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Genomics-based taxonomic rearrangement of Achlyodini and Carcharodini (Lepidoptera: Hesperiidae: Pyrginae)

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Genomics-based taxonomic rearrangement of Achlyodini and Carcharodini (Lepidoptera: Hesperiidae: Pyrginae)

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Abstract. Genomic analysis of Pyrginae Burmeister, 1878 (Lepidoptera: Hesperiidae Latreille, 1809) with an emphasis on the tribes Achlyodini Burmeister, 1878 and Carcharodini Verity, 1940 reveals many inconsistencies between the resulting phylogeny and the current classification. These problems are corrected by proposing new taxa, changing the ranks of others, or synonymizing them, and transferring species between genera. As a result, five subtribes, one genus, 20 subgenera, and one species are proposed as new: Cyclosemiina Grishin, **new subtribe** (type genus *Cyclosemia* Mabille, 1878), Ilianina Grishin, **new subtribe** (type genus *Iliana* E. Bell, 1937), Nisoniadina Grishin, **new subtribe** (type genus *Nisoniades* Hübner**, [1819]),** Burcina Grishin**, new subtribe** (type genus *Burca* E. Bell and W. Comstock, 1948), and Pholisorina Grishin, **new subtribe** (type genus *Pholisora* Scudder, 1872), all in Carcharodini; *Lirra* Grishin, **new genus** (type species *Leucochitonea limaea* Hewitson, 1868) in Pythonidina Grishin, 2019; *Trifa* Grishin, **new subgenus** (type species *Tagiades jacobus* Plötz, 1884), *Tuberna* Grishin, **new subgenus** (type species *Pythonides contubernalis* Mabille, 1883), *Ebona* Grishin, **new subgenus** (type species *Quadrus eboneus* E. Bell, 1947), *Noctis* Grishin, **new subgenus** (type species *Achlyodes accedens* Mabille, 1895), and *Cyrna* Grishin, **new subgenus** (type species *Achlyodes cyrna* Mabille, 1895) of *Quadrus* Lindsey, 1925; *Liddia* Grishin, **new subgenus** (type species *Helias pallida* R. Felder, 1869), *Minna* Grishin, **new subgenus** (type species *Achlyodes minna* Evans, 1953), and *Thilla* Grishin, **new subgenus** (type species *Eurypterus later* Mabille, 1891) of *Eantis* Boisduval, 1836; *Torgus* Grishin, **new subgenus** (type species *Ouleus gorgus* E. Bell, 1937) of *Iliana* E. Bell, 1937; *Fenops* Grishin, **new subgenus** (type species *Cabares enops* Godman and Salvin, 1894) of *Polyctor* Evans, 1953; *Bezus* Grishin, **new subgenus** (type species *Pellicia bessus* Möschler, 1877) and *Macarius* Grishin, **new**

