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Changes to North American butterfly names

Jing Zhang[2], **Qian Cong**[3], **Jinhui Shen**[2], **Paul A. Opler**[4], **Nick V. Grishin**[1,2,*]

[1]Howard Hughes Medical Institute, University of Texas Southwestern Medical Center, 5323 Harry Hines Blvd., Dallas, TX 75390-9050, USA

[2]Departments of Biophysics and Biochemistry, University of Texas Southwestern Medical Center, 5323 Harry Hines Blvd., Dallas, TX 75390-9050, USA

[3]Institute for Protein Design and Department of Biochemistry, University of Washington, 1959 NE Pacific Street, HSB J-405, Seattle, WA, 98195, USA

[4]Department of Bioagricultural Sciences and Pest Management, Colorado State University, Fort Collins, CO 80523-1177, USA.

Abstract

We obtained and analyzed whole genome shotgun sequences of all 845 species of butterflies recorded from Canada and the United States. Genome-scale phylogenetic trees constructed from the data reveal several non-monophyletic genera and suggest improved classification of species included in these genera. Here, these changes are formalized and 2 subgenera are described: *Amblyteria* Grishin, subgen. n. (type species *Goniloba exoteria* Herrich-Schäffer, 1869, parent genus *Amblyscirtes* Scudder, 1872), and *Coa* Grishin, subgen. n. (type species *Hesperia baracoa* Lucas, 1857, parent genus *Polites* Scudder, 1872). Furthermore, we resurrect 3 genera and 2 subgenera from synonymy, change the rank of 6 currently used genera to subgenus, synonymize 2 genera, transfer 3 (2 resurrected) subgenera and 11 additional species to different genera than those these taxa were assigned to, and raise one name from synonym to species rank. Namely, *Hedone* Scudder, 1872 and *Limochores* Scudder, 1872 are valid genera and not synonyms of *Polites* Scudder, 1872; *Pendantus* K. Johnson & Kroenlein, 1993 is a valid genus and not a synonym of *Electrostrymon* Clench, 1961; and *Sphaenogona* Butler, 1870 and *Lucidia* Lacordaire, 1833 are valid subgenera of *Abaeis* Hübner, [1819] (new placement) and not synonyms of *Eurema* Hübner, [1819]. The following taxa are best treated as subgenera: *Mimoides* Brown, 1991 of *Eurytides* Hübner, [1821] (sensu lato); *Philotiella* Mattoni, [1978] of *Euphilotes* Mattoni, [1978]; *Neominois* Scudder, 1875 of *Oeneis* Hübner, [1819]; *Agraulis* Boisduval & Le Conte, [1835] of *Dione* Hübner, [1819]; *Copaeodes* Speyer, 1877 of *Oarisma* Scudder, 1872; and *Problema* Skinner & R. Williams, 1924 of *Atrytone* Scudder, 1872. *Phaeostrymon* Clench, 1961 and *Saliana* Evans, 1955 are junior subjective synonyms of *Satyrium* Scudder, 1876 and *Calpodes* Hübner, [1819], respectively. The entire subgenus *Erynnides* Burns, 1964 is transferred from *Erynnis* Schrank, 1801 to *Gesta* Evans, 1953. New genus-species combinations resulting from transfer of species between genera are: *Nastra perigenes* (Godman, 1900) (not *Vidius* Evans, 1955); *Troyus fantasos* (Cramer, 1780), *Troyus onaca* (Evans, 1955), *Troyus aurelius* (Plötz, 1882), *Troyus marcus*

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[*]Corresponding author: grishin@chop.swmed.edu.

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(Fabricius, 1787), *Troyus diversa* (Herrich-Schäffer, 1869), and *Troyus drova* (Evans, 1955) (not *Vettius* Godman, 1901); *Oligoria percosius* (Godman, 1900), *Oligoria rindgei* (H. Freeman, 1969), *Oligoria lucifer* (Hübner, [1831]), and *Oligoria mustea* (H. Freeman, 1979) (not *Decinea* Evans, 1955). *Urbanus alva* Evans, 1952 is a valid species and not a synonym of *Urbanus belli* (Hayward, 1935), new status.

Keywords

taxonomy; classification; genomics; phylogeny; biodiversity

INTRODUCTION

Genome-scale phylogenetic approaches show promise to revolutionize our understanding of butterfly evolution and refine their taxonomy (Allio et al. 2019; Li et al. 2019; Zhang et al. 2019a; Zhang et al. 2019b). Accurate phylogenetic trees constructed from millions of base pairs give better confidence in the results and frequently reveal inconsistencies with the current classification. Most taxonomists agree that a genus-group taxon should be monophyletic, i.e., a group of species that consists of all descendants of their common ancestor. Thus, if a strongly supported by statistics phylogenetic tree reveals that a genus is not monophyletic (i.e., its member species are distributed across several clades in the tree intermixed with species from other genera, or the clade with this genus includes some species that are not currently placed in this genus), some action needs to be taken to restore monophyly of the genus. The genus could either be split into several genera, or species that are currently not included into it, but are in the same clade with it, could be transferred into this genus. An important consideration is to follow the type species of the genus, because it defines the genus. Only the clade with the type species could carry this genus name. In addition to monophyly, attention should be paid to the prominence of the genus and consistency with how other genera in this group of organisms are defined, see Taxonomic Appendix to Li et al. (2019) for discussion. In brief, the genus should be a major phylogenetic group, i.e., it is best if the phylogenetic tree branch leading to the last common ancestor of the genus is longer compared to other nearby branches, and the genetic diversity within different genera should be comparable, so that genera define more or less equivalent groups.

