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Fifty new genera of Hesperiidae (Lepidoptera)

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Abstract

Genomic sequencing and analysis of worldwide skipper butterfly (Lepidoptera: Hesperiidae) fauna points to imperfections in their current classification. Some tribes, subtribes and genera as they are circumscribed today are not monophyletic. Rationalizing genomic results from the perspective of phenotypic characters suggests two new tribes, two new subtribes and 50 new genera that are named here: Ceratrichiini Grishin, **trib. n.**, Gretnini Grishin, **trib. n.**, Falgina Grishin, **subtr. n.**, Apaustina Grishin, **subtr. n.**, *Flattoides* Grishin, **gen. n.**, *Aurivittia* Grishin, **gen. n.**, *Viuria* Grishin, **gen. n.**, *Clytius* Grishin, **gen. n.**, *Incisus* Grishin, **gen. n.**, *Perus* Grishin, **gen. n.**, *Livida* Grishin, **gen. n.**, *Festivia* Grishin, **gen. n.**, *Hoodus* Grishin, **gen. n.**, *Anaxas* Grishin, **gen. n.**, *Chiothion* Grishin, **gen. n.**, *Crenda* Grishin, **gen. n.**, *Santa* Grishin, **gen. n.**, *Canesia* Grishin, **gen. n.**, *Bralus* Grishin, **gen. n.**, *Ladda* Grishin, **gen. n.**, *Willema* Grishin, **gen. n.**, *Argemma* Grishin, **gen. n.**, *Nervia* Grishin, **gen. n.**, *Dotta* Grishin, **gen. n.**, *Lissia* Grishin, **gen. n.**, *Xanthonymus* Grishin, **gen. n.**, *Cerba* Grishin, **gen. n.**, *Avestia* Grishin, **gen. n.**, *Zetka* Grishin, **gen. n.**, *Turmosa* Grishin, **gen. n.**, *Mielkeus* Grishin, **gen. n.**, *Coolus* Grishin, **gen. n.**, *Daron* Grishin, **gen. n.**, *Barrolla* Grishin, **gen. n.**, *Brownus* Grishin, **gen. n.**, *Tava* Grishin, **gen. n.**, *Rigga* Grishin, **gen. n.**, *Haza* Grishin, **gen. n.**, *Dubia* Grishin, **gen. n.**, *Pares* Grishin, **gen. n.**, *Chitta* Grishin, **gen. n.**, *Artonia* Grishin, **gen. n.**, *Lurida* Grishin, **gen. n.**, *Corra* Grishin, **gen. n.**, *Fidius* Grishin, **gen. n.**, *Veadda* Grishin, **gen. n.**, *Tricrista* Grishin, **gen. n.**, *Viridina* Grishin, **gen. n.**, *Alychna* Grishin, **gen. n.**, *Ralis* Grishin, **gen. n.**, *Testia* Grishin, **gen. n.**, *Buzella* Grishin, **gen. n.**, *Vernia*

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Grishin, **gen. n.**, and *Lon* Grishin, **gen. n.** In addition, the following taxonomic changes are suggested. *Prada* Evans is transferred from Hesperiinae to Trapezitinae. *Echelatus* Godman and Salvin, *Systaspes* Weeks, and *Oenides* Mabille are removed from synonymy and are treated as valid genera. The following genera are new junior subjective synonyms: *Tosta* Evans of *Eantis* Boisduval; *Turmada* Evans of *Neoxeniades* Hayward, *Arita* Evans of *Tigasis* Godman, and *Alera* Mabille of *Perichares* Scudder. *Eantis pallida* (R. Felder) (not *Achlyodes* Hübner), *Gindanes kelso* (Evans) (not *Onenses* Godman and Salvin), *Isoteinon abjecta* (Snellen) (not *Astictopterus* C. and R. Felder), *Neoxeniades ethoda* (Hewitson) (not *Xeniades* Godman), *Moeris anna* (Mabille) (not *Vidius* Evans), and *Molo pelta* Evans (not *Lychnuchus* Hübner) are new genus-species combinations. The following are species-level taxa: *Livida assecla* (Mabille) (not a subspecies of *Livida grandis* (Mabille), formerly *Pythonides* Hübner) and *Alychna zenus* (E. Bell) (not a junior subjective synonym of *Alychna exclamationis* (Mabille), formerly *Psoralis* Mabille); and *Barrolla molla* E. Bell (formerly *Vacerra* Godman) is a junior subjective synonym of *Barrolla barroni* Evans (formerly *Paratrytone* Godman). All these changes to taxonomic status of names are propagated to all names currently treated as subspecies (for species), subgenera (for genera) and synonyms of these taxa. Finally, taxa not mentioned in this work are considered to remain at the ranks and in taxonomic groups they have been previously assigned to.

Keywords

Genomics; higher classification; taxonomy; biodiversity; phylogeny

Introduction

Hesperiidae, commonly known as skippers, are a charismatic group of butterflies that frequently look moth-like due to their stout bodies (Watson 1893), mostly brown and gray colors and fast wing beats. Some are crepuscular and even come to light (Austin 2008). However, recent DNA-based studies argue that they may have originated deep within butterfly radiation, after the swallowtails (Papilionidae) have split from the common ancestor (Wahlberg et al. 2005; Kawahara and Breinholt 2014; Espeland et al. 2018).

Having worldwide distribution, Hesperiidae are highly speciose with more than 3500 species described. However, they have received less attention than other butterfly families. The major milestone works remain those of Evans, who offered a comprehensive taxonomic treatment of the group in six volumes (Evans 1937, 1949, 1951, 1952, 1953, 1955). Refinement of this classification was catalyzed by new methodologies. The groundbreaking work of Warren et al. (2008, 2009) re-shaped the higher classification based on combination of DNA sequences of several genes with morphological characters. Several follow up studies employed a larger set of genes, up to several hundred (Sahoo et al. 2016, 2017; Toussaint et al. 2018). Then, a genome-scale revisionary work has followed (Li et al. 2019; Zhang et al. 2019b, c).

Genomic analyses revealed many nuances not readily apparent from a morphological standpoint. However, retrospective comparison of phenotypic characters is consistent with the picture emerging from the comparison of phylogenetic trees based on nuclear and

mitochondrial genomes (Li et al. 2019; Zhang et al. 2019c). We carried out genomic sequencing of representative Hesperiidae species from all known genera. As a result, we found inconsistencies in assignment of species to genera, and many genera and some tribes and subtribes were not monophyletic as currently defined. While the details of the phylogenetic analysis and their implications for the higher classification of Hesperiidae will be presented elsewhere, some of these inconsistencies are corrected here by proposing new names for two tribes, two subtribes and 50 genera detected in phylogenetic trees. Here, we show only a subset of data necessary to justify our conclusions.

Materials and Methods

This study is based on whole genomic shotgun DNA sequences that were mostly obtained from pinned and dried specimens in collections. Many of these specimens were collected more than a century ago and a number of them were primary type specimens. See Table 1 for a brief data summary of the specimens used in this work, and Table S1 in the Supplemental file deposited at https://osf.io/5cfht/?view_only=21eb53b6f8f344afaee3de2be90bf5d2 for details. We use either an abdomen, pieces of muscle tissue taken from the thorax through the abdomen attachment site (for previously dissected specimens), or a leg for DNA extraction. The abdomen is used when genitalic dissection is needed. Muscle tissue is a viable alternative to the leg when leg material is not sufficient or using a leg is not possible. Legs were the most convenient choice because they were easier to sample and often yielded better-quality DNA. Therefore, most specimens were sequenced from legs. The details of protocols for DNA extraction, genomic library preparation, sequencing and analysis are given in our previous publications (Cong et al. 2015a, b, 2016a, b, 2017a, b, 2018; Shen et al. 2015, 2016a, b, 2017; Zhang et al. 2017a, b; Li et al. 2019; Zhang et al. 2019a, b). In the methods employed, this study is identical to that of Li et al. (2019), and only difference is that a larger number of species and specimens were used.

Due to this very large number of specimens we have sequenced, the phylogenetic trees were built for smaller phylogenetic groups (subfamilies, tribes and subtribes) and analyzed together with the “backbone” tree for the entire family constructed with selected reference species and given in Li et al. (2019). Type species (or their close relatives when the type is not available) of available genus-level names (including the names treated as synonyms) were marked on the trees to ensure that any available name for each clade is used. Manual analysis of the trees involved searching for non-monophyletic genera and checking clades that are prominently separated from others. Both nuclear genome and mitogenome trees were checked side-by-side to evaluate the consistency between them. Statistical support values (bootstrap) were taken into consideration to judge the validity of each observed clade. When a clade without an available name was found, identification of specimens in the clade was confirmed by the analysis of their wing patterns and genitalia. These new clades and the genus of former placement of each species proposed as a type species of a new genus name were rationalized in terms of genitalic morphology and wing patterns to search for diagnostic characters in phenotype. Finally, genitalia and wing patterns were used to decide the generic placement of species for which DNA data were not available.

Diagnostic DNA characters were identified in nuclear genomic sequences using our recently published procedure (see SI Appendix to Li et al. 2019). The positions in exons were found that are most likely synapomorphic to the clade defined as a genus. For the clades where we had several species sequenced, positions that are invariant in all species from this clade and have a base pair different from a (mostly invariant) base pair in the outgroups were found and those with the smallest number of species with missing data were selected. If a genus has only one species sequenced, it is difficult to distinguish between characters of the genus and characters of the species. Therefore, we frequently resorted to a different method of defining DNA characters of a genus that would increase the robustness of these characters. First, we looked for characters to define the sister clade of the genus. Sister clades usually included more than one species, and thus characters for the sister clade were better defined. We find the characters for the sister clade and take their states that differ from those in the sister clade as diagnostic for the genus in question. Second, we found synapomorphic characters for the clade that leads to the common ancestor of the genus and its sister clade. We used the combination of these latter characters with the diagnostic ones to define the genus. Such a treatment increases the chances that the character found is not a random non-conserved change or a sequencing error. Number of sequence reads covering this position was taken into account in choosing the characters, and those positions with better coverage were given priority. The character states are given in diagnoses below as abbreviations. For example, aly728.44.1:G672C means position 672 in exon 1 of gene 44 from scaffold 728 of the *Cecropterus* [formerly *Achalarus*] *lyciades* (aly) reference genome (Shen et al. 2017) is C, changed from G in the ancestor. When characters were found for the sister clade of the diagnosed taxon, the following statement was used: aly5294.20.2:A548A (not C), which means that position 547 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). The sequences of exons from the reference genome with the positions used as character states highlighted in green are given in the supplemental file deposited at https://osf.io/5cfht/?view_only=21eb53b6f8f344afaee3de2be90bf5d2. Distribution of these sequences together with this publication ensures that the numbers given in the diagnoses can be easily associated with actual sequences. This publication has been registered with ZooBank as http://zoobank.org/BA35690A-FC73-4E5A-A805-FE9550275FEC and individual ZooBank registration numbers for each new name are given below.

The specimens were examined and sampled for sequencing in the following collections (abbreviations in parenthesis, used in Table 1 and Table S1 in the Supplemental file deposited at https://osf.io/5cfht/?view_only=21eb53b6f8f344afaee3de2be90bf5d2): American Museum of Natural History, New York, NY, USA (AMNH), Natural History Museum, London, UK (BMNH), Burke Museum of Natural History and Culture, Seattle, WA, USA (BMUW), Carnegie Museum of Natural History, Pittsburgh, PA, USA (CMNH), Colorado State University Collection, Fort Collins, CO, USA (CSUC), The Field Museum of Natural History, Chicago, FL, USA (FMNH), Los Angeles County Museum of Natural History, Los Angeles, CA, USA (LACM), Museum of Comparative Zoology, Harvard University, Cambridge, MA, USA (MCZ), Mississippi Entomological Museum, Starkville, MS, USA (MEM), Muséum National d'Histoire Naturelle, Paris, France (MNHP), Natural History Museum, Frankfurt, Germany (SMF), Texas A&M University Insect Collection,

College Station, TX, USA (TAMU), National Museum of Natural History, Smithsonian Institution, Washington, DC, USA (USNM), University of Texas Southwestern, freezers of the Grishin lab, Dallas, TX, USA (UTSW), Zentrum fur Biodokumentation des Saarlandes, Schiffweiler, Germany (ZfBS), Museum für Naturkunde, Berlin, Germany (ZMHB), Zoologische Staatssammlung München, Germany (ZSMC), and research collections of Jim P. Brock (JPBrock), Ernst Brockmann (EBrockmann), Robert Gallardo (RGallardo), Bernard Hermier (BHermier), Kiyoshi Maruyama (KMaruyama) James A. Scott (JAScott), Texas Lepidoptera Survey, Houston, TX, USA (TLS, since then donated to McGuire Center for Lepidoptera and Biodiversity, Gainesville, FL, USA, MGCL), and Mark Walker (MWalker).

Results and Discussion

Analysis of the trees revealed rampant inconsistencies in the current classification of Hesperiidae into genera. These inconsistencies were not evenly distributed among phylogenetic lineages of Hesperiidae. Fewer problems were observed among the Old World taxa due to better knowledge about them, and maybe due to their smaller number. Most problems involved non-monophyletic genera with one or more clades of the former genus not having an available name. In several instances, a genus remained monophyletic as currently circumscribed but was prominently divided into two clades. Genetic diversification within each clade was comparable to that in other genera. For instance, the COI barcode difference taken as a proxy for diversification was typically below 10%, and the distances in nuclear and mitochondrial genomic DNA trees were about the same as in other species-rich genera. However, the distance between the clades was prominently larger than within each clade, typically more than 10% identity in the barcode.

These clades are named here and the following are the standardized descriptions of new taxa found during this analysis. The names were chosen to be simple and short, and mostly either reflect names or properties of their type species to facilitate memorization, or are fusions of genus names, euphonized and shortened. For each genus, a ZooBank registration number is given. The type species name is listed in its original genus combination and spelling, followed by the author and year the name was made available (not a bibliographic reference, but part of the name). Definition section indicates closest genera, mostly sisters or a group of genera if there are no clear sister genera, states the generic placements prior to this study (type species are given where appropriate to help assign a clade to a genus), gives reference to diagnostic characters as they are given in previous publications mostly in the Evans volumes (Evans 1937, 1949, 1951, 1952, 1953, 1955). It was almost always possible to trace the genus observed in the phylogenetic trees to the morphological characters given in the Evans' identification keys. We think that referencing the keys rather than comprehensively listing all the characters would facilitate identification. Nevertheless, a brief morphological diagnosis for each genus is given, summarizing the most prominent phenotypic traits. DNA characters found by our recently developed method (Zhang et al. 2019c) are given at the end of each definition. This method should increase the robustness of the generic-level characters allowing for addition of species to a genus once they are sequenced. Then the gender of the name and an explanation about its origin is provided, species placed in the genus are listed (in their original genus-species name combinations with authors and dates),

a parent taxon (mostly a subtribe, tribe or subfamily per Li et al. (2019)) is given, sometimes followed by comments about species involved and proposed additional taxonomic changes.

All of the changes to taxonomic status of names are propagated to all names currently treated as subspecies (for species), subgenera (for genera) and synonyms of these taxa. For instance, we do not list subspecies and synonyms unless changes are made to their status, and we assume that these names go with the species they were previously placed with. Finally, taxa not mentioned in this work are considered to remain at the ranks and in taxonomic groups they have been previously assigned to (Evans 1937, 1949, 1951, 1952, 1953, 1955; Mielke 2005; Li et al. 2019; Zhang et al. 2019b).

Furthermore, several tribes and subtribes would no longer be monophyletic if the higher-level classification remained unchanged. To solve this problem, we establish two new tribes and two new subtribes, which are described here. The following sections follow the standardized format and are either new taxa descriptions or taxonomic changes to existing taxa, as stated in the titles of these sections. Sections dealing with family-group names are given first, so that the new names can be used in the following sections dealing with genus-group names. Then, the sections are arranged in phylogenetic order approximating how these taxa appear in the figured trees.

Ceratrichiini Grishin, new tribe

http://zoobank.org/FC72EB8A-495D-4439-AA53-C310CD0735DE

Type genus.—*Ceratrichia* Butler, [1870].

Definition.—Placed near the mostly African tribe Astictopterini Swinhoe, 1912, this tribe is a sister to all Hesperiinae except Aeromachini Tutt, 1906. Backed by the maximal statistical support in all trees (Fig. 1), this clade of closely related genera keys to VI.A.(b) or VII.B.(a)(a^1) in Evans (1937). Antennae long, longer than half of costa, 2nd segment of palpi directed up, forewing vein CuA_2 originates in the middle of discal cell, end of discal cell straight, hindwing vein M_2 prominent, originates closer to vein M_1 than M_3, vein CuA_2 originates before or opposite to RS, vein 3A long. Male genitalia simple in most species: uncus undivided (except *Herila*), terminally narrows to a point, narrow in lateral view, gnathos either short or lacking, valva 2–3 times longer than wide, without prominent elaborations, may have small teeth on harpe. In DNA, a combination of the following base pairs is diagnostic: aly1121.3.2:A429G, aly669.27.2:A50G, aly374.13.3:A242T, aly216.78.1:A568C, aly1155.14.6:T406G.

Genera included.—*Ceratrichia* Butler, [1870], *Meza* Hemming, 1939, *Herila* Larsen and Collins, 2012, *Pardaleodes* Butler, 1870, *Ankola* Evans, 1937, and a new genus described below.

Parent taxon.—Subfamily Hesperiinae Latreille, 1809.

Comments.—Judging from the genomic trees, this tribe consists of closely related species, but their wing patterns and colors are quite different from each other and may resemble

genera outside the tribe. We were not able to find an obvious morphological synapomorphy for the tribe and, as it frequently is the case, the tribe is best diagnosed by DNA characters.

Gretnini Grishin, new tribe

http://zoobank.org/E7F984DE-BC49-4617-8624-9630FCEE18F3

Type genus.—*Gretna* Evans, 1937.

Definition.—Placed as a sister to all other Hesperiinae but Aeromachini Tutt, 1906, Ceratrichiini trib. n. and Astictopterini Swinhoe, 1912 in all genomic trees, this stand-alone lineage has no close relatives (Fig. 1). Keys to VIII.B.(b)(b^1)(a^2)(a^3)(a^4) in Evans (1937), and the description of *Gretna* given by Evans (1937: 149) applies to the tribe. Most prominently it is distinguished from other Hesperiinae by a combination of large stout palpi with tiny 3rd segment, curved forewing vein 1A+2A, well-defined hindwing vein M_2, narrow hindwing cells M_1-M_2 and M_2-M_3 around it and unusual vein structure at the origin of vein RS in males, which is close to the origin of vein Sc+R_1, and veins M_1 and RS are curved at their divergence point, U-shaped rather than V-shaped. In DNA, a combination of the following base pairs is diagnostic: aly2012.5.1:A98C, aly2195.3.11:A37G, aly349.39.4:C152G, aly276378.25.8:A84T, aly6398.6.4:A46C.

Genera included.—Only the type genus.

Parent taxon.—Subfamily Hesperiinae Latreille, 1809.

Comments.—Uniqueness of *Gretna* as a stand-alone phylogenetic lineage of the tribal rank was not readily apparent from morphology and the genomic approach was critical in revealing its distinctness.

Falgina Grishin, new subtribe

http://zoobank.org/B32D24C6-8946-44DC-BFCF-15E5582B3ABE

Type genus.—*Falga* Mabille, 1898.

Definition.—An assemblage of genera previously placed in three subtribes (Carystina Mabille 1878, Anthoptina A. Warren, 2009 and Moncina A. Warren, 2008), the subtribe is characterized by the maximal statistical support values in all genomic trees (Fig. 1) and is in the same clade with Anthoptina and Moncina. Keys to I.1, I.2, J.8, J.13., J.16c, J.31, J.47, J.49, or K.1 in Evans (1955). The lack of spines on mid-tibiae is the unifying morphological character of this morphologically diverse group best diagnosed by the combination of the following synapomorphic DNA characters: aly1186.4.1:A962T, aly48.2.12:C1493A, aly345.16.5:A563T, aly536.1.3:A312G, aly276378.18.1:A1489G.

Genera included.—*Falga* Mabille, 1898, *Justinia* Evans, 1955, *Thargella* Godman, 1900, *Propapias* O. Mielke, 1992, *Synapte* Mabille, 1904, *Turesis* Godman, 1901, *Flaccilla* Godman, 1901, *Methion* Godman, 1900, *Mnasinous* Godman, 1900, *Miltomiges* Mabille, 1903, *Methionopsis* Godman, 1901 and a new genus described below.

Parent taxon.—Tribe Hesperiini Latreille, 1809.

Comments.—This subtribe is yet another unexpected assemblage of genera with disparate morphology. However, its monophyly is very strongly supported in all trees (Fig. 1). No phenotypic synapomorphy is apparent to unify these taxa, and the ultimate diagnosis is possible on the basis of synapomorphic DNA characters.

Apaustina Grishin, new subtribe

http://zoobank.org/05EF9D2F-DACA-45DC-B6D7-7960424D3C33

Type genus.—*Apaustus* Hübner, [1819].

Definition.—A subtribe without clear phylogenetic affinities within Hesperiini, but not a sister to Thymelicina (Fig. 1). Keys to J.1, M.1, or M4 or in Evans (1955). Characterized by elongated wings, weak flight, short antennae and gracile bodies. Diagnosed by a combination of: flattened antennal club without apiculus, long and thin 3rd segment of palpi extending beyond the 2nd segment (less so in *Adopaeoides*), the lack of spines on mid-tibiae (except *Apaustus*), and the lack of brands or stigmas on wings. In DNA, a combination of the following base pairs is diagnostic: aly3507.5.1:A578C, aly1297.14.4:A4190C, aly123.4.7:A70T, aly123.4.7:G71C, aly315.4.4:A453C.

Genera included.—*Apaustus* Hübner, [1819], *Adopaeoides* Godman, 1900, and *Ancyloxypha* C. Felder, 1862.

Parent taxon.—Tribe Hesperiini Latreille, 1809.

Comments.—Our genomic findings corroborate recent anchored phylogenomic results (Toussaint et al. 2018) in dividing the former Thymelicina into two phylogenetic lineages of different origins (Fig. 1). While the association of *Apaustus*, formerly placed in Moncina A. Warren, 2008, with the other two genera formerly placed in Thymelicina Tutt, 1905, was unexpected at first, it makes morphological sense considering similarities in wing shapes and the gracile bodies of these butterflies.

Composition of the subtribes Calpodina Clark, 1948 and Thymelicina Tutt, 1905

Separated from Carystina Mabille 1878 in Li et al. (2019), Calpodina is a sister and a close relative of Thymelicina (Fig. 1). In addition to the type genus *Calpodes* Hübner, [1819], we keep three genera in this subtribe: *Saliana* Evans, 1955, *Panoquina* Hemming, 1934, and *Zenis* Godman, 1900. All other genera previously placed in Calpodina (Warren et al. 2008, 2009) belong to Carystina or other subtribes as detailed in Li et al. (2019) and this work. Its sister Thymelicina, after removal of the two genera being placed in the new subtribe described above, is composed of only three genera: *Thymelicus* Hübner, [1819], *Oarisma* Scudder, 1872, and *Copaeodes* Speyer, 1877.

Flattoides Grishin, new genus

http://zoobank.org/9D7A5387-08F8-4C25-B584-B67F90EEC43A

Type species.—*Codatractus amazonensis* Bell, 1947.

Definition.—A sister genus to *Oileides* Hübner, [1825] (type species *Oileides vulpinus* Hübner, [1825]), where *C. amazonensis* was placed previously (Fig. 2). However large genetic distance between *O. vulpinus* and *O. amazonensis* (COI barcodes differ by 12.3%, the difference is typically smaller than 10% for species within a genus) argues for their distinction. Keys to D.9.4 in Evans (1952). Genitalia illustrated by Bell in his fig. 2 (Bell 1947). Distinguished from its relatives by the following combination of characters: shorter than tegumen and broad uncus with small (not longer than wide) arms; prominent gnathos not shorter than uncus; valva gradually curved dorsad, ending with two pointed teeth; tuft of apricot-colored modified scales in a groove along the vein near the base of ventral hindwing in males; forewing with a macular white band from mid-costa to tornus. In DNA, a combination of the following base pairs is diagnostic: aly8661.4.1:A916G, aly10226.44.1:C1975G, aly709.1.2:T194C, aly36556.1.1:T2416T (not A), aly274.33.1:A188A (not G), aly82.28.5:T398T (not G).

Etymology.—The name is a masculine noun in the nominative singular, for the type species that resembles butterflies from the genus *Celaenorrhinus* known as “Flats” in some English-speaking countries.

Species included.—Only the type species.

Parent taxon.—Subtribe Oileidina Grishin, 2019.

Aurivittia Grishin, new genus

http://zoobank.org/C2C0299C-67C8-4F0E-ACB8-29A7292E10BD

Type species.—*Plesioneura aurivittata* Moore, 1878.

Definition.—Surprisingly, a possible sister genus to *Alenia* Evans, 1935 (type species: *Pyrgus sandaster* Trimen, 1868), and in the same clade with *Apallaga* Strand, 1911 (type species *Apallaga separata* Strand, 1911), but genetically far removed from these and all other taxa (Fig. 3). Species in this genus were formerly placed in *Celaenorrhinus* Hübner, [1819] (type species *Papilio eligius* Stoll, [1781];) and key to B.6.30 in Evans (1949), notably lacking hair pencil on hind tibiae, which other *Celaenorrhinus*-like taxa possess. Morphologically, distinguished from *Celaenorrhinus* (sensu stricto) by essentially undivided uncus, sometimes with small knobs (not processes) as arms and the lack of hair pencil on hind tibiae; and from *Alenia* (a genus with undivided uncus) by the shape of valva that is not terminally split like a crab claw, and the presence of yellow band across the forewing. In male genitalia most similar to *Apallaga*, a genus with many species characterized by undivided uncus, but differs in longer gnathos (not less than half of the uncus length), thicker penis, valva with more robust and broad harpe that is gradually curved dorsad (not ventrad), does not carry any processes and is not forked, but narrows to a single point, and ampulla with a long process (style) along the harpe. In wing patterns, hindwing is not prominently variegated dorsally and is mostly unmarked, forewing with a compact yellow discal band with regular edges that does not extend into the discal cell and

frequently with a triplet of apical yellow spots. In DNA, a combination of the following base pairs is diagnostic: aly2532.2.1:T488A, aly997.12.1:C310A, aly527.19.4:T178A, aly822.15.1:C589A, aly235.8.18:G1178A.

Etymology.—The name is a feminine noun in the nominative singular, formed to reflect the golden stripe on the forewing, similar to the name of the type species.

Species included.—The type species, *Plesioneura cameroni* Distant, 1882, and *Celaenorrhinus viet-namicus* Devyatkin, 1998.

Parent taxon.—Tribe Celaenorrhinini Swinhoe, 1912.

Comments.—These south Asian butterflies are not so prominently distinct from the striped species of *Celaenorrhinus*. Therefore, their uniqueness was not apparent prior to our genomic study, although genitalic features revealed *a posteriori* can diagnose the genus morphologically. Phylogenetic placement of this Asian genus in the African clade of Celaenorrhinini Swinhoe, 1912 is interesting.

Viuria Grishin, new genus

http://zoobank.org/1D91E55F-38B7-4E1E-997F-49FBFD10CE02

Type species.—*Pellicia licisca* Plötz, 1882.

Definition.—A sister genus to *Viola* Evans, 1953, distant from *Pachyneuria* Mabille, 1888 (type species *Pachyneuria obscura* Mabille, 1888), where species of this genus were formerly placed (Fig. 4). Keys to E.20.7 in Evans (1953). Differs from *Pachyneuria* by the presence of long tufts of scales near hindwing costa above in males and swollen hindwing vein $Sc+R_1$, similar to *Viola* and *Nisoniades* Hübner, [1819], among others. Differ from *Viola* and other genera in genitalia and diagnosed by asymmetric uncus with asymmetric processes, reduced harpe of the right valva compared to the expanded rounded ampulla. In DNA, a combination of the following base pairs is diagnostic: aly1222.46.1:A28C, aly207.4.6:C1025G, aly1019.7.7:T59A, aly2012.7.7:C98G, aly638.27.5:T694A.

Etymology.—The name is a feminine noun in the nominative singular, a fusion of *Vi*[ola] and [Pachyne]*uria*.

Species included.—The type species, *Pachyneuria lista* Evans, 1953, and *Pellicia herophile* Hayward, 1940.

Parent taxon.—Tribe Carcharodini Verity, 1940.

Clytius Grishin, new genus

http://zoobank.org/AEAE278A-4A9B-45C3-9903-E886FBCEA5F7

Type species.—*Pholisora clytius* Godman and Salvin, [1897].

