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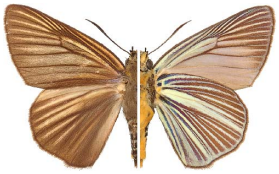

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New butterfly taxa and findings from genomic analyses

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ABSTRACT. Continuing our genomics-driven exploration of butterfly taxonomy, we integrate phylogenetic trees from all protein-coding genes with existing taxonomic and phenotypic knowledge and uncover further insights into butterfly systematics. As a result, one subgenus, 44 species, and 11 subspecies are proposed as new (type species in original combinations or type localities are listed in parentheses): *Porphaurea* Grishin, **subgen. n.** (*Phoenicops porphyropis* Meyrick & Lower, 1902) of *Chaetocneme* C. Felder, 1860 in Hesperiidae Latreille, 1809; *Dione* (*Agraulis*) *lamasi* Grishin, **sp. n.** (Peru: Cuzco) in Nymphalidae Rafinesque, 1815; *Lasaia* (*Lasaia*) *chiapis* Grishin, **sp. n.** (Mexico: Chiapas), *Lasaia* (*Lasaia*) *occalla* Grishin, **sp. n.** (Mexico: Oaxaca), *Lasaia* (*Lochris*) *oilenor* Grishin, **sp. n.** (Belize), *Lasaia* (*Lochris*) *oilepanor* Grishin, **sp. n.** (Panama: Colón), *Lasaia* (*Lochris*) *oilemarca* Grishin, **sp. n.** (Peru: Cajamarca), and *Emesis* (*Tenedia*) *peripore* Grishin, **sp. n.** (Trinidad) in Riodinidae Grote, 1895 (1827); and *Burara danata* Grishin, **sp. n.** (China: central Fujian), *Burara lawana* Grishin, **sp. n.** (Philippines: Palawan), *Bungalotis quadra* Grishin, **sp. n.** (Panama: Chiriquí), *Bungalotis barbalotis* Grishin, **sp. n.** (Peru: Loreto), *Cecropterus* (*Murgaria*) *eryssus* Grishin, **sp. n.** (Ecuador: Sucumbíos), *Cephise panuspe* Grishin, **sp. n.** (Panama: Panamá), *Noctuana haematoesta* Grishin, **sp. n.** (Colombia: Valle del Cauca), *Noctuana statonama* Grishin, **sp. n.** (Panama: Chiriquí), *Diaeus piura* Grishin, **sp. n.** (Peru: Piura), *Zopyrion* (*Zopyrion*) *cruise* Grishin, **sp. n.** (Mexico: Veracruz), *Chaetocneme triuna* Grishin, **sp. n.** (Papua New Guinea: Oro), *Chaetocneme brazza* Grishin, **sp. n.** (Indonesia: West Papua), *Ge pina* Grishin, **sp. n.** (Philippines: Mindanao), *Parnara guda* Grishin, **sp. n.** (India: West Bengal), *Parnara sulawesa* Grishin, **sp. n.** (Indonesia: South Sulawesi), *Tisias panamyna* Grishin, **sp. n.** (Panama: Panamá), *Xeniades* (*Tixe*) *lora* Grishin, **sp. n.** (Peru: Loreto), *Oligoria* (*Oligoria*) *costaria* Grishin, **sp. n.** (Costa Rica: Alajuela), *Oligoria* (*Oligoria*) *bahia* Grishin, **sp. n.** (Brazil: Bahia), *Alychna ventanilla* Grishin, **sp. n.** (Ecuador: Napo), *Thoon cuadius* Grishin, **sp. n.** (Ecuador: Napo), *Viridina viridella* Grishin, **sp. n.** (Peru: Cuzco), *Tricrista lingulata* Grishin, **sp. n.** (Brazil: Rondônia), *Tricrista taxolla* Grishin, **sp. n.** (Peru: Madre de Dios), *Vettius fuscapicalis* Grishin, **sp. n.** (Ecuador: Napo), *Mnasitheus oaxaceus* Grishin, **sp. n.** (Mexico: Oaxaca), *Tarmia bolivia* Grishin, **sp. n.** (Bolivia: La Paz), *Artines tines* Grishin, **sp. n.** (French Guiana), *Calpodes salma* Grishin, **sp. n.** (Panama: Colón), *Calpodes anabara* Grishin, **sp. n.** (Brazil: Rio de Janeiro), *Talides megamaca* Grishin, **sp. n.** (Mexico: Veracruz), *Perichares guatine* Grishin, **sp. n.** (Guatemala), *Perichares solamancha* Grishin, **sp. n.** (Peru: Cuzco), *Perichares indivisa* Grishin, **sp. n.** (Bolivia: La Paz), *Perichares amaletes* Grishin, **sp. n.** (Peru: Madre de Dios), *Perichares aura* Grishin, **sp. n.** (Peru: Cuzco), *Lycas gabriel* Grishin, **sp. n.** (Peru: Madre de Dios). *Burara danata himavata* Grishin, **ssp. n.** (Nepal), *Burara gomata burmana* Grishin, **ssp. n.** (Myanmar: Sagaing Region), *Burara gomata namata* Grishin, **ssp. n.** (China: Hong Kong), *Burara lorquini vichitra* Grishin, **ssp. n.** (unknown, likely in or around the Philippines), *Cecropterus* (*Murgaria*) *chales estales* Grishin, **ssp. n.** (USA: Texas, Starr Co.), *Pholisora mejicanus yuesanus* Grishin, **ssp. n.** (USA: Colorado, El Paso Co.), *Celotes sabinus verdinus* Grishin, **ssp. n.** (USA: Arizona, Yavapai Co.), *Ephyriades brunnea sansalva* Grishin, **ssp. n.** (Bahamas: San Salvador Island), *Ephyriades brunnea turcaica* Grishin, **ssp. n.** (Turks & Caicos Islands), *Ephyriades arcas norleewa* Grishin, **ssp. n.** (Anguilla), and *Calpodes hewitsoni supernalis* Grishin, **ssp. n.** (Mexico: Chiapas) in Hesperiidae. *Metron fas* Grishin, **nom. nov.** (Costa Rica: Heredia) is proposed as a new substitute name that replaces *Metron fascia* Grishin, 2025 preoccupied by *Metron fascia* Draudt, 1923. The following are valid species or subspecies (not subspecies or synonyms of taxa listed in parentheses): *Burara lara* (Leech, 1893), **stat. nov.**, *Burara vajra* (Fruhstorfer, 1911), **stat. nov.**, *Burara lorquini* (Mabille, 1876), **stat. rest.**, and *Burara radiosa* (Plötz, 1885), **stat. rest**. (not *Burara gomata* (Moore, [1866])), *Cecropterus* (*Murgaria*) *chales* (Godman & Salvin, 1893), **stat. rest.** (not *Cecropterus* (*Murgaria*) *doryssus* (Swainson, 1831)), *Noctuana bipuncta* (Plötz, 1884), **stat. rest.** (not *Noctuana lactifera* (Butler & H. Druce, 1872)), *Zopyrion* (*Timochreon*) *forta* (Evans, 1953), **stat. nov.** and *Zopyrion* (*Timochreon*) *tampa* (Evans, 1953), **stat. nov.** (not *Zopyrion* (*Timochreon*) *satyrus* (C. Felder & R. Felder, 1867)), *Parnara mangala* (F. Moore, 1866), **stat. rev.** (not *Parnara guttatus* (Bremer & Grey, [1852])), *Parnara philotas* (de Nicéville, 1895), **stat. rest.**, *Parnara daendeli* (Plötz, 1885), **stat. rest.**, and

Parnara bada nondoa (Plötz, 1886), **stat. nov.** (not *Parnara bada bada* (F. Moore, 1878)), *Xeniades corna* Evans, 1955, **stat. nov.** (not *Xeniades* (*Xeniades*) *chalestra* (Hewitson, 1866)), *Oligoria* (*Oligoria*) *pindar* (Schaus, 1913), **stat. rest.** (not *Oligoria* (*Oligoria*) *lucifer* (Hübner, [1829]), *Perichares crotona* (Hewitson, 1866), **stat. rest.** (not *Perichares seneca* (Latreille, [1824])), *Perichares fulvimargo* (Butler, 1873), **stat. rest.** and *Perichares luscinia* (Plötz, 1882), **stat. rest.** (not *Perichares deceptus* (Butler & H. Druce, 1872), *Perichares philetes trinitad* (Lucas, 1857), **stat. rev.** (not *Perichares philetes philetes* (Gmelin, [1790])), and *Lycas boisduvalii* (Ehrmann, 1909), **stat. rest.** (not *Lycas godart* (Latreille, [1824])). The following are new species-subspecies combination: *Burara lorquini minda* Chiba & Tsukiyama, 2009 (not *Burara gomata* (Moore, [1866])) and *Parnara mangala ormuzd* (Grum-Grshimailo, 1888) (not *Parnara guttatus* (Bremer & Grey, [1852])). The following are new synonyms: *Parnara guttatus batta* Evans, 1949, **syn. nov.** of *Parnara mangala* (F. Moore, 1866), **stat. rev.** and *Parnara kuwanoi* Seok, 1937, **syn. nov.** of *Pelopidas sinensis* (Mabille, 1877); and a new synonym placement, *Eudamus electra* Lintner, 1881, under *Ephyriades brunnea floridensis* E. Bell & W. P. Comstock, 1948, not *Ephyriades brunnea brunnea* (Herrich-Schäffer, 1865). Furthermore, we discuss and illustrate the following particulars: wing pattern differences between *Cercyonis silvestris* (W. H. Edwards, 1861) and *Cercyonis sthenele* (Boisduval, 1852) in the Sierra–Cascade ranges of California, USA; *Dione* (*Agraulis*) *galapagensis* (W. Holland, 1890) as a species-level taxon confirmed by genomic sequencing; female paratypes of recently described Hesperiidae species with strong sexual dimorphism not shown in the original descriptions; the third male of *Cecropterus* (*Thorybes*) *viridissimus* Grishin, 2023; all sequenced specimens of *Urbanus* (*Urbanus*) *viterboana* (Ehrmann, 1907) establishing this species as sister to *Urbanus* (*Urbanus*) *dubius* Steinhauser, 1981; *Windia sonoria* Grishin, 2025, and not *Windia windi* Freeman, 1969, recorded from the USA (Arizona, Cochise Co.); *Zopyrion* (*Zopyrion*) *xerxes* Grishin, 2025 as a species-level taxon confirmed by sequencing of additional specimens extending its range from Honduras to include El Salvador, Nicaragua, and Costa Rica; a second specimen of *Gorgythion cerrada* Grishin, 2025; a possible paralectotype of *Antigonus ruptifasciata* Plötz, 1884, also from Jamaica as deduced by genomic comparison; the holotype of *Pamphila philino* Möschler, 1879; a female of *Oligoria* (*Cobaloides*) *unica* (de Jong, 1983) from French Guiana; and a male of *Lychnuchus* (*Enosis*) *valle* Grishin, 2023 from Ecuador. We provide an updated list of the subtribe Euremina Grote, 1898 that comprises five genera (rather than one) and five additional subgenera. Finally, lectotypes are designated for eight taxa: *Helias haematospila* C. Felder & R. Felder, 1867 (Venezuela), *Tagiades editus* Plötz, 1885 (Indonesia: Maluku Province, Dobo), *Hesperia kolantus* Plötz, 1885 (India), *Hesperia daendeli* Plötz, 1885 (Indonesia: West Java, Jakarta), *Celaenorhinus* [sic] *lucifer* Hübner, [1829] (Suriname), *Cobalus pindar* Schaus, 1913 (Costa Rica: Limón), *Proteides hyas* Mabille, 1891 (Colombia: Valle del Cauca), and *Hesperia luscinia* Plötz, 1882 (Brazil: Santa Catarina, Blumenau), and a neotype is designated for *Thymele triton* Boisduval, 1832 (Papua New Guinea: northern half). The lectotype designation and phenotypic analysis indicate that the correct name for the South Texas species of *Oligoria* (*Oligoria*) Scudder, 1872 is *O.* (*O.*) *pindar* **stat. rest.**, and that *O.* (*O.*) *percosius* (Godman, 1900) should consequently be excluded from the U.S. fauna.

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

ZooBank registration: https://zoobank.org/5697F218-4587-4855-A40F-AE65BA978FF8

INTRODUCTION, CONCEPTS, AND METHODS

This work is a direct continuation of our earlier studies, incorporating additional specimens sequenced with the same methodologies and analyzed within the same conceptual framework (Cong et al. 2019a, b; Li et al. 2019; Zhang et al. 2019a–d; Cong et al. 2020; Zhang et al. 2020; Cong et al. 2021; Zhang et al. 2021; Robbins et al. 2022; Zhang et al. 2022b, d, 2023c–e, 2024a–c, 2025a–d). The objective of this study is to detect new species and subspecies of butterflies through genomic analysis. To accomplish this, we investigate a wide diversity of butterfly groups from across the globe. The specimens analyzed originate mainly from museum and private collections (see Acknowledgments for specific sources) and range in age from recently collected individuals to those preserved for several centuries. Whenever feasible, DNA is extracted from primary type specimens to provide an objective genomic reference for species names (Cong et al. 2021; Zhang et al. 2022a). Extraction is typically performed from a leg using a non-destructive method that preserves its structure, allowing subsequent morphological examination. For specimens whose DNA is not already degraded due to age, the DNA is fragmented prior to library construction. Sequencing is carried out on the Illumina next-generation platform, generating 150-base pair (bp) reads. The procedure does not rely on targeted gene or fragment amplification; instead, it sequences all recovered DNA fragments. Consequently, the method is equally suitable for old specimens with highly fragmented DNA, often around 30–50 bp in length.

For each specimen, we use all sequencing reads, not only complete 150 bp, but also shorter ones, to reconstruct exons of protein-coding genes. Assembly is guided by a reference genome of a closely related species for which a high quality complete genomic assembly is available. The reconstructed genes serve as the basis for phylogenetic inference. We generate three phylogenetic trees with IQ-TREE v1.6.12 using the GTR+GAMMA model (Nguyen et al. 2015): one based on the autosomal (nuclear) genome, another on genes inferred to be located on the Z chromosome, and a third from mitochondrial DNA. We include all well-covered codons for each specimen in the alignment that is generated "on the fly" and not stored, and the number of positions used in each nuclear genome tree is indicated in the figure legends, ranging from hundreds of thousands to several million. All mitogenomes are approximately 15,000 base pairs. We calculate ultrafast bootstrap as statistical support: values above 97% are considered reliable and below 90% the support is weak leaving the relationship uncertain (Hoang et al. 2018). Additional methodological details are provided in our previous studies (Li et al. 2019; Zhang et al. 2022b).

Phylogenetic trees are visualized, colored, and rearranged in FigTree (Rambaut 2018). Existing taxonomic classifications are mapped onto these trees to identify non-monophyletic taxa and to detect clades corresponding to previously unrecognized groups. Genome-wide trees often exhibit "levels"—evolutionary junctures where several lineages diversified simultaneously (Zhang et al. 2021). Such synchronous radiations are frequently linked to geological or climatic events that influenced multiple butterfly groups in parallel. These patterns offer a framework for aligning taxonomic ranks (tribe, subtribe, genus, subgenus) with the diversification levels revealed by genomic data. This strategy fosters a classification system that is both evolutionarily meaningful and internally consistent, grounded in genetic divergence and supported by paleontological context. Consistent application of these principles would contribute to greater taxonomic stability going forward. Our classification decisions are primarily guided by genomic phylogenies, with morphology serving as supporting evidence. This emphasis reflects the broader informational scope of genomes encompassing not only traits expressed in adult morphology that is the traditional foundation of butterfly taxonomy, but also signatures of life history, ecology, reproduction, and diet. Although phenotypes cannot yet be directly predicted from genomic sequences, aggregated protein-coding DNA data provide reliable genetic proxies, and robustly inferred phylogenies guide classification. Together, these elements enable a taxonomic framework consistent with both evolutionary relationships and genomic evidence.

In this study, our main emphasis is at the species and subspecies levels. Species boundaries are delineated using multiple criteria: differentiation in the Z chromosome with F_{st} values above 0.20 (typically marking species-level separation), G_{min} values below 0.05 (indicating limited gene flow) (Cong et al. 2019a), divergence in COI barcode sequences exceeding roughly 2% (Hebert et al. 2003) and their correlation with phenotypic distinction (Lukhtanov et al. 2016), and the existence of distinct, well-supported clades in phylogenetic trees (Zhang et al. 2022d). We keep in mind that mitochondrial markers such as COI frequently introgress between species (Bachtrog et al. 2006; Cong et al. 2017a), so some distinct species may share identical barcodes (Burns et al. 2008; Zhang et al. 2023b). Further explanations are provided by Zhang et al. (2022a), in the section "Species, subspecies, and genomics."

Conventionally, subspecies are defined as geographically distinct populations exhibiting consistent phenotypic differences (for example, when about 70% of individuals can be recognized by appearance alone, independent of locality) while remaining potentially interbreeding (Mayr 1982; Monroe 1982). In practice, reproductive compatibility is difficult to confirm, and in butterflies, subspecies are most often diagnosed solely by wing pattern differences. It is rarely evident whether these differences have a genetic basis or are environmentally influenced. Genomic analysis enables direct comparison of populations at the genetic level. In this study, we describe new subspecies corresponding to genomic clades, i.e., distinct groups visible in at least one of the phylogenetic trees, that are genetically differentiated and strongly supported (~100% bootstrap) but not sufficiently divergent to constitute separate species. Such subspecies represent initial stages of speciation: populations undergoing early differentiation that might not yet have achieved significant reproductive isolation. After identifying these clades, we examine wing patterns to determine diagnostic phenotypic features. As expected for

subspecies, these features are statistical in nature and exhibit variation. Because our subspecies definitions are based on genomic clades, the DNA characters supporting them are more reliable than morphological traits and apply to nearly all specimens. Accordingly, DNA-based diagnoses are provided for every new subspecies described herein.

The taxa in this work are ordered by the genome-wide phylogeny supplemented with morphological consideration. For all newly proposed taxa, we supply concise descriptions of diagnostic morphological traits that are often accompanied by references that provide identification keys, detailed accounts, and illustrations, alongside diagnostic DNA characters from the nuclear genome and, where possible, from the COI barcode. These DNA characters, derived from protein-coding regions, were identified using our established protocol (see SI Appendix in Li et al. (2019)). The procedure for selecting robust characters, detailed in Cong et al. (2019b), is designed to yield diagnostic characters that are expected to remain valid as additional specimens and species are incorporated into genomic datasets.

DNA character states are given for one of the three reference genomes: *Heliconius melpomene* (Linnaeus, 1758) (hm) (Davey et al. 2016), *Calephelis nemesis* (W. H. Edwards, 1871) (cne) (Cong et al. 2017b), or *Cecropterus lyciades* (Geyer, 1832) (aly, because this species was formerly in the genus *Achalarus* Scudder, 1872) (Shen et al. 2017). 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/sra4p >. By linking to this file, we ensure that the characters used in diagnoses can be traced to their actual sequences. Links to iNaturalist (2025) observations by observation number reported in figure legends are < https://www.inaturalist.org/observations/xxx >, where xxx is the number.

Whole genome shotgun datasets we obtained and used in this study are available from the NCBI database < https://www.ncbi.nlm.nih.gov/ > under BioProject PRJNA1356542. Associated BioSample records include locality data and other collection information for all specimens sequenced by us and shown in the trees. Tree figures list the following information for each specimen, separated by "|": taxon name with comments in square brackets, DNA sample code, type status, general locality, and year of collection ("old" if not dated and likely collected 100–150 years ago). Type status abbreviations are: HT holotype, LT lectotype, ST syntype, NT neotype, T type (could be ST, LT, paralectotype, or HT, status not investigated), PT paratype, AT allotype, PLT paralectotype, TT topotype (not a true type, but a specimen from the general area of the type locality of a taxon); and if a synonym name is given (in parentheses, preceded by "=", and in addition by "‡" for unavailable names), type status refers to the synonym. COI barcode sequences reported here will be deposited in GenBank once the U.S. government shutdown ends and NCBI services resume; accessions will be published as an update to this work. Abbreviations or acronyms for collections are listed in Acknowledgments.

Family Pieridae Swainson, 1820

The subtribe Euremina Grote, 1898 comprises five genera (not one) and five additional subgenera

Large-scale DNA analyses have provided unprecedented insights into the classification of life forms, including the family Pieridae (Braby et al. 2006). These pioneering researchers later proposed a more objective framework for the delineation of genera using DNA data (Talavera et al. 2012), suggesting that genera may correspond to clades diverging approximately 5 million years ago. We applied a similar approach using whole-genome data to classify the subtribe Euremina Grote, 1898, and to strike a balance between splitting (~5 Mya) and lumping (~25 Mya) (Zhang et al. 2023c). The whole-genome shotgun tree

we constructed in that work (Zhang et al. 2023c: fig. 2) is essentially identical to the target enrichment-based phylogeny published more recently in Leong et al. (2025). However, rather than fully utilizing their DNA data to refine the taxonomy of the group, Leong et al. (2025) default to citing Klots (1933) verbatim as support for their lumping of the entire subtribe into a single genus estimated to have diverged around 26 Mya. The taxonomic revision by Klots (1933), although significant for its time, is nearly a century old, and the role of DNA as the genetic material was not even known then.

The first indication that Klots's *Eurema* is an assemblage of several genera was provided in a groundbreaking study by Pollock et al. (1998). Although based on only a few genes, the study revealed deep divergence within *Eurema* sensu lato and formed the basis for splitting North American species into three genera, as suggested by Opler and Warren (2002) and reinforced by Pelham (2008). The argument for the split was straightforward: if genetic differentiation is too large, the organisms cannot belong to the same genus. Genetic differentiation is related to divergence time, which brings the argument back to Talavera et al. (2012) for the delineation of genera (~5 Mya, not >25 Mya). Therefore, although "*Eurema*" of Leong et al. (2025) is a valid taxon, it is not a genus but the subtribe Euremina, which consists of several genera because their divergence time exceeds 25 million years. Moreover, genetic differentiation is associated with phenotypic differences, which may not be limited to those reflected in wing patterns and shapes. For instance, another recent study questioned the validity of this *Eurema* super-lump based on the differences in egg structure (Nieves-Uribe et al. 2025).

Our partitioning of Euremina into genera (Zhang et al. 2023c) sought to achieve a compromise between splitting and lumping, while maintaining the established taxonomy of Lamas (2004) and Pelham (2008). We simply rearranged the species among genera restoring their monophyly (Zhang et al. 2019b, 2021, 2023c) but retaining the four genera of Lamas (2004). Our generic classification also makes biogeographical sense, allocating a separate genus for all Old World species, which form a clade of the same rank as each of the four New World genera. Euremina are mostly tropical, small, and non-migratory butterflies with a weak flight. Butterfly genera distributed in both the Old and New Worlds are typically found in temperate or arctic regions, i.e., with Holarctic distributions. Some notable exceptions, such as *Celaenorrhinus* Hübner, [1819], likely dispersed from Africa to South America across the Atlantic.

For all these reasons, we **reinstate** the classification proposed by Zhang et al. (2023c). The subtribe Euremina Grote, 1898 comprises the following five genera: *Terias* W. Swainson, 1821, **stat. rest.** (type species *Papilio hecabe* Linnaeus, 1758); *Eurema* Hübner, [1819] (type species *Papilio delia* Cramer, 1780, which is a junior homonym, and a valid name for this species is *Pieris daira* Godart, 1819); *Pyrisitia* A. Butler, 1870, **stat. rest.** (type species *Papilio proterpia* Fabricius, 1775); *Abaeis* Hübner, [1819], **stat. rest.** (type species *Papilio nicippe* Cramer, 1779); and *Teriocolias* Röber, 1909, **stat. rest.** (type species *Terias atinas* Hewitson, 1874, which is a junior subjective synonym of *Terias zelia* Lucas, 1852). The updated classification of the subtribe Euremina, including its subdivision into subgenera (five additional valid subgenera) and species, is given below. Only available genus-group names are listed; subspecies names are omitted but can be found on the Butterflies of America website (Warren et al. 2024). Old World species are not listed, as all belong to the genus *Terias*, which consists solely of Old World species. Type genera (for family-group names) or type species (for genus-group names) are indicated in parenthesis. Synonyms are preceded by =, and all but subjective synonyms also by ‡, with the valid name of the species following the colon. This list is updated from Zhang et al. (2023c) to incorporate findings from Zhang et al. (2024c).

Subtribe **Euremina** Grote, 1898 (*Eurema* Hübner, [1819])

Eurema section

Genus ***Terias*** W. Swainson, 1821 (*Papilio hecabe* Linnaeus, 1758), stat. rest.

Consists of all Old World species of *Euremini*

Subgenus *Maiva* Grose-Smith & W.F. Kirby, 1893 (=*M. sulphurea* Gr-Sm. & Kirby: *Papilio brigitta* Stoll, 1780), stat. rest.

=*Kibreeta* F. Moore, 1906 (=‡*Papilio libythea* Fabricius, 1798: *Terias brigitta rubella* Wallace, 1867)

=*Nirmula* F. Moore, 1906 (=*Terias venata* F. Moore, 1858: *Terias laeta* Boisduval, 1836)

Subgenus *Terias* W. Swainson, 1821 (*Papilio hecabe* Linnaeus, 1758)

Genus ***Eurema*** Hübner, [1819] (=‡*Papilio delia* Cramer, 1780: *Pieris daira* Godart, 1819)
- *Eurema priddyi* (Lathy, 1898)
- *Eurema lucina* (Poey, [1852])
- *Eurema daira* (Godart, 1819)
- *Eurema ella* (Röber, 1909)
- *Eurema elathea* (Cramer, 1777)
- *Eurema flavescens* (Chavannes, 1850)
- *Eurema nigrocincta* Dognin, 1889
- *Eurema millerorum* Llorente & Luis, 1987
- *Eurema agave* (Cramer, 1775)
- *Eurema phiale* (Cramer, 1775)

Genus ***Pyrisitia*** A. Butler, 1870 (*Papilio proterpia* Fabricius, 1775), stat. rest.

Subgenus *Pyrisitia* A. Butler, 1870 (*Papilio proterpia* Fabricius, 1775)
- *Pyrisitia proterpia* (Fabricius, 1775)
- *Pyrisitia westwoodii* (Boisduval, 1836)
- *Pyrisitia dina* (Poey, 1832)
- *Pyrisitia parvumbra* (Kaye, 1925)
- *Pyrisitia mayobanex* (M. Bates, 1939)
- *Pyrisitia memulus* (A. Butler, 1871)
- *Pyrisitia leuce* (Boisduval, 1836)
- *Pyrisitia larae* (Herrich-Schäffer, 1862)
- *Pyrisitia venusta* (Boisduval, 1836)
- *Pyrisitia chamberlaini* (A. Butler, 1898)
- *Pyrisitia nise* (Cramer, 1775)
- *Pyrisitia lisa* (Boisduval & Le Conte, [1830])
- *Pyrisitia euterpiformis* (Munroe, 1947)
- *Pyrisitia amelia* (Poey, [1852])
- *Pyrisitia portoricensis* (Dewitz, 1877)
- *Pyrisitia pyro* (Godart, 1819)
- *Pyrisitia messalina* (Fabricius, 1787)

Subgenus *Lirinia* Grishin, 2023 (*Terias lirina* H. Bates, 1861), stat. rest.
- *Pyrisitia lirina* (H. Bates, 1861)

Abaeis section

Genus ***Abaeis*** Hübner, [1819] (*Papilio nicippe* Cramer, 1779), stat. rest.

Subgenus *Leucidia* E. Doubleday, 1847 (*Pieris elvina* Godart, 1819), stat. rest.
- *Abaeis brephos* (Hübner, [1809])
- *Abaeis elvina* (Godart, 1819)

Subgenus *Lucidia* Lacordaire, 1833 (*Papilio albula* Cramer, 1775), stat. rest.
- *Abaeis albula* (Cramer, 1775)

Subgenus *Sphaenogona* Butler, 1870 (*Terias bogotana* C. & R. Felder, 1861: a ssp. of *T. mexicana* Boisd.), stat. rest.
- *Abaeis paulina* (H. Bates, 1861)
- *Abaeis xantochlora* (Kollar, 1850)
- *Abaeis fabiola* (C. Felder & R. Felder, 1861)
- *Abaeis tupuntenem* (Lichy, 1976)
- *Abaeis salome* (C. Felder & R. Felder, 1861)
- *Abaeis mexicana* (Boisduval, 1836)
- *Abaeis boisduvaliana* (C. Felder & R. Felder, 1865)
- *Abaeis angulata* (Wallengren, 1860)
- *Abaeis gratiosa* (E. Doubleday, 1847)
- *Abaeis arbela* (Geyer, 1832)
- *Abaeis adamsi* (Lathy, 1898)

Subgenus *Abaeis* Hübner, [1819] (*Papilio nicippe* Cramer, 1779)
- *Abaeis nicippe* (Cramer, 1779)
- *Abaeis nicippiformis* (Munroe, 1947)

Genus ***Teriocolias*** Röber, 1909 (=*Terias atinas* Hewitson, 1874: *Terias zelia* Lucas, 1852), stat. rest.
- *Teriocolias deva* (E. Doubleday, 1847)
- *Teriocolias doris* (Röber, 1909)
- *Teriocolias zelia* (Lucas, 1852)
- *Teriocolias reticulata* (A. Butler, 1871)

Wing pattern differences between *Cercyonis silvestris* (W. H. Edwards, 1861) and *Cercyonis sthenele* (Boisduval, 1852) in the Sierra–Cascade ranges of California, USA

As we have recently shown through genomic sequencing, the lectotype of *Satyrus silvestris* W. H. Edwards, 1861 (type locality in USA: California, likely Butte Co.) (Figs. 1, 2a, b), currently treated as a valid species in the genus *Cercyonis* Scudder, 1875 (type species *Papilio alope* Fabricius, 1793, which is a subspecies of *Papilio pegala* Fabricius, 1775), had been incorrectly regarded as conspecific with *Cercyonis sthenele* (Boisduval, 1852) (type locality USA: California, San Francisco), but instead is more closely related to *Cercyonis oetus* (Boisduval, 1869) (type locality in USA: California, Placer Co.) (Zhang et al. 2022c). We therefore proposed treating *S. silvestris* as a species-level taxon *Cercyonis silvestris* (W. H. Edwards, 1861), placing *Cercyonis incognita* J. Emmel, T. Emmel & Mattoon, 2012 (type locality in USA: California, Mendocino Co.) as its subspecies (Zhang et al. 2022c).

Although the two species, *C. silvestris* and *C. sthenele*, are not each other's closest relatives and are well differentiated genetically, they are notoriously difficult to distinguish by their wing patterns. This difficulty is likely the cause of the confusion about the taxonomic attribution of the *S. silvestris* lectotype (i.e., whether it is closer to *C. sthenele* or to *C. oetus*). Our ongoing genomic sequencing has revealed several specimens of *C. silvestris silvestris* and *C. sthenele* from the Sierra–Cascade ranges of California (Fig. 1). To aid in the identification of these species from their wing patterns, we illustrate these specimens here (Fig. 2). The differences between the two taxa are subtle and challenging to quantify. In general, *C. sthenele* (Fig. 2q–ab) tends to have larger eyespots; a better defined pattern of darker brown lines, curves, and striations on a darker ground color; and a more prominent break in the submarginal brown line at vein M_3 on the ventral hindwing (the posterior end of the lunule between veins M_1 and M_3 tends to be more strongly offset basad compared to the anterior end of the lunule in cell M_3-CuA_1 than in *C. silvestris*). Conversely, *C. silvestris* (Fig. 2a–p) tends to have a less regular discal brown line on the

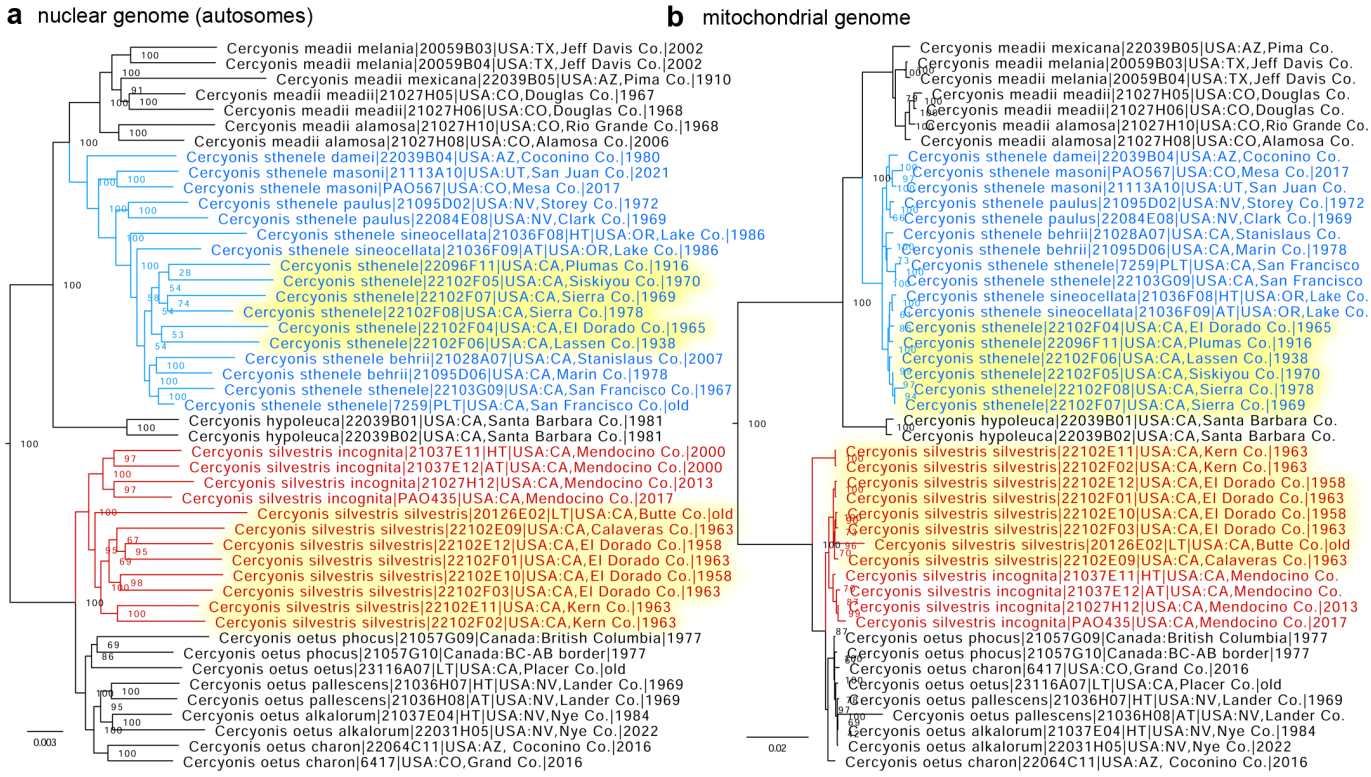

Fig. 1. Phylogenetic trees of *Cercyonis* specimens constructed from protein-coding regions in: **a)** the nuclear genome (autosomes), based on 3,851,532 positions, and **b)** the mitochondrial genome showing *C. sthenele* (blue) and *C. silvestris* (red). Specimens shown in Fig. 2 are highlighted yellow. Ultrafast bootstrap (Hoang et al. 2018) values are shown at nodes.

Fig. 2. Two *Cercyonis* species from USA: California in ventral (upper half, prior letter) and dorsal (lower half, subsequent letter) views, data in text: **a–p)** *C. silvestris* (gray dots) and **q–ab)** *C. sthenele* (ochre dots) ♂♂ unless indicated: **a–b)** lectotype NVG-20126E02 Butte Co., **c–d)** ♀ NVG-22102E09 Calaveras Co., **e–f)** NVG-22102E10 El Dorado Co., **g–h)** NVG-22102F03 El Dorado Co., **i–j)** NVG-22102E12 El Dorado Co., **k–l)** NVG-22102F01 El Dorado Co., **m–n)** NVG-22102F02 Kern Co., **o–p)** NVG-22102E11 Kern Co., **q–r)** NVG-22102F05 Siskiyou Co., **s–t)** ♀ NVG-22102F06 Lassen Co., **u–v)** NVG-22096F11 Plumas Co., **w–x)** NVG-22102F08 Sierra Co., **y–z)** NVG-22102F07 Sierra Co., **aa–ab)** NVG-22102F04 El Dorado Co.

ventral hindwing near the end of the discal cell, i.e., the dash between veins M_1 and M_3 is more strongly offset basad towards vein M_3 compared to the dash in cell M_3-CuA_1 than in *C. sthenele* (best seen in Fig. 2k). However, due to reduced mottling in many specimens, only the dash between M_1 and M_3 may be readily seen (e.g., Fig. 2g). It is a challenge to identify these species, and more specimens are needed to assess variation in these wing pattern characters.

Specimens shown in Fig. 2 are from USA, California, the Noel LaDue collection [CAS], unless indicated otherwise: *C. silvestris silvestris*: lectotype ♂ NVG-20126E02 hypothesized as Butte Co., North Fork Feather River Canyon, 2 mi SW of Pulga [CMNH] (Fig. 2a, b); ♀ NVG-22102E09, CASENT_8566999 Calaveras Co., 4 mi N of Mountain Ranch on road to Railroad Flat, 15-Jul-1963, (Fig. 2c, d); El Dorado Co., American River Canyon below Auburn, 1000': ♂ NVG-22102E10, CASENT_8567000 23-Jun-1958 (Fig. 2e, f), ♂ NVG-22102F03, CASENT_8567005 24-Jun-1963 (Fig. 2g, h), ♂ NVG-22102E12, CASENT_8567002 23-Jun-1958 (Fig. 2i, j), and ♂ NVG-22102F01, CASENT_8567003 24-Jun-1963 (Fig. 2k, l); and Kern Co., Tehachapi Mts., Pine Tree Mine, 19-Jun-1963: ♂ NVG-22102F02, CASENT_8567004 (Fig. 2m, n) and ♂ NVG-22102E11, CASENT_8567001 (Fig. 2o, p) and *C. sthenele*: ♂ NVG-22102F05, CASENT_8567007 Siskiyou Co., Kaiser Meadow, 16-Jul-1970, Jeff R. Smith leg. (Fig. 2q, r); ♀ NVG-22102F06, CASENT_8567008 Lassen Co., 13-Aug-1938, L. I. Hewes leg. (Fig. 2s, t); ♂ NVG-22096F11 Plumas Co., Portola, 17-Aug-1916, J. A. Comstock leg. [LACM] (Fig. 2u, v); Sierra Co., Sierra City, Jeff R. Smith leg.: ♂ NVG-22102F08, CASENT_8567010 26-Aug-1978 (Fig. 2w, x) and ♂ NVG-22102F07, CASENT_8567009 26-Jul-1969 (Fig. 2y, z); and ♂ NVG-22102F04, CASENT_8567006 El Dorado Co., American River Canyon below Auburn, 1000', 21-Jun-1965 (Fig. 2aa, ab).

Dione (*Agraulis*) *galapagensis* (W. Holland, 1890) is confirmed as a species-level taxon by genomic sequencing

In their detailed study, Núñez et al. (2022) did not obtain DNA sequences for *Agraulis vanillae* var. *galapagensis* Holland, 1890 (type locality in Ecuador: Galápagos, San Cristóbal Island), but nevertheless elevated this taxon to the species level based on a phenotypic comparison. Here, we confirm their

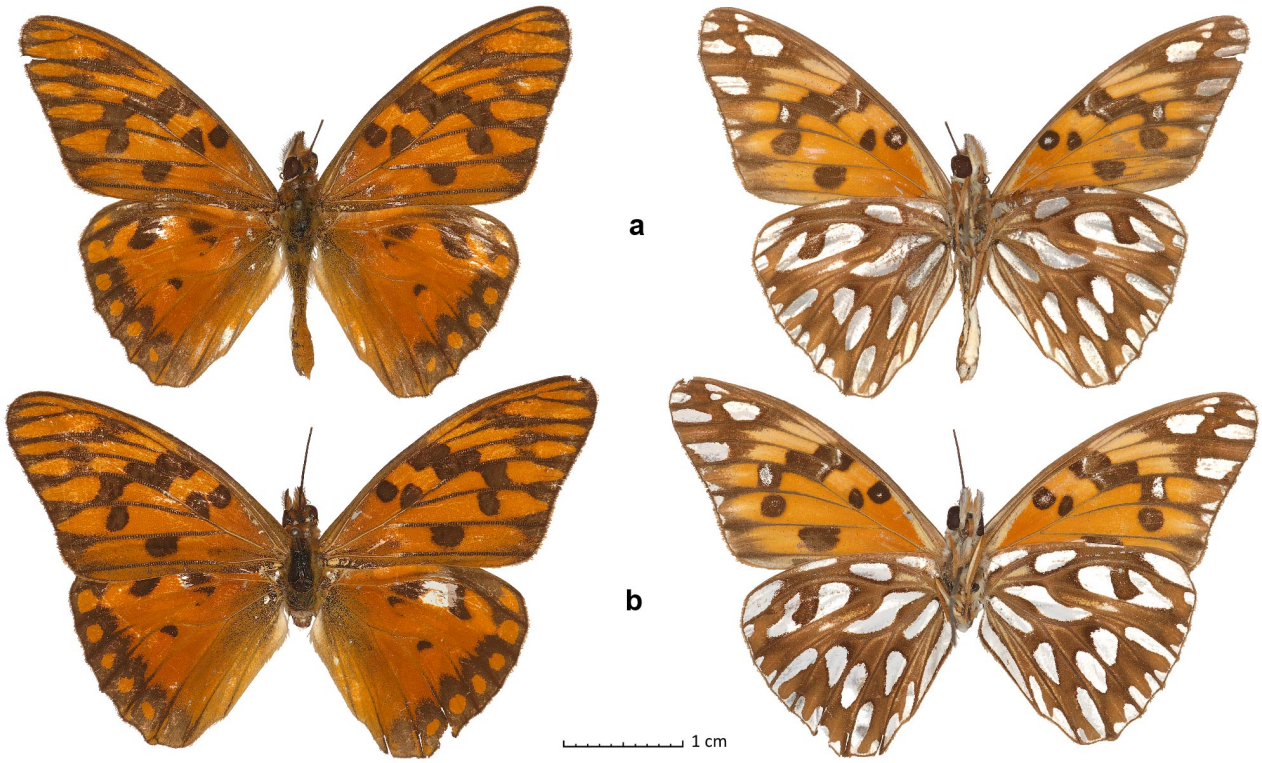

Fig. 3. Sequenced specimens of *Dione (Agraulis) galapagensis* ♂♂ from Galapagos [USNM] in dorsal (left) and ventral (right) views: **a)** topotype NVG-19094A07, USNMENT 01589530 San Cristóbal Island, 30-Mar-1891 and **b)** NVG-19094A04, USNMENT 01589527 Floreana Island, 1-Apr-1891.

taxonomic hypothesis by genomic sequencing of two specimens (Fig. 3), and show that *Dione* (*Agraulis*) *galapagensis* is genetically differentiated from congeners at the species level (Fig. 4), being confidently supported as sister to the clade comprising two species, *Dione* (*Agraulis*) *vanillae* Linnaeus, 1758 (type locality in America, possibly in Suriname) and *Dione* (*Agraulis*) *insularis* (Maynard, 1889) (type locality in Bahamas) in the nuclear genome trees (Fig. 4a, b). In addition to these two species, its sister clade in the mitochondrial genome tree also includes *Dione* (*Agraulis*) *lucina* (C. Felder & R. Felder, 1862) (type locality "Rio Negro") and *Dione* (*Agraulis*) *maculosa* Stichel, [1908] (type locality in Brazil: Espírito Santo and Paraguay) (Fig. 4c). The strongly supported incongruence between the trees suggests incomplete lineage sorting or introgression. The COI barcodes of *D.* (*A.*) *galapagensis* differ from other closely related species by 2.2% (15 bp) from *D.* (*A.*) *vanillae*, 1.8% (12 bp) from *D.* (*A.*) *insularis*, 2.0% (13 bp) from *D.* (*A.*) *lucina*, and 1.4% (9 bp) from *D.* (*A.*) *maculosa*. We note that the branch leading to *D.* (*A.*) *galapagensis* in the barcode dendrogram is particularly short (Fig. 4d red), indicating a comparatively low number of changes in the COI sequence of this species and thus leading to smaller barcode differences from congeners than expected from the nuclear genome differences. The COI barcode sequence of *D.* (*A.*) *galapagensis*, sample NVG-19094A07, 658 base pairs is:

TACTTTATATTTCATTTTTGGAATTTGAGCAGGAATAGTTGGAACATCTCTTAGTATTTTAATTCGAATAGAATTAGGTAATCCTGGATCATTAATTGGTGATGATCAAATTTATAATACT
ATTGTTACAGCTCATGCATTTATTATAATTTTTTTTATAGTTATACCTATTATAATTGGAGGATTTGGTAATTGATTAGTTCCATTAATATTAGGAGCCCCAGATATAGCATTTCCTCGAA
TAAATAATATAAGATTTTGACTTCTTCCCCCGTCATTAATCTTATTAATTTCTAGAAGAATTGTAGAAAATGGAGCAGGAACAGGATGAACTGTTTACCCCCCACTTTCATCAAATATTGC
TCATGGTGGTTCATCTGTAGATTTAGCTATTTTTTCTTTACATTTAGCTGGAATTTCCTCAATTTTAGGAGCAATTAATTTTATTACTACTATTATTAATATACGAATTAATAATATATCT
TTTGACCAATTACCTTTATTTATTTGAGCTGTAGGAATTACAGCACTTCTTTTATTATTATCTCTTCCAGTTTTAGCTGGAGCTATTACTATACTTTTAACAGATCGAAATTTAAATACAT
CATTTTTTGACCCTGCAGGAGGAGGAGATCCAATTTTATATCAACATTTATTT

The barcode sequence of the second specimen, sample NVG-19094A04, is identical.

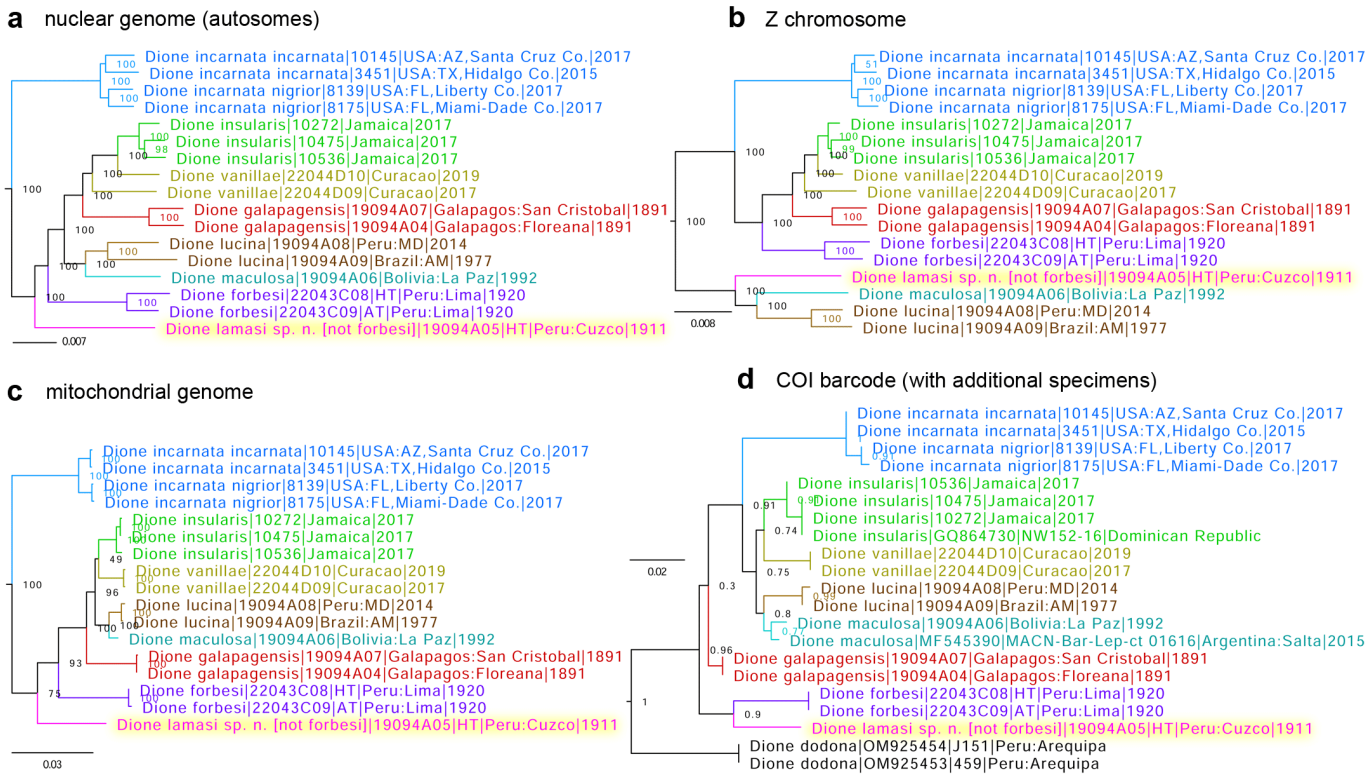

Fig. 4. Phylogenetic trees of all described *Dione* (*Agraulis*) species constructed from protein-coding regions in: **a)** the nuclear genome (autosomes), based on 11,226,555 positions, **b)** the Z chromosome, based on 623,562 positions, and **c)** the mitochondrial genome; and **d)** a FastTree (Price et al. 2009) dendrogram constructed from COI barcodes using NGPhylogeny.fr server (Lemoine et al. 2019). In the COI barcode dendrogram (d), specimens are added from GenBank with GenBank accessions (8 symbols starting from a letter, followed by a specimen ID) given for them. Sequences obtained by us are denoted by the sample ID starting from a number. Different species are colored differently: *D.* (*A.*) *incarnata* N. Riley, 1926 (blue), *D.* (*A.*) *insularis* (green), *D.* (*A.*) *vanillae* (olive), *D.* (*A.*) *galapagensis* (red), *D.* (*A.*) *lucina* (brown), *D.* (*A.*) *maculosa* (cyan), *D.* (*A.*) *forbesi* (purple), *D.* (*A.*) *lamasi* **sp. n.** (magenta, label highlighted in yellow), *D.* (*A.*) *dodona* (black, COI barcode only). Ultrafast bootstrap (Hoang et al. 2018) values are shown at nodes of the genomic trees.

Dione (*Agraulis*) *lamasi* Grishin, new species

https://zoobank.org/0FAA13AA-36A6-4BF3-A9BE-FC8312F403F4

(Figs. 4 part, 5a)

Definition and diagnosis. Genomic analysis reveals that a male of *Dione* (*Agraulis*) Boisduval & Le Conte, [1835] (type species *Papilio vanillae* Linnaeus, 1758) from the Andes in southern Peru is genetically differentiated from all known taxa at the species level (Fig. 4); e.g., COI barcodes of this male and the most similar species *Dione* (*Agraulis*) *forbesi* (Michener, 1942) (type locality in Peru: Lima) (Fig. 5b, c) differ by 2.7% (18 bp), and therefore this specimen represents a new species. This new species keys to "*Agraulis vanillae forbesi*" in Michener (1942), but differs from it and other relatives by the following combination of characters: the outer margin of the ventral hindwing bears a line of connected silver spots only separated by narrow brown overscaling along the veins, these spots are rounded and not elongated; the spots are the largest among *Dione* (*Agraulis*) species, except *Dione* (*Agraulis*) *dodona* Lamas & Farfán, 2022 (type locality in Peru: Arequipa), but *D. dodona* has a black-brown postdiscal spot in the dorsal hindwing cell CuA_1-CuA_2 (which the new species lacks) and the ventral hindwing discal cell silver spot has a distal segment separated by ground color (this spot is undivided in other species, including the new one); the dorsal hindwing has a broader marginal black-brown band with rounded orange spots that are a little over a third of its width; and the forewing discal cell black-brown spot is smaller and is separated from the postdiscal spot in cell M_3-CuA_1 by a distance larger than its width. Due to unexplored individual variation, this species is best identified by DNA, with diagnostic base pairs in the nuclear genome: hm2015211-RA.7:T42C, hm2015303-RA.23:T84C, hm2020017-RA.1:A129G, hm2007782-RA.3:A54G, hm2008275-RA.2:G123A, hm2003445-RA.15:C114C (not T), hm2015994-RA.2:G64G (not A), hm2005746-RA.15:A36A (not G), hm2007461-RA.2:G78G (not A), hm2007461-RA.2:G150G (not A); and the COI barcode: T106C, A403A, A466G, A517G, T646C.

Barcode sequence of the holotype. Sample NVG-19094A05, 658 base pairs:

TACTTTATATTTTATTTTTGGAATTTGAGCAGGAATAGTTGGAACATCTCTTAGTATTTTAATTCGAATAGAATTAGGTAATCCAGGATCATTAATTGGTGATGACCAAATTTATAATACT
ATTGTTACAGCTCATGCATTTATTATAATTTTTTTTATAGTTATACCTATTATAATTGGTGGATTTGGTAATTGATTAGTTCCATTAATATTAGGAGCCCCAGACATAGCATTTCCTCGAA
TAAATAATATAAGATTTTGACTTCTTCCCCCGTCATTAATTTTATTAATTTCTAGAAGAATTGTAGAAAATGGAGCAGGAACAGGATGAACCGTTTATCCCCCACTTTCATCAAATATTGC
TCATGGTGGCTCATCTGTAGATTTAGCTATTTTTTCTTTACATTTAGCTGGAATTTCCTCAATTTTAGGAGCAATTAATTTTATTACTACTATTATTAATATGCGAATTAATAATATATCT
TTTGATCAATTACCTCTATTTGTTTGAGCTGTGGGAATTACAGCTCTTCTTTTATTATTATCTCTTCCAGTTTTAGCTGGAGCTATTACTATACTTTTAACAGATCGAAATTTAAATACAT
CATTTTTTGACCCTGCAGGAGGAGGAGATCCAATTTTATACCAACATTTATTT

Type material. Holotype: ♂ currently deposited in the National Museum of Natural History, Smithsonian Institution, Washington, DC, USA (USNM), illustrated in Fig. 5a, bears the following six rectangular labels (2nd and 3rd handwritten, others printed with handwritten text shown in italics), five white: [Ollantaytambo | 9000ft. | *20*July,1911 | YalePeruvExp], [46], [Dione | vanillae | Linn | var.], [DNA sample ID: | NVG-19094A05 | c/o Nick V. Grishin], [USNMENT | {QR Code} | 01589528], and one red [HOLOTYPE ♂ | *Dione* (*Agraulis*) *lamasi* Grishin].

Type locality. Peru: Cuzco Region, Ollantaytambo.

Etymology. There is *Dione forbesi*, and we propose *Dione lamasi* **sp. n.** to honor Gerardo Lamas, a lepidopterist extraordinaire of unmatched knowledge and generosity in sharing it. Gerardo epitomizes the study of Neotropical butterflies, and essentially every major recent advance in the field is linked to his name. He discovered a new, and most unusual, species of *Dione* in Peru, and it is most fitting to dedicate another Peruvian *Dione* species to him. We are grateful to Gerardo for all his generous help over the years, for his kindness and patience. The name is a noun in the genitive case.

Distribution. Currently known only from the holotype collected on the eastern slopes of the Andes in southern Peru.

Comment. To facilitate further comparisons, here we report the COI barcode sequence of *D.* (*A.*) *forbesi* holotype ♂ (Fig. 5b), sample NVG-22043C08, 658 base pairs:

TACTTTATATTTTATTTTTGGAATTTGAGCAGGAATAGTTGGAACATCTCTTAGTATTTTAATTCGAATGGAATTAGGTAATCCTGGGTCATTAATTGGCGATGACCAAATTTATAATACT
ATTGTTACAGCTCATGCATTTATTATAATTTTTTTTCATAGTTATACCTATTATAATTGGTGGATTTGGTAATTGATTAGTTCCATTAATATTAGGAGCCCCAGATATAGCATTTCCTCGAA
TAAATAATATAAGATTTTGACTTCTCCCCCCGTCATTAATCTTATTAATTTCTAGAAGAATTGTAGAAAATGGAGCAGGAACAGGATGAACTGTATATCCCCCACTTTCATCAAATATTGC
TCATGGTGGCTCATCTGTAGATTTAGCTATTTTTTCTCTTCATTTAGCTGGAATTTCCTCAATTTTAGGAGCAATTAATTTTATTACTACTATTATTAATATACGAATTAATAATATATCT
TTTGACCAATTACCTCTATTTGTTTGAGCTGTAGGAATTACAGCACTTCTTTTATTATTATCTCTACCAGTTTTAGCTGGAGCTATTACTATACTTTTAACAGATCGAAATTTAAATACAT
CATTTTTTGACCCTGCAGGAGGAGGAGATCCAATTTTATATCAACATTTATTT

The barcode sequence of the allotype ♀ (Fig. 5c), sample NVG-22043C09, is identical.

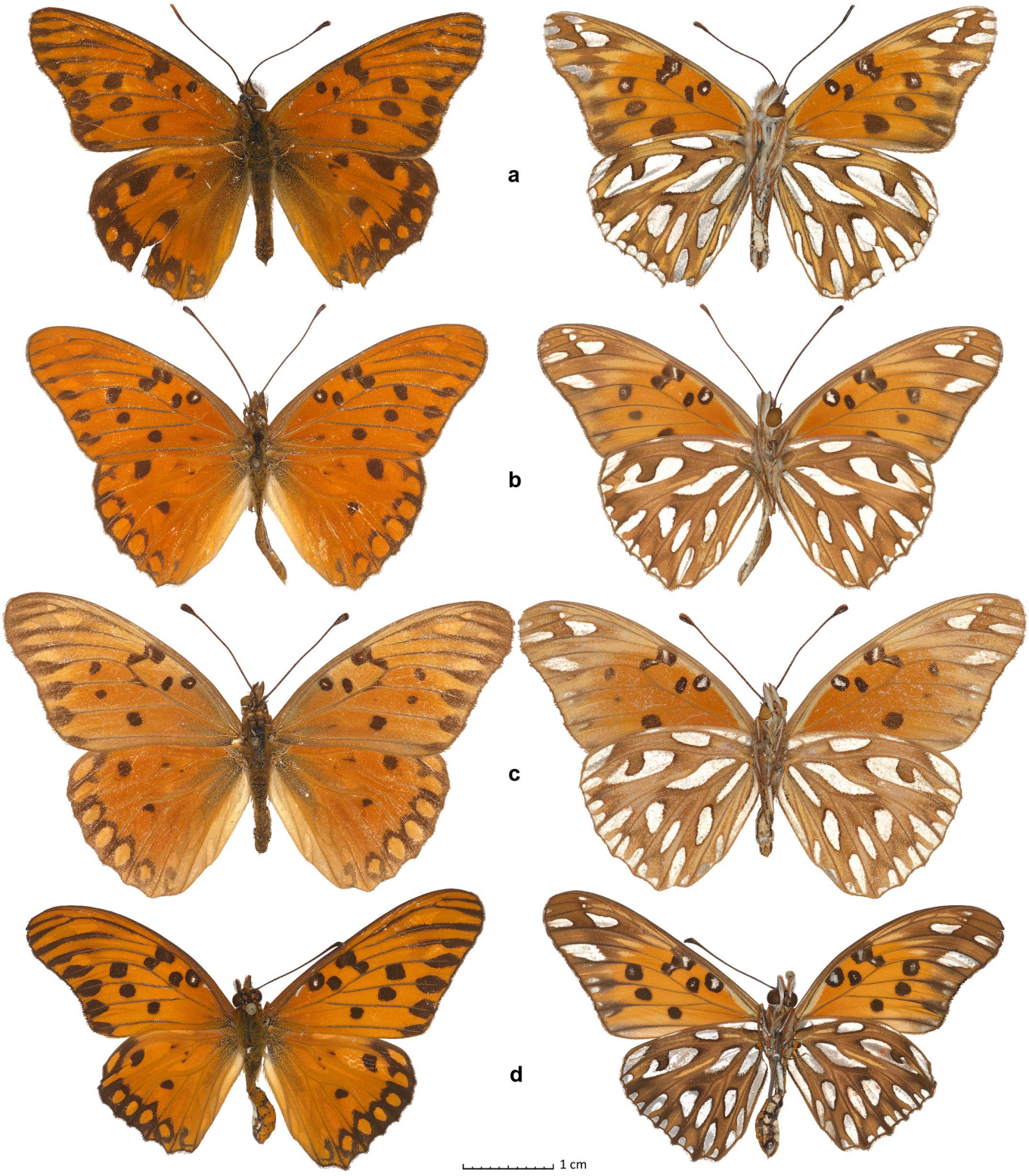

Fig. 5. *Dione (Agraulis)* species in dorsal (left) and ventral (right) views, data in text or below: **a)** holotype of *D.* (*A.*) *lamasi* **sp. n.** ♂ NVG-19094A05 from Peru: Cuzco; **b–c)** *D.* (*A.*) *forbesi* from Peru: Lima, 7-May-1920, Wm. T. M. Forbes leg. [CUIC]: **b)** holotype ♂ NVG-22043C08 and **c)** allotype ♀ NVG-22043C09; and **d)** *D.* (*A.*) *maculosa* ♂ NVG-19094A06, USNMENT 01589529 from Bolivia: La Paz, 10,700', 17-Jun-1992, R. D. Friesen leg. [USNM].

Family Riodinidae Grote, 1895 (1827)

Lasaia (*Lasaia*) *chiapis* Grishin, new species

https://zoobank.org/AD2867EE-6144-4B71-8591-6FE46682F3EB

(Figs. 6 part, 7a)

Definition and diagnosis. Genomic analysis reveals that a male from Chiapas, Mexico, identified in the MGCL collection as *Lasaia* (*Lasaia*) *meris* (Stoll, 1781) (type locality in Suriname) is sister to *Lasaia* (*Lasaia*) *arsis* Staudinger, [1887] (type locality in Brazil: Amazonas, lectotype sequenced as NVG-18054E09), being genetically differentiated at the species level (Fig. 6); e.g., their COI barcodes differ by 1.8% (12 bp), and therefore this male represents a distinct species. This Mexican species is not *L.* (*L.*) *meris*, currently known with confidence only from the original illustration (Stoll 1781; Clench 1972), because the Surinamese species has a stronger developed dark pattern of spots on the dorsal side (weakly developed in the posterior postdiscal part of the hindwing in the male from Chiapas); more contrasting ventral side with nearly black lines and bands and brown areas between them alternating with whitish bands and spots, equally developed in the posterior part of the hindwing (paler ventral side with the posterior half of the hindwing even paler in the male from Chiapas); and the lack of a pale spot in the postdiscal area of the dorsal forewing near the costal margin (present in the male from Chiapas). Therefore, this Chiapasian male represents a new species that is otherwise most similar in appearance to its sister *L.* (*L.*) *arsis* (see Clench (1972) for the description) and differs from it by males with more weakly expressed postdiscal dark spots in cells M_3-CuA_1 and CuA_1-CuA_2 on the dorsal hindwing, which has a smaller apical dark-brown spot, equally smaller on the ventral side; narrower elements of the dark-brown discal band on the dorsal side of both wings; more strongly overscaled with brown the pale costal

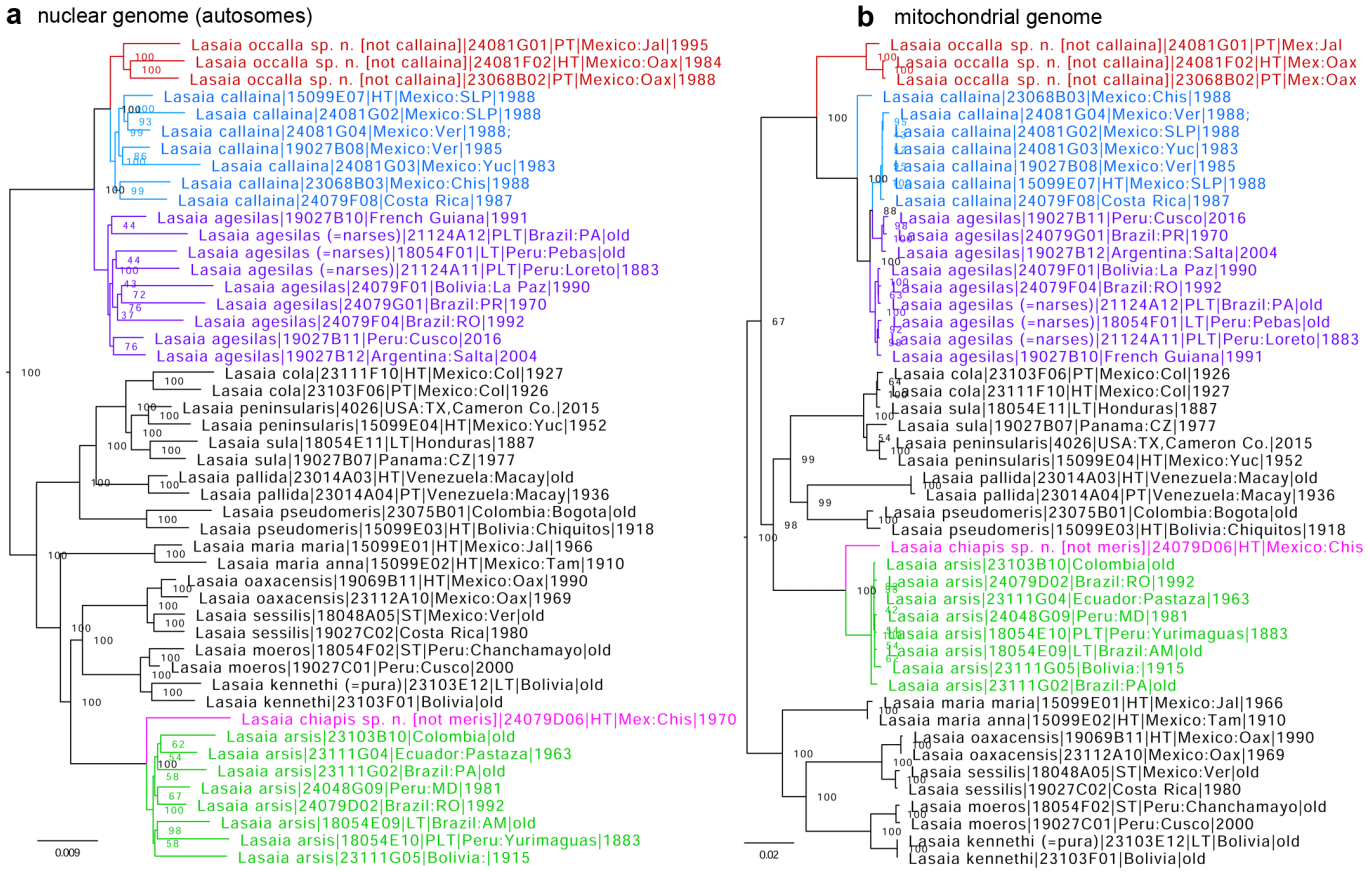

Fig. 6. Phylogenetic trees of selected *Lasaia* (*Lasaia*) species constructed from protein-coding regions in: **a)** the nuclear genome (autosomes), based on 5,789,646 positions, and **b)** the mitochondrial genome. Species discussed in the text are colored: *L.* (*L.*) *occalla* **sp. n.** (red), *L.* (*L.*) *callaina* (blue), *L.* (*L.*) *agesilas* (Latreille, [1809]) (purple), *L.* (*L.*) *chiapis* **sp. n.** (magenta), *L.* (*L.*) *arsis* (green). Ultrafast bootstrap (Hoang et al. 2018) values are shown at nodes.

Fig. 7. New *Lasaia* (*Lasaia*) species from Mexico in dorsal (left) and ventral (right) views, data in text:
a) *Lasaia* (*Lasaia*) *chiapis* **sp. n.** holotype ♂ NVG-24079D06 from Chiapas and **b–c)** *Lasaia* (*Lasaia*) *occalla* **sp. n.**:
b) holotype ♂ NVG-24081F02 from Oaxaca and **c)** paratype ♂ NVG-24081G01 from Jalisco.

area on the dorsal hindwing; and the dark brown spot near the base of the forewing cell CuA_1-CuA_2 not reaching its base, which is paler brown (the spot is thus more rounded, not triangular). Due to its cryptic nature and unexplored individual variation, this species is best identified by DNA, with diagnostic base pairs in the nuclear genome: cne1083.7.3:T474C, cne5233.1.2:A159G, cne5233.1.2:A300G, cne3097.3.1: T75C, cne2057.1.40:G78A, cne2850.2.2:A237A (not G), cne415.2.2:G69G (not A), cne16325.1.5:T57T (not C), cne907.9.3:T27T (not A), cne907.9.3:T42T (not G); and the COI barcode: A70G, T136C, A166G, A199G, T589C.

Barcode sequence of the holotype. Sample NVG-24079D06, 658 base pairs:

AACATTATATTTTATTTTTGGAATTTGAGCAGGAATAGTAGGTACATCTTTAAGTTTATTAATTCGTATGGAATTAGGTATACCAGGATCATTAATTGGTGATGATCAAATTTATAATACT
ATTGTTACAGCTCACGCTTTTATTATAATTTTTTTTATAGTTATGCCTATTATAATTGGAGGCTTTGGTAATTGATTGGTACCTTTAATATTAGGAGCTCCTGATATAGCATTTCCACGAA
TAAATAATATAAGATTTTGACTTTTACCTCCATCTTTATTTCTATTAATTTCAAGAAGTATTGTAGAAAATGGAGCAGGAACTGGATGAACAGTTTACCCCCCACTGTCTTCTAATATTGC
TCATGGAGGATCTTCAGTAGATTTAGCTATTTTTTCTTTACATTTAGCTGGTATTTCTTCAATTTTAGGAGCTATTAATTTTATTACAACTATTATTAATATACGTATTAATAATTTATCT
TTTGATCAAATACCATTATTTGTTTGATCTGTTGGTATTACTGCTCTATTATTATTATTATCATTACCTGTTTTAGCAGGAGCTATTACTATATTATTAACAGACCGTAATTTAAATACAT
CTTTTTTTGATCCTGCAGGAGGAGGTGATCCAATTTTATATCAACATTTATTT

Type material. Holotype: ♂ deposited in the McGuire Center for Lepidoptera and Biodiversity collection, Gainesville, FL, USA (MGCL), illustrated in Fig. 7a, bears the following seven rectangular labels (4th handwritten, others printed with handwritten text shown in italics), six white: [MEXICO: CHIAPAS | San Quintin | *9. vii* -197*0* | R. Wind], [A. C. Allyn | Acc. 1972-46], [MGCL/FMNH | Specimen no. | 4769], [Lasaia | meris ♂], [PHOTOGRAPHED | FOR BUTTERFLIES | OF AMERICA], [DNA sample ID: | NVG-24079D06 | c/o Nick V. Grishin], and one red [HOLOTYPE ♂ | Lasaia (Lasaia) | chiapis Grishin]. **Paratypes:** 3♂♂ from Mexico, Chiapas [MGCL]: 1♂ NVG-24079C11, MGCL/FLMNH no. 4768 data as the holotype but 3–5-Sep-1971; 1♂ NVG-24079C12, LEP-78351 Boca de Chajúl, Mar-1996, E. C. Knudson leg.; and 1♂ NVG-24079D07 Chiapas/Guatemala border, Usumacinta River, 29-Dec-1964, E. M. Shull leg.

Type locality. Mexico: Chiapas, San Quintín.

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

Distribution. Currently known only from eastern Chiapas in Mexico and expected at least in Guatemala.

Comment. At the time of publication, paratypes had not yet been sequenced and were assigned to this species based on phenotypic characters and collection locality.

Lasaia (*Lasaia*) *occalla* Grishin, new species

https://zoobank.org/AEE40B25-F9A0-4B61-9242-E8D2AB4298A6

(Figs. 6 part, 7b, c)

Definition and diagnosis. Genomic analysis reveals that males from Oaxaca, Mexico, initially identified as *Lasaia* (*Lasaia*) *callaina* Clench, 1972 (type locality in Mexico: San Luis Potosí) are genetically differentiated from it at the species level (Fig. 6); e.g., their COI barcodes differ by 2.9% (19 bp), and therefore these males represent a new species. This new species is most similar in appearance to its sister *L.* (*L.*) *callaina* (see Clench (1972) for the description), and differs from it by males with a greener dorsal side of wings, that has a greenish rather than bluish sheen, at least in the postdiscal area by the costa of the forewing; typically less expressed dark marginal pattern on the dorsal forewing; less developed dashes and spots in the posterior part of both wings dorsally; and the submarginal violaceous areas on the ventral hindwing reaching deeper towards the discal area. These differences appear to align more with subspecies-level characteristics, but prominent genetic differentiation argues for the species status of this new taxon. Due to its cryptic nature and unexplored individual variation, this species is best identified by DNA, with diagnostic base pairs in the nuclear genome: cne12317.1.1:G193A, cne12317.1.1:G576T, cne30446.5.1:C291T, cne30446.5.1:G981A, cne10656.1.3:A401T; and the COI barcode: T193C, T298A, T490C, T499A, T652C.

Barcode sequence of the holotype. Sample NVG-24081F02, 658 base pairs:

AACATTATATTTTATTTTTGGAATTTGAGCTGGAATAGTAGGTACATCTTTAAGTTTATTAATTCGTATAGAATTAGGTATACCCGGATCATTAATTGGTGATGATCAAATTTATAACACT
ATCGTTACAGCTCATGCTTTTATTATAATTTTTTTTATAGTTATACCTATTATAATTGGAGGTTTTGGAAACTGATTAGTACCTTTAATATTAGGAGCTCCTGATATAGCATTTCCACGAA
TAAATAATATAAGATTTTGACTTTTACCTCCATCATTATTTCTATTAATTTCAAGAAGTATTGTAGAAAATGGAGCAGGAACTGGATGAACAGTTTACCCCCCACTGTCTTCTAATATTGC
TCATGGAGGATCTTCCGTAGATTTAGCTATTTTTTCATTACATTTAGCTGGTATTTCTTCAATTTTAGGAGCTATTAATTTTATTACAACTATTATTAATATACGTATTAATAACCTATCT
TTTGACCAAATACCATTATTTGTTTGATCAGTTGGTATTACTGCTTTATTATTATTATTATCTTTACCTGTTTTAGCTGGAGCTATTACTATATTATTAACTGATCGTAATTTAAATACAT
CTTTTTTTGATCCTGCAGGAGGAGGTGATCCAATTTTATATCAACACTTATTT

Type material. Holotype: ♂ deposited in the McGuire Center for Lepidoptera and Biodiversity collection, Gainesville, FL, USA (MGCL), illustrated in Fig. 7b, bears the following five rectangular labels (first two handwritten, others printed), four white: [MEXICO, +500 M Candelaria Loxicha, Oaxaca | July 26, 1984], [Lasaia | agesilas | Det. E. C. Welling], [CV Covell colln. | MGCL Acc. | 2005-7], [DNA sample ID: | NVG-24081F02 | c/o Nick V. Grishin], and one red [HOLOTYPE ♂ | Lasaia (Lasaia) | occallaina Grishin]. **Paratypes:** 2♂♂: Mexico: 1♂ NVG-23068B02 Oaxaca, Candelaria Loxicha, 19-Jan-1988, C. Almaraz leg. [TMMC] and 1♂ NVG-24081G01 Jalisco, 15.5 km S of Mismaloya Hotel on rte. 200, 13–15-Nov-1995, B. O'Hara colln. [MGCL] (Fig. 7c).

Type locality. Mexico: Oaxaca, Candelaria Loxicha, elevation 500 m.

Etymology. In Latin, *occidens* means west and the name refers to the western distribution of the new species sister to *L. callaina*: *occ*[idens] + [c]*alla*[*ina*]. In Greek, καλλαΐνης (kallainēs) means turquoise (both the gemstone and the color), and κάλλος (kallos) means beauty. Thus, the name can be translated as 'western beauty' and is treated as a noun in apposition.

Distribution. Western Mexico, currently known from the states of Oaxaca and Jalisco.

Lasaia (*Lochris*) *oileus* Godman, 1903 is a complex of several species

Genomic sequencing of specimens identified as *Lasaia* (*Lochris*) *oileus* Godman, 1903 (type locality in southern Paraguay) reveals unexpected genetic diversity (Fig. 8). These specimens partitioned into four clades genetically differentiated at the species level (Fig. 8 magenta, blue, green, and red); e.g., their COI barcodes differ by 3% (20 bp) between the closest species. Therefore *L.* (*L.*) *oileus* is a complex that consists of at least four species. We identify the South American species distributed over the largest area with sequenced specimens from Venezuela to Brazil and southern Peru as *L.* (*L.*) *oileus*, and other three (from Belize, from Costa Rica and Panama, and from northern Peru) are new and described below. Females are chosen as the holotypes of these new species, because one of these species is known only from a single female, and females may be more straightforward to identify by wing patterns.

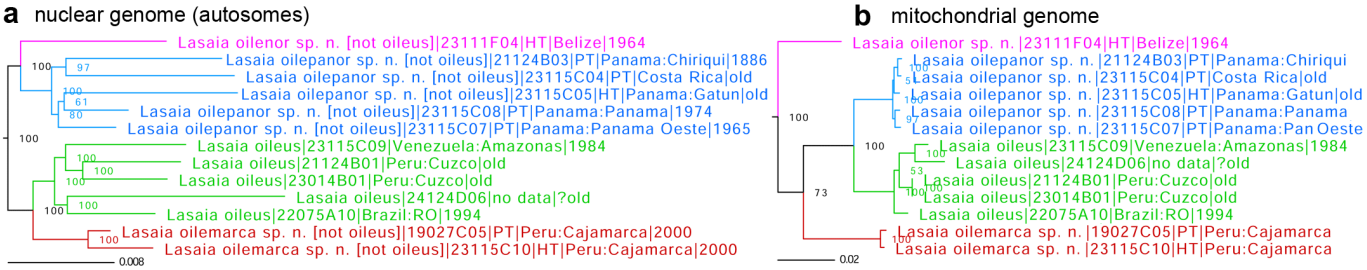

Fig. 8. Phylogenetic trees of all described *Lasaia* (*Lochris*) species constructed from protein-coding regions in: **a)** the nuclear genome (autosomes), based on 5,561,430 positions, and **b)** the mitochondrial genome. Different species are colored differently: *L.* (*Lochris*) *oilenor* **sp. n.** (magenta), *L.* (*Lochris*) *oilepanor* **sp. n.** (blue), *L.* (*Lochris*) *oileus* (green), and *L.* (*Lochris*) *oilemarca* **sp. n.** (red). Ultrafast bootstrap (Hoang et al. 2018) values are shown at nodes.

Lasaia (*Lochris*) *oilenor* Grishin, new species

https://zoobank.org/E7476C41-CED4-4DA0-98EA-5E22DA6D641B

(Figs. 8 part, 9a)

Definition and diagnosis. This is the first, and the northernmost, new species in the *Lasaia* (*Lochris*) *oileus* Godman, 1903 (type locality in southern Paraguay) complex, represented by a single specimen from Belize (Fig. 8 magenta). Its barcode differs from *L.* (*L.*) *oileus* by 3.5% (23 bp). The new species is similar to *L.* (*L.*) *oileus* and differs from it and other relatives by females having larger and darker submarginal brown spots on the ventral forewing; postdiscal spots in ventral forewing cells M_1-M_2 and M_2-M_3 are strongly overlapping with each other along M_2 vein (almost separated in *L.* (*L.*) *oileus*); the darker-brown framing of the ventral discal brown bands on both wings is relatively straight, with

Fig. 9 (this and the next page). Type series of new *Lasaia* (*Lochris*) species in dorsal (left) and ventral (right) views, data in text: **a)** *L. oilenor* **sp. n.** holotype ♀ NVG-23111F04 from Belize; **b–c)** *L. oilepanor* **sp. n.**: **b)** paratype ♀ NVG-23115C04 from Costa Rica, **c)** holotype ♀ NVG-23115C05 from Panama: Colón; **d)** *L. oilemarca* **sp. n.** holotype ♀ NVG-23115C10 from Peru: Cajamarca; **e–g)** *L. oilepanor* **sp. n.**: paratypes ♂♂ from Panama: **e)** NVG-21124B03 Chiriqui, **f)** NVG-23115C07 Panamá Oeste, **g)** NVG-23115C08 Panamá; and **h)** *L. oilemarca* **sp. n.** paratype ♂ NVG-19027C05 from Peru: Cajamarca.


e
f
g
h
1 cm

elements being dash-like, and less crescent-shaped; the white postdiscal spot in the ventral forewing cell R_{4+5}-M_1 is smaller than surrounding spots due to the dark brown element basad of it being larger; the discal and the basal brown spots in the ventral hindwing cell CuA_2-1A+2A are closer to each other; and the roundish brown spot between the basal and discal dark elongated spots in the ventral hindwing cell Sc+R_1-Rs is well-developed. Due to its cryptic nature and unexplored individual variation, this species is best identified by DNA, with diagnostic base pairs in the nuclear genome: cne6526.4.1:T759C, cne5645.4.3:A81T, cne10058.3.1:T209C, cne10058.3.1:T183A, cne937.1.9:C918T, cne3970.1.2:G66G (not A), cne2576.1.9:C195C (not T), cne4378.3.2:C180C (not T), cne13983.1.10:T3435T (not G), cne13983.1.10:T3513T (not C); and the COI barcode: T81C, A91C, T118C, T232C, 400T.

Barcode sequence of the holotype. Sample NVG-23111F04, 658 base pairs:

AACATTATATTTTATTTTTGGTATTTGAGCAGGAATAGTAGGAACATCTTTAAGTTTATTAATTCGAATAGAATTAGGTACACCAGGCTCCTTAATTGGAGATGATCAAATTTATAACACA
ATTGTTACCGCTCATGCTTTTATCATAATTTTTTTCATAGTTATACCTATTATAATTGGAGGATTCGGAAATTGATTAGTTCCATTAATATTAGGAGCTCCAGATATAGCCTTTCCACGAA
TAAATAATATAAGATTTTGATTATTACCCCCCTCATTATTTCTATTAATTTCAAGAAGTATTGTAGAAAATGGAGCAGGTACAGGATGAACAGTTTATCCCCCACTTTCATCTAATATTGC
CCATGGAGGTGCATCAGTAGATTTAGCTATTTTTTCTCTTCATTTAGCTGGAATTTCTTCAATTTTAGGAGCTATTAATTTTATTACAACTATTATTAATATACGAATTAATAATTTATCA
TTTGATCAAATACCTTTATTTGTTTGATCAGTTGGTATTACAGCTTTACTTCTACTTTTATCTTTACCTGTTTTAGCTGGAGCTATTACTATATTATTAACTGATCGTAATTTAAATACAT
CATTTTTCGATCCTGCTGGTGGAGGAGATCCTATTTTATATCAACATTTATTT

Type material. Holotype: ♀ deposited in the Carnegie Museum of Natural History, Pittsburgh, PA, USA (CMNH), illustrated in Fig. 9a, bears the following six rectangular labels (1st and 2nd handwritten, others printed with handwritten text shown in italics; 2nd on glassine paper, 5th pink, 6th red, others white): [Br. Hond: Stann Creek | Dist.: Middlesex 125 m. | 4. viii. 1964 E.C.Welling], [640 | ♀], [*LASAIA* | *OILEUS GODM* | det. H. Clench 1967], [Photo | 4.xi.70], [DNA sample ID: | NVG-23111F04 | c/o Nick V. Grishin], and [HOLOTYPE ♀ | Lasaia (Lochris) | oilenor Grishin].

Type locality. Belize: Stann Creek District, Middlesex, elevation 125 m.

Etymology. The name reflects the northernmost range for this *L. oileus* relative: *oile*[us from the]*nor*[th], and is treated as a noun in apposition.

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

Lasaia (*Lochris*) *oilepanor* Grishin, new species

https://zoobank.org/3343E429-47E7-42A3-9278-FE999ECBD5E7

(Figs. 8 part, 9b, c, e–g)

Definition and diagnosis. This is the second new species in the *Lasaia* (*Lochris*) *oileus* Godman, 1903 (type locality in southern Paraguay) complex, represented by a small series from Costa Rica to central Panama (Fig. 8 blue). Its barcode differs from *L.* (*L.*) *oileus* by 3% (20 bp) and from the new species described above by 4.7% (31 bp). The new species is similar to *L.* (*L.*) *oileus* and differs from it and other relatives by females having medium-sized and less prominent submarginal brown spots on the ventral forewing; postdiscal spots in ventral forewing cells M_1-M_2 and M_2-M_3 are strongly overlapping with each other along M_2 vein (almost separated in *L.* (*L.*) *oileus*); the darker-brown framing of the ventral discal brown bands on both wings is relatively straight, with elements being dash-like, and less crescent-shaped; the white postdiscal spot in the ventral forewing cell R_{4+5}-M_1 is similar in size to the surrounding spots and the dark brown element basad of it does not protrude distad; the discal and the basal brown spots in the ventral hindwing cell CuA_2-1A+2A are farther from each other; the roundish brown spot between the basal and discal dark elongated spots in the ventral hindwing cell Sc+R_1-Rs is well-developed; and males with typically more weakly developed grayish frosting towards the outer margin of the dorsal hindwing. Due to its cryptic nature and unexplored individual variation, this species is best identified by DNA, with diagnostic base pairs in the nuclear genome: cne836.4.12:G69T, cne836.4.12:C126T, cne505.2.16:T762A, cne505.2.16:A768T, cne505.2.16:C1308T; and the COI barcode: A334G, T463C, A484G, A526G, T547C.

Barcode sequence of the holotype. Sample NVG-23115C05, 658 base pairs:

AACATTATATTTTATTTTTGGTATTTGAGCAGGAATAGTAGGAACATCTTTAAGTTTATTAATTCGAATAGAATTAGGTATACCAGGTTCATTAATTGGTGATGATCAAATTTATAATACA
ATTGTCACCGCTCATGCTTTTATTATAATTTTTTTCATAGTTATACCTATTATAATTGGAGGATTTGGAAATTGATTAGTCCCATTAATATTGGGAGCCCCAGATATAGCTTTTCCACGAA
TAAATAATATAAGATTTTGATTATTACCCCCTTCATTATTTCTTTTAATTTCAAGAAGTATTGTAGAAAATGGAGCAGGTACAGGATGAACGGTTTACCCCCCACTTTCATCTAATATTGC
CCATGGAGGTGCATCAGTAGATTTAGCTATTTTTTCCCTTCATTTAGCAGGAATCTCATCAATTTTAGGAGCTATTAATTTTATTACTACTATTATTAACATACGAATTAATAATTTATCG
TTTGATCAAATACCTTTATTTGTTTGATCAGTTGGTATTACGGCTTTACTTCTACTTTTATCCTTACCTGTTTTAGCTGGAGCTATTACTATACTATTAACTGATCGTAATTTAAATACAT
CATTTTTTGACCCTGCTGGTGGGGGTGATCCCATTTTATATCAACATTTATTT

Type material. Holotype: ♀ deposited in the National Museum of Natural History, Smithsonian Institution, Washington, DC, USA (USNM), illustrated in Fig. 9c, bears the following six rectangular labels (3rd handwritten, others printed), five white: [Tabernilla | CanalZone | Panama], [AugBusck | Collector], [Lasaia | oileus | Godm.], [DNA sample ID: | NVG-23115C05 | c/o Nick V. Grishin], [USNMENT | {QR Code} | 01588439], and one red [HOLOTYPE ♀ | Lasaia (Lochris) | oilepanor Grishin]. **Paratypes:** 3♂♂ and 1♀ in USNM unless indicated: 1♀ NVG-23115C04, USNMENT 01588435 Costa Rica, Sixola River, Mar-old, Schaus and Barnes collection (Fig. 9b) and Panama: 1♂ NVG-21124B03 Chiriquí, 1886, Troetsch leg., coll. Staudinger [MFNB] (Fig. 9e); 1♂ NVG-23115C07, USNMENT 01588437 Panamá Oeste Province, Cerro Campana, 1500', 23-Jan-1965, G. B. Small (Fig. 9f); and 1♂ NVG-23115C08, USNMENT 01588436 Panamá Province, Bayano, 22-Oct-1974, G. B. Small (Fig. 9g).

Type locality. Panama: Colón Province, Gatún Lake area, former Tabernilla.

Etymology. The name reflects the range of this species mostly centered around Panama, and to the north of this *L. oileus* relative: *oile*[us from]*Pan*[ama and the n]*or*[th], and is treated as a noun in apposition.

Distribution. Currently known from Costa Rica and Panama.

Lasaia (*Lochris*) *oilemarca* Grishin, new species

https://zoobank.org/7393F683-B5BD-4409-BA7B-3A6D394DAA64

(Figs. 8 part, 9d, h)

Definition and diagnosis. This is the third new species in the *Lasaia* (*Lochris*) *oileus* Godman, 1903 (type locality in southern Paraguay) complex, represented by a pair from Cajamarca, Peru (Fig. 8 red). Its barcode differs from *L.* (*L.*) *oileus* by 3.5% (23 bp) and from the two new species described above by 3.6%–4.4% (24–29 bp). The new species is similar to *L.* (*L.*) *oileus* and differs from it and other relatives by females having smaller and the least prominent submarginal brown spots on the ventral forewing, which is generally paler and with more extensive whitish areas; postdiscal spots in ventral forewing cells M_1-M_2 and M_2-M_3 are strongly overlapping with each other along M_2 vein (almost separated in *L.* (*L.*) *oileus*); darker-brown framing of the ventral discal brown bands on both wings is strongly scalloped, with elements being crescent-shaped; the white postdiscal spot in the ventral forewing cell R_{4+5}-M_1 is similar in size to the surrounding spots and the dark brown element basad of it does not protrude distad; the discal and the basal brown spots in the ventral hindwing cell CuA_2-1A+2A are farther from each other; the roundish brown spot between the basal and discal dark elongated spots in the ventral hindwing cell Sc+R_1-Rs is vestigial and lacking in males; and males have more extensive whitish areas on the ventral side. Due to its cryptic nature and unexplored individual variation, this species is best identified by DNA, with diagnostic base pairs in the nuclear genome: cne5180.2.2:C396T, cne5180.2.2:T399A, cne256.3.4: A87T, cne2685.14.2:C42T, cne2685.14.2:T54C; and the COI barcode: T313C, A376C, T475C, T500C, A565G.

