick V. Grishin], [USNMNT | {QR Code} | 01544718], and one red [HOLOTYPE ♂ | *Euselasia* | *anapellos* Grishin].

Type locality. Peru: Loreto Region, ExplorNapo Lodge and the adjacent Amazon Center for Environmental Education and Research (ACEER) facility along the Río Sucusari, elevation 140 m, approx. GPS -3.2333, -72.9167.

Etymology. In classical Greek, *πελλός* (*pellos*) means dark-colored, dusky, blackish, or ashen-gray. The word was typically used to describe objects that were muted, dark, or somber in hue without being stark, pure black. The prefix *ἀνα-* (*ana-*) means up, upstream, or upriver, and refers to the upstream distribution of the new species compared to *E. pellos*. The name is treated as a noun in apposition.

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

Neotype designation for *Papilio eumene* Cramer, 1776

The name *Papilio eumene* Cramer, 1776 was proposed for an unspecified number of specimens from Suriname, and we translate the entire original description as: “The blue color of the dorsal side of the wings of this beautiful little Surinamese Grass-Butterfly [Dutch version] / Nymph [French version] is iridescent. The forelegs are short & without claws” (Cramer 1776). The description was accompanied by illustrations of the dorsal and ventral sides that show male(s) from the *Ectosemia eumene* group not confidently identifiable to species (Cramer 1776: pl. 92 F, G) (Fig. 18 shows photographs of the original drawings). Previously, when most species in the group were lumped under *E. eumene*, ambiguity in the illustrations and description did not cause a problem and was interpreted as variation. Genomic analysis reveals several species in the group (Zhang et al. 2023c), some new (Fig. 19), and it is necessary to define the name *E. eumene* objectively by a single name-bearing type specimen.

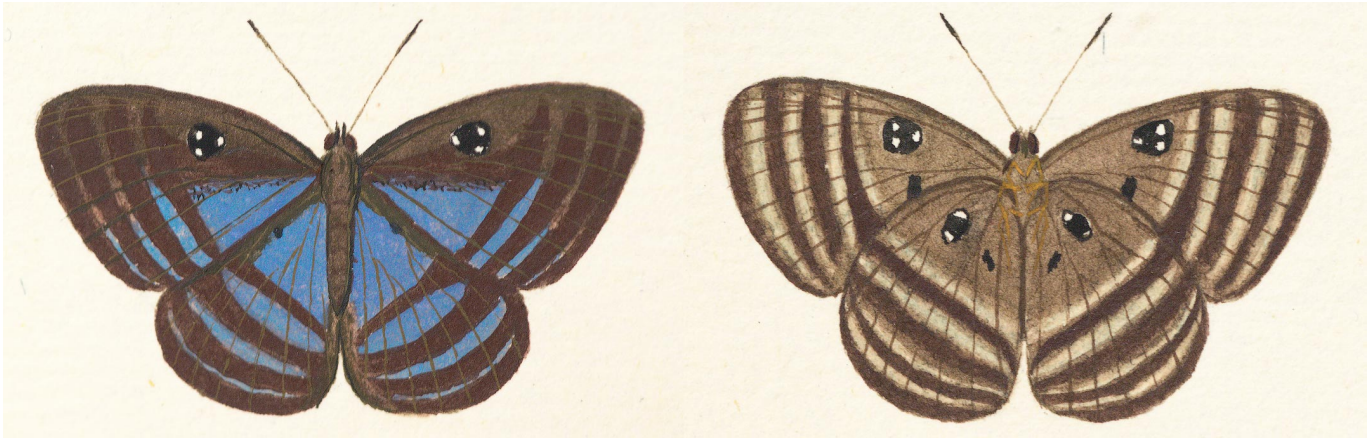


Fig. 18. *Papilio eumene* syntype(s), original drawings by Lambertz, in dorsal (left) and ventral (right) views; © The Trustees of the Natural History Museum, London, Creative Commons License 4.0 (<https://creativecommons.org/licenses/by/4.0/>).

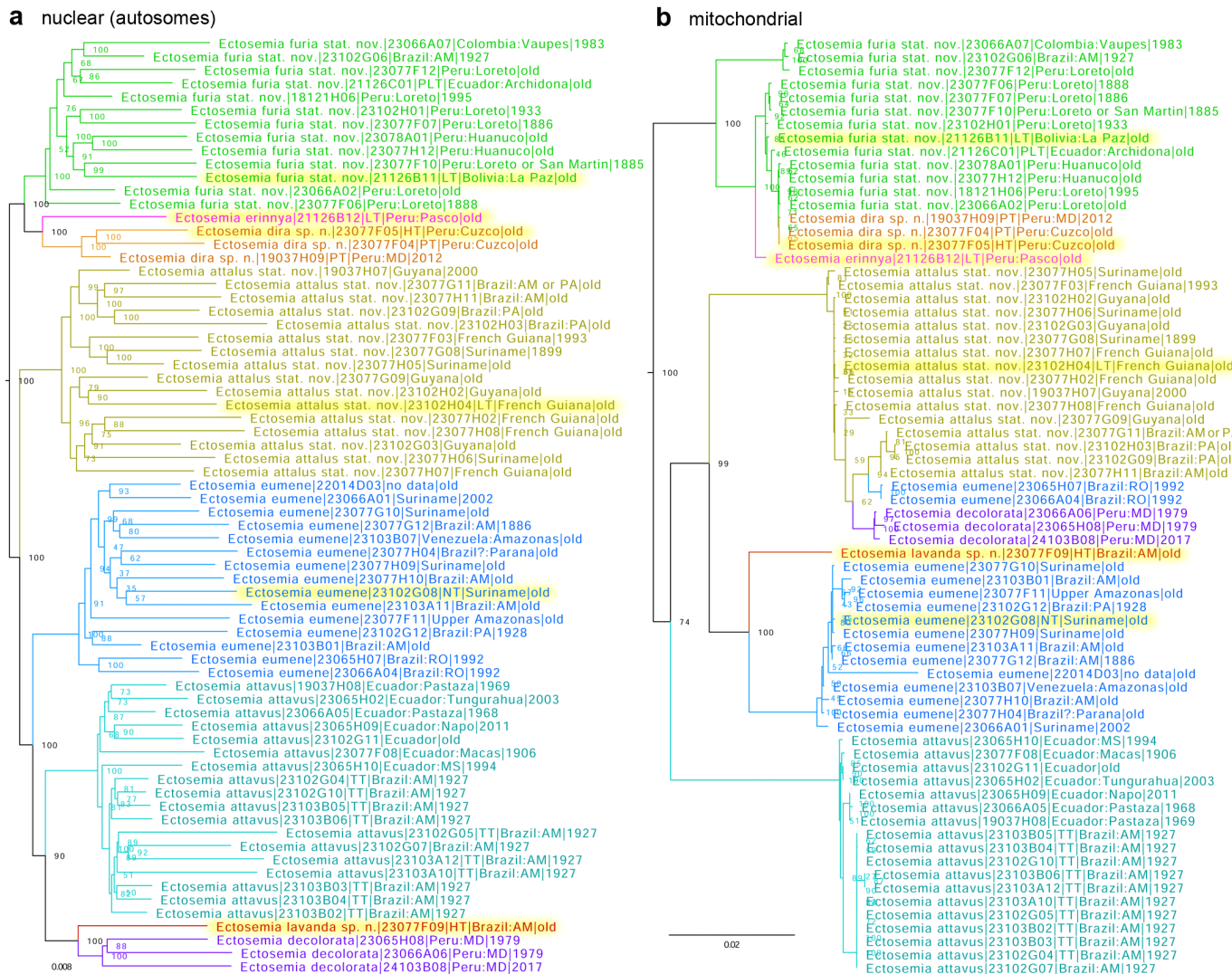


Fig. 19. Phylogenetic trees of species in the *Ectosemia eumene* group constructed from protein-coding regions in: **a)** the nuclear genome (autosomes), based on 340,968 positions, and **b)** the mitochondrial genome. Different species are colored differently: *E. furia* stat. nov. (green), *E. erinnya* (magenta), *E. dira* sp. n. (orange), *E. attalus* stat. nov. (olive), *E. eumene* (blue), *E. attavus* (cyan), *E. lavanda* (red), and *E. decolorata* (violet). Primary type specimens are highlighted in yellow. Sequenced topotypes (TT) of *E. attavus* in SMF were collected by J. F. Zikán at San Gabriel in 1927 and are likely part of the type series, with NVG-23103B03 (Figs. 25v, 27b) dated "14-XI-27", matching a syntype in the Zikán collection bearing labels "lectotypo" (unpublished) and "holotypus". A specimen of *E. furia* (NVG-23102G06) was collected by Zikán at the same locality on 19-Oct-1927, indicating sympatry of the two species. Ultrafast bootstrap (Hoang et al. 2018) values are shown at nodes.

We searched for *E. eumene* type specimens in two collections known to house Cramer's material: RMNH and BMNH. We were not able to find definitive types, and found only one possible candidate in the RMNH, an old specimen lacking data and bearing a single label: "Collectie Zoologisch Museum Amsterdam" (Fig. 20a). While this specimen generally agrees with the original illustration, we have no evidence to believe that it is a syntype. Moreover, this specimen is not set in the same manner as the illustration: because the forewings are not advanced forward enough to reveal the dark brown spot in the anterior part of the hindwing discal cell. Therefore, it is not likely to be the specimen illustrated. For these reasons we believe that syntypes of *P. eumene* have been lost.

There is an exceptional need for a neotype of *P. eumene* to define this taxon objectively and thus stabilize nomenclature by clarifying which species among several close relatives (some undescribed) corresponds to *P. eumene*. This is necessary, because different species have been called *P. eumene* over the years. For instance, according to our analysis, two different species were called *M. eumene* by Seitz (1916) and Brévignon and Gallard (1997) (see below). To form a better hypothesis about the identity of *P. eumene*, we inspected the original drawings by Gerrit Wartenaar Lambertz in the BMNH library, compiled and reproduced here (Fig. 18). Indeed, the drawing appears more accurate than the published engravings, at least in showing a narrower discal brown band on the dorsal hindwing, more characteristic of actual specimens than the broad band in the engraving.

Out of the two species we sequenced from Suriname (Fig. 19), the one that is more common in collections agrees best with the original drawing of *P. eumene* (Fig. 18). The old specimen in RMNH belongs to this species as well (Fig. 20a). Males of this species have more extensive blue coloration on the dorsal forewing, with three blue bands and a broader blue area in the basal half of the wings nearly reaching the discal cell; more extensive blue on the hindwing with the dark spot in the discal cell protruding into the blue area; and usually a metallic sky-blue rather than green color (Fig. 20a–c). This is the species Seitz (1916) considered "typical *eumene*." The second species has a more restricted and greener metallic color with two bands on the forewing (no submarginal bands near the tornus as seen in the original drawing of *P. eumene*) and the basal blue does not reach the discal cell; furthermore, the brown spot on the dorsal hindwing is completely within the brown area and not invading the greenish area (Fig. 20d). Therefore, a specimen of the first species is selected as the neotype. Hereby, N.V.G. designates the specimen in the SMF illustrated in Fig. 20b (DNA sample NVG-23102G08) as the **neotype** of *Papilio eumene* Cramer, 1776. This neotype stabilizes the current usage of this name as employed in historical works, such as Seitz (1916).

This neotype satisfies all requirements set forth by ICZN Article 75.3, namely: **75.3.1.** It is designated to clarify the taxonomic identity of *P. eumene*, which is necessary because the *E. eumene* group consists of several closely related species (including some described herein as new), and the original description and illustrations are insufficient to identify *P. eumene* with certainty; **75.3.2.** The characters to differentiate this taxon are the following, as inferred from the original drawing and the historical specimen in RMNH, which is likely conspecific with the syntype(s): three brown bands from costal to inner margin and a marginal brown band on both sides of both wings; a black spot with three white spots at the end of the forewing discal cell on both sides; a similar black spot in the hindwing discal cell but only on the ventral side, and with two white spots framing it at the base and outer margin; metallic sky-blue scaling on the dorsal side between and basad of the brown bands covering the posterior half of the forewing (from the discal cell to the inner margin) and nearly the entire hindwing except from the costal margin to the anterior part of the discal cell; the brown spot in the discal cell invading the blue area; and most prominently, three (not two) blue bands on the forewing, from the inner margin to at least vein CuA₁; **75.3.3.** The neotype specimen is a male bearing the following three rectangular printed labels (1st greenish, others white): [Surinam | V. – IX. | Fruhstorfer], [Coll. | A. Seitz], [DNA sample ID: | NVG-23102G08 | c/o Nick V. Grishin], and is illustrated in Fig. 20b; the neotype has a distinct hole in the left hindwing near the tornus, between the discal and postdiscal brown lines, and a narrowly chipped section of the outer margin of the right forewing just below the apex; **75.3.4.** We failed to find syntypes of *P. eumene* among the Riodinidae holdings and possible Cramer material in RMNH and BMNH (and in all

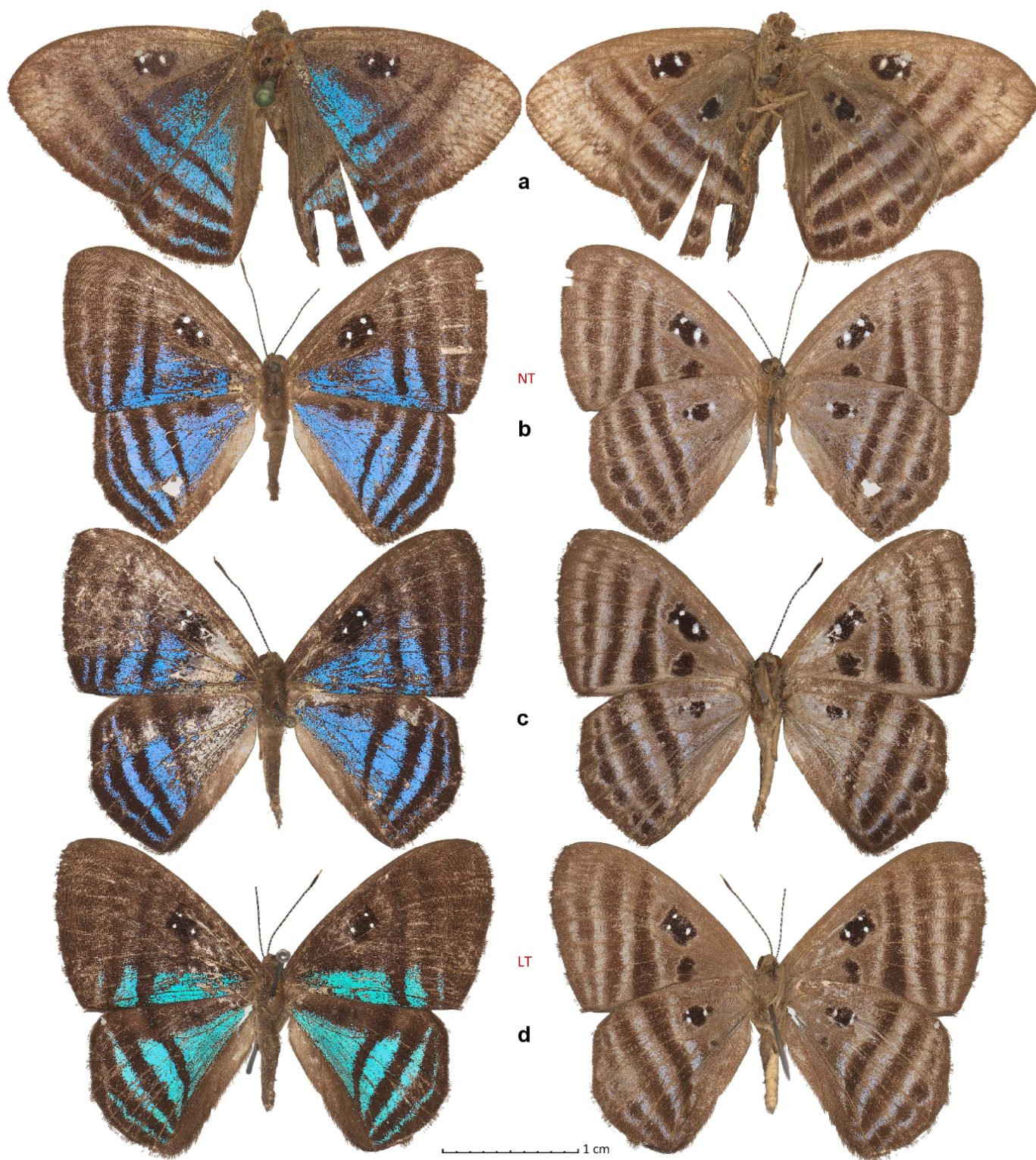


Fig. 20. *Ectosemia eumene* and *E. attalus* **stat. nov.** males in dorsal (left) and ventral (right) views, data in text or below: **a–c)** *E. eumene*: **a)** non-type NVG-22014D03 no data, old, labeled “Collectie Zoölogisch Museum Amsterdam” [RMNH]; **b)** neotype (designated herein) NVG-23102G08 from Suriname [SMF]; **c)** non-type NVG-23077H09 from Suriname [MFNB]; and **d)** *E. attalus* **stat. nov.** lectotype (designated herein) NVG-23102H04 from French Guiana: Nouveau Chantier [SMF].

other collections we visited, see Acknowledgments for the list) and therefore believe that they have been lost; **75.3.5.** The neotype closely agrees with the original description and illustrations in all characters, as evidenced by comparison of the neotype shown in Fig. 20b with the original Lambertz drawing (Fig. 18) and published engravings of the syntype(s) (Cramer 1776: pl. 92 F, G) and the characters listed for *P.*

eumene above (75.3.2.); **75.3.6.** The neotype is from Suriname, and the original type locality was given as Suriname; **75.3.7.** The neotype is deposited in the Senckenberg Naturmuseum, Frankfurt, Germany (SMF). The COI barcode sequence of the neotype, sample NVG-23102G08, GenBank [PZ516387](https://www.ncbi.nlm.nih.gov/nuclot/PZ516387), 658 base pairs, is:

```
TACATTATATTTTATTTTGAAGAGGTATAGTTGGATCTTCTCTAGTTTACTTATTCGAATAGAATTGGGTACACCTGGATCATTAAATGGAGATGATCAAATTTATAATAC
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TTTGATCAAAATACCTTTATTGTTATGATCTGTTGGTATTACAGCTTTATTATTACTTTTATCTTACCAGTTTACGAGGAGCTATTACCATATTATTAAGTATGATCGTAATTTAAATACTT
CTTTTTTGTATCTGCTGGTGGAGGTATCTATTCTTTATCAACATTATTATTT
```

Lectotype designation for *Mesosemia eumene* form. *attalus* Seitz, 1913

Mesosemia eumene form. *attalus* was described by Seitz (1913, 1916) from more than one specimen collected in French Guiana: “Nouveau Chantier, Amazon etc.” and, according to the original description (Seitz 1913, 1916), differs from other “forms” (i.e., subspecies) by the greenish area in the posterior part of the forewing not reaching “the median.” In the SMF collection, we found a specimen identified as a syntype of *M. eumene* form. *attalus* by Gerardo Lamas. According to its labels, this specimen is originally from the Seitz collection and is from the locality listed first in the original description. It agrees with the original description, and the greenish area on the forewing ends between one-quarter and one-third of the wing width from the inner margin and thus “does not reach the median” (Seitz 1916). Therefore, we agree with G. Lamas that this specimen is a syntype. To define the taxonomic identity of the name *M. eumene* form. *attalus* objectively, N.V.G. hereby designates the syntype in the SMF collection, a male illustrated in Fig. 20d bearing the following five rectangular white labels (4th handwritten, others printed): [GUYANE FRANÇ^{SE} | Nouveau Chantier | COLLECTION LE MOULT], [MAI], [Coll. | A. Seitz], [SYNTYPE ♂ | *Mesosemia eumene* | f. *attalus* Seitz, | 1916], and [DNA sample ID: | NVG-23102H04 | c/o Nick V. Grishin], as the **lectotype** of *Mesosemia eumene* form. *attalus* Seitz, 1913. The “syntype” label was written by Gerardo Lamas, who identified this specimen in the collection. The lectotype is missing the club of the left antenna, its head is tilted to the left, and the left hindwing has a prominent tear near its base. As a result of the lectotype designation, the type locality of *M. eumene* form. *attalus* becomes French Guiana: Nouveau Chantier. The COI barcode sequence of the lectotype, sample NVG-23102H04, GenBank [PZ516388](https://www.ncbi.nlm.nih.gov/nuclot/PZ516388), 658 base pairs, is:

```
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TCACAGAGGTTTCATCAGTAGATCTTGCTATTTTCTCTTCATTAGCAGGTATTTCTTCTATTTAGGTGCTATTAATTTTATTACTACTATTATTAATATACGAATTAATAATATATCA
TTTGATCAAAATACCTTTATTGTTATGATCTGTTGGTATTACAGCTTTATTATTACTTTTATCTTACCAGTTTACGCGGAGCTATTACTATATATTAACTGATCGTAATTTAAATACTT
CTTTTTTGTACCTGCTGGGGAGGTATCTATTCTTTATCAACATTATTATTT
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Ectosemia attalus (Seitz, 1913), stat. nov. is a valid species distinct from *Ectosemia eumene* (Cramer, 1776)

Genomic analysis of specimens in the *Ectosemia eumene* group reveals two clades genetically differentiated at the species level, with specimens from Suriname and Amazonian Brazil present in both clades (likely sympatric over a large area) (Fig. 19 blue and olive). Their COI barcodes differ by 2.6% (17 bp). Therefore, these clades represent two different species. The first clade contains the neotype of *Ectosemia eumene* (Cramer, 1776) (type locality in Suriname; NVG-23102G08) and represents this species (Fig. 19 blue). The second clade contains the lectotype of *Mesosemia eumene* form. *attalus* Seitz, 1913 (type locality French Guiana: Nouveau Chantier; NVG-23102H04) and represents this taxon, which is therefore a species (Fig. 19 olive). Thus, we propose that *Ectosemia attalus* (Seitz, 1913), **stat. nov.** is a valid species distinct from *Ectosemia eumene* (Cramer, 1776).

Males of the two species can be distinguished by the extend of bluish scaling on the dorsal forewing. In *E. eumene*, they reach the middle of the wing and the postmedian blue band extends from the inner margin to vein M₃ and frequently beyond towards the costal margin, and the submarginal blue band is usually present (Figs. 20 a–c, 25 m–o). In *E. attalus*, the postmedian bluish band does not reach vein M₃ and the submarginal blue band is not developed (Figs. 20 d, 25 h–j). Also, most specimens of *E.*

eumene, are bluer and most specimens of *E. attalus* are greener, although there is significant variation in the tint of the metallic areas.

Females of the two species can be distinguished by the relative darkness of the brown bands and the width and expression of the blue bands. In *E. eumene*, all four dark-brown bands of the dorsal forewing are approximately the same color and are more uniform from the inner margin to the costal margin; the dorsal hindwing blue bands are usually narrower; and the forewing postdiscal and submarginal blue bands on the dorsal forewing are more prominent (Figs. 25 p–r). In *E. attalus*, the submarginal band on the forewing is paler, especially towards the costal margin; the blue bands on the hindwing are typically broader; and the postdiscal and submarginal bands are weaker or vestigial on the dorsal forewing (Fig. 25 k–l).

***Mesosemia meyi* Brévignon, 1997 is a junior subjective synonym
of *Ectosemia eumene* (Cramer, 1776)**

Illustrations of “*Mesosemia eumene eumene*” in Brévignon and Gallard (1997) are identifiable as *Ectosemia attalus* (Seitz, 1913), **stat. nov.** (type locality in French Guiana). Both male and female possess characters of the latter species, even agreeing with its original description in that the greenish area in the posterior part of the forewing “does not reach the median” (Seitz 1913, 1916). Moreover, in the male, the submarginal greenish band on the dorsal forewing is vestigial, and the metallic color is greener rather than bluer. In the female, the blue bands on the dorsal forewing are less developed, and the brown submarginal band is paler (especially towards the costal margin) than the discal and postdiscal bands. However, the holotype and allotype of *Mesosemia meyi* Brévignon, 1997 are identifiable as *Ectosemia eumene* (Cramer, 1776) (type locality in Suriname). Indeed, the male displays more blue than green coloration, which is typical of *E. eumene*, and has more extensive blue on the forewing, including the submarginal bands that nearly reach the costal margin. These blue bands are equally prominent in the female, which also has a darker brown submarginal forewing band even towards the costal margin.

We agree with Brévignon and Gallard (1997) that their “*Mesosemia eumene eumene*” and *Mesosemia meyi* indeed represent two distinct species. However, these species are *Ectosemia attalus* and *Ectosemia eumene*, respectively. Thus, Brévignon and Gallard (1997) misidentified *Ectosemia eumene* (Cramer, 1776) and re-described it as *Mesosemia meyi* Brévignon, 1997, whereas the species they considered to be *E. eumene* is actually *E. attalus* (Seitz, 1913), which was previously treated as a junior subjective synonym of *E. eumene*. Following this phenotypic analysis, we propose that *Mesosemia meyi* Brévignon, 1997, **syn. nov.** is a junior subjective synonym of *Ectosemia eumene* (Cramer, 1776).

***Ectosemia lavanda* Grishin, new species**

<https://zoobank.org/E2ED2965-3344-42E9-B92A-F150E1B473DD>

(Figs. 19 part, 21a, 25y)

Definition and diagnosis. Genomic analysis reveals that a specimen from the western part of Amazonas, Brazil, initially identified by its wing pattern as *Ectosemia decolorata* (Lathy, 1932) (type locality in Brazil: Mato Grosso) is genetically differentiated from it at the species level (Fig. 19); e.g., their COI barcodes differ by 2.9% (19 bp), and therefore this specimen represents a new species. Males of this new species are similar to *E. decolorata* in having the anterior part of the forewing cell CuA₁-1A+2A brown basally on the dorsal side (instead of mostly blue); the discal cell on the dorsal hindwing mostly brown, with blue along its posterior and outer edge; and the discal dorsal forewing brown band reaching the inner margin, but differs from it and other relatives by the following combination of characters: the blue dorsal color is lavender, i.e., with a magenta tint (not pure blue or greenish), especially towards the outer margins between the brown bands; the areas between brown bands on the ventral side of the wings are less pale, browner, and mostly two-toned: browner basad and paler anterad [these bands are paler and less two-toned in *E. decolorata* (Fig. 21b, c)]; and the submarginal brown band on the ventral side of both wings is broader, with more prominent and darker spots in cells M₃-CuA₁ on both wings. Due to its

cryptic nature and unexplored individual variation, this species is best identified by DNA, with diagnostic base pairs in the nuclear genome: cne3037.1.9:C211A, cne4055.2.9:C158T, cne1383.4.14:C100T, cne9089.1.13:C162G, cne6120.1.6:A240G, cne41.6.2:A594A (not G), cne41.6.2:A459A (not G), cne2483.2.1:T531T (not C), cne2483.2.1:C555C (not A), cne32545.1.2:G81G (not T); and the COI barcode: T127C, T274A, 343T, 574C, T586C, G625T.

Barcode sequence of the holotype. Sample NVG-23077F09, GenBank [PZ516389](https://www.ncbi.nlm.nih.gov/nuclot/PZ516389), 658 base pairs:

TACATTATATTTTATTTTGGAAATTTGAAGAGGTATAGTTGGATCTTCTCTTAGTTTACTTATTTCGAATAGAATTAGGTACACCTGGATCATTAAATGGAGATGATCAAATTTATAATACT
ATTGTCAGTCTCATGCTTTTATTATAATTTTATAGTTATACCTATTATAATTTGGTGGATTTGGTAATTGACTTGTTCCTTTAATATTAGGGGCTCCTGATATAGCTTTTCTCGAA
TAAATAATATAAGATTTGACTTTTACCACCATCTTATTCTTTTAAATTTCAAGAAGAATTGTTGAAAATGGAGCAGGTACTGGATGAACAGTTTACCCTCTCTATCTTCTAATATTGC
TCATAGAGGTTTCATCAGTAGATCTTCTATTTTCTCTTCATTTAGCAGGTATTCTTCTATTTTAGGTGCTATTAATTTTATTACTACTATCATTAAATATACGAATTAATAATATATCA
TTTGATCAAATACCTTTATTGTATGATCTGTTGGTATTACAGCTTTATTATTACTTTTCTTTACCGGTTTAGCAGGAGCTATTACCATATTATTAACCGATCGTAATTTAAATACT
CTTTTTTGTATCTGCTGTTGGAGGTGACCCATTCTTTATCAACATTTATTT

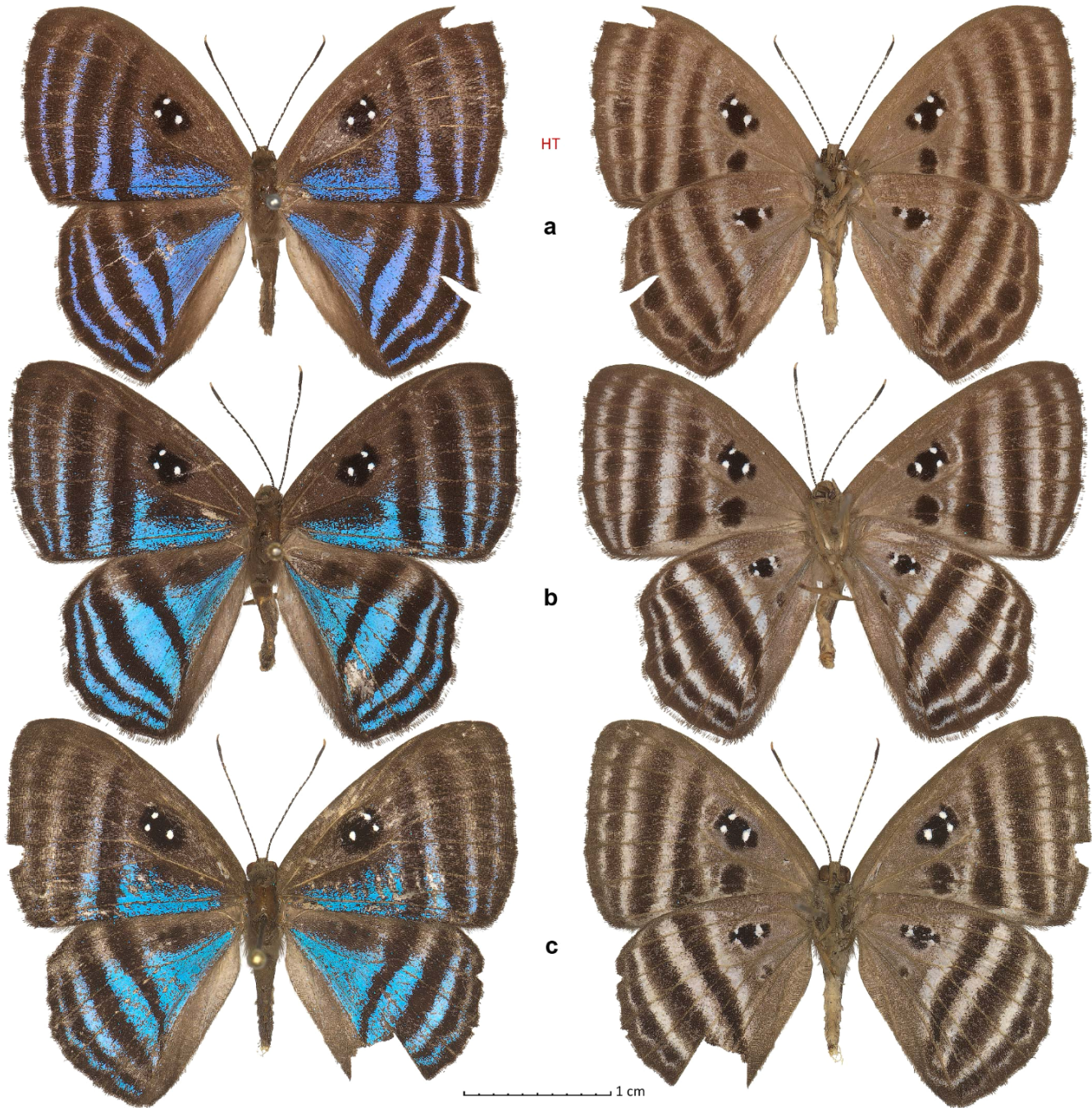


Fig. 21. *Ectosemia lavanda* sp. n. and *E. decolorata* males in dorsal (left) and ventral (right) views, data in text or below: **a)** *E. lavanda* sp. n. holotype NVG-23077F09 Brazil: Amazonas [MFNB]; and **b–c)** *E. decolorata* non-types from Peru: Madre de Dios: **b)** NVG-23065H08 Rio Tambopata, 15-Jul-1979, J. J. Bowe leg. [MGCL] and **c)** NVG-24103B08, WRD 15614 Alto Madre de Dios at Pantiacolla Lodge, 400 m, GPS –12.6500, –71.2167, 8-Nov-2017, W. R. Dempwolf leg. [WRDC].

Type material. Holotype: ♂ deposited in the Museum für Naturkunde, Berlin, Germany (MFNB), illustrated in Figs. 21a, 25y, bears the following three printed rectangular labels, two white: [S. P. Oliv. | Amaz. Sup. | Mich.], [DNA sample ID: | NVG-23077F09 | c/o Nick V. Grishin], and one red [HOLOTYPE ♂ | Ectosemia | lavanda Grishin]. According to its first label, the holotype was collected by Michaelis in São Paulo de Olivença, in the upper Amazonian region.

Type locality. Brazil: Amazonas, São Paulo de Olivença.

Etymology. Lavanda is the word for lavender in several languages, including Spanish, Portuguese, Italian, Catalan, and Galician. The name reflects the lavender color of the bluish stripes on the dorsal side of males in this species, which are redder rather than pure blue or greenish in its relatives. The name is treated as a noun in apposition.

Distribution. Currently known from the holotype collected near the western edge of Amazonian Brazil.

***Ectosemia furia* (Stichel, 1910), stat. nov. is a valid species distinct from *Ectosemia erinnya* (Stichel, 1910)**

Genomic analysis reveals that *Mesosemia eumene furia* Stichel, 1910 (type locality in Bolivia: La Paz, Farinas; lectotype sequenced as NVG-21126B11) currently treated as a junior subjective synonym of *Ectosemia erinnya* (Stichel, 1910) (type locality in Peru: Pasco, Pozuzo; lectotype sequenced as NVG-21126B12) is genetically differentiated from it at the species level in the nuclear genome (Fig. 19a), although the two taxa do not differ strongly in the mitochondrial genome (Fig. 19b). Genomic sequencing of 12 specimens from a wide range of localities extending from Colombia and Ecuador to Peru and Amazonas in Brazil reveals that they form a confidently supported clade containing the lectotype of *M. eumene furia* in the nuclear genome tree (Fig. 19a green) that is prominently separated from its sister clade with the lectotype of *E. erinnya* (Fig. 19a magenta and orange). Therefore, we propose that *Ectosemia furia* (Stichel, 1910), **stat. nov.** is a valid species distinct from *Ectosemia erinnya* (Stichel, 1910). It is possible that the two species are sympatric at least in central Peru.

Having sequenced only a single specimen of *E. erinnya*, the female lectotype, it is challenging to suggest confident wing pattern characters to separate it from *E. furia* **stat. nov.** Hypothetical characters of *E. furia* **stat. nov.** females include more extensive blue coloration between the brown bands on the dorsal forewing that reaches at least half the width of the wing from the inner margin towards the costa; broader brown bands equally dark towards the costa on both sides of the forewing (fading into the ground color towards the costa in *E. erinnya*); and less extensive blue scaling basad of the discal hindwing brown band.

***Ectosemia dira* Grishin, new species**

<https://zoobank.org/71B565C7-351B-49D1-83A4-E3F791797E35>

(Figs. 19 part, 22c–d, 23a, 25f–g)

Definition and diagnosis. Genomic analysis reveals that specimens from southeastern Peru initially identified as *Ectosemia erinnya* (Stichel, 1910) (type locality Peru: Pasco, Pozuzo; lectotype sequenced as NVG-21126B12) are genetically differentiated from it and their second close relative *Ectosemia furia* **stat. nov.** (type locality Bolivia: La Paz, Farinas; lectotype sequenced as NVG-21126B11) at the species level in the nuclear genome (Fig. 19) (COI barcodes do not differ among some specimens of these species, likely due to introgression), and therefore these specimens represent a new species. This new species is similar to *E. erinnya* and *E. furia* **stat. nov.**, but differs from them and other relatives by the following combination of characters in females (male of *E. erinnya* is unknown to us): more extensive pale areas between dark-brown bands on the ventral hindwing; typically narrower brown bands on the dorsal hindwing, which has more extensive blue overscaling basad of the discal band toward and around the dark spot (sometimes vestigial) in the discal cell; blue scaling reaches farther from the inner margin of the forewing toward the costa than in *E. erinnya* (Figs. 22b, 25s) but is broader than in *E. furia* **stat. nov.** (Figs. 22a, 25c, d); and this blue scaling is paler, with its tint being slightly greener (towards cyan) than in



a



LT

b



HT

c



d



1 cm

Fig. 22. (see the previous page). *Ectosemia erinnya* and relatives from Peru, females in dorsal (left) and ventral (right) views, data in text or below: **a)** *E. furia* non-type NVG-23066A02 Loreto, Iquitos, old, Le Moults leg. [MGCL]; **b)** *E. erinnya* lectotype NVG-21126B12 Pasco, Pozuzo [MFNB]; and **c–d)** *E. dira* **sp. n.**: **c)** holotype NVG-23077F05 Cuzco [MFNB] and **d)** paratype NVG-19037H09 Madre de Dios [USNM].

other species. Males of the new species can be separated from males of *E. furia* **stat. nov.** (Figs. 23b–d, 25a, b) by the following combination of characters: narrower brown bands on the dorsal hindwing with more extensive green area in the posterior part of the discal cell, and the postdiscal green band on the dorsal forewing does not reach the middle of the wing from the inner margin toward the costa [past the middle in *E. furia* **stat. nov.**, which also frequently has a developed submarginal green band]. Due to its cryptic nature and poorly explored individual variation, this species is best identified by DNA, with diagnostic base pairs in the nuclear genome: cne963.1.15:G63A, cne1817.2.9:T137C, cne3334.3.1:T111G, cne3334.3.1:T141C, cne29742.2.1:T282A; and the COI barcode is shared with several specimens of *E. furia* that we sequenced and therefore is not diagnostic.

Barcode sequence of the holotype. Sample NVG-23077F05, GenBank [PZ516390](#), 658 base pairs:

```
TACATTATATTTTATTTTGGAAATTTGAAGAGGTATAGTTGGATCTTCACTTAGTTTACTTATTCGAATAGATTAGGTTACCTGGTTCATTAATTGGAGACGATCAAATTTATAAATACT
ATTGTTACTGCTCATGCTTTTATTAATTTTATAGTTATACCTATTATAATTTGGTGGATTTGGTAATTGACTTGTTCCTTTAATATTAGGAGCTCCTGATATAGCTTTCCACGAA
TAAATAACATAAGATTTGACTTTTACCCCTTCTTATTCTTTTAATTTCAAGAAGAATTGTGAAATGGAGCAGGTACTGGATGAACAGTTTACCCCTTTATCTTCTAACATTGC
TCACAGAGGTTTCATCAGTAGATCTTGTCTATTTTCTCTTCATTAGCAGGTATTTCTTCTATTTAGGTGCTATTAATTTTATTACTACTATTATTAATATACGAATTAATAATATATCA
TTTGATCAAATACCTTTATTTGTATGATCTGTAGGTATTACAGCTTTATTATTACTTTTATCTTTACCAGTTTGTAGCAGGAGCTATTACTATATTATTAATGATCGTAATTTAAATACTT
CTTCTTTGTATCCTGCTGGAGGAGGTGATCCTATTCTTTATCAACATCTATTT
```

Type material. Holotype: ♀ deposited in the Museum für Naturkunde, Berlin, Germany (MFNB), illustrated in Figs. 22c, 25g, bears the following three rectangular labels (1st handwritten, others printed), two white: [Cuzco], [DNA sample ID: | NVG-23077F05 | c/o Nick V. Grishin], and one red [HOLOTYPE ♀ | *Ectosemia* | *dira* Grishin]. **Paratypes:** 1♂ and 1♀ from Peru: 1♂ NVG-23077F04 with the same data as the holotype (Figs. 23a, 25f) and 1♀ NVG-19037H09, USNMENT_01544939 Madre de Dios, Atalaya, 502 m, 18-May-2012, S. Kinyon leg. [USNM] (Fig. 22d).

Type locality. Peru: Cuzco.

Etymology. The word *erinnya* (or *erinyes*, plural *erinyes*; from the ancient Greek Ἐρινύς or Ἐρινύες) refers to the fierce chthonic deities of vengeance and retribution in Greek mythology, known in English as the Furies (or *Furiae* in Latin). This new species is closely related to *E. erinnya* and *E. furia*, and its name *dira* is an ancient Roman name for the Furies. All three words (*erinnya*, *furia*, and *dira*) have the same meaning: divine avengers associated with wrath, vengeance, punishment, madness, and relentless pursuit. It is unclear why these dark names were initially given to these appealing butterflies, but we are continuing the tradition, perhaps to reflect the taxonomic difficulties in this group of species. The name is a noun in apposition.

Distribution. Currently known from southeastern Peru.

Phenotypic variation in *Ectosemia eumene* group

Genomic analysis suggests that the *Ectosemia eumene* group consists of eight species (Figs. 19, 25). We sequenced over a dozen specimens for some of these species, which allows us to analyze intraspecific phenotypic variation. Many species reveal variation in size and tint of the metallic scales: from blue to green. For instance, the topotypical specimens of *Ectosemia attavus* (J. Zikán, 1952) (type locality Brazil: Amazonas, São Gabriel da Cachoeira municipality, Rio Negro) are smaller and cerulean blue, becoming larger and greener towards aquamarine and cyan in Ecuador (Figs. 24, 25s–x).

To aid identification of the eight species, all are illustrated here showing variation, including both sexes where known (Fig. 25). *Ectosemia erinnya* (Stichel, 1910) (type locality Peru: Pasco, Pozuzo) and *Ectosemia lavanda* **sp. n.** (type locality Brazil: Amazonas, São Paulo de Olivença) are currently known only from the female lectotype (Fig. 25e) and the male holotype (Fig. 25y), respectively. Males in the group have blue-green scaling in the posterior half of the dorsal wing surface, extending to the wing base, but the bases of all wings are brown in females. Identification and phenotypic diagnoses for some of these



Fig. 23. *Ectosemia dira* **sp. n.** and *E. furia* **stat. nov.** males in dorsal (left) and ventral (right) views, data in text or below: **a)** *E. dira* **sp. n.** paratype NVG-23077F04 Peru: Cuzco [MFNB] and **b–d)** *E. furia* **stat. nov.**: **b)** lectotype NVG-21126B11 Bolivia: La Paz, Farinas [SMF]; **c)** non-type NVG-23077H12 Peru: Huánuco, Monte Alegre, Río Pachitea, old, G. Tessmann leg. [MFNB]; and **d)** non-type NVG-18121H06 Peru: Loreto, Río Sucusari, ExplorNapo Lodge and ACEER, 140 m, GPS –3.2333, –72.9167, 16-Sep-1995, D. Harvey leg. [USNM].

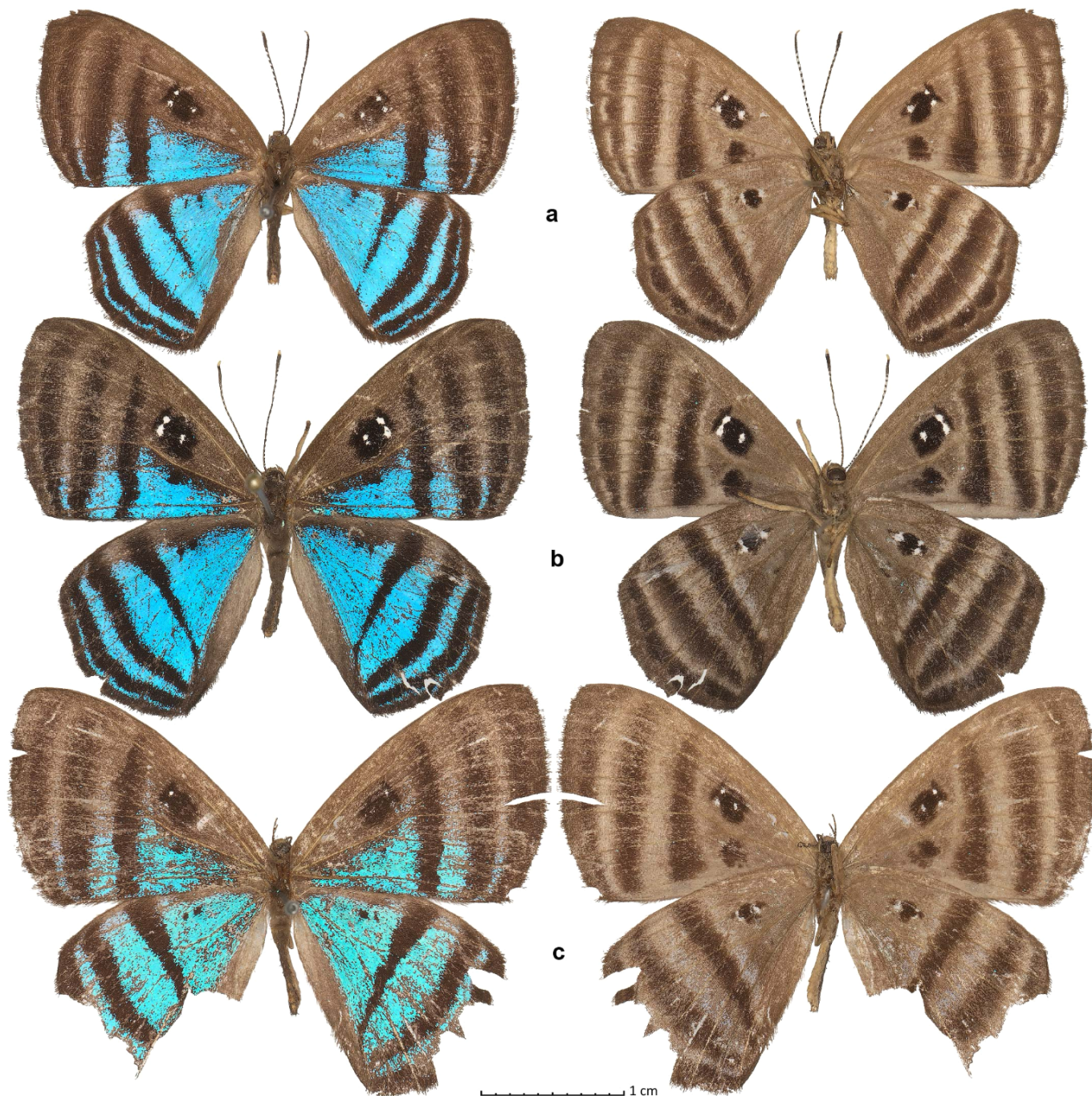


Fig. 24. Variation in *Ectosemia attavus* males shown in dorsal (left) and ventral (right) views: **a)** possible syntype NVG-23102G10 Brazil: Amazonas, San Gabriel, 1-Aug-1927, J. F. Zikán leg. [SMF]; **b)** NVG-23065H09 Ecuador: Napo, Tena, 650 m, Jun-2011, M. Simon leg. [MGCL]; and **c)** *E. attavus cyanea* **ssp. n.** paratype NVG-23102G11 Ecuador, old, Feyer leg. [SMF].

species are given above. The characters used to identify males of these species are the following: the extent of the metallic coloration in the basal half of the forewing; development of the submarginal and postdiscal pale bands on the forewing and the extent of blue/green scales in them; the extent of the metallic color in the basal half of the hindwing and the extent of brown color in the discal cell; and the tint of the metallic color (blue or green), although all these characters are subject to variation, especially the tint of the metallic coloration. For instance, the majority of *Ectosemia eumene* (Cramer, 1776) (type locality in Suriname) males are sky-blue (Fig. 25m, n), but some may be nearly as green (Fig. 25o) as typical *Ectosemia attalus* (Seitz, 1913), **stat. nov.** (type locality French Guiana: Nouveau Chantier) (Fig. 25h). Males of the latter species can be blue (Fig. 25i, j) instead of the typical green.

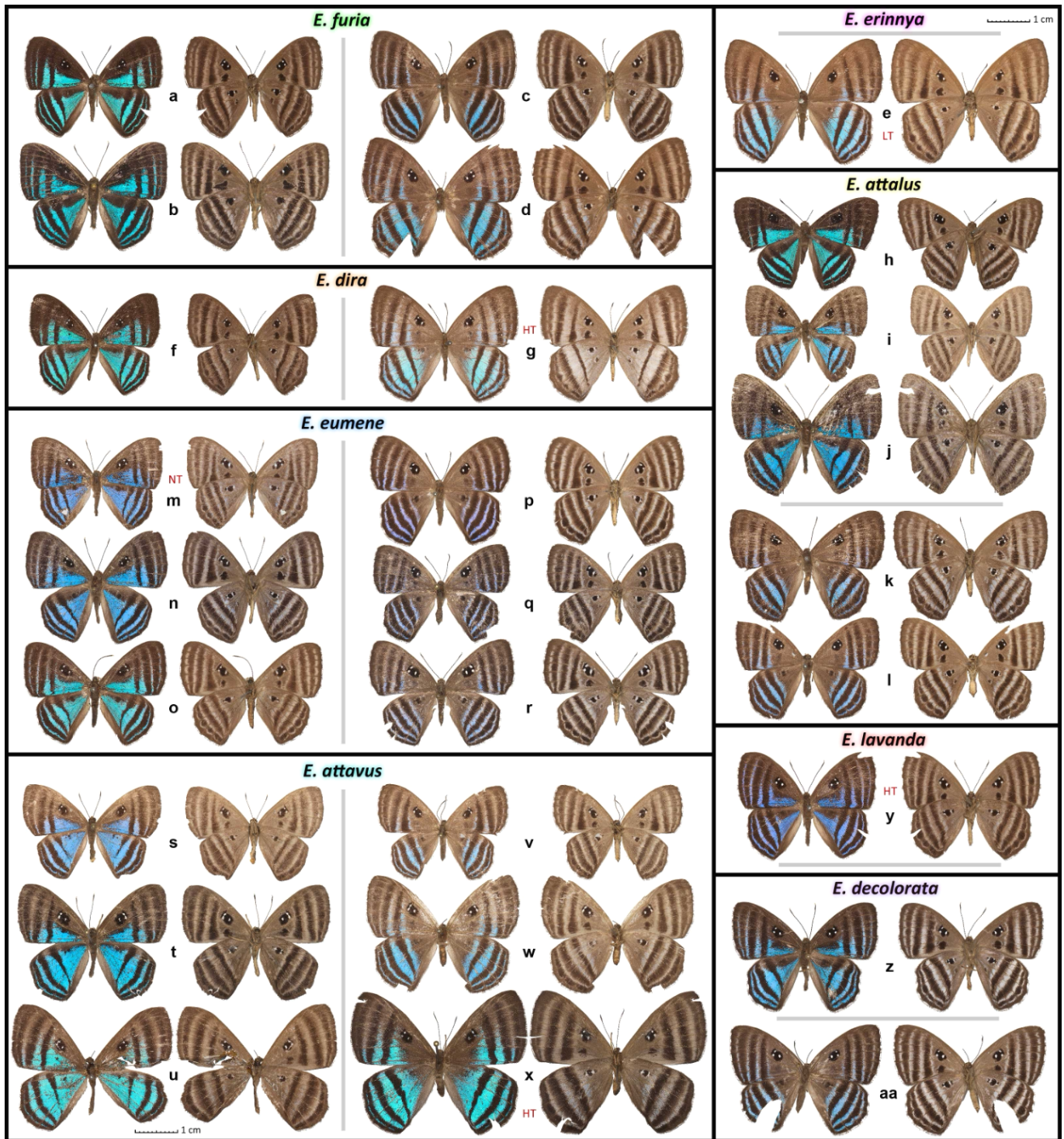


Fig. 25. All valid species of the *Ectosemia eumene* group in dorsal (left of the panel letter) and ventral (right) views, species are in black boxes, names highlighted in colors from Fig. 19, sexes separated by gray lines (males left or above the line, females right or below), detailed data in text: **a–d)** *E. furia* **stat. nov.**, **e)** *E. erinnya* lectotype ♀ NVG-21126B12 Peru: Pasco, **f–g)** *E. dira* **sp. n.** Peru: Cuzco, **h–l)** *E. attalus* **stat. nov.**, **m–r)** *E. eumene*, **s–x)** *E. attavus*, **y)** *E. lavanda* **sp. n.** holotype ♂ NVG-23077F09 Brazil: Amazonas, and **z–aa)** *E. decolorata* Peru: Madre de Dios; **a)** ♂ NVG-23077H12 Peru: Huánuco, **b)** ♂ NVG-18121H06 Peru: Loreto, **c)** ♀ NVG-23066A02 Peru: Loreto, **d)** paralectotype ♀ NVG-21126C01 Ecuador: Napo, **f)** paratype ♂ NVG-23077F04, **g)** holotype ♀ NVG-23077F05, **h)** ♂ NVG-23077H02 French Guiana, **i)** ♂ NVG-23077F03 French Guiana, **j)** ♂ NVG-19037H07 Guyana, **k)** ♀ NVG-23077H08 French Guiana, **l)** ♀ NVG-23077H06 Suriname, **m)** neotype ♂ NVG-23102G08 Suriname, **n)** ♂ NVG-23065H07 Brazil: Rondônia, **o)** ♂ NVG-23102G12 Brazil: Pará, **p)** ♀ NVG-23077G12 Brazil: Amazonas, **q)** ♀ NVG-23066A01 Suriname, **r)** ♀ NVG-23066A04 Brazil: Rondônia, **s)** possible syntype ♂ NVG-23102G05 Brazil: Amazonas, **t)** ♂ NVG-23065H09 Ecuador: Napo, **u)** ♂ NVG-23077F08 Ecuador: Morona-Santiago, **v)** possible syntype ♀ NVG-23103B03 Brazil: Amazonas, **w)** ♀ NVG-23066A05 Ecuador: Pastaza, **x)** *E. attavus cyanea* **ssp. n.** holotype ♀ NVG-23065H02 Ecuador: Tungurahua, **z)** ♂ NVG-23065H08, and **aa)** ♀ NVG-23066A06.

Females may be more difficult to identify, and their useful characters include the extent of blue between and basad of the brown bands; the width of the brown bands; the relative darkness of the forewing submarginal band compared to the other bands; the tint of the metallic scales; and the whiteness of pale scales between and basad of the brown bands on the ventral side of the wings.

Ectosemia attavus cyanea Grishin, new subspecies

<https://zoobank.org/F42C0624-E3F1-4038-B6E4-F1C4E18BD7D5>

(Figs. 24c, 25x, 26 part, 27a)

Definition and diagnosis. A female from the *Ectosemia eumene* group collected at an elevation of 2400 m in the eastern Andes of central Ecuador was remarkably different from known taxa in the group, both in size and the extensive cyan coloration on the dorsal wing surfaces (Figs. 25x, 27a). Despite its unique phenotype, genome-level phylogeny places it among specimens identified as *Ectosemia attavus* (J. Zikán, 1952) (type locality Brazil: Amazonas, São Gabriel da Cachoeira municipality, Rio Negro) and in a clade sister to its topotypes, which are also likely syntypes (Fig. 26). Due to the strong genetic similarity between this female and *E. attavus*, the insufficient number of sequenced specimens from various localities in Ecuador, and weakly supported clades insufficient to justify alternatives, we place it in *E. attavus*. A male from an unspecified locality in Ecuador collected about a century ago by E. Feyer (Fig. 24c) is strongly associated with this female in the nuclear genome tree (bootstrap support of 99%) (Fig. 26a red) and possesses the same mitochondrial haplotype (Fig. 26b red). Phenotypically, the male looks similar to the female, being larger in size and having greener metallic scales than the sky-blue color of topotypical *E. attavus*. These considerations are sufficient to recognize this pair as a distinct taxon, at least at the subspecies level. This new subspecies is similar to the nominotypical subspecies in that it has narrower brown bands on the dorsal hindwing (especially the discal band in males) and limited metallic coloration near the torus of the dorsal forewing that typically does not extend beyond vein CuA₂; but differs from it by larger size, cyan [rather than characteristic sky-blue in the nominotypical subspecies (Figs. 24a, 25s, v, 27b, c)] coloration of the metallic areas, a weakly developed submarginal pale-brown band on the ventral wing surfaces [which is more prominent and separated into elongated, slightly curved spots on the forewing in the nominotypical subspecies], and more extensive cyan scaling in the basal half of the dorsal side of the wings in females (only the hindwing base is brown). This subspecies can be identified by DNA, with diagnostic base pairs in the nuclear genome: cne2128.11.6:C60A, cne2128.11.6:G69T, cne585.3.5:T45A, cne2417.2.9:A81C, cne2417.2.9:G82A; although it remains unclear whether other specimens from Ecuador are best associated with this new subspecies. If they are, these DNA characters may be too restrictive because they apply to topotypical populations of the new subspecies. The COI barcode does not distinguish this subspecies from others.

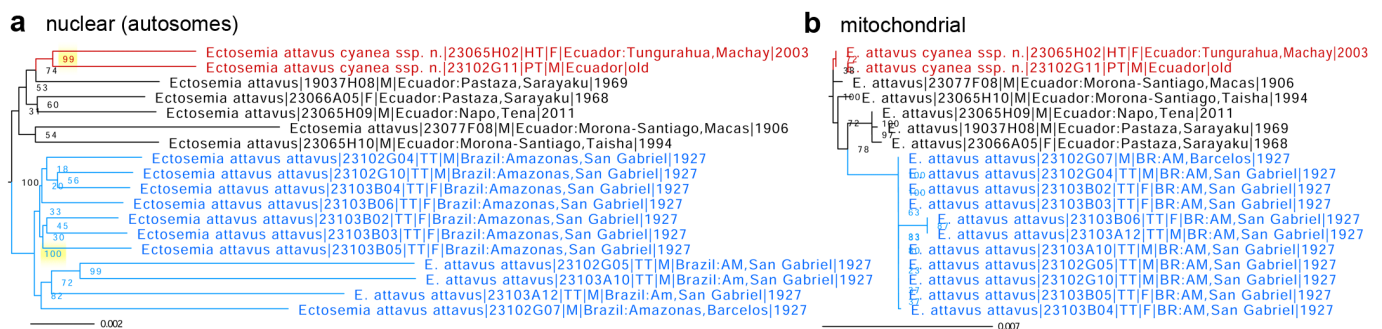


Fig. 26. Phylogenetic trees of *Ectosemia attavus* specimens constructed from protein-coding regions in: **a)** the nuclear genome (autosomes), based on 353,895 positions, and **b)** the mitochondrial genome: *E. attavus cyanea* ssp. n. type series (red), *E. attavus attavus* (blue), and various populations in Ecuador (black). Sequenced topotypes (TT) of *E. attavus* in SMF are likely part of the type series, with NVG-23103B03 (Figs. 25v, 27b) dated “14-XI-27”, matching a syntype in the Zikán collection bearing labels “lectotypo” (unpublished) and “holotypus”. M is male and F is female. Ultrafast bootstrap (Hoang et al. 2018) values are shown at nodes, with the high values supporting the clades of the two subspecies highlighted in yellow in (a).

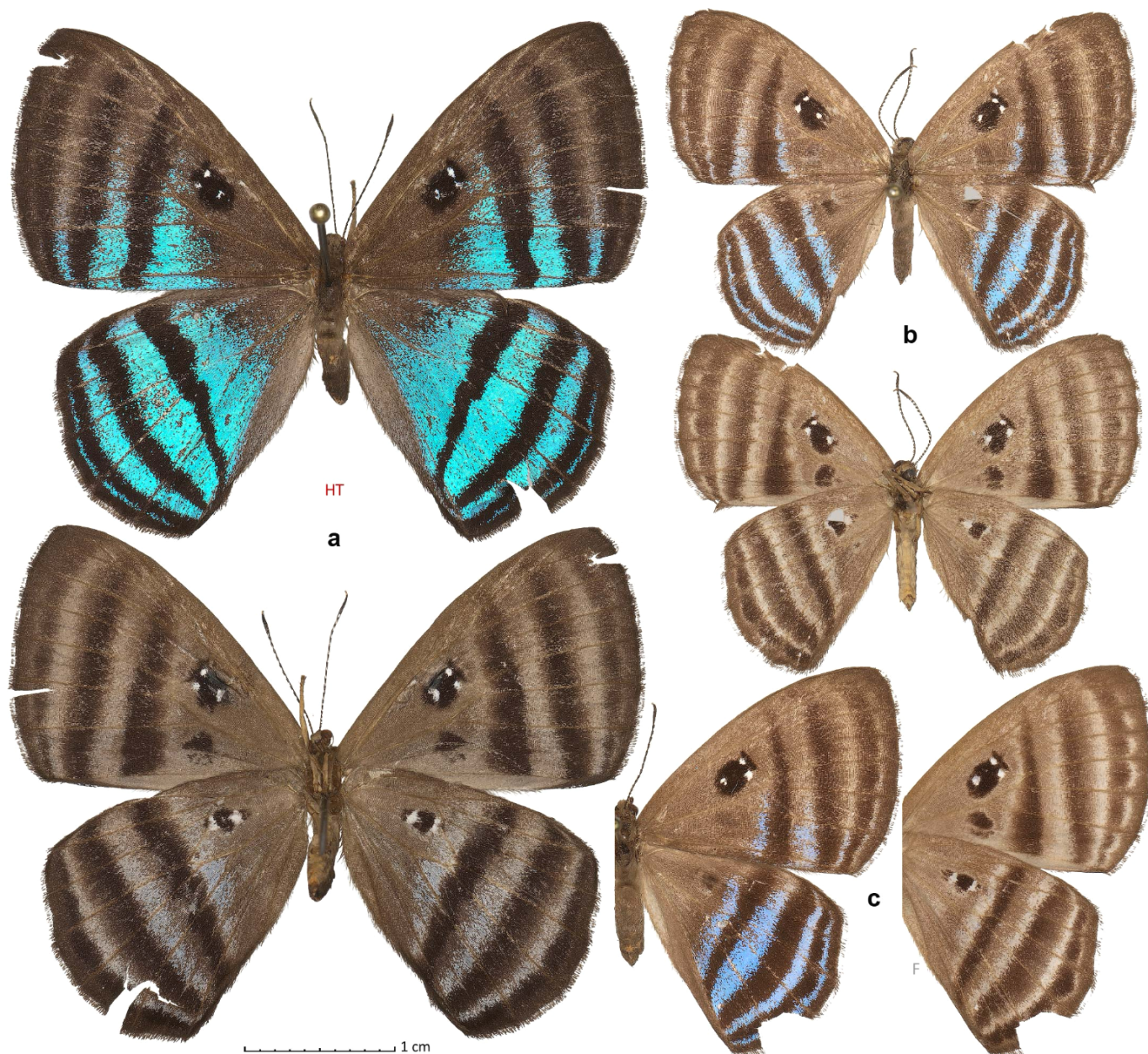


Fig. 27. Females of *Ectosemia attavus* subspecies in dorsal (above or left of the panel letter) and ventral (below or right) views: **a)** *E. attavus cyanea* ssp. n. holotype NVG-23065H02 Ecuador: Tungurahua, Machay, 2400 m, Feb-2003, M. Simon leg. [MGCL] and **b-c)** *E. attavus attavus* possible syntypes from Brazil: Amazonas, San Gabriel, J. F. Zikán leg. [SMF]: **b)** NVG-23103B03, 14-Nov-1927 and **c)** NVG-23103B05, 25-Aug-1927, F indicates flipped image (i.e. left-right inverted).

Barcode sequence of the holotype. Sample NVG-23065H02, GenBank [PZ516391](https://www.ncbi.nlm.nih.gov/nuotide/PZ516391), 658 base pairs:

TACATTATATTTTATTTTGGAACTCTGAAGAGGTATAGTTGGATCTTCTCTTAGTTACTTATCCGAATAGAATTAGGAACACCTGGCTCATTAAATTGGAGATGACCAAATTTATAATACT
ATTGTTACTGCTCATGCTTTTATTATAATTTTATGTTATACCAATTATAATTTGGTGGATTGGTAATTGACTTGTTCCTTTAATATTAGGAGCTCCTGATATAGCTTTCCCTCGAA
TAAATAACATAAGATTTGACTTTTACCCCTCTTTATTTCTTTTAAATTTCAAGAAGAATTGTTGAAATGGAGCAGGTACAGGATGAACAGTTTACCCCTTTTATCTTCTAATATTGC
TCATAGAGGTTTCATCAGTAGATCTTGTATTTTCTCTCCATTAGCGGGTATTTCTTCTATTTTAGGTGCTATTAAATTTTATTACTACTATTATTAATATACGAATTAATAGTATATCA
TTTGATCAAAATACCTCTATTGTATGATCTGTTGGTATTACAGCTTTACTATTACTTTTATCTTTACCGGTTTACGAGGAGCTATTACCATATTATTAAGTACCGTAACCTAAATACTT
CTTTTTTGTATCCTGCTGGAGGAGGTGATCCTATTCTTTATCAACATTTATTT

Type material. Holotype: ♀ deposited in the McGuire Center for Lepidoptera and Biodiversity collection, Gainesville, FL, USA (MGCL), illustrated in Figs. 25x, 27a, bears the following four rectangular labels (1st handprinted, other printed), three white: [ECUADOR | MACHAY | 2400 M | II-03], [Allyn Museum | Acc. 2003-9], [DNA sample ID: | NVG-23065H02 | c/o Nick V. Grishin], and one red [HOLOTYPE ♀ | *Ectosemia attavus* | *cyanea* Grishin]. Judging from the handwriting on the first label, the holotype was collected by M. Simon. **Paratype:** 1♂ NVG-23102G11 Ecuador (no detailed locality, likely eastern Andes), old, E. Feyer leg. (Fig. 24c).

Type locality. Ecuador: Tungurahua Province, Machay, elevation 2400 m.

Etymology. The name reflects the cyan color of the metallic scales characteristic of this subspecies compared to the brilliant-blue of the nominotypical subspecies. The name is an adjective.

Distribution. Currently known from the eastern Andes in central Ecuador.

Remarks. The holotype of this new subspecies is so different phenotypically from other taxa that its genomic identification as *E. attavus* was unexpected (compare Fig. 27a with b or c). Moreover, among the specimens we sequenced, the new subspecies was not strongly different genetically from the nominotypical subspecies (Figs. 19, 26). At this level of genomic similarity, a larger sample of specimens from various localities in Ecuador and Brazil (except the type locality that was sufficiently sampled) needs genomic sequencing to better understand the taxonomy of these populations. Regardless of these problems to be addressed, this Andean taxon is unconditionally described as a new subspecies here.

Lectotype designation for *Mesosemia albipuncta* Schaus, 1913

Mesosemia albipuncta Schaus, 1913 was described from an unspecified number of specimens from “Guapiles, Esperanza” in Costa Rica (Schaus 1913). We found a syntype in USNM with the word “type” written in the bottom left corner of its identification label in Schaus’s handwriting. Schaus labeled specimens he considered “types” (one per sex) with the handwritten word “type” but did not write this word on the identification labels of other specimens in his series. Therefore, even if there were other syntypes, this specimen was considered a name-bearing specimen by Schaus. To define the taxonomic identity of the name *M. albipuncta* objectively, N.V.G. hereby designates the syntype in the USNM collection, a male bearing the following four rectangular labels (3rd handwritten, others printed with handwritten text shown in italics; 4th red, others white): [Guapiles | CR], [Nov], [*Mesosemia albipuncta* | type Schs], and [Type | No. 16793 | U.S.N.M.], as the **lectotype** of *Mesosemia albipuncta* Schaus, 1913. The lectotype has a tear extending from above the tornus to near the middle of the left forewing, scales rubbed off from the costal area near its middle on both forewings (more extensive on the left), and a head that is tilted to the right. Images of this specimen, photographed by G. Lamas, are shown on the Butterflies of America website (Warren et al. 2024). The type locality of *M. albipuncta* remains Costa Rica: Limón, Guápiles, La Esperanza. The COI barcode sequence of the lectotype, sample NVG-22033F07, GenBank [PZ516392](https://www.ncbi.nlm.nih.gov/nuclot/PZ516392), 658 base pairs, is:

```
TACACTATATTTATTTTGGAAATTTGAGCTGGTATAGCTGGAACCTCATTAAAGTTTATTAATTCGTATAGAATTAGGAATACCAGGATCTTTAATGGGAATGACCAAAATTTATAATACT
ATTGTTACTGCTCATGCTTTTATTATAATTTTTCATGGTTATACCTATTATAATTGGAGGATTGGAAATTGACTTGTCCTCAATATTAGGAGCTCCTGATATAGCTTTCCCCCGTA
TAAATAATATAAGATTTGACTTTTACCCCTTCATTATTCCTACTTATTCTAGAGAATTGTTGAAAATGGAGCCGGAACCTGGATGAACGTTTATCCCCCTTTATCCTCCAATATCGC
CCACGGTGGATCTTCTGTGGATTAGCAATTTCTCTTTACATTAGCTGGTATTCTCTATTATTAGGAGCAATTAATTTTATTACTACTATTATTAATATACGAGTTAATAATATAAAG
TTTGATCAATACCATTATTTGTTTGATCAGTTGGTATTACAGCTTTATTATTATTGTTGTCATTACCAGTATTAGCCGGTGCATTACTATATTAATCACAGATCGTAATCTTAATACCT
CTTTTTTCGATCCTGCAGGAGGAGGAGATCCTATTCTTTATCAACATTTATT
```

Mesosemia tinypuncta Grishin, new species

<https://zoobank.org/8EED3480-8BEC-4A9C-AFCE-C1006FE6F6E5>

(Figs. 28, 29a–c part)

Definition and diagnosis. Genomic analysis reveals that a male from western Panama (Fig. 28) is sister to *Mesosemia albipuncta* Schaus, 1913 (type locality Costa Rica: Limón, Guápiles; lectotype sequenced as NVG-22033F07), but is genetically differentiated from it at the species level (Fig. 29); e.g., their COI barcodes differ by 1.8% (12 bp), and therefore this specimen represents a new species. This new species is similar to *M. albipuncta* and another relative, *Mesosemia mehida* Hewitson, 1869 (type locality in Ecuador) in lacking the black spot in the middle of the dorsal forewing (the black spot is present on the ventral side), but retaining the white spot (which forms the pupil of the black spot in other species) surrounded by blue ground color, and having blackish wing margins on the dorsal side; but differs from these species and other relatives by the following combination of characters in males: a narrower than in *M. albipuncta* dark-brown margin on the dorsal hindwing, which has an additional dark-brown submarginal band; this band is incomplete and fades towards the inner margin [absent in *M. albipuncta*;

about the same width throughout and as the marginal band in *M. mehida*]; a broad marginal dark brown area occupying more than a third of the dorsal forewing, as in *M. albipuncta* [narrower in *M. mehida*]; this area contains patches of blue scales or blue spots near the apex [absent in *M. albipuncta* and forming a narrow blue band from the costa to nearly the inner margin in *M. mehida*]; and a greenish tint to the blue coloration, rather than the purer blue seen in other species. Due to unexplored individual variation, this species is best identified by DNA, with diagnostic base pairs in the nuclear genome: cne2651.14.8:A117G, cne50.6.5:C54T, cne4191.5.14:T324C, cne369.4.3:A114T, cne16135.1.9:T90A, cne17082.9.9:T12T (not A), cne21273.1.10:A60A (not T), cne1775.24.10:A48A (not C), cne1370.11.2:A30A (not G), cne3598.6.12:T360T (not C); and the COI barcode: T39T, A286G, A373G, A382G, A583C.

Barcode sequence of the holotype. Sample NVG-23115G04, GenBank [PZ516393](#), 658 base pairs:

TACACTATATTTTATTTTGGAAATTTGAGCTGGTATAGTTGGAACCTTCATTAAGTTTATTAATTCGTATAGAATTAGGAATACCAGGGTCTTTAATTGGAATGACCAATTTATAATACT
ATTGTTACTGCTCATGCTTTTATTATAATTTTTCATAGTTATACCTATTATAATTTGGAGGATTTGGAAATTTGACTTGTACCATAATATTAGGAGCTCTGATATAGCTTTCCCGGTA
TAAATAATATAAGATTTTGACTTTTACCCCTTCATTATTCCTGCTTATTCTAGAGAATTGTTGAAATGGAGCCGGAACCTGGATGAATGTTTATCCCTTTTATCTTCCAATATCGC
CCACGGTGGGTCTTCTGTGGATTAGCAATTTCTCTTTACATTTAGCTGGTATTCTTCTATTATTTAGGAGCAATTAATTTTATTACTACTATTATTAATATACGAGTTAATAATATAAG
TTTGATCAAAATACCATTATTGTTGTATCAGTTGGAATTACAGCTTTATTATTATTGTTATCATTACCAGTATTAGCTGGTGTCTATTACTATATTACTACAGATCGTAATCTTAATACCT
CTTTTTCGATCCTGCAGGAGGAGATCTATTCTTTATCAACATTATTT

Type material. Holotype: ♂ deposited in the National Museum of Natural History, Smithsonian Institution, Washington, DC, USA (USNM), illustrated in Fig. 28, bears the following four rectangular

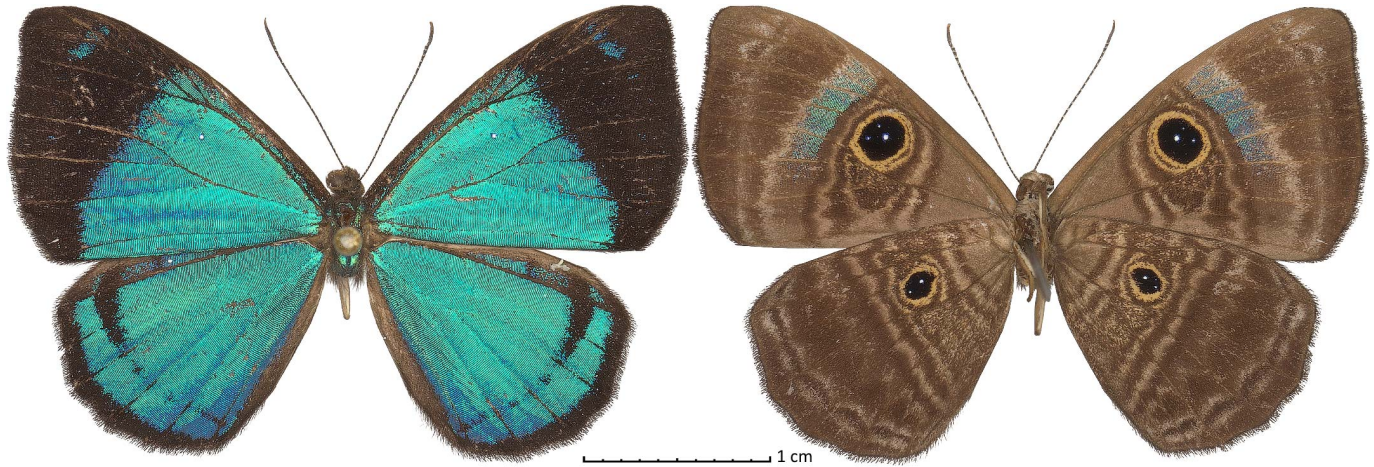


Fig. 28. *Mesosemia tinypuncta* sp. n. holotype ♂ NVG-23115G04 in dorsal (left) and ventral (right) views, data in text.

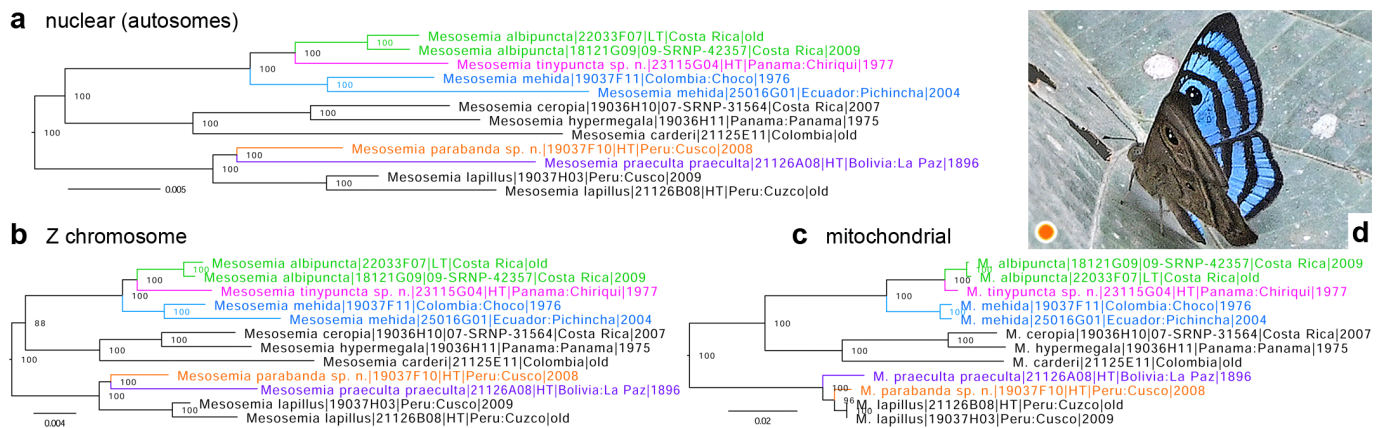


Fig. 29. Phylogenetic trees of selected *Mesosemia* Hübner, [1819] species constructed from protein-coding regions in: **a)** the nuclear genome (autosomes), based on 5,809,239 positions, **b)** the Z chromosome, based on 250,974 positions, and **c)** the mitochondrial genome; and **d)** *M. parabanda* sp. n. iNaturalist observation No. 187009157 Peru: Cuzco Region, Paucartambo Province, vic. Manu Lodge, GPS -13.0710, -71.5626, 6-Sep-2023 © Christoph Moning, brightened and cropped, CC BY 4.0 <https://creativecommons.org/licenses/by/4.0/>. Species mentioned in the text are colored: *M. albipuncta* (green), *M. tinypuncta* sp. n. (magenta), *M. mehida* (blue), *M. parabanda* sp. n. (orange), *M. praeculta* (violet). Ultrafast bootstrap (Hoang et al. 2018) values are shown at nodes.

labels (2nd handprinted, others printed with handwritten text shown in *italics*), three white: [PANAMA: CHIRIQUI | *Fortuna Dam Site* | *ca. 1000 m.* | *6 Jan. 1977* | G. B. Small], [1994-04], [DNA sample ID: | NVG-23115G04 | c/o Nick V. Grishin], and one red [HOLOTYPE ♂ | *Mesosemia tinypuncta* Grishin]. The second label is the genitalia dissection number. According to its label, the holotype was collected at the future site of Fortuna Dam (Presa Fortuna) just before its construction began.

Type locality. Panama: Chiriquí Province, Reserva Forestal de Fortuna, Presa Fortuna, ca. 1000 m.

Etymology. The name reflects the tiny white spot (*tiny* + *puncta*) in the dorsal forewing discal cell of this close relative of *M. albipuncta* named for a similar white spot, which is typically larger. The name is treated as a noun in apposition.

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

Mesosemia parabanda Grishin, new species

<https://zoobank.org/4BB2EB6D-4308-4E77-B277-C45FDD41F188>

(Figs. 29a–c part, 29d, 30a)

Definition and diagnosis. Genomic analysis reveals that a specimen from the northeastern slopes of the Andes in southern Peru initially identified as *Mesosemia praeculta* Stichel, 1910 (type locality Bolivia: La Paz, San Antonio; holotype sequenced as NVG-21126A08) is genetically differentiated from it at the species level (Fig. 29a–c); e.g., their COI barcodes differ by 2.1% (14 bp), and therefore this specimen represents a new species. This new species is most similar to *M. praeculta*, but differs from it and other relatives by the following combination of characters in males: a narrower dark-brown marginal band on the dorsal forewing and correspondingly broader blue submarginal band, with the two bands being of

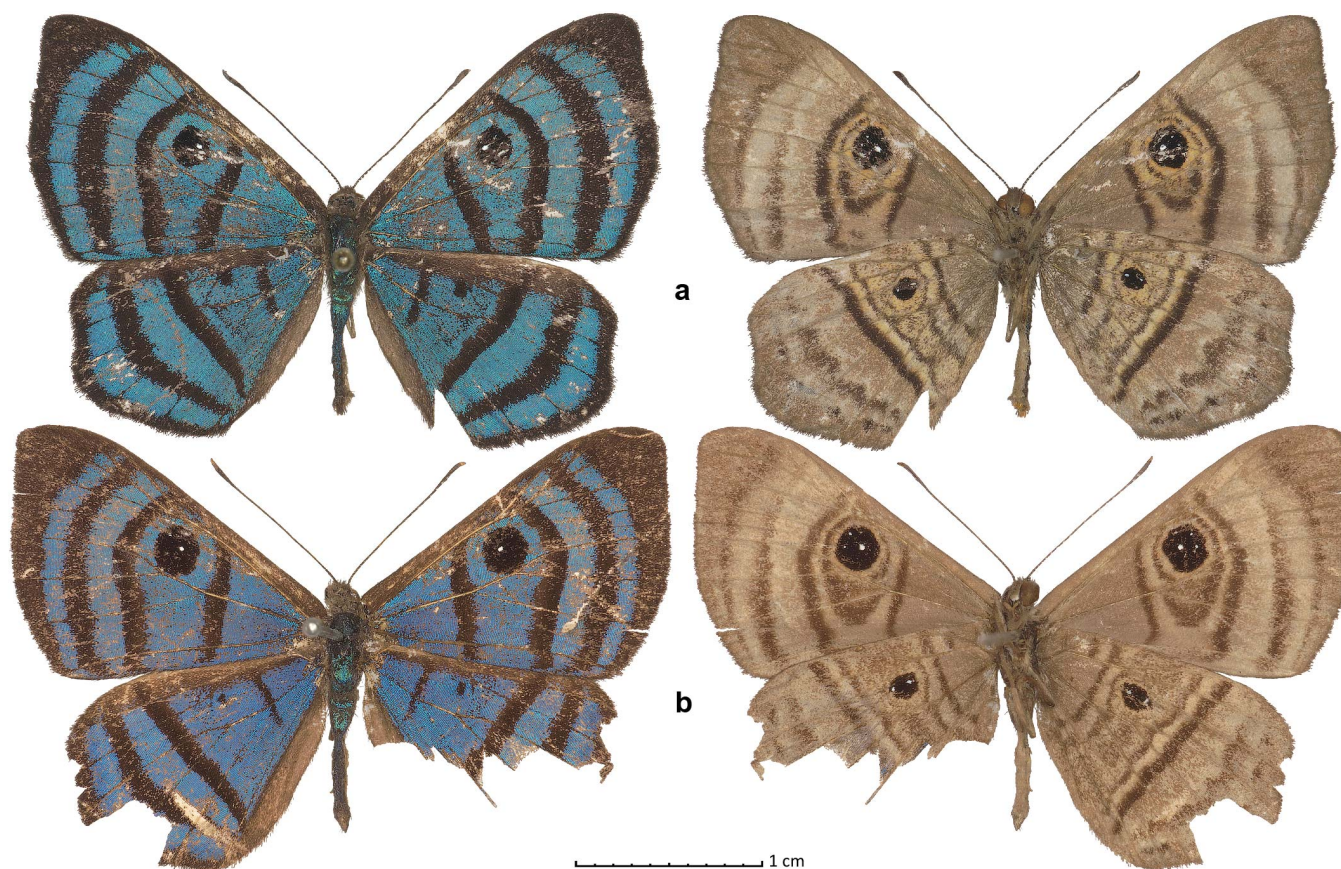


Fig. 30. *Mesosemia* holotypes ♂♂ in dorsal (left) and ventral (right) views, data in text or below:
a) *M. parabanda* sp. n. NVG-19037F10 from Peru: Cuzco [USNM] and **b)** *M. praeculta* NVG-21126A08 from Bolivia: La Paz, Yungas, San Antonio, 1800 m, 1895–1896, Garlepp leg. [MFNB].

approximately the same width or the blue band being broader (except near the apex) [broader marginal brown band and narrower blue submarginal band, the brown band is broader than the blue band in *M. praeculta* (Fig. 30b)]; no purple tint in the blue bands on the dorsal side, with the blue shifted towards cyan and teal [darker and purplish or indigo blue in *M. praeculta*]; and a relatively smaller distance between the postbasal and discal dark-brown bands on both wings, i.e., the central blue area is relatively narrower, especially towards the inner margin of the forewing [larger distance and broader area in *M. praeculta*]. Due to its cryptic nature and unexplored individual variation, this species is best identified by DNA, with diagnostic base pairs in the nuclear genome: cne1954.4.2:A27G, cne1954.4.2:A97T, cne48.1.2:A117G, cne1681.1.8:A183T, cne1681.1.8:T187C, cne961.2.4:G157G (not A), cne7435.1.1:C66C (not T), cne7435.1.1:C105C (not T), cne2604.2.4:T75T (not A), cne6349.7.11:G315G (not A); and the COI barcode: A160G, A244G, T337C, T421C, T634C, T640C.

Barcode sequence of the holotype. Sample NVG-19037F10, GenBank [PZ516394](https://www.ncbi.nlm.nih.gov/nuclot/PZ516394), 658 base pairs:

```
TACATTATATTTTCATTTTGGAAATTTGAGCTGGTATAGTTGGAACCTCTTAAAGTTTATTAATTCGTATAGAATTAGGAATACCAGGATCTTTAATTGGAGATGACCAAAATTTATAACACT
ATTGTTACTGCTCATGCTTTTATTATAATTTTTCATGGTTATACCTATTATAATTTGGAGGATTTGGAAATTTGACTTGTTCTCTTAATGTTAGGAGCTCCAGATATAGCTTTCCCCCGTA
TGAACAATATAAGATTTTGACTTTTACCTCCTTCTTATTTTACTTATTCTAGTAGAATCGTTGAAAATGGAGCTGGAACCTGGATGAACCTGTCTACCCCCCACTATCTTCCAATATTGC
CCATGGAGGATCTTCAGTAGATTAGCAATCTTTCTTTACATTTAGCTGGTATTTCCTCCATTTTAGGAGCAATTAATTTTATTACTACTATTATTAATATACGAGTTAATAATATAAAA
TTTGATCAAAATACCTTTATTGTTGATCAGTTGGAATCACAGCTTTACTATTACTATTATCTTTACCAGTATTAGCTGGAGCTATTACTATACTATTAAACAGATCGAAATCTTAATCTT
CTTTTTTGGACCTGCAGGAGGAGGAGACCTATCCTTTATCAACATTTATTT
```

Type material. Holotype: ♂ deposited in the National Museum of Natural History, Smithsonian Institution, Washington, DC, USA (USNM), illustrated in Fig. 30a, bears the following six rectangular labels (2nd handwritten, others printed with handwritten text shown in *italics*), five white: [PERU: Cuzco.Cosñipata Valley | Quebrada Moro Leguía 2,135m | 13° 08'11"S, 71° 34'51"W | 8 Nov. 2008 Brian Harris], [Mesosemia | metuana | glaucoma ♂], [TERRITORIAL | BEHAVIOR | 1030 hrs], [DNA sample ID: | NVG-19037F10 | c/o Nick V. Grishin], [USNMMENT | {QR Code} | 01544918], and one red [HOLOTYPE ♂ | Mesosemia | parabanda Grishin].

Type locality. Peru: Cuzco Region, Cosñipata Valley, Quebrada Moro Leguía, elevation 2135 m, GPS -13.13639, -71.58083.

Etymology. The name *parabanda*, meaning parallel band or equal band, is formed by adding the Greek prefix *para-*, meaning beside, alongside, or parallel to the Spanish word *banda*, meaning a band, stripe, or fascia. Furthermore, in Latin, *par* means equal, identical, or even. The name reflects parallel dark-brown and blue bands in the new species that are of more equal width than in its sister species, *M. praeculta*. The name is treated as a noun in apposition.

Distribution. Currently known from the northeastern slopes of the Andes in southern Peru.

Napaea extraperlata Grishin, new species

<https://zoobank.org/C2189E08-8618-4AAE-A2D7-220A7F59519D>

(Figs. 31 part, 32a, 33a–b)

Definition and diagnosis. Genomic analysis reveals that two males from the eastern slopes of the Andes in Ecuador initially identified as *Napaea sylva* (Möschler, 1877) (type locality in Suriname: Berg en Dal; holotype sequenced as NVG-21124E04) are genetically differentiated from it at the species level (Fig. 31); e.g., their COI barcodes differ by 2.4% (16 bp), and therefore these specimens represent a new species. Genetic differentiation of the new species from *N. sylva* is approximately the same as that of *Napaea rufolimba* J. Hall, 2005 (type locality in Costa Rica) from *Napaea tumbesia* J. Hall & Lamas, 2001 (type locality in Peru: Tumbes), which we confirm as two distinct species (Fig. 31). This new species is similar to *N. sylva* and was previously included in it, sharing all the characters listed by Hall (2005), but differs from it by the following combination of characters: additional pearly spots along the forewing margin in a row from the costa to the tornus; e.g., there is an extra spot between the submarginal row and the white segments of the fringe in both cells M₃-CuA₁ and CuA₂-1A+2A (the latter one, by the tornus, is easier to notice) [in *N. sylva*, the pearly submarginal spots are mostly constrained to the apical area (Figs. 32b, 33c, d)]; better-developed submarginal pearly dashes along the dorsal hindwing; e.g., there is a dash between veins M₁ and M₃ [typically lacking in *N. sylva*]; more elongated [rather than rounded]

postdiscal pearly spots on the dorsal hindwing; and a less defined lobe in the middle of the hindwing outer margin. Due to poorly explored individual variation and possible sexual dimorphism in the expression of pearly spots, this species is most confidently identified by DNA, with diagnostic base pairs in the nuclear genome: cne16401.5.2:A633G, cne922.11.3:A54G, cne922.11.3:A91C, cne953.7.1:C144T, cne2091.4.2:A237G; and the COI barcode: T4C, A208T, A310G, A349G, A565G, A586T.

Barcode sequence of the holotype. Sample NVG-18122B09, GenBank [PZ516395](https://www.ncbi.nlm.nih.gov/nuccore/PZ516395), 658 base pairs:

AACCTTATATTTTATTTTGAATTTGAGCAGGAATAGTAGGTACTTCTTTAAGTATTTTAATTCGTATAGAATTAGGTATACCTGGATCTTTAATGGAGATGATCAAATTTATAATACT
ATTGTTACAGCTCATGCTTTTATATAATTTTATAGTTATACCAATTATAATTTGGTGGTTTGGTAATTGATTAGTCCCCCTTATACTTGGTGCTCCAGATATAGCTTTTCCACGTA
TAAATAATATAAGATTTTGACTTTTACCTCCTTCTCTATTCCCTTTTAATCTCAAGAAGAATTGTTGAGAATGGAGCTGGTACTGGATGAACGTTTATCCCCGTTGTCTTCTAATATTGC
TCATAGTGGTTCTTCTGTAGATCTAGCTATTTTCTTTACATTTAGCAGGTATCTCATCTATTTTAGGAGCTATTAATTTTATTACTACAATTATTAATATACGAATTAATAATTTATCT
TTTGATCAAATACCTTTATTTATTTGATCTGTAGGTATTACTGCTTTTATTACTTTTATCTCTTCTGTTTGTAGCTGGGGCTATTACTATATTATTAAGTATCTTAATCTTAACTACT
CATTTTGTACCTGCTGGAGGAGGTGATCTATTCTTTATCAACATTTATTT

Type material. Holotype: ♂ deposited in the National Museum of Natural History, Smithsonian Institution, Washington, DC, USA (USNM), illustrated in Fig. 32a, bears the following four printed rectangular labels, three white: [ECUADOR: Morona-Santiago | Hilltop North of Santiago | 03° 02.3' S, 78° 00.3' W | 30 January 2014, 350 m. | R. C. Busby, D. H. Ahrenholz leg.], [DNA sample ID: | NVG-

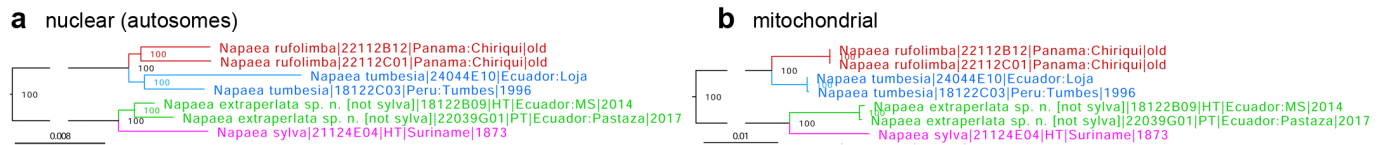


Fig. 31. Phylogenetic trees of selected *Napaea* Hübner, [1819] species constructed from protein-coding regions in: **a)** the nuclear genome (autosomes), based on 8,337,870 positions, and **b)** the mitochondrial genome. Different species are colored differently: *N. rufolimba* (red), *N. tumbesia* (blue), *N. extraperlata* sp. n. (green), and *N. sylvia* (magenta). Ultrafast bootstrap (Hoang et al. 2018) values are shown at nodes. Gaps in branches indicate where a vertical slice of the tree was removed to reduce its horizontal dimension (to allow an increase in the font size), i.e., branches with gaps are longer than shown.

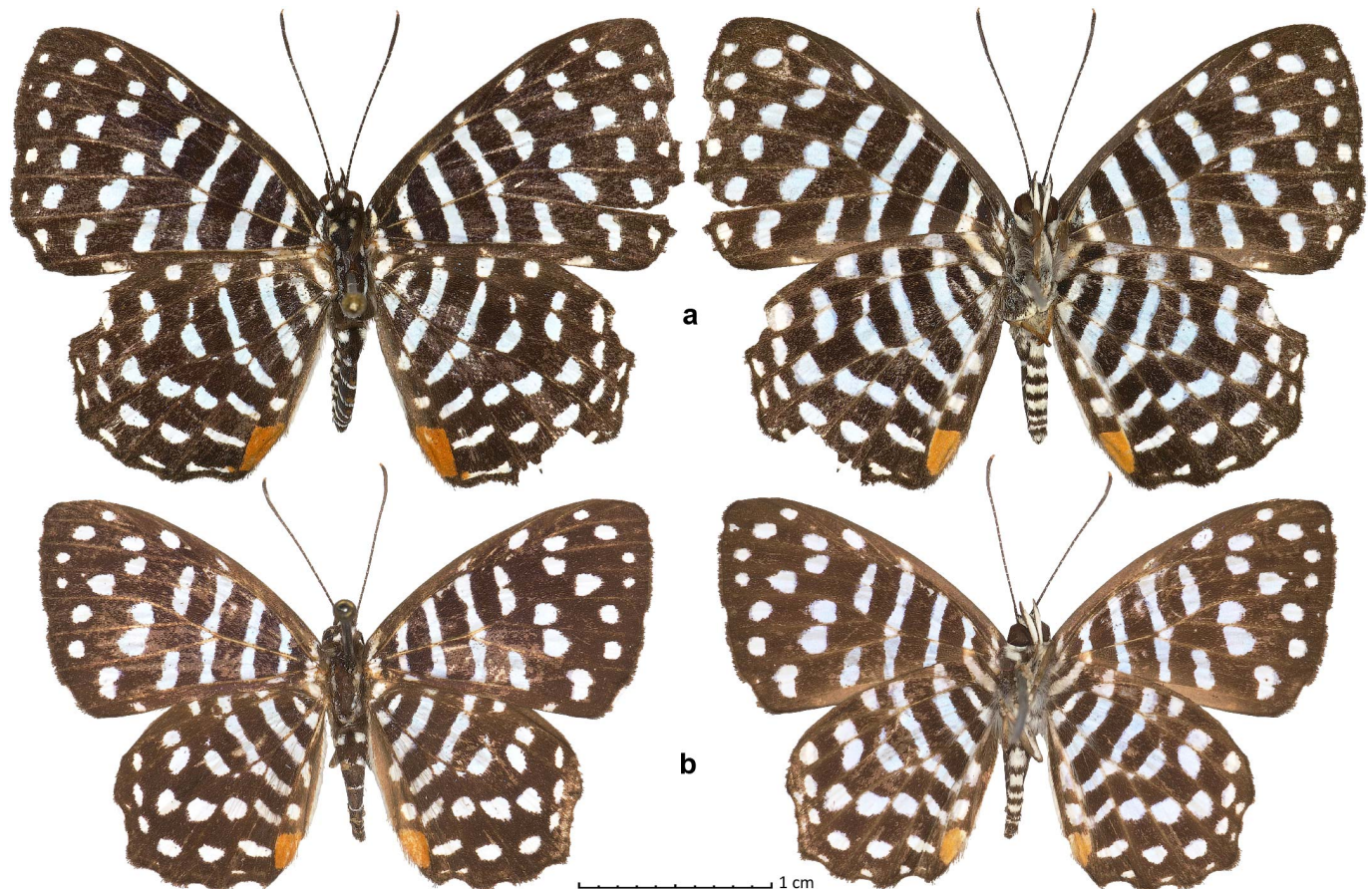


Fig. 32. *Napaea* holotypes in dorsal (left) and ventral (right) views, data in text or below: **a)** *N. extraperlata* sp. n. NVG-18122B09 Ecuador: Morona-Santiago [USNM] and **b)** *N. sylvia* NVG-21124E04 Suriname: Berg en Dal, 1873, [MFNB].

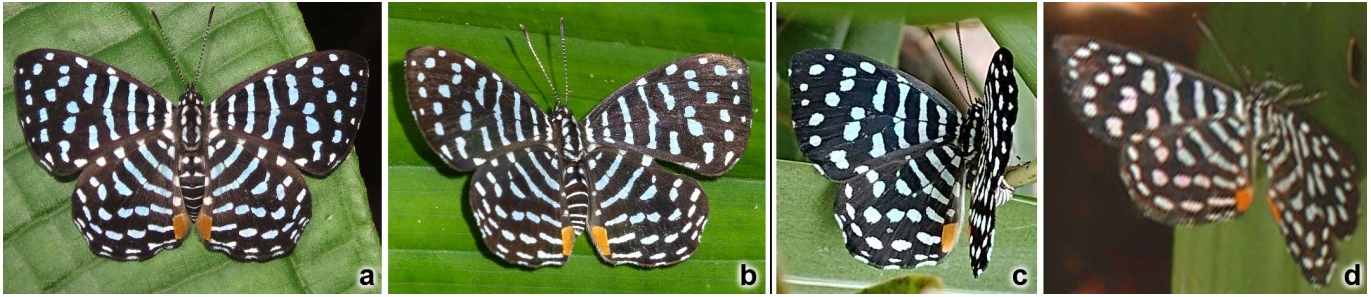


Fig. 33. iNaturalist observations of *Napaea*: **a–b)** *N. extraperlata* sp. n.: **a)** No. 235018793 Colombia: Putumayo, Mocoa, GPS 1.1269, –76.6305, 7-Aug-2024 © Lepidoptera Colombiana; **b)** No. 255224044 Ecuador, Napo, Tena, IKIAM Trail, GPS –0.9472, –77.8714, 23-Jul-2024 © Jackie Riley; and **c–d)** *N. sylva*: **c)** ovipositing, No. 135717774 Brazil, Amazonas, Manaus, Museu da Amazônia, GPS –3.0071, –59.9401, 19-Sep-2022 © Raymê Carvalho; **d)** No. 282353876 French Guiana, Saint-Laurent-du-Maroni, Maripasoula, GPS 2.5688, –54.1774, 3-May-2024 © Maël Dewynter; images are rotated, color-corrected, brightened, and cropped, CC BY-NC 4.0 <https://creativecommons.org/licenses/by-nc/4.0/>.

18122B09 | c/o Nick V. Grishin], [USNMNT | {QR Code} | 01532027], and one red [HOLOTYPE ♂ | *Napaea extraperlata* | Grishin]. **Paratype:** 1♂ NVG-22039G01 from Ecuador, Pastaza, Villa Villano vic. Puyo, 800 m [CHGC].

Type locality. Ecuador: Morona-Santiago Province, hilltop north of Santiago, elevation 350 m, GPS –3.0383, –78.005.

Etymology. The prefix *extra-* comes from the Latin, meaning outside, beyond, or exceeding the norm, and *perlatus* means pearly or pearly. The name *extraperlata* reflects the larger number of pearly spots in this species compared to *N. sylva*. The name is a feminine perfect passive participle in the nominative singular used as an adjective.

Distribution. Currently confirmed from the Amazonian slope transition zone of the Ecuadorian Andes and possibly found in southern Colombia (Fig. 33a).

Remarks. The holotype of *Napaea sylva* was listed as a male by Hall (2005), and it is similar in appearance to females (Fig. 33c). We have not seen females of the new species, and do not know the extent of sexual dimorphism in the expression of the pearly spots, so we advise caution in species identification. The most reliable characters currently are in DNA.

***Ithomiola (Ithomiola) cuscola* Grishin, new species**
<https://zoobank.org/7CA58538-AA9D-4C0D-AD55-BF353D6A7251>
 (Figs. 34 part, 35c)

Definition and diagnosis. Genomic analysis reveals that a female from Cuzco, Peru, listed as *Ithomiola (Ithomiola) orpheus* (Westwood, 1851) (type locality in Brazil: Amazonian region) by Hall (2005) and initially identified by us as *Ithomiola (Ithomiola) perutanos* Grishin, 2024 (type locality Peru: Cuzco, Cosñipata Valley, Quebrada Santa Isabel; holotype sequenced as NVG-19038C05) is not in the same clade as the former species and is also genetically differentiated from the latter at the species level (Fig. 34); e.g., their COI barcodes differ by 2.7% (18 bp), the same difference as that with *Ithomiola (Ithomiola) bajotanos* J. Hall, 2005 (type locality in Ecuador: Tungurahua), and therefore this specimen represents a new species. The female of this new species (male unknown) is most similar to *I. perutanos* (Fig. 35b) in that the discal dark-brown spots in cells M₁–M₂ and M₂–M₃ on the ventral hindwing are close to each other and are nearly touching [more separated in *I. bajotanos* (Fig. 35a)], but differs from other relatives by the following combination of characters in females: smaller size than *I. tanos*; broader than in *I. perutanos* dark-brown marginal area from the apex to the middle of the hindwing, similar to that in *I. bajotanos*; less extensive pattern of brown dots in the basal half of the ventral hindwing, especially in the posterior half; and postdiscal white spots in the forewing cells M₁–M₂ and M₂–M₃ that are closer to each other. Due to its cryptic nature, unexplored individual variation, and unknown males, this species is best

identified by DNA, with diagnostic base pairs in the nuclear genome: cne1620.4.7:G63T, cne7204.3.2:C84G, cne85.8.6:C135T, cne1093.15.10:A33G; and the COI barcode: G38A, T40C, T100C, T355A, T530C, T578C.

Barcode sequence of the holotype. Sample NVG-23078A07, GenBank [PZ516396](#), 658 base pairs:

```
AACTTTATATTTTATTTTGAATTTGAGCAGGAATAATCGGAACATCTTTAAGATTATTAATTCGTATAGAATTAGGTACACCAGGATCTTTAATTTGGCGATGATCAAATTTATAACT
ATCGTTACAGCTCATGCTTTTATTATAATTTCTTTATAGTTATGCTATTATAATTGGAGGTTTGGAAATGACTTGTCCCTTAATATTAGGAGCTCCAGATATAGCTTTCCCTCGTA
TAAATAATATAAGATTTTGACTCCTTCCCTTCTTTCTTTATTTCAAGAAGAATTGTTGAAATGGAGCAGGTACGGATGAACCTGTATATCTCTTATCTTCAAAATATTGC
TCATAGAGGATCTTCTGTTGATTAGCAATTTTCTTTACATTTAGCAGGTATTTTCATCAATTTAGGAGCTATTAACTTTATTACTACTATTATTAATATACGTATTAATAATTATCA
TTTGATCAAATACCTTTATTTGTATGATCAGTTGGTATTACAGCACTATTATTACTTTTATCTCTTCTGTATTAGCAGGAGCTATTACTATATACTATTACAGATCGAAATTTAAATACTT
CATTTTTTGATCCTGCTGGAGGAGGAGATCCTATTCTTTATCAACACTTATTT
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Type material. Holotype: ♀ deposited in the Museum für Naturkunde, Berlin, Germany (MFNB), illustrated in Fig. 35c, bears the following six printed rectangular labels, five white: [Vilcanota 3000 M. | Perú (Pr. Cuzco) | 1898. O. Garlepp], [Callan. | Perú | Garl.], [Coll. | Staudinger], [ex coll. | H. STICHEL], [DNA sample ID: | NVG-23078A07 | c/o Nick V. Grishin], and one red [HOLOTYPE ♀ | Ithomiola (Ithomiola) | cuscola Grishin]. The specimen bears two locality labels, either as a result of a mistake, or because the specimen came from a mixed lot from two localities, or because the second locality is a more precise area within a broader first locality. The two localities (upper Río Vilcanota and Callanga) are about 30–120 km apart, and 3000 m may be too high an elevation for this species.

Type locality. Peru: Cuzco Region, Vilcanota River valley (elevation ca. 3000 m) to Callanga (elevation ca. 1500 m).

Etymology. The name is derived from the type locality Cuzco (officially preferred spelling Cusco) to rhyme with the genus name *Ithomiola* and is treated as a noun in apposition.

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

Remarks. As a result of this study, there are currently three species in the *I. tanos* clade confirmed from Cuzco, Peru. Although we have not sequenced a female of *I. tanos*, this species is larger (compare males of *I. tanos* and *I. perutanos* in Fig. 36b–d), and females of the two smaller species, *I. perutanos* (all three confirmed specimens shown in Figs. 35b, 36c–d) and *I. cuscola* **sp. n.** (only a female known, Fig. 35c), differ as described above.

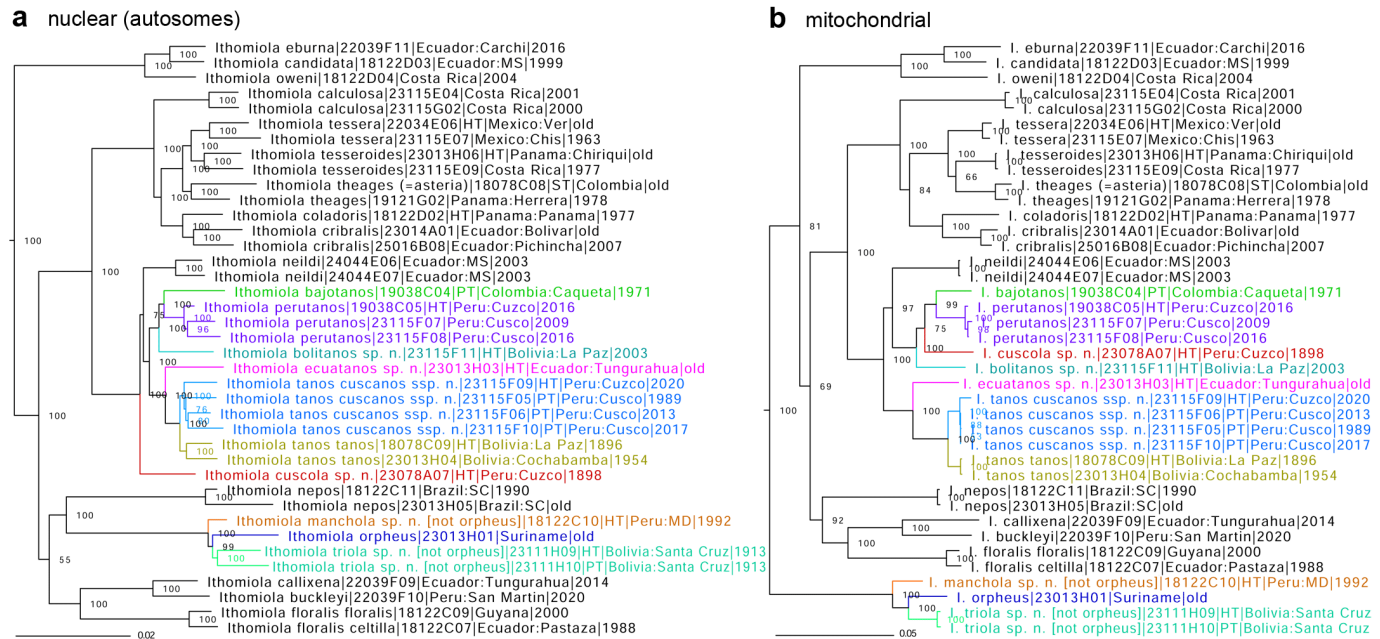


Fig. 34. Phylogenetic trees of all described *Ithomiola* C. Felder & R. Felder, 1865 species constructed from protein-coding regions in: **a**) the nuclear genome (autosomes), based on 1,002,927 positions, and **b**) the mitochondrial genome. The taxa discussed in the text are colored differently: *I. bajotanos* (green), *I. perutanos* (violet), *I. bolitanos* **sp. n.** (cyan), *I. ecuatano* **sp. n.** (magenta), *I. tanos cuscanos* **ssp. n.** (blue), *I. tanos tanos* (olive), *I. cuscola* **sp. n.** (red), *I. manchola* **sp. n.** (orange), *I. orpheus* (dark blue), and *I. triola* **sp. n.** (aquamarine). Ultrafast bootstrap (Hoang et al. 2018) values are shown at nodes.



Fig. 35. *Ithomiola* (*Ithomiola*) females in dorsal (left) and ventral (right) views: **a)** *I. bajotanos* paratype NVG-19038C04 Colombia: Caqueta, Sucre, 4000 ft, 23-Jan-1971, S. S. Nicolay [USNM]; **b)** *I. perutanos* non-type NVG-23115F07 Peru: Cuzco, Cosñipata Valley, Quebrada Quitacalzón, 1050 m, 12-Aug-2009, B. Harris leg. [USNM]; **c)** *I. cuscola* **sp. n.** holotype NVG-23078A07 Peru: Cuzco, Río Vilcanota or Callanga, 1898 or old, Garlepp leg. [MFNB]; and **d)** *I. bolitanos* **sp. n.** holotype NVG-23115F11 Bolivia: La Paz, 40 km N of Caranavi, Cumbre Alto Beni, 1500–1700 m, 12, 13, 15-Apr-2003, B. Harris leg. [USNM].

***Ithomiola* (*Ithomiola*) *bolitanos* Grishin, new species**

<https://zoobank.org/9A4094C9-83FB-4BB3-8332-94EC52DBFA93>

(Figs. 34 part, 35d)

Definition and diagnosis. Genomic analysis reveals that a female from western Bolivia is closely related to *Ithomiola* (*Ithomiola*) *perutanos* Grishin, 2024 (type locality Peru: Cuzco, Cosñipata Valley, Quebrada Santa Isabel; holotype sequenced as NVG-19038C05) and *Ithomiola* (*Ithomiola*) *bajotanos* J. Hall, 2005

(type locality in Ecuador: Tungurahua) in the nuclear genome tree, but is genetically differentiated from it at the species level (Fig. 34); e.g., its COI barcode differ by 3.0% (20 bp) from *I. perutanos*, 2.1% (14 bp) from *I. bajotanos*, and by 2.4% (16 bp) from the *I. cuscola* **sp. n.** (described right above). Another Bolivian species, *Ithomiola (Ithomiola) tanos* (Stichel, 1910) (type locality Bolivia: La Paz, Río Suapi), is more distantly related being in a different clade (Fig. 34). Therefore, the unique female represents a new species, which differs from its relatives by the following combination of characters in females: slightly smaller than *I. tanos*, but the holotype is larger than the close relatives mentioned above; the discal dark-brown spots in cells M₁-M₂ and M₂-M₃ on the ventral hindwing are farther from each other, as in *I. bajotanos*, but the spot in M₁-M₂ is narrower, dash-like [nearly touching in *I. perutanos* and *I. cuscola* **sp. n.**], postdiscal white spots in the forewing cells M₁-M₂ and M₂-M₃ are farther from each other and the spot in M₂-M₃ is close to the submarginal white spot; and the white patch approaches vein M₁ in the postdiscal area of the dorsal hindwing, being more extensive in cell M₁-M₂ [brown scaling more developed in the anterior part of cell M₁-M₂ in other species, or the marginal brown area is narrower in *I. perutanos*]. Due to its cryptic nature, unexplored individual variation, and unknown males, this species is best identified by DNA, with diagnostic base pairs in the nuclear genome: cne5683.4.1:A909T, cne2564.26.2:T96G, cne12935.2.4:T1071C, cne12935.2.4:A1086G, cne22301.1.2:C2106T, cne2722.5.5:C18C (not T), cne2722.5.5:A52A (not T), cne2722.5.5:C63C (not G), cne1992.2.1:A798A (not G), cne946.3.8:C330C (not T); and the COI barcode: G38A, T40T, T259C, T355A, A474G, T643C.

Barcode sequence of the holotype. Sample NVG-23115F11, GenBank [PZ516397](https://www.ncbi.nlm.nih.gov/GenBank/ accession=JF9516397), 658 base pairs:

```
AACTTTATATTTTATTTTGGGAATTTGAGCAGGAATAATTGGAACATCTTTAAGATTATTAATTCGTATAGAATTAGGAACACCAGGATCTTTAATTTGGTGATGATCAAATTTATAATACT
ATTGTTACAGCTCATGCTTTTATATAATTTTATAGTTATACCTATTATAATTTGGAGGTTTGGAAATTGACTTGTTCCTTTAATATTAGGAGCTCCAGATATAGCTTTCCCTCGTA
TAAATAATATAAGATTCTGACTTCTCCCTTCATTATTTCTTATTTCAGAGAATAATTGTTGAAATGGAGCAGGTACTGGATGAAGTGTATATCTCTCTTATCTTCAAATATTGC
TCATAGAGGATCTTCTGTTGATTAGCAATTTCTCTTTACATTTAGCAGGTATTTTCATCAATTTTAGGAGCTATTAATTTTATTACTACTATTATTAATATACGTATTAGTAATTTATCA
TTTGATCAAATACCTTTATTTGTATGATCAGTTGGTATTACAGCATTATTATTACTTTTATCTCTCTCTGATTAGCAGGAGCTATTACTATATTATTAACAGATCGAAATTTAAATCTT
CATTTTGTATCTGCTGGAGGAGGAGATCTTCTCTATCAACATTTATTT
```

Type material. **Holotype:** ♀ deposited in the National Museum of Natural History, Smithsonian Institution, Washington, DC, USA (USNM), illustrated in Fig. 35d, bears the following four printed rectangular labels (text in italics handwritten), three white: [BOLIVIA: La Paz Province | 40 km N Caranavi, Cumbre | Alto Beni 1500-1700 m. | 15°40.522'S, 67°29.348'W | road to radio tower | 12, 13, 15 April 2003 | Brian Harris, coll.], [*Napaea* | *nepos* ♀ | det. Brian Harris], [DNA sample ID: | NVG-23115F11 | c/o Nick V. Grishin], and one red [HOLOTYPE ♀ | *Ithomiola (Ithomiola)* | bolitanos Grishin].

Type locality. Bolivia: La Paz Province, 40 km north of Caranavi, Cumbre Alto Beni, elevation 1500–1700 m, GPS –15.67537, –67.48913.

Etymology. Similarly to how the names *bajotanos* and *perutanos* were formed (*bajo-* for lower and *peru-* for Peru + *tanos*), *bolitanos* means *tanos* from Bolivia. Although *I. tanos* itself is a Bolivian species, the new name *bolitanos* continues the practice of using locality prefixes in the names of related taxa. The name is treated as a noun in apposition.

Distribution. Currently known only from the holotype collected on the northeastern slopes of the Andes in western Bolivia.

Remarks. The type locality of the new species is close to the type locality of *I. tanos* with the distance between them being about 60 km, and the two species could be sympatric.

Ithomiola (Ithomiola) ecuatanos Grishin, new species

<https://zoobank.org/E1496BA1-E5A1-4507-BC16-C706297ECA0D>

(Figs. 34 part, 36a)

Definition and diagnosis. Genomic analysis reveals that a male from Santa Inés, Tungurahua, Ecuador, identified as *Ithomiola (Ithomiola) bajotanos* J. Hall, 2005 (type locality in Ecuador: Tungurahua) by Hall (2005) (while not being its paratype), is not closely related to *I. bajotanos*, belongs to a different clade, and instead is sister to *Ithomiola (Ithomiola) tanos* (Stichel, 1910) (type locality in Bolivia: La Paz, Río Suapi; holotype sequenced as NVG-18078C09), but is genetically differentiated from it at the species level (Fig. 34); e.g., their COI barcodes differ by 2.3% (15 bp), and therefore this specimen represents a

new species. This new species is most similar to *I. tanos* (Figs. 36b, 38), being larger in overall size than *Ithomiola (Ithomiola) perutanos* Grishin, 2024 (type locality Peru: Cuzco, Cosñipata Valley, Quebrada Santa Isabel; holotype sequenced as NVG-19038C05) (Fig. 36c, d) and *I. bajotanos*, but differs from it



Fig. 36. *Ithomiola (Ithomiola)* males in dorsal (left) and ventral (right) views: **a)** *I. ecuatanos* **sp. n.** holotype NVG-23013H03 Ecuador: Tungurahua, Santa Inés, old, R. Haensch leg. [ZSMC]; **b)** *I. tanos* holotype NVG-18078C09 Bolivia: La Paz, Río Suapi, 1000 m, 1895–1896, Garlepp leg. [MFNB]; and **c–d)** *I. perutanos*: Peru: Cuzco, Cosñipata Valley, Quebrada Santa Isabel, 1194 m, 27-Mar-2016, S. Kinyon leg. [USNM]: **c)** holotype NVG-19038C05 and **d)** non-type NVG-23115F08.



Fig. 37. Male genitalia of *Ithomiola ecuatanos* sp. n. holotype NVG-23013H03 in left lateral (left) and ventral (right) views.

and other relatives by the following combination of characters in males: slightly weaker pattern of violaceous streaks on the dorsal side of the wings (basal third to a half), and the streaks are grayer, less saturated in color; the postdiscal brown spot in the ventral hindwing cell M_2 - M_3 is offset distad from the small white spot in cell M_1 - M_2 [basad of this spot in other species] and the white area distad of the spot is correspondingly smaller; the dark-brown marginal area on the hindwing is narrower and more distinctly divided into spots; and the white spots are larger in the postdiscal triplet near the costa of the forewing. In male genitalia (Fig. 37), similar to *I. bajotanos* in having a longer aedeagus and irregularly sized cornuti, but the posterior margin between the lower spike of the valva and the upper lobe is evenly concave, as in *I. tanos*, without a hump in the middle that is present in *I. bajotanos*; and the spike is slightly upturned: less curved than in *I. tanos* but not as straight as in *I. bajotanos*. Due to its cryptic nature and unexplored individual variation, this species is best identified by DNA, with diagnostic base pairs in the nuclear genome: cne10764.3.1:G3726A, cne1387.2.3:C615T, cne1387.2.3:A648C, cne760.2.5:G738T, cne760.2.5:G762A, cne3383.2.1:C653C (not G), cne5326.4.3:C90C (not T), cne5326.4.3:G112G (not T), cne9535.2.1:G333G (not A), cne9535.2.1:G345G (not A); and the COI barcode: T25C, T292C, T346A, T451C, G506A, T536C, T595T.

Barcode sequence of the holotype. Sample NVG-23013H03, GenBank [PZ516398](https://www.ncbi.nlm.nih.gov/nuclot/PZ516398), 658 base pairs:

```
AACTTTATATTTATTTTGGAACTGAGCAGGAATAGTTGGAACATCTTTAAGATTATTAATTCGTATAGAATTAGGTACACCTGGATCTTTAATTGGTGATGATCAAATTTATAATACT
ATTGTTACAGCTCATGCTTTTATTATAATTTTATAGTTATACCTATTATAATTTGGAGGTTTGGAAATTGACTTGTTCTTTAATATTAGGAGCTCCAGATATAGCTTTTCCTCGTA
TAAATAATATAAGATTTGACTTCTTCCCCCTTCATTATTCTTCTTATCTCAAGAAGAATTGTTGAAATGGAGCAGGTACTGGATGAACAGTATACCCCCATTATCTTCTAATATTGC
TCATAGAGGATCTTCTGTTGACTTAGCAATTTCTCTTTACATTTAGCAGGAATTTTCATCAATTTTAGGAGCTATTAATTTTATTACCACTATTATTAATATACGTATTATAATTTATCA
TTTGATCAAATACCTTTATTATTGATCAGTTGGTATTACAGCATTTACTACTTTTATCTTACCTGTATTAGCAGGAGCTATTACTATATTATTAACAGATCGAAATTTAAATACTT
CATTTTTCGATCCTGCTGGAGGAGGAGATCCTATTCTTTATCAACACTTTATTT
```

Type material. Holotype: ♂ deposited in the Zoologische Staatssammlung München, Germany (ZSMC), illustrated in Fig. 36a (genitalia Fig. 37), bears the following five printed rectangular labels, four white: [Santa Jnéz | (Ecuad.) | R.Haensch S], [DNA sample ID: | NVG-23013H03 | c/o Nick V. Grishin], [DNA sample ID: | NVG-23087C10 | c/o Nick V. Grishin], [genitalia: | NVG260613-05 | c/o Nick V. Grishin], and one red [HOLOTYPE ♂ | *Ithomiola* (*Ithomiola*) | *ecuatanos* Grishin]. The first DNA sample ID refers to the extraction from a leg (sequenced), and the second from the abdomen (stored) prior to genitalia dissection.

Type locality. Ecuador: Tungurahua Province, Santa Inés, elevation 1100–1300 m.

Etymology. Similarly to how the names *bajotanos* and *perutanos* were formed (*bajo*- for lower and *peru*- for Peru + *tanos*), *ecuatanos* means *tanos* from Ecuador. The name is treated as a noun in apposition.

Distribution. Currently known only from the holotype collected in the Andes of central Ecuador.



Fig. 38. *Ithomiola* (*Ithomiola*) *tanos* males in dorsal (left) and ventral (right) views, data in text or below: **a–b**) *I. tanos cuscans* **ssp. n.** Peru, Cuzco [USNM]: **a**) holotype NVG-23115F09 and **b**) paratype NVG-23115F06; and **c–d**) *I. tanos tanos* Bolivia: **c**) holotype NVG-18078C09 La Paz, Río Suapi, 1000 m, 1895–1896, Garlepp leg. [MFNB]; and **d**) non-type NVG-23013H04 Cochabamba, Yungas del Palmar, 1000 m, 5-Jul-1954, R. Zischka leg. [ZSMC].

***Ithomiola (Ithomiola) tanos cuscanos* Grishin, new subspecies**

<https://zoobank.org/EF52E238-BA54-46C7-BBFD-3FD67BD0DAE9>

(Figs. 34 part, 38a–b)

Definition and diagnosis. Genomic analysis reveals that specimens of *Ithomiola (Ithomiola) tanos* (Stichel, 1910) (type locality in Bolivia: La Paz, Río Suapi; holotype sequenced as NVG-18078C09), from Cuzco Region in Peru, are genetically differentiated from the specimens near the type locality at the subspecies level (Fig. 34); e.g., their COI barcodes differ by 0.5% (3 bp), and therefore these specimens represent a new subspecies. This new subspecies is similar to the nominotypical subspecies (Fig. 38c, d), but differs from it by the following combination of characters in males: the white area on the dorsal hindwing protrudes towards the outer margin into the dark-brown marginal border in the middle of cell M_3 -CuA₁, [whereas the marginal band is entire in cell M_3 -CuA₁ in the nominotypical subspecies]; on the ventral side, this section of the brown margin is narrower; and the ventral hindwing area between veins M_1 and M_2 distad of the discal cell and basad of the brown margin is white [with brown scales in the anterior part in the nominotypical subspecies]; slightly larger white spots on the forewing; and a more pure blue [rather than lavender] color of markings in the basal half of the dorsal forewing. Due to poorly explored individual variation and females not yet confirmed, this subspecies is best identified by DNA, with diagnostic base pairs in the nuclear genome: cne3195.11.14:G2388A, cne3195.11.14:G2447A, cne9.7.3:A18G, cne4803.2.1:T1284C, cne5916.2.7:A21G; and the COI barcode: T106C, T202T, T401T, T428T, T595C.

Barcode sequence of the holotype. Sample NVG-23115F09, GenBank [PZ516399](https://www.ncbi.nlm.nih.gov/nuclot/PZ516399), 658 base pairs:

```
AACTTTATATTTTATTTTGGAAATTTGAGCAGGAATAGTTGGAACATCATTAAAGATTATTAATTCGTATAGAATTAGGTACACCTGGATCTTTAATTGGTGATGACCAAATTTATAATACT  
ATTGTTACAGCTCATGCTTTTATTATAATTTTATAGTTATACCTATTATAATTGGAGGTTTGGAAATTGACTTGTTCTCTTAATATTAGGAGCTCCAGATATAGCCTTTCCCTCGTA  
TAAATAATATAAGATTTTGACTTCTTCCCTTCATTAACTTACTTATTCAAGAAGAATTGTTGAAATGGAGCAGGTACTGGATGAAGTATACCCCCATTATCTTCTAATATTGC  
CCATAGAGGATCTTCTGTTGACTTAGCAATTTCTCTTTACATTTAGCAGGTATTTTCATCAATTTAGGAGCTATTAATTTTATTACTACTATTATTAATATACGTATTAATAATTATCA  
TTTGATCAAAATACCTTTATTGTTGATCAGTTGGTATTACAGCATTATTACTACTTTTATCTACCTGTATTAGCAGGAGCTATTACTATATTATTAACAGATCGAAACTTAAATACTT  
CATTTTTGATCCTGCTGGAGGAGGAGATCTATTCTTTATCAACACTTATT
```

Type material. Holotype: ♂ deposited in the National Museum of Natural History, Smithsonian Institution, Washington, DC, USA (USNM), illustrated in Fig. 38a, bears the following four printed rectangular labels (text in italics handwritten), three white: [PERU:Cuzco 2135 m. | Quebrada Morro Legua | Cosñipata Valley 6685 | 27-I-2020 Kinyon], [*Ithomiola tanos*], [DNA sample ID: | NVG-23115F09 | c/o Nick V. Grishin], and one red [HOLOTYPE ♂ | *Ithomiola (Ithomiola) tanos cuscanos* Grishin]. **Paratypes:** 3♂♂ from Peru, Cuzco, Cosñipata Valley [USNM]: 1♂ NVG-23115F06 Rocotal, 1970 m, 11-Nov-2017, S. Kinyon leg.; 1♂ NVG-23115F10 Cosñipata Rd., below Rocotal, 1950 m, 28-Jan-2013, S. Kinyon leg. (Fig. 38b); and 1♂ NVG-23115F05 San Pedro, 1400 m, 1-Sep-1989, R. K. Robbins leg., genitalia vial #1999-57, D. J. Harvey.

Type locality. Peru: Cuzco Region, Cosñipata Valley, Quebrada Morro Legua, elevation 2135 m.

Etymology. The name is derived from the type locality to rhyme with the species epithet. The name is treated as a noun in apposition.

Distribution. Currently known only from southeastern Peru.

***Ithomiola (Ithomiola) manchola* Grishin, new species**

<https://zoobank.org/A5EC6F15-94E9-4821-8C67-2D52854C43EB>

(Figs. 34 part, 39b)

Definition and diagnosis. Genomic analysis reveals that a male from southeastern Peru initially identified as *Ithomiola (Ithomiola) orpheus* (Westwood, 1851) (type locality in Brazil: Amazonian region) is genetically differentiated from it at the species level (Fig. 34); e.g., their COI barcodes differ by 2.7% (18 bp), and therefore this specimen represents a new species. This new species is most similar to *I. orpheus*, but differs from it by the following combination of characters, at least in males: conspicuously larger, fused white spots in the postdiscal area of forewing cells M_3 -CuA₁ and CuA₁-CuA₂ [smaller, frequently separated spots in *I. orpheus* (Fig. 39a)]; three [not two] broad triangular projections of the

white area on the dorsal hindwing directed towards the costa, and their outline resembles a maple leaf; and less extensive brown scaling along the dorsal hindwing outer margin, e.g., fully separated dark, somewhat rectangular marginal spots are present along the veins in the holotype [instead of a solid brown band with pale marginal spots inside it in *I. orpheus* (Fig. 39a). Due to poorly explored individual variation, this species is best identified by DNA, with diagnostic base pairs in the nuclear genome: cne6941.8.1:A135C, cne6941.8.1:A138T, cne4045.1.2:T40C, cne4045.1.2:A75T, cne703.2.8:T2970C, cne19895.1.5:C42C (not T), cne19895.1.5:C48C (not T), cne15245.2.5:C222C (not T), cne5160.13.1:A81A (not G), cne2359.5.12:C85C (not T); and the COI barcode: T4A, A208A, A256T, A298C, 370C, T442C, T581C.

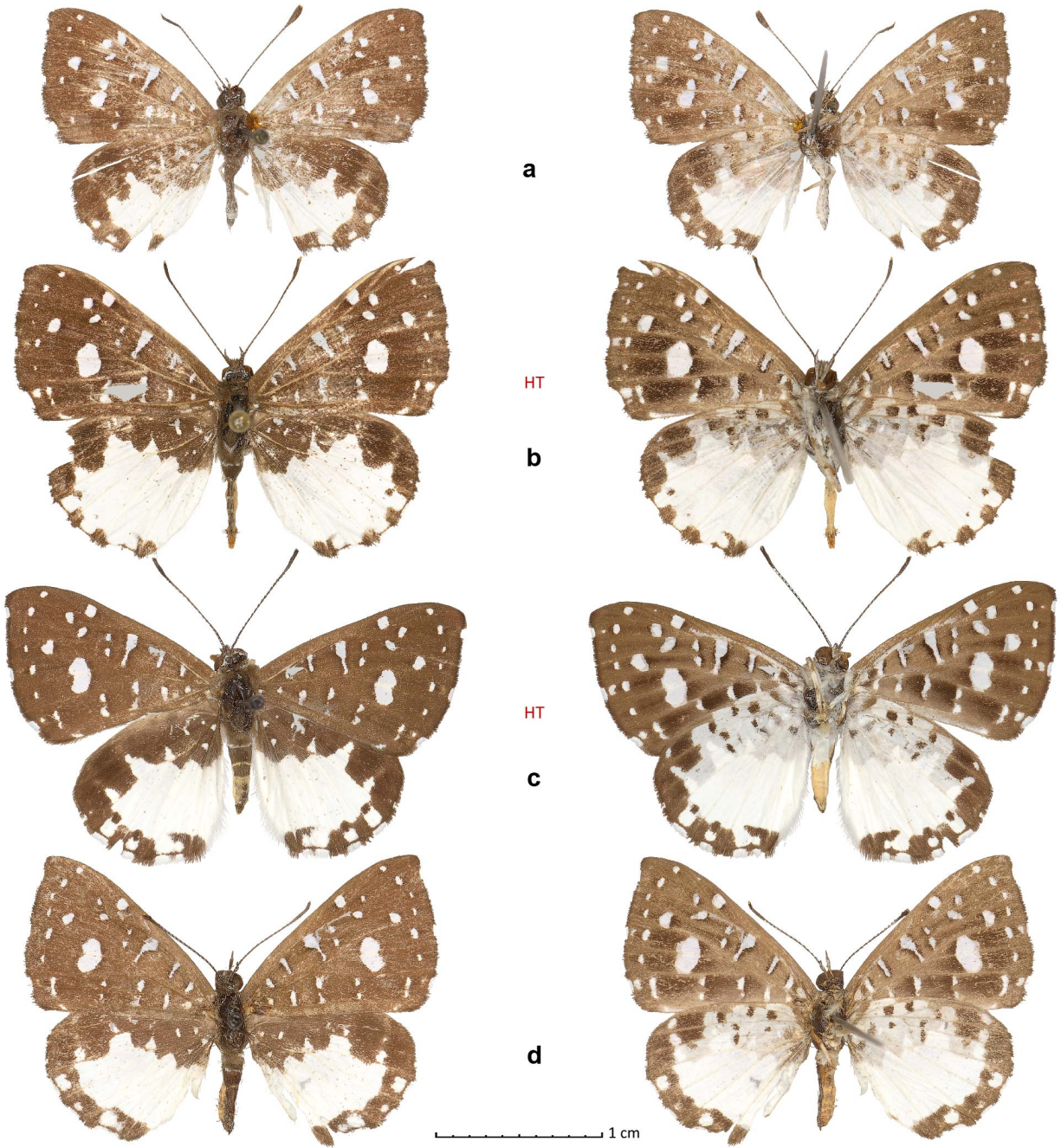


Fig. 39. *Ithomiola* (*Ithomiola*) *orpheus* and relatives, males in dorsal (left) and ventral (right) views: **a)** *I. orpheus* non-type NVG-23013H01 Suriname, old, Michaelis leg. [ZSMC]; **b)** *I. manchola* **sp. n.** holotype NVG-18122C10 Peru: Madre de Dios, 50 km WSW of Puerto Maldonado, Sep–Nov-1992, C. Tello leg. [USNM]; and **c–d)** *I. triola* **sp. n.** Bolivia, Santa Cruz, 1913, J. Steinbach leg. [CMNH]: **c)** holotype NVG-23111H09 Río Yapacaní, Aug and **d)** paratype NVG-23111H10 Las Juntas, Dec.