Definition.—Not closely related to any other genus. Formerly placed in *Bolla* (type species *Bolla pullata* Mabille, 1903, currently a junior subjective synonym of *Staphylus imbras* Godman and Salvin, [1896]), but is not monophyletic with *Bolla* species (Fig. 4). Keys to E.31.22 in Evans (1953). Morphologically, distinguished from *Bolla* species by broad-ended valva without processes, but with concave costa ending with bulky ampulla weakly separated from short serrated harpe, and the lack of gray or ochreous overscaling on wings above. In DNA, a combination of the following base pairs is diagnostic: aly997.12.1:G125C, aly536.106.2:A2067G, aly127.74.3:A1567G, aly320.9.2:A806G, aly1011.11.1:A34C.

Etymology.—The name, a masculine noun in the nominative singular, echoes the type species name.

Species included.—Only the type species.

Parent taxon.—Tribe Carcharodini Verity, 1940.

Incisus Grishin, new genus

http://zoobank.org/2ED74AC8-4CCF-4796-952B-0292620F0855

Type species.—*Antigonus incisus* Mabille, 1878.

Definition.—A genus without close relatives. Formerly placed in *Staphylus* Godman and Salvin, [1896], *incisus* is not monophyletic with the *Staphylus* type species *Helias ascalaphus* Staudinger, 1876, nor with *Scantilla opites* Godman and Salvin, [1896] (a junior subjective synonym of *Tagiades vincula* Plötz, 1886) the type species of *Scantilla* Godman and Salvin, [1896], a genus-group name treated as a subjective synonym of *Staphylus* (Fig. 4). Keys to E.32.35b in Evans (1953). Readily distinguished from its relatives by the wing shape: forewing inner margin concave, hindwing outer margin excavate; forewing with hyaline apical spots; uncus long and narrow, pointed at the tip, without side processes, no defined gnathos, valva less than twice longer than wide, penis shorter that in *Staphylus*, with a spined cornutus. In DNA, a combination of the following base pairs is diagnostic: aly23605.8.3:C247T, aly5294.23.1:A538C, aly9588.6.1:T843C, aly1370.7.2:A1760G, aly345.13.8:A62C.

Etymology.—The name, a masculine noun in the nominative singular, echoes the type species name.

Species included.—The type species, *Staphylus fasciatus* Hayward, 1933 and *Pholisora* (?) *angulata* Bell, 1937.

Parent taxon.—Tribe Carcharodini Verity, 1940.

Comments.—Steinhauser doubted the placement of some of these species in *Staphylus* on the basis of morphological analysis (Steinhauser 1989), and he was correct.

Perus Grishin, new genus

http://zoobank.org/349FEEDB-0503-4302-AA25-B985D8A8CB45

Type species.—*Pholisora cordillerae* Lindsey, 1925.

Definition.—Not closely related to any other genus. Formerly placed in *Staphylus* Godman and Salvin, [1896], *cordillerae* is not monophyletic with the *Staphylus* type species *Helias ascalaphus* Staudinger, 1876, nor with *Scantilla opites* Godman and Salvin, [1896] (a junior subjective synonym of *Tagiades vincula* Plötz, 1886) the type species of *Scantilla* Godman and Salvin, [1896], a genus-group name treated as a subjective synonym of *Staphylus* (Fig. 4). Keys to E.32.16, E.32.24b, E.32.26, or E.32.34 in Evans (1953). Distinguished from *Staphylus* species by the following combination of characters: head and palpi above mostly brown, more prominent submarginal pale spots on both wings above, harpe shorter than or the same length as moderately expanded ampulla, directed posteriad, end of uncus pointed, tegumen expanded on the sides, bulbous, with a pair of side processes in some species. In DNA, a combination of the following base pairs is diagnostic: aly3014.2.4:A833G, aly9588.14.1:C77A, aly171.12.3:A1360C, aly2532.10.1:A1294C, aly2790.11.3:A787C.

Etymology.—The name is a masculine noun in the nominative singular, derived from Peru, the locality of the type species and the county where many other species of this genus occur.

Species included.—The type species, *Staphylus mossi* Evans, 1953, *Staphylus minor* Schaus, 1902, *Antigonus coecatus* Mabille, 1891, and *Nisoniades menuda* Weeks, 1902.

Parent taxon.—Tribe Carcharodini Verity, 1940.

Tosta Evans, 1953 is a synonym of *Eantis* Boisduval, 1836

Phylogenetic analysis confidently reveals (Fig. 5) that *Tosta* Evans, 1953 (type species *Tosta tosta* Evans, 1953) originates within *Eantis* Boisduval, [1836] (type species *Urbanus thraso* Hübner, [1807]) and therefore is best considered its junior subjective synonym.

Eantis pallida (R. Felder, 1869), new combination

In all trees, *Helias pallida* R. Felder, 1869 is not monophyletic with *Papilio busirus* Cramer, [1779], the type species of *Achlyodes* Hübner, [1819], but originates within *Eantis* Boisduval, [1836] (type species *Urbanus thraso* Hübner, [1807]) (Fig. 5). Therefore, *H. pallida* is placed in this genus to form a new combination: *Eantis pallida*.

Pythonides assecla Mabille, 1883, reinstated status

We consider *Pythonides assecla* Mabille, 1883 to be a species distinct from *Pythonides grandis* Mabille, 1878 due to difference in size and extent of the blue coloration of the hindwing, both in males and females, and differences in shade of blue, being paler in *P. grandis*.

Livida Grishin, new genus

http://zoobank.org/24179CB6-20EF-4DF2-B545-CFF25554444C

Type species.—*Pythonides assecla* Mabille, 1883.

Definition.—A genus clearly near *Gindanes* Godman and Salvin, 1895, *Pythonides* Hübner, [1819], *Quadrus* Lindsey, 1925, *Zera* Evans, 1953 and *Ouleus* Lindsey, 1925, but without closer affinity to any one of them (Fig. 5). The species included here in this genus were formerly placed in *Pythonides*, but are not monophyletic with the type species of this genus, *Papilio jovianus* Stoll, 1782. Keys to E.41.5 in Evans (1953). Morphologically, distinguished from related genera by the combination of the shape of uncus (flattened at the tip with a short and thin central projection) with the shape of valva (broad at the base with concave costa and diamond-shaped harpe longer than the rest of the valva, with serrated dorsoposterior edge), only one upper spur on hind tibiae, the lack of tuft in hind tibiae and thoracic pouch in males, ventral hindwing mostly pale blue, dorsal hindwing pale blue in males at least near tornus. In DNA, a combination of the following base pairs is diagnostic: aly1672.3.1:T128G, aly1672.3.1:C110G, aly2618.5.1:C3626G, aly140.1.2:T1822T (not A), aly1349.7.9:C1010C (not G), aly1877.13.1:A785A (not C), aly23605.1.46:T5641T (not A), aly23605.1.46:C5642C (not G), aly536.102.1:C56C (not A), aly1935.2.1:G242G (not C), aly345.3.1:C328C (not G), aly767.12.13:C118C (not A).

Etymology.—The name is a feminine noun in the nominative singular, from the Latin lividus (blue), to indicate the distinctive cornflower blue color of the hindwing in males of the type species.

Species included.—The type species and *Pythonides grandis* Mabille, 1878.

Parent taxon.—Subtribe Pythonidina Grishin, 2019.

Comments.—Another genus that would be very difficult to detect without genomic data, because by appearance the adults of this species do not look noticeably different from *Pythonides*. However, genomic analysis suggests that the two are distant.

Gindanes kelso (Evans, 1953), new combination

Phylogenetic analysis shows (Fig. 5) that *Onenses kelso* Evans, 1953 falls within *Gindanes* Godman and Salvin, [1895] (type species *Gindanes panaetius* Godman and Salvin, [1895], treated as a subspecies of *Hesperia brebisson* Latreille, [1824]) and in a different tribe (Achlyodini) from *Onenses* Godman and Salvin, [1895] (type species *Leucochitonea hyalophora* R. Felder, 1869, tribe Pyrgini). Therefore, we introduce a new combination: *Gindanes kelso*.

Festivia Grishin, new genus

http://zoobank.org/16737C47-F8DA-40C1-8D05-B670F1E6FDD0

Type species.—*Syrichthus* [sic] *festiva* Erichson, [1849].

Definition.—A sister genus of *Sostrata* Godman and Salvin, 1895 (Type species. *Leucochitonea scintillans* Mabille, 1876, which is treated as a junior subjective synonym

of *Sostrata bifasciata* (Ménétriés, 1829)), where these species were placed before (Fig. 6). Keys to E.42.1a in Evans (1953). Distinguished from *Sostrata* by blue ventral hindwing, broader wings and in male genitalia by longer harpe, clearly separated from the rest of valva. In DNA, a combination of the following base pairs is diagnostic: aly276665.9.3:C95G, aly923.23.1:G274A, aly2790.3.6:A367C, aly923.23.1:T688G, aly2101.22.7:A31C.

Etymology.—The name is a feminine noun in the nominative singular, given for the type species and for the festive looks that distinguish this genus from *Sostrata*.

Species included.—The type species, *Leucochitonea cronion* C and R. Felder, 1867, *Pythonides caerulans* Mabille and Boullet, 1917, *Pythonides adamantinus* Mabille, 1898, *Sostrata grippa* Evans, 1953, and *Sostrata jinna* Evans, 1953.

Parent taxon.—Subtribe Erynnina Brues and Carpenter, 1932.

Comments.—Although this genus does not disrupt monophyly of the former concept of *Sostrata* that included these species, genetic distance between these sister genera is not less than that between *Potamanaxas* and *Anaxas*, gen. n., or between *Mylon* and *Anastrus*. This comparatively large genetic differentiation is present in both nuclear and mitochondrial genomes. The two genera are also clearly diagnosed by wing patterns and shapes.

Echelatus Godman and Salvin, [1894] is a valid genus

Echelatus Godman and Salvin, [1894] (type species *Anastrus varius* Mabille, 1883, which is a junior subjective synonym of *Achlyodes sempiternus* Butler and Druce, 1872) is reinstated as a valid genus from its synonymy with *Anastrus* Hübner, [1824], because the group of species that includes *Anastrus obscurus* Hübner, [1824] (the type species of *Anastrus*) is sister to *Mylon* Godman and Salvin, [1894] (type species *Leucochitonea lassia* Hewitson, 1868) and thus is not monophyletic with the type species of *Echelatus* (Fig. 6), as suggested by Austin (1998).

Hoodus Grishin, new genus

http://zoobank.org/CC847380-9804-439B-9370-DD2CE72BB0FE

Type species.—*Hesperia pelopidas* Fabricius, 1793.

Definition.—A sister genus to *Echelatus* Godman and Salvin, [1894] (type species *Anastrus varius* Mabille, 1883, which is a junior subjective synonym of *Anastrus sempiternus* (Butler and Druce, 1872)) (Fig. 6). Species of this new genus were placed in *Mylon* (type species *Leucochitonea lassia* Hewitson, 1868) previously, key to E.50.10 in Evans (1953), and were defined as the “pelopidas” group by Austin (2000) who gave a detailed morphological diagnosis on p. 5 and 7, which is not repeated here. Most importantly, the two unique diagnostic characters are: vinculum in male genitalia is expanded dorsad on both sides to cover most of tegumen and uncus arms are very short. In DNA, a combination of the following base pairs is diagnostic: aly1735.8.1:T625C, aly3616.13.2:A50G, aly1036.5.1:A436C, aly1735.8.1:C695T, aly1735.8.1:A772C.

Etymology.—The name is a masculine noun in the nominative singular, for the vinculum expanded as a hood over tegumen.

Species included.—The pelopidas species group as defined by Austin (2000), which consists of the type species, *Mylon cristata* Austin, 2000, *Leucochitonea jason* Ehrmann, 1907, *Mylon ozema* var. *exstincta* Mabille and Boullet, 1917, *Mylon simplex* Austin, 2000, and *Mylon argonautarum* Austin, 2000.

Parent taxon.—Subtribe Erynnina Brues and Carpenter, 1932.

Anaxas Grishin, new genus

http://zoobank.org/FE71A883-25C6-491B-B1BE-3EC4F82C62B1

Type species.—*Antigonus obliqua* Plötz, 1884.

Definition.—A likely sister genus to *Potamanaxas* Lindsey, 1925, and thus not monophyletic with *Anastrus* Hübner, [1824] (type species *Anastrus obscurus* Hübner, [1824]), where these species were formerly placed (Fig. 6). The need for this genus has been suggested previously (Austin 1998). Keys to F.6.3. in Evans (1953). Genitalia illustrated by Grishin in his fig. 30–39 (Grishin 2012). Morphologically, distinguished from *Anastrus* and *Echelatus* by having processes on sacculus of the valva and a second pair of uncus arms, from the ventral side of uncus, similar to some species of its sister *Potamanaxas*, but uncus itself is essentially undivided with arms reduced to small knobs. Primary uncus arms are well-developed in *Potamanaxas*. In facies, characterized by brown wings above with several dark-brown stripes and often with some bluish scaling between the stripes. Below, wings plain brown and some species with slate overscaling on the posterior third of hindwing. In DNA, a combination of the following base pairs is diagnostic: aly3570.7.4:A85T, aly3570.7.4:G86C, aly9673.2.5:T298A, aly1735.8.1:C820C (not T), aly16.28.2:C88C (not A), aly16.28.2:A89A (not T).

Etymology.—The name is a masculine noun in the nominative singular, a group of species that were formerly placed in *Ana*[strus], but are phylogenetically closer to [Potamana]*xas*.

Species included.—The type species, its sister *Anastrus isidro* Grishin, 2012 and *Pellicia petius* Möschler, 1877.

Parent taxon.—Subtribe Erynnina Brues and Carpenter, 1932.

Chiothion Grishin, new genus

http://zoobank.org/2A17E48E-AD11-46D1-B987-2213B42EEE24

Type species.—*Pyrgus georgina* Reakirt, 1868.

Definition.—A sister genus to *Gorgythion* Godman and Salvin, [1896]. Formerly placed in *Chiomara* Godman and Salvin, 1899 (type species *Achlyodes mithrax* Möschler, 1879), but are not monophyletic with the type species (Fig. 6). Keys to F.13.1a or F.13.4 in

Evans (1953). Morphologically, characterized by asymmetry in male and female genitalia and distinguished from all other Erynnini general by a likely synapomorphy: corpus bursae in female genitalia with an additional sack-like compartment stemming from its distal end, separated from the corpus by a narrow neck and folded inside the abdomen to point caudad. In wing patterns, distinguished from *Chiomara* and *Crenda* gen. n. by a discal dark bar in the cell of dorsal forewing, also present in its sister *Gorgythion*. In DNA, a combination of the following base pairs is diagnostic: aly1264.13.9:G91T, aly595.7.8:A121C, aly525.18.1:T1397A, aly536.219.9:C2312G, aly260.4.1:G877C.

Etymology.—The name is a masculine noun in the nominative singular, a fusion of *Chio*[mara], where these species were formerly placed, and [Gorgy]*thion*, near where they ended up.

Species included.—The type species, *Papilio asychis* Stoll, [1780], *Achlyodes basigutta* Plötz, 1884, and *Chiomara khalili* Riley, 1934.

Parent taxon.—Subtribe Erynnina Brues and Carpenter, 1932.

Crenda Grishin, new genus

http://zoobank.org/3E0B892C-FC8F-4FA4-A68F-4181F33333BF

Type species.—*Chiomara crenda* Evans, 1953.

Definition.—A genus without close relatives (Fig. 6). Keys to F.13.5 in Evans (1953) who gives a detailed diagnosis. Importantly, genitalia (except saccus and penis) are close to symmetrical, especially the uncus. Both uncus and valvae are highly asymmetrical in *Chiomara* Godman and Salvin, 1899 and other related genera such as *Theagenes* Godman and Salvin, 1896, *Gorgythion* Godman and Salvin, 1896. Symmetrical uncus with a pair of side processes on each side at its base, diagnostic of the genus. In DNA, a combination of the following base pairs is diagnostic: aly318.44.1:C664A, aly114.5.7:A142T, aly114.5.7:G143C, aly1294.17.1:A1681C, aly536.188.2:G103C.

Etymology.—The name is a feminine noun in the nominative singular, and is a tautonymous name.

Species included.—Only the type species.

Parent taxon.—Subtribe Erynnina Brues and Carpenter, 1932.

Santa Grishin, new genus

http://zoobank.org/86DDFA39-B2D5-44DB-843C-CA314846FBF4

Type species.—*Carrhenes santes* Bell, 1940.

Definition.—A genus related to *Plumbago* Evans, 1953, *Paches* Godman and Salvin, 1895 and *Carrhenes* Godman and Salvin, 1895 (Fig. 7). Keys to E.43.3 or E.52.4 in Evans

(1953), one species previously placed in *Paches* Godman and Salvin, [1895] (type species *Pythonides loxus* Westwood, [1852]) the other one in *Carrhenes* Godman and Salvin, 1895 (type species *Leucochitonea fuscescens* Mabille, 1891). Distinguished from others by brown wings with darker spots and stripes above and a black spot near the hindwing tornus below. Male genitalia with a process (style) from ampulla, uncus divided, arms about as long as wide, harpe longer than wide. In DNA, a combination of the following base pairs is diagnostic: aly5021.3.22:G847C, aly2103.4.2:G472A, aly528.2.2:G1190T, aly528.2.2:G1191T, aly839.26.5:A464T.

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

Species included.—The type species and *Paches trifasciatus* Lindsey, 1925.

Parent taxon.—Tribe Pyrgini Burmeister, 1878.

Comment.—While neither of these two species fit well into the genera they were assigned to previously, due to differences in genitalia and wing patterns between the two species, their sister relationship is not obvious without genomic analysis.

Systaspes Weeks, 1905 is a valid genus

Inspection of Pyrgini trees (Fig. 7) reveals that *Antigonus corrosus* Mabille, 1878, the type species of *Systaspes* Weeks, 1905, is a sister to *Celotes* Godman and Salvin, [1899] (type species *Pholisora nessus* Edwards, 1877) and is not monophyletic with *Antigonus* Hübner, [1819] (type species *Urbanus erosus* Hübner, [1812]). Therefore, we reinstate the genus *Systaspes* and the combination *Systaspes corrosus*.

Canesia Grishin, new genus

http://zoobank.org/38584341-521B-4D1E-8115-80FA17A39E30

Type species.—*Leucochitonea canescens* R. Felder, 1869.

Definition.—A sister genus to *Xenophanes* Godman and Salvin, 1895 (type species *Papilio tryxus* Stoll, 1780), not so closely related to *Carrhenes* Godman and Salvin, 1895 (type species *Leucochitonea fuscescens* Mabille, 1891), where these species were placed previously (Fig. 7). Keys to E.51.2b in Evans (1953), defined as the canescens group by Austin (2000), but excluding *C. santes*, a species placed here in *Santa*, gen. n. Morphologically, distinguished from *Carrhenes* by the lack of mushroom-shaped process from the ampulla. The ampulla process in this genus is small, and harpe is small and narrow giving valva the appearance of a crab claw. Forewing without hyaline discal spots near costa. In DNA, a combination of the following base pairs is diagnostic: aly1146.42.8:A2540T, aly27.16.1:A577C, aly275211.5.4:T821C, aly536.106.2:A296T, aly536.106.2:C295A.

Etymology.—The name is a feminine noun in the nominative singular, inspired by the name of the type species and a Latin word for crab (cancer), indicating the crab-claw shape of the genitalic valva.

Species included.—The “canescens” group of Austin (2000), including the type species, *Achlyodes leada* Butler, 1870, *Carrhenes lilloi* Hayward, 1947, *Carrhenes recurva* Austin, 2000, *Carrhenes callipetes* Godman and Salvin, [1895], *Carrhenes meridensis* Godman and Salvin, [1895].

Parent taxon.—Tribe Pyrgini Burmeister, 1878.

Bralus Grishin, new genus

http://zoobank.org/48DF0762-C1E2-4E1D-90C1-EA30A5063308

Type species.—*Anisochoria albida* Mabille, 1888.

Definition.—A genus related to *Zopyrion* Godman and Salvin, 1896 (type species *Zopyrion sandace* Godman and Salvin, [1896]), *Timochreon* Godman and Salvin, 1896 (type species *Helias satyrus* C. and R. Felder, [1867]), and *Anisochoria* Mabille, 1876 (type species *Anisochoria polysticta* Mabille, 1876, now considered a subspecies of *Anisochoria pedaliodina* (Butler, 1870)) with its junior subjective synonym *Dicrosema* Bryk, 1953 (type species *Dicrosema quadrifenestrata* Bryk, 1953), but without obvious affinity to either one of these genera (Fig. 7). Keys to E.59.8 in Evans (1953). Morphologically, distinguished from its relatives by almost symmetric valvae with smaller unmodified harpe, ampulla without a process (just with a small knob), and uncus with a pair of short and thin processes at its distal end, between the arms that are widely set apart. Hindwing above with a wide whitish area. In DNA, a combination of the following base pairs is diagnostic: aly8048.1.4:A65G, aly3881.2.1:A178G, aly1097.18.4:G805C, aly1443.3.4:T238T (not G), aly1443.3.4:C239C (not A), aly890.35.8:T164T (not A).

Etymology.—The name, a masculine noun in the nominative singular, is a fusion of *br*[unneis], *a*[lbum], and *lu*[teu]*s*: the three colors of the type species.

Species included.—Only the type species.

Parent taxon.—Tribe Pyrgini Burmeister, 1878.

Comments.—Yet another genus that would be difficult to detect without DNA analysis.

Ladda Grishin, new genus

http://zoobank.org/4BBF25C1-3C31-4B69-9499-516C8251D74E

Type species.—*Cyclopides eburones* Hewitson, 1877.

Definition.—A sister genus to *Dalla* Mabille, 1904 (type species *Cyclopides eryonas* Hewitson, 1877), where these species were placed previously (Fig. 8). Consists of the ibhara, part of quadristriga and part of caenides groups of Evans (1955) and keys to H.6.56b, H.6.44b, or H.6.53b. Distinguished by the combination of straight (non-concave) costa of forewing with unmarked, dark brown above hindwing. If hindwing is spotted above, then the spot is single, centered around the cell, ventral hindwing not plain yellow and without

a pale ray from base to margin and if a pale spot is present in M_3-CuA_1 cell, then it is either joined with the spot in CuA_1-CuA_2 cell, or closer the discal cell spot than to margin and ventral hindwing, and the pale spot in CuA_1-CuA_2 cell on ventral hindwing is not connected with distal margin by a broadening pale area (but could be connected with the area of the same width as the spot or narrower). In DNA, a combination of the following base pairs is diagnostic: aly103.37.1:A134T, aly638.15.11:T5060C, aly23605.1.35:A566G, aly1139.25.1:G552T, aly23605.1.35:C580G.

Etymology.—The name is a feminine noun in the nominative singular, a play of letters, from *Dalla*.

Species included.—The type species, *Dalla tona* Evans, 1955, *Dalla decca* Evans, 1955, *Butleria morva* Mabille, 1898, *Thanaos ibhara* Butler, 1870, *Carterocephalus plancus* Hopffer, 1874, *Cyclopides crithote* Hewitson, 1874, *Dalla calima* Steinhauser, 1991, *Dalla rosea* Evans, 1955, *Butleria granites* Mabille, 1898, *Dalla parma* Evans, 1955, *Dalla mars* Evans, 1955, *Pamphila cuadrada* Weeks, 1901, *Butleria quadristriga* Mabille, 1889, *Dalla rubia* Evans, 1955, *Argopteron xicca* Dyar, 1913, *Dalla pedro* Steinhauser, 2002, *Dalla connexa* Draudt, 1923, *Dalla disconnexa* Steinhauser, 2002, *Dalla vista* Steinhauser, 2002, *Butleria ticidas* Mabille, 1898, *Cyclopides caenides* Hewitson, 1868, *Dalla bos* Steinhauser, 1991, *Dalla pura* Steinhauser, 1991, *Dalla mora* Evans, 1955, *Dalla carnis* Evans, 1955, *Butleria monospila* Mabille, 1898, *Dalla simplicis* Steinhauser, 1991, *Dalla seirocastnia* Draudt, 1923, *Dalla celsus* Steinhauser, 2002, *Dalla pantha* Evans, 1955, *Dalla puracensis* Steinhauser, 1991, *Dalla ochrolimbata* Draudt, 1923.

Parent taxon.—Tribe Heteropterini Aurivillius, 1925.

Comments.—Although this genus does not disrupt the monophyly of *Dalla* when combined with it, *Ladda* is split from *Dalla*, due to the large genetic distance between the two genera, each forming a tight cluster of species well separated from the other. Genetic differentiation between these two genera is similar to that between traditional genera such as *Heteropterus* Duméril, 1806 and *Leptalina* Mabille, 1904, or *Carterocephalus* Lederer, 1852 and *Metisella* Hemming, 1934.

Willema Grishin, new genus

http://zoobank.org/D92BF2E1-F842-44C6-A924-023F495F9589

Type species.—*Heteropterus willemi* Wallengren, 1857.

Definition.—A sister genus to *Hovala* Evans, 1937 (type species *Cyclopides pardalina* Butler, 1879), more distant from *Metisella* Hemming, 1934 (type species *Papilio metis* Linnaeus, 1764), where it was placed previously (Fig. 8). Keys to IV.20.B in Evans (1937). Shares many features with *Metisella*, such as hindwing discal cell longer than half of the wing, forewing veins R_1 and R_2 very near each other or touching (not separated). Distinguished from its relatives by the pattern of hindwing underside, which is with dark web-like pattern along veins with some streaks across and orange, ochreous, yellow or white spots. Hindwing below pale-yellow with dark web-like pattern along veins with

some streaks across, but without darker markings. Genitalia with narrow and long penis, uncus with tegumen bulbous in dorsal view, uncus narrows to a point (except in *W. willemi* where distal end is mushroom-shaped and base of uncus with side processes), gnathos better developed than in Metisella, ampulla separated from harpe, protruding beyond its caudal end (except in *W. willemi* where harpe upturned embracing ampulla). In DNA, a combination of the following base pairs is diagnostic: aly363.37.1:A929C, aly1450.10.1:A576G, aly283.4.1:T1129C, aly3555.2.2:T116C, aly451.23.2:C1177A.

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

Species included.—The type species, *Cyclopides formosus* var. *tsadicus* Aurivillius, 1905, *Cyclopides angolana* Karsch, 1896, *Metisella kumbona* Evans, 1937, *Cyclopides carsoni* Butler, 1898, *Heteropterus formosus* Butler, 1894, and *Cyclopides perexcellens* Butler, 1896.

Parent taxon.—Tribe Heteropterini Aurivillius, 1925.

Prada Evans, 1949 belongs to Trapezitinae Waterhouse and Lyell, 1914

Prada (type species *Plastingia rothschildi* Evans, 1928) is transferred to Trapezitinae because it is monophyletic with this subfamily, receiving the strongest statistical support in all trees (Fig. 8), and is not monophyletic with Hesperiinae where it was formerly placed (Warren et al. 2009).

Argemma Grishin, new genus

http://zoobank.org/3A82BAF3-A287-4EBD-8969-327471780BC1

Type species.—*Apaustus argyrosticta* Plötz, 1879.

Definition.—A sister genus of *Ceratrichia* Butler, [1870] (type species *Papilio nothus* Fabricius, 1787), where these species were formerly placed, but separated from it by a prominent genetic distance consistent with how other genera are defined (Fig. 9). Keys to VI.31.B in Evans (1937) and differs from its relatives by pale apical spot on ventral hindwing in cell R_5-M_1 is in line with the spots in cells next to it (not offset strongly basad); uncus bulbous in ventral view, which gives tegumen with uncus a bowling duckpin shape; harpe widening distad, separated from ampulla; ventral hindwing ochreous with many small silvery spots, dorsal forewing brown with large orange-yellow spots. In DNA, a combination of the following base pairs is diagnostic: aly669.9.1:A231G, aly214.13.5:A98G, aly4389.5.1:G869A, aly1329.4.13:T479C, aly214.13.5:A97C.

Etymology.—The name is a feminine noun in the nominative singular, a fusion of the Latin words *Arg*[entum] (silver) and [g]*emma* (jewel), for the shiny, silvery gem-like spots on the hindwing below.

Species included.—The type species, *Ceratrichia aurea* Druce, 1910, *Ceratrichia maesseni* Miller, 1971, *Ceratrichia mabirensis* Riley, 1925, and *Ceratrichia bonga* Evans, 1946.

Parent taxon.—Tribe Ceratrichiini, trib. n.

Nervia Grishin, new genus

http://zoobank.org/22F7A77E-E3FF-448C-853D-165AB8D0582A

Type species.—*Hesperia nerva* Fabricius, 1793.