subgenus (type species *Pellicia macarius* Herrich-Schäffer, 1870) of *Nisoniades* Hübner, [1819]; *Quadralis* Grishin, **new subgenus** (type species *Pterygospidea extensa* Mabille, 1891) of *Gorgopas* Godman and Salvin, 1894; *Menuda* Grishin, **new subgenus** (type species *Nisoniades menuda* Weeks, 1902) and *Narycus* Grishin, **new subgenus** (type species *Pythonides narycus* Mabille, 1889) of *Perus* Grishin, 2019; *Bovaria* Grishin, **new subgenus** (type species *Achlyodes cyclops* Mabille, 1876), *Sebia* Grishin, **new subgenus** (type species *Nisoniades eusebius* Plötz, 1884), and *Stolla* Grishin, **new subgenus** (type species *Pholisora balsa* E. Bell, 1937) of *Bolla* Mabille, 1903; *Vulga* Grishin, **new subgenus** (type species *Achlyodes vulgata* Möschler, 1879) and *Capilla* Grishin, **new subgenus** (type species *Helias aurocapilla* Staudinger, 1876, currently a junior subjective synonym of *Hesperia musculus* Burmeister, 1875) of *Staphylus* Godman and Salvin, 1896; and *Quadrus* (*Zera*) *vivax* Grishin, **new species** (type locality in Brazil: Rio de Janeiro). The following 10 are **subgenera**, not genera or synonyms: *Ouleus* Lindsey, 1925 and *Zera* Evans, 1953 of *Quadrus* Lindsey, 1925; *Atarnes* Godman and Salvin, 1897 and *Eburuncus* Grishin, 2012 of *Milanion* Godman and Salvin, 1895; *Pachyneuria* Mabille, 1888 and *Austinus* O. Mielke and Casagrande, 2016 of *Sophista* Plötz, 1879; *Hemipteris* Mabille, 1889 and *Mictris* Evans, 1955 of *Pellicia* Herrich-Schäffer, 1870; and *Hesperopsis* Dyar, 1905 and *Scantilla* Godman and Salvin, 1896 of *Staphylus* Godman and Salvin, 1896. The following 7 are **species**, not subspecies: *Quadrus* (*Ebona*) *cristatus* (Steinhauser, 1989) (not *Quadrus* (*Ebona*) *negrus* (Nicolay, 1980)), *Quadrus* (*Quadrus*) *ophia* (A. Butler, 1870) (not *Quadrus* (*Quadrus*) *lugubris* (R. Felder, 1869)), *Quadrus* (*Zera*) *gellius* (Mabille, 1903) and *Quadrus* (*Zera*) *servius* (Plötz, 1884) (not *Quadrus* (*Zera*) *hyacinthinus* (Mabille, 1877)), *Mimia pazana* Evans,1953 (not *Mimia phidyle* (Godman and Salvin, 1894)), *Polyctor* (*Polyctor*) *dagua* Evans, 1953 (not *Polyctor* (*Polyctor*) *polyctor* (Prittwitz, 1868)), and *Staphylus* (*Vulga*) *satrap* Evans, 1953 (not *Staphylus* (*Vulga*) *saxos* Evans, 1953); and these 8 are species, not synonyms: *Quadrus* (*Zera*) *menedemus* (Godman and Salvin, 1894) (not *Quadrus* (*Zera*) *tetrastigma* (Sepp, [1847])), *Pellicia* (*Pellicia*) *bilinea* Mabille, 1889 (not *Pellicia* (*Pellicia*) *dimidiata* Herrich-Schäffer, 1870), *Pellicia* (*Hemipteris*) *nema* Williams and Bell, 1939 (not *Pellicia* (*Pellicia*) *theon* Plötz, 1882), *Bolla* (*Bovaria*) *sodalis* Schaus, 1913 (not *Bolla* (*Bolla*) *imbras* (Godman and Salvin, 1896)), *Bolla* (*Bovaria*) *aplica* (E. Bell, 1937) (not *Bolla* (*Sebia*) *eusebius* (Plötz, 1884)), *Bolla* (*Sebia*) *chilpancingo* (E. Bell, 1937) (not *Bolla* (*Bolla*) *subapicatus* (Schaus, 1902)), and *Bolla* (*Stolla*) *madrea* (R. Williams and E. Bell, 1940) and *Bolla* (*Stolla*) *hazelae* (Hayward, 1940) (not *Bolla* (*Stolla*) *zorilla* (Plötz, 1886)). The following 2 are junior subjective **synonyms**: *Achlyodes erisichthon* Plötz, 1884 of *Quadrus* (*Zera*) *servius* (Plötz, 1884) (not a subspecies of *Quadrus* (*Zera*) *tetrastigma* (Sepp, [1847]) and *Staphylus subapicatus* Schaus, 1902 of *Bolla* (*Bolla*) *imbras* (Godman and Salvin, 1896). Furthermore, we propose the following additional **new** genus-species **combination**: *Gindanes homer* (Evans, 1953), *Gindanes nides* (O. Mielke and Casagrande, 2002), *Gindanes maraca* (O. Mielke and Casagrande, 1992), *Gindanes jenmorrisae* (Shuey and Ramírez. 2022), *Gindanes tullia* (Evans, 1953), *Gindanes herennius* (Geyer, [1838]), *Gindanes proxenus* (Godman and Salvin, 1895), *Gindanes parallelus* (Mabille, 1898), *Gindanes braga* (Evans, 1953), *Gindanes hampa* (Evans, 1953), *Gindanes rosa* (Steinhauser, 1989), *Gindanes neivai* (Hayward, 1940), *Gindanes mundo* (H. Freeman, 1979), *Gindanes eminus* (E. Bell, 1934), *Quadrus* (*Trifa*) *francesius* Freeman, 1969, *Quadrus* (*Trifa*) *ineptus* (Draudt, 1922), *Quadrus* (*Trifa*) *jacobus* (Plötz, 1884), *Quadrus* (*Tuberna*) *lancea* (Hewitson, 1868), *Quadrus* (*Ebona*) *pescada* (E. Bell, 1956), *Lirra pteras* (Godman and Salvin, 1895), and *Lirra limaea* (Hewitson, 1868) (not *Pythonides* Hübner, 1819); *Quadrus (Cyrna) zora* (Evans, 1953) (not *Bolla* Mabille, 1903); *Eantis later* (Mabille, 1891) and *Eantis haber* (Mabille, 1891) (not *Aethilla* Hewitson, 1868); *Iliana* (*Torgus*) *gorgus* (E. Bell, 1937) and *Iliana* (*Torgus*) *taurus* (Evans, 1953) (not *Eantis* Boisduval, 1836); *Bolla* (*Stolla*) *evemerus* (Godman and Salvin, 1896), *Bolla* (*Stolla*) *chlora* (Evans, 1953), *Bolla* (*Stolla*) *astra* (R. Williams and E. Bell, 1940), *Bolla* (*Stolla*) *balsa* (E. Bell, 1937), *Bolla* (*Stolla*) *tridentis* (Steinhauser, 1989), *Bolla* (*Stolla*) *esmeraldus* (L. Miller, 1966), *Bolla* (*Stolla*) *chlorocephala* (Latreille, [1824]), and *Bolla* (*Stolla*) *incanus* (E. Bell, 1932) (not *Staphylus* Godman and Salvin, 1896). Finally, **lectotypes** are designated for *Achlyodes servius* Plötz, 1884 (type locality in Brazil: Rio de Janeiro), *Pellicia theon* Plötz, 1882 (type locality in South America), and *Nisoniades eusebius* Plötz, 1884 (type locality in Central America). Unless stated otherwise, all subgenera, species, subspecies, and synonyms of mentioned genera and species are transferred with their parent taxa, and others remain as previously classified.