Barcode sequence of the holotype. Sample NVG-18122C10, GenBank [PZ516400](https://www.ncbi.nlm.nih.gov/nuclot/PZ516400), 658 base pairs:

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AACATTATATTTTATTTTGAATTTGAGCAGGAATAGTTGGTACATCTTTAAGATTATTAATTCGTATAGAACTTGGTACTCCCGGCTCTTTAATTGGAGACGATCAAATTTATAATACT
ATTGTAACAGCTCATGCTTTTATTATAATTTTTCATAGTAATACCTATTATAATTTGGAGGATTTGGAAATTGACTTGTTCCTTTAATATTAGGAGCTCCAGATATAGCTTTCCCTCGTA
TAAATAATATAAGTTTTGATTACTTCCCTTCATTATTTCTTCTTATTTCAAGCAGAATTGTTGAAATGGTGCAGGACTGGATGAAGTGTATACCTCCCTTTATCATCTAATATTGC
CCACGGCGGATCTTCTGTTGATTAGCAATTTTCTTACATTAGCTGGTATTTTCATCAATTTAGGAGCTATTAACTTTTACTACTATTATAATATACGAATTAATAATTATCA
TTTGATCAAATACCTTTATTGTTGATCAGTTGGAATTACAGCTTTATTATTACTTTTATCTCTTCTGTTTAGCAGGTGCTATTACTATATTACTAACAGATCGAAATTTAAACACTT
CATTTTTTGATCCTGCTGGTGGAGGTGATCCAATTTTATATCAACATTTATTT
```

Type material. Holotype: ♂ deposited in the National Museum of Natural History, Smithsonian Institution, Washington, DC, USA (USNM), illustrated in Fig. 39b, bears the following four printed rectangular labels, three white: [PERU: Madre de Dios | 50Km WSW Pto. Maldo- | nado 12°45'S 69°35'W | 250m Sep-Nov 1992 | leg. Carlos Tello E.], [DNA sample ID: | NVG-18122C10 | c/o Nick V. Grishin], [USNMNT | {QR Code} | 01532037], and one red [HOLOTYPE ♂ | *Ithomiola* (*Ithomiola*) | *manchola* Grishin].

Type locality. Peru: Madre de Dios Region, 50 km west-southwest of Puerto Maldonado, elevation 250 m, GPS -12.75, -69.583.

Etymology. In Spanish, *mancha* means spot, stain, or patch. The name is formed to rhyme with *Ithomiola* and refers to a prominent white spot in the middle of the dorsal forewing in the new species that is distinctively larger than in *I. orpheus*. The name is treated as a noun in apposition.

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

Ithomiola (Ithomiola) triola Grishin, new species

<https://zoobank.org/B2449564-42AF-4C1B-B73E-263875446EA0>

(Figs. 34 part, 39c–d)

Definition and diagnosis. Genomic analysis reveals that two males from central Bolivia initially identified as *Ithomiola (Ithomiola) orpheus* (Westwood, 1851) (type locality in Brazil: Amazonian region) are genetically differentiated from it at the species level (Fig. 34); e.g., their COI barcodes differ by 3.2% (21 bp), and by 2.9% (19 bp) from *I. manchola* **sp. n.** (described right above), and therefore these specimens represent a new species. This new species is most similar to *I. orpheus* (Fig. 39a), but differs from it and other relatives by the following combination of characters: larger central white spot on the forewing spanning cells M₃-CuA₁ and CuA₁-CuA₂ as in *I. manchola* **sp. n.** [smaller, frequently separated spots in *I. orpheus*]; three [not two] narrower and more parallel to each other projections of the white area on the dorsal hindwing directed towards the costa (similar to a ghost head and two raised arms); and a more extensive, sometimes nearly complete, brown marginal border on the dorsal hindwing enclosing two or more white marginal spots. Due to its cryptic nature and poorly explored individual variation, this species is best identified by DNA, with diagnostic base pairs in the nuclear genome: cne5371.1.1:T210A, cne792.14.1:A66T, cne3077.8.1:T94G, cne9518.2.2:A66G, cne13680.1.3:C105A; and the COI barcode: T4A, T92C, T400T, A484G, T533C, T634C.

Barcode sequence of the holotype. Sample NVG-23111H09, GenBank [PZ516401](https://www.ncbi.nlm.nih.gov/nuclot/PZ516401), 658 base pairs:

```
AACATTATATTTTATTTTGAATTTGAGCAGGAATAGTTGGTACATCTTTAAGATTATTAATTCGTATAGAACTTGGTACTCCTGGTCTCTAATTGGAGACGATCAAATTTATAATACT
ATTGTAACAGCTCATGCTTTTATTATAATTTTTCATAGTAATACCTATTATAATTTGGAGGATTTGGAAATTGACTTGTTCCTTTAATACTAGGAGCTCCAGATATAGCTTTCCCTCGTA
TAAATAATATAAGTTTTGATTACTTCCCTTCATTATTTCTTCTTATTTCAAGCAGAATCGTTGAAATGGTGCAGGCACTGGATGAAGTGTATACCTCCCTTTATCATCTAATATTGC
CCATAGTGGATCTTCTGTTGATTAGCAATTTTCTTACATTTAGCTGGTATTTCATCAATTTTAGGAGCTATTAATTTTATTACTACTATTATTAATATACGAATTAATAATTTATCG
TTTGATCAAATACCTTTATTGTTGATCAGTTGGAATTACAGCTTTACTATTACTTTTATCTCTTCTGTTTAGCAGGTGCTATTACTATATTATTAACAGATCGAAATTTAAATACTT
CATTTTTTGACCTGCTGGTGGAGGTGACCAATTTTATATCAACATTTATTT
```

Type material. Holotype: ♂ deposited in the Carnegie Museum of Natural History, Pittsburgh, PA, USA (CMNH), illustrated in Fig. 39c, bears the following four printed rectangular labels (text in *italics* handwritten), three white: [Steinbach | Acc. 5047 | R. Japacani, Bol.], [Aug. | 1913], [DNA sample ID: | NVG-23111H09 | c/o Nick V. Grishin], and one red [HOLOTYPE ♂ | *Ithomiola* (*Ithomiola*) | *triola* Grishin]. **Paratype:** 1♂ NVG-23111H10 Bolivia, Santa Cruz, Las Juntas, Dec-1913, J. Steinbach leg. [CMNH] (Fig. 39d).

Type locality. Bolivia: Santa Cruz Department, Río Yapacaní.

Etymology. The name is constructed to rhyme with the genus name and reflects three white protuberances of the dorsal hindwing white area directed towards the costa in this new species; only two are prominent in *I. orpheus*. The name is treated as a noun in apposition.

Distribution. Currently known only from central Bolivia.

The type locality of *Apodemia (Apodemia) apache* Grishin, 2026

The type locality of *Apodemia (Apodemia) apache* Grishin, 2026 was indicated incorrectly in the original description (Zhang et al. 2026). Instead of “USA: Arizona, Apache Co., Greens Peak Road 8 mi west of US-60, elevation 7000 ft.” it should be “USA: Arizona, Apache Co., US-60, 8 mi west of Greens Peak Road, elevation 7000 ft.”, as stated on the label of the holotype. This locality is an arroyo on the south side of the highway, approximately 24 miles west of Springerville, where the larval foodplant, *Eriogonum jamesii* Benth., grows. We are grateful to Jim Brock for noticing this error and providing additional information.

Lectotype designation for *Apodemia multiplaga* Schaus, 1902

Apodemia multiplaga Schaus, 1902 was described from an unspecified number of specimens (No. 5912) from “Rinconada, Mexico” in the state of Veracruz (Schaus 1902). We found a syntype in USNM, originally from the W. Schaus collection, with No. 5912 and the word “type” written in the bottom left corner of its identification label. Schaus labeled specimens he considered “types” (one per sex) with the handwritten word “type” but did not write this word on identification labels of other specimens in his series. Therefore, even if there were other syntypes, this specimen was considered a name-bearing specimen by Schaus. To define the taxonomic identity of the name *A. multiplaga* objectively, N.V.G. hereby designates the syntype in the USNM collection, a male illustrated in Fig. 41c, bearing the following four rectangular labels (3rd handwritten, others printed with handwritten text shown in italics; last red, others white): [Rinconada, | V. Cruz], [Apodemia | multiplaga | type Schs], [Collection | W.Schaus], [Type | No. 5912 | U.S.N.M.], as the **lectotype** of *Apodemia multiplaga* Schaus, 1902. The lectotype is a specimen in good condition, the right pair of wings is spread closer together, its left antenna is missing the club, and its head is tilted to the left. Additional images of this specimen, photographed by G. Lamas, are shown on the Butterflies of America website (Warren et al. 2024). The type locality of *A. multiplaga* remains Mexico: Veracruz, Rinconada. The COI barcode sequence of the lectotype, sample NVG-17102D03, GenBank [PZ516402](https://www.ncbi.nlm.nih.gov/nuccore/PZ516402), 658 base pairs, is:

```
TACATTATATTTATTTTGGAAATTTGAGCAGGAATAATTGGAACATCATTAGATTATTAATTCGAATAGAATTAGGAACCTTCTGGATCTTTAATTGGAGATGATCAAATTTATAATACT  
ATTGTTACAGCTCATGCTTTTATTATAATTTTATATAGTAATCAATTATAATTGGAGGATTGGTAATTGATTAGTACCTTTAATACTAGGAGCTCCAGATATAGCTTTTCCCTCGAA  
TAAATAATATAAGATTTGACTTTTACCCCATCATTATTTTATTAATTTCTAGAGAAATTTGTAGAAAATGGGGCAGGAACAGGATGAACAGTATATCCCCCACTTCATCTAATATTGC  
CCATAGAGGATCTTCTGTTGATTAGCTATTTTTCCTTACATTAGCTGGTATTTCTTCTATTTTAGGAGCAATTAATTTTATTACCACCATTTAATACATACGTATCAATAACATATCC  
TTTGATCAAAATACCTTTATTTGTTTGATCTGTAGGAATTACAGCTTTTACTTCTACTATCTTTACCTGTATTAGCGGGAGCTATTACTATATTATTAAGTATCGTAATTTAAATACAT  
CATTTTGTGATCCAACAGGTGGAGGAGATCCAATTTTATACCAACATTTATTT
```

Apodemia (Apodemia) estrellada Grishin, new species

<https://zoobank.org/5924CC3B-0111-46C3-ABB2-6E0AC0B8C9BE>

(Figs. 40 part, 41a–b, 42a–c)

Definition and diagnosis. Genomic analysis reveals that specimens from Sonora, Mexico, initially identified as *Apodemia (Apodemia) multiplaga* Schaus, 1902 (type locality in Mexico: Veracruz) are

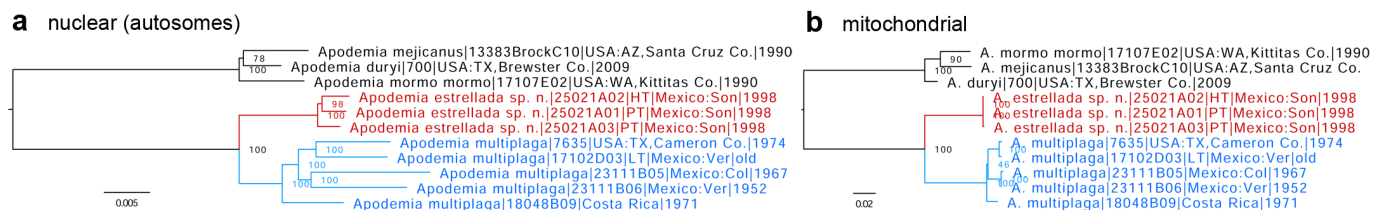


Fig. 40. Phylogenetic trees of selected *Apodemia* C. Felder & R. Felder, 1865 species constructed from protein-coding regions in: **a**) the nuclear genome (autosomes), based on 10,168,317 positions, and **b**) the mitochondrial genome: *A. estrellada* sp. n. (red) and *A. multiplaga* (blue). Ultrafast bootstrap (Hoang et al. 2018) values are shown at nodes.



Fig. 41 (legend continues on the next page). Specimens of *Apodemia* (*Apodemia*) in dorsal (left) and ventral (right) views, data below: a-b) *A. estrellada* sp. n. from Mexico: Sonora, 1 km E of Bahía San Carlos, 21-Mar-1998, J. P. Brock leg.:

a) holotype ♂ NVG-25021A02 [MGCL] and **b)** paratype ♀ NVG-25021A03 [JPBC]; and **c–d)** *A. multiplaga*: **c)** lectotype ♂ NVG-17102D03 Mexico: Veracruz, Rinconada, old [USNM] and **d)** non-type ♀ NVG-7635 USA: Texas, Cameron Co., Brownsville, US-281 at railroad crossing, 24-Oct-1974, W. W. McGuire & N. McGuire [TAMU].

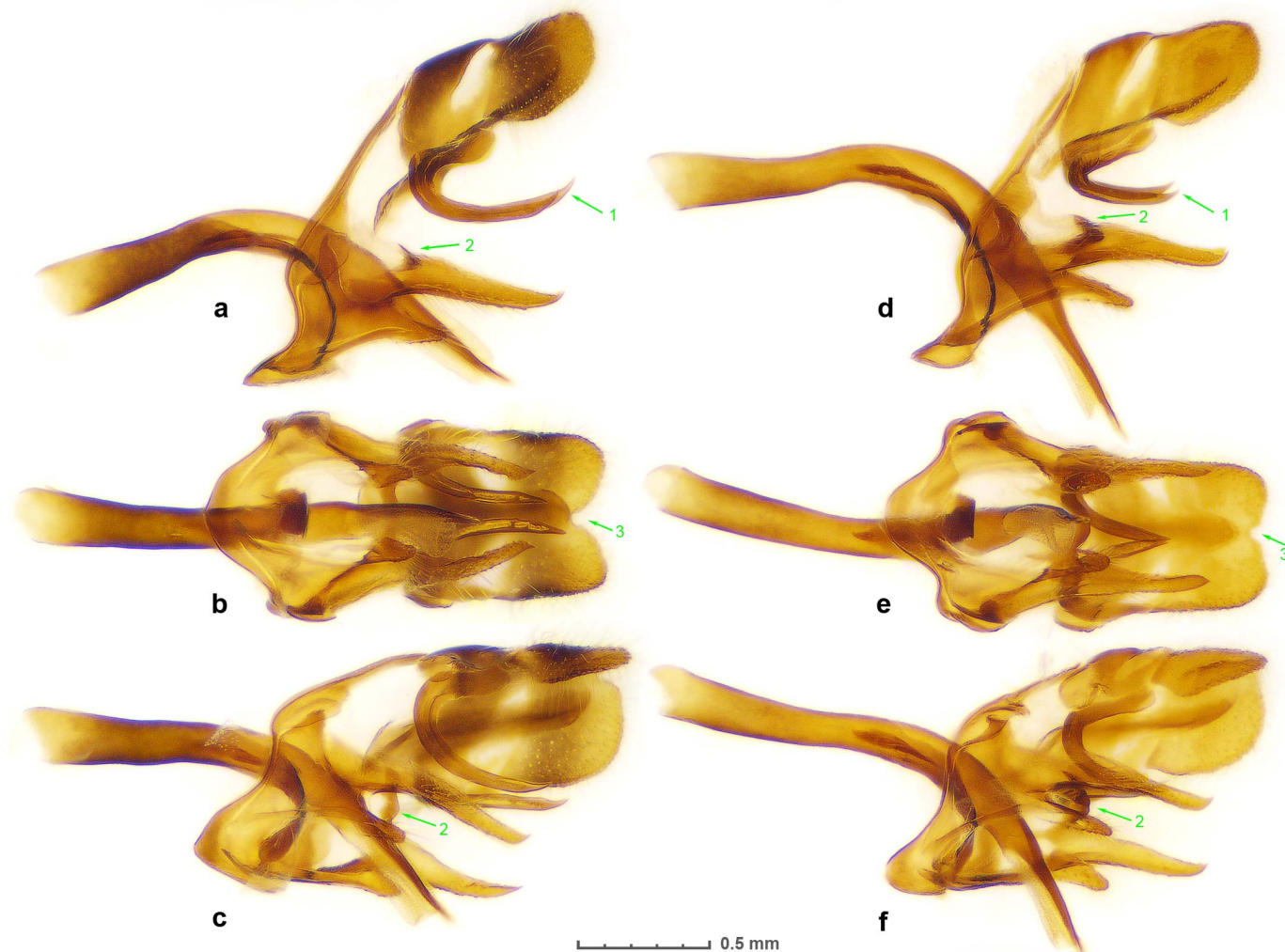


Fig. 42. Male genitalia of *Apodemia* (*Apodemia*) from Mexico: **a–c)** *A. estrellada* **sp. n.** holotype NVG-25021A02 Sonora, 1 km E of Bahía San Carlos, 21-Mar-1998, J. P. Brock leg., genitalia NVG260613-06 [MGCL]; and **d–f)** *A. multiplaga* non-type NVG-23111B06 Veracruz, San Andrés Tuxtla, Aug-1952, H. A. Freeman leg., genitalia NVG260613-07 [CMNH]. Views: **a, d)** left lateral, **b, e)** ventral, and **c, f)** left ventrolateral. Green arrows point to diagnostic characters, numbered 1 to 3, see text.

genetically differentiated from it at the species level (Fig. 40); e.g., their COI barcodes differ by 5.2% (34 bp), and therefore these specimens represent a new species. This species is most similar to its sister *A. multiplaga* (Fig. 41c, d), but differs from it by the following combination of characters: rounder hindwings in males; hindwing tornus is not as produced as in *A. multiplaga*; submarginal black streaks on the ventral hindwing are better developed and longer; the orange area in the basal half of the ventral forewing is narrower and does not reach the anterior edge of the discal cell as in *A. multiplaga*; and the discal pale spot on the ventral hindwing is narrower anteriorly. In male genitalia, compared to *A. multiplaga* the falces are longer and more curved (character 1 in Fig. 42), the transtilla is more weakly developed (character 2 in Fig. 42), the notch along the posterior margin of the uncus is deeper (character 3 in Fig. 42), and the aedeagus is shorter. Due to its cryptic nature and poorly explored individual and possibly seasonal variation, this species is best identified by DNA, with diagnostic base pairs in the nuclear genome: cne1621.2.10:T84C, cne2862.4.15:G36A, cne362.4.2:A333G, cne213.5.1:T2472C, cne2237.4.1:G156A; and the COI barcode: T40C, T91A, T157C, T386C, T484T.

TACATTATATTTTATTTTGGAAATTGTGACAGGAATAATCGGAACATCATTAAAGATTATTAATTGGAATAGAATTAGGAACTTCAGGATCATTAATTGGAGATGATCAAATTTATAACACT
ATTGTTACAGCTCATGCTTTTATTAATAATTTTTTCATAGTTATACCTAATTTATGAGGAGATTGGTAATTGATTAGTACCTTTAATATTAGGAGCTCCAGATATGCTGTTTCCACGAA
TAATAAATAAAGAAATTTGACTTTTACCCCCATCATATTTTATTAATTTCTAGAAGAAATGTAGAAAGGTGAGCTGGAACAGGATGAACAGTATACCCCACTGTTTCATCTAATATTGCG
TCATATGTTGATCTTCAGTTGATCTGGCAATTTTTCTTTACATTTTAGCTGGTATTTTCTTCTATTTTAGAGGCAATAATTTTATTACTATATTATTAATATACGTATTAAATAATATCT
TTTGATCAAATACCTTTATTTGTTTGTATCAGTAGGAATATACAGCTCTTTTACTTTTATTTATCTTCTTACCTGTATTAGCAGGAGCTATTAATAATATCTGATCGTAATTTAAATACAT
CTTTTTTTTACTCCAGCTAGGTGGAGGAGATCCAAATTTTATATCAACATTAATTTT

Type locality. Mexico: Sonora, 1 km east of Bahía San Carlos.

Distribution. Currently known from the type locality in Sonora, Mexico.

<https://zoobank.org/71068462-2758-49EA-9F47-8AC65AC97EFE>

Definition and diagnosis. Genomic analysis reveals that three *Synargis regulus* group males from French Guiana form a clade in both nuclear and mitochondrial genome trees genetically differentiated from others at the species level (Fig. 43); e.g., their COI barcodes differ from closest species such as *Synargis regina* Grishin, 2024 (type locality Peru: Junín, Chanchamayo) and *Synargis reginella* Grishin, 2024 (type locality Brazil: Pará, Itaituba) by 2% (13 bp) and 3% (20 bp), respectively. Therefore, these specimens represent a new species. This new species differs from its relatives by the following combination of characters in males: the postdiscal yellow band on the ventral hindwing does not reach (or barely approaches) vein Rs and does not penetrate into cell Sc+R₁-Rs, thus being shorter than in most other species; the band is narrower than the discal brown area, at least on the dorsal hindwing; only one submarginal yellow spot on the ventral hindwing, weakly developed and located near the tornus (the spot near the middle of the outer margin is not present) [similar to *Synargis gohia* Grishin, 2024 (Fig. 44e), but different from *Synargis flavicauda cosita* Grishin, 2024 (Fig. 44d) and *Synargis reginella* Grishin, 2024 (Fig. 44f)]; no submarginal yellow spots on the ventral forewing (possibly a weak yellow overscaling near the tornus); weakly defined, only slightly darker than the ground brown color, tornal area on the ventral hindwing; brown abdomen above (no yellow) but yellow beneath; dark fringes [slightly and sparsely checkered in *S. reginella* (Fig. 44f)]; concave outer edge of the discal yellow band on the dorsal forewing; typically smaller than some related species, and the type series, all from the same locality, exhibits variation in size (Fig. 44a–c). Due to its cryptic nature, poorly explored individual variation, and the lack of known females, this species is best identified by DNA, with diagnostic base pairs in the nuclear genome: cne3385.5.1:G448T, cne3385.5.1:A484T, cne3078.6.4:G48A, cne3078.6.4:C51T, cne1275.1.1:G141A; and the COI barcode: T238C, G371A, T400C, T403C, T499C.

AACTTTTATATTTTATTTTGGAACTGAGCAGGTATAAATAGGAACATCTCTTAGTTTATTAATTCGAATAGAATTAGGAACCTCGTGTCTTTAATGGAAATGATCAAATTTATAATACT
 AATTTGACAGCTCATGCATTTATATAATTTTATTTATAGTTATACCTATTATTAATGGAGGATTGGAAATGGATAGTTCATTAATATTAGGAGCTCCAGATATAGCTTTCCCCGGTA
 TAAATAATATAAGAAATTTGATTAATACCTCCATCTTTATTTATTAATTTCTAGAAGAAATTTAGAAATGAGGACAGGAATCGATGACTGCTGTACCCGCCACTTTCTATCAATAATGCG
 TCATAGAAGAGCTTCTGTTGATTAGCTATTTTTTCCCCTCCATTAGCTGGAAATTCATCAATTTTAGTGCAATTAATTTATTACAACCATTTATTAACATACGTATTAAATAATTTATCA
 TTGTGATCAAATACCCCTATTTATTTGATCAGTAGGAATTACTGCTCTTCTTTTATTTATTAATCTTTTACCTGTTTATAGCAGGAGCTATTACTATATTCAGATCGAAATTTAAATACAT
 CTTTTTTGTATCCCGCAGGAGGTGGAGATCCAAATTTATATCAACATTTCTTT

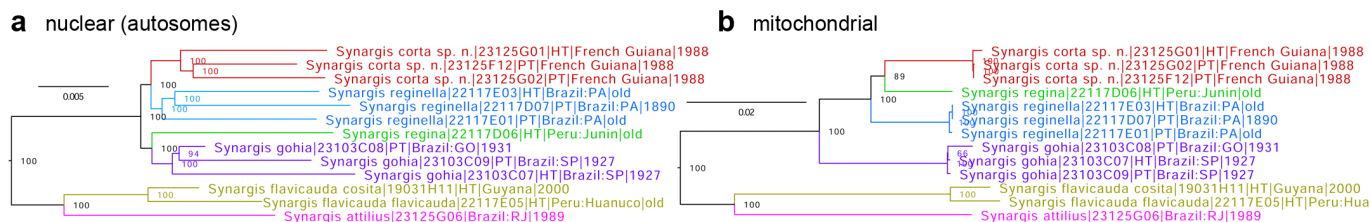


Fig. 43. Phylogenetic trees of selected *Synargis regulus* group species constructed from protein-coding regions in: **a)** the nuclear genome (autosomes), based on 1,406,502 positions, and **b)** the mitochondrial genome. Different species are colored differently: *S. corta* sp. n. (red), *S. reginella* (blue), *S. regina* (green), *S. gohia* (violet), *S. flavicauda* (olive), and *S. attilius* (magenta). Ultrafast bootstrap (Hoang et al. 2018) values are shown at nodes.

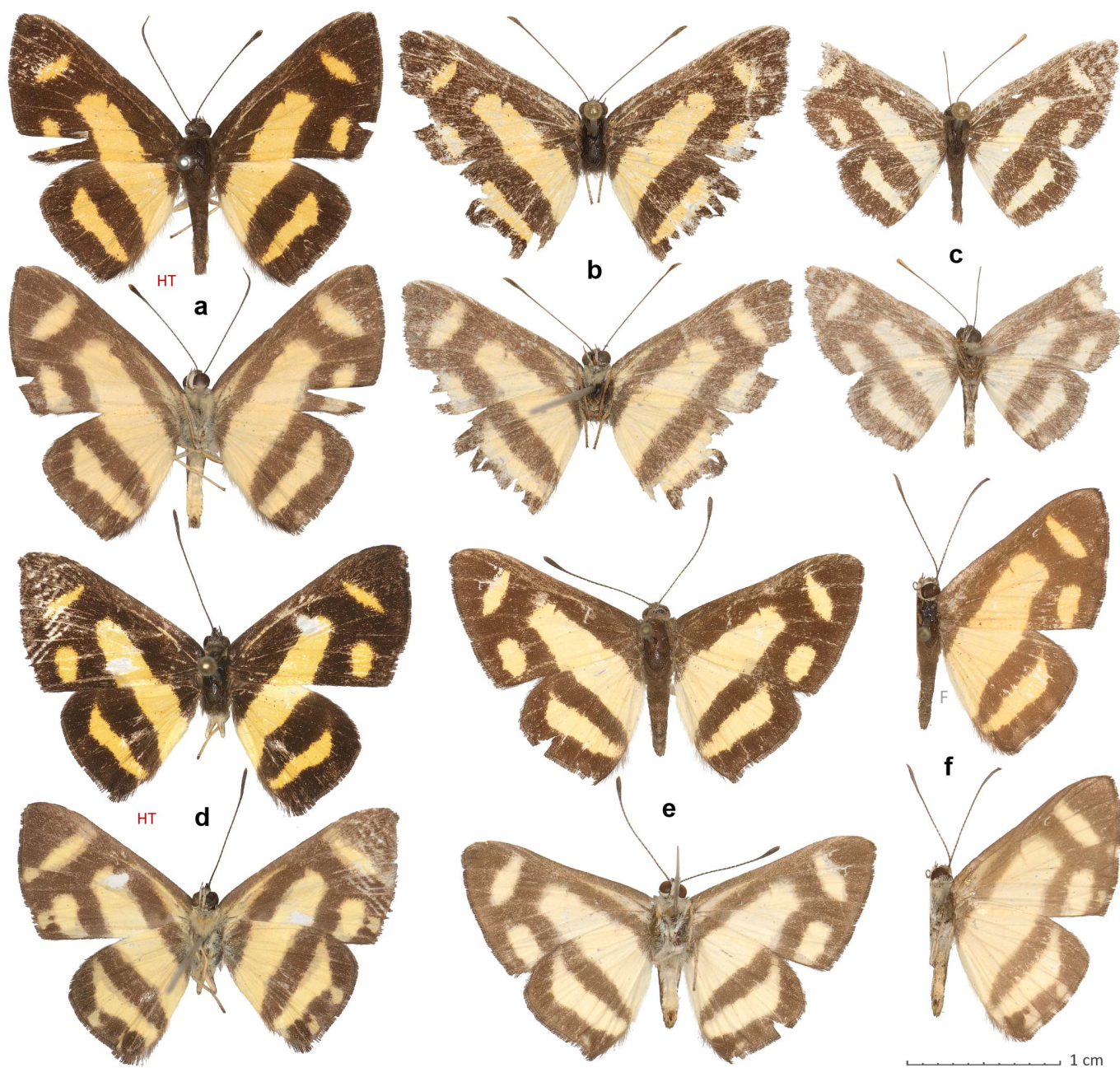


Fig. 44. Males of selected *Synargis regulus* group species in dorsal (above the panel letter) and ventral (below) views, data in text or below: **a–c)** *S. corta* sp. n. from French Guiana [USNM]: **a)** holotype NVG-23125G01 and paratypes: **b)** NVG-23125F12 and **c)** NVG-23125G02; **d)** *S. flavicauda cosita* holotype NVG-19031H11 from Guyana: Eastern Kanuku Mts., Two Hat Mountain S slope summit, 850'–1200', GPS 3.1133, –59.0983, S. Fratello et al. leg. [USNM]; **e)** *S. gohia* paratype NVG-23103C08 from Brazil: Goiás, Vianópolis, Nov-1921, Coll. R. Spitz [SMF]; and **f)** *S. reginella* non-type specimen NVG-23103C06 from Brazil: Pará, Tapajós, old (~1900) [SMF], F indicates flipped image (i.e. left-right inverted).

Type material. Holotype: ♂ deposited in the National Museum of Natural History, Smithsonian Institution, Washington, DC, USA (USNM), illustrated in Fig. 44a, bears the following four rectangular labels (1st handwritten, others printed), three white: [R^{te}. De l'Est | GUYANE | 12 Nov.88], [Donated to USNM by | Jean-Yves Gallard | November 1993], [DNA sample ID: | NVG-23125G01 | c/o Nick V. Grishin], and one red [HOLOTYPE ♂ | Synargis | corta Grishin]. The holotype must have been collected by J.-Y. Gallard in 1988. **Paratypes:** 2♂♂ with the same data as the holotype but Sep-1988, and J.-Y. Gallard is explicitly listed as the collector: 1♂ NVG-23125F12 (Fig. 44b) and 1♂ NVG-23125G02 (Fig. 44c), genitalia vial #2001-75 by Donald J. Harvey.

Type locality. French Guiana: Roura, Route de l'Est.

Etymology. In Spanish, *corto* means short, brief, small in length or duration, abrupt. The name reflects the shorter postdiscal yellow band on the ventral hindwing of this species that does not reach vein Rs. The name is treated as an adjective.

Distribution. Currently known only from the type locality in French Guiana.

Remarks. COI barcodes of the paratypes are identical to that of the holotype: NVG-23125F12, GenBank [PZ516405](#) and NVG-23125G02, GenBank [PZ516406](#).

Family Lycaenidae [Leach], [1815]

Rapala subguttata Elwes, [1893] belongs to *Ajenorix* Grishin, 2025 not *Virachola* F. Moore, 1881

Genomic analysis of *Rapala subguttata* Elwes, [1893] (type locality in Myanmar), currently placed in the genus *Virachola* F. Moore, 1881 (type species *Deudorix perse* Hewitson, 1863), reveals that it is not monophyletic with its type species but instead is sister to *Ajenorix* Grishin, 2025 (type species *Rapala hypargyria* Elwes, [1893]) (Fig. 45), although its wing pattern resembles that of *Virachola smilis* Hewitson, 1863 (type locality in India) more than those of species of *Ajenorix*. To restore the monophyly of *Virachola*, we place *R. subguttata* in the genus *Ajenorix* as *Ajenorix subguttata* (Elwes, [1893]), **comb. nov.** The ventral wing pattern of this species is novel for *Ajenorix*.

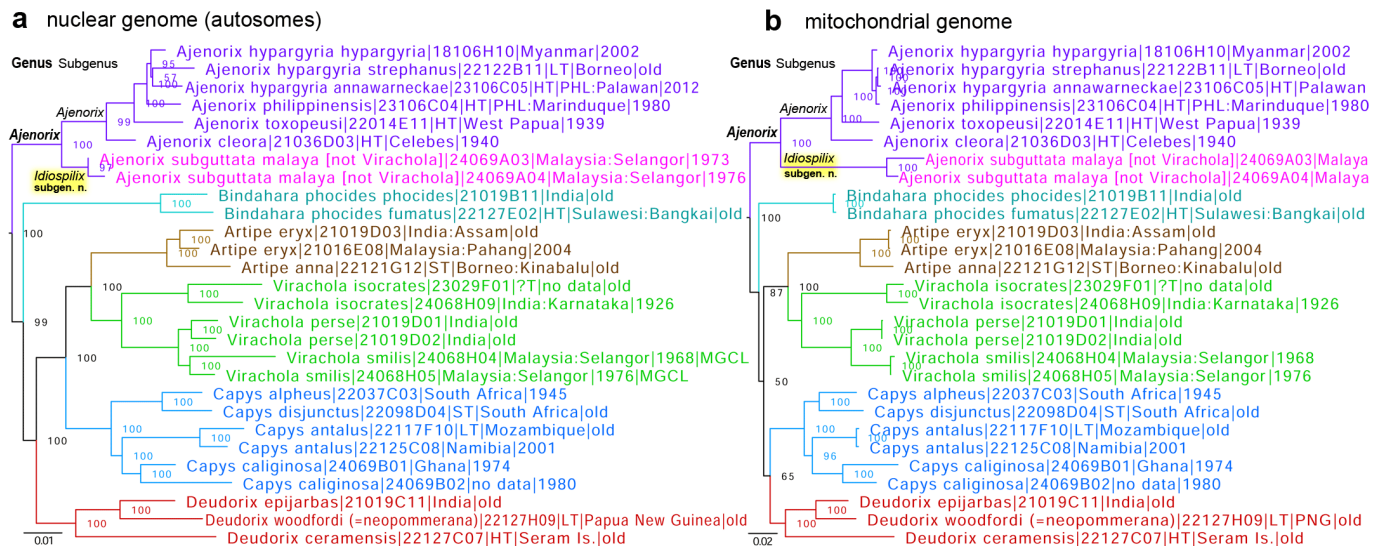


Fig. 45. Phylogenetic trees of selected species of Deudorini constructed from protein-coding regions in: **a**) the nuclear genome (autosomes), based on 478,089 positions, and **b**) the mitochondrial genome. Different genera are colored differently: *Ajenorix* (violet with *Idiospilix* subgen. n. labeled in magenta), *Bindahara* F. Moore, 1881 (cyan), *Artipe* Boisduval, 1870 (brown), *Virachola* (green), *Capys* Hewitson, 1865 (blue), and *Deudorix* (red). Genus *Ajenorix* and its subgenera are labeled by corresponding branches. Ultrafast bootstrap (Hoang et al. 2018) values are shown at nodes.

***Idiospilix* Grishin, new subgenus**

<https://zoobank.org/33180080-1281-49BD-804B-1732E4E111D2>

Type species. *Rapala subguttata* Elwes, [1893].

Definition. Genomic phylogeny of Deudorigini Doherty, 1886 reveals that *Ajenorix subguttata* (Elwes, [1893]), **comb. nov.** (type locality in Myanmar) is sister to all other species of *Ajenorix* Grishin, 2025 (type species *Rapala hypargyria* Elwes, [1893]) and is genetically differentiated from its type species at the subgenus level (Fig. 45), e.g., their COI barcodes differ by 7.4% (49 bp). Therefore, *A. subguttata* represents a new subgenus that differs from its relatives by the following combination of characters: the ventral side of the wing is vinous brown with a purplish tint, darker than in relatives, with brown spots framed in white; the ventral spotting is most similar to *Virachola smilis* Hewitson, 1863 (type locality in India) but differs in the lack of the discal spot in the hindwing cell Rs-M₁, which instead may have a more weakly developed submarginal spot. In DNA, a combination of the following characters is diagnostic in the nuclear genome: cce259.9.2:C165T, cce2450.8.10:G120C; and the COI barcode: A34T, T278C, T397C, T427C, A538T.

Etymology. The name is derived from the Greek ἴδιος (idios), meaning peculiar or distinctive, and σπῖλος (spílos), meaning spot. The name refers to the “[t]he peculiar spotting of the underside” as noted in the original description of the type species; the new subgenus was named to match the ending of the parent genus. The name is a feminine noun in the nominative singular.

Species included. Only the type species.

Parent taxon. Genus *Ajenorix* Grishin, 2025.

***Satyrium sylvinus* Boisduval, 1852, *Satyrium dryope* (W. H. Edwards, 1870). and *Satyrium californica* (W. H. Edwards, 1862)**

Zhang et al. (2022c) presented genomic evidence that *Satyrium dryope* (W. H. Edwards, 1870) (type locality in USA: California, Santa Clara Co.) is a species distinct from *Satyrium sylvinus* (Boisduval, 1852) (type locality in USA: California, Plumas Co.) and demonstrated that both are closely related to *Satyrium californica* (W. H. Edwards, 1862) (type locality in USA: California, Napa Co.). Moreover, in the nuclear genome trees constructed from concatenated protein-coding genes (both autosomes and the Z chromosome), it is *S. californica* and *S. sylvinus* that are sister taxa, and not the more phenotypically similar *S. sylvinus* and *S. dryope* as would be expected, because they were regarded as conspecific.

While the reason behind this apparent contradiction between wing pattern similarity and genetic relatedness is not clear, we reproduced the same phylogeny with a larger number of specimens from across the ranges of these taxa (Fig. 46a, b). This phylogeny may show the true relationship suggesting rapid phenotypic evolution of *S. californica*, which has differentiated substantially from the other two species. A longer branch supporting the *S. californica* clade (Fig. 46a violet) agrees with this hypothesis. Alternatively, it is possible that this tree topology results from a more extensive gene exchange between *S. californica* and *S. sylvinus*, who converged to be genetically closer. However, the Z-chromosome tree reveals the same topology despite the Z chromosome being more resistant to introgression (Fig. 46b).

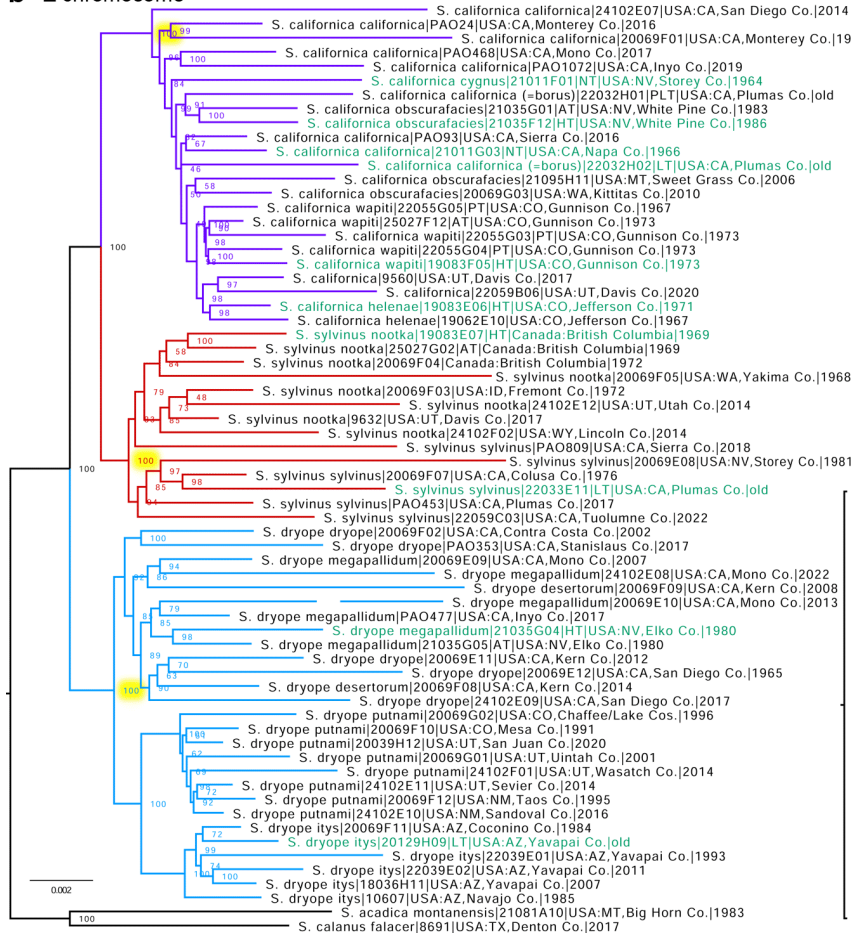
The clades of the three species are more prominent in the Z chromosome tree (Fig. 46b, yellow highlight of the bootstrap values) than in the autosome tree: i.e., the branches supporting the clades are comparatively longer than non-terminal branches within the clades in the Z-chromosome tree. Because the Z chromosome plays a special role in speciation (Cong et al. 2026a), this observation further supports species-level distinction among these three taxa. In contrast, the autosome tree separates subspecies better, because it is based on a much larger number of DNA positions, thus being more suitable for population-level analysis (Fig. 46a).

The mitochondrial genome tree reveals several haplotypes, with the most prominent being those of the eastern subspecies of *Satyrium dryope*: *S. dryope putnami* (Hy. Edwards, 1877) (type locality USA:

a nuclear (autosomes)



b Z chromosome



c mitochondrial

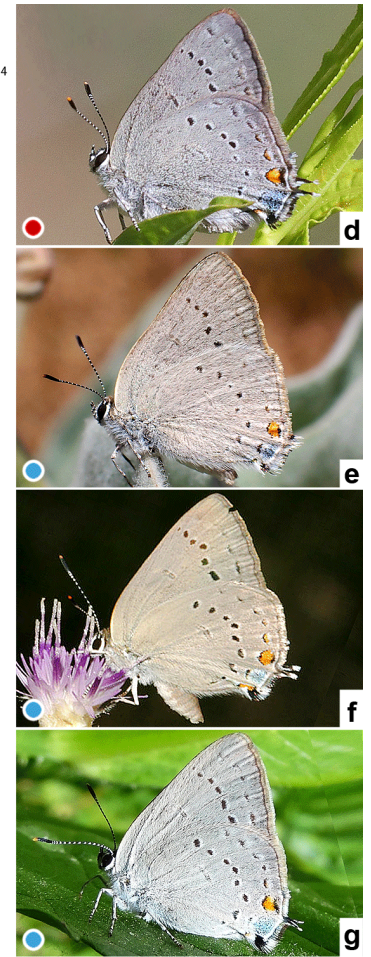
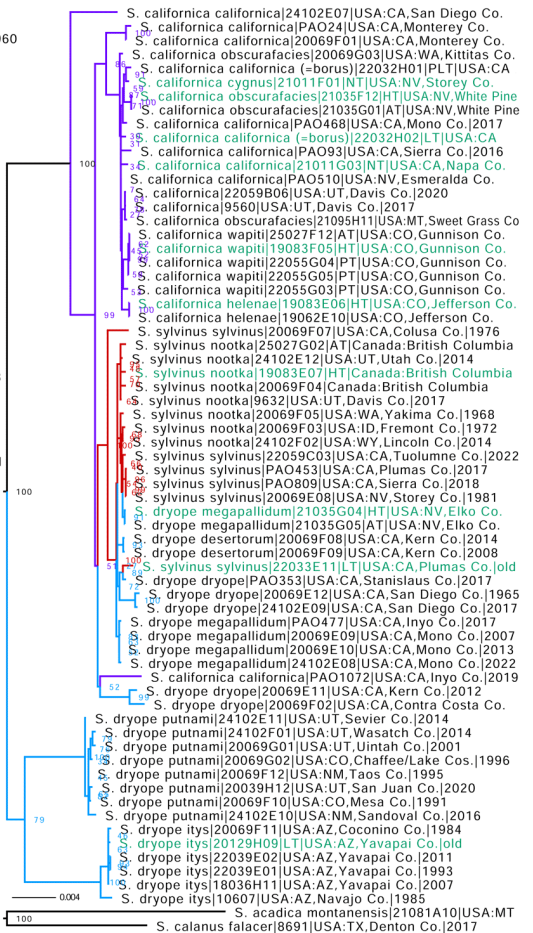


Fig. 46 (see the previous page). Phylogenetic trees of the *Satyrrium sylvinus* clade constructed from protein-coding regions in: **a)** the nuclear genome (autosomes), based on 2,055,747 positions, **b)** the Z chromosome, based on 237,948 positions, and **c)** the mitochondrial genome; and **d–g)** iNaturalist observations, males from the USA (color of the dot in the lower left of each image corresponds to the color of this taxon in the trees): **d)** *S. sylvinus sylvinus* possible topotype, observation No. 86817203, California, Plumas Co., Plumas National Forest, GPS 39.9908, –120.8514, 30-Jun-2021 © Paul G. Johnson; **e)** *S. dryope dryope* observation No. 338281189, California, San Diego Co., Roberts Ranch Trail, GPS 32.8235, –116.6274, 25-Jun-2025 © Mark Brown; **f)** *S. dryope putnami* observation No. 261650318, Colorado, Mesa Co., Unaweep Canyon, GPS 38.791, –108.655, 13-Jul-2005 © Tom Murray; **g)** *S. dryope itys* topotype, observation No. 138912170, Arizona, Yavapai Co., Prescott, GPS 34.6069, –112.4433, 9-Jun-2012 © jmbearce; images are color-corrected, brightened, rotated, cropped, and some flipped (i.e., left-right inverted), CC BY-NC 4.0 <https://creativecommons.org/licenses/by-nc/4.0/>. In the trees, primary type specimens are labeled in green font and clades are colored by species: *S. californica* (violet), *S. sylvinus* (red), and *S. dryope* (blue). Gaps in branches (in **c**) indicate where a vertical slice of the tree was removed to reduce its horizontal dimension, and a gap in a terminal branch (in **b**) indicates that a segment of a branch was cut out to reduce its length; i.e., branches with gaps are longer than shown (to allow an increase in the font size and fit the page). Ultrafast bootstrap (Hoang et al. 2018) values are shown at nodes. Bootstrap values supporting species-level clades (100%) are highlighted in yellow in the Z chromosome tree.

Utah, Juab-Utah Cos.) and *S. dryope itys* (W. H. Edwards, 1882) (type locality USA: Arizona, Yavapai Co.), which may eventually be regarded as species-level taxa (Fig. 46b). However, other species and subspecies of *S. californica*, *S. sylvinus*, and *S. dryope* do not prominently differ in their mitochondrial haplotypes and appear to exchange mitochondria among species.

Additional work is needed to better understand wing pattern characters separating *S. sylvinus* and *S. dryope* (Fig. 46d–g). Although nominotypical *S. dryope* is usually characterized by the lack of tails, tailed individuals (especially females) can be found, and the two more eastern subspecies of *S. dryope* possess prominent tails (Fig. 46f–g). Among the characters to look for would be the typically paler colors of *S. dryope* with reduced ventral spots giving it an overall more faded appearance (Fig. 46e–g). A typical *S. sylvinus* would be darker to brownish-gray beneath, with a crisper pattern of usually larger spots, including a more vivid and better outlined submarginal orange cap (Fig. 46d).

Finally, the genomic analysis supports *Satyrrium californica wapiti* M. Fisher, 2006, **stat. conf.** (type locality in USA: Colorado, Gunnison Co.) as a valid subspecies distinct from all others. Although *Satyrrium californica helenae* M. Fisher, 2009, **stat. rest.** (type locality in USA: Colorado, Jefferson Co.) is a close sister to *S. californica wapiti* in the autosome tree (Fig. 46a), the two specimens we sequenced (including the holotype) form a subclade prominently separated from it. Therefore, considering wing pattern differences, we treat *S. californica helenae* as a valid subspecies as well.

***Lacturnea* Nazari & Fric, 2025, *Huegelia* Nazari & Fric, 2025, and *Everes* Hübner, [1819] are subgenera of *Cupido* Schrank, 1801**

Analyzing gene marker-based phylogeny and morphology of genitalia, Nazari et al. (2025) proposed treating *Everes* Hübner, [1819] (type species *Papilio amyntas* [Schiffermüller], 1775, preocc. by *Papilio amyntas* Poda, 1761, valid name for this species is *Papilio argiades* Pallas, 1771) and *Sinocupido* Lee, 1963 (type species *Sinocupido lokiangensis* Lee, 1963) as genera distinct from *Cupido* Schrank, 1801 (type species *Papilio minimus* Fuessly, 1775) and described two new genera of their close relatives: *Lacturnea* Nazari & Fric, 2025 (type and only species *Polyommatus lacturnus* Godart, [1824]) and *Huegelia* Nazari & Fric, 2025 (type species *Lycaena huegelii* Gistel, 1857). The latter genus currently consists of two species.

Genomic phylogeny of Everina Tutt, 1907 and genera in related subtribes of Polyommata reveals that genetic differentiation among *Cupido* (Fig. 47 red), *Everes* (Fig. 47 magenta), and *Sinocupido* (Fig. 47 purple) is lower than that between other Polyommata genera and is comparable to the differentiation within genera; e.g., COI barcode differences are: 5.2% (34 bp) between *Cupido* and *Everes*, 4.7% (31 bp) between *Cupido* and *Sinocupido*, and 3.9% (26 bp) between *Everes* and *Sinocupido*. These barcode differences are rather small compared to typical differences between genera (around 10%) and fall within the range of distances between closely related congeners.

Genetic differentiation in the nuclear genome is illustrated by yellow rectangles within genera *Udara* Toxopeus, 1928 (type species *Polyommatus dilectus* F. Moore, 1879), *Eicochrysops* Bethune-Baker, 1924 (type species *Eicochrysops eicotrochilus* Bethune-Baker, 1924), *Icaricia* Nabokov, 1945 (type species *Lycaena icarioides* Boisduval, 1852), *Agriades* Hübner, 1819 (type species *Papilio glandon* Prunner, 1798), *Plebejus* Kluk, 1780 (type species *Papilio argus* Linnaeus, 1758), *Polyommatus* Latreille, 1804 (type species *Papilio icarus* Rottemburg, 1775), and *Aricia* L. R[eichenbach], 1817 (type species *Papilio agestis* Schiffermüller, 1775) (Fig. 47a). The horizontal dimension of yellow rectangles is proportional to genetic differentiation and is approximately the same in all these genera, being slightly larger than in the *Cupido* lineage that includes both *Everes* and *Sinocupido*. Although not marked in the mitochondrial genome tree, genetic differentiation within *Cupido* sensu lato is no more than that in most other genera (Fig. 47b).

We have not sequenced the whole genomes of *P. lacturnus* or *L. huegelii*, but their COI barcodes obtained in Nazari et al. (2025) differ from *C. minimus* by 6.5% (43 bp) and 5.2% (34 bp), respectively, revealing a similarly close congeneric relationship. These monotypic or species-poor lineages do not appear distinct enough to justify their genus status as originally described.

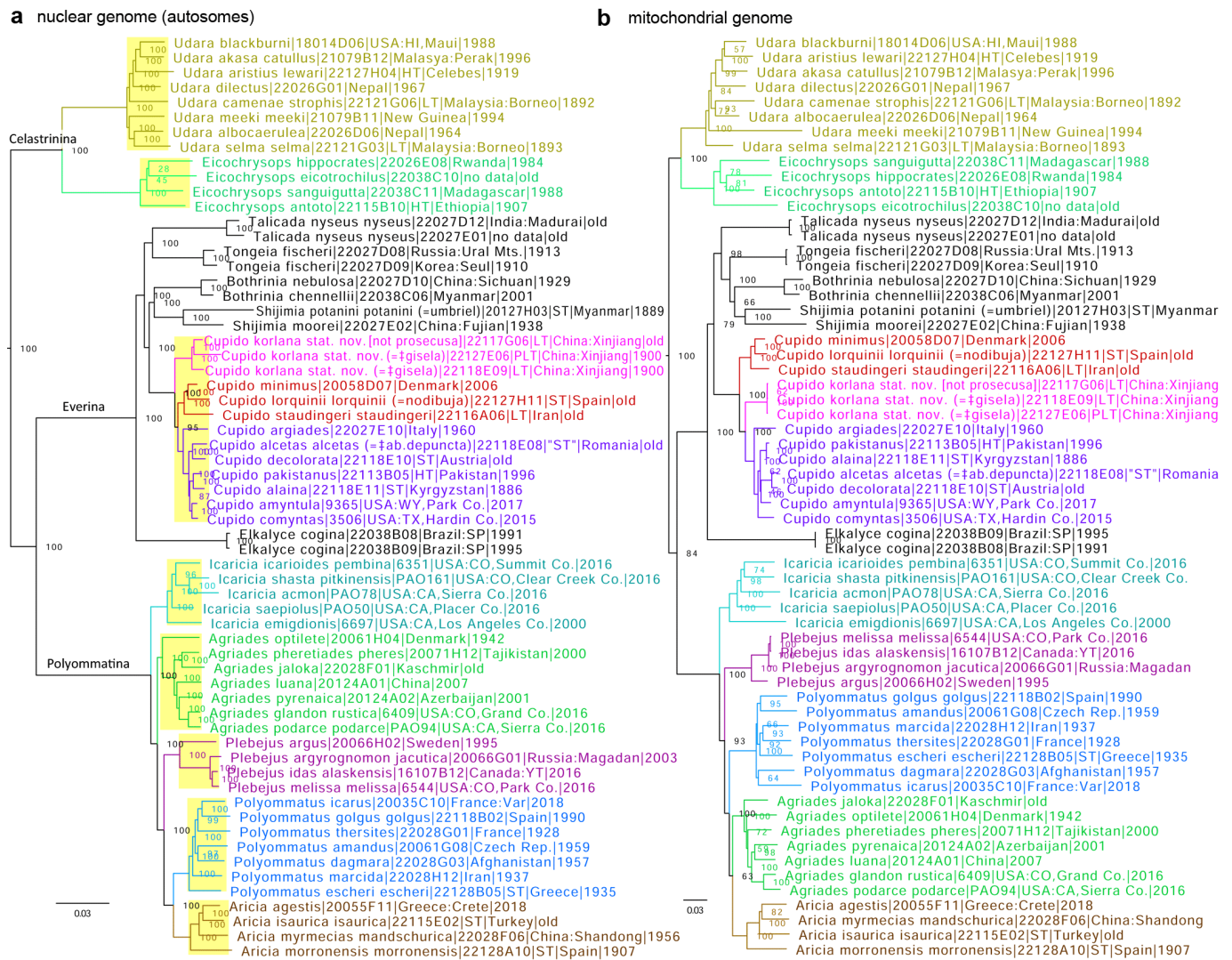


Fig. 47. Phylogenetic trees of selected Polyommataini constructed from protein-coding regions in: **a)** the nuclear genome (autosomes), based on 1,859,358 positions, and **b)** the mitochondrial genome. Genera and subgenera discussed in the text are colored: *Udara* (olive), *Eicochrysops* (aquamarine), *Cupido* (subgenera *Sinocupido* in magenta, *Cupido* in red, and *Everes* in violet), *Icaricia* (cyan), *Agriades* (green), *Plebejus* (magenta), *Polyommatus* (blue), and *Aricia* (brown). Yellow rectangles in the nuclear genome tree mark genetic differentiation in genera (horizontal dimension is similar in these rectangles). Ultrafast bootstrap (Hoang et al. 2018) values are shown at nodes.

This situation is reminiscent of *Plesioarida* Trujano & García, 2018 (type species *Apodemia walkeri* Godman & Salvin, 1886) and *Neoapodemia* Trujano, 2018 (type species *Chrysophanus nais* W. H. Edwards, 1877), initially proposed as genera based on detailed morphological analysis and indeed representing prominent phylogenetic lineages (Trujano-Ortega et al. 2018). Consistent with the current circumscription of Riodinidae genera, *Plesioarida* and *Neoapodemia* align more closely with subgeneric rank and are currently treated as such (Zhang et al. 2019d). Additionally, as genomic analysis shows, *Plesioarida* is best treated as a junior subjective synonym of *Roeberella* Strand, 1932 (type species *Lemonias calvus* Staudinger, [1887]) due to genetic and phenotypic similarities of the type species of these two genus-group names (Zhang et al. 2020).

For all the reasons put forward above, we propose treating *Lacturnea* Nazari & Fric, 2025, **stat. nov.**, *Huegelia* Nazari & Fric, 2025, **stat. nov.**, and *Everes* Hübner, [1819], **stat. rev.** as subgenera of *Cupido* Schrank, 1801.

Lectotype designation for *Lycaena gisela* Püngeler, 1901

Lycaena gisela Püngeler, 1901, a junior primary homonym of *Lycaena gisella* Staudinger, 1888, which is treated as a valid subspecies of *Phyliris helena* (Snellen, 1887), was described from an unspecified number of specimens; two males and one female were illustrated with the original description (Püngeler 1901). We found four male and four female syntypes of *L. gisela* in the MFNB collection, and one male in the MTD collection, all with the same locality label; and obtained a whole genome shotgun sequence dataset from a male syntype that was labeled as the “Type” (while others had the labels “Cotype” in MFNB and “Original” in MTD, the latter syntype was also sequenced as NVG-22127E06) and “abgebildet Iris 1901” (i.e., figured in Iris 1901), and was illustrated by Püngeler (1901) in fig. 12. The syntype’s appearance (it has now lost the right antenna and the right forewing is tilted posteriad) and label data agree with the original description and illustration, leaving little doubt that fig. 12 in Püngeler (1901) shows a photograph of this specimen. To stabilize nomenclature and define the name *L. gisela* objectively, N.V.G. hereby designates this syntype in the MFNB collection, a male illustrated in Fig. 48a, that bears the following five printed labels (2nd red, 4th yellow, others white; handwritten text shown in italics): [Ost-Turkestan | (Aksu) | Rückbeil 1900], [Type | *gisela* Püng. ♂ | *abgebildet Iris 1901* | Püngeler], [ex coll. 1/8 | PÜNGELER], [GART | Exemplar und Eti- | Ketten dokumentiert | Specimen and label | Data documented | RO | 17.5. 2002], and [DNA sample ID: | NVG-22118E09 | c/o Nick V. Grishin], as the **lectotype** of *Lycaena gisela* Püngeler, 1901. The lectotype is missing the right antenna, its head is turned to the right, and the right forewing is tilted posteriad compared to its original position. The type locality of *L. gisela* is given on the label of the lectotype as “Aksu” but is suggested to be China: Xinjiang, Tarim River area near Aksu by Huang and Xing (2023). The COI barcode sequence of the lectotype, sample NVG-22118E09, GenBank [PZ516407](#), 658 base pairs, is:

```
AACATTATATTTATTTTGGAAATTTGAGCAGGAATATTAGGAACATCTCTAAGAATTTAATTCGAATAGAAATAGGAATCCAGGATCATTAATTTGGAGATGATCAAATTTATAATACT
ATTGTCACAGCTCATGCTTTTATTATAATTTTTCATAGTAATACCAATTATAATTTGGAGGATTTGGAAATTTGATTAGTACCTTTAATATTAGGTGCCCCAGATATAGCATTTCCTCGAA
TAAATAATATAAGATTTTGATTATTGCCCCATCATTAATATTATTATTTCAAGAAGAATTTGTAGAAAATGGAGCAGGAACAGGATGAACAGTGTACCCCCACTTTCATCAAATATTGC
TCATGGAGGATCATCTGTAGACTTAGCAATTTTCTTTACATTTAGCAGGATTTCTTCAATTTTAGGAGCAATTAATTTTATTACAATATTATTAATATACGGGTTAATAATTTATCA
TTTGATCAAATATCTTTATTATTGAGCTGTAGGAATTACAGCATATTACTATTACTATCATTACCAGTTTTAGCTGGAGCTATTACAATATTATTAAGTATGCAAAATTTAAACACCT
CATTTTGTATCCTGCTGGAGGAGGAGATCCAATCTTATATCAACATTTATTC
```

Lectotype designation for *Lycaena prosecusa* v. *korlana* Staudinger, 1901

Lycaena prosecusa v. *korlana* Staudinger, 1901, currently regarded as a valid subspecies of *Cupido* (*Everes*) *prosecusa* (Erschoff, 1874) (type locality in Kazakhstan: vic. Turkestan city), was described from three females collected in China: Xinjiang, Korla (Staudinger and Rebel 1901). We obtained a whole genome shotgun dataset of one female syntype of *L. prosecusa* v. *korlana* in the MFNB collection illustrated in Fig. 48b. The syntype agrees with the original description, is determined to be a syntype of this taxon by Y. Nekrutenki in 1998 according to one of its labels, and bears two labels in Staudinger’s handwriting stating the locality and the taxon name. Therefore, there is little doubt that this female is one of the three syntypes. To stabilize nomenclature and define the name *L. prosecusa* v. *korlana* objectively, N.V.G. hereby designates the syntype in the MFNB collection, a female illustrated in Fig. 48b, that bears

the following six labels (1st purple, 4th and 5th yellow, others white; 1st without any text, 2nd and 3rd handwritten, others printed with handwritten text shown in *italics*): [], [von Korla], [*Prosecusa* var.? | *Korlana* Stgr.], [*prosecusa korlana* | Staudinger, 1901 | SYNTYPUS | Y. Nekrutenko det. 10.11.1998], [GART | Exemplar und Eti- | Ketten dokumentiert | Specimen and label | Data documented | RO | 18.6. 2002], and [DNA sample ID: | NVG-22117G06 | c/o Nick V. Grishin], as the **lectotype** of *Lycaena prosecusa* v. *korlana* Staudinger, 1901. The second and third labels are in Staudinger's handwriting, and the second label states "from Korla" in German. The lectotype is a specimen in good condition with some scales rubbed off posteriad of vein Rs near the middle of the right hindwing. As suggested on one of its labels, and consistently with the original description, the type locality of *L. prosecusa* v. *korlana* is

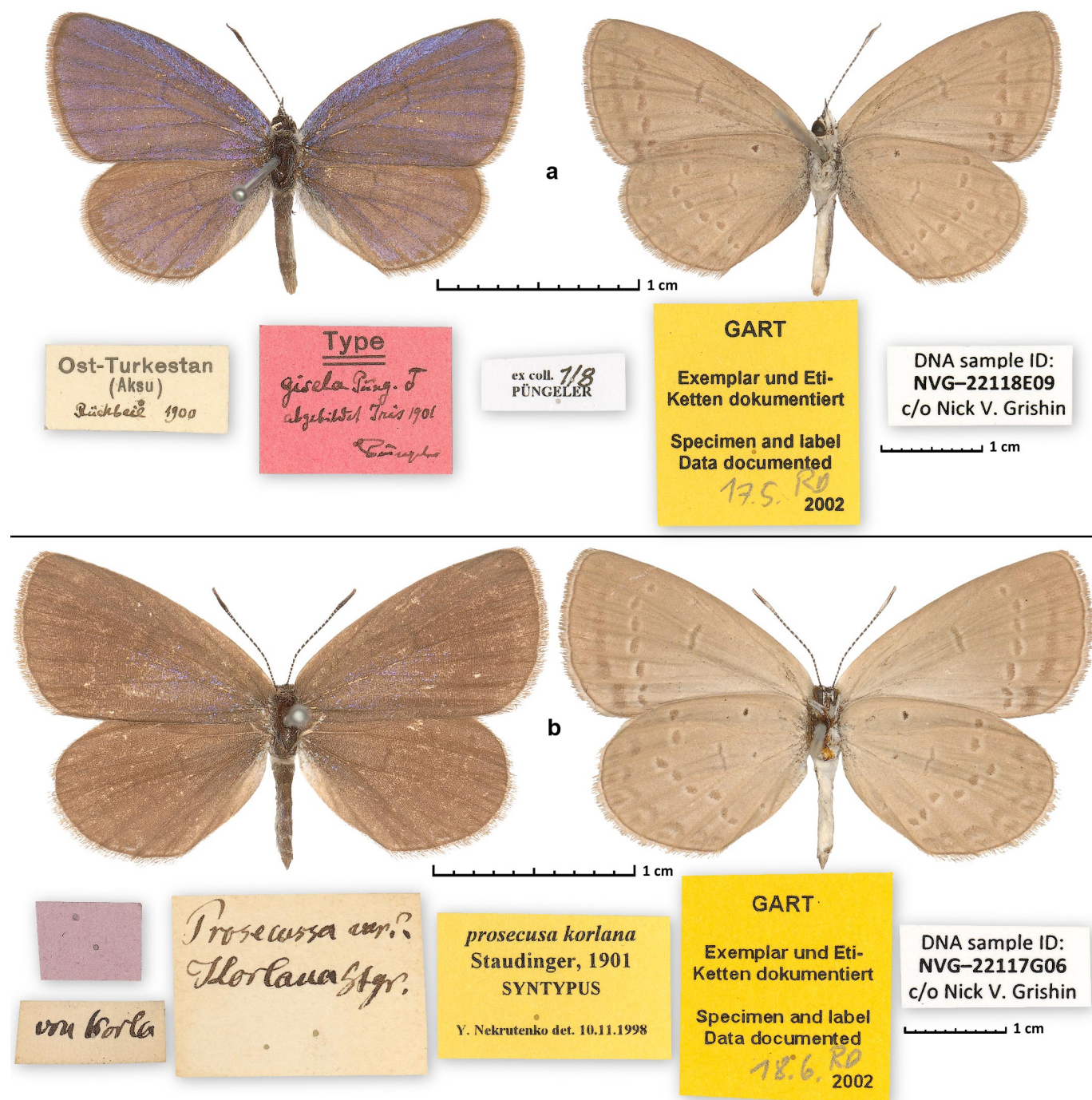


Fig. 48. Lectotypes (designated herein) of *Cupido* (*Sinocupido*) from China: Xinjiang in dorsal (left) and ventral (right) views, with their labels (below) [MFNB]: **a)** *Lycaena gisela* ♂ NVG-22118E09 from "Aksu" [Tarim River vicinity] and **b)** *Lycaena prosecusa* v. *korlana* ♀ NVG-22117G06 from Korla. Labels are reduced by ½ compared to the specimens. Larger and smaller scale bars refer to specimens and labels, respectively.

China: Xinjiang, Korla. The COI barcode sequence of the lectotype, sample NVG-22117G06, GenBank [PZ516408](#), 658 base pairs, is:

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AACATTATATTTTATTTTGGAAATTTGAGCAGGAATATTAGGAACATCTCTAAGAATTTTAATTCGAATAGAATTAGGAACCTCAGGATCATTAATTTGGAGATGATCAAATTTATAATACT
ATTGTCACAGCTCATGCTTTTATTATAATTTTTCATAGTAATACCAATTATAATTTGGAGGATTTGGAAATTTGATTAGTACCTTTAATATTAGGTGCCCGAGATATAGCATTTCTCGAA
TAAATAATATAAGATTTTGATTATTGCCCCATCATTAATATTATAATTTCAAGAAGAATTGTAGAAAATGGAGCAGGAACAGGATGAACAGTGTACCCCCACTTTCATCAAATATTGC
TCATGGAGGATCATCTGTAGACTTAGCAATTTTCTTTACATTAGCAGGGATTTCTTCAATTTAGGAGCAATTAATTTTATTACAATATTATTAATATACGGGTTAATAATTATCA
TTTGATCAATATCTTTATTATTGAGCTGTAGGAATTACAGCATTATTACTATTACTATCATTACCAGTTTGTAGTGGAGCTATTACAATATTATTAAGTATGCGAAATTTAAACACCT
CATTTTGTATCTGCTGGAGGAGGATCCAATCTTATATCAACATTTATTC
```

***Lycaena gisela* Püngeler, 1901 is a male of *Cupido (Sinocupido) korlana* Staudinger, 1901, stat. nov., which is a valid species, not a junior subjective synonym of *Cupido (Everes) proscusa duplex* (Alphéraky, 1887)**

Genomic phylogeny reveals that the lectotype (NVG-22118E09) and paralectotype (NVG-22127E06) of *Lycaena gisela* Püngeler, 1901-X-5 (type locality in China: Xinjiang, Tarim River area near Aksu), both males, and the lectotype of *Lycaena proscusa* v. *korlana* Staudinger, 1901-V (type locality China: Xinjiang, Korla) form a tight clade distinct from all other species, but displaying little genetic differentiation between the three type specimens consistent with their conspecificity (Fig. 47); e.g., their COI barcodes are 100% identical. They are phenotypically similar and come from nearby localities. Therefore, we propose that *Lycaena gisela* Püngeler, 1901 is a male of *Cupido (Sinocupido) korlana* Staudinger, 1901, stat. nov., which we regard as the valid name for this species, instead of treating this name as a junior subjective synonym of *Cupido (Everes) proscusa duplex* (Alphéraky, 1887) (type locality in China: Xinjiang, Lob-Noor area) as suggested by Nazari et al. (2025), the latter taxon being in a different subgenus. The taxonomic identity of the *C. (Sinocupido) korlana* lectotype implies that this name has been misapplied. The taxon previously referred to by this name is either *Everes acaudata* Lee, 1963 (type locality China: Xinjiang, Ruoqiang, Milan) treated as its junior subjective synonym by Huang and Xing (2023) or *Lycaena proscusa* var. *duplex* Alphéraky, 1887 treated as its senior subjective synonym by Nazari et al. (2025). The synonymy depends on whether one considers *E. acaudata* and *L. proscusa* var. *duplex*, which are from nearby localities in China: Xinjiang, to represent different subspecies, and Nazari et al. (2025) suggested synonymizing them.

***Sinocupido lokiangensis* Lee, 1963 is a junior subjective synonym of *Cupido (Sinocupido) korlana* Staudinger, 1901**

Nazari et al. (2025) used *Sinocupido lokiangensis* Lee, 1963 (type locality in China: Xinjiang, Alagan, north of Ruoqiang, alongside the Tarim River) as the valid name for the species, which Huang and Xing (2023) called *Cupido gisela* (Püngeler, 1901) (type locality in China: Xinjiang, Tarim River area near Aksu). The latter name, although available, is permanently invalid as a junior primary homonym of *Lycaena gisella* Staudinger, 1888, which is treated as a valid subspecies of *Philiris helena* (Snellen, 1887). As shown above, genomic analyses reveal that *Lycaena gisela* Püngeler, 1901 is conspecific with *Cupido (Sinocupido) korlana* Staudinger, 1901 (type locality China: Xinjiang, Korla). Therefore, we propose that *Sinocupido lokiangensis* Lee, 1963, syn. rev. is a junior subjective synonym of *Cupido (Sinocupido) korlana* Staudinger, 1901.

***Plebejus (Lycaeides) scudderii* (W. H. Edwards, 1861), stat. rest.**

As suggested by Toro-Delgado et al. (2026) and observed by us in a preliminary genomic analysis (data not shown), North American populations currently identified as *Plebejus (Lycaeides) idas* (Linnaeus, 1760) (type locality in Sweden) are not conspecific with the European nominotypical populations of that species and therefore represent a distinct species. The oldest available name for this species is *Plebejus (Lycaeides) scudderii* (W. H. Edwards, 1861), stat. rest. (type locality in Canada: Saskatchewan), which thus becomes its valid name. Consequently, pending more detailed studies, we treat all North American subspecies formerly assigned to *P. idas* as subspecies of *P. scudderii*.

Family HesperIIDae Latreille, 1809
Subfamily Eudaminae Mabilie, 1877
Tribe Entheini Grishin, 2019

***Drephalys (Paradrephalys) cremoreus* Grishin, new species**

<https://zoobank.org/698DF554-E2B1-457D-B7B3-25100C0B980E>

(Figs. 49 part, 50c)

Definition and diagnosis. Genomic analysis reveals that a female of *Drephalys* E. Watson, 1893 (type species *Eudamus helixus* Hewitson, 1877) from Bolivia is sister to *Drephalys (Paradrephalys) talboti* (Le Cerf, 1922) (type locality in French Guiana) and is genetically differentiated from it at the species level (Fig. 49); e.g., their COI barcodes differ by 3.8% (25 bp), and therefore this female represents a new species. This new species is most similar to its sister *D. talboti* (Fig. 50a, b), sharing with it two unique characters: the absence of a yellow postdiscal spot in cell Rs-M₁ on the dorsal hindwing in females, and a roundish cream spot at the end of the discal cell on the ventral hindwing that is separated from other pale markings rather than fused with the pale-yellow area along the inner margin (Fig. 50b, c vs. d); however, differs from it and other relatives by the following combination of characters in females (the male is unknown and may differ due to sexual dimorphism): paler, cream-colored wing bases on the ventral side [orange in *D. talboti*]; paler brown and violaceous areas on the ventral side of the wings and a black tornal area on the hindwing that contrasts more strongly with the paler ground color; a larger cream spot at the end of the discal cell on the ventral hindwing; and an elongated, tear-shaped yellow spot at the base of cell CuA₁-CuA₂ on the dorsal hindwing that does not extend posteriad beyond vein CuA₂ [extends in *D. talboti*]. Due to unexplored individual variation and males being unknown, this species is best identified by DNA, with diagnostic base pairs in the nuclear genome: aly3850.4.8:C141G, aly3850.4.8:A204G, aly423.17.9:A147G, aly4266.1.12:A318C, aly2790.9.2:T535A, aly671.40.5:C279C (not T), aly481.25.21:T117T (not C), aly322.41.77:G85G (not T), aly1539.18.2:G39G (not A), aly1146.50.11:G96G (not A); and the COI barcode: A100G, T355C, T337A, A373G, T415A, T581C.

Barcode sequence of the holotype. Sample NVG-24056H11, GenBank [PZ516409](https://www.ncbi.nlm.nih.gov/GenBank/698DF554-E2B1-457D-B7B3-25100C0B980E), 658 base pairs:

AACATTATATTTATTTTGGAAATTTGAGCAGGAATAGTTGGTACATCTTTAAGTCTTTTAATTCGAACATAGGAAGTCCAGGATCTTTAATTTGGGGATGATCAAATTTATAATACT
ATTGTTACAGCTCATGCTTTTATTATAATTTTATAGTTATACCTATTATAATTGGAGGATTTGGAAATTTGATTAGTTCTTTAATATTAGGAGCCCTGACATAGCATTCCCACGAA
TAAATAATATAAGATTTTGGTTATTACCCCCCTCATTAACCTTATTAAATTTCTAGAGAATTTAGAAAAATGGAGCTGGAACTGGATGAACAGTATATCCCCACTTTTCATCCAATATTGC
ACATCAAGGGTCTTCTGTAGATTTAGCTATTTTTCATTACATTTAGCTGGAATTTTCATCAATTTAGGAGCTATTAATTTTATTACAACAATTATTAATATACGAATTAATAATTTATCA
TTTGATCAAAATACCTTTATTTGTTGAGCTGTAGGTATTACAGCCTTATTATTACTTTTCATTACCTGTTTTCAGGAGCTATTACTATACCTTCTAACCCAGCCGAAATTTAAATACAT
CATTTTTCGATCTGCAGGAGGAGGATCTATTTTATATCAACATTTATTT

Type material. Holotype: ♀ deposited in the Natural History Museum of Denmark, University of Copenhagen, Copenhagen, Denmark (ZMUC), illustrated in Fig. 50c, bears the following three rectangular labels (2nd handwritten, others printed with handwritten text shown in *italics*), two white: [*Paradros oriander* ♀ | *Hew* | *Buenavista 450 m* | *Bolivia Steinbach*. | Modt. 11/11 1925 af | *José Steinbach. Bolivia*. | Coll.C.S.Larsen, Faaborg], [DNA sample ID: | NVG-24056H11 | c/o Nick V. Grishin], and one red [HOLOTYPE ♀ | *Drephalys (Paradrephalys) cremoreus* Grishin]. The date on the specimen label indicates when this specimen was received by Larsen, not collected by Steinbach (Danish: Modt[aget]. = received; af = from).