Definition.—A sister genus to *Tsitana* Evans, 1937 (type species *Cyclopides tsita* Trimen, 1870) and not monophyletic with *Kedestes* Watson, 1893 (type species *Hesperia lepenula* Wallengren, 1857), where it was previously placed (Fig. 9). Kedestes nerva group (Hancock and Gardiner 1982), keys to V.27.A. in Evans (1937). Distinguished from *Kedestes* by mostly dark below antennae (not pale or checkered), orange submarginal markings on forewing above (at least in females), rusty ventral hindwing margin, narrow uncus, upturned almost rectangular harpe with serrated dorsal edge, not separated from ampulla. In DNA, a combination of the following base pairs is diagnostic: aly6841.65.2:C1166G, aly2578.13.2:C1091A, aly127.64.1:A1342T, aly83.5.1:A418C, aly904.15.14:C3808G.

Etymology.—The name is a feminine noun in the nominative singular, formed from the type species name.

Species included.—The type species, *Hesperia mohozutza* Wallengren, 1857, *Kedestes protensa* Butler, 1901, *Pyrgus chaca* Trimen, 1873, *Kedestes heathi* Hancock and Gardiner, 1982, *Kedestes ekouyi* Vande weghe and Albert, 2009, *Kedestes michaeli* Gardiner and Hancock, 1982, *Kedestes monostichus* Hancock and Gardiner, 1982, *Kedestes nancy* Collins and Larsen, 1991, and *Kedestes pinheyi* Hancock and Gardiner, 1982.

Parent taxon.—Tribe Astictopterini Swinhoe, 1912.

Isoteinon abjecta (Snellen, 1872), new combination

Phylogenetic analysis shows (Fig. 9) that *Pamphila abjecta* Snellen, 1872 is not monophyletic with *Astictopterus jama* C. and R. Felder, 1860, the type species of the genus *Astictopterus* C. and R. Felder, 1860, where *Isoteinon abjecta* was previously placed, and instead forms a clade with *Isoteinon lamprospilus* C. and R. Felder, 1862, the type and the only species of *Isoteinon* C. and R. Felder, 1862. Therefore, we reinstate the combination *Isoteinon abjecta*.

Dotta Grishin, new genus

http://zoobank.org/1579BF7B-B1B2-4B01-B428-6593A087A665

Type species.—*Ceratrichia stellata* Mabille, 1891.

Definition.—A genus without close relatives, but not monophyletic with *Astictopterus* C. and R. Felder, 1860 (type species *Astictopterus jama* C. and R. Felder, 1860), *Kedestes* Watson, 1893 (type species *Hesperia lepenula* Wallengren, 1857), or *Isoteinon* C. and R. Felder, 1862 (type species *Isoteinon lamprospilus* C. and R. Felder, 1862) (Fig. 9). Keys to V.27.12 or IV.24.4 in Evans (1937). Distinguished from its relatives by long gnathos well-separated from and about the same length as uncus, terminally narrowing uncus, harpe terminally bulbous, finely serrated, separated from ampulla by a gap, black edged pale dots or spots on ventral hindwing, pale spots or dots above. In DNA, a combination of the following base pairs is diagnostic: aly274.20.6:A1605C, aly84.28.1:G1033C, aly274.20.6:T1601A, aly144.50.1:G193A, aly3194.1.2:C65A.

Etymology.—The name is a feminine noun in the nominative singular, for the white dots on the wings.

Species included.—The type species and *Cyclopides callicles* Hewitson, 1868 (formerly placed in *Kedestes*).

Parent taxon.—Tribe Astictopterini Swinhoe, 1912.

Comments.—Without DNA analysis, it would be challenging to pull these two species out of the genera they have been assigned to and join them in a single genus. Nevertheless, retrospectively observed genitalic similarity agrees with such placement.

Lissia Grishin, new genus

http://zoobank.org/C9B3D4FD-98CF-4117-B30A-8A3D80CFD7EA

Type species.—*Leona lissa* Evans, 1937.

Definition.—A genus more related to *Gamia* Holland, 1896 (type species *Proteides galua* Holland, 1891) and *Artitropa* Holland, 1896 (type species *Pamphila erynnis* Trimen, 1862) than to *Leona* Evans, 1937 (type species *Hesperia leonora* Plötz, 1879) (Fig. 9). Keys to VIII.59.C(b) in Evans (1937) and differs from its relatives, including *Leona*, by a well-defined gnathos reaching about half of uncus length (in lateral view); tegumen plus uncus twice as long as wide, hour-glass shaped in ventral view; uncus divided, arms short and stout, knob-like; valva with harpe close to rectangular; hindwing with a postdiscal band of spots above. In DNA, a combination of the following base pairs is diagnostic: aly127.66.15:T199A, aly1149.1.1:A1727G, aly822.30.12:A417C, aly490.3.1:A60A (not G), aly6339.4.1:G167G (not T), aly1121.3.2:C344C (not T).

Etymology.—The name is a feminine noun in the nominative singular, formed from the type species name.

Species included.—The type species and *Plastingia luehderi* Plötz, 1879.

Parent taxon.—Tribe Astictopterini Swinhoe, 1912.

Xanthonymus Grishin, new genus

http://zoobank.org/964F4410-339B-486C-8993-30E005481233

Type species.—*Pardaleodes xanthioides* Holland, 1892.

Definition.—A sister genus to *Hollandus* Larsen and Collins, 2015 (type species *Pardaleodes xanthopeplus* Holland, 1892), formerly placed in *Paronymus* Aurivillius, 1925 (type species *Hesperia ligora* Hewitson, 1876), but is not monophyletic with it (Fig. 9). Keys to VII.45.4 in Evans (1937) and differs from its relatives by narrow, beak-like uncus; tegumen narrowing into uncus gradually, their junctions slightly concave in ventral view; lack of gnathos; harpe gradually upturned, finely serrated at its short but nearly dorsal margin, with a tooth directed dorsad near its base; hindwing outer margin and tornus brown below. In DNA, a combination of the following base pairs is diagnostic: aly822.30.12:C365T, aly1089.8.4:G53A, aly164.3.1:A811G, aly5294.20.2:A547A (not T), aly5294.20.2:A548A (not C), aly838.12.1:T458T (not A).

Etymology.—The name is a masculine noun in the nominative singular, fusion of the type species name with the genus name where it was placed previously: *Xanth*[ioides] and [Par]*onymus*.

Species included.—The type species and *Xanthodisca astrape*.

Parent taxon.—Tribe Astictopterini Swinhoe, 1912.

Cerba Grishin, new genus

http://zoobank.org/199EACE1-E34F-4266-8CAA-46783F667A0A

Type species.—*Zea martini* Distant and Pryer, 1887.

Definition.—Previously placed in *Acerbas* de Nicéville, 1895 (type species *Hesperia anthea* Hewitson, 1868), this genus is not monophyletic with it and is sister to *Zela* de Nicéville, 1895 (type species *Zela zeus* de Nicéville, 1895) instead (Fig. 10). Keys to J.22.4 in Evans (1949). Diagnosed by the following combination of characters: mostly brown above wings with small forewing spots, milky areas by hindwing anal margin and broad central band on hindwing below; forewing vein CuA_2 originates in the middle between wing base and the origin of vein CuA_1; uncus broad, bilobed caudad, indistinctly separated from tegumen; tegumen with small side processes and a long central process; penis bulky and stout; valva twice as long as broad, with a prominent and rounded ampulla that is separated from a narrow but large harpe gradually upturned and rounded at the dorsal end protruding above ampulla. In DNA, a combination of the following base pairs is diagnostic: aly103.51.12:A1212T, aly2618.5.1:T1489A, aly420.23.4:A277C, aly276561.5.1:G1724G (not C), aly276561.5.1:A1721A (not G), aly1624.1.10:G534G (not A).

Etymology.—The name is a feminine noun in the nominative singular, formed by removing the first and last letters from the name of the genus that the type species was previously attributed to.

Species included.—Only the type species.

Parent taxon.—Tribe Erionotini Distant, 1886.

Avestia Grishin, new genus

http://zoobank.org/F54B9854-755F-4050-8D47-88EDB994DCED

Type species.—*Hesperia avesta* Hewitson, 1868.

Definition.—A genus sister to *Acerbas* de Nicéville, 1895 (type species *Hesperia anthea* Hewitson, 1868) with *Zela* de Nicéville, 1895 (type species *Zela zeus* de Nicéville, 1895), previously placed in *Lotongus* Distant, 1886 (type species *Eudamus calathus* Hewitson, 1876), but not monophyletic with it (Fig. 10). Keys to J.11.4 in Evans (1949). Morphologically, distinguished from its relatives by hourglass-shaped, terminally bulbous uncus in ventral view; harpe terminally rounded, not prominently separated from ampulla, with a single tooth directed caudad; ventral hindwing yellow band from costa to anal margin, closer to the base, veins brown below (not yellow). In DNA, a combination of the following base pairs is diagnostic: aly1838.39.2:A631G, aly2165.18.2:A22T, aly2096.50.1:A679T, aly1405.13.10:C136C (not G), aly537.26.8:A1279A (not G), aly1264.14.2:A37A (not T).

Etymology.—The name is a feminine noun in the nominative singular, formed from the type species name.

Species included.—Only the type species.

Parent taxon.—Tribe Erionotini Distant, 1886.

Zetka Grishin, new genus

http://zoobank.org/C331EB66-E1BB-4C06-9A8B-22A293353C6D

Type species.—*Mnasitheus zeteki* Bell, 1931.

Definition.—Formerly placed in *Styriodes* Schaus, 1913 (type species *Styriodes lyco* Schaus, 1913, in Moncina, Fig. 10–12) this genus does not have close relatives, but belongs in the same clade as *Neoxeniades* Hayward, 1938 (type species *Neoxeniades musarion* Hayward, 1938). Keys to K.2.6. in Evans (1955). Can be told apart from its relatives by the following combination of characters: males with long brands over vein 1A+2A and under vein CuA_2 but not above vein CuA_2, antennae as long as forewing discal cell, palpi broad, 3rd segment short, stout, wings and body brown. Genitalia illustrated by Bell (1931: fig. 1), uncus shorter than tegumen, stout, with small rounded arms, gnathos as long as uncus, saccus vestigial, valva twice as long as wide, harpe angled and squared caudad, upturned dorsocephalad, serrated at the dorsal end that protrudes from valva (Bell 1931).

In DNA, a combination of the following base pairs is diagnostic: aly1146.42.8:A1629G, aly1222.14.14:T7181A, aly1405.10.1:C373T, aly251.9.1:C1499T, aly103.32.1:A1000G.

Etymology.—The name is a feminine noun in the nominative singular formed from the type species name.

Species included.—Only the type species.

Parent taxon.—Subtribe Carystina Mabille 1878.

Neoxeniades ethoda (Hewitson, [1866]), new combination

Hesperia ethoda Hewitson, [1866] is transferred to *Neoxeniades*, where it is positioned in the genomic trees (Fig. 10), not being monophyletic with *Xeniades* Godman, [1900] (type species *Papilio orchamus* Cramer, [1777]), where it was placed previously, to form the new combination *Neoxeniades ethoda* (Hewitson, [1866]). The differences in unci between the two genera agree with this transfer. Uncus arms are well-developed and widely apart in *Xeniades*, but are vestigial (uncus almost undivided) in *Neoxeniades*.

Turmada Evans, 1955 is a synonym of *Neoxeniades* Hayward, 1938

Turmada originates within *Neoxeniades* (Fig. 10), and genetic distance between the type species of these genera is small (COI barcode difference 5.5%, and differences as much as 10% are frequent between congeners). Therefore, *Turmada* is designated a new junior subjective synonym of *Neoxeniades*.

Turmosa Grishin, new genus

http://zoobank.org/E6AD0703-A3E7-4397-84C6-F4D16308504E

Type species.—*Hesperia camposa* Plötz, 1886.

Definition.—A sister genus to *Orthos* Evans, 1955 (type species *Eutychide orthos* Godman, 1900) and in a different clade from *Turmada* Evans, 1955 (type species *Dion turmada* Druce, 1912), where it was placed previously (Fig. 10). Keys to K.16.2 in Evans (1955). Differs from other Hesperiidae by unspotted metallic blue-green wings above, hindwing below shiny orange-green with dark veins and narrow discal black band. In DNA, a combination of the following base pairs is diagnostic: aly276634.6.3:C296A, aly320.9.2:A59G, aly276634.6.3:C353T, aly5965.2.3:G988A, aly2582.35.2:A932T.

Etymology.—The name is a feminine noun in the nominative singular, a fusion of two words in a former name: *Turm*[ada] and [camp]*osa*.

Species included.—Only the type species.

Parent taxon.—Subtribe Carystina Mabille 1878.

Mielkeus Grishin, new genus

http://zoobank.org/DED1D74F-CC56-48CC-8F38-E4C6AE84D70B

Type species.—*Cobalus tertianus* Herrich-Schäffer, 1869.

Definition.—A genus in the same clade with *Neoxeniades* Hayward, 1938 (type species *Neoxeniades musarion* Hayward, 1938) and *Coolus* gen. n., and in a different subtribe (Carystina) from *Vettius* Godman, [1901] (type species *Papilio phyllus* Cramer, [1777]), which is in Moncina (Fig. 10). Keys to J.45.21 and J.45.15b. Distinguished from other Hesperiidae by the following combination of characters: uncus almost undivided, arms medium to short; gnathos small, narrow, about the same as uncus in lateral view; valva plate-like without processes, harpe about half of the valva, with a small notch on dorsal margin; no brands on forewing; mid tibiae smooth; milky-white areas on hindwing below, especially near the base, gradually turning brown towards outer margin; veins not darker. In DNA, a combination of the following base pairs is diagnostic: aly294.13.2:A968C, aly1249.14.7:A1222T, aly822.47.3:A218G, aly1838.8.2:A172C, aly127.74.5:T874C.

Etymology.—The name is a masculine noun in the nominative singular, named both for the milky pattern on the hindwing below and to honor skipper taxonomist Olaf H. H. Mielke.

Species included.—The type species, *Carystus klugi* Bell, 1941, *Hesperia lucretius* Latreille, [1824], and *Hesperia diana* Plötz, 1886.

Parent taxon.—Subtribe Carystina Mabille 1878.

Coolus Grishin, new genus

http://zoobank.org/64340957-82B3-48A9-BF06-16E2726987FE

Type species.—*Rhinthon bushi* Watson, 1937.

Definition.—A genus in the same clade with *Neoxeniades* Hayward, 1938 (type species *Neoxeniades musarion* Hayward, 1938) and far removed from *Rhinthon* Godman, [1900] (type species *Proteides chiriquensis* Mabille, 1889 treated as a junior subjective synonym of *Hesperia osca* Plötz, 1882) where it was previously placed, but does not belong (Fig. 10) in agreement with Burns et al. (Burns et al. 2010) and Smith et al. (Smith et al. 1994), who also questioned its position in *Rhinthon* but did not propose a proper genus for it. Keys to L.8.2 in Evans (1955). Distinguished from all other Hesperiidae by unique pattern in the basal half of brown ventral hindwing consisting of five spots: three connected, silvery-white, the one in the distal half of discal cell framed yellow, and two others towards tornus, and two small yellow ones, near the base of the cell and past it; and orange fringes in tornal area of both wings, dark brown elsewhere. In DNA, a combination of the following base pairs is diagnostic: aly2487.23.1:C242G, aly13410.9.1:G2107T, aly2700.17.1:G706A, aly1407.7.6:A2449C, aly1283.9.1:A694G.

Etymology.—The name is a masculine noun in the nominative singular meant to suggest the incredibly unique looks of this awesome skipper with icy patches on the hindwing below.

Species included.—Only the type species.

Parent taxon.—Subtribe Carystina Mabille 1878.

Daron Grishin, new genus

http://zoobank.org/D4A2E257-03F9-4DA7-B668-CDB6BBE9C420

Type species.—*Thracides seron* Godman, [1901].

Definition.—Removed from *Neoxeniades* Hayward, 1938 (type species *Neoxeniades musarion* Hayward, 1938) where it was formerly placed and a sister to *Damas* Godman, 1901 (type species *Goniloba clavus* Herrich-Schäffer, 1869), this genus differs from it by about 12% in the COI barcode region (Fig. 10). Keys to O.16.5 in Evans (1955). Distinguished from its relatives by the following combination of characters: antennae longer than 2/3 of costa, palpi flattened and pointed upwards, 3rd segment short, stout, mid-tibiae without spines, forewings elongated, discal cell without pale spots, as long as inner margin, uncus two times shorter than tegumen, with small knob-like rounded arms, penis undulate, valva simple, twice as long as wide, ampulla leveled with the rest of the valva, harpe about 1/3 of the valva length, slightly upturned, broad, with serrate dorsal margin. In DNA, a combination of the following base pairs is diagnostic: aly767.14.7:A754C, aly1775.4.5:A83T, aly140.7.3:T104A, aly851.3.4:C1900C (not T), aly536.9.2:A221A (not T), aly531.4.3:G193G (not T).

Etymology.—The name is a masculine noun in the nominative singular, a fusion of the type species names *Da*[mas+se]*ron*.

Species included.—Only the type species.

Parent taxon.—Subtribe Carystina Mabille 1878.

Vacerra molla E. Bell, 1959 is a synonym of *Paratrytone barroni* Evans, 1955

This species is known only from one female of *Paratrytone barroni* Evans, 1955 and one male of *Vacerra molla* E. Bell, 1959, both from Ecuador, which have similar distinct wing patterns. In particular, like in no other Hesperiidae, the hindwing below has a single cream band from mid-costa to the outer margin at cell CuA_2-1A+2A, continuing as white fringes, and partly seen on the dorsal surface as a straight streak of spots. Therefore, *V. molla* is designated a junior subjective synonym of *Paratrytone barroni* Evans, 1955.

Barrolla Grishin, new genus

http://zoobank.org/3BFA1AE8-9838-4E31-AC12-D139E3636083

Type species.—*Paratrytone barroni* Evans, 1955.

Definition.—A possible sister to *Falga* Mabille, 1898 (type species *Carystus jeconia* Butler, 1870) and in a different subtribe from *Vacerra* Godman, [1900] (type species *Hesperia litana* Hewitson, [1866]) (Fig. 10). Keys to M.23.9. in Evans (1955). Diagnosed by large and broad square palpi that are longer than the head, 2nd segment longer than usual and directed forward rather than dorsad, and 3rd segment very small; hindwing with a middle straight cream band on both sides. Genitalia illustrated by Bell (1959, fig. 18): uncus shorter than tegumen, arms rounded, gnathos longer than tegumen, saccus is very short, almost vestigial, valva broadens caudad, harpe short, upturned, joint with ampulla, without teeth or processes (Bell 1959). In DNA, a combination of the following base pairs is diagnostic: aly1603.20.1:G64A, aly84.28.1:C2633G, aly707.2.13:T749A, aly798.5.3:G284G (not A), aly291.21.2:T2561T (not G), aly102.6.2:G1936G (not A).

Etymology.—The name is a feminine noun in the nominative singular, formed as a fusion of the species names: senior and junior synonyms referring to the Type species. *Bar*[roni + m]*olla*.

Species included.—Only the type species.

Parent taxon.—Subtribe Falgina trib. n., described above.

Comments.—A genus with surprising phylogenetic placement that yet again indicates the value of DNA-based methods at the genomic scale, and instills confidence in the results due to the large datasets used for phylogeny reconstruction and highly confident nodes in phylogenetic trees.

Brownus Grishin, new genus

http://zoobank.org/99C1730A-E965-410D-A15A-D8754C5E3FF0

Type species.—*Paratrytone browni* Bell, 1959.

Definition.—Unexpectedly, a relative of *Amblyscirtes* Scudder, 1872 (type species *Hesperia vialis* Edwards, 1862) and is sister to *Remella* Hemming, 1939 (type species *Hesperia remus* Fabricius, 1798) with *Mnasicles* Godman, [1901] (type species *Mnasicles geta* Godman, 1901), which all are in a different subtribe (Moncina) from *Paratrytone* Godman, [1900] (type species *Paratrytone rhexenor* Godman, 1900) (in Hesperiina) where this lineage was placed previously (Fig. 11–12). Distinguished from its relatives by sacculus about as long as vinculum with tegumen in lateral view, valva simple, nearly diamond-shaped with vary narrow harpe ending in a point directed dorsoposteriad and not separated from ampulla, very long antennae reaching apical spots near costa, all (except the small cell spot) forewing spots forming a continuous line (separated by black veins only) and most spots in a line on ventral hindwing. In DNA, a combination of the following base pairs is diagnostic: aly28779.8.7:T461C, aly577.34.1:C115G, aly1370.21.5:A2861G, aly531.10.5:G517C, aly2124.3.99:A3193G.

Etymology.—The name is a masculine noun in the nominative singular, for the type species.

Species included.—Only the type species.

Parent taxon.—Subtribe Moncina A. Warren, 2008.

Tava Grishin, new genus

http://zoobank.org/A4C0707B-1BB7-410C-9682-7ACC79306988

Type species.—*Phanis tavola* Schaus, 1902.

Definition.—A genus without apparent close relatives, although in the same clade with *Phanes* Godman, [1901] (type species *Thracides aletes* Geyer, 1832), where it was placed previously but not monophyletic with it, *Cumbre* Evans, 1955 (type species *Phanis cumbre* Schaus, 1902), *Lamponia* Evans, 1955 (type species *Hesperia lamponia* Hewitson, 1876), and *Pheraeus* Godman, [1900] (type species *Carystus epidius* Mabille, 1891) among others (Fig. 11–12). Keys to J.23.5 in Evans (1955). Similar to many species in this group of relatives in having characteristic nearly square in many specimens, semi-hyaline spots near the bases of cells M_3-CuA_1 and CuA_1-CuA_2 on forewing. Differs from them by the combination of the following characters: antennae about 2/3 of costa length, nudum of 11 segments, palpi longer than wide in ventral view, 3rd segment short and conical, mid-tibiae with spines, forewing discal cell with well-developed recurrent vein, stigma V-shaped, inconspicuous, at the base of CuA_1-CuA_2 cell along veins, wings without apical spots, rufous brown below, hindwings mostly unspotted, in some specimens with a trace of small postdiscal yellowish spots (Bell 1940). Genitalia as figured by Bell (1940: fig. 6), distinctive in the shape of harpe, rather straight, only slightly upturned and narrowing to a point, ampulla with a small tooth, penis wider than harpe, longer than valva, tegumen and uncus shorter than harpe. In DNA, a combination of the following base pairs is diagnostic: aly671.22.3:T167A, aly374.12.1:G1087C, aly2874.22.6:A1535G, aly671.22.3:A155T, aly420.67.1:A1631T.

Etymology.—The name is a feminine noun in the nominative singular, derived from the beginning of the type species name.

Species included.—Only the type species.

Parent taxon.—Subtribe Moncina A. Warren, 2008.

Comments.—We sequenced a syntype of *Phanis tavola* and the holotype of *Phanes hoffmanni* Bell, 1940. Analysis of these genomic sequences confirms the synonymy previously suggested for these two taxa (Mielke 1995). For instance, their COI barcodes differ by only one position (0.15%).

Rigga Grishin, new genus

http://zoobank.org/5D98B6E8-8FF9-478D-B37B-D19DACCA9E31

Type species.—*Vorates auristriga* Draudt, 1923.

Definition.—A likely sister to *Misius* Evans, 1955 (type and the only species *Pamphila misius* Mabille, 1891), this genus is removed from *Parphorus* Godman, 1900 (type species *Phlebodes storax* Mabille, 1891), where it was placed previously (Fig. 11–12). Keys to J.34.9 or J.34.10a in Evans (1955). Diagnosed by long and prominent triangular hyaline yellow spot filling out forewing cell R_5-M_1 from the base to about a third of its length (except *paramus* E. Bell, 1947, which has typical for the genus genitalia), and no other apical forewing hyaline spots, hindwing below with more or less prominent pale ray along vein M_1 from wing base to outer margin. Genitalia differ from relatives by a combination of the following characters: uncus twice as long as tegumen, arms parallel and narrow, gnathos vestigial, valva twice as long as wide, harpe not extending much beyond bulky rounded ampulla, upturned and not separated from ampulla. In DNA, a combination of the following base pairs is diagnostic: aly536.116.6:A107G, aly2124.4.17:G268T, aly6377.1.2:A4462G, aly208.50.8:T236A, aly536.108.1:C2126T.

Etymology.—The name is a feminine noun in the nominative singular, containing the last four letters of the type species name with an extra ‘g’ added to avoid a homonym.

Species included.—The type species, *Hesperia hesia* Hewitson, 1870, *Apaustus ira* Butler, 1870, *Euroto oeagrus* Godman, [1900], *Vorates paramus* Bell, 1947, and *Vorates sapala* Godman, [1900].

Parent taxon.—Subtribe Moncina A. Warren, 2008.

Haza Grishin, new genus

http://zoobank.org/78B60979-8EA8-437D-8B48-24DE9AA92587

Type species.—*Hesperia hazarma* Hewitson, 1877.

Definition.—A sister to *Penicula* Evans, 1955 (type species *Pamphila bryanti* Weeks, 1906), this genus is away from *Cobalopsis* Godman, [1900] (type species *Pamphila edda* Mabille, 1891, which is a junior subjective synonym of *Hesperia autumna* Plötz, 1882) (Fig. 11–12). Keys to J.37.9 in Evans (1955), but very variable in hindwing patterns, from virtually brown unspotted to pale cream with brown-yellow veins and several central black spots surrounded by yellow or brown. Diagnosed by male genitalia with uncus not protruding from tegumen, very broad caudad with tiny knob-like arms on the side, uncus together with tegumen almost square in dorsal view, valva with very narrow extended hook-shaped harpe like no other Hesperiini. In DNA, a combination of the following base pairs is diagnostic: aly274.33.1:A430C, aly2202.27.1:C668A, aly2613.3.2:A2043C, aly2613.3.2:C2248A, aly587.20.1:T1522C.

Etymology.—The name is a feminine noun in the nominative singular, containing the first four letters of the type species name.

Species included.—Only the type species.

Parent taxon.—Subtribe Moncina A. Warren, 2008.

Dubia Grishin, new genus

http://zoobank.org/DBA6AFEC-D3DE-4C61-9FA9-7332B4BE5293

Type species.—*Euroto* (?) *dubia* Bell, 1932.

Definition.—A sister genus to *Phlebodes* Hübner, [1819] (type species *Papilio pertinax* Stoll, [1781]), but not monophyletic with and far removed from *Thoon* Godman, [1900] (type species *Proteides modius* Mabille, 1889), where it was previously placed (Fig. 11–12). Keys to J.48.4 in Evans (1955). Genitalia illustrated by Bell in his fig. 3 (Bell 1932). Distinguished from its relatives by elongated uncus with short arms; gnathos widely separated from uncus, about half of its length in lateral view; saccus long, about the same length as valva, valva hourglass shaped in lateral view, harpe rounded, with finely serrated dorsal margin, not separated from ampulla; dorsal forewing with two hyaline spots in discal cell and small brands at the origin and between veins CuA_1 and CuA_2; 2–5 small postdiscal dark spots, some with hyaline centers, placed along smooth curve on brown hindwing below. In DNA, a combination of the following base pairs is diagnostic: aly1281.8.1:A614T, aly390.17.1:T17C, aly1260.9.2:T347G, aly158825.1.3:A37A (not G), aly6286.5.7:A87A (not T), aly5543.13.1:A1601A (not G).

Etymology.—The name, a feminine noun in the nominative singular, echoes the type species name.

Species included.—Only the type species.

Parent taxon.—Subtribe Moncina A. Warren, 2008.

Pares Grishin, new genus

http://zoobank.org/2DD85F52-3615-4008-81A3-52AD86257662

Type species.—*Phlebodes pares* Bell, 1959.

Definition.—A genus near *Joanna* Evans, 1955 (type species *Joanna joanna* Evans, 1955) and *Vinpeius* Austin, 1997 (type and the only species *Pompeius tinga* Evans, 1955), and in same clade with *Niconiades* Hübner, [1821] (type species *Niconiades xanthaphes* Hübner, [1821]), where it was placed previously (Fig. 11–12). Indeed resembles some *Niconiades* species due to the presence of large hyaline spots on hindwing and green scaling of the body, but genitalia (illustrated by Bell 1959: fig. 22 and Nicolay 1980: fig. 8) quite distinctive and diagnostic: short uncus and tegumen, together not longer than valva height, uncus rounded and weakly bilobed caudad, saccus long, about half of vinculum length, penis narrowing caudad, valva broad, more than half of its length, ampulla transitions to harpe without a break, harpe projecting caudad as a broad straight tooth, indented before the tooth along ventral margin. (Bell 1959; Nicolay 1980). In DNA, a combination of the following base pairs is diagnostic: aly890.44.9:C94G, aly9673.13.1:C269G, aly3555.4.2:G923A, aly1041.12.1:T93T (not C), aly537.7.1:T984T (not C), aly1038.8.1:A1367A (not C), aly8857.2.1:G1234G (not A), aly1041.22.3:A377A (not G), aly517.17.2:G336G (not C).

Etymology.—The name, a masculine noun in the nominative singular, echoes the type species name.

Species included.—The type species and *Thoon maritza* Nicolay, 1980.