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

ZooBank registration. http://zoobank.org/B9AFA1A9-8664-4F31-B4D9-ACF7780C7CC6

Introduction

This work is a continuation of our efforts to improve the taxonomic classification of Hesperiidae Latreille, 1809 using large-scale DNA sequencing (Cong et al. 2019b; Li et al. 2019; Zhang et al. 2019a, 2019b, 2022b, 2023c, 2023d) and it complements the studies of others (Warren et al. 2008, 2009; Fan et al. 2016; Sahoo et al. 2016, 2017; Toussaint et al. 2018; Huang et al. 2019; Toussaint et al. 2019, 2021a, 2021b, 2022). Continuing with the whole genome shotgun sequencing of Hesperiidae, we focus on two tribes in the subfamily Pyrginae Burmeister, 1878, namely Achlyodini Burmeister, 1878 and Carcharodini Verity, 1940. These two tribes appear particularly problematic taxonomically, revealing that many taxa in the current classification are non-monophyletic.

In classification decisions, we strongly rely on nuclear genomic trees and use morphological considerations as secondary evidence to rationalize the results. This is because, contrary to a small set of gene markers, genomes offer a comprehensive picture of an organism richer than the morphology of adults typically used to classify butterflies. Genomes encode life histories, habitat and mating preferences, and food sources. All this information is present in the genomic sequence. While we lack the knowledge to extract it and predict phenotypes, we can use a genetic equivalent of this information in an aggregate to deduce phylogenetically sound taxonomic classification. We do so by selecting random codons from all protein-coding genes. This process yields a dataset that mirrors the natural balance of this information as found in the organism's genome.