We obtained and analyzed whole genome shotgun sequences of all butterfly species recorded from Canada and the United States (Pelham 2008; Pelham 2019). The manuscript describing this work is available from bioRxiv (Zhang et al. 2019c). Focusing on general evolutionary principles we can learn from butterflies, the manuscript does not go into taxonomic details. However, accurate phylogenetic trees we obtained from the genomic data reveal that some genera are not monophyletic, and some are either too broad or too narrow in terms of genetic divergence. Here, we propose taxonomic rearrangements that are supported by these phylogenetic trees. The following sections are in the standardized format. Taxonomic act is the title of each section. Relevant genera, subgenera and their type species, are listed giving valid names if the type species are synonyms. When the species are listed with their original genus name, author names are given without parenthesis. Currently used genus name for these species is clear from the context. Each section is illustrated by a small segment of a nuclear genomic tree with species that are needed to support the conclusion. The trees showing all US and Canada species are available from the bioRxiv preprint (Zhang et al. 2019c). Previous genus-species combinations (per Pelham 2019, version revised 7 October 2019) are used in the figures. New combinations are given in the text. Species of major focus are shown in red, other species in the genus of interest are shown in blue. Trees on gray background include species not recorded from the US. The section ends with a conclusion and in many cases with a list of species with revised genus-species names combinations. The sections are ordered by family and in their taxonomic order.

Family Papilionidae Latreille, [1802]

Mimoides Brown, 1991 is a subgenus of *Eurytides* Hübner, [1821]

Previously placed in the genus *Mimoides* Brown, 1991 (type species *Papilio ariarathes*, Esper, 1788), *Papilio phaon* Boisduval, 1836 is sister to *Eurytides marcellus* (Cramer, 1777) among butterflies of Canada and the US, and is phylogenetically close to *Eurytides philolaus* (Boisduval, 1836), suggesting that it should be placed in the genus *Eurytides* Hübner, [1821] (type species *Eurytides iphitas* Hübner, [1821]) (Fig. 1). Additionally taking into account that *Mimoides* species are close to each other as evidenced by their morphology (Tyler et al. 1994) and COI barcodes (Ratnasingham & Hebert 2007), we propose to treat *Mimoides* as a subgenus of *Eurytides* among its other subgenera: *Protesilaus* Swainson, [1832] (type species *Papilio protesilaus* Linnaeus, 1758) and *Neographium* Möhn, 2002 (type species *Papilio philolaus* Boisduval, 1836). Curiously, *Papilio marcellus* Cramer, 1777 is in the same clade with *Mimoides*, but is in a different clade from *Neographium*, and therefore should be included in the subgenus *Mimoides* despite the similarity in wing patterns to *Eurytides* (*Neographium*) *philolaus*. Finally, application of the genus *Protographium* Munroe (1961) (type species *Papilio leosthenes* E. Doubleday, 1846) to the New World is unwarranted, because genomic data show that the Australian endemic *P. leosthenes* is sister to another Old World genus *Graphium* Scopoli, 1777 (type species *Papilio sarpedon* Linnaeus, 1758) and is in a different clade from *Eurytides* (including *Mimoides* and *Neographium*) (Fig. 1). *Eurytides* versus *Protographium* is yet another case of striking wing pattern convergence in butterflies.

Family Pieridae Swainson, 1820

Sphaenogona Butler, 1870 and *Lucidia* Lacordaire, 1833 are subgenera of *Abaeis* Hübner, [1819] and not of *Eurema* Hübner, [1819], new placement

Previously junior subjective synonyms of *Eurema* Hübner, [1819] (type species *Papilio delia* Cramer, [1780], a junior subjective synonym of *Pieris daira* Godart, 1819), *Sphaenogona* Butler, 1870 (type species *Terias bogotana* C. & R. Felder, 1861, which is treated as a subspecies of *Terias mexicana* Boisduval, 1836) and *Lucidia* Lacordaire, 1833 (type species *Papilio albula* Cramer, 1775) are not monophyletic with *Eurema*, but are instead in the same clade with *Abaeis* Hübner, [1819] (type species *Papilio nicippe* Cramer, 1779) (Fig. 2). This genomic tree shows notable genetic divergence among *Abaeis*, *Sphaenogona* and *Lucidia* that is only slightly less than the divergence between *Eurema* and *Pyrisitia* Butler, 1870 (type species *Papilio proterpia* Fabricius, 1775) suggesting that *Sphaenogona* and *Lucidia* are not synonyms, but can be treated as subgenera of *Abaeis*. As a result, we use the following new or revised combination for the US species: *Abaeis (Sphaenogona) boisduvaliana* (C. Felder & R. Felder, 1865), *Abaeis (Sphaenogona) mexicana* (Boisduval, 1836), *Abaeis (Sphaenogona) salome* (C. Felder & R. Felder, 1861), and *Abaeis (Lucidia) albula* (Cramer, 1775). Consequently, only a single US species remains in *Eurema*, the type species of the genus: *Eurema daira*. Our proposed changes keep the number of genera in this group at 3 (*Eurema*, *Abaeis*, and *Pyrisitia*), and simply rearrange species between these genera. This rearrangement agrees with wing pattern characters on the dorsal side, making identification of the genus in the US easier. Both *Eurema* and *Pyrisitia* lack darker expanded area near forewing tornus and their males possess darker scaling along the outer margin of hindwing, at least by the veins. *Eurema* males can be distinguished by a long dark bar near forewing inner margin, which *Pyrisitia* species lack. Males of *Abaeis* species either have a dark forewing tornus (forewing mostly orange with a dark cell spot in the nominal subgenus and yellower, without the cell spot in the subgenus *Sphaenogona*), or lack dark scaling by the hindwing outer margin (USA only) and wings are mostly white with variable extent of dark margins (subgenus *Lucidia*). Although it is tempting to unite all these medium-sized white-yellow-orange butterflies in a single genus *Eurema*, their genetic divergence is very large (Fig. 2), and the group is divided into two prominent clades (*Eurema* + *Pyrisitia* and *Abaeis*), one of which splits into two more (*Eurema* and *Pyrisitia*). Therefore, we keep the three-genus arrangement of the group. Moreover, *Abaeis* as defined here is a broad and diverse genus. Comprehensive sequencing of the worldwide fauna of the group is likely to substantiate further splits rather than lumps.