Parent taxon.—Subtribe Moncina A. Warren, 2008.

Chitta Grishin, new genus

http://zoobank.org/BCD865CA-926C-43DB-9EEB-8E14E7296149

Type species.—*Phlebodes chittara* Schaus, 1902.

Definition.—A possible sister to the clade with *Thoon* Godman, [1900] (type species *Proteides modius* Mabille, 1889) and *Halotus* Godman, [1900] (type species *Hesperilla saxula* Mabille, 1891, a subjective junior synonym of *Hesperia angellus* Plötz, 1886) (Fig. 11–12). Not monophyletic with *Psoralis* Mabille, 1904 (type species *Psoralis sabaeus* Mabille, 1904, currently considered a junior subjective synonym of *Pamphila idee* Weeks, 1901) where it was placed previously (Fig. 11–12). Immediately distinguished from *Psoralis* by greenish ventral colors and a pattern of four pale dots on hindwing below, indeed reminiscent of *Thoon*. Genitalia illustrated by Bell (1959: fig. 24, as *Psoralis alis* Bell, 1959, a junior subjective synonym of *Chitta chittara*), quite distinctive and diagnostic: uncus and tegumen very short, look compressed, penis with a long titillator diverging from penis, valva peculiar, crooked with three teeth on harpe, directed dorsad, caudad and ventrad (Bell 1959). In DNA, a combination of the following base pairs is diagnostic: aly1107.9.6:A335C, aly13410.7.2:T37C, aly1838.8.3:G730G (not C), aly127.64.1:G1182G (not A), aly4966.20.2:A1499A (not G).

Etymology.—The name is a feminine noun in the nominative singular formed from the type species name.

Species included.—Only the type species.

Parent taxon.—Subtribe Moncina A. Warren, 2008.

Artonia Grishin, new genus

http://zoobank.org/48FE4172-440B-4E90-90E7-F0CD8BDA61F2

Type species.—*Hesperia artona* Hewitson, 1868.

Definition.—A likely sister to *Cobalopsis* Godman, [1900] (type species *Pamphila edda* Mabille, 1891, which is a subjective junior synonym of *Hesperia autumna* Plötz, 1882) and is in a different clade from *Vettius* Godman, [1901]; (type species *Papilio phyllus* Cramer, [1777]) (Fig. 11–12). Keys to J.45.13 in Evans (1955). Superficially indeed similar to some *Vettius* species in the gist of ventral wing patters, but differs from them in lacking brands in males, lacking white streak in cell 1A+2A-3A on dorsal hindwing, but having white spot in cell CuA_2-1A+2A on dorsal forewing and white veins on ventral hindwing.

In male genitalia, uncus short and broad, arms far apart, short, gnathos not expanded in lateral view, penis narrow, curved, harpe close to ampulla, upturned, ends in a finger-like process protruding dorsad from the valva. In DNA, a combination of the following base pairs is diagnostic: aly423.31.1:C427T, aly423.31.1:A428C, aly2548.21.8:T1491C, aly6841.51.2:A710T, aly1405.20.15:G592A.

Etymology.—The name is a feminine noun in the nominative singular formed from the name of the type species.

Species included.—Only the type species.

Parent taxon.—Subtribe Moncina A. Warren, 2008.

Lurida Grishin, new genus

http://zoobank.org/569CDC39-86BD-4E74-ABE2-E52FD84E8EEE

Type species.—*Cobalus lurida* Herrich-Schäffer, 1869.

Definition.—A genus near *Cymaenes* Scudder, 1872 (type species *Cobalus tripunctus* Herrich-Schäffer, 1865) and not monophyletic with *Nastra* Evans, 1955 (type species *Hesperia lherminier* Latreille, [1824]), where it was placed previously (Fig. 11–12). Keys to J.26.10 in Evans (1955). Distinguished from its relatives by terminally broad and concave nearly divided uncus; gnathos reaches the end of uncus, weakly separated from it; harpe ventrally excavated, shaped like can opener (with a notch); dark brown cheeks; wings rather rounded, with areas of violet-gray overscaling at outer margins below; a curve of small pale postdiscal spots on ventral hindwing. In DNA, a combination of the following base pairs is diagnostic: aly386.7.5:A205C, aly5582.8.1:A1097T, aly138.11.7:G998C, aly84.96.4:G40A, aly5582.8.1:C1037T.

Etymology.—The name, a feminine noun in the nominative singular, echoes the type species name.

Species included.—Only the type species.

Parent taxon.—Subtribe Moncina A. Warren, 2008.

Corra Grishin, new genus

http://zoobank.org/D013B16C-CC3F-43F5-8B00-6E861AA3B149

Type species.—*Hesperia coryna* Hewitson, [1866].

Definition.—A sister genus to *Lurida* gen. n. and is in a different clade from *Vettius* Godman, [1901] (type species *Papilio phyllus* Cramer, [1777]) where it was placed previously (Fig. 11–12). Keys to J.45.20 in Evans (1955). No brands or stigmas in males, forewing above with pale scaling along anal margin, hindwing below with dark costa and pale ray from base to outer margin above the middle of discal cell and a dark ray below it.

Uncus and gnathos deeply divided, arms narrow, far apart, gnathos the same length as uncus, saccus long, as vinculum in lateral view, valva broad, not longer than twice the width, harpe narrow, short and upturned, rounded at the tip. In DNA, a combination of the following base pairs is diagnostic: aly686.30.9:A280T, aly345.16.1:A127T, aly527.10.7:A209G, aly451.23.2:A331C, aly529.9.1:C862A.

Etymology.—The name is a feminine noun in the nominative singular, formed from the beginning of the type species name.

Species included.—Only the type species.

Parent taxon.—Subtribe Moncina A. Warren, 2008.

Fidius Grishin, new genus

http://zoobank.org/F4BFE58B-3E0D-4E6F-950D-8A3BD8430313

Type species.—*Vidius fido* Evans, 1955.

Definition.—A possible sister to *Cymaenes* Scudder, 1872 (type species *Cobalus tripunctus* Herrich-Schäffer, 1865) and far removed from *Vidius* Evans, 1955 (type species *Narga vidius* Mabille, 1891) where it was placed previously (Fig. 11–12). Keys to J.24.1 in Evans (1955). Genitalia illustrated by Mielke in his fig. 5–8 (Mielke 1980). Distinguished from its relatives by antennae shorter than half of costa length, wings rounded, broad, scales in fringes long, especially on forewing, nearly the same as palpi in length, wings almost entirely unmarked, chocolate brown, in some specimens, wings below with faint, blotchy yellowish spots consisting of a few scales and forming postdiscal bands and a discal cell spot on hindwing. Valva narrow, ~2–3 times longer than wide, harpe distally slightly to moderately upturned not well-separated from valva, costa of valva straight, uncus narrowly divided, arms short, close together, gnathos the same length as uncus, saccus as long as tegumen with uncus, penis narrow, twice as long as saccus. In DNA, a combination of the following base pairs is diagnostic: aly2096.50.1:A1451C, aly349.40.1:A898C, aly164.63.12:C436A, aly164.63.12:A437T, aly5965.2.3:C1150G.

Etymology.—The name is a masculine noun in the nominative singular. It is a fusion of the type species name with its original genus name: *Fid*[o] + [Vid]*ius*.

Species included.—The type species and *Vidius ochraceus* O. Mielke, 1980.

Parent taxon.—Subtribe Moncina A. Warren, 2008.

Veadda Grishin, new genus

http://zoobank.org/49E3A1A5-0F8B-4374-AA86-6EA2C1EEFCB6

Type species.—*Lerema veadeira* Mielke, 1968.

Definition.—Not closely related to any other genus, but falls near the clade of many Moncina genera, among which are *Parphorus* Godman, [1900] (type species *Phlebodes storax* Mabille, 1891), *Phlebodes* Hübner, [1819] (type species *Papilio pertinax* Stoll, 1781), *Cantha* Evans, 1955 (type species *Cantha calva* Evans, 1955), *Saturnus* Evans, 1955 (type species *Papilio saturnus* Fabricius, 1787), *Penicula* Evans, 1955 (type species *Pamphila bryanti* Weeks, 1906), and *Duroca* Grishin, 2019 (type species *Hesperia duroca* Plötz, 1882). Not closely related to *Lerema* Scudder, 1872 (type species *Papilio accius* Smith, 1797), where it was originally placed (Fig. 11–12). Distinguished from them by a combination of the following characters: uncus divided, arms long, very close together; gnathos broader than uncus in ventral view, about 2/3 of uncus length; saccus nearly the same length as vinculum in lateral view; harpe short, less than 1/3 of valva, upturned, ending in a tooth directed dorsad, not separated from ampulla and not serrated; dorsal forewing with small ochre spots and tripartite gray stigma, lined with black scales basad; mostly ferruginous (a rather unusual color for Hesperiidae) below, with faint ochreous spots on both wings. In DNA, a combination of the following base pairs is diagnostic: aly318.7.1:A1032G, aly1042.23.2:G113T, aly1042.23.2:A115G, aly1487.4.1:A662G, aly164.9.1:A1676T.

Etymology.—The name is a feminine noun in the nominative singular, formed from the first part of the type species name.

Species included.—Only the type species.

Parent taxon.—Subtribe Moncina A. Warren, 2008.

Tricrista Grishin, new genus

http://zoobank.org/97A09601-6840-4813-A346-31A073A507D4

Type species.—*Penicula crista* Evans, 1955.

Definition.—A sister genus to *Vettius* Godman, [1901] (type species *Papilio phyllus* Cramer, 1777) and far removed from *Penicula* Evans, 1955 (type species *Pamphila bryanti* Weeks, 1906) (Fig. 11–12), where these species were placed previously due to the characteristic tuft of hair-like scales in the discal area of hindwing above, apparently a convergent feature different in details between them. Keys to L.10.2a in Evans (1955). Distinguished from its relatives (including *Penicula*) by the structure of its dorsal hindwing area with the tuft of scales: the dense (not thin) tuft from upper part of discal cell at its base, covering gray (not black) area by the thickened bases of veins CuA_2 and CuA_2 (not reaching vein 1A+2A). No hyaline spots in forewing cell M_2-M_3. In DNA, a combination of the following base pairs is diagnostic: aly2041.22.2:G133A, aly563.7.2:A292G, aly208.38.3:A886T, aly536.2.4:A94A (not T), aly3721.1.24:A167A (not G), aly3721.1.24:A169A (not C).

Etymology.—The name is a feminine noun in the nominative singular, and it denotes that three species in the genus have “crist” in their names.

Species included.—The type species, *Penicula cristina* Evans, 1955, *Cobalus cristatus* Bell, 1930, *Penicula roppai* Mielke, 1980, and *Rinthon* [sic] *advena* Draudt, 1923.

Parent taxon.—Subtribe Moncina A. Warren, 2008.

Viridina Grishin, new genus

http://zoobank.org/0A14CB25-9511-4311-8B76-746AA38011C1

Type species.—*Lerema* (?) *viridis* Bell, 1942.

Definition.—A close sister genus to *Moeris* Godman, [1900] (type species *Talides striga* Geyer, [1832]). Not in the same clade as *Lerema* Scudder, 1872 (type species *Papilio accius* Smith, 1797), *Tigasis* Godman, [1900] (type species *Tigasis zalates* Godman, [1900]) or its subjective synonym *Alerema* Hayward, 1942 (type species *Alerema aeteria* Hayward, 1942 treated as junior subjective synonym of *Phlebodes simplex* Bell, 1930), where species from this genus were placed previously (Fig. 11–12). Keys to J.44.10 or J.41.6. in Evans (1955). Genitalia illustrated by Bell in his fig. 9 (Bell 1942). Distinguished from its relatives by a combination of the following characters: uncus undivided, narrowing to a point; in ventral view: uncus sides slightly concave, gnathos arms widely apart, crescent-shaped, the same length as uncus, forming an φ together with it; saccus short, about the length of uncus, penis stout; harpe shorter than 1/3 of valva, slightly upturned, finely serrated at the distal margin, with a small tooth near ampulla, separated from it by a small notch; antennae longer than half of costa, checkered; wings produced; narrow complete stigma on forewing from base of vein CuA_1 to vein 1A+2A in males; hindwing below greenish-ochreous with a postdiscal irregular row of indistinct pale blotch-like spots. In DNA, a combination of the following base pairs is diagnostic: aly1019.13.1:C3748G, aly208.17.4:G1754C, aly1475.19.1:A667G, aly1041.11.5:G116G (not A), aly1294.15.2:A1078A (not T), aly272.12.6:A338A (not G).

Etymology.—The name is a feminine noun in the nominative singular, and denotes that all three species placed in this genus have “virid” in their names.

Species included.—The type species, *Pamphila viridenex* Weeks, 1901, which is a very close relative, and *Oeonus subviridis* Hayward, 1940.

Parent taxon.—Subtribe Moncina A. Warren, 2008.

Moeris anna (Mabille, 1898), new combination

Pamphila anna Mabille, 1898 was previously placed in *Vidius* Evans, 1955 (type species *Narga vidius* Mabille, 1891), but is not monophyletic with it (Fig. 11–12). Instead, it groups closely with *Moeris* Godman, [1900] (type species *Talides striga* Geyer, [1832]): compare with its sister, the *Viridina*, gen. n., cluster in Fig. 11 and 12. Despite obvious differences in wing patterns, the wing shapes and genitalia structures (even the shape of the valva with a somewhat expanded harpe) are quite similar between these species. The COI barcode difference between *P. anna* and *M. striga* is 7.4%, suggesting a close relationship. For

these reasons, instead of proposing a new genus name for *P. anna*, we establish a new combination, *Moeris anna*.

Arita Evans, 1955 is a synonym of *Tigasis* Godman, [1900]

Inspection of *Tigasis* reveals its close relationship with *Arita* Evans, 1955 (type species *Cobalus arita* Schaus, 1902) (Fig. 11–12). For instance, COI barcodes of the type species in these genera differ by only about 3%. Therefore, we treat *Arita* as a new junior subjective synonym of *Tigasis*.

Alychna Grishin, new genus

http://zoobank.org/D9C177B1-6CE7-4A1E-9B76-BD7D29AE18E6

Type species.—*Pamphila exclamationis* Mabille, 1898.

Definition.—A sister genus of *Zalomes* Bell, 1947 (type species *Zalomes colobus* Bell, 1947, considered to be a junior subjective synonym of *Hesperia biforis* Weymer, 1890) and in a different clade from both *Psoralis* Mabille, 1904 (type species *Psoralis sabaeus* Mabille, 1904, which is a junior subjective synonym of *Pamphila idee* Weeks, 1901) and from *Lychnuchus* Hübner, [1831] (type species *Lychnuchus olenus* Hübner, [1831] considered to be a junior subjective synonym of *Hesperia celsus* Fabricius, 1793), where species of this genus were placed previously (Fig. 11–12). Keys to J.43.3d, J.43.6, or K.12.1 in Evans (1955). Morphologically, distinguished from its relatives by a combination of the following characters: uncus broad, the same width and length, if divided, arms very short, spike-like; gnathos not shorter than uncus, close to it in lateral view; valva broad, harpe not well-separated from ampulla, varying in shape depending on species, mostly rectangular with irregular margins, in the type species with a hook-like projections narrowly separated from harpe; stigma black, di- or tripartite; pale scales or hyaline spot distad of stigma on forewing; frequently a curved line of small pale spots in discal area of hindwing below. In DNA, a combination of the following base pairs is diagnostic: aly4645.10.1:T700C, aly4645.10.1:G701T, aly1877.13.1:T1118A, aly1877.13.1:G1159A, aly274.43.1:C170A.

Etymology.—The name is a feminine noun in the nominative singular, formed from the first five letters of *Lychnuchus* (where one species was formerly placed) with “a” added on both sides to stress that it is not that genus.

Species included.—The type species, *Lychnuchus victa* Evans, 1955, *Oeonus zenus* Bell, 1942, *Psoralis mirnae* Siewert, Nakamura and Mielke, 2014, *Psoralis darienensis* Gaviria, Siewert, Mielke and Casagrande, 2018, *Hesperia degener* Plötz, 1882, and *Psoralis venta* Evans, 1955.

Parent taxon.—Subtribe Moncina A. Warren, 2008.

Comments.—The two species *Lychnuchus celsus* and *Alychna victa* are so close to each other in wing patterns that their placement in two distantly related genera is totally unexpected. This is probably the most surprising discovery in our analysis. Retrospective

analysis of genitalia reveals significant differences between these two species that agree with the DNA-guided placement (Fig. 11–12).

Molo pelta (Evans, 1955), new combination

To add to the *Lychnuchus* surprise, we transfer another mimic, *Lychnuchus pelta* Evans, 1955, to *Molo* Godman, [1900] (type species *Hesperia heraea* Hewitson, 1868, considered to be a junior subjective synonym of *Hesperia mango* Guenée, 1865), because it is not in the same clade as *Lychnuchus celsus* (the type species of *Lychnuchus*) but instead is closely related to *Molo mango* (COI barcode difference only 2.7%, indicating congeneric relationship). Therefore, we form the new combination *Molo pelta* (Fig. 10–12).

Alychna zenus (E. Bell, 1942), reinstated species status

We conclude that *Oeonus zenus* E. Bell, 1942 (type locality Ecuador) is a species-level taxon, not a junior subjective synonym of *Pamphila exclamationis* Mabille, 1898 (type locality Bolivia). COI barcodes differ by more than 3% (Fig. 12), the stigma is broader and more curved in *A. zenus* compared to *Alychna exclamationis* and has more extensive black overscaling around it, and the hindwing is more produced at the tornus in *A. zenus*.

Ralis Grishin, new genus

http://zoobank.org/55719473-C71C-4492-B44C-00BB0CFFE700

Type species.—*Lerema coyana* Schaus, 1902.

Definition.—A genus without close relatives, but not monophyletic with *Psoralis* Mabille, 1904 (type species *Psoralis sabaeus* Mabille, 1904, which is a junior subjective synonym of *Pamphila idee* Weeks, 1901) (Fig. 11–12). Keys to J.43.9 in Evans (1955). Morphologically, distinguished from its relatives by a very conspicuous, large gray stigma and nearly unmarked dark brown hindwing ventral (sometimes with small pale dots). Male genitalia distinctive, see Nicolay (1980: fig. 7): uncus broad, not narrowing in the middle, tegumen with a pair of long dorsal processes directed caudad, gnathos the same length and width as uncus, prominent in lateral view, penis stout caudad with elongated phallobase, valva nearly oval, twice as long and wide with shirt harpe pointed dorsad, closely approaching ampulla (Nicolay 1980). In DNA, a combination of the following base pairs is diagnostic: aly25.7.1:A134C, aly2532.12.2:A142C, aly594.9.1:G589A, aly423.4.2:C199G, aly25.7.1:A226G.

Etymology.—The name is a masculine noun in the nominative singular, denoting the second half of [Pso] *Ralis*, the genus where these species were placed previously.

Species included.—The type species and *Psoralis concolor* Nicolay, 1980.

Parent taxon.—Subtribe Moncina A. Warren, 2008.

Testia Grishin, new genus

http://zoobank.org/7063BAAB-1F7C-4EF5-905C-DF50960CCB02

Type species.—*Atrytone* (?) *potesta* Bell, 1941.

Definition.—A sister genus to *Oxynthes* Godman, [1900] (type species *Goniloba corusca* Herrich-Schäffer, 1869) combined with *Oeonus* Godman, [1900] (type species *Oeonus pyste* Godman, [1900]) and in the same clade with *Lindra* Evans, 1955 (type species *Carystus simulius* Druce, 1876) (Fig. 13). Not monophyletic with *Orthos* Evans, 1955 (type species *Eutychide orthos* Godman, [1900]), which is in a different subtribe (Carystina Mabille 1878). Keys to L.15.5 in Evans (1955). Distinguished from its relatives by a combination of the following characters (Bell 1941). Antennae about 2/3 of costa in length, male no secondary sexual characters, wings unmarked dark brown above with shiny green hair-like scales in tornal area of hindwing (and on body), with cream spots below: on hindwing near its middle plus diffuse cream area in distal half of CuA_2-1A+2A cell, small spots on hindwing in discal cell and as a postdiscal row in each cell between veins M_2 and 1A+2A. Male genitalia (see Bell 1941: fig. 3 for illustration) with uncus deeply divided, arms long (only slightly shorter than tegumen), parallel, near each other, penis widening terminally (nearly as wide as valva), bulky, with terminal spikes, valva nearly rectangular, sacculus without processes, harpe short (shorter than 1/3 of valva), angular, with a stout tooth pointed dorsad, separated from ampulla by a narrow notch. In DNA, a combination of the following base pairs is diagnostic: aly2874.22.9:G1030A, aly3512.12.2:T234C, aly2811.6.1:T166C, aly1139.93.1:C452C (not G), aly862.12.2:A1755A (not C), aly5021.5.1:G1325G (not C), aly537.7.1:A181A (not G), aly2012.14.2:T317T (not C), aly577.34.1:A485A (not T).

Etymology.—The name is a feminine noun in the nominative singular, formed from the type species name.

Species included.—Only the type species.

Parent taxon.—Subtribe Hesperiina Latreille, 1809.

Buzella Grishin, new genus

http://zoobank.org/3B8255CA-FE24-4197-B04C-0876533EABF7

Type species.—*Buzyges mellanaformis* Austin and A. Warren, 2009.

Definition.—Not monophyletic with *Buzyges idothea* Godman, [1900], the type species of *Buzyges* Godman, [1900], this genus is placed in a different clade instead (Fig. 13). Detailed diagnosis of *mellanaformis* given by Austin and Warren (2009:28, fig. 70, 82, 90) can be applied to this genus (Austin and Warren 2009). In brief, differs from related genera by long antennae, the lack of stigma, short tegumen and uncus and relatively small valva with broad trapezoid harpe (shared with *Buzyges*), but penis narrower and cornuti are smaller than in *Buzyges* (see Fig. 70 and 82 in Austin and Warren (2009)), mid- and hind-tibiae without spines characteristic of *Buzyges* and forewing outer margin more convex. In DNA, a combination of the following base pairs is diagnostic: aly386.7.5:A874T, aly207.4.6:A367T, aly320.7.8:G428A, aly128.6.20:C131C (not G), aly708.6.1:A1197A (not G), aly1838.58.4:T1070T (not C), aly536.174.1:A1825A (not C), aly2582.33.4:A512A (not T), aly3071.1.1:C135C (not T).

Etymology.—The name is a feminine noun in the nominative singular, formed from the type species original name *Buz*[yges m]*ella*[naformis].

Species included.—Only the type species.

Parent taxon.—Subtribe Hesperiina Latreille, 1809.

Vernia Grishin, new genus

http://zoobank.org/980834C1-C6C5-4172-B5BB-151246B12F1A

Type species.—*Pamphila verna* Edwards, 1862.

Definition.—A genus in the same clade with *Hesperia* Fabricius, 1793 (type species: *Papilio comma* Linnaeus, 1758), *Atalopedes* Scudder, 1872 (type species *Hesperia huron* Edwards, 1863), and *Pseudocopaeodes* Skinner and Williams, 1923 (type species *Copaeodes eunus* Edwards, 1881), but not closely related with any particular one. *Pompeius* Evans, 1955 (type species *Hesperia pompeius* Latreille, [1824]), where species from this genus were placed previously, is in a different clade from them (Fig. 13). Keys to M.15.2 or M.15.5 in Evans (1955). Distinguished from its relatives by divided uncus with short and stout arms; thin gnathos arms, longer than uncus; valva with harpe about half of its length, unturned, terminating with two broad teeth directed dorsocaudad, no bristles; apiculus of six segments, nudum not black; stigma tripartite on dorsal forewing of males; pale spot distad of stigma segment in dorsal forewing cell CuA_1-CuA_2 occupies the whole width of the cell. In DNA, a combination of the following base pairs is diagnostic: aly443.32.2:G99C, aly2487.36.2:T119G, aly443.32.2:A97G, aly887.14.12:A1715G, aly2096.38.5:A32C.

Etymology.—The name, a feminine noun in the nominative singular, reflects the type species name.

Species included.—The type species and *Hesperia dares* Plötz, 1883.

Parent taxon.—Subtribe Hesperiina Latreille, 1809.

Lon Grishin, new genus

http://zoobank.org/4CFECC3F-DEDA-4533-9F5C-4418BADA0ABB

Type species.—*Hesperia zabulon* Boisduval and Le Conte, [1837].

Definition.—A sister genus to *Stinga* Evans, 1955 (type species *Pamphila morrisoni* Edwards, 1878) combined with *Poanes* Scudder, 1872 (type species *Hesperia massasoit* Scudder, 1863) including its junior subjective synonym *Phycanassa* Scudder, 1872 (type species *Hesperia viator* Edwards, 1865) (Fig. 13). Species of this genus were formerly placed in *Poanes*, but are not monophyletic with it if *Stinga* is considered a valid genus, because *Stinga* is sister to *Poanes* with exclusion of this genus. This genus constitutes the “ordinary terrestrial species” subgroup of Burns (Burns 1992) who gave and illustrated diagnostic genitalic characters for it, in contrast to “marsh dwellers” that

are the true *Poanes*. Most obvious diagnostic character is a very long (extending well beyond the body of aedeagus) and armed with spikes titillator in penis (in addition to two smaller ones), so prominent that it is even shown on Evans sketches (Evans 1955). Harpe upturned and touches ampulla, instead of being directed largely distad and leaving a gap between it at ampulla in *Poanes*. In DNA, a combination of the following base pairs is diagnostic: aly525.55.2:G476C, aly378.21.7:A1612G, aly84.28.1:A602G, aly2631.4.13:T68A, aly85.22.2:T1259C.

Etymology.—The name is a masculine noun in the nominative singular, and is formed from the last syllable of the type species name.

Species included.—The type species, *Hesperia hobomok* T. Harris, 1862, *Pamphila inimica* Butler and Druce, 1872, *Pamphila taxiles* Edwards, 1881, *Pamphila azin* Godman, 1900, *Poanes macneilli* Burns, 1992, *Hesperia ulphila* Plötz, 1883, *Atrytone monticola* Godman, [1900], *Pamphila niveolimbus* Mabille, 1889, *Hesperia melane* Edwards, 1869.

Parent taxon.—Subtribe Hesperiina Latreille, 1809.

Alera Mabille, 1891 is a synonym of *Perichares* Scudder, 1872

We find (Fig. 13) that *Alera furcata* Mabille, 1891 and *Perichares philetes* (Gmelin, [1790]), the type species of both genera (technically, *Papilio coridon* Fabricius, 1775, a homonym, considered to refer to *Perichares philetes*, is the type species of *Perichares*) are genetically close (COI barcodes differ by about 6.5%). Moreover, several species of *Alera* that we sequenced are not monophyletic and are interspersed between species of *Perichares*. For these reasons, we consider *Alera* to be a subjective junior synonym of *Perichares*.

Oenides Mabille, 1904 is a valid genus

Hesperia vulpina C. and R. Felder, 1867 is not monophyletic with *Alera furcata*, the type species of *Alera*, where *H. vulpina* was previously placed, and since it is the type species of the available genus-group name *Oenides* Mabille, 1904, that was considered a subjective synonym of *Alera*, we resurrect this genus from synonymy and use it as a monotypic valid genus with the species *Oenides vulpina* (Fig. 13).

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

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Literature Cited

Austin GT 1998. Hesperiidae of Rondônia, Brazil: *Anastrus* and *Tosta*, with descriptions of two new species (Lepidoptera: Hesperiidae: Pyrginae). Tropical Lepidoptera 9(suppl. 2): 19–25.

Austin GT 2000. Hesperiidae of Rondônia, Brazil: "*Antigonus*" genus group (Pyrginae), with taxonomic comments and descriptions of new species from Brazil and Guatemala. Journal of the Lepidopterists' Society 54(1): 1–28.

Austin GT 2008. Hesperiidae of Rondonia, Brazil: Taxonomic comments on 'night' skippers, with descriptions of new genera and species (Lepidoptera: Eudaminae). Insecta Mundi 29: 1–36.

Austin GT, and Warren AD. 2009. New looks at and for *Onespa*, *Buzyges*, and *Librita* (Lepidoptera: Hesperiidae: Hesperiinae), with new combinations and descriptions of a new genus and six new species. Insecta Mundi 89: 1–55.

Bell EL 1931. A list of Hesperiidæ from Barro Colorado Island, Canal Zone, and adjacent Panama, with a description of a new species. Journal of The New York Entomological Society 39(1): 81–108.

Bell EL 1932. Notes on some American Hesperiidae and descriptions of new species (Lepidoptera, Rhopalocera). Bulletin of the Brooklyn Entomological Society 12(3): 131–141.

Bell EL 1940. A new genus and some new species of neotropical Hesperiidae (Lepidoptera, Rhopalocera). American Museum Novitates 1064: 1–5.

Bell EL 1941. New species of neotropical Hesperiidae (Lepidoptera, Rhopalocera). American Museum Novitates 1125: 1–10.