We see that phylogenetic trees based on nuclear genomes are particularly suited to address the questions of higher classification and offer guidance on discretizing continuous evolutionary processes of speciation and extinction, fitting the clades to taxonomic ranks. Genome-based phylogenies frequently reveal levels, i.e., timepoints when diversification occurred in several lineages independently (Zhang et al. 2021, 2023b). These synchronized diversifications result from geological events affecting all major lineages at the same time, offering an opportunity to match taxonomic ranks (we utilize tribe, subtribe, genus, and subgenus) to the levels in genome-based phylogenies, which leads to a more objective and consistent classification tied to both genetic differentiation and paleontological history. We attempt to define secondary levels (subtribes and subgenera) in the classification whenever possible if we see noteworthy clustering of genera or species into groups of relatives prominently differentiated from other such groups. We find these subdivisions useful in taxonomic lists, even if for no other reason than to place closer relatives close to each other in alphabetically sorted hierarchical lists.

Species are delineated by a combination of criteria that include genetic differentiation in the Z chromosome measured by F_{st} (>0.20 usually corresponds to distinct species) and gene exchange G_{min} (<0.05 for distinct species) (Cong et al. 2019a), COI barcode difference (typically >2% for distinct species) (Hebert et al. 2003) and its correlation with phenotypic differences (Lukhtanov et al. 2016), and the prominence of species-level clades (Zhang et al. 2022c). However, COI barcodes (together with mitochondria) can be transfer between species through occasional hybridization (Bachtrog et al. 2006; Cong et al. 2017), and some distinct species may possess highly similar or identical barcodes (Burns et al. 2008; Zhang et al. 2023a). See the "Species, subspecies, and genomics" section in Zhang et al. (2022a) for further discussion.

Following the logic outlined above, we are reclassifying two tribes in the subfamily Pyrginae Burmeister, 1878 based on the phylogeny inferred from whole genome shotgun datasets. The nuclear genomic tree we obtain is strongly supported, and the taxa we propose are confidently monophyletic. Moreover, their taxonomic ranks are consistent because they are tied to levels in the phylogenetic tree.

Materials and Methods

Methods employed in this study are the same as detailed in our previous publications (Li et al. 2019; Zhang et al. 2019a, 2022b; Cong et al. 2021). First, we obtain whole genome shotgun sequence datasets from butterfly specimens using our previously established experimental protocols (Li et al. 2019; Zhang et al. 2019a). Typically, a leg of a dry pinned specimen is used for DNA extraction. Our protocol is non-destructive, and legs are preserved. Specimens of any age are amenable to this protocol (Cong et al. 2021). We do not rely on the amplification of specific genes or segments, and every extracted DNA piece is sequenced. Therefore, the protocol succeeds with very old specimens, in which DNA may be fragmented into 30–50 bp segments. Second, these genomic datasets composed of 150 bp (or less) DNA segments are subjected to computational analysis to identify and assemble (i.e., stitch together) protein-coding regions using DIAMOND (Buchfink et al. 2015) and a reference set of all proteins encoded in a previously assembled reference genome of *Cecropterus lyciades* (Geyer, 1832) (Shen et al. 2017). This procedure results in a master-slave alignment of all these regions (i.e., coding regions in each specimen are aligned to the reference). These alignments (about 18 million positions) are too large for time-efficient phylogenetic analysis. They are randomly subsampled for 300,000 positions (by codon) that are used to infer phylogenetic trees as described previously (Zhang et al. 2022b). Third, we construct phylogenetic trees using IQ-tree v1.6.12 under the GTR+GAMMA model (Nguyen et al. 2015) from these randomly sampled positions in the nuclear genome (300 thousand positions) and estimate statistical significance by standard codon resampling from the original complete alignment (18 million positions). The trees are visualized, manipulated, and colored to prepare illustrations using FigTree (Rambaut 2018).