Family Lycaenidae [Leach], [1815]

Philotiella Mattoni, [1978] is a subgenus of *Euphilotes* Mattoni, [1978]

Philotiella Mattoni, [1978] (type species *Lycaena speciosa* Hy. Edwards, 1877) is phylogenetically close to *Euphilotes* Mattoni, [1978] (type species *Lycaena enoptes* Boisduval, 1852) (COI barcodes differ by only 3.3%) and does not prominently stand out from it in the tree (Fig. 3). Therefore *Philotiella* is better treated as a subgenus, new status. *Euphilotes* is a genus distinct from *Philotes* Scudder, 1876 (type species *Lycaena regia* Boisduval, 1869, a junior subjective synonym of *Lycaena sonorensis* C. Felder & R. Felder, 1865), because they are not monophyletic. *Philotes* is sister to *Glaucopsyche* Scudder, 1872 (type species *Polyommatus lygdamus* E. Doubleday, 1841) (Fig. 3). However, these three genera are close to each other and, if one prefers, can be combined under *Glaucopsyche*. The tight cluster of species comprising *Euphilotes*, (Fig. 3) contrasts with the two rather distant species of *Glaucopsyche* and the monotypic *Philotes* at about the same distance from them. Apparently, not all genera form prominent assemblages of species, and some genera may not be that distinct from each other, like *Glaucopsyche* and *Philotes*.

Phaeostrymon Clench, 1961 is a junior subjective synonym of *Satyrium* Scudder, 1876

Phaeostrymon Clench, 1961 (type and the only species *Thecla alcestis* W. H. Edwards, 1871) was previously considered a valid genus, but it originates within *Satyrium* Scudder, 1876 (type species *Lycaena fuliginosa* W. H. Edwards, 1861), thus rendering *Satyrium* paraphyletic (Fig. 4). Because *Satyrium* is a tight (but diverse) group of close relatives prominently separated from other genera (Fig. 4), *Phaeostrymon* is a close sister to the clade with the type species of *Satyrium*, and *Phaeostrymon* is not prominently distinct from this clade, it is best to treat *Phaeostrymon* as a junior subjective synonym of *Satyrium*, new status.

Pendantus K. Johnson & Kroenlein, 1993 is a valid genus

Previously placed in the genus *Electrostrymon* Clench, 1961 (type species *Papilio endymion* Fabricius, 1775), *Thecla guzanta* Schaus, 1902 is not monophyletic with it and instead is sister to *Calycopis* Scudder, 1876 (type species *Rusticus poeas* Hübner, [1811], which is a junior subjective synonym of *Hesperia cecrops* Fabricius, 1793) (Fig. 5). Not willing to place *guzanta* in *Calycopis* due to genetic and morphological divergence of about the same magnitude as that between *Electrostrymon* and *Kisutam* K. Johnson, 1993 (*Thecla syllis* Godman & Salvin, 1887), we resurrect from synonymy the genus *Pendantus* K. Johnson & Kroenlein, 1993 (type species *Thecla plusios* Godman & Salvin 1887, currently treated as a junior subjective synonym of *Tmolus denarius* Butler & H. Druce, 1872) and form new or revised combinations: *Pendantus guzanta*, *Pendantus thurman* (Thompson & Robbins, 2016), *Pendantus denarius* (A. Butler & H. Druce, 1872), and *Pendantus perisus* (H. Druce, 1907).

Family Nymphalidae Rafinesque, 1815

Neominois Scudder, 1875 is a subgenus of *Oeneis* Hübner, [1819]

In agreement with the previous study (Kleckova et al. 2015), we find that *Neominois* Scudder, 1875 (type species *Satyrus ridingsii* W. H. Edwards, 1865) originates within *Oeneis* Hübner, [1819] (type species *Papilio norna* Thunberg, 1791, represented by *O. polixenes* (Fabricius, 1775) in the US) as it is currently defined, and is sister to the subgenus *ueneis*. COI barcode difference between *ridingsii* and *polixenes* is only 6.2%. However, subgenus *Protoeneis* Gorbunov, 2001 (type species *Chionobas nanna* Ménétriés, 1858, represented by *Oeneis uhleri* (Reakirt, 1866) in the US fauna) that is placed in the genus *Oeneis*, is a sister to the clade consisting of *Neominois* and subgenus *Oeneis* (Fig. 6). The entire group of 3 taxa is compact (Fig. 6), prominent, and genetic divergence within it agrees with the expected divergence within a genus. Therefore, we treat *Neominois* as a subgenus of *Oeneis*.