Barcode sequence of the holotype. Sample NVG-23115C10, 658 base pairs:

AACATTATATTTTATTTTTGGTATTTGAGCAGGAATAGTAGGAACATCTTTAAGTTTATTAATTCGAATAGAATTAGGTATACCAGGCTCATTAATTGGTGATGATCAAATTTATAATACT
ATTGTTACCGCTCATGCTTTTATTATAATTTTTTTCATAGTTATACCTATTATAATTGGAGGATTTGGAAATTGATTAGTCCCATTAATATTAGGAGCTCCAGATATAGCATTTCCACGAA
TAAATAATATAAGATTTTGATTATTACCTCCCTCATTATTTCTTTTAATTTCAAGAAGTATTGTAGAAAACGGAGCAGGTACAGGATGAACAGTTTACCCCCCACTTTCATCTAATATTGC
CCATGGAGGTGCCTCAGTAGATTTAGCTATTTTTTCTCTTCATTTAGCGGGAATTTCATCAATTTTAGGAGCTATTAATTTTATTACTACTATTATTAATATACGAATTAACAATATATCA
TTTGATCAAATACCCCTATTTGTTTGATCAGTTGGTATTACAGCTTTACTTCTACTTTTATCTTTACCTGTTTTAGCTGGGGCTATTACTATATTACTAACTGATCGTAATTTAAATACAT
CATTTTTTGATCCTGCTGGTGGAGGAGATCCTATTTTATATCAACATTTATTT

Type material. Holotype: ♀ currently deposited in the National Museum of Natural History, Smithsonian Institution, Washington, DC, USA (USNM), illustrated in Fig. 9d, bears the following four printed rectangular labels, three white: [PERU: Cajamarca: | Chilasque, 1200m, | 06°01'S 79°12'W | 12 June 2000 | Robbins & Lamas Leg.], [DNA sample ID: | NVG-23115C10 | c/o Nick V. Grishin], [USNMENT | {QR Code} | 01588443], and one red [HOLOTYPE ♀ | Lasaia (Lochris) | oilemarca Grishin]. **Paratype:** 1♂ NVG-19027C05, USNMENT 01544152 with the same data as the holotype (Fig. 9h).

Type locality. Peru: Cajamarca, Chilasque, elevation 1200 m, GPS −6.0167, −79.2000.

Etymology. The name reflects the type locality of this *L. oileus* relative: *oile*[us from Caja]*marca*, and is treated as a noun in apposition.

Distribution. Currently known only from the type locality in Cajamarca, Peru.

Emesis (*Tenedia*) *peripore* Grishin, new species

https://zoobank.org/F221899B-0B0D-4B4F-9BB4-4F2BDC005965

(Figs. 10 part, 11)

Definition and diagnosis. Genomic analysis reveals that specimens from Trinidad initially identified as *Emesis* (*Tenedia*) *ocypore aethalia* H. Bates, 1868 (type locality in Colombia: Santa Marta) are genetically differentiated from it at the species level (Fig. 10); e.g., their COI barcodes differ by 4.2% (28 bp), and therefore these specimens represent a new species that is sister to *Emesis* (*Tenedia*) *ocypore ocypore* (Geyer, 1837) (type locality in "Africa", likely an Amazonian species), including the nominotypical subspecies and *E.* (*T.*) *ocypore aethalia*, in both nuclear (Fig. 10a) and mitochondrial (Fig. 10b) genome trees. This new species is phenotypically most similar to *E.* (*T.*) *ocypore aethalia*, but differs from it and the nominotypical subspecies by males with a more prominent dark-brown pattern on a brown ground color, e.g., the submarginal and postdiscal rows on the dorsal forewing consist of thicker lunules and the discal band is composed of thicker dashes; the submarginal and postdiscal lunules are more strongly bowed and more sharply defined on both sides of both wings, and on the ventral side, some are boomerang-shaped (postdiscal towards the tornus), but the submarginal ones ventrally are mostly reduced to rounded or somewhat elongated latitudinally spots, which are typically larger than in *E. ocypore*; the dark-brown dashes in the discal row on the ventral hindwing are more aligned with each other, e.g., the dashes in cells M_3-CuA_1 and CuA_1-CuA_2 are closer to each other and the second one is shifted basad less prominently; and the costal margin of the forewing is moderately concave in the middle and strongly convex towards the apex. These phenotypic differences are more in line with this taxon being a subspecies, but the very prominent genetic differentiation both in the nuclear and mitochondrial genome points to its species level. Due to its cryptic nature and unexplored individual variation, this species is best identified by DNA, with diagnostic base pairs in the nuclear genome: cne2783.8.1:A219C, cne1493.28.10:C87T, cne1493.28.10:C114T, cne776.4.3:G88A, cne2685.11.8:G33A; and the COI barcode: T55C, A73G, T163C, T364C, A388T.

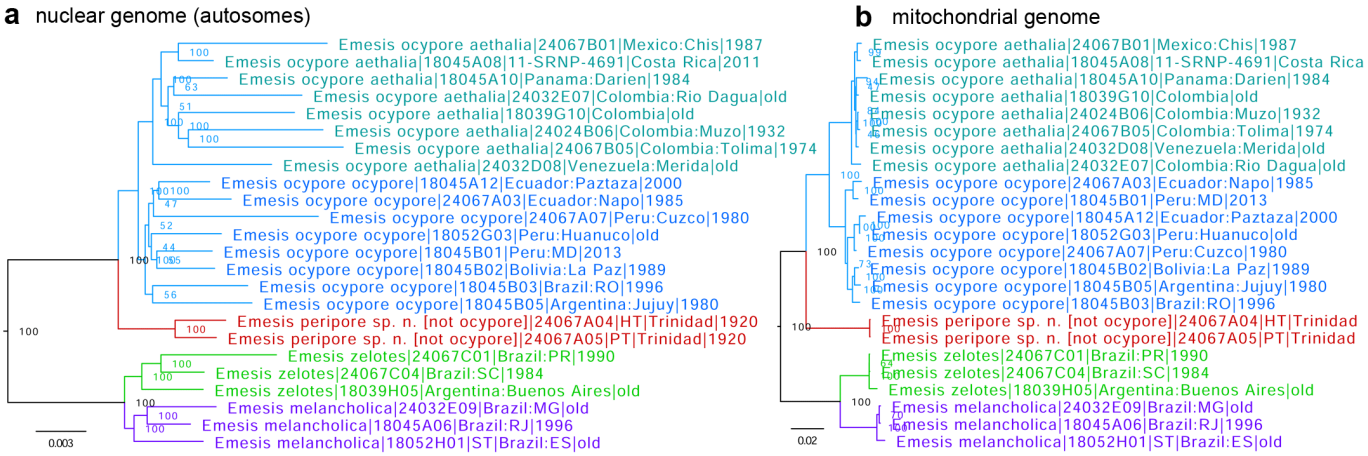

Fig. 10. Phylogenetic trees of *Emesis* (*Tenedia*) *ocypore* and close relatives constructed from protein-coding regions in: **a)** the nuclear genome (autosomes), based on 4,151,547 positions, and **b)** the mitochondrial genome. Different species are colored differently: *E.* (*T.*) *ocypore* (blue, with *E.* (*T.*) *ocypore aethalia* labeled in cyan), *E.* (*T.*) *peripore* **sp. n.** (red), *E.* (*T.*) *zelotes* (green), and *E.* (*T.*) *melancholica* (purple). Ultrafast bootstrap (Hoang et al. 2018) values are shown at nodes.

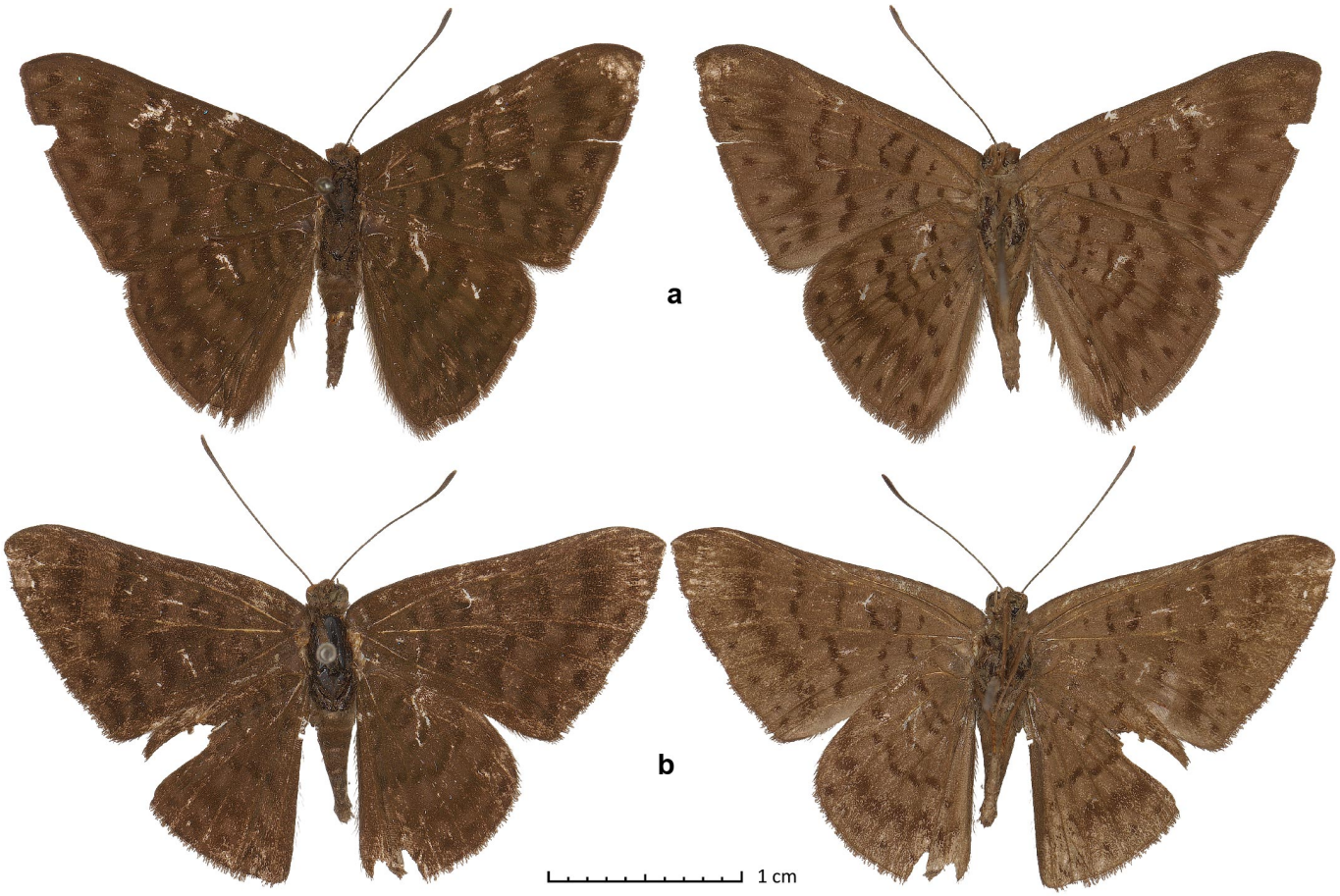

Fig. 11. *Emesis* (*Tenedia*) *peripore* **sp. n.** type series from Trinidad, in dorsal (left) and ventral (right) views, data in text: **a)** holotype ♂ NVG-24067A04 and **b)** paratype ♂ NVG-24067A05.

Barcode sequence of the holotype. Sample NVG-24067A04, 658 base pairs:

AACATTATATTTTATTTTTGGAATTTGAGCAGGAATAGTAGGTACATCTTTAAGCTTATTAATTCGAATAGAGCTAGGAACTTCAGGATCTTTAATTGGAGATGATCAAATTTATAATACT
ATTGTCACAGCTCATGCTTTTATTATAATTTTTTTTATAGTCATACCAATTATAATCGGAGGATTTGGAAATTGATTAGTCCCATTAATATTAGGAGCCCCAGATATAGCTTTTCCACGAA
TAAATAATATAAGATTTTGATTACTACCCCCATCACTAATTTTATTAATTTCAAGAAGAATTGTTGAAAATGGAGCTGGAACAGGATGAACAGTGTACCCCCCACTTTCATCTAATATTGC
CCATAGAGGATCATCAGTAGATCTTGCTATTTTTTCTCTTCATTTAGCTGGTATTTCTTCTATTTTAGGAGCAATTAATTTTATTACTACTATTATTAATATACGAATTAATAATTTATCA
TTTGATCAAATACCCCTTTTTATCTGATCGGTAGGTATTACAGCTCTTTTACTCTTATTATCTTTACCTGTATTAGCGGGAGCTATTACTATACTATTAACAGATCGTAATTTAAATACAT
CATTTTTTGACCCAGCAGGAGGAGGAGATCCAATTTTATACCAACATTTATTT

Type material. Holotype: ♂ deposited in the McGuire Center for Lepidoptera and Biodiversity collection, Gainesville, FL, USA (MGCL), illustrated in Fig. 11a, bears the following four rectangular labels (2nd handwritten, others printed with handwritten text shown in italics), three white: [*Siparia* | Trinidad. | Oct.—Dec., 1920. | A. Hall.], [Emesis | aethalia,Bates], [DNA sample ID: | NVG-24067A04 | c/o Nick V. Grishin], and one red [HOLOTYPE ♂ | Emesis (Tenedia) | peripore Grishin]. **Paratype:** 1♂ NVG-24067A05 with the same data as the holotype (Fig. 11b).

Type locality. Trinidad and Tobago: Trinidad, Siparia.

Etymology. The name of its sister species, *E.* (*T.*) *ocypore*, could mean 'swift passage' or 'fast-moving way', possibly originating from the Ancient Greek words: ὠκύς (ōkys) meaning 'swift', 'quick', or 'fast', and πόρος (poros) meaning 'passage', 'way', or 'pore'. Occupying a vast range from Mexico to South Brazil, *E. ocypore*, has a sister species living on a periphery of this 'way' and named here *peripore*, from Greek περί (peri) meaning 'around' or 'on the outskirts'. The name is treated as a noun in apposition.

Distribution. Currently known only from the type locality in Trinidad.

Comment. Genetic differentiation between this new species (Fig. 10 red) and *E.* (*T.*) *ocypore* (Fig. 10 blue) is about the same as — if not smaller than — that between *E.* (*T.*) *zelotes* Hewitson, 1872 (type locality in Brazil, likely Southeast or South) (Fig. 10 green), and *E.* (*T.*) *melancholica* Stichel, 1916 (type locality in Brazil: Espírito Santo) (Fig. 10 purple); e.g., the COI barcodes of the latter pair differ by 3.8% (25 bp).

Female paratypes of recently described species with strong sexual dimorphism

Here, we illustrate female paratypes of most strongly sexually dimorphic species described in Zhang et al. (2025b) that were not shown in the original publication. To highlight the degree of sexual dimorphism and facilitate comparison, holotypes are also illustrated (Figs. 12a, 13a, 14a) next to paratypes (Figs. 12b, 13b, 14b).

The female paratype of *Bungalotis lotis* Grishin, 2025 (type locality in Belize: Cayo) (Fig. 12b) is brown with white hyaline forewing spots and diffuse darker brown (in some specimens white-centered) ventral hindwing spots, thus differing strongly from orange or orange-yellow males, but is similar to females of the closely related *Bungalotis midas* (Cramer, 1775) (type locality in Suriname), differing from them by slightly narrower forewing hyaline spots in the discal band (e.g., the spot in cell CuA_1-CuA_2 is narrowing more strongly towards the vein CuA_2) and better developed small hyaline submarginal spots in cell M_2-M_3 than subapical spots between veins R_3 and M_2. The opposite is typically true for *B. midas* (i.e., the subapical spots are better developed than submarginal, or lacking altogether), but additional specimens of *B. lotis* are needed to substantiate these putative differences. Data for illustrated specimens: holotype ♂ NVG-23109C01 (abdomen), NVG-24015D03 (leg) Belize, Cayo District, San Ignacio, Cristo Ray Rd., 17-Jun-1990, Morton S. Adams leg., genitalia vial NVG250720-47 [CMNH] (Fig. 12a) and paratype ♀ NVG-23109C02 with the same data but 17–18-May-1990 and "Cristo Ray Rd." not specified on the label (Fig. 12b).

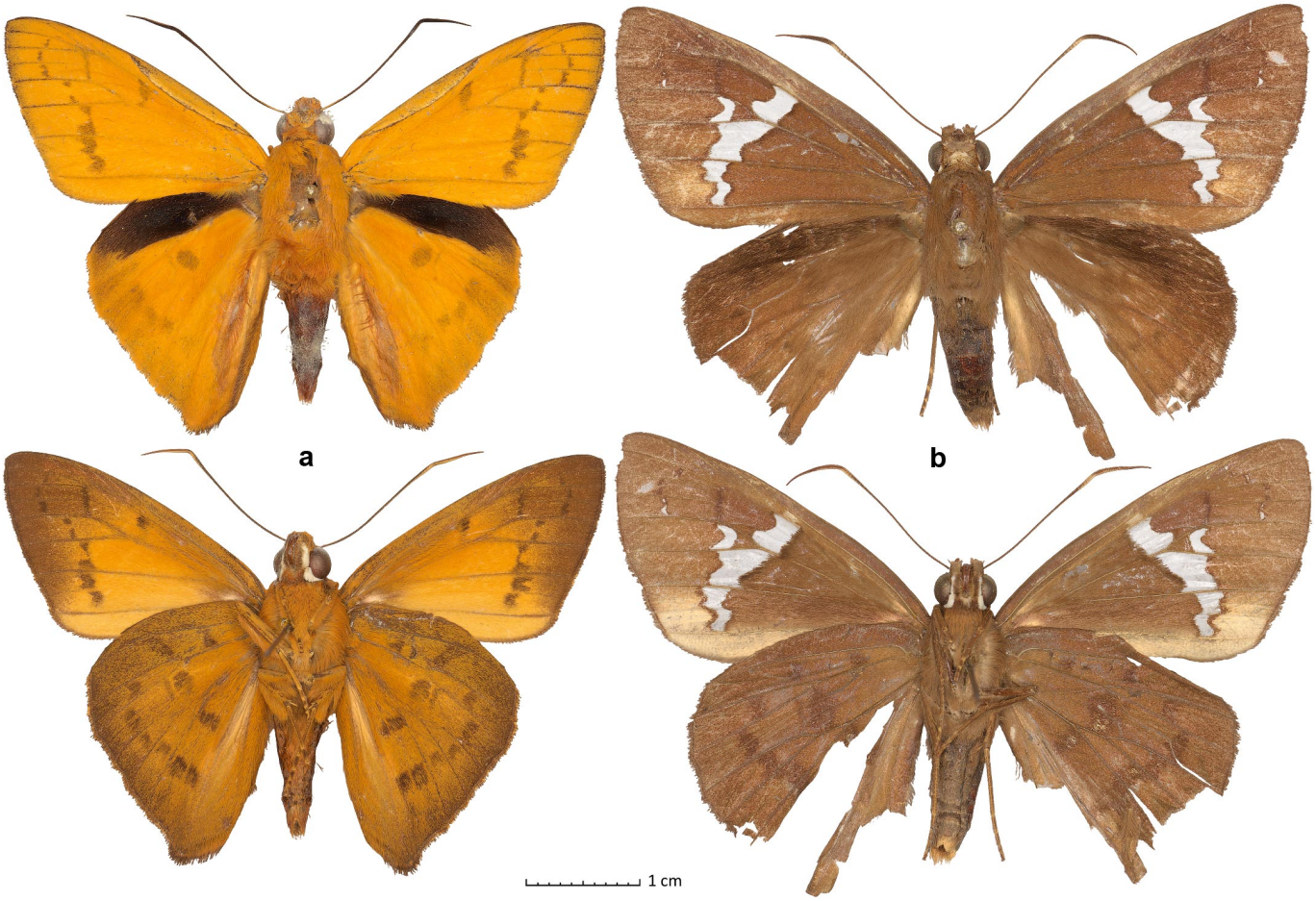

Fig. 12. *Bungalotis lotis* from Belize in dorsal (top) and ventral (bottom) views, data in text: **a)** holotype ♂ NVG-23109C01 and **b)** paratype ♀ NVG-23109C02.

The female paratype of *Molo reticulatus* Grishin, 2025 (type locality in Ecuador: Esmeraldas) (Fig. 13) has an entirely dark-brown hindwing (paler and with reddish tint beneath with vestigial postdiscal orange spots) and reduced orange-yellow spots on the forewing and may not be easy to recognize as this species without association by DNA. Data for illustrated specimens: Ecuador, Esmeraldas Province [USNM]: holotype ♂ NVG-18117B06 (leg), NVG-23121C06 (abdomen), USNMENT 01531677, Río Cachaví, 1 km W of Alto Tambo, 725 m, GPS 0.9123, −78.5472, 2-Mar-2001, D. H. Ahrenholz leg., genitalia vial NVG241121-73 (Fig. 13a) and paratype ♀ NVG-18117C04, USNMENT 01531687 37 km N of Pero Vicente Maldonado, Ruminahui, 500 m, GPS 0.2788, −78.9983, Apr-2001. I. Aldas leg. (Fig. 13b).

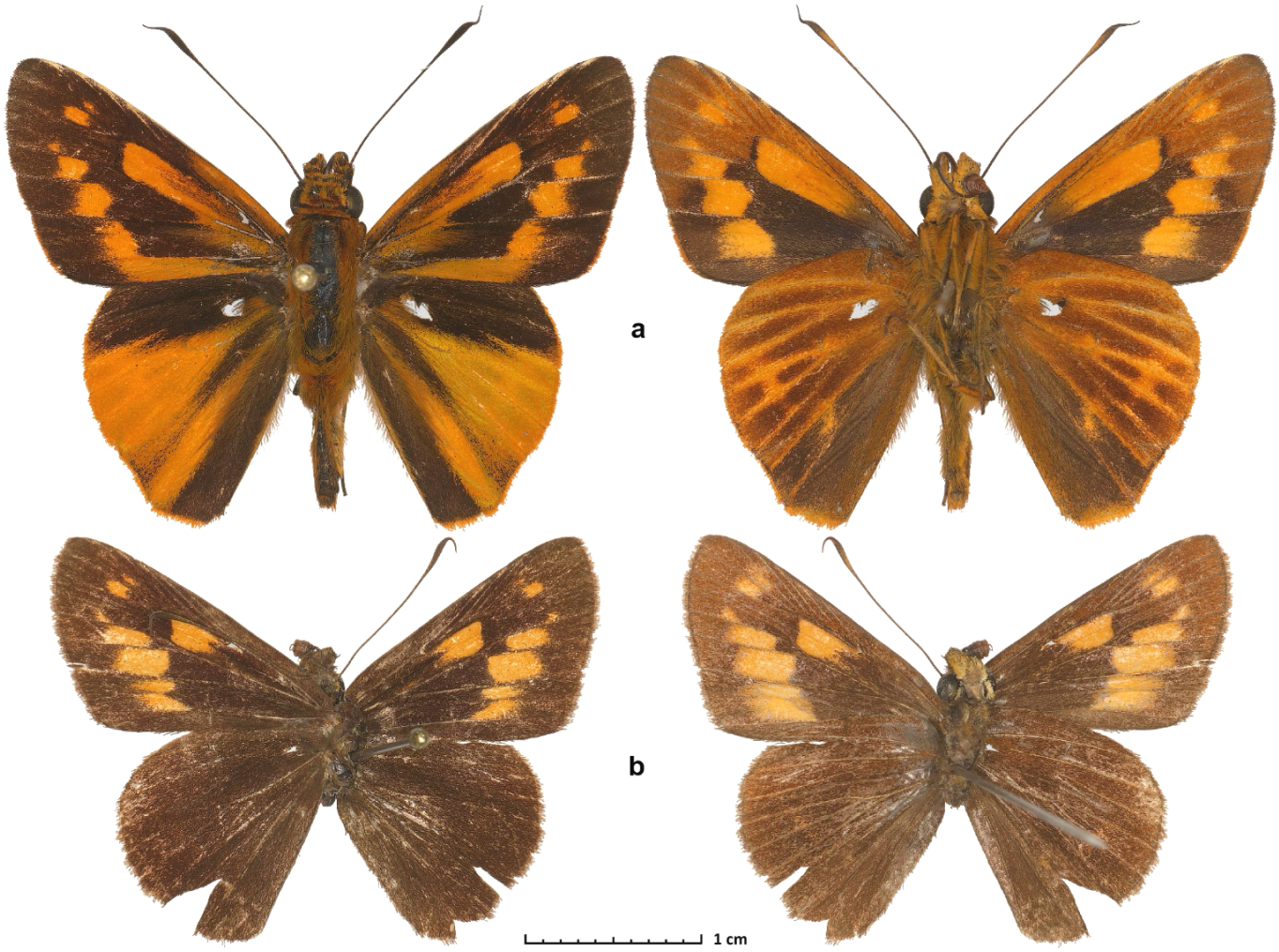

Fig. 13. *Molo reticulatus* from Ecuador in dorsal (left) and ventral (right) views, data in text: **a)** holotype ♂ NVG-18117B06 and **b)** paratype ♀ NVG-18117C04.

The female paratype of *Calvetta calva* Grishin, 2025 (type locality in Panama: Colón) (Fig. 14) differs from a male by having a ventral hindwing discal pale band rather than a central spot, a larger whitish area near the anal margin on the ventral forewing, and broader subapical semihyaline white spots. The female differs from its sister species *Calvetta calvina* (Hewitson, 1866) (type locality in Brazil: Pará) mostly by the outer edge of the pale spots in the ventral hindwing cell Rs-M_1 aligned with the edge of the rest of the oblique pale band and not strongly offset distal. Data for illustrated specimens: Panama, Colón Province [USNM]: holotype ♂ NVG-23122E09, Santa Rita Arriba, 1500', 31-Dec-1968, S. S. Nicolay leg., genitalia vial NVG250720-52 (Fig. 14a) and paratype ♀ NVG-23122E11 Gatún, 27-Jan-1973, G. B. Small leg. (Fig. 14b).

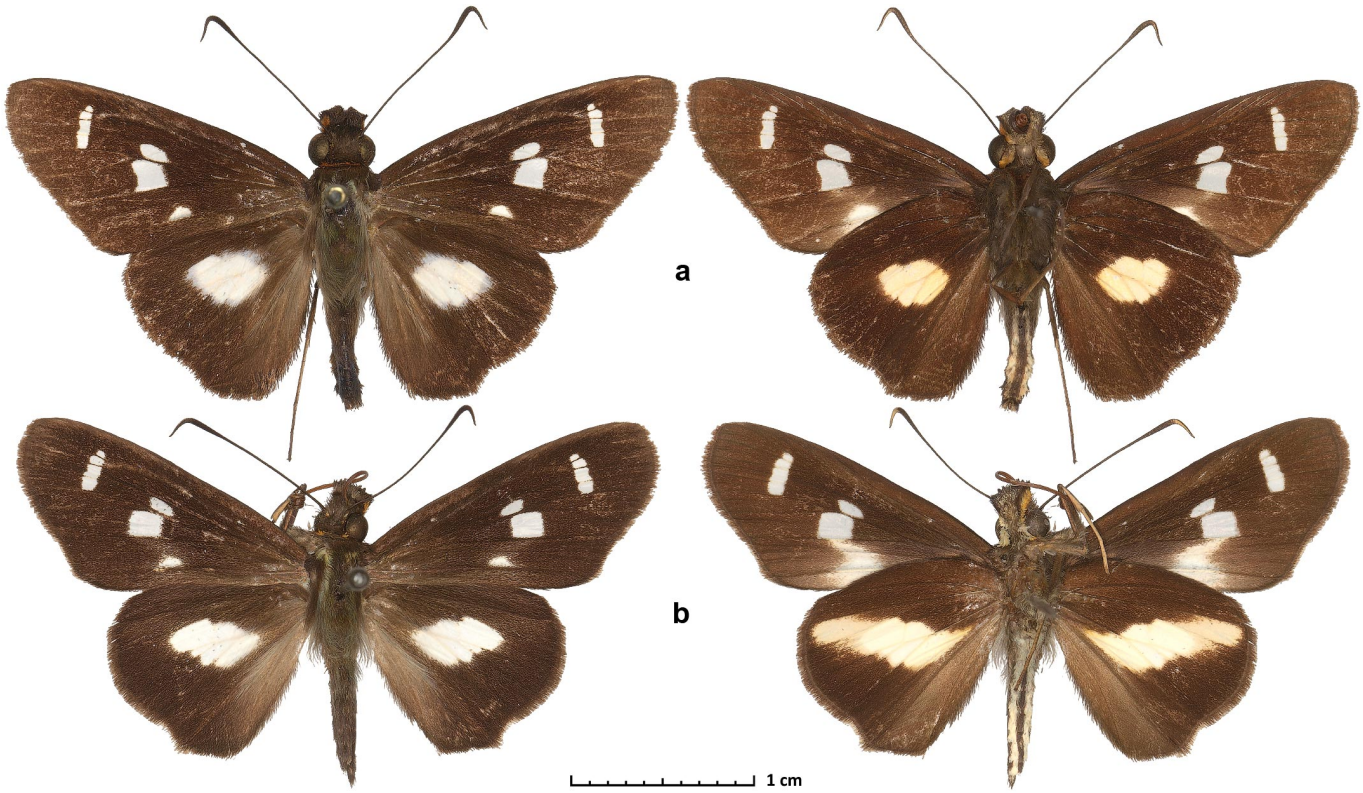

Fig. 14. *Calvetta calva* from Panama in dorsal (left) and ventral (right) views, data in text: **a)** holotype ♂ NVG-23122E09 and **b)** paratype ♀ NVG-23122E11.

Subfamily Coeliadinae Evans, 1937

Burara gomata (Moore, [1866]) is a complex of several species

Burara gomata (Moore, [1866]) was described from more than one specimen, only males, from "N.E. Bengal" in the collections of A. E. Russell and F. Moore (two different collections mentioned, which means more than one specimen). Localities of higher precision, e.g., Darjeeling (which is within northeastern Bengal), were listed by Moore for some other species in the same work (Moore [1866]). Because no specific single locality was given for *B. gomata*, it is likely that the type series came from several localities in this broader region of "N.E. Bengal" and could have been polytypic. The description of *B. gomata* stated that the ventral side of wings of this species was "dark brown" (Moore [1866]). Swinhoe (1911–1912), continuing the work of Moore, illustrated *B. gomata* consistently with the original description and showing the ventral side of a darker male with limited pale overscaling along the veins within brown areas between pale streaks. However, this drawing (Swinhoe 1911–1912: pl. 748, fig. 3[b]) does not seem to be particularly accurate in details of the wing pattern and may not be identifiable to species, because it combines characters of more than one species.

Evans (1949) treated *B. gomata* as a polytypic species with five additional subspecies (noting that their genitalia were similar) and two junior subjective synonyms, listed here in their original combinations and type localities (in parentheses): *Ismene gomata lara* Leech, 1893 (western China), *Ismene gomata kanara* Evans, 1926 (India: North Kanara), *Ismene gomata lalita* Fruhstorfer, 1911 (West Sumatra) with its junior subjective synonym *Ismene gomata vajra* Fruhstorfer, 1911 (West Java), *Ismene lorquini* Mabille, 1876 (Philippines: Luzon) with its junior subjective synonym *Ismene mindorana* Fruhstorfer, 1911 (Philippines: Mindoro), and *Ismene radiosa* Plötz, 1885 (Sulawesi). This treatment has not changed since, and was adopted in the latest revision of the subfamily Coeliadinae by Chiba (2009) with an additional subspecies described from Mindanao, Philippines as *Burara gomata minda* Chiba & Tsukiyama, 2009.

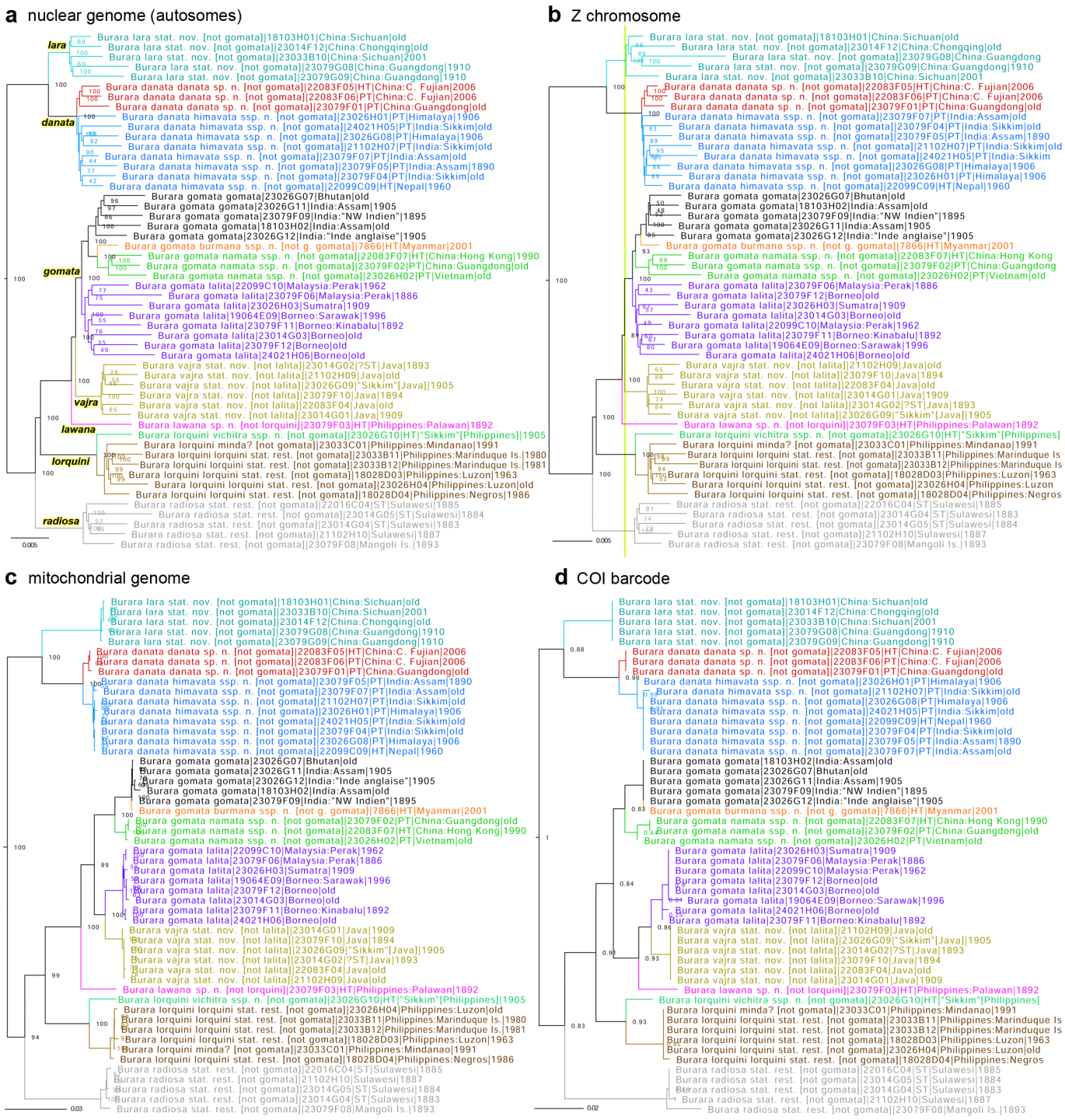

Fig. 15. Phylogenetic trees of the *Burara gomata* group taxa constructed from protein-coding regions in: **a)** the nuclear genome (autosomes), based on 2,971,287 positions, **b)** the Z chromosome, based on 155,799 positions, and **c)** the mitochondrial genome; and **d)** a FastTree (Price et al. 2009) dendrogram constructed from COI barcodes using NGPhylogeny.fr server (Lemoine et al. 2019). Different taxa are colored differently: *B. lara* **stat. nov.** (cyan), *B. danata danata* **sp. n.** (red), *B. danata himavata* **ssp. n.** (blue), *B. gomata gomata* (black), *B. gomata burmana* **ssp. n.** (orange), *B. gomata namata* **ssp. n.** (green), *B. gomata lalita* (purple), *B. vajra* **stat. nov.** (olive), *B. lawana* **sp. n.** (magenta), *B. lorquini vichitra* **ssp. n.** (aquamarine), *B. lorquini lorquini* **stat. rest.** (brown, together with a possible specimen of *B. lorquini minda* **comb. nov.**), *B. radiosa* **stat. rest.** (gray). Species names are placed by their clades in the autosome tree (a), and a pale-green line cuts through the Z chromosome tree (b) at the species level. Ultrafast bootstrap (Hoang et al. 2018) values are shown at nodes of genomic trees.

We sequenced whole genome shotgun datasets of all these taxa except *Burara gomata kanara* (Evans, 1926) and *Ismene mindorana* Fruhstorfer, 1911. Without genomic data, we do not see a reason to challenge the current taxonomic placement of these two names and maintain the former as a subspecies of

B. gomata and the latter as a junior subjective synonym of *I. lorquini*. However, genomic analysis of all other taxa does not support *B. gomata* as a single polytypic species, but reveals that *B. gomata* is a complex consisting of seven species (two new) and seven additional subspecies (four new), including *B. gomata kanara* (which we have not sequenced) and *B. gomata minda*, although a male from Mindanao that we tentatively identified as this taxon did not differ significantly from *I. lorquini* in its DNA (Fig. 15 brown). Thus, we define the *B. gomata* group to consist of these seven species and discuss the species delineation process that led to this conclusion after describing the new taxa below. We regard major clades in the nuclear genome trees as species (Fig. 15a, b), labeled by species names in the autosome tree (Fig. 15a); and the greenish vertical line in the Z chromosome tree is placed to cut through the species clades (Fig. 15b). Geographic variation within species is denoted by subspecies names and major genomic clusters within species

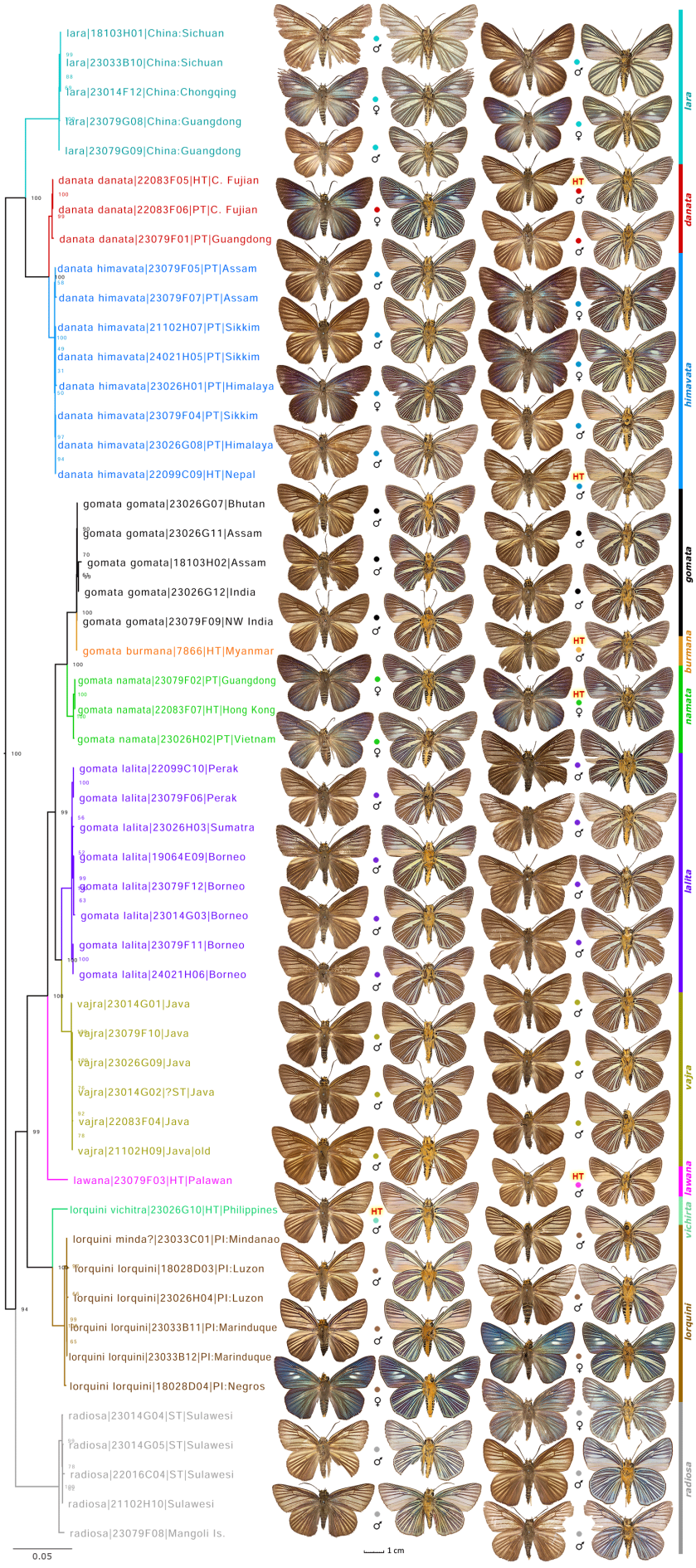

Fig. 16. Sequenced specimens of the *Burara gomata* group in dorsal (left of the dot) and ventral (right of the dot) views, aligned with the mitochondrial genome tree shown on the left (duplicated from Fig. 15c). Specimens are arranged following the tree order, in two alternating columns: one specimen in the left column, the next in the right column slightly lower, then next in the left column, etc., such that each specimen's thorax is best aligned with its corresponding label in the tree. Holotypes are marked by red 'HT' label highlighted yellow. A dot between the dorsal and ventral image of the same specimen is colored according to the taxon color used in the tree and in the right bar: *B. lara* **stat. nov.** (cyan), *B. danata danata* **sp. n.** (red), *B. danata himavata* **ssp. n.** (blue), *B. gomata gomata* (black), *B. gomata burmana* **ssp. n.** (orange), *B. gomata namata* **ssp. n.** (green), *B. gomata lalita* (purple), *B. vajra* **stat. nov.** (olive), *B. lawana* **sp. n.** (magenta), *B. lorquini vichitra* **ssp. n.** (aquamarine), *B. lorquini* **stat. rest.** (brown, with a possible male of *B. lorquini minda* **comb. nov.**), *B. radiosa* **stat. rest.** (gray).

are defined as subspecies, which typically have unique mitochondrial genome (and COI barcode) haplotypes (Fig. 15c, d). Due to having discrete haplotypes, different taxa stand out more clearly in the mitochondrial genome tree (Fig. 15c), and therefore, images of all *B. gomata* group specimens we sequenced are shown projected on the mitogenome tree (Fig. 16).

The most surprising result of our analysis is that two *B. gomata* group species are sympatric in the "N.E. Bengal" area (Figs. 15, 16 black and blue, Fig. 19, compare c and d with a and b), which is the type locality of *B. gomata*. Males of the first species have "dark brown" (Moore [1866]) ventral side of wings thus agreeing with the original description of *B. gomata* (although the type series might have been polytypic); a paler base of the dorsal forewing cell CuA_1-CuA_2 that is more prominent than pale streaks in the subapical area and a larger, broader in the middle, lanceolate pale patch (not a streak) in cell Rs-M_1 of the dorsal hindwing, both dorsal characters illustrated in Swinhoe (1911–1912: pl. 748, fig. 3, the left half is more clear, although Swinhoe amalgamates characters of both species in the ventral illustration 3^b); "narrowly pale" veins on the ventral forewing (Evans 1949); and was illustrated by an unambiguously identifiable photograph in the comprehensive Coeliadinae revision as *B. gomata gomata* by Chiba (2009) (Fig. 19c, d). In addition, this species has a developed broad pale "tooth" (sometimes with a small notch basad of it) in the middle of the posterior side of the central pale ray on the ventral hindwing (Chiba 2009: pl. 4, fig. 1), as also illustrated by de Nicéville (1883 [1884]), although his illustration refers to *B. gomata kanara* female from India: Kerala, Wayanad. This "tooth" is a pale spot on the discocellular vein that merges with the pale ray and extends beyond the ray's posterior margin—and, if the ray is narrow, also beyond the anterior margin (Fig. 19c, d). Finally, the pale streak in the ventral hindwing cell Sc+R_1-Rs is narrow, similar to the streaks in other cells, and not broader in the middle (Figs. 16 black, 19c, d); and the ventral hindwing vein M_2 is broadly overscaled with cream scales in it basal half, thus the dark brown ground color is absent on both sides of the vein, which is fused with the pale streaks in the middle of cells M_1-M_2 and M_2-M_3 being entirely cream-colored (i.e., two brown streaks, one on each side of the paler M_2 vein, extend from the outer wing margin to approximately half of the distance form the margin to the discal cell, where they do not merge with each other, but the two pale streaks are merged from that point basad) (Fig. 19c, d).

Males of the second species (Fig. 19a, b) are characterized by a paler ventral side, which is mostly pale yellow to tan with brown streaks; the pale streaks in the subapical area of the dorsal forewing that are more prominent than the pale coloration in cell CuA_1-CuA_2; a narrow pale streak (broader at the base) in cell Rs-M_1 of the dorsal hindwing (not a lanceolate patch broader in the middle); more extensive pale overscaling along the veins on the ventral forewing; the lack of the tooth in the middle of the posterior margin of the ventral hindwing pale ray; the pale streak in the ventral hindwing cell Sc+R_1-Rs, which is more prominent than in other cells and is broader in the middle in this species (Fig. 16 blue, 19a, b); and the ventral hindwing vein M_2 is narrowly overscaled with cream scales that are nearly lacking in its basal part, thus the dark-brown ground color is present on both sides of the vein from its base (i.e., two dark-brown streaks, one on each side of the paler M_2 vein, extend from the outer wing margin to the discal cell, where they merge with each other) (Fig. 19a, b).

The original description, Swinhoe (1911–1912: pl. 748 fig. 3, 3^b) illustrations (imperfectly for the ventral side drawing 3^b), Evans's (1949) treatment (incompletely), and the revision of Coeliadinae by Chiba (2009) (see pl. 4 fig. 1 for his illustration definitively of a darker species) agree better with the darker species being *B. gomata*, although these workers may not have distinguished between the two species, likely viewing the differences (if noticed) as individual variation. According to our analysis, this darker species has a wider distribution, ranging from southern India through the Himalayas to the Malay Peninsula and the islands of Sumatra and Borneo, thus agreeing with the historical treatment of *B. gomata* in literature and its curation in collections. For the stability of nomenclature ("The objects of the Code are to promote stability and universality in the scientific names of animals …" quoted from the preamble of the ICZN Code, 1999), in this work, we apply the name *B. gomata* to this darker species and are searching for additional specimens from the type series of *B. gomata* to possibly formalize this choice by a lectotype designation.

We note that mentions of “The type male” by Swinhoe (1911–1912), “type B.M.” by Evans (1949) and “Holotype: Male, [INDIA], "Darjiling 79.57," BMNH H2406” by Chiba (2009) do not seem to be valid lectotype designations, because “the original work reveals that the taxon had been based on more than one specimen” (Art. 74.5), neither Swinhoe nor Evans “have unambiguously selected a particular syntype to act as the unique name-bearing type of the taxon” (Art. 74.5), it is not true that “the original description neither implies nor requires that there were syntypes” (Art. 74.6), and Chiba (2009) was published after 1999 (Art. 74.7) (ICZN 1999). The original description lists two collections for *B. gomata* specimens (A. E. Russell collection and F. Moore collection) and therefore implies that more than one specimen was included in the type series (i.e., “there were syntypes”). Furthermore, neither Swinhoe (1911–1912: 238) nor Evans (1949: 50) made it clear which specific specimen they were referring to as “type” (it could have been two different specimens, one of Swinhoe and the other of Evans). While Chiba (2009: 12) explicitly gave the specimen number in the BMNH collection that can be traced to a particular (possible) syntype, his work was published after 1999. We also note that Swinhoe (1911–1912: 238) stated “The type male is marked N.E. Bengal” and Chiba (2009: 12) referred to “Darjiling” (the latter being a specific locality within the former) and may have referenced different specimens.

Having defined *B. gomata* for the purpose of this work as the darker species (Figs. 15, 16 black), we proceeded by assigning available names to clades in the genomic trees (Fig. 15). Only one clade was objectively defined by primary type specimens, *Ismene radiosa*, with two male (NVG-22016C04, NVG-23014G05) and one female (NVG-23014G04) syntypes sequenced (Figs. 15, 16 gray). A possible syntype (NVG-23014G02, a specimen labeled by H. Fruhstorfer as collected by him in Aug 1893 on Mount Gede, West Java, in ZMSC, but not explicitly labeled as a syntype) of *I. gomata vajra* is used to assign the name to that clade (Figs. 15, 16 olive). The remaining names were attributed based on phenotype (agreeing with the original descriptions and extant primary type specimens) and geographic locality by genomic sequencing of topotypical specimens. Specimens from Sichuan, China (NVG-18103H01, NVG-23033B10), with a broad pale, cream-colored, central ray on the hindwing that covers the entire discal cell on both sides of the wing, bifurcates and extends nearly to the outer margin on the dorsal side, and reaches the outer margin as an almost equal width band on the ventral side, were identified as *I. gomata lara* (Figs. 15, 16 cyan). A specimen from Medan, Sumatra (NVG-23026H03), with a slightly darker dorsal hindwing and narrower pale streaks on the dorsal hindwing was used as a reference for *I. gomata lalita* (Figs. 15, 16 purple). Finally, males from Luzon, Philippines (NVG-18028D03, NVG-23026H04), which are paler above and have cream-colored forewing discal cell below (except a narrow brown streak in the middle, better expressed towards the distal end of the cell) are *I. lorquini*; and a single male from near Mount Kalatungan, Mindanao (NVG-23033C01) was tentatively identified (by the locality only, because this taxon has been described from female(s)) as *B. gomata minda* (Figs. 15, 16 brown). Genomic sequencing of this male did not reveal strong genetic differentiation from *I. lorquini* specimens and placed it among them in all trees (Figs. 15, 16 brown).

Genomic analysis reveals that the following taxa are genetically differentiated from *B. gomata* at the species level (Fig. 15, see discussion below), and therefore we propose to treat them as species: *Burara lara* (Leech, 1893), **stat. nov.**, *Burara vajra* (Fruhstorfer, 1911), **stat. nov.**, *Burara lorquini* (Mabille, 1876), **stat. rest.**, and *Burara radiosa* (Plötz, 1885), **stat. rest**. Due to lower, but notable, genetic differentiation, we keep *Burara gomata lalita* Fruhstorfer, 1911 as a subspecies of *B. gomata* pending additional studies. We tentatively propose a new species-subspecies combination (a taxonomic category, not a new combination in nomenclature, which is defined as a combination with a genus-group name) *Burara lorquini minda* Chiba & Tsukiyama, 2009, **comb. nov.**, because a specimen we sequenced from near the type locality of this taxon was placed among *B. lorquini* specimens in genomic trees, an issue to be further investigated by genomic sequencing of the holotype of this subspecies.

Species- and subspecies-level clades of the genomic trees that do not correspond to described taxa represent new taxa that are described next: two new species and four new subspecies.

Burara danata Grishin, new species

https://zoobank.org/F6174F66-8961-40B1-B46E-1AA9D7F33C12

(Figs. 15–16 part, 17, 22b)

Definition and diagnosis. Genomic analysis reveals that specimens from southeastern China initially identified as *Burara gomata* (Moore, [1866]) (type locality in N.E. Bengal) are genetically differentiated from it at the species level (Fig. 15, 16 red vs. black); e.g., their COI barcodes differ by 4.3% (28 bp), and therefore these specimens represent a new species. This new species keys to "*Bibasis gomata gomata*" (A.1.13(c)) in Evans (1949), but differs from it and other relatives by the following combination of characters in both sexes: paler ventral side, predominantly pale yellow to tan with brown streaks; more extensive pale overscaling along the veins of the ventral forewing; absence of a tooth in the middle of the posterior margin of the ventral hindwing pale ray; the pale streak in the ventral hindwing cell Sc+R_1-Rs,

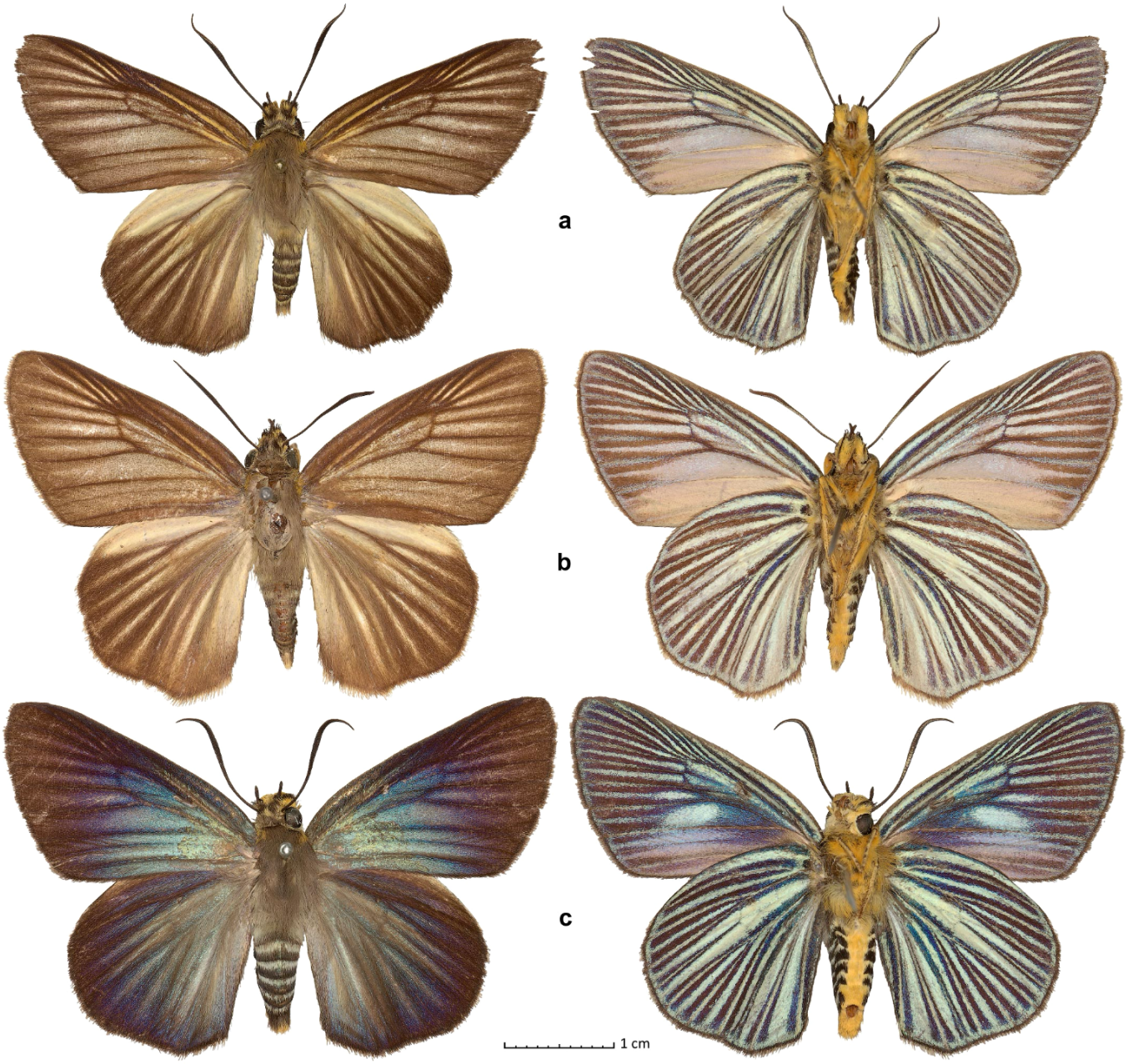

Fig. 17. *Burara danata danata* **sp. n.** type series from China in dorsal (left) and ventral (right) views, data in text: **a)** holotype ♂ NVG-22083F05 from central Fujian and paratypes: **b)** ♂ NVG-23079F01 from Guangdong and **c)** ♀ NVG-22083F06 from central Fujian.

which is more prominent than those in other cells and broader in the middle; and the ventral hindwing vein M_2 is narrowly overscaled with cream scales, which are almost absent in its basal portion; consequently, the dark brown ground color is visible on both sides of the vein from its base (i.e., two dark brown streaks, one on each side of the paler M_2 vein, extend from the outer wing margin to the discal cell, where they fuse with each other). In males of this new species, the pale streaks in the subapical area of the dorsal forewing are more prominent than the pale coloration in cell CuA_1-CuA_2; and the pale streak is narrow (broader at the base) in cell Rs-M_1 of the dorsal hindwing (not a lanceolate patch broader in the middle). Due to poorly explored individual variation, this species is best identified by DNA, with diagnostic base pairs in the nuclear genome: aly345.17.3:C75T, aly345.17.3:C117T, aly1294.6.1:T784C, aly23726.1.1:C162T, aly23726.1.1:G171A; and the COI barcode: T205T, T385C, A568G, T616T, T619C.

Barcode sequence of the holotype. Sample NVG-22083F05, 658 base pairs:

AACATTATATTTTATTTTTGGAATTTGAGCAGGTATAGTTGGAACTTCATTAAGTTTATTAATTCGAACAGAATTAGGTAATCCCGGATCTTTAATTGGAGATGATCAAATTTATAATACT
ATTGTTACAGCCCATGCCTTTATTATAATTTTTTTTATAGTAATACCAATTATAATTGGAGGATTTGGAAATTGATTAGTACCTTTAATATTAGGAGCTCCTGATATAGCTTTTCCTCGAA
TAAATAATATAAGTTTTTGACTTTTACCCCCATCATTAACTTTATTAATTTCAAGAAGAATTGTAGAAAATGGAGCAGGTACTGGATGAACTGTTTATCCCCCCTTATCTGCTAATATTGC
ACATCAAGGTTCATCTGTTGACTTAGCAATTTTTTCTTTACACCTAGCAGGAATTTCTTCTATTTTAGGAGCTATTAATTTTATTACAACTATTATTAATATACGAATTAATAATTTATCT
TTTGATCAAATACCTTTATTTGTTTGAGCTGTAGGTATTACCGCTTTATTATTACTTTTATCTTTACCAGTTTTAGCTGGAGCGATTACTATATTATTAACAGATCGAAATTTAAATACTT
CTTTTTTTGATCCCGCAGGTGGTGGAGATCCTATTTTATATCAACATTTATTT

Type material. Holotype: ♂ deposited in the McGuire Center for Lepidoptera and Biodiversity collection, Gainesville, FL, USA (MGCL), illustrated in Fig. 17a, bears the following five rectangular labels (first two handwritten, others printed), four white: [CHINA | CENTRAL FUJIAN | VI-VII-06], [Bibasis gomata | lara (Leech, 1894)], [M. Simon colln. | MGCL Accession | # 2007-3], [DNA sample ID: | NVG-22083F05 | c/o Nick V. Grishin], and one red [HOLOTYPE ♂ | Burara danata | Grishin]. **Paratypes:** 1♂ and 1♀: 1♀ NVG-22083F06 data as the holotype (Fig. 17c) and 1♂ NVG-23079F01 China: Guangdong Province, ca. 30 km SE of Meizhou City ("Tong cung san"), old, S. V. Mell leg. [MFNB] (Fig. 17b).

Type locality. China: central Fujian.

Etymology. In Chinese (Mandarin), 淡 (dàn) means light or faint in color, and this word is fused with the name of its relative, *B. gomata*, a species darker on the ventral side: *dan* + [gom]*ata* to reflect paler ventral color of the new species. The name is treated as a noun in apposition.

Distribution. Currently confirmed from southeastern China (Fujian and Guangdong).

Burara danata himavata Grishin, new subspecies

https://zoobank.org/242934D3-6E79-483E-A692-F2F7A8CF6BA7

(Figs. 15–16 part, 18, 19a–b, 22c)

Definition and diagnosis. Genomic analysis reveals that specimens from the Himalayan region initially identified as *Burara gomata* (Moore, [1866]) (type locality in N.E. Bengal) are genetically differentiated from it at the species level (Fig. 15, 16 blue vs. black); e.g., their COI barcodes differ by 4.7% (31 bp), and therefore these specimens represent a new taxon. This taxon is phenotypically and genetically similar to *Burara danata* **sp. n.** described above (Fig. 15, 16 blue vs. red); e.g., their COI barcodes differ by 0.8% (5 bp), and therefore it is a subspecies. This new subspecies keys to "*Bibasis gomata gomata*" (A.1.13(c)) in Evans (1949) and was included by him in this taxon, but differs from it and other relatives by the characters listed above for *Burara danata* **sp. n.**, differing from the nominate subspecies by yellower pale rays on the ventral side of wings and a broader ray in the ventral hindwing cell Sc+R_1-Rs. Due to poorly explored individual variation, this subspecies is best identified by DNA, with diagnostic base pairs in the nuclear genome: aly1838.60.2:C6T, aly1838.60.2:C78T, aly127.31.2:G381A, aly1603.33.3:A218G, aly272.20.1:T165C; and the COI barcode: T205C, T385C, A568A, T616C, T619C.

Barcode sequence of the holotype. Sample NVG-22099C09, 658 base pairs:

AACATTATATTTTATTTTTGGAATTTGAGCAGGTATAGTTGGAACTTCATTAAGTTTATTAATTCGAACAGAATTAGGTAATCCCGGATCTTTAATTGGAGATGATCAAATTTATAATACT
ATTGTTACAGCCCATGCCTTTATTATAATTTTTTTTATAGTAATACCAATTATAATTGGAGGATTTGGAAATTGATTAGTACCCTTAATATTAGGAGCTCCTGATATAGCTTTTCCTCGAA
TAAATAATATAAGTTTTTGACTTTTACCCCCATCATTGACTTTATTAATTTCAAGAAGAATTGTAGAAAATGGAGCAGGTACTGGATGAACTGTTTATCCCCCCTTATCTGCTAATATTGC
ACATCAAGGTTCATCTGTTGACTTAGCAATTTTTTCTTTACACCTAGCAGGAATTTCTTCTATTTTAGGAGCTATTAATTTTATTACAACTATTATTAATATACGAATTAATAATTTATCT
TTCGATCAAATACCTTTATTTGTTTGAGCTGTAGGTATTACCGCTTTATTATTACTTTTATCTTTACCAGTTTTAGCTGGAGCAATTACTATATTATTAACAGATCGAAATTTAAATACTT
CTTTTTTTGACCCCGCAGGTGGTGGAGATCCTATTTTATATCAACATTTATTT

Type material. Holotype: ♂ deposited in the collection of the California Academy of Sciences, San Francisco, CA, USA (CAS), illustrated in Fig. 18a, bears the following six rectangular labels (3rd handwritten, others printed with handwritten text shown in italics), five white: [NEPAL:God- | avari School | Kathmandu | *5400':IX-15-60* | E. L. Watrin], [Bibasis | gomata | gomata Moore | DET C.D.MACNEILL 89], [Collection of C. D. MacNeill], [DNA sample ID: | NVG-22099C09 | c/o Nick V. Grishin], [{QR Code} | CASENT | 8566783], and one red [HOLOTYPE ♂ | Burara danata | himavata Grishin]. **Paratypes:** 5♂♂ and 3♀♀: Himalaya, "Inde anglaise", 1906, W. Harcourt Bath leg. [MNHP]: 1♂ NVG-23026G08, EL83690 and 1♀ NVG-23026H01; 1♂ NVG-21102H08 "Northern India", old, Knyvett leg. [CMNH]; India, Sikkim, old: 1♂ NVG-21102H07, Möller leg. [CMNH] (Fig. 18b), 1♂ NVG-23079F04 Möller leg. [MFNB] (Fig. 19b), and 1♀ NVG-24021H05 coll. A. Seitz [SMF] (Fig. 18c); India, Meghalaya ("Assam"), Khasi Hills, 1890, Hamilton leg. [MFNB]: 1♂ NVG-23079F05 (Fig. 19a) and 1♀ NVG-23079F07.

Fig. 18. *Burara danata himavata* **sp. n.** type specimens in dorsal (left) and ventral (right) views, data in text:
a) holotype ♂ NVG-22099C09 from Nepal and paratypes from India, Sikkim: **b)** ♂ NVG-21102H07 and **c)** ♀ NVG-24021H05.

Fig. 19. *Burara gomata* group males from India in dorsal (left) and ventral (right) views, data in text or below: **a–b)** *B. danata himavata* **sp. n.** paratypes: **a)** NVG-23079F05 Khasi Hills and **b)** NVG-23079F04 Sikkim; **c–d)** *B. gomata gomata*: **c)** NVG-23079F09 "NW. Indien", 1895 [MFNB] and **d)** NVG-18103H02 Khasi Hills, old. B. Neumögen collection [USNM].

Type locality. Nepal: Bagmati Province, Lalitpur District, ca. 15 km south of Kathmandu, Godawari, St. Xavier's School, elevation 5400'.

Etymology. The name is derived from the Sanskrit word हिमवत् (Himavat), meaning 'frosty,' 'possessing snow,' or 'snowy' and is the personification of the Himalayan mountains in Hindu mythology. The name reflects the distribution of this subspecies centered around the Himalayas, its paler ("frostier") ventral side, and is treated as a feminine noun in apposition.

Distribution. Currently known from Himalayan region, confirmed from Nepal and Northeast India: Sikkim and Meghalaya ("Assam").

Burara gomata burmana Grishin, new subspecies

https://zoobank.org/451821A0-136B-49C7-BED8-999D8A1922BD

(Figs. 15–16 part, 20a)

Definition and diagnosis. Genomic analysis reveals that a specimen from northwestern Myanmar initially identified as *Burara gomata* (Moore, [1866]) (type locality in N.E. Bengal) is genetically differentiated from it at the subspecies level and not even monophyletic with it in the phylogenetic tree constructed from the autosome genes (Fig. 15a) (although their COI barcodes do not differ), and therefore this specimen represents a new subspecies. This new subspecies keys to "*Bibasis gomata lalita*" (A.1. 13(d)) in Evans (1949), but differs from it and other relatives by the following combination of characters in males: dorsal forewing is darker in the middle and does not have an obvious pale patch in the basal half of cell CuA_1-CuA_2; ventral forewing discal cell is mostly pale except the central brown streak and dark scaling along the posterior side; veins on the ventral side of wings are more weakly overscaled with pale or completely dark; and the ventral hindwing central pale ray ends with a narrower pair of prongs at the outer margin. Pale overscaling of ventral forewing veins is only vestigial (pale streaks between veins are prominent), and the ventral hindwing central pale streak is narrower with a larger and broader central "tooth" (a pale spot at the discocellular vein that is fused with the streak). Due to its somewhat cryptic nature and unexplored individual variation, this subspecies is best identified by DNA, with diagnostic base pairs in the nuclear genome: aly171.17.1:C543T, aly171.17.1:G900A, aly171.3.3:A37C, aly171.3.3:A66G, aly171.12.3:T918A, aly2612.7.2:A497A (not C), aly2612.7.2:C552C (not T), aly102.26.2:C93C (not A), aly102.26.2:A102A (not T), aly276558.30.1:T174T (not C); and the COI barcode: G38G, T121C, T367C, T536C, T607T.

Barcode sequence of the holotype. Sample NVG-7866, 658 base pairs:

AACATTATATTTTATTTTTGGAATCTGAGCAGGAATAGTAGGAACTTCACTAAGTTTATTAATTCGAACAGAACTAGGTAATCCAGGATCTTTAATTGGAGATGATCAAATTTATAATACC
ATTGTTACAGCTCATGCTTTTATTATAATTTTTTTTATAGTAATACCAATTATAATTGGAGGATTTGGAAATTGATTAGTACCTTTAATATTAGGAGCTCCTGATATAGCTTTTCCTCGAA
TAAATAATATAAGTTTTTGACTTCTCCCCCCCTCACTAACTTTATTAATTTCAAGAAGAATTGTAGAAAATGGAGCAGGTACAGGATGAACTGTTTACCCCCCCTTATCTGCTAATATTGC
ACACCAAGGTTCATCTGTTGATTTAGCAATTTTTTCTTTACATTTAGCAGGAATTTCTTCTATTTTAGGTGCTATTAATTTTATTACCACTATTATTAATATACGAGTTAATAATTTATCT
TTTGATCAAATACCCCTATTTGTTTGAGCTGTAGGTATTACCGCTTTATTACTACTTTTATCTTTACCAGTTTTAGCTGGAGCAATTACAATATTATTAACAGATCGAAATTTAAATACTT
CTTTTTTTGATCCTGCAGGTGGTGGAGATCCTATTTTATATCAACATTTATTT

Type material. Holotype: ♂ deposited in the National Museum of Natural History, Smithsonian Institution, Washington, DC, USA (USNM), illustrated in Fig. 20a, bears the following five printed rectangular labels (text in italics handwritten), four white: [MYANMAR, Mandalay Div | Alaungdaw Khattapa NP | N22°19.4' E94°28.8' El 1,600' | 22-IX-2001 Leg S. Kinyon | *855*], [DNA sample ID: | NVG-7866 | c/o Nick V. Grishin], [genitalia | NVG170206-51 | Nick V. Grishin], [USNMENT | {QR Code} | 01321706] and one red [HOLOTYPE ♂ | Burara gomata | burmana Grishin].

Type locality. Myanmar: Sagaing Region, Alaungdaw Kathapa National Park, elevation 1600', GPS 22.323, 94.480.

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

Distribution. Currently known only from the holotype collected in northern Myanmar.

Comment. A noteworthy feature of this subspecies is its different phylogenetic affinities in the autosomes and the Z chromosome trees. While in the Z chromosome tree, it is monophyletic with the geographically closer nominotypical subspecies (Fig. 15b orange and black, and also in the mitogenome trees Fig. 15c, d), in the autosome tree, it is in the clade with the new subspecies from the southeastern parts of the Asian continent that is described next (Fig. 15a orange and green).

Fig. 20. *Burara gomata* group type specimens in dorsal (left) and ventral (right) views, data in text: **a)** *B. gomata burmana* **ssp. n.** holotype ♂ NVG-7866 from Myanmar and **b–d)** *B. gomata namata* **ssp. n.** type series ♀♀ from China: **b)** holotype NVG-22083F07 from Hong Kong and paratypes: **c)** NVG-23079F02 from Guangdong and **d)** NVG-23026H02 from Vietnam.

Burara gomata namata Grishin, new subspecies

https://zoobank.org/ED00C1D1-DCD6-4647-B52D-84545F22E8F6

(Figs. 15–16 part, 20b–d, 22f)

Definition and diagnosis. Genomic analysis reveals that specimens from southern Asia identified as *Burara gomata* (Moore, [1866]) (type locality in N.E. Bengal) are genetically differentiated from it at the

subspecies level (Fig. 15, 16); e.g., their COI barcodes differ by 0.8% (5 bp), and therefore these specimens represent a new subspecies. This new subspecies keys to "*Bibasis gomata lalita*" (A.1.13(d)) in Evans (1949), but differs from it and other relatives in the following ways. It shares with the nominotypical subspecies the following characters: dark brown ventral surface of the wings; narrowly pale veins on the ventral forewing; a prominent broad "tooth" (sometimes with a small notch basad of it) in the middle of the posterior margin of the central pale ray on the ventral hindwing; a pale streak in the ventral hindwing cell Sc+R_1-Rs that is narrow—comparable to the streaks in other cells—and not broader in the middle; and the ventral hindwing vein M_2 is broadly overscaled with cream scales in its basal half, so that the dark brown ground color is absent on both sides of the vein, which is fused with the pale streaks in the middle of cells M_1-M_2 and M_2-M_3, these being entirely cream-colored (i.e., two brown streaks, one on each side of the paler M_2 vein, typically extend from the outer wing margin to about half the distance from the margin to the discal cell, where they do not merge, while the two pale streaks are merged from that point basad). This new subspecies differs from the nominotypical by the following combination of characters: the ventral side of wing is less bluish and is more reddish-brown; brown streaks in the central pale ray on the ventral hindwing (along the pale vein M_2) reach closer to the discal cell from the outer margin. Males, share with the nominotypical subspecies a paler base of the dorsal forewing cell CuA_1-CuA_2 that is more prominent than the pale streaks in the subapical area, but the pale streak in the dorsal hindwing cell Sc+R_1-Rs is usually not expanded into a broad lancelet as in the nominotypical subspecies and *B. gomata burmana* **ssp. n.**, but is narrower. Due to its somewhat cryptic nature and poorly explored individual variation, this subspecies is best identified by DNA, with diagnostic base pairs in the nuclear genome: aly2612.7.2:A497C, aly2612.7.2:C552T, aly102.26.2:C93A, aly102.26.2:A102T, aly276558.30.1:T174C; and the COI barcode: G38A, T121C, T367T, T536T, T607C.

Barcode sequence of the holotype. Sample NVG-22083F07, 658 base pairs:

AACATTATATTTTATTTTTGGAATCTGAGCAGGAATAATAGGAACTTCACTAAGTTTATTAATTCGAACAGAACTAGGTAATCCAGGATCTTTAATTGGAGATGATCAAATTTATAATACC
ATTGTTACAGCTCATGCTTTTATTATAATTTTTTTTATAGTAATACCAATTATAATTGGAGGATTTGGAAATTGATTAGTACCTTTAATATTAGGAGCTCCTGATATAGCTTTTCCTCGAA
TAAATAATATAAGTTTTTGACTTCTCCCCCCCTCACTAACTTTATTAATTTCAAGAAGAATTGTAGAAAATGGAGCAGGTACAGGATGAACTGTTTACCCCCCCTTATCTGCTAATATTGC
ACATCAAGGTTCATCTGTTGATTTAGCAATTTTTTCTTTACATTTAGCAGGAATTTCTTCTATTTTAGGTGCTATTAATTTTATTACCACTATTATTAATATACGAGTTAATAATTTATCT
TTTGATCAAATACCCCTATTTGTTTGAGCTGTAGGTATTACTGCTTTATTATTACTTTTATCTTTACCAGTTTTAGCTGGAGCAATTACAATATTATTAACAGATCGAAATTTAAATACTT
CCTTTTTTGATCCTGCAGGTGGTGGAGATCCTATTTTATATCAACATTTATTT

Type material. Holotype: ♀ deposited in the McGuire Center for Lepidoptera and Biodiversity collection, Gainesville, FL, USA (MGCL), illustrated in Fig. 20b, bears the following four printed rectangular labels, three white: [HONG KONG: I. nr. LANTAU I. | Chek Lap Kok; 15-17.v.1990 | Coll. Don Thomas], [D Thomas colln. | Allyn Museum | Acc. 1990-17], [DNA sample ID: | NVG-22083F07 | c/o Nick V. Grishin], and one red [HOLOTYPE ♀ | Burara gomata | namata Grishin]. **Paratypes:** 2♀♀: 1♀ NVG-23079F02 China, Guangdong Province, Guangzhou ("Su-Lie-Kum"), old, S. V. Mell leg. [MFNB] (Fig. 20c) and 1♀ NVG-23026H02, EL83696 Northern Vietnam, around Hanoi ("Tonkin"), old, L. Seraphin leg. [MNHP] (Fig. 20d).

Type locality. China: Hong Kong, Chek Lap Kok Island.

Etymology. In Vietnamese, nam means south and is fused with species epithet for the southern subspecies with the center of the range around Vietnam: *nam* + [gom]*ata*. The name is treated as a noun in apposition.

Distribution. Currently confirmed from Southern China and Northern Vietnam, is expected in neighboring countries: Laos, eastern Myanmar, Thailand, and Cambodia.

***Burara lawana* Grishin, new species**

https://zoobank.org/2286BA36-FDB9-4640-A93D-B2138199E8BF

(Figs. 15–16 part, 21a)

Definition and diagnosis. Genomic analysis reveals that a male from Palawan, Philippines, initially identified as *Burara lorquini* (Mabille, 1876), **stat. rest.** (type locality Philippines: Luzon, Manila) because of its provenance in the Philippines is genetically differentiated from it and other relatives at the species level (Fig. 15, 16); e.g., their COI barcodes differ by 3.2% (21 bp) from *B. lorquini* and by 2.3%

(15 bp) from *B. gomata*, and therefore this male represents a new species. This new species keys (incompletely) to "*Bibasis gomata lalita*" (A.1.13(d)) in Evans (1949), but differs from it and other relatives by the following combination of characters in males: ventral side of wings with browner, warmer ground color and beige (not yellowish) rays; the presence of a tooth in the middle of the posterior margin of the central beige ray on the ventral hindwing; the dark pattern in the beige ventral forewing discal cell that consists of a central line and dark-brown scaling in the basal half posteriad of the discal line; and possibly smaller size. Due to unexplored individual variation, this species is best identified by DNA, with diagnostic base pairs in the nuclear genome: aly1838.8.3:T891G, aly1139.31.7:A72G, aly1139.31.7 :G96A, aly1222.14.26:T96C, aly1222.14.26:A370G, aly86.15.1:T1419T (not C), aly2954.5.2:T1140T (not C), aly2954.5.2:C567C (not T), aly1294.17.1:C520C (not T), aly1294.17.1:T537T (not C); and the COI barcode: T13C, T157C, 220C, T278C, T385C, T484C, T547C.

Barcode sequence of the holotype. Sample NVG-23079F03, 658 base pairs:

AACATTATATTTCATTTTTGGAATTTGAGCAGGAATAGTAGGAACTTCATTAAGTTTATTAATTCGAACAGAATTAGGTAATCCAGGATCTTTAATTGGAGATGATCAAATTTATAATACT
ATTGTTACAGCTCATGCTTTTATTATAATTTTTTTCATAGTAATACCAATTATAATTGGAGGATTTGGAAATTGATTAGTACCTTTAATATTAGGAGCCCCTGATATAGCTTTTCCTCGAA
TAAATAATATAAGTTTTTGACTTCTCCCCCCCCTCACTAACTTTATTAATTTCAAGAAGAATTGTAGAAAATGGAGCAGGTACAGGATGAACTGTTTATCCCCCCTTATCTGCTAATATTGC
ACATCAAGGTTCATCTGTTGACTTAGCAATTTTTTCTTTACACTTAGCAGGAATCTCTTCTATTTTAGGTGCTATTAATTTTATTACCACTATTATTAATATACGAGTTAATAATTTATCC
TTTGATCAAATACCCCTATTTGTTTGAGCTGTAGGTATTACCGCTTTATTATTACTTTTATCCTTACCAGTTTTAGCTGGAGCAATTACAATATTATTAACAGATCGAAATTTAAATACTT
CTTTTTTTGATCCTGCAGGTGGTGGAGATCCTATTTTATATCAACATTTATTT

Type material. Holotype: ♂ deposited in the Museum für Naturkunde, Berlin, Germany (MFNB), illustrated in Fig. 21a, bears the following five rectangular labels (3rd handwritten, others printed with handwritten text shown in italics), four white: [Palawan | *92* Platen], [♀ wohl auch | blau oben | (Erh.) vide K 26.], [Coll. | Staudinger], [DNA sample ID: | NVG-23079F03 | c/o Nick V. Grishin], and one red [HOLOTYPE ♂ | Burara lawana | Grishin]. According to its 1st label, the holotype was collected by Carl Constantin Platen (1843–1927) in 1892 (the handwritten 92 is written over printed 88).

Type locality. Philippines: Palawan.

Etymology. The name is derived from the type locality in [Pa]*lawan* + *a* to go along with *lara*, *lalita*, and *lorquini*, and is treated as a noun in apposition.

Distribution. Currently known only from the holotype collected in Palawan, Philippines.

Burara lorquini vichitra Grishin, new subspecies

https://zoobank.org/93CBD45A-A016-451D-9573-2EF6FBFF17F8

(Figs. 15–16 part, 21b)

Definition and diagnosis. Genomic analysis reveals that a male labeled from "Sikkim" (most likely mislabeled, see below) identified as *Burara gomata* (Moore, [1866]) (type locality in N.E. Bengal) is not close to this species in the genomic trees and instead groups with *Burara lorquini* (Mabille, 1876), **stat. rest.** (type locality Philippines: Luzon, Manila), while being genetically differentiated from the latter at the subspecies level (Fig. 15, 16); e.g., their COI barcodes differ by 1.5% (10 bp), and therefore this likely mislabeled specimen represents a new subspecies. This new subspecies keys to "*Bibasis gomata lorquini*" (A.1.13(e)) in Evans (1949), but differs from it and other relatives by the following combination of characters in males: darker dorsal side of wings with darker posterior pars of the dorsal forewing discal cell; paler brown color of the ventral side; more diffuse, wider, and merging with the costal beige area streak in the dorsal forewing cell Sc+R_1-Rs; and possibly larger size. Due to its cryptic nature and unexplored individual variation, this subspecies is best identified by DNA, with diagnostic base pairs in the nuclear genome: aly84.47.1:G1062A, aly84.47.1:A2856G, aly390.9.2:T45C, aly390.9.2:C78T, aly499. 27.3:G45A, aly216.7.1:C1234C (not T), aly536.176.1:C907C (not T), aly116.20.1:G1857G (not A), aly7376.5.5:C45C (not T), aly103.51.12:A2275A (not G); and the COI barcode: T97C, T400C, T401T, C451T, T463C, 526C, T578C.

Barcode sequence of the holotype. Sample NVG-23026G10, 658 base pairs:

AACATTATATTTTATTTTTGGAATCTGAGCAGGAATAGTAGGAACTTCATTAAGTTTATTAATTCGAACAGAATTAGGTAATCCAGGATCTTTAATCGGAGATGATCAAATTTATAATACT
ATTGTTACAGCTCATGCTTTTATTATAATTTTTTTTATAGTAATACCAATTATAATTGGAGGATTTGGAAATTGATTAGTACCTTTAATATTAGGAGCTCCTGATATAGCTTTTCCTCGAA
TAAATAATATAAGTTTTTGACTTCTCCCCCCCTCATTAACTTTATTAATTTCAAGAAGAATTGTAGAAAATGGAGCAGGTACAGGATGAACTGTTTATCCCCCCTTATCTGCTAATATTGC
ACATCAAGGTTCATCTGTAGATTTAGCAATTTTTTCCTTACATTTAGCAGGAATTTCTTCTATTTTAGGTGCTATTAATTTTATTACTACTATTATTAACATACGAGTTAATAATTTATCT
TTTGATCAAATACCTTTATTTGTTTGAGCTGTAGGTATTACCGCTTTATTATTACTTTTATCTTTACCAGTTTTAGCTGGAGCTATTACAATACTATTAACAGATCGAAATTTAAATACTT
CTTTTTTTGATCCTGCAGGTGGTGGAGATCCTATTTTATATCAACATTTATTT

Fig. 21. *Burara gomata* group males from the Philippines in dorsal (left) and ventral (right) views, data in text or below: **a)** *B. lawana* **sp. n.** holotype ♂ NVG-23079F03 from Palawan; **b)** *B. lorquini vichitra* **ssp. n.** holotype ♂ NVG-23026G10; and **c–d)** *B. lorquini lorquini*: **c)** NVG-18028D03, USNMENT 01465232 from Luzon, Laguna, College of Forestry, 1-Dec-1963, W. L. Stern [USNM] and **d)** NVG-23033B11 from Marinduque Is., 1980, R. Aronheim leg. [MGCL].

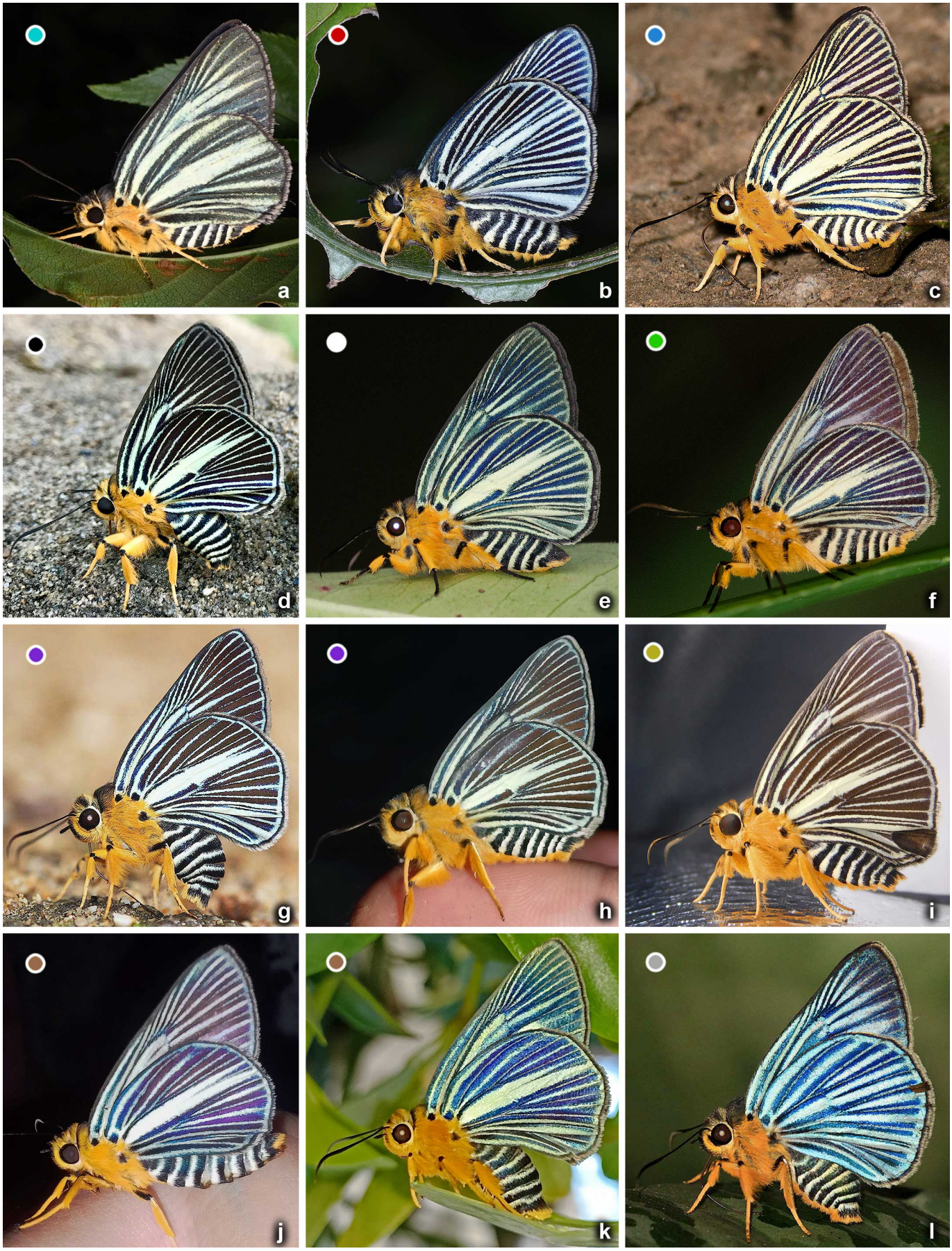

Fig. 22 (legend continues on the next page). *Burara gomata* group live photographs. iNaturalist (2025) observations: **a)** *B. lara* **stat. nov.** (cyan dot) 249040369 China: Sichuan, Leshan, GPS 28.9160, 103.5601, 11-Aug-2025 © KrabX; **b)** *B. danata*

danata **sp. n.** (red dot) 109634327 China: Fujian, Ningde, GPS 26.6306, 119.5345, 24-Nov-2021 © 甲殼蟲翻身; **c)** *B. danata himavata* **ssp. n.** (blue dot) 249040369 India: Mizoram, Reiek, GPS 23.6917, 92.6033, 13-Oct-2024 © Subhajit Roy; **d)** *B. gomata gomata* (black dot) 291413614 India: Assam, Golaghat, GPS 26.6114, 93.5030, 12-Oct-2017 © Rofikul Islam; **e)** *B. gomata kanara* (white dot) 19781534 India: Kerala, Kannur, GPS 11.9224, 75.7925, 10-Jan-2015 © Firos AK; **f)** *B. gomata namata* **ssp. n.** (green dot) 226393908 China: Hong Kong, Tai Po, GPS 22.4769, 114.2194, 1-Jul-2024 © Tree Fong; **g–h)** *B. gomata lalita* (purple dot): **g)** 24483609 Thailand: Yala, Bannang Star, GPS 6.2213, 101.1588, 20-Jun-2015 © Les Day and **h)** 180895349 Borneo: Sarawak, Marudi, 4.0417, 114.8153, 15-Aug-2023, © Andrea Vannini; **i)** *B. vajra* **stat. nov.** (olive dot) 265011195 West Java, Jatinangor, −6.9328, 107.7715, 12-Mar-2025 © Ganjar Cahyadi; **j–k)** *B. lorquini lorquini* **stat. rest.** (brown dot), Philippines, Luzon: **j)** 289774982 Albay, Guinobatan, GPS 13.1410, 123.5984, 12-Dec-2024 © mikey maykol and **k)** 259348019 Cavite, Indang, GPS 14.2000, 120.8826, 23-Jan-2025 © Adiel Balanza; **l)** *B. radiosa* **stat. rest.** (gray dot) 39516930 Indonesia: Sulawesi Utara, Minahasa, GPS 1.2169, 124.8183, 19-May-2012 © Les Day. Photographs were taken by different photographers using different equipment in different lighting conditions. Therefore, color reproduction is not expected to be fully comparable between images. Photographs were color-corrected, brightened, rotated, cropped, and some flipped (left-right inverted).

Type material. Holotype: ♂ deposited in the Muséum National d'Histoire Naturelle, Paris, France (MNHP), illustrated in Fig. 21b, bears the following four rectangular labels (1st handwritten, others printed; 1st tan with a golden framing depicting grasses and flowers, 4th red, others white): [Sikkim | Inde anglaise | 1905 | O. Staudinger], [DNA sample ID: | NVG-23026G10 | c/o Nick V. Grishin], [MNHN, Paris {QR Code} | EL83692], and [HOLOTYPE ♂ | Burara lorquini | vichitra Grishin].

Type locality. Unknown, likely in or around the Philippines as deduced by DNA comparison. "Sikkim Inde anglaise" is specified on the label, but the holotype is almost certainly mislabeled due to its close genetic similarity with specimens from the Philippines. Furthermore, we found another specimen in the same collection (MNHP) with the same labels as the holotype, but placed within specimens from Java in the genomic trees (Fig. 15, 16, NVG-23026C09), and therefore also almost certainly mislabeled. The type locality will be determined by future genomic comparisons with additional specimens.

Etymology. In Sanskrit, विचित्र (vičitra) means variegated, colorful, unusual, strange, wonderful, extraordinary, curious, etc., and this new subspecies is all that, including its (likely incorrect) locality label and unexpected genetic differentiation from the nominotypical subspecies. The name is a phonetic transliteration Latinized to be treated as a feminine adjective.

Distribution. Currently known only from the holotype.

Delineation of species and subspecies in the *Burara gomata* (Moore, [1866]) complex

We found that two genetically distinct entities of the *Burara gomata* complex are sympatric in the Himalayan region and in southern China (Figs. 15 & 16 blue with black, and red with green). Their F_{st}/COI barcode differences are: 0.75/4.7% (31 bp) in the Himalayan region, and 0.79/4.2% (29 bp) in southern China. Therefore, these entities are decisively species-level taxa, not subspecies, and the complex consists of at least two species. These two species belong to two different clades of the first bifurcation in all four phylogenetic trees, denoted by their oldest names as *B. gomata* and *B. lara* **stat. nov.** (Fig. 15).