The current taxonomic classification was overlaid on the trees to find non-monophyletic taxa and clades corresponding to taxa without names. Taxa we define are monophyletic groups in nuclear genome trees that correspond to prominent clades. By "prominent," we mean tree branches strongly supported statistically (typically by 100% of replicates) and usually longer than neighboring branches. The length of a branch is proportional to the number of base-pair substitutions along the branch. Not only are longer branches better supported statistically, but the larger number of genetic changes along them likely leads to more pronounced phenotypic changes that should be reflected in some morphological characters, not necessarily in adults, but could be in immature stages or other aspects of the phenotype. Nevertheless, due to highly non-linear relationships between the number of genetic changes and visually drastic phenotypic differences (Zhang et al. 2019a), there are short tree branches that correspond to visually recognizable taxa, and each case should be considered individually. It is unclear, however, if some drastic phenotypic change in adult appearance that was caused by a small number of genetic changes (maybe even a single inversion of a genomic segment) should be grounds for the erection of a separate taxon for this lineage because all other characters, e.g., those of caterpillars, would remain rather similar to the relatives of this lineage. Generally, we prefer to avoid monotypic (or nearly monotypic, i.e., consisting of very close relatives) higher taxa unless they cannot be confidently assigned to other taxa of the same rank or show prominent genetic differentiation from them at the level of the tree that corresponds to their rank. Furthermore, currently employed taxonomy is considered, and currently used names and their taxonomic ranks serve, on average, as a reference point to define levels in the trees and new taxa.

All taxa in this work are listed in their suggested phylogenetic order that agrees with phylogenetic trees augmented with the considerations of phenotypic similarity so that more similar species are closer to each other in the list (under the constraints of the trees). In addition to phenotypic diagnoses, we provide diagnostic DNA characters, both in the nuclear genome and the COI barcode. DNA characters are found in nuclear protein-coding regions using our previously developed procedure (see SI Appendix to Li et al. 2019). The logic behind the character selection was detailed in Cong et al. (2019b). The character states are provided in species diagnoses as abbreviations. E.g., aly728.44.1:G672C means position 672 in exon 1 of gene 44 from scaffold 728 of the *Cecropterus lyciades* (Geyer, 1832) (formerly in *Achalarus* Scudder, 1872, thus "aly") reference genome (Shen et al. 2017) is C, changed from G in the ancestor. When characters are given for the sister clade of the diagnosed taxon, the following notation is used: aly5294.20.2:A548A (not C), which means that position 548 in exon 2 of gene 20 on scaffold 5294 is occupied by the ancestral base pair A, which was changed to C in the sister clade (so it is not C in the diagnosed taxon). The same notation is used for COI barcode characters but without a prefix ending with ':'. The sequences of exons from the reference genome with the positions used as character states highlighted in green are given in the supplemental file (Zhang et al. 2023d). Linking to the DNA sequences accessible from this publication ensures that DNA characters given in the diagnoses can be readily associated with actual sequences. General locality and collection year for specimens are given in the tree figures, and detailed data are provided in Table S1 of the supplemental file (Zhang et al. 2023d). COI barcode sequences have been deposited in GenBank with accessions OR665721–OR665734 and OR721875–OR721877. All new names have been registered with ZooBank, and registration numbers are provided for each.

The specimens were examined and sampled for sequencing in the following collections (abbreviations, which are not necessarily acronyms of the current names of these institutions, are given in parenthesis and used in Table S1 of the supplemental file (Zhang et al. 2023d)): American Museum of Natural History, New York, NY, USA (AMNH), Natural History Museum, London, UK (BMNH), Carnegie Museum of Natural History, Pittsburgh, PA, USA (CMNH), Colorado State University Collection, Fort Collins, CO, USA (CSUC), 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), Museum für Naturkunde, Berlin, Germany (MFNB), McGuire Center for Lepidoptera and Biodiversity, Gainesville, FL, USA (MGCL), Muséum National d'Histoire Naturelle, Paris, France (MNHP), Museo de Historia Natural, Lima, Peru (MUSM), Texas A&M University Insect Collection, College Station, TX, USA (TAMU), Biodiversity Center, University of Texas at Austin, Austin, TX, USA (TMMC), Bohart Museum of Entomology, University of California, Davis, CA, USA (UCDC), National Museum of Natural History, Smithsonian Institution, Washington, DC, USA (USNM), University of Texas Southwestern, freezers of the Grishin lab, Dallas, TX, USA (UTSW), Zoologische Staatssammlung München, Germany (ZSMC), and research collections of Ernst Brockmann, Germany (EBrockmann), Matthew J. W. Cock, UK (MJWCock), Bill Dempwolf, USA (WRDempwolf), Bernard Hermier, French Guiana (BHermier), and the late James A. Scott, USA (JAScott).