Agraulis Boisduval & Le Conte, [1835] is a subgenus of *Dione* Hübner, [1819]

Monotypic genus *Agraulis* Boisduval & Le Conte, [1835] (type species *Papilio vanillae* Linnaeus, 1758) is a close sister to *Dione* Hübner, [1819] (type species *Papilio juno* Cramer, 1779) (Fig. 7). COI barcode difference between *A. vanillae* and *Dione moneta* Hübner, [1825] is 7.9%. Time-calibrated nuclear genomic tree shows that genetic divergence (Fig. 7) between *Agraulis* and *Dione* is nearly the same as the divergence among species of *Boloria* Moore, 1900 (type species *Papilio pales* [Denis & Schiffermüller], 1775) and smaller than the divergence between *Heliconius* Kluk, 1780 (type species *Papilio charithonia* Linnaeus, 1767) and *Eueides* Hübner, 1816 (type species *Nereis dianasa* Hübner, [1806]) (Fig. 7). Therefore, we treat *Agraulis* as a subgenus of *Dione*.

Family Hesperiidae Latreille, 1809

Urbanus alva Evans, 1952, new status

Described as a subspecies of *Urbanus viterboana* (Ehrmann, 1907) by Evans (1952), *alva* (the holotype, male, from Mexico: Veracruz, Atoyac, examined by NVG) was placed in synonymy with *Urbanus belli* (Hayward, 1935) (the holotype, female, from Argentina: Salta, photographs examined) by Steinhauser (1981), who was unable to see the *belli* holotype. Our genomic analysis of *U. belli* from Argentina indicates that it is not conspecific with belli-like specimens from Mexico or anywhere else in North America due to genetic divergence between them. Evans noted shorter hindwing tails in *alva* compared to *belli*, and this character holds true comparing the holotypes of these taxa and additional *belli* specimens from Argentina we sequenced, including males. For these reasons we resurrect *alva* from synonymy with *belli* and treat it as a distinct species *Urbanus alva*, new status. Consequently, we exclude *Urbanus belli* (Hayward, 1935) from the North American fauna.

Erynnides Burns, 1964 is a subgenus of *Gesta* Evans, 1953 and not of *Erynnis* Schrank, 1801, new placement

Gesta Evans, 1953 (type species *Thanaos gesta* Herrich-Schäffer, 1863) is a sister to subgenus *Erynnides* Burns, 1964 (type species *Nisoniades propertius* Scudder & Burgess, 1870), with the exclusion of subgenus *Erynnis* Schrank, 1801 (type species *Papilio tages* Linnaeus, 1758, represented by *Erynnis brizo* (Boisduval & Le Conte, [1837]) and *Erynnis icelus* (Scudder & Burgess, 1870) in the US), thus rendering *Erynnis* paraphyletic (Fig. 8). There are three possible solutions. First (splitting), treat all three (*Erynnis*, *Gesta*, and *Erynnides*) as valid genera. However, genetic divergence between *Gesta*, and *Erynnides* is moderate (about 8% in the COI barcode), and no prominent tree branches separate the two taxa. Their genitalia are also quite similar. Therefore, these two taxa are best viewed as subgenera. Second (lumping), treat all three as subgenera of *Erynnis*, thus eliminating genus-species combinations involving *Gesta*. However, genetic divergence between *Erynnis* (sensu stricto) and *Gesta* + *Erynnides* is prominent (Fig. 8), comparable to that between other Erynnini Brues & F. Carpenter, 1932 genera. While the lumping solution is more compatible with how these taxa were viewed historically, it is not consistent with how other members of Erynnini are partitioned into genera. Third (middle ground), is a two-genus solution, i.e., to transfer *Erynnides* from *Erynnis* to *Gesta*. Phylogenetic trees show the two prominent clades corresponding to these two genera, and the clade leading to their common ancestor is shorter and thus less prominent (Fig. 8). Genetic divergence between these two genera is the same magnitude as between other sister genera of Erynnini. This divergence is equally profound in nuclear (autosomes and Z chromosome) and mitochondrial genomes. Therefore, we prefer this two-genus solution. As a result, all species formerly placed in the subgenus *Erynnides* of *Erynnis* would change their genus name to *Gesta*. This action results in many name changes, but highlights deep genetic divergence between mostly Old Worth *Erynnis* and exclusively New World *Gesta* and thus seems to be more biologically meaningful. Although the switch of names is bothersome in short run, it may be beneficial long term.

Copaeodes Speyer, 1877 is a subgenus of *Oarisma* Scudder, 1872

Previously placed in the genus *Oarisma* Scudder, 1872 (type species *Hesperia powesheik* Parker, 1870), *Thymelicus edwardsii* W. Barnes, 1897 is not monophyletic with it, and is a close sister to the two US species from the genus *Copaeodes* Speyer, 1877, including its type species *Heteropterus procris* W. H. Edwards, 1871, a junior subjective synonym of *Ancy-loxipha* [sic!] *aurantiaca* Hewitson, 1868 (Fig. 9). Investigation of other *Oarisma* and *Copaeodes* species reveals that they are close to each other and difficult to partition between the two genera (Fig. 9). Only the close cluster of 3 species *O. poweshiek* (Parker, 1870), *O. garita* (Reakirt, 1866), and *O. era* Dyar, 1927 constitute *Oarisma* sensu stricto. Others fall in a different and broad clade, which in addition to *Copaeodes* includes other species previously placed in *Oarisma*, e.g., *O. edwardsii* (W. Barnes, 1897) and *O. nanus* (Herrich-Schäffer, 1865), and we treat this clade as a subgenus *Copaeodes* within a broader-defined *Oarisma*.