At the next level, one of these major clades splits into two (Fig. 15 top clade, with *B. lara* **stat. nov.**), and the other one splits into three (Fig. 15 bottom clade, with *B. gomata*) clades of approximately equal genetic differentiation comparable to that between *B. gomata* and *B. lara* **stat. nov**. In the first clade, F_{st}/COI barcode differences are 0.55/2.6% (17 bp) between *B. lara* **stat. nov**. and *B. danata* **sp. n.** In the second clade, the statistics are 0.65/2.7% (18 bp) between *B. gomata* and *B. lorquini* **stat. rest.**, 0.63/4.3% (28 bp) between *B. gomata* and *B. radiosa* **stat. rest.**, and 0.62/4.0% (26 bp) between *B. lorquini* **stat. rest.** and *B. radiosa* **stat. rest**. Note that *B. radiosa* **stat. rest.** strongly differs in its mitochondrial genome (and hence the COI barcode) from all other taxa in the complex (Fig. 15c, d). Moreover, *B. lara* **stat. nov.** and *B. danata* **sp. n.**, approach each other in Guangdong Province, China, and may be sympatric there. Therefore, we regard *B. danata* **sp. n.** as a species distinct from *B. lara* **stat.**

nov., and *B. lorquini* **stat. rest.** and *B. radiosa* **stat. rest.** as species distinct from *B. gomata*, not subspecies.

At the third level of the nuclear genome trees, the clade with *B. gomata* splits into three subclades (Fig. 15a, b magenta, olive, and the rest). While at the previous two levels, the topology between clades is the same in all four trees (Fig. 15), the mitochondrial genome and COI barcode trees (Fig. 15c, d) exhibit incongruence with the nuclear genome trees (Fig. 15a, b) for some of the subclades at the third level. This incongruence indicates evolutionary irregularities at this level, such as incomplete lineage sorting or introgression. First, *B. lawana* **sp. n.** is sister to the other two groups in all but the COI barcode tree (Fig. 15d). The barcode sequence might be too short to yield a reliable phylogenetic signal, which may explain this incongruence without evolutionary cause. While we cannot compute F_{st} for a taxon represented by only one specimen, COI barcode difference 2.3% (15 bp) between *B. lawana* **sp. n.** and *B. gomata gomata* is characteristic of distinct but closely related species in the presence of phenotypic differences and nuclear genome distinction. Second, *B. vajra* **stat. nov.** is sister to *B. gomata* in the nuclear genome (Fig. 15a, b), while being most confidently supported sister to *B. gomata lalita* in the mitochondrial genome tree (Fig. 15c olive and purple), mirrored by the COI barcode dendrogram (Fig. 15d olive and purple). This incongruence is unlikely due to methodological imperfections and may indeed be caused by different evolutionary paths of the nuclear and mitochondrial genes. Although *B. vajra* **stat. nov.** has been previously treated as a junior subjective synonym of *B. gomata lalita*, we find that the former taxon exhibits species-level Z chromosome F_{st} with subspecies of *B. gomata*: 0.44 with *B. gomata gomata*, 0.43 with *B. gomata namata* **ssp. n.**, and 0.29 with *B. gomata lalita*, and therefore we propose to treat *B. vajra* **stat. nov.** as a species.

The COI barcode differences of *B. vajra* **stat. nov.** from the abovementioned subspecies are lower: 1.8% (12 bp), 2.3% (15 bp), and 0.9% (6 bp), respectively. It is possible that *B. vajra* **stat. nov.** might have acquired mitochondria from *B. gomata lalita* at some point in the past, thus the two taxa are sisters in the mitogenome trees (Fig. 15c, d olive and purple) explaining less than 1% difference in the COI barcode. In the nuclear genome trees, *B. gomata lalita* confidently belongs to the clade with *B. gomata gomata* (Fig. 15a, b purple goes with black, orange, and green, not with olive). All four *B. gomata* subspecies (*B. gomata gomata* (black), *B. gomata burmana* **ssp. n.** (orange), *B. gomata namata* **ssp. n.** (green), and *B. gomata lalita* (purple)) are particularly close in the Z chromosome tree (Fig. 15b) that sets them farther apart from *B. vajra* **stat. nov.** (olive). Alternatively, it is possible that the mitochondrial genome reveals the true relationship, and *B. gomata lalita* experienced strong nuclear genome introgression from *B. gomata namata* **ssp. n.**, pulling it into the clade with *B. gomata gomata*. In this scenario, *B. gomata lalita*, may even be a hybrid species-level taxon. However, overall genetic differentiation between *B. gomata lalita* and *B. gomata namata* **ssp. n.** is low even in the Z chromosome with F_{st} of 0.18, suggesting conspecificity, and we conservatively leave *B. gomata lalita* as a subspecies pending further studies.

Thus, we treat the three subclades at the third level as species (*B. lawana* **sp. n.**, *B. vajra* **stat. nov.**, and *B. gomata*) due to genetic differentiation in the Z chromosome (F_{st} above 0.25), or COI barcode differences (above 2%), or both, although these species may be incipient due to their closer relationship with each other. A vertical line crossing the Z chromosome tree at approximately this level (Fig. 15b) cuts the tree into seven clades corresponding to species. We regard other genetically distinct entities that form clades below the species level (i.e., to the right in the tree) as subspecies because their overall genetic differentiation in the Z chromosome and the COI barcode is typically lower, e.g., F_{st}/COI barcode difference is 0.14/0.8% (5 bp) between *B. danata* **sp. n.** and *B. danata himavata* **ssp. n.**, and 0.14/1.8% (12 bp) between *B. gomata gomata* and *B. gomata lalita*. These subspecies-level clades are more conspicuous in the mitochondrial genome tree (Figs. 15c, 16), because mitogenomes do not usually recombine and persist as distinct haplotypes. However, it is possible that some of these taxa that we treat here as subspecies are recently differentiated distinct species that differ strongly in some specific regions of the genome thus causing incompatibility in crosses, but do not stand out in the overall genetic differentiation. The *B. gomata* complex can be a model for future studies of speciation in butterflies and this work is the first step in this direction.

A summary of characters for the taxa in the *Burara gomata* (Moore, [1866]) complex

Here, we summarize the key characters and geographical ranges distinguishing the taxa denoted by 14 valid names in the *B. gomata* group. Due to individual variation, some characters may not hold in all specimens of each taxon. Geographical ranges given are only approximate and are incompletely known. Abbreviations: C central, CPR central pale ray on the ventral hindwing, D dorsal side, DC discal cell, DT "discal tooth", i.e., a protrusion of pale scales in the middle of the posterior margin of the central pale ray on the ventral hindwing (i.e., the discocellular pale spot that protrudes posteriad from the central pale ray), DFW dorsal forewing, DHW dorsal hindwing, E east, FW forewing, N north, NE northeast, NW northwest, OD original description, S south, SE southeast, SW southwest, TL type locality, V ventral side, VFW ventral forewing, VHW ventral hindwing, W west.

Burara lara (Leech, 1893), **stat. nov.**: Figs. 16 cyan, 22a.
CPR broad till the outer margin; other pale rays broad on V; no DT; ♂ DHW discal cell entirely pale.
SW to C & SE China; TL: western China.

Burara danata danata Grishin, **sp. n.**: Figs. 16 red, 17, 22b.
V pale rays broad; brown streaks from outer margin in CPR reach DC; no DT; ♂ DHW cell Sc+R_1-Rs narrow pale streak.
SE China; TL: China: central Fujian.

Burara danata himavata Grishin, **ssp. n.**: Figs. 16 blue, 18, 19a–b, 22c.
As nominotypical, but V rays yellower; VHW cell Sc+R_1-Rs ray broader.
Himalayan region; TL: Nepal: Bagmati Province, Lalitpur District, ca. 15 km S of Kathmandu.

Burara gomata gomata (Moore, [1866]): Figs. 16 black, 19c–d, 22d.
V pale rays narrow; brown streaks from outer margin in CPR end before DC; has DT; ♂ DHW cell Sc+R_1-Rs pale lancelet.
Himalayan region; TL: NE Bengal.

Burara gomata kanara (Evans, 1926): Fig. 22e.
As nominotypical, but more diffuse pale overscaling of V veins towards outer margin.
SW India; TL: India: N Kanara.

Burara gomata burmana Grishin, **ssp. n.**: Figs. 16 orange, 20a.
As nominotypical, but ♂ DFW darker in the middle; V veins less to not pale; CPR with narrower prongs to outer margin.
NW Myanmar; TL: Myanmar: Mandalay Division, Alaungdaw Kathapa National Park.

Burara gomata namata Grishin, **ssp. n.**: Figs. 16 green, 20b–d, 22f.
As nominotypical, but V less bluish; brown streaks reach closer to DC in CPR; ♂ DHW cell Sc+R_1-Rs pale streak.
SE China to E Myanmar and Cambodia; TL: China: Hong Kong, Chek Lap Kok Island.

Burara gomata lalita (Fruhstorfer, 1911): Figs. 16 purple, 22g–h.
As nominotypical, but V warmer brown, less greenish; ♂ DFW darker in the middle; ♂ DHW cell Sc+R_1-Rs pale streak.
S China to Sumatra and Borneo; TL: W Sumatra.

Burara vajra (Fruhstorfer, 1911), **stat. nov.**: Figs. 16 olive, 22i.
As *B. g. lalita*, but no DT; ♂ D darker (e.g., DHW basal part).
Java; TL: W Java.

Burara lawana Grishin, **sp. n.**: Figs. 16 magenta, 21a.
♂ as *B. lorquini* but VFW DC with dark pattern; V ground color browner, rays beige (not yellowish); has DT.
Palawan in the Philippines; TL: Philippines: Palawan.

Burara lorquini vichitra Grishin, **ssp. n.**: Figs. 16 aquamarine, 21b.
♂ as nominotypical, but D darker with darker DFW DC posterior part; V paler brown ground color.
unknown, likely in the Philippines; TL: unknown, likely in or around the Philippines.

Burara lorquini lorquini (Mabille, 1876), **stat. rest.**: Figs. 16 brown (except NVG-23033C01), 21c–d, 22j–k.
Paler D; VFW DC mostly pale in ♂; FW pale spots in ♀; CPR posterior prong narrows less to outer margin; no DT.
Philippine Islands except Palawan and (possibly) Mindanao; TL: Philippines: Luzon, Manila.

Burara lorquini minda Chiba & Tsukiyama, 2009, **comb. nov.**: possible ♂ Fig. 16 brown NVG-23033C01.
As nominotypical, but (per OD) ♀ head darker above; FW spots reduced; VHW bluish (Chiba, 2009).
Mindanao in the Philippines; TL: Philippines: Mindanao, Surigao.

Burara radiosa (Plötz, 1885), **stat. rest.**: Figs. 16 gray, 22l.
VHW rays bluish (not greenish or yellowish), similar in width, CPR not much broader than others; no DT.
Sulawesi and the islands E of it; TL: Sulawesi.

Subfamily Eudaminae Mabille, 1877
Tribe Phocidini Tutt, 1906

Bungalotis quadra Grishin, new species

https://zoobank.org/B5005E2A-A2D0-4F7B-956D-A6E69B570B9D

(Figs. 23 part, 24)

Definition and diagnosis. Genomic analysis reveals that specimens from Panama initially identified as *Bungalotis quadratum quadratum* (Sepp, [1845]) (type locality in Suriname) are genetically differentiated from it at the species level (Fig. 23); e.g., their COI barcodes differ by 4.7% (31 bp), and therefore these specimens represent a new species. This new species keys to *B. quadratum quadratum* (D.1.6(a)) in Evans (1952) and was likely included by him in this taxon, but differs from it and other relatives by the following combination of characters: males have yellower wings (orange to tawny in *B. quadratum*), the ventral hindwing with brown spots and margins more sharply defined and strongly contrasting with the yellow ground color (suffused with tawny or nearly brown in other species and less contrasting), females with more weakly developed or missing subapical semihyaline spots and typically narrower semihyaline spot in the forewing cell M_3-CuA_1. Due to poorly documented individual variation, this species is best identified by DNA, with diagnostic base pairs in the nuclear genome: aly50.21.1:C48T, aly770.15.11: G60T, aly1042.21.15:G81C, aly1042.21.15:C90T, aly216.63.2:C75T; and the COI barcode: T133A, T145C, T574C, T641C, T646C.

Barcode sequence of the holotype. Sample NVG-23125H01, 658 base pairs:

AACATTATATTTTATTTTTGGTATTTGAGCAGGAATAATTGGTACTTCTTTAAGATTACTAATTCGAACTGAATTAGGAACCCCCGGATCTTTAATTGGAGATGATCAAATTTATAACACT
ATTGTTACTGCACATGCTTTTATCATAATTTTTTTTATAGTTATACCTATTATAATTGGAGGATTTGGAAATTGATTAGTACCTCTAATACTTGGAGCTCCTGATATAGCATTTCCTCGAA
TAAATAATATAAGATTTTGATTATTACCACCTTCTTTAACTTTATTAATTTCAAGAAGTATTGTCGAAAATGGAGCTGGCACAGGTTGAACAGTTTACCCTCCTTTATCTGCTAATATTGC
ACACCAAGGTTCTTCTGTTGATCTAGCAATTTTTTCTTTACATTTAGCTGGAATTTCATCTATTTTAGGAGCTATTAATTTTATTACAACAATTATTAACATACGAATTAGAAATTTATCA
TTTGATCAAATACCTTTATTTATTTGAGCTGTAGGAATTACAGCTCTTTTATTATTACTTTCATTACCTGTTTTAGCTGGTGCTATTACCATATTATTAACAGATCGAAATCTTAATACAT
CATTTTTTGATCCTGCAGGTGGAGGAGATCCAATTCTATACCAACATTTATTT

Type material. Holotype: ♂ deposited in the National Museum of Natural History, Smithsonian Institution, Washington, DC, USA (USNM), illustrated in Fig. 24a, bears the following seven rectangular labels (2nd–5th handwritten, others printed), six white: [Bugaba | Panama], [July], [Bungalotis | midas | Cr], [D 26], [♂ genitalia | Slide. 27 Dec. | W.D.F. # 430 1940], [DNA sample ID: | NVG-23125H01 | c/o Nick V. Grishin], and one red [HOLOTYPE ♂ | Bungalotis | quadra Grishin]. **Paratypes:** 1♂ and 1♀ from Panama [USNM]: 1♂ NVG-17104A12, USNMENT 00913836 Bocas del Toro, Changuinola, 6-May-1980 and 1♀ NVG-17104B01, USNMENT 00913837 Colón, Barro Colorado Is., 10-17-May-1964, W. D. & S. S. Duckworth (Fig. 24b).

Type locality. Panama: Chiriquí Province, Bugaba.

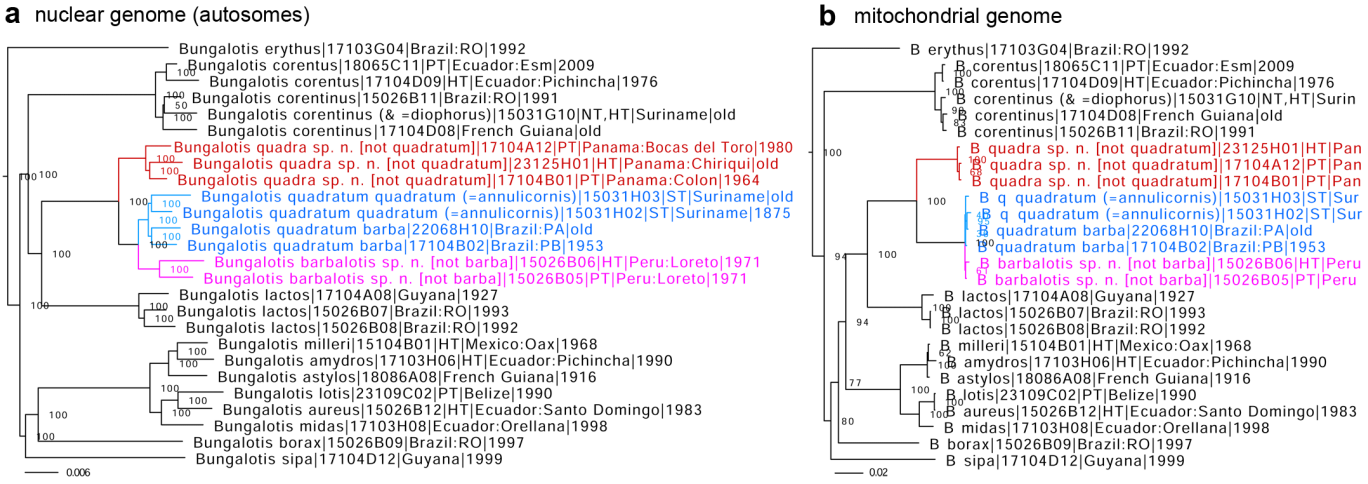

Fig. 23. Phylogenetic trees of selected *Bungalotis* species constructed from protein-coding regions in: **a)** the nuclear genome (autosomes), based on 6,291,114 positions, and **b)** the mitochondrial genome. Species mentioned in the text are colored: *B. quadra* **sp. n.** (red), B. quadratum (blue), and *B. barbalotis* **sp. n.** (magenta). Ultrafast bootstrap (Hoang et al. 2018) values are shown at nodes.

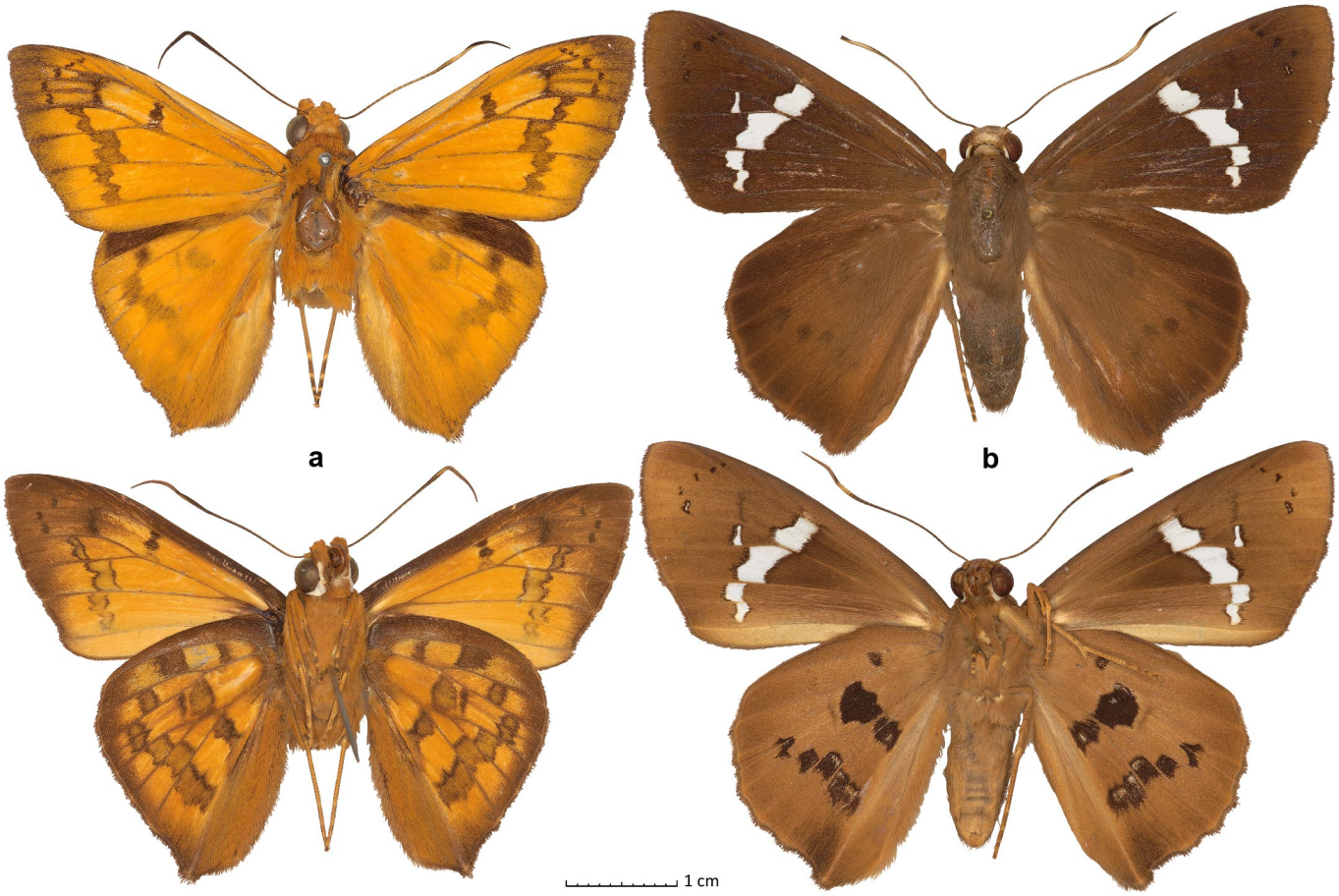

Fig. 24. *Bungalotis quadra* **sp. n.** from Panama in dorsal (left) and ventral (right) views, data in text: **a)** holotype ♂ NVG-23125H01 and **b)** paratype ♀ NVG-17104B01.

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

Distribution. Currently known only from Panama.

Bungalotis barbalotis Grishin, new species

https://zoobank.org/3B6DD7BF-BA00-45AA-9BFD-3681889A0C8F

(Figs. 23 part, 25–26)

Definition and diagnosis. Genomic analysis reveals that two males from Loreto, Peru, identified as *Bungalotis quadratum barba* Evans, 1952 (type locality in Brazil: Para) are genetically differentiated from it at the species level in the nuclear genome (Fig. 23); e.g., their F_{st} is 0.31 (COI barcodes do not differ), and therefore these males represent a new species. This new species keys to *B. quadratum barba* (D.1.6(b)) in Evans (1952), but differs from it and other relatives by the following combination of characters: males with the orange dorsal side of the wings, brighter than the tawny coloration of *B. quadratum barba*, the brown spiderweb-like pattern on the dorsal side is reduced but more sharply defined, and spots are paler inside with darker framing (in *B. quadratum barba*, ventral forewing spots are frequently darker at their centers, e.g., the spot in cell CuA_1-CuA_2); forewings are more rounded; the harpe is about the same length as the rest of the valva, narrower at the base and upturned, broadening towards the tooth at the distal margin and rounded at the dorsal margin; the tooth is twice as large as the costal tooth-like smooth (not serrated) process but about half of the length of the dorsally directed section of the harpe dorsad of the tooth; both the tooth and the dorsal segment of the harpe are serrated along the

margin, the serrations are denser (approximately eight small teeth) at the very dorsal rounded part of the margin and very sparse (total around eight) elsewhere. Due to its partly cryptic nature and unexplored individual variation, this species is best identified by DNA, with diagnostic base pairs in the nuclear genome: aly6654.3.4:C119G, aly420.60.2:C99T, aly26.12.4:C765T, aly26.12.4:C771G, aly1911.2.8:G57A; and only one difference from *B. quadratum* is observed in the COI barcode, A628A.

Fig. 25. *Bungalotis barbalotis* **sp. n.** holotype ♂ NVG-15026B06 in dorsal (left) and ventral (right) views, data in text.

Fig. 26. Male genitalia of *Bungalotis barbalotis* **sp. n.** holotype NVG-15026B06 from Peru: Loreto in **a)** left lateral, **b)** dorsal, and **c)** posterolateral views.

Barcode sequence of the holotype. Sample NVG-15026B06, 658 base pairs:

AACACTATATTTTATTTTTGGTATTTGAGCAGGAATAGTTGGTACTTCTTTAAGATTACTAATTCGAACTGAATTAGGAACCCCCGGATCTTTAATTGGAGATGATCAAATTTACAATACT
ATTGTTACTGCGCACGCTTTTATTATAATTTTCTTTATAGTTATACCTATTATAATTGGAGGATTTGGAAATTGATTAGTACCTTTAATACTTGGAGCCCCTGATATAGCATTTCCTCGAA
TAAATAATATAAGATTTTGATTATTACCTCCTTCTTTAACTTTATTAATTTCAAGAAGTATTGTCGAAAATGGGGCTGGTACAGGTTGAACAGTTTACCCCCCTTTATCCGCTAATATTGC
ACATCAAGGTTCTTCTGTTGATCTAGCAATTTTTTCCTTACATTTAGCTGGAATTTCATCTATTTTAGGAGCTATCAATTTTATTACAACAATTATTAATATACGAATTAGAAACTTATCA
TTCGATCAAATACCTTTATTTGTTTGAGCTGTAGGAATTACAGCACTTTTATTATTACTTTCATTACCTGTCTTAGCTGGTGCTATTACTATATTACTAACAGATCGAAATCTTAACACAT
CATTTTTTGATCCTGCAGGAGGAGGAGATCCAATTTTATATCAACATTTATTT

Type material. Holotype: ♂ currently deposited in the McGuire Center for Lepidoptera and Biodiversity collection, Gainesville, FL, USA (MGCL), illustrated in Fig. 25 (genitalia Fig. 26), bears the following seven printed rectangular labels (text in italics handwritten), six white: [PERU: LORETO | Colonia Callaria 18-20 km. from R. | Ucayali; 11.X | 1971; ex M. Simon], [Allyn Museum | Acc. 1983-38], [> a leg is glued to this label, no text, [DNA sample ID: | NVG-15026B06 | c/o Nick V. Grishin], [DNA sample ID: | NVG-24127F08 | c/o Nick V. Grishin], [genitalia | NVG250720-28 | c/o Nick V. Grishin], and one red [HOLOTYPE ♂ | Bungalotis | barbalotis 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-15026B05 with the same data as the holotype.

Type locality. Peru: Loreto Region, Colonia Callaría, 18–20 km from Rio Ucayali.

Etymology. The name is derived from the subspecies it was misidentified as, *B. quadratum barba*, and is treated as a noun in apposition.

Distribution. Currently known from the type locality in northern Peru.

Tribe Eudamini Mabille, 1877
Subtribe Eudamini Mabille, 1877

The third confirmed male of *Cecropterus* (*Thorybes*) *viridissimus* Grishin, 2023

Cecropterus (*Thorybes*) *viridissimus* Grishin, 2023 (type locality in Ecuador: Zamora-Chinchipe) is currently known from two males and one female confirmed by genomic sequencing (Zhang et al. 2023a, 2025a). Due to the unusual nature of this species revealed by strongly supported incongruence of phylogenetic trees constructed from autosomes and the Z chromosome, every additional specimen may be of interest. We sequenced a *C. viridissimus* male NVG-24072F03 from Ecuador: Pastaza Province, Sarayaku, Nov-1967, R. de Lafebre leg. [MGCL], illustrated here for comparison (Fig. 27).

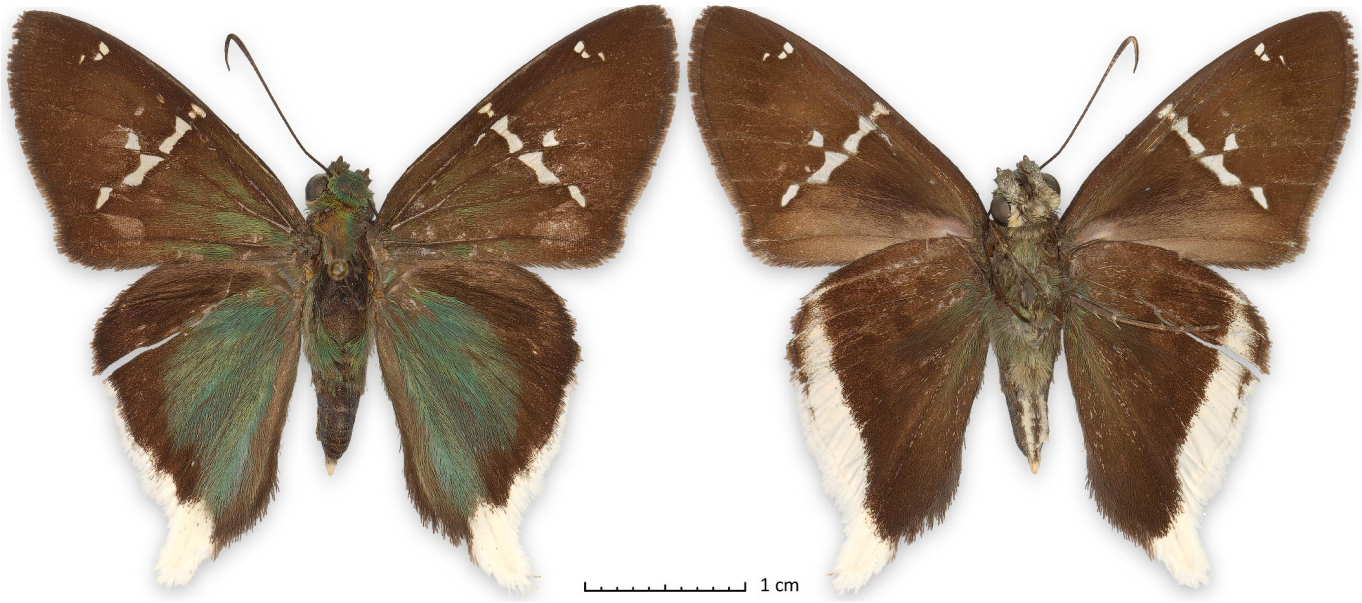

Fig. 27. *Cecropterus* (*Thorybes*) *viridissimus* NVG-24072F03 in dorsal (left) and ventral (right) views, data in text.

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

https://zoobank.org/6CEE9373-0A64-4E91-BB6C-D4D60723C01C

(Figs. 28 part, 29)

Definition and diagnosis. Genomic analysis reveals that a male from northeastern Ecuador initially identified as *Cecropterus* (*Murgaria*) *doryssus* (Swainson, 1831) (type locality in Brazil: Bahia) is genetically differentiated from it at the species level (Fig. 28); e.g., their COI barcodes differ by 4.3% (28 bp), and therefore this male represents a new species. This new species keys to "*Urbanus doryssus doryssus*" (C.13.25a) in Evans (1952), but differs from it and other relatives by the following combination of characters: three costal-most subapical hyaline spots on the forewing are small, dot-like, and the 4th (in cell R_5-M_1) is dash-like, strongly offset distad from the rest; the hyaline dash in the forewing cell M_3-CuA_1 is more strongly tilted away from the central hyaline band, forming a less acute angle with it from the costa; the white tornal area in the dorsal hindwing is moderately wide compared to other species, but with more strongly invading dark-brown "tooth" in cell CuA_2-1A+2A, and more developed white to pale overscaling broadly along the vein 1A+2A towards the base for more than its third from the tail end; dark-brown anal area penetrating deeper along the tail at its base; longer tail; and darker inner marginal area on the ventral forewing. Due to its cryptic nature and unexplored individual variation, this species is best identified by DNA, with diagnostic base pairs in the nuclear genome: aly2700.13.6:C139T, aly3595.5.4:T87C, aly3595.5.4:C117G, aly16031.2.1:T201C, aly5547.1.1:G396A, aly16287.1.1:T89T (not C), aly1222.26.6:G42G (not A), aly709.3.1:G63G (not T), aly2781.3.5:G918G (not A), aly536.26.2:G51G (not T); and the COI barcode: T197C, A466G, A481G, T556A, A622C.

Barcode sequence of the holotype. Sample NVG-24021B02, 658 base pairs:

AACTTTATATTTTATTTTTGGAATTTGAGCAGGATTAGTCGGAACTTCATTAAGTTTACTTATTCGAACTGAACTAGGAACTCCAGGATCTTTAATTGGAGATGATCAAATTTATAATACT
ATTGTAACAGCCCATGCTTTTATTATAATTTTTTTTATAGTTATACCTATTATAATTGGAGGATTTGGTAATTGACTAATTCCTCTTATACTAGGAGCCCCAGATATAGCTTTCCCCCGTA
TAAATAATATAAGATTTTGATTATTACCCCCATCTTTAACTCTTCTAATCTCGAGAAGAATTGTAGAAAATGGTGCAGGTACTGGATGAACAGTTTACCCCCCCTTATCATCTAATATTGC
CCATCAAGGAGCATCCGTAGATTTAGCAATTTTCTCTTTACATTTAGCTGGAATTTCTTCTATTCTTGGAGCCATTAATTTTATTACAACTATCATTAATATGCGAATTAATAATTTGTCA
TTTGATCAAATACCATTATTTATTTGAGCAGTCGGAATTACAGCCCTACTATTATTATTATCATTACCTGTACTAGCTGGAGCTATTACTATATTATTAACTGATCGAAATTTAAATACCT
CTTTCTTTGATCCAGCCGGTGGAGGAGATCCTATTTTATATCAACATTTATTC

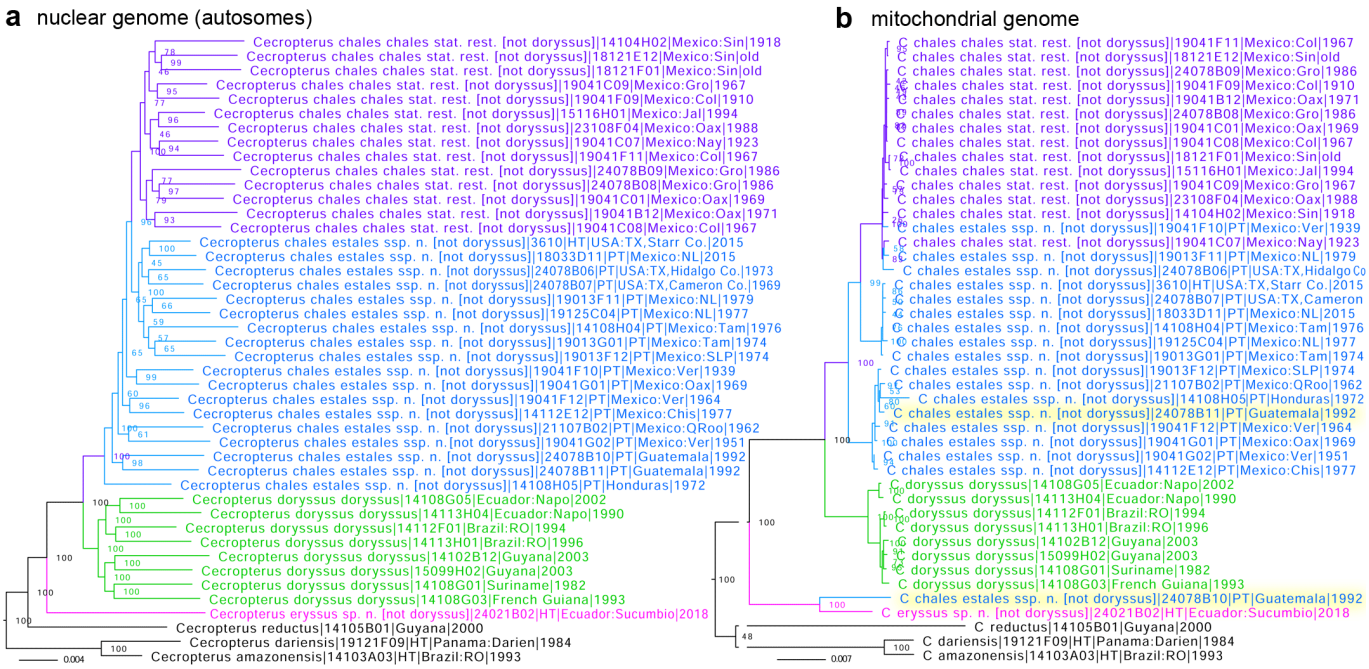

Fig. 28. Phylogenetic trees of selected *Cecropterus* (*Murgaria*) species constructed from protein-coding regions in: **a)** the nuclear genome (autosomes), based on 7,641,234 positions, and **b)** the mitochondrial genome. Different species discussed in this work are colored differently: *C.* (*M.*) *chales chales* **stat. rest.** (purple), *C.* (*M.*) *chales estales* **ssp. n.** (blue), *C.* (*M.*) *doryssus* (green), and *C.* (*M.*) *eryssus* **sp. n.** (magenta). Two specimens from Guatemala with the same label data but strongly different COI barcodes (due to introgression) are highlighted in yellow in (b). 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. 29. *Cecropterus* (*Murgaria*) *eryssus* **sp. n.** holotype ♂ NVG-24021B02 in dorsal (left) and ventral (right) views, data in text.

Type material. Holotype: ♂ deposited in the Senckenberg Natural History Museum collection, Frankfurt, Germany (SMF), illustrated in Fig. 29, bears the following three printed rectangular labels, two white: [Ecuador | Prov. Sucumbio | Playas de Cuyabeno | Aguarico River | XI.2018 210 m NN | S 0° 15' 50" | W 75° 53' 34" | leg. local collector], [DNA sample ID: | NVG-24021B02 | c/o Nick V. Grishin], and one red [HOLOTYPE ♂ | Cecropterus (Murgaria) | eryssus Grishin]. The specimen originally comes from the Ernst Brockmann collection.

Type locality. Ecuador: Sucumbíos Province, Playas de Cuyabeno, Aguarico River, elevation 210 m, GPS −0.2639, −75.8928.

Etymology. The name is derived from the *E*[cuadorian origin of this do]*ryssus* relative. Furthermore, the Ancient Greek verb ερύω (eryō) may mean to draw, to pull, or to drag, and reflects the phylogenetic distinction of this new species, which is "dragged away" in the trees from *C. doryssus* and its relatives. The name is treated as a noun in apposition.

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

Cecropterus (*Murgaria*) *chales* (Godman & Salvin, 1893), stat. rest. is a species distinct from *Cecropterus* (*Murgaria*) *doryssus* (Swainson, 1831)

Genomic analysis reveals that *Eudamus chales* Godman & Salvin, 1893 (type locality Mexico: Guerrero, Acapulco) currently regarded as a subspecies of *Cecropterus* (*Murgaria*) *doryssus doryssus* (Swainson, 1831) (type locality in Brazil: Bahia) is genetically differentiated from it at the species level (Fig. 28); e.g., their F_{st}/COI barcode difference are 0.29/1.1% (7 bp) (mitochondrial DNA is prone to introgression in this group, Fig. 28b). Therefore, we propose that *Cecropterus* (*Murgaria*) *chales* (Godman & Salvin, 1893), **stat. rest.** is a species distinct from *Cecropterus* (*Murgaria*) *doryssus* (Swainson, 1831).

Cecropterus (*Murgaria*) *chales estales* Grishin, new subspecies

https://zoobank.org/FBE25002-D2B6-4E0B-B78A-D6B9093B7EF5

(Figs. 28 part, 30–31a–d)

Definition and diagnosis. Genomic analysis reveals that specimens from eastern Mexico and surroundings initially identified as *Cecropterus* (*Murgaria*) *doryssus* (Swainson, 1831) (type locality in

Brazil: Bahia) are genetically differentiated from it at the subspecies level in the nuclear genome (Fig. 28), also showing a notable difference in COI barcodes of 1.1% (7 bp), but are genetically closer to *Cecropterus* (*Murgaria*) *chales* (Godman & Salvin, 1893), **stat. rest.** (type locality Mexico: Guerrero, Acapulco) with the barcode difference of only 0.3% (2 bp), and therefore represent its new subspecies due to their different wing pattern. This new subspecies keys to "*Urbanus doryssus doryssus*" (C.13.25a) in Evans (1952), but differs from it and other relatives by the following combination of characters: forewing with hyaline spots in both sexes, larger and broader in females (some *C. chales* females may have narrow spots), white area by the dorsal hindwing margin near the tornal tail is narrower than in *C. doryssus doryssus* but typically wider than in the nominotypical *C. chales*, the ventral hindwing margin is with strongly developed brown overscaling or spots within the white marginal band from the apex to past mid-wing (more weakly developed and confined to the apical area in *Cecropterus* (*Murgaria*) *doryssus albicuspis* (Herrich-Schäffer, 1869)), typically three or less subapical hyaline spots on the forewing, and the hyaline spot in the forewing cell M_3-CuA_1 tends to be narrower or lacking. Male genitalia (Fig. 31a–d) are similar to those of the nominotypical subspecies (Fig. 31e–f). Due to its partly cryptic nature and extensive individual variation, this subspecies is best identified by DNA, with diagnostic base pairs in the nuclear genome: aly138.12.1:G1068T, aly259.26.3:A114T, aly259.26.3:T900C, aly259.26.3:C1450A, aly259.

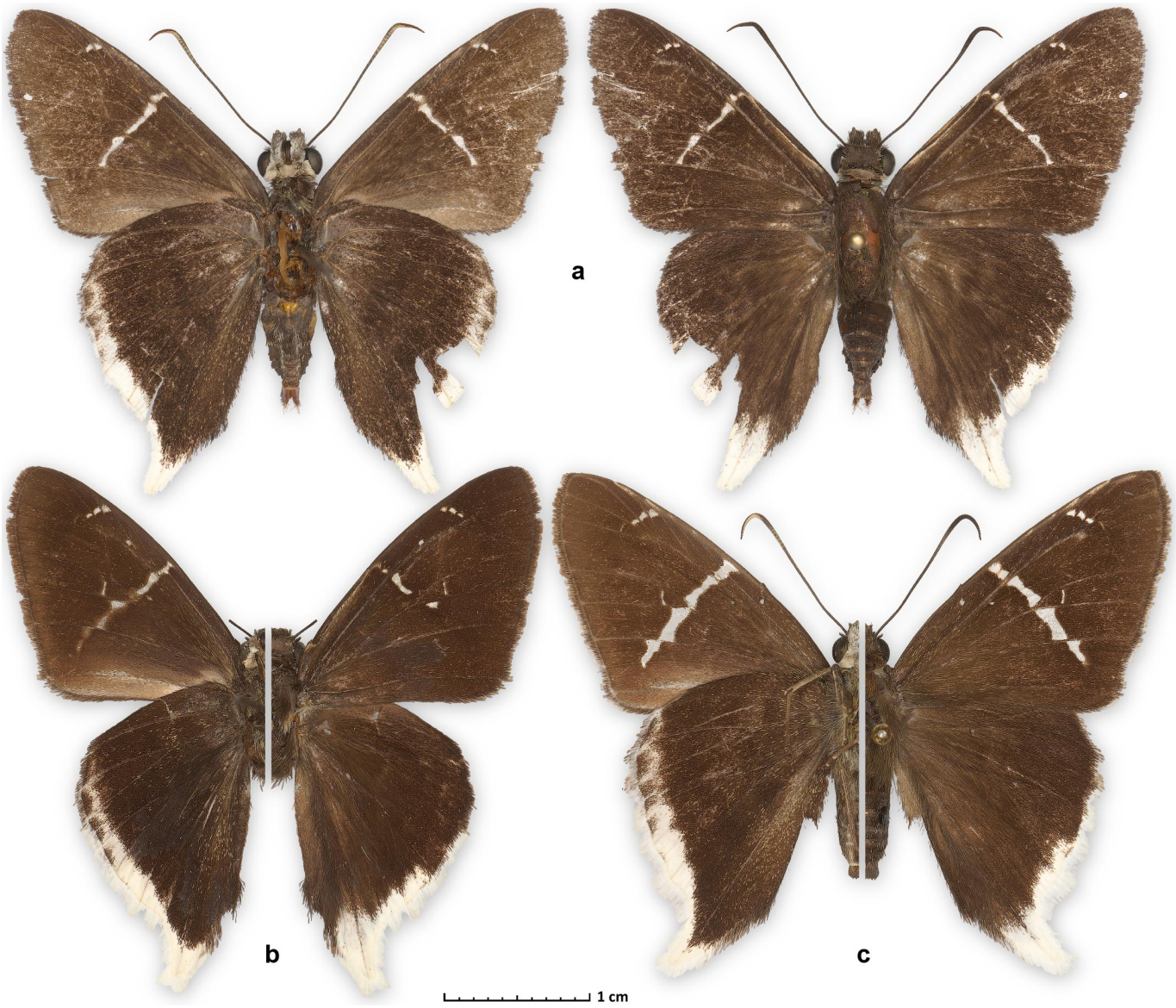

Fig. 30. *Cecropterus (Murgaria) chales estales* **ssp. n.** from USA: TX in ventral (left) and dorsal (right) views, data in text: **a)** holotype ♂ NVG-3610 Starr Co. and paratypes: **b)** ♂ NVG-24078B06 Hidalgo Co. and **c)** ♀ NVG-24078B07 Cameron Co.

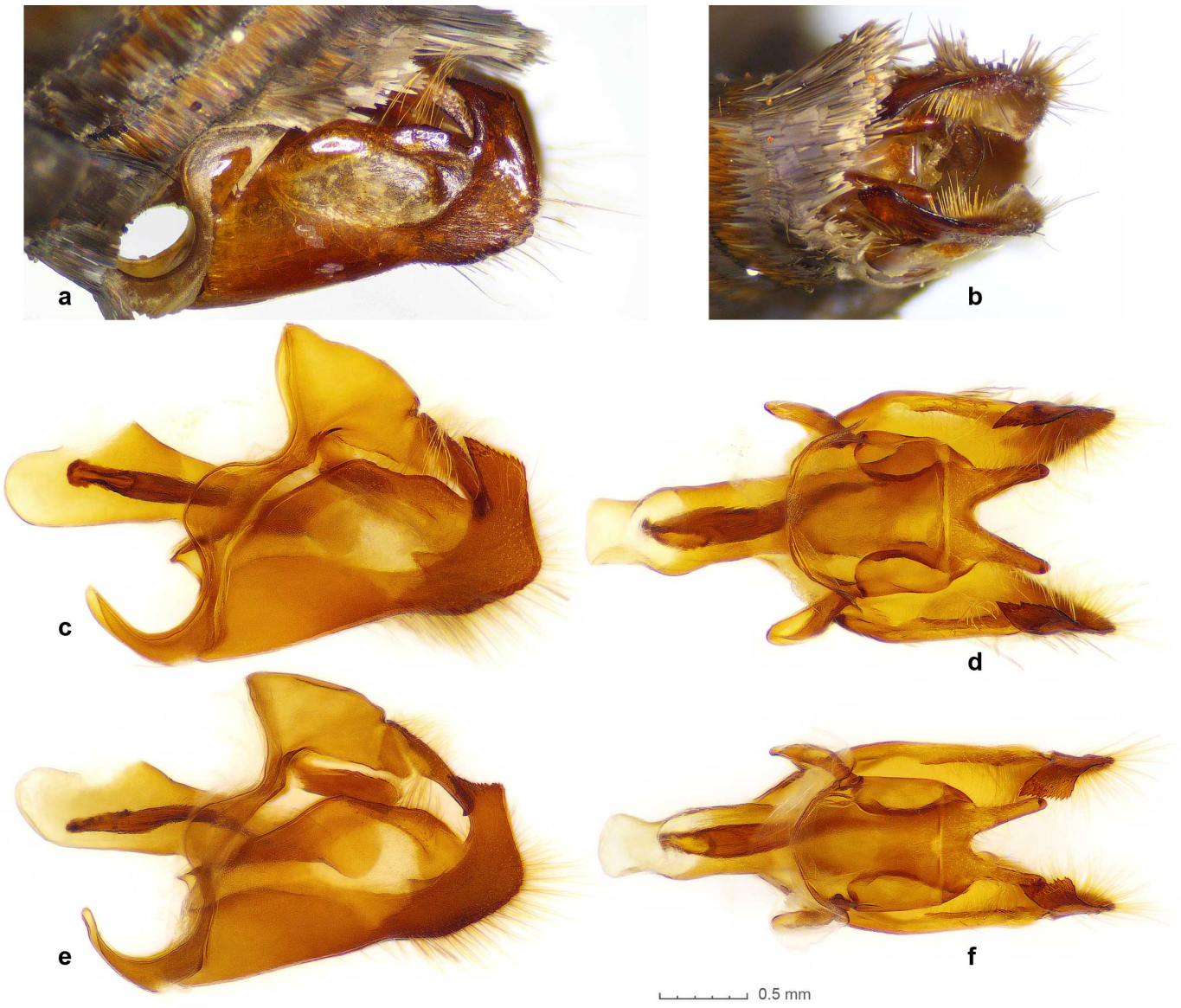

Fig. 31. Male genitalia of *Cecropterus* (*Murgaria*) *chales*, data in text or below: **a–d)** *C.* (*M.*) *chales estales* **ssp. n.** from USA, Texas: **a–b)** holotype NVG-3610 in situ and **c–d)** paratype NVG-24078B06; and **e–f)** *C.* (*M.*) *chales chales* NVG-15116H01, CSU_ENT1045547 Mexico: Jalisco, Mismaloya, ca. 16 km SW of Puerto Vallarta on Hwy 200, 26-Dec-1994, A. D. Warren leg., genitalia NVG241220-13 [CSUC]. Views: **a**, **c**, **e)** left lateral, **b)** dorsoposterior, and **d**, **f)** dorsal.

26.3:T2004G, aly138.12.1:G1068G (not T), aly259.26.3:A114A (not T), aly259.26.3:T900T (not C), aly259.26.3:C1450C (not A), aly259.26.3:T2004T (not G); and the COI barcode does not differentiate some specimens of this new subspecies from those of the nominotypical subspecies.

Barcode sequence of the holotype. Sample NVG-3610, 658 base pairs:

AACTTTATATTTTATTTTTGGAATTTGAGCAGGATTAGTCGGAACTTCATTAAGTTTACTTATTCGAACTGAATTAGGAACTCCAGGATCTTTAATTGGAGATGATCAAATTTATAATACT
ATTGTAACAGCCCATGCTTTTATTATAATTTTTTTTATAGTTATACCTATTATAATTGGAGGATTTGGTAATTGATTAATTCCTCTTATATTAGGAGCCCCCGATATAGCTTTCCCCCGTA
TAAATAATATAAGATTTTGATTATTACCCCCATCTTTAACACTCCTAATCTCAAGAAGAATTGTAGAAAATGGTGCAGGTACTGGATGAACAGTTTACCCCCCCTTATCATCTAATATTGC
CCATCAGGGAGCATCCGTAGATTTAGCAATTTTCTCATTACATTTAGCTGGAATTTCTTCTATTCTTGGAGCTATTAATTTTATTACAACTATCATTAATATACGAATTAATAATTTATCA
TTTGATCAAATACCATTATTTATTTGAGCAGTCGGAATTACAGCCCTATTATTATTATTATCATTACCTGTTTTAGCTGGAGCTATTACTATATTATTAACTGATCGAAATTTAAATACTT
CTTTTTTTGATCCAGCAGGTGGAGGAGACCCCATCTTATACCAACATTTATTT

Type material. Holotype: ♂ deposited in the McGuire Center for Lepidoptera and Biodiversity collection, Gainesville, FL, USA (MGCL), illustrated in Fig. 30a (genitalia Fig. 31a, b), bears the following three printed rectangular labels (text in italics handwritten), two white: [USA: TEXAS: Starr Co., | Roma, near International | Bridge, 26.4052, −99.0192 | 14-Jun-2015, leg. N. V. Grishin], [DNA sample ID: | NVG-3610 | c/o Nick V. Grishin], and one red [HOLOTYPE ♂ | Cecropterus (Murgaria) | chales estales Grishin]. **Paratypes:** 11♂♂ and 7♀♀: USA, Texas [MGCL]: 1♂ NVG-14112E11 Starr Co.,

Fronton, 4-Nov-2004, D. Clark leg., TLS collection; 1♂ NVG-24078B06 Hidalgo Co., Bentsen-Rio Grande Valley State Park, 14-Apr-1973, W. W. McGuire leg., genitalia GTA-2184 (Figs. 30b, 31c, d); and 1♀ NVG-24078B07 Cameron Co., W edge of Brownsville along irrigation canals by railroad tracks, 24-Jun-1969, J. R. Heitzman leg. [MGCL] (Fig. 30c); and Mexico: Nuevo León: 1♀ NVG-18033D11 Charco Azul, GPS 25.5894, −100.1856, 26-Aug-2015, M. Walker leg. [MWC] and Cola de Caballo: 1♂ NVG-19125C04 19-Aug-1977, C. J. Durden leg. [TMMC] and 1♀ NVG-19013F11 26-Oct-1979, R. O. Kendall & C. A. Kendall leg., BOLD sample TAMUICEGR-0039 [TAMU]; Tamaulipas: 1♂ NVG-14108H04 Ciudad Victoria, 11-Oct-1976, E. C. Knudson [USNM] and 1♀ NVG-19013G01 Sierra de las Cucharas, nr. rock quarry, 24-Feb-1974, R. O. Kendall & C. A. Kendall leg. [TAMU]; 1♂ NVG-19013F12 San Luis Potosí, Hwy 70, ca. [empty space, no number] km W of Ciudad Valles, 17-Jun-1974, W. W. McGuire leg. [TAMU]; Veracruz [AMNH]: 1♂ NVG-19041F10, AMNH_IZC 00337796 Presidio, 1939, C. C. Hoffmann leg.; 1♂ NVG-19041G02, AMNH_IZC 00337800 Presidio, Sep-1951, T. Escalante leg.; and 1♀ NVG-19041F12, AMNH_IZC 00337798 Catemaco, Sep-1964, T. Escalante leg.; 1♂ NVG-19041G01, AMNH_IZC 00337799 Oaxaca, El Naranjal–Chitepec, 35 m, May-1969, P. Hubbell leg. [AMNH]; 1♂ NVG-21107B02 Quintana Roo, X-cán, 14-Aug-1962, E. C. Welling leg. [CMNH]; 1♂ NVG-14112E12 Chiapas, Ejido Las Delicias, 4-Aug-1977, RLA leg., TLS collection [MGCL]; Guatemala, Petén, Parque Nacional Tikal, G. T. Austin collection [MGCL]: 1♀ NVG-24078B10 12-Jun-1992 and 1♂ NVG-24078B11 29-Jul-1992; and 1♀ NVG-14108H05 Honduras, San Pedro Sula, Santa Ana River, 14-Jul-1972, R. D. Lehman [USNM].

Type locality. USA: Texas, Starr Co., Roma, near the international bridge, GPS 26.4052, −99.0192.

Etymology. The name is derived from Spanish el este meaning east and reflects the eastern distribution of this subspecies. The name is treated as a noun in apposition.

Distribution. South Texas through eastern Mexico to Honduras.

The identity of *Urbanus* (*Urbanus*) *viterboana* (Ehrmann, 1907)

Genomic sequencing of the holotype of *Urbanus* (*Urbanus*) *viterboana* (Ehrmann, 1907) (type locality in Colombia: Socorro, sequenced as NVG-15095A01) revealed that this species has been misidentified by Evans (1952) and Steinhauser (1981) (Zhang et al. 2025b), and specimens previously identified as *U. viterboana* belong to several other species, such as *Urbanus* (*Urbanus*) *oplerorum* Grishin, 2023 (type locality in USA: Texas) and *Urbanus* (*Urbanus*) *viterbo* Grishin, 2025 (type locality in eastern Colombia), none of which is *U. viterboana*'s close relative (Fig. 32). Instead, *U. viterboana* is most closely related to *Urbanus* (*Urbanus*) *dubius* Steinhauser, 1981 (type locality in Colombia: Valle del Cauca), e.g., their COI barcodes differ by 2.4% (16 bp). This magnitude of difference is characteristic of closely related, but distinct species.

In contrast to *U. viterbo*, which is a common Central American species previously misidentified as *U. viterboana*, the true *U. viterboana* is rare in collections. In addition to the holotype (Fig. 33a), genomic analysis revealed only five other specimens, all males, that we identify as this species, because they form a clade sister to *U. dubius* that contains the holotype of *U. viterboana*. To aid in the identification of *U. viterboana*, we illustrate all 6 genetically identified specimens (Fig. 33), which come from the eastern Andes above 1000 m elevation in Colombia, Ecuador, and Peru (northern and southern). Data for illustrated specimens are: holotype ♂ NVG-15095A01 Colombia, Santander Department, Socorro, old, genitalia M-3218 J. Y. Miller [CMNH] (Fig. 33a); Ecuador, Tungurahua, Rio Encanto, 1400 m, Jan-1971, R. de Lafebre [MGCL]: 1♂ NVG-24078C10 genitalia SRS-470 (Fig. 33b) and 1♂ NVG-24078C11 genitalia SRS-472 (Fig. 33c); 1♂ NVG-14104A11 Peru, Cuzco, Quitacalzone, Cosñipata Rd., 1050 m, 20-May-2012, S. Kinyon leg. [USNM] (Fig. 33d); Peru, San Martin, ex coll. Michael Büche [EBC]: 1♂ NVG-20095B06a Jorge Chávez-Afluente, 1300-1800 m, Feb-2012 (Fig. 33e) and 1♂ NVG-20095B07a, 1500-1800 m, Jul-2012 (Fig. 33f).

Comparisons of wing patterns among these specimens and to other species of *Urbanus* Hübner, [1807] (type species *Papilio proteus* Linnaeus, 1758) suggest that *U. viterboana* males may be identifiable

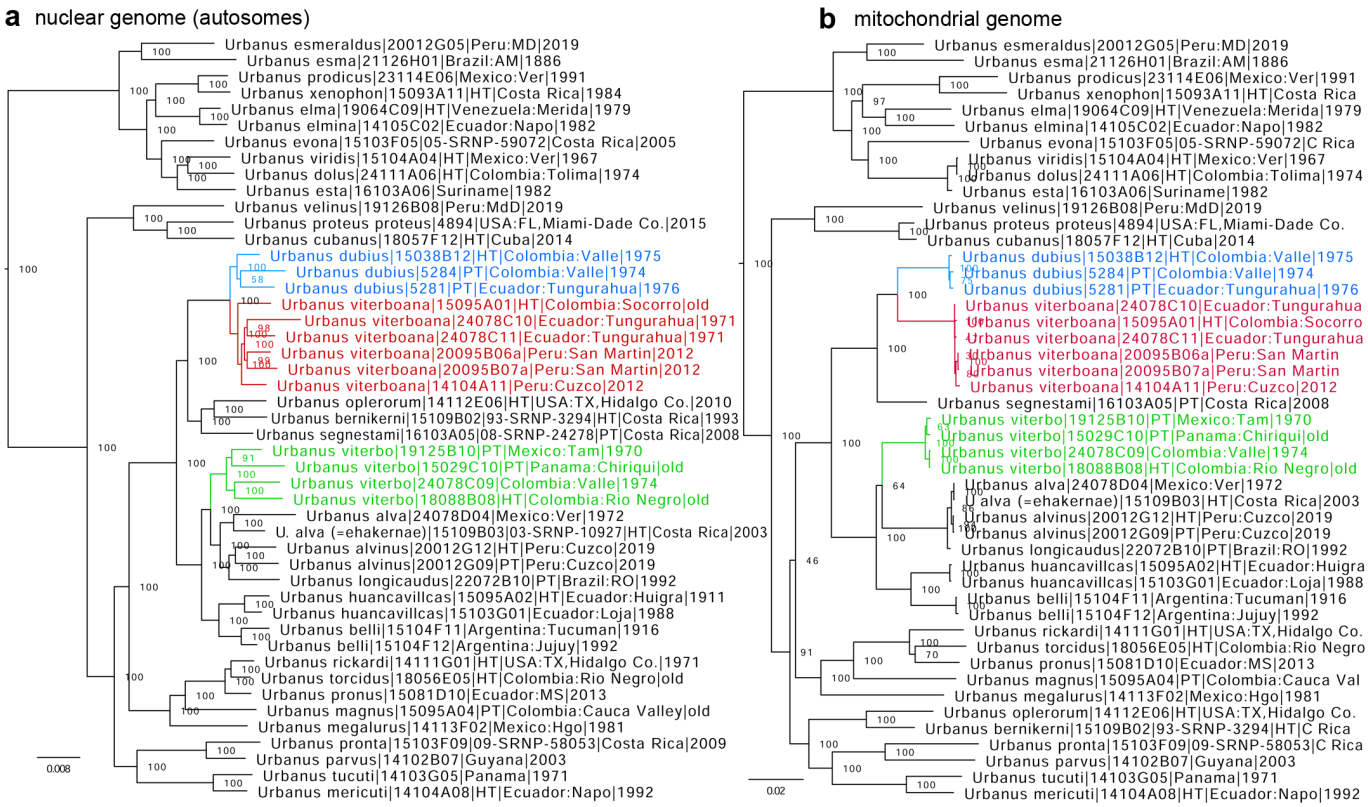

Fig. 32. Phylogenetic trees of selected *Urbanus* species constructed from protein-coding regions in: **a)** the nuclear genome (autosomes), based on 5,421,354 positions, and **b)** the mitochondrial genome. Species discussed in this work are colored: *U. dubius* (blue), *U. viterboana* (red), and *U. viterbo* (green, previously misidentified as *U. viterboana*). Ultrafast bootstrap (Hoang et al. 2018) values are shown at nodes.

from photographs. In particular, all specimens have reduced in size and more strongly yellow semihyaline forewing spots; the spot in the discal cell is nearly triangular and the elongated rectangular costal spot overlaps with it over the entire length, the spot in cell CuA_1-CuA_2 tends to be smaller than the spot in cell M_3-CuA_1 (which is usually the largest spot on the forewing) and is frequently pear-shaped; the third from the costa subapical semihyaline spot is the smallest and slightly offset distad from the other two; the basal dark band on the ventral hindwing is forked at the costal margin with the two sides of the brown fork nearly parallel to each other and the costal cell is darker than the ground color, thus creating an impression that the basal dark band contains a paler spot near the costa; the base of the ventral hindwing cell Rs-M_1 is paler than the dark band (except the very base) forming a notch at the outer edge of the band. The female of *U. viterboana* remains unknown.

To further facilitate recognition of these species, we provide COI barcodes of the holotypes of *U. viterboana* and *U. dubius* but caution that the barcodes may introgress between species. As a result, other species may have barcodes close to these, and, conversely, there might be specimens of these two species having different barcodes. Therefore, nuclear genomic sequences or total evidence approach should be used for more confident identification. The COI barcode sequence of the *U. viterboana* holotype, sample NVG-15095A01, 658 base pairs is:

AACTTTATATTTTATTTTTGGAATTTGAGCAGGATTAATTGGAACTTCTCTAAGATTACTTATTCGAACTGAATTAGGAACCCCAGGATCTTTAATTGGAGATGATCAAATTTATAATACT
ATTGTAACAGCTCATGCATTTATTATAATTTTTTTTATAGTTATACCTATTATAATTGGAGGATTTGGTAATTGACTAGTGCCTTTGATAATAGGAGCTCCTGATATAGCTTTCCCCCGTA
TAAATAATATAAGATTTTGATTATTACCCCCCTCCTTAACTTTATTAATTTCAAGAAGAATTGTTGAAAATGGTGCTGGTACTGGATGAACAGTTTATCCCCCCCTTTCATCTAATATTGC
TCATCAAGGAGCTTCTGTTGATTTAGCAATTTTCTCCCTTCATCTTGCAGGTATTTCATCAATTCTTGGAGCTATTAATTTTATTACAACAATTATTAATATACGAATTAATAGATTATCT
TTTGATCAAATACCATTATTTGTATGAGCTGTAGGAATTACAGCATTATTATTATTACTTTCTTTACCCGTTTTAGCTGGAGCTATTACTATATTATTAACTGATCGAAACTTAAATACTT
CATTTTTTGATCCAGCTGGAGGAGGAGATCCAATCCTATATCAACATTTATTT

The sequence of the *U. dubius* holotype, sample NVG-15038B12, 658 base pairs is:

AACTTTATATTTTATTTTTGGAATTTGAGCAGGATTAATTGGAACTTCTCTAAGATTACTTATTCGAACTGAATTAGGAACTCCAGGATCTTTAATTGGAGATGATCAAATTTATAATACT
ATTGTAACAGCCCATGCATTTATTATAATTTTTTTTATAGTTATACCTATTATAATCGGAGGATTTGGTAATTGATTAGTACCTTTAATAATAGGAGCTCCTGATATAGCTTTCCCCCGTA
TAAATAATATAAGATTTTGATTATTACCCCCATCATTAACTTTATTAATTTCAAGAAGAATTGTTGAAAATGGTGCTGGTACTGGATGAACAGTTTATCCCCCTCTTTCATCTAATATTGC
TCATCAAGGAGCTTCTGTTGATTTAGCAATTTTCTCCCTCCATCTTGCAGGAATTTCATCAATTCTTGGAGCTATTAATTTTATTACAACAATTATTAATATACGAATCAATAGATTATCT
TTTGATCAAATACCATTATTTGTATGAGCTGTAGGAATTACAGCATTATTATTATTACTTTCTTTACCCGTTTTAGCTGGAGCTATTACTATATTATTAACTGACCGAAACTTAAATACTT
CATTTTTTGATCCCGCTGGAGGAGGGGATCCAATCCTATACCAACATTTATTT

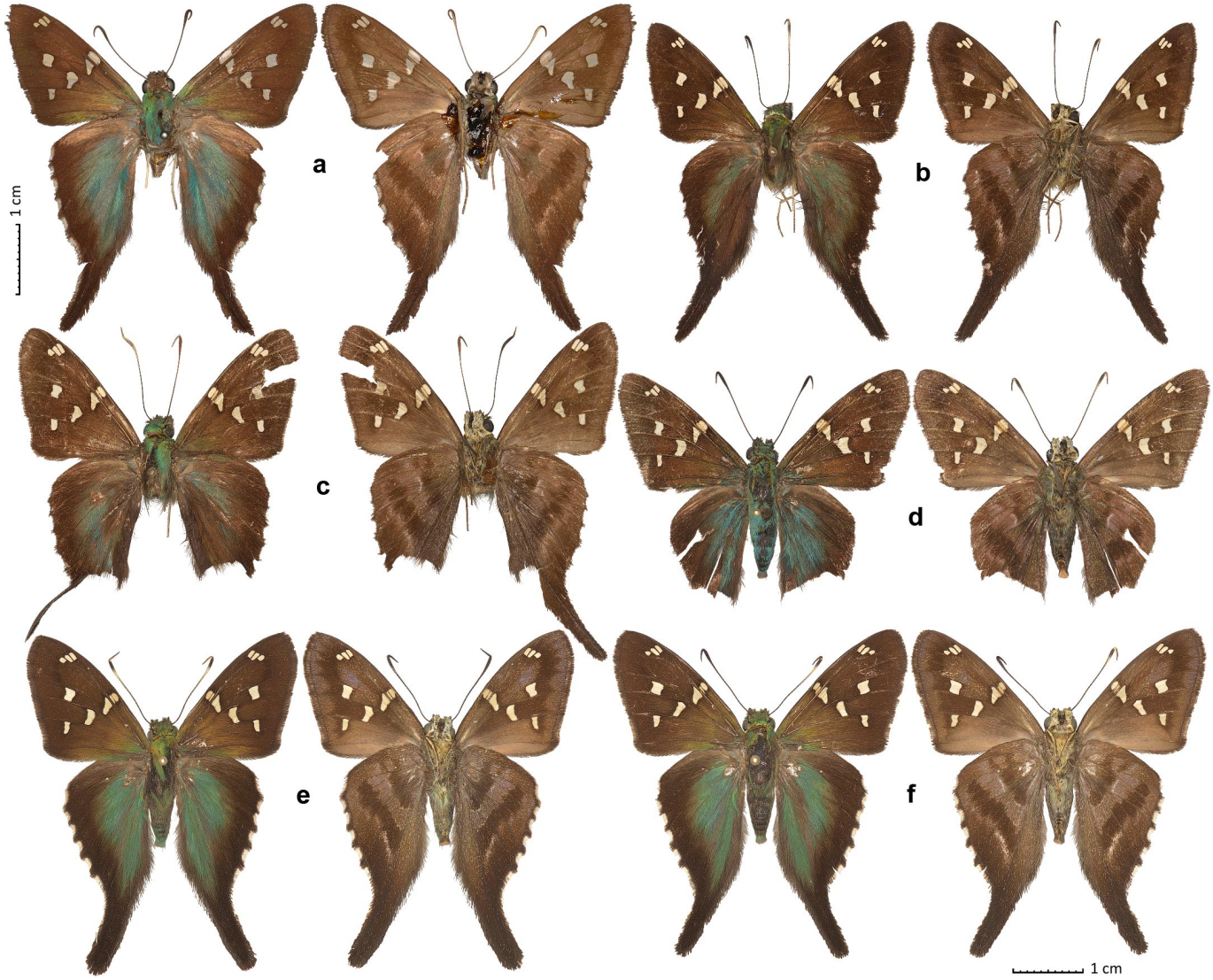

Fig. 33. Males of *Urbanus viterboana* in dorsal (left) and ventral (right) views, data in text: **a)** holotype NVG-15095A01 from Colombia: Santander; **b)** NVG-24078C10 and **c)** NVG-24078C11 from Ecuador: Tungurahua; **d)** NVG-14104A11 from Peru: Cuzco; and **e)** NVG-20095B06a and **f)** NVG-20095B07a from Peru: San Martín. Photographs e, f) are by Ernst Brockmann.

Subtribe Cephisina Grishin, 2019

Cephise panuspe Grishin, new species

https://zoobank.org/A1AA6EDC-43C7-450D-86B7-73BD63691E14

(Figs. 34 part, 35)

Definition and diagnosis. Genomic analysis reveals that a specimen from Panama initially identified as *Cephise nuspesez* Burns, 1996 (type locality in Costa Rica, holotype sequenced as NVG-22032F10) is genetically differentiated from it at the species level (Fig. 34); e.g., their COI barcodes differ by 2% (13 bp), and therefore this specimen represents a new species. This new species keys to "*Cephise cephise cephise*" (Herrich-Schäffer, 1869) (D.6(a)) in Evans (1952), but differs from it and other relatives by the following combination of characters in males: only two subapical spots on the forewing (the middle spot is absent), similar to *Cephise burnsi* Austin & O. Mielke, 2000 (type locality in Brazil: Espírito Santo), but the costal-most spot is smaller than in *C. burnsi*; semihyaline spots appear yellower (at least in the holotype); the hindwing tornus is more extended and the wing appears narrower; and the semihyaline spot in the forewing cell CuA_2-1A+2A is smaller and appears nearly detached from the discal band. Due to its cryptic nature and unexplored individual variation, this species is best identified by DNA, with diagnostic

base pairs in the nuclear genome: aly2850.3.5:A225G, aly2850.3.5:C270T, aly322.13.2:A1564T, aly322.13.2:T1632C, aly5181.7.2:A96T, aly770.15.10:A63A (not T), aly118415.1.3:G30G (not A), aly118415.1.3:A33A (not G), aly1916.6.3:G39G (not C), aly85.23.28:A72A (not G); and the COI barcode: T16C, G200G, A307T, A319T, T487C.

Barcode sequence of the holotype. Sample NVG-2072, 658 base pairs:

AACTTTATATTTTATCTTTGGTATTTGAGCTGGAATAATTGGATCATCCTTAAGTTTATTAATTCGAACTGAATTAGGAACTTGTGGATCTTTAATTGGAGATGATCAAATTTATAATACT
ATTGTTACAGCTCATGCTTTTATTATAATTTTCTTTATAGTAATACCTATTATAATTGGAGGATTTGGAAATTGATTAGTTCCTTTAATATTAGGAGCTCCAGATATAGCATTTCCACGAA
TAAATAATATAAGATTTTGATTACTTCCCCCATCTTTAACTTTATTAATTTCAAGAAGTATTGTTGAAAATGGAGCTGGAACTGGATGAACAGTATATCCTCCTTTATCTTCTAATATTGC
CCACCAAGGTTCTTCTGTTGATCTAGCAATTTTTTCCTTACATTTAGCAGGTATCTCTTCAATTTTAGGAGCTATTAATTTCATTACAACAATTATTAATATACGAATTAATAATATATCT
TTCGATCAAATACCTTTATTTATTTGAGCAGTAGGAATTACAGCATTATTATTATTACTTTCATTACCTGTATTAGCAGGAGCTATTACTATACTTTTAACAGATCGTAATTTAAATACTT
CTTTTTTTGATCCTGCTGGAGGAGGAGATCCTATTCTATACCAACATTTATTC

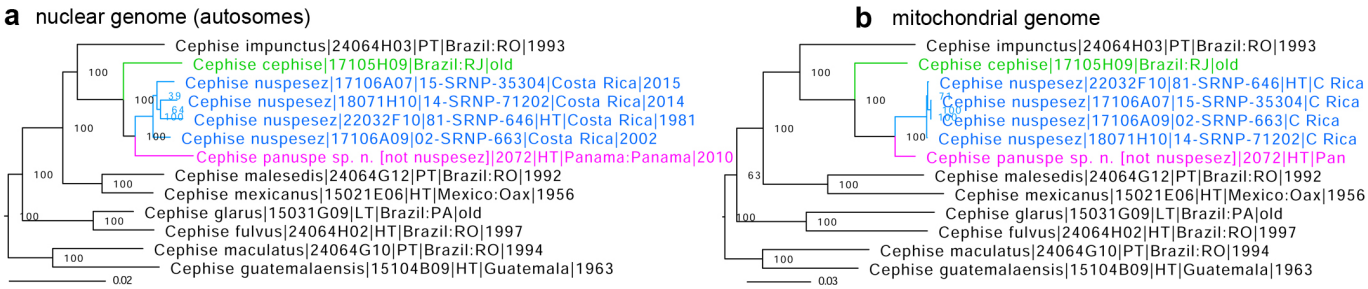

Fig. 34. Phylogenetic trees of selected *Cephise* species constructed from protein-coding regions in: **a)** the nuclear genome (autosomes), based on 8,515,890 positions, and **b)** the mitochondrial genome. Species mentioned in the text are colored: *C. cephise* (green), *C. nuspesez* (blue), *C. panuspe* **sp. n.** (magenta). Ultrafast bootstrap (Hoang et al. 2018) values are shown.

Fig. 35. *Cephise panuspe* **sp. n.** holotype ♂ NVG-2072 in dorsal (left) and ventral (right) views, data in text.

Type material. Holotype: ♂ deposited in the Mississippi Entomological Museum, Starkville, MS, USA (MEM), illustrated in Fig. 35, bears the following five printed rectangular labels (text in italics handwritten), four white: [Panama: Panama | ca. 12 km. E of | Bayano bridge | N 09° 09' 11.5" | W 078° 41' 34.2" | Aug. 20, 2010 | J. R. MacDonald], [Genit. Vial No. | RAA 0573], [*Cephise sp.* | *nr. cephise* | Det. R. Anderson], [DNA sample ID: | NVG-2072 | c/o Nick V. Grishin], and one red [HOLOTYPE ♂ | Cephise panuspe | Grishin].

Type locality. Panama: Panamá Province, ca. 12 km east of Bayano bridge, GPS 9.1532, −78.6928.

Etymology. The name is a fusion: *Pa*[nama] + *nuspe*[sez], to reflect its type locality and sister species name. The name is treated as a noun in apposition.

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

Subfamily Pyrginae Burmeister, 1878
Tribe Carcharodini Verity, 1940
Subtribe Pholisorina Grishin, 2023

Pholisora mejicanus yuesanus Grishin, new subspecies

https://zoobank.org/6093D113-DD73-4EB1-8630-66D43FC8AAD4

(Fig. 36 part, 37)

Definition and diagnosis. Genomic analysis of *Pholisora mejicanus* (Reakirt, [1867]) (type locality Mexico: Veracruz, Presidio, neotype sequenced as NVG-23054E11) specimens from across the range reveals that they partition into two clades in all three trees (autosomes in the nuclear genome, the Z chromosome, and the mitochondrial genome; Fig. 36). These clades may not be distinct enough to justify the species level for the taxa they represent, but they are genetically distinct to be treated as subspecies. Even COI barcodes that frequently do not differ between subspecies have diverged between the two clades by 0.8% (5 bp), which is a non-trivial difference for subspecies. The southern clade with Mexican populations contains the neotype of *P. mejicanus* and corresponds to this taxon. The northern clade with the U.S. populations represents a new subspecies. This new subspecies keys to *P. mejicanus* (G.4.2) in Evans (1953) and differs from the nominotypical subspecies by rounder (compared to more elongated) submarginal white spots (if developed) on the dorsal forewing, weaker black overscaling around ventral hindwing veins, usually better developed pale scales in the fringe at the forewing apex; and a slightly smaller ampulla connected with the costa though a smaller concavity instead of the broader and more convex dorsal margin. Due to the cryptic nature of this subspecies, most reliable identification is achieved by DNA, and a combination of the following base pairs is diagnostic in the nuclear genome: aly747.7.4: C99T, aly747.7.4:G126A, aly747.7.4:A153C, aly887.14.4:A166C, aly393.14.1:C133T, and the COI barcode does not always distinguish this new subspecies from the nominotypical subspecies.

Barcode sequence of the holotype. Sample NVG-19013D11, 658 base pairs:

AACTTTATATTTTATTTTTGGTATTTGAGCAGGTATAGTAGGGACTTCTTTAAGTATCCTTATTCGTTCTGAATTAGGAACACCTGGATCTTTAATTGGTGATGATCAAATTTATAATACT
ATTGTAACAGCTCATGCTTTTATTATAATTTTTTTATAGTTATACCTATTATAATTGGAGGATTTGGAAATTGACTAGTACCCCTTATATTAGGAGCTCCTGATATAGCTTTCCCACGAA
TAAATAATATAAGATTTTGACTTTTACCTCCTTCACTTATATTATTAATTTCTAGTAGTATTGTAGAAAATGGTGCAGGTACTGGATGAACTGTATATCCCCCACTTTCAGCTAATATTGC
TCATCAAGGTTCATCTGTAGATTTAGCAATTTTTTCACTTCATCTTGCTGGTATTTCTTCAATTTTAGGTGCAATTAATTTTATTACAACAATTATTAATATACGAATTAATAATTTATCA
TTTGATCAAATACCTTTATTTGTTTGAGCTGTAGGTATTACAGCTTTACTTCTATTACTATCTTTACCAGTATTAGCGGGTGCTATTACTATATTATTAACTGATCGAAATCTTAATACAT
CATTTTTTGATCCTGCTGGAGGAGGAGACCCTATTTTATATCAACATTTATTT

Type material. Holotype: ♂ deposited in the Texas A&M University Insect Collection, College Station, TX, USA (TAMU), illustrated in Fig. 37, bears the following four labels (1st handwritten, others printed with handwritten text shown in italics), three white: [COLORADO | El Paso Co.: Woodmen | Valley Rd., 17-VII-82 | leg Mike Fisher], [HESPERIIDAE, | Pyrginae: | Pholisora mejicana | (Reakirt, [1867]) | ♂ det. R.O. Kendall | M. & B. No. 116], [DNA sample ID: | NVG-19013D11 | c/o Nick V. Grishin], and one red [HOLOTYPE ♂ | Pholisora mejicanus | yuesanus Grishin]. **Paratypes:** 7♂♂ and 3♀♀ from USA: Colorado: 1♂ NVG-24105G11 El Paso Co., S of Crystola, 7-Jul-1962, C. J. Durden leg., genitalia

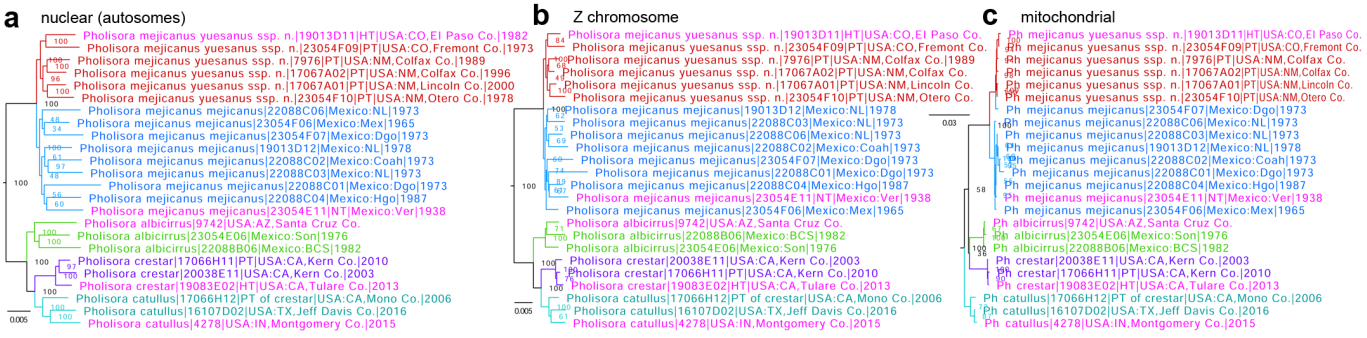

Fig. 36. Phylogenetic trees of *Pholisora* constructed from protein-coding regions in: **a)** the nuclear genome (autosomes), **b)** the Z chromosome, and **c)** the mitochondrial genome: *P. mejicanus yuesanus* **ssp. n.** (red), *P. mejicanus mejicanus* (blue), *P. albicirrus* Glassberg, 2023 (green), *P. crestar* Scott & Davenport, 2017 (purple), and *P. catullus* (Fabricius, 1793) (cyan). Specimens used as name references are labeled in magenta.

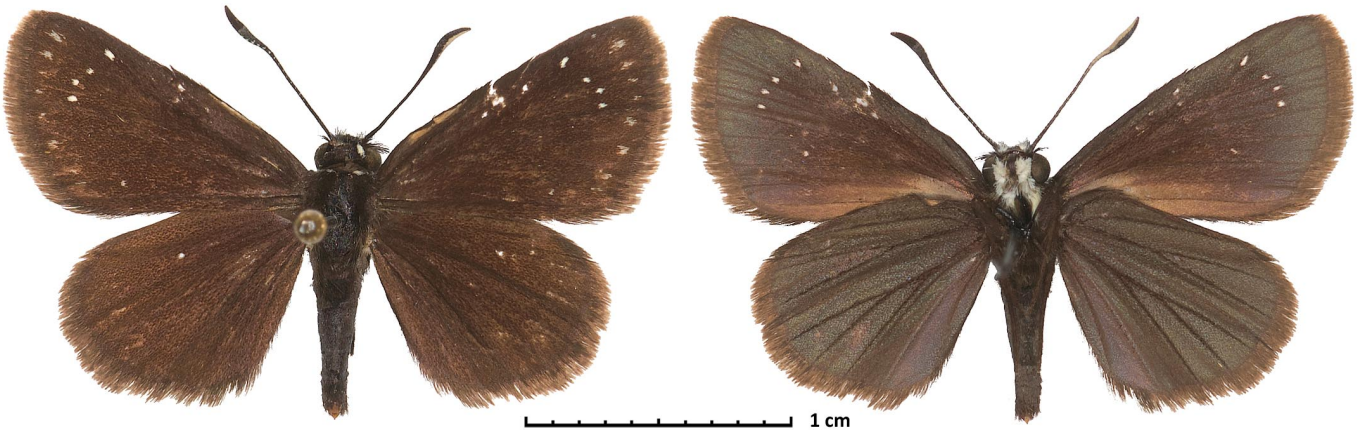

Fig. 37. *Pholisora mejicanus yuesanus* **ssp. n.** holotype ♂ NVG-19013D11 in dorsal (left) and ventral (right) views.

NVG250720-59 [TMMC] and 1♂ NVG-23054F09 Fremont Co., Kerr Gulch, 19-Aug-1973, J. A. Scott leg. [MGCL] and New Mexico: Colfax Co.: 1♀ NVG-7976, USNMENT_01321816 Cimarron, 6430 ft, 7-Aug-1989, J. M. & S. N. Burns leg., genitalia NVG170207-61 [USNM] and 1♂ NVG-17067A02, CSU_ENT1040718 Maxwell National Wildlife Refuge, Lakes 12 & 13, 6500 ft, 4-Jul-1996, R. W. Holland & S. J. Cary leg. [CSUC]; 1♂ NVG-25027G09, CSU_ENT1040746 Bernalillo Co., E. slope of Sandia Mountains, Dry Sink, 8100 ft, 29-Jul-1968, J. Lane leg., genitalia No. 6267 by Kilian Roever [CSUC]; Torrance Co.: 1♀ NVG-24102G09, WRD 21815 Cibola National Forest, Rd. A013, 6869 ft, GPS 34.7603, −106.3163, 16-Jul-2022, W. R. Dempwolf leg. [WRDC] and 1♂ NVG-25027G10, CSU_ENT1040711 Manzano Mountains, New Campground Rd., ca. 2 mi E of Manzano, 7300 ft, 30-Jul-1968, J. Lane leg., genitalia No. 6265 by Kilian Roever [CSUC]; 1♂ NVG-24102G08, WRD 23252 Sierra Co., Hwy 52, 6897 ft, GPS 33.3836, −107.6042, 11-Jun-2023, W. R. Dempwolf leg. [WRDC]; 1♂ NVG-17067A01, CSU_ENT1040733 Lincoln Co., Sacramento Mts., Cedar Creek, 5 mi N of Ruidoso, NMSU station, 7200 ft, 1-Jul-2000, R. W. Holland leg. [CSUC]; and 1♀ NVG-23054F10 Otero Co., 3.5 mi SW of Mayhill, Lightning Spring, 4-Jul-1978, K. Roever leg. [MGCL].

Type locality. USA: Colorado, El Paso Co., Woodmen Valley Rd.

Etymology. The name is a spelled-out version of "U.S." to end like the name of the nominate subspecies *mejicanus*, reflecting the distribution of this subspecies. The name is treated as an indeclinable adjective.

Distribution. Southern Rocky Mountain region of the USA (confirmed from Colorado and New Mexico).

Subtribe Carcharodini Verity, 1940

Lectotype designation for *Helias haematospila* C. Felder & R. Felder, 1867

Helias haematospila C. Felder & R. Felder, 1867, presently a valid species of *Noctuana* Bell, 1937 (type species *Helias noctua* C. Felder & R. Felder, 1867), was described from both males and females, from Venezuela, and Colombia: Bogota (Felder and Felder 1867). To stabilize nomenclature, narrow down the type locality, and define the name *H. haematospila* objectively, N.V.G. hereby designates a syntype in the BMNH collection, a female that bears the following seven labels (first two, 4th, 7th round, others rectangular; 1st with a red circle on one side, 2nd blue, 7th yellow, others white; 2nd–4th, 7th handwritten, others printed): (Type) and on the other side of this label handwritten (H | 848), (Venezu | ela), [61 Helias | haematospila], [♀], (FELDER | COLL$^{N.}$), [{QR Code} | BMNH(E) 1669579], (276), as the **lectotype** of *Helias haematospila* C. Felder & R. Felder, 1867. The lectotype is missing both antennae, its head is tilted to the right, and it has a pinhole of the size of the subapical hyaline spot at the base of the right hindwing. Images of this specimen photographed by N.V.G. are shown on the Butterflies of America website (Warren et al. 2024). The type locality of *H. haematospila* becomes Venezuela.

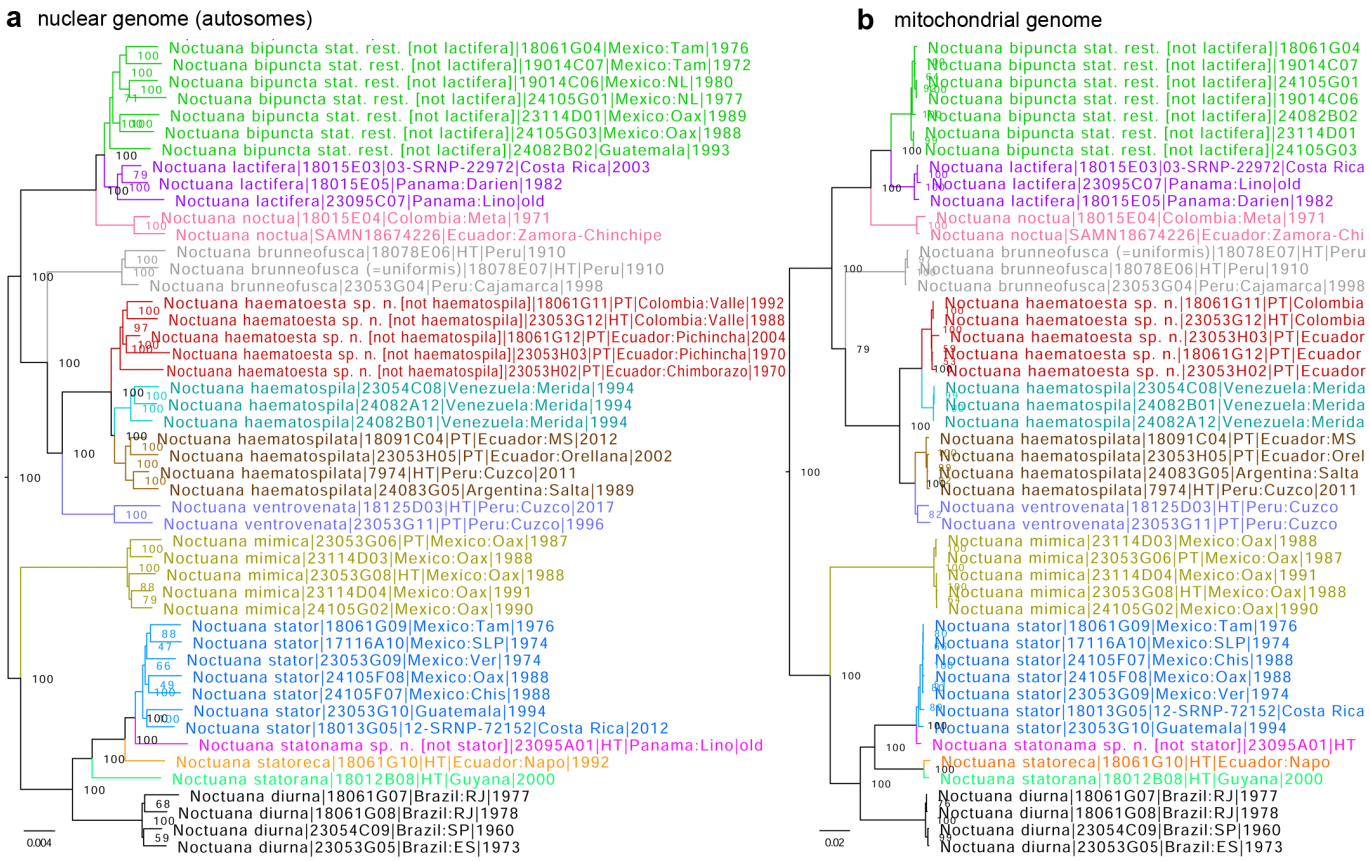

Fig. 38. Phylogenetic trees of all described *Noctuana* species constructed from protein-coding regions in: **a)** the nuclear genome (autosomes), based on 1,468,671 positions, and **b)** the mitochondrial genome. Different species are colored differently: *N. bipuncta* **stat. rest.** (green), *N. lactifera* (purple), *N. noctua* (C. Felder & R. Felder, 1867) (pink), *N. brunneofusca* (Mabille & Boullet, 1917) (gray), *N. haematoesta* **sp. n.** (red), *N. haematospila* (cyan), *N. haematospilata* Grishin, 2025 (brown), *N. ventrovenata* Grishin, 2025 (lavender), *N. mimica* Grishin, 2025 (olive), *N. stator* (blue), *N. statonama* **sp. n.** (magenta), *N. statoreca* Grishin, 2025 (orange), *N. statorana* Grishin, 2025 (aquamarine). The sequence of SAMN18674226 is taken from the alignment provided in Kawahara et al. (2023). Ultrafast bootstrap (Hoang et al. 2018) values are shown at nodes.