Bell EL 1942. New genera and new species of neotropical Hesperiidae (Lepidoptera, Rhopalocera). American Museum Novitates 1205: 1–9.

Bell EL 1947. A new genus and some new species and subspecies of neotropical Hesperiidae (Lepidoptera, Rhopalocera). American Museum Novitates 1354: 1–12.

Bell EL 1959. Descriptions of some new species of neotropical Hesperiidae (Lepidoptera, Rhopalocera). American Museum Novitates 1962: 1–16.

Burns JM 1992. Genitalic recasting of *Poanes* and *Paratrytone* (Hesperiidae). Journal of the Lepidopterists' Society 46(1): 1–23.

Burns JM, Janzen DH, Hallwachs W, Hajibabaei M, and Hebert PDN. 2010. Genitalia, DNA barcodes, larval facies, and foodplants place the mimetic species *Neoxeniades molion* in *Rhinthon* (Hesperiidae: Hesperiinae). Journal of the Lepidopterists' Society 64(2): 69–78.

Cong Q, Borek D, Otwinowski Z, and Grishin NV. 2015a. Skipper genome sheds light on unique phenotypic traits and phylogeny. BMC Genomics 16: 639. [PubMed: 26311350]

Cong Q, Borek D, Otwinowski Z, and Grishin NV. 2015b. Tiger swallowtail genome reveals mechanisms for speciation and caterpillar chemical defense. Cell Reports 10(6): 910–919. [PubMed: 25683714]

Cong Q, Li W, Borek D, Otwinowski Z, and Grishin NV. 2018. The bear giant-skipper genome suggests genetic adaptations to living inside yucca roots. Molecular Genetics and Genomics 294(1): 211–226. [PubMed: 30293092]

Cong Q, Shen J, Borek D, Robbins RK, Opler PA, Otwinowski Z, and Grishin NV. 2017a. When COI barcodes deceive: complete genomes reveal introgression in hairstreaks. Proceedings of the Royal Society B: Biological Sciences 284(1848): 20161735.

Cong Q, Shen J, Borek D, Robbins RK, Otwinowski Z, and Grishin NV. 2016a. Complete genomes of hairstreak butterflies, their speciation, and nucleo-mitochondrial incongruence. Scientific Reports 6: 24863. [PubMed: 27120974]

Cong Q, Shen J, Li W, Borek D, Otwinowski Z, and Grishin NV. 2017b. The first complete genomes of metalmarks and the classification of butterfly families. Genomics 109: 485–493. [PubMed: 28757157]

Cong Q, Shen J, Warren AD, Borek D, Otwinowski Z, and Grishin NV. 2016b. Speciation in cloudless sulphurs gleaned from complete genomes. Genome Biology and Evolution 8(3): 915–931. [PubMed: 26951782]

Espeland M, Breinholt J, Willmott KR, Warren AD, Vila R, Toussaint EFA, Maunsell SC, Aduse-Poku K, Talavera G, Eastwood R, Jarzyna MA, Guralnick R, Lohman DJ, Pierce NE, and Kawahara AY. 2018. A comprehensive and dated phylogenomic analysis of butterflies. Current Biology 28(5): 770–778. [PubMed: 29456146]

Evans WH 1937. A catalogue of the African Hesperiidae indicating the classification and nomenclature adopted in the British Museum. British Museum (Natural History); London. xii + 212 p., 30 pl.

Evans WH 1949. A catalogue of the Hesperiidae from Europe, Asia, and Australia in the British Museum (Natural History). British Museum (Natural History); London. xix + 502 p., 53 pl.

Evans WH 1951. A catalogue of the American Hesperiidae indicating the classification and nomenclature adopted in the British Museum (Natural History). Part I. Introduction and Group A Pyrrhopyginae. British Museum (Natural History); London. x + 92 p., pl. 1–9

Evans WH 1952. A catalogue of the American Hesperiidae indicating the classification and nomenclature adopted in the British Museum (Natural History). Part II. Pyrginae. Section I. British Museum (Natural History). London. v + 178 p., pl. 10–25

Evans WH 1953. A catalogue of the American Hesperiidae indicating the classification and nomenclature adopted in the British Museum (Natural History). Part III. Pyrginae. Section 2. British Museum (Natural History); London. v + 246 p., pl. 26–53

Evans WH 1955. A catalogue of the American Hesperiidae indicating the classification and nomenclature adopted in the British Museum (Natural History). Part IV. Hesperiinae and Megathyminae. British Museum (Natural History); London. v + 499 p., pl. 54–88

Grishin NV 2012. A new Central American *Anastrus* with unexpectedly distinct genitalia (Lepidoptera, Hesperiidae, Pyrginae). Tropical Lepidoptera Research 22(1): 1–7.

Hancock DL, and Gardiner AJ. 1982. The *Kedestes nerva* group of species (Lepidoptera: Hesperiidae). Arnoldia Zimbabwe 9(8): 105–123.

Kawahara AY, and Breinholt JW. 2014. Phylogenomics provides strong evidence for relationships of butterflies and moths. Proceedings of the Royal Society B: Biological Sciences 281(1788): 20140970.

Li W, Cong Q, Shen J, Zhang J, Hallwachs W, Janzen DH, and Grishin NV. 2019. Genomes of skipper butterflies reveal extensive convergence of wing patterns. Proceedings of the National Academy of Sciences of the United States of America 116(13): 6232–6237. [PubMed: 30877254]

Mielke CGC 1995. Papilionoidea e Hesperioidea (Lepidoptera) de Curitiba e seus arrededores, Paraná, Brasil, com notas taxonômicas sobre Hesperiidae. Revista brasileira de Zoologia 11(4): 759–776.

Mielke OHH 1980. Contribuição ao estudo faunístico dos Hesperiidae americanos. VI. Nota suplementar às espécies de Hesperiinae do Rio Grande do Sul, Brasil (Lepidoptera). Acta Biologica Paranaense 8–9: 127–172.

Mielke OHH 2005. Catalogue of the American Hesperioidea: Hesperiidae (Lepidoptera). Sociedade Brasileira de Zoologia; Curitiba, Paraná, Brazil. xiii + 1536 p.

Nicolay SS 1980. Descriptions of new Hesperiidae from Panama and Ecuador (Pyrginae and Hesperiinae). Bulletin of the Allyn Museum 59: 1–17.

Sahoo RK, Warren AD, Collins SC, and Kodandaramaiah U. 2017. Hostplant change and paleoclimatic events explain diversification shifts in skipper butterflies (Family: Hesperiidae). BMC Evolutionary Biology 17(1): 174. [PubMed: 28768477]

Sahoo RK, Warren AD, Wahlberg N, Brower AV, Lukhtanov VA, and Kodandaramaiah U. 2016. Ten genes and two topologies: an exploration of higher relationships in skipper butterflies (Hesperiidae). PeerJ 4: e2653. [PubMed: 27957386]

Shen J, Cong Q, Borek D, Otwinowski Z, and Grishin NV. 2017. Complete genome of *Achalarus lyciades*, the first representative of the Eudaminae subfamily of skippers. Current Genomics 18(4): 366–374. [PubMed: 29081692]

Shen J, Cong Q, and Grishin NV. 2015. The complete mitochondrial genome of *Papilio glaucus* and its phylogenetic implications. Meta Gene 5: 68–83. [PubMed: 26106582]

Shen J, Cong Q, and Grishin NV. 2016a. The complete mitogenome of *Achalarus lyciades* (Lepidoptera: Hesperiidae). Mitochondrial DNA Part B: Resources 1(1): 581–583. [PubMed: 28367503]

Shen J, Cong Q, Kinch LN, Borek D, Otwinowski Z, and Grishin NV. 2016b. Complete genome of *Pieris rapae*, a resilient alien, a cabbage pest, and a source of anti-cancer proteins. F1000Research 5: 2631. [PubMed: 28163896]

Smith DS, Miller LD, and Miller JY. 1994. The butterflies of the West Indies and South Florida. Oxford Univ. Press; Oxford, New York, Tokyo. x + 264 p.

Steinhauser SR 1989. Taxonomic notes and descriptions of new taxa in the Neotropical Hesperiidae. Part I. Pyrginae. Bulletin of the Allyn Museum 127: 1–70.

Toussaint EFA, Breinholt JW, Earl C, Warren AD, Brower AVZ, Yago M, Dexter KM, Espeland M, Pierce NE, Lohman DJ, and Kawahara AY. 2018. Anchored phylogenomics illuminates the skipper butterfly tree of life. BMC Evolutionary Biology 18(1): 101. [PubMed: 29921227]

Wahlberg N, Braby MF, Brower AV, de Jong R, Lee MM, Nylin S, Pierce NE, Sperling FA, Vila R, Warren AD, and Zakharov E. 2005. Synergistic effects of combining morphological and molecular data in resolving the phylogeny of butterflies and skippers. Proceedings of the Royal Society B: Biological Sciences 272(1572): 1577–1586.

Warren AD, Ogawa JR, and Brower AVZ. 2008. Phylogenetic relationships of subfamilies and circumscription of tribes in the family Hesperiidae (Lepidoptera: Hesperioidea). Cladistics 24(5): 642–676.

Warren AD, Ogawa JR, and Brower AVZ. 2009. Revised classification of the family Hesperiidae (Lepidoptera: Hesperioidea) based on combined molecular and morphological data. Systematic Entomology 34(3): 467–523.

Watson EY 1893. A proposed classification of the Hesperiidae, with a revision of the genera. Proceedings of the Zoological Society of London 1893(1): 3–132.

Zhang J, Cong Q, Rex EA, Hallwachs W, Janzen DH, Grishin NV, and Gammon DB. 2019a. Gypsy moth genome provides insights into flight capability and virus-host interactions. Proceedings of the National Academy of Sciences of the United States of America 116(5): 1669–1678. [PubMed: 30642971]

Zhang J, Cong Q, Shen J, Brockmann E, and Grishin NV. 2019b. Genomes reveal drastic and recurrent phenotypic divergence in firetip skipper butterflies (Hesperiidae: Pyrrhopyginae). Proceedings of the Royal Society B: Biological Sciences 286(1903): 20190609.

Zhang J, Cong Q, Shen J, Brockmann E, and Grishin NV. 2019c. Three new subfamilies of skipper butterflies (Lepidoptera, Hesperiidae). Zookeys 861: 91–105. [PubMed: 31333327]

Zhang J, Cong Q, Shen J, Fan XL, Wang M, and Grishin NV. 2017a. The complete mitogenome of *Euschemon rafflesia* (Lepidoptera: Hesperiidae). Mitochondrial DNA Part B: Resources 2(1): 136–138. [PubMed: 30931394]

Zhang J, Cong Q, Shen J, Wang R, and Grishin NV. 2017b. The complete mitochondrial genome of a skipper *Burara striata* (Lepidoptera: Hesperiidae). Mitochondrial DNA Part B: Resources 2(1): 145–147. [PubMed: 29376128]

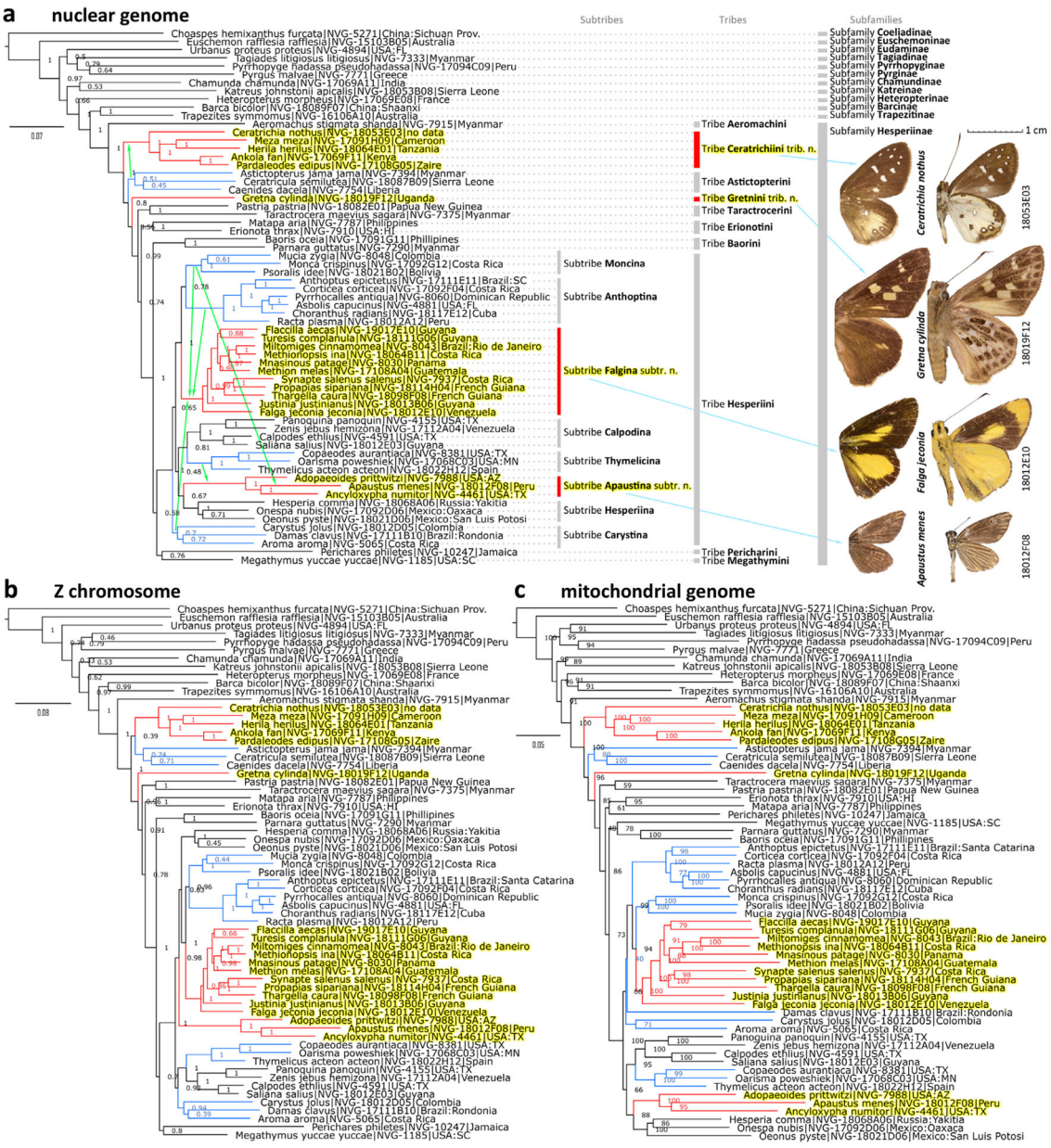

Figure 1.

Genomic trees of representative Hesperiidae. The trees are built from protein-coding regions in different genomic partitions: **a)** Nuclear genome; **b)** Z chromosome; **c)** Mitochondrial genome. The trees are rooted with *Pterourus glaucus* (NVG-1670), not shown. See Table 1 and Table S1 in the Supplemental file deposited at https://osf.io/5cfht/?view_only=21eb53b6f8f344afaee3de2be90bf5d2 for additional data about these specimens. Names of species placed in new tribes and subtribes described in this work are highlighted in yellow and clades representing new taxa are colored in red. Clades for tribes and subtribes where species of the new taxa were placed previously are colored in blue and green arrow points from the former taxon to the new taxon (only on nuclear genome tree). Statistical support values are shown by nodes in all but the COI barcode trees. COI barcode NJ

dendrogram is given for comparison and is not expected to reflect phylogeny. Subfamilies, tribes and subtribes for species included in the trees are shown to the right of the nuclear tree. Sequenced specimens of the type species of the new tribes and subtribes are illustrated in dorsal (left) and ventral (right) views and indicated by blue arrows.

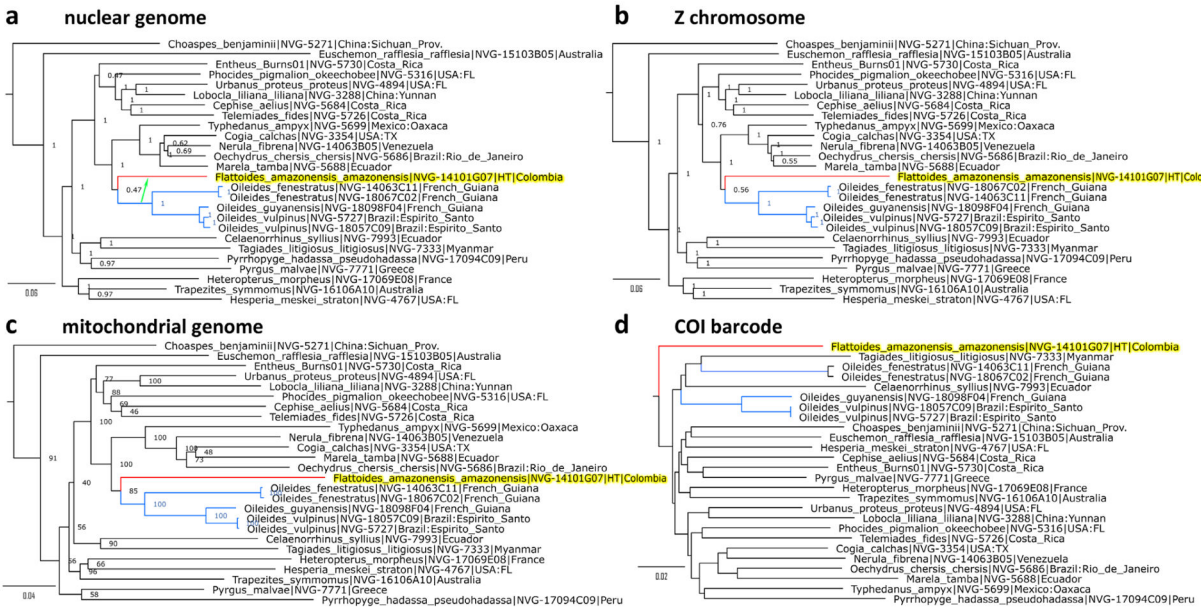

Figure 2.

Genomic trees of Eudaminae and representatives of other Hesperiidae subfamilies. The trees are built from protein-coding regions in different genomic partitions: **a)** Nuclear genome. **b)** Z chromosome. **c)** Mitochondrial genome; **d)** COI barcode. The trees are rooted with *Pterourus glaucus* (NVG-1670), not shown. See Table 1 and Table S1 in the Supplemental file deposited at https://osf.io/5cfht/?view_only=21eb53b6f8f344afaee3de2be90bf5d2 for additional data about these specimens. Where possible, taxa are ordered similarly to that in the nuclear genome tree. Names of species placed in new genera described in this work are highlighted in yellow and clades of these genera are colored in red. Clades for genera where these species were placed previously are colored in blue and green arrow points from the former genus to the new genus (only on nuclear genome tree). Names of genera resurrected from synonymy are highlighted in cyan. Names of genera that form new genus-species combinations proposed in this work are highlighted in magenta. Statistical support values are shown by nodes in all but the COI barcode trees. COI barcode NJ dendrogram is given for comparison and is not expected to reflect phylogeny. The same notations are used in Fig. 2–13.

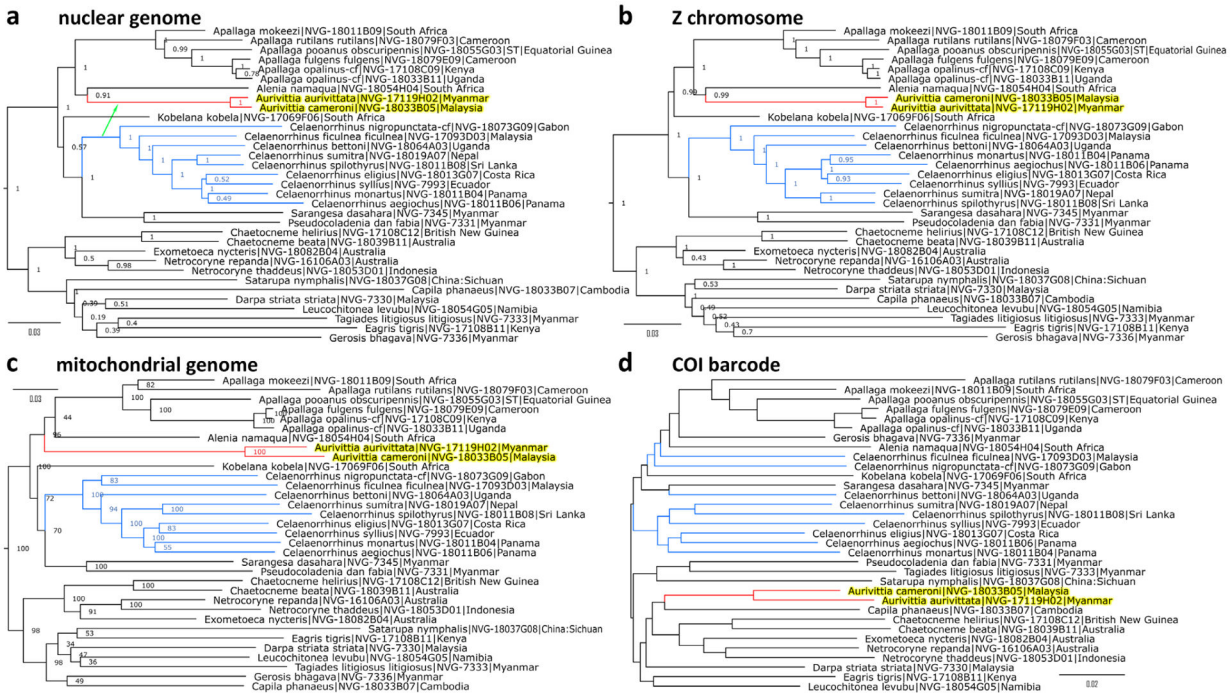

Figure 3.

Genomic trees of Tagiadinae. See Fig. 2 legend for notations.

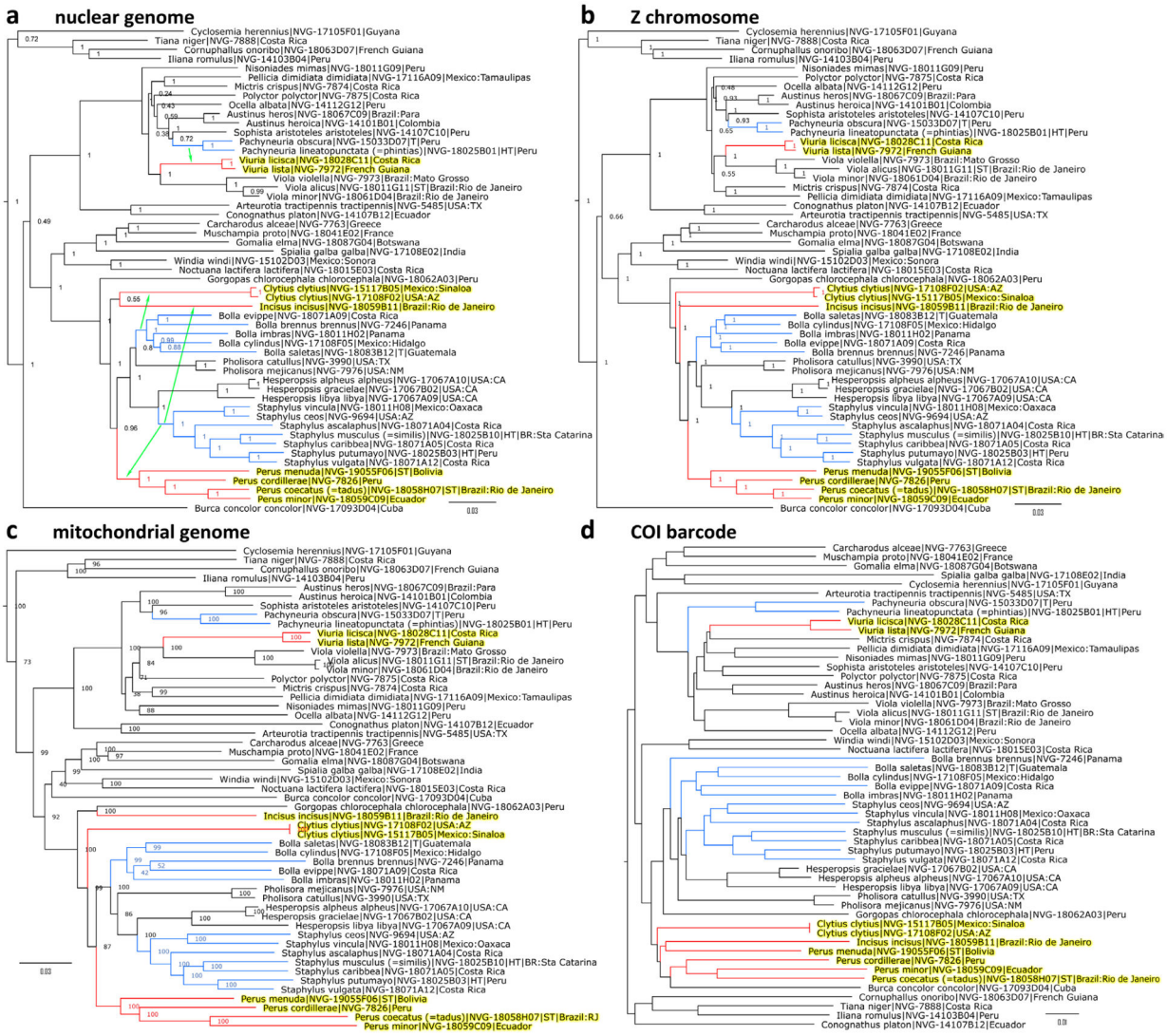

Figure 4.

Genomic trees of Carcharodini. See Fig. 2 legend for notations.

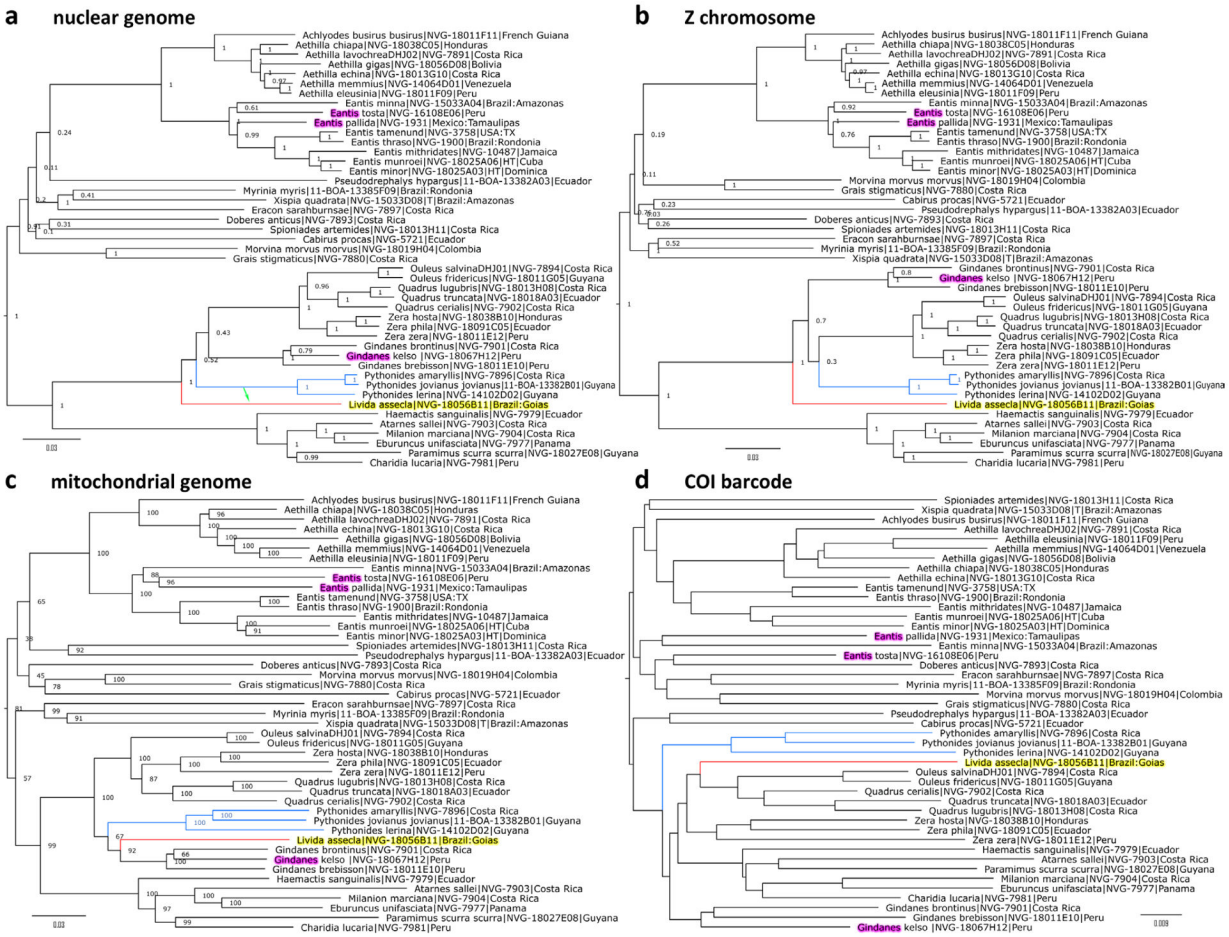

Figure 5.