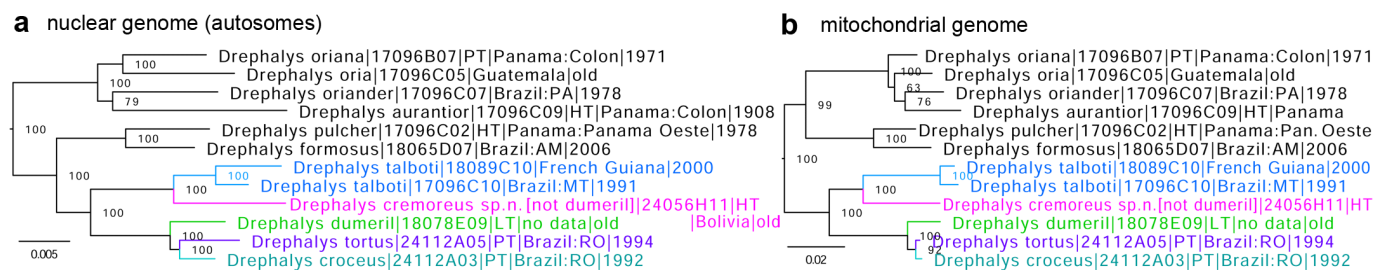


Fig. 49. Phylogenetic trees of all valid species of the subgenus *Paradrephalys* Burns, 2000 constructed from protein-coding regions in: **a**) the nuclear genome (autosomes), based on 2,748,546 positions, and **b**) the mitochondrial genome. Species discussed in the text are colored: *D. talboti* (blue), *D. cremoreus* sp. n. (magenta), *D. dumeril* (green), *D. tortus* (violet), and *D. croceus* (cyan). Ultrafast bootstrap (Hoang et al. 2018) values are shown at nodes.



Fig. 50. Specimens of *Drephalys* in dorsal (left) and ventral (right) views, data in text or below: **a–b)** *D. talboti* non-types: **a)** ♂ NVG-17096C10, USNM_{ENT} 00894941 Brazil: Mato Grosso, Diamantino, Alto Rio Arinos, 350-400 m, GPS -14.217, -56.200, 23-Feb-1991, E. Furtado leg., genitalia X-4259 J. M. Burns 1997 [USNM] and **b)** ♀ NVG-18089C10, H-18636 French Guiana: Pointe Malmanoury, GPS 5.283, -53.825, 13-Oct-2000, C. Faynel leg. [EBC]; **c)** *D. cremoreus* **sp. n.** holotype ♀ NVG-24056H11 from Bolivia; and **d)** *D. tortus* Austin, 1995 paratype ♀ NVG-24112A05 Brazil: Rondônia, Linha C-10 (at Rio Pardo), off B-65, 5 km S of Cacaulândia, 15-Jun-1994, O. Gomes leg., genitalia GTA-5134 [MGCL].

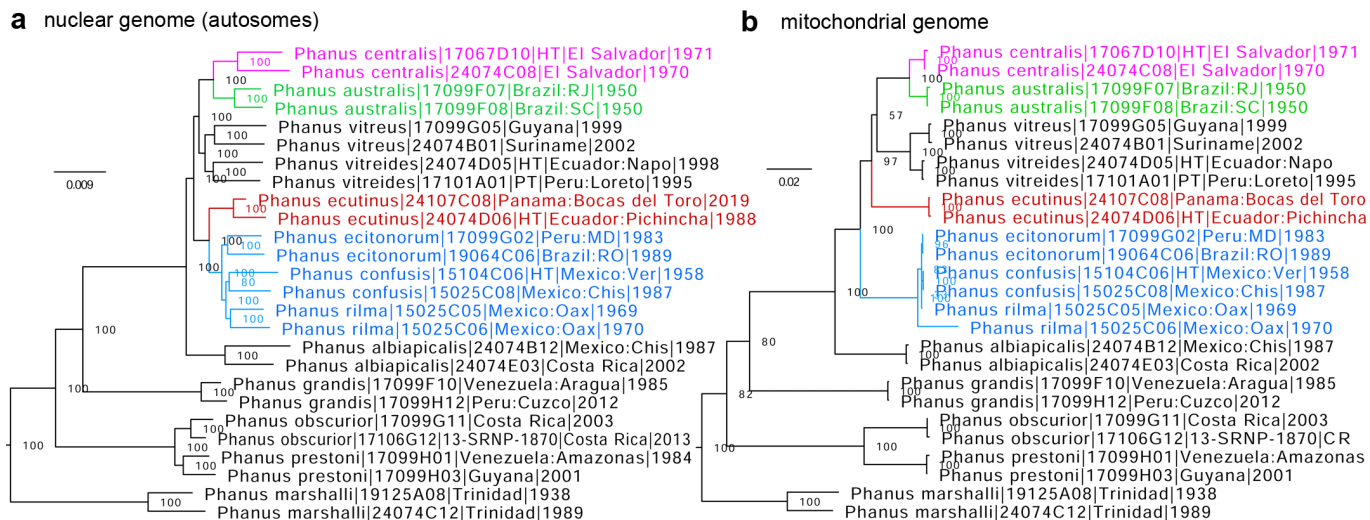


Fig. 51. Phylogenetic trees of all valid *Phanus* species constructed from protein-coding regions in: **a)** the nuclear genome (autosomes), based on 4,427,214 positions, and **b)** the mitochondrial genome. Species previously known from a single specimen and their sister groups, are colored: *P. centralis* (magenta), *P. australis* (green), *P. ecutinus* (red), and a trio of species in blue: *P. ecitonorum*, *P. confusus*, and *P. rilma*. Ultrafast bootstrap (Hoang et al. 2018) values are shown at nodes.

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

Etymology. In Latin, *cremoreus* means made of cream, creamy, cream-like, or cream-colored. The name reflects paler colors of this new species and is an adjective.

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

***Phanus centralis* Grishin, 2025 is confirmed as a species by sequencing a second specimen from El Salvador**

Genomic analysis of newly sequenced specimens of *Phanus* Hübner, [1819] (type species *Papilio vitreus* Stoll, 1781) reveals a male of *Phanus centralis* Grishin, 2025 (type locality El Salvador: San Salvador; holotype sequenced as NVG-17067D10), a species previously known only from a single female (Zhang et al. 2025b) (Fig. 51). The male, sequenced as NVG-24074C08 from El Salvador: Santa Tecla, 700 m, 16-Jul-1970, L. M. Steinhauser leg., genitalia SRS-1231 [MGCL] (Fig. 52a), is similar to the female holotype (Fig. 52b) and confirms the validity of *P. centralis* as a distinct species and sister to *Phanus australis* L. Miller, 1965 (type locality in Brazil: Santa Catarina) rather than an atypical or mislabeled specimen. No genitalia were present in the vial SRS-1231, which contained only the abdominal skin; therefore, another male is needed to illustrate the male genitalia of *P. centralis*. The COI barcode sequence of the male, sample NVG-24074C08, GenBank [PZ516410](https://www.ncbi.nlm.nih.gov/nuclot/PZ516410), 658 base pairs, is identical to that of the holotype:

```
AACTTTATATTTTATTTTGGAAATTTGAGCTGGAATAGTAGGTACATCTCTAAGTTTATTAATTCGAACAGAATTAGGAACCTCTGGATCTTTAATTTGGAGATGATCAAAATTTATAATACT
ATTGTCACATGCACATGCAATTTATTATAATTTTTCATAGTAATACCAATTATAATTTGGAGGATTTGGAAATTTGATTAGTACCTTTAATATTAGGAGCTCCCGATATAGCTTTCCCTCGAA
TAAATAATATAAGTTTGTACTTCTCCCCATCATTAACCTTTATTAAATTTCAAGAAGAAATTTAGAAAATGGAGCCGGAACCTGGATGAACAGTTTATCCCTCTTTCATCTAATATTGC
TCATCAAGGTTTCATCTGTCGATTAGCAATTTTCTTTACACTTAGCTGGAATTTTCATCTATTTTAGGTGCAATTAATTTTATTACCACAATTATTAATATACGTATTAGAAATTTATCT
TTTGATCAAAATACCTTTATTATTGAGCTGTTGGAATTACTGCTTTATTATTACTTTCTCTCTCTGTTTGTAGCAGGAGCTATCACAATACTTTTAACTGATCGAAATTTAAATACAT
CATTTTTTGATCTGCTGGTGGAGGAGATCCCATCTTTATCAACATTTATTT
```

***Phanus ecutinus* Grishin, 2025 is confirmed as a species and its range extended to include Panama**

Genomic analysis of newly sequenced specimens of *Phanus* Hübner, [1819] (type species *Papilio vitreus* Stoll, 1781) reveals a second female of *Phanus ecutinus* Grishin, 2025 (type locality Ecuador: Pichincha, 12 km E of Santo Domingo de los Colorados, Tinalandia Lodge) (Fig. 52c), previously known only from

the female holotype (Fig. 52d), thus confirming it as a species-level taxon sister to *Phanus ecitonorum* Austin, 1993 (type locality in Brazil: Rondônia) in the nuclear genome (Fig. 51a). The newly found female, sequenced as NVG-24107C08 from Panama: Bocas del Toro, Fortuna Cabins, GPS 8.7814,



Fig. 52. Specimens of *Phanus* in dorsal (top or left) and ventral (bottom or right) views, data in text or below:
a–b) *P. centralis* from El Salvador: **a)** non-type ♂ NVG-24074C08 and **b)** holotype ♀ NVG-17067D10; and
c–d) *P. ecutinus*: **c)** non-type ♀ NVG-24107C08 from Panama and **d)** holotype ♀ NVG-24074D06 from Ecuador.

–82.1909, 28-Apr–7-May-2019, collected by E. Riley at UV light [TAMU] (Fig. 52c), extends the known distribution of this species to western Panama in addition to northwestern Ecuador, which includes the type locality. The COI barcode sequence of the female from Panama, sample NVG-24107C08, GenBank [PZ516411](https://www.ncbi.nlm.nih.gov/nuclot/PZ516411), 658 base pairs, is identical to that of the holotype from Ecuador:

```
AACTTTTATATTTTATTTTGGAAATTTGAGCCGGAATAGTAGGTACATCTTTAAGTTTATTAATTCGAACAGAATTAGGAACCCCTGGATCTTTAATTGGAGATGATCAAATTTATAATACT
ATTGTTACTGCTCATGCATTATTATAATTTTATAGTAATACCAATTATAATTTGGAGGATTTGGAAATTGATTAGTAGTACCTTTAATATTGGGTGCCCCAGACATAGCTTTCCCTCGAA
TAAATAATATAAGTTTGTGACTCCTCCCCCATCATTAACTTTTATTAATCTCAAGAAGAATTGTAGAAAATGGAGCCGGAAGTGGATGAACAGTTTATCCCTCTTTTCATCTAATATTGC
TCACCAAGGTTTCATCTGTCGATTAGCAATCTTTTCCCTTACACTTAGCTGGAATTTTCATCTATTTTAGGTGCAATTAATTTTATTACTACAATTATTAATATACGTATTAGAAATTTATCT
TTTGATCAAAATACCCTTATTCATTGAGCGGTTGGAATTACTGCTTATTATTATTACTTCTCTCTCTGTTTAGCAGGAGCTATTACAATACTTTTAAGTACCGAAATTTAAATACAT
CATTTTGTATCTGCTGGAGGAGATCCAATTTTACCAACATTTATTT
```

Tribe Phocidini Tutt, 1906

Dyscophellus megaporsena Grishin, new species

<https://zoobank.org/C12017E0-9E51-4336-B022-6F0AC57C3592>

(Figs. 53d, 54 part)

Definition and diagnosis. Genomic analysis reveals that a male of *Dyscophellus* Godman and Salvin, 1893 (type species *Papilio sebalus* Stoll, 1781) from Argentina is in the clade with other tawny species characterized by a broad pale area along the costal margin of the dorsal hindwing, extending to about half of the wing length, preceded by the dark basal spot and followed by the dark-brown longitudinal stripe between veins Sc+R₁ and M₁: *Dyscophellus porsena* E. Bell, 1934 (type locality Peru: Loreto, Iquitos; holotype sequenced as NVG-15104B04) (Fig. 53a), *Dyscophellus basialbus* Grishin, 2022 (type locality in Brazil: Rondônia; holotype sequenced as NVG-15026C05) (Fig. 53b), and *Dyscophellus porsenica* Grishin, 2025 (type locality in Peru: Madre de Dios; holotype sequenced as NVG-17104C04) (Fig. 53c), but is genetically differentiated from every one of them at the species level (Fig. 54); e.g., their COI barcodes differ by at least 2.1% (14 bp) (with *D. porsenica* being the closest species in the mitochondrial genome tree), and therefore this specimen represents a new species. This new species keys to “*Dyscophellus diaphorus*” (misidentification) (D.4.8) in Evans (1952), but differs from it and other relatives by the following combination of characters (including the tawny dorsal color and the white hindwing area mentioned above and shared with other species in this clade): larger in overall size; slightly rounder wings; more prominent spots in the apical third of the forewing, especially on the dorsal side in cell M₃-CuA₁; this spot is elongated and curved (or possibly divided into two spots) with gray scales along its center; more prominent pale scaling within the ventral hindwing brown spots, especially in cell M₃-CuA₁ (as on the forewing); and a more diffuse transition between the costal dark-brown area of the dorsal hindwing and the tawny ground color submarginally [more sharply defined in *D. porsena*]. Due to its cryptic nature and unexplored individual variation, this species is best identified by DNA, with diagnostic base pairs in the nuclear genome: aly10672.5.1:T2019C, aly2178.6.3:G120A, aly2178.6.3:C126T, aly320.4.1:T108C, aly420.60.7:A72C, aly420.60.7:A90A (not G), aly528.39.8:G552G (not A), aly1432.15.3:G36G (not A), aly127.46.1:T27T (not C), aly127.46.1:C51C (not T); and the COI barcode: A31G, C81T, C287C, T292C, A328G, T500C.

Barcode sequence of the holotype. Sample NVG-24019E12, GenBank [PZ516412](https://www.ncbi.nlm.nih.gov/nuclot/PZ516412), 658 base pairs:

```
AACTCTTTATTTTATTTTCGGAATTTGAGCCGGAATAGTAGGTACATCATTAAAGATTATTAATTCGAACGTAATTAGGAATTTAGGTTCTTTAATTGGTGATGATCAAATTTATAATACT
ATTGTTACAGCTCATGCTTTTATTATAATTTTATGTTAATACCTATTATAATTTGGAGGATTTGGAAATTGATTAGTAGTACCTAATATTAGGAGCTCCTGATATAGCTTTTCCACGAA
TAAATAATATAAGATTTGATTATTACCCCATCTTAACTTTTACTAATCTCAAGAAGAATTGTTGAAAATGGTGACAGGAGGTTGAAGTGTATCTCTCTTTATCTTCTAATATTGC
TCATCAAGGATCTTCTGTTGATTAGCAATTTTCTTTACATTTAGCAGGAATTTTCATCAATTTTAGGAGCTATTAAATTTTATTACTACAATTATTAATATACGAATTAGAAATTTATCA
TTTGATCAAAATACCCTATTTGTTTGTATCTGTTGGAATTACAGCTTTTATTATTATTACTTCTTTACCTGTATTAGCAGGAGCTATTACAATACTTCTCACTGATCGAAATTTAAATACAT
CATTTTGTATCTGCTGGTGGAGGAGACCAATTTTATATCAACATTTATTT
```

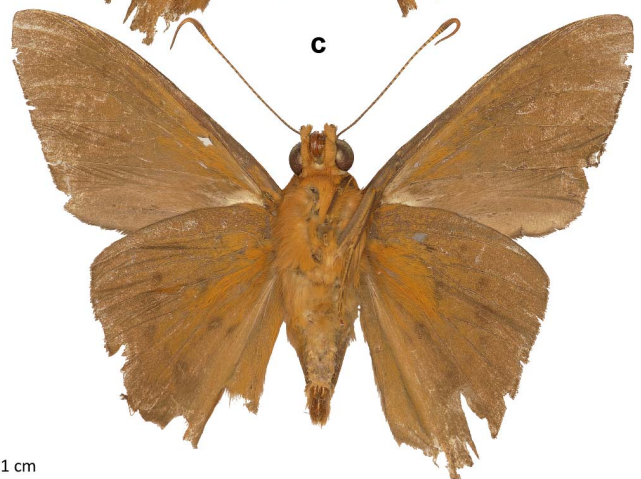
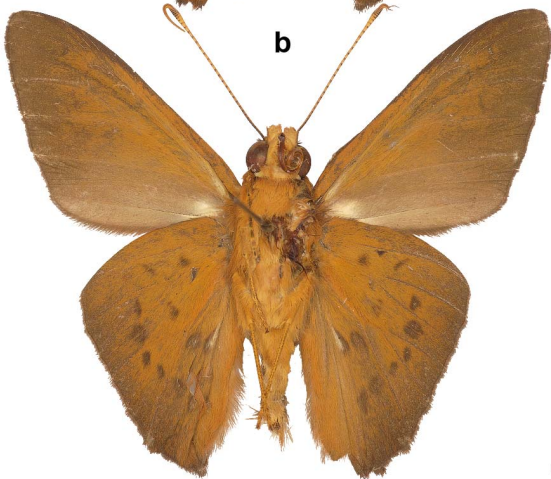
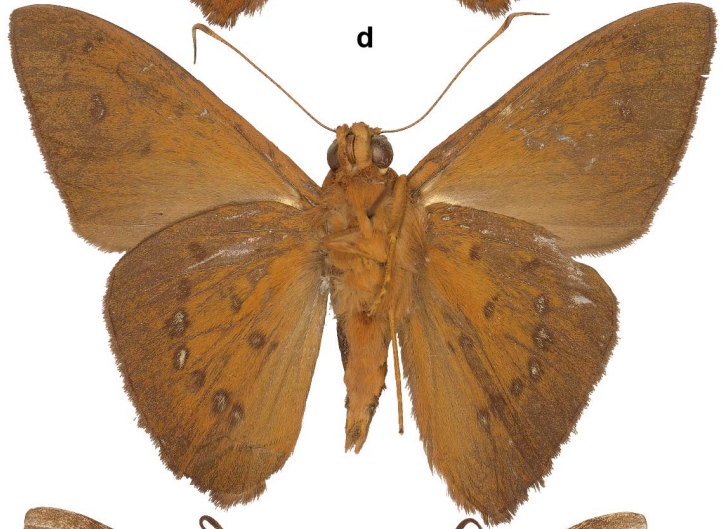
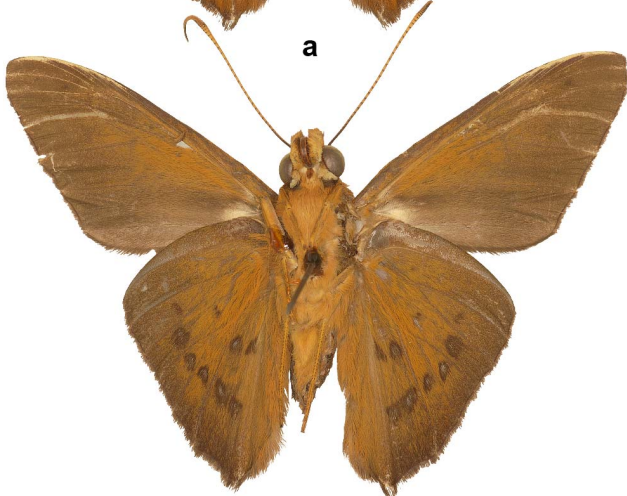
Type material. Holotype: ♂ deposited in the Senckenberg Natural History Museum, Frankfurt, Germany (SMF), illustrated in Fig. 53d, bears the following four rectangular labels (1st handwritten, others printed), three white: [patria ? | N. Argent.], [Coll. | A. Seitz], [DNA sample ID: | NVG-24019E12 | c/o Nick V. Grishin], and one red [HOLOTYPE ♂ | *Dyscophellus* | megaporsena Grishin]. The first label (locality label) questions the origin of this specimen in Argentina (“patria?”, literally translated as “fatherland?”, meaning “locality?”). The locality of the holotype will be determined by genomic comparison with other specimens belonging to this clade as they become available.



a



d



1 cm

Fig. 53 (see the previous page). Holotypes of *Dyscophellus porsena* and relatives, males in dorsal (above) and ventral (below) views: **a)** *D. porsena* NVG-15104B04 Peru: Loreto, Iquitos, 7-Apr-1931, genitalia G827 [AMNH]; **b)** *D. basialbus* NVG-15026C05 Brazil: Rondônia, 65 km S of Ariquemes, Linha C-20, 7 km E of B-65, Fazenda Rancho Grande, 9-Jun-1993, G. T. Austin leg. [MGCL]; **c)** *D. porsenica* NVG-17104C04 Peru: Madre de Dios, 30 km SW of Puerto Maldonado, 330 m, 24-Oct-1983, S. S. Nicolay leg. [USNM]; and **d)** *D. megaporsena* **sp. n.** NVG-24019E12 northern Argentina ?, old, coll. A. Setiz [SMF].

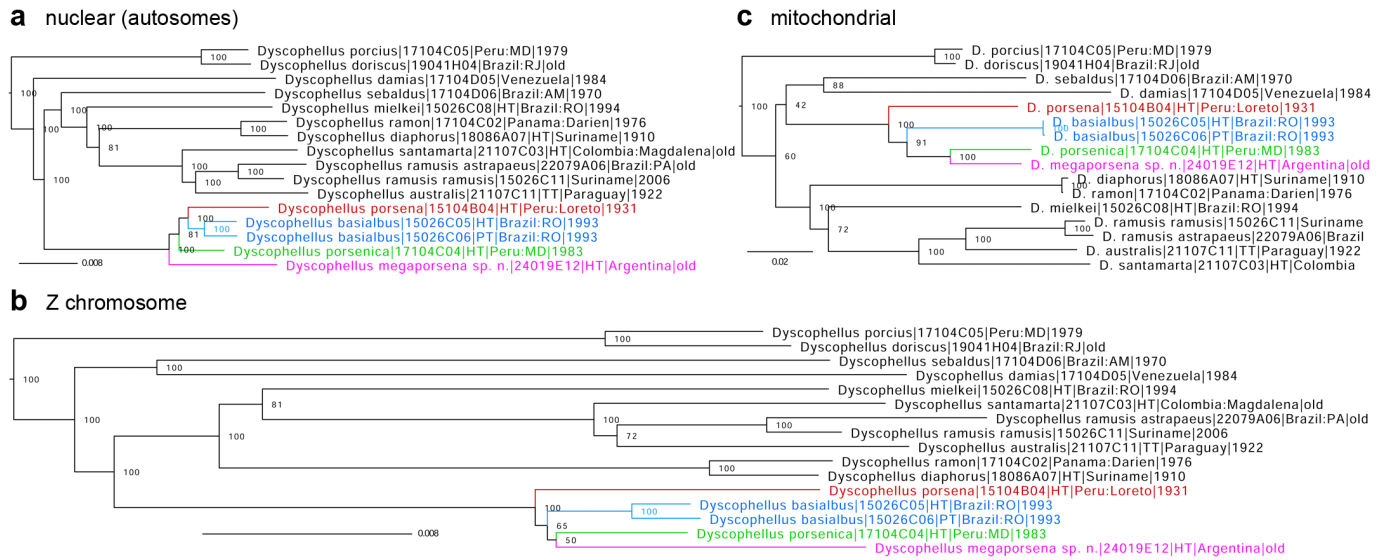


Fig. 54. Phylogenetic trees of all valid *Dyscophellus* taxa constructed from protein-coding regions in: **a)** the nuclear genome (autosomes), based on 7,833,465 positions, **b)** the Z chromosome, based on 217,755 positions, and **c)** the mitochondrial genome. Species discussed in the text are colored: *D. porsena* (red), *D. basialbus* (blue), *D. porsenica* (green), and *D. megaporsena* **sp. n.** (magenta). Ultrafast bootstrap (Hoang et al. 2018) values are shown at nodes.

Type locality. Argentina: northern part (possibly Misiones), although questionable according to the holotype label.

Etymology. The name reflects the large size of this species related to *D. porsena* and is treated as a noun in apposition.

Distribution. Currently known only from the holotype, possibly collected in northern Argentina.

Tribe Eudamini Mabilie, 1877

Cecropterus (Cecropterus) capys Godman & Salvin, 1894, stat. rest. is a valid species distinct from *Cecropterus (Cecropterus) longipennis* Plötz, 1882

Genomic analysis of *Cecropterus (Cecropterus) longipennis* Plötz, 1882 (type locality in South America; no locality data on possible syntypes but Brazil: Rio de Janeiro hypothesized from genomic comparison, see the next section) specimens from across the range reveal that they partition into two clades genetically differentiated at the species level (Fig. 55), e.g., their COI barcodes differ by 2.3% (15 bp). The name *C. longipennis* applies to the South American clade. The name *Cecropterus capys* Godman & Salvin, 1894 (type locality Panama, Colón, “Lion Hill”, now submerged beneath the waters of Gatun Lake; holotype by the original designation: “our type specimen is from Panama” (Godman and Salvin 1894)) applies to the clade consisting of specimens from Central America and Northeastern South America. Therefore, we propose that *Cecropterus (Cecropterus) capys* Godman & Salvin, 1894, **stat. rest.** is a valid species distinct from *Cecropterus (Cecropterus) longipennis* Plötz, 1882. We note that both names are used as originally proposed (except for the addition of a subgenus name), in their original status and combination.

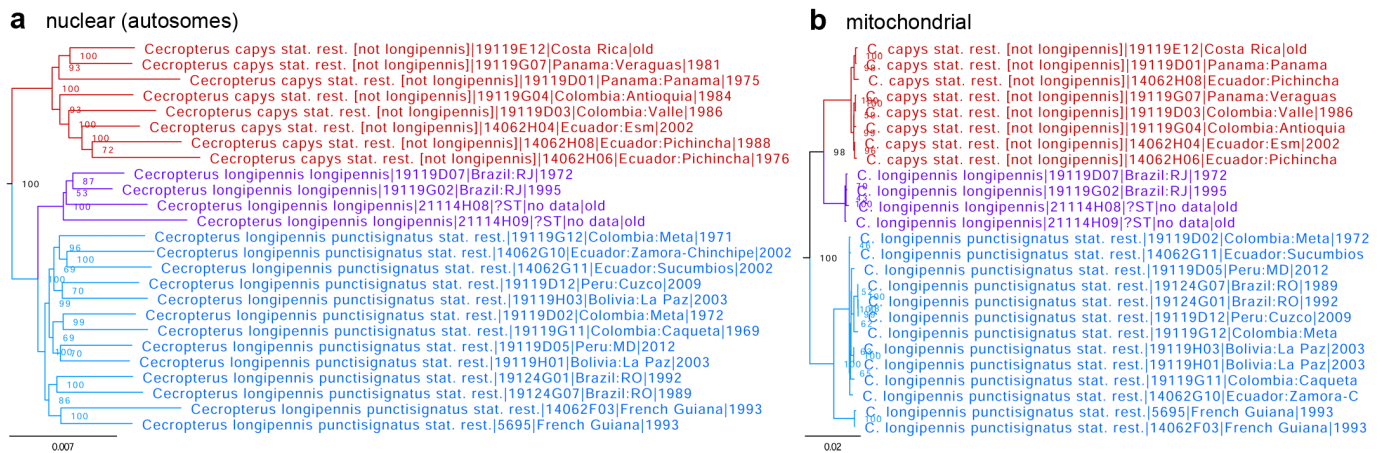


Fig. 55. Phylogenetic trees of the clade previously identified as *Cecropterus (Cecropterus) longipennis* constructed from protein-coding regions in: **a)** the nuclear genome (autosomes), based on 3,962,679 positions, and **b)** the mitochondrial genome. Different taxa are colored differently: *C. capys stat. rest.* (red), *C. longipennis longipennis* (magenta), and *C. longipennis punctisignatus stat. rest.* (blue). Ultrafast bootstrap (Hoang et al. 2018) values are shown at nodes.

***Cecropterus (Cecropterus) longipennis punctisignatus* Bryk, 1953, stat. rest. is a valid subspecies distinct from *Cecropterus (Cecropterus) longipennis* Plötz, 1882**

Genomic analysis of specimens of *Cecropterus (Cecropterus) longipennis* Plötz, 1882 (type locality in South America) from across the range reveals that they partition into two non-sister clades by their mitochondrial haplotypes (Fig. 55b violet and blue), and the same clades are present (although less prominently) as sisters in the nuclear genome tree (Fig. 55a violet and blue). Therefore, the two clades correspond to two distinct taxa. Conservatively, we treat them as subspecies pending further research. One clade includes specimens from Rio de Janeiro in Brazil (Fig. 55b violet). Two possible syntypes of *C. longipennis* that we found in MFNB are in this clade. The possible syntypes do not bear locality labels, consistent with the fact that no specific locality was given in the original description, which referenced Herrich-Schäffer *in litteris* (Plötz 1882). However, the close clustering of the possible syntypes with specimens from Rio de Janeiro, Brazil, suggests that the type locality of *C. longipennis* was likely in southeastern Brazil, and possibly in Rio de Janeiro, where many pre-1880s specimens, like those seen by Herrich-Schäffer, originated. Therefore, pending additional studies and a more extensive search for *C. longipennis* syntypes, we tentatively consider populations in southeastern Brazil to represent the nominotypical subspecies. The second clade consists of specimens from the remainder of the range (Fig. 55b blue), which includes the type locality of the only available name applicable to it: *Cecropterus aunus* form *punctisignatus* Bryk, 1953 (type locality Peru: Loreto, Iquitos). Therefore, we propose that *Cecropterus (Cecropterus) longipennis punctisignatus* Bryk, 1953, **stat. rest.** is a valid subspecies distinct from *Cecropterus (Cecropterus) longipennis* Plötz, 1882.

***Cecropterus (Murgaria) perichales* Grishin, new species**

<https://zoobank.org/4F0B6553-BF10-4B81-8699-5C4A89EBA6D9>

(Figs. 56 part, 57)

Definition and diagnosis. Genomic analysis reveals that a male from Peru initially identified as *Cecropterus (Murgaria) chales* (Godman & Salvin, 1893) (type locality Mexico: Guerrero, Acapulco) is not monophyletic with it and instead is sister to both *C. chales* and *Cecropterus (Murgaria) doryssus* (Swainson, 1831) (type locality in Brazil: Bahia) in the nuclear genome tree (Fig. 56a), while occupying an even more distant position in the mitochondrial genome tree (Fig. 56b). Therefore, this male represents a new species genetically distant from *C. chales*, e.g., their COI barcodes differ by 5.8% (38 bp). This new species keys to “*Urbanus chales*” (C.13.23) in Evans (1952), but differs from it and other relatives

by the following combination of characters: mostly brown wings without bands except for the marginal white band of the hindwing, extending from the middle of the outer margin through the tornal tail on the dorsal side and from near the apex of the ventral side; three small but well-defined subapical forewing hyaline spots in a relatively straight row; two small semihyaline spots near the forewing mid-costa; the absence of discal spots on the forewing (except for a vestigial paler brown streak in the anterior part on the ventral side); the absence of marginal brown spots within the pale marginal band of the ventral hindwing; and more extensive marginal white overscaling on the ventral forewing, especially towards the tornus. Due to its cryptic nature and unexplored individual variation, this species is best identified by DNA, with diagnostic base pairs in the nuclear genome: aly1121.5.7:C75T, aly4683.2.1:G96A, aly13410.5.2:C118T, aly6954.5.15:C132T, aly6954.5.15:T141C, aly529.6.2:A204A (not G), aly529.6.2:C207C (not T), aly1113.9.3:T48T (not C), aly9588.17.4:C63C (not T), aly9588.17.4:C66C (not A); and the COI barcode: T16C, A100G, T287T, T325C, A494T, 557C.

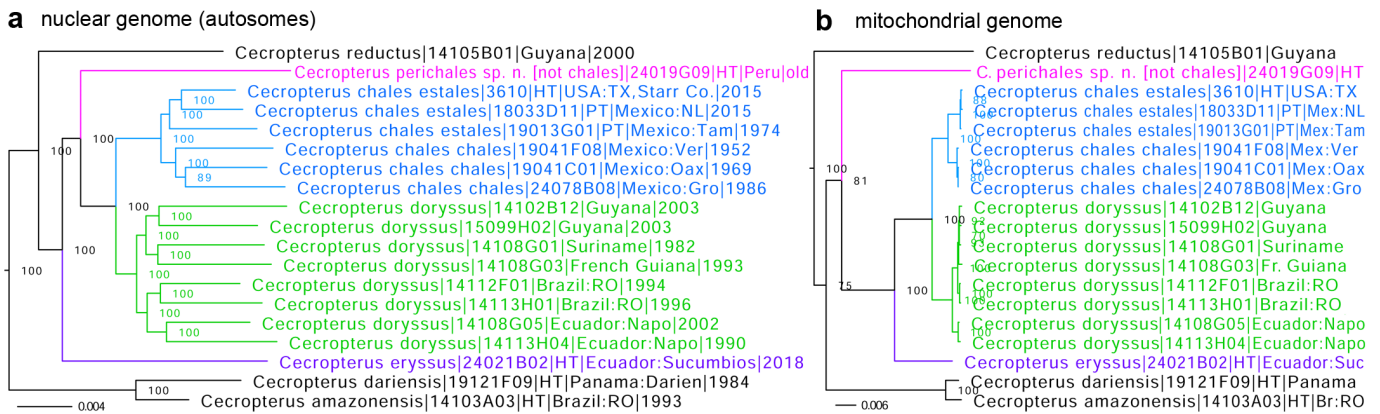


Fig. 56. Phylogenetic trees of the clade with *C. doryssus* constructed from protein-coding regions in: **a)** the nuclear genome (autosomes), based on 16,643,085 positions, and **b)** the mitochondrial genome. Four closely related species are colored differently *C. perichales* sp. n. (magenta), *C. chales* (blue), *C. doryssus* (green), and *C. eryssus* (violet). Ultrafast bootstrap (Hoang et al. 2018) values are shown at nodes.



Fig. 57. *Cecropterus* (*Murgaria*) *pechales* sp. n. holotype ♂ NVG-24019G09 in dorsal (left) and ventral (right) views.

Barcode sequence of the holotype. Sample NVG-24019G09, GenBank [PZ516413](https://www.ncbi.nlm.nih.gov/nuclot/PZ516413), 658 base pairs:

```
AACTTTATATTTTATCTTTGGAATTTGAGCAGGATTAGTTGGAACCTCACTAAGTTTACTTATTCGAACCTGAATTAGGAACCTCAGGATCTTTAATTTGGGGATGATCAGATTTATAATACT
ATTGTAACAGCTCATGCTTTTATTATAATTTTATGTTATACCTATTATAATTGGAGGATTTGGTAATTGATTAATTCCTTATATTAGGAGCCCCGATATAGCCTTCCCCGTA
TAAACAATATAAGATTTTGATTATTACCCCCATCCCTAACTCTTTTAATTTCAAGAAGAATTGTAGAAAATGGTGCAGGCACCGGATGAACAGTTTACCCCCCTATCATCTAATATTGC
CCATCAAGGAGCATCTGTAGATTAGCAATCTTCTCATTACATTTAGCTGGGATTTCTTCTATCTTGGAGCTATTAATTTTATTACAACCTATTATTAATATACGAATTAATAACTTATCC
TTTGATCAATTACCATTATTATTGAGCAGTTGGAATTACAGCTTACTATTACTATCATTACCTGTTCTAGCTGGAGCTATTACTATATTATACTGATCGAAATTTAAATCTT
CTTTTTCGACCCAGCAGGTGGAGGAGACCTATCTTATATCAACATTTATTT
```

Type material. Holotype: ♂ deposited in the Senckenberg Natural History Museum, Frankfurt, Germany (SMF), illustrated in Fig. 57, bears the following four rectangular labels (first two handwritten, others printed), three white: [Peru | Rolle], [chales], [DNA sample ID: | NVG-24019G09 | c/o Nick V. Grishin], and one red [HOLOTYPE ♂ | *Cecropterus* (Murgaria) | perichales Grishin]. This specimen was collected by Franz Hermann Rolle (1864–1929) and according to its second label, its dorsal side was illustrated as “chales” on Plate 160, row f, image [7] in Draudt (1921–1924).

Type locality. Peru. No other details are known. The type locality will be inferred by genomic sequence comparison when additional specimens of this species are discovered.

Etymology. The name is a fusion for this *Per*[uv]/[an species that resembles]*chales*. Furthermore, in Greek, *περί* (*peri*) means around, near, or bordering and indicates that this new species is “near” *C. chales*. The name is treated as a noun in apposition.

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

***Cecropterus* (Murgaria) *guatemalensis* Grishin, new species**

<https://zoobank.org/286049D7-46E8-476E-8CEA-5B1C1EEB3789>

(Figs. 58 part, 59, 60b)

Definition and diagnosis. Genomic analysis reveals that a series of specimens from Parque Nacional Tikal in Guatemala form a clade sister to *Cecropterus* (Murgaria) *nigrociliata* (Mabille & Boulet, 1912) (type locality in Mexico; holotype sequenced as NVG-18086A11) that is genetically differentiated from it at the species level in the nuclear genome (Fig. 58a); e.g., F_{st}/G_{min} are 0.39/0.2% (although their COI barcodes are identical), and therefore these specimens represent a new species. This new species keys to “*Achalarus toxus*” (C.17.4) in Evans (1952), who misidentified *Aethilla toxus* Plötz, 1882 (type locality in Mexico; lectotype sequenced as NVG-15032A10), currently treated as a junior subjective synonym of *Cecropterus* (Murgaria) *albociliatus albociliatus* (Mabille, 1877) (type locality in Colombia, Panama, and Guatemala) (Zhang et al. 2023d). Evans’s “*A. toxus*” corresponds to the species group including *Cecropterus* (Murgaria) *coyote* (Skinner, 1892) (type locality in USA: Southern Texas), *Cecropterus* (Murgaria) *roeveri* Grishin, 2025, and *C. nigrociliata*; these species representing at least some of the genitalic variants noted by Evans for his “*toxus*”: “The cuiller of the clasp varies considerably” (Evans 1952: 128). The new species differs from its relatives by the following combination of characters in males: well-developed costal fold on the forewing; more angular wings: forewings with a straighter outer margin and hindwings with a straight to mildly concave outer margin; white hindwing fringe with some brown scaling at the wing margin, mostly around the apex and the tornus; faint to vestigial pale semihyaline spots on the forewing, not prominent even in the subapical area; most strongly developed pattern of darker spots on the ventral forewing; the uncus is shorter relatively to the tegumen in lateral view, similar to *C. roeveri* (Fig. 60c) [in *C. nigrociliata*, the tegumen is less elongated and is nearly square in dorsal view], but the arms are narrower in dorsal view, similar to *C. nigrociliata* (Fig. 60a) [in *C. roeveri* the arms are more strongly curved ventrad and thicker]; the harpe is bent but not as upturned as in *C. roeveri*, broader in lateral view and slightly more curved dorsad at the caudal end than in *C. nigrociliata*, the caudal end is serrated and rounder than a sharp tooth-like end of *C. roeveri*; the costa-ampulla of the valva is with a more prominent and angled hump in the middle than in *C. nigrociliata*, being more similar to that of *C. roeveri*. Due to its cryptic nature and poorly explored individual variation, this species is best identified by DNA, with diagnostic base pairs in the nuclear genome: aly2582.37.3: A144T, aly2582.37.3:G185T, aly638.4.4:A1988G, aly1297.4.6:A79C, aly1297.4.6:C93T; and the COI barcode does not differentiate this species from some others.

Barcode sequence of the holotype. Sample NVG-25012D08, GenBank [PZ516414](#), 658 base pairs:

AAC TT TATAT TTTTAT TTTTGA A TTTGAG CAGGATTA A TTTGGA A C T T CATT AAGAT TACTAT TCGAA C TGA A TTAGGT ACCC CAGGAT CTTT AAT TGGAG ATGAT CAAAT TTTATA TACT
ATTGTAACAGCTCATGCTTTTATTATAATTTTTTTATAGTTATACCTATTATAATTTGGAGGATTTGGAAATGATTAATCCCTTTATATTAGGGGCCCCGATATAGCTTTCCCTCGTA
TAAATAATATAAGATTTTGATTATACCCCATCTTTAACCCCTCTTAATTTCAAGAAGAAATGTAGAAAATGGTGCAGGTACTGGATGAACAGTTTATCCCCCTTTATCATCCAATATTGC
CCATCAAGGAGCATCAGTAGATTTAGCAATTTTTTCATTACATTTAGCTGGAAATTTCTTCTATTCTTGGAGCTATTAATTTTATTACAAC TATTATTAATATACGAATTAATATTATCA
TTTGATCAAATACCATTATTATCTGAGCTGTTGGAATTACAGCTTTATTATTATTACTTTCATTACCTGTTTGTAGCAGGAGCTATTACTATATTATTAAGTATGATGAAATTTAAATACTT
CTTTTTTGTATCCAGCAGGTGGAGGTGATCTATTTTATACCAACATTTATT

Type material. Holotype: ♂ deposited in the McGuire Center for Lepidoptera and Biodiversity collection, Gainesville, FL, USA (MGCL), illustrated in Fig. 59 (genitalia Fig. 60b), bears the following five printed rectangular labels, four white: [GUATEMALA | Petén, Parque | Nacional Tikal | # 32, 08:30-09:00 | 5 February 1992 | leg. G. T. Austin], [G.T. Austin colln. | MGCL Accession | # 2004-5], [DNA

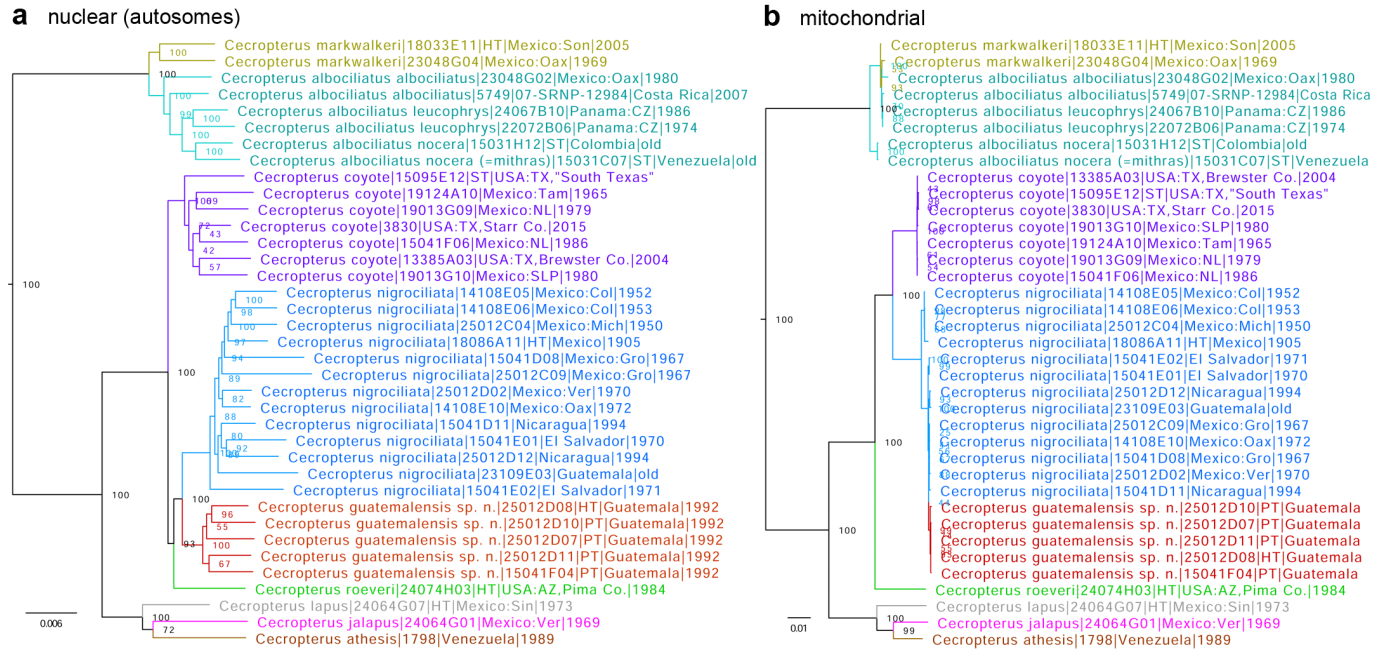


Fig. 58. Phylogenetic trees of selected *Cecropterus* (*Murgaria*) species constructed from protein-coding regions in: **a)** the nuclear genome (autosomes), based on 1,480,014 positions, and **b)** the mitochondrial genome. Different species are colored differently: *C. markwalkeri* Grishin, 2023 (olive), *C. albociliatus* (Mabille, 1877) (cyan), *C. coyote* (violet), *C. nigrociliata* (blue), *C. guatemalensis* sp. n. (red), *C. roeveri* (green), *C. lapus* Grishin, 2025 (gray), *C. jalapus* (Plötz, 1881) (magenta), and *C. athesis* (Hewitson, 1867) (brown). Ultrafast bootstrap (Hoang et al. 2018) values are shown at nodes.



Fig. 59. *Cecropterus* (*Murgaria*) *guatemalensis* sp. n. holotype ♂ NVG-25012D08 in dorsal (left) and ventral (right) views.

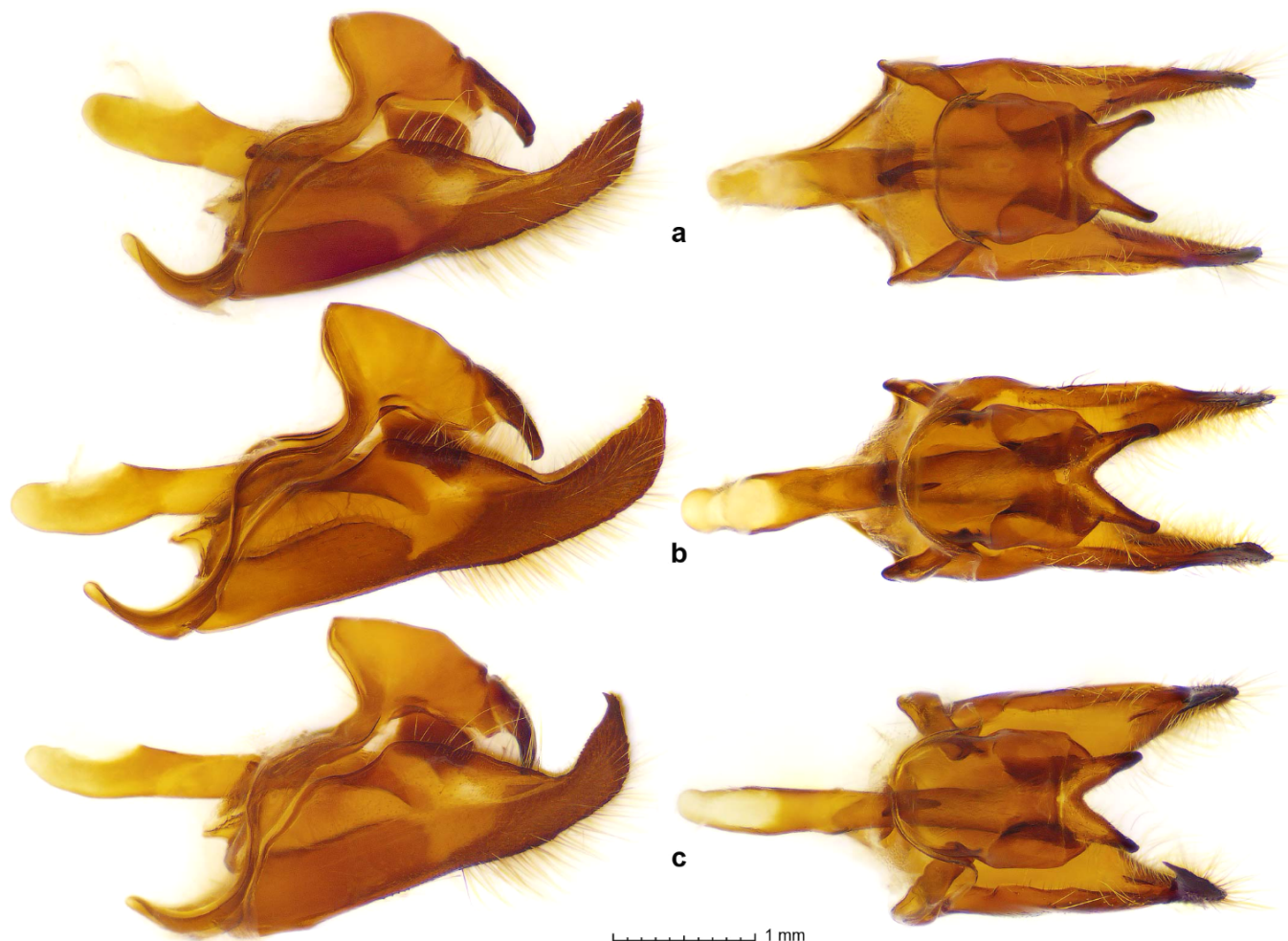


Fig. 60. Male genitalia of *Cecropterus* (*Murgaria*) in left lateral (left) and dorsal (right) views [MGCL]: **a)** *C. nigrociliata* NVG-24064F03 Mexico: Colima, Comala, 14-Nov-1982, D. W. Jenkins leg., genitalia NVG241111-11; **b)** *C. guatemalensis* **sp. n.** holotype NVG-25012D08 Guatemala: Petén Department, Parque Nacional Tikal, 5-Feb-1992, G. T. Austin leg., genitalia NVG250720-40 [MGCL]; and **c)** *C. roeveri* holotype NVG-24074H03 USA: AZ, Pima Co., 7 mi W of Arivaca, Arivaca Creek, elevation 3600 ft, 22-Sep-1984, K. Roever leg., genitalia NVG241111-34.

sample ID: | NVG-25012D08 | c/o Nick V. Grishin], [genitalia | NVG250720-40 | c/o Nick V. Grishin], and one red [HOLOTYPE ♂ | *Cecropterus* (*Murgaria*) | *guatemalensis* Grishin]. **Paratypes:** 6♂♂ and 3♀♀ with the same data as the holotype except as indicated: 1♀ NVG-25012D10, 2-Feb-1992; 1♂ NVG-25012D07, 4-Feb-1992; 1♂ NVG-15041F04, 19-Aug-1992, genitalia GTA-4590; 1♀ 4-Nov-1992; 1♂ 6-Nov-1992, JVO leg.; 2♂♂ 11-Nov-1992; 1♀ NVG-25012D11, 12-Nov-1992; and 1♂ 20-Oct-1993, JVO leg.

Type locality. Guatemala: Petén Department, Parque Nacional Tikal.

Etymology. The name is derived from the country of the type locality and is an adjective.

Distribution. Currently known only from Guatemala.

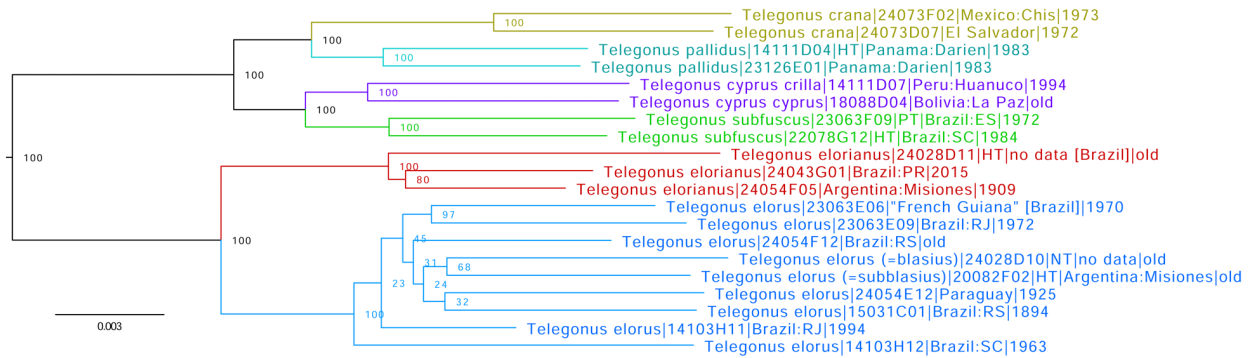
***Telegonus* (*Rhabdoides*) *elorianus* Grishin, 2025 is confirmed as a species-level taxon from South Brazil and Argentina**

First, to aid identification in the field, we show iNaturalist (2026) photographs that we identified as *Telegonus* (*Rhabdoides*) *elorus* (Hewitson, 1867) (type locality in Brazil, likely Southeast or South) (Fig. 61a) and *Telegonus* (*Rhabdoides*) *elorianus* Grishin, 2025 (type locality likely in Southeast or Southern Brazil) (Fig. 61b, c), both individuals are from Brazil: São Paulo. Second, genomic sequencing

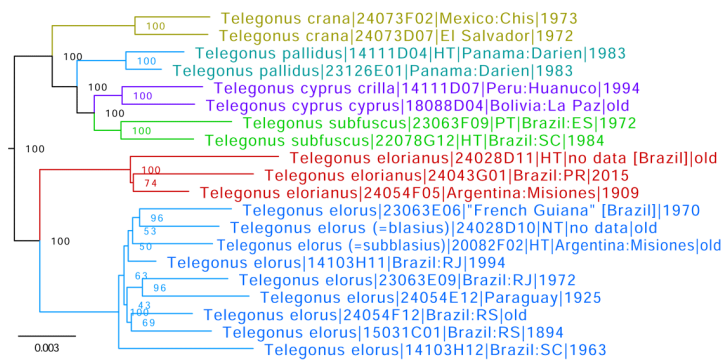


Fig. 61. *Telegonus (Rhabdoides)* from Brazil: São Paulo, iNaturalist (2026) live photographs (with observation numbers): **a)** *T. (R.) elorus* (102661047) Vila Água Funda, GPS -23.6393, -46.6270, 28-Dec-2013 © rick costa, and **b–c)** *T. (R.) elorianus* (143753688) Serra do Japi, GPS -23.2385, -46.9376, 15-Jan-2019 © Ken Kertell, in **b)** dorsal and **c)** ventral views. Photographs were brightened, rotated, and cropped. CC BY-NC 4.0 <https://creativecommons.org/licenses/by-nc/4.0/>.

a nuclear genome (autosomes)



b Z chromosome



c mitochondrial genome

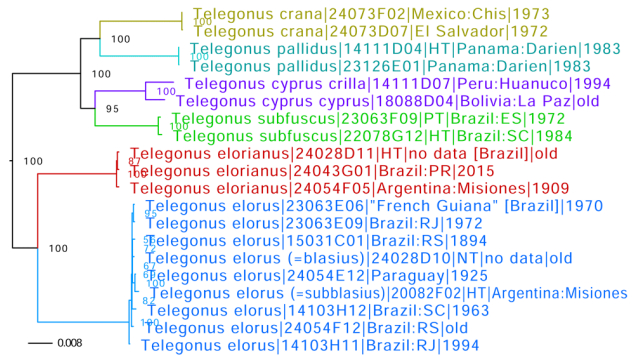


Fig. 62. Phylogenetic trees of all described *Telegonus (Rhabdoides) elorus* group species constructed from protein-coding regions in: **a)** the nuclear genome (autosomes), based on 8,564,061 positions, **b)** the Z chromosome, based on 376,926 positions, and **c)** the mitochondrial genome. Different species are shown in different colors: *T. crana* (Evans, 1952) (olive), *T. pallidus* Grishin, 2025 (cyan), *T. cyprus* (Evans, 1952) (violet), *T. subfuscus* Grishin, 2025 (green), *T. elorianus* (red), and *T. elorus* (blue). Ultrafast bootstrap (Hoang et al. 2018) values are shown at nodes.

revealed two more specimens of *T. (R.) elorianus* (Fig. 62), a recently described species sister to *T. (R.) elorus* (Fig. 63a), previously known from a single specimen of unspecified provenance (Fig. 63b). These two additional specimens are: NVG-24043G01, CEP-7167, Brazil: Paraná, Guarapuava–Guará, Rio das Pedras, 1000–1050 m, 16-Feb-2015, T. Pyrez leg. [CEPUJ] (Fig. 63c) and NVG-24054F05, Argentina: Misiones, 27-Mar-1909, P. Jörgensen leg. [ZMUC]. These records further substantiate the species status of this taxon described only from the holotype (rather than suggesting that it was an aberrant or poorly sequenced specimen), support the hypothesized type locality, and confirm this species from South

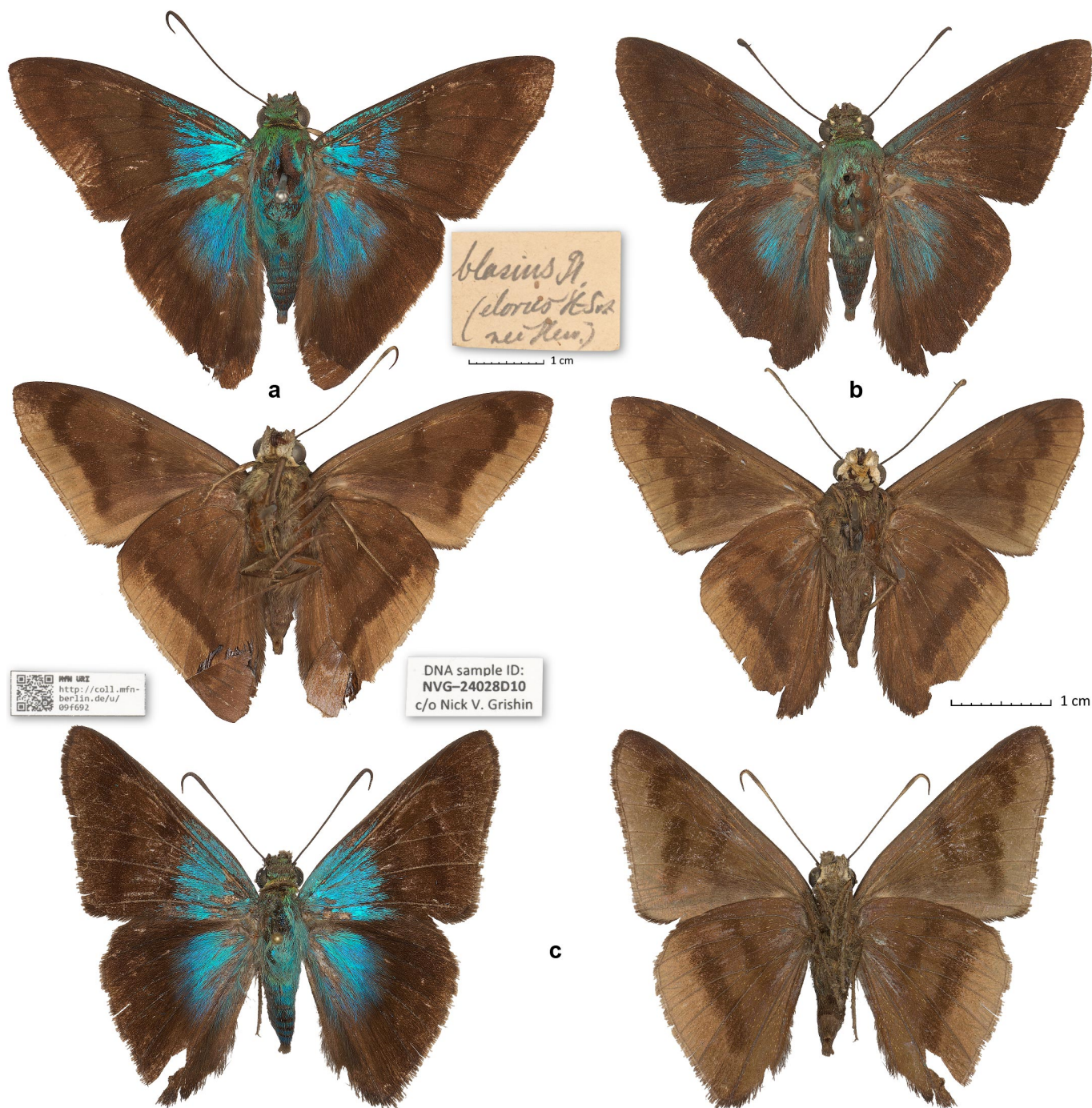


Fig. 63. Specimens of *Telegonus* (*Rhabdoides*) in dorsal (top or left) and ventral (bottom or right) views, data in text or below:
a) *T. (R.) elorus* (neotype of *Eudamus blasius* Plötz, 1881) NVG-24028D10 [MFNB] with its labels reduced to $\frac{3}{4}$ of the specimen scale (the scale for labels is below the handwritten label) and **b–c)** *T. (R.) elorianus* (no labels are shown):
b) holotype NVG-24028D11 of unknown provenance [MFNB] and **c)** non-type NVG-24043G01 from Brazil: Paraná.

Brazil and northeastern Argentina. As the tree shows (Fig. 62), *T. (R.) elorus* and *T. (R.) elorianus* are sympatric at least in Misiones, Argentina. Wing patterns of the two newly sequenced specimens of *T. (R.) elorianus* are similar to that of the holotype and corroborate that *T. (R.) elorianus* differs from *T. (R.) elorus* by the browner (instead of yellow) pale submarginal areas of the ventral side of the wings and by having a dark postdiscal band on the ventral forewing that is partly broken into spots. This band appears indented along vein M_3 , and its outer margin is less regular and more concave outward, thus leaving a wider submarginal pale area than in *T. (R.) elorus*. Furthermore, the fringes are darker than in typical *T. (R.) elorus* specimens, most noticeably near the middle of the hindwing.

Lectotype designation for *Eudamus calchas* Herrich-Schäffer, 1869

Eudamus calchas Herrich-Schäffer, 1869, currently a valid species in the genus *Cogia* Butler, 1870 (type species *Cogia hassan* Butler, 1870), was described from an unspecified number of specimens from tropical America (Herrich-Schäffer 1869). We found a single syntype of *E. calchas* in the MFNB collection, which is known to house a large number of Herrich-Schäffer's type specimens. The syntype agrees with the original description, is labeled as "Origin." (i.e., a syntype), and bears a characteristic label with "Coll. H.—Sch." indicating that it came from Herrich-Schäffer's collection. To stabilize nomenclature and define the name *E. calchas* objectively, N.V.G. hereby designates the syntype in the MFNB collection, a female that bears the following six labels (1st purple, others white; 3rd and 4th handwritten, others printed with handwritten text shown in *italics*): [Origin.], [Coll. H.—Sch. | *Rio*], [Calchas | HS. | Achlyodes], [Calchas | H.-Sch.], [{QR Code} <http://coll.mfn-berlin.de/u/940b61>], and [DNA sample ID: | NVG-15032A06 | c/o Nick V. Grishin], as the **lectotype** of *Eudamus calchas* Herrich-Schäffer, 1869. The third label is in Staudinger's handwriting, and although this specimen lacks a label indicating that it is from the Staudinger collection, it was most likely part of that collection together with other Herrich-Schäffer type specimens. The word "Rio" on the second label is written in the same hand as the fourth and was probably added when Herrich-Schäffer's specimens were curated into the scientific collection of Staudinger. The lectotype has damage at the tornus of both hindwings and a large pinhole near the middle of the right forewing. Images of this specimen, photographed by B. Hermier, are shown on the Butterflies of America website (Warren et al. 2024). As suggested by one of its labels, the type locality of *E. calchas* is in Brazil: Rio de Janeiro, which is consistent with our genomic comparison results placing it among South American specimens (Fig. 64). The COI barcode sequence of the lectotype, sample NVG-15032A06, GenBank [PZ516415](#), 658 base pairs, is:

```
AAC TT TATATTTTATTTTGGGATTTGAGCAGGAATAATTGGAACCTTCATTAAGTTTATTAATTCGTACTGAATTAGGTACTCTGGATCATTAAATTGGAGATGACCAAAATTTATAATACT
ATTGTAAGTCTCATGCTTTATTTATTAATTTTCTCATAGTTATACCAATTATAATTTGGTGGATTTGGAAATTTGATTAGTTCCTTTAATATTTAGGTGCTCTGATATAGCTTTCCCGGTA
TAAACAATATAAGATTTTGATTACTTCCCTTCATTAACCCATTAATTTCAAGAGCATCGTAGAAAATGGTGGTACTGGATGAACATTTATCCCTCTTTCATCTAATATTGC
TCATCAAGGATCCTCAGTAGATTAGCTATTTTTCATTACATTTAGCAGGTATTTCTTCTATTTTAGGAGCTATTAATTTTATTACTACAATTATTAATATACGAATTAGAAATTTATCA
TTCGATCAAATACCTTTATTTGATGAGCAGTAGGAATTACAGCTTTATTTATTTACTCTCTTACCCTTTTAGCAGGAGCTATTACTATATCTTTAACAGACCGAAATCTTAATACTT
CATTTTGTATCCTGCTGGTGGAGGGATCCCATTTTATATCAACATTTATTT
```

Cogia terranea (Butler, 1874) is a valid species distinct from *Cogia calchas* (Herrich-Schäffer, 1869)

Genomic analysis of specimens identified as *Cogia calchas* (Herrich-Schäffer, 1869) (type locality in Brazil: Rio de Janeiro, lectotype sequenced as NVG-15032A06) from across its range reveals their partitioning into two prominent clades genetically differentiated at the species level in the nuclear genome (Fig. 64a), although their COI barcodes along with the mitochondrial genomes do not differ strongly (Fig. 64b), while partitioning the specimens into two clades similarly to the nuclear genome (with likely

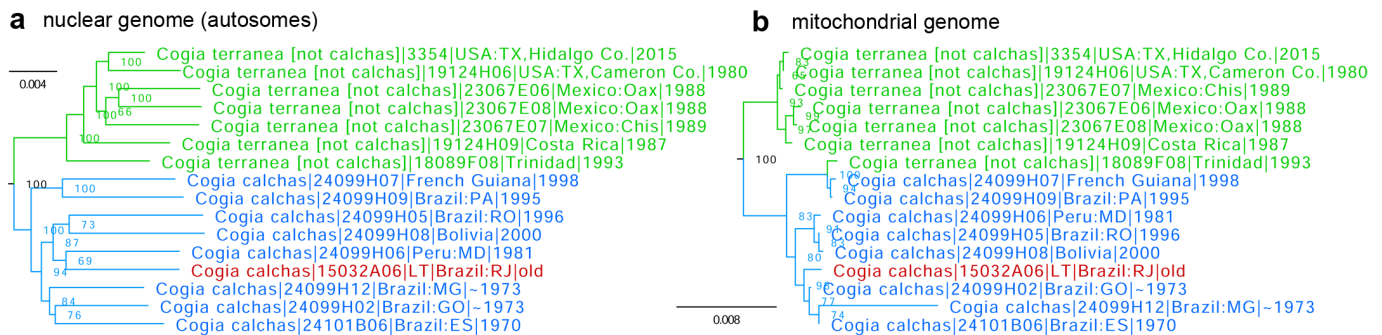


Fig. 64. Phylogenetic trees of specimens previously identified as *Cogia calchas* constructed from protein-coding regions in: **a)** the nuclear genome (autosomes), based on 4,008,378 positions, and **b)** the mitochondrial genome: *C. terranea* **stat. rest.** (green) and *C. calchas* (blue with the lectotype labeled in red). Ultrafast bootstrap (Hoang et al. 2018) values are shown at nodes.

mitogenome introgression in one specimen from Trinidad). Due to genetic differentiation in the nuclear genome, these two clades correspond to two distinct species. The lectotype of *C. calchas* (Fig. 64 labeled in red) is in the clade that consists of South American specimens (Fig. 64 blue) and therefore this clade represents this species. The second clade (Fig. 64 green) consists of specimens from North and Central America and one specimen from Trinidad. The clade includes a specimen from Costa Rica, which is the country containing the type locality (Cartago) of *Spathilepia terranea* Butler, 1874, currently regarded as a junior subjective synonym of *C. calchas*, and the only available name for this group. Therefore, we propose to treat *Cogia terranea* (Butler, 1874), **stat. rest.** as a valid species distinct from *Cogia calchas* (Herrich-Schäffer, 1869).