Noctuana haematoesta Grishin, new species

https://zoobank.org/106337C1-BFE3-4388-8834-AB8BA9900FDB

(Figs. 38 part, 39, 40a)

Definition and diagnosis. Genomic analysis reveals that specimens from the Andes in western Colombia and Ecuador initially identified as *Noctuana haematospila* (C. Felder and R. Felder, 1867) (type locality in Venezuela) are genetically differentiated from it and other relatives at the species level (Fig. 38); e.g., their COI barcodes differ by 1.4% (9 bp) (the barcode difference is lower than expected from the nuclear genome divergence, possibly due to introgression because nuclear and mitochondrial trees are incongruent: Fig. 38a vs. b), and therefore these specimens represent a new species. This new species keys to *N. haematospila* (E.22.5) in Evans (1953) and was included by him in this species, but differs from it (Fig. 40b–d) and other relatives by the following combination of characters in males: more elongated hindwing towards the tornus; ventral forewing with a more strongly developed pattern of beige lunules and dashes in the submarginal area, particularly towards the tornus; and the red spots in the ventral hindwing discal cell and cell M_3-CuA_1 overlap with each other to a lesser extent. Due to its cryptic nature and unexplored individual variation, this species is best identified by DNA, with diagnostic base pairs in the nuclear genome: aly1454.5.2:G313A, aly1454.5.2:C324T, aly3721.1.16:G1110A, aly2919.2.1:C72T, aly1282.24.6:T72C; and the COI barcode: G38A, C85T, 433A, A622T, A631G.

Fig. 39. Type specimens of *Noctuana haematoesta* **sp. n.** ♂♂ in dorsal (left) and ventral (right) views, data in text: from Colombia: Valle del Cauca: **a)** holotype NVG-23053G12, **b)** paratype NVG-18061G11; and paratypes from Ecuador: Pichincha: **c)** NVG-18061G12 and **d)** NVG-23053H03.

Fig. 40. Males of specimens of *Noctuana* in dorsal (left) and ventral (right) views, data in text: **a)** *Noctuana haematoesta* **sp. n.** paratype NVG-23053H02 from Ecuador: Chimborazo and *Noctuana haematospila* from Venezuela: Merida: **b)** NVG-24082A12, **c)** NVG-24082B01, and **d)** NVG-23054C08.

Barcode sequence of the holotype. Sample NVG-23053G12, 658 base pairs:

AACCTTATATTTTATTTTTGGTATTTGAGCAGGAATAATAGGAACTTCTTTAAGATTAATTATTCGCTCTGAATTAGGAACCCCTGGATCTTTAATTGGAGATGATCAAATTTACAATACT
ATTGTAACAGCTCACGCCTTTATTATAATTTTTTTTATAGTAATACCAATTATAATCGGAGGTTTTGGAAATTGACTAGTCCCCCTTATGTTGGGAGCCCCTGACATAGCTTTTCCACGAA
TAAATAATATAAGATTTTGACTTTTACCTCCTTCACTTATGCTACTAATTTCAAGAAGTATCGTAGAAAATGGAGCTGGAACAGGATGAACAGTTTATCCCCCTTTATCAGCCAATATTGC
TCACCAAGGATCCTCAGTAGATTTAGCTATTTTCTCCCTCCACTTAGCAGGAATTTCTTCAATTTTAGGAGCAATTAATTTCATTACAACAATTATTAATATACGAATTAATAATTTATCA
TTTGATCAAATACCCTTATTTATTTGAGCTGTAGGAATTACAGCATTACTTTTACTATTATCTTTACCAGTTTTAGCTGGAGCTATCACTATACTTTTAACTGATCGAAATCTTAATACAT
CTTTTTTTGACCCTGCTGGAGGGGGGGATCCAATTTTATATCAACATTTATTT

Type material. Holotype: ♂ deposited in the McGuire Center for Lepidoptera and Biodiversity collection, Gainesville, FL, USA (MGCL), illustrated in Fig. 39a, bears the following four rectangular labels (1st handwritten, others printed with handwritten text shown in italics), three white: [COLOMBIA-VALLE | CALIMA V. | 1200 M | XI-2-88], [Allyn Museum | Acc. *1988-26*], [DNA sample ID: | NVG-23053G12 | c/o Nick V. Grishin], and one red [HOLOTYPE ♂ | Noctuana | haematoesta Grishin]. Judging from the handwriting, the holotype was collected by Mark Simon. **Paratypes:** 4♂♂: 1♂ NVG-18061G11, USNMENT 01466900 Colombia: Valle del Cauca, Calima Dam, 1000 m, GPS 3.8833, −76.5667, 25-Jan-1992, J. Bolling Sullivan leg. [USNM] (Fig. 39b) and Ecuador: Pichincha: 1♂ NVG-18061G12, USNMENT 01466901 Hacienda Santa Isabel, jct. of new & old Quito–Sto. Domingo Rd., 900–1200 m, J. P. W. Hall & I. Aldas, 30-Mar-2004 [USNM] (Fig. 39c) and 1♂ NVG-23053H03 San Pablo, 1100 m, Jun-1970, R. de Lafebre [MGCL] (Fig. 39d); and 1♂ NVG-23053H02 Chimborazo, Pallatanga, 1700 m, Jul-1970, R. de Lafebre [MGCL] (Fig. 40a).

Type locality. Colombia: Valle del Cauca Department, Calima River Valley.

Etymology. The name reflects the western distribution of this relative of *N. haematospila* and is treated as a noun in apposition.

Distribution. Currently known from the mid-elevation Andes in western Colombia and Ecuador.

Noctuana bipuncta (Plötz, 1884) is a species distinct from *Noctuana lactifera* (Butler & H. Druce, 1872)

Genomic analysis reveals that *Antigonus bipuncta* Plötz, 1884 (type locality in Mexico) currently regarded as a subspecies of *Noctuana lactifera* (Butler & H. Druce, 1872) (type locality in Costa Rica) is genetically differentiated from it at the species level (Fig. 38), e.g., their COI barcodes differ by 3.3% (22 bp). Therefore, we propose that *Noctuana bipuncta* (Plötz, 1884), **stat. rest.** is a species distinct from *Noctuana lactifera* (Butler & H. Druce, 1872).

Noctuana statonama Grishin, new species

https://zoobank.org/B93FCD35-007D-4A56-B909-CD2CE0E6113D

(Figs. 38 part, 41)

Definition and diagnosis. Genomic analysis reveals that a specimen from western Panama identified as *Noctuana stator* (Godman, 1899) (type locality Mexico, Veracruz, Atoyac) is genetically differentiated from it at the species level in the nuclear genome (Fig. 38), although their COI barcodes do not differ strongly (0.5%, 3 bp), and therefore this specimen represents a new species. This new species keys to *N. stator* (E.23.4) in Evans (1953) and was included by him in it, but differs from *N. stator* and other relatives by the following combination of characters in males: the hyaline spot in the forewing cell R_4-R_5 is shifted distad from the spot in cell R_3-R_4, and the two spots (of the same size or larger, but not smaller) overall are less aligned with each other than in *N. stator*; the two orange spots in the ventral hindwing cell Sc+R_1-Rs are closer to each other; and orange submarginal spots are framed by better-expressed darker brown lunules on both sides (basal-side lunules are weakly developed in *N. stator*). Due to its cryptic nature and unexplored individual variation, this species is best identified by DNA, with diagnostic base pairs in the nuclear genome: aly793.1.9:C90T, aly793.1.9:T123C, aly890.20.6:A114T, aly890.20.6:T132C, aly1313.19.12:G48A, aly16031.2.1:C171C (not T), aly16031.2.1:T66T (not C), aly1838.32.6:G70G (not A), aly18826.17.1:A66A (not T), aly208.60.1:C117C (not T); and the COI barcode does not distinguish this species from *N. stator*.

Fig. 41. *Noctuana statonama* **sp. n.** holotype ♂ NVG-23095A01 in dorsal (left) and ventral (right) views, data in text.

Barcode sequence of the holotype. Sample NVG-23095A01, 658 base pairs:

AACTTTATATTTTATTTTTGGTATTTGAGCAGGTATAGTAGGAACCTCTTTAAGTTTAATTATTCGTTCAGAATTAGGAACTCCTGGTTCTTTAATCGGAGATGATCAAATTTATAATACT
ATTGTAACAGCTCATGCTTTTATTATAATTTTTTTTATAGTTATACCAATTATAATTGGAGGCTTTGGAAATTGACTAGTTCCCCTTATATTAGGAGCCCCTGACATAGCTTTCCCACGAA
TAAATAATATAAGATTTTGACTTTTACCTCCATCACTTATATTATTAATTTCAAGAAGTATTGTTGAAAATGGGGCAGGAACAGGATGAACAGTTTACCCCCCTCTTTCAGCTAATATTGC
CCATCAAGGATCTTCAGTAGATTTAGCTATTTTTTCACTTCATTTAGCTGGTATTTCTTCTATTTTAGGGGCAATTAATTTCATCACAACAATTATTAATATACGAATTAATAATTTATCT
TTTGATCAAATACCTTTATTTGTTTGAGCAGTAGGAATTACAGCATTACTTTTATTATTATCTTTACCAGTTTTAGCTGGAGCTATTACTATACTTTTAACTGATCGAAATCTTAATACAT
CATTTTTTGACCCTGCAGGAGGAGGAGATCCAATTTTATATCAACATTTATTT

Type material. Holotype: ♂ deposited in the Zentrum für Biodokumentation des Saarlandes collection, Schiffweiler, Germany (ZfBS), illustrated in Fig. 41, bears the following four rectangular labels (2nd handwritten, others printed), three white: [Lino Panama | 800 m | Coll. Fassl], [stator U], [DNA sample ID: | NVG-23095A01 | c/o Nick V. Grishin], and one red [HOLOTYPE ♂ | Noctuana | statonama Grishin]. According to its 2nd label, the ventral side of the holotype right wings was illustrated in Draudt (1923) as "*stator*" (plate 177, row f, first image from the left).

Type locality. Panama: Chiriquí Province, Lino, elevation 800 m.

Etymology. The name for this *stato*[r] relative from [Pa]*nama* is a fusion and is treated as a noun in apposition.

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

Windia sonoria Grishin, 2025 has been recorded from the USA

Genomic sequencing reveals a specimen of *Windia sonoria* Grishin, 2025 (type locality in Mexico: Sonora) in the MGCL, collected by Kilian Roever in USA: Arizona, Cochise Co., Peloncillo Mts.,

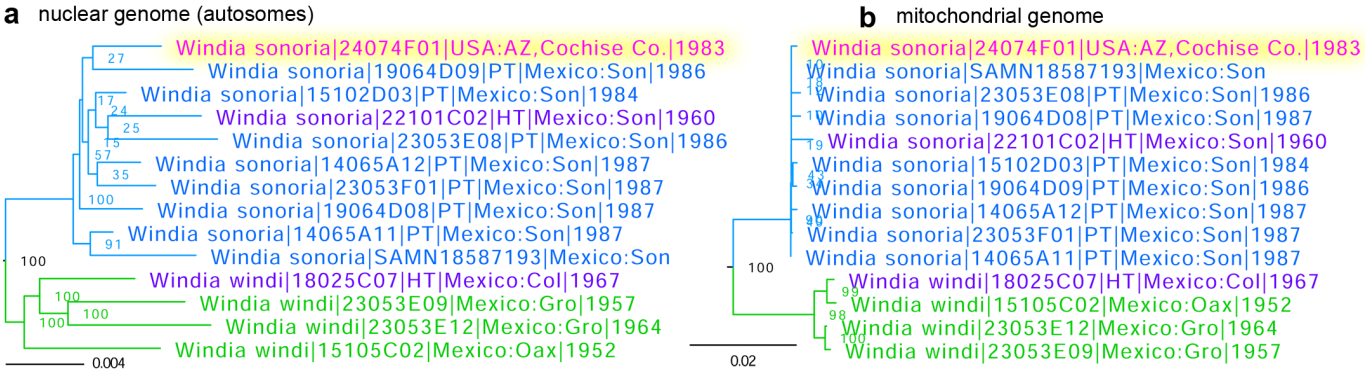

Fig. 42. Phylogenetic trees of *Windia* species constructed from protein-coding regions in: **a)** the nuclear genome (autosomes), based on 1,403,574 positions, and **b)** the mitochondrial genome. Different species are colored differently: *W. sonoria* (blue, the specimen from USA: Arizona is labeled in magenta and highlighted in yellow) and *W. windi* (green). Holotypes are labeled in purple. The sequence of SAMN18587193 is taken from the alignment provided in Kawahara et al. (2023). Ultrafast bootstrap (Hoang et al. 2018) values are shown at nodes.

Fig. 43. *Windia sonoria* ♂ NVG-24074F01 from USA: Arizona in dorsal (left) and ventral (right) views, data in text.

Cottonwood Creek, 5000–5200 ft, 23-Aug-1983 (NVG-24074F01) (Figs. 42, 43). In publications (Opler and Warren 2002; Pelham 2008), this specimen was referred to by the name of its sister species, *Windia windi* H. Freeman, 1969 (type locality in Mexico: Colima), which is unlikely to enter the U.S. Our analysis suggests that USA records of *Windia* H. Freeman, 1969 (type species *W. windi*) are *W. sonoria*.

Tribe Pyrgini Burmeister, 1878

Celotes sabinus verdinus Grishin, new subspecies

https://zoobank.org/C81446AC-BAF3-41A7-BE61-D966587DFE69

(Fig. 44 part, 45)

Definition and diagnosis. Genomic analysis of specimens of *Celotes sabinus* (type locality USA: Arizona, Pima Co., Santa Catalina Mts., Sabino Canyon) across the range from northwestern Arizona to Sonora in Mexico reveals that specimens from the southeastern Arizona and northwestern Mexico form a strongly supported clade in nuclear genome trees (100% bootstrap in all trees), genetically differentiated from the rest at the subspecies level (Fig. 44a, b, d blue). These specimens belong to the nominate subspecies, and the specimens from other parts of Arizona are therefore a new subspecies. COI barcodes of some of them differ by 2.3% (15 bp) from the holotype of *C. sabinus* (the difference is large due to introgression, some specimens have identical barcodes: Fig. 44c). A specimen from Pinal Co. AZ (NVG-8304) is sister to the rest of *C. sabinus sabinus* thus being placed closer to specimens of the new subspecies, likely due to gene exchange between the two subspecies (Fig. 44a). Furthermore, specimens from Gila Co. AZ form a clade sister to all *C. sabinus sabinus* in the autosome tree (Fig. 44a, albeit with low confidence) thus showing intermediate genotype and further supporting the notion of gene exchange. Due to this gene exchange, which is increased between geographically closest populations, the two taxa are regarded as subspecies. This new subspecies is similar to the nominotypical in all aspects, but differs in the dorsal side, which tends to have more contrasting dark-brown streaks and areas in the basal half of the wings, a paler distal half of the wings, and pale submarginal streaks that are usually longer. Ventrally, the contrast between darker and paler areas is also stronger in most specimens; the bases of the wings tend to be paler overall; and the palpi are distally whiter beneath, where the nominotypical subspecies typically has more extensive beige scaling. Due to its cryptic nature, this subspecies is best identified by DNA, with diagnostic base pairs in the nuclear genome: aly5788.1.8:G114A, aly85.33.2:G84A, aly85.33.2:G459A, aly3319.1.11:G84T, aly14145.2.6:G6A, aly971.3.4:G129G (not A), aly971.3.4:C132C (not G), aly971.3.4:C30C (not T), aly15586.2.1:G72G (not A), aly2011.25.2:C690C (not T); the COI barcodes of this new subspecies are represented by at least two distinct haplotypes and do not differ even between species of *Celotes* Godman & Salvin, 1899 (type species *Pholisora nessus* W. Edwards, 1877).

Barcode sequence of the holotype. Sample NVG-23054H06, 658 base pairs:

AACTTTATATTTCATTTTTGGAATTTGAGCAGGTATAGTAGGTACTTCTTTAAGTTTATTAATTCGAACTGAATTAGGAAATCCAGGATCTCTAATTGGAGATGATCAAATTTATAATACT
ATTGTAACAGCACATGCTTTCATTATAATTTTTTTCATAGTAATACCTATTATAATTGGAGGATTTGGAAATTGATTGGTACCTTTAATACTAGGAGCTCCTGATATAGCATTTCCACGTA
TAAATAATATAAGATTTTGATTATTACCTCCTTCTTTAACACTTCTTATTTCAAGAAGTATTGTAGAAAACGGAGCAGGAACAGGATGAACAGTTTACCCCCCCCTATCATCTAATATTGC
TCATCAAGGTTCATCTGTTGATTTGGCTATCTTTTCCTTACATCTAGCAGGAATTTCATCAATTTTAGGAGCAATTAACTTCATTACAACCATTATTAATATACGAATTAGAAATTTATCA
TTTGATCAAATACCTTTATTCGTATGAGCTGTAGGAATTACAGCATTACTTTTATTATTATCTTTACCTGTTTTAGCTGGAGCTATTACAATATTATTAACTGATCGAAATTTAAATACAT
CTTTCTTTGATCCTGCTGGAGGAGGAGATCCAATTTTATATCAACACTTATTT

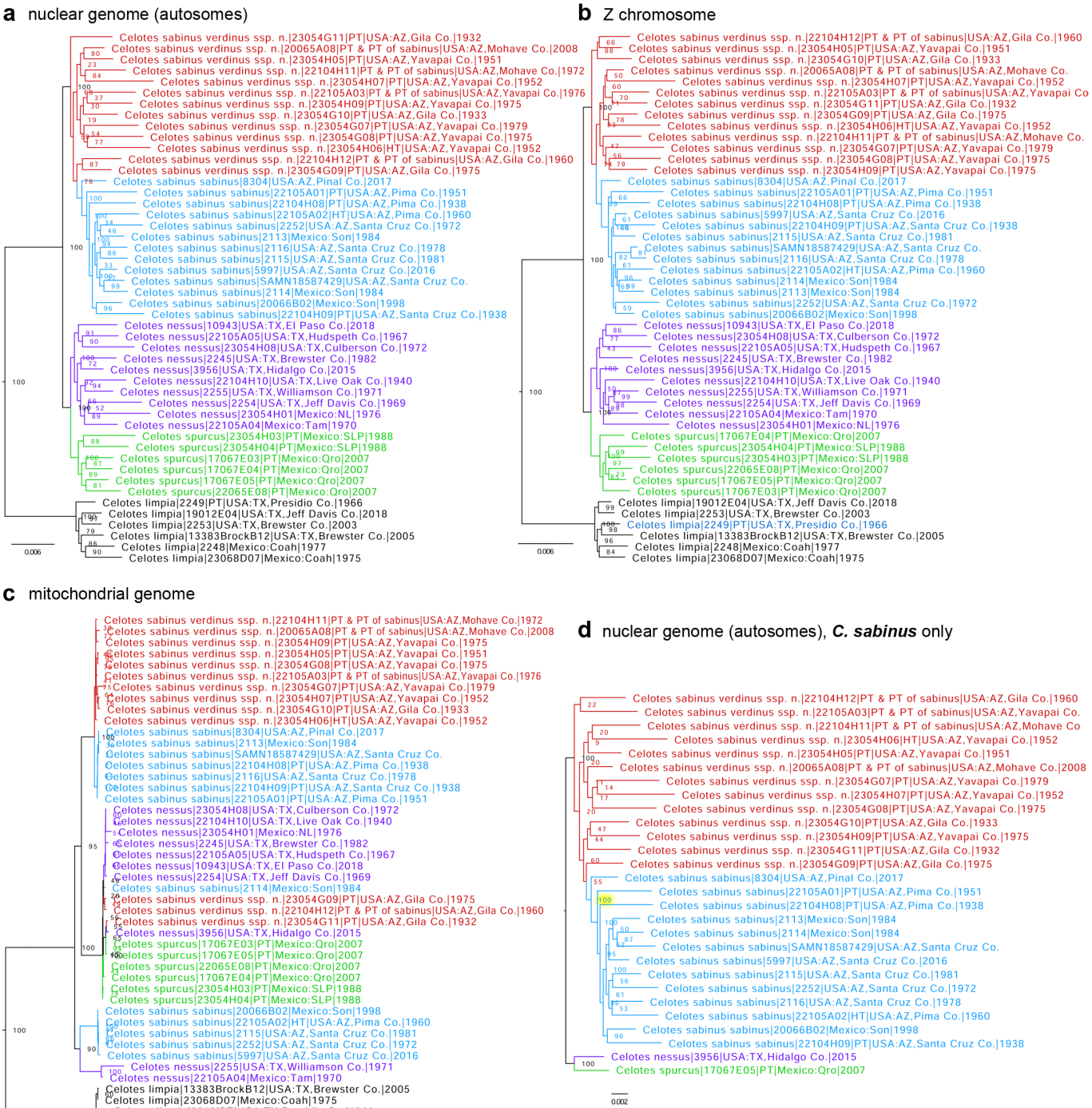

Fig. 44. Phylogenetic trees of all described *Celotes* species constructed from protein-coding regions in: **a)** the nuclear genome (autosomes), based on 1,030,491 positions, **b)** the Z chromosome, based on 349,008 positions, and **c)** the mitochondrial genome; and **d)** the nuclear genome (autosomes) constructed from *C. sabinus* specimens only, based on 1,263,519 positions. Different taxa are colored differently: *C. sabinus verdinus* **ssp. n.** (red), *C. sabinus sabinus* (blue), *C. nessus* (purple), and *C. spurcus* (green). The sequence of SAMN18587429 is taken from the alignment provided in Kawahara et al. (2023). Ultrafast bootstrap (Hoang et al. 2018) values are shown at nodes of genomic trees and the 100% support value for the *C. sabinus sabinus* clade in (d) is highlighted in yellow.

Fig. 45. *Celotes sabinus verdinus* **ssp. n.** holotype ♂ NVG-23054H06 in dorsal (left) and ventral (right) views, data in text.

Type material. Holotype: ♂ deposited in the McGuire Center for Lepidoptera and Biodiversity collection, Gainesville, FL, USA (MGCL), illustrated in Fig. 45, bears the following four rectangular labels (1st handprinted, others printed), three white: [Celotes nessus | Cottonwood, Yavapai Co. | Ariz. August 18,1952 | D.L.Bauer], [JD Turner coll. | Ex. D. Bauer colln. | MGCL Accession | # 2010-29], [DNA sample ID: | NVG-23054H06 | c/o Nick V. Grishin], and one red [HOLOTYPE ♂ | Celotes sabinus | verdinus Grishin]. **Paratypes:** 8♂♂ and 5♀♀ from USA: Arizona, in MGCL unless indicated otherwise: Mohave Co.: 1♀ NVG-20065A08, CSU_ENT1024696 Hualapai Mts., lower el., 16-Apr-2008, K. Davenport leg. [CSUC] and 1♂ NVG-22104H11, CASENT_8568341 nr. Wickieup, 30-Mar-1972, J. W. Tilden leg. [CAS]; Yavapai Co.: 1♀ NVG-22105A03, CASENT_8568345 8 mi SW of Prescott, 21-Apr-1976, J. W. Tilden leg. [CAS]; 1♂ NVG-23054G07 Bradshaw Mts, 4 mi SW of Cleator, 19-May-1979, J. P. Brock leg.; 1♂ NVG-23054H07 nr. Bumble Bee, 16-Jul-1952, D. L. Bauer leg.; 1♂ NVG-23054G08 Verde River valley nr. IH17, 5-Sep-1975, BH leg., T. Allen colln.; 1♂ NVG-23054H05 Cottonwood, Mingus Mt., Black Canyon, 6-May-1951, D. L. Bauer leg.; and 1♂ NVG-23054H09 7.5 mi W of Strawberry, Fossil Creek, 3450 ft, J. L. Harry leg.; 1♂ NVG-2250 Maricopa Co., Camp Creek on Cave Creek Rd., 12 mi NE of Jct. of Cave Creek and Scottsdale Rds., 8-Apr-1968, J. A. Miller leg., genitalia NVG140320-91 [TAMU]; and Gila Co.: 1♀ NVG-23054G09, UF FLMNH MGCL 1048000 10 mi W of Globe, 27-Aug-1975, J. P. Brock leg.; Globe, 3300 ft, DKD leg., ex coll. R. G. Wind: 1♀ NVG-23054G10 15-Apr-1933 and 1♀ NVG-23054G11 12-May-1932, genitalia #08-10 by A. D. Warren; and 1♂ NVG-22104H12, CASENT_8568342 Sevenmile Wash, 22-Aug-1960, P. A. Opler leg. [CAS].

Type locality. USA: Arizona, Yavapai Co., Cottonwood.

Etymology. The name is derived from the Verde River in central Arizona, which is in the center of the range of this subspecies. The name is treated as a noun in apposition.

Distribution. In the transition zone of Arizona (Mohave, Yavapai, Maricopa, and Gila counties).

Comment. Mitochondrial genomes of *Celotes* Godman & Salvin, 1899 (type species *Pholisora nessus* W. H. Edwards, 1877) are represented by five haplotypes. However, except that of *Celotes limpia* Burns, 1974 (type locality in USA: Texas, Jeff Davis Co.), which is unique to this species, the other four haplotypes do not uniquely correlate with taxa, and mitochondrial exchange appears common between species (Fig. 44c, colors do not sort by clades as in Fig. 44a, b).

Diaeus piura Grishin, new species

https://zoobank.org/4C3B5EDA-D267-4661-831E-51154614BBE7

(Figs. 46 part, 47)

Definition and diagnosis. Genomic analysis reveals that a specimen from northern Peru initially identified as *Diaeus ambata* Evans, 1953 (type locality in Ecuador: Ambato) is sister to *Diaeus varna*

Evans, 1953 (type locality in Mexico: Veracruz) in the nuclear genome and is genetically differentiated at the species level (Fig. 46); e.g., their COI barcodes differ by 1.7% (11 bp) from *D. ambata* and by 2.6% (17 bp) from *D. varna*, and therefore this specimen represents a new species. This new species keys to "*Diaeus lacaena ambata*" (E.35(c)) in Evans (1953), but differs from it and other relatives by the following combination of characters in females: forewing discal cell hyaline spot is larger than in *D. ambata*, not crescent-shaped; the forewing is not divided into three zones of contrasting colors, as it is in *D. varna*; and the ventral hindwing is paler, not variegated, but with submarginal dark areas towards tornus, somewhat similar to *Diaeus lacaena* (Hewitson, 1869) (type locality in Brazil). Due to its cryptic nature and unexplored individual variation, this species is best identified by DNA, with diagnostic base pairs in the nuclear genome: aly1063.2.1:C195T, aly1063.2.1:A240G, aly16812.3.2:A291C, aly16812.3.2:C294T, aly1651.43.2:C55A, aly12063.20.15:C138C (not T), aly2012.16.1:C144C (not T), aly2012.16.1:T147T (not C), aly234.10.9:C144C (not A), aly234.10.9:G81G (not A); and the COI barcode: T16C, T226C, A421G, A470G, T646C.

Barcode sequence of the holotype. Sample NVG-23124A12, 658 base pairs:

AACTTTATATTTTATCTTTGGAATTTGAGCAGGAATAGTAGGTACTTCTTTAAGTTTATTAATTCGAACTGAATTAGGTAATCCAGGATCTTTAATTGGAGATGATCAAATTTATAATACT
ATCGTTACAGCTCATGCTTTTATTATAATTTTTTTTATAGTTATACCTATTATAATTGGAGGATTTGGAAATTGATTAGTGCCATTAATATTAGGAGCTCCAGACATAGCTTTCCCCCGTA
TAAATAATATAAGATTTTGATTATTACCCCCCTCTTTAACACTCTTAATTTCTAGAAGTATCGTAGAAAACGGAGCAGGAACTGGATGAACAGTATACCCCCCTCTTTCAGCAAATATTGC
TCATCAAGGTTCTTCTGTTGATTTAGCTATTTTTTCTTTACATTTAGCGGGAATTTCATCAATTTTAGGAGCAATTAATTTTATTACTACAATTATTAATATACGAGTTAATAATCTATCT
TTTGATCAAATACCATTATTTGTTTGAGCAGTCGGAATTACAGCTTTACTTTTATTATTATCTTTACCAGTATTAGCTGGTGCTATTACTATATTATTAACTGATCGTAATTTAAATACAT
CTTTTTTTGATCCTGCAGGAGGAGGAGATCCTATTTTATACCAACACTTATTT

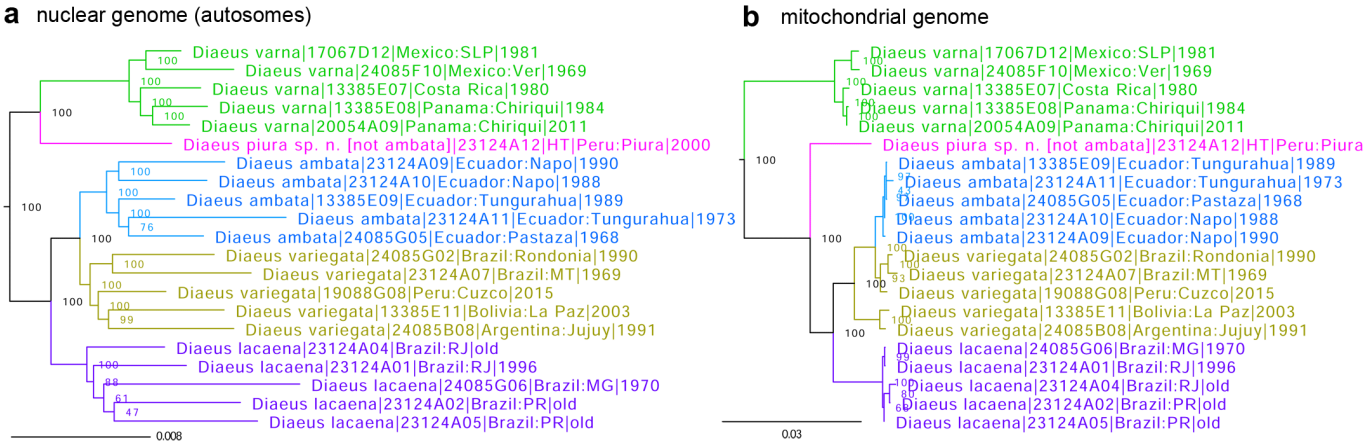

Fig. 46. Phylogenetic trees of all described *Diaeus* species constructed from protein-coding regions in: **a)** the nuclear genome (autosomes), based on 2,819,034 positions, and **b)** the mitochondrial genome. Different species are colored differently: *D. varna* (green), *D. piura* **sp. n.** (magenta), *D. ambata* (blue), *D. variegata* (Plötz, 1884) (olive), and *D. lacaena* (purple). Ultrafast bootstrap (Hoang et al. 2018) values are shown at nodes.

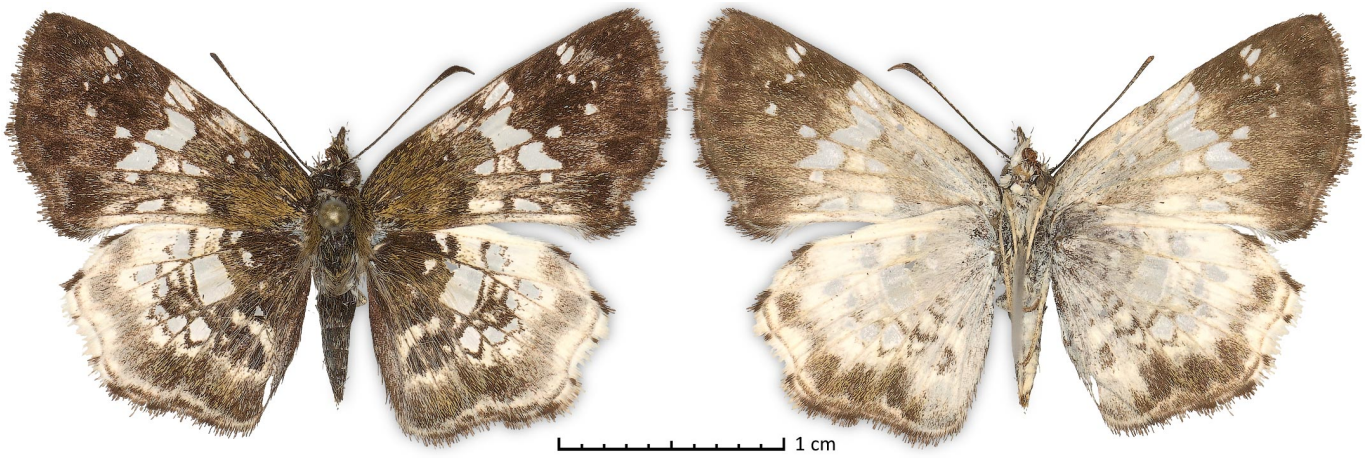

Fig. 47. *Diaeus piura* **sp. n.** holotype ♂ NVG-23124A12 in dorsal (left) and ventral (right) views, data in text.

Type material. Holotype: ♀ currently deposited in the National Museum of Natural History, Smithsonian Institution, Washington, DC, USA (USNM), illustrated in Fig. 47, bears the following three printed rectangular labels, two white: [PERU: Piura: 3km W | Canchaque, 1300m, | 05°22'S 79°37'W | 4 June 2000 | Robbins & Lamas Leg.], [DNA sample ID: | NVG-23124A12 | c/o Nick V. Grishin], and one red [HOLOTYPE ♀ | Diaeus piura | Grishin].

Type locality. Peru: Piura Region, 3 km W of Canchaque, elevation 1300 m, GPS −5.3667, −79.6167.

Etymology. The name originates from the Peruvian region containing the type locality and is treated as a noun in apposition.

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

Zopyrion (*Zopyrion*) *xerxes* Grishin, 2025 is confirmed as a species and its range extended to include El Salvador, Nicaragua, and Costa Rica

Originally proposed from a single specimen, the holotype, *Zopyrion* (*Zopyrion*) *xerxes* Grishin, 2025 (type locality Honduras: San Pedro Sula) (Zhang et al. 2025a) is confirmed as a species-level taxon by genomic analysis of five additional specimens (Fig. 48 green). These specimens were collected in El Salvador, Nicaragua, and Costa Rica, thus extending the range of this species southward. Its sister species, *Zopyrion* (*Zopyrion*) *sandace* Godman & Salvin, 1896 (type locality Mexico: Guerrero, Río Papagayo), is currently known only from western and southern Mexico (Sinaloa, Nayarit, Jalisco, Colima, Guerrero, Oaxaca, Veracruz, and Chiapas) (Fig. 48 blue). The two species are sisters in both nuclear and mitochondrial genome trees (Fig. 48) and are well differentiated in the mitochondrial genome, with a 2.6% (17 bp) difference in the COI barcode. We have not detected any mitochondrial introgression between the two species among the sequenced specimens (Fig. 48b).

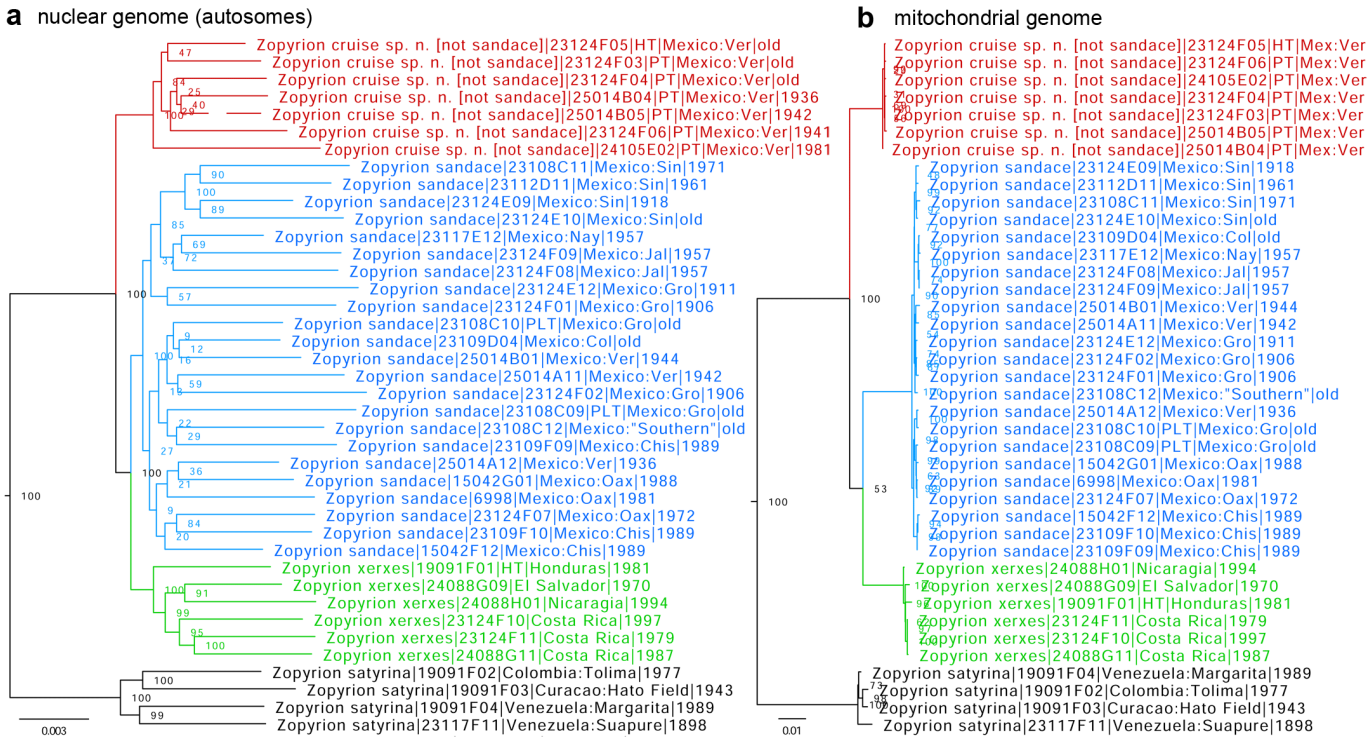

Fig. 48. Phylogenetic trees of selected *Zopyrion* (*Zopyrion*) species constructed from protein-coding regions in: **a)** the nuclear genome (autosomes), based on 594,411positions, and **b)** the mitochondrial genome. Different species are colored differently: *Z.* (*Z.*) *cruise* **sp. n.** (red), *Z.* (*Z.*) *sandace* (blue), and *Z.* (*Z.*) *xerxes* (green). A gap in a terminal branch indicates that a segment of the branch was cut out to reduce its length (to allow an increase in the font size), i.e., the branch with the gap is longer than shown. Ultrafast bootstrap (Hoang et al. 2018) values are shown at nodes.

Zopyrion (*Zopyrion*) *cruise* Grishin, new species

https://zoobank.org/1349FA4A-E7C7-4CBE-A1C8-E38E613BF692

(Figs. 48 part, 49–50)

Definition and diagnosis. Genomic analysis reveals that several specimens from central Veracruz, Mexico, identified as *Zopyrion* (*Zopyrion*) *sandace* Godman & Salvin, 1896 (type locality Mexico: Guerrero, Río Papagayo) are genetically differentiated from it and its sister *Zopyrion* (*Zopyrion*) *xerxes* Grishin, 2025 (type locality Honduras: San Pedro Sula) at the species level (Fig. 48); e.g., their COI barcodes differ by 2.4% (16 bp) from *Z. sandace* and by 2.3% (15 bp) from *Z. xerxes*, and therefore these specimens represent a new species. This new species is similar to *Z. sandace* and keys to it (E.58.1) Evans (1953), but differs from it and other relatives by the following combination of characters: the harpe is not terminally pointed, but not fully rounded either, narrower than in *Z. sandace*, irregular, and rather straight,

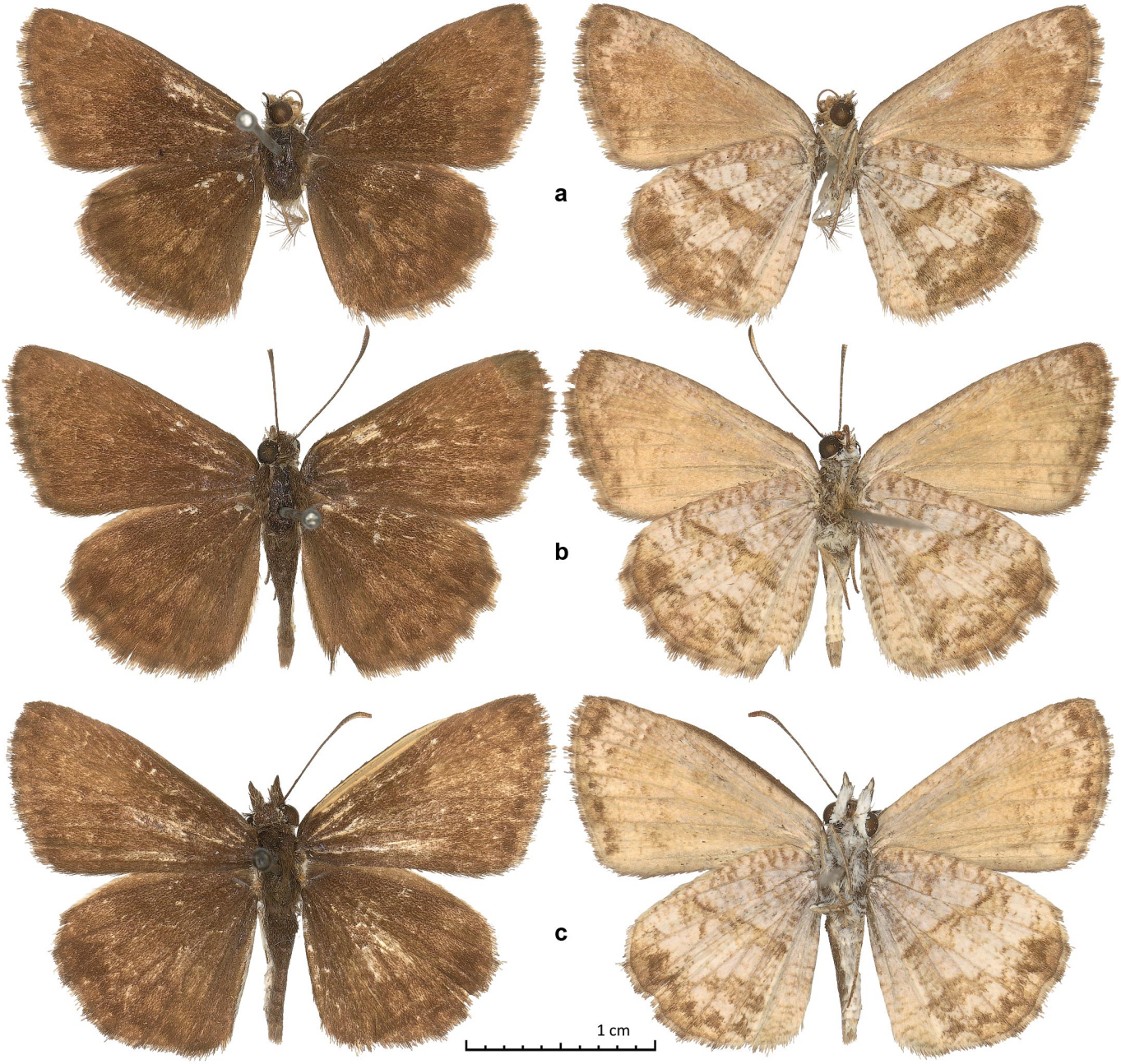

Fig. 49. *Zopyrion* (*Zopyrion*) *cruise* **sp. n.** males from Mexico: Veracruz in dorsal (left) and ventral (right) views, data in text: **a)** holotype NVG-23124F05 and paratypes: **b)** NVG-23124F04 and **c)** NVG-23124F06.

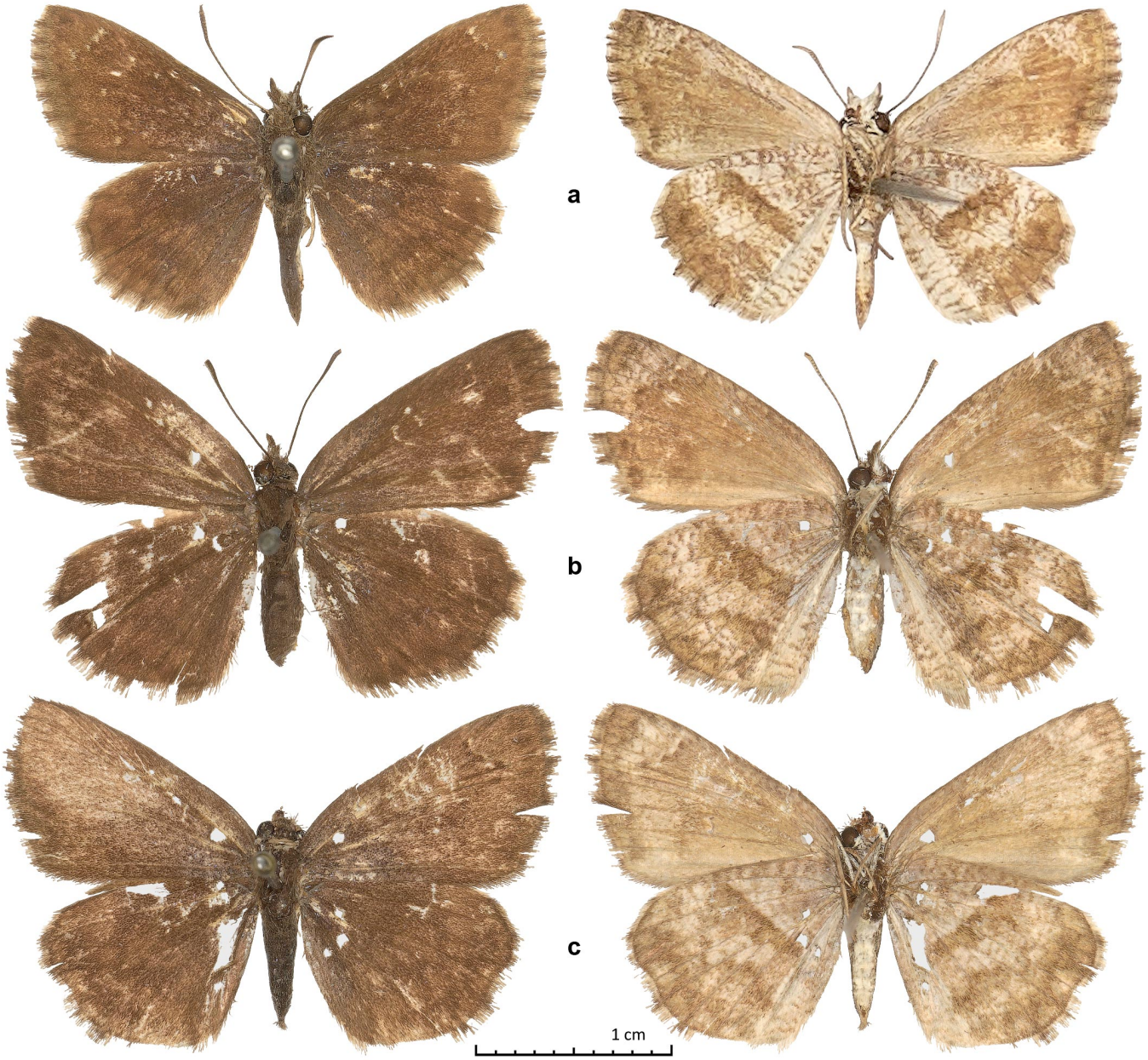

Fig. 50. *Zopyrion* (*Zopyrion*) *cruise* **sp. n.** paratypes from Mexico: Veracruz in dorsal (left) and ventral (right) views, data in text: **a)** ♂ NVG-23124F03, **b)** ♀ NVG-25014B04, and **c)** ♀ NVG-25014B05.

not turning dorsad at the distal end (turning dorsad in *Z. sandace*), which is armed with teeth; the ventral side of wings is typically darker, more variegated, and with heavier brown scaling (including spots, patches, and lunules) along the margin of the hindwing, particularly in cell R_1-M_3 (compare with *Z. sandace* from Mexico: Veracruz shown in Fig. 51). Due to its cryptic nature and unexplored individual variation, this species is best identified by DNA, with diagnostic base pairs in the nuclear genome: aly86.8.21:C135T, aly923.9.3:T537C, aly923.9.3:C525T, aly127.64.1:A1152T, aly3499.12.1:A261C; and the COI barcode: A34G, T226C, T263C, T424C, A508G.

Barcode sequence of the holotype. Sample NVG-23124F05, 658 base pairs:

AACTTTATACTTCATTTTTGGAATTTGAGCAGGGATAGTTGGTACTTCTTTAAGTTTATTAATTCGAACTGAATTAGGAAATCCAGGATCTCTAATTGGTGATGATCAAATTTATAATACT
ATCGTAACAGCTCATGCTTTTATTATAATTTTTTTTATAGTTATACCTATTATAATTGGAGGATTTGGAAATTGATTAGTACCATTAATACTTGGAGCCCCAGACATAGCTTTCCCCCGTA
TAAATAATATAAGATTTTGACTATTACCTCCTTCATTAACATTATTAATTTCTAGAAGTATTGTAGAAAATGGAGCAGGAACAGGATGAACAGTTTACCCCCCCCTTTCAGCTAACATTGC
TCATCAAGGTTCTTCTGTTGATTTAGCAATTTTTTCCTTACATTTAGCAGGTATTTCATCCATTTTAGGAGCTATTAATTTTATTACAACAATTATTAATATACGAATTAGAAATTTATCT
TTTGATCAAATACCTTTATTTGTGTGAGCTGTAGGAATTACAGCTTTACTTTTATTATTATCATTACCTGTATTAGCAGGAGCTATTACTATACTTTTAACTGATCGAAATTTAAATACAT
CTTTTTTTGATCCAGCTGGAGGGGGAGATCCTATTCTTTATCAACACTTATTT

Type material. Holotype: ♂ deposited in the National Museum of Natural History, Smithsonian Institution, Washington, DC, USA (USNM), illustrated in Fig. 49a (genitalia Fig. 52), bears the following

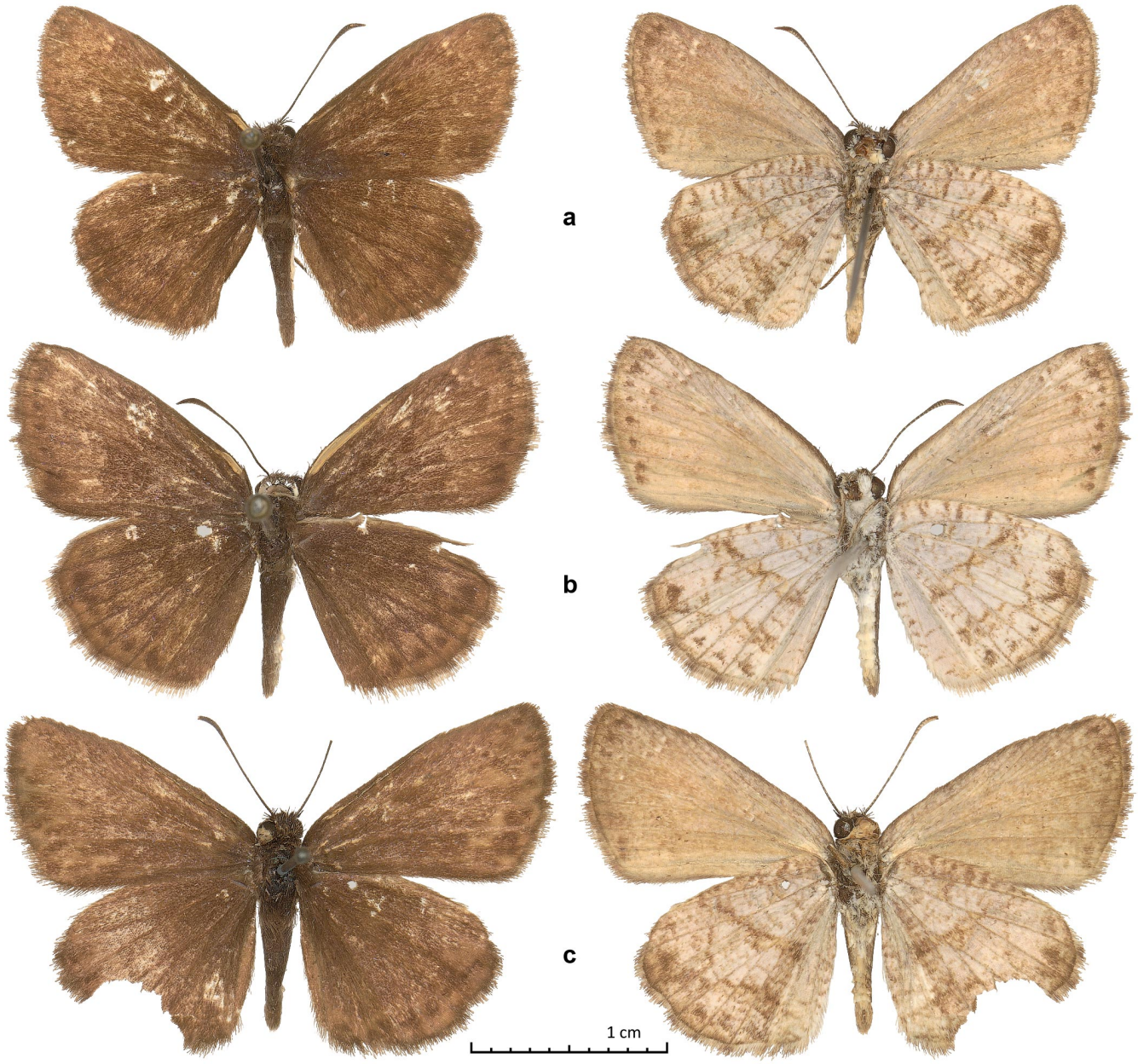

Fig. 51. *Zopyrion* (*Zopyrion*) *sandace* males from Mexico: Veracruz, Presidio, T. Escalante leg. [MGCL] in dorsal (left) and ventral (right) views: **a)** NVG-25014A12 Aug-1936, genitalia NVG250720-46; **b)** NVG-25014A11 Sep-1942, genitalia NVG250720-45, and **c)** NVG-25014B01 Aug-1944.

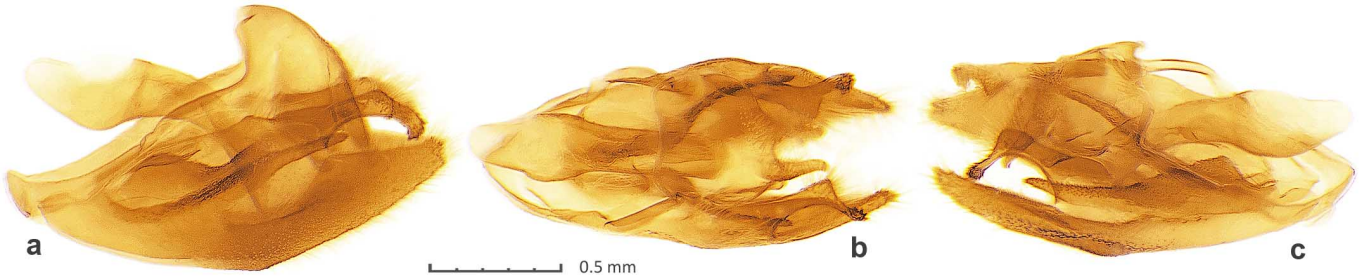

Fig. 52. Male genitalia of *Zopyrion* (*Zopyrion*) *cruise* **sp. n.** holotype NVG-23124F05 in **a)** left lateral, **b)** dorsal, and **c)** right dorsolateral views.

six rectangular labels (2nd handwritten, others printed with handwritten text shown in italics), five white: [Rinconada, | V. Cruz.], [Zapyrion | sandace | G. S.], [Collection | W. Schaus], [GENITALIA NO. | X- *43 78* | J.M.Burns 1998], [DNA sample ID: | NVG-23124F05 | c/o Nick V. Grishin], and one red [HOLOTYPE ♂ | Zopyrion (Zopyrion) | cruise Grishin]. **Paratypes:** 3♂♂ and 3♀♀ from Mexico: Veracruz: 1♂ NVG-23124F06 Palo Gancho, Aug-1941, J. Camelo G. leg. [USNM] (Fig. 49c); 2♂♂ NVG-23124F03 (Fig. 50a) and NVG-23124F04 (Fig. 49b) Veracruz, Rinconada, old, coll. W. Schaus [USNM]; 1♀ NVG-24105E02, 4.5 km SW of Omealca, 6-Aug-1981, C. J. Durden leg. [TMMC]; and Presidio, T. Escalante leg. [MGCL]: 1♀ NVG-25014B04 Apr-1936 (Fig. 50b) and 1♀ NVG-25014B05 Jul-1942 (Fig. 50c).

Type locality. Mexico: Veracruz, Rinconada.

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

Distribution. Currently known only from the State of Veracruz in Mexico.

Distribution. According to the labels of specimens in collections, this species is sympatric with *Z. sandace* in Presidio, Veracruz, Mexico.

Zopyrion (*Timochreon*) *forta* (Evans, 1953) and *Zopyrion* (*Timochreon*) *tampa* (Evans, 1953) are species distinct from *Zopyrion* (*Timochreon*) *satyrus* (C. Felder & R. Felder, 1867)

Genomic analysis reveals that *Timochreon satyrus forta* Evans, 1953 (type locality in Brazil: Pará) and *Timochreon satyrus tampa* Evans, 1953 (type locality in Brazil: Matto Grosso, Chapada) originally proposed and currently regarded as subspecies of *Zopyrion* (*Timochreon*) *satyrus* (C. Felder & R. Felder, 1867) (type locality in Colombia: Bogotá) (Fig. 54a) are genetically differentiated from it at the species level (Fig. 53), e.g., their COI barcodes differ by 7.4% (49 bp) and 4.4% (29 bp), respectively. Moreover, *Z. satyrus tampa* is not monophyletic with the nominotypical *Z. satyrus* and is instead sister to *Zopyrion* (*Timochreon*) *doria* (Plötz, 1884) (type locality in Brazil) (Fig. 53), differing from it by 3% (20 bp) in the COI barcode. Furthermore, as Evans (1953) noted, these taxa differ from each other in male genitalia and wing shape. E.g., we find that the wings of *Z. satyrus forta* are more elongated (Fig. 54b) and those of *Z. satyrus tampa* more rounded (Fig. 54c). Therefore, we propose that *Zopyrion* (*Timochreon*) *forta* (Evans, 1953), **stat. nov.** and *Zopyrion* (*Timochreon*) *tampa* (Evans, 1953), **stat. nov.** are species distinct from *Zopyrion* (*Timochreon*) *satyrus* (C. Felder & R. Felder, 1867). In wing patterns, we find that *Z. forta* has a better-developed, darker, and more triangular submarginal spot in the ventral hindwing cell CuA_2-1A+2A (Fig. 54b), and *Z. tampa* has a more uniformly colored ventral wing surface (Fig. 54c). *Zopyrion doria* is recognized by golden-brown to tawny-orange ventral forewing discal cell contrasting with paler and more violaceous ground color distad of it (Fig. 54d). Data for specimens shown in Fig. 54, males in MGCL, unless indicated: NVG-24088G04 Colombia: Tolima, Las Guayabas, Río Cucuana, 1300-1600 m, 8-Mar-1974, S. & L. Steinhauser leg. (Fig. 54a); NVG-22018H06 from "Am. m.", i.e., South America, no other data, old specimen [ZSMC] (Fig. 54b); NVG-24076E04 Brazil: Rondônia, 62 km S of Ariquemes off B-65, vic. Fazenda Rancho Grande, 180 m, 24-Oct-1989, G. T. Austin leg. (Fig. 54c); NVG-15042F10 Brazil: Minas Gerais, Reserva da Serra Belo Horizonte, 9–12-Apr-1971, C. Callaghan leg. (Fig. 54d).

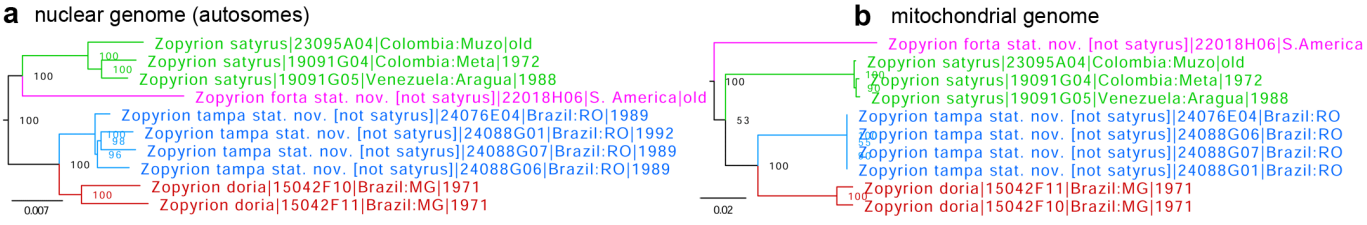

Fig. 53. Phylogenetic trees of all described *Zopyrion* (*Timochreon*) species constructed from protein-coding regions in: **a)** the nuclear genome (autosomes), based on 5,767,263 positions, and **b)** the mitochondrial genome. Different species are colored differently: *Z.* (*T.*) *satyrus* (green), *Z.* (*T.*) *forta* **stat. nov.** (magenta), *Z.* (*T.*) *tampa* **stat. nov.** (blue), and *Z.* (*T.*) *doria* (red). Ultrafast bootstrap (Hoang et al. 2018) values are shown at nodes.

Fig. 54. *Zopyrion* (*Timochreon*) males in dorsal (left) and ventral (right) views, detailed data in text: **a)** *Z.* (*T.*) *satyrus* NVG-24088G04 from Colombia: Tolima; **b)** *Z.* (*T.*) *forta* **stat. nov.** NVG-22018H06 from South America; **c)** *Z.* (*T.*) *tampa* **stat. nov.** NVG-24076E04 from Brazil: Rondônia; and **d)** *Z.* (*T.*) *doria* NVG-15042F10 from Brazil: Minas Gerais.

A second specimen of *Gorgythion cerrada* Grishin, 2025

Our ongoing genomic sequencing efforts identified a second specimen of recently described *Gorgythion cerrada* Grishin, 2025 (type locality in Brazil: Goiás) from Brazil: Minas Gerais, Km 231 Belo-Brasília, Paracatu, collected by C. Callaghan during April 17–18, before and around 1973 (no year given, the specimen was donated to MGCL in 1973), genitalia SRS-1758 dissected by S. R. Steinhauser, DNA

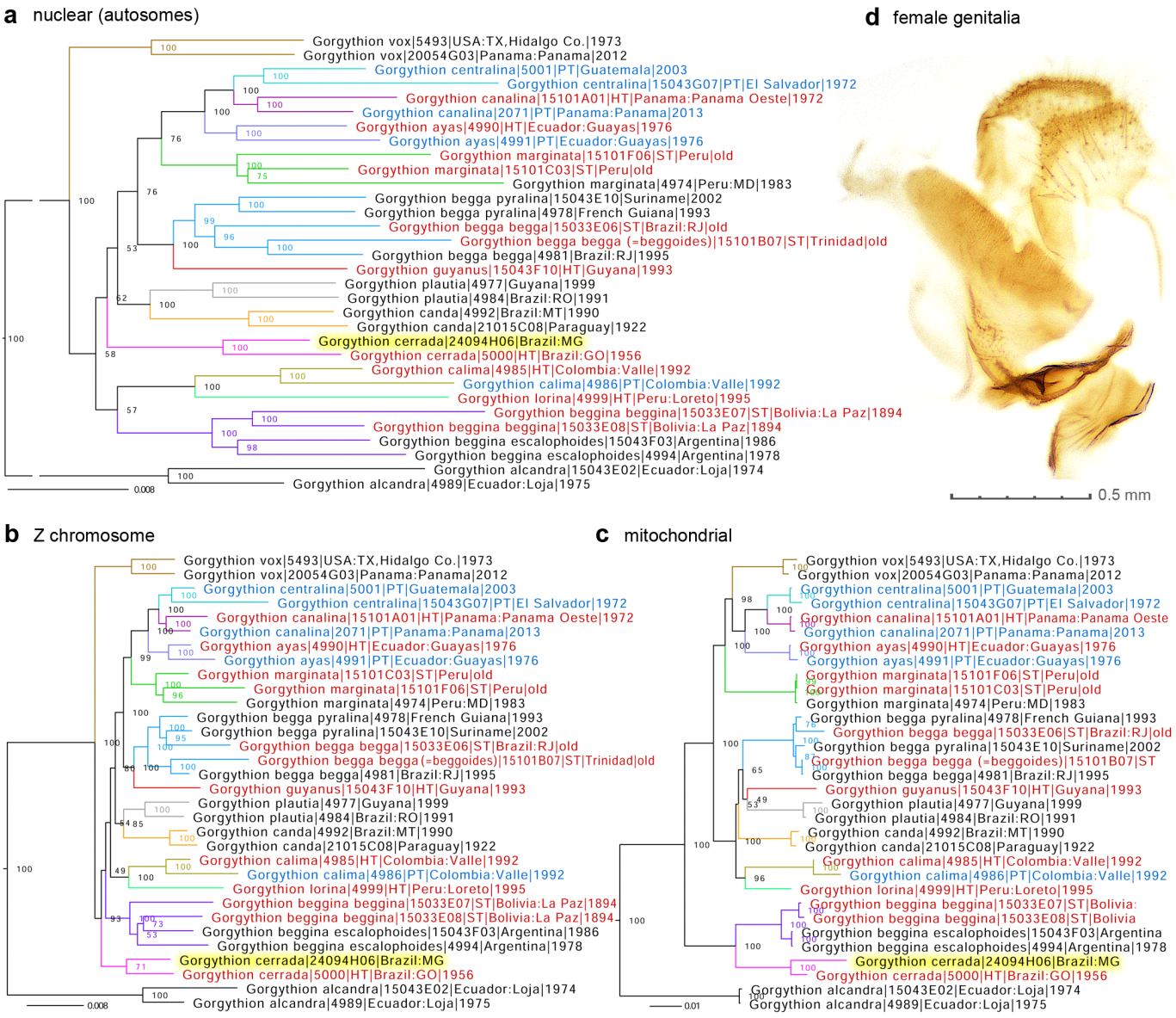

Fig. 55. *Gorgythion* Godman & Salvin, 1896 trees and female genitalia: **a–c)** phylogenetic trees of all described species constructed from protein-coding regions in: **a)** the nuclear genome (autosomes), based on 1,028,877 positions, **b)** the Z chromosome, based on 286,974 positions, and **c)** the mitochondrial genome; and **d)** female genitalia of *G. cerrada* NVG-24094H06 in ventral view. In trees, different species are colored differently: *G. vox* Evans, 1953 (brown), *G. centralina* Grishin, 2025 (cyan), *G. canalina* Grishin, 2025 (maroon), *G. ayas* Grishin, 2025 (lavender), *G. marginata* Schaus, 1902 (green), *G. begga* (Prittwitz, 1868) (blue), *G. guyanus* Grishin, 2023 (red), *G. plautia* (Möschler, 1877) (gray), *G. canda* Evans, 1953 (orange), *G. calima* Grishin, 2025 (olive), *G. lorina* Grishin, 2025 (aquamarine), *G. beggina* Mabille, 1898 (purple), *G. cerrada* (magenta). Primary type specimens are labeled in red font and paratypes are labeled in blue font. The label of the second known specimen of *G. cerrada* is highlighted in yellow. 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 (and accommodate the photograph of genitalia), i.e., two branches with gaps are longer than shown.

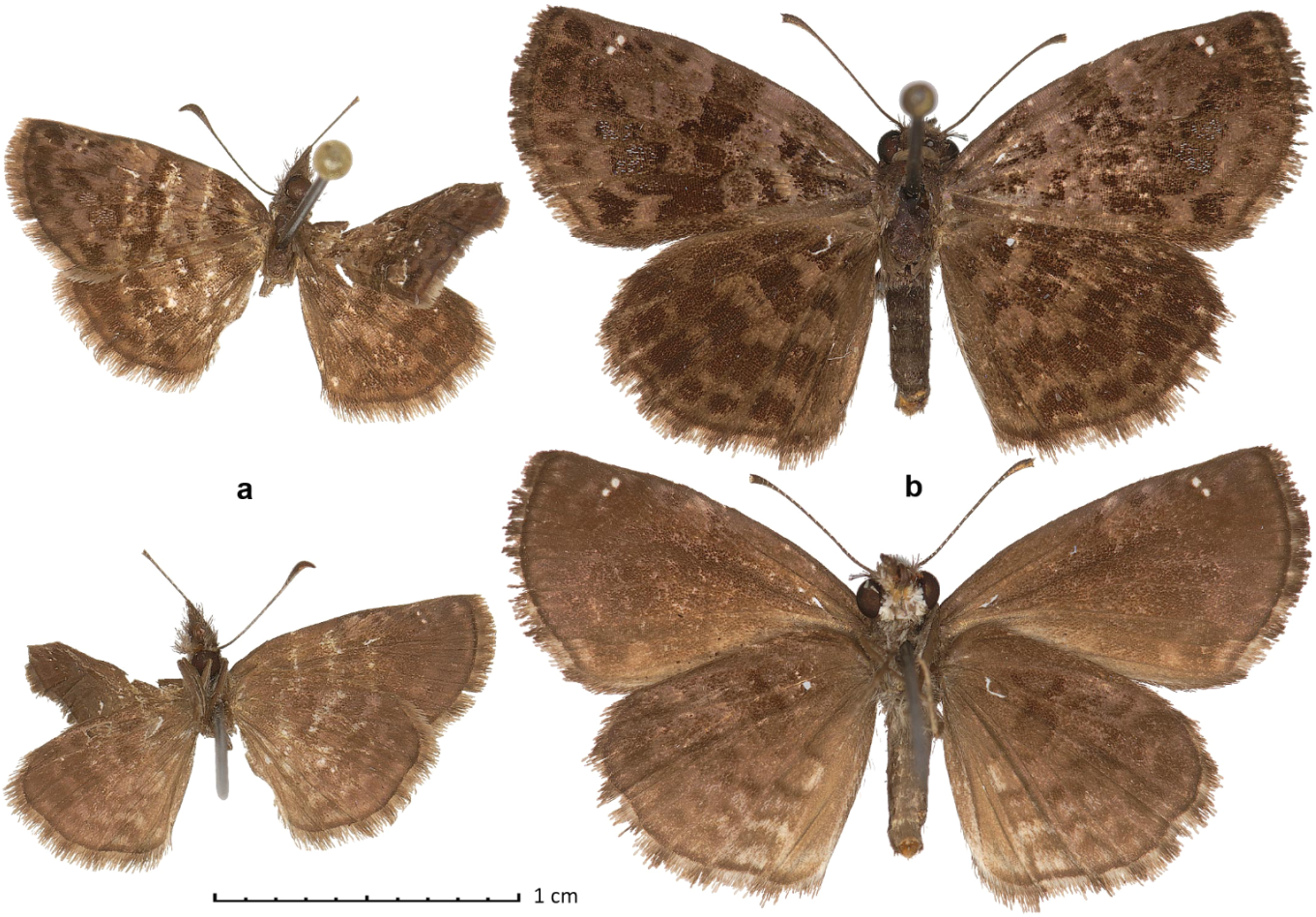

Fig. 56. *Gorgythion cerrada* from Brazil in dorsal (above) and ventral (below) views, data in text: **a)** non-type specimen ♀ NVG-24094H06 from Minas Gerais and **b)** holotype ♀ NVG-5000 from Goiás.

sample NVG-24094H06 (Fig. 55a–c yellow highlight). It is also a female, illustrated here (Fig. 56a), with its genitalia (Fig. 55d). It is significantly smaller in size (possibly a dwarf) than the holotype (Fig. 56b), but its COI barcode is identical.

A possible paralectotype of *Antigonus ruptifasciata* Plötz, 1884 is also from Jamaica

Previously, we found a syntype of *Antigonus ruptifasciata* Plötz, 1884 in the MFNB collection and designated it a lectotype (Zhang et al. 2024b). Genomic comparison of the lectotype with specimens from known localities revealed that it was collected in Jamaica, which was unexpected and resulted in several changes in nomenclature (Zhang et al. 2024b). As a result, the Jamaican species is referred to by this name: *Timochares ruptifasciata* (Plötz, 1884), and *Timochares ruptifasciata runia* Evans, 1953 (type locality in Jamaica) became its junior subjective synonym. A continental species was described as new: *Timochares fuscifasciata* Grishin, 2024 (USA: Texas, Hidalgo Co.).

Recently, we completed genomic sequencing of a *Timochares* Godman & Salvin, 1896 (type species *Leucochitonea trifasciata* Hewitson, 1868) specimen placed on the left of the lectotype under the same header label “ruptifasciatus | Plötz” (NVG-24029B03) (Fig. 57d). In contrast to the lectotype (Fig. 57a, b) (Zhang et al. 2024b), this specimen has no direct indication on its labels suggesting it was part of the type series (Fig. 57c). However, it bears the only original label “Antigonus | ruptifasciata | Plötz” likely handwritten by J. Peter Maassen (9 December 1810 – 2 August 1890). Because Maassen was 74 years old and nearing the end of his life when the description of *A. ruptifasciata* was published (1884),

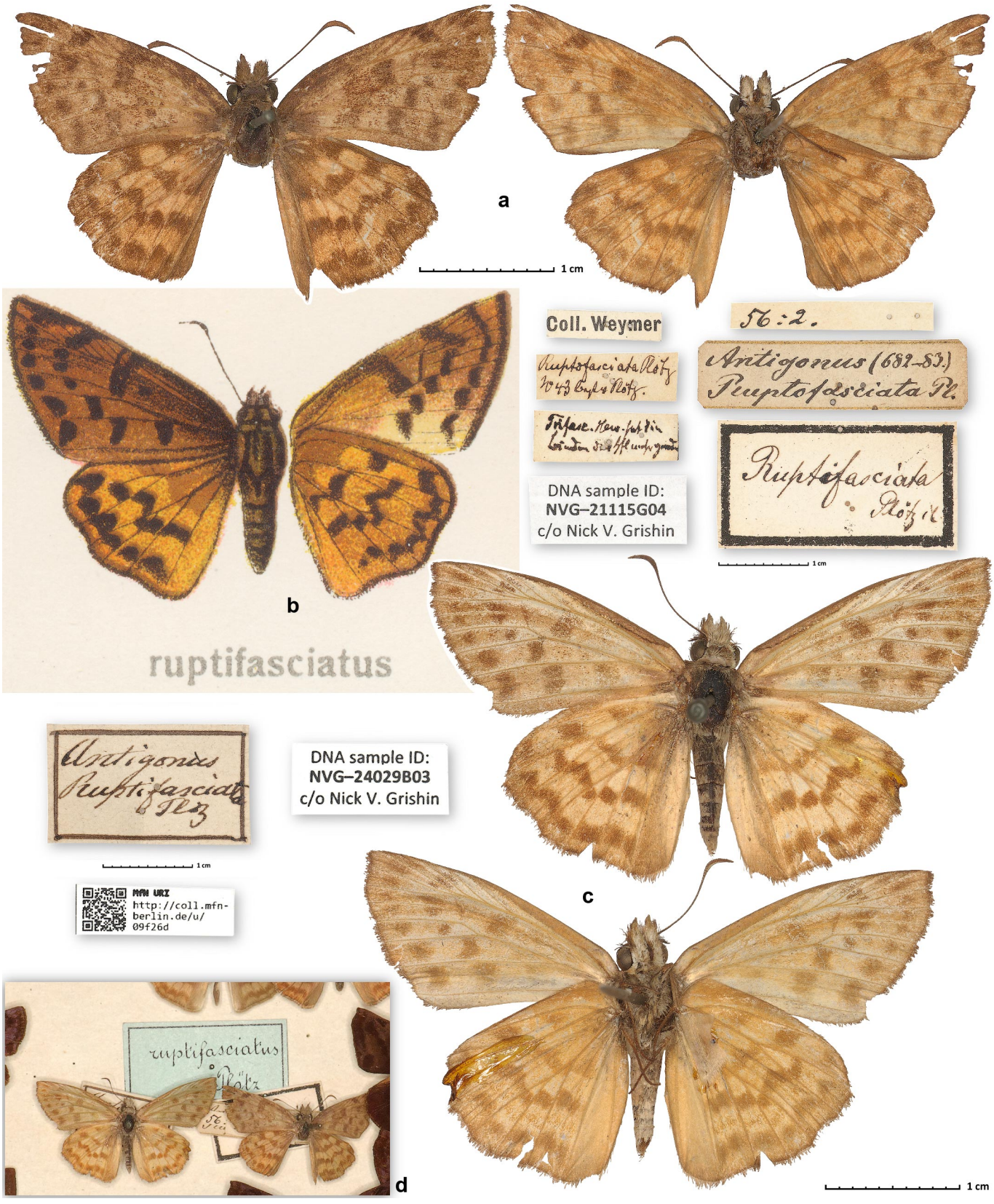

Fig. 57. *Antigonus ruptifasciata* from Jamaica in MFNB: **a)** lectotype ♀ NVG-21115G04 with its labels below the ventral image, **b)** illustration from Draudt (1923), likely a copy of the unpublished Plötz drawing t. 1019, **c)** a possible paralectotype ♂ NVG-24029B03 with its labels shown on the left of the images, **d)** these two specimens in the MFNB Hesperiidae drawer No. 70 under the header label "ruptifasciatus | Plötz." Dorsal and ventral views are shown on the left (or above) and right (or below) of the figure panel letter. The larger scale bar refers to specimens. Labels are reduced by a third compared to specimens and smaller scale bars are placed near them.

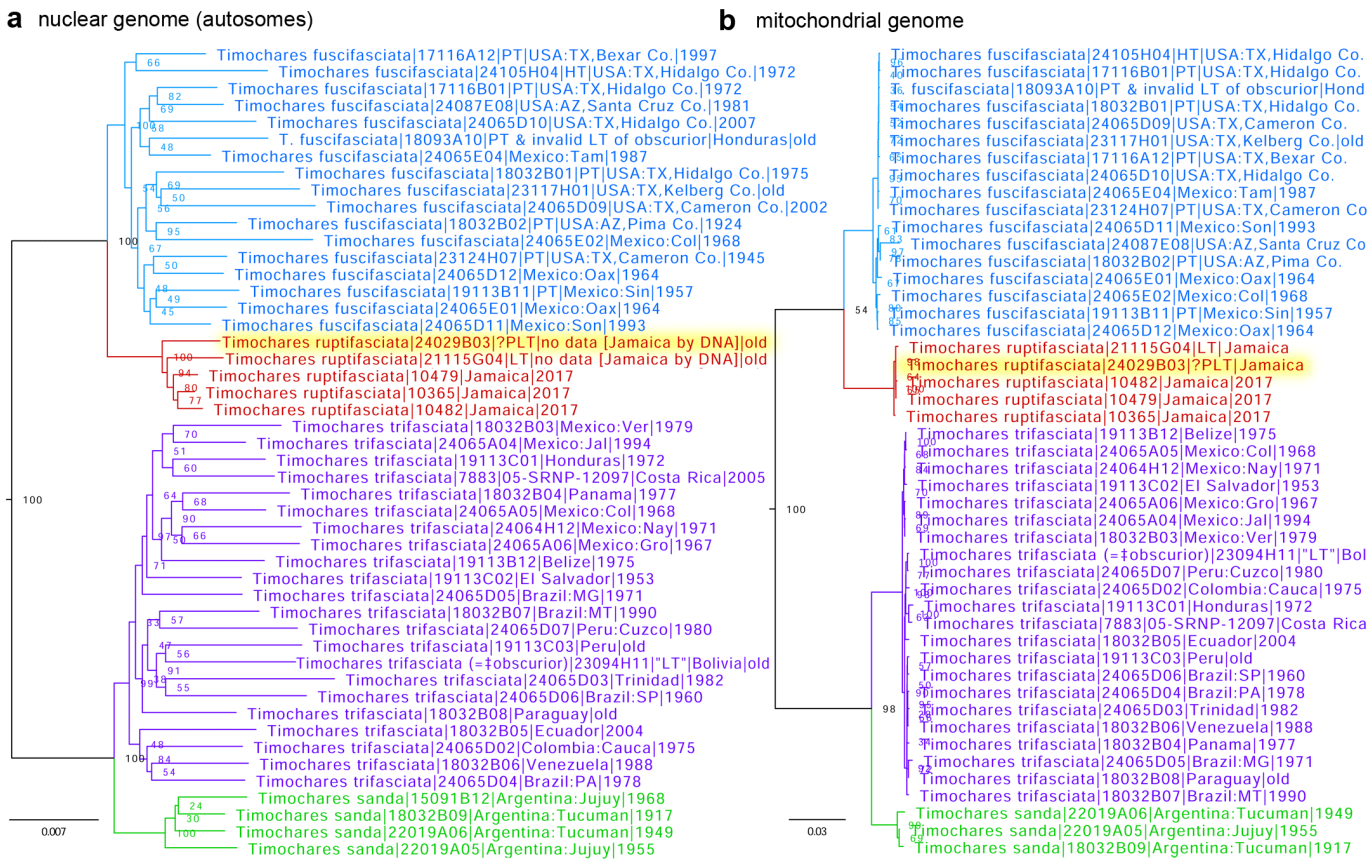

Fig. 58. Phylogenetic trees of all described *Timochares* species constructed from protein-coding regions in: **a)** the nuclear genome (autosomes), based on 504,312 positions, and **b)** the mitochondrial genome. Different species are shown in different colors: *T. fuscifasciata* (blue), *T. ruptifasciata* (red, a possible paralectotype discussed in the text is highlighted in yellow), *T. trifasciata* (purple), and *T. sanda* (green). Ultrafast bootstrap (Hoang et al. 2018) values are shown at nodes.

it seems likely that this specimen was collected before the description. Furthermore, genomic comparison places this specimen among specimens from Jamaica (Fig. 58). Because both specimens (the lectotype, and the specimen NVG-24029B03) are located next to each other in the collection (Fig. 57d), were identified as the same taxon, are the only specimens of this taxon in the historical MFNB collections, and have the same provenance being collected in Jamaica likely around the same time, it is possible that the specimen NVG-24029B03 is a paralectotype of *A. ruptifasciata*. While there is no nomenclatural significance to this finding, all specimens of *A. ruptifasciata* that we found in the MFNB collection (two) being collected in Jamaica increases the likelihood that the majority of *A. ruptifasciata* syntypes and specimens known at the time had Jamaican origin and supports our choice of the lectotype for this taxon.

Eudamus electra Lintner, 1881 is a junior subjective synonym of *Ephyriades brunnea floridensis* E. Bell & W. P. Comstock, 1948 and not of *Ephyriades brunnea brunnea* (Herrich-Schäffer, 1865)

Genomic analysis of the holotype of *Eudamus electra* Lintner, 1881 likely mislabeled from Canada: Ontario, Hamilton (sequenced as NVG-15096A09), currently regarded as a junior subjective synonym of *Ephyriades brunnea brunnea* (Herrich-Schäffer, 1865) (type locality in Cuba), reveals that it is not monophyletic with it in both nuclear and mitochondrial genome trees (Fig. 59), and instead is sister to specimens of *Ephyriades brunnea floridensis* E. Bell & W. P. Comstock, 1948 (type locality in USA: Florida, Monroe Co., Key Largo) from Florida. Therefore, we propose to regard *Eudamus electra* Lintner, 1881 as a junior subjective synonym of *E. brunnea floridensis* instead of *E. brunnea brunnea*.

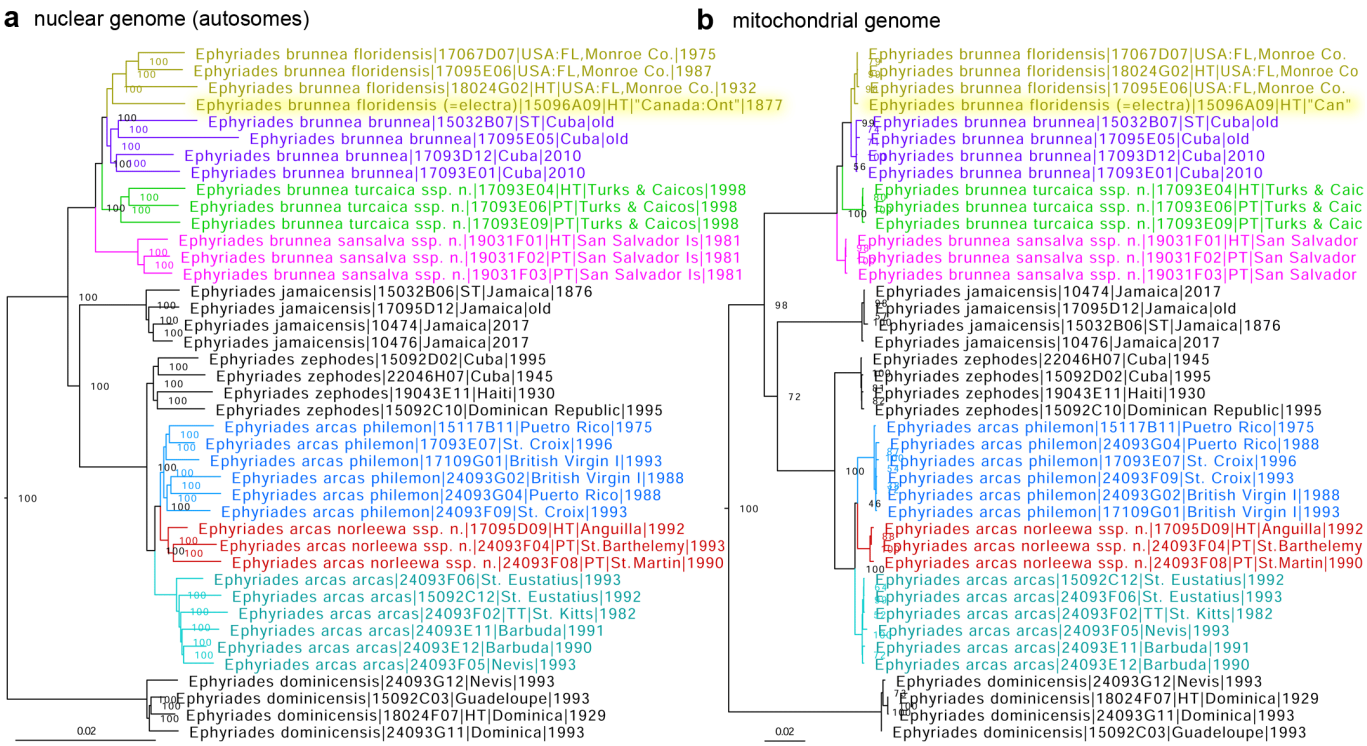

Fig. 59. Phylogenetic trees of all described *Ephyriades* species constructed from protein-coding regions in: **a)** the nuclear genome (autosomes), based on 9,520,194 positions, and **b)** the mitochondrial genome. Subspecies discussed in the text are colored: *E. brunnea floridensis* (olive), *E. brunnea brunnea* (purple), *E. brunnea turcaica* **ssp. n.** (green), *E. brunnea sansalva* **ssp. n.** (magenta), *E. arcas philemon* (blue), *E. arcas norleewa* **ssp. n.** (red), *E. arcas arcas* (cyan). The holotype of *Eudamus electra* is highlighted in yellow. Ultrafast bootstrap (Hoang et al. 2018) values are shown at nodes.

Ephyriades brunnea sansalva Grishin, new subspecies

https://zoobank.org/740A14C9-FD96-4277-A1C0-84E44384F4C8

(Figs. 59 part, 60)

Definition and diagnosis. Genomic analysis reveals that specimens from San Salvador Island, Bahamas, identified as *Ephyriades brunnea brunnea* (Herrich-Schäffer, 1865) (type locality in Cuba) are genetically differentiated from it at least at the subspecies level (Fig. 59); e.g., their COI barcodes differ by 1.5% (10 bp), and therefore we conservatively consider these specimens to represent a new subspecies rather than a species. This new subspecies keys to "*Ephyriades brunnea brunnea*" (F.15.3(b)) in Evans (1953), but differs from it and other relatives by being more spotted than a typical *Ephyriades brunnea floridensis* E. Bell & W. P. Comstock, 1948 (type locality in USA: Florida, Monroe Co., Key Largo); e.g., the male holotype has a white hyaline dash in the forewing cell CuA_1-CuA_2 and the three subapical hyaline spots on the forewing are in a concave (outward) line, i.e., the spot in cell R_4-R_5 is offset distad from the other two; and females have an elongated (rather than squarish) hyaline spot in the forewing cell M_3-CuA_1, but subapical spots are rounder than in a typical *E. brunnea brunnea*, and the submarginal section of the dorsal side is paler and more contrasting with the darker base in females. 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: aly456.1.2:C73T, aly456.1.2:C78T, aly6209.3.1:C951T, aly6209.3.1:T2145C, aly363.33.4:C94T; and the COI barcode: T50C, T121C, T178C, T319C, T586A, A622A.

Barcode sequence of the holotype. Sample NVG-19031F01, 658 base pairs:

AACTTTATATTTTATTTTTGGAATTTGAGCAGGAATAGTAGGAACTTCCCTAAGTTTATTAATTCGAACAGAATTAGGTAATCCTGGATCTTTAATTGGAGATGATCAAATTTATAATACC
ATTGTTACAGCTCATGCTTTTATTATAATTTTTTTTATAGTAATACCAATTATAATCGGAGGATTTGGAAATTGACTTGTACCCCTTATATTAGGAGCTCCTGATATAGCATTCCCACGAA
TAAATAATATAAGATTTTGACTTTTACCTCCTTCTTTAATATTATTAATTTCAAGAAGAATTGTAGAAAATGGAGCCGGAACAGGTTGAACTGTTTATCCCCCTCTTTCAGCTAATATTGC
TCATCAAGGATCATCAGTAGATTTAGCTATTTTCTCTTTACATTTAGCTGGAATTTCCTCTATTTTAGGAGCTATTAATTTTATTACAACAATTATTAATATACGAATTAGAAACTTATCT
TTTGATCAAATACCTTTATTTGTTTGAGCTGTAGGAATTACAGCTTTACTTTTACTATTATCTTTACCAGTATTAGCAGGAGCTATTACTATACTATTAACAGATCGAAATTTAAATACAT
CATTTTTTGATCCTGCAGGAGGAGGTGATCCAATTCTTTATCAACATTTATTT

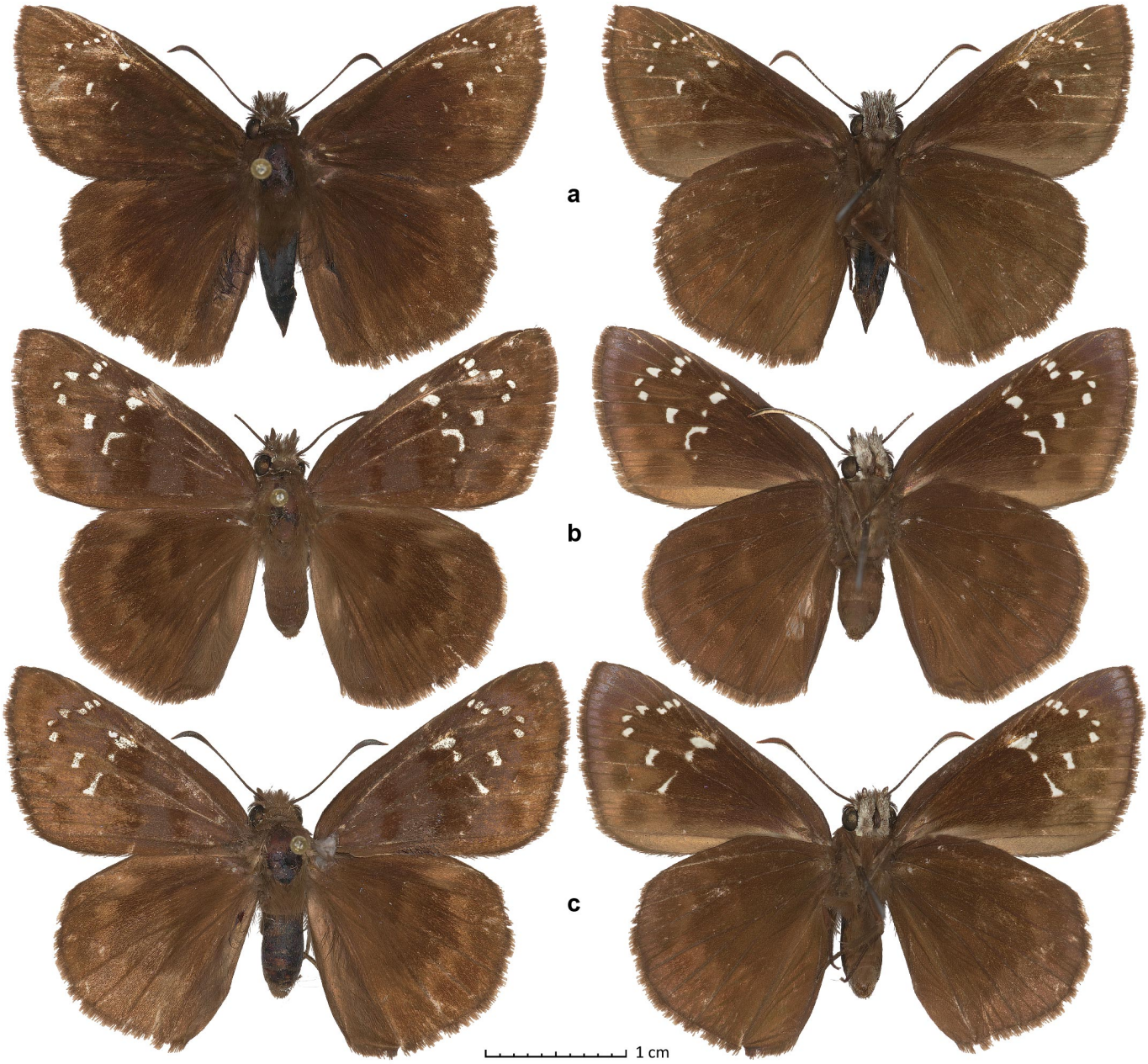

Fig. 60. *Ephyriades brunnea sansalva* **ssp. n.** type series from Bahamas: San Salvador Island in dorsal (left) and ventral (right) views, data in text: **a)** holotype ♂ NVG-19031F01 and paratypes ♀♀: **b)** NVG-19031F02 and **c)** NVG-19031F03.