Genomic trees of Achlyodini. See Fig. 2 legend for notations.

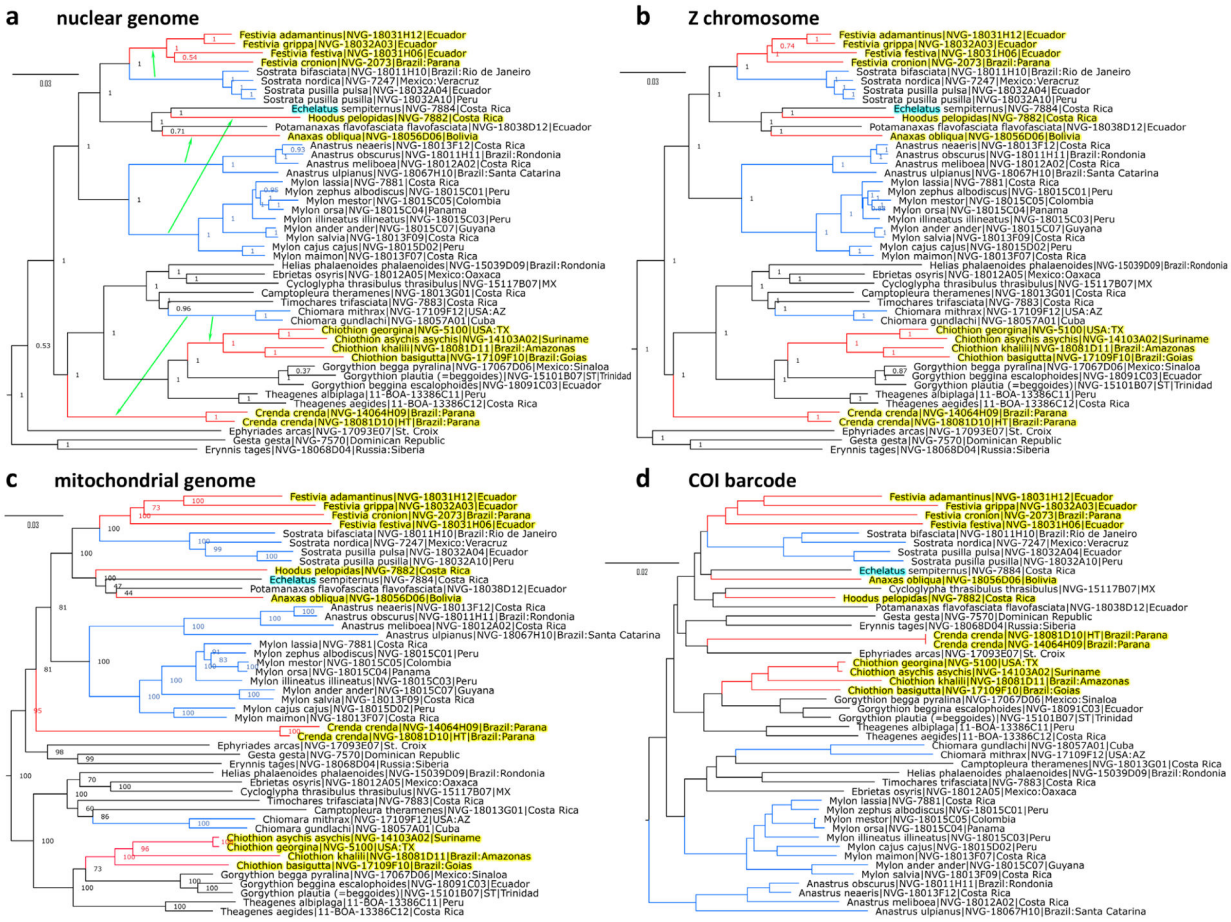

Figure 6.
Genomic trees of Erynnini. See Fig. 2 legend for notations.

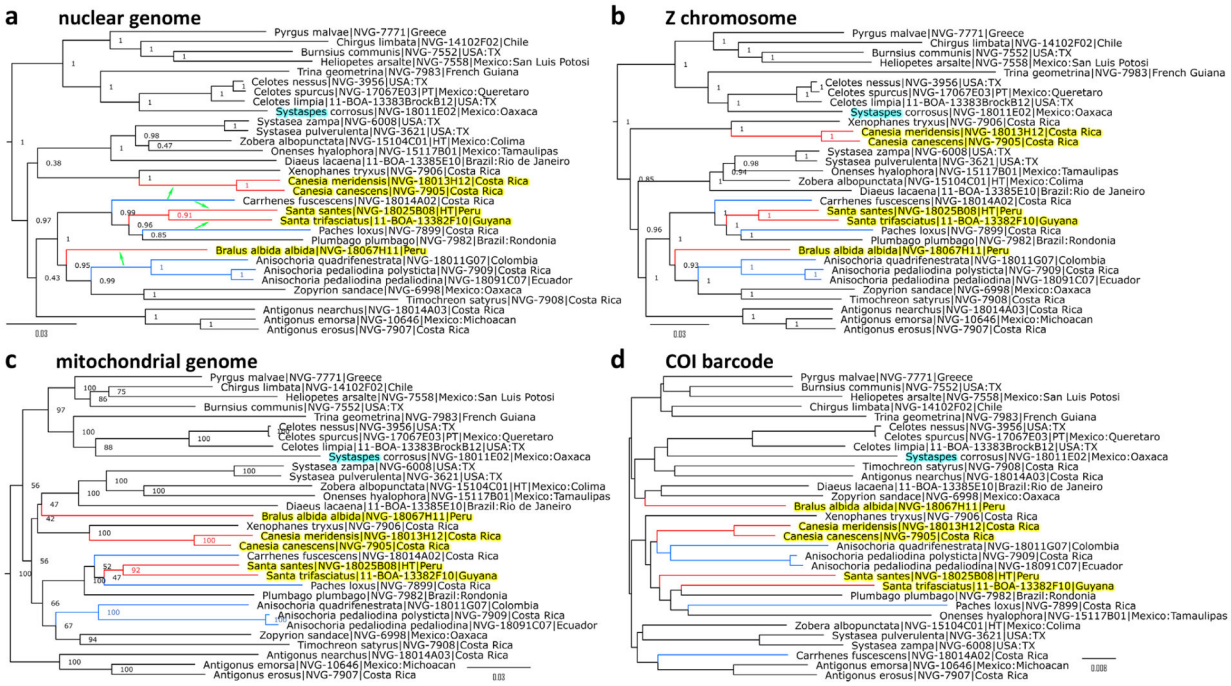

Figure 7.
Genomic trees of Pyrgini. See Fig. 2 legend for notations.

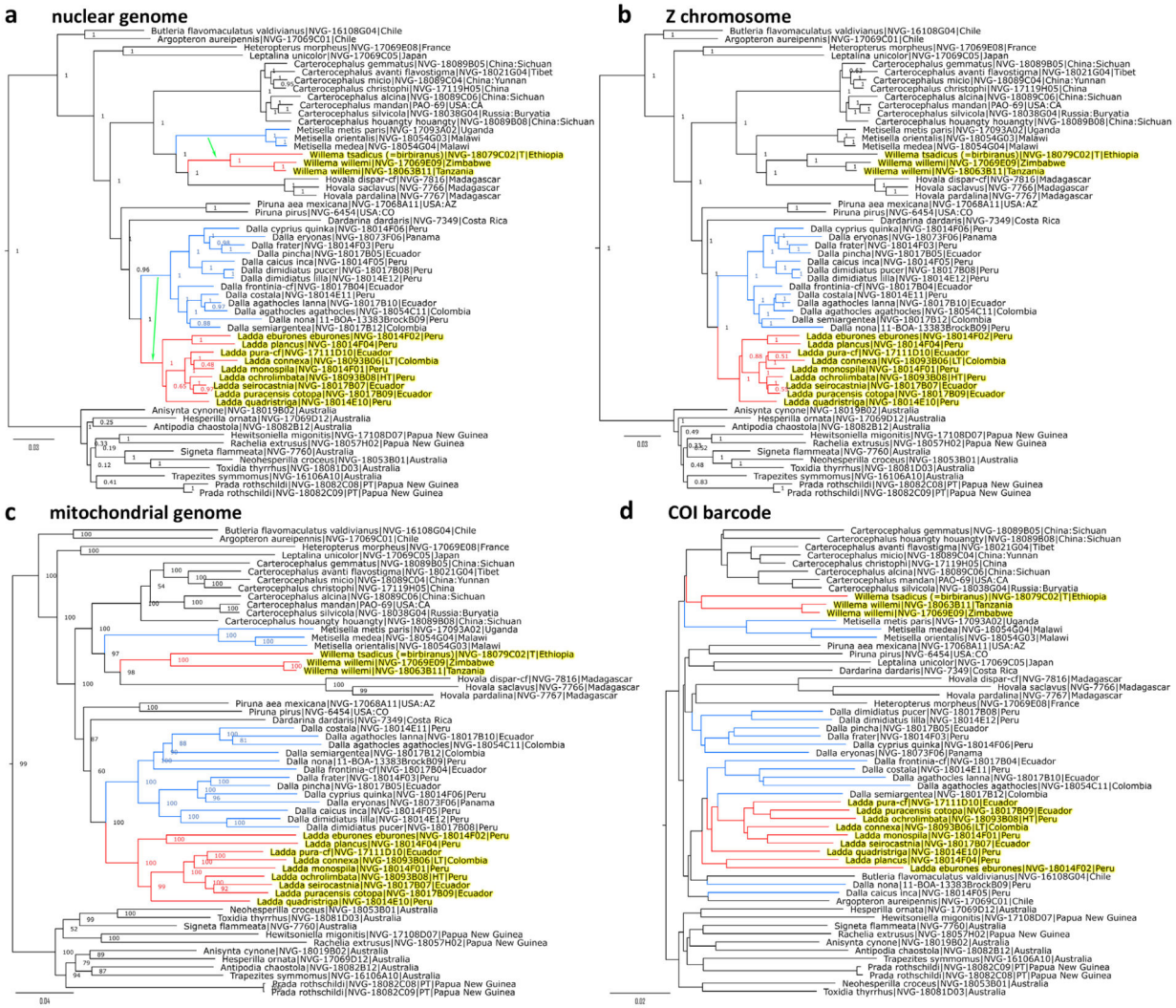

Figure 8.

Genomic trees of Heteropterinae and Trapezitinae. See Fig. 2 legend for notations.

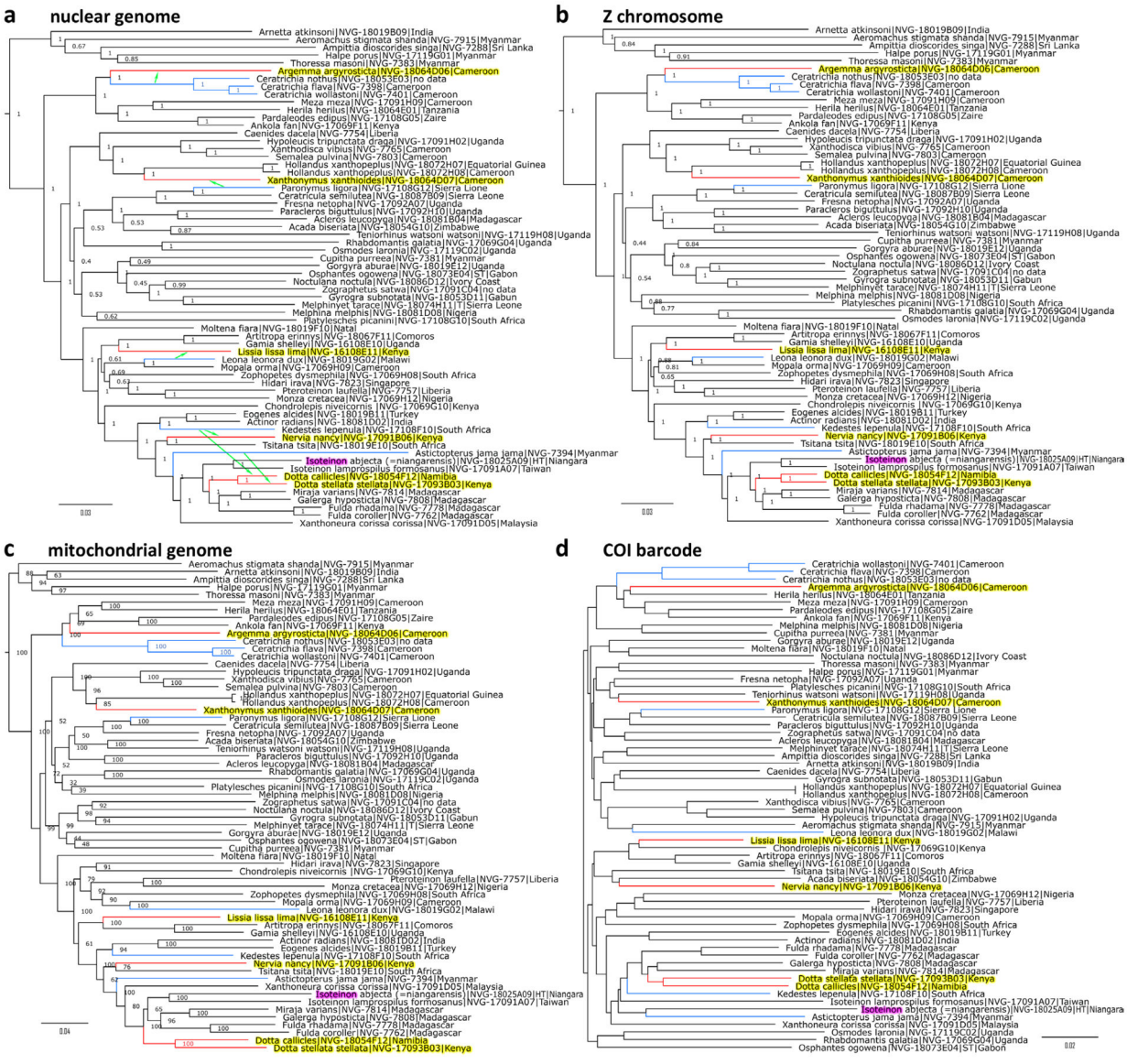

Figure 9.

Genomic trees of Astictopterini and relatives. See Fig. 2 legend for notations.

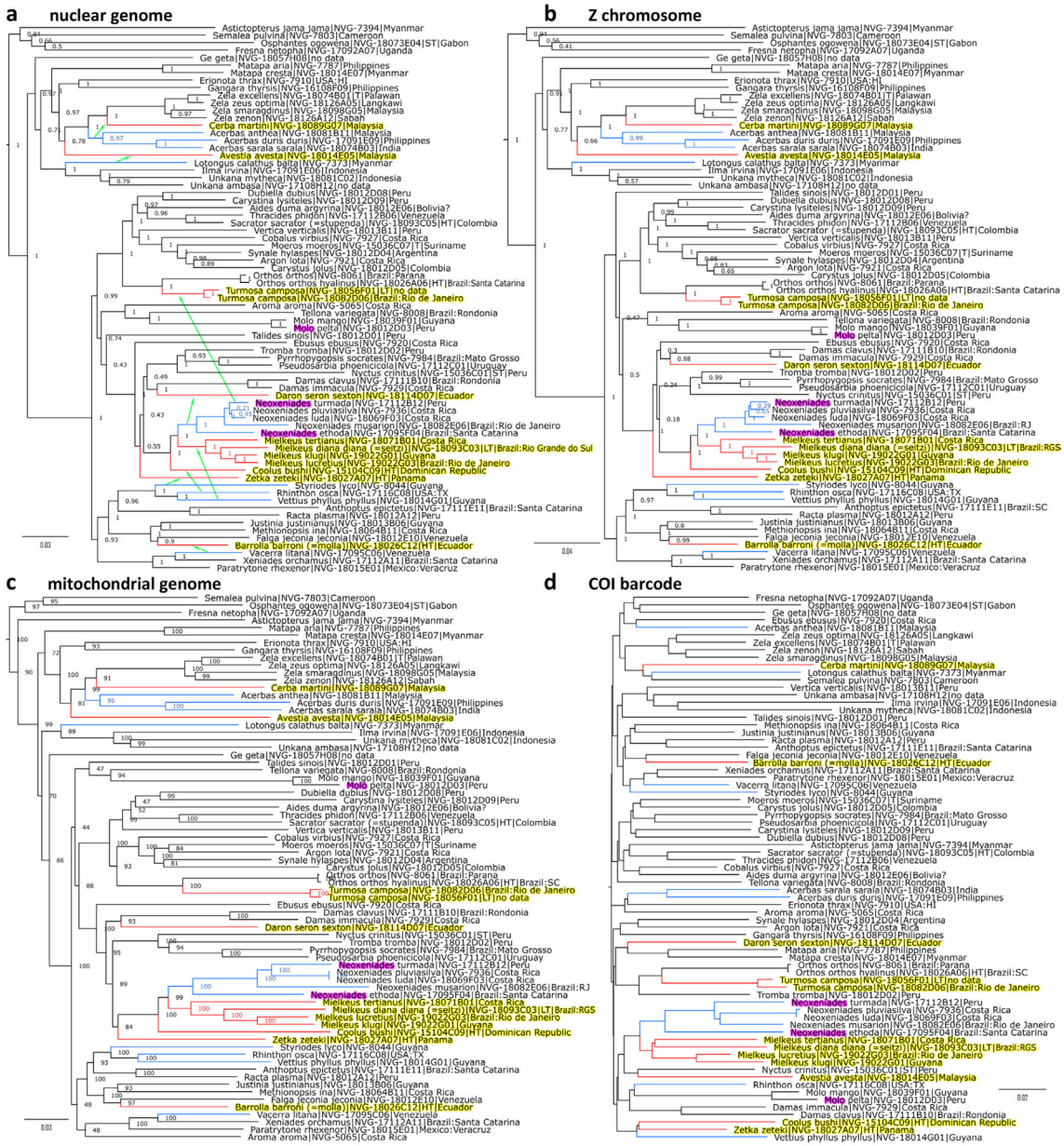

Figure 10.
Genomic trees of Erionotini, Carystina and relatives. See Fig. 2 legend for notations.

Figure 11.

Nuclear genome and Z chromosome trees of Moncina and relatives. See Fig. 2 legend for notations.

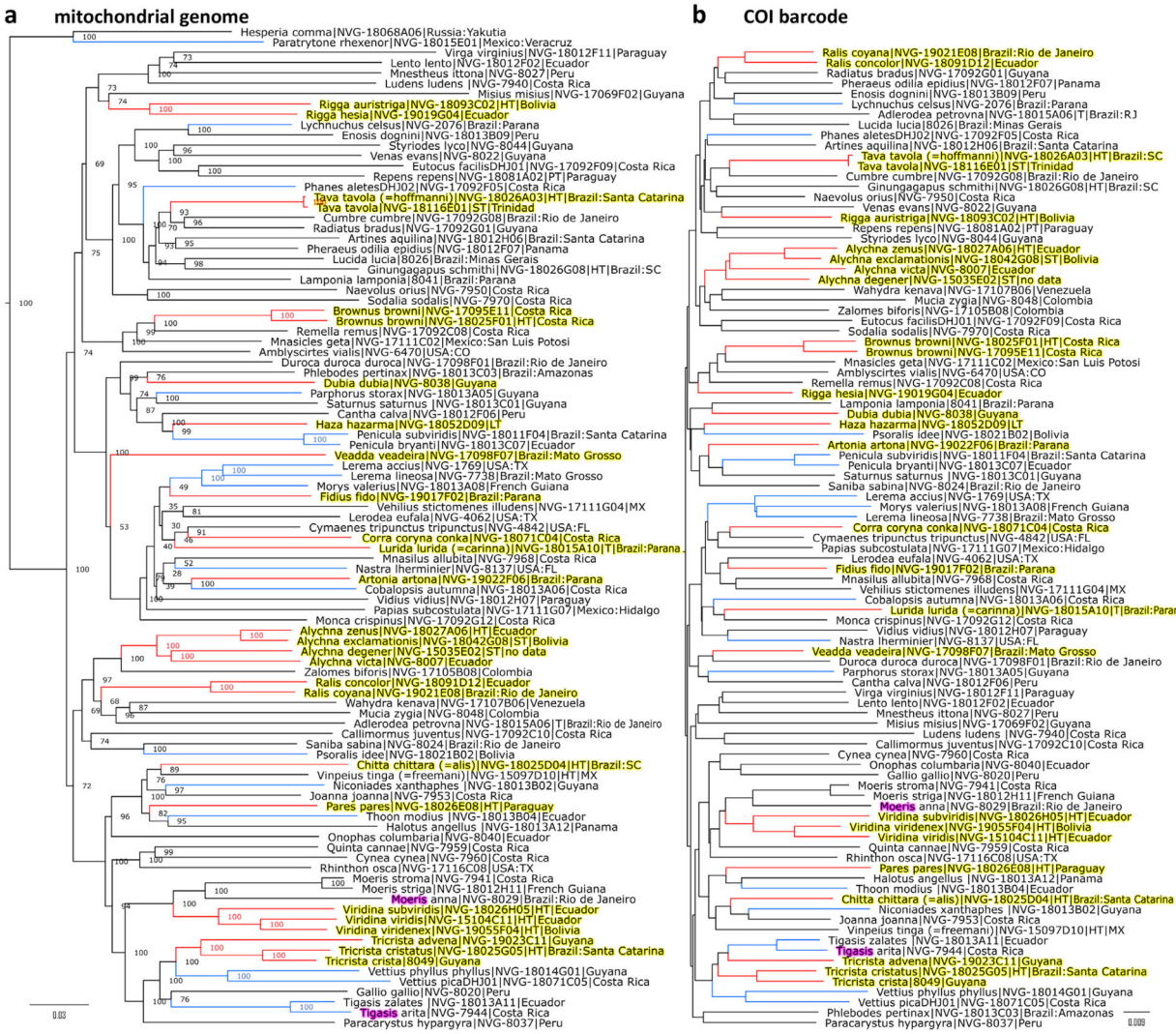

Figure 12.

Mitochondrial genome and COI barcode trees of Moncina and relatives. See Fig. 2 legend for notations.

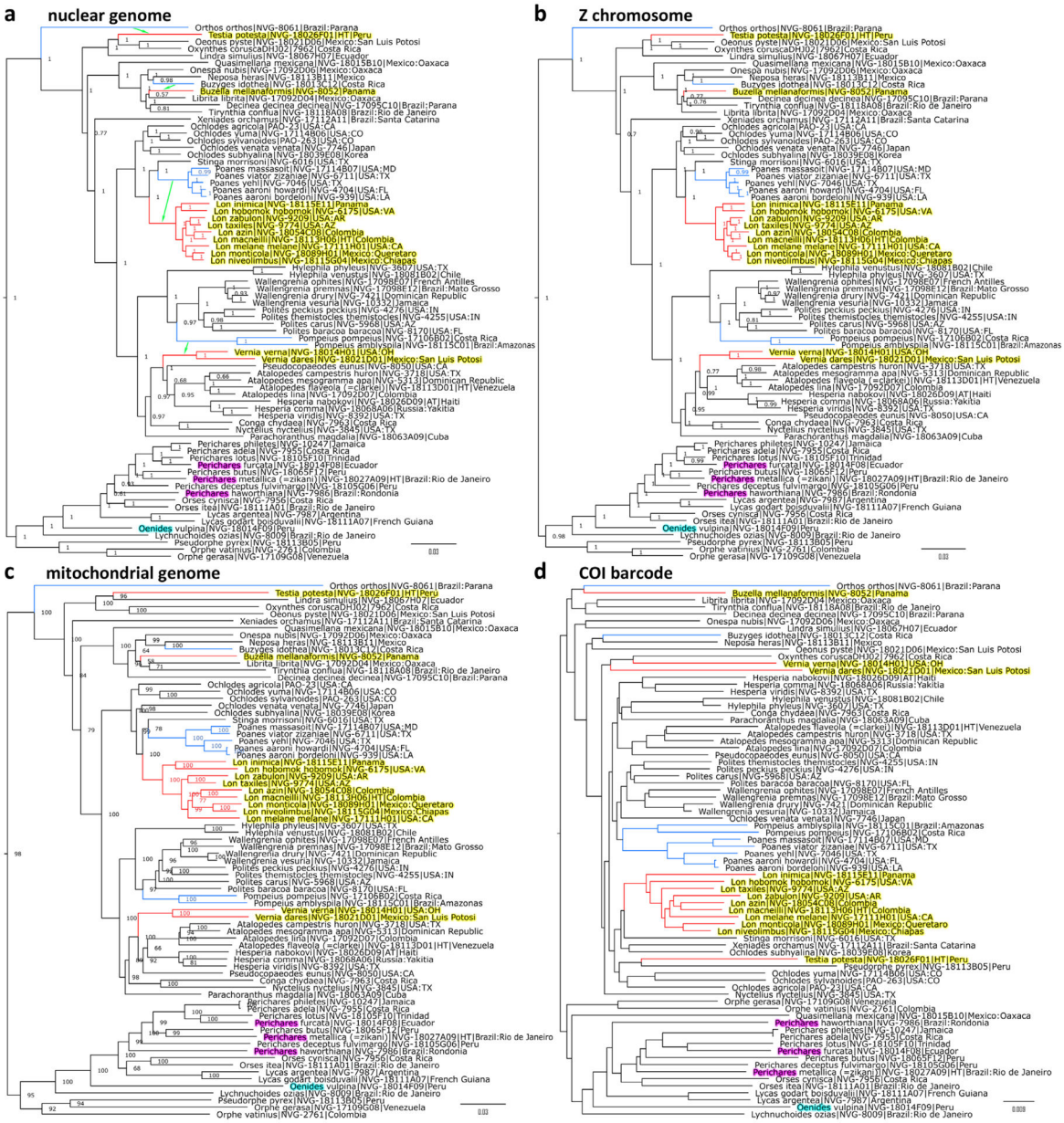

Figure 13.
Genomic trees of Hesperiina, Pericharini and relatives. See Fig. 2 legend for notations.

Table 1.

Data for 620 sequenced Hesperiidae specimens. See Table S1 in the Supplemental file deposited at https://osf.io/5cfht/?view_only=21eb53b6f8f344afaee3de2be90bf5d2 for detailed information about these specimens and Materials and Methods section for collection abbreviations. Type status abbreviations are: AT, allotype; HT, holotype; LT, lectotype; PT, paratype, ST, syntype; T, type.