Saliana Evans, 1955 is a junior subjective synonym of *Calpodes* Hübner, [1819]

Monotypic genus *Calpodes* Hübner, [1819] (type species *Papilio ethlius* Stoll, 1782) is genetically close to *Saliana* Evans, 1955 (type species *Papilio salius* Cramer, 1775) (Fig. 10) and their type species differ by only about 6.5% in COI barcodes. Moreover, *Calpodes* + *Saliana* clade experienced rapid radiation over a short period of time and, as a result, the tree looks more like a comb than a bi-branching structure (Fig. 10). It is not clear whether *Saliana* is monophyletic: 64% bootstrap in the nuclear genome tree suggests that it is not, and that *Saliana fusta* Evans, 1955 is sister to the rest of *Saliana* + *Calpodes*. Due to rapid radiation, this genus is difficult to partition into meaningful subgenera, because no clear clusters of species are apparent in the tree (Fig. 10). For all these reasons, we propose that *Saliana* is a junior subjective synonym of *Calpodes*, new status. Interestingly, *C. ethlius* diverged strongly in wing shapes and patterns from all other members of the genus (although their male genitalia are similar) and this new synonymy is unexpected. Therefore, we tested the results using multiple specimens of *C. ethlius* (7 shown in Fig. 10) and they all cluster together, within former *Saliana*. The newly expanded *Calpodes* is a strongly supported (bootstrap 100%) and prominent (long tree branch is leading to it) genus.

Nastra perigenes (Godman, 1900), new combination

Previously placed in the genus *Vidius* Evans, 1955 (type species *Narga vidius* Mabille, 1891), *Mastor perigenes* Godman, 1900 is not monophyletic with the type species of *Vidius*, and instead forms a clade with *Nastra* Evans, 1955 (type species *Hesperia lherminier* Latreille, [1824]) (Fig 11) and therefore is transferred to this genus to form a new combination *Nastra perigenes*.

Amblyteria Grishin, new subgenus

http://zoobank.org/C1F98F8D-C366-4065-9317-EA039D15CB22

Type species.—*Goniloba exoteria* Herrich-Schäffer, 1869.

Definition.—A prominent clade within *Amblyscirtes* Scudder, 1872 (type species *Hesperia vialis* W. H. Edwards, 1862) without a name (Fig. 11, 12). Keys to N.2.2, 6, 8, or 22 in Evans (1955). Phenotypically diverse lineage of species that differs from its relatives by the following combination of characters: males either with stigma long, narrow and rather straight, hindwing below with many small white spots in some species, and size small (forewing length mostly < 15mm), or if larger, then forewing pale spot in cell M_1-M_2 strongly offset towards outer margin; or with brands at the base of vein CuA_2, and brands either very conspicuous on bronze-colored wings, or wings black, head orange and fringes not orange but pale. Due to this pronounced phenotypic variation, the subgenus is best defined by DNA characters. A combination of the following base pairs in the standard DNA COI barcode region (658 bp) is diagnostic: T548C, A550T (these two characters are synapomorphic), 343(not G as in *Stomyles*), T346T(not C as in *Stomyles*), T553T(not A as in the nominal subgenus), and A637A(not T as in *Stomyles*).

Etymology.—The name is a feminine noun in the nominative singular, a fusion of the type species name epithets: *Ambly*[scirtes] + [exo]*teria*.

Species included.—*Amblyscirtes elissa* Godman, [1900], *Pamphila oslari* Skinner, 1899, *Amblyscirtes brocki* Freeman, 1992, *Goniloba exoteria* Herrich-Schäffer, 1869, and *Pamphila phylace* Edwards, 1878.

Parent taxon.—Genus *Amblyscirtes* Scudder, 1872.

Assignment of species to subgenera.—With the description of *Amblyteria* subgen. n., we consider that the genus *Amblyscirtes* consists of 4 subgenera (Fig. 12). Subgenus *Stomyles* Scudder, 1872 (Eastern US clade) consists of *A. carolina* (Skinner, 1892), *A. reversa* F. Jones, 1926, *A. aesculapius* (Fabricius, 1793), and *A. hegon* (Scudder, 1863). Subgenus *Mastor* Godman, [1900] (Southern clade) consists of *A. fimbriata* (Plötz, 1882) (the only USA species), *A. anubis* (Godman, 1900), *A. novimmaculatus* A. Warren, 1998, *A. raphaeli* H. Freeman, 1973, *A. patriciae* (E. Bell, 1959), and *A. folia* Godman, 1900. Names of type species are underlined. Other *Amblyscirtes* species (Mielke 2005; Pelham 2008) not mentioned here belong to the nominal subgenus.

Comment.—A surprising result is that two very similar-looking species *A. (Amblyteria) phylace* and *A. (Mastor) fimbriata* are not each other's closest relatives and belong to different subgenera (Fig. 12).