Results and Discussion

Tribe Achlyodini Burmeister, 1878, subtribe Pythonidina Grishin, 2019

Genomic analysis of the subtribe Pythonidina Grishin, 2019 reveals a large number of inconsistencies within the current classification (Fig. 1). Out of traditionally used genera, only *Gindanes* Godman and Salvin, 1895 (type species *Gindanes panaetius* Godman and Salvin, 1895) (Fig. 1 cyan) was monophyletic (but also included a species from a different genus), while species of other genera, such as *Pythonides* Hübner, 1819 (type species *Papilio jovianus* Stoll, 1782) (Fig. 1 red), *Ouleus* Lindsey, 1925 (type species *Achlyodes fridericus* Geyer, 1832) (Fig. 1 blue), *Quadrus* Lindsey, 1925 (type species *Papilio cerialis* Stoll, 1782) (Fig. 1 green), and *Zera* Evans, 1953 (type species *Achlyodes zera* Butler, 1870) (Fig. 1 magenta) were scattered among several clades. The tree reveals two major levels (genus and subgenus) in the clade containing all these species. We observe five prominent clades at the genus level (Fig. 1) that represent genera *Livida* Grishin, 2019 (type species *Pythonides assecla* Mabille, 1883), *Pythonides*, *Gindanes*, *Quadrus*, and the unnamed genus described below. To restore the monophyly of all taxa and to provide an internally consistent classification of this subtribe, we propose taxonomic changes detailed below.

Ouleus Lindsey, 1925 and *Zera* Evans, 1953 are subgenera of *Quadrus* Lindsey, 1925

The genome-based phylogeny reveals that *Ouleus* Lindsey, 1925 (type species *Achlyodes fridericus* Geyer, 1832) and *Zera* Evans, 1953 (type species *Achlyodes zera* Butler, 1870) currently treated as genera, in addition to being polyphyletic are at a subgenus level (second from the root major level) (Fig. 1). Therefore, we propose that *Ouleus* Lindsey, 1925, **new status,** and *Zera* Evans, 1953, **new status,** are subgenera of *Quadrus* Lindsey, 1925 (type species *Papilio cerialis* Stoll, 1782) and restore their monophyly as detailed below. We note that *Ouleus* and *Quadrus* were proposed in the same work issued on the same date, and we give precedence to the name *Quadrus* acting as First Revisers (ICZN Code Art. 24.2.2.) (ICZN 1999).

Taxonomic rearrangement of *Pythonides* Hübner, 1819

Inspection of the genome-based phylogeny reveals that *Pythonides* Hübner, 1819 (type species *Papilio jovianus* Stoll, 1782) as currently circumscribed (Fig. 1 red) is not monophyletic with its species dispersed among three genera: *Gindanes* Godman and Salvin, 1895 (type species *Gindanes panaetius* Godman and Salvin, 1895), *Quadrus* Lindsey, 1925 (type species *Papilio cerialis* Stoll, 1782), and a new genus described below. Clades corresponding to these genera receive 100% statistical support, and to restore the monophyly of *Pythonides*, we transfer all of its species, but two that remain in *Pythonides* (*P. lerina* (Hewitson, 1868) and *P. jovianus* (Stoll, 1782)), in these other genera to form the following **new combinations**: *Gindanes homer* (Evans, 1953), *Gindanes nides* (O. Mielke and Casagrande, 2002), *Gindanes maraca* (O. Mielke and Casagrande, 1992), *Gindanes jenmorrisae* (Shuey and Ramírez. 2022), *Gindanes tullia* (Evans, 1953), *Gindanes herennius* (Geyer, [1838]), *Gindanes proxenus* (Godman and Salvin, 1895), *Gindanes parallelus* (Mabille, 1898), *Gindanes braga* (Evans, 1953),