DNA voucher	Taxon name	Type	Brief data	Collection
NVG-18054G10	*Acada biseriata*		Zimbabwe, 1993	ZMHB
NVG-18081B11	*Acerbas anthea*		Malaysia, 1917, NHMUK_010430824, 0247275554	BMNH
NVG-17091E09	*Acerbas duris duris*		Philippines, old (around 1900)	USNM
NVG-18074B03	*Acerbas sarala sarala*		India, 1890	ZMHB
NVG-18011F11	*Achlyodes busirus busirus*		French Guiana, 1988	USNM
NVG-18081B04	*Acleros leucopyga*		Madagascar, 1921, NHMUK_010430828, 0247274717	BMNH
NVG-18081D02	*Actinor radians*		India, 1885, NHMUK_010430809, 0247275546	BMNH
NVG-18015A06	*Adlerodea petrovna*	**T**	Brazil: Rio de Janeiro, old (around 1900)	USNM
NVG-7988	*Adopaeoides prittwitzi*		USA: AZ, Santa Cruz Co., 1999	USNM
NVG-7915	*Aeromachus stigmata shanda*		Myanmar, 2002	USNM
NVG-18038C05	*Aethilla chiapa*		Honduras	RGallardo
NVG-18013G10	*Aethilla echina*		Costa Rica, 2005, 05-SRNP-20	USNM
NVG-18011F09	*Aethilla eleusinia*		Peru, 2012	USNM
NVG-18056D08	*Aethilla gigas*		Bolivia, old (around 1900)	ZfBS
NVG-7891	*Aethilla lavochrea*DHJ02		Costa Rica, 2013, 13-SRNP-22231	USNM
NVG-14064D01	*Aethilla memmius*		Venezuela, 1985	USNM
NVG-18012E06	*Aides duma argyrina*		Bolivia?, no date?1970	USNM
NVG-18054H04	*Alenia namaqua*		South Africa, 2002	ZMHB
NVG-15035E02	*Alychna degener*	**ST**	no data	ZMHB
NVG-18042G08	*Alychna exclamationis*	**ST**	Bolivia, old (around 1900)	ZMHB
NVG-8007	*Alychna victa*		Ecuador, 2004	USNM
NVG-18027A06	*Alychna zenus*	**HT**	Ecuador, 1939	AMNH
NVG-6470	*Amblyscirtes vialis*		USA: CO, Grand Co., 2016	UTSW
NVG-7288	*Ampittia dioscorides singa*		Sri Lanka, 1971	USNM
NVG-18012A02	*Anastrus meliboea*		Costa Rica, 1977	USNM
NVG-18013F12	*Anastrus neaeris*		Costa Rica, 2008, 08-SRNP-2106	USNM
NVG-18011H11	*Anastrus obscurus*		Brazil: Rondonia, 1991	USNM
NVG-18067H10	*Anastrus ulpianus*		Brazil: Santa Catarina, 2000	EBrockmann
NVG-18056D06	*Anaxas obliqua*		Bolivia, old (around 1900)	ZfBS
NVG-4461	*Ancyloxypha numitor*		USA: TX, Dallas Co., 2015	UTSW
NVG-18091C07	*Anisochoria pedaliodina pedaliodina*		Ecuador, 2012	EBrockmann
NVG-7909	*Anisochoria pedaliodina polysticta*		Costa Rica, 2004, 04-SRNP-15751	USNM
NVG-18011G07	*Anisochoria quadrifenestrata*		Colombia, old (around 1900)	USNM
NVG-18019B02	*Anisynta cynone*		Australia, 1961	AMNH

DNA voucher	Taxon name	Type	Brief data	Collection
NVG-17069F11	*Ankola fan*		Kenya, 1955	USNM
NVG-17111E11	*Anthoptus epictetus*		Brazil: Santa Catarina, 1999	LACM
NVG-10646	*Antigonus emorsa*		Mexico: Michoacan, 1994	TAMU
NVG-7907	*Antigonus erosus*		Costa Rica, 2013, 13-SRNP-56479	USNM
NVG-18014A03	*Antigonus nearchus*		Costa Rica, 2006, 06-SRNP-32799	USNM
NVG-18082B12	*Antipodia chaostola*		Australia, 1934, NHMUK_012824109, 0247278477	BMNH
NVG-18079E09	*Apallaga fulgens fulgens*		Cameroon, 1987, EL63116	MNHP
NVG-18011B09	*Apallaga mokeezi*		South Africa, 1978	USNM
NVG-17108C09	*Apallaga opalinus*-cf		Kenya, 2001	LACM
NVG-18033B11	*Apallaga opalinus*-cf		Uganda, 2008	MWalker
NVG-18055G03	*Apallaga pooanus obscuripennis*	**ST**	Equatorial Guinea, 1906	ZMHB
NVG-18079F03	*Apallaga rutilans rutilans*		Cameroon, 1991, EL63122	MNHP
NVG-18012F08	*Apaustus menes*		Peru, 2011	USNM
NVG-18064D06	*Argemma argyrosticta*		Cameroon, old (around 1900)	USNM
NVG-7921	*Argon lota*		Costa Rica, 2007, 07-SRNP-55877	USNM
NVG-17069C01	*Argopteron aureipennis*		Chile, 1982	USNM
NVG-18019B09	*Arnetta atkinsoni*		India, 1927	AMNH
NVG-5065	*Aroma aroma*		Costa Rica, 04-SRNP-1707	USNM
NVG-5485	*Arteurotia tractipennis tractipennis*		USA: TX, Hidalgo Co., 1972	TAMU
NVG-18012H06	*Artines aquilina*		Brazil: Santa Catarina, 1999	USNM
NVG-18067F11	*Artitropa erinnys*		Comoros, 1987	EBrockmann
NVG-19022F06	*Artonia artona*		Brazil: Parana, 1995	USNM
NVG-4881	*Asbolis capucinus*		USA: FL, Monroe Co., 2015	UTSW
NVG-7394	*Astictopterus jama jama*		Myanmar, 2001	USNM
NVG-3718	*Atalopedes campestris huron*		USA: TX, Dallas Co., 2015	UTSW
NVG-18113D01	*Atalopedes flaveola (=clarkei)*	**HT**	Venezuela, 1985	USNM
NVG-17092D07	*Atalopedes lina*		Colombia, 1991	USNM
NVG-5313	*Atalopedes mesogramma apa*		Dominican Republic, 2015	UTSW
NVG-7903	*Atarnes sallei*		Costa Rica, 2007, 07-SRNP-59529	USNM
NVG-17119H02	*Aurivittia aurivittata*		Myanmar, 2002	USNM
NVG-18033B05	*Aurivittia cameroni*		Malaysia, 2003	MWalker
NVG-14101B01	*Austinus heroica*		Colombia, 1946	AMNH
NVG-18067C09	*Austinus heros*		Brazil: Para, 2009	EBrockmann
NVG-18014E05	*Avestia avesta*		Malaysia, old (around 1900)	USNM
NVG-17091G11	*Baoris oceia*		Phillipines, 1914	USNM
NVG-18089F07	*Barca bicolor*		China: Shaanxi, 2009	EBrockmann
NVG-18026C12	*Barrolla molla*	**HT**	Ecuador	AMNH
NVG-7246	*Bolla brennus brennus*		Panama, 1981	USNM
NVG-17108F05	*Bolla cylindus*		Mexico: Hidalgo, 1982	LACM

DNA voucher	Taxon name	Type	Brief data	Collection
NVG-18071A09	*Bolla evippe*		Costa Rica, 2009, 09-SRNP-57008	USNM
NVG-18011H02	*Bolla imbras*		Panama, 1984	USNM
NVG-18083B12	*Bolla saletas*	**T**	Guatemala, BMNH(E)_1669828, 0247277236	BMNH
NVG-18067H11	*Bralus albida albida*		Peru, 1994	EBrockmann
NVG-18025F01	*Brownus browni*	**HT**	Costa Rica, 1946	AMNH
NVG-17095E11	*Brownus browni*		Costa Rica, 2006	USNM
NVG-17093D04	*Burca concolor concolor*		Cuba, 2010	USNM
NVG-7552	*Burnsius communis*		USA: TX, Bexar Co., 1977	TAMU
NVG-16108G04	*Butleria flavomaculatus valdivianus*		Chile, 1979, USNMENT 00894446	USNM
NVG-8052	*Buzella mellanaformis*		Panama, 1982	USNM
NVG-18013C12	*Buzyges idothea*		Costa Rica, 1980	USNM
NVG-5721	*Cabirus procas*		Ecuador, 2004	USNM
NVG-7754	*Caenides dacela*		Liberia, 1988	USNM
NVG-17092C10	*Callimormus juventus*		Costa Rica, 2012, 12-SRNP-20224	USNM
NVG-4591	*Calpodes ethlius*		USA: TX, Cameron Co., 2015	UTSW
NVG-18013G01	*Camptopleura theramenes*		Costa Rica, 2015, 15-SRNP-45798	USNM
NVG-7905	*Canesia canescens*		Costa Rica, 2014, 14-SRNP-1649	USNM
NVG-18013H12	*Canesia meridensis*		Costa Rica, 1997, 97-SRNP-1522	USNM
NVG-18012F06	*Cantha calva*		Peru, 1986	USNM
NVG-18033B07	*Capila phanaeus*		Cambodia, 2006	MWalker
NVG-7763	*Carcharodus alceae*		Greece, 1990	USNM
NVG-18014A02	*Carrhenes fuscescens*		Costa Rica, 1995, 95-SRNP-6819	USNM
NVG-18089C06	*Carterocephalus alcina*		China: Sichuan, 2006	EBrockmann
NVG-18021G04	*Carterocephalus avanti flavostigma*		Tibet, 1944	AMNH
NVG-17119H05	*Carterocephalus christophi*		China, old (around 1900)	USNM
NVG-18089B05	*Carterocephalus gemmatus*		China: Sichuan, 2002	EBrockmann
NVG-18089B08	*Carterocephalus houangty houangty*		China: Sichuan, 2007	EBrockmann
PAO-69	*Carterocephalus mandan*		USA: CA, Sierra Co., 2016	UTSW
NVG-18089C04	*Carterocephalus micio*		China: Yunnan, 2006	EBrockmann
NVG-18038G04	*Carterocephalus silvicola*		Russia: Buryatia, 2016, 5195	UTSW
NVG-18012D09	*Carystina lysiteles*		Peru, 1999	USNM
NVG-18012D05	*Carystus jolus*		Colombia, 1971	USNM
NVG-18011B06	*Celaenorrhinus aegiochus*		Panama, 1981	USNM
NVG-18064A03	*Celaenorrhinus bettoni*		Uganda, 1952	USNM
NVG-18013G07	*Celaenorrhinus eligius*		Costa Rica, 2010, 10-SRNP-20588	USNM
NVG-17093D03	*Celaenorrhinus ficulnea ficulnea*		Malaysia, old (around 1900)	USNM
NVG-18011B04	*Celaenorrhinus monartus*		Panama, 1981	USNM
NVG-18073G09	*Celaenorrhinus rosetta*		Gabon, old (around 1900)	ZMHB
NVG-18011B08	*Celaenorrhinus spilothyrus*		Sri Lanka, 1976	USNM

DNA voucher	Taxon name	Type	Brief data	Collection
NVG-18019A07	*Celaenorrhinus sumitra*		Nepal, 1937	AMNH
NVG-7993	*Celaenorrhinus syllius*		Ecuador, 2002, USNMENT 01321833	USNM
11-BOA-13383BrockB12	*Celotes limpia*		USA: TX, Brewster Co.	JPBrock
NVG-3956	*Celotes nessus*		USA: TX, Hidalgo Co., 2015	UTSW
NVG-17067E03	*Celotes spurcus*	**PT**	Mexico: Queretaro, 2007, CSU_ENT1024631	CSUC
NVG-5684	*Cephise aelius*		Costa Rica, 2014, 14-SRNP-70854	USNM
NVG-7398	*Ceratrichia flava*		Cameroon, 1989	USNM
NVG-18053E03	*Ceratrichia nothus*		no data	ZMHB
NVG-7401	*Ceratrichia wollastoni*		Cameroon, 1989	USNM
NVG-18087B09	*Ceratricula semilutea*		Sierra Leone, 1906, EL62955	MNHP
NVG-18089G07	*Cerba martini*		Malaysia, 1993	EBrockmann
NVG-18039B11	*Chaetocneme beata*		Australia, old (around 1900)	FMNH
NVG-17108C12	*Chaetocneme helirius*		British New Guinea, 1962	LACM
NVG-17069A11	*Chamunda chamunda*		India, old (around 1900)	USNM
NVG-7981	*Charidia lucaria*		Peru, 2008	USNM
NVG-18057A01	*Chiomara gundlachi*		Cuba, 2014	ZSMC
NVG-17109F12	*Chiomara mithrax*		USA: AZ, Santa Cruz Co., 1992	LACM
NVG-14103A02	*Chiothion asychis asychis*		Suriname	USNM
NVG-17109F10	*Chiothion basigutta*		Brazil: Goias, 1956	LACM
NVG-5100	*Chiothion georgina*		USA: TX, Starr Co., 2015	UTSW
NVG-18081D11	*Chiothion khalili*		Brazil: AM, 1929, NHMUK_010430875, 0247277240	BMNH
NVG-14102F02	*Chirgus limbata*		Chile, 1952	FMNH
NVG-18025D04	*Chitta chittara (=alis)*	**HT**	Brazil: Santa Catarina, old (around 1900)	AMNH
NVG-5271	*Choaspes hemixanthus furcata*		China: Sichuan Prov., 2015	UTSW
NVG-17069G10	*Chondrolepis niveicornis*		Kenya, 1951	USNM
NVG-18117E12	*Choranthus radians*		Cuba, 2010	USNM
NVG-14107C04	*Clito aberrans*-cf		Peru, 1982	USNM
NVG-15117B05	*Clytius clytius*		Mexico: Sinaloa, 2003, CSU_ENT1039479	CSUC
NVG-17108F02	*Clytius clytius*		USA: AZ, Santa Cruz Co., 1991	LACM
NVG-18013A06	*Cobalopsis autumna*		Costa Rica, old (around 1900)	USNM
NVG-7927	*Cobalus virbius*		Costa Rica, 2012, 12-SRNP-22162	USNM
NVG-3354	*Cogia calchas*		USA: TX, Hidalgo Co., 2015	UTSW
NVG-7963	*Conga chydaea*		Costa Rica, 2009, 09-SRNP-68418	USNM
NVG-14107B12	*Conognathus platon*		Ecuador, 1989	USNM
NVG-15104C09	*Coolus bushi*	**HT**	Dominican Republic	AMNH
NVG-8381	*Copaeodes aurantiaca*		USA: TX, Blanco Co., 2017	UTSW
NVG-18063D07	*Cornuphallus onoribo*		French Guiana, 2004, H21114	BHermier
NVG-18071C04	*Corra coryna conka*		Costa Rica, 2007, 07-SRNP-35032	USNM

DNA voucher	Taxon name	Type	Brief data	Collection
NVG-17092F04	*Corticea corticea*		Costa Rica, 2012, 12-SRNP-70085	USNM
NVG-14064H09	*Crenda crenda*		Brazil: Parana, old (around 1900)	USNM
NVG-18081D10	*Crenda crenda*	**HT**	Brazil: Parana, NHMUK_010430876, 0247278431	BMNH
NVG-17092G08	*Cumbre cumbre*		Brazil: Rio de Janeiro, 1994	USNM
NVG-7381	*Cupitha purreea*		Myanmar, 2001	USNM
NVG-15117B07	*Cycloglypha thrasibulus thrasibulus*		Mexico: Sinaloa, 2003, CSU_ENT1039523	CSUC
NVG-17105F01	*Cyclosemia herennius*		Guyana, 2000	USNM
NVG-4842	*Cymaenes tripunctus tripunctus*		USA: FL, Collier Co., 2015	UTSW
NVG-7960	*Cynea cynea*		Costa Rica, 2010, 10-SRNP-35740	USNM
NVG-18054C11	*Dalla agathocles agathocles*		Colombia, 1921	ZMHB
NVG-18017B10	*Dalla agathocles lanna*		Ecuador, 1993	USNM
NVG-18014F05	*Dalla caicus inca*		Peru, 2011	USNM
NVG-18014E11	*Dalla costala*		Peru, 2011	USNM
NVG-18014F06	*Dalla cyprius quinka*		Peru, 2013	USNM
NVG-18014E12	*Dalla dimidiatus lilla*		Peru, 2011	USNM
NVG-18017B08	*Dalla dimidiatus pucer*		Peru, 1992	USNM
NVG-18073F06	*Dalla eryonas*		Panama, old (around 1900)	ZMHB
NVG-18014F03	*Dalla frater*		Peru, 2013	USNM
NVG-18017B04	*Dalla frontinia*-cf		Ecuador, 1986	USNM
11-BOA-13383BrockB09	*Dalla nona*		Peru	JPBrock
NVG-18017B05	*Dalla pincha*		Ecuador, 1982	USNM
NVG-18017B12	*Dalla semiargentea*		Colombia, 1965	USNM
NVG-17111B10	*Damas clavus*		Brazil: Rondonia, 1993	LACM
NVG-7929	*Damas immacula*		Costa Rica, 2010, 10-SRNP-67003	USNM
NVG-7349	*Dardarina dardaris*		Costa Rica, 2004, 04-SRNP-13073	USNM
NVG-18114D07	*Daron seron sexton*		Ecuador, 2001	USNM
NVG-7330	*Darpa striata striata*		Malaysia, old (around 1900)	USNM
NVG-17095C10	*Decinea decinea decinea*		Brazil: Parana, 1995	USNM
11-BOA-13385E10	*Diaeus lacaena*		Brazil: Rio de Janeiro, 1996	USNM
NVG-7893	*Doberes anticus*		Costa Rica, 2004, 03-SRNP-23600	USNM
NVG-18054F12	*Dotta callicles*		Namibia, 1992	ZMHB
NVG-17093B03	*Dotta stellata stellata*		Kenya, 1957	USNM
NVG-8038	*Dubia dubia*		Guyana, 1999	USNM
NVG-18012D08	*Dubiella dubius*		Peru, 1989	USNM
NVG-17098F01	*Duroca duroca duroca*		Brazil: Rio de Janeiro, 1996, USNMENT 00913432	USNM
NVG-17108B11	*Eagris tigris*		Kenya, 1985	LACM
NVG-15033A04	*Eantis minna*		Brazil: Amazonas, 1886	ZMHB
NVG-18025A03	*Eantis minor*	**HT**	Dominica, 1934	AMNH

DNA voucher	Taxon name	Type	Brief data	Collection
NVG-10487	*Eantis mithridates*		Jamaica, 2017	UTSW
NVG-18025A06	*Eantis munroei*	**HT**	Cuba	AMNH
NVG-1931	*Eantis pallida*		Mexico: Tamaulipas, 1974	TAMU
NVG-3758	*Eantis tamenund*		USA: TX, Hidalgo Co., 2015	UTSW
NVG-1900	*Eantis thraso*		Brazil: Rondonia	TAMU
NVG-16108E06	*Eantis tosta*		Peru, 1999	USNM
NVG-18012A05	*Ebrietas osyris*		Mexico: Oaxaca, 1992	USNM
NVG-7977	*Eburuncus unifasciata*		Panama, 1984	USNM
NVG-7920	*Ebusus ebusus*		Costa Rica, 2013, 13-SRNP-30669	USNM
NVG-7884	*Echelatus sempiternus*		Costa Rica, 2007, 07-SRNP-12147	USNM
NVG-18013B09	*Enosis dognini*		Peru, 1998	USNM
NVG-5730	*Entheus Burns01*		Costa Rica, 2008, 08-SRNP-35619	USNM
NVG-18019B11	*Eogenes alcides*		Turkey, old (around 1900)	AMNH
NVG-17093E07	*Ephyriades arcas*		St. Croix, 1996	USNM
NVG-7897	*Eracon sarahburnsae*		Costa Rica, 2010, 10-SRNP-67957	USNM
NVG-7910	*Erionota thrax*		USA: HI, Molokai, 2005	USNM
NVG-18068D04	*Erynnis tages*		Russia: Siberia, 1999	EBrockmann
NVG-15103B05	*Euschemon rafflesia rafflesia*		Australia	USNM
NVG-17092F09	*Eutocus facilis*DHJ01		Costa Rica, 2006, 06-SRNP-47351	USNM
NVG-18082B04	*Exometoeca nycteris*		Australia, NHMUK_010430873, 0247277190	BMNH
NVG-18012E10	*Falga jeconia jeconia*		Venezuela, 1985	USNM
NVG-18031H12	*Festivia adamantinus*		Ecuador, 2002	USNM
NVG-2073	*Festivia cronion*		Brazil: Parana, 2011	MEM
NVG-18031H06	*Festivia festiva*		Ecuador, 1990	USNM
NVG-18032A03	*Festivia grippa*		Ecuador, 2002	USNM
NVG-19017F02	*Fidius fido*		Brazil: Parana, old (around 1900)	USNM
NVG-19017E10	*Flaccilla aecas*		Guyana, 2000	USNM
NVG-14101G07	*Flattoides amazonensis amazonensis*	**HT**	Colombia, 1946	AMNH
NVG-17092A07	*Fresna netopha*		Uganda, 1960	USNM
NVG-7762	*Fulda coroller*		Madagascar, 1991	USNM
NVG-7778	*Fulda rhadama*		Madagascar, 1990	USNM
NVG-7808	*Galerga hyposticta*		Madagascar, 1990	USNM
NVG-8020	*Gallio gallio*		Peru, 1986	USNM
NVG-16108E10	*Gamia shelleyi*		Uganda, 1953	USNM
NVG-16108F09	*Gangara thyrsis*		Philippines, 1987	USNM
NVG-18057H08	*Ge geta*		no data, 1894	ZSMC
NVG-7336	*Gerosis bhagava*		Myanmar, 2003	USNM
NVG-7570	*Gesta gesta*		Dominican Republic, 1981	TAMU
NVG-18011E10	*Gindanes brebisson*		Peru, 2016	USNM

DNA voucher	Taxon name	Type	Brief data	Collection
NVG-7901	*Gindanes brontinus*		Costa Rica, 2008, 08-SRNP-57426	USNM
NVG-18067H12	*Gindanes kelso*		Peru, 2000	EBrockmann
NVG-18026G08	*Ginungagapus schmithi*	**HT**	Brazil: Santa Catarina	AMNH
NVG-18087G04	*Gomalia elma*		Botswana, 1997	EBrockmann
NVG-18062A03	*Gorgopas chlorocephala chlorocephala*		Peru, 2016	USNM
NVG-18019E12	*Gorgyra aburae*		Uganda, 1954	AMNH
NVG-17067D06	*Gorgythion begga pyralina*		Mexico: Sinaloa, 2003, CSU_ENT1039357	CSUC
NVG-18091C03	*Gorgythion beggina escalophoides*		Ecuador, 2012	EBrockmann
NVG-15101B07	*Gorgythion plautia (=beggoides)*	**ST**	Trinidad, Type No. 5981 U.S.N.M.	USNM
NVG-7880	*Grais stigmaticus*		Costa Rica, 2014, 14-SRNP-30242	USNM
NVG-18019F12	*Gretna cylinda*		Uganda, 1953	AMNH
NVG-18053D11	*Gyrogra subnotata*		Gabun, 1892	ZMHB
NVG-7979	*Haemactis sanguinalis*		Ecuador, 1991	USNM
NVG-18013A12	*Halotus angellus*		Panama, 1976	USNM
NVG-17119G01	*Halpe porus*		Myanmar, 2001	USNM
NVG-18052D09	*Haza hazarma*	**LT**	no data	ZMHB
NVG-15039D09	*Helias phalaenoides phalaenoides*		Brazil: Rondonia, 1993	FMNH
NVG-7558	*Heliopetes arsalte*		Mexico: San Luis Potosi, 1980	TAMU
NVG-18064E01	*Herila herilus*		Tanzania, 1951	USNM
NVG-18068A06	*Hesperia comma*		Russia: Yakutia, 1990	EBrockmann
NVG-4767	*Hesperia meskei straton*		USA: FL, Levy Co., 2015	UTSW
NVG-18026D09	*Hesperia nabokovi*	**AT**	Haiti, 1922	AMNH
NVG-8392	*Hesperia viridis*		USA: TX, Blanco Co., 2017	UTSW
NVG-17069D12	*Hesperilla ornata*		Australia, old (around 1900)	USNM
NVG-17067A10	*Hesperopsis alpheus alpheus*		USA: CA, Kern Co., 2012, CSU_ENT1039256	CSUC
NVG-17067B02	*Hesperopsis gracielae*		USA: CA, Riverside Co., 1997, CSU_ENT1039348	CSUC
NVG-17067A09	*Hesperopsis libya libya*		USA: CA, Inyo Co., 2009, CSU_ENT1039161	CSUC
NVG-17069E08	*Heteropterus morpheus*		France, 1966, USNMENT 00894386	USNM
NVG-17108D07	*Hewitsoniella migonitis*		Papua New Guinea, 1996	LACM
NVG-7823	*Hidari irava*		Singapore, 1989	USNM
NVG-18072H08	*Hollandus xanthopeplus*		Cameroon, 1895	ZMHB
NVG-18072H07	*Hollandus xanthopeplus*		Equatorial Guinea, 1906	ZMHB
NVG-7882	*Hoodus pelopidas*		Costa Rica, 2008, 08-SRNP-55556	USNM
NVG-7816	*Hovala dispar*-cf		Madagascar, 1988	USNM
NVG-7767	*Hovala pardalina*		Madagascar, 1988	USNM
NVG-7766	*Hovala saclavus*		Madagascar, 1988	USNM
NVG-3607	*Hylephila phyleus*		USA: TX, Starr Co., 2015	UTSW
NVG-18081B02	*Hylephila venustus*		Chile, 1960, NHMUK_010430840, 0247274697	BMNH
NVG-17091H02	*Hypoleucis tripunctata draga*		Uganda, 1960	USNM

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NVG-14103B04	*Iliana romulus*		Peru	USNM
NVG-17091E06	*Ilma irvina*		Indonesia, old (around 1900)	USNM
NVG-18059B11	*Incisus incisus*		Brazil: Rio de Janeiro, 1995	USNM
NVG-18025A09	*Isoteinon abjecta (=niangarensis)*	**HT**	Niangara, 1910	AMNH
NVG-17091A07	*Isoteinon lamprospilus formosanus*		Taiwan, 1980	USNM
NVG-14107C02	*Jera tricuspidata*		Ecuador, 1984	USNM
NVG-7953	*Joanna joanna*		Costa Rica, 2004, 04-SRNP-14377	USNM
NVG-18013B06	*Justinia justinianus*		Guyana, 2000	USNM
NVG-18053B08	*Katreus johnstonii apicalis*		Sierra Leone, 1887	ZMHB
NVG-17108F10	*Kedestes lepenula*		South Africa, 1943	LACM
NVG-17069F06	*Kobelana kobela*		South Africa, 1978	USNM
NVG-18093B06	*Ladda connexa*	**LT**	Colombia	SMF
NVG-18014F02	*Ladda eburones eburones*		Peru, 2008	USNM
NVG-18014F01	*Ladda monospila*		Peru, 2010	USNM
NVG-18093B08	*Ladda ochrolimbata*	**HT**	Peru, old (around 1900)	SMF
NVG-18014F04	*Ladda plancus*		Peru, 2013	USNM
NVG-18017B09	*Ladda puracensis cotopa*		Ecuador, 1993	USNM
NVG-17111D10	*Ladda pura*-cf		Ecuador, 1992	LACM
NVG-18014E10	*Ladda quadristriga*		Peru, 2013	USNM
NVG-18017B07	*Ladda seirocastnia*		Ecuador, 1986	USNM
8041	*Lamponia lamponia*		Brazil: Parana, 1995	USNM
NVG-18012F02	*Lento lento*		Ecuador, 1998	USNM
NVG-18019G02	*Leona leonora dux*		Malawi, 1938	AMNH
NVG-17069C05	*Leptalina unicolor*		Japan, 1951	USNM
NVG-1769	*Lerema accius*		USA: TX, Dallas Co., 2013	USNM
NVG-7738	*Lerema lineosa*		Brazil: Mato Grosso, 1991	USNM
NVG-4062	*Lerodea eufala*		USA: TX, Dallas Co., 2015	UTSW
NVG-18054G05	*Leucochitonea levubu*		Namibia, 2002	ZMHB
NVG-17092D04	*Librita librita*		Mexico: Oaxaca, 1992	USNM
NVG-18067H07	*Lindra simulius*		Ecuador, 2012	EBrockmann
NVG-16108E11	*Lissia lissa lima*		Kenya, 1956	USNM
NVG-18056B11	*Livida assecla*		Brazil: Goias, 1929	ZfBS
NVG-3288	*Lobocla liliana liliana*		China: Yunnan, 2009	UTSW
NVG-18054C08	*Lon azin*		Colombia, 1920	ZMHB
NVG-6175	*Lon hobomok hobomok*		USA: VA, Augusta Co., 2016	UTSW
NVG-18115E11	*Lon inimica*		Panama, 2007	USNM
NVG-18113H06	*Lon macneilli*	**HT**	Colombia, 1975	USNM
NVG-17111H01	*Lon melane melane*		USA: CA, San Luis Obispo Co., 1994	LACM
NVG-18089H01	*Lon monticola*		Mexico: Queretaro, 2004	EBrockmann