Troyus fantasos (Cramer, 1780), *Troyus onaca* (Evans, 1955), *Troyus aurelius* (Plötz, 1882), *Troyus marcus* (Fabricius, 1787), *Troyus diversa* (Herrich-Schäffer, 1869), and *Troyus drova* (Evans, 1955), new combinations

Previously placed in the genus *Vettius* Godman, 1901 (type species *Papilio phyllus* Cramer, 1777), *Papilio fantasos* Cramer, 1780 is not monophyletic with *Vettius* type species, and is a close relative of the monotypic genus *Troyus* A. Warren & Turland, 2012 (type and the only included species *Troyus turneri* A. Warren & Turland, 2012). Their sister genus is *Monca* Evans, 1955 (type species *Cobalus telata* Herrich-Schäffer, 1869) (Fig. 13). Therefore, we establish a new combination *Troyus fantasos* Due to genetic and morphological similarities, we additionally propose the following new combinations: *Troyus onaca* (Evans, 1955), *Troyus aurelius* (Plötz, 1882), *Troyus marcus* (Fabricius, 1787), *Troyus diversa* (Herrich-Schäffer, 1869), and *Troyus drova* (Evans, 1955). All these species were in *Vettius* before.

Hedone Scudder, 1872 is a valid genus

We find that *Polites* Scudder, 1872 (type species *Hesperia peckius* W. Kirby, 1837) is paraphyletic with respect to *Wallengrenia* Berg, 1897 (type species *Hesperia premnas* Wallengren, 1860). Genetic divergence within *Polites* that includes *Wallengrenia* is too large compared to how most Hesperiidae genera are defined. Therefore, instead of including *Wallengrenia* into *Polites*, it makes sense to restore monophyly of these genera by splitting *Polites* into genera with divergence consistent with that of most other Hesperiidae genera. Previously a junior subjective synonym of *Polites* Scudder, 1872 (type species *Hesperia peckius* W. Kirby, 1837), *Hedone* Scudder, 1872 (type species *Hesperia brettus* Boisduval & Le Conte, [1837], a junior subjective synonym of *Thymelicus vibex* Geyer, 1832) forms a clade sister to the rest of *Polites* + *Wallengrenia* (Fig. 14). Therefore, *Hedone* is a valid genus, and *Hedone vibex* (Geyer, 1832) is a revised combination. Due to morphological similarities, we additionally propose the following new combinations: *Hedone bittiae* (Lindsey, 1925), *Hedone vibicoides* (de Jong, 1983), and *Hedone dictynna* (Godman & Salvin, 1896).

Limochores Scudder, 1872 is a valid genus

Sister to the rest of *Polites* + *Wallengrenia* excluding *Hedone, Limochores* Scudder, 1872 (type species *Hesperia manataaqua* Scudder, 1863, which is a junior subjective synonym of *Hesperia origenes* Fabricius, 1793) was treated as a junior subjective synonym of *Polites* (Fig. 14). For the reasons given above for *Hedone*, we propose the following new or revised combinations: *Limochores origenes* (Fabricius, 1793), *Limochores mystic* (W. H. Edwards, 1863), *Limochores sonora* (Scudder, 1872), *Limochores puxillius* (Mabille, 1891), and *Limochores pupillus* (Plötz, 1882). Interestingly, two difficult-to-distinguish species that frequently fly together at the same location, *L. origenes* and *Polites themistocles* (Latreille, [1824]), ended up in different genera. Even though their genitalia are similar, they belong to distant from each other clades in the tree (Fig. 14): *P. themistocles* is closely related to *P. peckius*, the type genus of *Polites*, while *L. origenes* is closer to *L. mystic*.

Coa Grishin, new subgenus

http://zoobank.org/CD8143FC-839D-408E-A114-3FFEEA7AE349

Type species.—*Hesperia baracoa* Lucas, 1857.

Definition.—A sister to subgenus *Yvretta* Hemming, 1935 (type species *Pamphila citrus* Mabille, 1889, which is treated as a junior subjective synonym *Hesperia subreticulata* Plötz, 1883), *Hesperia baracoa* Lucas, 1857 prominently stands out from other *Polites* (Fig. 14). Therefore, this lineage is given a subgenus status and a name. This new subgenus keys to M.13.4 in Evans (1955). Distinguished from its relatives within *Polites* by the combination of the following characters: presence of apiculus (longer than 1 segment); diagnostic shape of stigma: rather short, relatively straight and narrower than in other species with defined apiculus; the lack of spot before the end of discal cell on plain gray-brown ventral hindwing without dark spots (but sometimes with a row of pale discal spots) combined with orange area by the forewing costa below, stemming from the wing base and reaching apical spots.

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

Species included.—Only the type species.

Parent taxon.—Genus *Polites* Scudder, 1872.

Assignment of species to subgenera.—With the description of *Coa* subgen. n., we consider that *Polites* consists of 3 subgenera (Fig. 14). Subgenus *Yvretta* consists of *P. subreticulata* (Plötz, 1883), *P. carus* (W. H. Edwards, 1883), and *P. rhesus* (W. H. Edwards, 1878). Other *Polites* species (Mielke 2005; Pelham 2008) not mentioned in this work belong to the nominal subgenus. Interestingly, *Wallengrenia* Berg, 1897 (type species *Hesperia premnas* Wallengren, 1860) is not prominently distinct genetically from *Polites* (green branch in Fig. 14) and may therefore be included in *Polites* as the 4th subgenus, depending on researcher's taste.