Subfamily Pyrginae Burmeister, 1878

Tribe Achlyodini Burmeister, 1878

Charidia paronia Grishin, new species

<https://zoobank.org/6CF8D53A-28F1-441A-8A92-BA5CCB051C7A>

(Figs. 65 part, 66a–b, 67a–b)

Definition and diagnosis. Genomic analysis (Fig. 65) reveals that two females from the Amazonian region of Brazil (Fig. 66a, b) initially identified as *Charidia ronda* Grishin, 2023 (type locality in Brazil: Rondônia) (Fig. 66c, d) are genetically differentiated from it and its sister *Charidia lucaria* (Hewitson, 1868) (type locality in French Guiana) (Fig. 66e) at the species level; e.g., their COI barcodes differ by 2.4% (16 bp), and therefore these specimens represent a new species. This new species keys to “*C. lucaria lucaria*” (E.48.1(b)) in Evans (1953), but differs from it and other relatives by the following combination of characters: the pale yellowish area on the hindwing is large and has rather straight or gently curved edges, occupies about half of the wing [narrower and with a coarsely irregular basal edge in *C. lucaria*], and is slightly paler on the ventral side [typically more tan in *C. ronda* and *C. lucaria*]; the base of the forewing cell M_3-CuA_1 is cream-colored [brown in *C. ronda*]; and the partly hyaline pale discal forewing band extends into cell CuA_1-CuA_2 [does not extend beyond the discal cell in *C. ronda*]. In female genitalia, compared to *C. ronda* (Fig. 67c–d), the lamella postvaginalis is less robust and is rounder at the corners, a difference most conspicuous in ventrolateral view (Fig. 67a–b vs. Fig. 67c–d, lower row), and the lamella antevaginalis is likewise less robust and not expanded anteriad into the

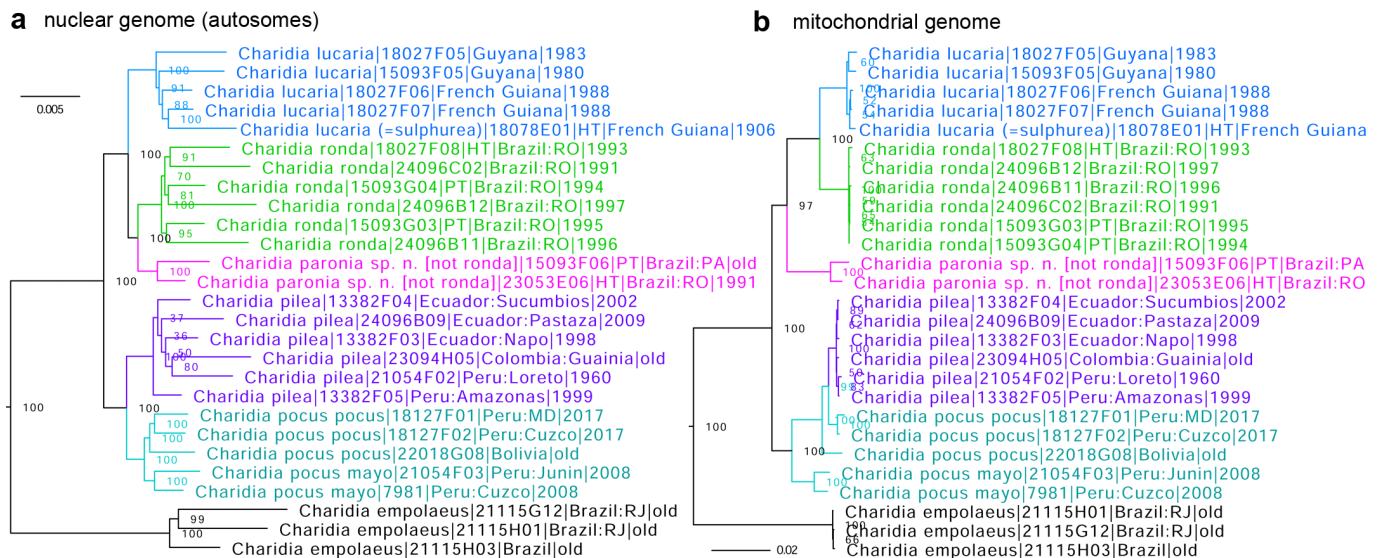


Fig. 65. Phylogenetic trees of all described species of *Charidia* constructed from protein-coding regions in: **a)** the nuclear genome (autosomes), based on 2,924,181 positions, and **b)** the mitochondrial genome. Different species are colored differently: *C. lucaria* (blue), *C. ronda* (green), *C. paronia* sp. n. (magenta), *C. pilea* Evans, 1953 (violet), *C. pocus* Evans, 1953 (cyan), and *C. empolaesus* (Westwood, 1852) (black). Ultrafast bootstrap (Hoang et al. 2018) values are shown at nodes.

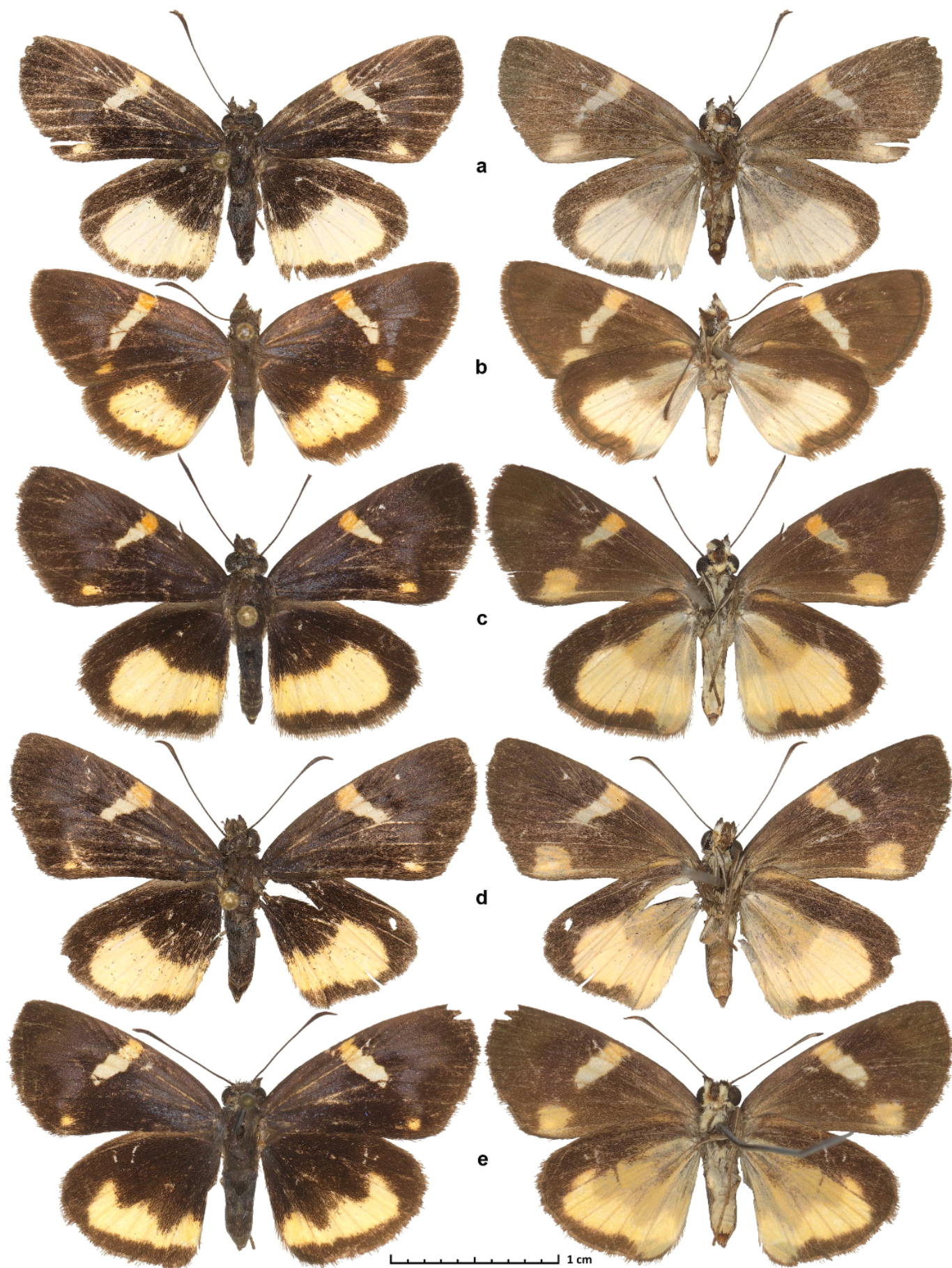


Fig. 66 (legend continues on the next page). Females of *Charidia* in dorsal (left) and ventral (right) views: **a–b**) *C. paronia* sp. n. type series from Brazil [MGCL]: **a**) holotype NVG-23053E06 Rondônia, 62 km S of Ariquemes, Linha C-20, 7 km E of

B-65, Fazenda Rancho Grande, 11-Jul-1991, G. Bongioio leg. and **b**) paratype NVG-15093F06 Pará, Santarém, ex. coll. E. Le Moul; **c–d**) *C. ronda* from Brazil, Rondônia, 5 km S of Cacaulândia, Linha C-10 at Rio Pardo off B-65, O. Gomes leg. [MGCL]: **c**) paratype NVG-15093G04, 7-Jul-1994 and **d**) non-type NVG-24096B12, UF FLMNH MGCL 1043450, 16-May-1997; and **e**) *C. lucaria* (holotype of *C. lucaria* var. *sulphurea* Mabilie & Boulet, 1917) NVG-18078E01 French Guiana, Cayenne, 1906, H. Donckier leg. [MNHP].

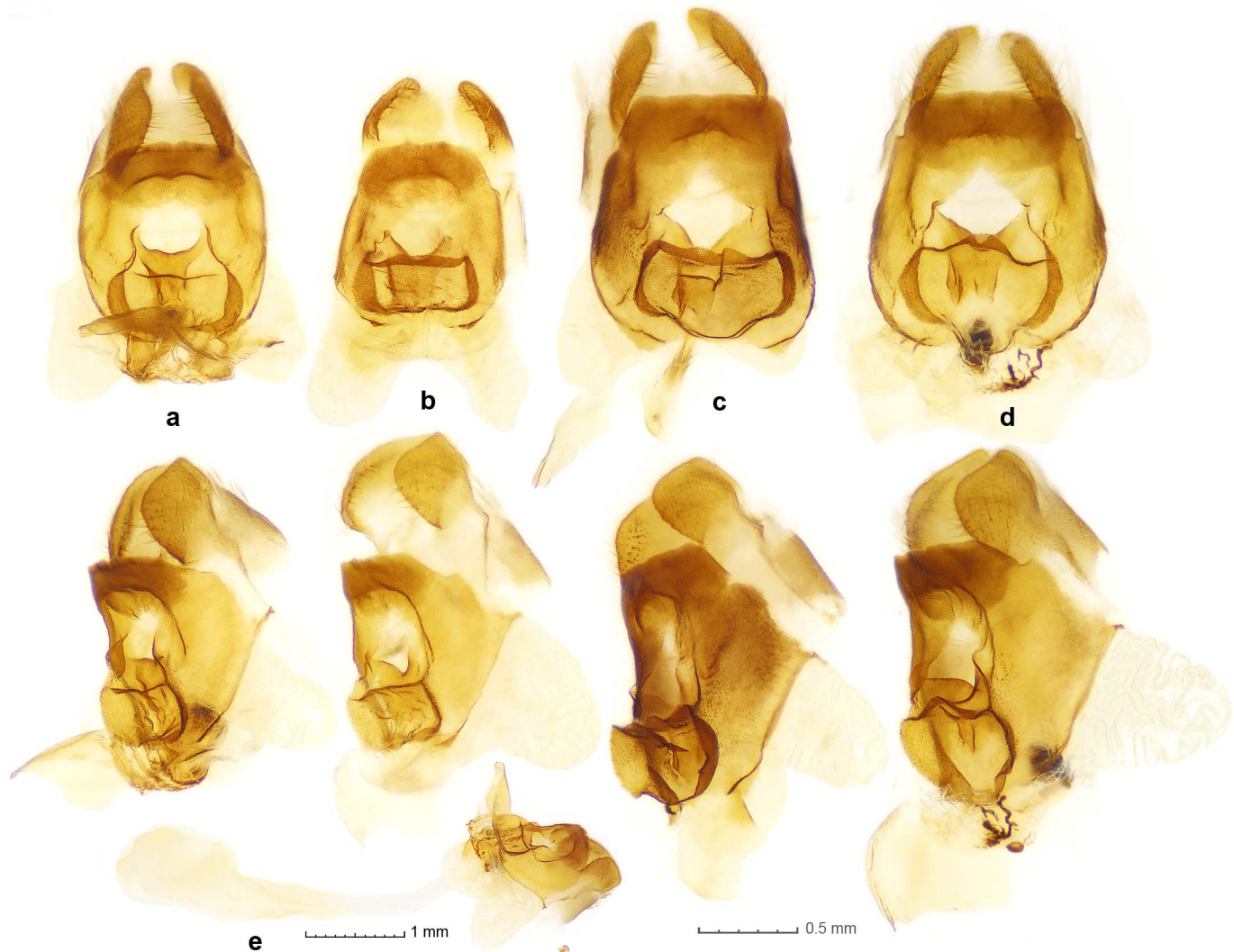


Fig. 67. Female genitalia of *Charidia* from Brazil [MGCL] in ventral (above the panel letter) and right ventrolateral (below) views (ductus and corpus bursae not shown), except **e**), which shows complete genitalia in right ventrolateral view, reduced in size with the scale below: **a–b, e**) *C. paronia* sp. n. type series: **a, e**) holotype NVG-23053E06 Rondônia, 62 km S of Ariquemes, Linha C-20, 7 km E of B-65, Fazenda Rancho Grande, 11-Jul-1991, G. Bongioio leg., genitalia NVG260613-10 (specimen Fig. 66a) and **b**) paratype NVG-15093F06 Pará, Santarém, ex. coll. E. Le Moul, genitalia NVG260613-13 (specimen Fig. 66b); and **c–d**) *C. ronda* from Rondônia, 5 km S of Cacaulândia, Linha C-10 at Rio Pardo off B-65, O. Gomes leg.: **c**) paratype NVG-15093G04, 7-Jul-1994, genitalia NVG260613-11 (specimen Fig. 66c) and **d**) non-type NVG-24096B12, UF FLMNH MGCL 1043450, 16-May-1997, genitalia NVG260613-12 (specimen Fig. 66d).

shallow lobe present in *C. ronda*. Due to its cryptic nature and unexplored individual variation, this species is best identified by DNA, with diagnostic base pairs in the nuclear genome: aly274.20.22:C102T, aly813.3.6:G120A, aly84.26.4:G30C, aly159.15.6:114G, aly320.21.4:C102T; and the COI barcode: T55C, T130C, C271T, T434C, T601C.

Barcode sequence of the holotype. Sample NVG-23053E06, GenBank [PZ516416](https://www.ncbi.nlm.nih.gov/nuclot/PZ516416), 658 base pairs:

```
AACTTTATATTTTATTTTGGAAATTTGAGCAGGAATAGTAGGAACCTCTTTAAGCTTATTAATTCGAACCTGAACTAGGAAATCCAGGATCTTTAATTTGGAAATGATCAAATTTATAATACT
ATTGTTACCGCTCATGCATTATTATAATTTTATAGTAATACCAATTATAATTGGAGGATTTGGAAATTTGACTAGTACCCCTTATACAGGAAGTCCAGATATAGCTTTTCCACGAA
TAAATAATATAAGATTTTGATTATTACCTCCATCTCTTATATTATTAATTTCAAGAAGTATTGTAGAAATGGAGCAGGAACCTGGATGAACAGTTTATCTCTCTTTCCGCTAATATTGC
TCATCAAGGTTTCATCTGTAGATTAGCAATTTTTCATTACATTTAGCTGGAATTTCTTCAATTTTAGGAGCTATTAAATTTTATTACCACATATTATTAATATACGAGTAAATAACTTATCA
TTTGATCAAATACCATTTATTGTATGAGCTGTAGGAATTACAGCCTTACTTTTATTATTATCATTACCTGTATTAGCAGGAGCTATTACTATATTATTAAGTATCGAAATTTAAACACAT
CATTTTGTATCTGCTGGAGGAGGATCCAATTTTATATCAACATTTATTT
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Type material. Holotype: ♀ currently deposited in the McGuire Center for Lepidoptera and Biodiversity collection, Gainesville, FL, USA (MGCL), illustrated in Fig. 66a (genitalia Fig. 67a), bears the following six printed labels (1st triangular, others rectangular; 3rd buff-colored, last red, others white): <] right antenna and a leg are glued to this otherwise blank label, [BRASIL: Rondonia | 62 km S Ariquemes | linea C-20, 7 km E | B-65, Fazenda | Rancho Grande | 11 July 1991 | leg. G. Bongioiolo], [photographed | G.T. Austin & | J. P. Brock | March 1992], [Charidia lucaria], [DNA sample ID: | NVG-23053E06 | c/o Nick V. Grishin], [DNA sample ID: | NVG-25071F11 | c/o Nick V. Grishin], [genitalia: | NVG260613-010 | c/o Nick V. Grishin], and [HOLOTYPE ♀ | Charidia | paronia Grishin]. The first DNA sample ID refers to the extraction from a leg (sequenced), and the second from the abdomen (stored) prior to genitalia dissection. **Paratype:** 1♀ NVG-15093F06 (leg, DNA sequenced), NVG-25071G02 (abdomen, DNA stored) Brazil: Pará, Santarém, ex. coll. E. Le Moul, genitalia NVG260613-13 [MGCL] (Figs. 66b, 67b). **Type locality.** Brazil: Rondônia, 62 km south of Ariquemes, Linha C-20, 7 km east of B-65, Fazenda Rancho Grande.

Etymology. The name is a fusion derived from the known localities for this species: *par*[a] + *[rond]onia*, and is treated as a noun in apposition.

Distribution. Currently known from Rondônia and Pará in Brazil.

***Quadrus (Quadrus) teelatus* Grishin, new species**
<https://zoobank.org/4099DEE8-E10D-4F76-BE2F-97B5AB5679DF>
 (Figs. 68 part, 69a, 70)

Definition and diagnosis. Genomic analysis reveals that a male from the Venezuelan Coastal Range similar in appearance to *Quadrus (Quadrus) tee* Grishin, 2025 (type locality Colombia: Antioquia, Medellín) (Fig. 69b) is genetically differentiated from it at the species level (Fig. 68); e.g., their COI barcodes differ by 3.6% (24 bp), and therefore this specimen represents a new species, also related to *Quadrus (Quadrus) truncata* (Hewitson, 1870) (type locality in Ecuador) (Fig. 69c, d). This new species keys to *Q. truncata* (E.39.8) in Evans (1953), but differs from it and other relatives by the following combination of characters: the discal cell semihyaline spot on the forewing is broken along its posterior

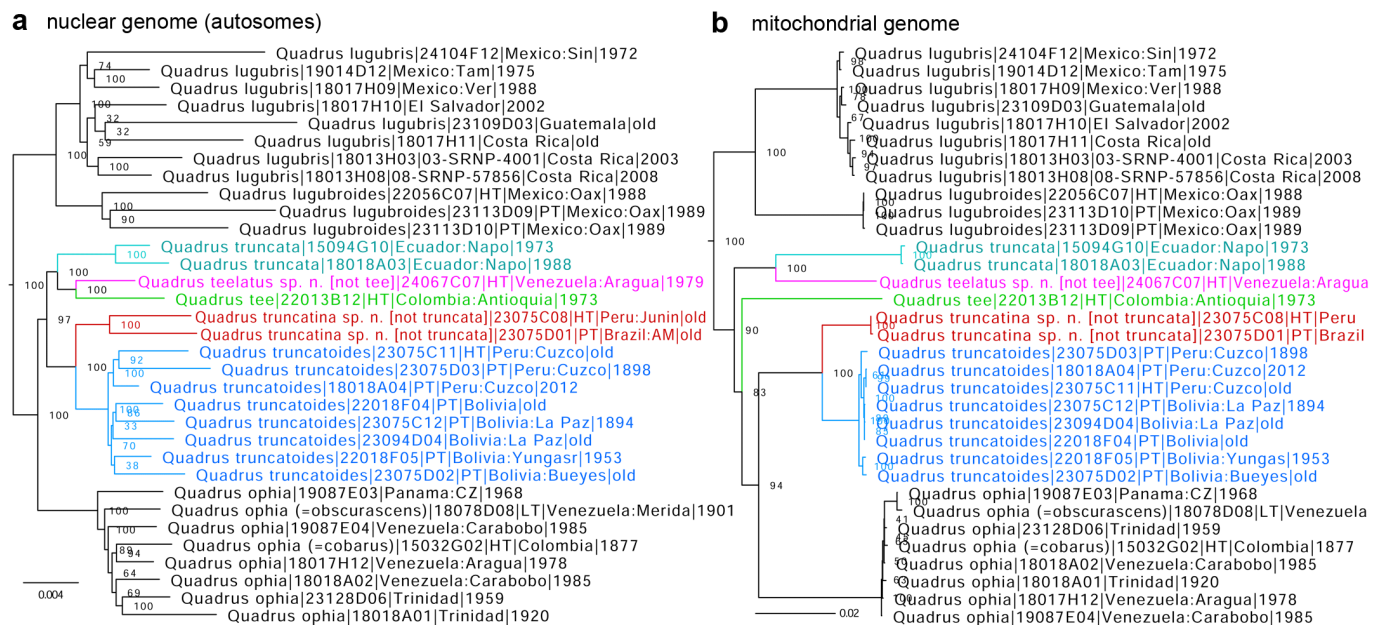


Fig. 68. Phylogenetic trees of selected *Quadrus* species constructed from protein-coding regions in: **a**) the nuclear genome (autosomes), based on 2,702,610 positions, and **b**) the mitochondrial genome. Species mentioned in the text are colored differently: *Q. truncata* (cyan), *Q. teelatus* sp. n. (magenta), *Q. tee* (green), *Q. truncatina* sp. n. (red), and *Q. truncatoides* (blue). Ultrafast bootstrap (Hoang et al. 2018) values are shown at nodes.



Fig. 69. Males of *Quadrus* (*Quadrus*) in dorsal (left) and ventral (right) views: **a)** *Q. (Q.) teelatus* **sp. n.** holotype NVG-24067C07 from Venezuela, Aragua, Henri Pittier National Park, 20-Jul-1979, R. Anderson leg. [MGCL]; **b)** *Q. (Q.) tee* holotype NVG-22013B12 Colombia, Antioquia Province, Medellín, 14-Sep-1973 [RMNH]; and **c-d)** *Q. (Q.) truncata* non-types from Ecuador, Napo: **c)** NVG-15094G10 Río Oyacachi, 1650 m, 25-May-1973, N. Vénédictioff leg. [MGCL] and **d)** NVG-18018A03, USNMENT_01450921 Baeza, 2000 m, 5-Nov-1988, S. S. Nicolay leg. [USNM].



Fig. 70. Genitalia of *Quadrus (Quadrus) teelatus* sp. n. holotype ♂ NVG-24067C07 in left lateral (left) and dorsal (right) views.

arm, T-shaped (T with a distal extra lower dot) rather than C-shaped or U-shaped; smaller and more sharply defined darker spots in the discal row on the hindwing (both sides); less extensive pale-bluish-white (glaucous) areas on the ventral side [glaucous areas distad of the hyaline spots in cell CuA₂-1A+2A in *Q. truncata*]; no blue distad of the postdiscal brown spot in the ventral hindwing cell Sc+R₁-Rs [basal half of the segment distad of the spot is glaucous in *Q. tee*]; the postdiscal row of brown spots on the dorsal hindwing is midway between the distal edge of the basal brown area and the outer margin of the wing [closer to the basal brown area in *Q. tee*]; and a broader subapical semihyaline forewing band (i.e., composed of longer spots aligned at their outer edges) [narrower zigzag band (composed of shorter spots with the spot in cell R₄-R₅ being offset basad from the rest) in *Q. tee*]. Due to its cryptic nature and unexplored individual variation, this species is best identified by DNA, with diagnostic base pairs in the nuclear genome: aly1022.5.7:G240A, aly1022.5.7:T279C, aly2844.3.2:G318A, aly798.8.12:C72T, aly707.7.2:T42C, aly814.8.12:C133C (not A), aly536.141.3:A42A (not T), aly155.6.8:T96T (not C); and the COI barcode: T232C, C318T, T463C, A487G, T508C, T646C.

Barcode sequence of the holotype. Sample NVG-24067C07, GenBank [PZ516417](https://www.ncbi.nlm.nih.gov/GenBank/AB111111), 658 base pairs:

```
AACTTTATATTTCTTTTCGGAATTTGAGCCGGAATAATTGGAACCTCTTAAGTTTATTAATTGGAACCTGAATTAGGAAACCCAGGATCTTTAATTGGTGATGATCAAAATTTATAATACT
ATTGTAAGTCTCATGCTTTTATTATAATTTCTTTATAGTTATACCAATTATAAATTGGTGGGATTTGGAACTGACTAGTACCCCTTATACTAGGAGCTCCAGATATAGCCTTTCCACGAA
TAAATAATATAAGTTTGTGATTATTACCTCCATCCCTTTTATTGTTAAATTTCAAGAAGTATTGTAGAAAATGGAGTAGGAACAGGTTGAACAGTTTACCCACCTCTTTCTGCTAATATTGC
TCATCAAGGATCCTCTGTTGATTAGCTATTTTTCCTTACATTAGCAGGTATTTCTTCAATTTAGGAGCTATTAAATTCATTACTACAATTATTAACATACGAATTAATAATCTTTCA
ATGGATCAAAATACCTTTATTGTTCTGAGCTGTAGGAATTACAGCATTACTTTTACTTTTATCATTACCTGTTTAGCTGGAGCTATTACTATACTATTAAACAGATCGAAATTTAAATACAT
CATTTTTTGATCCTGCGAGGAGGAGGTGATCCAATTTTATACCAACATTTATTT
```

Type material. **Holotype:** ♂ currently deposited in the McGuire Center for Lepidoptera and Biodiversity collection, Gainesville, FL, USA (MGCL), illustrated in Fig. 69a (genitalia Fig. 70), bears the following seven rectangular labels (1st handwritten, others printed with text in italics handwritten), six white: [Venezuela | Aragua | Henri Pittier Pk. | 20 July 1979], [Allyn Museum | Acc. 1999-17], [*Quadras truncata* | Det. R. Anderson], [DNA sample ID: | NVG-24067C07 | c/o Nick V. Grishin], [DNA sample ID: | NVG-25072A05 | c/o Nick V. Grishin], [genitalia: | NVG260613-14 | c/o Nick V. Grishin], and one red [HOLOTYPE ♂ | *Quadrus (Quadrus) teelatus* Grishin]. The first DNA sample ID refers to the extraction from a leg (sequenced), and the second from the abdomen (stored) prior to genitalia dissection. The genus name is misspelled on the first identification label.

Type locality. Venezuela: Aragua, Henri Pittier National Park.

Etymology. The name of this new species related to *Q. tee* reflects its broader (in Latin, *latus* means broad) subapical semihyaline band on the forewing. The name is treated as an adjective.

Distribution. Currently known only from the holotype collected in the Venezuelan Coastal Range.

Quadrus (Quadrus) truncatina Grishin, new species

<https://zoobank.org/A9078A1A-5DA4-42CB-BDC9-97C6B1EA3847>

(Figs. 68 part, 71a–b)

Definition and diagnosis. Genomic analysis reveals that two specimens (from central Peru and, unless mislabeled, the Upper Amazonian Region in Brazil) initially identified as *Quadrus (Quadrus) truncata*

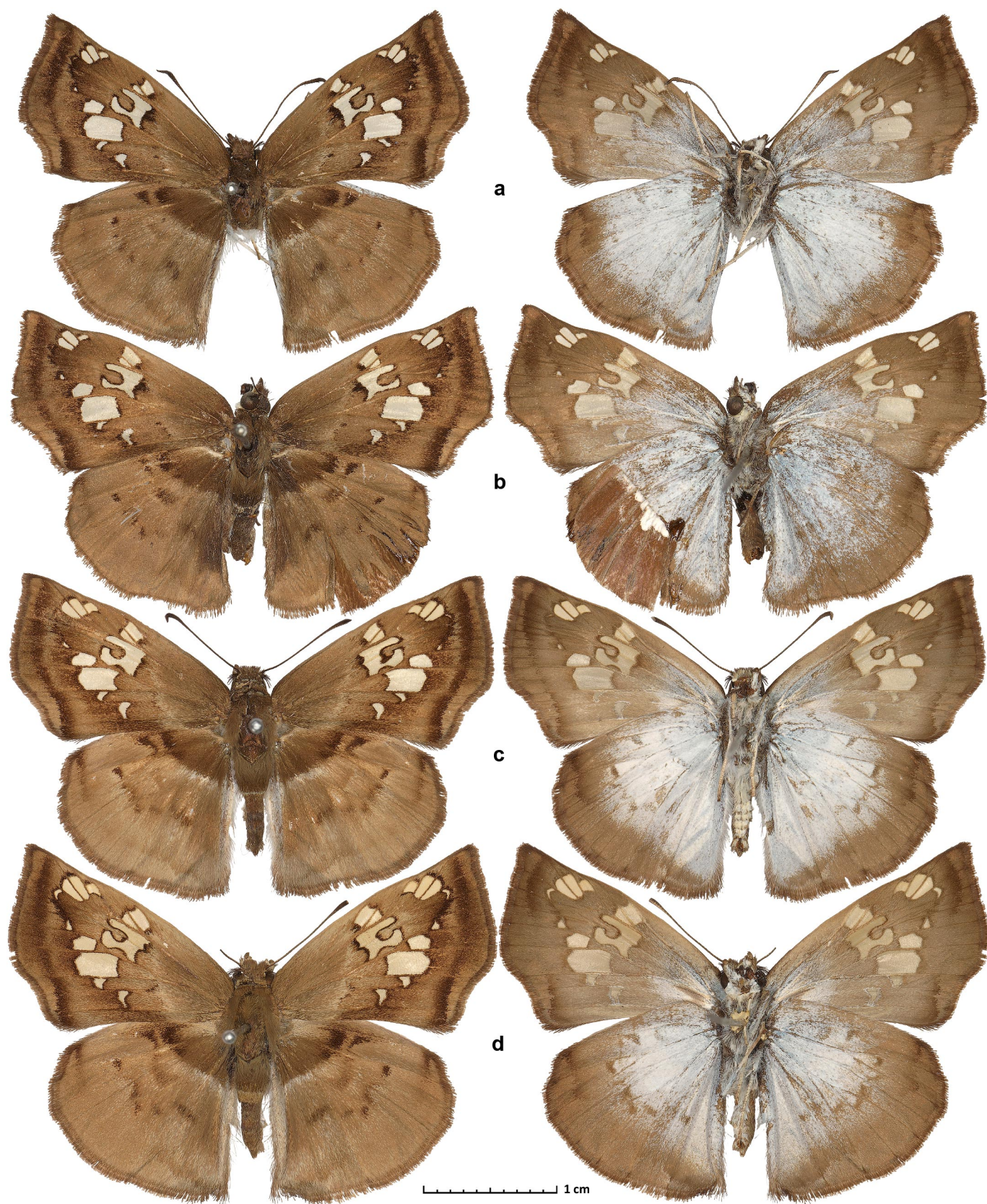


Fig. 71. Males of *Quadrus* (*Quadrus*) in MFNB, in dorsal (left) and ventral (right) views: **a–b**) *Q. (Q.) truncatina* sp. n.: **a**) holotype NVG-23075C08 Peru, Junín, Chanchamayo, old, F. Thamm leg. and **b**) paratype NVG-23075D01 Brazil: Amazonas, Tefé, old and **c–d**) *Q. (Q.) truncatoides*: **c**) holotype NVG-23075C11 Peru, Cuzco, Marcapata, old and **d**) paratype NVG-23075C12 Bolivia, La Paz, Río Tanampaya, 1894, Garlepp leg.

(Hewitson, 1870) (type locality in Ecuador) (Fig. 69c, d) form a clade sister to *Quadrus* (*Quadrus*) *truncatoides* Grishin, 2025 (type locality Peru: Cuzco, Marcapata) (Fig. 71c, d), but are genetically differentiated from it at the species level (Fig. 68); e.g., their COI barcodes differ by 2.0% (13 bp), and therefore these specimens represent a new species. This new species keys to *Q. truncata* (E.39.8) in Evans (1953), but differs from it and other relatives by the following combination of characters: C- or U-shaped (not T.-shaped) semihyaline spots in the forewing discal cell; pale-bluish-white (glaucous) coloration on the ventral forewing reaches and spreads around the semihyaline spots (the base of cell CuA₁-CuA₂ is glaucous), but no prominent glaucous areas distad of the hyaline spots in cell CuA₂-1A+2A [such areas are present in *Q. truncata*, whereas in *Q. truncatoides* the glaucous scaling does not reach the spots; the base of cell CuA₁-CuA₂ is mostly brown in these two species]; and the glaucous area is more strongly expressed on the ventral hindwing, so that postdiscal brown spots do not strongly stand out against the glaucous background. Due to its cryptic nature and unexplored individual variation, this species is best identified by DNA, with diagnostic base pairs in the nuclear genome: aly274.40.12:C220T, aly274.40.12:C225T, aly318.25.17:C154T, aly37338.20.4:C51T, aly37338.20.4:G75A; and the COI barcode: A22T, A100C, A181G, A265G, G389A.

Barcode sequence of the holotype. Sample NVG-23075C08, GenBank [PZ516418](https://www.ncbi.nlm.nih.gov/nuclot/PZ516418), 658 base pairs:

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AACCTTATATTTTATTTTCGGTGTGAGCTGGAATAATTGGAACCTTCATTAAAGTTTATTAATTCGAACTGAATTAGGAAATCCAGGATCTTTAATTGGCGATGATCAAATTTATAATACT
ATTGTAACCTGCTCATGCTTTTATTATAATTTCTTTATAGTTATACCAATTATAATTGGGGGATTGGAACTGACTAGTACCCCTTATACTAGGAGCTCCAGATATAGCTTTCCCCCGAA
TAAATAATATAAGTTTTTGATTGTTACCTCCATCTCTTTTATTATTAAATTCAGAAGTATTGTAGAAAATGGGGCAGGAACAGGTTGAACAGTTTACCCACCTCTCTCTCTAATATTGC
TCATCAAGGATCCTCTGTTGATTAACTATTTTCTTTACATTTAGCTGGTATTCTTCAATTTTAGGAGCTATTAATTTTATTACTACAATTATTAATATACGAATTAATAATCTTTCA
ATAGATCAAATACCTTTATTTGTTGAGCTGTAGGAATTACAGCATTACTTTTACTTTTATCCTTACCTGTTTATAGCTGGAGCTATTACTATATATTAAACAGATCGAAATTTAATATACAT
CATTTTGTATCCTGCTGGAGGAGGAGATCCAATTTTATATCAACATTATTT
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Type material. Holotype: ♂ deposited in the Museum für Naturkunde, Berlin, Germany (MFNB), illustrated in Fig. 71a, bears the following four rectangular labels (2nd handwritten, others printed), three white: [Chanchamayo | Thamm], [Truncata | Hew.], [DNA sample ID: | NVG-23075C08 | c/o Nick V. Grishin], and one red [HOLOTYPE ♂ | *Quadrus* (*Quadrus*) | *truncatina* Grishin]. The holotype is missing the abdomen. **Paratype:** 1♂ NVG-23075D01 in MFNB from J. P. Maassen's collection labeled "Achlyodes | truncata | Hw. | Ega.", i.e., Brazil: Amazonas, Tefé (unless mislabeled) (Fig. 71b).

Type locality. Peru: Junín Region, Chanchamayo.

Etymology. The name is derived from the names of its relatives *Q. truncata* and *Q. truncatoides*, and the intermediate length of the name reflects the geographic position of its range between those of the other two species. The name is treated as a noun in apposition.

Distribution. Central Peru and possibly the Upper Amazonian Region of Brazil.

Gindanes vittatus Grishin, new species

<https://zoobank.org/3DB7D0FB-FF66-41D3-B377-80977F5CAF13>

(Figs. 72 part, 73a–b, 74)

Definition and diagnosis. Genomic analysis (Fig. 72) reveals that a male from Rondônia, Brazil (Fig. 73a), initially identified as *Gindanes variegatus* Grishin, 2023 (type locality in Brazil: Mato Grosso) (Fig. 73b–d) and sympatric with it, is genetically differentiated from *G. variegatus* at the species level;

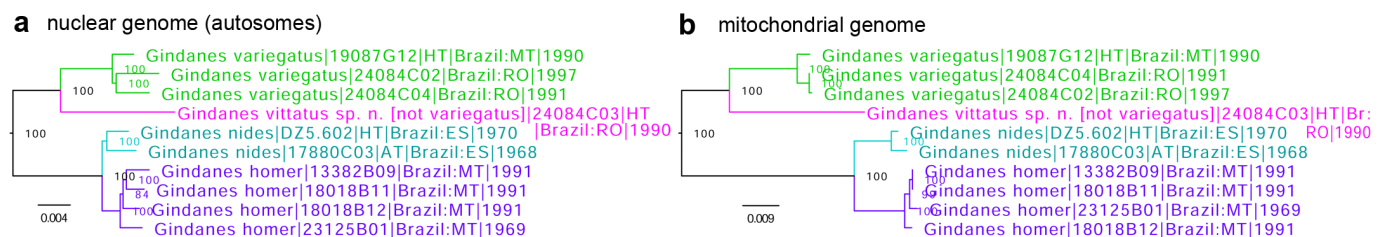


Fig. 72. Phylogenetic trees of selected *Gindanes* species constructed from protein-coding regions in: **a**) the nuclear genome (autosomes), based on 2,296,584 positions, and **b**) the mitochondrial genome. Different species are colored differently: *G. variegatus* (green), *G. vittatus* sp. n. (magenta), *G. nides* (cyan), and *G. homer* (violet). Ultrafast bootstrap (Hoang et al. 2018) values are shown at nodes.

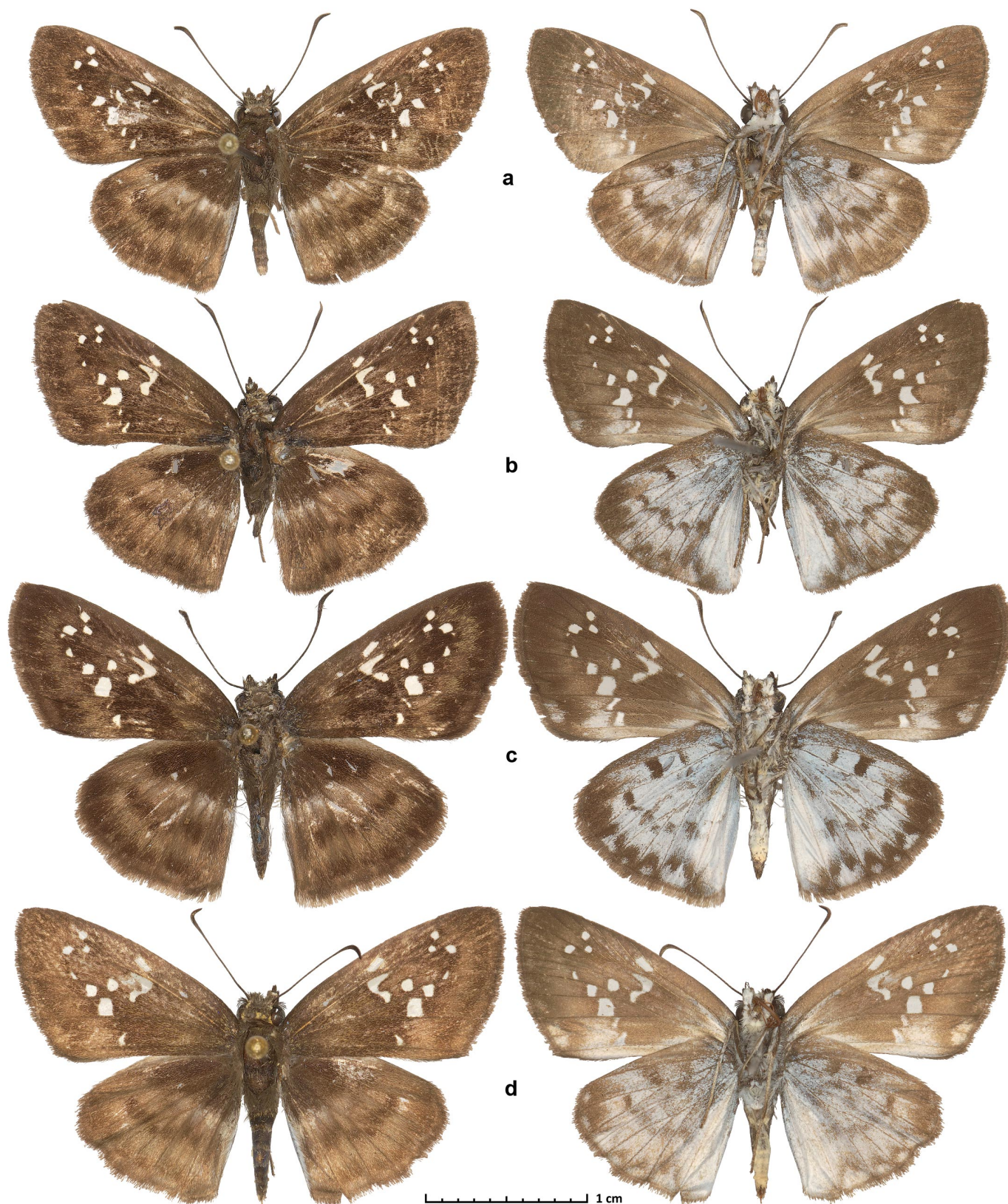


Fig. 73. Males of *Gindanes* in dorsal (left) and ventral (right) views: **a)** *G. vittatus* **sp. n.** holotype NVG-24084C03 Brazil: Rondônia, 62 km S of Ariquemes, Linha C-20, 7 km E of B-65, Fazenda Rancho Grande, 30-Oct-1990, J. P. Brock leg. [MGCL] and **b-d)** *G. variegatus*: **b-c)** non-types from Brazil: Rondônia [MGCL]: **b)** NVG-24084C04 62 km S of Ariquemes, Linha C-20, 7 km E of B-65, Fazenda Rancho Grande, 17-Mar-1991, C. V. Covell leg., genitalia GTA-3211, and **c)** NVG-24084C02 5 km S of Cacaulândia, Linha C-10 (at Rio Pardo) off B-65, Station #13 forest, 23-Feb-1997, O. Gomes leg.; and **d)** holotype NVG-19087G12 (leg), NVG-22032E01 (abdomen), USNMMENT_01588890 Brazil: Mato Grosso, Diamantino, Alto Rio Arinos, 350-400 m, 18-Aug-1990, E. Furtado leg., genitalia NVG230216-15 [USNM].



Fig. 74. Male genitalia of *Gindanes vittatus* sp. n. holotype NVG-24084C03 in left lateral (left) and dorsal views (right).

e.g., their COI barcodes differ by 4.4% (29 bp), and therefore this specimen represents a new species. The new species keys (incompletely) to “*Pythonides homer*” (E.41.10) or “*Pythonides herennius herennius*” (E.41.7b) in Evans (1953), but is more similar to the recently described *G. variegatus*, and possibly also to *Gindanes nides* (Mielke and Casagrande, 2002) (type locality in Brazil: Espírito Santo), differing from them by the following combination of characters: a more variegated appearance, larger forewing hyaline spots (similar to *G. variegatus*), a divided forewing discal cell spot (i.e., three spots in the discal cell: a longer anterior one and two shorter posterior spots), pale-bluish-white (glaucous) coloration extending into the anterior portion of the ventral hindwing: a prominent central brown spot near the costa is framed by glaucous on both sides (as in *G. variegatus*), a broader and more diffuse and more uniform brown outer marginal band on the ventral hindwing [narrower, and separated into crescent-shaped spots band in *G. variegatus*], and a broader brown discal band on the hindwing [narrower and frequently separated into spots in *G. variegatus*, best seen on the ventral side]. In male genitalia (Fig. 74), compared to *G. variegatus*, the uncus is longer relative to the tegumen; the harpe is terminally narrower; the ampulla is more strongly developed; and the saccus is shorter than the valva [of approximately equal length in *G. variegatus*]. Due to its cryptic nature and unexplored individual variation, this species is best identified by DNA, with diagnostic base pairs in the nuclear genome: aly103.39.11:C132G, aly103.39.11:A147C, aly420.49.1:T512C, aly420.49.1:A519G, aly37338.40.1:C1410T, aly2423.3.7:C139C (not T), aly2423.3.7:C153C (not T), aly923.17.4:G27G (not A), aly923.17.4:C45C (not G), aly168.11.6:A102A (not G); and the COI barcode: T56T, T127C, T157C, T478C, A565T.

Barcode sequence of the holotype. Sample NVG-24084C03, GenBank [PZ516419](#), 658 base pairs:

```
AACTTTATATTTTATTTTGGGAATTTGGGCAGGAATAATTGGAACATCCTTAAGTTTATTAATTCGAACTGAATTAGGTAATCCAGGATCTTTAATTTGGAGATGATCAAATTTATAATACT
ATTGTCACCTGCTCATGCTTTTATTATAATTTTTCATAGTTATACCAATTATAAATGGAGGATTTGGAAATTGATTAGTACCTTTAATGTTAGGAGCCCCAGATATAGCTTTTCTCGAA
TAAATAATATAAGATTTTGATTATTACCTCCATCTTTATTATTATTATTAATTTCAAGTAGTATTGTTGAAATGGAGCAGGACAGGATGAACCTTTTACCCACCTCTTTCTGCTAATATTGC
TCATCAAGGTTTCATCTGTAGATTTAGCTATTTCTTTTACATTTAGCGGGGATTTTCATCAATTTTAGGAGCTATTAACTTTATTACCACAATTATTAATATACGAATTAATAACCTTTCA
TTTGATCAAATACCTTTATTATTATTGAGCAGTAGGAATTACAGCATTAATATTATTATCTCTCTGTTTGTAGCAGGTGCTATTACTATATTATTAATGATGCAAAATTTAAATACAT
CATTTTTGATCCTGCGGGTGGAGGAGATCCAATTTTATATCAACATCTATTT
```

Type material. Holotype: ♂ currently deposited in the McGuire Center for Lepidoptera and Biodiversity collection, Gainesville, FL, USA (MGCL), illustrated in Fig. 73a (genitalia Fig. 74), bears the following six printed rectangular labels (2nd dark mustard-yellow, last red, others white): [30 October 1990 | Fazenda Rancho Grande, | rd C-20, 7 km E of B-65, | 62 km S of Ariquemes, | Rondonia, BRAZIL | leg. Jim P. Brock], [photographed | G.T. Austin & | J. P. Brock | March 1992], [DNA sample ID: | NVG-24084C03 | c/o Nick V. Grishin], [DNA sample ID: | NVG-25071H06 | c/o Nick V. Grishin], [genitalia: | NVG260613-15 | c/o Nick V. Grishin], and [HOLOTYPE ♂ | *Gindanes vittatus* Grishin]. The first DNA sample ID refers to the extraction from a leg (sequenced), and the second from the abdomen (stored) prior to genitalia dissection.

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

Etymology. In Latin, *vittatus* means striped, banded, or bound with a ribbon. Rather than being variegated, this sister species of *G. variegatus* has a more striped pattern of the hindwing. The name is an adjective.

Distribution. Currently known only from the holotype collected in Rondônia, Brazil.

Species ranges in *Arteurotia* Butler & H. Druce, 1872

The original description of *Arteurotia artistella* Grishin, 2023 (type locality in USA: Texas, Hidalgo Co., Mission) was based on only two specimens, from USA: Texas and Mexico: Tamaulipas (Zhang et al. 2023a), and demonstrated that *Arteurotia tractipennis* A. Butler & H. Druce, 1872 (type locality in Costa Rica), the type species of *Arteurotia* Butler & H. Druce, 1872, ranges from El Salvador to Venezuela. Because *Arteurotia* species are cryptic and variable, their distribution and possible sympatry in Mexico and Central America remains unknown.

Here, we sequence specimens sampled from across Mexico and Central America and find that both species, *A. artistella* and *A. tractipennis*, occur in eastern Chiapas (Mexico), and Guatemala. The specimens were identified using the Z chromosome tree (Fig. 75a), in agreement with their phenotypes. Two males from eastern Chiapas, one of each species, are illustrated in Fig. 76a, b for comparison. The mitochondrial genome tree is incongruent with the nuclear genome tree and reveals evidence of mitochondrial haplotype exchange between taxa (Fig. 75b).

In wing patterns, both males (Fig. 76a, b) and females (Fig. 76c, d) differ in the relative position of the subapical hyaline spots, as stated in the original description of *A. artistella* (Zhang et al. 2023a): the spot in cell R₃-R₄ tends to be closer to the spot in cell R₄-R₅ in *A. artistella*, although these spots vary in position, shape, and size. The shapes and orientations of these spots also differ. In *A. tractipennis*, the spots are generally narrower; the spot in cell R₄-R₅ is elongated and frequently points away from the spot in cell R₃-R₄; while in *A. artistella*, this R₄-R₅ spot is usually rounder and may curve towards the spot in cell R₃-R₄ along vein R₄.

Additionally, phylogenetic analysis of Z chromosome genes reveals that the *A. artistella* clade partitions into two subclades genetically differentiated at the subspecies level (Fig. 75a). One subclade includes the holotype together with specimens from the eastern and central parts of the range and corresponds to the nominotypical subspecies. The other subclade consists of specimens from western Mexico and is not associated with an available name. Therefore, it represents a new subspecies that is described below.

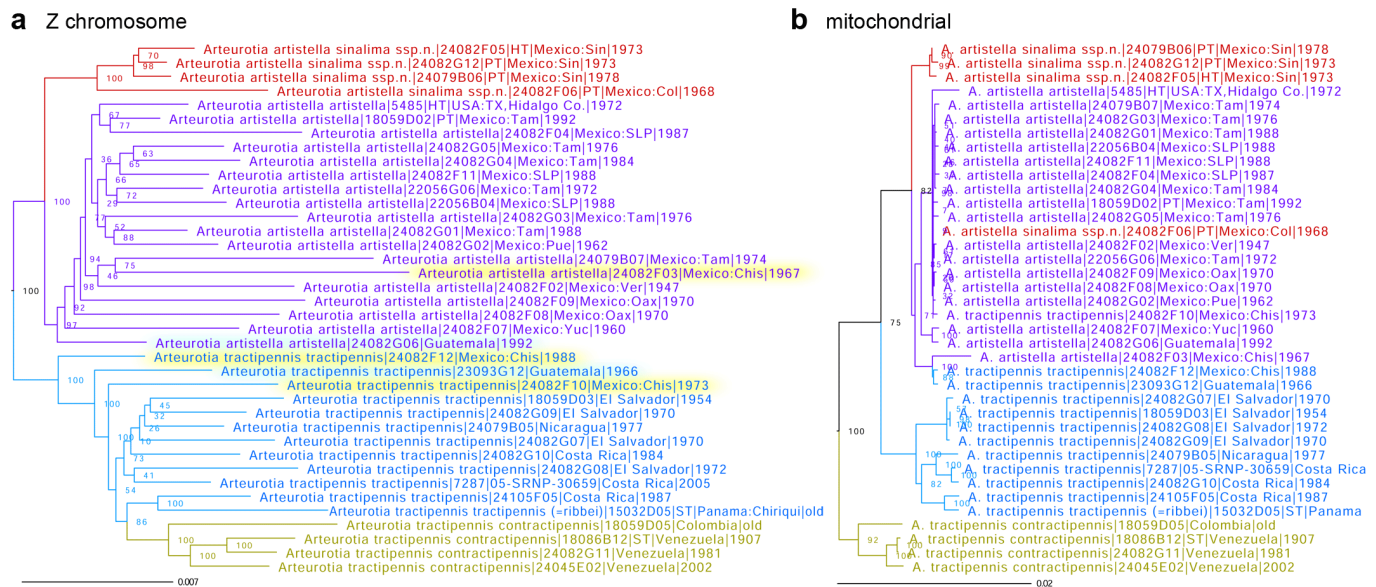


Fig. 75. Phylogenetic trees of all described *Arteurotia* taxa constructed from protein-coding regions in: **a)** the Z chromosome, based on 376,674 positions, and **b)** the mitochondrial genome. Different subspecies are colored differently: *A. artistella sinalima* ssp. n. (red), *A. artistella artistella* (violet), *A. tractipennis tractipennis* (blue), and *A. tractipennis contractipennis* (olive). Ultrafast bootstrap (Hoang et al. 2018) values are shown at nodes. Specimens from Mexico: Chiapas and Guatemala are highlighted in yellow and blue, respectively.

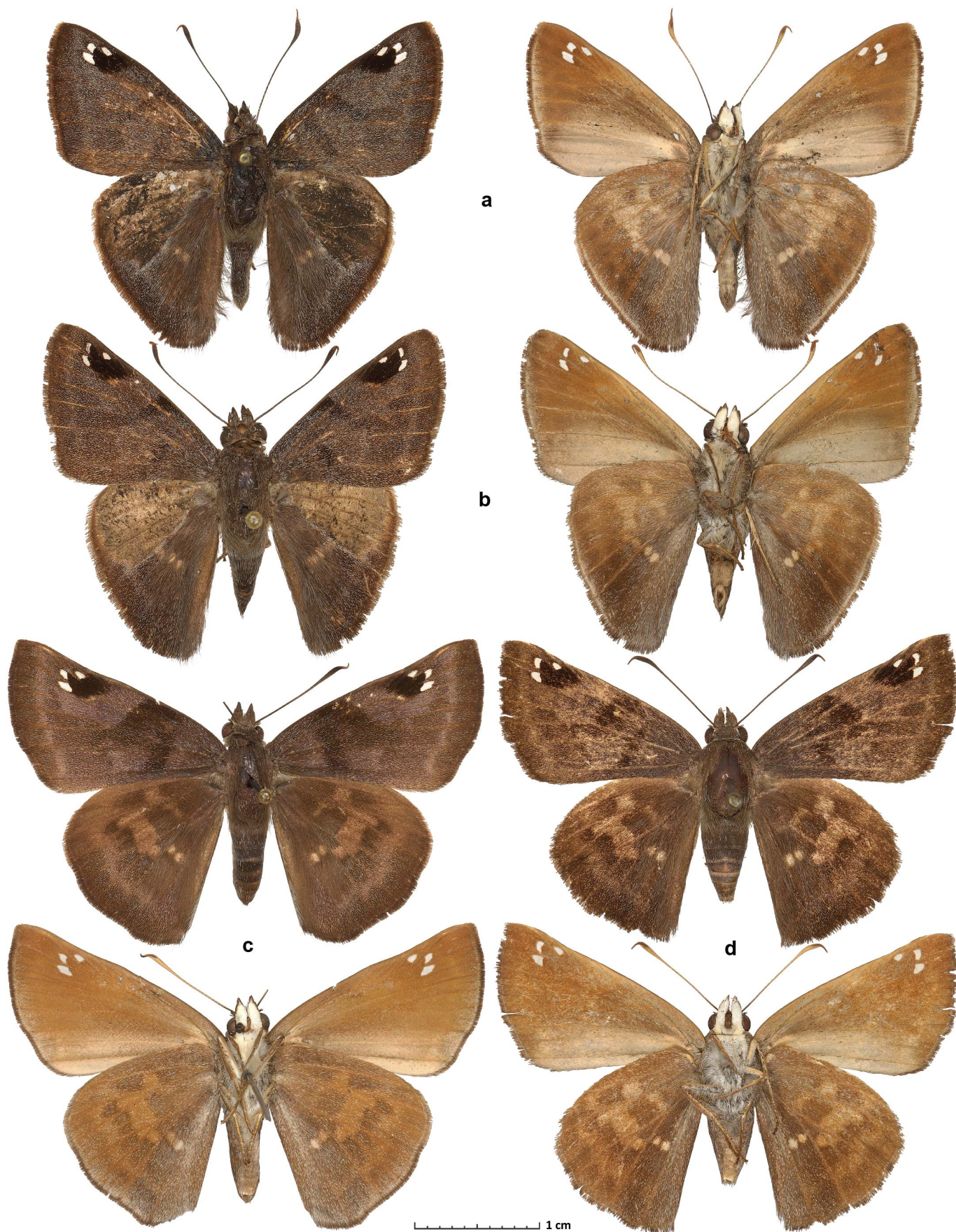


Fig. 76. *Arteurotia* species in dorsal (left or above panel letter) and ventral (right or below) views, data in text: **a, c)** *A. artistella* *artistella* from Mexico: **a)** ♂ NVG-24082F03 Chiapas, Santa Rosa and **c)** ♀ NVG-24082G05 Tamaulipas; and **b, d)** *A. tractipennis*: **b)** ♂ NVG-24082F10 from Mexico: Chiapas, San Jeronimo and **d)** ♀ NVG-24082G09 from El Salvador.

Arteurotia artistella sinalima Grishin, new subspecies
<https://zoobank.org/AE5384D7-9A62-465A-9DA0-9D3B4DA90607>

(Figs. 75 part, 77)

Definition and diagnosis. Genomic analysis reveals that specimens from western Mexico (Sinaloa and Colima) initially identified as *Arteurotia artistella* Grishin, 2023 (type locality in USA: Texas, Hidalgo Co., Mission) is genetically differentiated from it at the subspecies level in the Z chromosome (Fig. 75) (their COI barcodes differ by only 0.3%, 2 bp), and therefore these specimens represent a new subspecies. This new subspecies keys to *Arteurotia tractipennis tractipennis* (E.12(a)) in Evans (1953), but differs from it and the more similar *A. artistella* by the following combination of characters: generally rounder wings and hindwings are less produced at the tornus in males; usually smaller subapical hyaline spots on the forewing; paler ground color; and more variegated appearance, especially on the ventral side of wings, with more prominent paler bands and spots. Due to poorly explored individual variation, this subspecies is best identified by DNA, with diagnostic base pairs in the nuclear genome: aly16.15.1:A111G, aly1651.3.2:T114A, aly1139.45.1:G30C, aly1139.45.1:T105C, aly276890.6.5:G48A; and the COI barcode does not distinguish this subspecies from others, possibly due to introgression.

Barcode sequence of the holotype. Sample NVG-24082F05, GenBank [PZ516420](https://www.ncbi.nlm.nih.gov/nuclot/PZ516420), 658 base pairs:

```
TAC TTTATATTTTATTTTGGTATTTGATCAGGAATAGTAGGAACATCTTTAAGTATACTTATTCGATCAGAATTAGGAATACCTGGATCTTTAATTTGGAGATGATCAAATTTATAATACT  
ATCGTAACGCTCATGCTTTTATATAATTTTATATAGTTATACCTATCATAATTGGAGGATTTGGAATTTGATTAGTACCCCTTATATTAGGAGCACCTGATATAGCTTTTCCCGAA  
TAAATAACATAAGATTTGACTTTTACCTCCTTCTTAATATTATTAATTTCAAGAAGTGTTGTAGAAAATGGTGCTGGAACAGGTTGAAGTGTATCCCCCTTCAGCTAATATTGC  
TCATCAAGGATCTTCTGTAGATTTAACTATTTTCCCTTCATTTAGCTGGAATTTCCCTCTATTTTAGGGGCAATTAATTTTATTACAATATTATTAATATACGAATTAATAATTTATCT  
TTTGATCAAATACCTCTATTGCTATGAGCTGTAGGTATTACTGCTTTACTTTTATTATTATCTTTACCCGTTTGTAGCTGGAGCTATTACCATATTATTAAGTATCGTAATTTAAACACAT  
CTTTTTTGTATCCAGCTGGAGGAGGAGATCCAATTTTATATCAACATTTATTTT
```

Type material. Holotype: ♂ deposited in the McGuire Center for Lepidoptera and Biodiversity collection, Gainesville, FL, USA (MGCL), illustrated in Fig. 77a, bears the following five printed rectangular labels, four white: [MEXICO: SINALOA | 6 mi. N Mazatlán | 30 m.; dense scrub | 25.viii.1973; L. D. & J. Y. Miller | Sta. No. 1973-44], [A. C. Allyn | Acc. 1973-38], [MGCL/FLMNH | Specimen no. | 22160], [DNA sample ID: | NVG-24082F05 | c/o Nick V. Grishin], and one red

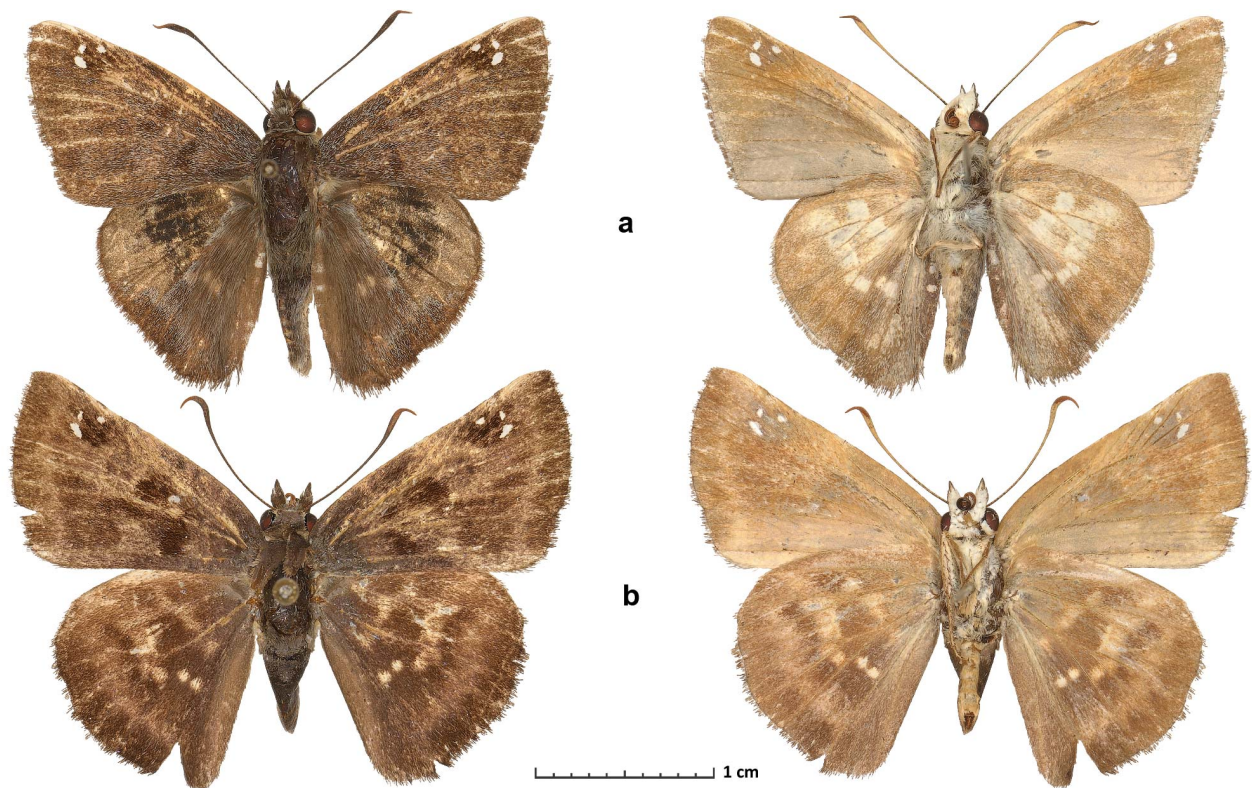


Fig. 77. *Arteurotia artistella sinalima* ssp. n. type specimens from Mexico: Sinaloa, 6 mi N of Mazatlán [MGCL], in dorsal (left) and ventral (right) views, data in text: **a)** holotype ♂ NVG-24082F05 and **b)** paratype ♀ NVG-24082G12.

[HOLOTYPE ♂ | *Arteurotia artistella* | sinalima Grishin]. **Paratypes:** 1♂ and 2♀♀ from Mexico in MGCL: Sinaloa: 1♀ NVG-24079B06 20–25 mi N of Mazatlán, Santa Fe, 19-Oct-1978, R. Wuttken leg. and 1♀ NVG-24082G12 with the same data as the holotype but 25-Aug-1973 (Fig. 77b); and 1♂ NVG-24082F06 Colima, La Salada, 1000 ft, 4-5-May-1968, R. Wind leg.

Type locality. Mexico: Sinaloa, 6 mi north of Mazatlán, elevation 30 m.

Etymology. The name is a fusion of the names of the Mexican states from which this subspecies is known: *Sinal*[oa] + *[Col]ima*, and is treated as a noun in apposition.

Distribution. Currently known from western Mexico (Sinaloa and Colima).

Bolla (Sebia) azora Grishin, new species

<https://zoobank.org/7CC61161-DBC9-4070-8571-DB9F03C1E20A>

(Figs. 78 part, 79, 80)

Definition and diagnosis. Genomic analysis reveals that specimens of *Bolla (Sebia)* Grishin, 2023 (type species *Nisoniades eusebius* Plötz, 1884) from east-central and southern Mexico form a prominent clade sister to several species: *Bolla (Sebia) brennus* (Godman & Salvin, 1896) (type locality in Panama: Chiriquí), *Bolla (Sebia) antha* Evans, 1953 (type locality Colombia: Valle del Cauca, Juntas) and *Bolla (Sebia) dorsolaciniæ* Steinhauser, 1989 (type locality Colombia: Tolima, Río Chili) in both nuclear and mitochondrial genome trees (Fig. 78). Therefore, these specimens represent a new species with prominent genetic differentiation, e.g., its COI barcodes differ by at least 3.5% (23 bp) (the difference from *B. brennus*) compared with those of the other species. This new species keys to *B. brennus brennus* (E.31.16a) in Evans (1953) and was likely included by him in this taxon, but differs from it and other relatives by the following combination of characters: males without a trace of subapical hyaline spots, females with two well-developed spots in cells R₃-R₄ and R₅-M₁, as in *Bolla (Uniphylus) zorilla* (Plötz, 1886) (type locality in Panama) (not a close relative, with which these females were previously confused), and a vestigial or small spot in cell R₄-R₅; males with a slightly produced forewing apex and a concavity along the outer margin near the apex [the forewing is rounder and the outer margin is evenly convex in *B. brennus* and *B. antha*]; both males and females are more variegated above and beneath, with better-developed paler bands and spots alternating with darker brown patches; the alignment of these spots into bands is less definitive, and the bands have more irregular edges, giving this species a somewhat

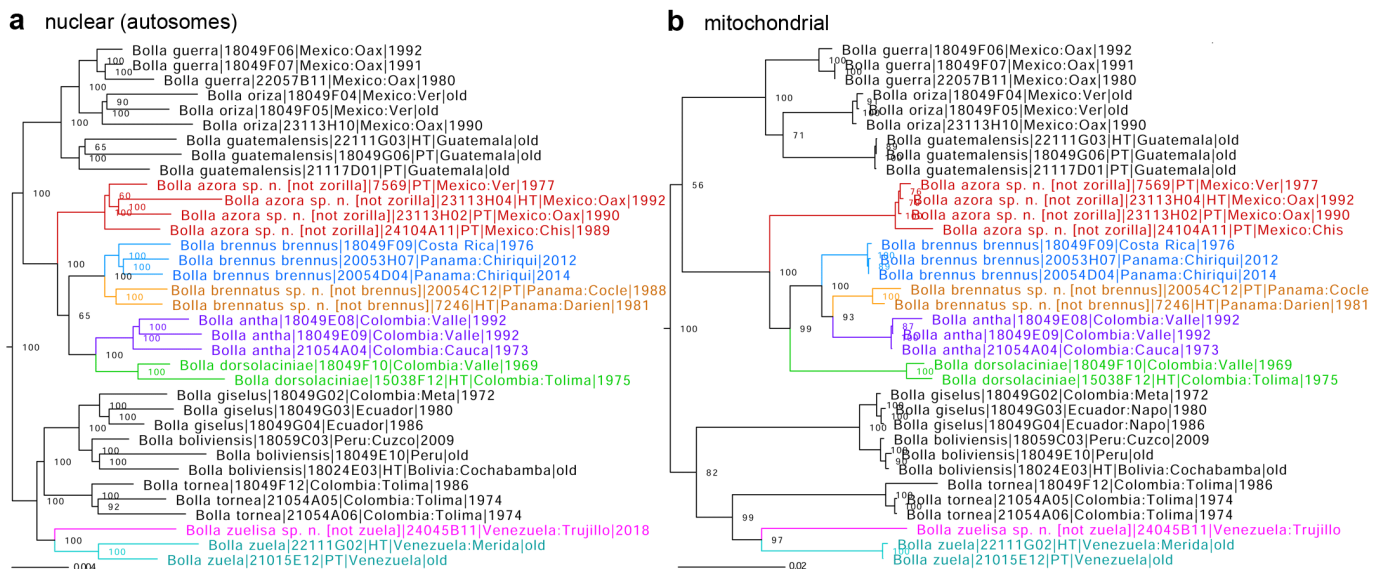


Fig. 78. Phylogenetic trees of a clade of *Bolla (Sebia)* species constructed from protein-coding regions in: **a**) the nuclear genome (autosomes), based on 2,551,185 positions, and **b**) the mitochondrial genome. New species and species in their sister clades are colored: *B. azora* sp. n. (red), *B. brennus* (blue), *B. brennatus* sp. n. (orange), *B. antha* (violet), *B. dorsolaciniæ* (green), *B. zuelisa* sp. n. (magenta), and *B. zuela* (cyan). Ultrafast bootstrap (Hoang et al. 2018) values are shown at nodes.



Fig. 79. Type specimens of *Bolla (Sebia) azora* **sp. n.** from Mexico in dorsal (left) and ventral (right) views, detailed data in text: **a)** holotype ♂ NVG-23113H04 Oaxaca and **b–c)** paratypes ♀♀: **b)** NVG-23113H02 Oaxaca and **c)** NVG-7569 Veracruz.

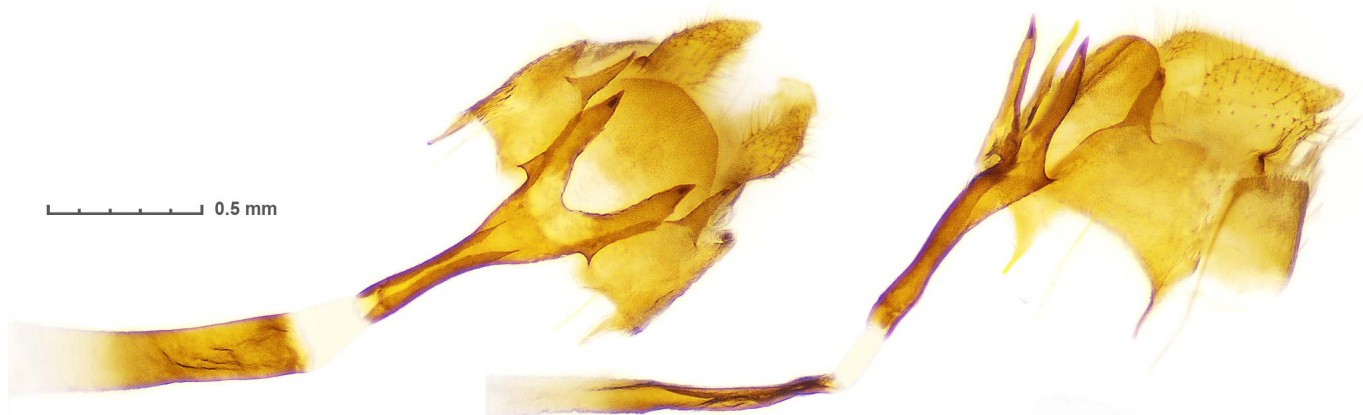


Fig. 80. Female genitalia of *Bolla (Sebia) azora* **sp. n.** paratype NVG-24104A11 Chiapas, ca. 3 mi. S of Simojovel, 3000 ft, 5–6-Sep-1989, J. Kemner leg., genitalia NVG260613-17, in ventral (left) and right ventrolateral (right) views.

checkered appearance [other closely related species are typically more uniformly brown, with paler spots better aligned into smoothly curved bands]. Due to its cryptic nature and unexplored individual variation, this species is best identified by DNA, with diagnostic base pairs in the nuclear genome: aly1041.22.2: A435G, aly11945.14.2:C58T, aly904.15.28:T51G, aly904.15.28:G74T, aly2096.13.5:C228A; and the COI barcode: T181A, T263C, A334G, A511G, T523C.

Barcode sequence of the holotype. Sample NVG-23113H04, GenBank [PZ516421](https://www.ncbi.nlm.nih.gov/nuclot/PZ516421), 658 base pairs:

```
AACTTTATATTTTATTTTGGTATTTGATCAGGTATAATTGGAACCTCATTAAAGTATTCTTATTCGTTCTGAATTAGGAATACCTGGATCTTTAATCGGAGATGATCAAATCTATAATACA  
ATTGTAAGTCTCATGCTTTTATTTATATAATTTTATGGTTATACCTATTATAATTGGAGGATTCGGAATTTGGTTAGTACCCCTAATATTAGGAGCCCTGATATAGCTTTCCCCCGAA  
TAAATAACATAAGATTTGACTATTACCCCATCTCTTATACCTATTAAATTTCAAGTAGTATTGTAGAAAATGGAGCAGGAACAGGATGAACGGTTTATCCCCCTTCATCTAATATTGC  
TCACCAAGGTTTCATCAGTTGATTAGCTATTTTCTCTTCATTTAGCAGGTATTCTTCAATTTTAGGAGCAATTAATTTTATTACAATATTATTAATATACGAATTAATAATTTATCA  
TTTGATCAAATACCTTTATTTGTATGGGCGGTAGGAATCACAGCTCTTTATTACTCTTTCCTTACCAGTATTAGCAGGAGCTATTACAATACTCTTAACAGATCGTAATTTAAATCTT  
CATTTTGTATCCTGCGAGGAGGTGATCCTATTTTATACCAACACTTATTT
```

Type material. Holotype: ♂ deposited in the Carnegie Museum of Natural History, Pittsburgh, PA, USA (CMNH), illustrated in Fig. 79a, bears the following three rectangular labels (1st handprinted, others printed), two white: [Mex: Oaxaca | Yetla-Puerto Eligio | 15 Aug.1992-el. 2000' | John Kemner], [DNA sample ID: | NVG-23113H04 | c/o Nick V. Grishin], and one red [HOLOTYPE ♂ | Bolla (Sebia) | azora Grishin]. **Paratypes:** 3♀♀: Mexico: 1♀ NVG-23113H02 the same data as the holotype but 21-Apr-1990 (Fig. 79b); 1♀ NVG-7569 Veracruz, Fortín de las Flores, Motel Posada Loma, ca. 900 m, 30-Mar-1977, Roy O. Kendall & C. A. Kendall leg., genitalia NVG170107-25 [TAMU] (Fig. 79c); and 1♀ NVG-24104A11 (leg, sequenced), NVG-25052F07 (abdomen, stored), Chiapas, ca. 3 mi. S of Simojovel, 3000 ft, 5–6-Sep-1989, J. Kemner leg., genitalia NVG260613-17 (Fig. 80) [TMMC].

Type locality. Mexico: Oaxaca, Mpio. Santiago Comaltepec, 3 mi north of Puerto Eligio toward Yetla, elevation 2000 ft.

Etymology. Due to superficial similarity, a female of this new species was misidentified by H. A. Freeman as *B. zorilla*, which is a distantly related species belonging to a different subgenus. The name means not-*zorilla* with negating a- for not: *a+* *zor*[ill]*a*, and is treated as a noun in apposition.

Distribution. Widely distributed in east-central and southern Mexico, confirmed from Veracruz, Oaxaca, and Chiapas.

***Bolla (Sebia) brennatus* Grishin, new species**

<https://zoobank.org/AB9C48B4-80B8-41B2-A8F9-DFC61AE1ED1C>

(Figs. 78 part, 81a–b, 82a)

Definition and diagnosis. Genomic analysis reveals that two males from central and eastern Panama initially identified as *Bolla (Sebia) brennus brennus* (Godman & Salvin, 1896) (type locality in Panama Chiriquí) (Fig. 81c–e) are genetically differentiated from it at the species level (Fig. 78); their COI barcodes differ by 1.5% (10 bp) but they are not sister species in the mitochondrial genome tree (Fig. 78b), and therefore these specimens represent a new species. This new species keys to *B. brennus brennus* (E.31.16a) in Evans (1953), but differs from it and other relatives by the following combination of characters in males: lack of hyaline spots [*Bolla (Sebia) brennus vexta* Evans, 1953 (type locality in Colombia: Manizales) has at least one spot]; rounder wings [*B. brennus vexta* has a more angular forewing apex]; the ventral side of the wings is slightly paler along the margins, in particular, near the hindwing tornus and the forewing apex, the postdiscal paler band across the ventral hindwing is usually better defined; and hindwing yellowish postdiscal spots (when developed, best seen in fresher specimens) are slightly smaller and better separated from each other. In male genitalia (Fig. 82a), compared to *B. brennus* (Fig. 82b, c), the ventrally pointed side lobes of the tegumen adjacent to the uncus are less developed, as best seen in lateral view: a round, down-pointed hump in the new species vs. a right triangle in *B. brennus*; the harpe is relatively shorter and broader, with teeth along the posterior margin extending farther dorsad, and the lobe by the ampulla is nearly level with the costa of the valva, not conspicuously protruding dorsad beyond of it as in *B. brennus*. Due to its cryptic nature and poorly explored individual variation, this species is best identified by DNA, with diagnostic base pairs in the nuclear genome: aly331.24.3:T93A, aly1313.9.8:C69A, aly1313.9.8:A93G, aly6841.13.2:A261T, aly636.10.2:A42G; and the COI barcode: T91C, T169C, G253A, A466G, G514A.



Fig. 81. Specimens of *Bolla* (*Sebia*) in dorsal (left) and ventral (right) views, data in text or below: **a–b)** *B. brennatus* **sp. n.**: from Panama: **a)** holotype ♂ NVG-7246 and **b)** paratype ♂ NVG-20054C12 and **c–e)** *B. brennus* non-types: **c–d)** ♂♂ Panama, Chiriqui [MEM]: **c)** ♂ NVG-20053H07 and **d)** ♂ NVG-20054D04, and **e)** ♀ NVG-18049F09 Costa Rica, Heredia. 'F' indicates mirror image (i.e., left-right inverted).

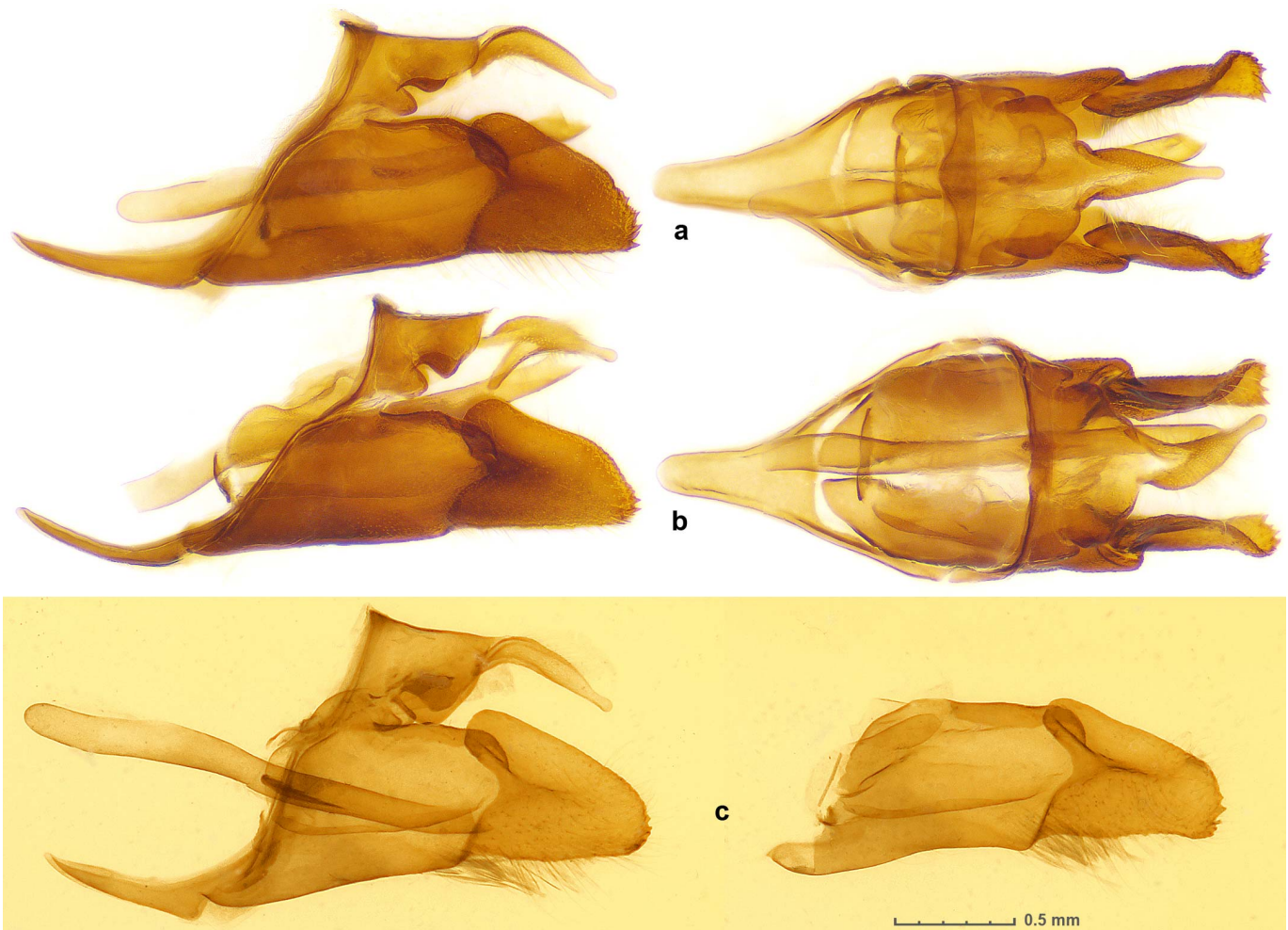


Fig. 82. Male genitalia of *Bolla* (*Sebia*) in left lateral (left) and dorsal views (right, except for (c), which shows the lateral view of the valva): **a)** *B. (S.) brennatus* sp. n. paratype NVG-20054C12 from Panama, Coclé [MEM]; and **b–c)** *B. (S.) brennatus* from Panama: Chiriquí: **b)** non-type NVG-20053H07 Santa Clara, Río Candela, 1830 m, GPS 8.89925, –82.73836, J. R. MacDonald leg., 25-May-2012, genitalia RAA 0555 by R. A. Anderson; the uncus is partly detached and the anterior part of the phallobase is broken off [MEM]; and **c)** syntype BMNH(E) 1669527, Volcán Barú, 2500–4000 ft, G. C. Champion leg., minislide 724 affixed to the same pin as the specimen and used by Godman and Salvin (1896) to describe and illustrate the genitalia on pl. 89, fig. 23 (the still attached valva appears flattened, and the detached valva is mounted at an angle, resulting in apparent differences in shape despite the genitalia being symmetrical); © The Trustees of the Natural History Museum, London, Creative Commons License 4.0 (<https://creativecommons.org/licenses/by/4.0/>) [BMNH].

Barcode sequence of the holotype. Sample NVG-7246, GenBank [PZ516422](https://www.ncbi.nlm.nih.gov/nuccore/PZ516422), 658 base pairs:

```
AACTTTATATTTTATTTTCGGTATTTGATCCGGTATAATTGGAACCTCATTAGTATCCTTATTCGTTCTGAACTAGGTATACCTGGATCCTTAATCGGAGATGATCAAATCTATAATACA
ATTGTAACCTGCTCATGCTTTTATTATAAATTTTTTTATAGTTATACCCATTATAATTGGTGGATTTCGGAAATTTGGTTAGTACCCCTAATATTAGGAGCCCTGATATAGCTTTCCCCCGAA
TAAATAACATAAGATTTTGATTATTACCCCATCTCTTATACTATTAAATTTCAAGTAGTATTGTAGAAAATGGAGCAGGAACAGGATGAACAGTTTATCCCCCCTTTCATCTAATATTGC
TCATCAAGGTTTCATCAGTTGACTTAGCTATTTTCTCCCTTCATTAGCAGGTATTTCTTCAATTTAGGAGCAATTAACCTTTATTACAACCTATTATTAATATGCGAATTAATAATTTATCG
TTTGATCAAAATACCTTTATTTGTATGAGCAGTAGGAATTACAGCTCTTTTATTACTTCTTTCCTTACCAGTATTAGCTGGAGCTATTACAATACTCTTAACAGATCGTAATTTAAATACTT
CATTTTTTGATCCTGCAGGAGGAGGGATCCTATTTTATACCAACACTTATTT
```

Type material. **Holotype:** ♂ deposited in the National Museum of Natural History, Smithsonian Institution, Washington, DC, USA (USNM), illustrated in Fig. 81a, bears the following six printed rectangular labels (text in *italics* handwritten), five white: [PANAMA: Darien | Cana 750m | 21.VII.1981 | leg. G.B.Small], [*Bolla* ♂ | *brennatus* (Godman | and Salvin) | det. H.A. Freeman], [DNA sample ID: | NVG-7246 | c/o Nick V. Grishin], [genitalia | NVG161005-73 | Nick V. Grishin], [USNMMENT | {QR Code} | 01321094], and one red [HOLOTYPE ♂ | *Bolla* (*Sebia*) | *brennatus* Grishin]. **Paratype:** 1♂ NVG-20054C12 Panama, Coclé, El Valle, 800–900 m, 3-5-Jan-1988, J. MacDonald & Schiefer leg., genitalia NVG260613-16 [MEM] (Figs. 81b, 82b).

Type locality. Panama: Darién Province, Cana, elevation 750 m.

Etymology. The name is derived from that of its close relative *B. brennus* and was lengthened to reflect the more southern distribution of this species. The name is treated as a noun in apposition.

Distribution. Currently known from central and eastern Panama.



Fig. 83. Type specimens of *Bolla (Sebia)* ♂♂ from Venezuela in dorsal (left) and ventral (right) views, data in text or below: **a)** *B. zuelisa* **sp. n.** holotype NVG-24045B11 and **b–c)** *B. zuelisa* type series: **b)** holotype NVG-22111G02 Mérida, old, Hahnel leg. [MFNB] and **c)** paratype NVG-21015E12 no locality details, old [ca. 1900], Holland collection [CMNH].

***Bolla (Sebia) zuelisa* Grishin, new species**

<https://zoobank.org/B7EFCC60-0411-4B4F-9304-0D286EBB03B6>

(Figs. 78 part, 83a)

Definition and diagnosis. Genomic analysis reveals that a male from the Venezuelan Andes is sister to *Bolla (Sebia) zuela* Grishin, 2025 (type locality in Venezuela, Mérida) but is genetically differentiated

from it at the species level (Fig. 78); e.g., their COI barcodes differ by 3.3% (22 bp), and therefore this male represents a new species, also related to *Bolla (Sebia) boliviensis* (Bell, 1937) (type locality in Bolivia: Cochabamba). This new species keys to “*B. tetra boliviensis*” (E.31.17(c)) in Evans (1953), but differs from it and particularly its sister *B. zuela* (included by Evans in “*B. tetra boliviensis*”) by the following combination of characters: absent hyaline spotting anywhere on the wings, including the subapical spots characteristic of *B. zuela* (Fig. 83b, c); smaller overall size; rounder forewings; a paler brown and more uniform coloration on both wing surfaces; no pale spots on the ventral side, and only a diffuse pale postdiscal band is present instead. Due to its cryptic nature and unexplored individual variation, this species is best identified by DNA, with diagnostic base pairs in the nuclear genome: aly275209.6.11:C174G, aly127.86.7:C87T, aly127.86.7:T144C, aly671.22.1:C392T, aly671.22.1:T945C, aly423.30.2:A39A (not G), aly423.30.2:C30C (not T), aly412.4.17:T88T (not G), aly252.21.21:A178A (not T), aly1603.83.1:A597A (not G); and the COI barcode: T247C, A268G, C343T, T421C, T499C, A550A, A628A.

Barcode sequence of the holotype. Sample NVG-24045B11, GenBank [PZ516423](https://www.ncbi.nlm.nih.gov/GenBank/entry/view.cgi?accession=PZ516423), 658 base pairs:

```
AACTTTATATTTTATTTTGGTATTTGATCAGGTATAATTGGAACCTCATTAAAGTATTCCTATTCGTTCTGAATTAGGTATACCTGGATCTTTAATGGAGATGATCAAATTTATAATACA
ATTGTAACGCTCATGCTTTTATTATAATTTTATAGTTATACCTATTATAATTTGGTGGATTGGAAATGATTAGTACCCCTAATATTAGGAGCTCCTGATATAGCTTTCCCGCGAA
TAAACACATAAGATTTTGATTATGCCCCATCCCTAATACTATTAAATTTCAAGTAGTGTGTAGAAAATGGAGCAGGAACAGGATGAACAGTTTATCCTCCTCTTTCATCTAATATTGC
TCATCAAGGTTTCATCAGTTGATTTAGCTATTTTTCCTTCATTAGCAGGTATTTCCCTCAATTTTAGGAGCAATTAATTTTATTACAACATATCATTAAATATACGAATTAATATTATCA
TTTGATCAATACCCCTTATTGTATGAGCTGTAGGAATTACAGCTCTTTTATTACTTCTTCTTACCAGTATTAGCAGGAGCTATTACAATACTCTTAACAGATCGTAATTTAAATACAT
CATTTTGTATCCAGCTGGAGGAGGAGATCCTATTTTATACCAACACTTATT
```

Type material. Holotype: ♂ deposited in the collection of the Nature Education Centre of the Jagiellonian University, Kraków, Poland (CEPUJ), illustrated in Fig. 83a, bears the following five printed rectangular labels (2nd blue, 3rd green, 5th red, others white): [VENEZUELA | Estado Trujillo | Boconó | Arbol Redondo | 2000-2500 m | 27.V.18 | M. Sánchez leg.], [M.Sanchez | CEP-MZUJ 03/2019], [CEP-DNA | 7309 | | tissue | sample], [DNA sample ID: | NVG-24045B11 | c/o Nick V. Grishin], and [HOLOTYPE ♂ | Bolla (Sebia) | zuelisa Grishin].

Type locality. Venezuela: Trujillo, Boconó, Árbol Redondo, 2000–2500 m.

Etymology. In Spanish, liso means smooth, plain, unpatterned, or unspotted. The name reflects the plain and unspotted pattern of this species compared to its relatives and is treated as a noun in apposition.

Distribution. Currently known only from the holotype collected in the cloud forest of the Andes in northwestern Venezuela.

Bolla (Uniphylus) marteia Grishin, new species

<https://zoobank.org/E60F817A-5496-4322-8397-4929A6F3AB68>

(Figs. 84 part, 85a–b)

Definition and diagnosis. Genomic analysis reveals that a pair from the Sierra Nevada de Santa Marta in northern Colombia is sister to the clade of two species: *Bolla (Uniphylus) hazelae* (Hayward, 1940) (type locality Ecuador, Tungurahua, Mapoto at Río Pastaza) and *Bolla (Uniphylus) vena* Grishin, 2023 (type

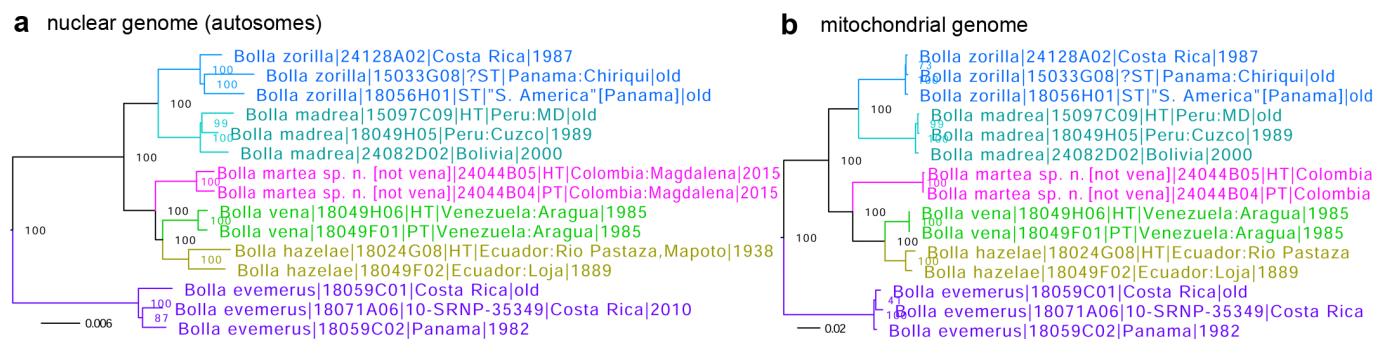


Fig. 84. Phylogenetic trees of all valid species of *Bolla (Uniphylus)* constructed from protein-coding regions in: **a**) the nuclear genome (autosomes), based on 6,997,494 positions, and **b**) the mitochondrial genome. Different species are colored differently: *B. zorilla* (blue), *B. madrea* (cyan), *B. marteia* sp. n. (magenta), *B. vena* (green), *B. hazelae* (olive), and *B. evemerus* (violet). Ultrafast bootstrap (Hoang et al. 2018) values are shown at nodes.



Fig. 85. Type specimens of *Bolla* (*Uniphylus*) in dorsal (left) and ventral (right) views, data in text or below: **a–b)** *B. martea* **sp. n.**: from Colombia: **a)** holotype ♂ NVG-24044B05 and **b)** paratype ♀ NVG-24044B04 and **c–d)** *B. vena* from Venezuela, Aragua, Rancho Grande, 1100 m, S. S. Nicolay leg. [USNM]: **c)** holotype ♂ NVG-18049H06, USNMENT_01466668, 18-May-1985 and **d)** paratype ♀ NVG-18049F01, USNMENT_01466639, 7-Jun-1985.

locality Venezuela: Aragua, Rancho Grande) (Fig. 85c–d), and is genetically differentiated from them at the species level (Fig. 84); e.g., their COI barcodes differ by 8.3% (55 bp) (from *B. hazelae*) and by 7.6% (50 bp) (from *B. vena*), and therefore this pair of specimens represents a new species that is also related to *Bolla* (*Uniphylus*) *zorilla* (Plötz, 1886) (type locality in Panama) and *Bolla* (*Uniphylus*) *madrea* (R. Williams & E. Bell, 1940) (type locality in Peru: Madre de Dios) (Fig. 84). This new species keys to *B. zorilla* (E.31.21) in Evans (1953), but differs from it and other relatives by the following combination of characters: larger hyaline spots on the forewing, including the subapical triplet [smaller in *B. vena*], a dot (larger in females) at the base of cell M₃-CuA₁, and, in females, a dash fully crossing cell CuA₁-CuA₂, accompanied by a smaller spot near vein CuA₂ in cell CuA₂-1A+2A; and the ventral wing pattern closely resembles the dorsal pattern, with more prominent pale hindwing bands and correspondingly more contrasting darker postdiscal bands on both wings. Due to its cryptic nature and unexplored individual variation, this species is best identified by DNA, with diagnostic base pairs in the nuclear genome: aly528.24.7:A186C, aly29.1.2:T45C, aly1139.63.6:A123G, aly1019.14.44:C87T, aly529.13.54:C204T; and the COI barcode: T5C, A7T, A59G, T277C, A493G, A583C.

Barcode sequence of the holotype. Sample NVG-24044B05, GenBank [PZ516424](https://www.ncbi.nlm.nih.gov/nuclot/PZ516424), 658 base pairs:

```
AACTCTTTATTTTATTTTGGCATCTGATCTGGTATAGTTGGAACCTCTTTAAGAATGCTTATTCGTTTCTAGAACTAGGAACCTCCCGGATCTTTAATCGGAGATGATCAAAATTTATAATACT
ATCGTAACAGCTCATGCTTTTATTATAATTTTATATAGTTATACCTATTATAATCGGAGGATTTGGAAATTGATTAGTCCCATTAATATTAGGAGCCCTGATATAGCTTTTCTCGAA
TAAATAATATAAGATTTGACTTTTACCCCTTCCCTAATACTATTAAATTTCTAGAGTGTGGTAGAAAAATGGGGCAGGAACCGGGTGAACCTGTTATCCCTCTTTCAGCTAATATTGC
TCACCAAGGATCTTCTGTAGATTAGCTATTTTCCCTTCATTAGCTGGTATTTCCTCAATTTAGGGGCAATTAATTTTATTACAACATTGTTAATATACGAATTAATAACTTATCA
TTTGATCAGATACCTTTATTGTATGAGCAGTTGGTATTACTGCCTTACTTTTATTATTATCTTTACCTGTATTGGCAGGGGCTATTACTATACCTCTCACAGATCGAAATTTAAATACTT
CATTTTGTATCCCGCAGGAGGGGGGAGCCCATTTTATACCAACATTTATTT
```

Type material. Holotype: ♂ deposited in the collection of the Nature Education Centre of the Jagiellonian University, Kraków, Poland (CEPUJ), illustrated in Fig. 85a, bears the following five printed rectangular labels (2nd blue, 3rd green, 5th red, others white): [COLOMBIA | Magdalena | Sierra Nevada de SM | San Pedro | 1500-1600 m | 03–05.02.2015 | A.Zubek, C.Prieto, | J.Lorenc leg.], [NCN A.Zubek | MZUJ 4/2017], [CEP-DNA | 7207 | | tissue | sample], [DNA sample ID: | NVG-24044B05 | c/o Nick V. Grishin], and [HOLOTYPE ♂ | *Bolla* (*Uniphylus*) | *martea* Grishin]. **Paratype:** 1♀ NVG-24044B04, CEP-7206 with the same data as the holotype (Fig. 85b).

Type locality. Colombia: Magdalena Department, Sierra Nevada de Santa Marta, elevation 1500–1600 m.

Etymology. Similarly to its relative *B. madrea*, the name of this new species is derived from the type locality in [Sierra Nevada de Santa]*Mart{e}a* and is treated as an adjective.

Distribution. Currently known only from the type locality in northern Colombia.

Lectotype designation for *Nisoniades braco* Herrich-Schäffer, 1865

Nisoniades braco was described by Herrich-Schäffer (1865) from an unspecified number of specimens. The title of the work implies that at least some syntypes should have been from Cuba, however, at least a pair of syntypes from “Mexico” was also mentioned in the description. We translate the description from German as “Entirely uniform brown; the male with a costal fold on the forewing, without hair tufts on the hind tibiae. Underside of the palpi and thorax somewhat moldy gray. In somewhat larger specimens from Mexico, which I otherwise cannot distinguish, I observe three rows of paler spots faintly indicated on the underside of the hindwing, this is found also in a female from the same locality, while a female sent by H. G[undlach]. as belonging here probably belongs to another species because of distinct hyaline spots in cells 3, 6–8” (Herrich-Schäffer 1865). We found three specimens curated as syntypes of *Nisoniades braco*, all males, one in each collection: MFNB, ZSMC, and ANSP.

The syntype in MFNB sequenced as NVG-15033G10 is from the Herrich-Schäffer collection, later incorporated into the Staudinger collection (Fig. 86a). The syntype is labeled as “Origin.” (a pink label characteristic of type specimens in the Staudinger collection) and bears a label in Herrich-Schäffer’s handwriting “braco m” with “Cuba” added in a different ink and probably at a later time. This specimen is a syntype (unless the “braco” label was transferred from the original specimen to this one), because “m” after “braco” (written by Herrich-Schäffer) is an abbreviation of “mihi” (Latin for “of me”), added after a species name to attribute the new species to the writer. This way of attribution was frequently used over a

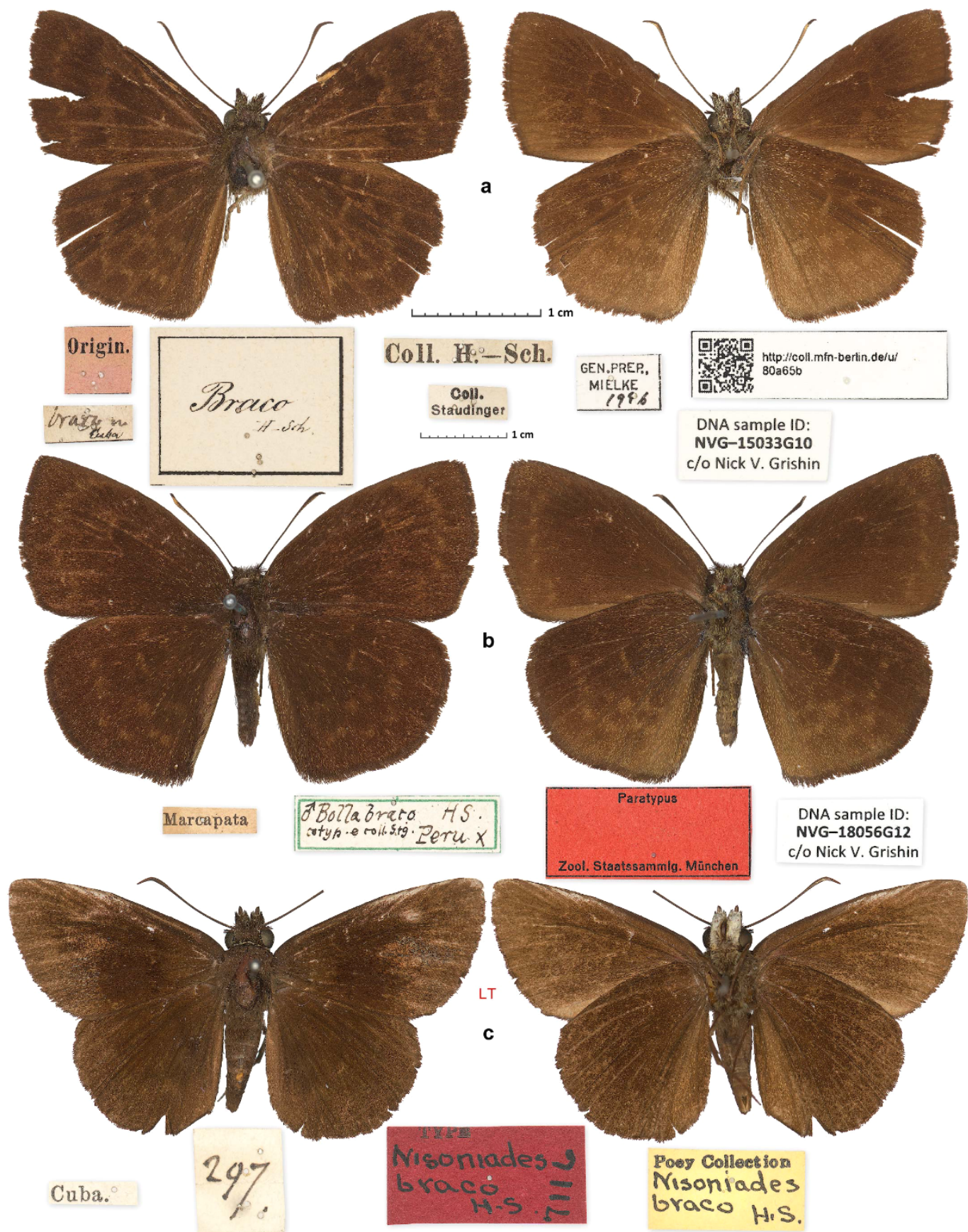


Fig. 86. Males curated as type specimens of *Burca braco* in dorsal (left) and ventral (right) views, labels below, data in text: **a)** *Bolla catharina* NVG-15033G10 in MFNB; **b)** *Bolla nigerrima* NVG-18056G12 from Peru: Marcapata in ZSMC; and **c)** lectotype (designated herein) NVG-20112B09 from Cuba in ANSP. Labels are reduced by a third compared to specimens; the smaller scale below one of the labels refers to labels and the larger scale below the first specimen refers to specimens.

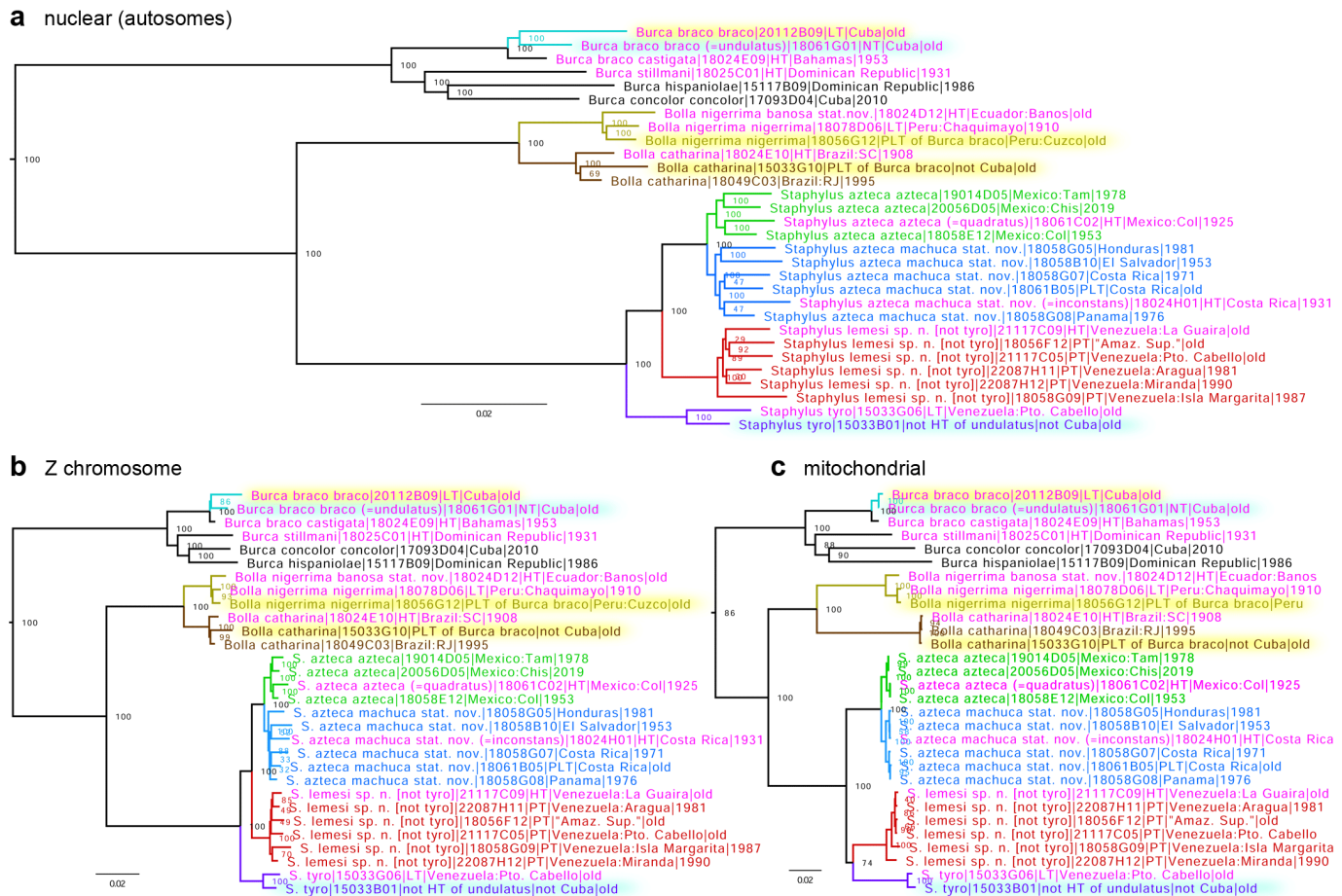


Fig. 87. Phylogenetic trees of selected Carcharodini taxa constructed from protein-coding regions in: **a)** the nuclear genome (autosomes), based on 3,594,045 positions, **b)** the Z chromosome, based on 252,132 positions, and **c)** the mitochondrial genome. Primary type specimens are labeled in magenta and different taxa discussed in the text are colored differently: *Burca braco braco* (cyan, but types are labeled in magenta, as for all primary types), *Bolla nigerrima* (olive), *Bolla catharina* (brown), *Staphylus azteca azteca* (green), *Staphylus azteca machuca stat. nov.* (blue), *Staphylus lemesi sp. n.* (red), and *Staphylus tyro* (violet). The three specimens (of three different species) that are likely from the type series of *Burca braco* are highlighted in yellow and the two specimens associated with the name *Nisoniades undulatus* Herrich-Schäffer, 1865 are highlighted in blue. Ultrafast bootstrap (Hoang et al. 2018) values are shown at nodes.

century ago, instead of the author's name being added to the species name. However, genomic phylogeny places this syntype in the clade with the holotype of *Bolla* (*Bolla*) *catharina* (E. Bell, 1937) (type locality Brazil: Santa Catarina, Nova Bremen), thus identifying it as this species known only from southeastern Brazil (Fig. 87). Therefore, the locality "Cuba" was added to this specimen by mistake, probably from the title of the Herrich-Schäffer's work, likely because this specimen did not have a locality label. The appearance of this specimen agrees with Herrich-Schäffer's description of the Mexican syntype, and it might have been considered to originate from Mexico (Herrich-Schäffer 1865). In any case, this syntype is not the best candidate for a lectotype, because it will change the long-established application of the name to a Cuban species, thus going against the stability of nomenclature.

A possible syntype in ZSMC sequenced as NVG-18056G12 is labeled as "cotyp[us]. e[x] coll[ectione]. St[audin]g[er]." and "Paratypus"; however, its locality label, "Marcapata", which is in Peru: Cuzco, is not consistent with Cuba and Mexico from the original description (Fig. 86b). Therefore, it is either not a syntype or was mislabeled or referred to as being from "Mexico" in the original description. Genomic analysis places this possible syntype in the clade with the lectotype (designated herein) of *Bolla* (*Bolla*) *nigerrima* Mabilie & Boullet, 1917 (type locality Peru: Puno, Chaquimayo) thus identifying it as this species, sister to *B. catharina*, which is not known from Cuba or Mexico, but recorded from Peru and Ecuador (Fig. 87). Therefore, the locality label of this possible syntype is likely accurate, and even if this

specimen is a syntype, it is also not the right candidate for a lectotype for the same reason as the syntype in MFNB.

A syntype in ANSP sequenced as NVG-20112B09 is from the Felipe Poey collection, which is known to have type material of Herrich-Schäffer, is labeled from “Cuba” and curated as a “type” of *Nisoniades braco* (Fig. 86c). Genomic analysis places this syntype with specimens currently considered to be *Burca braco* (Fig. 87), and therefore it represents this species thus being a candidate for a lectotype that would preserve the stability of nomenclature. To stabilize nomenclature and define the name *N. braco* objectively, N.V.G. hereby designates the syntype in the ANSP collection, a male illustrated in Fig. 86c that bears the following four labels (3rd red, 4th yellow, others white; 2nd handwritten, others printed with handwritten text shown in *italics*): [Cuba.], [297.], [TYPE | *Nisoniades* | *braco* | *H-S.* | 7116], where the number is rotated 90° counterclockwise relative to the rest of the text and written along the right edge of the label, [Poey Collection | *Nisoniades* | *braco* | *H-S.*], as the **lectotype** of *Nisoniades braco* Herrich-Schäffer, 1865. The lectotype is missing the club of the right antenna, and both of its hindwings are chipped near the tornus. The type locality of *N. braco* remains in Cuba. The COI barcode sequence of the lectotype, sample NVG-20112B09, GenBank [PZ516425](https://www.ncbi.nlm.nih.gov/nuclot/PZ516425), 658 base pairs, is:

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AACTTTATATTTTATTTTGGTATTTGATCTGGAATAGTAGGAACCTTCATTAAGATTACTAATTCGATCAGAATTAGGAACCCCTGGATCTTTAATTGGAGATGATCAAATTTATAATACT
ATTGTACAGCTCATGCTTTTATTATAATTTTATAGTTATACCTATTATAATTGGAGGATTTGGTAACCTGATTAGTACCCCTTATATTAGGAGCTCCCGATATAGCCTTTCCACGAA
TAAATAATATAAGATTTGACTTTTACCTCCATCATTAATATTATTAATTTCTAGAAGTATTGTAGAAAATGGAGCAGGAACAGGTTGAACAGTTTACCTCCTTTATCAGCTAATATCGC
ACATCAAGGATCTTCTGTTGATTAGCCATTTTCCCTTCATTAGCAGGTATTCTCAATTCCTGGGGCAATTAATTTATTACAACATATTATTAATATACGAATTAATAATTTATCT
TTTGATCAATTACCTTTATTTGTGTGAGCAGTAGGAATTACTGCTTTATTATTACTACTTTCTTTACCAGTATTAGCTGGAGCTATTACAATACTTTTAACAGATCGTAATCTTAATACAT
CCTTTTGTGACCCCTGCTGGAGGAGGAGATCCAATTTATACCAACATTTATTT
```

Neotype designation for *Nisoniades undulatus* Herrich-Schäffer, 1865

The name *Nisoniades undulatus* Herrich-Schäffer, 1865 regarded as a junior subjective synonym of *Burca braco* (Herrich-Schäffer, 1865) (type locality in Cuba) was proposed for a female (holotype by monotypy) from Cuba (as inferred from the title of the work and the collector being Gundlach), and we translate the entire original description from German as: “A single female, which H. G[undlach]. sent as belonging to *N. braco*. Closest to *N. potrerillo* [sic. *potrillo*], with the same cut of the margin of the hindwings, but the four hyaline spots on the middle of the forewing costal margin are absent; the three costal spots are more uniform, and the underside is not clouded with violaceous-grey”; complemented with a phrase referring to this female from the description of *B. braco* on the previous page: “a female sent by H. G[undlach]. as belonging here probably belongs to another species because of distinct hyaline spots in cells 3, 6–8” (Herrich-Schäffer 1865).

Genomic sequencing of a female (originally from the Herrich-Schäffer collection) curated in MFNB as a type (“Origin.”) of *N. undulatus* (Fig. 88a; NVG-15033B01) reveals that it belongs to the subgenus *Capilla* Grishin, 2023 (type species *Helias aurocapilla* Staudinger, 1875, currently a junior subjective synonym of *Hesperia musculus* Burmeister, 1875) of *Staphylus* Godman & Salvin, 1896 (type species *Helias ascalaphus* Staudinger, 1876) (subtribe Pholisorina Grishin, 2023), and not to *Burca* E. Bell and W. Comstock, 1948 (type species *Nisoniades concolor* Herrich-Schäffer, 1865) (subtribe Burcina Grishin, 2023) (Fig. 87). Moreover, this female is sister to the lectotype of *Staphylus* (*Capilla*) *tyro* (Mabille, 1878) (type locality Venezuela: Carabobo, Puerto Cabello) and we identify it as this species. *S. tyro* is not known from Cuba and is not likely to occur there. The female lacks the original Herrich-Schäffer’s label with the name *undulatus* and “m” after it, there is no attribution of this specimen to Gundlach, and the locality label “Cuba(?)” in Staudinger’s handwriting is with a question mark (Fig. 88a). The identification label “Undulatus | HS. ♀ | var. Federici ♀ au. | bon. spec. ? (Mab.)” has also been written by Staudinger and added after the original description of *N. undulatus*. The label mentions *Quadrus* (*Ouleus*) *fridericus* (Geyer, 1832), a species recorded from Cuba, but with rounded hindwings (not more angular as in the original description) and without hyaline spots. Staudinger probably considered this specimen (and *N. undulatus*?) to be a variation of *Q. fridericus*, or questionably a valid species, per P. Mabille (“bon. spec. ? (Mab.)”). We conclude that while being from the Herrich-Schäffer collection, this female is not the holotype of *N. undulatus*. Finally, although this female of *S. tyro* is missing most of its wings, it may not agree with the original description of *N. undulatus*, mentioning a

hyaline spot in the forewing cell 3 (M_3-CuA_1) which *S. tyro* typically lacks. Searches for other candidates for the holotype of *N. undulatus* in MFNB, ZSMC, SMNS, BMNH, and ANSP have failed. Therefore, we believe that the holotype of *N. undulatus* is lost.

There is an exceptional need for a neotype of *N. undulatus* to define this taxon objectively and thus stabilize nomenclature by clarifying the taxonomic identity of this species, largely because a specimen of *S. tyro* is currently curated as a type of *N. undulatus*, creating potential for instability. Hereby, N.V.G. designates a female in the USNM illustrated in Fig. 88b (DNA sample NVG-18061G01) as the **neotype** of *Nisoniades undulatus* Herrich-Schäffer, 1865. To stabilize nomenclature, we selected an old female of *B. braco* from Cuba: Matanzas as the neotype of *N. undulatus*, because it agrees with its original description. Gundlach was stationed in the Matanzas province (Ramsden 1915), and it is possible that the holotype was collected there.

This neotype satisfies all requirements set forth by ICZN Article 75.3, namely: **75.3.1.** It is designated to clarify the taxonomic identity of *N. undulatus*, which is necessary to stabilize nomenclature, because a specimen of *S. tyro* is curated as a type of *N. undulatus* in MFNB, and the original description is insufficient to identify *N. undulatus* with certainty; **75.3.2.** The characters that differentiate females of this taxon are given in the original description translated above, and we summarize them as follows: brown and somewhat similar in appearance to *Autochton* (*Autochton*) *potrillo* (Lucas, 1857) (type locality in Cuba), in particular in the shape of the hindwing with outer margin slightly angular in the middle, but lacking hyaline spots by the costal margin in the middle of the forewing, and the ventral side of the wings is not overscaled with violaceous-gray; the forewing has three apical hyaline spots of about the same size in cells between veins R_3 and M_1 , and one at the base of cell M_3-CuA_1 ; **75.3.3.** The neotype is a female

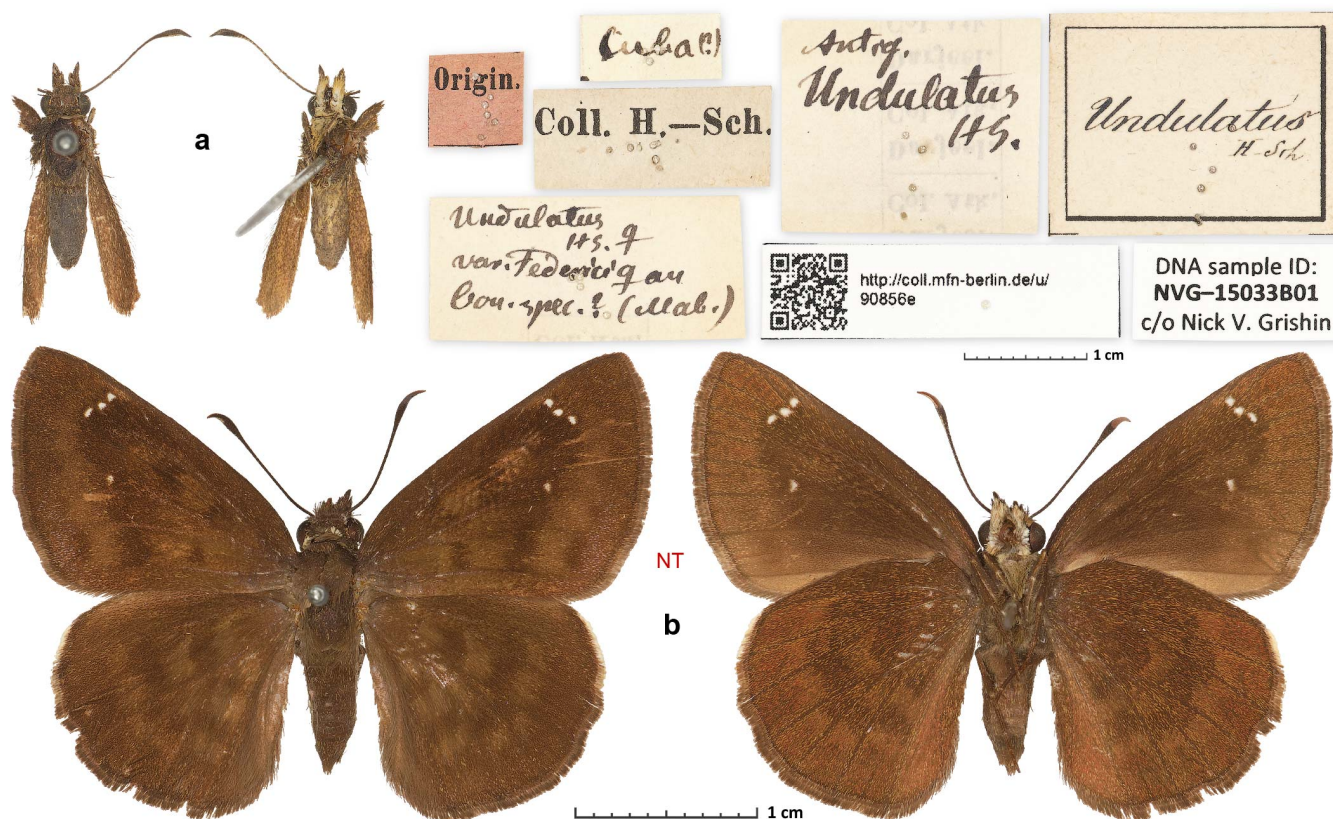


Fig. 88. Females associated with the name *Nisoniades undulatus* Herrich-Schäffer, 1865 in dorsal (left) and ventral (right) views, detailed data in text: **a)** *Staphylus* (*Capilla*) *tyro* NVG-15033B01 curated as a type of *N. undulatus* with its labels on the right (no labels are shown for the other specimen) and **b)** neotype of *N. undulatus* (designated herein, a junior subjective synonym of *Burca braco*) NVG-18061G01 from Cuba: Matanzas in USNM. Labels are reduced by a third compared to specimens; the smaller scale below one of the labels refers to labels and the larger scale at the bottom refers to specimens.

bearing the following five rectangular printed white labels: [Matanzas, | Cuba], [Oct.], [Collection | WmSchaus], [DNA sample ID: | NVG-18061G01 | c/o Nick V. Grishin], [USNM | {QR Code} | 01466890], and is illustrated in Fig. 88b; the neotype is a specimen in good condition with some damage to the fringe of the left hindwing and some scales rubbed off the area posteriad of the discal cell on the right hindwing; **75.3.4.** We failed to find the holotype of *N. undulatus* in dedicated searches in MFNB, ZSMC, SMNS, BMNH, and ANSP known to house Herrich-Schäffer's type specimens (and in all other collections we visited, see Acknowledgments for the list) and therefore believe that it has been lost; **75.3.5.** The neotype closely agrees with the original description in all characters, as evidenced by comparing the neotype shown in Fig. 88b with the characters listed for *N. undulatus* above (75.3.2.); **75.3.6.** The neotype is from Matanzas, Cuba, and the original type locality was inferred as Cuba from the title of the work; **75.3.7.** The neotype is deposited in the National Museum of Natural History, Smithsonian Institution, Washington, DC, USA (USNM). The type locality of *N. undulatus* becomes Cuba: Matanzas. The COI barcode sequence of the neotype, sample NVG-18061G01, GenBank [PZ516426](#), 658 base pairs, is:

```
AACTTTATATTTTATTTTGGTATTTGATCTGGAATAGTAGGAACCTCATTAAAGATTACTAATTCGATCAGAATTAGGAACCCCTGGATCTTTAATTTGGAGATGATCAAAATTTATAATACT
ATTGTAACAGCTCATGCTTTTATATAATTTTATAGTTATACCTATTATAATTTGGAGGATTTGGTAAGTATTAGTACCCCTTATATTAGGAGCTCCCGATATAGCCTTTCCACGAA
TAAATAATATAAGATTTTGACTTTTACCTCCATCATTAAATATTATTAATTTCTAGAAGTATTGTAGAAAATGGAGCAGGAACAGGTTGAACAGTTTACCCCTCCTTTATCAGCTAATATCGC
ACATCAAGGATCTTCTGTTGATTTAGCCATTTTCCCTTCATTTAGCAGGATTTCTTCAATTTCTGGGGCAATTAATTTTATTACAACATATTATTAATATACGAATTAATAATTTATCT
TTTGATCAATACCTTTATTTGTGTGAGCAGTAGGAATTACTGCTTTATTATTACTACTTTCTTTACCAGTATTAGCTGGAGCTATTACAATACTTTTAACAGATCGTAATCTTAATACAT
CCTTTTGTGACCTGCTGGAGGAGGAGATCCAATTTTATACCAACATTTATTT
```

Lectotype designation for *Bolla nigerrima* Mabille & Boulet, 1917

Bolla nigerrima Mabille & Boulet, 1917 was described from two males from Peru originally in the Boulet collection (Mabille and Boulet 1917), now in the MNHP. Both syntypes are extant and bear the same locality/other data label. We sequenced the syntype with the red “Type” label as NVG-18078D06. To stabilize nomenclature and define the name *B. nigerrima* objectively, N.V.G. hereby designates the syntype in the MNHP collection, a male that bears the following seven labels (1st red, 2nd white with red printed text COLL. BOULET and MUSEUM PARIS along the left and the right edges, rotated 90° counterclockwise and clockwise to the handwritten text, respectively, 3rd pistachio green, others white; 2nd–4th handwritten, others printed with handwritten text shown in *italics*): [TYPE], [Chaquimayo | S. Pérou | 3000' – 6.VII 1910 | Rosenberg (Watkins)], [B.Nigerrimus. | Mab. et Boull], [Bolla | nigerrima | Mabille-Boulet | Bull Soc. ent. Fr. 1917: 99], [GEN. PREP. | MIELKE | 1996], [DNA sample ID: | NVG-18078D06 | c/o Nick V. Grishin], and [MNHN, Paris | EL63005 {QR code}], as the **lectotype** of *B. nigerrima* Mabille & Boulet, 1917. The lectotype was collected by Harry Watkins and acquired through W. F. H. Rosenberg. The lectotype is a specimen in good condition, missing the right palpus and with some scale loss on the dorsal side of the right forewing near the base of the discal cell. Images of this specimen photographed by B. Hermier are shown on the Butterflies of America website (Warren et al. 2024). The type locality of *B. nigerrima* is Peru: Puno, Chaquimayo, 3000'. The COI barcode sequence of the lectotype, sample NVG-18078D06, GenBank [PZ516427](#), 658 base pairs, is:

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AACTTTATATTTTATTTTGGTATTTGATCAGGGATAGTAGGAACCTCTTAAGTATTTCTTATTCGTTTCAGAATTAGGAACCTCTAGATCTTTAATTTGGTATGATCAAAATTTATAATACT
ATTGTAACAGCTCATGCTTTTATATAATTTTATAGTAATACCAATTATAATTTGGAGGATTCGGAATTTGGTTAGTACCCCTTATATTAGGAGCTCCTGATATAGCTTTCCCGGAA
TAAATAACATAAGTTTTTGATTATTACCTCCCTCTTAATATTATTAATTTCAAGAAGTATCGTTGAAAATGGAGCAGGAACAGGATGAACAGTTTACCCCTCCTTTCAACTAATATTGC
CCATCAAGGTTTCTGTTAGACTTAGCTATTTTCCCTTCATTTAGCAGGATTTCTCTATTCTAGGGGCAATTAATTTTATTACAACATATTATTAATATACGAATTAATAATTTATCT
TTTGATCAAATACCTTTATTTGTCTGAGCTGTTGGAATTACTGCATTACTTTATTATTATCTCTCCAGTATTAGCAGGTGCTATTACTATACTTTTAACAGATCGTAATTTAAATACAT
CATTTTTTGATCTGTCAGGAGGAGGAGATCCTATTTTATATCAACATTTGTTT
```

Bolla (Bolla) nigerrima banosa (Bell, 1937), stat. nov. is a valid subspecies and not a synonym of *Bolla (Bolla) nigerrima* Mabille & Boulet, 1917

Genomic analysis of the holotype of *Pholisora banosa* Bell, 1937 (type locality Ecuador: Tungurahua, Baños) currently treated as a junior subjective synonym of *Bolla (Bolla) nigerrima* Mabille & Boulet, 1917 (type locality Peru: Puno, Chaquimayo; lectotype sequenced as NVG-18078D06) reveals that it is genetically differentiated from it at least at the subspecies level (Fig. 87); e.g., their COI barcodes differ by 1.7% (11 bp). Therefore, we propose that *Bolla (Bolla) nigerrima banosa* (Bell, 1937), **stat. nov.** is a

valid subspecies and not a synonym of *Bolla (Bolla) nigerrima* Mabilie & Boulet, 1917, pending broader sampling to assess whether the two taxa warrant recognition as distinct species. The COI barcode sequence of the *B. nigerrima banosa* **stat. nov.** holotype, sample NVG-18024D12, GenBank [PZ516428](#), 658 base pairs, is:

```
AACCTTTATATTTTATTTTGGTATTTGATCAGGAATAGTAGGAACCTCTTAAAGTATTCTTATTCGTTTCAGAATTAGGAACCTCTAGATCTTTAATTGGTGACGATCAAATTTATAATACT
ATTGTAACAGCTCATGCTTTTATTATAATTTTATAGTAATACCAATTATAATTGGAGGATTCGAAATTGGTTAGTACCCCTTATATTAGGAGCTCTGTATAGCTTTCCCCCGAA
TAAATAACATAAGTTTGTGATTGTTACCTCCCTCTTAAATATTATTAATTTCAAGAAGTATCGTTGAAATGGAGCAGGAACAGGATGAACAGTTTACCCCTCTTTTCAGCTAATATTGC
CCATCAAGGTTTCATCTGTAGACTTAGCTATTTTCCCTTCATTTAGCAGGATTTCCCTCTATTTAGGGGCAATTAAATTTATTACAATATTATAATATACGAATTAATAATTATCT
TTTGATCAAAATACCTTTATTGTTGAGCTGTTGGAATTACTGCATTACTTTTATTACTATCTCTCCAGTATTAGCAGGTGCTATTACTATACTTTTAACAGATCGTAATTTAAATACAT
CATTTTGTATCCCGCAGGAGGAGGATCTATTTTATACCAACATTTATTT
```

Type specimens by William Schaus and the lectotype of *Bolla machuca* Schaus, 1913

Inspecting specimens described by Schaus as new species and labeled by him with handwritten identification labels (Schaus 1913), we found that while his article did not mention type specimens (and therefore the names were based on syntypes, except for holotypes by monotypy), Schaus made a distinction between his “types” and other specimens he identified as his new species. Specimens he considered “types” invariably have the word “type” written in the lower left corner of the identification label, before his signature “Schs” (Zhang et al. 2023e). For all Schaus’s species, there is only one such “type” label per sex. If a description included both sexes, there were two “type” specimens: a male and a female. If the description was based on one sex, there was only one “type” specimen.

Curiously, while Schaus wrote “In British Museum” for many of his species (Schaus 1913), the specimens of these species that he considered “types” were retained in the USNM. The USNM specimens most likely served as the models for his illustrations, because they agree better with the illustrations in cases where the difference is obvious. Moreover, we deduce that the original descriptions by Schaus were based on these “type” specimens, because the text reads as though it describes a single specimen (per sex), and the “type” specimen is a better match to the description than other specimens identified by Schaus as these species (where they exist and differ). It remains unclear whether Schaus temporarily kept the “type” specimens in the USNM (e.g., to describe them and make illustrations) and intended to send them to the BMNH later. See Zhang et al. (2025d) for a detailed discussion of one such case. These details may be important if the type series is polytypic, especially given the existence of cryptic species that are best uncovered and distinguished through genomic sequencing.

The question remains whether specimens identified by Schaus as his new species but not labeled as “types” can be regarded as syntypes, or whether only those that Schaus considered to be “types” constitute the type series. This question is not trivial for several reasons. First, judging from his descriptions, Schaus described and sometimes illustrated one specimen (of each sex if available), apparently the “type”, and not the series, although this was not stated explicitly by Schaus and is more a hypothesis than a solid inference (Zhang et al. 2023e). Second, according to Art. 72.4.1.1 of the ICZN Code, any evidence, published and unpublished, can be used to identify the type series for species described before 2000. We presented evidence from specimen labels that Schaus marked his type specimens with the word “type” and did not put this word on the identification labels of other specimens. Third, in a remotely similar case involving *Chionobas chryxus* Doubleday, 1849 (currently *Oeneis chryxus*), the ICZN Commission voted to regard the specimen illustrated as the holotype of this taxon, although there was evidence that additional specimens might have been part of the type series (one of which, of a different sex, was designated as a lectotype) (ICZN 2019). To avoid this problem altogether, we recommend that lectotypes be designated from specimens labeled as “type” by Schaus.

Lemes et al. (2026) designated as the lectotype a specimen in the BMNH identified by Schaus as *Bolla machuca* Schaus, 1913 (type locality Costa Rica: San Mateo) but not labeled as “type” by him. Although the nomenclatural implications of our findings remain uncertain, we are confident that the specimen designated as the lectotype of *B. machuca*, although it is in the BMNH as stated in the original description, was not considered by Schaus to be a “type” of this taxon, because it lacks the word “type” on its identification label written by Schaus. Moreover, the original description gives “Expanse 26 mm”

(Schaus 1913), but the lectotype is significantly larger (30 mm), and the smaller specimen is in the USNM. This USNM specimen has slightly more apparent “traces of ... darker ... small marginal spots” and more conspicuous “three white points outwardly between veins 6 and 9” on the dorsal forewing (Schaus 1913). This raises the question of whether the lectotype designation is valid, because the lectotype does not fully agree with the original description and might not have been part of the type series. Schaus’s “type” specimen is currently in the USNM, the only specimen of *B. machuca* with the word “type” written by Schaus in the lower left corner of the identification label. Images of both specimens, photographed by N.V.G. (at the BMNH and USNM) and B. Hermier (USNM), are shown on the Butterflies of America website (Warren et al. 2024). The COI barcode sequence of the “type” specimen of *B. machuca* in the USNM, sample NVG-18061B05, GenBank [PZ516429](#), 658 base pairs, is:

```
AACTTTATATTTTATTTTGGTATTTGATCAGGAATAGTAGGAACCTCTTTAAGTATCTTATTCGTTTCAGAACTAGGAACCCCTGGATCTTTAATTGGAGATGACCAATTTATAATACT
ATTGTAACCTGCTCATGCTTTTATTATAATTTTATAGTTATACCTATTATAATTGGAGGATTTGGAAATTGACTAGTACCCCTTATACTAGGAGCTCCTGATATAGCTTTTCTCGAA
TAAATAATATAAGTTTGGTATTACCACCATCTTTAATACTATTAAATTCAGTAGTATTGTAGAAAATGGAGCAGGAACCTGGATGAAGTATATCCCCACTTTCAGCCAATATTGC
CCATCAAGGTTCTTCTGTTGATTAGCTATTTCTCTTTACACCTAGCAGGTATTTCTCTATTTTAGGAGCAATTAATTTTATTACAACCTATTATTAATATACGAATTAATAATTTATCA
TTTGATCAAAATACCTTTATTGTTTGGAGCGTAGGAATTACAGCTTTACTTCTACTTTTATCTCTACCAGTATTAGCAGGAGCTATTACCATATTATTAAGTATGATCGAAATCTTAATACAT
CATTTTGTATCTGTCAGGAGGAGGAGATCCTATCTTATACCAACATTTATTT
```

***Staphylus (Capilla) azteca machuca* (Schaus, 1913), stat. nov. is a valid subspecies and *Staphylus inconstans* Bell, 1932 is its junior subjective synonym**

Genomic analysis of *Staphylus (Capilla) azteca* (Scudder, 1872) (type locality Mexico: Oaxaca, Tehuantepec) from across its range reveals that specimens partition into two clades (in both nuclear and mitochondrial genome trees) genetically differentiated at the subspecies level (Fig. 87), e.g., their COI barcodes differ by 1.1–1.2% (7–8 bp). One clade consists of specimens from Mexico and corresponds to *S. azteca*. The other clade consists of specimens to the south of the Mexican border (Honduras, El Salvador, Costa Rica, and Panama) and includes type specimens of *Bolla machuca* Schaus, 1913 (type locality Costa Rica: San Mateo) and *Staphylus inconstans* Bell, 1932 (type locality Costa Rica: Orotina), both currently treated as junior subjective synonyms of *S. azteca*. We conclude that the second clade represents a valid subspecies of *S. azteca* that should be referred to by the senior name *Staphylus (Capilla) azteca machuca* (Schaus, 1913), **stat. nov.**, with *Staphylus inconstans* Bell, 1932 being its junior subjective synonym (new placement of a synonym). *Thanaos quadratus* Dyar, 1926 (type locality in Mexico: Colima) is kept as a junior subjective synonym of *Staphylus (Capilla) azteca azteca*. Furthermore, we report the COI barcodes of the two holotypes. The COI barcode sequence of the *S. inconstans* holotype in the AMNH, sample NVG-18024H01, GenBank [PZ516430](#), 658 base pairs, is:

```
AACTTTATATTTTATTTTGGTATTTGATCAGGAATAGTAGGAACCTCTTTAAGTATCCTTATTCGTTTCAGAACTAGGAACCCCTGGATCTTTAATTGGGATGATCAAAATTTATAATACT
ATTGTAACCTGCTCATGCTTTTATTATAATTTTATAGTTATACCTATTATAATTGGAGGATTTGGAAATTGACTAGTACCCCTTATACTAGGAGCTCCTGATATAGCTTTTCTCGAA
TAAATAATATAAGTTTGGTATTACCACCATCTTTAATACTATTAAATTCAGTAGTATTGTAGAAAATGGAGCAGGAACCTGGATGAAGTATATCCCCACTTTCAGCCAATATTGC
CCATCAAGGTTCTTCTGTTGATTAGCTATTTCTCTTTACACCTAGCAGGTATTTCTCTATTTTAGGAGCAATTAATTTTATTACAACCTATTATTAATATACGAATTAATAATTTATCA
TTTGATCAAAATACCTTTATTGTTTGGAGCGTAGGAATTACAGCTTTACTTCTACTTTTATCTCTACCAGTATTAGCAGGAGCTATTACCATATTATTAAGTATGATCGAAATCTTAATACAT
CATTTTGTATCTGTCAGGAGGAGGAGATCCTATCTTATACCAACATTTATTT
```

The COI barcode sequence of the *T. quadratus* holotype in the USNM, sample NVG-18061C02, GenBank [PZ516431](#), 658 base pairs, is:

```
AACTTTATATTTTATTTTGGTATTTGATCAGGAATAGTAGGAACCTCTTTAAGTATCCTTATTCGTTTCAGAACTGGGAACCCCTGGATCTTTAATTGGAGATGATCAAAATTTATAATACT
ATTGTAACCTGCTCATGCTTTTATTATAATTTTATAGTTATACCTATTATAATTGGAGGATTTGGAAATTGACTAGTACCCCTTATACTAGGAGCTCCTGATATAGCTTTTCTCGAA
TAAATAATATAAGTTTGGTATTACCACCATCTTTAATACTATTAAATTCAGTAGTATTGTAGAAAATGGAGCAGGAACCTGGATGAAGTATATCCCCACTTTCAGCCAATATTGC
CCATCAAGGTTCTTCTGTTGATTAGCTATTTCTCTTTACACCTAGCAGGTATTTCTCTATTTTAGGAGCAATTAATTTTATTACAACCTATTATTAATATACGAATTAATAATTTATCA
TTTGATCAAAATACCTTTATTGTTTGGAGCTGTAGGAATTACAGCTTTACTTCTACTTTTATCTCTACCAGTATTAGCAGGAGCTATTACTATATATTAAGTATGATCGAAATCTTAATACAT
CATTTTGTATCTGTCAGGAGGAGGAGATCCTATCTTATATCAACATTTATTT
```

***Staphylus (Capilla) tyro nicoleae* Lemes, 2026, stat. nov.**

The analysis of the lectotype of *Staphylus (Capilla) tyro* (Mabille, 1878) (type locality Venezuela: Carabobo, Puerto Cabello; sequenced as NVG-15033G06) reveals that it is not the species identified as such by Lemes et al. (2026) (except the lectotype itself), who also designated this lectotype. Instead, both its COI barcode and wing patterns indicate that the lectotype of *S. tyro* is more closely allied to *Staphylus (Capilla) nicoleae* Lemes, 2026 (type locality Colombia: Cundinamarca, El Boquerón) and would have been identified by Evans (1953) as “*Staphylus imperspicua*” (misidentification).

We used COI barcodes reported by Lemes et al. (2026) for the *S. nicoleae* holotype (Fig. 89a, magenta) and for a specimen they identified as *S. tyro* (Fig. 89a, labeled in brown) combined with barcodes assembled from our whole-genome shotgun reads to support this conclusion. The holotype of *S. nicoleae* is in the same clade as the lectotype of *S. tyro* (Fig. 89a, highlighted in yellow), but the specimen identified as *S. tyro* by Lemes et al. (2026) belongs to a different clade and therefore may be misidentified, unless there has been introgression of COI barcodes (Fig. 89a). The COI barcode sequence of the *S. tyro* lectotype in the MFNB, sample NVG-15033G06, GenBank [PZ516432](#), 658 base pairs, is:

```
AACTTTATATTTTATTTTGGTATTTGATCAGGAATAGTAGGAACCTCTTTAAGTATTCTTATTCGCTCAGAATTAGGAACCTCTGGATCTTTAATTGGAGATGATCAAATTTATAATACT
ATTGTAACCTGCTCATGCTTTTATATAATTTTATAGTTATACCTATTATAATTTGGAGGATTTGGAAATTGATTAGTCCCTCATATTAGGAGCTCTGATATAGCTTTTCTCGAA
TAAATAATATAAGTTTGTATTTGATTTGCCCATCTTTAATACTATTAAATTTCAAGTAGTATTGTAGAAATGGAGCAGGAAGTGAATGAAGTCTCTATCCCTTCTAGCAATATTGC
CCATCAAGGTTCTTCTATTGATTAGCTATTTTCTTTACATTTAGCAGGTATTCTTCTATTTTAGGAGCAATTAATTTTATTACAATATTATTAATATACGAATTAATAATTTATCA
TTTGATCAAATACCTTTATTTGTTGAGCTGTAGGAATTACAGCTCTACTCTTACTTCTATCTTTACCAGTGTTAGCAGGTGCTATTACTATATTATTAAGTATGATCGAAATCTTAATACAT
CATTTTTGTATCTGTCAGGAGGAGGATCTATTCTATATCAACATTTATTT
```

In wing patterns, the holotype of *S. nicoleae* (Fig. 89b) and the lectotype of *S. tyro* (Fig. 90a) share more distinct and separated yellow spots (composed of sparse yellow overscaling) on the ventral hindwing; the lack of a more prominent discal darker area (broad band) on the ventral hindwing; and the lack of three pale or semihyaline subapical spots on the forewing. The specimen that Lemes et al. (2026) identified as *S. tyro* (Fig. 89c) has more diffuse yellow spots on the ventral hindwing that are almost merged into a postdiscal band; a more prominent discal area, darker than the ground brown color (i.e., a darker broad discal band) on the ventral hindwing; and a triplet of small, but present, pale or semihyaline subapical spots on the forewing. This *S. “tyro”* specimen shares these characters with specimens from the same clade that we sequenced (Figs. 89a red, 90b–d). These wing pattern differences agree with the COI barcode species assignment (i.e., no mitochondrial introgression was observed), and we therefore conclude that *S. tyro* was in part (except the lectotype) misidentified by Lemes et al. (2026).

Lemes et al. (2026) considered two related species in South America (misidentified *S. tyro* and *S. nicoleae*), not three (misidentified *S. tyro*, *S. nicoleae* [Colombia] and true *S. tyro* [Venezuela]). Lemes et al. (2026) placed Colombian and Venezuelan specimens in *S. nicoleae*. Following their two-species logic, the topotypical *S. nicoleae* and the lectotype of *S. tyro* from Venezuela would be conspecific. Therefore, it is conceivable to regard *S. nicoleae* as a junior subjective synonym of *S. tyro*. However, we have not sequenced genomes of topotypical *S. nicoleae* and it is likely that this taxon is distinct from Venezuelan *S. tyro* due to biogeographical differences and some difference in the COI barcode (0.7%; the barcode of *S. nicoleae* holotype is incomplete and missing a region in the middle). Without a better understanding of this species complex, we follow Lemes et al. (2026) in recognizing two species, which implies that *S.*



Fig. 89. *Staphylus* (*Capilla*) *tyro nicoleae* stat. nov. and relatives. **a)** COI barcode dendrogram constructed using FastME (Lefort et al. 2015) with default parameters as implemented on the NGPhylogeny.fr server (Lemoine et al. 2019). Different taxa are colored differently: *S. azteca azteca* (green), *S. azteca machuca* stat. nov. (blue), *S. tyro* (violet, with the *S. tyro nicoleae* stat. nov. holotype in magenta), *S. lemesi* sp. n. (red, with a specimen misidentified as *S. tyro* in Lemes et al. (2026) labeled in brown). The lectotype of *S. tyro* is highlighted in yellow, and two specimens with barcodes reported in Lemes et al. (2026) and downloaded from GenBank are highlighted in orange. **b–c)** Males in dorsal (left) and ventral (right) views; images © José Ricardo Assmann Lemes et al., taken from Lemes et al. (2026), color-corrected, brightened, and reproduced here under the CC BY 4.0 License, <https://creativecommons.org/licenses/by/4.0/>: **b)** *S. tyro nicoleae* stat. nov. holotype DZ 45.163 from Colombia: Cundinamarca, El Boquerón and **c)** specimen DZ 22.893 from Venezuela, Aragua, Ocumare de la Costa misidentified as *S. tyro* by Lemes et al. (2026), which we identify as *S. lemesi* sp. n. (a paratype).

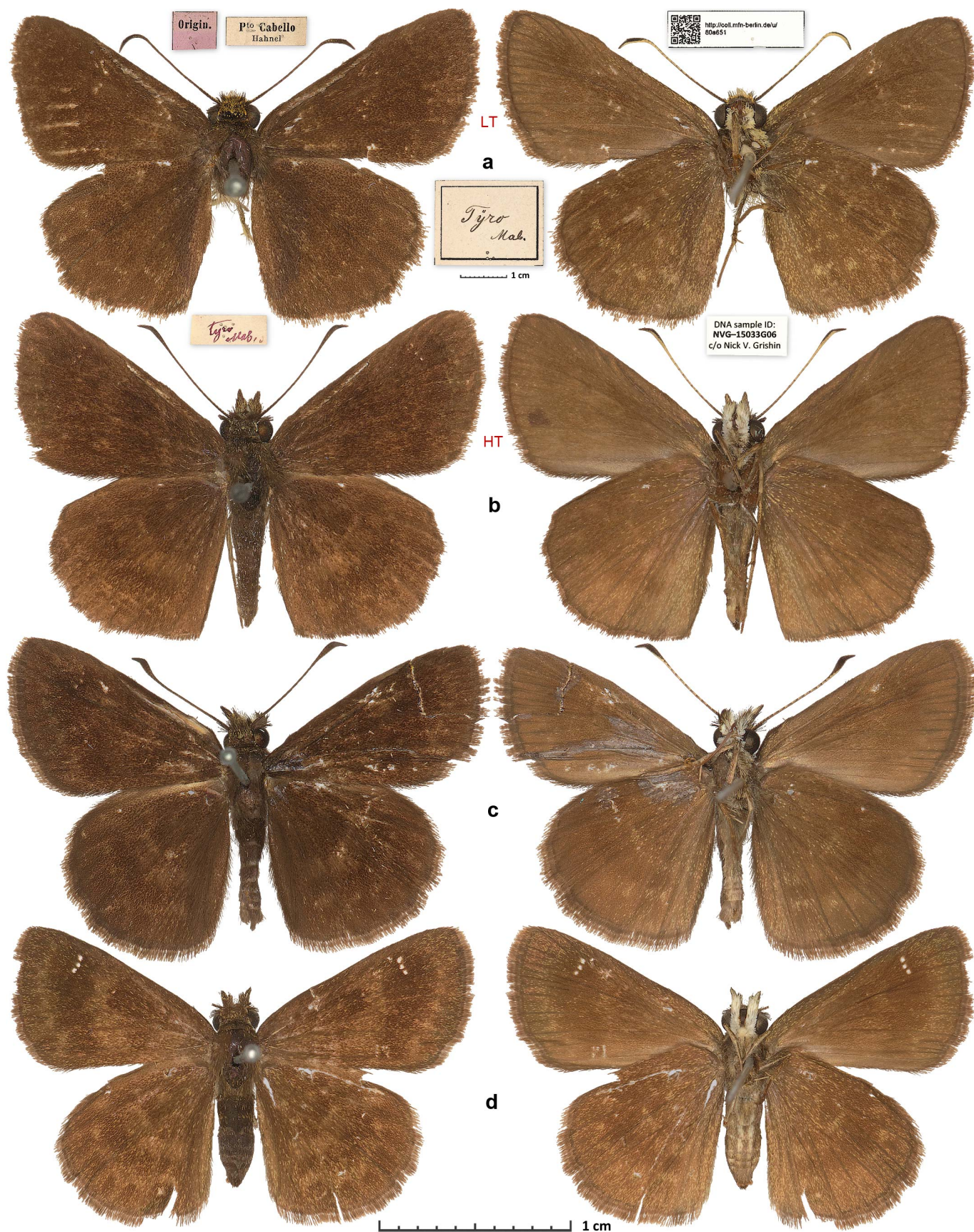


Fig. 90. *Staphylus* (*Capilla*) type specimens from Venezuela in MFNB (unless indicated) in dorsal (left) and ventral (right) views, data in text: **a)** *S. tyro* lectotype ♂ NVG-15033G06 with its labels (labels are not shown for the other specimens); **b–c)** *S. lemesi* **sp. n.**: **b)** holotype ♂ NVG-21117C09 and paratypes; **c)** ♂ NVG-18056F12 “Amaz. sup.” in ZSMC and **d)** ♀ NVG-21117C05. Labels are reduced to one-quarter of their original size relative to the specimens; the smaller scale below one of the labels refers to labels and the larger scale at the bottom of the figure refers to specimens.

tyro” [ZSMC] (Fig. 90c) and Venezuela: 1♂ NVG-18058G09, USNMENT_01466743 Nueva Esparata, Isla Margarita, La Sierra, 2200-2600 ft, GPS 11.0167, -63.8667, 16-Aug-1987, J. Glassberg leg., genitalia X-2480 J. M. Burns 1987 [USNM]; 1♀ NVG-21117C05 Carabobo, Puerto Cabello, old, Staudinger collection [MFNB] (Fig. 90d); and 23♂♂ and 8♀♀ listed as specimens of *S. tyro* from Venezuela (but not Colombia) in Lemes et al. (2026). See Lemes et al. (2026: 170) for data. In their data, we correct SRS-13001 to SRS-1301, this specimen was sequenced as NVG-22087H11; and 1♂ listed from Miranda in MGCL (we add D. Dukes as the third collector) was sequenced as NVG-22087H12, specimen UF FLMNH MGCL 1112057.

Type locality. Venezuela: La Guaira, La Guaira.

Etymology. The name, a noun in the genitive case, honors José Ricardo Assmann Lemes, who spearheaded the lectotype designation of *Helias tyro* and the comprehensive revision of *Staphylus* (*Capilla*) that led to the discovery of several new species, and who has made many other important contributions to our knowledge of Hesperiididae (Lemes et al. 2020; Lemes et al. 2023a, b; Lemes et al. 2024; Lemes et al. 2025a, b).

Distribution. Currently known with confidence from Venezuela and is likely present in Colombia.

Remarks. Mabilles did not identify the holotype of this new species as his *H. tyro*; instead he identified it as a variety of *A. unifascia*, thus indirectly agreeing with the species choice for *S. tyro* lectotype designation by Lemes et al. (2026). However, the holotype of the new species is not a paralectotype of *Antigonus unifascia* Mabilles, 1889 (currently *Clytius unifascia*) because, according to the original description, the type series was from Honduras and did not include specimens from Venezuela.

Tribe Pyrgini Burmeister, 1878

Lectotype designation for *Anisochoria minorella* Mabilles, 1898

Anisochoria minorella was described by Mabilles (1898) from an unspecified number of specimens from “Bolivie: Tanampaya” in collections of Staudinger and Mabilles. Because the Staudinger collection (now in MFNB) is listed first and it contains several syntypes, all from the type locality and by the same collector (Bolivia: Tanampaya, Garlepp leg.) (Fig. 91d–g), we selected a specimen from this collection as the lectotype. Several syntypes bear the purple “Origin.” label typical of type specimens in the Staudinger collection, and two of them bear identification labels written by Mabilles. One of these two syntypes is smaller than the others (Fig. 91g) with Mabilles’s identification label “a. minorella | form. minor.” indicating that Mabilles did not consider this specimen to represent typical *minorella*. The name “minor” was not published and appeared only on specimen labels. The second syntype is of typical size, agrees well with the original description, and is the most suitable candidate for the lectotype designation. To stabilize nomenclature and define the name *A. minorella* objectively, N.V.G. hereby designates the syntype in the MFNB collection, a male illustrated in Fig. 91d that bears the following five labels (1st purple, 3rd greenish, others white; 3rd handwritten, others printed): [Origin], [Tanamp. | Bol. | Garl.], [anisoch. | minorella | Mab], [{QR Code} http://coll.mfn-berlin.de/u/ | 9085f3], and [DNA sample ID: | NVG-21117B03 | c/o Nick V. Grishin], as the **lectotype** of *Anisochoria minorella* Mabilles, 1898. The first two labels are typical of specimens from the Staudinger collection, the second label states that the specimen was collected by Garlepp (Otto or Gustav) in Tanampaya, Bolivia, and the third label is in Mabilles’s handwriting. The lectotype is a specimen in good condition with its left antenna touching the costal margin of the forewing, its abdomen tilted to the right, and some damage to the fringe near the apex of the left forewing and near the tornus of the right hindwing. The type locality of *A. minorella* remains Bolivia: La Paz Department, Río Tanampaya. The COI barcode sequence of the lectotype, sample NVG-21117B03, GenBank [PZ516434](https://www.ncbi.nlm.nih.gov/nuccore/PZ516434), 658 base pairs, is:

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AACTTTATATTTTATTTTGGAAATTTGAGCAGGAATAGTAGGAACCTCTTAAGTTTATTAATTCGAAGTGAATAGGAAGTCCAGGATCATTAAATCGGAGATGATCAAAATTTATAATACT
ATTGTCACAGCTCATGCTTTTATTATAATTTTATAGTTATACCCATTATAATGGAGGATTTGGAAATTTGACTAGTACCTTTAATATTGGGAGCCCTGATATAGCTTTCCCGCGAA
TAAATAATATAAGATTTTGATTATGACCTCTCTTAACACTGCTAATTTCTAGAAGTATTGTAGAAAATGGAGCAGGAAGTGGATGAACAGTTTACCCCCACTTTCATCTAATATTGC
CCATCAAGGTTTCATCTGTTGATTAGCTATTTTTCCCTACATTTAGCAGGTATTTTCATCAATTTTAGGAGCTATCAACTTTTACTACAATTATTAATATACGAATTAATAATTTATCT
TTTGATCAAAATACCTTTATTGTATGAGCAGTAGGAATTACTGCTTTACTTTTATTATTATCATTACCTGTTTTAGCAGGAGCTATTACTATATTATTAACAGACCGAAATTTAAATACAT
CTTTTTTGTATCTGCCGAGGAGGAGATCCAATTTTATATCAACATTTATTT
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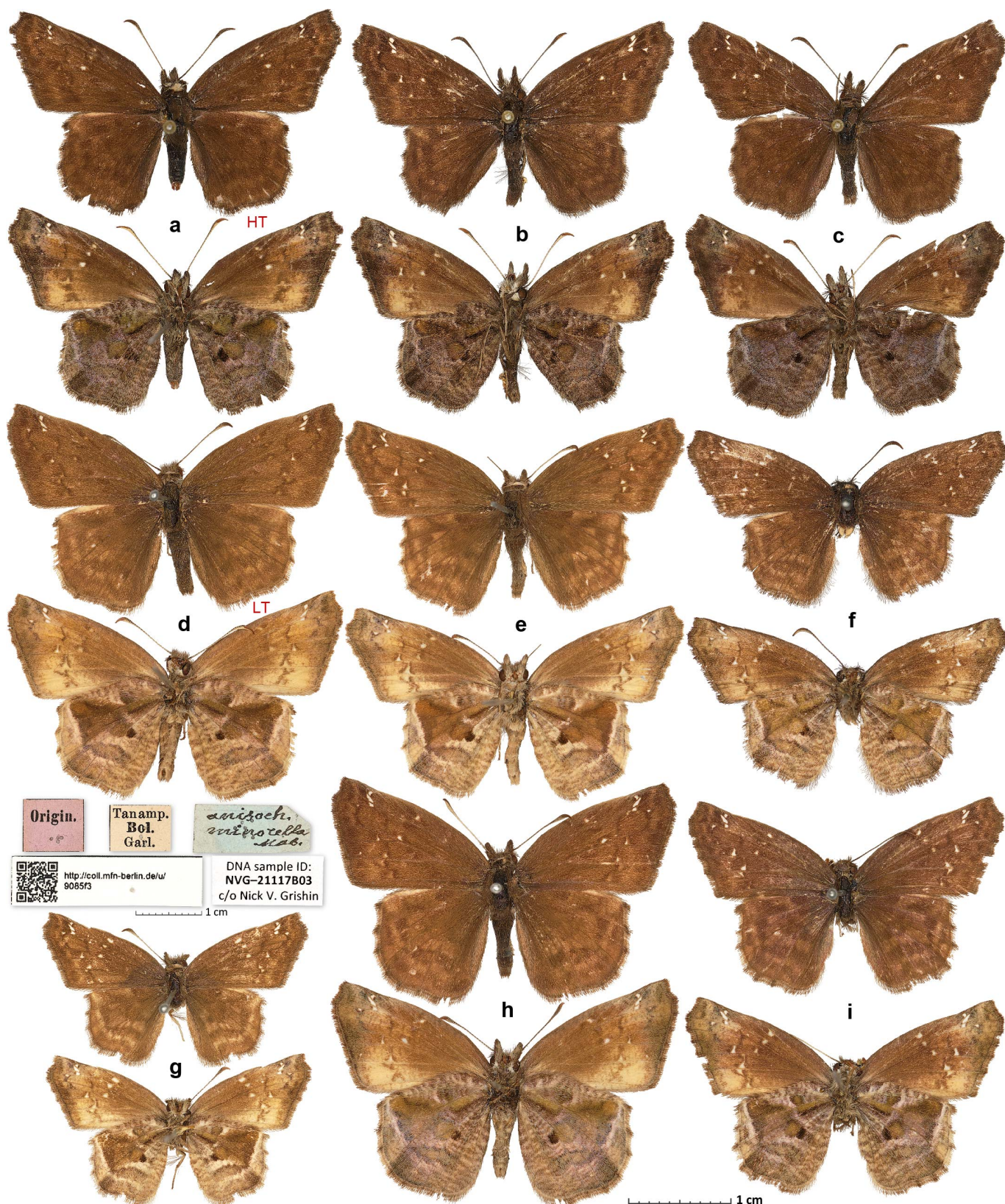



Fig. 91. *Anisochoria* males in dorsal (above) and ventral (below) views, data in text or below: **a–c)** *A. minorella hermierei* ssp. n. type series from Argentina: **a)** holotype NVG-19091H10 Salta and **b–c)** paratypes: **b)** NVG-24085A09 Salta and **c)** NVG-24085A08 Jujuy; and **d–i)** *A. minorella minorella* from Bolivia, La Paz, Río Tanampaya, old, Garlepp leg., in MFNB, except as indicated (but likely the same locality and collector): **d)** lectotype NVG-21117B03 with its labels below (no labels are shown for other specimens); **e–g)** paralectotypes: **e)** NVG-21117B04; **f)** BMNH(E) 1669582 “Bolivie” from the Mabilie collection in BMNH, abdomen lost; **g)** NVG-15033E03, genitalia vial by O. Mielke, 1996; and **h–i)** specimens not labeled as types: **h)** NVG-21117B01 and **i)** NVG-22018H11 “Bolivia” in ZSMC, abdomen lost. Labels are reduced by a third relative to specimens; the smaller scale below the labels refers to labels and the larger scale at the bottom of the figure refers to specimens.

Anisochoria minorella hermeri Grishin, new subspecies

<https://zoobank.org/122133BC-AFE5-460A-9608-C3621474CE3E>

(Figs. 91a–c, 92 part)

Definition and diagnosis. Identifying HesperIIDae specimens, Bernard Hermier noticed a different, darker appearance of specimens from Argentina and Bolivia, traditionally identified as *Anisochoria minorella* Mabilie, 1898 (type locality in Bolivia: La Paz, Río Tanampaya; lectotype sequenced as NVG-21117B03) and informed N.V.G. about it. We already had three such specimens sequenced (Fig. 91a–c), which differ in their wing color and contrast from typical *A. minorella* (Fig. 91d–i). While the genomic analysis indeed reveals some separation of the Argentine specimens from the Bolivian specimens (including the lectotype of *A. minorella*) in the autosome tree (Fig. 92a), the two groups do not form separate clades in the Z chromosome tree, which is usually more indicative of speciation (Fig. 92b). The Argentinian and Bolivian specimens separate into two clades in the mitochondrial genome, but genetic differentiation between them is low, and their COI barcodes differ by 0.8% (5 bp). Therefore, we could not confidently support recognition of the two groups as separate species. However, due to their phenotypic distinction and some degree of separation in both nuclear and mitochondrial genomes, Argentine specimens represent a distinct subspecies. This new subspecies keys to *Anisochoria minorella minorella* (E.59.4(b)) in Evans (1953), and was likely included by him in this subspecies as one of its seasonal forms, but differs from typical *A. minorella* and other relatives by being darker overall: darker brown color of the dorsal side of the wings with a less variegated hindwing; and a less contrasting and darker, more uniform ventral wing pattern, especially on the hindwing, which does not have the prominent pale postdiscal lines and paler apical submarginal half characteristic of nominotypical *A. minorella*. This subspecies does not appear to be cryptic, but due to unexplored individual variation and the possible existence of seasonal forms, it is best identified by DNA, with diagnostic base pairs in the nuclear genome: aly491.1.1:A1293G, aly491.1.1:G1353A, aly188.26.2:C90T, aly7032.5.16:C27A, aly7032.5.16:A54G; and the COI barcode: A37G, T97C, T439T.

Barcode sequence of the holotype. Sample NVG-19091H10, GenBank [PZ516435](https://www.ncbi.nlm.nih.gov/nuclot/PZ516435), 658 base pairs:

```
AACTTTATATTTATTTATTTTGGAAATTTGAGCAGGAATGGTAGGAACCTCTTTAAGTTTATTAATCGAAGTGAATAGGAATCCAGGATCATTAAATCGGAGATGATCAAAATTTATAATACT  
ATTGTCACAGCTCATGCTTTTATTATAATTTTATTTATAGTTATACCCATTATAATTTGGAGGATTTGGAAATTTGACTAGTACCTTTAATATTGGGAGCCCTGATATAGCTTTCCCCCGAA  
TAAATAATATAAGATTTTGATTATTACACCTCTTTAACACTACTAATTTCTAGAAGTATTTAGAAAATGGAGCAGGAAGTGAACAGTTTACCCCCACTTTTCATCTAATATTGC  
CCATCAAGGTTTCATCTGTTGATTAGCTATTTTCCCTACATTAGCAGGATTTTCATCAATTTAGGAGCTATTAACCTTATTACTACAATTTAATATACGAATTAATAATTTATCT  
TTTGATCAAAATACCTTTATTTGTATGAGCAGTAGGAATTACTGCTTTTACTTTTATTATTATCATTACCTGTTTGTAGCAGGAGCTATTACTATATTATTAACAGACCGAAATTTAAATACAT  
CTTTTTTGTATCTGCCGAGGAGGAGATCCAATTTTATATCAACATTTATT
```

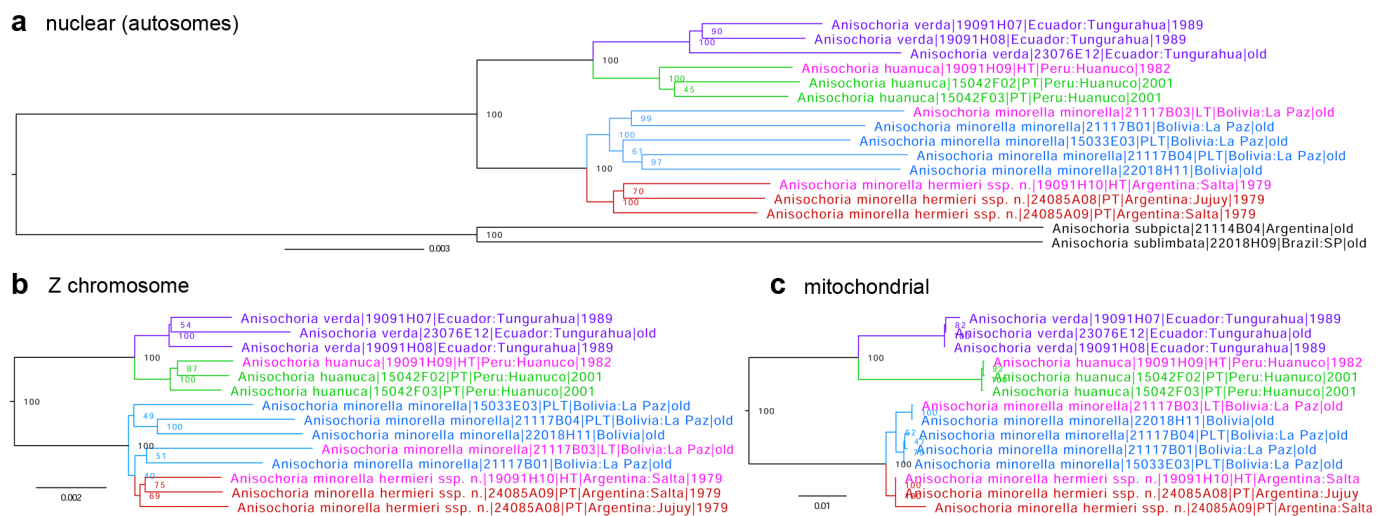


Fig. 92. Phylogenetic trees of selected *Anisochoria* Mabilie, 1877 species constructed from protein-coding regions in: **a)** the nuclear genome (autosomes), based on 3,906,948 positions, **b)** the Z chromosome, based on 273,522 positions, and **c)** the mitochondrial genome. Different taxa discussed in the text are colored differently: *A. verda* (violet), *A. huanuca* (green), *A. minorella minorella* (blue), and *A. minorella hermeri* ssp. n. (red). Primary type specimens are labeled in magenta. Ultrafast bootstrap (Hoang et al. 2018) values are shown at nodes.

Type material. Holotype: ♂ deposited in the National Museum of Natural History, Smithsonian Institution, Washington, DC, USA (USNM), illustrated in Fig. 91a, bears the following four rectangular labels (first two handprinted, others printed), three white: [ARGENTINA | Salta, 1 km. | ne. Cerrillos | 3. Feb. 1979 | R. C. Eisele], [Anisochoria ♂ | minorella det. | minorella Eisele], [DNA sample ID: | NVG-19091H10 | c/o Nick V. Grishin], and one red [HOLOTYPE ♂ | Anisochoria minorella | hermiere Grishin]. **Paratypes:** 2♂♂ from Argentina, R. Eisele leg. [MGCL]: 1♂ NVG-24085A09 Salta, Cerrillos, 1250 m, 24-Feb-1979 (Fig. 91b) and 1♂ NVG-24085A08, UF FLMNH MGCL 1048092 Jujuy, Rio Lozano, 1600 m, 11-Jan-1979 (Fig. 91c).

Type locality. Argentina: Salta, 1 km northeast of Cerrillos.

Etymology. The subspecies is named in honor of Bernard Hermier (French Guiana), who recognized this distinctive phenotype and suggested looking into it. Bernard is a distinguished specialist in Neotropical HesperIIDae, who has generously shared his extensive knowledge and devoted considerable time to thoughtful and illuminating discussions of challenging questions in nomenclature and taxonomy. His insight, clarity of judgment, and willingness to tackle the most difficult problems have been invaluable, and his encouragement played a decisive role in bringing this and many other taxa to formal description. Bernard's exceptional kindness and intellectual generosity are widely recognized and deeply appreciated by naturalists worldwide. The name is a masculine noun in the genitive case.

Distribution. Currently known only from Argentina.

Remarks. It is possible that the dark phenotype of this new subspecies is a seasonal form. However, the new subspecies is genetically differentiated from the nominotypical subspecies in both the nuclear and mitochondrial genomes, forming a separate clade (except in the Z chromosome tree). Thus, even if it has another seasonal form similar in appearance to the nominotypical subspecies, its distinction is supported by the unique gene set that may be responsible for other, yet undiscovered, unique phenotypic traits.

Subfamily HesperIIDae Latreille, 1809
Tribe Aeromachini Tutt, 1906

***Thoressa justini* Inoué & Kawazoé, 1969 belongs to the genus *Halpe* F. Moore, 1878**

Since its description, *Thoressa justini* Inoué & Kawazoé, 1969 (type locality Philippines, Luzon, Baguio) has been kept in its original genus *Thoressa* Swinhoe, 1913 (type species *Pamphila masoni* F. Moore, 1879). Our genomic phylogeny indicates that *T. justini* is not monophyletic with *Thoressa* and instead is sister to all other species of *Halpe* F. Moore, 1878 (type species *Halpe moorei* Watson, 1893) that we sequenced (Fig. 93). Therefore, we transfer it to the latter genus as *Halpe justini* (Inoué & Kawazoé, 1969), **comb. nov.**

Halpe raphaeli* (Nuyda & Kitamura, 1994), **comb. et stat. nov.** is a species distinct from *Halpe justini* (Inoué & Kawazoé, 1969), **comb. nov.*

Genomic analysis reveals that *Halpe justini justini* (Inoué & Kawazoé, 1969) **comb. nov.** (type locality Philippines, Luzon, Baguio) and *Halpe justini raphaeli* (Nuyda & Kitamura, 1994), **comb. nov.** (type locality in Philippines, Leyte) are genetically differentiated at the species level (Fig. 93), e.g., their COI barcodes differ by 5.3% (35 bp), and differ phenotypically as well. Therefore, we recognize *Halpe raphaeli* (Nuyda & Kitamura, 1994), **comb. et stat. nov.** as a species distinct from *Halpe justini* (Inoué & Kawazoé, 1969), **comb. nov.**

***Justa* Grishin, new subgenus**

<https://zoobank.org/114AB547-D26B-46D1-8490-B0DDEED98EA5>

Type species. *Thoressa justini* Inoué & Kawazoé, 1969.

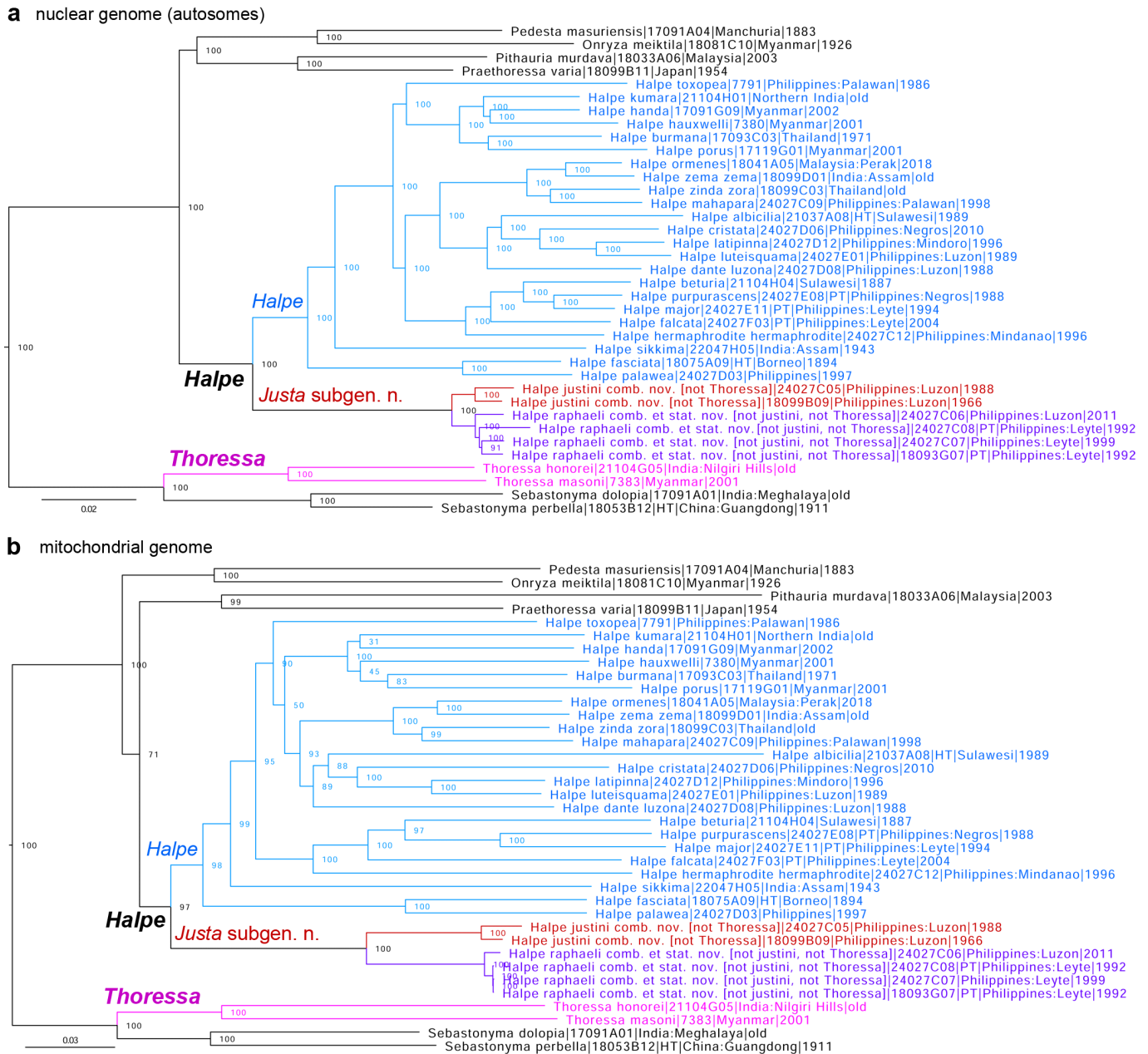


Fig. 93. Phylogenetic trees of selected *Aeromachini* species constructed from protein-coding regions in: **a**) the nuclear genome (autosomes), based on 9,195,531 positions, and **b**) the mitochondrial genome. Taxa are colored as follows: subgenus *Halpe* (blue), *H. justini* **comb. nov.** (red), *H. raphaeli* **comb. et stat. nov.** (violet), and genus *Thoressa* (magenta). Genera and subgenera discussed in the text are labeled at their respective clades in larger bold italic and smaller italic fonts, respectively. Ultrafast bootstrap (Hoang et al. 2018) values are shown at nodes.

Definition. Genomic phylogeny of *Aeromachini* Tutt, 1906 reveals that *Halpe justini* (Inoué & Kawazoé, 1969), **comb. nov.** (type locality Philippines, Luzon, Baguio) belongs to the clade sister to all other species of *Halpe* F. Moore, 1878 (type species *Halpe moorei* Watson, 1893, which is a junior subjective synonym of *Hesperilla porus* Mabille, 1876) and is genetically differentiated from its type species at the subgenus level (Fig. 93); e.g., their COI barcodes differ by 9.7% (64 bp). Therefore, *H. justini* represents a new subgenus that differs from the nominotypical subgenus by the following combination of characters: well-developed gnathos [vestigial or absent in the nominotypical subgenus], deeply divided scaphium at the posterior end [shallowly excavated in most species of the nominotypical subgenus], and symmetrical, elongated valvae with the harpe shaped more similarly to *Halpe* than to the genera with a developed gnathos: reniform, even slightly bilobed, with a dorsally rounded and ventrally right-angled distal end and

a rounded basal lobe directed anterodorsad, the dorsal margin of the harpe is finely serrated. In DNA, a combination of the following characters is diagnostic in the nuclear genome: aly1937.14.2:C99A, aly1877.13.1:A538G, aly1877.13.1:G1090C, aly1838.49.7:T1089C, aly1838.49.7:A1239T; and the COI barcode: A31T, T223A, T529A.

Etymology. The name is derived from the type species name and is a feminine noun in the nominative singular.

Species included. The type species and *Thoressa justini raphaeli* Nuyda & Kitamura, 1994.

Parent taxon. Genus *Halpe* F. Moore, 1878.

Tribe Taractrocerini Voss, 1952

Lectotype designation for *Hesperia euria* Plötz, 1883

Hesperia euria Plötz, 1883 (currently *Potanthus (Potanthus) euria*) was described from an unspecified number of specimens from unknown localities, with the name attributed to Weymer: “*Euria* Wym. i. 1.” (Plötz 1883). We translate from German the last section of the original description of *H. euria* given within the identification key as: “Hindwing with a reddish-yellow, narrow band of spots from cell 1c to 5, placed quite far from the margin; the spot in cell 1 is divided; beneath, in cell 7, there are 2 more spots. The dorsal side is black-brown. Forewing with a reddish-yellow inner margin and similar spots in cells 1–3 and 6–8; in the discal cell, 2 longitudinal lines and some short slanted streaks near the costal margin. The ventral side of the forewing is black, reddish-brown along the margin; the hindwing is reddish-brown,

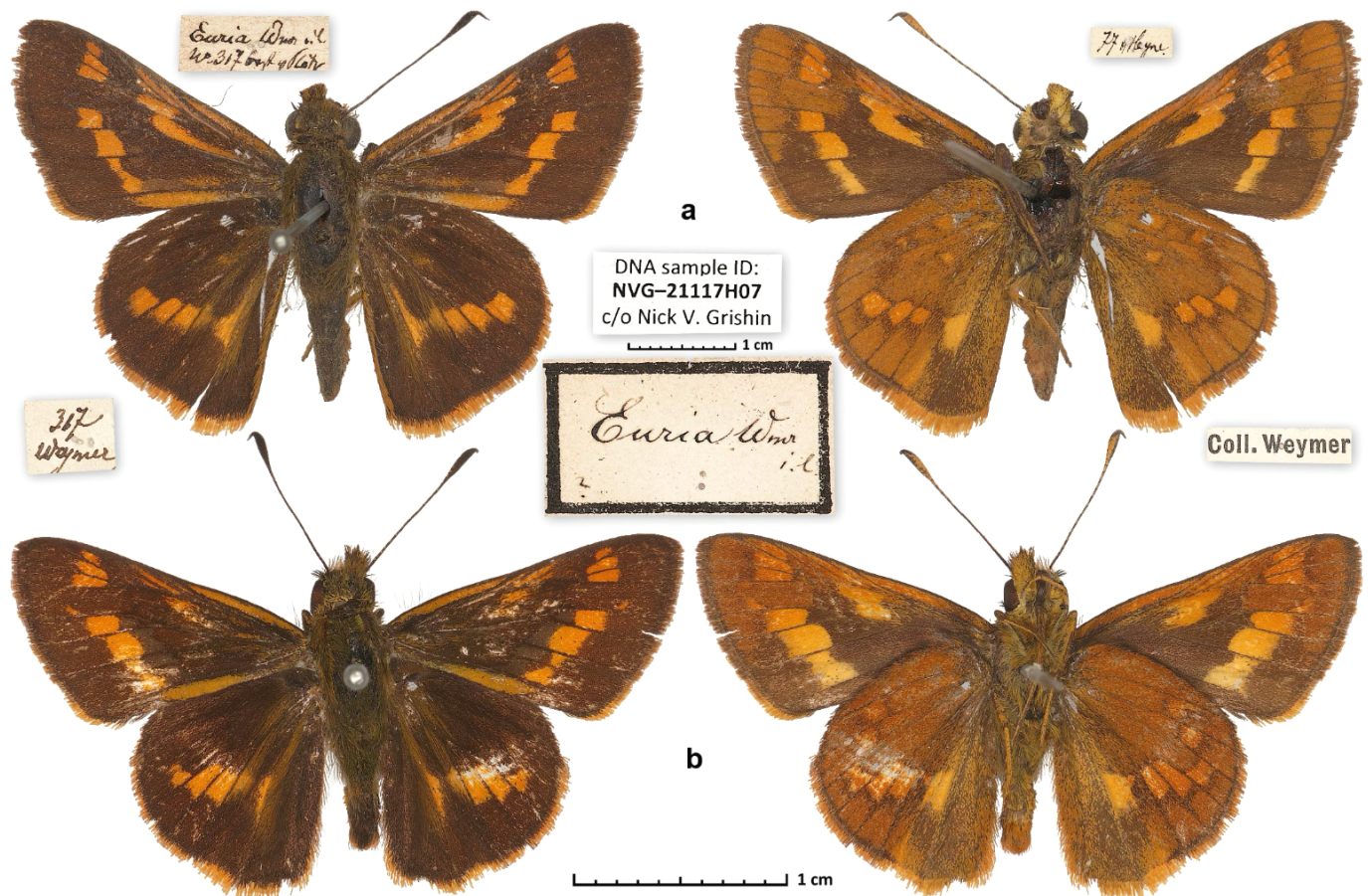


Fig. 94. Males of *Potanthus (Potanthus)* in dorsal (left) and ventral (right) views [MFNB]: **a**) *P. (P.) euria* lectotype (designated herein) NVG-21117H07 with no locality data, from/by Heyne, 1877; labels are shown at half the specimen scale (the label scale is between the two labels) and **b**) *P. (P.) pavor* **stat. rest.** non-type specimen NVG-21117H06 from Indonesia: Sumatra, Medan region (“Deli”), old; no labels are shown for this specimen.

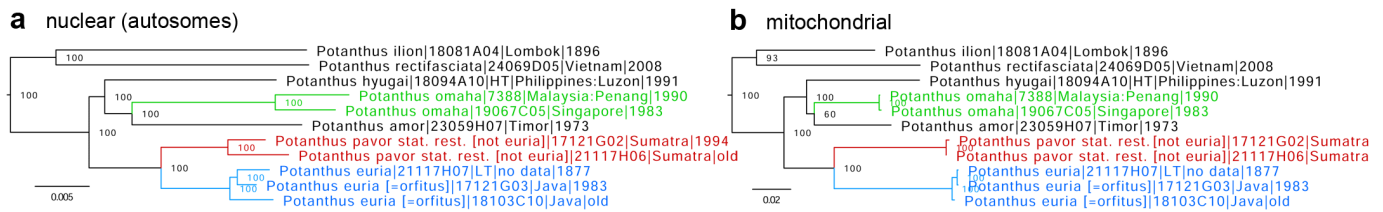


Fig. 95. Phylogenetic trees of selected *Potanthus* species constructed from protein-coding regions in: **a)** the nuclear genome (autosomes), based on 3,212,502 positions, and **b)** the mitochondrial genome. Different taxa are colored as follows: *P. omaha* (green), *P. pavor stat. rest.* (red), and *P. euria* (blue). Ultrafast bootstrap (Hoang et al. 2018) values are shown at nodes.

black at the inner margin, with a short reddish-yellow ray in cell 1c and brown-edged spots. Antennae are quite long and thin. 502. *Euria* Weym. i. l. — Pl. Suppl. 14 mm. Partia?” (Plötz 1883). Note the two spots in the ventral hindwing cell 7 (i.e., Sc+R₁-Rs) mentioned in the original description. The two spots are usually present in specimens from Java, but the basal spot is absent in populations from Sumatra.

In the MFNB, we found a specimen originally from Weymer’s collection labeled “*Euria* Wmr | i. l.” in Weymer’s handwriting, with “i. l.” standing for *in litteris* (literally meaning “in letters” or “in correspondence”) usually added to yet unpublished names. Moreover, according to one of its labels, it was identified by Plötz as “*Euria* Wmr i.l.” and is lacking a locality label; thus, its provenance was likely unknown. This specimen matches the original description, was collected prior to its publication, dated 1877, and is a syntype of *H. euria*. To define the taxonomic identity of the name *H. euria* objectively, N.V.G. hereby designates this syntype in the MFNB collection, a male illustrated in Fig. 94a bearing the following six rectangular labels (the last two printed, others handwritten): [77 v. Heyne], [*Euria* Wmr. i.l. | n° 317 best. v. Plötz], [*Euria* Wmr | i. l.], [317 | Weymer], [Coll. Weymer], and [DNA sample ID: | NVG-21117H07 | c/o Nick V. Grishin], as the **lectotype** of *Hesperia euria* Plötz, 1883. The first four labels are in Weymer’s handwriting. According to the first label, the specimen was received from (or collected by?) Heyne in 1877. According to the second label, this specimen was identified by Plötz (“best[immet]. v[on]. Plötz”) as “*Euria* Wmr.”, and this label with the name was added to the specimen prior to publication (“i[n].l[itteris]”). The number 317 is likely an unpublished specimen number in the Weymer collection, or the number of a specimen among those identified by Plötz. There is no locality stated on the labels. The lectotype is missing the left antenna, and its right hindwing is torn near the inner margin from the base and at the outer margin. The type locality of *H. euria* is in Indonesia: Java, as inferred by genomic comparison of the lectotype with specimens from known localities (Fig. 95). The COI barcode sequence of the lectotype, sample NVG-21117H07, GenBank [PZ516436](#), 658 base pairs, is:

AACCTTATACCTTTATTTTGGTATTTGAGCAGGCATATTAGGAACCTTCACTTAGAATGTTAATTCGTAAGTATAGGAAACCCAGGCTCATTAAATGGAGATGATCAAATTTATACACT
ATTGTTACTGCTCATGCTTTTATTATAATTTTATAGTTATACCTATTATAATTTGGAGGATTTGGTAATTTGATTAGTTCCCTTAATATTGGGGGCCCTGATATAGCTTTCCACGAA
TAAATAATATAAGTTTCTGGATACTCCCTTCACTTAACCTTAACTTTAGAGAAGATCGTAGAAAATGGTGGGACTGGTTGAACCTGTTACCCCTCTTTCTCTTAATATTGC
CCACCAAGGATCGTCTGTTGACCTAGCAATTTTCTTTACATTTAGCAGGAATCTCTTCAATTTTAGGAGCTATTAATTTTATTACTACAATTTAATATATGCGAATTAATTAATTTATCA
TTTGACCAATACCGTTATTTGTTGATCAGTTGGGATTACAGCTTTATTTATTAATTTCACTACCTGTTTATAGCAGGCGCTATTACCATACTCTTACTGATCGAAATTTAAATACCT
CATTTTGTGACCCGTGCTGGGGGGGAGATCCAAATTTTATATCAACATTTATTC

***Potanthus (Potanthus) pavor* (De Niceville, 1894), stat. rest. is a valid species and
Pamphila orfitus Mabilie, 1883 is a junior subjective synonym
of *Potanthus (Potanthus) euria* (Plötz, 1883)**

Genomic analysis of *Potanthus* Scudder, 1872 (type species *Hesperia omaha* Edwards, 1863) places the lectotype of *Hesperia euria* Plötz, 1883 (type locality not stated; sequenced as NVG-21117H07) among specimens from Indonesia: Java (Fig. 95 blue) and away from the clade of specimens from Indonesia: Sumatra (Fig. 95 red). *Pamphila orfitus* Mabilie, 1883 (published in May) (type locality in Indonesia: Java), the name currently applied to populations from Java, is junior to *H. euria* Plötz, 1883 (published in mid-January). Therefore, we propose that *Pamphila orfitus* Mabilie, 1883, **syn. nov.** is a junior subjective synonym of *Potanthus (Potanthus) euria* (Plötz, 1883). Evans (1949) misapplied the name *P. euria* to populations in Sumatra (misidentification), with *Padraona pavor* De Niceville, 1894 (type locality in Indonesia: northeastern Sumatra, Batak Mountains) (Fig. 94b) being treated as its junior subjective

synonym. The lectotype designation suggests synonymy of *P. euria* and *Pamphila orfitus*, and not of *P. euria* and *Padraona pavor*. Once *P. euria* is restricted to the Javan taxon, the senior available name for populations in Sumatra is *Padraona pavor*. Moreover, genomic comparison reveals species-level genetic differentiation between populations in Java and Sumatra (Fig. 95); e.g., their COI barcodes differ by 7.0% (46 bp). Coupled with morphological differences in secondary sexual characters (stigma in Sumatra vs. brands in Java) and male genitalia (e.g., ampulla shape and uncus width), DNA differences strongly support the recognition of these two taxa as distinct species. Therefore, we propose that *Potanthus* (*Potanthus*) *pavor* (De Niceville, 1894), **stat. rest.** is a valid species distinct from *Potanthus* (*Potanthus*) *euria* (Plötz, 1883).

Tribe Erionotini Distant, 1886

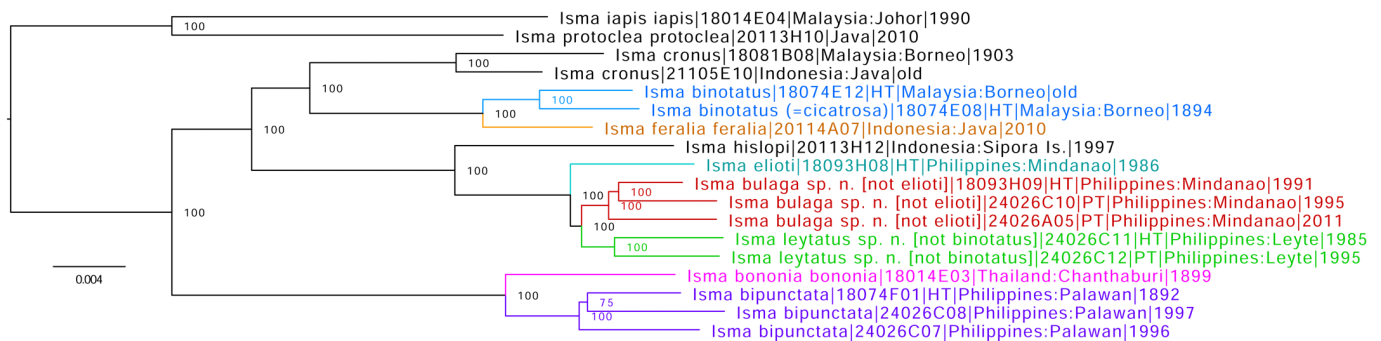
Isma bulaga Grishin, new species

<https://zoobank.org/C1859CE3-341A-4A3C-91FF-CBBA312DB491>

(Figs. 96 part, 97b–d)

Definition and diagnosis. Genomic analysis reveals that two sequenced paratypes of *Isma elioti* de Jong & Treadaway, 2007 (type locality in Philippines, Mindanao; holotype sequenced as NVG-18093H08) (Fig. 97a), prior to its description regarded as a new subspecies of *Isma feralia* (Hewitson, 1868) (type locality in Java), together with a female that was unidentified in the Treadaway collection, form a clade sister to but genetically differentiated from the *I. elioti* holotype at the species level (Fig. 96); e.g., their COI barcodes differ by 5.0% (33 bp), and therefore these specimens represent a new species. This new species keys to *I. feralia* (J.9.5) in Evans (1949), but differs from it and other relatives by the following combination of characters: it lacks a pair of pale spots near the end of the discal cell on the ventral forewing and a diffuse pale spot on the dorsal side at the place of the distal ventral spot [spots present in *I.*

a nuclear genome (autosomes)



b mitochondrial genome

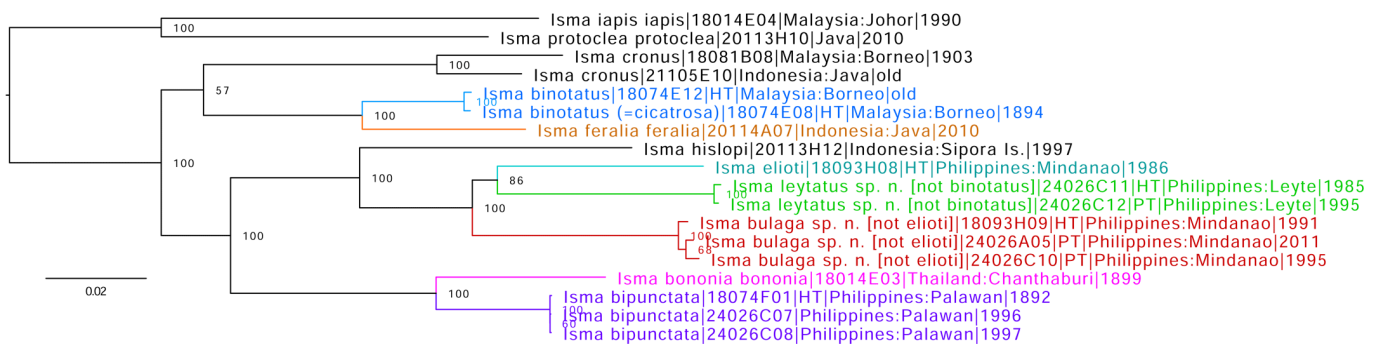


Fig. 96. Phylogenetic trees of selected *Isma* Distant, 1886 species constructed from protein-coding regions in: **a)** the nuclear genome (autosomes), based on 3,273,813 positions, and **b)** the mitochondrial genome. Species discussed in the text are colored as follows: *I. binotatus* (blue), *I. feralia* (orange), *I. elioti* (cyan), *I. bulaga* sp. n. (red), *I. leytatus* sp. n. (green), *I. bononia* (magenta), and *I. bipunctata* (violet). Ultrafast bootstrap (Hoang et al. 2018) values are shown at nodes.



Fig. 97. Type specimens of *Isma* from the Philippines, Mindanao [SMF], in dorsal (left) and ventral (right) views: **a)** *I. elioti* holotype ♂ NVG-18093H08 Surigao, Jun-1986, R. Lunawig leg. and **b–d)** *I. bulaga* sp. n.: **b)** holotype ♂ NVG-18093H09 Bukidnon, Mount Kitanglad, 17-Dec-1991, **c)** paratype ♂ NVG-24026C10 Zamboanga del Norte Province, Mount Dapiak, 9-Jul-1994, and **d)** paratype ♀ NVG-24026A05 Mt. Apo, 10-Feb-2011.

elioti]; the posterior semihyaline discal cell spot on the forewing is not as long as in *I. elioti* and is sometimes shorter than the anterior spot [in *I. elioti*, the posterior spot is approximately twice as long as the anterior spot]; the female (Fig. 97d) is darker than most relatives, lacks discal cell spots and, dorsally, subapical spots, has an unspotted dorsal hindwing, two semihyaline round spots on the dorsal forewing (larger in the basal third of cell CuA₁-CuA₂ and smaller near the base of cell M₃-CuA₁) and, ventrally, has two additional (and smaller) beige spots (near the base of cells R₅-M₁ and M₂-M₃) on the forewing and three diffuse postdiscal beige spots in a row between veins M₂ and CuA₂. Due to its cryptic nature and unexplored individual variation, this species is best identified by DNA, with diagnostic base pairs in the nuclear genome: aly127.90.5:C117T, aly127.90.5:C132T, aly905.4.1:T37C, aly905.4.1:G75A, aly905.4.1:G83A; and the COI barcode: A100G, T145C, T193C, T232C, 400A, A433T.

Barcode sequence of the holotype. Sample NVG-18093H09, GenBank [PZ516437](https://www.ncbi.nlm.nih.gov/nuclot/PZ516437), 658 base pairs:

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AACCTTTATATTTTATCTTTGGTATTTGAGCTGGATTATTAGGAACATCATTAAAGATTATTAATTCGTACTGAATTAGGAAATCCTGGATCTTTAATTGGGGACGATCAAATTTATAACACA
ATTGTAACAGCTCATGCTTTTATCATAATTTTTTTCATAGTTATACCAATTATAATTGGAGGATTTGGTAACTGATTAGTTCCTTAATATTAGGGGCCCTGATATAGCCTTTCCACGAA
TAAATAATATAAGATTTGAATATTACCCCTTCATTAACCTTACTTATTTCAGAGAAGATTGTAGAAAATGGTGCCGGAAGTGAACAGTTTACCCCTTTCATCTAATATTGC
CCATCAAGGATCTTCTGTTGATTAGCAATTTTTCATTACATTAGCTGGAATTTCTCCATCTTAGGTGCTATTAAATTTATTACTACAATTATTAATATGCGAATTAATAATTTATCT
TTTGATCAAAATATCCCTTTTCATTTGATCTGTTGGGATCACAGCATTATTACTTTTCTTCTTACCTGTTTGTAGCAGGTGCTATTACCATACTTCTTACTGATCGAAATTTAAATACTT
CTTTTTTGTATCCAGCGGGAGGAGGATCCAATTTTATCAACATTTATTT
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Type material. Holotype: ♂ deposited in the Senckenberg Natural History Museum collection, Frankfurt, Germany (SMF), illustrated in Fig. 97b, bears the following seven printed rectangular labels (1st, 5th, and 6th handwritten, others printed; 3rd and 7th red, 4th blue, others white): [17 Dec | 1991 | Philippines | MINDANAO | Bukidnon | mt Kitanlad], the first two lines are rotated 90° counterclockwise and written along the left edge of this label, which bears the following text on the opposite side: [♂ | leg Jeanhomi], [Collection | C.G. Treadaway], [Para- | typus], [] no text on this label, [Photo 2 IX 1992 # 13A/14A], [PHOTO VI 15 | 1995 25A/26A] and on the other side of this label: [Isma | ferralia | n ssp], [DNA sample ID: | NVG-18093H09 | c/o Nick V. Grishin], and [HOLOTYPE ♂ | Isma bulaga | Grishin]. **Paratypes:** 1♂ and 1♀ from Philippines, Mindanao [SMF]: 1♂ NVG-24026C10 Zamboanga del Norte Province, Mount Dapiak, 9-Jul-1994, “Abella” leg. (Fig. 97c) and 1♀ NVG-24026A05 Mt. Apo, 10-Feb-2011, “Pedro” leg. (Fig. 97d).

Type locality. Philippines: Mindanao, Bukidnon, Mount Kitanglad.

Etymology. In the Filipino/Tagalog language, bulaga is a playful expression of surprise, and reflects a surprising discovery of this species, initially included among the paratypes of *I. elioti*, through genomic analysis, as well as its unusual female that Treadaway kept among only two unidentified HesperIIDae specimens in his collection. The name is treated as a noun in apposition.

Distribution. Currently known from the island of Mindanao in the Philippines.

Isma leytatus Grishin, new species

<https://zoobank.org/655F0EA5-63DD-4D06-A45D-78F18B62765E>

(Figs. 96 part, 98b–c)

Definition and diagnosis. Genomic analysis reveals that two females from Leyte, Philippines, identified by Treadaway as *Isma binotatus* (Elwes & Edwards, 1897) (type locality in Malaysia: Borneo, Mt. Kinabalu; holotype sequenced as NVG-18074E12) (Fig. 98a), are not closely related to it and instead form a clade in the nuclear genome tree sister the new species described immediately above, but are genetically differentiated from it at the species level (Fig. 96); e.g., their COI barcodes differ by 5.2% (34 bp), and therefore these females represent a new species. This new species keys to *I. binotatus* (J.9.4) in Evans (1949), but differs from it and other relatives by the following combination of characters in females: larger semihyaline spots on the forewing; the forewing discal cell has one or two semihyaline spots (the posterior spot is smaller or absent); the semihyaline spot in cell CuA₁-CuA₂ is nearly square, not elongated; and the ventral hindwing has two smaller pale discal spots (sometimes semihyaline) between veins M₂ and CuA₂. Due to its cryptic nature, unknown males, and unexplored individual variation, this species is best identified by DNA, with diagnostic base pairs in the nuclear genome: aly275215.2.10:A33C, aly1656.25.1:T519C, aly1656.25.1:C531T, aly1656.40.1:T1116C, aly1139.27.1:G126T; and the COI barcode: T50C, T85C, T139C, T250C, A298T, T436C.

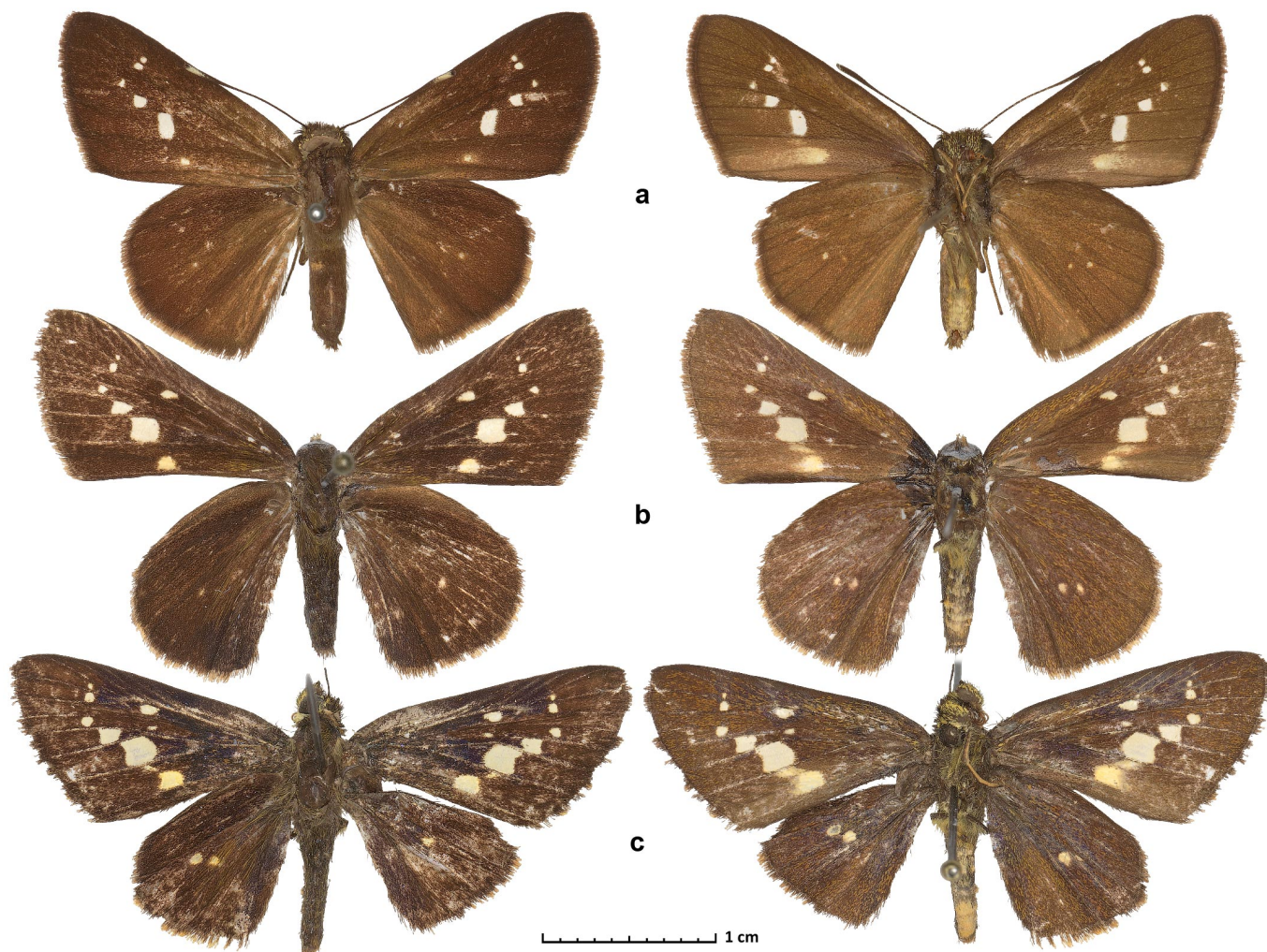


Fig. 98. Type specimens of *Isma* in dorsal (left) and ventral (right) views, data in text or below: **a)** *I. binotatus* holotype ♀ NVG-18074E12 Malaysia: Borneo, Mt. Kinabalu, old, Waterstradt leg. [MFNB] and **b–c)** *I. leytatus* sp. n. ♀♀ from Philippines, Leyte, Mount Balocawe [SMF]: **b)** holotype NVG-24026C11, 26-Jul-1985 and **c)** paratype NVG-24026C12, 17-Jun-1995.

Barcode sequence of the holotype. Sample NVG-24026C11, GenBank [PZ516438](https://www.ncbi.nlm.nih.gov/nuclot/PZ516438), 658 base pairs:

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AACTTTATATTTTATCTTTGGTATTTGAGCCGGATTATTAGGAACATCACTAAGATTATTAATTCGTACTGAATTAGGAAATCCCGGATCTTTAATTGGAGATGATCAAATTTATAATACA
ATTGTAAGTCCCATGCGCTTTATTATAATTTTTTTATAGTAATACCAATTATAAATTGGAGGATTGGTAATTGATTAGTCCCTTAATATTAGGGGCCCTGATAGCTTTCCCTCGAA
TAAATAATATAAGATTTTGAATATTACCCCTTCATTAACCTTTACTTATTTCAAGTAGAATTGTAGAAAATGGTGCAGGAACAGGATGAAGTGTTCACCCCACTTTTCATCTAATATTGC
CCATCAAGGATCTTCTGTTGATTAGCAATCTTTCCCTTACATTAGCTGGAATTTCCCTCCATTTAGGAGCCATTAATTTTATTACTACAATTATTAATATACGAATTAATAATTTATCT
TTTGATCAAATATCCCTTTTCATTTGATCTGTTGGAATCACAGCATTATTACTTTTACTCTCTTACCTGTTTACGAGGTGCTATTACCATACTTCTTACTGATCGAAATTTAAATACTT
CTTTTTTGTATCCGGCAGGAGGAGGTGATCCAATTTCTTACCAACATTATTT
```

Type material. Holotype: ♀ deposited in the Senckenberg Natural History Museum collection, Frankfurt, Germany (SMF), illustrated in Fig. 98b, bears the following seven rectangular labels (3rd, 4th, and 5th handwritten, others printed), six white: [26 VII | 1985 | Phil 700 m | C Leyte | mt Balocawe], the first two lines are rotated 90° counterclockwise and written along the left edge of this label, which bears the following text on the opposite side: [*Isma* (?) | ♀ | leg Rodong], [Collection | C.G. Treadaway], [Photo 11 III | 1994 23/34], [PHOTO VI 15 | 1995 27A/28A], [Film 7.II.2007 | Photos 13/14], [13. *Isma binotatus* ♀], [DNA sample ID: | NVG-24026C11 | c/o Nick V. Grishin], and one red [HOLOTYPE ♀ | *Isma leytatus* | Grishin]. **Paratype:** 1♀ NVG-24026C12 with the same collection data as the holotype, but 500 m, 17-Jun-1995, “Bebot” leg. (Fig. 98c).

Type locality. Philippines: Leyte Island, Mount Balocawe, 700 m.

Etymology. The name of this new species from *Leyt*[e identified by Treadaway as *Isma binot*]atus is treated as a noun in apposition.

Distribution. Currently known only from the type locality in the mountains of central Leyte, Philippines.

***Isma bipunctata* Elwes & Edwards, 1897 is confirmed as a species
distinct from *Isma bononia* (Hewitson, 1868)**

Genomic analysis reveals that *Isma bipunctata* Elwes & Edwards, 1897 (type locality in Philippines: Palawan; holotype sequenced as NVG-18074F01), formerly treated as a subspecies of *Isma bononia* (Hewitson, 1868) (type locality in Singapore), is genetically differentiated from it at the species level (Fig. 96), e.g., their COI barcodes differ by 5.9% (39 bp). Therefore, we confirm *Isma bipunctata* Elwes & Edwards, 1897, **stat. conf.** as a species distinct from *Isma bononia* (Hewitson, 1868).

Tribe Hesperini Latreille, 1809

***Decinea buenia* Grishin, new species**

<https://zoobank.org/69A6CC1A-9512-407A-B876-D5A9D56002F6>

(Figs. 99 part, 100a)

Definition and diagnosis. Genomic analysis reveals that a Bolivian male of *Decinea* Evans, 1955 (type species *Hesperia decinea* Hewitson, 1876) with a unique wing pattern is a distant sister to *Decinea notata* Grishin, 2023 (type locality in Ecuador: Napo) but is not similar to it phenotypically and is markedly differentiated genetically from all species in the genus (Fig. 99); e.g., COI barcodes differ by 7.9% (52 bp) from its sister *D. notata*, and therefore this male represents a new species. This new species keys to *Decinea decinea* (L.11.2) in Evans (1955), and was possibly misidentified by him as a female of *Decinea denta denta* Evans, 1955 (type locality in Peru: Junín, La Merced; a species that Evans proposed as a subspecies of *D. decinea*) from Bolivia, but differs from all other species in the genus by the following combination of characters in males: boldly patterned with semihyaline cream spots larger than those of its relatives and more extensive ferruginous areas and cream overscaling on the ventral surfaces of the wings; an hourglass-shaped, nearly divided forewing discal cell spot [not only the upper spot as in *D. denta*]; a prominent semihyaline cream dash in the forewing cell M₂-M₃ [lacking in most other species] in addition to well-developed [but smaller than in *Decinea denta pruda* Evans, 1955 (type locality Paraguay: Sapucaí)] semihyaline spots in cells CuA₁-CuA₂ (the largest, with concave outer margin), M₃-CuA₁ (smaller, elongated), and three elongated spots in cells between veins R₃ and M₁ in a slightly curved row; a cream roundish spot in the middle of the posterior half of the dorsal forewing cell CuA₂-1A+2A; in addition to a smaller spot in cell Rs-M₁ [usually absent in males of other *Decinea* taxa], subequal elongated semihyaline discal spots in hindwing cells M₃-CuA₁ and CuA₁-CuA₂ and a small cream spot in cell M₂-M₃; ventrally, more than half of the forewing cell CuA₂-1A+2A is cream-colored; ferruginous

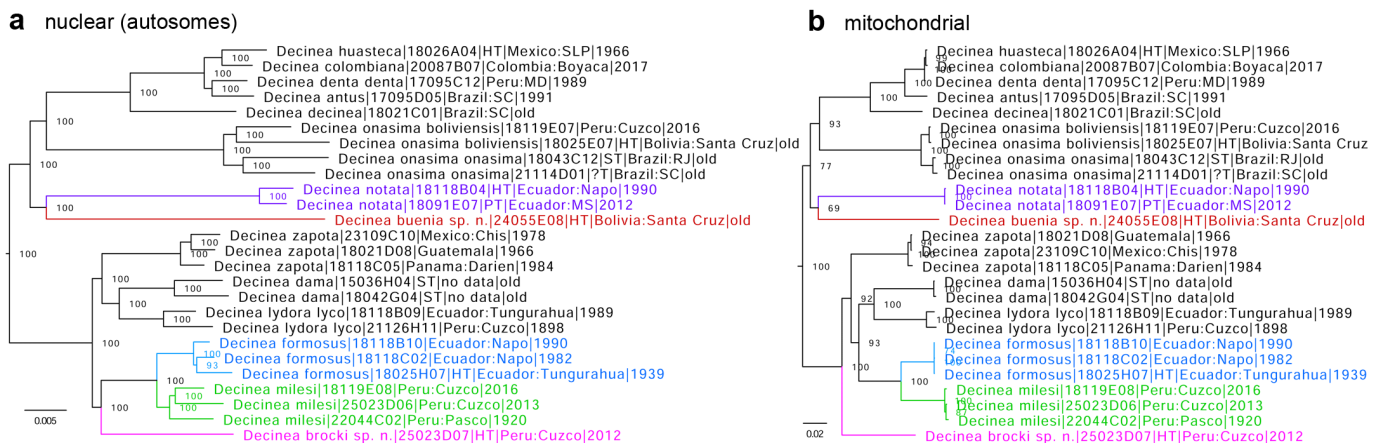


Fig. 99. Phylogenetic trees of all valid *Decinea* species constructed from protein-coding regions in: **a)** the nuclear genome (autosomes), based on 13,130,205 positions, and **b)** the mitochondrial genome. Nuclear genome clades containing new species are colored: *D. notata* (violet), *D. buenia* sp. n. (red), *D. formosus* (blue), *D. milesi* (green) and *D. brocki* sp. n. (magenta). Ultrafast bootstrap (Hoang et al. 2018) values are shown at nodes.