Figure 1. The nuclear genome-based phylogeny of Achlyodini (continued in Fig. 3). Only the segment of the tree corresponding to the subtribe Pythonidina is shown. The bottom segment of the tree (subtribe Achlyodinia) is replaced with four dots and is shown in Fig. 3. The tree is constructed from protein-coding regions in autosomes. The tree is rooted with *Carcharodus alceae* (NVG-18087F02, GenBank barcode OR665734), not displayed. Statistical support values are shown by nodes. For each specimen, its name adopted in this work is given first, and a previously used name is listed in square brackets (if different), supplemented with the DNA sample number, type status (HT holotype, LT lectotype, ST syntype, T type, PT paratype, and PLT paralectotype), general locality and collection year ("old" means collection year known, but likely before 1950, mostly around the turn of 20th century). See Table S1 in the Supplemental file (Zhang et al. 2023d) for additional data about these specimens. Synonyms are given in parentheses preceded by "=". The type status refers to this synonym if the synonym name is provided. Names of genera (larger font, more prominent tree branches, on the left) and subgenera (smaller font, less prominent tree branches, on the right) are shown by the clades corresponding to these taxa. New genus-group names are highlighted in yellow. Branches leading to the type species (or their closest sequenced relatives) of valid genus-group names are marked with large black dots and refer to the subgenus (in parenthesis) given in the corresponding name, or the genus if the subgenus is not specified. The same notations are used in Fig. 3–6. Names of taxa that before this work were placed in genera *Pythonides* (red), *Gindanes* (cyan), *Quadrus* (green), *Oulеus* (blue), and *Zera* (purple) are shown in color to illustrate rampant violations of monophyly in these taxa, corrected here.

Gindanes hampa (Evans, 1953), *Gindanes rosa* (Steinhauser, 1989), *Gindanes neivai* (Hayward, 1940), *Gindanes mundo* (H. Freeman, 1979), *Gindanes eminus* (E. Bell, 1934), *Quadrus lancea* (Hewitson, 1868), *Quadrus pescada* (E. Bell, 1956), and the remaining two in the new genus described below.

Lirra Grishin, new genus

http://zoobank.org/C0278D7F-5AF8-4C68-8306-35A67EA4AC52

Type species. *Leucochitonea limaea* Hewitson, 1868.

Definition. Currently in *Pythonides* Hübner, 1819 (type species *Papilio jovianus* Stoll, 1782), two closely related sister species *Ate pteras* Godman and Salvin, 1895 (type locality Panama: Chiriqui) and *Leucochitonea limaea* Hewitson, 1868 (type locality in French Guiana) are genetically distant from it and statistical support for their monophyly with species included here in *Pythonides* is not strong in the genomic tree (54%) (Fig. 1). The clade formed by these two species corresponds to a genus-level taxonomic category based on its position in the phylogeny and comparison to established genera-level clades. Therefore, we propose that this clade corresponds to a new genus that keys to E.41.11 in Evans (1953) and is distinguished from its relatives by the following characters: hind tibiae with one upper spur and with a tuft in males, forewing without hyaline spots, dorsal hindwing broadly blue at the margin, ventral hindwing without black overscaling of veins; uncus undivided, semi-triangular, gradually narrowing towards its end, aedeagus straight, not downturned or upturned, harpe approximately the same length as valva, narrowing distad, upturned and ending in a broad tooth pointing dorsad, costa slightly convex, ampulla with long process over harpe reaching its half. In DNA, a combination of the following nuclear genomic base pairs is diagnostic: aly531.8.1:T654C, aly536.138.5:A1345C, aly1603.75.1:C49G, aly74.2.4:A627G, aly1656.25.1:A333G.

Etymology. The name is a feminine noun in the nominative singular formed as a modified fusion of species names: *Li*[maea]+[pte]{*r*}*ra*[s].

Species included. *Ate pteras* Godman and Salvin, 1895 and *Leucochitonea limaea* Hewitson, 1868.

Parent taxon. Subtribe Pythonidina Grishin, 2019.

Trifa Grishin, new subgenus

http://zoobank.org/80AA9B97-38A1-4668-9A65-1B2D621F6DEA

Type species. *Tagiades jacobus* Plötz, 1884.