Problema Skinner & R. Williams, 1924 is a subgenus of *Atrytone* Scudder, 1872

Currently monotypic genus *Atrytone* Scudder, 1872 (type species *Hesperia iowa* Scudder, 1868) is sister to *Problema* Skinner & R. Williams, 1924 (type genus *Pamphila byssus* W. H. Edwards, 1880), a genus of two species, including also *Hesperia bulenta* Boisduval & Le Conte, [1837]. All three species are close in their genomic sequences (Fig. 15). Their genetic divergence is more consistent with them being congeners. Therefore, we treat *Problema* as a subgenus of *Atrytone* to form new or revised combinations *Atrytone byssus* and *Atrytone bulenta*.

Oligoria percosius (Godman, 1900), *Oligoria rindgei* (H. Freeman, 1969), *Oligoria lucifer* (Hübner, [1831]), and *Oligoria mustea* (H. Freeman, 1979), new combinations

Previously placed in the genus *Decinea* Evans, 1955 (type species *Hesperia decinea* Hewitson, 1876), *Cobalus percosius* Godman, 1900 is not monophyletic with *Decinea* type species, which is in the same clade with *Buzyges* Godman, 1900. Instead, *percosius* is a very close sister of the monotypic genus *Oligoria* Scudder, 1872 (type species *Hesperia maculata* W. H. Edwards, 1865) (Fig. 16), which is in the same clade with *Xeniades* Godman, 1900. COI barcode difference between *maculata* and *percosius* is only 4%. Therefore, we establish a new combination: *Oligoria percosius*. Due to morphological and genetic DNA similarities, we additionally propose the following new combinations: *Oligoria rindgei* (H. Freeman, 1969), *Oligoria lucifer* (Hübner, [1831]), and *Oligoria mustea* (H. Freeman, 1979) (Fig. 16). All these species were previously placed in *Decinea*.

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LITERATURE CITED

Allio R, Scornavacca C, Benoit N, Clamens AL, Sperling FAH, and Condamine FL. 2019. Whole genome shotgun phylogenomics resolves the pattern and timing of swallowtail butterfly evolution. Systematic Biology: ahead of print May 7. pii: syz030.

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 pp., pls. 10–25.

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 pp., pls. 54–88.

Kleckova I, Cesanek M, Fric Z, and Pellissier L. 2015. Diversification of the cold-adapted butterfly genus Oeneis related to Holarctic biogeography and climatic niche shifts. Molecular Phylogenetics and Evolution 92: 255–265. [PubMed: 26166775]

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

Pelham JP 2008. Catalogue of the Butterflies of the United States and Canada. Journal of Research on the Lepidoptera 40: 1–658.

Pelham JP 2019. Catalogue of the Butterflies of the United States and Canada. Revised 7 Oct 2019. Accessed 8 Oct 2019 (http://www.butterfliesofamerica.com/US-Can-Cat.htm).

Ratnasingham S, and Hebert PD. 2007. BOLD: The Barcode of Life Data System (http://www.barcodinglife.org). Molecular Ecology Notes 7(3): 355–364. [PubMed: 18784790]

Steinhauser SR 1981. Revision of the *proteus* group of the genus *Urbanus* Hubner (Lepidoptera: Hesperiidae). Bulletin of the Allyn Museum 62: 1–41.

Tyler HA, Brown KS, and Wilson KH. 1994. Swallowtail butterflies of the Americas: a study in biological dynamics, ecological diversity, biosystematics, and conservation. Scientific Publishers; Gainesville, FL. 376 pp.

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

Zhang J, Cong Q, Shen J, Opler PA, and Grishin NV. 2019c. Genomics of a complete butterfly continent. bioRxiv preprint.

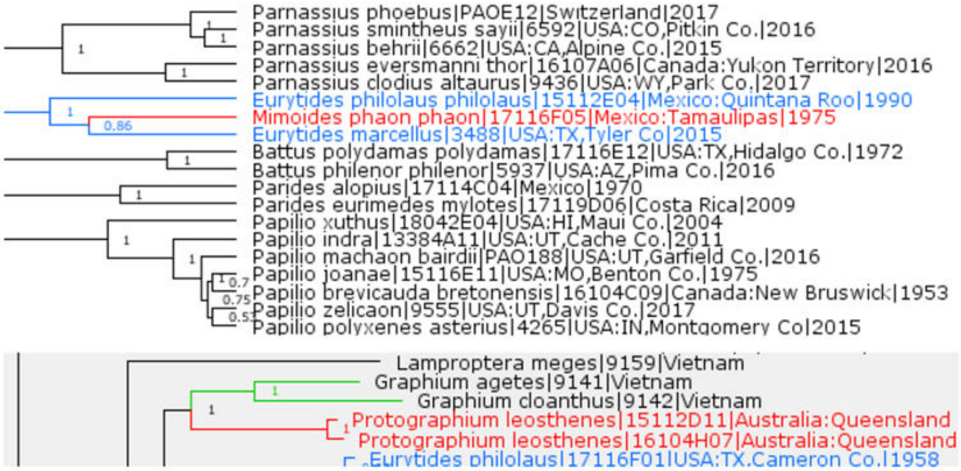

Fig. 1.

Eurytides, *Mimoides* and *Protographium*.