Etymology. The name is derived from the type locality and reflects the appearance of this arguably most beautiful species in the genus. The name is treated as a noun in apposition.

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

Decinea brocki Grishin, new species

<https://zoobank.org/8228FA9E-5E81-4615-A845-41DBB01A2DC3>

(Figs. 99 part, 100b, 101)

Definition and diagnosis. Genomic analysis reveals that a male of *Decinea* Evans, 1955 (type species *Hesperia decinea* Hewitson, 1876) from the foothills of the Andes in southeastern Peru is most strongly differentiated genetically from all known species in the genus, being sister to the clade of *Decinea formosus* (Hayward, 1940) (type locality Ecuador: Tungurahua, Río Topo) and *Decinea milesi* (Weeks, 1901) (type locality Bolivia, La Paz, nr. Coroico) in the nuclear genome tree (Fig. 99); their COI barcodes differ by 9.7% (64 bp) (from *D. formosus*) and 9.1% (60 bp) (from *D. milesi*), and therefore this male represents a new species. This new species keys to “*Decinea dama*” (L.11.6) in Evans (1955), under which he lumped several distinct species, but differs from them and other relatives by the following combination of characters in males: no white on antennae [*D. milesi* has a white side of the club]; cream-colored distal half of the abdomen on the ventral side [as in *D. milesi*]; only traces of hyaline subapical spots on the forewing; no pale spot in the forewing discal cell; elongated semihyaline cream spots with convex outer margins in cells M₃-CuA₁ (longitudinally elongated, but close to square) and CuA₁-CuA₂ (latitudinally elongated, at least twice as long as wide); on the ventral forewing, a cream-colored longitudinally elongated patch nearly parallel in its axis to the costal margin and occupying a quarter of cell CuA₂-1A+2A from its middle distad, ending about a quarter of the wing length from the outer margin; two semihyaline approximately rectangular cream spots on the hindwing in cells M₂-CuA₁ (larger) and CuA₁-CuA₂ (smaller); and, apart from the mentioned markings, dark brown wings on both sides. Due to its cryptic nature and unexplored individual variation, this species is best identified by DNA, with diagnostic base pairs in the nuclear genome: aly686.40.1:T39G, aly103.12.2:A609T, aly587.24.4:A57G, aly1603.37.5:T90C, aly971.11.1:A129G, aly1624.2.1:T183T (not C), aly925.44.1:G315G (not C), aly4305.27.6:T90T (not C), aly2692.7.22:C58C (not T), aly7600.1.2:C391C (not A); and the COI barcode: G81A, A199G, A262G, T397C, T529C, T604T, T610T.

Barcode sequence of the holotype. Sample NVG-25023D07, GenBank [PZ516440](https://www.ncbi.nlm.nih.gov/nuccore/PZ516440), 658 base pairs:

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AACTTTATATTTTATTTTGGTATTTGAGCAGGTACTAGGAACCTTCATTAAGTTTATTAATTCGTACTGAATTAGGAAATCCAGGATCTTTAATTGGAGATGATCAAATTTATAATACT
ATTGTTACAGCTCATGCTTTTATTATAATTTTATAGTAATACCCATTATAATCGGAGGATTCGGAAATTGACTGGTACCTTTAATACTAGGAGCCCAGATATAGCTTTCCCTCGAA
TAAATAATATAAGATTTTGGATATTACCCCCCTCATTAACCTTTATTAATTTCAAGAAGAATCGTAGAAAATGGTGCAGGAACCTGGATGAACAGTTTATCCCCCTTTATCATCAAATATTGC
TCACCAAGGAGCCTCTGTTGATTTAGCTATTTCTCCCTTCATTTAGCTGGTATTTCTTCTATTTTAGGGGCTATTAATTTTATTACTACAATTATTAACATACGAATTAATAATTTATCA
TTTGATCAAATACCTTTATTGTTATGATCTGTAGGAATTACAGCCTTATTATTACTACTATCTTTACCTGTTTAGCAGGTGCTATTACAATATTACTTACAGACCGAAATTTAAATACTT
CATTTTTTGACCTGCTGGAGGTGGGATCCTATTTTATACCAACATTTATTT
```

Type material. **Holotype:** ♂ currently deposited in the McGuire Center for Lepidoptera and Biodiversity collection, Gainesville, FL, USA (MGCL), illustrated in Fig. 100b (genitalia Fig. 101), bears the following



Fig. 101. Male genitalia of *Decinea brocki* sp. n. holotype NVG-25023D07 in left lateral (left) and dorsal (right) views.

five printed rectangular labels, four white: [PERU: Cuzco: | Cosñipata Valley | Pilcopata, 522 m | 7 xi 2012 | leg. J P Brock], [DNA sample ID: | NVG-25023D07 | c/o Nick V. Grishin], [DNA sample ID: | NVG-26012C03 | c/o Nick V. Grishin], [genitalia: | NVG260613-08 | c/o Nick V. Grishin], and one red [HOLOTYPE ♂ | *Decinea brocki* | Grishin]. The first DNA sample ID refers to the extraction from a leg (sequenced), and the second from the abdomen (stored) prior to genitalia dissection.

Type locality. Peru: Cuzco Region, Cosñipata Valley, Pilcopata, elevation 522 m.

Etymology. The specific epithet honors Jim P. Brock (Tucson, Arizona), who collected the holotype. Jim is widely recognized as an extraordinary lepidopterist whose uncanny intuition for finding butterflies and their caterpillars borders on a sixth sense, as he frequently discovers immature stages and adults where others find none. His profound contributions to our understanding of butterflies and their identification span decades of research, published articles and books, outreach presentations, and field tours. Yet, the impact of his work is rivaled only by his vibrant spirit, sparkling humor and wit, an open generosity in sharing expertise, and unsurpassed kindness. We express our deepest gratitude to Jim for his continuous and invaluable support of our research over the years. The name is a noun in the genitive case.

Distribution. Currently known only from the holotype collected in the Andean-Amazonian transition zone of southeastern Peru.

Zenis parlatus Grishin, new species

<https://zoobank.org/D94C996B-8215-4AE1-AC2E-DE86E1C8E944>

(Figs. 102 part, 103a, 104)

Definition and diagnosis. Genomic analysis reveals that a female from Rondônia, Brazil, initially identified as *Zenis par* Grishin, 2022 (type locality Peru: Cuzco, Cosñipata Valley, Quebrada Santa Isabel) is genetically differentiated from it at the species level (Fig. 102); e.g., their COI barcodes differ by 4.7% (31 bp), and therefore this female represents a new species. This new species keys to “*Zenis jebus melaleuca*” (O.3.2.(b)) in Evans (1955), and, together with *Z. par*, was likely included by Evans in this taxon, which he misidentified (Mielke and Casagrande 2002). The new species is most similar to *Z. par*, possessing its characters as described in Zhang et al. (2022c); but differs from *Z. par* by the following combination of characters (at least in females): broader discal white band on the hindwing, but a less prominent and smaller pale spot near the middle of the inner margin of the ventral hindwing; two longer subapical hyaline spots that are less equal in size: the spot in cell R₅-M₁ is conspicuously smaller than the spot in cell M₂-M₃ and does not overlap the spot in cell R₄-R₅ along vein R₅ [in *Z. par* (Fig. 103b), the spots are approximately equal in size, or the anterior one, which usually overlaps the spot

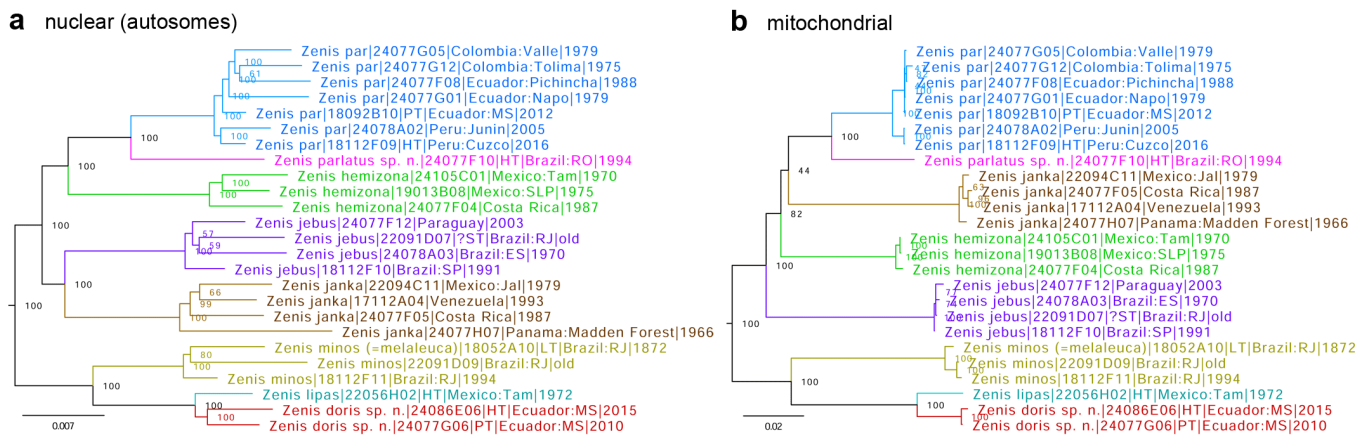


Fig. 102. Phylogenetic trees of all valid *Zenis* Godman, 1900 species constructed from protein-coding regions in: **a)** the nuclear genome (autosomes), based on 7,841,604 positions, and **b)** the mitochondrial genome. Different species are colored differently: *Z. par* (blue), *Z. parlatus* sp. n. (magenta), *Z. hemizona* (green), *Z. jebus* (violet), *Z. janka* (brown), *Z. minos* (olive), *Z. lipas* (cyan), *Z. doris* sp. n. (red). Ultrafast bootstrap (Hoang et al. 2018) values are shown at nodes.

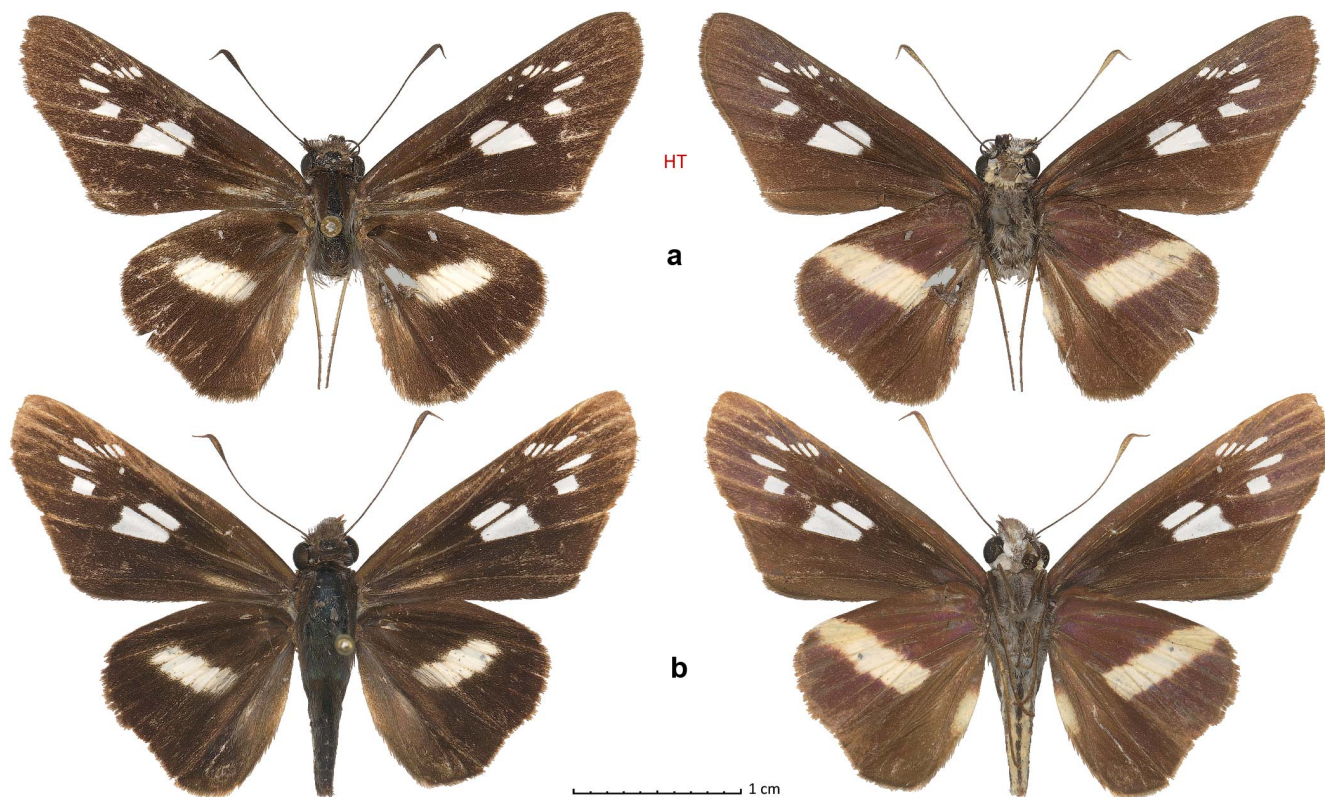


Fig. 103. Type specimens of *Zenis*, females in dorsal (left) and ventral (right) views: **a)** *Z. parlatus* sp. n. holotype NVG-24077F10 Brazil: Rondônia, 5 km S of Cacauplandia, Linha C-10 at Rio Pardo, off B-65, 19-Jul-1994, O. Gomez leg. [MGCL] and **b)** *Z. par* paratype NVG-18092B10 Ecuador: Morona-Santiago, Mendez, 800 m, -2.42, -78.20, 16-Nov-2012, J.-C. Petit leg. [EBC].

in cell R_4-R_5 , is only slightly smaller]; and a more conspicuous pale narrow ray along the basal half of the ventral hindwing vein $1A+2A$. Due to its cryptic nature, unexplored individual variation, and males being unknown, this species is best identified by DNA, with diagnostic base pairs in the nuclear genome: *aly525.91.6:A315G*, *aly525.91.6:T930C*, *aly536.169.1:A1176T*, *aly318.29.1:G230A*, *aly272.17.2:G84A*, *aly577.35.2:A57A* (not T), *aly577.35.2:G66G* (not A), *aly1454.3.2:A45A* (not G), *aly1454.3.2:A57A* (not T), *aly188.16.7:A1713A* (not G); and the COI barcode: A202T, T284C, A295C, T373G, T490T, T658A.

Barcode sequence of the holotype. Sample NVG-24077F10, GenBank [PZ516441](https://www.ncbi.nlm.nih.gov/nuclot/PZ516441), 658 base pairs:

```
AACTTTATATTTATTTTGGGATCTGAGCAGGAATATTAGGTACCTCATTAAGTTTAT
TAATTCGAACAGAAATTAGGAAATCCTGGTTCTTTAATTTGGAGATGATCAAATTTATAAT
ACTATTGTTACAGCACATGCTTTTATTATAATTTTATAGTTATACCTATTATAAT
TGGAGGATTTGGAAATTGATTAGTTCCTTTAATATTAGGGGCTCCAGATATAGCCTTTC
CTCGAATAAATAATATAAGATTTTGAATATTACCCCTTCATTAACCTATTAAATTTCC
AGAAGAATTGTTGAAATGGTGCAGGAACAGGATGAACCGTATATCCTCCTTTCTTC
TAATATTGCCCATCAAGGGGCATCTGTTGATTAGCAATTTTCTTTACATTAGCAG
GAATTCATCAATCCTAGGAGCTATTAATTTTATTACCACAATTATTAATATACGAATT
AAAAATTTATCATTTGATCAAATACCTTTATTTGTTGATCAGTAGGTATTACAGCTTT
ATTATTACTTTTATCTCTTCTGTATTAGCTGGAGCAATTACTATATTATTGACTGATC
GAAATTTAAATACATCTTCTTTGATCCTGCTGGAGGAGAGATCTATTTTATATCAA
CATTTATTT
```

Type material. **Holotype:** ♀ deposited in the McGuire Center for Lepidoptera and Biodiversity collection, Gainesville, FL, USA (MGCL), illustrated in Fig. 103a (genitalia Fig. 104), bears the following five printed rectangular labels (text in italics handwritten), four white: [BRASIL: Rondônia | linea C-10 (at Rio | Pardo), off B-65 | 5 km S Cacauplandia | 19 July 1994 | leg. O. Gomes], [Genetalic Vial | GTA - 10229], [G T Austin colln | MGCL Acc. | 2004-5], [DNA sample ID: |

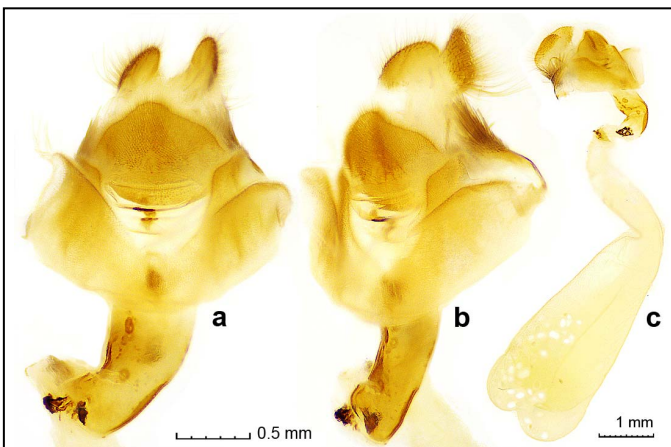


Fig. 104. Female genitalia of *Zenis parlatus* sp. n. holotype NVG-24077F10: **a–b)** without the bursa copulatrix: **a)** ventral and **b)** right ventrolateral views, scale between the images; and **c)** complete, left ventrolateral view, scale on the right.

NVG-24077F10 | c/o Nick V. Grishin], and one red [HOLOTYPE ♀ | *Zenis parlatus* | Grishin].

Type locality. Brazil: Rondônia, 5 km south of Cacaupônia, Linha C-10 at Rio Pardo, off B-65.

Etymology. In Latin, *latus* means broad, fused to the name of the sister species *Z. par*, reflecting the broader white band on the hindwing of the new species. The name is treated as an adjective.

Distribution. Currently known only from the holotype collected in Rondônia, Brazil.

***Zenis doris* Grishin, new species**

<https://zoobank.org/C1C9C7D5-91FE-4FBD-8FCD-5E7B8AAA2E7E>

(Figs. 102 part, 105a–b, 106a–c)

Definition and diagnosis. Genomic analysis reveals that two males from Ecuador initially identified as *Zenis minos* (Latreille, [1824]) (type locality in Brazil, likely Rio de Janeiro) are instead most closely



Fig. 105. Type specimens of *Zenis* ♂♂ in dorsal (left) and ventral (right) views: **a–b)** *Z. doris* **sp. n.** Ecuador: Morona-Santiago, M. Simon leg. [MGCL]: **a)** holotype NVG-24086E06 San Isidro, 1100 m, Nov-2015 and **b)** paratype NVG-24077G06 Méndez, 1000 m, May-2010; and **c)** *Z. lipas* holotype NVG-19013F05 Mexico: Tamaulipas, Xicoténcatl, 3.5 km SE of Azteca, Río Sabinas, 130 m, 27-Dec-1972, C. J. Durden leg. [TMMC].

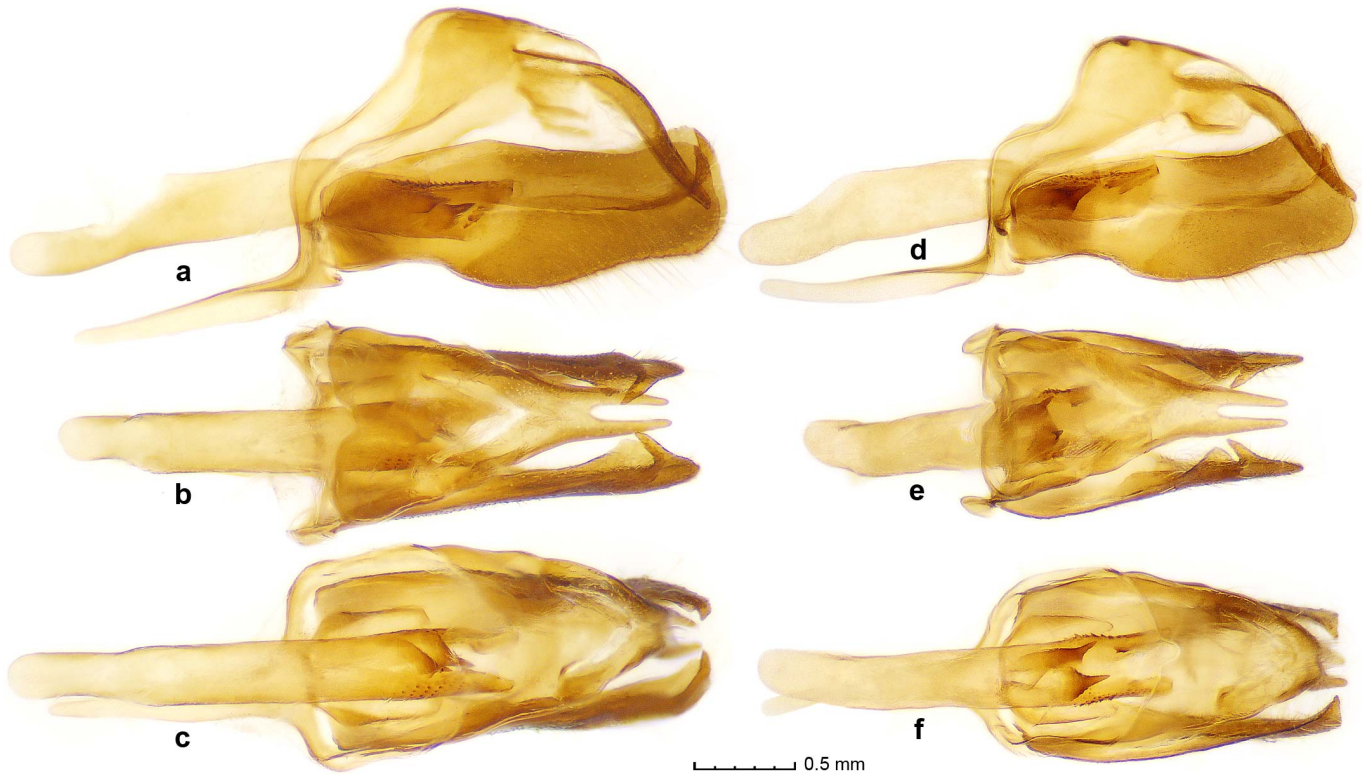


Fig. 106. Male genitalia of *Zenis*: **a–c)** *Z. doris* **sp. n.** holotype NVG-24086E06 Ecuador: Morona-Santiago, San Isidro, 1100 m, Nov-2015, M. Simon leg., genitalia NVG260613-18 [MGCL]; and **d–f)** *Z. lipas* holotype NVG-19013F05 Mexico: Tamaulipas, Xicoténcatl, 3.5 km SE of Azteca, Río Sabinas, 130 m, 27-Dec-1972, C. J. Durden leg., genitalia NVG241121-71 [TMMC]. Views: **a, d)** left lateral, **b, e)** dorsal, and **c, f)** anterodorsal, tilted to the right.

related to *Zenis lipas* Grishin, 2025 (type locality in Mexico: Tamaulipas, Xicoténcatl) but are genetically differentiated from it at the species level (Fig. 102); e.g., their COI barcodes differ by 3.3% (24 bp), and therefore these males represent a new species. This new species keys to *Z. minos* (O.3.1) in Evans (1955) and was probably included by him in this species, but differs from it and *Z. lipas* (Fig. 105c) by the following combination of characters in males: the subapical hyaline spots are shorter, and the spot in cell R₃-R₄ is not much longer than the spot in cell R₄-R₅ [longer in *Z. lipas*]; the more uneven inner margin of the discal hyaline band on the dorsal hindwing, with the spot in cell Rs-M₁ being more strongly separated from the others; and more conspicuous brands. In male genitalia (Fig. 106a–c), compared to *Z. lipas* (Fig. 106d–f), the valva is longer and narrower in its distal third; the ampulla is longer and narrower, about three times as long as wide; the dorsally directed terminal spike of the harpe nearly reaches the dorsal edge of the ampulla in lateral view [the ampulla extends distad of the spike in *Z. lipas*]; and the posteroventral corner of the harpe is rounded and not bulging posteriad. Due to its cryptic nature and poorly explored individual variation, this species is best identified by DNA, with diagnostic base pairs in the nuclear genome: aly6370.12.1:G579A, aly6841.59.5:C115G, aly2582.7.5:C110G, aly2582.7.5:T111C, aly4988.2.2:A24G; and the COI barcode: T16C, A211G, A289T, T346C, A566G, T547C.

Barcode sequence of the holotype. Sample NVG-24086E06, GenBank [PZ516442](https://www.ncbi.nlm.nih.gov/sequence/oln/pz516442), 658 base pairs:

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AACTTTATATTTTATCTTTGGAATTTGAGCAGGAATATTAGGTACTTCATTAAGTTTATTAATTCGAACAGAATTAGGAAACCCCGGCTCTTTAATTTGGTGATGATCAAAATTTACAACACT
ATTGTTACAGCACATGCTTTTATTATAATTTTTTTATAGTAATACCTATTATAATTTGGAGGATTCGGAAACTGATTAGTACCTTTAATGCTAGGAGCACCAGATATAGCTTTTCCTCGAA
TAAATAATATAAGATTTTGAATATTACCCCTTCATTAACCTTTACTTATCTCAAGAAGAATTGTAGAAAATGGTGCTGGCACAGGATGAACCGTATACCCCTTTCTTCTAATATTGC
CCATCAAGGAGCATCTGTTGATTTAGCCATTTTCTCTTCATTAGCAGGAATTTTCATCAATTCAGGAGCTATTAAATTTTATTACTACAATTATTAATATGCGAATTAATAATTTATCA
TTTGATCAAAATACCTTTATTGTTTGATCAGTAGGTATTACAGCTTTTATTACTTTTATCCTTACCTGTATTAGCAGGTGCTATTACTATACTATTAACTGATCGAAATCTAAATACAT
CTTTCTTTGATCCAGCTGGAGGAGGAGATCCTATTTTATATCAACATTTATTT
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Type material. Holotype: ♂ deposited in the McGuire Center for Lepidoptera and Biodiversity collection, Gainesville, FL, USA (MGCL), illustrated in Fig. 105a (genitalia Fig. 106a–c), bears the following five rectangular labels (1st handprinted, others printed), four white: [ECUADOR · M.S. | SAN ISIDRO 1100M | XI-2015], [DNA sample ID: | NVG-24086E06 | c/o Nick V. Grishin], [DNA sample ID: | NVG-25068C01 | c/o Nick V. Grishin], [genitalia: | NVG260613-18 | c/o Nick V. Grishin], and

one red [HOLOTYPE ♂ | Zenis doris Grishin]. From the handwriting on the first label, the specimen was collected by Mark Simon. The first DNA sample ID refers to the extraction from a leg (sequenced), and the second from the abdomen (stored) prior to genitalia dissection. **Paratype:** 1♂ NVG-24077G06 Ecuador: Morona-Santiago, Méndez, 1000 m, May-2010, M. Simon leg. [MGCL] (Fig. 105b).

Type locality. Ecuador: Morona-Santiago Province, San Isidro, elevation 1100 m.

Etymology. The name for this [Ecu]dor[ian Zen]is species is a fusion and is treated as a noun in apposition.

Distribution. Currently known from the eastern slopes of the Andes in southeastern Ecuador.

Mucia rustana Grishin, new species

<https://zoobank.org/D48F36B5-DAFA-4754-8FBE-433100D5B5F1>

(Figs. 107 part, 108b, 109a–c)

Definition and diagnosis. Genomic analysis reveals that a specimen from the cloud forest in southeastern Peru initially identified as *Mucia rusta* (Evans, 1955) (type locality in Venezuela) is not monophyletic with it and is genetically differentiated from it at the species level (Fig. 107); e.g., their COI barcodes differ by 3.3% (22 bp), and therefore this specimen represents a new species. This new species keys to *Psoralis rusta* (J.43.7) in Evans (1955) and is similar to it (Fig. 108a) in having a thicker stigma [not a thin one as in *Mucia castana* Grishin, 2025 (type locality in Ecuador: Zamora) (Fig. 108c)] but differs from it and other relatives by the following combination of characters in males: a postdiscal row of faint, but more conspicuous than in relatives, gray spots on the ventral hindwing, with one spot in each cell between veins Sc+R₁ and CuA₂ (five or six spots, each composed of a few scales); less ferruginous, browner scaling on the ventral side of the wings; and a slightly narrower and straighter anterior segment of the stigma. In male genitalia (Fig. 109a–c), the tegumen has a deeper notch at the anterior margin; the harpe is rounder, less strongly produced anteriorly at its end, with smaller teeth along the dorsal margin [in *M. rusta* male genitalia (Fig. 109d–h), the ventroposterior margin of the harpe is relatively straight and even mildly concave, which makes the harpe appear narrower near its base; and the end of the harpe is conspicuously produced anteriorly]; the costa of the valva is shallowly concave, lacking the central hump observed in *Mucia rusta* (Fig. 109e–f); and the phallobase may be less curved and longer. Due to its cryptic nature and unexplored individual variation, this species is best identified by DNA, with diagnostic base pairs in the nuclear genome: aly18826.6.1:C72A, aly437.6.1:A408G, aly36.1.3:G51A, aly2643.2.4:A75T, aly1398.3.3:T153C, aly525.92.5:A144A (not C), aly10226.27.6:A96A (not T), aly577.17.1:A223A (not C), aly767.16.1:A360A (not G), aly50.26.1:C25C (not T); and the COI barcode: T79C, 88C, A265G, T424T, T613C, A631G.

Barcode sequence of the holotype. Sample NVG-25022G07, GenBank [PZ516443](https://www.ncbi.nlm.nih.gov/nuclot/PZ516443), 658 base pairs:

AACTTTATATTTATTTTGGTATTTGAGCAGGAATATTAGGAACCTCTTAAGTTTATTAATTCGTACAGAATTAGGCAACCTGGCTCATTAATTGGAGATGATCAAATTTATAATACT
ATTGTTACAGCACATGCTTTTATTATAATTTTATAGTTATACCTATTATAATTGGAGGATTGGAAATGATTAGTTCTCTTAATATTAGGTGCTCCTGATATAGCTTTCCACAGAA
TAAATAATATAAGATTTGAATGCTTCCCTCTTAAATATTATTAATTTCAAGAGAATTGTAGAAAATGGAGCAGGAACCTGGTGAACAGTTTATCCACCTCTTCTTCTAATATTGC
TCATCAAGGATCCTCTGTTGATTAGCAATTTTCTCTTCATTAGCAGGAATTTCTCTATTCTAGGAGCTATTAACCTTATTACTACAATTATTAATATACGAATTAGAAATATATCA
TTTGATCAAATACCTTTATTGTATGATCTGTGCGAATTACTGCTTTATTATTACTTTTATCATTACCTGTATTAGCAGGAGCTATTACAATACTTCTTACTGACCGAACTTAAATACAT
CTTTTTCGATCCTGCAGGAGGAGGGATCCTATTCTTTATCAACATTTATT

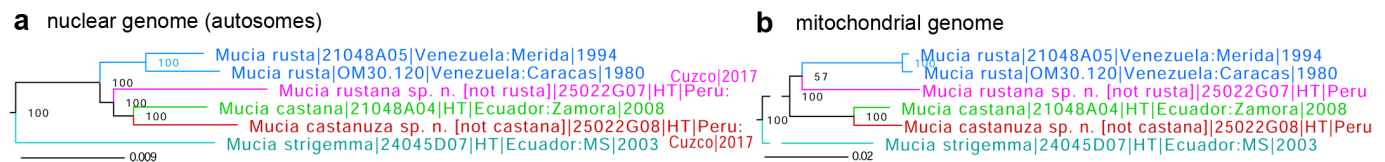


Fig. 107. Phylogenetic trees of selected *Mucia* species constructed from protein-coding regions in: **a**) the nuclear genome (autosomes), based on 10,665,363 positions, and **b**) the mitochondrial genome. Different species are colored differently: *M. rusta* (blue), *M. rustana* sp. n. (red), *M. castana* (green), *M. castanuza* sp. n. (red), and *M. strigemma* (cyan). Ultrafast bootstrap (Hoang et al. 2018) values are shown at nodes. Gaps in branches indicate where a vertical slice of the tree was removed to reduce its horizontal dimension (allowing the font size increase), i.e., branches with gaps are longer than shown.



Fig. 108. (see the previous page). Males of *Mucia* in dorsal (left) and ventral (right) views [MGCL]: **a)** *M. rusta* non-type NVG-21048A05 Venezuela: Mérida, 2 km N of La Hechicera, Monte Zerpa, 5-Nov-1994, D. L. Lindsley leg.; **b)** *M. rustana* sp. n. holotype NVG-25022G07 Peru: Cuzco, Cosñipata Valley, Quebrada Morro Leguía, 2135 m, 11-Nov-2017, J. P. Brock leg.; **c)** *M. castana* holotype NVG-21048A04 Ecuador: Zamora-Chinchipe, Zamora, elevation 2000 m, Sep-2008, M. Simon leg.; and **d)** *M. castanuzza* sp. n. holotype NVG-25022G08 Peru: Cuzco, Cosñipata Valley, Quebrada Quitacalzón, km 81, ca. 1050 m, 2-Nov-2017, J. P. Brock leg.

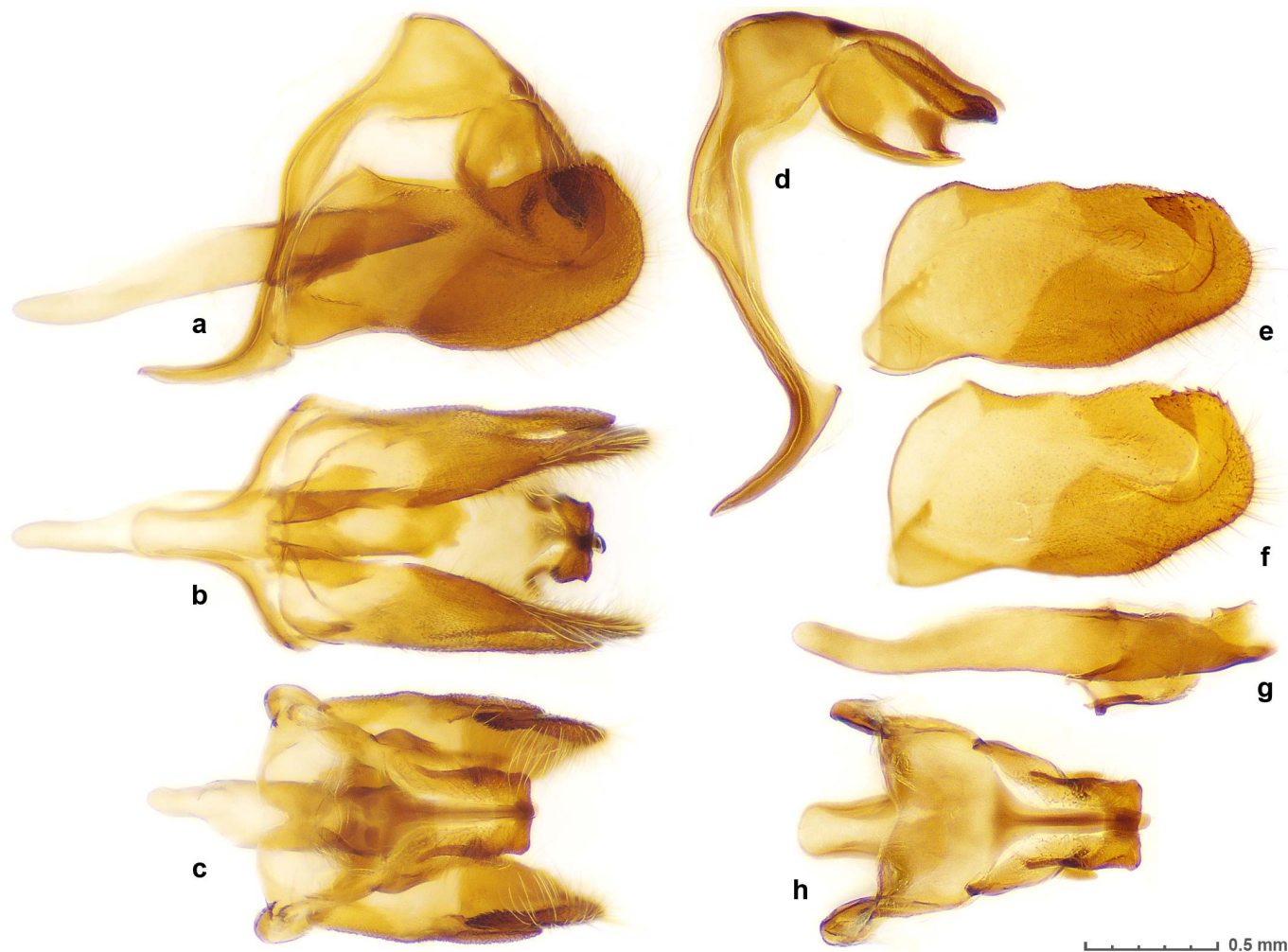


Fig. 109. Male genitalia of *Mucia*: **a–c)** *M. rustana* sp. n. holotype NVG-25022G07 in: **a)** left lateral, **b)** ventral, and **c)** dorsal views; and **d–h)** *M. rusta* non-type NVG-21048A05 Venezuela: Mérida, 2 km N of La Hechicera, Monte Zerpa, 5-Nov-1994, D. L. Lindsley leg., in: **d–g)** left lateral and **h)** dorsal views with detached structures: **e)** right and **f)** left valva, and **g)** aedeagus.

Type material. Holotype: ♂ currently deposited in the McGuire Center for Lepidoptera and Biodiversity collection, Gainesville, FL, USA (MGCL), illustrated in Fig. 108b (genitalia Fig. 109a–c), bears the following five printed rectangular labels, four white: [PERU, CU, Cosñipata | Valley, Quebrada | Morro Leguía, 2135 m, | 11 Nov 2017. JP Brock], [DNA sample ID: | NVG-25022G07 | c/o Nick V. Grishin], [DNA sample ID: | NVG-26012C04 | c/o Nick V. Grishin], [genitalia: | NVG260613-09 | c/o Nick V. Grishin], and one red [HOLOTYPE ♂ | *Mucia rustana* | Grishin]. The first DNA sample ID refers to the extraction from a leg (sequenced), and the second from the abdomen (stored) prior to genitalia dissection.

Type locality. Peru: Cuzco Region, Cosñipata Valley, Quebrada Morro Leguía, elevation 2135 m.

Etymology. The name is derived from its relative *M. rusta* with the suffix added to make it longer thus reflecting the more southern distribution of this new species, and is treated as a noun in apposition.

Distribution. Currently known only from the holotype collected in the cloud forest zone of southeastern Peru.

Mucia castanuza Grishin, new species

<https://zoobank.org/26328CEA-44EB-4046-BD73-98073213D46F>

(Figs. 107 part, 108d)

Definition and diagnosis. Genomic analysis reveals that a specimen from the Andean foothills in southeastern Peru initially identified as *Mucia castana* Grishin, 2025 (type locality in Ecuador: Zamora) is genetically differentiated from it at the species level (Fig. 107); e.g., their COI barcodes differ by 2.1% (14 bp), and therefore this specimen represents a new species. This new species keys to *Psoralis rusta* (J.43.7) in Evans (1955), but differs from it and other relatives by the following combination of characters: a thin stigma, more similar to that in *M. castana* (Fig. 108c) than in *Mucia rusta* (Evans, 1955) (type locality in Venezuela) (Fig. 108a) and *Mucia rustana* sp. n. described above, but the stigma is slightly thicker, especially its two posterior segments, which are rounder, dot-like, rather than the elongated streaks seen in *M. castana*; dark-brown fringes [redder, more ferruginous in *M. castana*]; less prominent ferruginous overscaling in the apical third of the ventral forewing; a more conspicuous division of the ventral forewing cell CuA₂-1A+2A into a darker, grayer base (basad of the stigma) and a paler, browner distal half; and a rounder, somewhat less produced hindwing tornus. Due to its cryptic nature and unexplored individual variation, this species is best identified by DNA, with diagnostic base pairs in the nuclear genome: aly536.229.1:C267T, aly666.28.3:T90C, aly3905.12.2:T105C, aly1041.26.1:A1029G, aly2954.8.5:G126C, aly2154.7.3:C78C (not T), aly1019.27.2:G258G (not A), aly361.11.1:A18A (not G), aly151.24.2:T150T (not A), aly420.17.3:T60T (not C); and the COI barcode: A40G, T193C, A316G, C347T, T394C, T553C.

Barcode sequence of the holotype. Sample NVG-25022G08, GenBank [PZ516444](https://www.ncbi.nlm.nih.gov/nuclot/PZ516444), 658 base pairs:

```
AACTTTATATTTTATTTTGGAAATTTGAGCAGGAATATTGGGAACCTCTTTAAGTTTACTAATTCGAACAGAATTAGGTAACCTGGCTCTTTAATTGGAGATGATCAAATTTATAATACT
ATTGTTACAGCACATGCTTTTATATAATTTTATAGTTATACCTATTATAATTTGGAGGATTTGGAACTGATTAATTCCTTTAATATTAGGTGCTCCTGATATAGCTTTTCCACGAA
TAAACAATATAAGATTTTGAATACTTCCACCTCTTTAATATTATTAAATTTCAAGAAGAATTGTAGAAAATGGGGCAGGAAGTGGTTGAACAGTTTATCCACCTTTATCTTCTAATATTGC
CCACCAAGGATCTTCTGTTGATTTAGCAATCTTCTCTTCATTTAGCAGGAATTTCTTCTATTTTAGGAGCTATTAATTTTATTACTACAATTATTAATATACGAATTAGAAATATATCA
TTTGATCAAATACCTTTATTTGTATGATCTGTTGGAATTACTGCTTTATTATTACTTTTATCTTTACCGTATTAGCAGGAGCTATTACAATACTTCTTACTGATCGAAATTTAAATACAT
CTTTTTTGTATCTGTCAGGAGGAGGAGACCTATTCTTTATCAACATTATTC
```

Type material. Holotype: ♂ currently in the research collection of Jim P. Brock (Tucson, AZ, USA), to be deposited in the McGuire Center for Lepidoptera and Biodiversity collection, Gainesville, FL, USA (MGCL), illustrated in Fig. 108d, bears the following three printed rectangular labels, two white: [PERU, CU, Cosñipata | Quebrada Quitacalzón, | km 81, 2 Nov 2017 | leg. JP Brock], [DNA sample ID: | NVG-25022G08 | c/o Nick V. Grishin], and one red [HOLOTYPE ♂ | *Mucia castanuza* | Grishin].

Type locality. Peru: Cuzco Region, Cosñipata Valley, Quebrada Quitacalzón, km 81, elevation ca. 1050 m.

Etymology. The name of the new species is derived from *M. castana* and refers to its occurrence in the Cuzco region. It is treated as a noun in apposition.

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

Alerema uniplex Grishin, new species

<https://zoobank.org/E7B84519-7BA2-4D1A-A273-6DE7C8F825E9>

(Figs. 110 part, 111c)

Definition and diagnosis. Genomic phylogeny (Fig. 110) reveals that a male from Bolivia initially identified as *Alerema simplex* (Bell, 1930) (type locality in Brazil: Santa Catarina) (Fig. 111b) is genetically differentiated from both it and its sister *Alerema complex* Grishin, 2025 (type locality in USA: Texas) (Fig. 111a) at the species level; e.g., its COI barcode differs by 5.3% (35 bp) from *A. simplex* and 5.8% (38 bp) from *A. complex*, and therefore this male represents a new species. This new species keys to

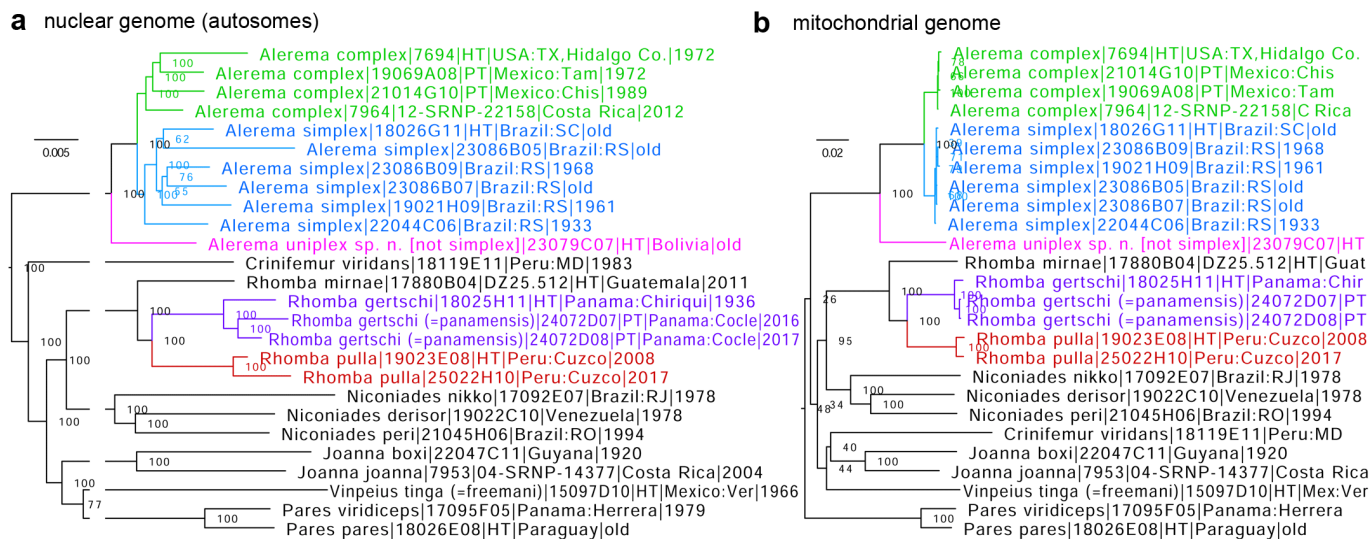


Fig. 110. Phylogenetic trees of the clade containing *Niconiades* Hübner, [1821] and relatives (only selected species are shown in some genera) constructed from protein-coding regions in: **a)** the nuclear genome (autosomes), based on 1,394,616 positions, and **b)** the mitochondrial genome: *Alerema complex* (green), *Alerema simplex* (blue), *Alerema uniplex* sp. n. (magenta), *Rhomba gertschi* (E. Bell, 1937) (violet, with paratypes of *Psoralis panamensis* Anderson & Nakamura, 2019), and *Rhomba pulla* (red). Ultrafast bootstrap (Hoang et al. 2018) values are shown at nodes. Gaps in branches indicate where a vertical slice of the tree was removed to reduce its horizontal dimension (allowing an increase in font size), i.e., branches with gaps are longer than shown.

“*Tigasis simplex*” (J.44.8) in Evans (1955), but differs from it and other relatives by the following combination of characters in males: rounder wings; a large oval paler patch occupying about a fifth of the ventral hindwing instead of a pale discal cell spot and a row of postdiscal spots with a darker ground color in between them; a ventral hindwing area distad of vein 1A+2A that is paler and the same color as the patch; gray, not yellowish, cheeks (i.e., scaled areas ventrad of the eyes); and a more robust brand, especially the oval segment near the base of cell CuA₁-CuA₂. Due to its cryptic nature and unexplored individual variation, this species is best identified by DNA, with diagnostic base pairs in the nuclear genome: aly997.12.1:C765T, aly997.12.1:C777T, aly3215.4.4:C63T, aly2976.10.1:C408T, aly2976.10.1:C420T, aly5719.4.21:C87C (not T), aly1222.19.36:C75C (not T), aly2012.43.17:T96T (not C), aly577.15.3:G45G (not C), aly208.58.35:A24A (not G); and the COI barcode: T97C, T250C, T445C, G506G, A529A, T610C.

Barcode sequence of the holotype. Sample NVG-23079C07, GenBank [PZ516445](https://www.ncbi.nlm.nih.gov/nuccore/PZ516445), 658 base pairs:

```
AACTTTATACTTTATTTTGAATTTGAGCAGGAATATTAGGAACCTCTCTTAGATTACTAATTCGTACAGAATTGGGAAATCCAGGATCTTTAATCGGAGATGACCAAAATTTATAATACT
ATTGTAACAGCTCATGCTTTTCATTATAATTTTTTTATAGTAATACCTATTATAATTTGGAGGATTTGGAAATGATTAGTAGTACCTTTAATATTAGGAGCTCCTGATATAGCTTTTCCACGAA
TAAATAACATAAGATTTTGAATATTACCTCCTTCATTAATACTTTTAAATTTCAAGAAGAATTGTAGAAAATGGTGCTGGAACCTGGTTGAACAGTTTATCTCTCTTTATCATCAAAATATCGC
TCATCAAGGTTTCATCTGTTGATTTAGCAATTTTCTCTTCACCTAGCAGGAATCTCATCAATTTAGGAGCTATTAAATTTCTTACTACTACAATTTAATATACGAATTAATAATCTATCA
TTTGATCAAAATACCTTTATTGTTGATCTGTAGGTATTACAGCATTATTACTTTTATCTCTCCCGTATTAGCAGGAGCTATTACCATACTTTTAAACAGATCGAAATTTAAATCTT
CATTTCTTTGACCCAGCTGGAGGAGGAGATCCAATTTTATACCAACATTTATTT
```

Type material. Holotype: ♂ deposited in the Museum für Naturkunde, Berlin, Germany (MFNB), illustrated in Fig. 111c, bears the following five rectangular labels (2nd handwritten, others printed), four white: [Corvico | Bol. | Garl.], [Stgr.], [Coll. | Staudinger], [DNA sample ID: | NVG-23079C07 | c/o Nick V. Grishin], and one red [HOLOTYPE ♂ | Alerema | uniplex Grishin]. The second label is in Staudinger’s handwriting, and the upper part of the text is cut off.

Type locality. Bolivia: La Paz Department, Coroico.

Etymology. The name is formed similarly to its congeners to reflect the presence of a single (*uni-*) patch on the ventral hindwing instead of several smaller spots in other species. The name is treated as a noun in apposition.

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

Remarks. Although this new species is geographically closer to *A. simplex* than *A. simplex* is to *A. complex*, it is more genetically differentiated from both of them than they are from each other.

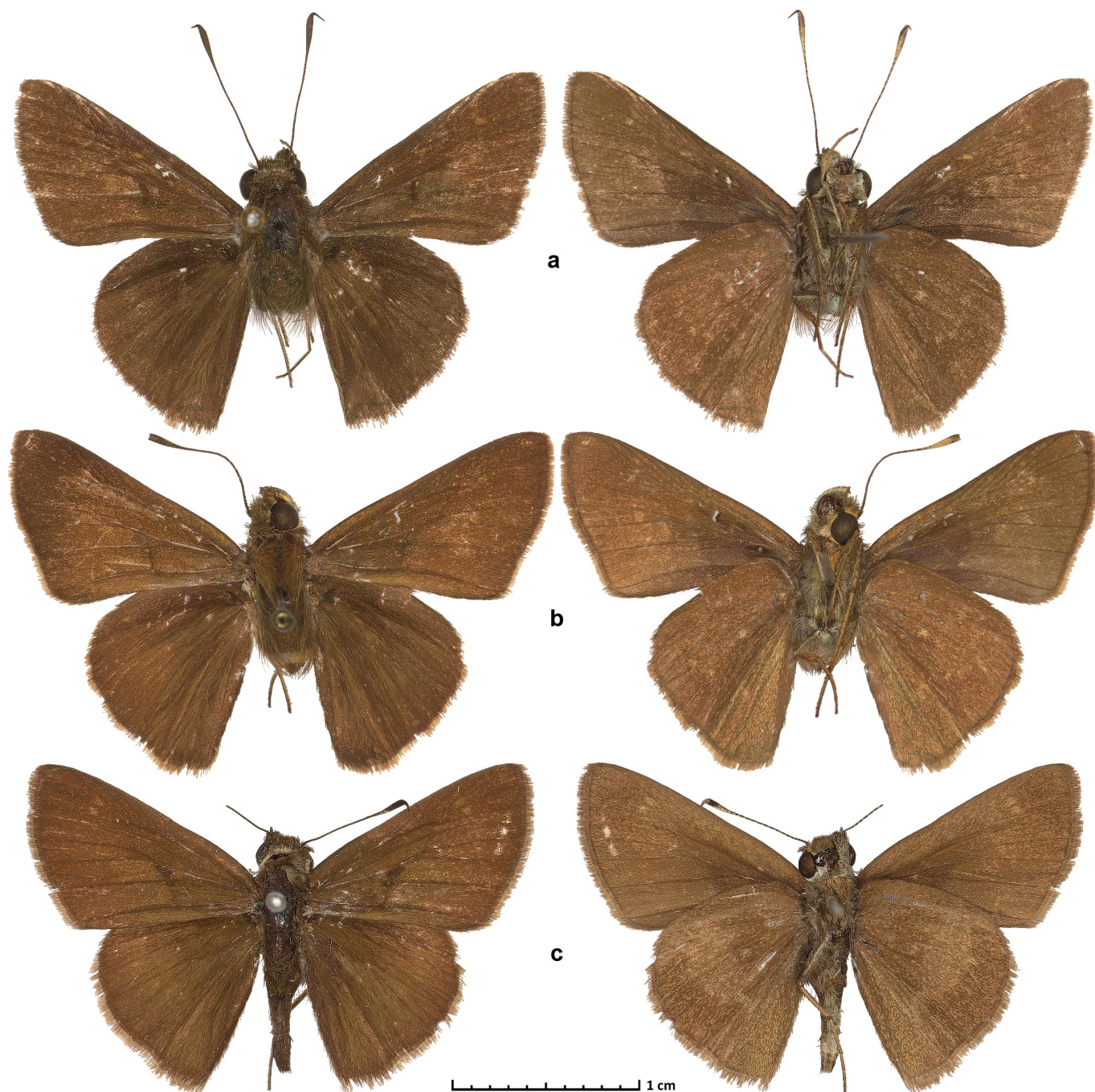


Fig. 111. Males of all described species of *Alerema* in dorsal (left) and ventral (right) views: **a)** *A. complex* paratype NVG-21014G10 Mexico: Chiapas, 3 mi S of Simojovel, 3000', 5-Sep-1989, J. Kemner leg., genitalia H-939 by H. A. Freeman [CMNH]; **b)** *A. simplex* non-type NVG-22044C06 Brazil: Rio Grande do Sul, Guarani, 2-Jan-1933, C. M. de Biezanko leg., genitalia #1 slide 12-II-537 SK [CUIC]; and **c)** *A. uniplex* **sp. n.** holotype NVG-23079C07 Bolivia: La Paz Department, Coroico, old, Staudinger colln. [MFNB].

Individual variation in *Rhomba pulla* Grishin, 2023

Genomic analysis confirms the identity of a second specimen of *Rhomba pulla* Grishin, 2023 (type locality in Peru: Cuzco), which was described from a single male (Fig. 110). Both specimens are illustrated here (Fig. 112). The two males are similar in their wing shape, the structure of the brand, and their dark coloration; however, the second male has a rounded semihyaline spot near the base of the forewing cell M_3-CuA_1 and a dot near the base of the forewing cell R_5-M_1 . In the holotype, the spot is present only as a small patch of pale scales on the ventral side of the wing, and the dot is absent. On the

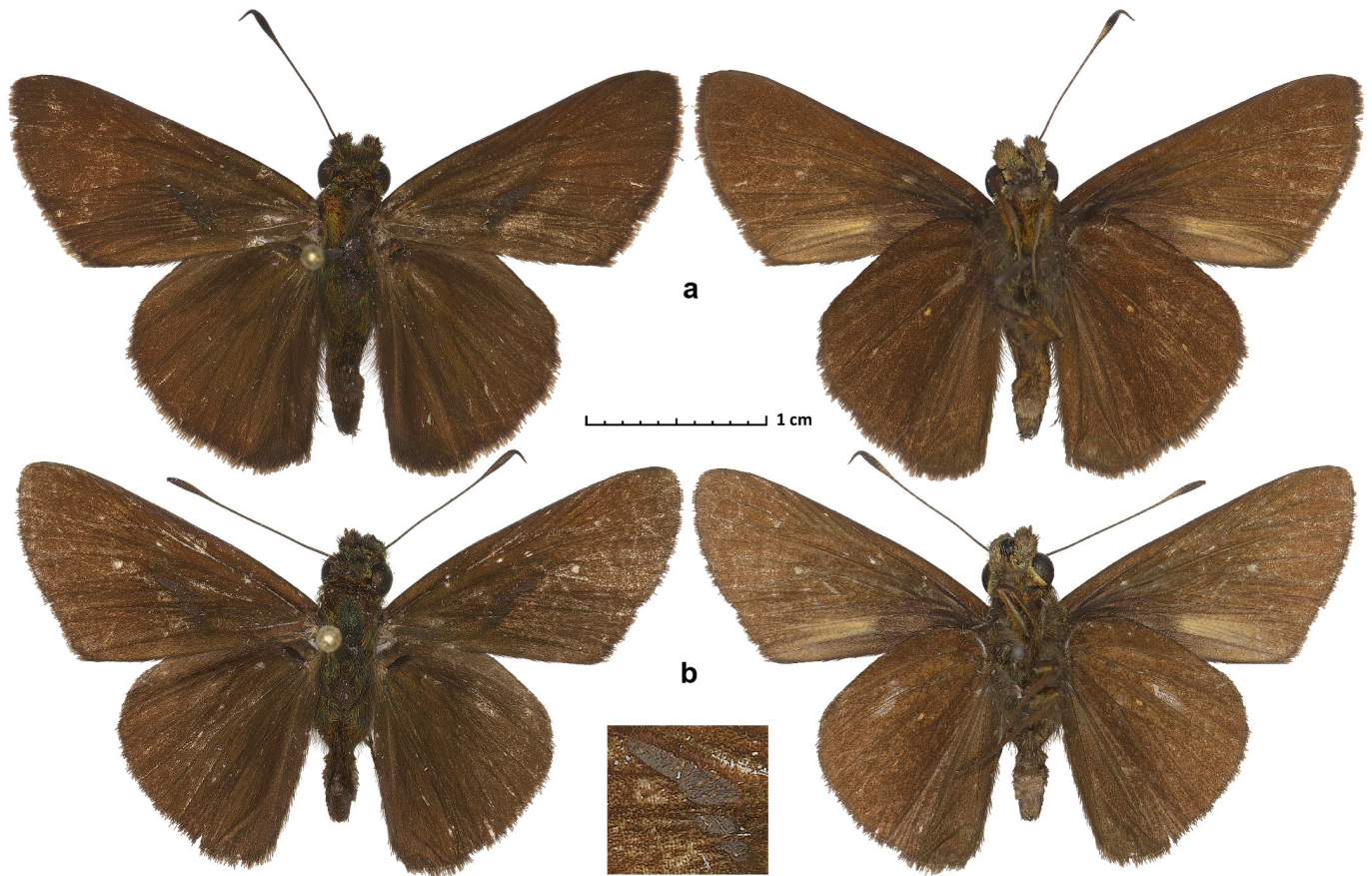


Fig. 112. Males of *Rhomba pulla* from Peru: Cuzco Region, Cosñipata Road in dorsal (left) and ventral (right) views: **a)** holotype NVG-19023E08 San Pedro Lodge, 1450 m, 9-Nov-2008, S. Kinyon leg. [USNM] and **b)** non-type NVG-25022H10 Quebrada Quitacalzón, km 81, 2-Nov-2017, J. P. Brock leg. [JPBC]; the inset shows a magnified and digitally enhanced image of the left forewing brand.

ventral hindwing, both specimens have a yellowish elliptical spot near the end of the discal cell; the holotype has a smaller elongated postdiscal spot in cell M_1 - M_2 , and the second male has a vestigial, narrow postdiscal spot consisting of a few yellow scales in cell M_3 - CuA_1 , suggesting that some specimens of this species may develop a postdiscal row of small yellowish spots.

Racta racteca Grishin, new species

<https://zoobank.org/1C42986E-A34C-4F22-96CC-F3D94D841948>

(Figs. 113 part, 114a–b)

Definition and diagnosis. Genomic analysis of *Racta* Evans, 1955 (type species *Racta racta* Evans, 1955) reveals that specimens identified as *Racta racta* Evans, 1955 (type locality Peru: Puno, Urohuasi;

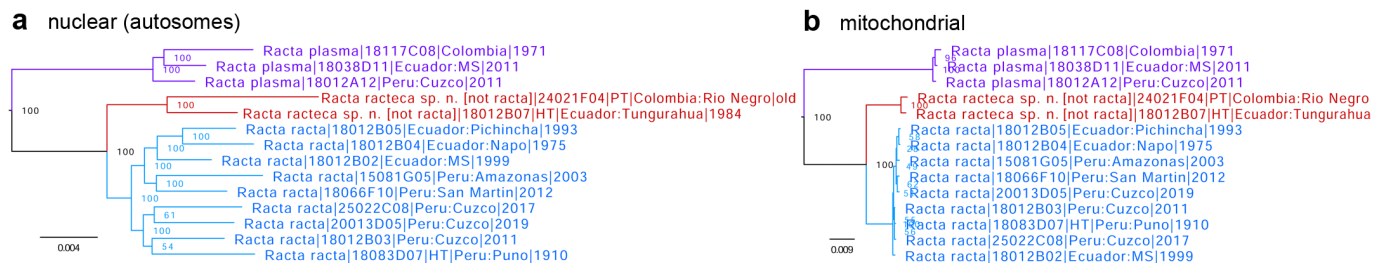


Fig. 113. Phylogenetic trees of a clade of *Racta* species constructed from protein-coding regions in: **a)** the nuclear genome (autosomes), based on 2,043,810 positions, and **b)** the mitochondrial genome: *R. plasma* Evans, 1955 (violet), *R. racteca* sp. n. (red), and *R. racta* (blue). Ultrafast bootstrap (Hoang et al. 2018) values are shown at nodes.



Fig. 114. Females of *Racta* in dorsal (left) and ventral (right) views: **a–b)** *R. racteca* **sp. n.** type series: **a)** holotype NVG-18012B07, USNMENT_01450272 Ecuador, Tungurahua, Río Negro, 1500 m, 10-Nov-1984, S. S. Nicolay leg. [USNM] and **b)** paratype NVG-24021F04 Colombia: Upper Río Negro [Meta, nr. Villavicencio], old, Fassl leg. [SMF]; and **c–d)** *R. racta* non-types: **c)** NVG-18012B02, USNMENT_01450267 Ecuador: Morona-Santiago, Nueve de Octubre, 1800 m, 10-Sep-1999, GPS -2.217, -78.217, Robbins, Busby, Estevez, and Aldas leg. [USNM] and **d)** NVG-20013D05, WRD 17110 Peru: Cuzco, Cosñipata Valley, Rocotal, ca. 2000 m, GPS -13.100, -71.567, 17-Jun-2019, W. R. Dempwolf leg. [WRDC].

holotype NHMUK_012824210 sequenced as molecular sample NHMUK_0247279216, internally processed as NVG-18083D07) partition into two clades genetically differentiated at the species level in the nuclear genome (Fig. 113), and their COI barcodes differ by 1.4% (9 bp). The clade containing the holotype corresponds to *R. racta* and includes specimens ranging from northern Ecuador to southeastern Peru. The second clade consists of two females collected in the eastern Andean foothills in Colombia and Ecuador and represents a new species. This new species is expected to key to *Racta racta* (I.14.3) in Evans (1955) and was probably included by him in this species, but differs from it and other relatives by having females that are similar to males in wing pattern: a brown dorsal side of the wings with an orange band from near the apex towards the middle of the inner margin on both wings; an orange spot in the forewing discal cell that is separated from the band; an orange spot in the forewing cell M₂-M₃ that is shorter than the spot in cell M₃-CuA₁ [typically longer at least in *Racta apella apella* (Schaus, 1913) (type locality in Costa Rica)]; and a broader postdiscal band of pale spots on the ventral hindwing. All females of *R. racta* are, in contrast, dark (Fig. 114c, d), without a band on the dorsal hindwing and with a broad orange forewing band from the discal cell towards the tornus (plus some orange subapical spots); the discal cell bar is connected to the other spots of the band; and the ventral hindwing postdiscal band is narrower or vestigial. Due to poorly explored individual variation, possible dimorphism in females, and males being unknown, this species is best identified by DNA, with diagnostic base pairs in the nuclear genome: aly506.6.6:C156T, aly2976.15.10:A45C, aly84.42.4:A189G, aly1651.22.5:A114G, aly991.2.1:G84A; and the COI barcode: C38C, T118C, T499A, T613C, T634T.

Barcode sequence of the holotype. Sample NVG-18012B07, GenBank [PZ516446](#), 658 base pairs:

```
AACTTTATATTTTATTTTGGTATTTGAGCAGGATTACTTGGAACCTTCATTAAGATTACTAATTCGAACAGAATTAGGTACCCCGGATCTTTAATTGGAGATGACCAAATTTATAACACT
ATCGTAACAGCTCATGCTTTTATTATAATTTTATAGTTATACCAATTATAATTTGGAGGATTTGGAAATTGATTAGTTCCTTTAATATTAGGAGCACCTGATATAGCTTTCCACGAA
TAAATAATATAAGATTTTGAATATTACCTCCATCATTAAACATTATTAATTTCAAGAAGTATTGTAGAAAATGGTGCAGGTACAGGATGAACAGTTTATCCTCCTCTTTCATCTAATATTGC
TCATCAAGGTTCTCTGTAGATTAGCAATTTTCTTTACATTAGCAGGAATTTCTTCTATTTAGGAGCAATTAATTTTATTACTACAATTATTAATATACGAGTTAGAAATTTATCA
TTTGATCAAATACCATTTATTTGTATGATCAGTAGGAATTACAGCTTTTATTACTTTTATCTTTACCTGTATTAGCAGGAGCTATTACTATACTTTTAAACAGATCGAAATTTAAATACTT
CTTTTTTCGATCCAGCAGGAGGAGGAGATCCAATTTTATACCAACATTTATTT
```

Type material. Holotype: ♀ deposited in the National Museum of Natural History, Smithsonian Institution, Washington, DC, USA (USNM), illustrated in Fig. 114a, bears the following five printed rectangular labels (text in *italics* handwritten), four white: [ECUADOR Tung. | Rio Negro 1500m | 10 Nov. 84 | S. S. Nicolay], [*Racta* ♀ | *racta* | Det. | S.S. Nicolay], [DNA sample ID: | NVG-18012B07 | c/o Nick V. Grishin], [USNMMENT | {QR Code} | 01450272], and one red [HOLOTYPE ♀ | *Racta racteca* | Grishin]. **Paratype:** 1♀ NVG-24021F04 Colombia, Upper Rio Negro [Meta, nr. Villavicencio], 800 m, old, Fassl leg. [SMF] (Fig. 114b). According to one of its labels, the dorsal side of the paratype is illustrated on Plate 188, row c, the third image in Draudt (1921–1924), misidentified as a female of *Molo humeralis* Mabille, 1878, which is currently regarded as a junior subjective synonym of *Molo mango* (Guenée, 1865) (type locality in America, incorrectly stated as Madagascar). The illustration appears remarkably accurate.

Type locality. Ecuador: Tungurahua Province, Río Negro, 1500 m.

Etymology. The name is a modified fusion that reflects the phylogenetic affinity and the type locality of this species: *ract*[a] + *Ec*[u]a[dor], and is treated as a noun in apposition.

Distribution. Currently known from the eastern foothills of the Andes in Colombia and Ecuador.

Remarks. Females of *R. racta* are often misidentified as a species of *Molo* Godman, 1900 (type species *Hesperia heraea* Hewitson, 1868, currently a junior subjective synonym of *Hesperia mango* Guenée, 1865), while females of the new species are misidentified as *R. racta*. Whether both species exhibit female dimorphism (dark, *racta*-like vs. similar to males, *racteca*-like) remains unknown, and if they do, DNA-based identification is required to learn about this variation.

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