Type material. Holotype: ♂ deposited in the National Museum of Natural History, Smithsonian Institution, Washington, DC, USA (USNM), illustrated in Fig. 60a, bears the following five printed rectangular labels (text in italics handwritten), four white: [BAHAMA ISLS. | San Salvador Isl. | May 15, 1981 | J.R.Powers.Collr.], [om flowering | sea grapes], [DNA sample ID: | NVG-19031F01 | c/o Nick V. Grishin], [USNMENT | {QR Code} | 01544422], and one red [HOLOTYPE ♂ | Ephyriades brunnea | sansalva Grishin]. **Paratypes:** 2♀♀ with the same data as the holotype except as indicated: 1♀ NVG-19031F02, USNMENT 01544423, 19-May-1981 (Fig. 60b) and 1♀ NVG-19031F03, USNMENT 01544424 (Fig. 60c).

Type locality. Bahamas: San Salvador Island.

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

Distribution. Currently known only from the type locality in San Salvador Island, Bahamas.

Ephyriades brunnea turcaica Grishin, new subspecies

https://zoobank.org/A0386DEA-AFB6-4D6C-B752-B0BC9B32629B

(Figs. 59 part, 61)

Definition and diagnosis. Genomic analysis reveals that specimens from Providenciales Island (Turks & Caicos Islands) identified as *Ephyriades brunnea brunnea* (Herrich-Schäffer, 1865) (type locality in Cuba) are genetically differentiated from it at least at the subspecies level (Fig. 59); e.g., their COI barcodes differ by 1.2% (8 bp), and therefore we conservatively consider these specimens to represent a new subspecies rather than a species. This new subspecies keys to "*Ephyriades brunnea brunnea*" (F.15.3(b)) in Evans (1953), but differs from it and other relatives by males that are paler and have warmer brown colors rather than blackish and females that are also paler, with narrower dark cross-bands on the forewing and broader middle paler-brown area. 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: aly2532.7.4:C126T, aly2532.7.4:C136T, aly6841.76.2:T126A, aly6841.76.2:G129A, aly127.44.1:G144A; and the COI barcode: T50C, T319T, T340C, T401C, T457C, A622G.

Barcode sequence of the holotype. Sample NVG-17093E04, 658 base pairs:

AACTTTATATTTTATTTTTGGAATTTGAGCAGGAATAGTAGGAACTTCCCTAAGTTTATTAATTCGAACAGAATTAGGTAATCCTGGATCTTTAATTGGAGATGATCAAATTTACAATACT
ATTGTTACAGCTCATGCTTTTATTATAATTTTTTTCATAGTAATACCAATTATAATTGGAGGATTTGGAAATTGACTTGTACCCCTTATATTAGGAGCTCCTGATATAGCATTCCCACGAA
TAAATAATATAAGATTTTGACTTTTACCTCCTTCTTTAATATTATTAATTTCAAGAAGAATTGTAGAAAATGGAGCTGGAACAGGTTGAACTGTTTACCCCCCTCTTTCAGCTAATATTGC
TCATCAAGGATCATCAGTAGATTTAGCTATTTTCTCTCTACATTTAGCTGGAATTTCCTCTATTTTAGGAGCTATTAATTTTATTACAACAATCATTAATATACGAATTAGAAACTTATCT
TTTGATCAAATACCTTTATTTGTTTGAGCTGTAGGAATTACAGCTTTACTTTTACTATTATCTTTACCAGTATTAGCAGGAGCTATTACTATACTATTAACTGATCGAAATTTAAATACAT
CATTTTTTGATCCTGCGGGAGGAGGTGATCCAATTCTTTATCAACATTTATTT

Type material. Holotype: ♀ deposited in the National Museum of Natural History, Smithsonian Institution, Washington, DC, USA (USNM), illustrated in Fig. 61a, bears the following five printed rectangular labels, four white: [TURKS & CAICOS ISLS. | Providenciales | Long Bay Beach | 21°48'N, 72°12'W | 1 February 1998], [Coastal scrub and | dune vegetation; | W. E. Steiner & J. M. Swearingen | collectors], [DNA sample ID: | NVG-17093E04 | c/o Nick V. Grishin], [USNMENT | {QR Code} | 00894691], and one red [HOLOTYPE ♀ | Ephyriades brunnea | turcaica Grishin]. **Paratypes:** 3♂♂ and 1♀ with the same data as the holotype except as indicated: 1♂ NVG-17093E09, USNMENT 00894716 (Fig. 61d) and 1♀ NVG-17093E03, USNMENT 00894691 (Fig. 61b–c); 1♂ NVG-17093E05, USNMENT 00894696 Northwest Point, approx. GPS 21.850, −72.333, 31-Jan-1998; and 1♂ NVG-17093E06, USNMENT 00894701 Crystal Bay (nr. Northwest Point), approx. GPS 21.8333, −72.3167 (Fig. 61e–f).

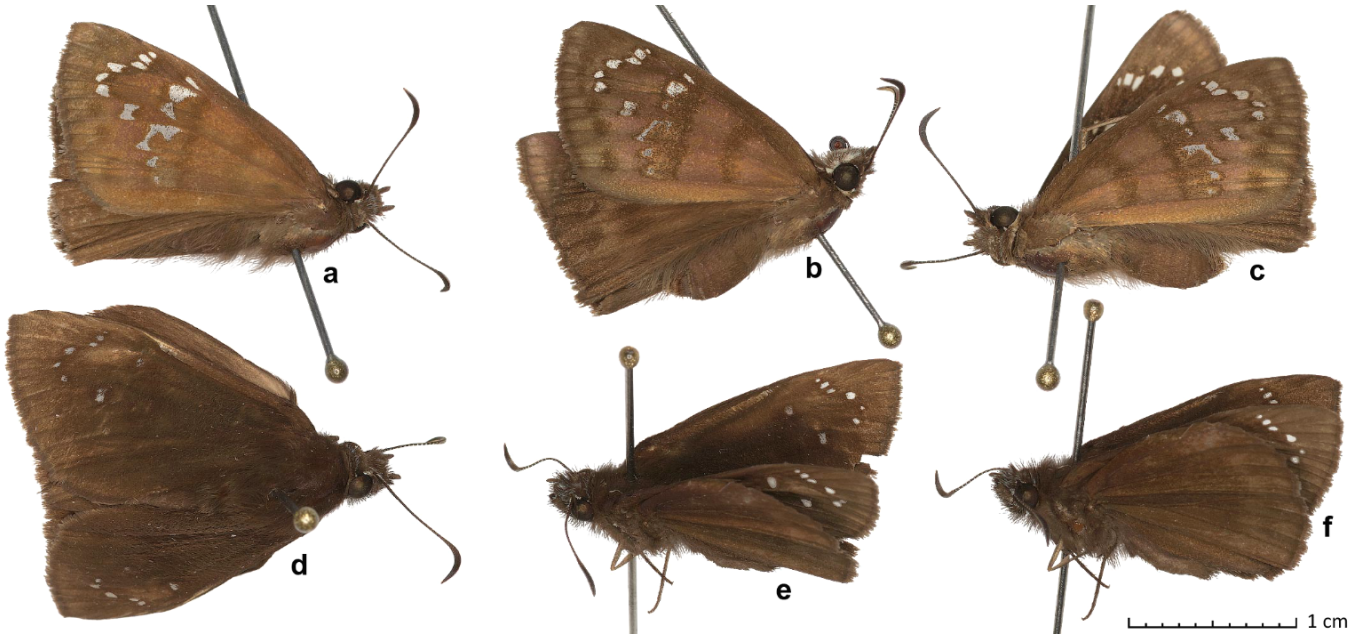

Fig. 61. *Ephyriades brunnea turcaica* **ssp. n.** from Providenciales, Turks & Caicos Islands, data in text:
a) holotype ♀ NVG-17093E04 and paratypes: **b–c)** ♀ NVG-17093E03, **d)** ♂ NVG-17093E09, and **e–f)** ♂ NVG-17093E06.

Type locality. Turks & Caicos Islands: Providenciales Island, Long Bay Beach.

Etymology. The name is derived from the type locality in *Tur*[ks &]*Caic*[os Isl]*a*[nds] and is treated as a noun in apposition.

Distribution. Currently known only from Providenciales Island in Turks & Caicos Islands.

Distribution. GPS coordinates on the holotype label point to the ocean and do not correspond to the locality given in words, and GPS coordinates on the paratype labels are equally misleading.

Ephyriades arcas norleewa Grishin, new subspecies

https://zoobank.org/91C1D926-37B0-4723-BF99-661C9D322A93

(Figs. 59 part, 62)

Definition and diagnosis. Genomic analysis reveals that specimens from the northernmost Leeward Islands (Anguilla, St. Martin, and St. Barthélemy) identified as *Ephyriades arcas philemon* (Fabricius, 1775) (type locality in "America", possibly in St. Croix) or *Ephyriades arcas arcas* (Drury, 1773) (type locality in St. Kitts) are genetically differentiated from them at least at the subspecies level (Fig. 59); e.g.,

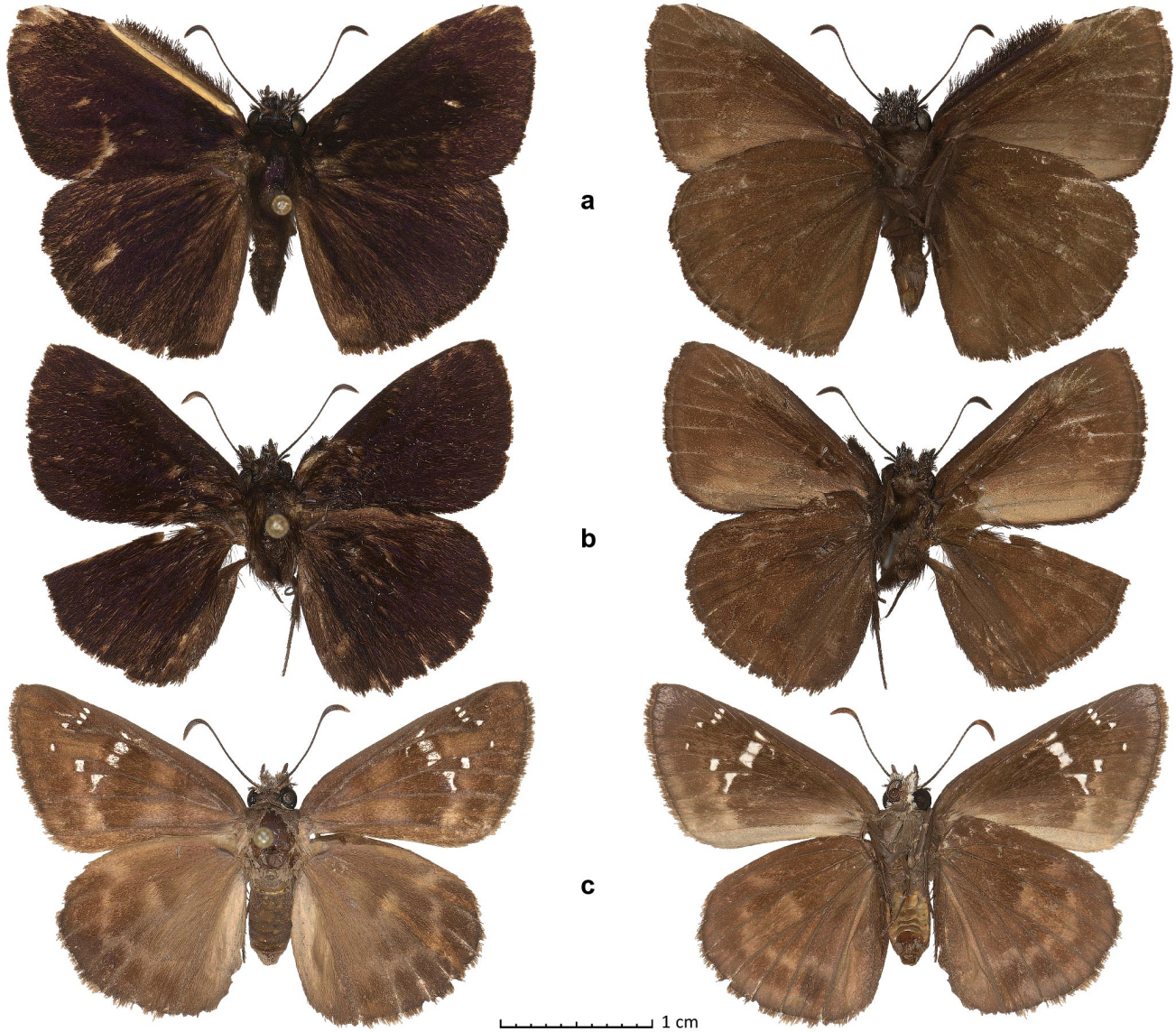

Fig. 62. *Ephyriades arcas norleewa* **sp. n.** type series in dorsal (left) and ventral (right) views, data in text: **a)** holotype ♂ NVG-17095D09 Anguilla, **b)** paratype ♂ NVG-24093F08 St. Martin and **b)** paratype ♀ NVG-24093F04 St. Barthélemy.

their COI barcodes differ by 1.7% (11 bp) from both *E. arcas philemon* and *E. arcas arcas* (the latter two subspecies differing by the same number of base pairs from each other), and therefore we conservatively consider these specimens to represent a new subspecies rather than a species. This new subspecies keys to *E. arcas philemon* (F.15.1(b)) in Evans (1953), but has characters intermediate between the two subspecies. Males lack the pale spot of *E. arcas arcas* in the ventral forewing discal cell thus being *E. arcas philemon*-like, but are usually smaller, more similar to *E. arcas arcas* in size. Females are also smaller and typically have reduced or missing semihyaline spot in the forewing cell M_1-M_2 and three subapical spots by the costal margin in a straight row and small, with the posterior-most spot being the smallest. Females appear more variegated on the ventral hindwing, with the area distad of the discal cell being paler, similar in color to the postdiscal pale band. Due to its cryptic nature and significant individual variation, this subspecies is best identified by DNA, with diagnostic base pairs in the nuclear genome: aly2668.11.1:G58C, aly2668.11.1:G81T, aly2984.10.3:C90T, aly2984.10.3:T114A, aly379.6.6:C64T; and the COI barcode: T46T, T85C, 112T, T463C, 562C.

Barcode sequence of the holotype. Sample NVG-17095D09, 658 base pairs:

AACTTTATATTTTATTTTTGGAATTTGAGCAGGAATAGTAGGAACTTCTTTAAGTTTATTAATTCGAACAGAATTAGGTAATCCCGGATCTTTAATTGGAGATGATCAAATTTATAATACT
ATTGTTACAGCTCATGCTTTTATTATAATTTTTTTTATAGTAATACCAATTATAATTGGAGGATTTGGAAATTGACTTGTACCCCTTATATTAGGAGCTCCTGATATAGCATTCCCACGAA
TAAATAATATAAGATTTTGACTTTTACCCCCATCTTTAATATTATTAATTTCAAGAAGAATCGTAGAAAATGGAGCCGGAACAGGTTGAACCGTTTACCCCCCTCTTTCAGCTAATATTGC
CCATCAAGGATCATCAGTAGATTTAGCTATTTTTTCTTTACATTTAGCTGGAATTTCTTCTATTCTAGGAGCTATTAATTTTATTACAACAATTATTAACATACGAATTAAAAATTTATCT
TTTGATCAAATACCTTTATTTGTTTGAGCCGTAGGAATTACAGCATTACTCTTACTTTTATCTTTACCTGTCTTAGCCGGAGCTATTACTATATTATTAACTGATCGAAATTTAAATACAT
CATTTTTTGATCCCGCAGGAGGAGGAGATCCAATTCTTTATCAACATTTATTT

Type material. Holotype: ♂ deposited in the National Museum of Natural History, Smithsonian Institution, Washington, DC, USA (USNM), illustrated in Fig. 62a, bears the following four printed rectangular labels (text in italics handwritten), three white: [ANGUILLA: Brimegin | 18°14'50"N, 63°03'00"W | 24 March 1992 | collrs. W. E. Steiner | & J. M. Swearingen], [DNA sample ID: | NVG-17095D09 | c/o Nick V. Grishin], [USNMENT | {QR Code} | 00894795], and one red [HOLOTYPE ♂ | Ephyriades arcas | norleewa Grishin]. **Paratypes:** 1♂ and 1♀ in MGCL: 1♂ NVG-24093F08 Saint Martin, N slope Pic Paradis, 280 m, 25-Sep-1990, L. D. & J. Y. Miller leg., genitalia vial RG0139 by Riley J. Gott (Fig. 62b) and 1♀ NVG-24093F04 Saint Barthélemy, NE shore Grande Saline, 2-Nov-1993, L. D. Miller leg. (Fig. 62c).

Type locality. Anguilla: Brimegin, GPS 18.2472, −63.0500.

Etymology. The name is derived from the range of this species in *nor*[thern] *Leewa*[rd Islands] and is treated as a noun in apposition.

Distribution. Currently known from the northernmost Leeward Islands: Anguilla, Saint Martin, and Saint Barthélemy.

Subfamily Tagiadinae Mabille, 1878
Tribe Netrocorynini Grishin, 2019

Neotype designation for *Thymele triton* Boisduval, 1832

Thymele triton Boisduval, 1832, currently a valid species in the genus *Chaetocneme* C. Felder, 1860 (type species *Chaetocneme corvus* C. Felder, 1860, which is a junior subjective synonym of *Papilio helirius* Cramer, 1775), was described from an unstated number of specimens from New Guinea (Boisduval 1832). We translate (the first sentence from Latin and the rest from French) the entire original description as "4. T. Triton. Wings dark reddish and unspotted; all beneath blackish-brown; legs and palps yellowish-tawny. Wings of a dark reddish-brown, without spots; underside of the four [wings] of a blackish-brown; legs and palps of a yellowish-tawny. It is the size of [Augiades] Crinisus, and it is found in New Guinea." Both the description and the type locality are vague and incomplete and agree with several distinct species of *Chaetocneme*.

To confidently determine the taxonomic identity of *T. triton*, we searched for its syntypes in all collections we examined (see Acknowledgments for their list), more carefully the collection with extant

Boisduval type specimens, such as BMNH, USNM, and MNHP, and we searched not just in the segregated type drawers, but among their entire Hesperiidae holdings. Inspection of Hesperiidae specimens in these collections failed to uncover syntypes of *T. triton*. Next, we proceeded with the neotype designation because there is an exceptional need to clarify both the taxonomic identity and the type locality of *T. triton*. Considering new species present among its close relatives, it is important to define *T. triton* objectively. Hereby, N.V.G. designates the specimen in MTD, a male shown in Fig. 63a (DNA sample NVG-18095F02), as the **neotype** of *Thymele triton* Boisduval, 1832. We selected a specimen of this species as the neotype, because in addition to fully agreeing with the original description, it lacks orange fringes (not mentioned in the original description), is smaller than some other species (thus more similar in size to *Augiades crinisus* (Cramer, 1780)), and has been identified in collections and literature as *T. triton* (Evans 1949). Therefore, our designation satisfies both the historical accuracy and nomenclatural stability in the application of this name.

This neotype satisfies all requirements set forth by the ICZN Article 75.3, namely: **75.3.1.** It is designated to clarify the taxonomic identity of *T. triton*, which is necessary because new species are present among its close relatives and the original description was too incomplete to differentiate between them, and to better define the type locality, which was stated in the original description very broadly as "New Guinea"; **75.3.2.** The characters to differentiate this taxon from others, as stated in the original description, are: dark reddish and unspotted wings; darker on the ventral side, blackish-brown; orange legs and palpi; and the size of *A. crinisus*, i.e., wingspan of about 4–5 cm; **75.3.3.** The neotype specimen is a male bearing four rectangular white labels (1st handwritten, others printed): [D.N.=Guin.] meaning Deutsch-Neuguinea, i.e., German New Guinea, [Stauding.& Bang-Haas | Dresden, Ankauf 1961], [Staatl. Museum für | Tierkunde Dresden], [DNA sample ID: | NVG-18095F02 | c/o Nick V. Grishin] and shown in Fig. 63a; the neotype is a specimen in good condition but with an elongated scratch near the end of the discal cell on the dorsal side of the left forewing; **75.3.4.** We failed to find syntypes of *T. triton* among Hesperiidae holdings in all collections we examined (see Acknowledgments for their list, in particular BMNH, USNM, and MNHP with other Boisduval types) and therefore believe that they were lost; **75.3.5.** The neotype closely agrees with the original description of *T. triton* in all characters, as evidenced by finding these characters (listed in 75.3.2 above) in the neotype photographs shown in Fig. 63a, the wingspan of the neotype being 4.7 cm; **75.3.6.** The neotype is from "German New Guinea" which falls within the original type locality given as "New Guinea"; **75.3.7.** The neotype is in the collection of the Museum für Tierkunde, Dresden, Germany (MTD). As a result of the neotype designation, the type locality of *T. triton* becomes Papua New Guinea: northern half (i.e., former German New Guinea), to be refined by genomic comparison. The COI barcode sequence of the neotype, sample NVG-18095F02, 658 base pairs, is:

AACTTTATATTTTATTTTTGGAATTTGATCAGGAATAGTTGGTACCTCTTTAAGTCTTTTAATTCGTACTGAATTAGGTAATCCAGGTTCTTTAATTGGAGATGATCAAATTTATAATACA
ATCGTTACAGCTCATGCTTTTATTATAATTTTTTTTATAGTAATACCTATTATAATTGGAGGATTTGGTAATTGATTAGTTCCTTTAATATTAGGAGCTCCTGATATAGCTTTCCCACGAA
TAAATAATATAAGATTTTGACTTTTACCCCCCCTCATTAGTTTTACTAATTTCAAGAAGAATCGTAGAAAATGGAGCAGGAACTGGTTGAACAGTATATCCCCCTCTTTCAGCTAATATTGC
TCACCAAGGAGCTTCAGTAGATTTAGCAATTTTTTCATTACATTTAGCTGGTATTTCTTCTATCTTAGGAGCTATTAACTTTATTACAACAATTATTAATATACGAATTAAAAATTTATCT
TTTGATCAAATACCTTTATTCGTGTGAGCTGTAGGAATTACAGCTTTACTTTTACTTCTTTCCTTACCTGTATTAGCTGGAGCTATTACAATACTTTTAACAGATCGAAATTTAAATACTT
CCTTTTTCGATCCAGCGGGAGGAGGAGATCCTATTTTATATCAACATTTATTT

Lectotype designation for *Tagiades editus* Plötz, 1885

Tagiades editus Plötz, 1885, currently placed in the genus *Chaetocneme* C. Felder, 1860 (type species *Chaetocneme corvus* C. Felder, 1860, which is a junior subjective synonym of *Papilio helirius* Cramer, 1775), was described from an unstated number of specimens collected in the Aru Islands by Carl Ribbe (Plötz 1885). We located and sequenced a single syntype of *T. editus* in the ZSMC collection (NVG-22016C12) (Fig. 63b) with the locality "Aru-Jnsel" and collected by C. Ribbe in 1883 (i.e., before the description was published), as stated on one of the labels, and with another label "editus" in Plötz's handwriting. To define the taxonomic identity of the name *T. editus* objectively, N.V.G. hereby designates this syntype in the ZSMC collection, the female with the following six rectangular labels (3rd purple, 5th red, others white; 2nd and 4th handwritten, others printed): [Aru-Jnsel | Wamma Dobbo | C.Ribbe 1883], [editus], [Original], [♀ Celaen. editus Pl.typ. | (sec.Mab.sp) Aru Ins.], [Holotypus | | Zool. Staatssammlg.

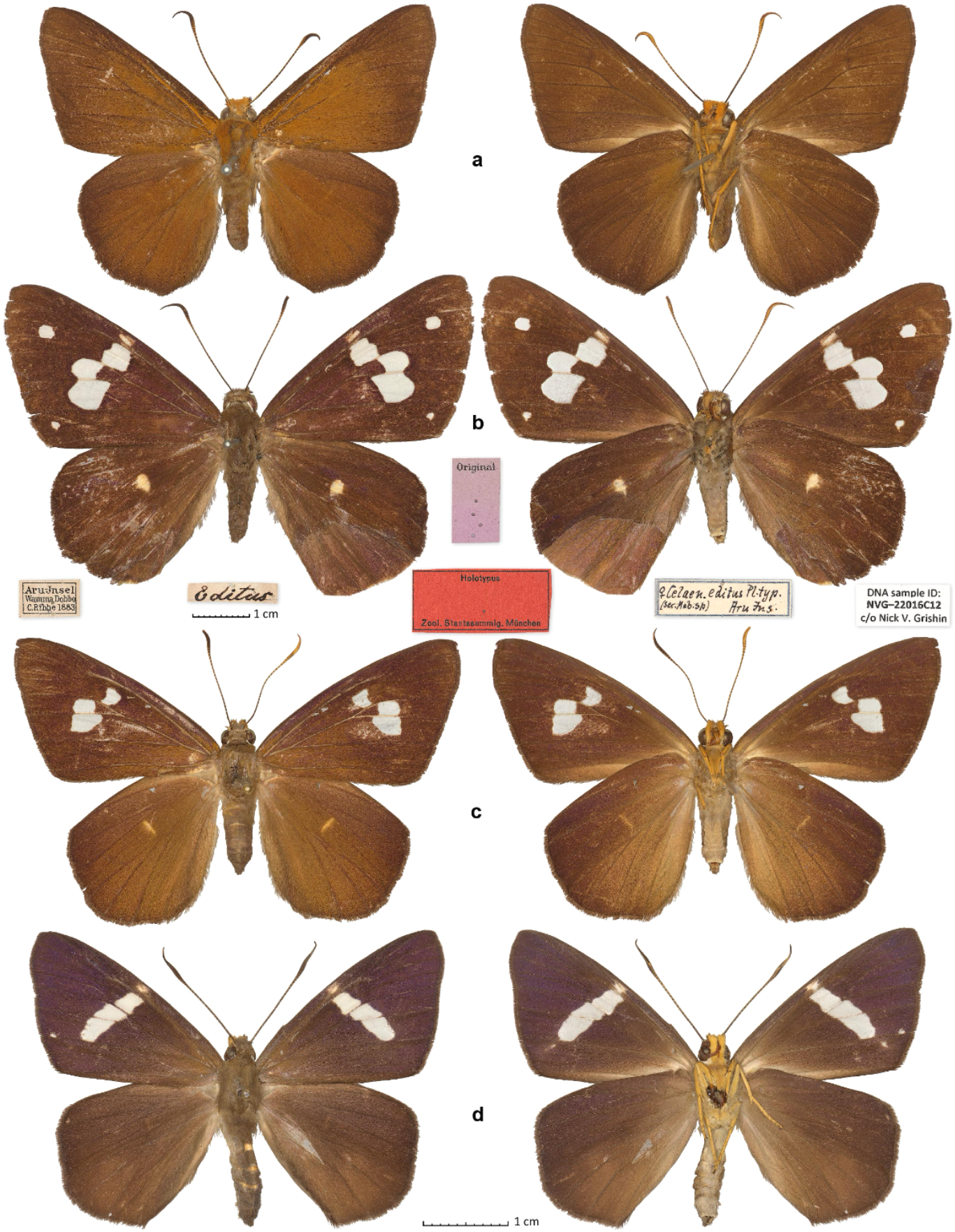

Fig. 63. Primary type specimens of *Chaetocneme* in dorsal (left) and ventral (right) views, data in text: **a)** *C. triton* neotype ♂ NVG-18095F02, **b)** *C. editus* lectotype ♂ NVG-22016C12 with its labels, reduced by ⅓ compared to specimens, as indicated by a smaller scale bar, **c)** *C. triuna* **sp. n.** holotype ♀ NVG-17068G02, **d)** *C. brazza* **sp. n.** holotype ♀ NVG-23086B10.

München], and [DNA sample ID: | NVG-22016C12 | c/o Nick V. Grishin] as the **lectotype** of *Tagiades editus* Plötz, 1885. The lectotype is missing the apiculus of the right antenna and has the tornus on both hindwings repaired (i.e., basically replaced) with wing segments of other specimens. These wing segments of unknown species are excluded from the lectotype. According to the label of the lectotype, the type locality of *T. editus* becomes Indonesia: Maluku Province, Aru Islands, Wamar Island, Dobo. The COI barcode sequence of the lectotype, sample NVG-22016C12, 658 base pairs is:

AACTTTATATTTTATTTTTGGAATTTGATCAGGAATAGTTGGTACATCTTTAAGTCTTTTAATTCGTACTGAATTAGGTAATCCTGGTTCTTTAATTGGAGATGATCAAATTTATAATACA
ATTGTTACAGCTCATGCTTTTATTATAATTTTTTTTATGGTAATACCTATCATAATTGGAGGATTTGGTAATTGATTAGTTCCCTTAATATTAGGAGCCCCTGATATAGCCTTTCCACGAA
TAAATAACATAAGATTTTGACTTTTACCCCCTTCATTAGTTTTATTAATTTCAAGAAGAATTGTAGAAAATGGAGCAGGAACTGGTTGAACAGTATACCCCCCTCTCTCAGCTAATATTGC
TCATCAAGGAGCTTCAGTAGATTTAGCAATTTTTTCATTACATTTAGCTGGTATTTCTTCTATTCTAGGAGCTATTAACTTTATTACAACAATTATTAATATACGAATTAAAAATTTATCT
TTTGATCAAATACCTTTATTCGTATGAGCTGTAGGAATTACAGCTTTACTTTTACTTCTTTCATTACCTGTATTAGCTGGAGCTATTACAATACTTTTAACAGATCGAAATTTAAATACTT
CTTTTTTTGATCCTGCAGGAGGAGGAGATCCTATTTTATATCAACATTTATTT

Chaetocneme triuna Grishin, new species

https://zoobank.org/2A46EED6-DBD4-4741-B28B-BBC58E0EF5BF

(Figs. 63c, 64 part)

Definition and diagnosis. Genomic analysis reveals that a female collected in the southeastern New Guinea is sister to *Chaetocneme triton* (Boisduval, 1832) (type locality in New Guinea) but is genetically differentiated from it at the species level (Fig. 64), e.g., their COI barcodes differ by 4.6% (30 bp); and strongly differs in wing pattern by having a cluster of three semihyaline white spots in the middle of the forewing instead of a forewing pale band, and therefore this female represents a new species. This new species is phenotypically more similar to *Chaetocneme editus* (Plötz, 1885) (type locality in Indonesia: Maluku province, Wamar Island, Dobo; lectotype sequenced as NVG-22016C12) and keys to it (B.2.4a) in Evans (1949), but differs from it and other relatives by females lacking any trace of an apical white spot on the forewing and only having a cluster of three semihyaline white spots in the middle: a discal cell spot and distad of it two aligned spots in cells M_3-CuA_1 and CuA_1-CuA_2; and a yellowish dash (not an oval spot) at the end of the hindwing discal cell on both sides of the wing. Due to unexplored individual variation, this species is best identified by DNA, with diagnostic base pairs in the nuclear genome: aly133.39.7:A1740T, aly3446.8.19:G54A, aly1313.19.16:C39T, aly1313.19.16:G48C, aly2011.3.2:C72T, aly1405.13.10:T90T (not G), aly2874.9.1:T75T (not C), aly2627.2.2:C33C (not T), aly10226.37.5: G158G (not A), aly323.1.11:C120C (not T); and the COI barcode: T124C, A268G, T436C, A517T, T610C.

Barcode sequence of the holotype. Sample NVG-17068G02, 658 base pairs:

AACTTTATATTTTATTTTTGGAATTTGATCAGGAATAGTTGGTACATCTTTAAGTCTTTTAATTCGTACCGAATTAGGTAATCCTGGTTCTTTAATTGGAGATGATCAAATTTATAATACA
ATCGTTACAGCTCATGCTTTTATTATAATTTTTTTTATAGTAATACCTATCATAATTGGGGGGTTTGGTAATTGATTAGTTCCTTTAATATTAGGGGCTCCTGATATAGCTTTCCCACGAA
TAAATAACATAAGATTTTGACTTTTGCCTCCCTCATTAGTTTTACTAATTTCAAGAAGAATCGTAGAAAATGGAGCAGGAACTGGTTGAACAGTATACCCCCCTCTTTCAGCTAATATTGC
TCATCAAGGAGCTTCAGTAGATTTAGCAATTTTCTCATTACATTTAGCTGGTATTTCTTCCATTTTAGGGGCCATTAATTTTATTACAACAATTATTAATATACGAATTAAAAATTTATCT
TTTGATCAAATACCCTTATTCGTATGAGCTGTTGGAATTACAGCTTTACTTTTACTTCTTTCTCTACCTGTATTAGCTGGAGCTATTACAATACTTTTAACAGATCGAAATTTAAATACTT
CCTTCTTTGACCCCGCAGGAGGGGGAGATCCTATTTTATACCAACATTTATTT

Type material. Holotype: ♀ deposited in the National Museum of Natural History, Smithsonian Institution, Washington, DC, USA (USNM), illustrated in Fig. 63c, bears the following five rectangular labels (2nd handwritten, others printed), four white: [J. Hotota | Popondetta | NEW GUINEA | 19], [Casyapa | corvus | dissimilis ♂ | Swh,], [AUGUST SCHMITT | COLLECTION | To Smithsonian | 1990], [DNA sample ID: | NVG-17068G02 | c/o Nick V. Grishin], and one red [HOLOTYPE ♀ | Chaetocneme | triuna Grishin].

Fig. 64. Phylogenetic trees of selected *Chaetocneme* species constructed from protein-coding regions in: **a)** the nuclear genome (autosomes), based on 7,639,971positions, and **b)** the mitochondrial genome. Species discussed in the text are colored: *C. editus* (purple), *C. triuna* **sp. n.** (red), *C. triton* (green), *C. brazza* **sp. n.** (magenta), and *C. tenuis* (blue). Ultrafast bootstrap (Hoang et al. 2018) values are shown at nodes.

Type locality. Papua New Guinea: Oro Province, Popondetta.

Etymology. The name is derived from the three-in-one white spots that are near each other in the middle of the forewing and are the only pale forewing markings. The name is a noun in apposition.

Distribution. Currently known only from the holotype collected near the northern coast of the southeastern part of New Guinea.

Chaetocneme brazza Grishin, new species

https://zoobank.org/79D226C7-A117-4AE5-8650-92B7996E8123

(Figs. 63d, 64 part)

Definition and diagnosis. Genomic analysis reveals that a female collected south of the Maoke Mountains in central New Guinea is sister to *Chaetocneme tenuis* (van Eecke, 1924) but is genetically differentiated from it at the species level in the nuclear genome (Fig. 64), and therefore this female represents a new species. However, their COI barcodes do not differ. This new species keys to *Chaetocneme tenuis* (B.2.12) in Evans (1949), but differs from it and other relatives by females lacking any trace of the white spot in the forewing cell CuA_2-1A+2A that is present near the tornus in all of its close relatives (at least as a trace). Due to unexplored individual variation, this species is best identified by DNA, with diagnostic base pairs in the nuclear genome: aly2188.7.6:T84C, aly2188.7.6:A62T, aly1468.7.7:T168A, aly198.2.3:C387T, aly4966.20.2:C414T, aly322.16.14:G48G (not C), aly1432.14.2:G393G (not A), aly1952.2.8:C45C (not T), aly6841.72.12:G90G (not A), aly923.25.1:C1212C (not T); and the COI barcodes of specimens we sequenced do not distinguish this new species from *C. tenuis*.

Barcode sequence of the holotype. Sample NVG-23086B10, 658 base pairs:

AACTCTATATTTTATTTTTGGAATTTGATCAGGAATAGTTGGCACATCTTTAAGTCTTTTAATTCGTACTGAATTAGGTAACCCTGGTTCTTTAATTGGGGATGATCAAATTTATAATACA
ATTGTTACAGCCCATGCTTTTATTATAATTTTTTTTATAGTAATACCTATTATAATTGGAGGATTTGGTAATTGATTAGTTCCTTTAATATTAGGGGCACCTGATATAGCTTTCCCACGAA
TAAATAATATAAGATTTTGACTTTTACCTCCCTCATTAATTTTACTAATTTCAAGAAGAATCGTAGAAAATGGAGCTGGAACTGGTTGAACAGTATACCCCCCCCTTTCAGCTAATATTGC
CCACCAAGGGGCTTCTGTAGATTTAGCAATTTTTTCATTACATTTAGCTGGTATTTCTTCTATTTTAGGAGCTATTAATTTTATTACAACAATTATCAATATACGAATTAAAAATTTATCT
TTTGATCAAATACCTTTATTCGTATGAGCTGTGGGAATTACAGCTTTACTTTTACTTCTTTCATTACCTGTATTAGCTGGAGCTATTACAATACTTTTAACGGATCGAAATTTAAATACTT
CTTTTTTTGATCCAGCAGGAGGAGGAGATCCTATTTTATATCAACATTTATTT

Type material. Holotype: ♀ deposited in the Zoologische Staatssammlung München, Germany (ZSMC), illustrated in Fig. 63d, bears the following three printed rectangular labels (text in italics handwritten), two white: [Staatsslg. | München | NEU GUINEA | Irian Barat | Brazza River 250 m | *18.XI.*1971 | leg. G. Konrad], [DNA sample ID: | NVG-23086B10 | c/o Nick V. Grishin], and one red [HOLOTYPE ♀ | Chaetocneme | brazza Grishin]. First two lines on the first label are rotated 90° counterclockwise and are placed along the left side of the label.

Type locality. Indonesia: West Papua region, Brazza River, elevation 250 m.

Etymology. The name is derived from the type locality and is a noun in apposition.

Distribution. Currently known only from the holotype collected south of the Maoke Mountains in central New Guinea.

Porphaurea Grishin, new subgenus

https://zoobank.org/14C4E0F3-7626-4917-9FBD-FD2004ADB805

Type species. *Phoenicops porphyropis* Meyrick & Lower, 1902.

Definition. Genomic phylogeny of *Chaetocneme* C. Felder, 1860 (type species *Chaetocneme corvus* C. Felder, 1860, which is a junior subjective synonym of *Papilio helirius* Cramer, 1775) reveals that all species except one form a compact clade in both the nuclear and mitochondrial genome trees (Fig. 65). Only *Chaetocneme porphyropis* (Meyrick & Lower, 1902) stands out as an isolated lineage sister to all other sequenced *Chaetocneme* species that is genetically differentiated from them at least at the subgenus level, e.g., its COI barcode differs by 10.6% (70 bp) from the type species of *Chaetocneme*. Therefore, not willing to erect a new monotypic genus, we propose that this lineage corresponds to a subgenus. This new subgenus differs from its relatives by a combination of the following characters: an expanded ampulla and

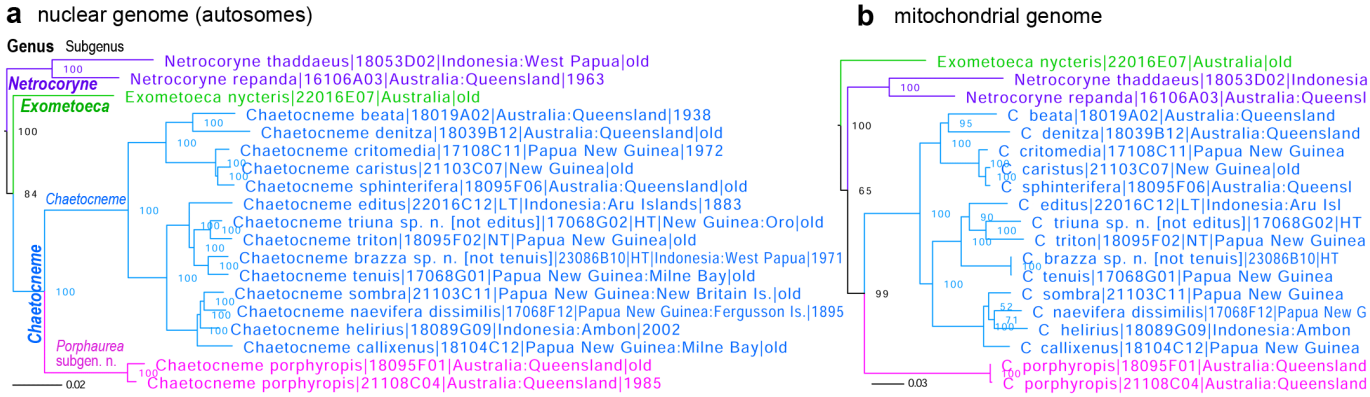

Fig. 65. Phylogenetic trees of Netrocorynini constructed from protein-coding regions in: **a)** the nuclear genome (autosomes), based on 4,889,442 positions, and **b)** the mitochondrial genome. Different genera and subgenera are colored differently: *Netrocoryne* (purple), *Exometoeca* (green), *Chaetocneme* (blue with *Porphaurea* **subgen. n.** in magenta). Ultrafast bootstrap (Hoang et al. 2018) values are shown at nodes.

reduced harpe giving the valva a nearly triangular shape, less robust and thinner body, stronger purplish reflection off the wings, especially in the basal part, and a yellow hindwing apex combined with a yellow discal forewing band. In DNA, a combination of the following characters is diagnostic in the nuclear genome: aly3850.3.3:T159C, aly3850.3.3:T168A, aly1018.6.2:T496C, aly577.55.2:G408A, aly151.38.1:A189G and COI barcode: T19C, A211G, C497T, G512T, T568A.

Etymology. The name is given for the golden (*aureus* in Latin) bands across the purplish (πορφύρα (*porphyra*) in Greek) ground color of this species and is derived from the name of the type species. The name is a feminine noun in the nominative singular.

Species included. Only the type species (i.e., *Phoenicops porphyropis* Meyrick & Lower, 1902).

Parent taxon. Genus *Chaetocneme* C. Felder, 1860.

Subfamily Hesperiinae Latreille, 1809
Tribe Erionotini Distant, 1886

Ge pina Grishin, new species

https://zoobank.org/D76D31A6-AA29-476E-A5D7-DAC10CC5742D

(Figs. 66 part, 67)

Definition and diagnosis. Genomic analysis reveals that a pair of specimens from eastern Mindanao, Philippines, identified as *Ge geta* de Nicéville, 1895 (type locality in Malaysia: Penang and Indonesia: northeastern Sumatra) is genetically differentiated from it at the species level (Fig. 66); e.g., their COI barcodes differ by 5% (33 bp), and therefore this pair represents a new species. This new species keys (incompletely for females) to *G. geta* (J.16) in Evans (1949), but differs from it by the following combination of characters: in males, the forewing androconial patch is rounder (somewhat more circular and not that elongated in antero-posterior direction); paler-beige color on the ventral hindwing does not reach anteriad of the vein CuA_2, and the ventral hindwing lacks a slightly paler reddish-brown segment around and along the vein 1A+2A; and females lack a conspicuous beige-yellow coloration of the outer half of the ventral hindwing, which is brown, paler towards the inner margin; and pale spots on the forewing are more weakly developed and more diffuse. Due to its cryptic nature and unexplored individual variation, this species is best identified by DNA, with diagnostic base pairs in the nuclear genome: aly1139.50.8:C189T, aly16.26.2:G40A, aly16.26.2:T51A, aly16.26.2:T135C, aly522.20.7:T120C; and the COI barcode: T10C, T13C, T145C, C235T, T499A.

Fig. 66. Phylogenetic trees of *Ge* de Nicéville, 1895 species and relatives constructed from protein-coding regions in: **a)** the nuclear genome (autosomes), based on 1,745,187 positions, and **b)** the mitochondrial genome. Different *Ge* are colored differently: *Ge geta* (blue) and *Ge pina* **sp. n.** (red). The sequence of SAMN18587889 is taken from the alignment provided in Kawahara et al. (2023). Ultrafast bootstrap (Hoang et al. 2018) values are shown at nodes.

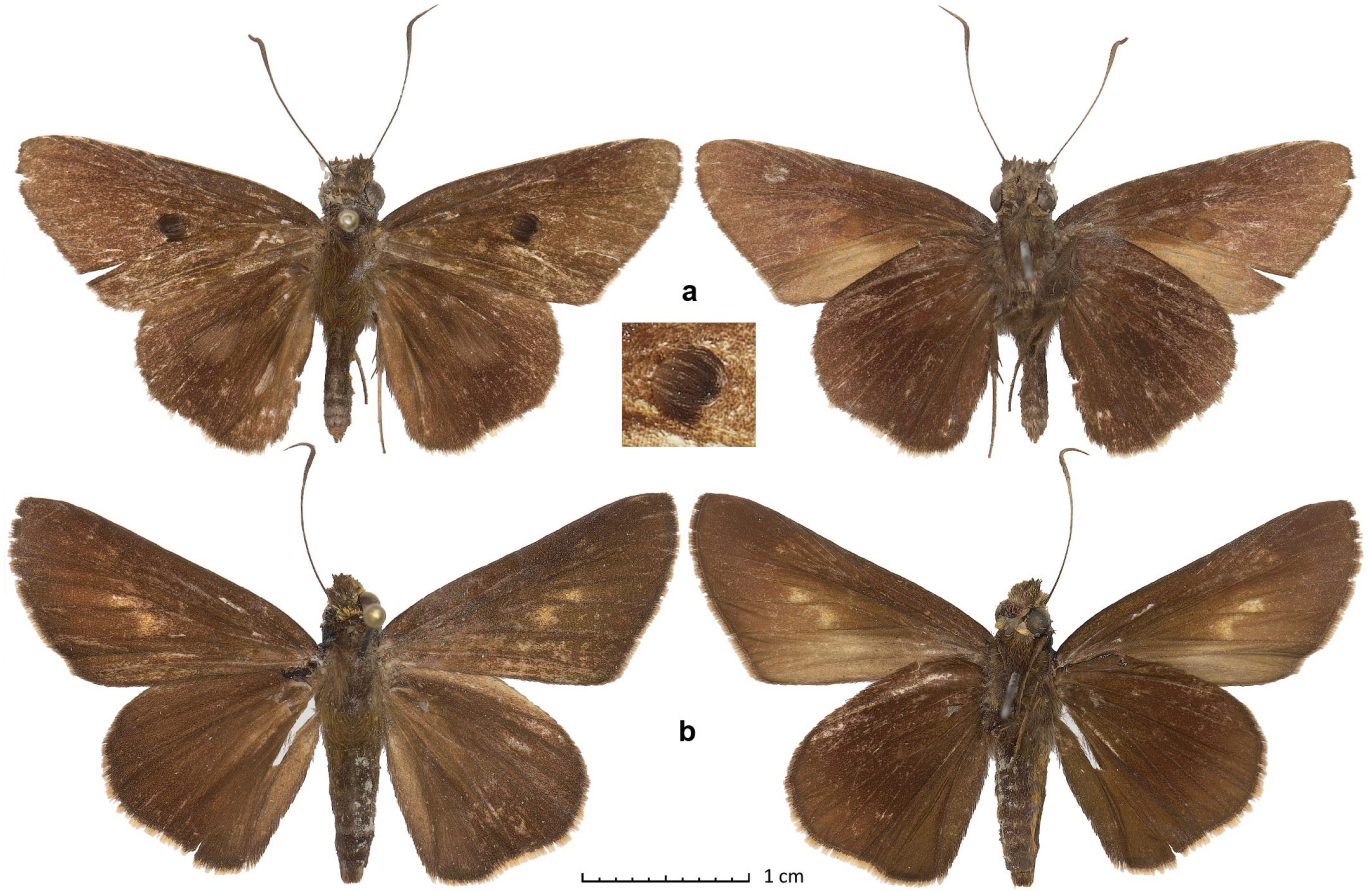

Fig. 67. *Ge pina* **sp. n.** type series in dorsal (left) and ventral (right) views, data in text: **a)** holotype ♂ NVG-24026F12, inset magnifies the right androconial patch, brightened for clarity, and **b)** paratype ♀ NVG-24026F11.

<u>Barcode sequence of the holotype.</u> Sample NVG-24026F12, 658 base pairs:

AACTTTATACTTCATTTTTGGAATTTGAGCTGGTATATTAGGTTCATCATTAAGTTTATTAATCCGAACTGAATTAGGTAACCCTGGATCTTTAATTGGAGATGATCAAATTTATAATACA
ATTGTTACCGCTCATGCTTTTATCATAATTTTTTTTATAGTTATGCCTATTATAATTGGAGGATTTGGAAATTGATTAGTACCCTTAATATTAGGAGCTCCTGATATAGCTTTTCCACGAT
TAAATAATATAAGATTTTGATTATTACCTCCTTCATTAACTTTATTAATCTCTAGAAGAATTGTAGAAAATGGTGCCGGAACTGGCTGAACTGTTTACCCCCCTCTTTCTTCTAATATTGC
TCATCAAGGTTCATCTGTTGATTTAGCAATTTTTTCTCTTCATTTAGCTGGAATTTCTTCTATTCTTGGAGCTATTAATTTTATTACAACAATTATCAATATACGAATTAGAAATTTATCT
TTTGATCAAATACCATTATTTATTTGATCAGTAGGAATTACAGCTTTATTACTACTTCTTTCCTTACCAGTTTTAGCTGGTGCTATTACTATACTTTTAACTGATCGAAATTTAAATACTT
CCTTTTTTGACCCAGCTGGAGGTGGTGATCCTATTTTATATCAACATTTATTT

Type material. Holotype: ♂ deposited in the Senckenberg Natural History Museum collection, Frankfurt, Germany (SMF), illustrated in Fig. 67a, bears the following six rectangular labels (1st and 3rd handwritten, others printed), five white: [PHIL. 6.IX.2005 | E. Mindanao | Surigao Sur | Mt DIWATA] and on the other side of this label [leg Noel], [Ge geta ♂], [SPECIAL], [Collection | C.G. Treadaway], [DNA sample ID: | NVG-24026F12 | c/o Nick V. Grishin], and one red [HOLOTYPE ♂ | Ge pina | Grishin]. **Paratype:** 1♀ NVG-24026F11 the same data as the holotype but 3-Sep-2006 (Fig. 67b). The type series was collected by Noel Mohagan ("leg Noel").

Type locality. Philippines: Mindanao, Surigao del Sur Province, Mount Diwata.

Etymology. The name is derived from the type locality in the [Philip]*pin*[es] + *a* and is treated as a noun in apposition.

Distribution. Currently known only from the type locality in eastern Mindanao Island, Philippines.

Tribe Baorini Doherty, 1886

Holotype of *Pamphila philino* Möschler, 1879

Pamphila philino Möschler, 1879, currently a junior subjective synonym of *Parnara guttatus guttatus* (Bremer & Grey, [1852]) (type locality in China: Beijing), was described from "a single ♂ from the Himalayas" ("Ein ♂ vom Hymalaja"), the holotype by monotypy (Möschler 1878). We found the holotype in the MFNB collection and sequenced its whole genome shotgun. This specimen (Fig. 68a), collected in 1877 according to its label, is originally from the Möschler collection, incorporated in the Staudinger scientific collection that is currently housed in MFNB, bears labels characteristic of the Möschler type specimens, and agrees with the original description in all details, leaving no doubt that it is the holotype. The COI barcode sequence of the holotype, sample NVG-18074G07, 658 base pairs is:

AACTTTATATTTTATTTTTGGTATTTGAGCAGGAATATTAGGAACATCTTTAAGACTTTTAATTCGTACGGAACTAGGAAATCCAGGTTCATTAATTGGAGATGATCAAATTTATAATACA
ATCGTAACAGCTCATGCTTTTATTATAATTTTTTTTATAGTTATACCTATTATAATTGGAGGATTTGGAAATTGATTAGTTCCATTAATATTAGGGGCCCCTGATATAGCTTTCCCACGTA
TAAACAATATAAGATTTTGAATGCTTCCCCCTTCTTTAACCTTATTAATCTCTAGAAGAATTGTAGAAAATGGTGCAGGAACTGGTTGAACAGTTTATCCCCCACTCTCATCTAATATTGC
CCATCAAGGTTCTTCTGTTGACTTAGCAATTTTTTCCCTTCATTTAGCAGGAATTTCTTCTATTTTAGGAGCTATTAATTTTATTACAACAATTATTAATATACGAATTAAAAATATAACA
TTTGATCAAATACCTTTATTTGTATGATCAGTGGGAATTACAGCTTTATTATTACTCTTATCATTGCCAGTATTAGCTGGTGCTATCACTATACTTCTTACAGATCGAAATCTTAATACTT
CATTTTTTGATCCTGCAGGAGGAGGTGATCCTATCCTATATCAACACTTATTT

Lectotype designation for *Hesperia kolantus* Plötz, 1885

Hesperia kolantus Plötz, 1885, currently a junior subjective synonym of *Parnara guttatus guttatus* (Bremer & Grey, [1852]) (type locality in China: Beijing), was described from an unstated number of specimens from India (Plötz 1885). We found a single syntype of *H. kolantus* in the ZSMC collection known to house Plötz's type material (Fig. 68b). The syntype agrees well with the original description, which we translate from German as: "Upperside dark brown, underside brownish gray, fringes gray. The forewings, as in *Guttatus* Brem., have eight transparent spots: two in the discal cell, three in cells 2, 3, and 4, and three elongated apical spots placed close together. The hindwings have three transparent spots and, beneath, an additional small white spot in cell 5. 18 mm — India" (Plötz 1885). The agreement even includes the small pale spot in cell M_1-M_2 (cell 5) on the ventral hindwing largely missing above. The discrepancies in the assessment of color are characteristic of Plötz's descriptions and may suggest that he was, at least partly, color-blind, or worked under poor lighting. The syntype is labeled as "Holotypus" (it is likely that the description was based on a single specimen, but we avoid the assumption of the holotype to follow the ICZN Code Recommendation 73F), and the label "Kolantus" is in Plötz's handwriting, further supporting the type status of this specimen. To stabilize nomenclature and define the name *H. kolantus* objectively, N.V.G. hereby designates the syntype in the ZSMC collection, a male that bears the following six labels (3rd purple, 5th red, others white; 2nd and 4th handwritten, others printed): [Brit. | Ost-Jndien], [Kolantus], [Original], [Parnara type | Kolantus Pl. O. Ind.], [Holotypus | | Zool. Staatssammlg. München], and [DNA sample ID: | NVG-22016H06 | c/o Nick V. Grishin], as the **lectotype** of *Hesperia kolantus* Plötz, 1885. The lectotype is missing both antennae, and its both hindwings are slightly chipped at the outer margin near the vein 1A+2A. The type locality of *H. kolantus* remains in India. The COI barcode sequence of the lectotype, sample NVG-22016H06, 658 base pairs is:

AACTTTATATTTTATTTTTGGTATTTGAGCAGGAATATTAGGAACATCTTTAAGACTTTTAATTCGTACGGAACTAGGAAATCCAGGTTCATTAATTGGAGATGATCAAATTTATAATACA
ATCGTAACAGCTCATGCTTTTATTATAATTTTTTTTATAGTTATACCTATTATAATTGGAGGATTTGGAAATTGATTAGTTCCATTAATATTAGGGGCCCCTGATATAGCTTTCCCACGTA
TAAACAATATAAGATTTTGAATGCTTCCCCCTTCTTTAACCTTATTAATCTCTAGAAGAATTGTAGAAAATGGTGCAGGAACTGGTTGAACAGTTTATCCCCCACTCTCATCTAATATTGC
CCATCAAGGTTCTTCTGTTGACTTAGCAATTTTTTCCCTTCATTTAGCAGGAATTTCTTCTATTTTAGGAGCTATTAATTTTATTACAACAATTATTAATATACGAATTAAAAATATAACA
TTTGATCAAATACCTTTATTTGTATGATCAGTGGGAATTACAGCTTTATTATTACTCTTATCATTGCCAGTATTAGCTGGTGCTATCACTATACTTCTTACAGATCGAAATCTTAATACTT
CATTTTTTGATCCTGCAGGAGGAGGTGATCCTATCCTATATCAACACTTATTT

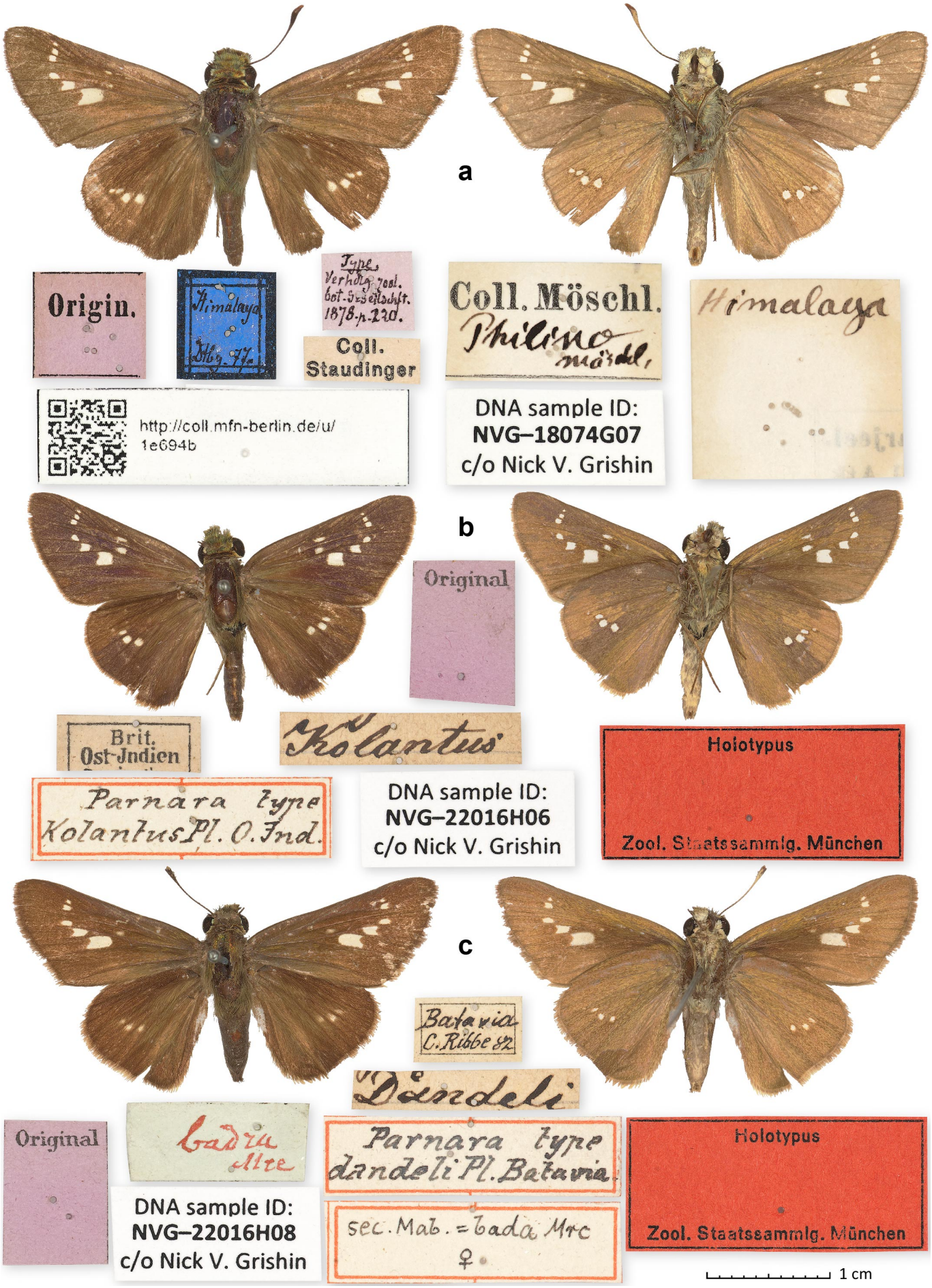
a
Origin.
Himalaya
Type
Verhdlg. zool.
bot. Gesellschft.
1878. p. 220.
Coll.
Staudinger
Coll. Möschl.
Philippo
Himalaya
http://coll.mfn-berlin.de/u/
1e694b
DNA sample ID:
NVG–18074G07
c/o Nick V. Grishin
b
Original
Brit.
Ost-Indien
Kolantus
Parnara type
Kolantus Pl. O. Ind.
DNA sample ID:
NVG–22016H06
c/o Nick V. Grishin
Holotypus
Zool. Staatssammlg. München
c
Batavia
C. Ribbe 92
Dandeli
Original
Gadra
Mre
Parnara type
dandeli Pl. Batavia
sec. Mab. = Gada Mre
♀
DNA sample ID:
NVG–22016H08
c/o Nick V. Grishin
Holotypus
Zool. Staatssammlg. München
1 cm

Fig. 68 (see the previous page). Sequenced primary type specimens of *Parnara* in dorsal (left) and ventral (right) views with their labels (below each specimen), all to scale, detailed data in text: **a)** *Pamphila philino* Möschler, 1879 holotype ♂ NVG-18074G07 Himalaya [MFNB]; established here as a junior subjective synonym of *Parnara mangala* (F. Moore, 1866), **stat. rev.**; **b)** *Hesperia kolantus* Plötz, 1885 lectotype (designated herein) ♂ NVG-22016H06 India [ZSMC]; established here as a junior subjective synonym of *P. mangala* **stat. rev.**; **c)** *Hesperia daendeli* Plötz, 1885 lectotype (designated herein) ♀ NVG-22016H08 Indonesia: Java, Jakarta [ZSMC]; established here as a valid species *Parnara daendeli* (Plötz, 1885), **stat. rest**.

Lectotype designation for *Hesperia daendeli* Plötz, 1885

Hesperia daendeli Plötz, 1885, currently a junior subjective synonym of *Parnara bada bada* (Moore, 1878) (type locality in Sri Lanka), was described from an unstated number of specimens from Jakarta (referred to by its old name Batavia), Java (Plötz 1885). We found a single syntype of *H. daendeli* in the ZSMC collection, known to house Plötz's type material (Fig. 68c). The syntype agrees well with the original description, which we translate from German as: "Dark brown, forewings with yellowish-white hyaline spots: a very small narrow one on the hind margin of the discal cell, three of decreasing size in an oblique row in cells 2, 3, and 4, and two spots placed one above the other in cells 6 and 7. The hindwings have, in a slightly curved row, three hyaline spots side by side in cells 2, 3, and 4, their fringes are gray, as are thorax and abdomen, while the palpi are more whitish. 18 mm — Batavia" (Plötz 1885). The agreement even includes the very small pale spot exactly in the posterior part of the forewing discal cell. Moreover, the syntype is similar in wing pattern to the illustration of *daendeli* in Seitz (1907–1924), which is likely a copy of the original Plötz's drawing of this taxon.

The syntype is labeled as "Holotypus" (it is likely that the description was based on a single specimen, but we avoid the assumption of the holotype to follow the ICZN Code Recommendation 73F), and the label "Dändeli" (spelled as *daendeli* in the publication) is in Plötz's handwriting, further supporting the type status of this specimen. To stabilize nomenclature and define the name *H. daendeli* objectively, N.V.G. hereby designates the syntype in the ZSMC collection, a female that bears the following eight labels (3rd pale greenish, 4th purple, 7th red, others white; 4th, 7th, and 8th handwritten, others printed): [Batavia | C.Ribbe 82], [Dändeli], [badra | Mre], [Original], [Parnara type | dandeli Pl.Batavia], [sec.Mab.=bada Mre | ♀], [Holotypus | | Zool. Staatssammlg. München], and [DNA sample ID: | NVG-22016H08 | c/o Nick V. Grishin], as the **lectotype** of *Hesperia daendeli* Plötz, 1885. The 2nd and 3rd labels are in C. Plötz's and in P. Mabille's handwriting, respectively. The lectotype is missing the right antenna, and its left hindwing is nicked at the outer margin near the vein 1A+2A. The type locality of *H. daendeli* remains as Indonesia: West Java, Jakarta. The COI barcode sequence of the lectotype, sample NVG-22016H08, 658 base pairs is:

AACTTTATACTTTATTTTTGGTATTTGATCAGGGATATTAGGAACATCATTAAGACTTTTAATTCGTACTGAATTAGGAAACCCAGGTTCATTAATTGGAGATGATCAAATTTACAATACA
ATTGTTACAGCTCATGCTTTTATTATAATTTTTTTTATAGTTATACCCATTATAATCGGAGGATTTGGAAATTGATTAGTTCCATTAATATTAGGAGCTCCTGATATAGCTTTTCCACGAA
TAAATAATATAAGATTTTGAATACTTCCCCCTTCTTTAACTTTATTAATTTCTAGAAGAATTGTAGAAAATGGTGCAGGAACTGGTTGAACAGTTTACCCACCCCTGTCATCTAACATTGC
TCATCAAGGTTCTTCTGTTGATTTAGCAATTTTTTCTCTTCATTTAGCTGGTATTTCTTCTATTTTAGGGGCTATCAATTTTATTACAACAATTATTAATATACGAATTAAAAATATATCA
TTTGATCAAATACCTTTATTTGTATGATCGGTAGGAATTACAGCTTTATTATTACTTTTATCATTACCAGTATTAGCTGGGGCTATTACAATACTCCTTACAGATCGTAATCTTAATACCT
CATTTTTCGATCCTGCTGGAGGAGGAGATCCTATTTTGTATCAACATTTATTT

Parnara mangala (F. Moore, 1866) is a valid species distinct from *Parnara guttatus* (Bremer & Grey, [1852])

Genomic analysis of *Parnara* F. Moore, 1881 (type species *Eudamus guttatus* Bremer & Grey, [1852]) reveals that specimens identified as *Parnara guttatus* (Bremer & Grey, [1852]) (type locality in China: Beijing) partition into two prominent clades genetically differentiated at the species level (Fig. 69); e.g., their COI barcodes differ by 3.2% (21 bp), and therefore the clades represent two distinct species. The first clade contains specimens from Korea, eastern China, and Vietnam, and we identify them as the nominotypical *P. guttatus* in agreement with Huang et al. (2019). The second clade corresponds to the species that, judging from the COI barcode sequences, Huang et al. (2019) identified as *Parnara batta* Evans, 1949 (type locality in China: Fujian Province, "Kuatuni", 2300 m, approximate GPS 27°40'N 117°40'E). However, *P. batta* cannot be a valid name for the species represented by this clade (assuming

the clade represents only one species), because the clade includes primary type specimens of two older names: *Pamphila philino* Möschler, 1879 (type locality in Himalaya, holotype sequenced as NVG-18074G07) and *Hesperia kolantus* Plötz, 1885 (type locality in eastern India, lectotype, designated herein, sequenced as NVG-22016H06). At the very least, *P. philino*, having priority over *P. batta*, may become a valid name for this species.

Evans (1949) treated both *P. philino* and *H. kolantus* as junior subjective synonyms of *Hesperia mangala* F. Moore, 1866 (type locality in "Bengal"). The latter taxon, placed by Evans (1949) as a subspecies of *P. guttatus*, was synonymized with it by Huang et al. (2019) based on phenotypic assessment of specimens from China (mostly southeastern), but none from India or the Bengal region (where the type locality of *H. mangala* is). Curiously, specimens from Kashmir and Nepal, which are in the general area of the type locality of *H. mangala*, were identified by Huang et al. (2019) as *P. batta*, despite the type locality of the latter taxon being in southeastern China. While we have not sequenced primary specimens of *H. mangala* and *P. batta*, our sequenced specimens from "N Bengal" and Myanmar were in the same clade with the primary types of *P. philino* and *H. kolantus* and were phenotypically similar to the specimen curated in the BMNH as the type of *H. mangala*. Hence, in agreement with Evans (1949), we consider that the names *P. philino*, *H. kolantus*, and *H. mangala* refer to the same species that according to Li et al. (2017) (called this species *P. mangala*), Huang et al. (2019) (called this species *P. batta*), and our genomic results, is distinct from *P. guttatus*. Therefore, we propose to treat *Parnara mangala* (F. Moore, 1866), **stat. rev.** as a valid species distinct from *Parnara guttatus* (Bremer & Grey, [1852]), in agreement with Li et al. (2017). Furthermore, we keep *Pamphila philino* Möschler, 1879 and

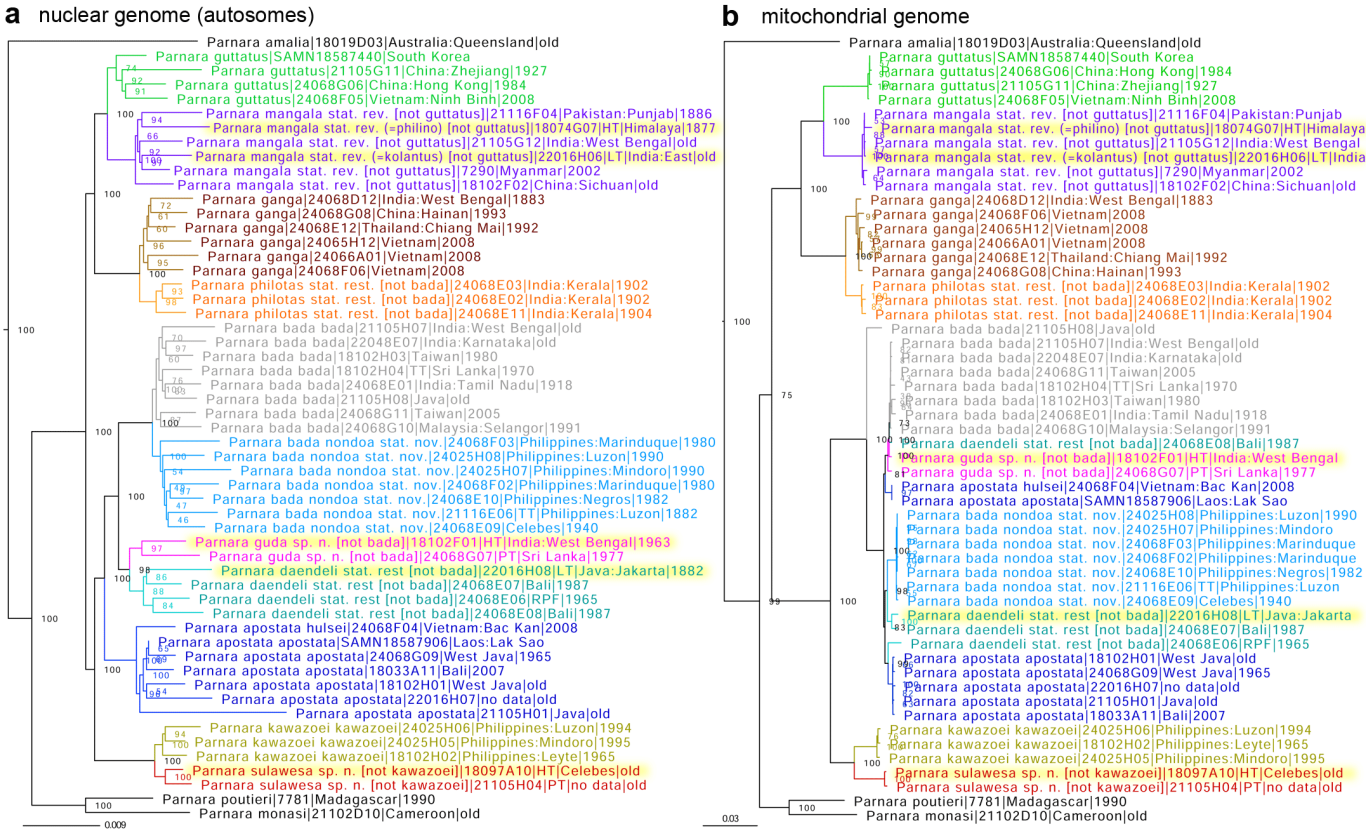

Fig. 69. Phylogenetic trees of selected *Parnara* species constructed from protein-coding regions in: **a)** the nuclear genome (autosomes), based on 607,791 positions, and **b)** the mitochondrial genome. Taxa discussed in the text are colored: *P. guttatus* (green), *P. mangala* **stat. rev.** (purple), *P. ganga* (brown), *P. philotas* **stat. rest.** (orange), *P. bada bada* (gray), *P. bada nondoa* **stat. nov.** (blue), *P. guda* **sp. n.** (magenta), *P. daendeli* (cyan), *P. apostata* (dark blue), *P. kawazoei* (olive), and *P. sulawesa* **sp. n.** (red). Primary type specimens discussed or designated in this work are highlighted in yellow. Sequences of SAMN18587440 and SAMN18587906 are taken from the alignment provided in Kawahara et al. (2023). Ultrafast bootstrap (Hoang et al. 2018) values are shown at nodes.

Fig. 70. Sequenced non-type specimens of *Parnara* in dorsal (above or left of each panel letter) and ventral (below or right of each letter) views, detailed data in text: **a–c)** *P. guttatus* (marked with black dots) and **d–g)** *P. mangala* **stat. rev.** (marked with ochre dots): **a)** ♀ NVG-24068F05 Vietnam: Ninh Binh Province; **b)** ♀ NVG-24068G06 China: Hong Kong (greased specimen); **c)** ♀ NVG-21105G11 China: Zhejiang Province; **d)** ♂ NVG-21116F04 Pakistan: Punjab Province; **e)** ♂ NVG-21105G12 India: West Bengal State; **f)** ♂ NVG-18102F02 China: Sichuan Province; **g)** ♀ NVG-7290 Myanmar: South Shan State.

Hesperia kolantus Plötz, 1885 as junior subjective synonyms of *P. mangala*, in agreement with Evans (1949).

We have not sequenced the holotype of *P. batta,* and the identity of this taxon remains unclear to us. However, we recommend following Chiba and Eliot (1991) in treating it as a junior subjective

synonym and, taking into account the work of Huang et al. (2019) and specimens from the Fujian Province, China, that they analyzed and identified as *P. batta*, tentatively propose that *Parnara guttatus batta* Evans, 1949, **syn. nov.** is a junior subjective synonym of *Parnara mangala* (F. Moore, 1866), **stat. rev**. Finally, and also tentatively, based on the original description and geographic proximity, we regard *Pamphila ormuzd* Grum-Grshimailo, 1888 (type locality in Tajikistan: Qubodiyon) as a subspecies of *P. mangala* and not of *P. guttatus*: *Parnara mangala ormuzd* (Grum-Grshimailo, 1888), **comb. nov**.

To aid further studies of these taxa, we illustrate all seven non-type specimens of this group we sequenced in this work (Fig. 70). Data for these specimens are: *P. guttatus* (three specimens): ♀ NVG-24068F05 Vietnam: Ninh Binh Province, Cuc Phuong N.P., nr. guest house, 140 m, GPS 20.2509, 105.7150, 8-Jun-2008, I. Nakamura leg. [MGCL] (Fig. 70a); ♀ NVG-24068G06, UF_FLMNH_MGCL_1048723 China: Hong Kong, Kowloon, 4 km N of Kowloon, 3-6-Oct-1984, J. B. Heppner leg. [MGCL] (Fig. 70b); and ♀ NVG-21105G11 China: Zhejiang Province, Jiaxing, 22-Sep-1927, KY. Zey, Holland collection [CMNH] (Fig. 70c); and *P. mangala* **stat. rev.** (four specimens): ♂ NVG-21116F04 Pakistan: Punjab Province, Murree Hill, approx. GPS 33.91, 73.39, 1886, Donckier leg., Weymer collection [MFNB] (Fig. 70d); ♂ NVG-21105G12 India: West Bengal State, Kalimpong, old [CMNH] (Fig. 70e); ♂ NVG-18102F02, USNMENT_01491878 China: Sichuan Province, Mount Emei, vic. Baoguo Temple, 4400', Aug-old, D. C. Graham [USNM] (Fig. 70f); and ♀ NVG-7290, USNMENT_01321138 Myanmar: South Shan State, Kalaw City, 29-May-2002, S. Kinyon leg., genitalia NVG161007-17 [USNM] (Fig. 70g). For the illustrations of primary type specimens of the names that are junior subjective synonyms of *P. mangala*, see Fig. 70a, b.

Parnara kuwanoi Seok, 1937 is a junior subjective synonym of *Pelopidas sinensis* (Mabille, 1877)

Parnara kuwanoi Seok, 1937 was described from a female holotype collected in Beijing, China (Seok 1937). This taxon largely escaped attention, was not mentioned in Evans (1949), and by default has been treated as a valid species of *Parnara* F. Moore, 1881 (type species *Eudamus guttatus* Bremer & Grey, [1852]), e.g., by Bridges (1994). While we have not sequenced the holotype, we inspected the photographs of its dorsal and ventral sides published with the original description by Seok (1937) as figs. 7 and 8, respectively, and available from the National Diet Library Digital Collections, Japan (NDL Digital Collections 2025), reproduced here in Fig. 71a. The photographs are consistent with the text of the description that compares *P. kuwanoi* with *Zinaida pellucida* (Murray, 1875) (type locality in Japan), *Pelopidas jansonis* (A. Butler, 1878) (type locality in Japan), and *Parnara guttatus* (Bremer & Grey, [1852]) (type locality in China: Beijing).

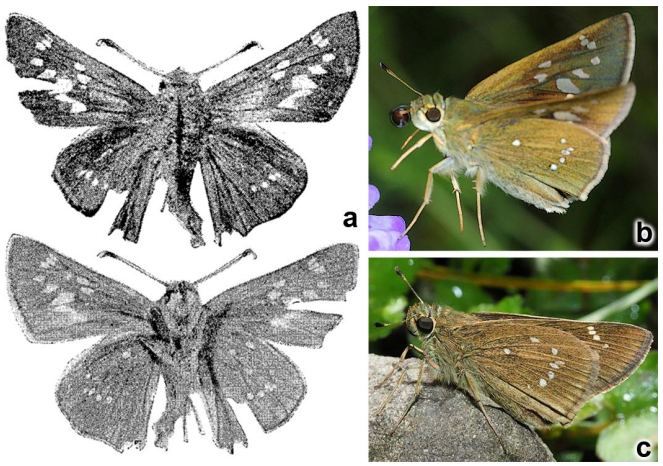

Fig. 71. *Pelopidas sinensis*: **a)** holotype of *Parnara kuwanoi* Seok, 1937 in dorsal (above) and ventral (below) views, reproduced from Seok (1937) downloaded from the National Diet Library Digital Collections, Japan (2025); and iNaturalist (2025) observations: **b)** 54612847 China: Beijing, GPS 40.6423, 117.4637, 11-Aug-2025 © Homemountain/Shan Gui; **c)** 111071218 Taiwan: Chiayi Co., GPS 23.4792, 120.8248, 10-Apr-2022 © Ray Tsai. Photographs were brightened, rotated, and cropped. CC BY-NC 4.0 https://creativecommons.org/licenses/by-nc/4.0/.

We agree with Seok (1937) that *P. kuwanoi* is unlikely to be any of these species. In *Z. pellucida*, hindwing pale spots have sharper edges, are somewhat elongated, and form a better-defined "3" (ventral left) due to the spots in cells M_1-M_2 and M_3-CuA_1 being strongly offset distad from the rest. In *P. kuwanoi*, these spots are more weakly expressed and form a straighter line. In *P. jansonis*, ventral hindwing pale spots in cells M_1-M_2 and M_2-M_3 are larger than others and typically merge into a single spot. In *P. kuwanoi*, these spots are approximately the same size as some others and are separated. In *P.*

guttatus, forewing semihyaline pale spots are typically smaller, and the pale spot in cell CuA_2-1A+2A is either absent or much smaller, and the anterior part of the ventral hindwing discal cell lacks a pale spot (in some specimens, there is a pale spot in the posterodistal part), however, if the forewing spots are larger, then the hindwing spots are larger as well. In *P. kuwanoi*, these forewing spots are prominent, especially the pale spot in cell CuA_2-1A+2A, but the hindwing spots are smaller, and there is a prominent spot in the anterior part of the ventral hindwing discal cell.

However, we find that the wing pattern of the *P. kuwanoi* holotype is consistent with that of *Pelopidas sinensis* (Mabille, 1877) (type locality in China: Shanghai) (Fig. 71b, c), although many individuals of the latter species have larger hindwing pale spots. Moreover, *P. sinensis* is the only known species that may closely resemble *P. kuwanoi*. As recorded on iNaturalist (2025), *P. sinensis* is still found in Beijing, with several individuals similar in facies to the female holotype (e.g., Fig. 71b). In addition to *Pelopidas sinensis* and *P. jansonis*, the only other congener currently recorded from Beijing is *Pelopidas mathias* (Fabricius, 1798) (type locality in India: Tharangambadi) (iNaturalist 2025), which has noticeably smaller semihyaline spots on the forewing. Therefore, due to wing pattern similarities combined with localities of these taxa, we propose that *Parnara kuwanoi* Seok, 1937, **syn. nov.** is a junior subjective synonym of *Pelopidas sinensis* (Mabille, 1877).

Parnara philotas (de Nicéville, 1895) is a valid species distinct from *Parnara bada bada* (Moore, 1878)

Genomic analysis reveals that specimens from southwestern India initially identified as *Parnara bada* (F. Moore, 1878) (type locality in Sri Lanka) are instead a close sister to *Parnara ganga* Evans, 1937 (type locality in India: Manipur) but are genetically differentiated from it at the species level (Fig. 69); e.g., their COI barcodes differ by 1.7% (11 bp), and therefore these specimens represent a distinct species. The facies of these specimens (Fig. 73a–c) agree with the original description of *Baoris* (*Parnara*) *philotas* de Nicéville, 1895 (type locality in India: Kerala, Thiruvananthapuram) and the original illustration (de Nicéville 1895: pl. Q, fig. 60), reproduced here as Fig. 73d. These similarities include two hyaline spots on each wing: a larger, squarish one in the forewing cell CuA_1-CuA_2, a smaller and roundish one in the forewing cell M_3-CuA_1, and two small, elongated spots on the hindwing. Therefore, we identify these specimens as *B.* (*P.*) *philotas*, which is currently regarded as a junior subjective synonym of *P. bada bada*, and propose that *Parnara philotas* (de Nicéville, 1895), **stat. rest.**, is a valid species distinct from *Parnara bada bada* (F. Moore, 1878). Barcode sequence of *P. philotas* (sample NVG-24068E02, 658 base pairs) is:

AACTTTATATTTTATTTTTGGTATTTGAGCAGGAATATTAGGAACATCTTTAAGACTTTTAATT
CGTACTGAATTAGGGAACCCAGGTTCACTAATTGGAGATGATCAAATTTACAATACAATTGTAA
CAGCTCATGCTTTTATTATAATTTTTTTTATAGTTATACCTATTATAATTGGAGGATTTGGAAA
TTGATTAGTTCCATTAATATTAGGAGCCCCTGATATAGCTTTCCCACGTATAAATAATATAAGA
TTTTGAATACTTCCCCCTTCTTTAACCTTATTAATTTCTAGAAGAATTGTGGAAAATGGTGCAG
GAACTGGTTGAACAGTTTATCCCCCACTTTCATCTAATATTGCCCATCAAGGTTCTTCTGTTGA
TTTAGCAATTTTTTCCCTTCATTTAGCAGGAATTTCCTCTATTCTAGGAGCTATTAATTTTATT
ACAACAATTATTAATATACGAATTAAAAATATAACATTTGATCAAATACCTTTATTTGTATGAT
CAGTAGGAATTACAGCTTTACTATTACTTTTATCATTACCAGTATTAGCAGGAGCTATTACTAT
ACTTCTCACAGATCGAAATCTTAATACTTCATTTTTTGACCCTGCAGGAGGAGGTGATCCTATT
TTATACCAACATTTATTT

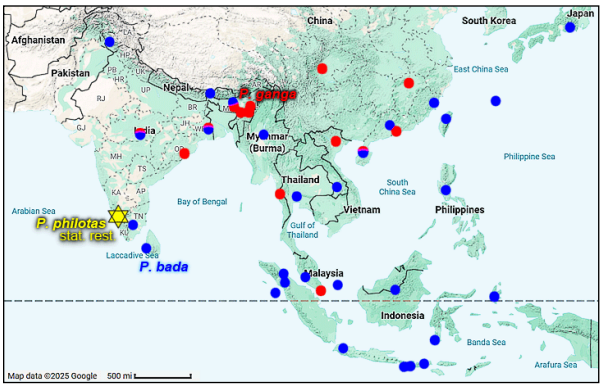

Fig. 72. A map of approximate localities of *Parnara ganga* (red) and *Parnara bada* (blue) as given by Evans (1949) showing his concept of these taxa. Identifications of these specimens were not checked. The localities are not precise and dots are placed approximately in the middle of each locality as we interpret it, e.g., 'C. India' corresponds to the two overlapping dots (red above blue) overlaying the word 'India' on the map, and the locality '"Japan"' (given in quotes by Evans, meaning that he believed the specimen was likely mislabeled) corresponds to the blue dot in Japan. The locality of sequenced specimens of *Parnara philotas* **stat. rest.** is marked with a yellow star. Species names are placed on the map near their type localities.

To aid further studies of the group, we show a map of localities for *P. ganga* and *P. bada* referenced by Evans (1949) and our *P. philotas* **stat. rest.** specimens (Fig. 72) and photographs of selected specimens we sequenced (Fig. 73). Data for these specimens are: *P. philotas* **stat. rest.** (three specimens) from India: Kerala, Brodie coll. [MGCL]: ♂ NVG-24068E02 Kozhikode

Fig. 73. Sequenced non-type specimens of *Parnara* in dorsal (above or left of each panel letter) and ventral (below or right of each letter) views, detailed data in text: **a–d)** *P. philotas* **stat. rest.** from India: Kerala (marked with black dots), **e–f)** *P. ganga* (marked with gray dots), and **g–k)** *P. bada* (marked with ochre dots): **a)** ♂ NVG-24068E02; **b)** ♂ NVG-24068E11; **c)** ♀ NVG-24068E03; **d)** original illustration of *P. philotas* holotype ♂ (de Nicéville 1895); **e)** ♂ NVG-24068E12 Thailand: Chiang Mai; **f)** ♀ NVG-24068D12 India: West Bengal; **g)** topotype ♂ NVG-18102H04 Sri Lanka; **h)** ♀ NVG-22048E07 India: Karnataka; **i)** ♂ NVG-24068E01 India: Tamil Nadu; **j)** ♀ NVG-21105H07 India: West Bengal; **k)** ♀ NVG-24068G10 Malaysia: Selangor.

("Calicut"), 31-Jul-1902, (Fig. 73a); ♂ NVG-24068E11 Tirur, 19-Jun-1904 (Fig. 73b); and ♀ NVG-24068E03 Kozhikode ("Calicut"), 25-Jul-1902, [MGCL] (Fig. 73c); *P. ganga* (two specimens): ♂ NVG-24068E12, UF_FLMNH_MGCL_1048811 Thailand: Chiang Mai, 2500-3000 m, 16-Nov-1992, D. Thomas [MGCL] (Fig. 73e) and ♀ NVG-24068D12 India: West Bengal, Kolkata, Mangal Pandey ("Barrackpore") Park, May-1883, G. A. J. Rothney pres. [MGCL] (Fig. 73f); *P. bada bada* (five specimens): topotype ♂ NVG-18102H04, USNMENT_01491904 Sri Lanka: Kandy District, Kandy, Peak View Motel, 1800', 15-24-Jan-1970, Davis & Rowe leg. [USNM] (Fig. 73g); ♀ NVG-22048E07 India: Karnataka, Uttara Kannada ("N. Kanara"), T. R. Bell [CUIC] (Fig. 73h); ♂ NVG-24068E01 India: Tamil Nadu, Chennai ("Madras City") residential quarter, Nungambakkam, seal level, 17-Dec-1918, Colonel C. Donovan leg. [MGCL] (Fig. 73i); ♀ NVG-21105H07 India: West Bengal, Kalimpong, old [CMNH] (Fig. 73j); and ♀ NVG-24068G10 Malaysia: Selangor, 24 km N of Kuala Lumpur, Taman Eko Rimba Kanching (Kanching Eco-Forest Park), 350', 27-May-1991, John J. Bowe leg. [MGCL] (Fig. 73k).

Parnara daendeli (Plötz, 1885) is a valid species distinct from *Parnara bada bada* (Moore, 1878)

Genomic analysis reveals that specimens we initially identified as *Parnara bada* (Moore, 1878) (type locality in Sri Lanka) partition into two clades (Fig. 69 gray with blue vs. cyan). The first clade (Fig. 69 gray with blue) includes specimens from across the range of *P. bada* including a topotypical specimen NVG-18102H04 and a specimen labeled from Java (NVG-21105H08). The second clade (Fig. 69 cyan) comprises specimens from Java and Bali and is genetically differentiated from the first clade at the species level based on the nuclear genome. Therefore, the two clades represent two distinct species that are possibly sympatric in Java. The first clade corresponds to *P. bada*, and the second clade contains the lectotype of *Hesperia daendeli* Plötz, 1885 (type locality Indonesia: West Java, Jakarta, lectotype designated above and sequenced as NVG-22016H08), which may be the oldest name associated with this clade. Therefore, we propose that *Parnara daendeli* (Plötz, 1885), **stat. rest.** is a valid species distinct from *Parnara bada bada* (Moore, 1878). We note that, in agreement with Huang et al. (2019), mitochondrial DNA does not differ strongly among species of this group and is prone to introgression (Fig. 69b).