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NVG-18115G04	*Lon niveolimbus*		Mexico: Chiapas, 1992	USNM
NVG-9774	*Lon taxiles*		USA: AZ, Cochise Co., 2017	UTSW
NVG-9209	*Lon zabulon*		USA: AR, Montgomery Co., 2017	UTSW
NVG-7373	*Lotongus calathus balta*		Myanmar, 2003	USNM
8026	*Lucida lucia*		Brazil: Minas Gerais, 1994	USNM
NVG-7940	*Ludens ludens*		Costa Rica, 2012, 11-SRNP-33493	USNM
NVG-18015A10	*Lurida lurida (=carinna)*	**T**	Brazil: Parana, old (around 1900)	USNM
NVG-7987	*Lycas argentea*		Argentina, 1998	USNM
NVG-18111A07	*Lycas godart boisduvalii*		French Guiana, 1993	USNM
NVG-8009	*Lychnuchoides ozias*		Brazil: Rio de Janeiro, 1995	USNM
NVG-2076	*Lychnuchus celsus*		Brazil: Parana, 2011	MEM
NVG-5688	*Marela tamba*		Ecuador, 1991	USNM
NVG-7787	*Matapa aria*		Philippines, 1986	USNM
NVG-18014E07	*Matapa cresta*		Myanmar, 2001	USNM
NVG-1185	*Megathymus yuccae yuccae*		USA: SC, Aiken Co., 2013	UTSW
NVG-18081D08	*Melphina melphis*		Nigeria, 1958, NHMUK_010430880, 0247278457	BMNH
NVG-18074H11	*Melphinyet tarace*	**T**	Sierra Leone, 1889	ZMHB
NVG-17108A04	*Methion melas*		Guatemala, 1963	BMUW
NVG-18064B11	*Methionopsis ina*		Costa Rica, 2010, 10-SRNP-43176	USNM
NVG-18054G04	*Metisella medea*		Malawi, 1996	ZMHB
NVG-17093A02	*Metisella metis paris*		Uganda, 1958	USNM
NVG-18054G03	*Metisella orientalis*		Malawi, 1996	ZMHB
NVG-17091H09	*Meza meza*		Cameroon, old (around 1900)	USNM
NVG-7874	*Mictris crispus*		Costa Rica, 2009, 09-SRNP-71399	USNM
NVG-18093C03	*Mielkeus diana diana (=seitzi)*	**LT**	Brazil: Rio Grande do Sul, old (around 1900)	SMF
NVG-19022G01	*Mielkeus klugi*		Guyana, 1999	USNM
NVG-19022G03	*Mielkeus lucretius*		Brazil: Rio de Janeiro, 1995	USNM
NVG-18071B01	*Mielkeus tertianus*		Costa Rica, 2010, 10-SRNP-72549	USNM
NVG-7904	*Milanion marciana*		Costa Rica, 2005, 05-SRNP-41228	USNM
NVG-8043	*Miltomiges cinnamomea*		Brazil: Rio de Janeiro, 1995	USNM
NVG-7814	*Miraja varians*		Madagascar, 1988	USNM
NVG-17069F02	*Misius misius*		Guyana, 2001	USNM
NVG-17111C02	*Mnasicles geta*		Mexico: San Luis Potosi, 1981	LACM
NVG-7968	*Mnasilus allubita*		Costa Rica, 2002, 02-SRNP-13739	USNM
NVG-8030	*Mnasinous patage*		Panama, 1996	USNM
NVG-8027	*Mnestheus ittona*		Peru, 2012	USNM
NVG-8029	*Moeris anna*		Brazil: Rio de Janeiro, 1994	USNM
NVG-18012H11	*Moeris striga*		French Guiana, 1993	USNM
NVG-7941	*Moeris stroma*		Costa Rica, 2013, 13-SRNP-56538	USNM

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NVG-15036C07	*Moeros moeros*	**T**	Suriname, 1874	ZMHB
NVG-18039F01	*Molo mango*		Guyana, 2003	FMNH
NVG-18012D03	*Molo pelta*		Peru, 2012	USNM
NVG-18019F10	*Moltena fiara*		Natal, 1924	AMNH
NVG-17092G12	*Monca crispinus*		Costa Rica, 2006, 06-SRNP-55847	USNM
NVG-17069H12	*Monza cretacea*		Nigeria, 1951	USNM
NVG-17069H09	*Mopala orma*		Cameroon, old (around 1900)	USNM
NVG-18019H04	*Morvina morvus morvus*		Colombia, 1945	AMNH
NVG-18013A08	*Morys valerius*		French Guiana, 1993	USNM
NVG-8048	*Mucia zygia*		Colombia, 1992	USNM
NVG-18041E02	*Muschampia proto*		France, 2012	EBrockmann
NVG-18015C07	*Mylon ander ander*		Guyana, 2000	USNM
NVG-18015D02	*Mylon cajus cajus*		Peru, 2016	USNM
NVG-18015C03	*Mylon illineatus illineatus*		Peru, 2016	USNM
NVG-7881	*Mylon lassia*		Costa Rica, 2009, 09-SRNP-36601	USNM
NVG-18013F07	*Mylon maimon*		Costa Rica, 2015, 15-SRNP-21203	USNM
NVG-18015C05	*Mylon mestor*		Colombia, 1992	USNM
NVG-18015C04	*Mylon orsa*		Panama, 1975	USNM
NVG-18013F09	*Mylon salvia*		Costa Rica, 2006, 06-SRNP-1769	USNM
NVG-18015C01	*Mylon zephus albodiscus*		Peru, 2008	USNM
11-BOA-13385F09	*Myrinia myris*		Brazil: Rondonia, 1989	USNM
NVG-7950	*Naevolus orius*		Costa Rica, 2010, 10-SRNP-72281	USNM
NVG-8137	*Nastra lherminier*		USA: FL, Liberty Co., 2017	UTSW
NVG-18053B01	*Neohesperilla croceus*		Australia, 1892	ZMHB
NVG-17095F04	*Neoxeniades ethoda*		Brazil: Santa Catarina, 1991	USNM
NVG-18069F03	*Neoxeniades luda*		Costa Rica, 2012, 12-SRNP-1402	USNM
NVG-18082E06	*Neoxeniades musarion*		Brazil: RJ, NHMUK_012824133, 0247279800	BMNH
NVG-7936	*Neoxeniades pluviasilva*		Costa Rica, 2012, 12-SRNP-30105	USNM
NVG-17112B12	*Neoxeniades turmada*		Peru, 1986	LACM
NVG-18113B11	*Neposa heras*		Mexico, old (around 1900)	BMNH
NVG-14063B05	*Nerula fibrena*		Venezuela, 1985	USNM
NVG-17091B06	*Nervia nancy*		Kenya, 1960	USNM
NVG-16106A03	*Netrocoryne repanda*		Australia, 1963	LACM
NVG-18053D01	*Netrocoryne thaddeus*		Indonesia, 1894	ZMHB
NVG-18013B02	*Niconiades xanthaphes*		Guyana, 2000	USNM
NVG-18011G09	*Nisoniades mimas*		Peru, 1982	USNM
NVG-18015E03	*Noctuana lactifera lactifera*		Costa Rica, 2003, 03-SRNP-22972	USNM
NVG-18086D12	*Noctulana noctula*		Ivory Coast, EL63203	MNHP
NVG-3845	*Nyctelius nyctelius*		USA: TX, Cameron Co., 2015	UTSW

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NVG-15036C01	*Nyctus crinitus*	**ST**	Peru, old (around 1900)	ZMHB
NVG-17068C03	*Oarisma poweshiek*		USA: MN, Pipestone Co., 1986, CSU_ENT1025108	CSUC
NVG-14112G12	*Ocella albata*		Peru, no date	TLS
PAO-23	*Ochlodes agricola*		USA: CA, Sierra Co., 2016	UTSW
NVG-18039E08	*Ochlodes subhyalina*		Korea, 1956	FMNH
PAO-263	*Ochlodes sylvanoides*		USA: CO, Larimer Co., 2016	UTSW
NVG-7746	*Ochlodes venata venata*		Japan, 1933	USNM
NVG-17114B06	*Ochlodes yuma*		USA: CO, Mesa Co., 2001, LepNet 1024498	CSUC
NVG-5686	*Oechydrus chersis chersis*		Brazil: Rio de Janeiro, 1996, 14063A12	USNM
NVG-18014F09	*Oenides vulpina*		Peru, 2016	USNM
NVG-18021D06	*Oeonus pyste*		Mexico: San Luis Potosi, 1967	AMNH
NVG-14063C11	*Oileides fenestratus*		French Guiana, 1993, Hermier No 4771	USNM
NVG-18067C02	*Oileides fenestratus*		French Guiana, 2009	EBrockmann
NVG-18098F04	*Oileides guyanensis*		French Guiana, 2002, H19994	BHermier
NVG-18057C09	*Oileides vulpinus*		Brazil: Espirito Santo, old (around 1900)	ZSMC
NVG-5727	*Oileides vulpinus*		Brazil: Espirito Santo, 1969	USNM
NVG-15117B01	*Onenses hyalophora*		Mexico: Tamaulipas, 2003, CSU_ENT1039476	CSUC
NVG-17092D06	*Onespa nubis*		Mexico: Oaxaca, 1990	USNM
NVG-8040	*Onophas columbaria*		Ecuador, 2002	USNM
NVG-17109G08	*Orphe gerasa*		Venezuela, 1993	LACM
NVG-2761	*Orphe vatinius*		Colombia, 1976	JAScott
NVG-7956	*Orses cynisca*		Costa Rica, 2008, 08-SRNP-40358	USNM
NVG-18111A01	*Orses itea*		Brazil: Rio de Janeiro, 1995	USNM
NVG-8061	*Orthos orthos*		Brazil: Parana, 1991	USNM
NVG-18026A06	*Orthos orthos hyalinus*	**HT**	Brazil: Santa Catarina, old (around 1900)	AMNH
NVG-17119C02	*Osmodes laronia*		Uganda, 1961	USNM
NVG-18073E04	*Osphantes ogowena*	**ST**	Gabon, 1888	ZMHB
NVG-18011G05	*Ouleus fridericus*		Guyana, 2000	USNM
NVG-7894	*Ouleus salvina*DHJ01		Costa Rica, 2011, 11-SRNP-57460	USNM
NVG-14113A02	*Oxynetra aureopecta*	**HT**	Mexico: Hidalgo, 1987	LACM
7962	*Oxynthes corusca*DHJ02		Costa Rica, 2011, 11-SRNP-23410	USNM
NVG-7899	*Paches loxus*		Costa Rica, 2003, 03-SRNP-30995	USNM
NVG-18025B01	*Pachyneuria lineatopunctata (=phintias)*	**HT**	Peru, 1931	AMNH
NVG-15033D07	*Pachyneuria obscura*	**T**	Peru, old (prior to 1888)	ZMHB
NVG-4155	*Panoquina panoquin*		USA: TX, Jefferson Co., 2015	UTSW
NVG-17111G07	*Papias subcostulata*		Mexico: Hidalgo, 1981	LACM
NVG-8037	*Paracarystus hypargyra*		Peru, 2013	USNM
NVG-18063A09	*Parachoranthus magdalia*		Cuba, 2009	EBrockmann
NVG-17092H10	*Paracleros biguttulus*		Uganda, 1956	USNM

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NVG-18027E08	*Paramimus scurra scurra*		Guyana, 2001	USNM
NVG-18015E01	*Paratrytone rhexenor*		Mexico: Veracruz, old (around 1900)	USNM
NVG-17108G05	*Pardaleodes edipus*		Zaire, 1981	LACM
NVG-18026E08	*Pares pares*	**HT**	Paraguay	AMNH
NVG-7290	*Parnara guttatus*		Myanmar, 2002	USNM
NVG-17108G12	*Paronymus ligora*		Sierra Lione, 1974	LACM
NVG-18013A05	*Parphorus storax*		Guyana, 2000	USNM
NVG-17094H03	*Passova gellias*		Costa Rica, 2013, 13-SRNP-6248	USNM
NVG-18082E01	*Pastria pastria*		Papua NG, 1982, NHMUK_010430882, 0247277187	BMNH
NVG-17116A09	*Pellicia dimidiata dimidiata*		Mexico: Tamaulipas, 1974	TAMU
NVG-18013C07	*Penicula bryanti*		Ecuador, 2001	USNM
NVG-18011F04	*Penicula subviridis*		Brazil: Santa Catarina, 1990	USNM
NVG-7955	*Perichares adela*		Costa Rica, 2013, 13-SRNP-65013	USNM
NVG-18065F12	*Perichares butus*		Peru, 2015	EBrockmann
NVG-18105G06	*Perichares deceptus fulvimargo*		Peru, 2013	USNM
NVG-18014F08	*Perichares furcata*		Ecuador, 1976	USNM
NVG-7986	*Perichares haworthiana*		Brazil: Rondonia, 1992	USNM
NVG-18105F10	*Perichares lotus*		Trinidad, 2000	USNM
NVG-18027A09	*Perichares metallica (=zikani)*	**HT**	Brazil: Rio de Janeiro	AMNH
NVG-10247	*Perichares philetes*		Jamaica, 2017	UTSW
NVG-18058H07	*Perus coecatus (=tadus)*	**ST**	Brazil: Rio de Janeiro	USNM
NVG-7826	*Perus cordillerae*		Peru, 1999	USNM
NVG-19055F06	*Perus menuda*	**ST**	Bolivia, 1899	MCZ
NVG-18059C09	*Perus minor*		Ecuador, 1988	USNM
NVG-17092F05	*Phanes aletes*DHJ02		Costa Rica, 2015, 15-SRNP-71060	USNM
NVG-18012F07	*Pheraeus odilia epidius*		Panama, 1982	USNM
NVG-18013C03	*Phlebodes pertinax*		Brazil: Amazonas, 1993	USNM
NVG-5316	*Phocides pigmalion okeechobee*		USA: FL, Monroe Co., 2015	UTSW
NVG-3990	*Pholisora catullus*		USA: TX, Starr Co., 2015	UTSW
NVG-7976	*Pholisora mejicanus*		USA: NM, Colfax Co., 1989	USNM
NVG-17068A11	*Piruna aea mexicana*		USA: AZ, Santa Cruz Co., 2016, CSU_ENT1033276	CSUC
NVG-6454	*Piruna pirus*		USA: CO, Grand Co., 2016	UTSW
NVG-17108G10	*Platylesches picanini*		South Africa, 1944	LACM
NVG-7982	*Plumbago plumbago*		Brazil: Rondonia, 1989	USNM
NVG-939	*Poanes aaroni bordeloni*		USA: LA, 2011	UTSW
NVG-4704	*Poanes aaroni howardi*		USA: FL, Levy Co., 2015	UTSW
NVG-17114B07	*Poanes massasoit*		USA: MD, Dorchester Co., 1976, LepNet 1031028	CSUC
NVG-6711	*Poanes viator zizaniae*		USA: TX, Dallas Co., 2016	UTSW
NVG-7046	*Poanes yehl*		USA: TX, Hopkins Co., 2016	UTSW

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NVG-8170	*Polites baracoa baracoa*		USA: FL, Miami-Dade Co., 2017	UTSW
NVG-5968	*Polites carus*		USA: AZ, Santa Cruz Co., 2016	UTSW
NVG-4276	*Polites peckius peckius*		USA: IN, Montgomery Co., 2015	UTSW
NVG-4255	*Polites themistocles themistocles*		USA: IN, Montgomery Co., 2015	UTSW
NVG-7875	*Polyctor polyctor*		Costa Rica, 2012, 12-SRNP-4870	USNM
NVG-18115C01	*Pompeius amblyspila*		Brazil: Amazonas, 1993	USNM
NVG-17106B02	*Pompeius pompeius*		Costa Rica, 2010, 10-SRNP-103576	USNM
NVG-18038D12	*Potamanaxas flavofasciata flavofasciata*		Ecuador, 2008	EBrockmann
NVG-18082C08	*Prada rothschildi*	**PT**	Papua NG, 1899, NHMUK_012824115, 0247281590	BMNH
NVG-18082C09	*Prada rothschildi*	**PT**	Papua NG, 1899, NHMUK_010430826, 0247278442	BMNH
NVG-18114H04	*Propapias sipariana*		French Guiana, 1993	USNM
NVG-7331	*Pseudocoladenia dan fabia*		Myanmar, 2001	USNM
NVG-8050	*Pseudocopaeodes eunus*		USA: CA, Inyo Co., 1950	USNM
11-BOA-13382A03	*Pseudodrephalys hypargus*		Ecuador	USNM
NVG-18113B05	*Pseudorphe pyrex*		Peru, 1992	USNM
NVG-17112C01	*Pseudosarbia phoenicicola*		Uruguay, 1967	LACM
NVG-18021B02	*Psoralis idee*		Bolivia, old (around 1900)	AMNH
NVG-7757	*Pteroteinon laufella*		Liberia, 1988	USNM
NVG-7771	*Pyrgus malvae*		Greece, 1992	USNM
NVG-8060	*Pyrrhocalles antiqua*		Dominican Republic, 1994	USNM
NVG-17094C09	*Pyrrhopyge hadassa pseudohadassa*		Peru, 2013, USNMENT 00894886	USNM
NVG-7984	*Pyrrhopygopsis socrates*		Brazil: Mato Grosso, 1991	USNM
NVG-7896	*Pythonides amaryllis*		Costa Rica, 2006, 06-SRNP-7674	USNM
11-BOA-13382B01	*Pythonides jovianus jovianus*		Guyana, 2000	USNM
NVG-14102D02	*Pythonides lerina*		Guyana, 2003	FMNH
NVG-7902	*Quadrus cerialis*		Costa Rica, 2008, 08-SRNP-1186	USNM
NVG-18013H08	*Quadrus lugubris*		Costa Rica, 2008, 08-SRNP-57856	USNM
NVG-18018A03	*Quadrus truncata*		Ecuador, 1988	USNM
NVG-18015B10	*Quasimellana mexicana*		Mexico: Oaxaca, 1989	USNM
NVG-7959	*Quinta cannae*		Costa Rica, 2012, 12-SRNP-75508	USNM
NVG-18057H02	*Rachelia extrusus*		Papua New Guinea, old (around 1900)	ZSMC
NVG-18012A12	*Racta plasma*		Peru, 2011	USNM
NVG-17092G01	*Radiatus bradus*		Guyana, 1999	USNM
NVG-18091D12	*Ralis concolor*		Ecuador, 2012	EBrockmann
NVG-19021E08	*Ralis coyana*		Brazil: Rio de Janeiro, 1996	USNM
NVG-17092C08	*Remella remus*		Costa Rica, 2006, 06-SRNP-6640	USNM
NVG-18081A02	*Repens repens*	**PT**	Paraguay, 1904, NHMUK_010430831, 0247279233	BMNH
NVG-17069G04	*Rhabdomantis galatia*		Uganda, 1958	USNM

DNA voucher	Taxon name	Type	Brief data	Collection
NVG-17116C08	*Rhinthon osca*		USA: TX, Hidalgo Co., 1974	TAMU
NVG-18093C02	*Rigga auristriga*	**HT**	Bolivia, old (around 1900)	SMF
NVG-19019G04	*Rigga hesia*		Ecuador, 2002	USNM
NVG-18093C05	*Sacrator sacrator (=stupenda)*	**HT**	Colombia, old (around 1900)	SMF
NVG-18012E03	*Saliana salius*		Guyana, 2000	USNM
NVG-8024	*Saniba sabina*		Brazil: Rio de Janeiro, 1996	USNM
NVG-18025B08	*Santa santes*	**HT**	Peru, 1924	AMNH
11-BOA-13382F10	*Santa trifasciatus*		Guyana	USNM
NVG-7345	*Sarangesa dasahara*		Myanmar, 2001	USNM
NVG-18037G08	*Satarupa nymphalis*		China: Sichuan, 2010	UTSW
NVG-18013C01	*Saturnus saturnus*		Guyana, 2000	USNM
NVG-7803	*Semalea pulvina*		Cameroon, 1989	USNM
NVG-7760	*Signeta flammeata*		Australia, 1985	USNM
NVG-7970	*Sodalia sodalis*		Costa Rica, 2011, 11-SRNP-75366	USNM
NVG-14107C10	*Sophista aristoteles aristoteles*		Peru, 2013	USNM
NVG-18011H10	*Sostrata bifasciata*		Brazil: Rio de Janeiro, 1995	USNM
NVG-7247	*Sostrata nordica*		Mexico: Veracruz, 1906	USNM
NVG-18032A04	*Sostrata pusilla pulsa*		Ecuador, 1976	USNM
NVG-18032A10	*Sostrata pusilla pusilla*		Peru, 1989	USNM
NVG-17108E02	*Spialia galba galba*		India, 1961	LACM
NVG-18013H11	*Spioniades artemides*		Costa Rica, 2010, 10-SRNP-67995	USNM
NVG-18071A04	*Staphylus ascalaphus*		Costa Rica, 2016, 16-SRNP-56091	USNM
NVG-18071A05	*Staphylus caribbea*		Costa Rica, 2009, 09-SRNP-42728	USNM
NVG-9694	*Staphylus ceos*		USA: AZ, Santa Cruz Co., 2017	UTSW
NVG-18025B10	*Staphylus musculus (=similis)*	**HT**	Brazil: Sta Catarina, old (around 1900)	AMNH
NVG-18025B03	*Staphylus putumayo*	**HT**	Peru, 1931	AMNH
NVG-18011H08	*Staphylus vincula*		Mexico: Oaxaca, 1988	USNM
NVG-18071A12	*Staphylus vulgata*		Costa Rica, 2010, 10-SRNP-55088	USNM
NVG-6016	*Stinga morrisoni*		USA: TX, Jeff Davis Co., 2016	UTSW
NVG-8044	*Styriodes lyco*		Guyana, 2000	USNM
NVG-18012D04	*Synale hylaspes*		Argentina, 1998	USNM
NVG-7937	*Synapte salenus salenus*		Costa Rica, 2007, 07-SRNP-21744	USNM
NVG-3621	*Systasea pulverulenta*		USA: TX, Duval Co., 2015	UTSW
NVG-6008	*Systasea zampa*		USA: TX, El Paso Co., 2016	UTSW
NVG-18011E02	*Systaspes corrosus*		Mexico: Oaxaca, 1992	USNM
NVG-7333	*Tagiades litigiosus litigiosus*		Myanmar, 2001	USNM
NVG-18012D01	*Talides sinois*		Peru, 2015	USNM
NVG-7375	*Taractrocera maevius sagara*		Myanmar, 2003	USNM
NVG-18116E01	*Tava tavola*	**ST**	Trinidad, old (around 1900)	USNM

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NVG-18026A03	*Tava tavola (=hoffmanni)*	**HT**	Brazil: Santa Catarina, 1913	AMNH
NVG-5726	*Telemiades fides*		Costa Rica, 2011, 11-SRNP-20768	USNM
NVG-8008	*Tellona variegata*		Brazil: Rondonia, 1993	USNM
NVG-17119H08	*Teniorhinus watsoni watsoni*		Uganda, 1961	USNM
NVG-18026F01	*Testia potesta*	**HT**	Peru, 1931	AMNH
NVG-18098F08	*Thargella caura*		French Guiana, 2005, H22106	BHermier
11-BOA-13386C12	*Theagenes aegides*		Costa Rica, 1980	USNM
11-BOA-13386C11	*Theagenes albiplaga*		Peru, 2008	USNM
NVG-18013B04	*Thoon modius*		Ecuador, 1992	USNM
NVG-7383	*Thoressa masoni*		Myanmar, 2001	USNM
NVG-17112B06	*Thracides phidon*		Venezuela, 1993	LACM
NVG-18022H12	*Thymelicus acteon acteon*		Spain, 1953	AMNH
NVG-7888	*Tiana niger*		Costa Rica, 2011, 11-SRNP-35371	USNM
NVG-7944	*Tigasis arita*		Costa Rica, 2011, 11-SRNP-32281	USNM
NVG-18013A11	*Tigasis zalates*		Ecuador, 1977	USNM
NVG-7883	*Timochares trifasciata*		Costa Rica, 2005, 05-SRNP-12097	USNM
NVG-7908	*Timochreon satyrus*		Costa Rica, 2007, 07-SRNP-58884	USNM
NVG-18118A08	*Tirynthia conflua*		Brazil: Rio de Janeiro, 1995	USNM
NVG-18081D03	*Toxidia thyrrhus*		Australia, 1911, NHMUK_010430805, 0247281664	BMNH
NVG-16106A10	*Trapezites symmomus*		Australia, 1963	LACM
NVG-19023C11	*Tricrista advena*		Guyana, 2000	USNM
8049	*Tricrista crista*		Guyana, 2000	USNM
NVG-18025G05	*Tricrista cristatus*	**HT**	Brazil: Santa Catarina, old (around 1900)	AMNH
NVG-7983	*Trina geometrina*		French Guiana, 1993	USNM
NVG-18012D02	*Tromba tromba*		Peru, 2014	USNM
NVG-18019E10	*Tsitana tsita*		South Africa, 1924	AMNH
NVG-18111G06	*Turesis complanula*		Guyana, 2000	USNM
NVG-18082D06	*Turmosa camposa*		Brazil: RJ, 1883, NHMUK_012824124, 0247279797	BMNH
NVG-18056F01	*Turmosa camposa*	**LT**	no data	ZSMC
NVG-5699	*Typhedanus ampyx*		Mexico: Oaxaca, 1992, 14104H07	USNM
NVG-17108H12	*Unkana ambasa*		no data, no date	LACM
NVG-18081C02	*Unkana mytheca*		Indonesia, 1914, NHMUK_010430823, 0247278996	BMNH
NVG-4894	*Urbanus proteus proteus*		USA: FL, Miami-Dade Co., 2015	UTSW
NVG-17095C06	*Vacerra litana*		Venezuela, 1975	USNM
NVG-17098F07	*Veadda veadeira*		Brazil: Mato Grosso, 1991	USNM
NVG-17111G04	*Vehilius stictomenes illudens*		Mexico: San Luis Potosi, 1980	LACM
NVG-8022	*Venas evans*		Guyana, 2000	USNM
NVG-18021D01	*Vernia dares*		Mexico: San Luis Potosi, 1966	AMNH

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NVG-18014H01	*Vernia verna*		USA: OH, Summit Co., 2012	USNM
NVG-18013B11	*Vertica verticalis*		Peru, 1983	USNM
NVG-18014G01	*Vettius phyllus phyllus*		Guyana, 2001	USNM
NVG-18071C05	*Vettius pica*DHJ01		Costa Rica, 2015, 15-SRNP-71571	USNM
NVG-18012H07	*Vidius vidius*		Paraguay, old (around 1900)	USNM
NVG-15097D10	*Vinpeius tinga (=freemani)*	**HT**	Mexico: Veracruz	CMNH
NVG-18011G11	*Viola alicus*	**ST**	Brazil: Rio de Janeiro, old (around 1900)	USNM
NVG-18061D04	*Viola minor*		Brazil: Rio de Janeiro, 1995	USNM
NVG-7973	*Viola violella*		Brazil: Mato Grosso, 1991	USNM
NVG-18012F11	*Virga virginius*		Paraguay, 1986	USNM
NVG-18026H05	*Viridina subviridis*	**HT**	Ecuador, 1938	AMNH
NVG-19055F04	*Viridina viridenex*	**HT**	Bolivia, 1899	MCZ
NVG-15104C11	*Viridina viridis*	**HT**	Ecuador, 1938	AMNH
NVG-18028C11	*Viuria licisca*		Costa Rica, 2003, 03-SRNP-27671	USNM
NVG-7972	*Viuria lista*		French Guiana, 1988	USNM
NVG-17107B06	*Wahydra kenava*		Venezuela, 1978	USNM
NVG-7421	*Wallengrenia drury*		Dominican Republic, 1981	USNM
NVG-17098E07	*Wallengrenia ophites*		French Antilles, 1989	USNM
NVG-17098E12	*Wallengrenia premnas*		Brazil: Mato Grosso, 1990	USNM
NVG-10332	*Wallengrenia vesuria*		Jamaica, 2017	UTSW
NVG-18079C02	*Willema tsadicus (=birbiranus)*	**T**	Ethiopia, 1925, EL63085	MNHP
NVG-18063B11	*Willema willemi*		Tanzania, old (around 1900)	ZSMC
NVG-17069E09	*Willema willemi*		Zimbabwe, 1961	USNM
NVG-15102D03	*Windia windi*		Mexico: Sonora, 1984	USNM
NVG-7765	*Xanthodisca vibius*		Cameroon, 1987	USNM
NVG-17091D05	*Xanthoneura corissa corissa*		Malaysia, old (around 1900)	USNM
NVG-18064D07	*Xanthonymus xanthioides*		Cameroon, old (around 1900)	USNM
NVG-17112A11	*Xeniades orchamus*		Brazil: Santa Catarina, 1999	LACM
NVG-7906	*Xenophanes tryxus*		Costa Rica, 2010, 10-SRNP-103428	USNM
NVG-15033D08	*Xispia quadrata*	**T**	Brazil: Amazonas, prior to 1889	ZMHB
NVG-17105B08	*Zalomes biforis*		Colombia, 1965	USNM
NVG-18074B01	*Zela excellens*	**T**	Palawan, 1888	ZMHB
NVG-18098G05	*Zela smaragdinus*		Malaysia, 2016	UTSW
NVG-18126A12	*Zela zenon*		Sabah, 1984	KMaruyama
NVG-18126A05	*Zela zeus optima*		Langkawi, 2018	UTSW
NVG-17112A04	*Zenis jebus hemizona*		Venezuela, 1993	LACM
NVG-18038B10	*Zera hosta*		Honduras	RGallardo
NVG-18091C05	*Zera phila*		Ecuador, 2012	EBrockmann
NVG-18011E12	*Zera zera*		Peru, 2014	USNM

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NVG-18027A07	*Zetka zeteki*	**HT**	Panama, 1928	AMNH
NVG-15104C01	*Zobera albopunctata*	**HT**	Mexico: Colima	AMNH
NVG-17091C04	*Zographetus satwa*		no data	USNM
NVG-17069H08	*Zophopetes dysmephila*		South Africa, 1953	USNM
NVG-6998	*Zopyrion sandace*		Mexico: Oaxaca, 1981	TAMU
NVG-1670	*Pterourus glaucus glaucus*		USA: TX, Denton Co., 2013	USNM