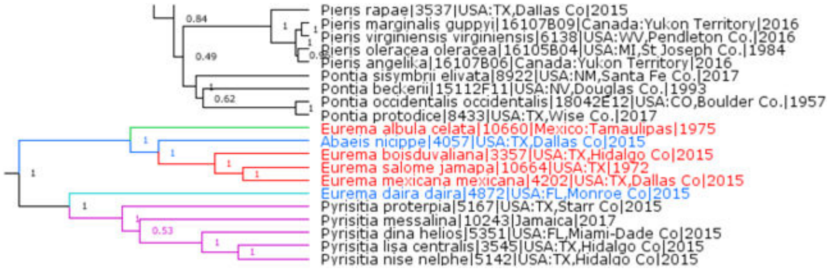

Fig. 2.

Eurema, *Abaeis*, *Sphaenogona*, and *Lucidia*.

Fig. 3.

Euphilotes, *Philotiella*, and *Philotes*.

Fig. 4.

Satyrium and *Phaeostrymon*.

Fig. 5.

Electrostrymon, *Calycopis*, and *Pendantus*.

Fig. 6.

Oeneis and *Neominois*.

Fig. 7.

Agraulis and *Dione*.

Fig. 8.

Erynnis and *Gesta*.

Fig. 9.

Oarisma and *Copaeodes*. US species (tree above) and including others (gray tree below, asterisks mark type species).

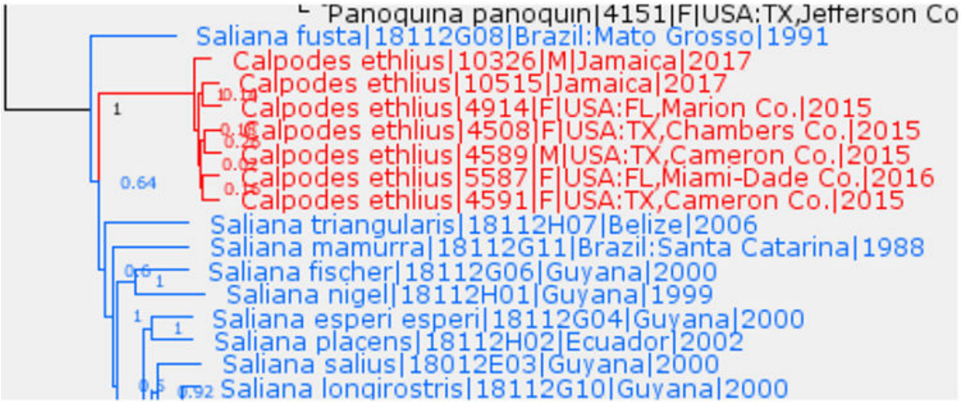

Fig. 10.

Calpodes and *Saliana*.

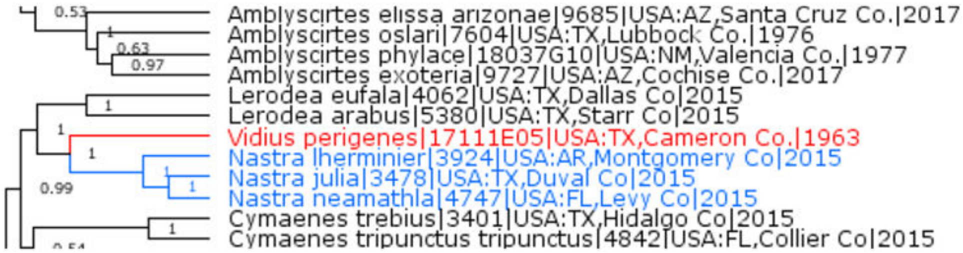

Fig. 11.

Nastra and no *Vidius*.

Fig. 12.

Amblyscirtes.

Fig. 13.

Troyus, *Monca*, and no *Vettius*.

Fig. 14.

Polites, *Wallengrenia*, *Hedone*, and *Limochores*.

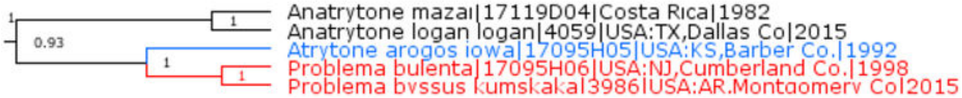

Fig. 15.

Atrytone and *Problema*.

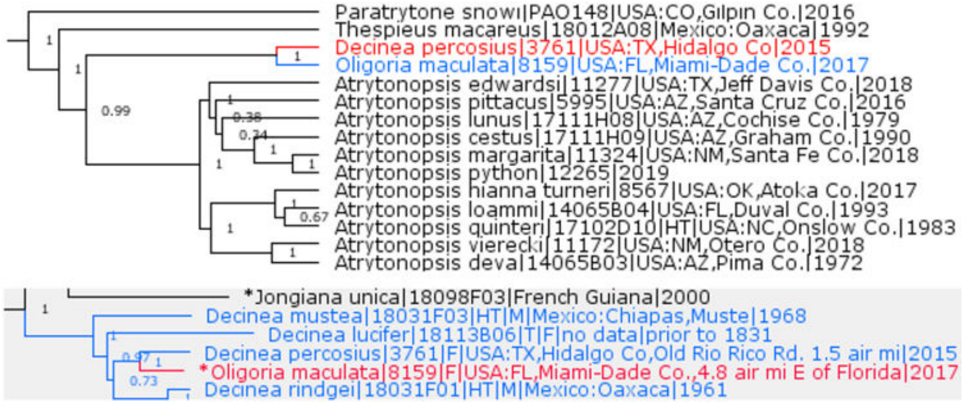

Fig. 16.

Oligoria and no *Decinea*. US species (tree above) and including others (gray tree below, asterisks mark type species).