Hesperia nondoa Plötz, 1886 is a valid subspecies of *Parnara bada* (Moore, 1878)

Hesperia nondoa Plötz, 1886 (type locality in Philippines: Luzon, Manila) is currently regarded as a junior subjective synonym of *Parnara bada bada* (Moore, 1878) (type locality in Sri Lanka). Genomic analysis reveals that specimens from the Philippines that we identified as *Parnara bada* (Fig. 69 blue) are in a clade separate from but closely related to the clade of *Parnara bada bada* (Fig. 69 gray). Genetic differentiation between the two clades is less than typical for distinct species, hence we consider that the clades represent two subspecies. Thus, we propose that *Parnara bada nondoa* (Plötz, 1886), **stat. nov.** is a valid subspecies, confirmed by DNA from several islands in the Philippines (Fig. 69 blue: Mindoro, Marinduque, and Negros). Furthermore, a specimen from Sulawesi is identified as *P. bada nondoa* by DNA (Fig. 69, NVG-24068E09).

Parnara guda Grishin, new species

https://zoobank.org/19105787-104B-45D7-9DAB-854928CA3317

(Figs. 69 part, 74a–b)

Definition and diagnosis. Genomic analysis reveals that specimens from northeastern India and Sri Lanka initially identified as *Parnara bada* (Moore, 1878) (type locality in Sri Lanka) are genetically differentiated from it at the species level in the nuclear genome (Fig. 69); e.g., the Z chromosome F_{st} is

0.57 comparing with *P. bada*, and F_{st} is the smallest (0.27) with the sister species *Parnara daendeli* (Plötz, 1885), **stat. rest.** (type locality Indonesia: West Java, Jakarta), and therefore these specimens represent a new species. Species in this group do not differ strongly from each other in COI barcodes. This new species keys to "*Parnara naso bada*" (M.2.3(a)) in Evans (1949), but differs from it and other relatives by males having a small round spot in the posterior part of the forewing discal cell, just basad of the large spot in cell M_3-CuA_1, and females are characterized by: a hyaline spot in the hindwing cell RS-M_1 being only slightly smaller than the spot in cell M_1-M_2; four prominent hyaline spots in a straight row on the hindwing between veins M_1 and CuA_2; a small pale spot near the vein 1A+2A at about 1/3 from the outer margin in cell CuA_2-1A+2A on both sides of the forewing; olive (yellower than in other species, not brownish) overtones of the ventral side with the ventral hindwing being entirely olive-colored (with hyaline spots); two prominent (size of the hindwing spots) hyaline subapical forewing spots; and a pale dot in cell R_2-R_3 on both sides of the forewing shifted distad from the row of hyaline spots. Due to its cryptic nature and unexplored individual variation, this species is best identified by DNA, with diagnostic base pairs in the nuclear genome: aly1139.65.8:C106A, aly1139.65.8:G120A, aly2532.4.8:C465T, aly2532.4.8:T471C, aly322.12.5:T543C; and the COI barcode does not distinguish this new species from several others, likely due to introgression.

Barcode sequence of the holotype. Sample NVG-18102F01, 658 base pairs:

AACTTTATACTTTATTTTTGGTATTTGATCAGGAATATTAGGAACATCATTAAGACTTTTAATTCGTACTGAATTAGGAAACCCAGGTTCATTAATTGGAGATGATCAAATTTACAATACA
ATTGTAACAGCTCATGCTTTTATTATAATTTTTTTTATAGTTATACCCATTATAATTGGAGGATTTGGAAATTGATTAGTTCCATTAATATTAGGAGCTCCTGATATAGCTTTCCCACGAA
TAAATAATATAAGATTTTGAATACTTCCCCCTTCTTTAACTTTATTAATTTCTAGAAGAATTGTAGAAAATGGTGCAGGAACTGGTTGAACAGTTTACCCACCCCTGTCATCTAACATTGC
TCATCAAGGTTCCTCTGTTGATTTAGCAATTTTTTCTCTTCATTTAGCTGGTATTTCTTCTATTTTAGGGGCTATCAATTTTATTACAACAATTATTAATATACGAATTAAAAATATATCA
TTTGATCAAATACCTTTATTTGTATGATCAGTAGGAATTACAGCTTTATTATTACTTTTATCATTACCAGTATTAGCTGGGGCTATTACAATACTCCTTACAGATCGTAATCTTAATACCT
CATTTTTTGATCCTGCTGGAGGAGGAGATCCTATTTTATATCAACATTTATTT

Type material. Holotype: ♀ deposited in the National Museum of Natural History, Smithsonian Institution, Washington, DC, USA (USNM), illustrated in Fig. 74b, bears the following seven rectangular labels (first four handwritten, others printed), six white: [HOOGLY | W. Bengal | 19. IX. 1963], [Adult of larva | feeding on leaf | of winter paddy], [CIBC-IS], [112], [DNA sample ID: | NVG-18102F01 | c/o Nick V. Grishin], [USNMENT | {QR Code} | 01491877], and one red [HOLOTYPE ♀ | Parnara guda | Grishin]. A pupal shell is pinned among the labels. **Paratype:** 1♂ NVG-24068G07 Sri Lanka: Western Province, Colombo, 26-Dec-1977, G. T. Austin leg. [MGCL] (Fig. 74a).

Type locality. India: West Bengal, Hooghly.

Etymology. The name is a wordplay of bad vs. good. If there is *P. bada*, there should be *P. guda*. The name is treated as a noun in apposition.

Distribution. Currently known from northeastern India and Sri Lanka.

Comment. For comparison, we illustrate selected sequenced specimens of taxa from this group. Data for these specimens are: *P. daendeli* **stat. rest.** from Indonesia (four specimens): ♂ NVG-24068E07 Bali, W. Sari, 6-Jan-1987, Joel Miller leg. [MGCL] (Fig. 74c); ♂ NVG-24068E08 Bali, Mar-1987, Joel Miller leg. [MGCL] (Fig. 74d); ♀ NVG-24068E06 "RPF" 12-Jan-1965, McCartney collection [MGCL] (Fig. 74e); and lectotype ♀ NVG-22016H08 West Java, Jakarta, 1882, C. Ribbe leg. [ZSMC] (Fig. 74f); *P. apostata apostata* from Indonesia (four specimens): ♂ NVG-18102H01, USNMENT_01491901 West Java, Sukabumi, old, Bryant & Palmer coll. [USNM] (Fig. 74g); ♂ NVG-24068G09 West Java, Djatiluhur, Purwakarta, Darangdan, 24-Oct-1965, B. Turlin leg. [MGCL] (Fig. 74h); ♂ NVG-21105H01 Java, old, Lindsay collection [CMNH] (Fig. 74i); and ♂ NVG-22016H07 no locality data (Fig. 75a); *P. apostata hulsei* ♀ NVG-24068F04 Vietnam: Bac Kan Province, E of Ba Be N. P., S of Don Den Peak, nr. Cang Lo, 758 m, GPS 22.3881, 105.6839, 20-Jun-2008, I. Nakamura leg. [MGCL] (Fig. 75b); *P. bada bada* (two specimens): ♂ NVG-21105H08 Indonesia: Java, old, Lindsay collection [CMNH] (Fig. 75c); ♀ NVG-18102H03, USNMENT_01491903 Taiwan: Tainan City, ~2–3 km S of Guanziling, ca. 350 m, 26–28-Jun-1980, D. R. Davis leg. [USNM] (Fig. 75d); *P. bada nondoa* **stat. nov.** (two specimens): ♂ NVG-24068E10 Philippines: Negros Is., Mt. Kanlaon, 1982, M. Simon leg., genitalia SRS-5501 [MGCL] (Fig. 75e) and ♀ NVG-24068F03, UF_FLMNH_MGCL_1048843 Philippines: Marinduque Is., vic. Boac, Jun–Jul 1980, ex R. Aronheim [MGCL] (Fig. 75f).

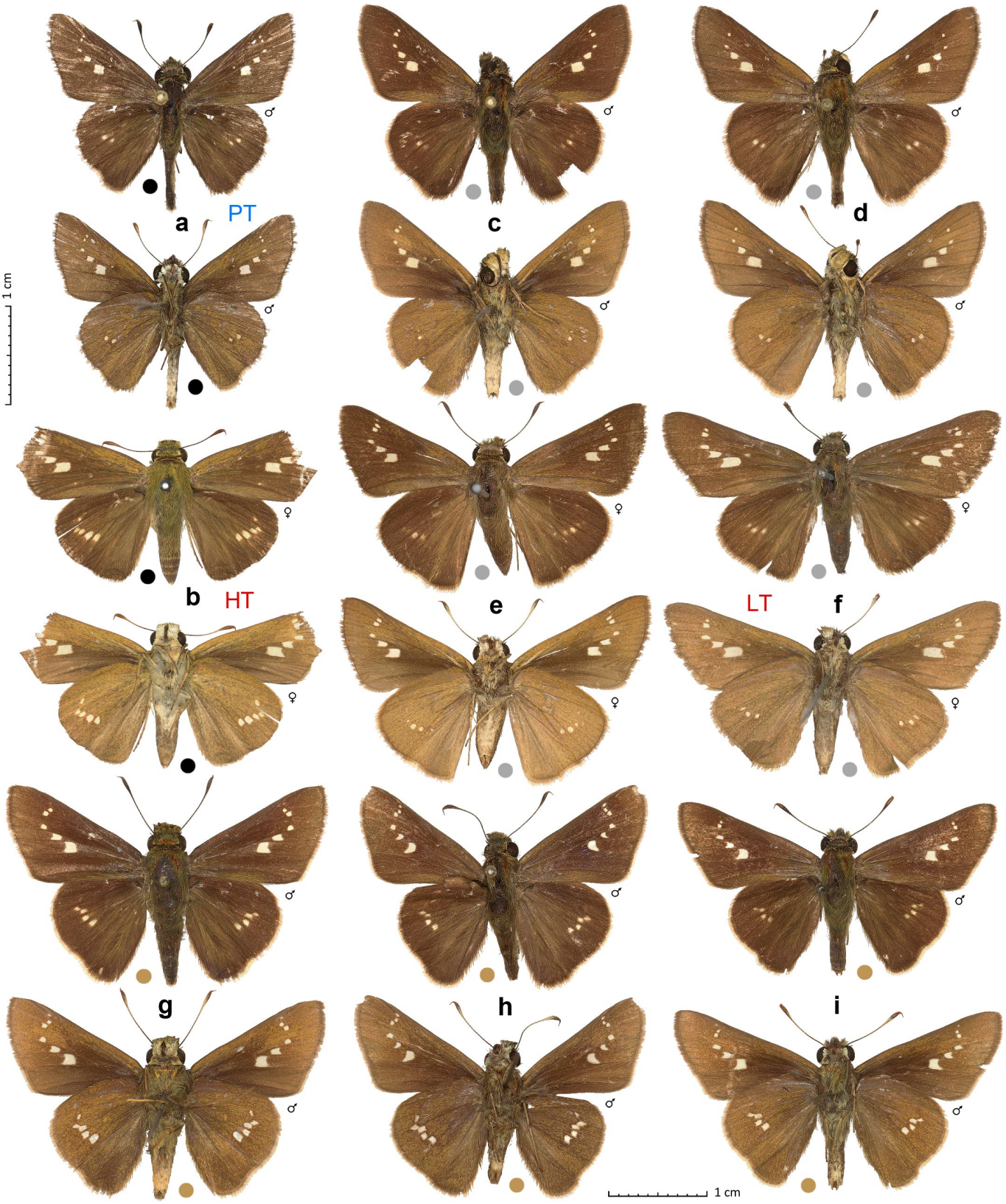

Fig. 74. Sequenced specimens of *Parnara* in dorsal (above each panel letter) and ventral (below each letter) views, detailed data in text: **a–b)** *P. guda* **sp. n.** (marked with black dots), **c–f)** *P. daendeli* **stat. rest.** from Indonesia (marked with gray dots), and **g–i)** *P. apostata* from Indonesia (marked with ochre dots): **a)** paratype ♂ NVG-24068G07 Sri Lanka: Western Province; **b)** holotype ♀ NVG-18102F01 India: West Bengal; **c)** ♂ NVG-24068E07 Bali; **d)** ♂ NVG-24068E08 Bali; **e)** ♀ NVG-24068E06 "RPF"; **f)** lectotype ♀ NVG-22016H08 West Java; **g)** ♂ NVG-18102H01 West Java; **h)** ♂ NVG-24068G09 West Java; **i)** ♂ NVG-21105H01 Java.

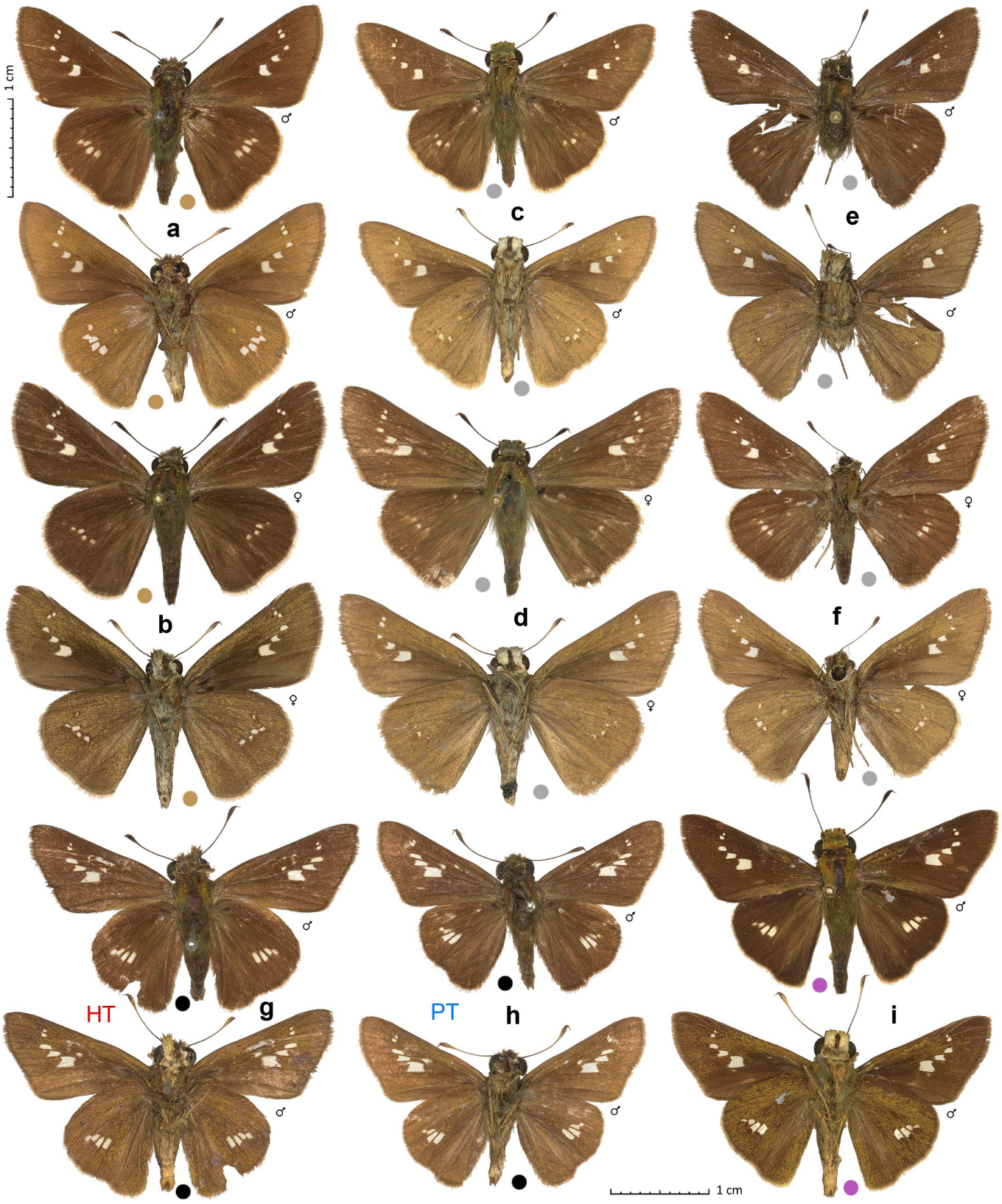

Fig. 75. Sequenced specimens of *Parnara* in dorsal (above each panel letter) and ventral (below each letter) views, detailed data in text: **a–b)** *P. apostata* (marked with ochre dots): **a)** *P. apostata apostata* and **b)** *P. apostata hulsei*, **c–f)** *P. bada* (marked with gray dots): **c–d)** *P. bada bada* and **e–f)** *P. bada nondoa* **stat. nov.**, **g–h)** *P. sulawesa* **sp. n.** (marked with black dots), and **i)** *P. kawazoei* (marked with purple dots): **a)** ♂ NVG-22016H07 no locality data; **b)** ♀ NVG-24068F04 Vietnam: Bac Kan; **c)** ♂ NVG-21105H08 Indonesia: Java; **d)** ♀ NVG-18102H03 Taiwan; **e)** ♂ NVG-24068E10 Philippines: Negros; **f)** ♀ NVG-24068F03 Philippines: Marinduque; **g)** holotype ♂ NVG-18097A10 Indonesia: South Sulawesi; **h)** paratype ♂ NVG-21105H04 no locality data; **i)** ♂ NVG-18102H02 Philippines: Leyte.

Parnara sulawesa Grishin, new species

https://zoobank.org/BB9303F5-15DB-46EA-B8B7-40D26D2C74A1

(Figs. 69 part, 75g–h)

Definition and diagnosis. Genomic analysis reveals that two specimens (from Sulawesi and without a locality label) initially identified as *Parnara kawazoei* Chiba & Eliot, 1991 (type locality in Philippines: Luzon) are genetically differentiated from it at the species level (Fig. 69); e.g., their COI barcodes differ by 2.9% (19 bp), and therefore these specimens represent a new species. This new species keys to *Parnara kawazoei* in Chiba and Eliot (1991), and was included in this species as paratypes by the original authors, but differs from it by males with longer and better developed hyaline spots on the hindwing, longer hyaline spots in forewing cells M_2-M_3 and M_3-CuA_1, and by having a small pale spot in the posterior part of the forewing discal cell. Due to its cryptic nature and unexplored individual variation, this species is best identified by DNA, with diagnostic base pairs in the nuclear genome: aly318.38.4:G117A, aly318.38. 4:T135C, aly1146.38.13:C79A, aly54.28.3:G1910C, aly54.28.3:G2000C; and the COI barcode: A181G, T287C, A508G, T533C, A553G, T589C.

Barcode sequence of the holotype. Sample NVG-18097A10, 658 base pairs:

AACTTTATACTTTATTTTTGGTATTTGATCAGGAATATTAGGAACATCATTAAGACTTTTAATTCGTACTGAATTAGGAAATCCAGGTTCATTAATTGGAGATGATCAAATTTATAATACA
ATTGTTACAGCTCATGCTTTTATTATAATAATTTTTTTTATAGTTATACCTATTATAATTGGGGGATTTGGAAATTGACTAGTTCCATTAATATTAGGGGCTCCTGATATAGCTTTCCCACGAA
TAAATAATATAAGATTTTGAATACTTCCCCCTTCTTTAACTTTACTAATTTCTAGAAGAATTGTAGAAAATGGTGCAGGAACTGGTTGAACAGTTTATCCACCCCTTTCATCTAATATTGC
TCATCAAGGTTCTTCTGTTGATTTAGCAATTTTTTCTCTTCACTTAGCTGGAATTTCTTCTATTTTAGGGGCTATTAATTTTATTACAACAATTATTAATATACGAATTAAAAATTTATCA
TTTGATCAAATACCTTTATTTGTGTGATCAGTAGGAATTACAGCTTTACTATTACTTTTATCATTGCCGGTATTAGCTGGAGCTATTACAATACTCCTTACAGACCGAAATCTTAATACCT
CATTTTTTGATCCTGCTGGAGGAGGGGATCCTATTTTATATCAACATTTATTT

Type material. Holotype: ♂ deposited in the Museum für Tierkunde collection, Dresden, Germany (MTD), illustrated in Fig. 75g, bears the following six rectangular labels (1st and 2nd handwritten, others printed), five white: [S.-W.-Celebes, IV | Bantimurung], [Parnara | guttatus | apostata], [Stauding.& Bang-Haas | Dresden, Ankauf 1961], [Staatl. Museum für | Tierkunde Dresden], [DNA sample ID: | NVG-18097A10 | c/o Nick V. Grishin], and one red [HOLOTYPE ♂ | Parnara sulawesa | Grishin]. **Paratypes:** 2♂♂ and 1♀: 1♂ NVG-21105H04 no data, old specimen [CMNH] (Fig. 75h) and Sulawesi, J. N. Eliot leg. [BMNH], not sampled for DNA; paratypes of *P. kawazoei*: 1♂ Makasser, 20-Mar-1937 and 1♀ Malino, 3000 ft, 8-Apr-1937.

Type locality. Indonesia: South Sulawesi, Bantimurung.

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

Distribution. Sulawesi.

Comment. For comparison, we illustrate a male of *P. kawazoei* NVG-18102H02, USNMENT_01491902 Philippines: Leyte Province, 5 km E of Ormoc, 200 m, 3–11-Oct-1965, D. R. Davis leg. [USNM] (Fig. 75i).

Tribe Hesperiini Latreille, 1809

Subtribe Hesperiina Latreille, 1809

Metron fas Grishin, nom. nov. is a new substitute name to replace *Metron fascia* Grishin, 2025

https://zoobank.org/2CAD78ED-C6AC-4968-B9E7-B0A40963514A

Metron fascia Grishin, 2025 (type locality in Costa Rica: Heredia) is a junior primary homonym of *Metron fascia* Draudt, 1923 (type locality in Colombia, Rio Aguacatal), currently a junior synonym of *Metrocles leucogaster leucogaster* Godman, 1900 (type locality in Panama: Chiriqui). Here, according to Article 60.3 of the International Code of Zoological Nomenclature (1999), *Metron fas* Grishin, **nom. nov.** is proposed as a new substitute name that replaces *Metron fascia* Grishin, 2025. The new name, treated as a noun in apposition, is a shortened version of *fascia*. According to the ICZN Code Article 72.7, the holotype of *M. fascia* is also the holotype of *M. fas*, and the type locality of *M. fas* is therefore Costa Rica: Heredia Province, 3.8 km west of Santa Clara.

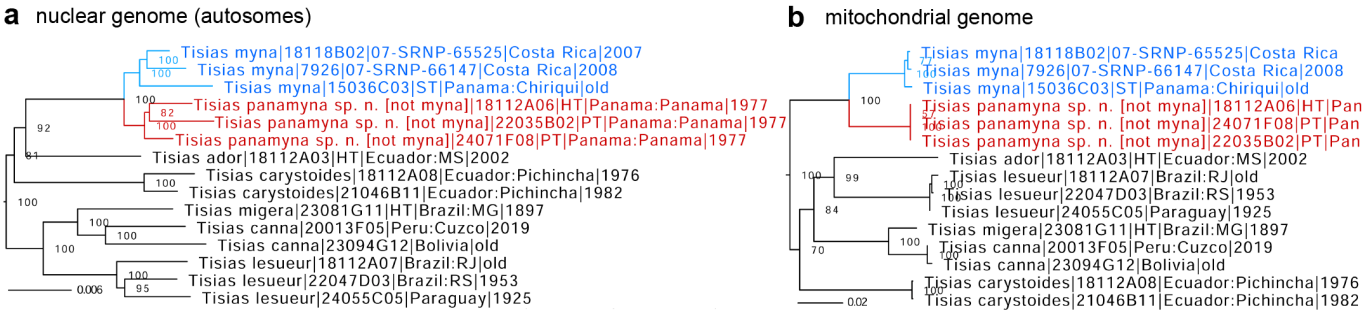

Fig. 76. Phylogenetic trees of selected *Tisias* species constructed from protein-coding regions in: **a)** the nuclear genome (autosomes), based on 2,399,367 positions, and **b)** the mitochondrial genome. Species mentioned in the text are colored: *T. myna* (blue) and *T. panamyna* **sp. n.** (red). Ultrafast bootstrap (Hoang et al. 2018) values are shown at nodes.

Fig. 77. *Tisias panamyna* **sp. n.** type series from Panama: Cerro Jefe in dorsal (left) and ventral (right) views, data in text: **a)** holotype ♂ NVG-18112A06, **b)** paratype ♂ NVG-22035B02, and **b)** paratype ♀ NVG-24071F08.

Tisias panamyna Grishin, new species

https://zoobank.org/133236CF-C532-401C-8E0D-D5988308958A

(Figs. 76 part, 77–78)

Definition and diagnosis. Genomic analysis reveals that a specimen from Panama identified as *Tisias myna* (Mabille, 1889) (type locality in Panama: Chiriquí, syntype sequenced as NVG-15036C03) is genetically differentiated from it at the species level (Fig. 76); e.g., their COI barcodes differ by 4.3% (28 bp), and therefore this specimen represents a new species. This new species keys to *T. myna* (K.20.3) in Evans (1955), but differs from it and other relatives by the following combination of characters: males with a more strongly divided semihyaline spot in the forewing discal cell, smaller hindwing semihyaline spots, and wide segments of the brand with the two anterior ones being joined in a horseshoe-like fashion; and females with more strongly developed cream-colored scaling around the semihyaline spot in the ventral forewing cell CuA_2-1A+2A. The male genitalia have a terminally rounded harpe bearing a broad dorsal tooth ending at a right angle, knob-shaped ampulla and a convex sclerotized costa, blade-shaped uncus arms that are narrow in dorsal view, and at least two cornuti are saw-like. Due to its cryptic nature and unexplored individual variation, this species is best identified by DNA, with diagnostic base pairs in the nuclear genome: aly770.27.4:G198A, aly276634.2.2:C72T, aly276634.2.2:T73C, aly6370.7.5:A33G, aly6370.7.5:G72A; and the COI barcode: T232C, C282T, T376A, T457C, A628G.

Barcode sequence of the holotype. Sample NVG-18112A06, 658 base pairs:

AACTTTATATTTTATTTTTGGTATTTGAGCAGGAATATTAGGAACTTCTTTAAGTTTATTAATTCGAACAGAATTAGGAAATCCAGGATCTTTAATTGGAGATGATCAAATTTATAATACT
ATTGTCACAGCTCATGCTTTTATTATAATTTTTTTTATAGTTATACCTATTATAATTGGAGGATTTGGAAACTGATTAGTTCCATTAATATTAGGAGCCCCAGATATAGCCTTCCCTCGAA
TAAATAATATAAGATTTTGAATATTACCCCCTTCTTTAATATTATTAATTTCAAGAAGAATCGTAGAAAATGGTGCTGGAACTGGTTGAACAGTTTATCCACCTTTATCTTCTAATATTGC
TCATCAAGGATCATCTGTTGATTTAGCAATTTTCTCCCTTCATTTAGCTGGTATTTCATCTATTCTAGGAGCTATTAATTTTATTACAACAATCATTAATATACGAATTAAAAATTTATCA
TTTGATCAAATACCTTTATTTGTTTGATCTGTAGGTATTACAGCATTATTATTACTTTTATCTTTACCTGTATTAGCTGGAGCTATTACAATATTACTTACCGATCGAAATTTAAATACTT
CATTCTTTGACCCAGCAGGAGGGGGAGATCCAATTCTATATCAACATTTATTT

Type material. Holotype: ♂ deposited in the National Museum of Natural History, Smithsonian Institution, Washington, DC, USA (USNM), illustrated in Fig. 77a (genitalia in Fig. 78), bears the following six printed rectangular labels (text in italics handwritten), five white: [PANAMA: PANAMA | *Cerro Jefe ca. 900 m.* | *III-11-*.1977 | G. B. Small], [DNA sample ID: | NVG-18112A06 | c/o Nick V. Grishin], [DNA sample ID: | NVG-23121D04 | c/o Nick V. Grishin], [genitalia | NVG251025-06 | c/o Nick V. Grishin], [USNMENT | {QR Code} | 01531353], and one red [HOLOTYPE ♂ | Tisias panamyna | Grishin]. **Paratypes:** 1♂ and 1♀ with the same data as the holotype except collected on 15-Apr-1977 and as indicated: 1♂ NVG-22035B02 800 m, GPS 9.2333, −79.3667 (Fig. 77b) and 1♀ NVG-24071F08 genitalia vial SRS-5476 [MGCL] (Fig. 77c).

Fig. 78. Male genitalia of *Tisias panamyna* **sp. n.** holotype NVG-18112A06 in left lateral (above), and dorsal (below) views.

Type locality. Panama: Panamá Province, Cerro Jefe, elevation ca. 900 m.

Etymology. The name for this sister species of *T. myna* is a fusion: *Pana*[manian] + *myna*, and is treated as a noun in apposition.

Distribution. Currently known only from the type locality in central Panama.

Xeniades (*Tixe*) *lora* Grishin, new species

https://zoobank.org/2169CFB0-F231-4C83-AECA-1CF014878651

(Figs. 79 part, 80a)

Definition and diagnosis. Genomic analysis reveals that a male from northern Peru initially identified as *Xeniades* (*Tixe*) *quadrata* (Herrich-Schäffer, 1869) (type locality not specified, likely in South or Southeast Brazil as deduced by genomic analysis of a syntype sequenced as NVG-15036C04) is genetically differentiated from it at the species level (Fig. 79); e.g., their COI barcodes differ by 2.6% (17 bp), and therefore this male represents a new species. This new species keys to "*Tisias quadrata quadrata*" (K.20.1(b)) in Evans (1955), but differs from it and other relatives by the following combination of characters in males: no apical hyaline spots similarly to *T. quadrata* (Fig. 80b, c), thus differing from *Xeniades* (*Tixe*) *hermoda* (Hewitson, 1870) (type locality in Ecuador: Pastaza, Canelos), and no darker ventral forewing subapical spots of *T. quadrata* either; the distal part of the ventral hindwing is only slightly paler than the basal half (stronger contrast between the halves in males of *T. quadrata*); slightly smaller postdiscal semihyaline spots on the hindwing; the semihyaline spot in the forewing cell CuA_1-CuA_2 is smaller, narrower, and crescent-shaped, with the branches of the brand posterior of the vein CuA_1 and anterior of the vein CuA_2 reaching distad of the spot and ending closer to the outer margin; branches of the brand are generally slightly wider and longer than in *T. quadrata*. Due to its cryptic nature and unexplored individual variation, this species is best identified by DNA, with diagnostic base pairs in the nuclear genome: aly671.48.2:T225C, aly671.48.2:T264C, aly798.33.86:C120T, aly4645.7.1:G321A, aly5196.5.4:A165G, aly390.36.1:A96A (not C), aly528.35.5:C30C (not T), aly2582.33.4:C2655C (not T), aly481.19.3:G72G (not A), aly12063.21.6:G504G (not A); and the COI barcode: A70C, T112C, T172C, T385C, T508T.

Barcode sequence of the holotype. Sample NVG-24071F05, 658 base pairs:

AACTTTATATTTTATTTTTGGAATTTGAGCAGGAATATTAGGAACTTCTTTAAGATTATTAATTCGTACCGAATTAGGTAACCCTGGATCTTTAATTGGAGACGATCAAATCTATAACACT
ATTGTAACAGCTCATGCTTTTATTATAATTTTTTTTATAGTTATACCTATCATAATTGGAGGATTTGGAAATTGACTAGTTCCTTTAATATTAGGAGCTCCTGATATAGCTTTCCCACGAA
TAAACAATATAAGATTTTGAATACTACCTCCCTCATTAACTCTATTAATTTCAAGAAGTATTGTTGAAAATGGTGCAGGAACTGGATGAACAGTATACCCACCTTTATCTTCTAATATCGC
TCATCAAGGATCTTCTGTTGACTTAGCTATTTTTTCACTTCATTTAGCTGGTATTTCTTCTATTTTAGGAGCTATTAATTTTATTACAACAATTATTAATATACGAATTAAAAATTTATCA
TTTGATCAAATACCTTTATTTGTTTGATCTGTAGGTATTACTGCATTATTATTACTTTTATCTTTACCTGTTTTAGCAGGAGCTATTACTATACTTCTTACAGATCGAAATTTAAATACTT
CTTTTTTCGATCCAGCTGGAGGAGGAGATCCTATTTTATATCAACACTTATTT

Type material. Holotype: ♂ currently deposited in the McGuire Center for Lepidoptera and Biodiversity collection, Gainesville, FL, USA (MGCL), illustrated in Fig. 80a, bears the following four printed rectangular labels (text in italics handwritten), three white: [PERU: DEPT. OF LORETO, | EXPLORAMA LODGE, | 65 MI. E. OF IQUITOS | ON AMAZON RIVER | *14 MAR 84* | LINWOOD C. DOW], [FSCA | Florida

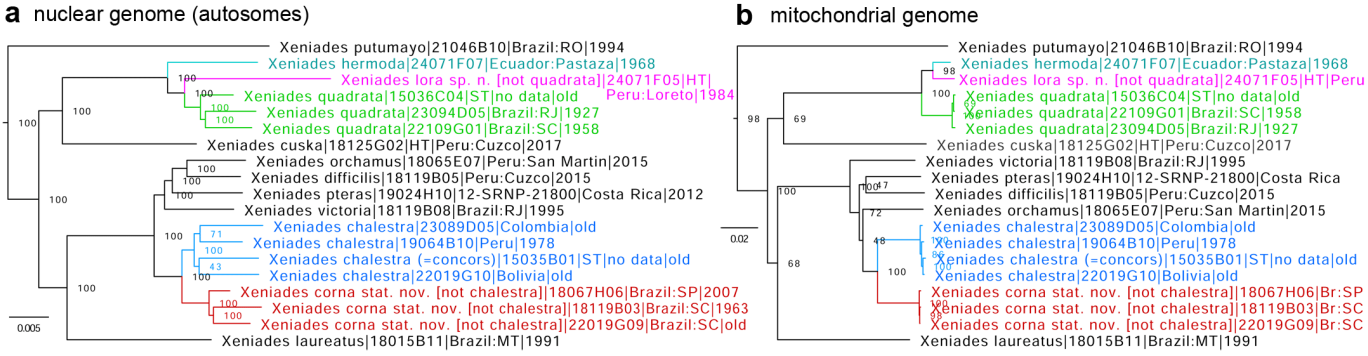

Fig. 79. Phylogenetic trees of selected *Xeniades* species constructed from protein-coding regions in: **a)** the nuclear genome (autosomes), based on 5,533,281 positions, and **b)** the mitochondrial genome. Species mentioned in the text are colored: *X. hermoda* (cyan), *X. lora* **sp. n.** (magenta), *X. chalestra* (blue), and *X. corna* **stat. nov.** (red). Ultrafast bootstrap (Hoang et al. 2018) values are shown at nodes.

Fig. 80. Males of *Xeniades* (*Tixe*) in dorsal (left or above) and ventral (right or below) views, data in text or below: **a)** *X.* (*T.*) *lora* **sp. n.** holotype NVG-24071F05 from Peru: Loreto and *X.* (*T.*) *quadrata* from Brazil: **b)** NVG-23094D05 Rio de Janeiro, vic. Itatiaia National Park, Jan-1927, R. Spitz leg. [ZfBS] and **c)** NVG-24071F06 Espirito Santo, Sta. Teresa, 900 m, 22-Mar-1971, C. Callaghan leg. [MGCL].

State Collection | of Arthropods], [DNA sample ID: | NVG-24071F05 | c/o Nick V. Grishin], and one red [HOLOTYPE ♂ | Xeniades (Tixe) | lora Grishin].

Type locality. Peru: Loreto Region, 65 mi east of Iquitos, Amazon River, Explorama Lodge.

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

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

Xeniades (*Xeniades*) *corna* Evans, 1955 is a species distinct from *Xeniades* (*Xeniades*) *chalestra* (Hewitson, 1866)

Genomic analysis reveals that *Xeniades chalestra corna* Evans, 1955 (type locality in Brazil: São Paulo) originally proposed and currently regarded as a subspecies of *Xeniades* (*Xeniades*) *chalestra* (Hewitson, 1866) (type locality in Brazil: Minas Gerais) is genetically differentiated from it at the species level (Fig. 79), e.g., their COI barcodes differ by 2.3% (15 bp). Therefore, we propose that *Xeniades corna* Evans,

1955, **stat. nov.** is a species distinct from *Xeniades* (*Xeniades*) *chalestra* (Hewitson, 1866). In wing patterns, *X. corna* differs from *X. chalestra* by having larger forewing semihyaline spots, e.g., the spot in cell CuA_1-CuA_2 fully overlaps the discal cell spot, and the proximal edges of these spots are in line (Evans 1955).

Female of *Oligoria* (*Cobaloides*) *unica* (de Jong, 1983)

Here, we illustrate the first known female of *Oligoria* (*Cobaloides*) *unica* (de Jong, 1983) (type locality in Suriname), NVG-23119C02, Hermier n° 3443 from French Guiana: Saül, 11-Jun-1992, L. Senecaux & A. Docquin leg., ex coll. Hermier, genitalia X-3671 J. M. Burns 1993 [USNM] (Fig. 81), confirmed by genomic comparison that included the holotype (Fig. 82). Comparing with the male holotype, the female has smaller semihyaline spots on the hindwing (but a larger doublet of spots in the forewing discal cell) and less developed ochreous scaling on the dorsal side in the basal part of wings, thus hindering its identification. The anterior part of its left forewing appears to be discolored.

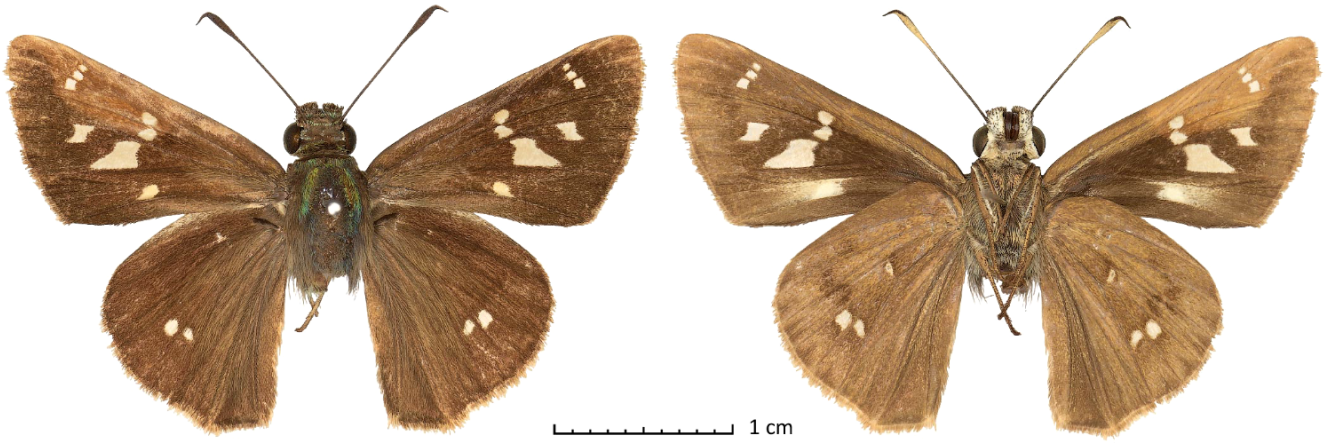

Fig. 81. *Oligoria* (*Cobaloides*) *unica* ♀ NVG-23119C02 from French Guiana in dorsal (left) and ventral (right) views.

Lectotype designation for *Celaenorhinus* [sic] *lucifer* Hübner, [1829]

Celaenorhinus [sic] *lucifer* Hübner, [1829], currently a valid species in the nominotypical subgenus of the genus *Oligoria* Scudder, 1872 (type species *Hesperia maculata* W. H. Edwards, 1865), was described from an unstated number of specimens from Suriname, one (or two) of which was (were) illustrated in figs. 579, 580, and a male explicitly mentioned (Hübner [1827]–[1829]). However, the illustrations depict female specimen(s) judging from the wing shape. The entire description is brief, and we (literally) translate it from German as: "As far as Cramer's illustration can be discerned, his Sergestus resembles the present butterfly on the upperside very much; however, of the underside of the species in question, Cramer has given no figure. In the male specimen communicated to me by Mr. Grimm, a corner spot [or angular spot?] on the underside of the wings is furthermore to be noted. – Homeland: Suriname." (Hübner [1827]–[1829]).

We located and sequenced a single syntype of *C. lucifer*, a female from the MFNB collection (NVG-18113B06, currently on loan in USNM) labeled as "Origin" (typical of most types originating from the Staudinger collection) and "lucifer HZ 579" likely written by Herrich-Schäffer, with "HZ" for "Hübner Zuträge" as a reference to the original description, and "579" refers to the figure number of the dorsal illustration of *C. lucifer* in Hübner ([1827]–[1829]). The syntype agrees with the original description, in particular, the "corner spot" likely refers to a prominent pale area near the tornus of the ventral forewing (Fig. 83a right). It is a conspicuous feature of this specimen (and this species) shaped as an acute isosceles triangle with a diffuse side towards the outer wing margin. Furthermore, although the syntype lacks a locality label, genomic sequencing places it among specimens from Suriname and French Guiana (Fig. 82) in agreement with the original description.

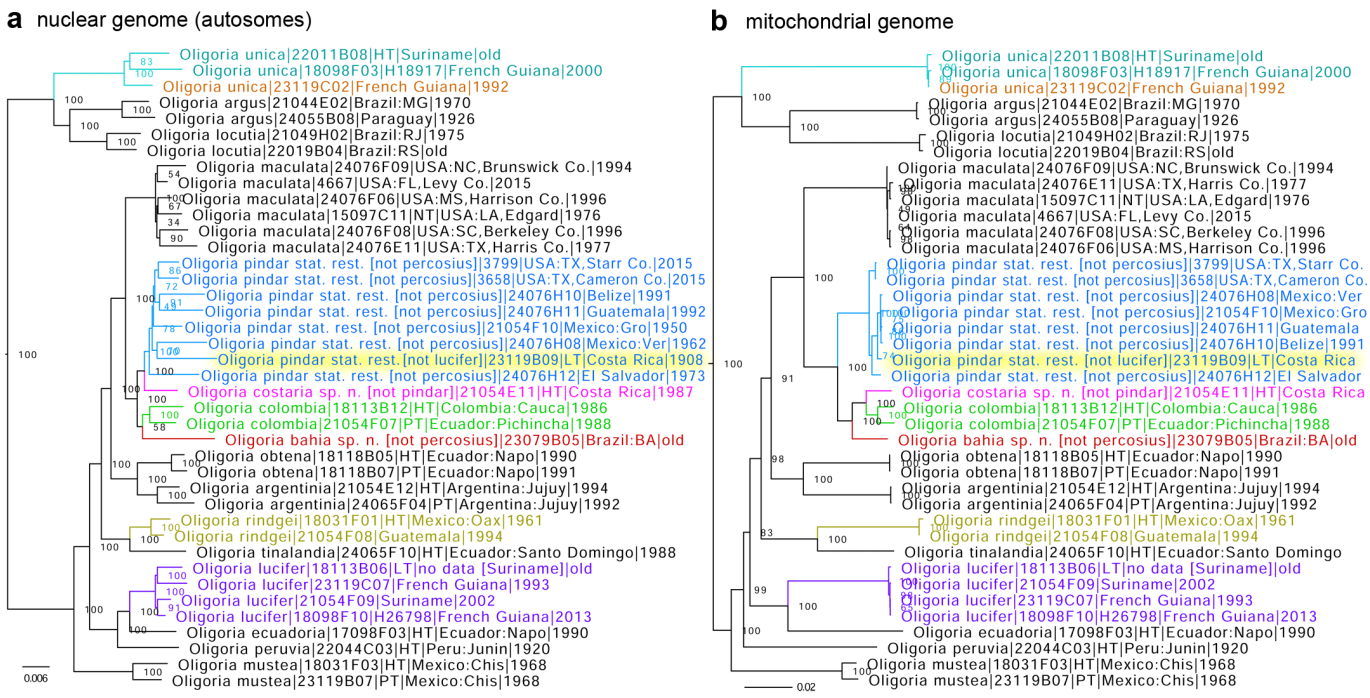

Fig. 82. Phylogenetic trees of *Oligoria* species constructed from protein-coding regions in: **a)** the nuclear genome (autosomes), based on 886,728 positions, and **b)** the mitochondrial genome. Species mentioned in the text are colored: *O.* (*Cobaloides*) *unica* (cyan, with the female specimen labeled in orange), *O.* (*Oligoria*) *pindar* **stat. rest.** (blue, the lectotype highlighted in yellow), *O.* (*Oligoria*) *costaria* **sp. n.** (magenta), *O.* (*Oligoria*) *colombia* (green), *O.* (*Oligoria*) *bahia* **sp. n.** (red), *O.* (*Oligoria*) *rindgei* (olive, *O.* (*Oligoria*) *percosius* is expected to be closely related to or conspecific with this species), and *O.* (*Oligoria*) *lucifer* (purple). Ultrafast bootstrap (Hoang et al. 2018) values are shown at nodes.

The syntype resembles Hübner's original illustrations (figs. 579, 580) in wing shape and spotting, but the illustration shows larger hyaline spots, in particular, on the hindwing that has three additional spots in the anterior part. The depicted pattern of five hyaline spots on the hindwing is not observed among documented Hesperiidae: the costal-most spot is typically offset basad from the band (not distad as in the drawing). The distal position of the costal-most spot is known in some *Metrocles* Godman, 1900 (type species *Metrocles leucogaster* Godman, 1900) species, but these species have a complete and rather straight band of spots which are not hyaline and present on the ventral side only. However, the left hindwing of the *C. lucifer* syntype has spot-like damage in the postdiscal area that forms a pattern similar to Hübner's illustration: in addition to two pale posterior spots, there are three anterior "spots" (i.e., damage) with the middle "spot" offset basad as in Hübner's figures. It is possible that this pattern, which is a combination of damage with real spotting, was illustrated.

Finally, we note that the holotype of another species shown on the same plate with *C. lucifer* and described directly after it, i.e., *Celaenorhinus* [sic!] *phaeomelas* Hübner, [1829] (type locality in Brazil), currently in the subgenus *Methionopsis* Godman, 1901 (type species *Methionopsis modestus* Godman, 1901) of the genus *Mnasinous* Godman, 1900 (type species *Mnasinous patage* Godman, 1900), is also extant, and is in the MFNB collection as well, discussed and illustrated in Zhang et al. (2022c). For all these reasons, we conclude that the specimen NVG-18113B06 is indeed a syntype of *C. lucifer*.

To define the taxonomic identity of the name *C. lucifer* objectively, N.V.G. hereby designates this syntype from the MFNB collection, a female illustrated in Fig. 83a, with the following seven rectangular labels (1st purple, others white; 2nd and 3rd handwritten, others printed): [Origin], [lucifer HZ 579], [Lucifer | Hb.], [Coll. H.–Sch.], [Coll. | Staudinger], [Zool. Mus. | Berlin], and [DNA sample ID: | NVG-18113B06 | c/o Nick V. Grishin] as the **lectotype** of *Celaenorhinus* [sic] *lucifer* Hübner, [1829]. The lectotype is missing the abdomen, both antennae, and the right hindwing tornus, has tears near the base of both hindwings (left also from the outer margin near tornus). The type locality of *C. lucifer* remains in Suriname. The COI barcode sequence of the lectotype, sample NVG-18113B06, 658 base pairs

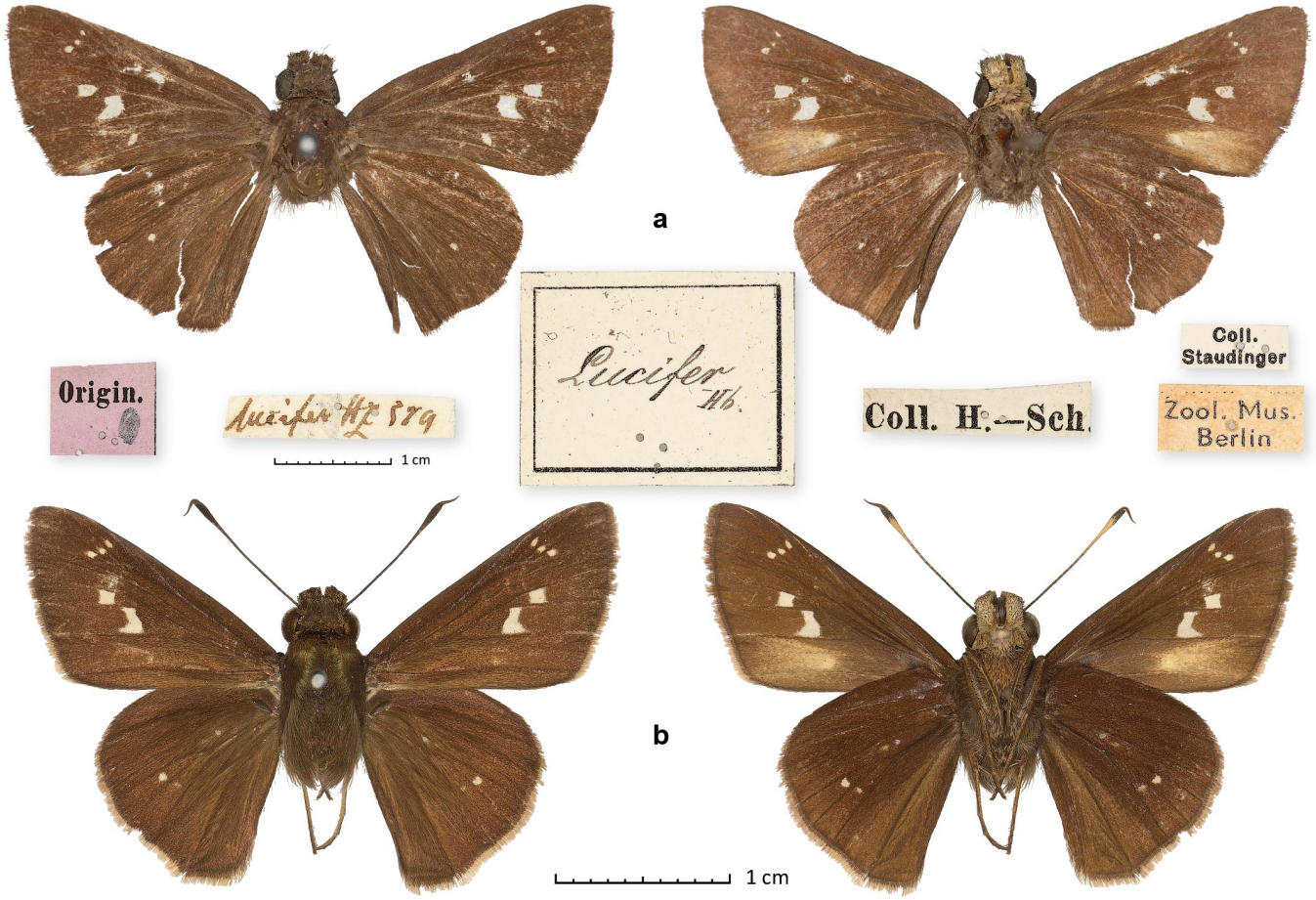

Fig. 83. Specimens of *Oligoria* (*Oligoria*) *lucifer* in dorsal (left) and ventral (right) views, data in text or below: **a)** lectotype (designated herein) ♀ NVG-18113B06 from Suriname with its original labels shown below and **b)** non-type ♂ NVG-23119C07, Hermier n° 4678 from French Guiana: Saül, Batardeau, 24-Feb-1993, B. Hermier leg., genitalia X-3578 J. M. Burns [USNM].

is:

AACTTTATATTTCATCTTTGGTATTTGAGCAGGAATATTAGGAACCTCATTAAGATTGTTAATTCGTACAGAATTAGGTAACCCAGGGTCATTAATTGGTGATGATCAAATTTATAACACT
ATTGTTACAGCTCATGCTTTTATTATAATTTTTTTTATAGTTATACCTATTATAATTGGAGGATTTGGAAATTGATTAGTCCCTCTTATACTAGGAGCCCCTGACATAGCTTTCCCACGAA
TAAATAATATAAGATTTTGAATACTACCACCTTCTTTAACATTGCTAATCTCAAGAAGAATTGTGGAAAATGGAGCAGGAACTGGTTGAACAGTTTACCCCCCCCTATCTTCTAATATTGC
CCACCAAGGATCTTCTGTTGATTTAGCAATTTTTTCTCTTCACTTAGCTGGTATTTCTTCAATTCTAGGAGCTATTAATTTTATTACAACAATTATTAATATACGAATTAAAAATCTATCA
TTTGATCAAATACCTTTATTTGTCTGATCTGTAGGTATTACTGCTTTATTATTACTCTTATCTTTACCTGTTTTAGCAGGAGCTATTACTATATTACTTACTGATCGAAATATTAATACTT
CATTTTTTGATCCTGCAGGAGGAGGAGATCCAATTTTATACCAACATTTATTT

Using genomic sequencing, we associated a male with the female lectotype. The male (Fig. 83b) is similar to the female (Fig. 83a) in wing pattern and only differs in having more angular wings, different from those illustrated in Hübner ([1827]–[1829]), and lacks the spot-like wing damage present in the lectotype.

Lectotype designation for *Cobalus pindar* Schaus, 1913

Cobalus pindar Schaus, 1913, currently treated as a junior subjective synonym of *Oligoria* (*Oligoria*) *lucifer* (Hübner, [1829]) (type locality in Suriname, lectotype sequenced as NVG-18113B06), was described from at least two specimens collected in "Port Limon" (i.e., Limón in Limón Province) and "Juan Vinas" (i.e., Juan Viñas in Cartago Province) in Costa Rica (Schaus 1913). We located two syntypes, one from each locality. Although both are supposed to be in BMNH according to the original description (Schaus 1913), one, from "Port Limon," is in USNM. Both syntypes bear characteristic identification labels written by Schaus and were collected prior to the description (1906 and 1908). However, only the syntype from "Port Limon" in USNM has "type" written on the identification label. The syntype from "Juan Vinas" in BMNH lacks the word "type" on the label. Furthermore, the USNM

"type" syntype agrees better with the original description and illustration (Schaus 1913: pl. 54, fig. 18) in having three well-defined apical hyaline spots in a straight line and the hyaline spot in the forewing cell CuA_1-CuA_2 is more arrowhead- than crescent-shaped. Finally, the "Port Limon" locality is given first in the original description. For these reasons, we believe that the "Port Limon" "type" syntype in USNM represents Schaus's concept of *C. pindar* best.

To define the taxonomic identity of the name *C. pindar* objectively, N.V.G. hereby designates this syntype in the USNM collection, a male illustrated in Fig. 84a, with the following seven rectangular labels (5th red, others white; 3rd handwritten, others printed with handwritten text shown in italics): [July | '08], [PortLimon | CR], [Cobalus | pindar | type Sch.], [Collection | WmSchaus], [Type | No. *16823* | U.S.N.M.], [GENITALIA NO. | X- *33 43* | J.M.Burns 199*2*], and [DNA sample ID: | NVG-23119B09 | c/o Nick V. Grishin] as the **lectotype** of *Cobalus pindar* Schaus, 1913. The lectotype's right antenna is bent near the base, the left one is straight, and the left forewing has conspicuous pinholes near the end of

Fig. 84. Primary type specimens of *Oligoria* (*Oligoria*) in dorsal (left) and ventral (right) views, data in text: **a)** of *O.* (*O.*) *pindar* **stat. rest.** lectotype ♂ NVG-23119B09 from Costa Rica: Limón with its labels; **b)** *O.* (*O.*) *costaria* **sp. n.** holotype ♂ NVG-21054E11 from Costa Rica: Alajuela, and **c)** *O.* (*O.*) *bahia* **sp. n.** holotype ♀ NVG-23079B05 from Brazil: Bahia.

the discal cell. According to the label of the lectotype, the type locality of *C. pindar* becomes Costa Rica: Limón Province, Limón. The COI barcode sequence of the lectotype, sample NVG-23119B09, 658 base pairs is:

AACTTTATATTTTATTTTTGGTATTTGAGCAGGAATATTAGGAACTTCATTAAGATTATTAATTCGTACAGAATTAGGTAATCCAGGATCATTAATTGGAGATGATCAAATTTATAATACT
ATTGTTACAGCTCATGCTTTTATTATAATTTTTTTTATAGTTATACCTATTATAATTGGAGGATTTGGAAATTGATTAGTTCCACTTATATTAGGAGCTCCTGATATAGCTTTTCCACGAA
TAAATAATATAAGATTTTGAATACTACCCCCTTCTTTAACATTATTAATTTCAAGAAGAATTGTAGAAAATGGAGCAGGAACAGGTTGAACAGTTTATCCTCCTTTATCTTCTAATATTGC
TCACCAAGGATCTTCAGTTGATTTAGCAATCTTTTCTCTTCATTTAGCTGGTATTTCTTCTATTTTAGGAGCTATTAATTTTATTACAACAATTATTAATATACGAATTAAAAATCTATCA
TTTGATCAAATACCTTTATTTGTTTGATCTGTAGGTATCACTGCATTATTATTACTTTTATCTTTACCTGTTTTAGCTGGAGCTATTACTATACTACTCACTGATCGAAATCTTAATACTT
CATTTTTTGATCCTGCAGGAGGAGGAGATCCAATTTTATATCAACATTTATTT

Oligoria (*Oligoria*) *pindar* (Schaus, 1913) is a valid species distinct from *Oligoria* (*Oligoria*) *lucifer* (Hübner, [1829]) and *Oligoria* (*Oligoria*) *percosius* (Godman, 1900)

Genomic analysis places the lectotype of *Cobalus pindar* Schaus, 1913 (from Costa Rica: Limón, sequenced as NVG-23119B09), a taxon currently treated as a junior subjective synonym of *Oligoria* (*Oligoria*) *lucifer* (Hübner, [1829]) (type locality in Suriname, lectotype sequenced as NVG-18113B06), in a clade different from it (Fig. 82 purple) and among specimens traditionally identified as *Oligoria* (*Oligoria*) *percosius* (Godman, 1900) (type locality Mexico: Veracruz, Atoyac) (Fig. 82 blue). However, the lectotype of *O.* (*O.*) *percosius* together with topotypical paralectotypes differ from *C. pindar* (Fig. 84a) and these "*O. percosius*" specimens (Fig. 85c, d) by having a prominent pale area in the distal half of the ventral forewing cell CuA_2-1A+2A while being darker overall otherwise as reflected in smaller subapical forewing semihyaline spots, usually one or two (not three) in males, and darker ventral hindwing with smaller elongated and somewhat angular (rather than round) postdiscal semihyaline spot(s); lacking the darker postdiscal band passing though the hyaline spot(s) on the ventral hindwing; having a broader and more rounded harpe, smaller ampulla, and less concave transition from the ampulla to the costa, which is not notched towards the base but evenly convex. Phenotypically, the topotypical specimens in the type series of *O.* (*O.*) *percosius* (which we have not sequenced) are more similar to *Oligoria* (*Oligoria*) *rindgei* (H. Freeman, 1969) (type locality in Mexico: Oaxaca, holotype sequenced as NVG-18031F01) than to "*O. percosius*," are expected to belong to the clade with *O.* (*O.*) *rindgei* (Fig. 82 olive), and may be conspecific with it. Therefore, we propose that *Oligoria* (*Oligoria*) *pindar* (Schaus, 1913), **stat. rest.** is a valid species distinct from both *Oligoria* (*Oligoria*) *lucifer* (Hübner, [1829]) and *Oligoria* (*Oligoria*) *percosius* (Godman, 1900) but refrain from synonymizing *O.* (*O.*) *rindgei* with *O.* (*O.*) *percosius* prior to the genomic analysis of the lectotype. Because *Oligoria* specimens from the U.S. previously misidentified as *O.* (*O.*) *percosius* are in the clade with *O.* (*O.*) *pindar* and are likely conspecific with it, we identify them as this species instead of *O.* (*O.*) *percosius.* As a result, the name for the South Texas species becomes *O.* (*O.*) *pindar*, and *O.* (*O.*) *percosius* is excluded from the U.S. fauna.

Oligoria (*Oligoria*) *costaria* Grishin, new species

https://zoobank.org/D3E29477-8BAD-410B-A7FD-7E51755E8CE4

(Fig. 82 part, 84b, 85a–b)

Definition and diagnosis. Genomic analysis reveals that a specimen from central Costa Rica initially identified as *Oligoria* (*Oligoria*) *pindar* (Schaus, 1913), **stat. rest.** (type locality Costa Rica: Limón, lectotype sequenced as NVG-23119B09) is genetically differentiated from it and other relatives at the species level (Fig. 82); e.g., their COI barcodes differ by 2.9% (19 bp), and therefore this specimen represents a new species. This new species keys to "*Decinea percosius*" (L.11.7.) in Evans (1955), but differs from it and other relatives by the following combination of characters in males: hyaline spots are larger, with the spot in the forewing cell CuA_1-CuA_2 more arrowhead-like, with longer sides and deeper outer indentation; the central spot in the triad by the forewing apex is not the smallest in size; the ventral hindwing has a larger discal cell spot and the spot in the middle of cell M_3-CuA_1, the two spots are approximately the same size; the ground color of the ventral hindwing is darker, the coloration is more uniform without a prominent darker postdiscal band crossing the hyaline spot; the valva is shorter and

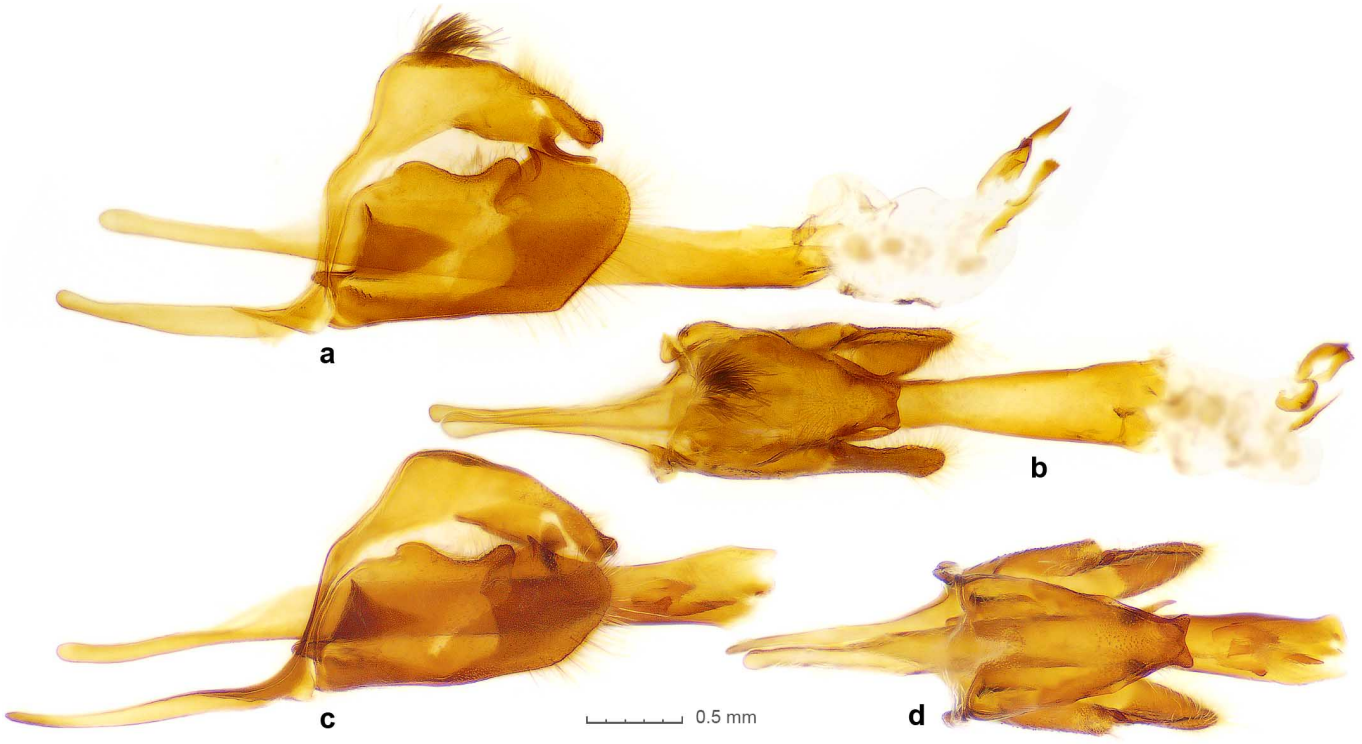

Fig. 85. Male genitalia of *Oligoria* (*Oligoria*), data in text or below: **a–b)** *O.* (*O.*) *costaria* **sp. n.** holotype NVG-21054E11 (data in text) and **c–d)** *O.* (*O.*) *pindar* **stat. rest.** NVG-3799 from USA: Texas, Starr Co., Roma, nr. Citizens State Bank, 28-Jun-2015, N. V. Grishin leg., genitalia NVG251025-08 in: **a, c)** left lateral and **b, d)** dorsal views.

broader; the harpe is angled at the ventral margin and more broadly rounded distally with a broader dorsal tooth by the ampulla, and the ampulla is slightly broader. Due to its cryptic nature and unexplored individual variation, this species is best identified by DNA, with diagnostic base pairs in the nuclear genome: aly923.5.2:C151T, aly923.5.2:C219G, aly216.60.2:A114G, aly216.69.1:G123A, aly216.69.1:A201G, aly1019.13.1:T1698T (not A), aly1019.13.1:T5439T (not C), aly1019.13.1:T5604T (not G), aly1019.13.1:G2199G (not A), aly1656.26.1:A258A (not G); and the COI barcode: T59C, T142C, T202A, C271C, T499A, T508C.

Barcode sequence of the holotype. Sample NVG-21054E11, 658 base pairs:

AACTTTATATTTTATTTTTGGTATTTGAGCAGGAATATTAGGAACTTCATTAAGATTACTAATTCGTACAGAATTAGGTAATCCAGGATCATTAATTGGAGATGATCAAATTTATAATACT
ATTGTTACAGCTCATGCTTTCATTATAATTTTTTTTATAGTTATACCTATTATAATTGGAGGATTTGGAAATTGATTAGTACCACTTATATTAGGAGCTCCTGATATAGCTTTTCCACGAA
TAAATAATATAAGATTTTGAATATTACCCCCTTCTTTAACATTATTAATTTCAAGAAGAATTGTAGAAAATGGAGCAGGAACAGGTTGAACAGTTTATCCCCCTTTATCTTCTAATATTGC
CCATCAAGGATCTTCAGTTGATTTAGCAATTTTTTCCCTTCATTTAGCTGGTATTTCTTCTATTTTAGGAGCTATTAATTTTATTACAACAATTATTAATATACGAATTAAAAATTTATCA
TTTGATCAAATACCATTATTTGTCTGATCTGTAGGTATTACTGCATTACTATTACTCTTATCTTTACCTGTTTTAGCTGGAGCTATTACTATATTACTTACTGATCGAAATCTTAATACTT
CATTTTTTGACCCCGCAGGAGGAGGAGATCCAATTTTATATCAACATTTATTT

Type material. Holotype: ♂ deposited in the McGuire Center for Lepidoptera and Biodiversity collection, Gainesville, FL, USA (MGCL), illustrated in Fig. 84b (genitalia Fig. 85a, b), bears the following six printed (text in italics handwritten) rectangular labels, five white: [COSTA RICA | Alajuela Province | Rio Virilla, 5.5 | km SW Guacima | 2 Oct. 1987 | leg G&A Austin], [Genit. Vial | SRS-*3105*], [*Decinea* | *lucifer* | ♂ | Det: S. R. Steinhauser], [G.T. Austin colln. | MGCL Accession | # 2004-5], [DNA sample ID: | NVG-21054E11 | c/o Nick V. Grishin], and one red [HOLOTYPE ♂ | Oligoria | costaria Grishin].

Type locality. Costa Rica: Alajuela Province, Río Virilla, 5.5 km southwest of Guácima.

Etymology. The name is formed from the type locality: *costa* + *ri*[c]*a* and is treated as a feminine noun in apposition.

Distribution. Currently known only from the holotype collected in central Costa Rica.

Oligoria (*Oligoria*) *bahia* Grishin, new species

https://zoobank.org/A17DCB4C-5707-4684-8F10-B22F48335A16

(Figs. 82 part, 84c)

Definition and diagnosis. Genomic analysis reveals that a specimen from Bahia, Brazil, initially identified as *Oligoria* (*Oligoria*) *percosius* (Godman, 1900) (type locality in Mexico: Veracruz), the latter species being misidentified *Oligoria* (*Oligoria*) *pindar* (Schaus, 1913), **stat. rest.** (type locality Costa Rica: Limón, lectotype sequenced as NVG-23119B09), is genetically differentiated from it at the species level (Fig. 82); e.g., their COI barcodes differ by 2.3% (15 bp), and therefore this specimen represents a new species. This new species keys to "*Decinea percosius*" (L.11.7.) in Evans (1955), but differs from it and other relatives by the following combination of characters in females: a semihyaline spot in the anterior part of the forewing discal cell near its distal end that is the size of apical spots, typically larger semihyaline spots on the forewing, weaker brown framing around semihyaline spots on the ventral hindwing, and darker fringes. Due to its cryptic nature, lack of known males, and poorly explored individual variation, this species is best identified by DNA, with diagnostic base pairs in the nuclear genome: aly155.6.11:G36A, aly2096.25.2:A108G, aly1651.3.1:G72T, aly276558.15.8:A45A (not T), aly235.6.4:G75G (not C), aly10226.27.8:A72A (not T); and the COI barcode: T59C, T64C, T428C, T460C, A628T.

Barcode sequence of the holotype. Sample NVG-23079B05, 658 base pairs:

AACTTTATATTTTATTTTTGGTATTTGAGCAGGAATATTAGGAACTTCATTAAGATTACTAATCCGTACAGAATTAGGTAATCCAGGATCATTAATTGGAGATGATCAAATTTATAATACT
ATTGTTACAGCTCATGCTTTTATTATAATTTTTTTTATAGTTATACCTATTATAATTGGAGGATTTGGAAATTGATTAGTTCCACTTATATTAGGAGCTCCTGATATAGCTTTTCCACGAA
TAAATAATATAAGATTTTGAATATTACCTCCTTCTTTAACATTATTAATTTCAAGAAGAATTGTAGAAAATGGAGCAGGAACAGGTTGAACAGTTTATCCCCCTTTATCTTCTAATATTGC
CCATCAAGGATCTTCAGTTGATTTAGCAATTTTTTCTCTTCATTTAGCTGGTATTTCTTCTATTCTAGGAGCTATTAATTTTATTACAACAATTATCAATATACGAATTAAAAATTTATCA
TTTGATCAAATACCTTTATTTGTTTGATCTGTAGGTATTACTGCATTACTATTATTTTTATCTTTACCTGTTTTAGCTGGAGCTATTACTATATTACTTACTGATCGAAATCTTAATACTT
CATTTTTTGATCCCGCAGGAGGTGGAGATCCAATTTTATATCAACATTTATTT

Type material. Holotype: ♀ deposited in the Museum für Naturkunde, Berlin, Germany (MFNB), illustrated in Fig. 84c, bears the following four rectangular labels (2nd handwritten, others printed; 2nd green, last red, and others white): [5599], [Bahia Sello], [DNA sample ID: | NVG-23079B05 | c/o Nick V. Grishin], and [HOLOTYPE ♀ | Oligoria (Oligoria) | bahia Grishin]. On the first label, 5599 is a lot number of specimens registered in the historical collection catalog written by Hopffer. The entry in the catalogue shows three specimens in this lot, all from Bahia collected by Sello, as also stated on one the holotype's labels. Friedrich Sello[w] (1789–1831) collected in Bahia in 1817–1818 and sent a significant amount of collected material from Bahia to MFNB in October of 1817 (Pacheco and Whitney 2001). **Paratypes:** 2♀♀ from the same specimen lot as the holotype, not sampled for DNA.

Type locality. Brazil: Bahia.

Etymology. The name is given for the type locality and is as a feminine noun in apposition.

Distribution. Currently known only from Bahia, Brazil.

Subtribe Moncina A. Warren, 2008

Alychna ventanilla Grishin, new species

https://zoobank.org/50227B13-BF84-44D1-91E5-86A69A686556

(Figs. 86 part, 87a–b, 88a–c)

Definition and diagnosis. Genomic analysis reveals that specimens from the Andes in Ecuador and Peru identified as *Alychna victa* (Evans, 1955) (type locality Peru: Puno Region, Carabaya Province, Uruhuasi) are genetically differentiated from it at the species level (Fig. 86); e.g., their COI barcodes differ by 5.8% (38 bp), and therefore these specimens represent a new species. This new species keys to "*Lychnuchus victa*" (K.12.1) in Evans (1955), but differs from it and other relatives by the following combination of characters in males: the anterior arrowhead-shaped segment of the brand reaches the orange band; the semihyaline area of the orange band in the forewing cell CuA_1-CuA_2 is smaller and does not reach the distal edge of the band as in *A. victa* and *Alychna bogotana* Grishin, 2025 (type locality in Colombia: Bogotá); the outer edge of the forewing orange band is more diffuse; the harpe has a narrower and more pointed dorsal tooth, is concave distad of it and terminally angled, the dorsal margin of the harpe is longer

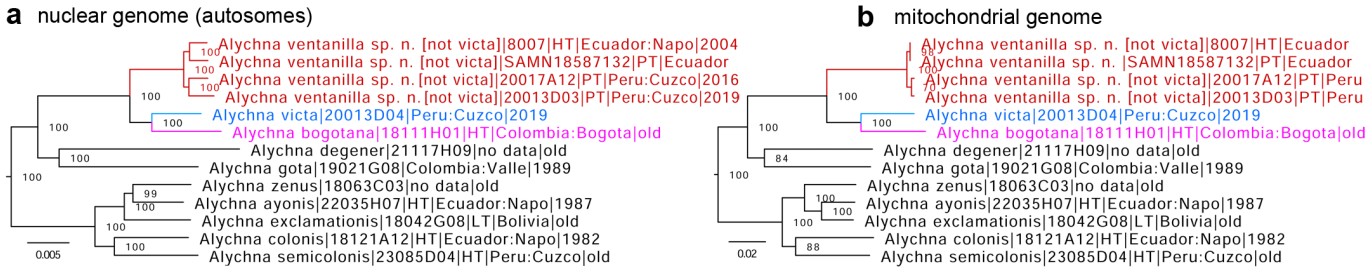

Fig. 86. Phylogenetic trees of selected *Alychna* species constructed from protein-coding regions in: **a)** the nuclear genome (autosomes), based on 1,955,025 positions, and **b)** the mitochondrial genome. Species discussed in the text are colored: *A. ventanilla* **sp. n.** (red), *A. victa* (blue), and *A. bogotana* (magenta). The sequence of SAMN18587132 is taken from the alignment provided in Kawahara et al. (2023). Ultrafast bootstrap (Hoang et al. 2018) values are shown at nodes.

basally from the tooth, ending in a comparatively narrow tooth directed basad (Fig. 88a) [the harpe is more compact and rounded along the distal margin, with a broader dorsal tooth and with a narrower but longer upturned section, basal end of which forms a broader tooth in *A. victa* (Fig. 88d); distally rounded, but with a shorter upturned section, especially its basal margin, which is rounded and not extended into a tooth, in *A. bogotana* (Fig. 88g)]; a narrower ampulla (Fig. 88a) [broader in *A. victa* (Fig. 88d) and the broadest in *A. bogotana* (Fig. 88g)]; and a narrower tegumen and uncus, which is undivided with vestigial terminal "knobs" on the sides (Fig. 88b, c) [the uncus is broader and divided in the other two species (Fig. 88e, h), which have a broader tegumen (Fig. 88e, f, h) with a deeper central notch along the anterior margin in *A. bogotana* (Fig. 88h)]. Due to poorly explored individual variation, this species is best identified by DNA, with diagnostic base pairs in the nuclear genome: aly2012.60.4:G75A, aly671.39.2: T426C, aly3560.2.2:G84A, aly595.11.2:A189G, aly1350.19.4:C153T; and the COI barcode: A49C, T106C, T442C, T536C, T586C.

Barcode sequence of the holotype. Sample NVG-8007, 658 base pairs:

AACTTTATATTTTATTTTTGGTATTTGAGCAGGAATACTAGGAACTTCCTTAAGTTTATTAATTCGTACTGAATTAGGAAATCCCGGATCTTTAATTGGAGATGACCAAATTTATAATACC
ATTGTAACTGCCCATGCTTTTATTATAATTTTTTTCATAGTAATACCAATTATAATTGGAGGATTTGGAAATTGATTAGTTCCTCTAATATTAGGAGCCCCTGATATAGCTTTCCCCCGAA
TAAACAATATAAGATTTTGAATATTACCACCCTCATTAACATTATTAATTTCAAGAAGAATTGTTGAAAATGGTGCAGGTACTGGATGAACTGTATATCCCCCCCTTTCTTCTAATATTGC
CCATCAAGGATCATCTGTTGACTTAGCAATTTTTTCTTTACACTTAGCAGGAATTTCATCTATTTTAGGAGCTATTAACTTTATCACCACAATTATTAATATACGAATTAGAAACTTATCA
TTTGATCAAATACCTTTATTTGTATGATCTGTAGGAATTACAGCTTTATTACTACTTTTATCTTTACCTGTATTAGCTGGAGCTATTACAATACTTTTAACCGATCGAAATTTAAATACTT
CTTTTTTTGATCCAGCTGGAGGAGGAGATCCAATTTTATATCAACATTTATTT

Type material. Holotype: ♂ deposited in the National Museum of Natural History, Smithsonian Institution, Washington, DC, USA (USNM), illustrated in Fig. 87a, bears the following five printed rectangular labels, four white: [ECUADOR: Napo, | Km. 49 Tena-Loreto rd. | 0° 42.74'S, 77° 44.44' W | 1300 m, 18 Mar 2004 | J.P.W. Hall & I. Aldas], [DNA sample ID: | NVG-8007 | c/o Nick V. Grishin], [genitalia | NVG170207-92 | Nick V. Grishin], [USNMENT | {QR Code} | 01321847], and one red [HOLOTYPE ♂ | Alychna ventanilla | Grishin]. **Paratypes:** 3♂♂: 1♂ LEP-61199, SAMN18587132 (NCBI BioSample accession) Ecuador, Lodge, J. D. Turner leg. [MGCL] and Peru, Cuzco, Quebrada Quitacalzón, 1050–1100 m, approx. GPS −13.0167, −71.4833: 1♂ NVG-20017A12, 2-Sep-2016, G. Lamas leg. [MUSM] and 1♂ NVG-20013D03 (leg, DNA sequenced), NVG-25031C12 (abdomen, DNA stored, genitalia dissected), WRD 17211, 15-Jun-2019, W. R. Dempwolf leg., genitalia NVG251025-02 [WRDC] (Figs. 87b, 88a–c).

Type locality. Ecuador: Napo Province, km 49 of Tena–Loreto road, elevation 1300 m, GPS −0.7123, −77.7407.

Etymology. In Spanish, ventanilla means a small window, like those in an airplane; and the name, a noun in apposition, reflects smaller and squarish semihyaline areas in the forewing discal band of this species.

Distribution. Known from the eastern slopes of the Andes from northern Ecuador to southern Peru.

Comment. For comparison, we illustrate *A. victa* ♂ NVG-20013D04 from Peru: Cuzco, Cosñipata Valley, Quebrada Morro Leguía, 2135 m, GPS −13.1167, −71.5667, 14-Jun-2019, W. R. Dempwolf leg. [WRDC] (Fig. 87c) sympatric with the new species; the holotype of *A. bogotana* ♂ NVG-18111H01 Colombia: Bogotá [USNM] (Fig. 87d); and their genitalia (Fig. 88b, c).

Fig. 87. *Alychna* ♂♂ in dorsal (left) and ventral (right) views, data in text: **a–b)** *A. ventanilla* **sp. n.**: **a)** holotype NVG-8007 from Ecuador: Napo and **b)** paratype NVG-20013D03 from Peru: Cuzco; **c)** *A. victa* NVG-20013D04 from Peru: Cuzco; and **d)** *A. bogotana* holotype NVG-18111H01 from Colombia: Bogotá. Insets show a magnified section with brands, flipped in (d).

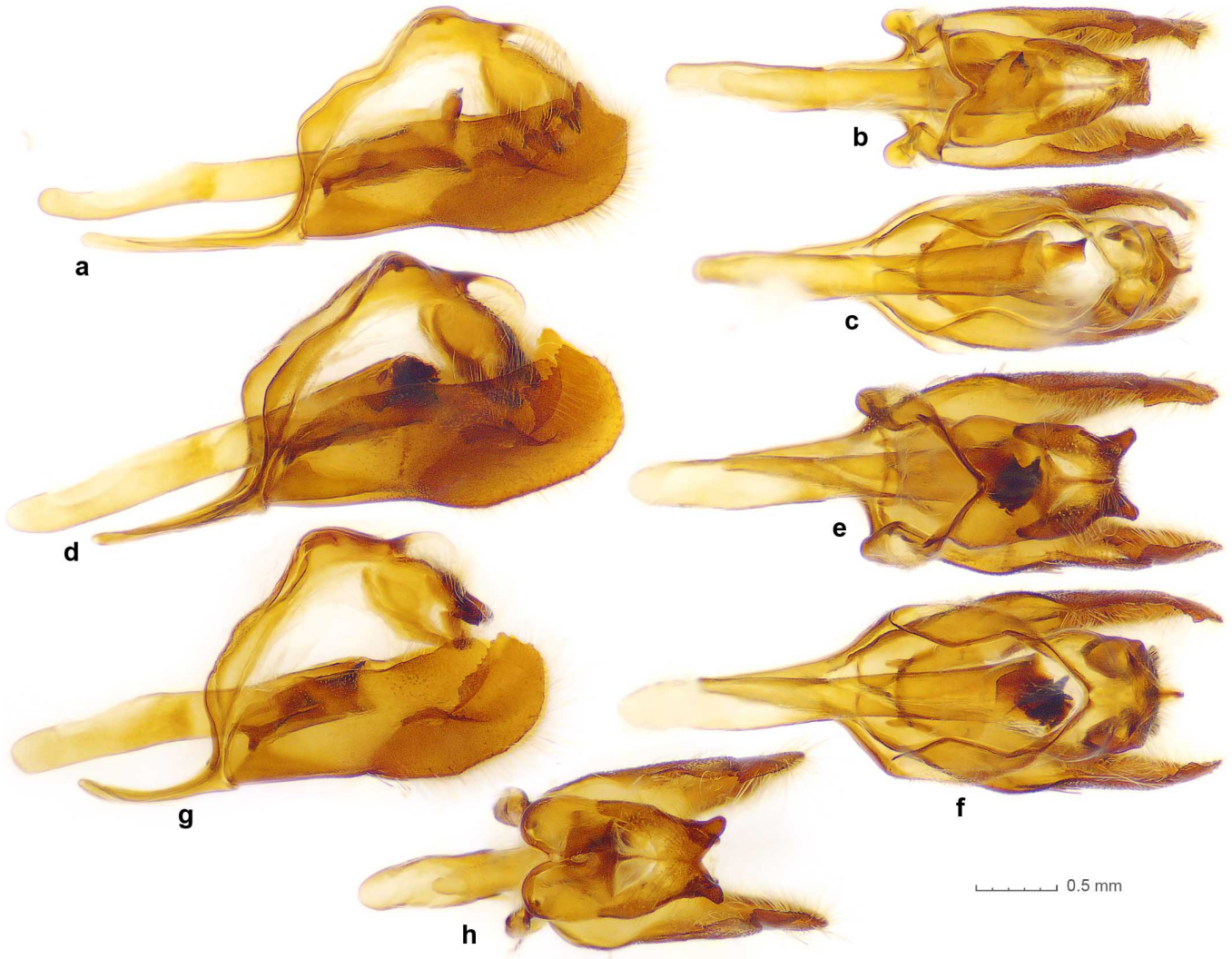

Fig. 88. Male genitalia of *Alychna*, data in text: **a–c)** *A. ventanilla* **sp. n.** paratype NVG-20013D03 from Peru: Cuzco; **d–f)** *A. victa* NVG-20013D04 from Peru: Cuzco, and **g–h)** *A. bogotana* holotype NVG-18111H01 from Colombia: Bogotá in: **a, d, g)** left lateral, **b, e, h)** dorsal, and **c, f)** anterodorsal views.

Thoon cuadius Grishin, new species

https://zoobank.org/DA881C63-B996-40EB-8C03-6A2B4AD77F6D

(Fig. 89 part, 90–91)

Definition and diagnosis. Genomic analysis reveals that specimens from Ecuador initially identified as *Thoon modius* (Mabille, 1889) (type locality in Panama: Chiriquí, syntype sequenced as NVG-15035C04) are genetically differentiated from it at the species level (Fig. 89); e.g., their F_{st}/COI barcode difference are 0.39/1.2% (8 bp), and therefore these specimens represent a new species. This new species keys to *T. modius* (J.48.3) in Evans (1955) and was likely included by him in this species, but differs from it and other relatives by the following combination of characters: the ground color of the ventral hindwing is dark yellow-brown, darker than in *T. modius* and not mauve or violaceous as in *Thoon dius* Grishin, 2025 (type locality in Mexico: Tamaulipas) or *Thoon rondius* Grishin, 2025 (type locality in Brazil: Rondônia); dorsal yellow overscaling at wing bases and the forewing inner margin is not prominent and is darker, more brown; the second semihyaline apical forewing spot is vestigial or lacking; the central spot in the ventral hindwing cell CuA_1-1A+2A is smaller and with weaker pale overscaling around it; the postdiscal spot between the hindwing veins M_1 and M_3 is more weakly expressed on both sides; the forewing discal cell spot in its anterior part is developed above and beneath; the dorsal tooth-shaped process of the harpe is broader and well-separated from the broad, smaller tooth at its base; and the inner dorsal margin of the

harpe is shorter and more slanted basad of the dorsal ridge. Due to its cryptic nature and unexplored individual variation, this species is best identified by DNA, with diagnostic base pairs in the nuclear genome: aly4456.8.4:C214A, aly4456.8.4:C234T, aly1405.13.8:T87C, aly1405.13.8:C113T, aly707.14.1:A69T; and the COI barcode: T178C, C184A, T205A, G631G, C646C.

Barcode sequence of the holotype. Sample NVG-23056D04, 658 base pairs:

AACTTTATATTTTATTTTTGGTATTTGAGCAGGTATATTAGGAACTTCTCTTAGTTTATTAATTCGTTCAGAATTAGGAAATCCAGGATCTTTAATTGGAGATGATCAAATTTATAATACT
ATTGTCACAGCTCATGCATTTATTATAATTTTTTTTATAGTTATACCTATTATAATCGGAGGATTTGGAAATTGATTAGTACCATTAATATTAGGAGCCCCAGATATAGCTTTCCCACGAA
TAAATAATATAAGATTTTGAATATTACCTCCTTCATTAATATTATTAATTTCAAGAAGAATTGTAGAAAATGGTACTGGAACAGGTTGAACAGTATACCCCCCTCTTTCTGCTAATATCGC
TCATCAAGGTTCATCTGTTGATTTAGCTATTTTTTCACTTCATTTAGCTGGAATTTCATCAATTTTAGGAGCTATTAATTTCATTACAACAATTATTAATATACGAATTAAAAATTTATCA
TTTGATCAAATACCTTTATTTGTTTGATCTGTAGGTATTACAGCTTTATTATTACTTTTATCTTTACCAGTTTTAGCTGGTGCTATTACTATACTTTTAACAGATCGAAATCTTAATACTT
CTTTTTTTGATCCTGCTGGAGGAGGGGATCCTATTTTATACCAACATTTATTT

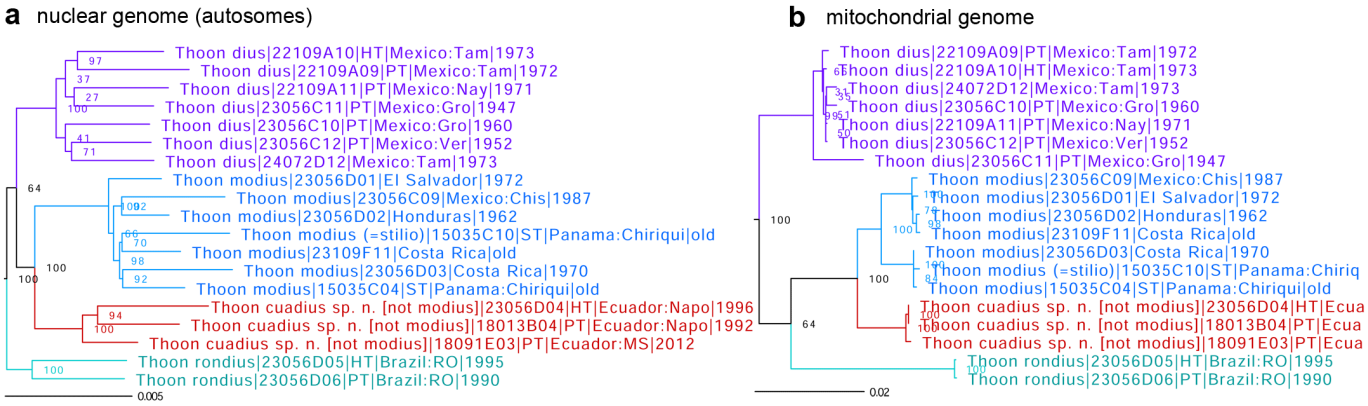

Fig. 89. Phylogenetic trees of all described *Thoon* species constructed from protein-coding regions in: **a)** the nuclear genome (autosomes), based on 2,789,211 positions, and **b)** the mitochondrial genome. Different species are shown in different colors: *T. dius* (purple), *T. modius* (blue), *T. cuadius* **sp. n.** (red), and *T. rondius* (cyan). Ultrafast bootstrap (Hoang et al. 2018) values are shown at nodes.

Fig. 90. *Thoon cuadius* **sp. n.** holotype ♂ NVG-23056D04 in dorsal (left) and ventral (right) views, data in text.

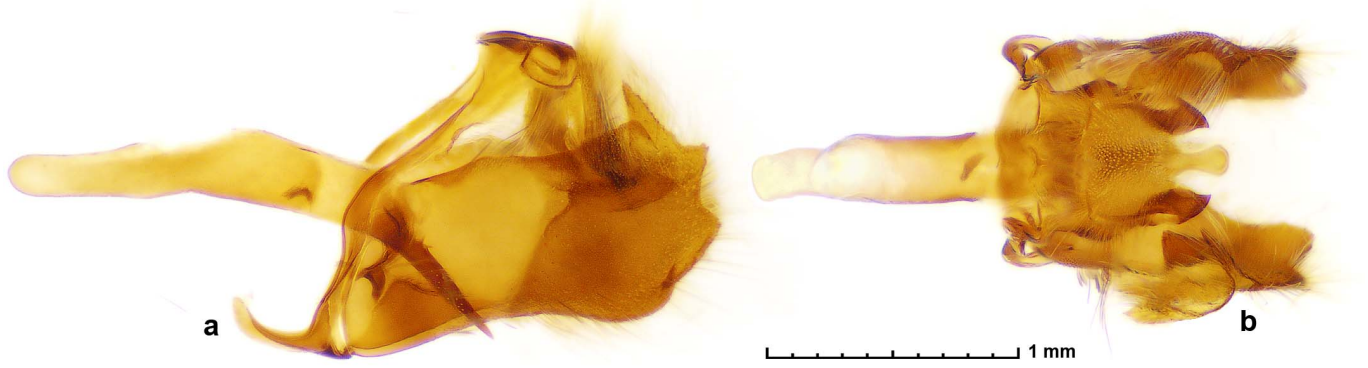

Fig. 91. Male genitalia of *Thoon cuadius* **sp. n.** holotype NVG-23056D04 (data in text) in: **a)** right lateral (flipped, i.e., left-right inverted) and **b)** dorsal views.

Type material. Holotype: ♂ deposited in the McGuire Center for Lepidoptera and Biodiversity collection, Gainesville, FL, USA (MGCL), illustrated in Fig. 90 (genitalia Fig. 91), bears the following six printed (text in italics handwritten) rectangular labels, five white: [Pusuno, Rio Napo | NapoPoviince,Ecuador | September 10, 1996 | D & J Lindsley], [Thoon Godman | modius (Mabille)], [D.L. Lindsley colln | MGCL Accession | # 2008-20], [DNA voucher | LEP-79977], [DNA sample ID: | NVG-23056D04 | c/o Nick V. Grishin], and one red [HOLOTYPE ♂ | Thoon cuadius | Grishin]. Unnumbered genitalia vial is pinned together with the labels. **Paratypes:** 1♂ and 1♀ from Ecuador: 1♂ NVG-18013B04, USNMENT 01450363 Napo, 8 km Napo-Ahano, 480 m, GPS −1.0417, −77.7250, 9-Nov-1992, S. S. Nicolay leg. [USNM]; 1♀ NVG-18091E03 Morona-Santiago, San Isidro, Macas, 1250 m, GPS −2.12, −78.10, 15-Nov-2012, J.-C. Petit leg. [EBC].

Type locality. Ecuador: Napo Province, Pusuño, Río Napo.

Etymology. The name is formed from the name of its relative: [e]*cua*[dorian] + [mo]*dius*. The name is a feminine noun in apposition.

Distribution. Currently known only from Ecuador.

Viridina viridella Grishin, new species

https://zoobank.org/6845A703-EA23-4634-A710-2E1D5C65E497

(Fig. 92 part, 93, 94a–d)

Definition and diagnosis. Genomic analysis reveals that specimens from southern Peru and western Bolivia initially identified as *Viridina viridenex* (Weeks, 1901) (type locality in Bolivia, 200 mi north of Cochabamba, holotype sequenced as NVG-19055F04) are genetically differentiated from it at the species level in the nuclear genome (Fig. 92); e.g., their COI barcodes differ by 4.3% (28 bp), and therefore these specimens represent a new species. This new species keys to "*Tigasis viridenex*" (J.44.10) in Evans (1955), but differs from it and *Viridina viridis* (Bell, 1942) (type locality Ecuador, Tungurahua, Runtun) by a narrower anterior segment of the stigma; ventral hindwing postdiscal pale violaceous spots between veins M_1 and M_3 and in cell M_3-CuA_1 that are closer aligned with each other; darker palpi beneath; nearly trapezoidal valva with a prominent notch between the harpe and ampulla, the ampulla that is slightly humped, the costa-ampulla that is nearly straight with a slight hump basad of the ampulla, and the ventral margin of the valva that is concave basad of the harpe (Fig 94a, d) [the valva is more rounded and with a vestigial notch, stronger serrated at the rounder distal margin, the ampulla is not developed, and the costa-ampulla margin is mildly convex in *V. viridenex* (Fig. 94e, h); the valva is similar in *V. viridis*, but the harpe is separated from the ampulla by a broad and shallow concavity, the ampulla is better developed and the dorsal margin of the harpe is broadly humped at the ampulla]; nearly undivided (only partly split at the distal end) and narrower uncus (Fig. 94b) [broader and divided uncus with parallel arms touching each other over their entire length in *V. viridenex* (Fig. 94f)]; shorter uncus comparatively to the tegumen (Fig 94a, d) [in *V. viridenex*, the uncus is relatively longer as best observed in lateral view (Fig. 94e, h); the uncus is similar, but slightly shorter in *V. viridis*]; and a longer, straighter phallobase (Fig. 94a, c) [shorter and upturned in *V. viridenex* (Fig. 94e, g)]. Due to its partly cryptic nature and unexplored

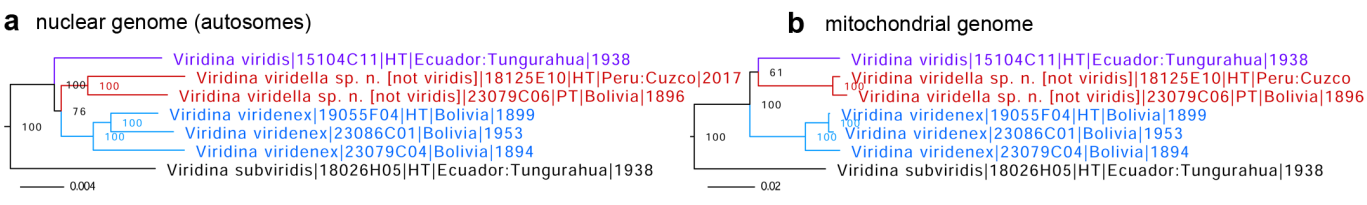

Fig. 92. Phylogenetic trees of all described *Viridina* species constructed from protein-coding regions in: **a)** the nuclear genome (autosomes), based on 1,511,886 positions, and **b)** the mitochondrial genome. Different species are shown in different colors: *V. viridis* (purple), *V. viridella* **sp. n.** (red), *V. viridenex* (blue), and *V. subviridis* (Hayward, 1940) (black). Ultrafast bootstrap (Hoang et al. 2018) values are shown at nodes.

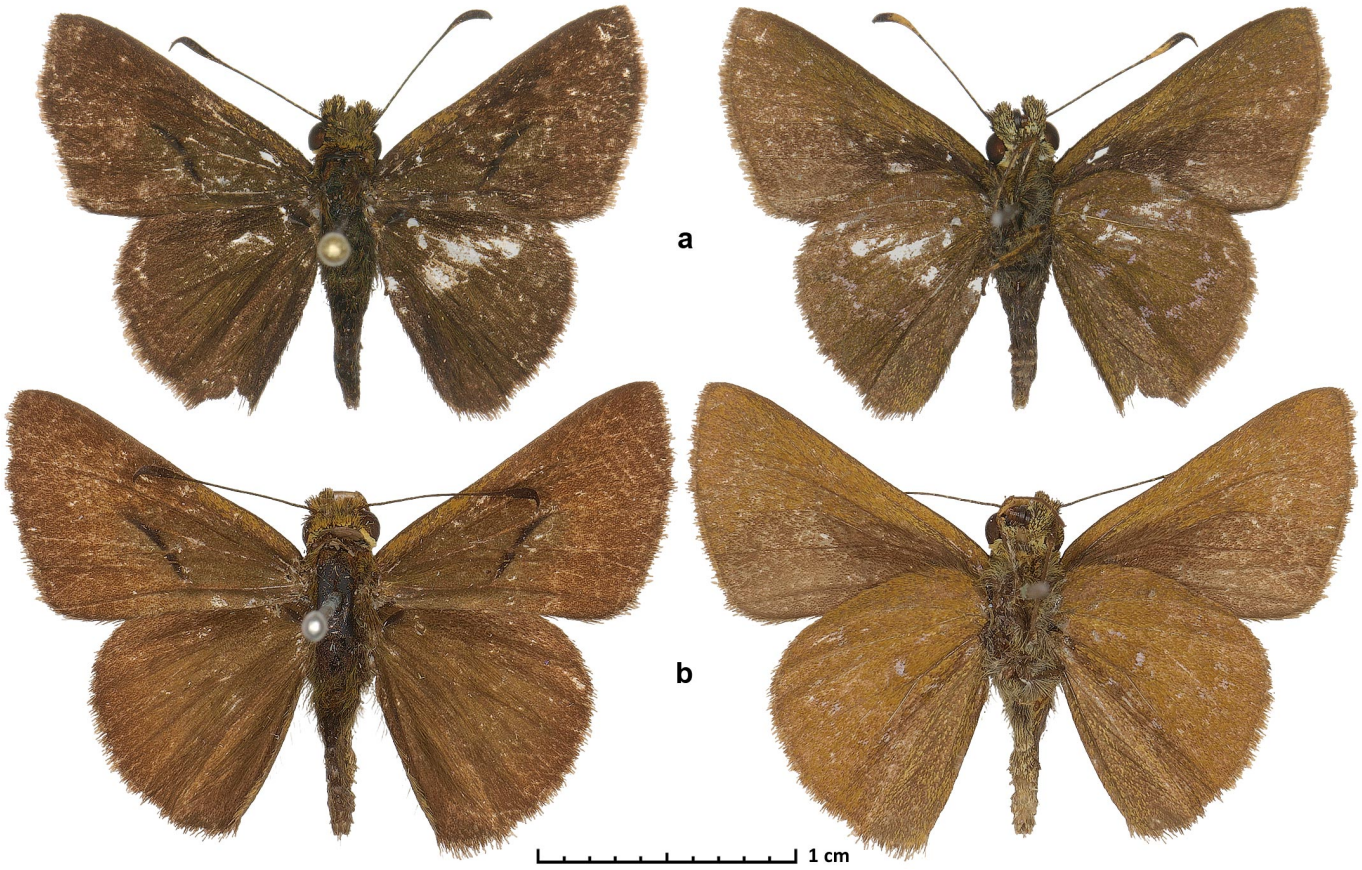

Fig. 93. Type series of *Viridina viridella* **sp. n.** in dorsal (left) and ventral (right) views, data in text: **a)** holotype ♂ NVG-18125E10 from Peru: Cuzco and **b)** paratype ♂ NVG-23079C06 from Bolivia.

individual variation, this species is best identified by DNA, with diagnostic base pairs in the nuclear genome: aly23605.23.10:C111T, aly125.1.4:A123G, aly12063.29.23:A39G, aly12063.29.23:A69G, aly2096.41.14:G6A; and the COI barcode: A49C, T50C, T238C, T428C, A622T.

Barcode sequence of the holotype. Sample NVG-18125E10, 658 base pairs:

AACTTTATATTTTATTTTTGGAATTTGAGCAGGAATATTAGGAACTTCCCTAAGATTATTAATTCGTACAGAATTAGGTAATCCAGGTTCTTTAATTGGAGATGATCAAATTTATAATACT
ATTGTTACAGCTCATGCTTTCATTATAATTTTTTTTATAGTTATACCTATTATAATTGGAGGATTTGGAAATTGATTAGTACCATTAATATTAGGGGCACCTGATATAGCTTTCCCCCGAA
TAAATAATATAAGATTTTGAATACTACCCCCCCTCTTTATTATTATTAATTTCAAGAAGAATTGTAGAAAATGGTGCAGGAACAGGATGAACTGTTTACCCCCCCCTTTCTTCAAATATTGC
CCATCAAGGATCTTCTGTTGATTTAGCAATTTTTTCCTTACATTTAGCTGGAATTTCATCTATTCTAGGAGCTATTAATTTTATTACAACTATTATTAATATACGAATTAGTAATATAACA
TTTGATCAAATACCATTATTTATTTGATCTGTAGGAATTACAGCACTTTTATTACTTTTATCTTTACCTGTATTAGCAGGAGCTATCACTATACTATTAACAGACCGAAATTTAAATACTT
CATTTTTTGATCCTGCTGGAGGAGGAGATCCAATTTTATACCAACATTTATTT

Type material. Holotype: ♂ currently in the Dempwolf collection (Austin, Texas, USA), to be deposited in the Museo de Historia Natural, Lima, Peru (MUSM), illustrated in Fig. 93a (genitalia Fig. 94a–d), bears the following seven printed (text in italics handwritten) rectangular labels, six white: [Peru: Cuzco Dept, 2350m | Cosñipata Valley, Yanamayo | 13° 08' S, 71° 35' W | November 14, 2017 | Leg: J. Brock], [Tigasis viridenex | ♂ | Coll of: W R Dempwolf], [DNA sample ID: | NVG-18125E10 | c/o Nick V. Grishin], [DNA sample ID: | NVG-25031D02 | c/o Nick V. Grishin], [genitalia | NVG251025-04 | c/o Nick V. Grishin], [WRD 14,895], and one red [HOLOTYPE ♂ | Viridina | viridella 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-23079C06 Bolivia, Yungas Region, La Paz Department, San Antonio, 1800 m, 1895–1896, Garlepp leg. [MFNB].

Type locality. Peru: Cuzco, Cosñipata Valley, Yanamayo, elevation 2350 m, GPS −13.1333, −71.5833.

Etymology. The name is derived from the names of its relatives: *V. viridis*, *V. viridenex*, and *V. subviridis*, and is treated as a noun in apposition.

Distribution. Currently known only from the higher Andes in southern Peru and western Bolivia.

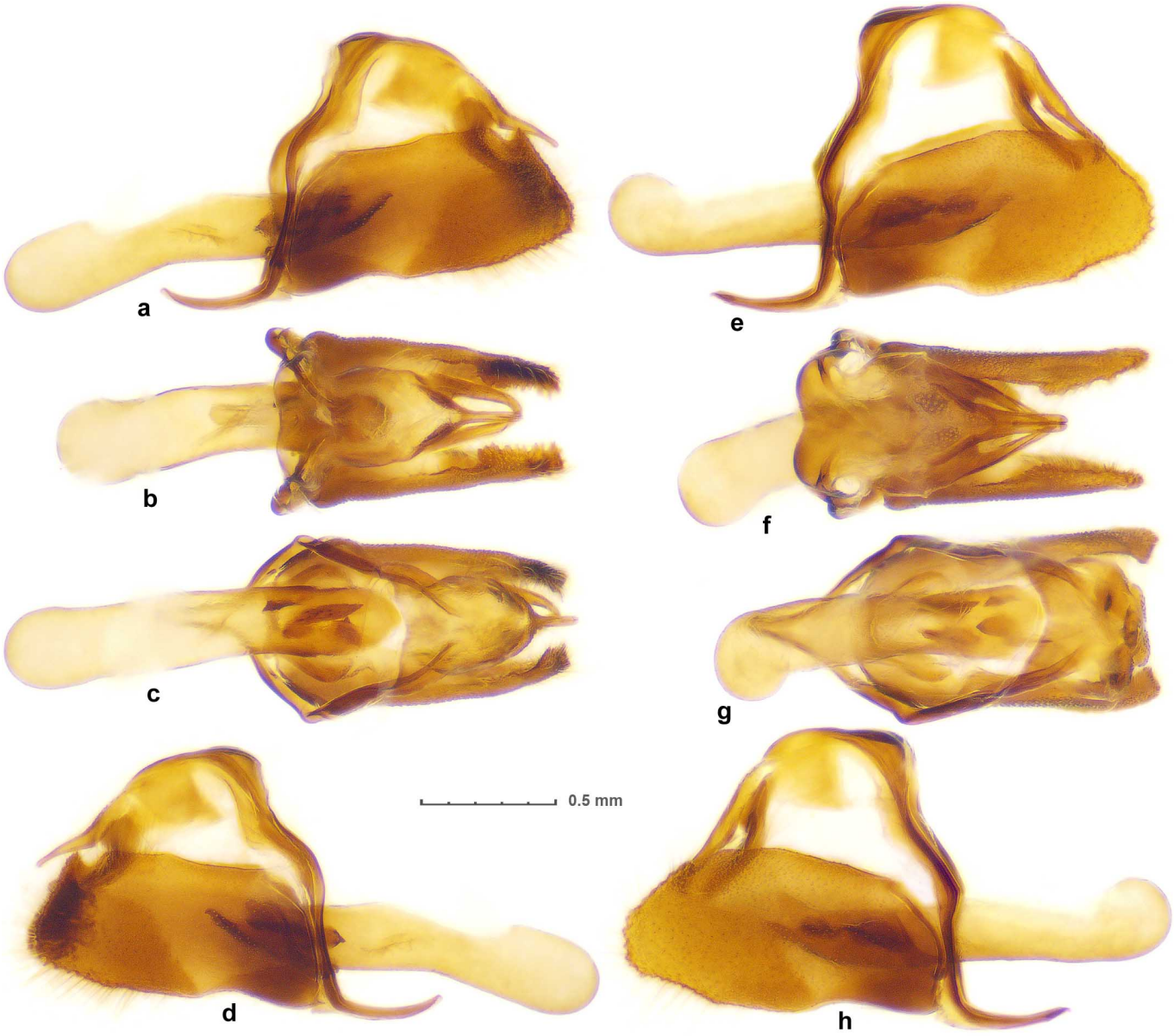

Fig. 94. Male genitalia of *Viridina* holotypes, data in text or below: **a–d)** *V. viridella* **sp. n.** NVG-18125E10 from Peru: Cuzco and **e–h)** *V. viridenex* NVG-19055F04 from Bolivia, 5 days N from Cochabamba, 25-VIII-1899 [MCZ].
Views: **a, e)** left lateral; **b, f)** dorsal; **c, g)** anterodorsal, and **d, h)** right lateral.

Tricrista lingulata Grishin, new species

https://zoobank.org/4AD658F3-6A19-4BA6-ADE2-3DD4AE0B794C

(Figs. 95 part, 96–97)

Definition and diagnosis. Genomic analysis reveals that a male from Rondônia, Brazil, was placed in *Tricrista* Grishin, 2019 (type species *Penicula crista* Evans, 1955) as sister to both *Tricrista cristatus* (Bell, 1930) (type locality in Brazil: Santa Catarina) and *Tricrista crista* (Evans, 1955) (type locality in Venezuela: Suapure) being genetically differentiated from them at the species level (Fig. 95); e.g., their COI barcodes differ by 6.4% (42 bp) (from sympatric *T. crista*), and therefore this male represents a new species. Although we have not sequenced *T. cristina* (Evans, 1955) (type locality in Colombia: Cundinamarca), the new species differs from it by genitalia as detailed below. This new species keys to "*Penicula crista*" (L.10.4) in Evans (1955), but differs from it and other relatives by a more elongated and rounded distal part of the harpe distinct from all congeners (Fig. 97). In facies, mostly dark brown with some ochreous overscaling above, forewing with two discal hyaline spots, a larger and rectangular in cell CuA_1-CuA_2 and a smaller and square in cell M_3-CuA_1 (these two spots are slightly larger than in *T. crista*

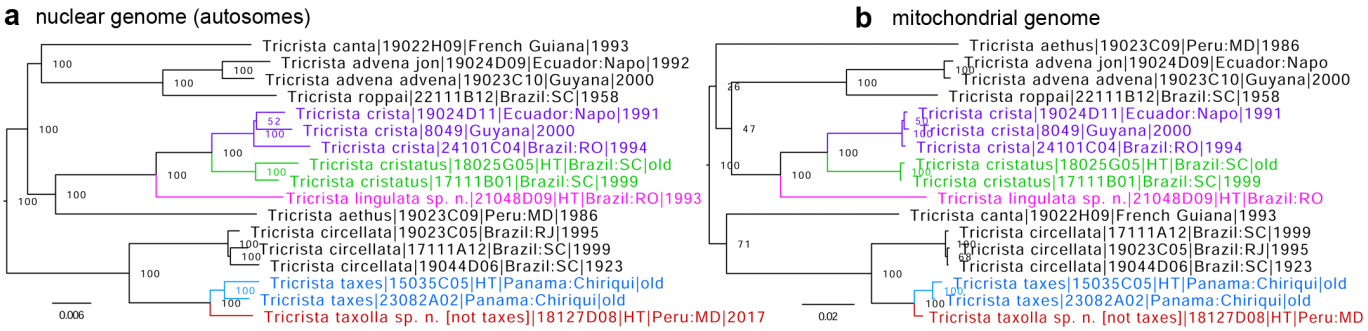

Fig. 95. Phylogenetic trees of selected *Tricrista* species constructed from protein-coding regions in: **a)** the nuclear genome (autosomes), based on 5,081,976 positions, and **b)** the mitochondrial genome. Species discussed in the text are colored: *T. crista* (purple), *T. cristatus* (green), *T. lingulata* **sp. n.** (magenta), *T. taxes* (blue), and *T. taxolla* sp. n. (red). Ultrafast bootstrap (Hoang et al. 2018) values are shown at nodes.

Fig. 96. *Tricrista lingulata* **sp. n.** holotype ♂ NVG-21048D09 in dorsal (left) and ventral (right) views, data in text.

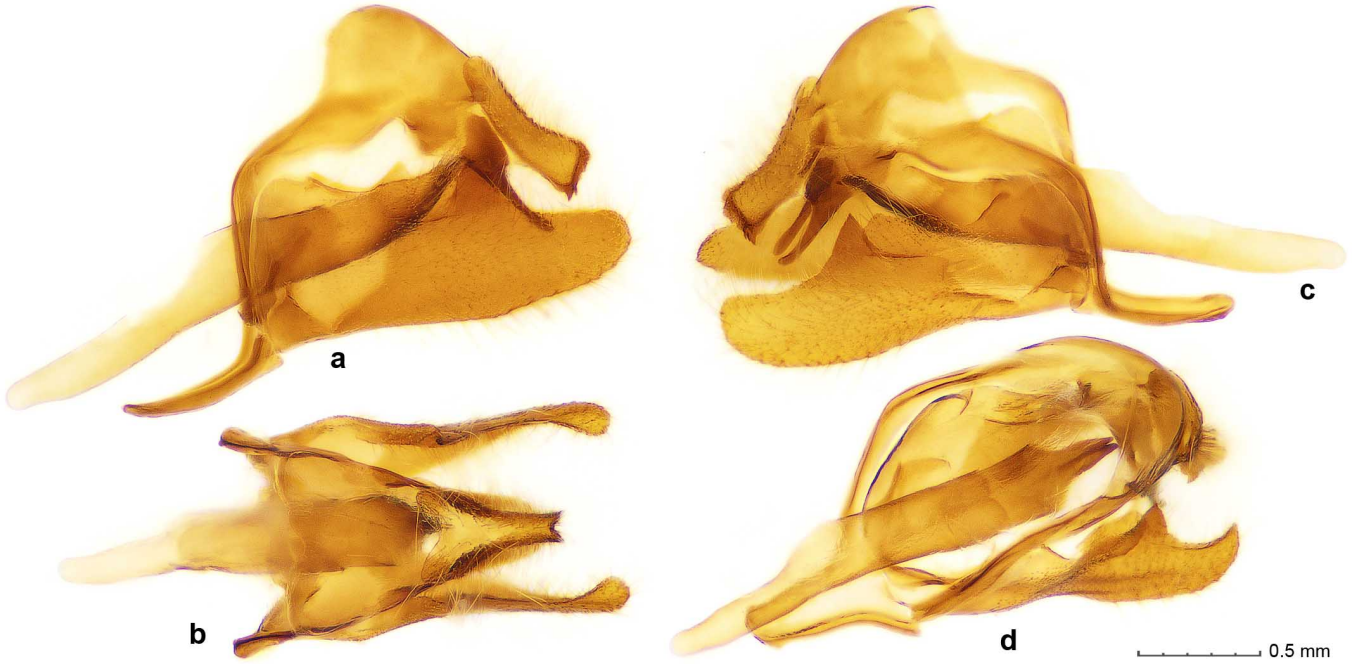

Fig. 97. Male genitalia of *Tricrista lingulata* **sp. n.** holotype NVG-21048D09 in **a)** left lateral, **b)** dorsal, **c)** right dorsolateral, and **d)** left anterodorsal (tilted to the right) views.

and *T. cristina*); a subapical dot in cell R_5-M_1 and a small oval near the anterior margin in the middle of the discal cell; hindwing with a prominent cream-colored spot in cell CuA_2-1A+2A beneath and some weakly expressed postdiscal dots. This species is not cryptic and is confidently identified by phenotype. In DNA, the following are diagnostic base pairs in the nuclear genome: aly536.163.5:A45G, aly536.163.5:A48G, aly536.37.5:A285C, aly536.37.5:C297T, aly671.8.1:C69T, aly1097.14.14:T111T (not A), aly5.7.1:C1806C (not T), aly21.15.3:T255T (not G), aly283.8.3:C342C (not T), aly2096.13.7:A48A (not G); and the COI barcode: A37G, T74C, A100T, T169C, A565G.

Barcode sequence of the holotype. Sample NVG-21048D09, 658 base pairs:

AACTTTATATTTTATTTTTGGAATTTGAGCAGGAATGTTAGGAACTTCCTTAAGATTATTAATTCGTACAGAACTAGGTAATCCTGGATCTTTAATTGGTGATGATCAAATTTATAATACT
ATTGTTACAGCTCATGCTTTTATTATAATTTTTTTTATAGTTATACCCATTATAATTGGTGGATTTGGAAATTGATTAGTTCCATTAATATTAGGGGCTCCTGATATAGCTTTCCCTCGAA
TAAATAATATAAGATTCTGAATACTCCCCCCTTCATTAATATTATTAATTTCAAGAAGAATTGTAGAAAATGGTGCAGGTACTGGATGGACAGTTTACCCCCCTCTTTCTTCTAATATTGC
CCATCAAGGATCATCTGTTGATCTAACAATTTTTTCCCTTCATTTAGCGGGAATTTCTTCCATTTTAGGAGCTATTAATTTCATTACTACAATTATTAATATACGAATTAAAAACCTATCA
TTTGATCAAATACCATTATTTGTATGATCAGTAGGAATTACTGCATTATTATTACTTTTATCTTTACCTGTTTTAGCTGGGGCTATTACAATACTTTTAACAGATCGAAATTTAAATACTT
CTTTTTTTGATCCAGCTGGAGGAGGAGATCCAATTTTATACCAACATTTATTT

Type material. Holotype: ♂ deposited in the McGuire Center for Lepidoptera and Biodiversity collection, Gainesville, FL, USA (MGCL), illustrated in Fig. 96 (genitalia Fig. 97), bears the following four printed rectangular labels (text in italics handwritten), three white: [BRASIL:Rondonia | 67 km S Ariquemes | linea C-10, 5 km S | Cacaulandia | *5* July 1993 | leg. O. Gomes], [Genitalia Vial | GTA-*3645*], [DNA sample ID: | NVG-21048D09 | c/o Nick V. Grishin], and one red [HOLOTYPE ♂ | Tricrista | lingulata Grishin].

Type locality. Brazil: Rondônia, 67 km south of Ariquemes, linha C-10, 5 km south of Cacaulândia.

Etymology. In Latin, *lingulatus* means tongue-shaped and the name, an adjective, reflects the elongated and rounded distal part of the harpe of this new species.

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

Tricrista taxolla Grishin, new species

https://zoobank.org/3D66650E-9CC2-4916-9105-43D3A9B52B2A

(Figs. 95 part, 98a, 99)

Definition and diagnosis. Genomic analysis reveals that a female from southern Peru initially identified as *Tricrista taxes* (Godman, 1900) (type locality in Panama: Chiriquí, holotype sequenced as NVG-15035C05) is genetically differentiated from it at the species level in the nuclear genome (Fig. 95) (although it does not differ strongly in the COI barcode), and therefore this female represents a new species. This new species keys to "*Thoon taxes*" (J.48.5) in Evans (1955), but differs from it and other relatives by females with darker ventral forewing tornus (not with a large pale blotch as in *T. taxes*, Fig. 98b), white cheeks (not yellow), more purplish sheen of the ventral side of the wings (less yellowish), the lamella antevaginalis with sclerotized ridge-like side lobes, and the lamella postvaginalis with an equally sclerotized subulate (but terminally rounded) process on each side. Due to its cryptic nature and unexplored individual variation, this species is best identified by DNA, with diagnostic base pairs in the nuclear genome: aly1350.9.1:T1251A, aly1350.9.1:A1254T, aly536.163.5:A42G, aly974.8.2:C162T, aly2012.8.3:C315G; and the COI barcode: T136C, T313T, T367C, T607T, 616C.

Barcode sequence of the holotype. Sample NVG-18127D08, 658 base pairs:

AACTTTATATTTTATTTTTGGAATTTGAGCAGGAATATTAGGAACTTCTTTAAGAATATTAATCCGAACAGAATTAGGTAATCCAGGATCTTTAATTGGAGATGATCAAATTTATAATACT
ATTGTAACAGCTCACGCTTTTATTATAATTTTTTTTATAGTAATACCTATTATAATTGGAGGATTTGGAAATTGATTAGTTCCTTTAATACTAGGTGCCCCTGATATAGCTTTCCCACGAA
TAAACAATATAAGATTTTGAATACTACCCCCTTCATTAACATTATTAATTTCAAGAAGAATTGTTGAAAATGGTGCAGGAACTGGATGAACAGTATATCCCCCTCTTTCTTCTAATATTGC
CCACCAAGGATCTTCTGTTGATCTAGCAATTTTTTCCCTTCATTTAGCAGGAATTTCTTCTATTCTAGGAGCTATTAATTTTATTACTACAATTATTAATATACGAATTAAAAATTTATCT
TTTGATCAAATACCTTTATTTGTTTGATCTGTAGGAATTACTGCACTTTTATTACTTTTATCATTACCAGTATTAGCAGGAGCTATTACTATATTATTAACAGATCGAAATTTAAATACCT
CTTTTTTTGACCCTGCTGGAGGAGGAGATCCTATTTTATATCAACATTTATTT

Type material. Holotype: ♀ currently in the Dempwolf collection (Austin, Texas, USA), to be deposited in the Museo de Historia Natural, Lima, Peru (MUSM), illustrated in Fig. 98a (genitalia Fig. 99), bears the following seven printed rectangular labels, six white: [Peru: Madre de Dios Dept, | 400m Alto Madre de Dios at | Pantiacolla Lodge 12° 39' S, | 71° 13' W November 7, 2017 | Leg: W. Dempwolf], [Orthos·orthos orthos | ♂ | Coll of: W R Dempwolf], [DNA sample ID: | NVG-18127D08 | c/o Nick V. Grishin], [DNA sample ID: | NVG-24015F11 | c/o Nick V. Grishin], [genitalia | NVG241114-43 | c/o Nick V. Grishin], [WRD 14,945], and one red [HOLOTYPE ♀ | Tricrista | taxolla 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: Madre de Dios Region, Alto Madre de Dios at Pantiacolla Lodge, elevation 400 m, GPS −12.6500, −71.2167.

Etymology. The name reflects the type locality of this new species that is a relative of *tax*[es from Pantiac]*olla* and is treated as a feminine noun in apposition.

Distribution. Currently known only from the holotype collected in the northeastern foothills of the Andes in southern Peru.

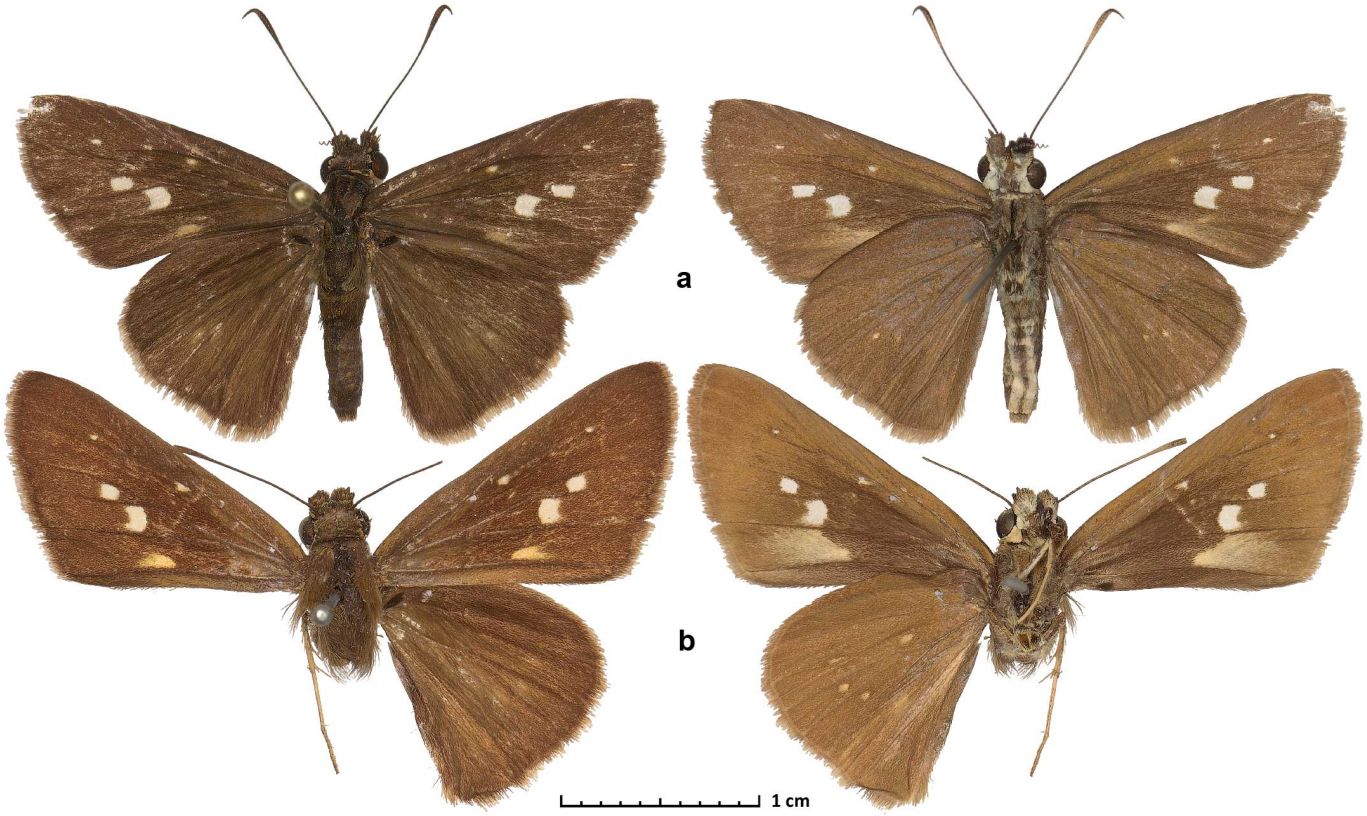

Fig. 98. Females of *Tricrista* in dorsal (left) and ventral (right) views, data in text or below: **a)** *T. taxolla* **sp. n.** holotype NVG-18127D08 Peru: Madre de Dios and **b)** *T. taxes* NVG-23082A02 Panama: Chiriquí, old, C. Ribbe leg. [MFNB].

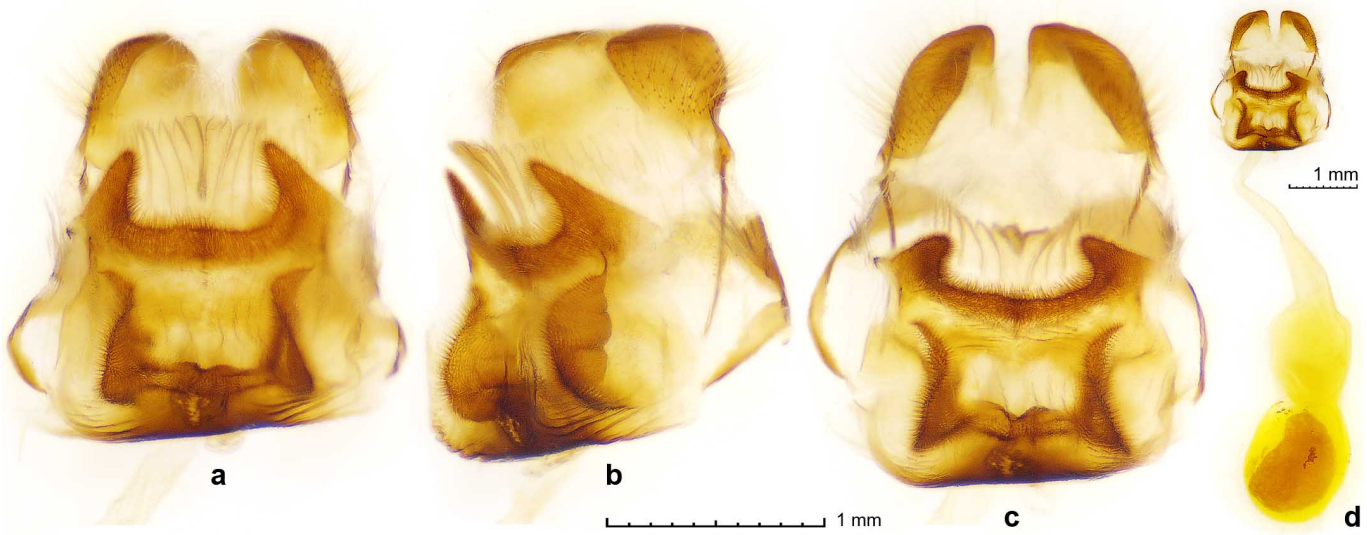

Fig. 99. Female genitalia of *Tricrista taxolla* **sp. n.** holotype NVG-18127D08: **a–c)** sterigma in: **a)** ventral, **b)** right ventrolateral, and **c)** posteroventral views and **d)** complete genitalia in ventral view, reduced, scale shown on the right.

Vettius fuscapicalis Grishin, new species

https://zoobank.org/7E12DF59-EFB1-4506-9AED-EAA30540117F

(Fig. 100 part, 101)

Definition and diagnosis. Genomic analysis reveals that a specimen from eastern Ecuador initially identified as *Vettius richardi* (Weeks, 1906) (type locality in Venezuela: Suapure) is genetically differentiated at the species level (Fig. 100); e.g., their COI barcodes differ by 6.2% (41 bp), and therefore this specimen represents a new species. This new species keys to *Vettius richardi* (J.45.2) in Evans (1955), but differs from it and other relatives by the following combination of characters in males: from *V. richardi* by essentially lacking white overscaling distad of the apical spots on the ventral forewing, a larger central white area of the dorsal hindwing, and a more expressed white area at the ventral hindwing inner margin; and has a spot in the forewing discal cell that most relatives lack. *Vettius crispa* Evans, 1955 (type locality in Brazil: Amazonas) has more extensive white at the hindwing apex beneath, and nearly ½ of the costal cell is white, but the new species has an entirely brown costal cell. *Vettius triangularis* (Hübner, [1829]) (type locality in Brazil) has a more straight outer edge of the white ventral hindwing area, without strongly invading brown in cell CuA_2-1A+2A. Due to its partly cryptic nature and unexplored individual variation, this species is best identified by DNA, with diagnostic base pairs in the nuclear genome: aly536.27.1:G937A, aly694.2.2:A219G, aly270.1.9:T69C, aly270.1.9:G90A, aly270.1.9:A168C, aly890.57.2:G48G (not A), aly1146.42.7:A51A (not G), aly1146.42.7:A63A (not G), aly536.173.1:G147G (not A), aly536.173.1:G162G (not A); and the COI barcode: T5C, T118C, T533C, T610C, A622G, 637C.

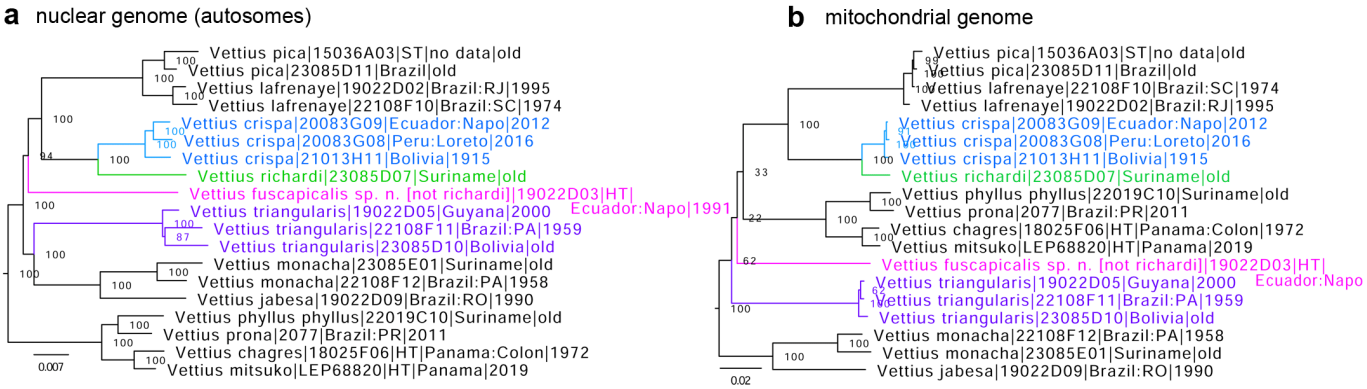

Fig. 100. Phylogenetic trees of selected *Vettius* species constructed from protein-coding regions in: **a)** the nuclear genome (autosomes), based on 4,029,753 positions, and **b)** the mitochondrial genome. Species discussed in the text are colored: *V. crispa* (blue), *V. richardi* (green), *V. fuscapicalis* **sp. n.** (magenta), and *V. triangularis* (purple). Ultrafast bootstrap (Hoang et al. 2018) values are shown at nodes.

Fig. 101. *Vettius fuscapicalis* **sp. n.** holotype ♂ NVG-19022D03 from Ecuador in dorsal (left) and ventral (right) views.

Barcode sequence of the holotype. Sample NVG-19022D03, 658 base pairs:

AACTCTATATTTTATTTTTGGAATTTGAGCAGGAATATTAGGAACTTCTTTAAGCCTTCTTATCCGTACAGAATTAGGTAACCCAGGTTCTTTAATTGGAGATGATCAAATTTATAACACT
ATTGTTACAGCTCATGCTTTTATTATAATTTTTTTTTATAGTTATACCTATCATAATTGGTGGATTTGGAAATTGATTAGTTCCTCTAATACTAGGTGCCCCTGATATAGCTTTCCCCCGAA
TAAATAATATAAGATTCTGAATATTACCTCCCTCTTTAATATTATTAATTTCAAGAAGAATTGTAGAAAATGGTGCAGGAACTGGATGAACAGTTTACCCCCCTCTTTCTTCCAATATTGC
TCATCAAGGATCTTCAGTAGATTTAGCAATTTTTTCCCTTCATTTAGCAGGAATTTCTTCTATTTTAGGAGCTATTAATTTTATTACTACAATTATTAATATACGAATTAGAAATTTATCT
TTTGATCAAATACCTTTATTTGTATGATCAGTAGGTATTACAGCATTACTTTTACTTTTATCTTTACCTGTATTAGCAGGTGCCATTACTATACTTCTAACAGATCGAAATTTAAATACTT
CTTTCTTTGATCCTGCGGGAGGAGGAGATCCCATTTTATACCAACATCTTTTT

Type material. Holotype: ♂ deposited in the National Museum of Natural History, Smithsonian Institution, Washington, DC, USA (USNM), illustrated in Fig. 101, bears the following four printed (text in italics handwritten) rectangular labels, four white: [ECUADOR: Napo Pr | 14 km E Puerto Napo | 01° 03' S, 77° 41' W | 6 Oct 1991 470 m | S S Nicolay leg], [DNA sample ID: | NVG-19022D03 | c/o Nick V. Grishin], [USNMENT | {QR Code} | 01532762], and one red [HOLOTYPE ♂ | Vettius fuscapicalis | Grishin].

Type locality. Ecuador: Napo Province, 14 km east of Puerto Napo, elevation 470 m, GPS −1.0500, −77.6833.

Etymology. The name reflects the dark (*fuscus* in Latin) forewing apex beneath, setting this species apart from its most similar relative *V. richardi*. The name is an adjective.

Distribution. Currently known only from the holotype collected east of the Andes (Oriente) in north-central Ecuador.

Mnasitheus oaxaceus Grishin, new species

https://zoobank.org/FE40EC74-5BBE-4DED-B038-D0778116DCBF

(Fig. 102 part, 103)

Definition and diagnosis. Genomic analysis reveals that a specimen from Oaxaca, Mexico, initially identified as *Mnasitheus chrysophrys* (Mabille, 1891) (type locality in Colombia: Río San Juan) is genetically differentiated from it at the species level in the nuclear genome (Fig. 102) (although it does not differ strongly in the COI barcode), and therefore this specimen represents a new species. This new species keys to *Mnasitheus chrysophrys* (J.32.1) in Evans (1955), but differs from it and other relatives by the following combination of characters in males: a more pointed forewing, paler ventral hindwing with better developed cream-colored overscaling and traces of spots, and a more diffuse cream area at the place of a better defined spot of *M. chrysophrys* in cell CuA_1-CuA_2 on the ventral forewing. Due to its cryptic nature and unexplored individual variation, this species is best identified by DNA, with diagnostic base pairs in the nuclear genome: aly1838.39.2:T2136C, aly159.10.4:A94C, aly1260.26.1:G237A, aly1651.11.2:G225A, aly318.5.6:C102T, aly330.11.2:T1227T (not C), aly1660.8.1:A1314A (not G), aly322.15.3:T279T (not A), aly322.15.3:T324T (not C), aly2563.2.2:A261A (not G); and the COI barcode: A265G, C343C, 352C, A415G, T580C.

Barcode sequence of the holotype. Sample NVG-23114B03, 658 base pairs:

AACTTTATATTTTATTTTTGGTATTTGAGCAGGAATATTAGGAACTTCTTTAAGTTTACTAATTCGAACAGAATTAGGCAATCCTGGATTTTTAATTGGAGATGATCAAATCTATAATACA
ATTGTAACAGCTCATGCTTTTATTATAATTTTTTTTATAGTTATACCAATTATAATTGGAGGATTTGGAAACTGATTAGTTCCTTTAATATTAGGTGCCCCTGATATAGCTTTCCCCCGAA
TAAATAATATAAGATTTTGAATGCTCCCCCCTTCATTAATAATATTAATTTCAAGAAGAATTGTAGAAAATGGTGCTGGAACTGGTTGAACAGTATACCCCCCTTTATCCTCAAATATTGC
TCACCAAGGATCTTCAGTTGATTTAGCAATTTTTTCTCTACATTTAGCTGGGATTTCATCTATTTTAGGAGCTATTAATTTTATTACTACAATTATTAATATACGAATTACAAACATATCA
TTTGATCAAATACCATTATTTGTTTGATCAGTTGGTATTACAGCTTTATTACTACTTTTATCCTTACCTGTATTAGCAGGAGCTATTACTATACTCCTTACTGATCGAAATTTAAATACTT
CATTTTTTGATCCAGCAGGAGGAGGAGATCCTATTCTCTATCAACATTTATTT

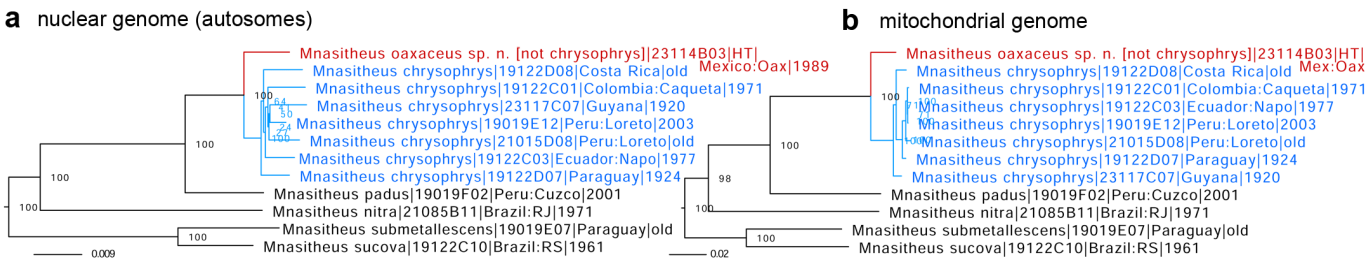

Fig. 102. Phylogenetic trees of selected *Mnasitheus* species constructed from protein-coding regions in: **a)** the Z chromosome, based on 201,813 positions, and **b)** the mitochondrial genome. Species discussed in the text are colored: *M. oaxaceus* **sp. n.** (magenta), *M. chrysophrys* (blue). Ultrafast bootstrap (Hoang et al. 2018) values are shown at nodes.

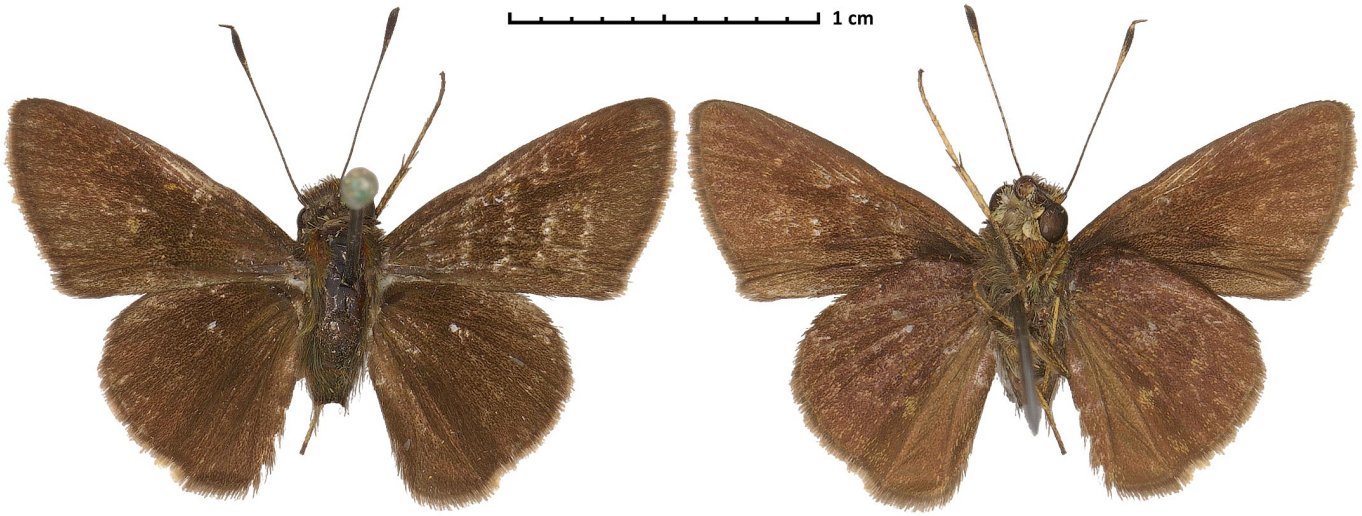

Fig. 103. *Mnasitheus oaxaceus* **sp. n.** holotype ♂ NVG-23114B03 in dorsal (left) and ventral (right) views, data in text.

Type material. Holotype: ♂ deposited in the Carnegie Museum of Natural History, Pittsburgh, PA, USA (CMNH), illustrated in Fig. 103, bears the following six rectangular labels (first three handwritten, others printed, five white: [Mex:Oaxaca:Pluma | Hidalgo - 13Jan1989 | John Kemner], [H-944], [Mnasitheus ♂ | chrysophrys | (Mabille) | det. H.A.Freeman], [Specimen with | abdomen lost | or damaged], [DNA sample ID: | NVG-23114B03 | c/o Nick V. Grishin], and one red [HOLOTYPE ♂ | Mnasitheus | oaxaceus Grishin]. The distal half of the abdomen is missing in the holotype, and H-944 is the number for a genitalia dissection prepared by H. A. Freeman. However, the vial with H-944 was not located in the collection.

Type locality. Mexico: Oaxaca, Pochutla District, Pluma Hidalgo.

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

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

A male of *Lychnuchus* (*Enosis*) *valle* Grishin, 2023

Lychnuchus (*Enosis*) *valle* Grishin, 2023 (type locality in Colomba: Valle del Cauca, nr. Cali) was described from females only and males remained unknown. Genomic sequencing reveals the first male of this species (Fig. 104, NVG-23121E05) illustrated here in Fig. 105 from Ecuador: Pichincha, Tandapi, 1500 m, 12-Sep-1976, S. S. Nicolay leg. [USNM]. The male is very similar to its sister species *Lychnuchus* (*Enosis*) *topo* Nicolay, 1980 (type locality Ecuador: Tungurahua, Río Topo) and differs from it by a more rounded basal section of the anterior segment of the brand and a smaller area of darker scales (androconia?) around the brand. It is likely that the two species are sympatric in Colombia and Ecuador.

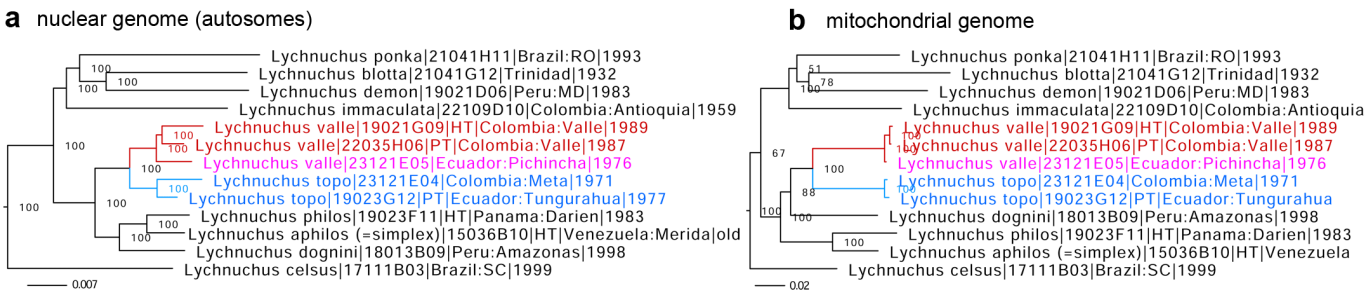

Fig. 104. Phylogenetic trees of selected *Lychnuchus* species constructed from protein-coding regions in: **a)** the nuclear genome (autosomes), based on 4,375,047 positions, and **b)** the mitochondrial genome. Species discussed in the text are colored: *L. (Enosis) valle* (red, with the male specimen labeled in magenta) and *L. (Enosis) topo* (blue). Ultrafast bootstrap (Hoang et al. 2018) values are shown at nodes.

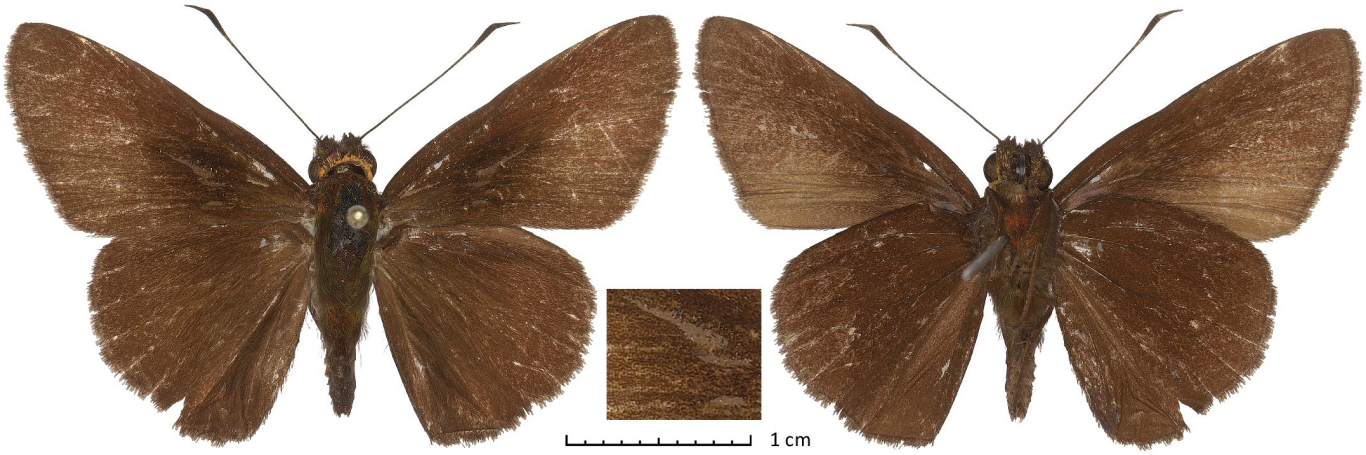

Fig. 105. *Lychnuchus* (*Enosis*) *valle* ♂ NVG-23121E05 from Ecuador in dorsal (left) and ventral (right) views, data in text. The inset shows a magnified view (brightened for clarity) of the brand on the left forewing.

Tarmia bolivia Grishin, new species

https://zoobank.org/42AAF903-A85E-4E1D-8499-948CA815D522

(Fig. 106 part, 107)

Definition and diagnosis. Genomic analysis reveals that a specimen from Bolivia initially identified as *Tarmia monastica* Lindsey, 1925 (type locality Peru: Junín, Río Tarma, Huacapistana) is genetically differentiated at the species level in the nuclear genome (Fig. 106); e.g., their COI barcodes differ by 4.6% (30 bp). This new species keys to "*Phanes monastica*" (J.23.7) in Evans (1955), but differs from it and other relatives by more prominent pale spots in the postdiscal area of the forewing and better developed dark spots on the ventral hindwing framing paler postdiscal spots distad. 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: aly798.33.74:T66G, aly233.6.2:T48G, aly2178.42.3:T136C, aly5434.3.1:T180C, aly5434.3.1:T186C, aly707.14.14:C54C (not T), aly2012.17.5:G81G (not C), aly728.8.7: C39C (not T); and the COI barcode: T38C, T163C, T169C, T562G, C616T.

Barcode sequence of the holotype. Sample NVG-23079C05, 658 base pairs:

AACTTTATATTTTATTTTTGGAATTTGAGCAGGAATACTAGGAACTTCTTTAAGTTTACTAATTCGTACAGAATTAGGAAATCCAGGCTCATTAATTGGAGATGATCAAATTTATAATACT
ATTGTTACAGCTCATGCTTTTATTATAATTTTTTTTATAGTCATACCCATTATAATTGGAGGATTTGGAAATTGATTAATTCCATTAATATTAGGAGCACCTGATATAGCCTTCCCACGAA
TAAATAATATAAGATTCTGAATATTACCCCCTTCATTAATATTACTAATTTCAAGAAGAATTGTTGAAAATGGGGCAGGAACTGGATGAACAGTTTATCCCCCTCTTTCTTCTAATATTGC
TCATCAAGGTTCTTCTGTTGATTTAGCAATTTTTTCTCTTCATTTAGCAGGAATTTCTTCTATTTTAGGAGCTATTAATTTTATTACAACAATCATTAATATACGAATTAGAAATTTATCA
TTTGACCAAATACCCCTATTTGTCTGATCAGTGGGAATTACAGCTTTATTATTACTTTTATCTTTACCTGTATTAGCGGGAGCTATTACCATACTTTTAACTGACCGAAATTTAAATACTT
CTTTTTTTGATCCTGCAGGAGGAGGAGATCCAATTTTATATCAACATTTATTT

Type material. Holotype: ♀ deposited in the Museum für Naturkunde, Berlin, Germany (MFNB), illustrated in Fig. 107, bears the following four printed rectangular labels, three white: [Songo | Bol. | Garl.], [Coll. Staudinger], [DNA sample ID: | NVG-23079C05 | c/o Nick V. Grishin], and one red [HOLOTYPE ♀ | Tarmia bolivia | Grishin]. According to its label, the holotype was collected in Bolivia: Rio Zongo by O. Garlepp. The abdomen is missing in the holotype.

Type locality. Bolivia: La Paz Department, Rio Zongo.

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

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

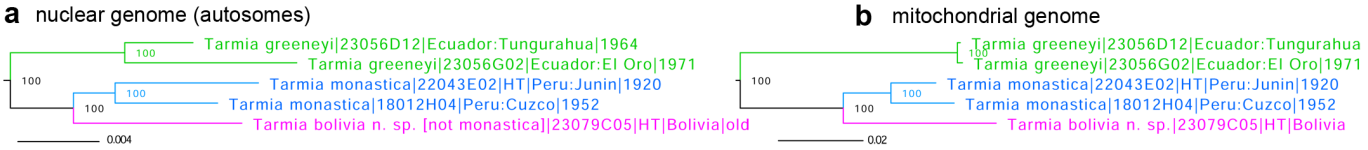

Fig. 106. Phylogenetic trees of *Tarmia* species constructed from protein-coding regions in: **a)** the nuclear genome (autosomes), based on 3,103,833 positions, and **b)** the mitochondrial genome. Different species are colored differently: *T. greeneyi* (green), *T. monastica* (blue), and *T. bolivia* **sp. n.** (magenta). Ultrafast bootstrap (Hoang et al. 2018) values are shown at nodes.

Fig. 107. *Tarmia bolivia* **sp. n.** holotype ♀ NVG-23079C05 in dorsal (left) and ventral (right) views, data in text.

Artines tines Grishin, new species

https://zoobank.org/CF5A1026-F4BB-4053-9D8C-8B037CA7F2FA

(Figs. 108 part, 109a–b, 110)

Definition and diagnosis. Genomic analysis reveals that specimens from the eastern part of the Guianas initially identified as *Artines focus* Evans, 1955 (Guyana: Roraima) are genetically differentiated from it at the species level (Fig. 108); e.g., their COI barcodes differ by 1.8% (12 bp), and therefore these specimens represent a new species. This new species keys to *A. focus* (J.12.2) in Evans (1955) and was probably included by him in this species, but differs from it and other relatives by the following combination of characters: the spike at the end of the harpe is longer, the uncus is narrower in lateral view, and the spike on the aedeagus is narrower; the ventral forewing typically has a darker area just distad of the discal cell (ground color in *A. focus* (Fig. 109c) and *Artines cofus* Medeiros & Dolibaina, 2019 (type locality in Brazil: Rondônia) (Fig. 109d)), the ventral hindwing tornus is not overscaled with darker brown in the middle, the central black spot on the ventral hindwing is larger than in *A. focus* (similar in size to *A. cofus*), and the bluish spots around it are slightly smaller. 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: aly1984.5.3:G1176A, aly2124.3.16:A40G, aly2124.3.16:G84A, aly536.173.5:A70G, aly536.173.5:A96T; and the COI barcode: A28A, T151C, C343T, T424C, A517A.

Barcode sequence of the holotype. Sample NVG-21046H10, 658 base pairs:

AACTTTATATTTTATTTTCGGAATCTGAGCAGGTATATTAGGAACTTCTCTAAGTTTATTAATTCGAACAGAATTAGGTAATCCTGGTTCTTTAATTGGAGATGATCAAATTTATAATACT
ATTGTAACAGCCCATGCTTTTATTATAATCTTTTTTATAGTTATACCTATTATAATTGGAGGATTTGGAAATTGATTAGTTCCTTTAATATTAGGTGCCCCTGATATAGCTTTCCCACGAA
TAAATAATATAAGATTCTGAATACTACCCCCTTCTTTAATACTATTAATTTCTAGAAGAATTGTTGAAAATGGTGCAGGTACTGGTTGAACTGTTTACCCTCCTCTTTCTTCAAATATTGC
TCATCAAGGATCTTCAGTAGATTTAGCAATTTTTTCTTTACATCTAGCAGGAATTTCTTCCATTTTAGGAGCTATTAATTTTATTACTACTATCATTAATATACGAGTTAGAAATTTATCT
TTTGATCAAATACCCCTATTTGTTTGATCTGTAGGAATTACAGCTTTATTATTACTTTTATCTCTGCCTGTTTTAGCTGGAGCTATTACTATACTTCTTACCGATCGAAATTTAAATACTT
CATTTTTTGATCCTGCTGGAGGAGGAGATCCAATCTTATATCAACATTTATTT

Type material. Holotype: ♂ deposited in the McGuire Center for Lepidoptera and Biodiversity collection, Gainesville, FL, USA (MGCL), illustrated in Fig. 109a (genitalia Fig. 110), bears the following six printed rectangular labels, five white: [FR. GUIANA, Montagne de Kaw | Roura, 38km E | 14 Dec 1997 Leg: WHR JG166], [W. Russell coll. | MGCL Accession | # 2010-27], [DNA sample ID: |

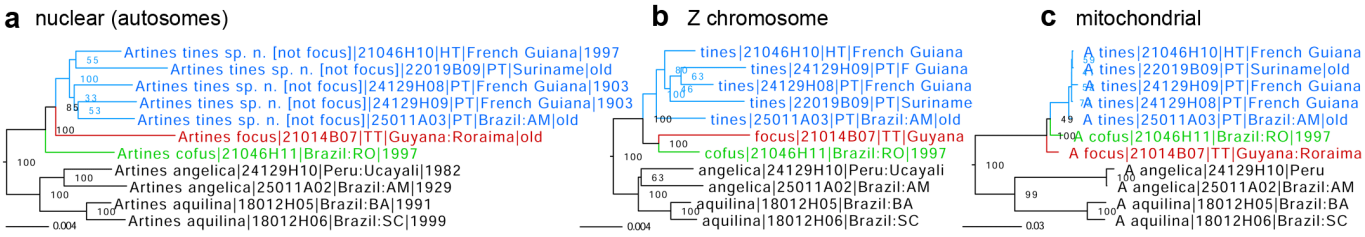

Fig. 108. Phylogenetic trees of selected *Artines* species constructed from protein-coding regions in: **a)** the nuclear genome (autosomes), based on 1,570,428 positions, **b)** the Z chromosome, based on 224,166 positions, and **c)** the mitochondrial genome. Different species discussed in the text are colored differently: *A. tines* **sp. n.** (blue), *A. focus* (red), and *A cofus* (green). Ultrafast bootstrap (Hoang et al. 2018) values are shown at nodes.

NVG-21046H10 | c/o Nick V. Grishin], [DNA sample ID: | NVG-24129H06 | c/o Nick V. Grishin], [genitalia | NVG250720-39 | c/o Nick V. Grishin], and one red [HOLOTYPE ♂ | Artines tines | 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♂♂ and 1♀: French Guiana, Maroni River,

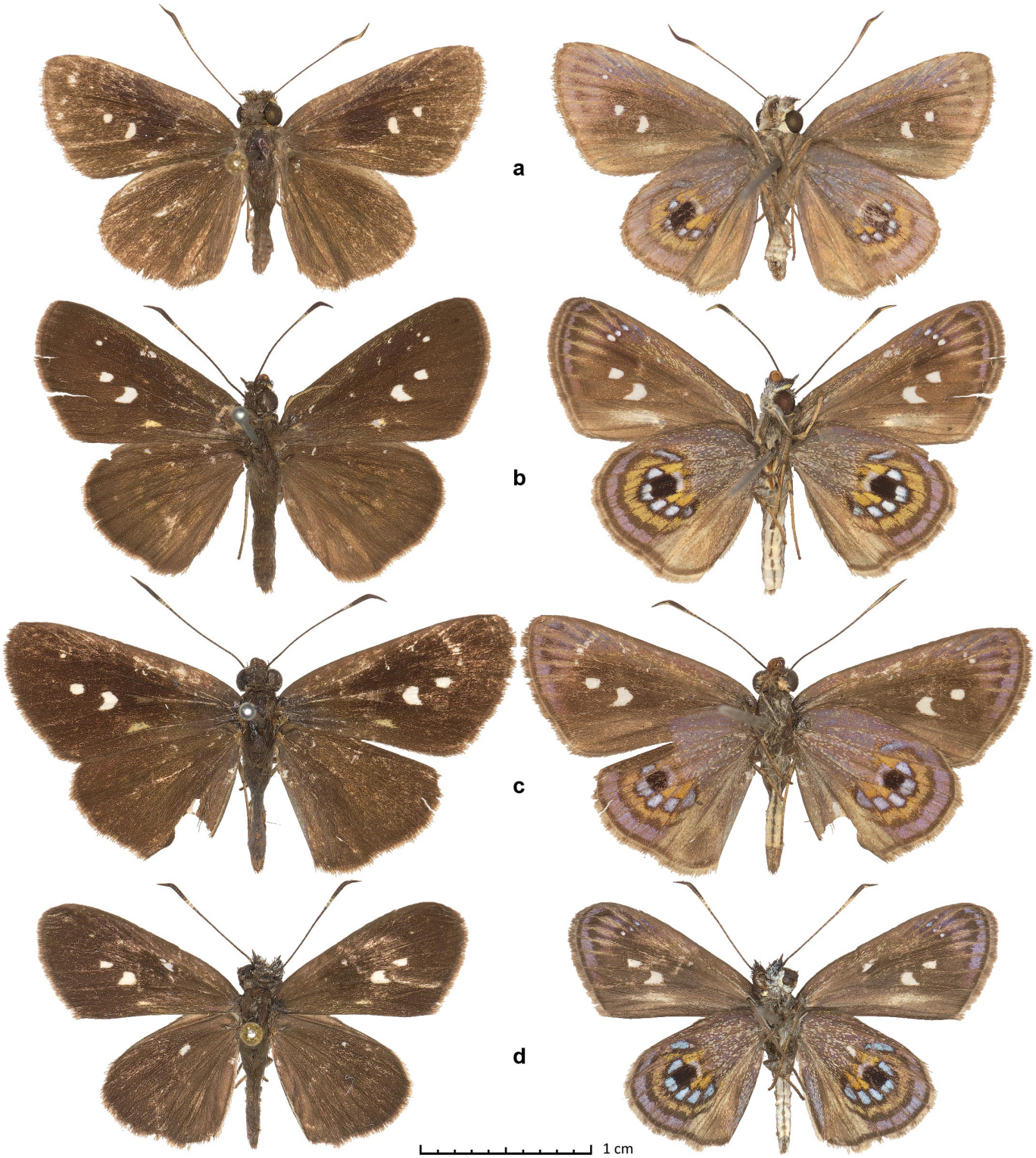

Fig. 109. Specimens of *Artines* in dorsal (left) and ventral (right) views, data in text and below: **a)** *A. tines* **sp. n.** holotype ♂ NVG-21046H10 from French Guiana, **b)** *A. tines* **sp. n.** paratype ♀ NVG-22019B09 from Suriname, **c)** *A. focus* topotype ♂ NVG-21014B07 from the same series as the holotype, Guyana: Roraima, old, H. Whitely leg. [CMNH], **d)** *A. cofus* ♂ NVG-21046H11 from Brazil: Rondônia, 62 km S of Ariquemes, linha C-10, 5 km S of Cacaulândia, 15-Apr-1997, G. T. Austin leg. [MGCL].

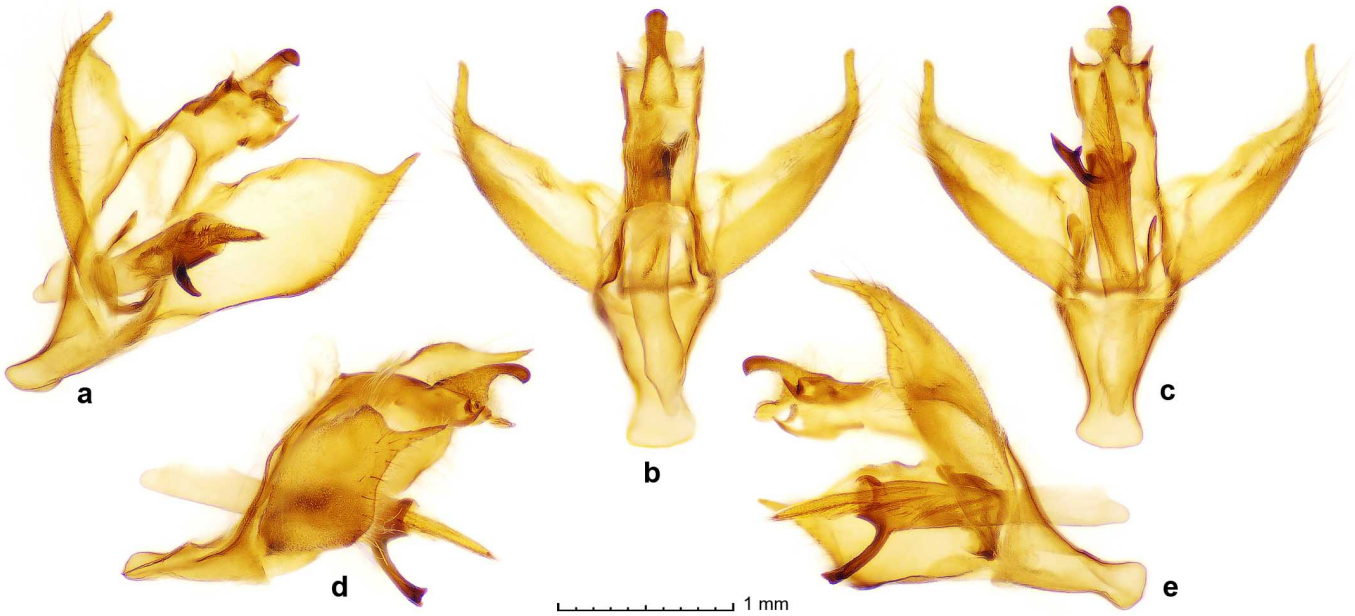

Fig. 110. Male genitalia of *Artines tines* **sp. n.** holotype NVG-21046H10 (valvae open) in: **a)** left posterolateral, right valva aligned with the plane of the image, **b)** dorsal, **c)** ventral, **d)** left lateral, and **e)** right ventrolateral views.

ex coll. E. Le Moult [MGCL]: 1♂ NVG-24129H08 1903 and 1♂ NVG-24129H09 Oct-Nov-1903, genitalia SRS-2641; 1♀ NVG-22019B09 Suriname, May-Sep-old, Fruhstorfer [ZSMC] (Fig. 109b); and 1♂ NVG-25011A03 Brazil: Amazonas, Ipiranga, Purus River, old, ex coll. E. Le Moult [MGCL].

Type locality. French Guiana: Roura, 38 km east of Montagne de Kaw.

Etymology. The specific epithet *tines* (treated as a noun in apposition) is derived from the English word 'tines', meaning pointed, projecting spikes or prongs. The name refers to the sharp, long spike on the valva and a narrower, spike-like uncus in the male genitalia of this new species. The Latinized pronunciation is 'TEE-nes'. It rhymes with the genus name 'ahr-TEE-nees', which we assume to be a Greek word Ἀρτίνης (Artínēs), a masculine proper name, and pronounce it accordingly.

Distribution. Currently known from French Guiana, Suriname and Brazil: Amazonas.

Subtribe Calpodina A. Clark, 1948

Calpodes hewitsoni supernalis Grishin, new subspecies

https://zoobank.org/83FB8184-258E-46D3-8BCC-BAC7354C5935

(Figs. 111 part, 112)

Definition and diagnosis. Genomic analysis reveals that specimens from southern Mexico identified as *Calpodes hewitsoni* (Riley, 1926) (type locality in Peru: Loreto) are genetically differentiated from it at the subspecies level in the nuclear genome, forming a prominent strongly supported clade (Fig. 111 green vs. brown), although their COI barcodes do not differ, and therefore these specimens represent a new subspecies. This new subspecies keys to "*Saliana hewitsoni*" (O.14.10) in Evans (1955), but differs from it by the following combination of characters: forewing large semihyaline spots are rounder; the anterior arm of the discal cell spot is less developed and not prominently separated from the rest of the spot; the semihyaline spot in the hindwing cell CuA_1-CuA_2 is larger; and the spot between veins M_1 and M_3 is more strongly notched by the vein M_2 and narrows in the middle. 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: aly536.216.4:T127C, aly536.216.4:T174C, aly827.2.1:C438T, aly827.2.1:T456A, aly320.21.3:C105A; and the COI barcodes do not differ from the nominotypical subspecies.

Barcode sequence of the holotype. Sample NVG-24129E05, 658 base pairs:

AACTTTATATTTTATTTTTGGTATTTGAGCAGGAATATTAGGTACTTCATTAAGTTTATTAATTCGTACTGAATTAGGTAATCCTGGCTCATTAATTGGAGATGATCAAATTTATAATACT
ATTGTTACAGCTCACGCTTTTATTATAATTTTTTTTATAGTTATACCTATTATAATTGGAGGATTTGGAAATTGATTAGTTCCTTTAATATTAGGTGCTCCTGATATAGCTTTCCCTCGAA
TAAATAATATAAGATTTTGAATACTTCCCCCTTCATTAACTTTATTAATTTCAAGAAGAATTGTAGAAAATGGTGCAGGAACAGGTTGAACAGTTTATCCCCCCCTTTCATCTAATATTGC
TCACCAAGGATCATCAGTTGATTTAGCAATTTTTTCTTTACATTTAGCAGGAATCTCATCAATTTTAGGAGCTATTAATTTCATCACTACAATTATTAATATACGAATTAAAAATTTAATA
TTTGACCAAATACCTTTATTTGTTTGATCTGTAGGAATTACAGCACTATTATTATTATTATCATTACCAGTTTTAGCAGGAGCTATCACTATACTTCTTACAGATCGAAATTTAAATACAT
CTTTTTTTGACCCTGCAGGAGGAGGTGACCCTATCTTATATCAACATTTATTT

Type material. Holotype: ♂ deposited in the McGuire Center for Lepidoptera and Biodiversity collection, Gainesville, FL, USA (MGCL), illustrated in Fig. 112a, bears the following eight rectangular labels (6th handwritten, others printed with handwritten text shown in italics; 4th pink, last red, others white): [T. Escalante | *Santa Rosa* | *Comitan* | *IX-65*], [A. C. Allyn | Acc. 1973-48], [MGCL/FMNH | Specimen no. | 36247], [ ] no text on this label, [Saliana | hewitsoni ♂], [PHOTOGRAPHED | FOR BUTTERFLIES | OF AMERICA], [DNA sample ID: | NVG-24129E05 | c/o Nick V. Grishin], and [HOLOTYPE ♂ | Calpodes hewitsoni | supernalis Grishin]. **Paratype:** 1♂ NVG-24129E06 Mexico: Oaxaca, Río Sarabia, Aug-1958, T. Escalante leg. [MGCL] (Fig. 112b).

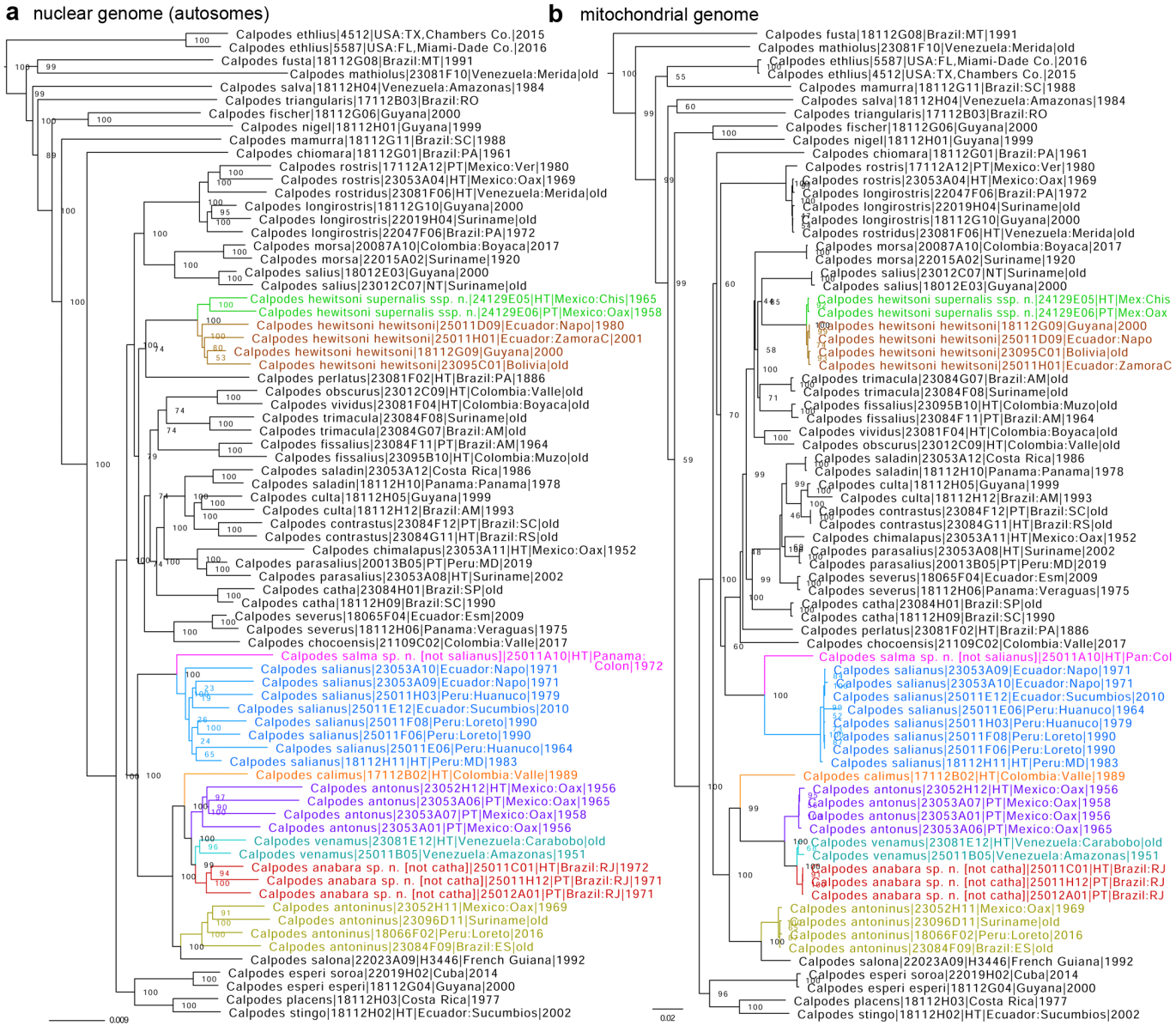

Fig. 111. Phylogenetic trees of all described *Calpodes* species constructed from protein-coding regions in: **a)** the nuclear genome (autosomes), based on 2,161,233 positions, and **b)** the mitochondrial genome. Taxa discussed in the text are colored: *C. hewitsoni supernalis* **ssp. n.** (green), *C. hewitsoni hewitsoni* (brown), *C. salma* **sp. n.** (magenta), *C. salianus* (blue), *C. calimus* (orange), *C. antonus* (purple), *C. venamus* (cyan), *C. anabara* **sp. n.** (red), and *C. antoninus* (olive). Ultrafast bootstrap (Hoang et al. 2018) values are shown at nodes.

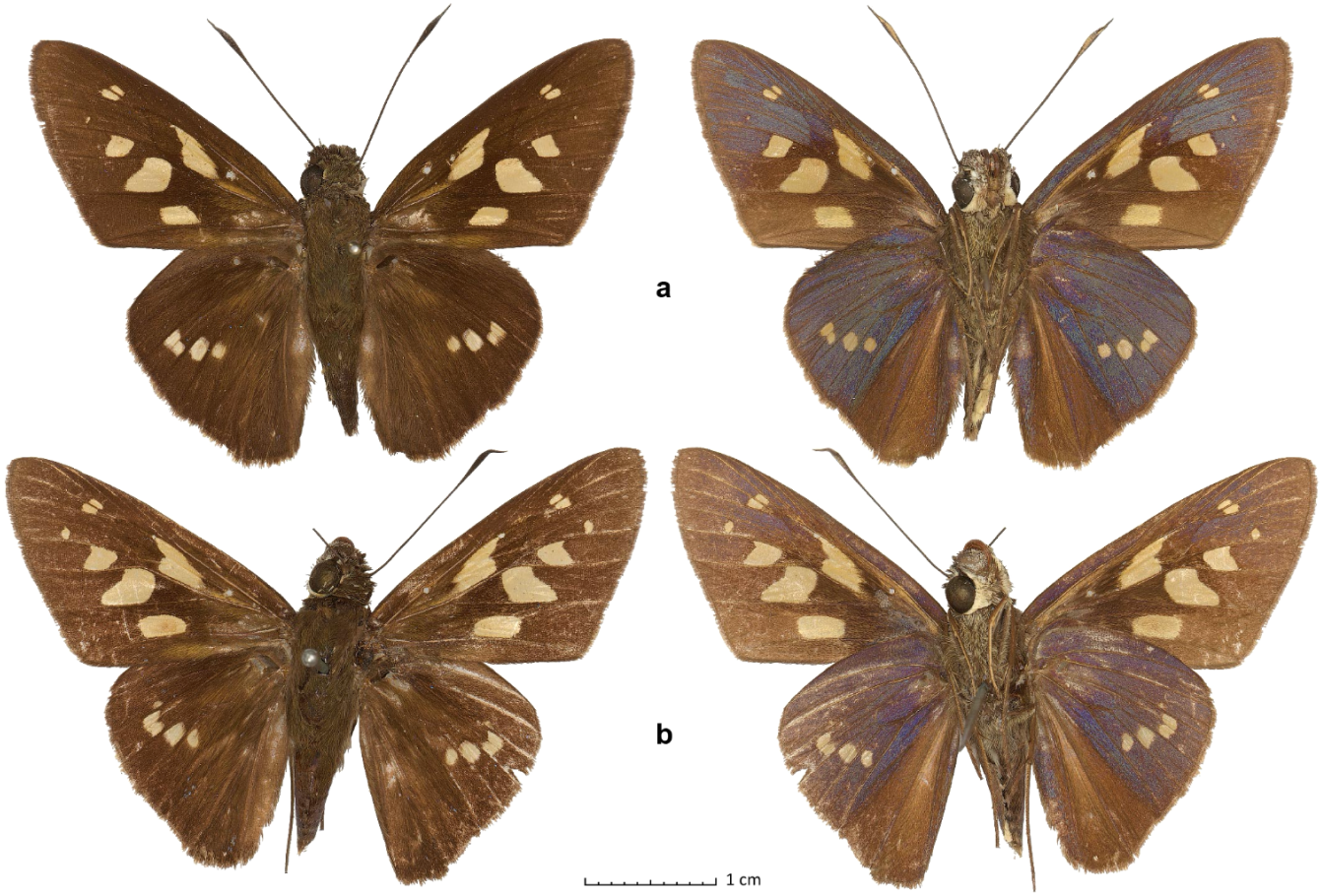

Fig. 112. Type series of *Calpodes hewitsoni supernalis* **ssp. n.** from Mexico in dorsal (left) and ventral (right) views, data in text: **a)** holotype ♂ NVG-24129E05 from Chiapas and **b)** paratype ♂ NVG-24129E06 from Oaxaca.

Type locality. Mexico: Chiapas, Santa Rosa Comitán.

Etymology. The name is formed from Latin *supernus* (meaning upper or above) with a suffix *-alis* (meaning pertaining to, relating to), and refers to the northernmost range of this subspecies. The name is an adjective.

Distribution. Currently known from the states of Oaxaca and Chiapas in Mexico.

Calpodes salma Grishin, new species

https://zoobank.org/275EDB9D-0281-4244-AA15-E9DF107C61F1

(Figs. 111 part, 113)

Definition and diagnosis. Genomic analysis reveals that a female from central Panama initially identified as *Calpodes salianus* Grishin, 2023 (type locality in Peru: Madre de Dios) is indeed its sister but is genetically differentiated at the species level (Fig. 111); e.g., their COI barcodes differ by 5.8% (38 bp), and therefore this female represents a new species. This new species keys to "*Saliana salius*" (O.14.17) in Evans (1955), but differs from it and other relatives by the following combination of characters in females: three (not two as in various species keying to "*Saliana salius*" in Evans) semihyaline subapical spots on the forewing; a more tawny (less yellow) costal area in the basal half of the ventral forewing; a straighter boundary between the pale base and dark marginal half of the ventral hindwing from costa to the vein CuA_1; nearly absent whitish suffusion around the ventral forewing semihyaline spot in cell CuA_2-1A+2A; and a less elongated semihyaline spot in the forewing cell CuA_1-CuA_2. Due to its cryptic nature and unexplored individual variation, this species is best identified by DNA, with diagnostic base pairs in the nuclear genome: aly527.15.2:T63G, aly527.15.2:C99T, aly6002.6.6:A169G, aly1651.27.7:C39T, aly1651.27.

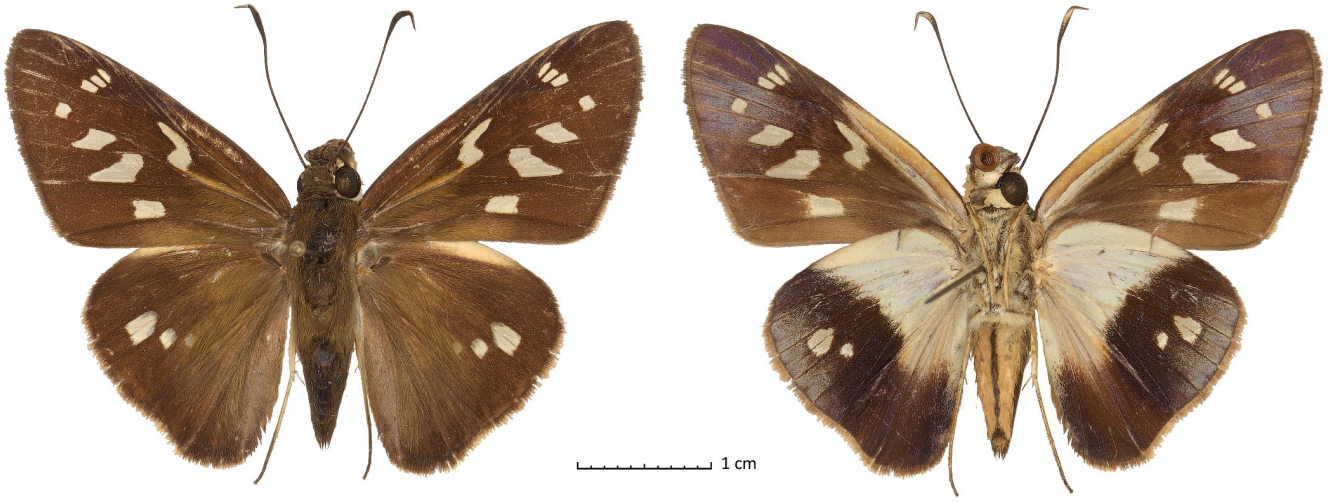

Fig. 113. *Calpodes salma* **sp. n.** holotype ♀ NVG-25011A10 in dorsal (left) and ventral (right) views, data in text.

7:C57T, aly8937.5.1:G762G (not A), aly8937.5.1:A1740A (not C), aly8937.5.1:G1971G (not A), aly5294.22.3:A630A (not T), aly5294.22.3:C666C (not A); and the COI barcode: T13C, T38C, A202G, T397C, A474G.

Barcode sequence of the holotype. Sample NVG-25011A10, 658 base pairs:

AACTTTATACTTCATTTTCGGTATTTGAGCAGGAATACTAGGTACTTCTTTAAGTTTATTAATTCGTACTGAATTAGGTAATCCTGGTTCATTAATTGGAGATGACCAAATTTATAATACT
ATTGTTACAGCTCATGCTTTTATTATAATTTTTTTTATAGTAATACCTATTATAATTGGAGGATTTGGAAATTGATTAGTGCCATTAATATTAGGTGCTCCTGATATGGCCTTCCCCCGAA
TGAATAATATAAGATTTTGAATACTTCCCCCTTCATTAACCTTACTAATTTCGAGAAGAATTGTAGAAAATGGTGCAGGAACAGGTTGAACAGTTTATCCCCCTCTTTCAGCTAATATCGC
TCACCAAGGATCCTCCGTTGATTTAGCAATTTTCTCTTTACATTTAGCAGGAATTTCATCAATTTTAGGAGCTATTAATTTTATTACTACAATTATTAATATACGAATTAGAAATTTAATA
TTTGATCAAATACCATTATTTGTTTGATCTGTAGGAATTACAGCATTATTATTATTATTATCATTACCAGTTTTAGCAGGAGCTATCACAATACTTCTTACTGATCGAAATTTAAACACAT
CATTTTTTGATCCTGCAGGAGGAGGTGACCCTATTTTATACCAACATTTATTT

Type material. Holotype: ♀ deposited in the McGuire Center for Lepidoptera and Biodiversity collection, Gainesville, FL, USA (MGCL), illustrated in Fig. 113, bears the following four printed rectangular labels (text in italics handwritten), three white: [PANAMA: COLON | Piña, 100 m. | *31.vii-1972* | H. L. King], [A. C. Allyn | Acc. 1972-5], [DNA sample ID: | NVG-25011A10 | c/o Nick V. Grishin], and one red [HOLOTYPE ♀ | Calpodes | salma Grishin].

Type locality. Panama: Colón Province, Piña, elevation 100 m.

Etymology. The name is derived from the name of its sister species, *C. salianus*, made shorter and to indicate the type locality in Panama. The name is treated as a noun in apposition.

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

Calpodes anabara Grishin, new species

https://zoobank.org/6810B53D-75A5-41C7-9514-540C90113744

(Figs. 111 part, 114)

Definition and diagnosis. Genomic analysis reveals that specimens from Rio de Janeiro, Brazil, identified as *Calpodes catha* (Evans, 1955) (type locality in Brazil: Santa Catarina) are not monophyletic with it and instead form a clade sister to *Calpodes venamus* Grishin, 2025 (type locality in Venezuela: Carabobo, Puerto Cabello) genetically differentiated from it at the species level in the nuclear genome (Fig. 111), although not differing strongly in the COI barcode, and therefore these specimens represent a new species. This new species keys (incompletely) to "*Saliana saladin catha*" (O.14.18(c)) in Evans (1955), but differs from it and other relatives by the following combination of characters in males: a more weakly developed orange-yellow area between the veins 1A+2A and 3A from the base of the ventral hindwing to the brown half of the wing, where the color is redder than yellower, the wings are broader and the hindwing is more rounded with a longer discal cell and this comparatively wider pale basal area; the semihyaline spot in the forewing discal cell has a rounder posterior segment and a more elongated and thinner anterior segment; and the posterior segment of the semihyaline doublet between hindwing veins

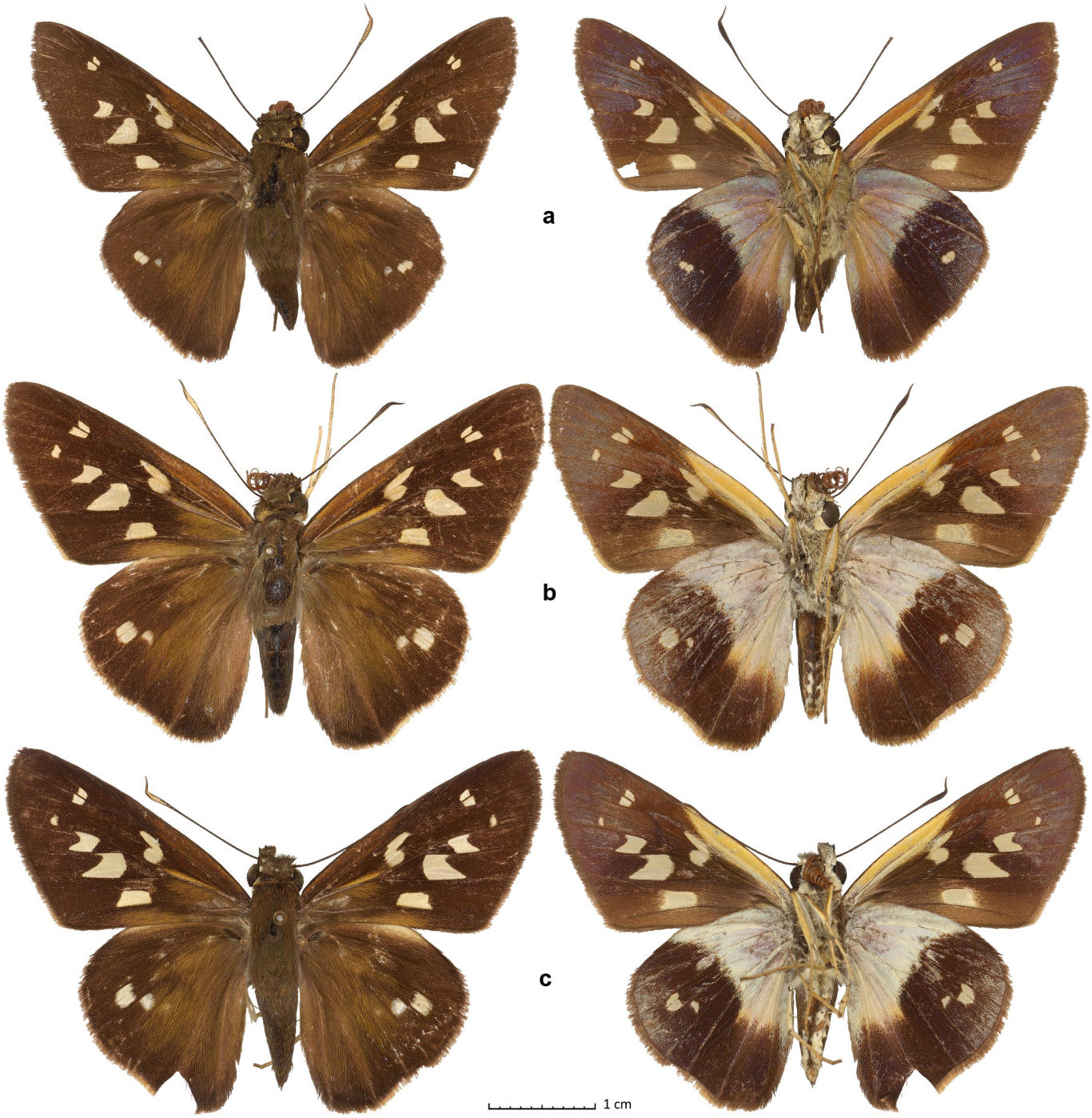

Fig. 114. Type series of *Calpodes anabara* **sp. n.** from Brazil: Rio de Janeiro in dorsal (left) and ventral (right) views, data in text: **a)** holotype ♂ NVG-25011C01 and paratypes ♀♀: **b)** NVG-25011H12, and **c)** ♀ NVG-25012A01.

M_1 and M_3 is slightly shifted basad rather than distad compared to *C. venamus*. Due to its cryptic nature and unexplored individual variation, this species is best identified by DNA, with diagnostic base pairs in the nuclear genome: aly1139.48.12:G36A, aly1229.9.12:C1779T, aly1651.36.1:A930G, aly1487.3.7:C99T, aly1487.3.7:G108C; and the COI barcode: T439C, T553C, A562C, T601C, T646C.

Barcode sequence of the holotype. Sample NVG-25011C01, 658 base pairs:

AACTTTATATTTTATTTTTGGTATTTGAGCAGGAATATTAGGTACTTCATTAAGATTATTAATTCGTACTGAATTAGGTAATCCTGGATCATTAATTGGAGATGATCAAATTTATAATACT
ATTGTTACAGCTCATGCTTTTATTATAATTTTCTTTATAGTTATACCTATTATAATTGGAGGATTTGGAAATTGATTAGTTCCATTAATACTAGGAGCCCCTGATATAGCTTTTCCTCGAA
TAAATAATATAAGATTTTGAATACTCCCCCCTTCATTAACTTTATTAATTTCAAGAAGAATTGTAGAAAATGGTGCAGGAACAGGTTGAACAGTTTATCCCCCTCTTTCAGCTAATATTGC
TCATCAAGGATCCTCTGTTGATTTAGCAATTTTTTCTCTTCATTTAGCAGGAATTTCATCAATTTTAGGAGCTATCAATTTTATTACCACAATTATTAATATACGAGTTAAAAACTTAATG
TTTGATCAAATACCATTATTTGTTTGATCTGTAGGAATTACAGCATTATTATTACTTTTATCTTTACCCGTTTTAGCCGGAGCTATTACCATATTACTTACTGATCGAAATTTAAACACAT
CTTTTTTTGACCCCGCAGGAGGAGGTGATCCTATTTTATACCAACATTTATTT

Type material. Holotype: ♂ deposited in the McGuire Center for Lepidoptera and Biodiversity collection, Gainesville, FL, USA (MGCL), illustrated in Fig. 114a, bears the following four printed rectangular labels (text in italics handwritten), three white: [BRASIL: GUANABARA | Gavea Pequena | 25. III. 1972 | C. Callaghan], [A. C. Allyn | Acc. 1972-30], [DNA sample ID: | NVG-25011C01 | c/o Nick V. Grishin], and one red [HOLOTYPE ♂ | Calpodes anabara | Grishin]. **Paratypes:** 2♀♀ from Brazil: Rio de Janeiro, C. Callaghan leg. [MGCL]: NVG-25011H12 nr. Suruí, km 14 of Rio-Teresópolis Hwy, 5-Jul-1971 (Fig. 114b) and NVG-25012A01 Magé, km 20 of Rio-Petrópolis Hwy, 2-May-1971 (Fig. 114c).

Type locality. Brazil: Rio de Janeiro, Gávea Pequena.

Etymology. The name is derived from the type locality in the former state of [Gu]*anabara* and is treated as a noun in apposition.

Distribution. Currently known from the Southeast Region in Brazil.

Subtribe Carystina Mabille 1878

Talides megamaca Grishin, new species

https://zoobank.org/C2FFE293-8093-4FC8-9239-5587050F329D

(Figs. 115 part, 116)

Definition and diagnosis. Genomic analysis reveals that specimens from southern Mexico initially identified as *Talides alternata* E. Bell, 1941 (type locality in Brazil: Santa Catarina, holotype sequenced as NVG-18025D05) are genetically differentiated from it at the species level (Fig. 115); e.g., their COI barcodes differ by 6.2% (41 bp), and therefore these specimens represent a new species. This new species keys to "*Talides alternata alternata*" (K.13.3(a)) in Evans (1955), but differs from it and other relatives by the following combination of characters: semihyaline spots on the forewing are larger than in all described species in the genus, in particular the discal cell spot, which may be longer than wide; the semihyaline spot in the forewing cell CuA_1-CuA_2 does not adjoin the spot in cell M_3-CuA_1, as it does in *Talides cantra* Evans, 1955 (type locality in Guatemala), but is placed in the middle between the latter spot and the origin of the vein CuA_1; and the wings are not as produced as in *T. cantra*, but are less rounded than in *T. alternata*. Due to poorly explored individual variation, this species is best identified by DNA, with diagnostic base pairs in the nuclear genome: aly2487.23.1:T1086A, aly808.4.3:C114T, aly1402.9.1:T199A, aly1402.9.1:G202A, aly1402.9.1:C273T; and the COI barcode: T74C, T121C, G200A, T457C, A631T.

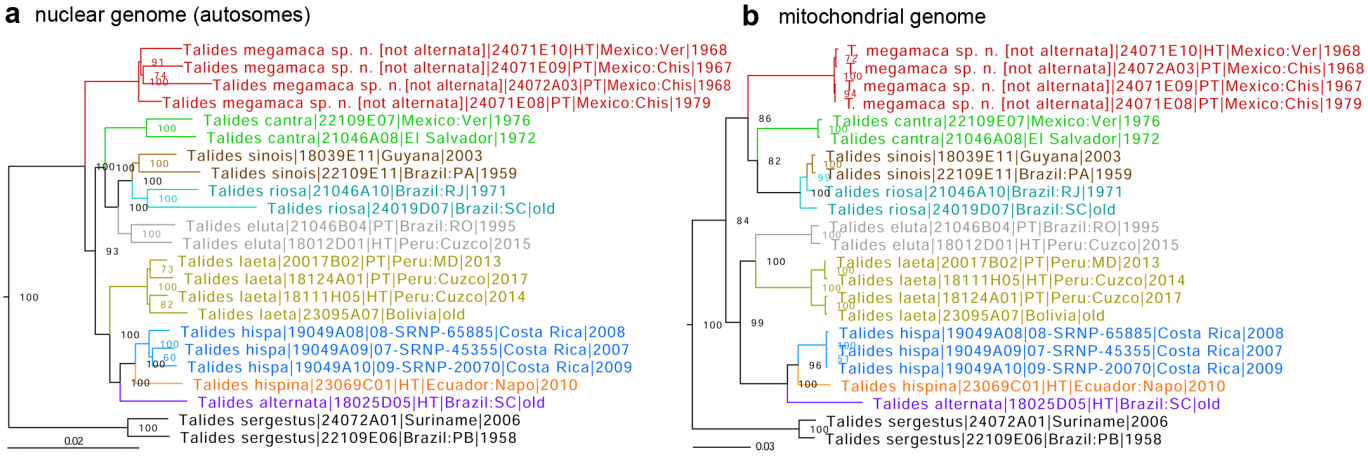

Fig. 115. Phylogenetic trees of all described *Talides* species constructed from protein-coding regions in: **a)** the nuclear genome (autosomes), based on 6,995,334 positions, and **b)** the mitochondrial genome. Different species are colored differently: *T. megamaca* **sp. n.** (red), *T. cantra* (green), *T. sinois* Hübner, [1819] (brown), *Talides riosa* Evans, 1955 (cyan), *T. eluta* Grishin, 2023 (gray), *T. laeta* Grishin, 2023 (olive), *T. hispa* Evans, 1955 (blue), *T. hispina* Grishin, 2025 (orange), *T. alternata* (purple), *T. sergestus* (Cramer, 1775) (black). Ultrafast bootstrap (Hoang et al. 2018) values are shown at nodes.

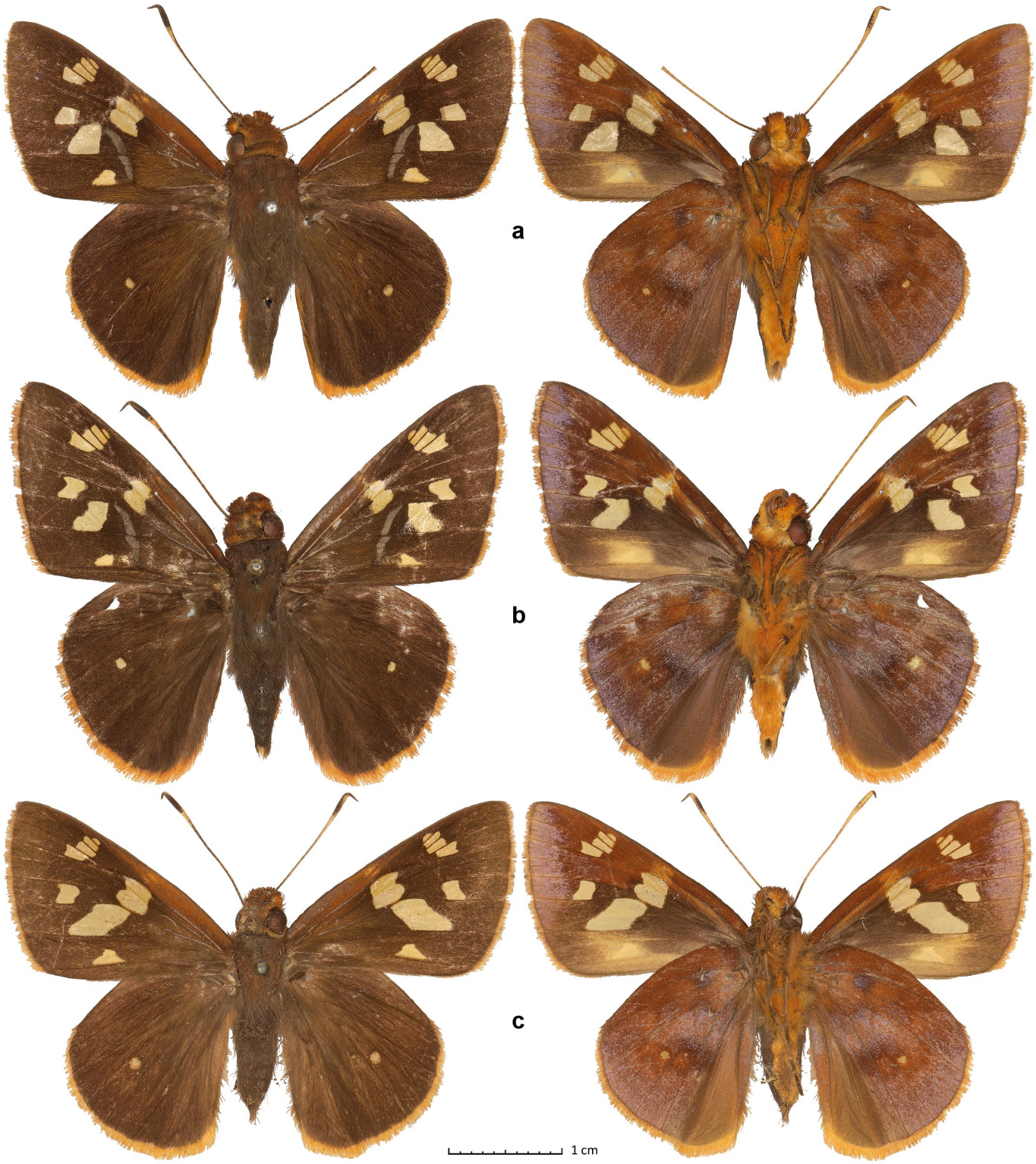

Fig. 116. *Talides megamaca* **sp. n.** type specimens from Mexico in dorsal (left) and ventral (right) views, data in text: **a)** holotype ♂ NVG-24071E10 Veracruz, **b)** paratype ♂ NVG-24071E08 Chiapas, and **c)** paratype ♀ NVG-24071E09 Chiapas.

Barcode sequence of the holotype. Sample NVG-24071E10, 658 base pairs:

AACTTTATATTTTATTTTTGGAATTTGAGCAGGAATATTAGGAACTTCATTAAGATTATTAATTCGAACAGAACTAGGTAATCCAGGATTTTTAATCGGAGATGATCAAATTTATAATACC
ATTGTAACAGCTCATGCTTTTATTATAATTTTTTTCATAGTTATACCTATTATAATTGGAGGATTTGGAAATTGATTAATCCCCCTTATATTAGGAGCCCCTGATATAGCTTTCCCCCGAA
TAAATAATATAAGATTTTGAATACTTCCACCCTCTTTAATATTATTAATTTCAAGAAGAATTGTAGAAAATGGTGCCGGTACTGGATGGACCGTATACCCCCCTCTTTCAGCTAATATTGC
TCATCAAGGTTCTTCTGTTGATTTAGCAATTTTTTCCTTACATTTAGCAGGAATTTCTTCTATTTTAGGAGCTATTAATTTTATTACAACAATCATCAATATACGAATTAAAAATTTATTA
TTTGACCAAATACCCTTATTTGTTTGATCTGTAGGAATTACAGCTTTATTATTATTATTATCTTTACCTGTATTAGCAGGAGCTATTACAATACTTCTTACTGATCGTAATTTAAATACTT
CATTTTTTGATCCTGCAGGTGGAGGTGATCCTATTTTATATCAACATTTATTT

Type material. Holotype: ♂ deposited in the McGuire Center for Lepidoptera and Biodiversity

collection, Gainesville, FL, USA (MGCL), illustrated in Fig. 116a, bears the following six printed rectangular labels (text in italics handwritten; 4th pink, last red, others white): [T. Escalante | *Catemaco* | *Ver·VI·68*], [A. C. Allyn | Acc. 1973-48], [MGCL/FLMNH | Specimen no. | 35311], [ ] no text on this label, [DNA sample ID: | NVG-24071E10 | c/o Nick V. Grishin], and [HOLOTYPE ♂ | Talides megamaca | Grishin]. **Paratypes:** 1♂ and 2♀♀: Mexico: Chiapas [MGCL]: 1♂ NVG-24071E08, MGCL/FLMNH 35312 San Antonio, 4000', 19-Sep-1979, R. Wind leg. (Fig. 116b) and Santa Rosa Comitán, T. Escalante leg.: 1♀ NVG-24071E09, MGCL/FLMNH 35313, Mar-1967 (Fig. 116c) and 1♀ NVG-24072A03, Jul-1968.

Type locality. Mexico: Veracruz, Catemaco.

Etymology. The name reflects large spots in this new species: *mega* + *mac*[ul]*a*[e], as treated as a noun in apposition.

Distribution. Currently known from the states of Veracruz and Chiapas in Mexico.

Tribe Pericharini Grishin, 2019; Subtribe Pericharina Grishin, 2019

Perichares guatine Grishin, new species

https://zoobank.org/65374B0F-76D2-4FE6-A210-28561D8D9BC5

(Figs. 117 part, 118)

Definition and diagnosis. Genomic analysis reveals that a pair from Guatemala identified as *Perichares saptine* Godman & Salvin, 1879 (type locality in Costa Rica: Irazú) is genetically differentiated from it at the species level (Fig. 117); e.g., their COI barcodes differ by 2.4% (16 bp), and therefore this pair represents a new species. This new species keys to *Lychnucoides* [sic] *saptine* (K.29.2) in Evans (1955), but differs from it and other relatives by the following combination of characters: forewing fringes are not prominently yellow by the forewing tornus; the semihyaline spot in the forewing cell CuA_1-CuA_2 is rounded at the proximal margin and does not reach the boomerang-shaped brand in the male; and the darker marginal patch in the anterior half of the ventral hindwing cell CuA_1-1A+2A is longer and reaching farther basad, in the male more contrasting with the paler and warmer brown color of the patch in cell CuA_1-CuA_2. Due to its cryptic nature and unexplored individual variation, this species is best identified by DNA, with diagnostic base pairs in the nuclear genome: aly203.5.1:T198C, aly517.8.2: T111C, aly320.2.13:T336C, aly349.7.6:C249T, aly6841.59.8:A57G; and the COI barcode: A37G, T154C, T287C, T349G, T376C, T616C.

Barcode sequence of the holotype. Sample NVG-18111G04, 658 base pairs:

AACTTTATATTTTATTTTTGGTATTTGAGCAGGTATGTTAGGTACATCTTTAAGTTTATTAATTCGTACTGAATTAGGTAACCCAGGATCCTTAATTGGAGATGATCAAATTTATAATACT
ATTGTTACAGCTCATGCTTTTATTATAATTTTCTTTATAGTTATACCTATTATAATTGGAGGATTTGGAAATTGATTAGTACCTCTTATATTAGGGGCCCCCGATATAGCTTTCCCCCGAA
TAAATAATATAAGATTTTGAATATTACCCCCATCCTTAACTCTTCTAATTTCAAGAAGAATTGTTGAAAATGGTGCCGGAACTGGATGAACAGTTTATCCCCCCCTGTCATCCAATATTGC
ACATCAAGGATCCTCAGTTGATTTAGCAATTTTTTCCTTACATTTAGCAGGAATTTCCTCAATTTTAGGAGCTATTAACTTTATTACTACCATTATTAATATACGAATTATAAATATAACA
TTTGATCAAATACCATTATTTGTTTGATCTGTAGGTATTACAGCATTATTATTATTATCTTTACCAGTATTAGCAGGAGCTATTACTATACTTTTAACTGATCGAAATTTAAATACTT
CTTTTTTTGACCCAGCTGGAGGTGGAGATCCTATTTTATACCAACATTTATTT

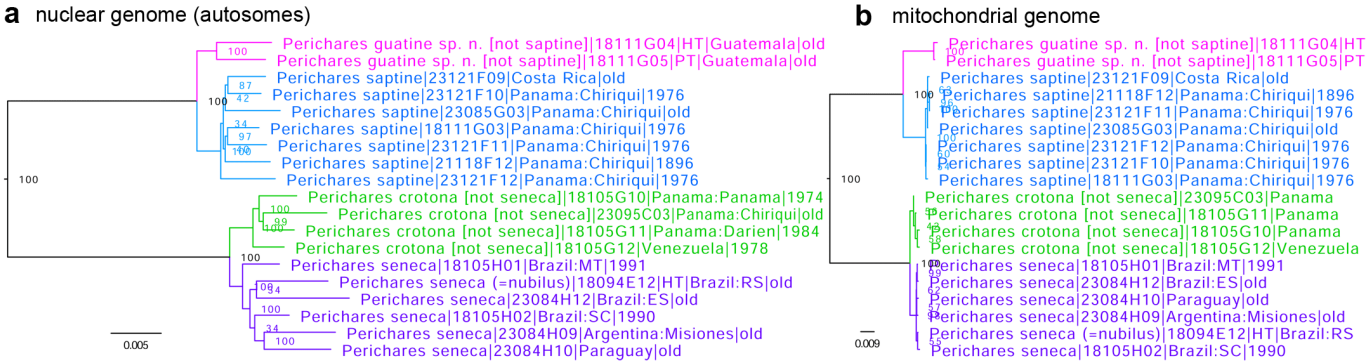

Fig. 117. Phylogenetic trees of several *Perichares* species constructed from protein-coding regions in: **a)** the nuclear genome (autosomes), based on 11,092,893 positions, and **b)** the mitochondrial genome. Different species are colored differently: *P. guatine* **sp. n.** (magenta), *P. saptine* (blue), *P. crotona* **stat. rest.** (green), and *P. seneca* (purple). Ultrafast bootstrap (Hoang et al. 2018) values are shown at nodes.

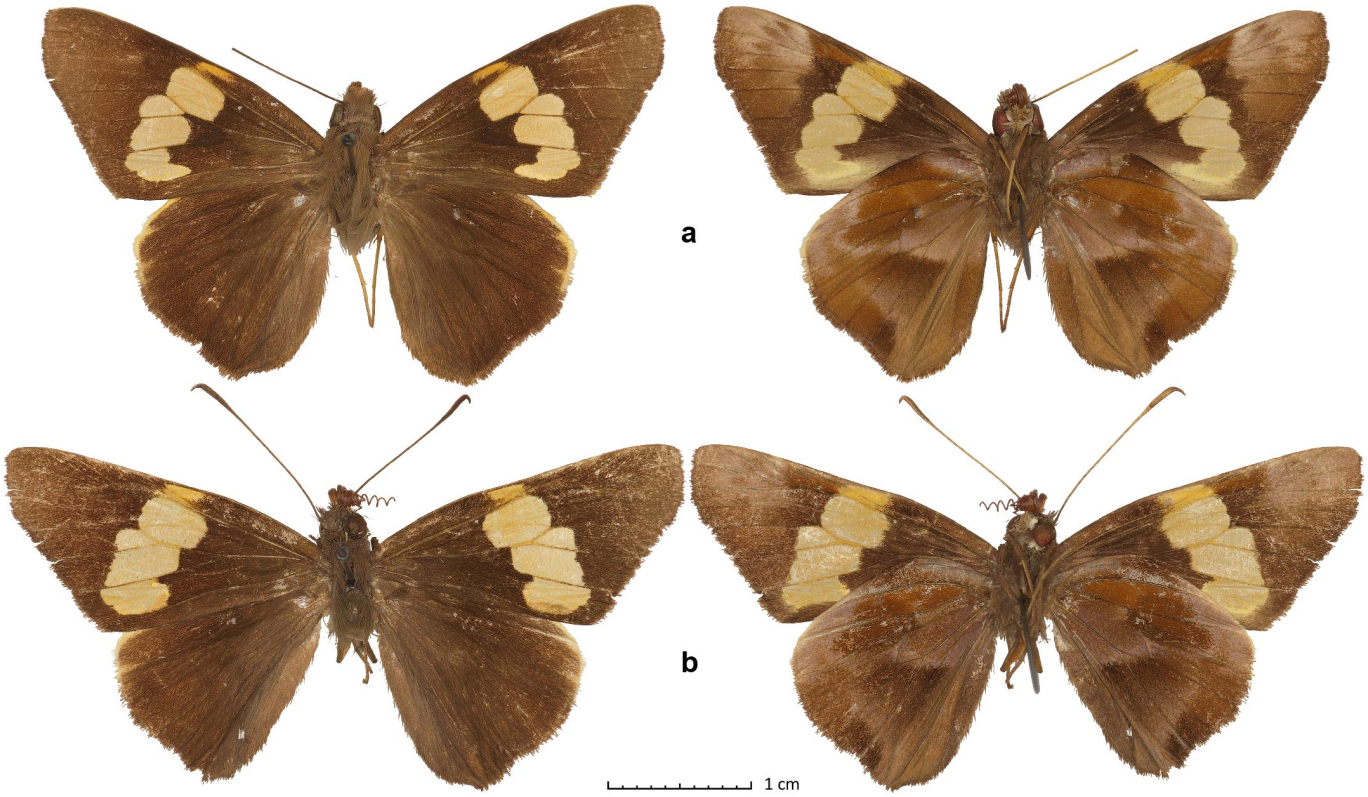

Fig. 118. *Perichares guatine* **sp. n.** from Guatemala in dorsal (left) and ventral (right) views, data in text: **a)** holotype ♂ NVG-18111G04 and **b)** paratype ♀ NVG-18111G05.

Type material. Holotype: ♂ deposited in the National Museum of Natural History, Smithsonian Institution, Washington, DC, USA (USNM), illustrated in Fig. 118a, bears the following seven printed rectangular labels (text in italics handwritten), six white: [Volcan |StaMaria | Guat], [Nov.], [Schaus and | Barnes | coll], [GENITALIA NO. | X-*1878* | J.M.Burns 198*3*], [DNA sample ID: | NVG-18111G04 | c/o Nick V. Grishin], [USNMENT | {QR Code} | 01531330], and one red [HOLOTYPE ♂ | Perichares guatine | Grishin]. **Paratype:** 1♀ NVG-18111G05 with the same data as the holotype, genitalia X-1879 (Fig. 118b).

Type locality. Guatemala: Quetzaltenango Department, Santa María Volcano.

Etymology. The name is a fusion: *guat*[emalan] + [sapt]*ine*, and is treated as a noun in apposition.

Distribution. Currently known only from Guatemala.

Perichares crotona (Hewitson, 1866) is a species distinct from *Perichares seneca* (Latreille, [1824])

Genomic analysis reveals that *Hesperia crotona* Hewitson, 1866 (type locality in Venezuela) currently regarded as a subspecies of *Perichares seneca* (Latreille, [1824]) (type locality in Brazil, likely in Southeast Brazil) is genetically differentiated from it at the species level in the nuclear genome (COI barcodes do not differ strongly) (Fig. 117) and therefore is a species-level taxon. Thus, *Perichares crotona* (Hewitson, 1866), **stat. rest.** is a species distinct from *Perichares seneca* (Latreille, [1824]).

Lectotype designation for *Proteides hyas* Mabille, 1891

Proteides hyas Mabille, 1891, currently a junior subjective synonym of *Perichares deceptus fulvimargo* (Butler, 1873) (type locality in Venezuela), was described from an unstated number of males (probably

only one, but we avoid the assumption of the holotype to follow the ICZN Code Recommendation 73F) from "Cauca" [Colombia] (Mabille 1891). We found a single syntype of *P. hyas* in the MFNB collection known to house part of Mabille's type material. The syntype agrees well with the original description, which we translate from French as: "Brown; forewings with four white hyaline spots, namely: two small spots in the cell, each against the opposite margin; two median spots in spaces 4 and 3; in addition, an apical dot, and an oblique scaly streak running from vein 3 to vein 1. Fringe dirty yellowish. Wing base metallic blue. Hindwings with base covered with metallic blue hairs; a yellow border and fringe along the posterior margin. Underside reddish brown, with the apical and outer part of the forewings lilac, crossed beneath the apex by a brown band ending at vein 2. Hindwings lilac with two reddish-brown bands, the first along the anterior margin, the second toward the middle, posterior margin yellow as well as the fringe. Body blackish. Collar hair-like scales metallic blue. Abdomen beneath yellow; palpi shaded with gray. Legs long and slender, reddish brown. 43 mm. — ♂ — Cauca." (Mabille 1891). To stabilize nomenclature and define the name *P. hyas* objectively, N.V.G. hereby designates the syntype in the MFNB collection, a male that bears the following eight labels (1st purple, others white; 2nd–5th handwritten, others printed): [Origin.], [Cauca | Kalbr.], [Prot. Hyas | Mb.], [Proteid. | Hyas | Mab.], [Hÿas | Mab.], [Coll. | Staudinger], [{QR Code} http://coll.mfn-berlin.de/u/ | 44a042], and [DNA sample ID: | NVG-18043B07 | c/o Nick V. Grishin], as the **lectotype** of *Proteides hyas* Mabille, 1891. According to the second label, the lectotype was collected by Wilhelm (Guillermo) Kalbreyer (1847–1912). The 3rd and 4th labels are in Mabille's (likely the original identification label by the author of the name) and Staudinger's handwriting, respectively. The lectotype is missing the club of the left antenna, and its right hindwing is shallowly torn in the middle of the outer margin. Images of this specimen photographed by B. Hermier are shown on the Butterflies of America website (Warren et al. 2024). The type locality of *P. hyas* remains in Colombia: Valle del Cauca. The COI barcode sequence of the lectotype, sample NVG-18043B07, 658 base pairs is:

AACTTTATATTTTATTTTTGGAATTTGAGCAGGAATATTGGGTACATCTCTAAGTTTATTAATTCGTACTGAATTAGGTAATCCAGGATCTTTAATTGGAGATGATCAAATTTATAATACT
ATTGTTACAGCTCATGCTTTTATTATAATTTTTTTTATAGTTATACCTATTATAATTGGAGGATTTGGTAATTGACTTGTCCCTTTAATATTAGGAGCCCCCGACATAGCTTTCCCCCGTA
TAAATAACATAAGATTTTGAATATTACCTCCTTCCTTAACTCTTTTAATTTCAAGAAGAATTGTTGAAAATGGTGCTGGAACTGGATGAACAGTTTATCCCCCCCTTTCATCTAATATTGC
CCATCAAGGATCTTCAGTTGACTTAGCAATTTTTTCCCTTCATTTAGCAGGTATTTCTTCTATTTTAGGAGCTATTAATTTTATTACTACAATTATTAATATACGAATTATAAATTTATCA
TTTGATCAAATACCTTTATTTATTTGATCTGTAGGTATCACAGCTTTATTATTATTATTATCTTTACCTGTTTTAGCTGGTGCTATTACTATACTTCTTACAGATCGAAATTTAAATACTT
CATTTTTTGATCCTGCAGGAGGAGGAGATCCTATTTTATATCAACATTTATTT

Lectotype designation for *Hesperia luscinia* Plötz, 1882

Hesperia luscinia Plötz, 1882 (Weymer in litt.), currently a subspecies of *Perichares deceptus* (Butler & H. Druce, 1872) (type locality in Costa Rica), was described from an unstated number of specimens from "Blumenau" [Santa Catarina, Brazil] (Plötz 1882). We found a single syntype of *H. luscinia*, originally from the Weymer's collection, now in the MFNB collection known to house part of Plötz's type material. The syntype agrees well with the original description, which we assemble from the identification key and translate from German as: "Upperside brown or black, forewings with 3–4 hyaline spots, without a hyaline dot before the apex, but with brown spots on the underside. Underside lilac-gray and clouded with brown. Hindwings unicolorous above. Fringes not checkered. Forewings with 3 white hyaline spots; the two in cells 2 and 3 shifted toward the margin; the middle spot elongated parallel to the margin and constricted in the middle. ♂ with stigma" (Plötz 1882). To stabilize nomenclature and define the name *H. luscinia* objectively, N.V.G. hereby designates the syntype in the MFNB collection, a male that bears the following eight labels (1st red, others white; 2nd–5th handwritten, others printed): [Typus], [Blumenau | 1876 Peters], [197 | Weymer], [Luscinia Wmr | Nº197 best. v. Plötz], [Luscinia Wmr | i l. | Blumenau], [Coll. Weymer], [{QR Code} http://coll.mfn-berlin.de/u/ | 44a054], and [DNA sample ID: | NVG-18043C01 | c/o Nick V. Grishin], as the **lectotype** of *Hesperia luscinia* Plötz, 1882. The lectotype was collected in 1876 possibly by Wilhelm Peters (1815–1883), a curator in the Berlin collection. The 2nd, 4th, and 5th labels are in Weymer's handwriting and the 4th label states that the specimen was identified by Plötz ("best[immt]. v[on]. Plötz"). The lectotype is missing the clubs of both antennae and the right hindwing tornus. Images of this specimen photographed by B. Hermier are shown on the Butterflies of America website (Warren et al. 2024). The type locality of *H. luscinia* remains as Brazil: Santa Catarina,

Blumenau. The COI barcode sequence of the lectotype, sample NVG-18043C01, 658 base pairs is:

AACTTTATATTTTATTTTCGGAATTTGAGCAGGAATACTAGGTACATCTTTAAGTTTATTAATTCGTACTGAATTAGGTAATCCAGGATTTTTAATTGGAGATGATCAAATCTATAACACT
ATTGTTACAGCTCATGCTTTTATTATAATTTTTTTTTATAGTTATACCTATCATAATTGGAGGATTTGGAAATTGACTTGTTCCTTTAATATTAGGAGCCCCCGACATAGCTTTTCCTCGTA
TAAATAACATAAGATTCTGAATATTGCCACCTTCTTTAACTCTTTTAATTTCAAGAAGAATTGTTGAAAATGGTGCAGGAACTGGATGAACAGTTTACCCCCCACTTTCATCCAATATTGC
ACATCAAGGATCTTCAGTTGATTTAGCAATTTTTTCCCTTCATTTAGCAGGTATTTCTTCTATTTTAGGAGCTATTAACTTTATTACTACAATTATTAACATACGAATCATAAATTTATCA
TTTGATCAAATACCTTTATTTATTTGATCAGTAGGTATTACAGCTTTATTATTACTACTATCTTTACCTGTTTTAGCTGGAGCTATTACTATACTTCTCACAGATCGAAATTTAAATACTT
CATTTTTTGATCCTGCAGGAGGAGGAGATCCTATTTTATACCAACATTTATTT

Perichares fulvimargo (Butler, 1873) and *Perichares luscinia* (Plötz, 1882) are species distinct from *Perichares deceptus* (Butler & H. Druce, 1872)

Genomic analysis reveals that *Carystus fulvimargo* Butler, 1873 (type locality in Venezuela) and *Hesperia luscinia* Plötz, 1882 (type locality in Brazil: Santa Catarina) currently regarded as subspecies of *Perichares deceptus* (Butler & H. Druce, 1872) (type locality in Costa Rica) are genetically differentiated from it and each other at the species level (Fig. 119), e.g., their COI barcodes differ by 1.2% (8 bp) from *Carystus fulvimargo*, 4.9% (32 bp) from *Hesperia luscinia*, and 4.9% (32 bp) between them. Therefore, we propose that *Perichares fulvimargo* (Butler, 1873), **stat. rest.** and *Perichares luscinia* (Plötz, 1882), **stat. rest.** are species distinct from *Perichares deceptus* (Butler & H. Druce, 1872).

Perichares solamancha Grishin, new species

https://zoobank.org/AD7B67E0-2D2F-434F-8FB6-4EF57F169D75

(Figs. 119 part, 120c, 121)

Definition and diagnosis. Genomic analysis reveals that a male from Cuzco, Peru, initially identified as *Perichares colenda* (Hewitson, 1866) (type locality in Venezuela) is genetically differentiated from it at the species level (Fig. 119); e.g., their COI barcodes differ by 5.0% (33 bp), and therefore this specimen represents a new species. This new species keys to *P. colenda* (K.30.6) in Evans (1955), but differs from it and other relatives by the following combination of characters: the hindwing has a semihyaline pale slightly yellowish spot around the middle of cell M_3-CuA_1 more obvious on the dorsal side and unique to this species; tornal orange scaling on the ventral hindwing is more extensive and forms a crescent rounded on all sides and the vein 1A+2A within this crescent lacks brown overscaling; the ventral hindwing has a stronger contrast between pale and dark areas; the brown area at the base of the ventral hindwing along the costa is pierced by a ray of pale-violaceous scales; the inner edge of the apical pale-violaceous scaling on the ventral forewing forms a tooth directed basad in cell M_1-M_2, because the area in cell M_2-M_3 anteriad of the semihyaline spot in cell M_3-CuA_1 is partly brown basad; the valva is longer and narrower, especially towards the base; the harpe is terminally broader and rounder with smaller serrations along the dorsal margin, which is mildly convex to nearly straight towards the ampulla; the uncus is broader at its base in dorsal view and stronger humped in the middle in lateral view, and the side processes of the uncus

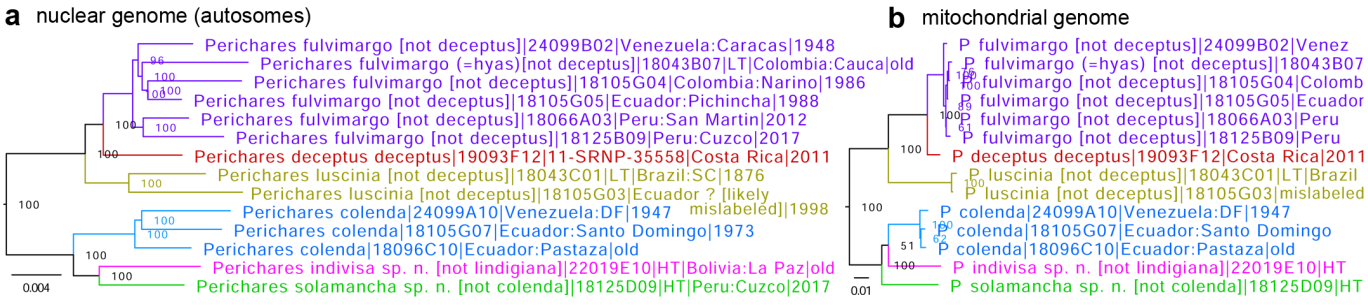

Fig. 119. Phylogenetic trees of selected *Perichares* Scudder, 1872 species constructed from protein-coding regions in: **a)** the nuclear genome (autosomes), based on 3,553,272 positions, and **b)** the mitochondrial genome. Different species are colored differently: *P. fulvimargo* **stat. nov.** (purple), *P. deceptus* (red), *P. luscinia* **stat. nov.** (olive), *P. colenda* (blue), *P. indivisa* **sp. n.** (magenta), and *P. solamancha* **sp. n.** (green). Ultrafast bootstrap (Hoang et al. 2018) values are shown at nodes.

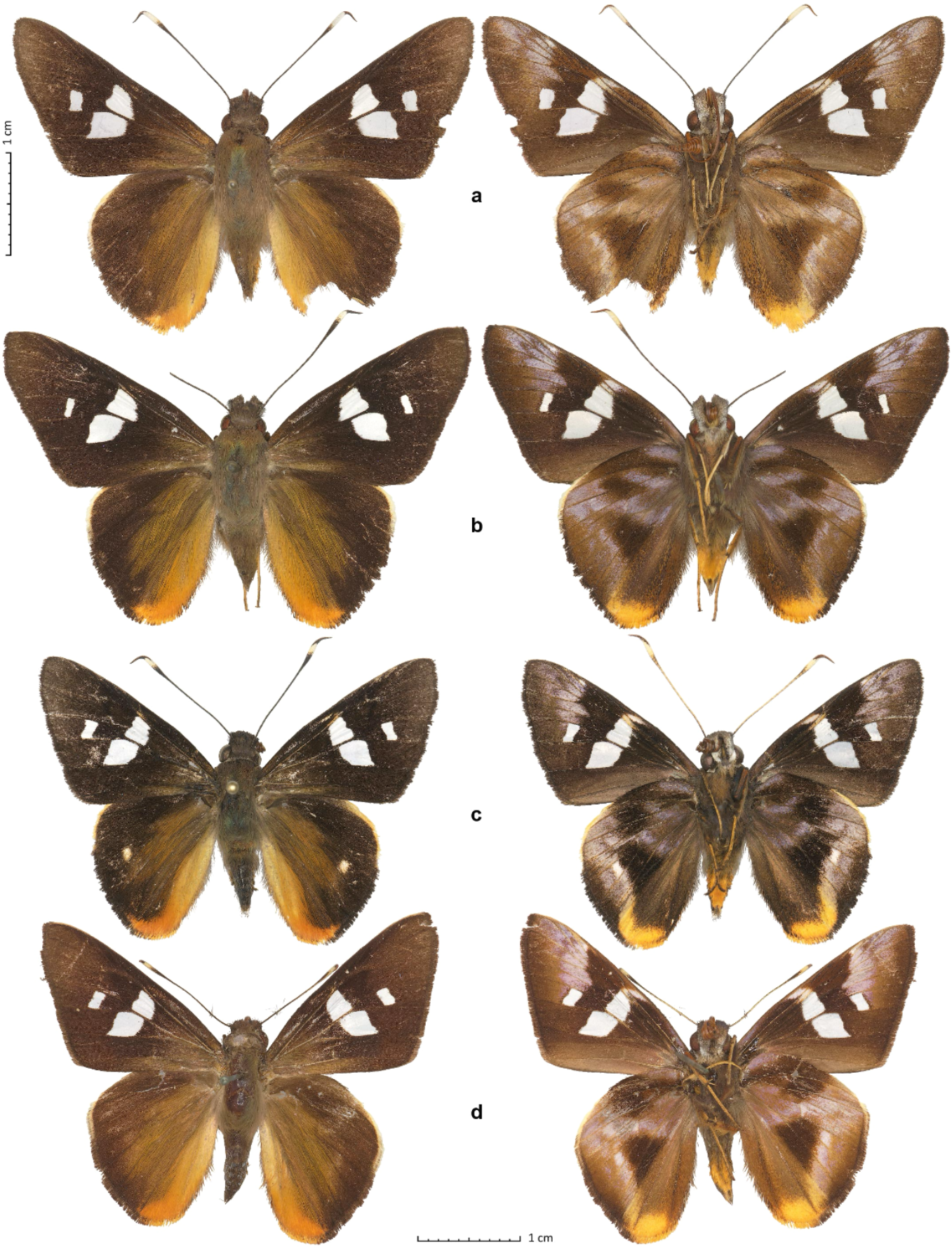

Fig. 120. Males of *Perichares* in dorsal (left) and ventral (right) views, data in text: **a–b)** *P. colenda*: **a)** NVG-24099A10 from Venezuela: DF and **b)** NVG-18105G07 from Ecuador: Sto. Domingo; **c)** *P. solamancha* **sp. n.** holotype NVG-18125D09 from Peru: Cuzco; and **d)** *P. indivisa* **sp. n.** holotype NVG-22019E10 from Bolivia: La Paz.

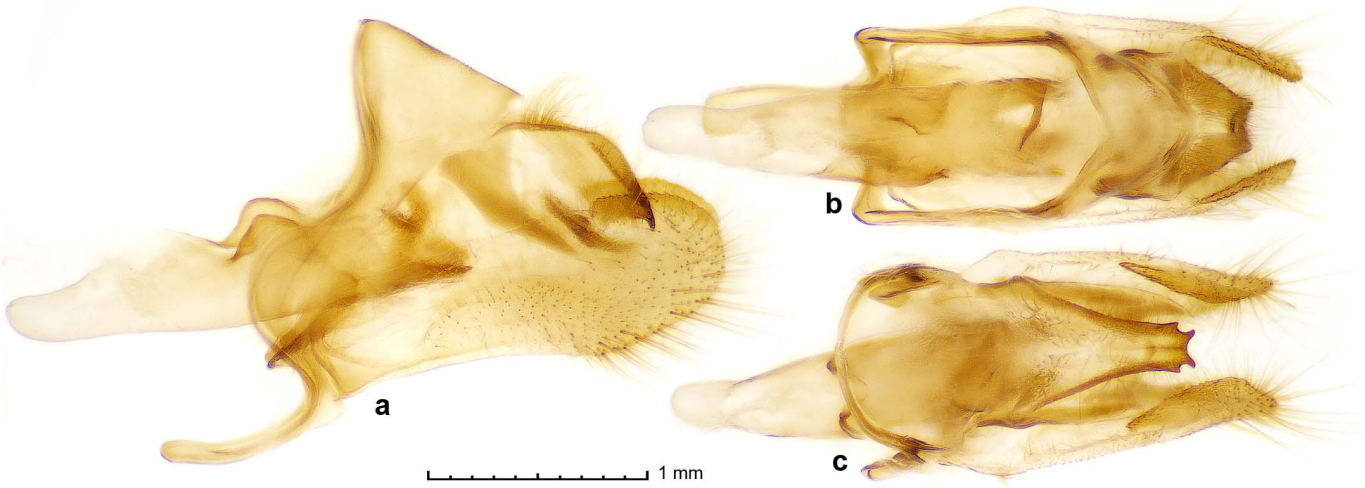

Fig. 121. Male genitalia of *Perichares solamancha* **sp. n.** holotype NVG-18125D09 in: **a)** left lateral, **b)** anterodorsal, and **c)** dorsal views.

near its distal end are smaller and closer to the uncus arms, which are narrow, finger-like. Due to its cryptic nature and unexplored individual variation, this species is best identified by DNA, with diagnostic base pairs in the nuclear genome: aly2752.3.1:T1548G, aly2752.3.1:C1569T, aly580.5.5:A447G, aly580.5.5:G713A, aly13163.1.1:G39A, aly13163.1.1:C45C (not T), aly13163.1.1:C63C (not T), aly2012.26.8:G97G (not T), aly1042.7.1:A3054A (not G), aly7429.1.5:G15G (not C); and the COI barcode: T10C, T70C, T187C, T325A, A466G, T533C.

Barcode sequence of the holotype. Sample NVG-18125D09, 658 base pairs:

AACTTTATACTTTATTTTTGGTATTTGAGCCGGAATATTGGGTACATCTTTAAGTTTATTAATTCGTACCGAATTAGGTAACCCAGGATCTTTAATTGGAGATGATCAAATCTATAACACT
ATTGTTACAGCTCATGCTTTTATTATAATTTTTTTTATAGTTATACCTATTATAATTGGAGGATTCGGAAATTGGCTTGTTCCTCTCATATTGGGAGCCCCCGACATAGCTTTCCCCCGTA
TAAATAACATAAGATTTTGAATATTACCTCCTTCATTAACTCTTTTAATTTCAAGAAGAATTGTTGAAAATGGTGCTGGAACAGGATGAACAGTTTACCCCCCCCTTTCATCTAATATTGC
ACACCAAGGATCTTCAGTTGATTTAGCAATTTTCTCTCTTCATTTAGCAGGAATTTCTTCTATTTTAGGAGCTATTAATTTTATTACTACAATTATTAATATGCGAATTATAAATTTATCA
TTTGATCAAATACCTTTATTTATTTGATCAGTAGGTATTACAGCTTTACTATTATTATTATCTTTACCAGTATTAGCAGGTGCTATTACTATACTTCTTACAGATCGAAATTTAAATACTT
CATTTTTTGACCCTGCAGGAGGGGGAGATCCTATTTTATATCAACATTTATTT

Type material. Holotype: ♂ currently in the Dempwolf collection (Austin, Texas, USA), to be deposited in the Museo de Historia Natural, Lima, Peru (MUSM), illustrated in Fig. 120c (genitalia Fig. 121), bears the following seven printed rectangular labels, six white: [Peru: Cuzco Dept, 1375m | Cosñipata Valley, San Pedro | 13° 03'S, 71° 33'W | November 1, 2017 | Leg: W. Dempwolf], [Perichares colenda | ♂ | Coll of: W R Dempwolf], [DNA sample ID: | NVG-18125D09 | c/o Nick V. Grishin], [DNA sample ID: | NVG-25031D03 | c/o Nick V. Grishin], [genitalia | NVG251025-05 | c/o Nick V. Grishin], [WRD 14,927], and one red [HOLOTYPE ♂ | Perichares | solamancha 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 Department, Cosñipata Valley, San Pedro, elevation 1375 m, GPS −13.05, −71.55.

Etymology. In Spanish, mancha means spot. The name reflects the sole white spot on the hindwing characteristic of this new species and is treated as a noun in apposition.

Distribution. Currently known only from the holotype collected on the eastern slopes of the Andes in southern Peru.

Comments. We sequenced three males that we identify as *P. colenda* by phenotypic similarity and the locality of one in Venezuela. These three specimens form a tight clade in the trees, do not differ in their COI barcodes, and we consider them to be the same species. Two of them are illustrated in Fig. 120a, b. Data for these specimens are: NVG-24099A10 Venezuela: DF, El Junquito, 2100 m, 3-Apr-1947, coll. René Lichy [MGCL] (Fig. 120a); NVG-18105G07, USNMENT 01531265 Ecuador: Santo Domingo de los Tsáchilas, Old Sto. Domingo Rd., 9-Oct-1973, S. S. Nicolay leg. [USNM] (Fig. 120b); and NVG-18096C10 Ecuador: Pastaza, “Zarayaquilio”, old [MTD].

Perichares indivisa Grishin, new species

https://zoobank.org/1A31C907-2CAA-457E-9144-CE48C325DB21

(Figs. 119 part, 120d)

Definition and diagnosis. Genomic analysis reveals that a male from Bolivia initially identified as *Perichares colenda* (Hewitson, 1866) (type locality in Venezuela) is genetically differentiated from it and its relatives at the species level (Fig. 119); e.g., their COI barcodes differ by 4.9% (32 bp) from *P. colenda* and by 6.0% (40 bp) from the new species described above, and therefore this male represents a new species. This new species keys to *P. colenda* (K.30.6) in Evans (1955) and was included by him in this species, but differs from it and other relatives by the following combination of characters: the hindwing lacks pale spots; tornal orange scaling on the ventral hindwing is shaped more like a patch that is cut through by brown overscaling along the vein 1A+2A; the ventral hindwing is less variegated and appears more uniformly colored within paler and darker areas; the brown area at the base of ventral hindwing along the costa is nearly entire and this difference would be clear on live individuals (i.e., in resting pose, *P. colenda* displays three conspicuous pale-violaceous rays through the ventral hindwing, but this new species lacks the middle ray and has the brown spot only slightly notched by pale scales along the inner side and not cut through); tawny-orange scales reach the middle of the dorsal hindwing and extend farther towards the margin, e.g., for more than a third of cell M_3-CuA_1 from its base; the inner edge of the apical pale-violaceous scaling on the ventral forewing is relatively straight and aligned in cells M_1-M_2 and M_2-M_3, and aligned with the inner edge of the semihyaline spot in cell M_3-CuA_1 with the area anteriad of the semihyaline spot in cell M_2-M_3 being mostly violaceous-beige rather than brown ground color; and the harpe is shorter and more angular rendering the valva trapezoidal. Due to its cryptic nature and unexplored individual variation, this species is best identified by DNA, with diagnostic base pairs in the nuclear genome: aly2165.4.3:A2008G, aly2165.4.3:G2025A, aly13163.1.1:G39A, aly13163.1.1:T69G, aly2752.3.1:T1548G, aly13163.1.1:G42G (not T), aly6128.4.6:C78C (not T), aly4305.32.1:C439C (not T), aly274.44.1:C273C (not A), aly669.15.1:C594C (not A); and the COI barcode: T49C, A85T, A265G, A373T, A412G, T499C.

Barcode sequence of the holotype. Sample NVG-22019E10, 658 base pairs:

AACTTTATATTTTATTTTTGGTATTTGAGCCGGAATATTAGGTACATCCTTAAGCTTACTAATTCGTACAGAATTAGGTAACCCTGGATCTTTAATTGGAGATGATCAAATCTATAATACT
ATTGTTACAGCTCATGCTTTTATTATAATTTTTTTTATAGTTATACCTATTATAATTGGAGGATTTGGTAATTGACTTGTCCCTCTTATACTAGGAGCCCCCGACATAGCTTTCCCCCGTA
TAAATAATATAAGATTTTGAATGCTGCCCCCTTCATTAACTCTTTTAATTTCAAGAAGAATTGTTGAAAACGGTGCTGGAACTGGATGAACAGTTTACCCCCCACTTTCATCTAATATTGC
CCATCAAGGTTCCTCAGTTGATTTAGCAATTTTTTCCCTTCATTTAGCGGGAATTTCTTCTATTTTAGGAGCTATTAATTTTATTACTACAATTATTAATATACGAATTATAAACTTATCA
TTTGATCAAATACCCCTATTTATTTGATCAGTAGGTATTACAGCTTTATTATTATTATTGTCATTACCAGTATTAGCTGGTGCTATTACTATACTTCTTACAGATCGAAATTTAAATACTT
CATTTTTTGACCCTGCAGGAGGAGGAGATCCTATTTTATACCAACATTTATTT

Type material. Holotype: ♂ deposited in the Zoologische Staatssammlung München, Germany (ZSMC), illustrated in Fig. 120d, bears the following three rectangular labels (1st handwritten in pencil, others printed), two white: [Farinas | Boliv], [DNA sample ID: | NVG-22019E10 | c/o Nick V. Grishin], and one red [HOLOTYPE ♂ | Perichares | indivisa Grishin].

Type locality. Bolivia: La Paz Region, Fariñas.

Etymology. In Latin, *indivisa* means undivided. The name reflects the undivided brown area from the base of ventral hindwing to mid-costa characteristic of this new species and is a feminine adjective.

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

Comments. After this work was completed, we found that Suênia-Bastos et al. (2025) identified specimens from Bolivia phenotypically similar to this new species as *Perichares lindigiana* (C. Felder & R. Felder, 1867) (type locality in Bolivia). Our analysis does not agree with this identification due to phenotypic differences between the two taxa (the Bolivian species and the lectotype of *P. lindigiana* from Venezuela), as discussed above. Conversely, we do not have strong evidence to support the distinction of *P. lindigiana* from *P. colenda*, both collected in Venezuela, and suggest that until lectotypes of the two taxa are more thoroughly analyzed and sequenced, it is best to regard *Hesperia lindigiana* C. Felder & R. Felder, 1867, **stat. rev.** as a junior subjective synonym of *P. colenda* due to the lack of prominent phenotypic differences between their lectotypes also originating in the same country (Venezuela). The similarities between the lectotypes of *H. lindigiana* and *P. colenda* that differentiate them from other taxa

include: the brown area from the base of the ventral hindwing to mid-costa is cut through by a violaceous-beige ray and the hindwing appears more variegated than in Bolivian specimens; tawny-orange scales reach the middle of the dorsal hindwing, but do not extend farther; brown overscaling along the vein 1A+2A on the ventral hindwing is absent in the orange area near the tornus, and the vein does not conspicuously cut through the orange tornus; violaceous-beige scaling in the ventral forewing cell M_2-M_3 does not reach the basal edge of the hyaline spot in the ventral forewing cell M_3-CuA_1 and is not aligned with the violaceous-beige scaling in cell M_1-M_2 (that reaches the base of the cell), thus the scaling in cell M_1-M_2 forms a "tooth" protruding basad from the inner edge of the violaceous-beige band. The differences between the two taxa are in the size of the semihyaline spot in the forewing cell M_3-CuA_1 and the extent of the orange scaling along the hindwing tornus, but these differences may be due to individual variation and should be investigated further.

Perichares philetes trinitad (Lucas, 1857), stat. rev. is a valid subspecies of *Perichares philetes* (Gmelin, [1790])

Nuclear genomic phylogeny partitions specimens identified as *Perichares philetes* (Gmelin, [1790]) (type locality in Jamaica) into two prominent clades that are genetically differentiated at least at the subspecies level (the Z chromosome tree is shown in Fig. 122a). The first clade corresponds to specimens from Jamaica and represents the nominotypical taxon. The second clade includes specimens from a larger geographical area covering at least three islands: Cuba, Hispaniola, and Puerto Rico. Note that genetic differentiation among specimens from the three islands is limited and they form a compact clade. Therefore, we propose that *Eudamus trinitad* Lucas, 1857 (type locality in Cuba), which belongs to this clade and is the only available name for the taxon represented by it, is not a synonym, but a subspecies of *P. philetes*: *Perichares philetes trinitad* (Lucas, 1857), **stat. rev**. Further research will clarify whether it constitutes a species-level taxon.

Perichares amaletes Grishin, new species

https://zoobank.org/87BE5162-E06D-490A-8B6F-4A04DEAE3888

(Figs. 122 part, 123a, 124a–c)

Definition and diagnosis. Genomic analysis reveals that a specimen from the Amazonian region in the southeastern Peru initially identified as *Perichares philetes* (Gmelin, [1790]) (type locality in Jamaica) is genetically differentiated from it at the species level (Fig. 122); e.g., their COI barcodes differ by 0.9% (6 bp) (COI barcodes do not differ strongly between species in this group (Burns et al. 2007)), and therefore this specimen represents a new species. This new species keys to "*Perichares philetes philetes*" (K.30.2(b)) in Evans (1955) and was likely included by him in this taxon, but differs from it and other relatives by the following combination of characters in males: the wings are less rounded, the hindwing is more extended towards the tornus; forewing semihyaline spots are paler yellow and smaller: no spot in cell CuA_2-1A+2A dorsally and an oval spot ventrally, the discal cell spot is a shallow C on the right wing, the anterior segment is not strongly extended but slightly narrower and twice as long as the posterior segment, the spot in cell M_3-CuA_1 is nearly rectangular and slightly convex/concave along the basal/distal edges, respectively, the spot in cell CuA_1-CuA_2 is approximately the same in size as the previous, from trapezoidal with at least two times shorter anterior edge than the posterior edge to almost triangular, nearly straight/slightly convex along the basal/distal edges; two weakly developed dashes of yellow scales anteriad of the forewing discal cell spot on the dorsal side and two more strongly developed spots (but weaker than in some other species) separated by the Sc vein on the ventral side; the brown spots in the ventral hindwing postdiscal row are larger, e.g., the spot in cell Sc+R_1-Rs is separated from the discal brown spot by a narrower pale violaceous area; body and wing bases are overscaled with shiny greenish scales dorsally; the abdomen is broadly orange ventrally without the central brown stripe; the stigma is broader, especially the segment in cell CuA_1-CuA_2; the valva is less constricted towards its base with the

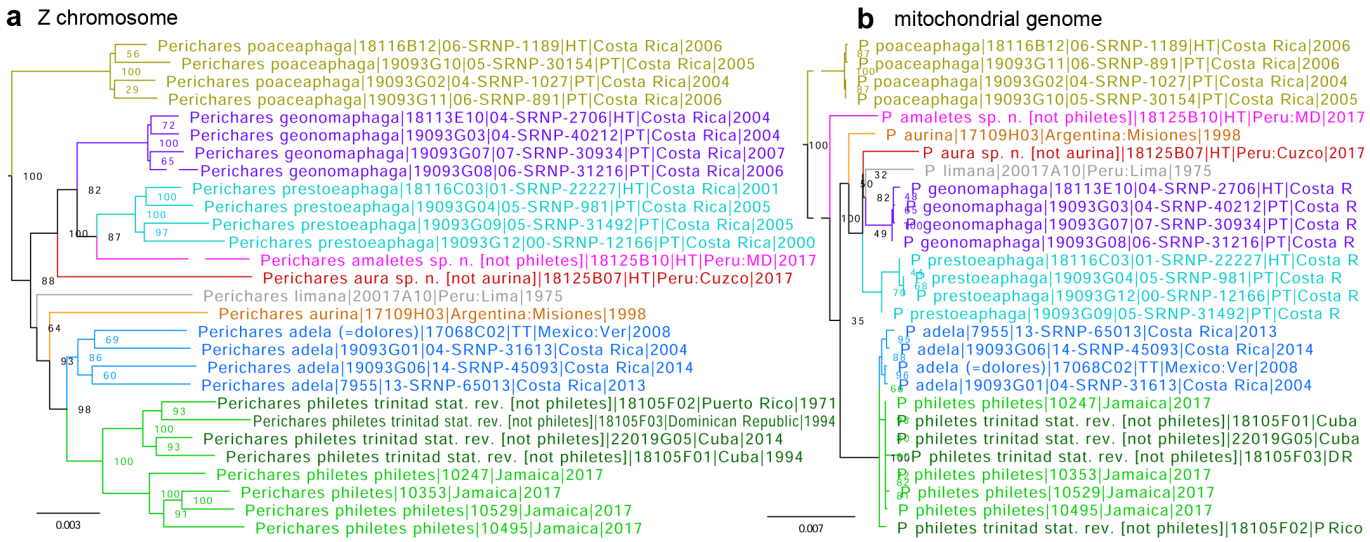

Fig. 122. Phylogenetic trees of selected *Perichares philetes* group species constructed from protein-coding regions in: **a)** the Z chromosome, based on 405,726 positions and **b)** the mitochondrial genome. Different species are colored differently: *P. poaceaphaga* Burns, 2008 (olive), *P. geonomaphaga* Burns, 2008 (purple), *P. prestoeaphaga* Burns, 2008 (cyan), *P. amaletes* **sp. n.** (magenta), *P. aura* **sp. n.** (red), *P. limana* Evans, 1955 (gray), *P. aurina* Evans, 1955 (orange), *P. adela* (Hewitson, 1867), and *P. philetes* (green with its subspecies *P. philetes trinitad* **stat. rev.** labeled in dark-green). Ultrafast bootstrap (Hoang et al. 2018) values are shown at nodes. Gaps in terminal branches indicate that a segment of a branch was cut out to reduce its length (to allow an increase in the font size), i.e., a branch with a gap is longer than shown. Similarly, gaps in other branches indicate where a vertical slice of the tree was removed to reduce its horizontal dimension.

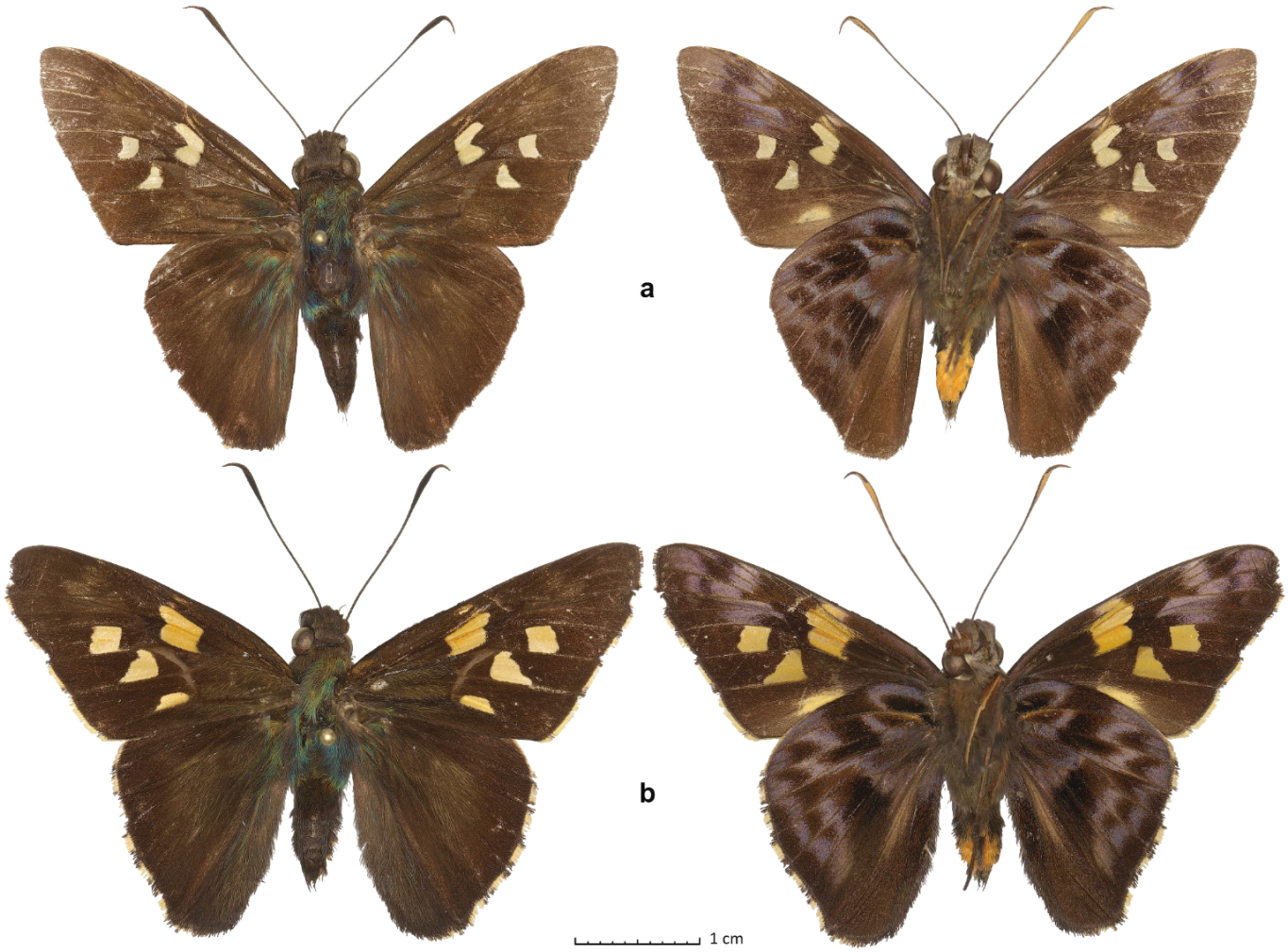

Fig. 123. New species of *Perichares*, holotypes from Peru, in dorsal (left) and ventral (right) views, data in text: **a)** *Perichares amaletes* **sp. n.** ♂ NVG-18125B10 Madre de Dios and **b)** *Perichares aura* **sp. n.** ♂ NVG-18125B07 Cuzco.

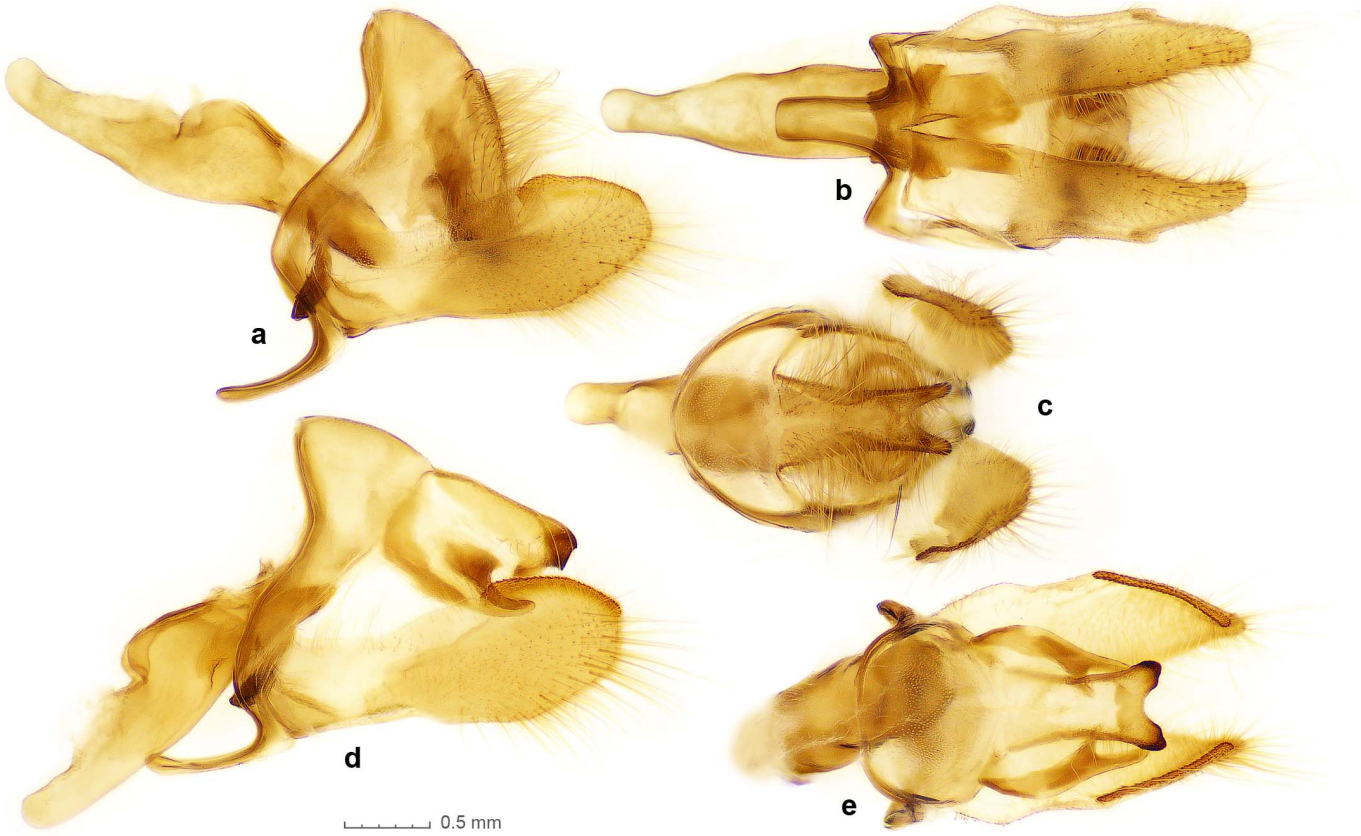

Fig. 124. Male genitalia of *Perichares* holotypes from Peru: **a–c)** *P. amaletes* **sp. n.** NVG-18125B10 Madre de Dios and **d–e)** *P. aura* **sp. n.** NVG-18125B07 Cuzco in: **a, d)** left lateral, **b)** ventral, **c)** posterior, showing dorsal view of uncus, and **e)** dorsal.

ventral margin nearly straight and only slightly convex, the harpe is terminally rounded, its dorsal margin more rounded and very finely serrated, not much stronger sclerotized than the rest of the harpe and only slightly darker along the margin; and the uncus arms are narrower, finger-like. Due to its cryptic nature and unexplored individual variation, this species is best identified by DNA, with diagnostic base pairs in the nuclear genome: aly54.10.6:C6T, aly1402.10.3:T45A, aly361.35.2:T81C, aly1698.2.5:C288G, aly8211.8.4:T216G, aly2178.19.2:A75A (not G), aly2178.42.17:C375C (not T), aly2178.42.17:G381G (not A), aly2178.42.17:G390G (not A), aly2178.42.17:C429C (not T); and the COI barcode: C206T, T271T, T340T, 364C, G477A.

Barcode sequence of the holotype. Sample NVG-18125B10, 658 base pairs:

AACTTTATATTTTATTTTTGGTATTTGAGCAGGAATATTAGGAACATCTTTAAGTTTATTAATTCGTACTGAATTAGGAAATCCAGGATCTTTAATTGGTGATGATCAAATTTATAATACC
ATTGTTACAGCTCATGCTTTTATTATAATTTTTTTTATAGTTATACCTATTATAATTGGAGGATTTGGTAATTGACTTGTTCCTTTAATACTAGGAGCCCCTGATATAGCTTTCCCCCGTA
TAAATAATATAAGATTTTGAATATTACCTCCATCATTAACTCTTTTAATCTCAAGAAGAATTGTTGAAAATGGTGCTGGAACTGGATGAACAGTTTATCCCCCACTTTCATCTAACATTGC
CCATCAAGGATCTTCAGTTGATTTAGCAATTTTCTCCTTACATTTAGCAGGAATTTCTTCTATTTTAGGAGCTATTAACTTTATTACAACAATTATTAATATACGAATTATAAACTTATCT
TTTGATCAGATACCTTTATTTGTTTGATCAGTAGGTATTACAGCTTTATTATTACTTTTATCTCTACCAGTATTAGCAGGAGCTATTACAATACTTCTTACAGATCGAAATTTAAATACTT
CATTTTTTGATCCTGCAGGAGGAGGAGATCCAATTTTATACCAACATTTATTT

Type material. Holotype: ♂ currently in the Dempwolf collection (Austin, Texas, USA), to be deposited in the Museo de Historia Natural, Lima, Peru (MUSM), illustrated in Fig. 123a (genitalia Fig. 124a–c), bears the following seven printed rectangular labels (text in italics handwritten), six white: [Peru: Madre de Dios Dept, | 400m Alto Madre de Dios at | Pantiacolla Lodge 12° 39' S, | 71° 13' W November 6, 2017 | Leg: W. Dempwolf], [Perichares philetes simplex | ♂ | Coll of: W R Dempwolf], [DNA sample ID: | NVG-18125B10 | c/o Nick V. Grishin], [DNA sample ID: | NVG-24015F08 | c/o Nick V. Grishin], [genitalia | NVG241114-40 | c/o Nick V. Grishin], [WRD 14,930], and one red [HOLOTYPE ♂ | Perichares | amaletes 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: Madre de Dios Region, Alto Madre de Dios at Pantiacolla Lodge, elevation 400 m, GPS −12.6500, −71.2167.

Etymology. The name reflects *Ama*[zonian distribution of this species that is most similar to P. phi]*letes* and is treated as a noun in apposition.

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

Perichares aura Grishin, new species

https://zoobank.org/3CD3A758-C8A8-4910-8FB4-E910752249FC

(Figs. 122 part, 123b, 124d–e)

Definition and diagnosis. Genomic analysis reveals that a specimen from the Andes in southern Peru initially identified as *Perichares aurina* Evans, 1955 (type locality Brazil: Paraná, Castro) is genetically differentiated from it at the species level (Fig. 122); e.g., their COI barcodes differ by 0.5% (3 bp) (COI barcodes do not differ strongly between species in this group (Burns et al. 2007)), and therefore this specimen represents a new species. This new species keys to "*Perichares philetes aurina*" (K.30.2(c)) in Evans (1955) and was included by him in this species, but differs from it and other relatives by the following combination of characters in males: the wings are more rounded, the hindwing less extended towards the tornus; forewing semihyaline spots are deeper, more saturated yellow and larger: a well-developed elongated spot in cell CuA_2-1A+2A dorsally and a larger oval spot ventrally, the discal cell spot is longitudinally elongated, basally convex and distally notched, the spot in cell M_3-CuA_1 is nearly square, the spot in cell CuA_1-CuA_2 is approximately the same in size as the previous, nearly a right triangle with a slightly convex basal margin and dorsally rounded (ventrally a short straight line) anterior angle; two weakly developed dashes of yellow scales anteriad of the forewing discal cell spot on the dorsal side and two well defined spots (the posterior one is joint with the discal cell spot) weakly separated by the Sc vein on the ventral side; the violaceous pattern on the ventral side is better developed and broader, e.g., the discal and postdiscal brown spots in cell Sc+R_1-Rs are separated from each other by a broader violaceous area; body and wing bases are overscaled with shiny greenish scales dorsally, more ochreous on the forewings; the abdomen is orange ventrally in its distal half with the central brown stripe; the stigma is narrower, with its basal margin more angled at the vein CuA_2; the valva is more strongly constricted towards its base with the ventral margin nearly straight and then humped ventrad at the harpe, the harpe is terminally more angled with the distal margin nearly straight, its dorsal margin more angled in the middle and finely serrated, stronger sclerotized than the rest of the harpe appearing as a darker stripe along the margin; and the uncus arms are broader, knob-like. Due to its cryptic nature and unexplored individual variation, this species is best identified by DNA, with diagnostic base pairs in the nuclear genome: aly1080.21.5:T204A, aly594.3.7:A84G, aly310.1.12:A60G, aly86.5.7:C84C (not T), aly86.5.7:G114G (not A), aly594.3.7:T69T (not C), aly594.3.7:C105C (not A), aly594.3.7:T132T (not C); and the COI barcode: C206T, T271T, T340C, 364C, G477G.

Barcode sequence of the holotype. Sample NVG-18125B07, 658 base pairs:

AACTTTATATTTTATTTTTGGTATTTGAGCAGGAATATTAGGAACATCTTTAAGTTTATTAATTCGTACTGAATTAGGAAATCCAGGATCTTTAATTGGTGATGATCAAATTTATAATACC
ATTGTTACAGCTCATGCTTTTATTATAATTTTTTTTATAGTTATACCTATTATAATTGGAGGATTTGGTAATTGACTTGTTCCTTTAATACTAGGAGCCCCTGATATAGCTTTCCCCCGTA
TAAATAATATAAGATTTTGAATATTACCTCCATCATTAACTCTTTTAATCTCAAGAAGAATTGTTGAAAATGGTGCTGGAACTGGATGAACAGTTTACCCCCCACTTTCATCTAACATTGC
CCATCAAGGATCTTCAGTTGATTTAGCAATTTTCTCCTTACATTTAGCAGGAATTTCTTCTATTTTAGGAGCTATTAACTTTATTACAACAATTATTAATATACGAATTATAAGCTTATCT
TTTGATCAGATACCTTTATTTGTTTGATCAGTAGGTATTACAGCTTTATTATTACTTTTATCTCTACCAGTATTAGCAGGAGCTATTACAATACTTCTTACAGATCGAAATTTAAATACTT
CATTTTTTGATCCTGCAGGAGGAGGAGATCCAATTTTATACCAACATTTATTT

Type material. Holotype: ♂ currently in the Dempwolf collection (Austin, Texas, USA), to be deposited in the Museo de Historia Natural, Lima, Peru (MUSM), illustrated in Fig. 123b (genitalia Fig. 124d, e), bears the following seven printed rectangular labels (text in italics handwritten), six white: [Peru: Cuzco Dept, 1375m | Cosñipata Valley, San Pedro | 13° 03' S, 71° 33' W | November 1, 2017 | Leg: W. Dempwolf], [Perichares adela | ♂ | Coll of: W R Dempwolf], [DNA sample ID: | NVG-18125B07 | c/o Nick V. Grishin], [DNA sample ID: | NVG-24015F09 | c/o Nick V. Grishin], [genitalia | NVG241114-41 | c/o Nick V. Grishin], [WRD 14,929], and one red [HOLOTYPE ♂ | Perichares | aura 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, San Pedro, elevation 1375 m, GPS −13.05, −71.55.

Etymology. The name reflects phenotypic similarity to *P. aurina* in having larger and yellower forewing semihyaline spots, made shorter for this more northern species, and is treated as a noun in apposition.

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

Lycas boisduvalii (Ehrmann, 1909) is a species distinct from *Lycas godart* (Latreille, [1824])

Genomic analysis reveals that *Eudamus boisduvalii* Ehrmann, 1909 (type locality Venezuela: Suapure, holotype sequenced as NVG-15096D09) currently regarded as a subspecies of *Lycas godart* (Latreille, [1824]) (type locality in Brazil, likely in Southeast Brazil) is genetically differentiated from it at the species level (Fig. 125); e.g., their COI barcodes differ by 4.4% (29 bp), and therefore the former is a species-level taxon. Thus, we propose that *Lycas boisduvalii* (Ehrmann, 1909), **stat. rest.** is a species distinct from *Lycas godart* (Latreille, [1824]).

Lycas gabriel Grishin, new species

https://zoobank.org/9161ACDF-BD6C-4EA1-AD58-AD02B2954E21

(Figs. 125 part, 126)

Definition and diagnosis. Genomic analysis reveals that a specimen from southeastern Peru identified as *Lycas boisduvalii* (Ehrmann, 1909) (type locality Venezuela: Suapure, holotype sequenced as NVG-15096D09) is genetically differentiated from it at the species level (Fig. 125); e.g., their COI barcodes differ by 3.6% (24 bp), and therefore this specimen represents a new species. This new species keys to "*Lycas godart boisduvalii*" (K.33.1(a)) in Evans (1955), but differs from it and other relatives by the following combination of characters in females: wider silver bands on the ventral hindwing, bands with rather straight margins (no prominent tooth in the middle of the inner margin of the outer band); the CuA_1-CuA_2 semihyaline forewing spot that is well-separated from the discal cell spot and not only does not overlap with it, but its anterior side is narrower and pointing towards the costa at about ⅓ from the apex; and this spot being nearly triangular, not rectangular. Due to its cryptic nature and unexplored individual variation, this species is best identified by DNA, with diagnostic base pairs in the nuclear genome: aly123.8.1:G90T, aly123.8.1:G135T, aly361.2.2:A258G, aly887.24.9:T64C, aly887.24.9:T78C,

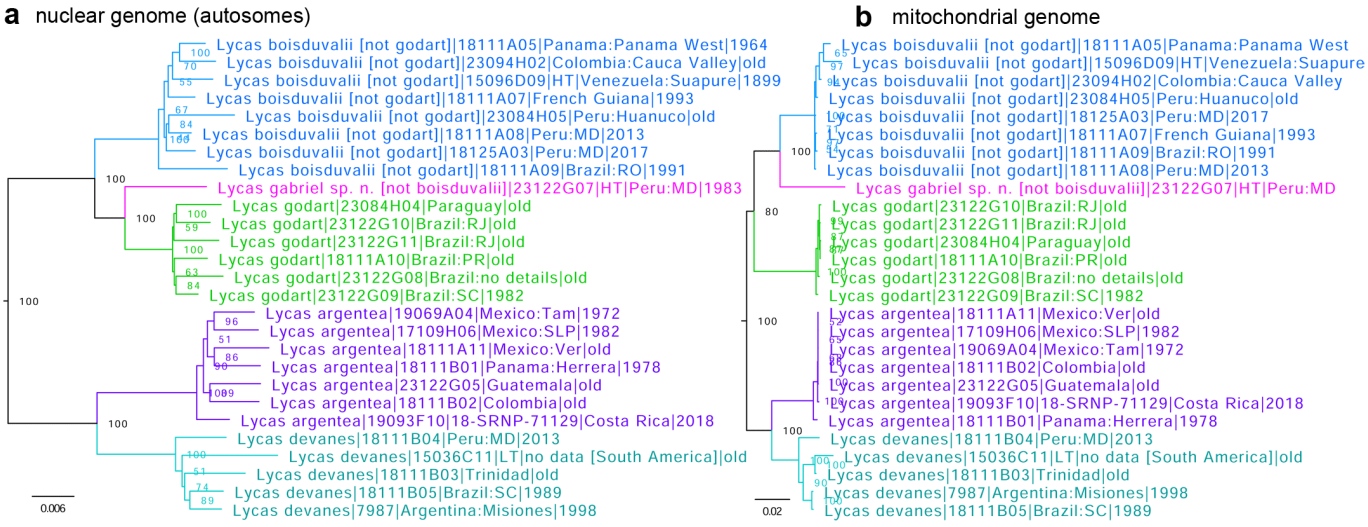

Fig. 125. Phylogenetic trees of *Lycas* Godman, 1901 species constructed from protein-coding regions in: **a)** the nuclear genome (autosomes), based on 2,290,164 positions, and **b)** the mitochondrial genome. Different species are colored differently: *L. boisduvalii* **stat. rest.** (blue), *L. gabriel* **sp. n.** (magenta), *L. godart* (green), *L. argentea* (Hewitson, 1866) (purple), and *L. devanes* (Herrich-Schäffer, 1869) (cyan). Ultrafast bootstrap (Hoang et al. 2018) values are shown at nodes.

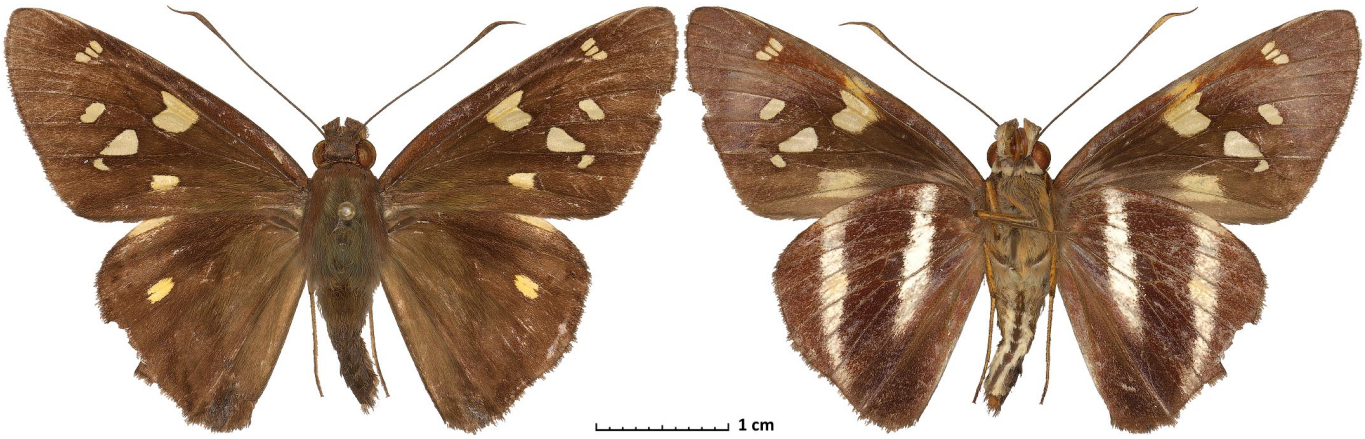

Fig. 126. *Lycas gabriel* **sp. n.** holotype ♀ NVG-23122G07 in dorsal (left) and ventral (right) views, data in text.

aly104.3.6:C444C (not A), aly104.3.6:T468T (not C), aly6370.4.4:A729A (not G), aly6370.4.4:C736C (not T), aly994.6.8:G51G (not A); and the COI barcode: A14C, T16A, T106C, T250C, T445C, T604C.

Barcode sequence of the holotype. Sample NVG-23122G07, 658 base pairs:

AACTTTATATTTTCTATTTGGTATTTGAGCAGGTATATTAGGAACATCATTAAGTTTATTAATTCGTACAGAATTAGGAAATCCAGGATCTTTAATTGGAGATGACCAAATTTATAATACT
ATTGTTACAGCACATGCTTTTATTATAATTTTTTTTATAGTTATACCAATTATAATTGGAGGATTTGGAAATTGATTAGTACCTTTAATATTAGGAGCCCCAGATATAGCTTTCCCCCGTA
TAAATAACATAAGATTTTGAATATTACCCCCCTCATTAATACTCTTAATTTCAAGAAGAATTGTTGAAAATGGTGCTGGAACTGGTTGAACTGTATACCCCCCTCTTTCATCTAATATTGC
TCATCAAGGATCTTCAGTAGATTTAGCAATTTTTTCTCTTCACTTAGCTGGAATTTCTTCAATTTTAGGAGCAATTAATTTCATTACCACAATTATTAATATACGAATTATAAATTTATCT
TTTGATCAAATACCTTTATTTATTTGATCTGTTGGTATTACAGCATTATTATTACTTTTATCTCTACCAGTATTAGCAGGGGCTATTACTATACTTCTTACAGATCGTAATTTAAATACCT
CATTTTTTGATCCTGCTGGTGGAGGAGATCCAATTTTATATCAACATTTATTT

Type material. Holotype: ♀ currently deposited in the National Museum of Natural History, Smithsonian Institution, Washington, DC, USA (USNM), illustrated in Fig. 126, bears the following four printed rectangular labels (text in italics handwritten), three white: [PERU 300m | 30 Km S.W. | Pto. Maldonado | *27 Oct. '83* | S. S. Nicolay], [*Lycas ♀* | *argentea* | Det. *Hew.* | S. S. Nicolay], [DNA sample ID: | NVG-23122G07 | c/o Nick V. Grishin], and one red [HOLOTYPE ♀ | Lycas gabriel | Grishin].

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

Etymology. The name of its sister species, godart, can be interpreted as 'God-hard,' 'good and strong,' 'brave God,' or 'God's strong one.' A Spanish equivalent to that may be Gabriel, originating from Hebrew 'strong man of God.' The name is a masculine noun in apposition.

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

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