Definition. The newly expanded genus *Quadrus* Lindsey, 1925 (type species *Papilio cerialis* Stoll, 1782) can be divided into eight clades at the subgenus level in the tree (Fig. 1). In addition to the nominotypical subgenus, two of these clades correspond to traditional subgenera, previously treated as genera: *Ouleus* Lindsey, 1925 (type species *Achlyodes fridericus* Geyer, 1832) and *Zera* Evans, 1953 (type species *Achlyodes zera* Butler, 1870), and five clades represent new subgenera. One of these new subgenera forms a clade sister to the rest and is stronger differentiated from them genetically. It keys to E.39.1 (in part, as a synonym of *cerealis* [sic], a synonymy probably based on a misidentification) or E.13.2 in Evans (1953) and is distinguished from its relatives by the following characters: dorsal hindwing with dark-brown base and two bands (postdiscal and submarginal), ventral hindwing mostly blue except submarginal brown area, forewing with one or two dash-like (not collected into a "C") hyaline spots in discal cell; valva with a process from mid-costa, not from the ampulla area; harpe longer than valva, with strongly convex distal margin, narrowing to a point. In DNA, a combination of the following nuclear genomic base pairs is diagnostic: aly3312.4.6:C55A, aly84.97.14:C160T, aly84.97.14:G171T, aly276558.35.2:T64A, aly276558.35.2:C65G.

Etymology. The name is a feminine noun in the nominative singular, inspired by the three dark bands on dorsal hindwings of these species: *Tri-fa*[scia].

Species included. *Pythonides ineptus* Draudt, 1922, *Quadrus francesius* Freeman, 1969, and *Tagiades jacobus* Plötz, 1884.

Parent taxon. Genus *Quadrus* Lindsey, 1925.

Tuberna Grishin, new subgenus

http://zoobank.org/7C63B146-7D14-42AC-B8EC-071C103D39D4

Type species. *Pythonides contubernalis* Mabille, 1883.

Definition. The newly expanded genus *Quadrus* Lindsey, 1925 (type species *Papilio cerialis* Stoll, 1782) can be divided into eight clades at the subgenus level in the tree (Fig. 1). In addition to the nominotypical subgenus, two of these clades correspond to traditional subgenera, previously treated as genera: *Ouleus* Lindsey, 1925 (type species *Achlyodes fridericus* Geyer, 1832) and *Zera* Evans, 1953 (type species *Achlyodes zera* Butler, 1870), and five clades represent new subgenera. One of these new subgenera is sister to all others except *Trifa* **new subgenus** and keys to or E.39.4a or E.41.1 in Evans (1953) and is distinguished from its relatives by the following characters: dorsal hindwing either with 2 bright shiny blue bands, or primarily blue with dark veins and central white streak; uncus undivided, stem-shaped, rounded at its end, with parallel sides in dorsal view, ampulla with projection (or a hump), harpe longer than valva, either with concave dorsal margin or rounded, nearly oval, merged with valva and ampulla with a small hump. In DNA, a combination of the following nuclear genomic base pairs is diagnostic: aly2116.6.1:T200C, aly2116.6.1:C326T, aly1475.25.1:A1840C, aly1475.25.1:T1200A, aly1838.49.3:G435T.

Etymology. The name is a feminine noun in the nominative singular, formed from the type species name: [con] *Tuberna*[lis].

Species included. *Pythonides contubernalis* Mabille, 1883, *Pythonides deyrollei* Mabille, 1877, and *Leucochitonea lancea* Hewitson, 1868.

Parent taxon. Genus *Quadrus* Lindsey, 1925.

Ebona Grishin, new subgenus

http://zoobank.org/8A1637CD-1681-42BC-AE8A-04FF28148C42

Type species. *Quadrus eboneus* E. Bell, 1947.

Definition. The newly expanded genus *Quadrus* Lindsey, 1925 (type species *Papilio cerialis* Stoll, 1782) can be divided into eight clades at the subgenus level in the tree (Fig. 1). In addition to the nominotypical subgenus, two of these clades correspond to traditional subgenera, previously treated as genera: *Ouleus* Lindsey, 1925 (type species *Achlyodes fridericus* Geyer, 1832) and *Zera* Evans, 1953 (type species *Achlyodes zera* Butler, 1870), and five clades represent new subgenera. One of these new subgenera brings together species dispersed among three genera (*Ouleus*, *Zera*, and *Pythonides*). It keys to E.37.3a in Evans (1953) and is distinguished from its relatives by mostly dark wings without blue, hind-tibiae with one pair of spurs, tapered to a point uncus tip, and stout ampulla process. In DNA, a combination of the following base nuclear genomic pairs is diagnostic: aly770.31.1:C235A, aly770.31.1:A588G, aly6311.5.2:A42G, aly6311.5.2:A60G, aly1370.7.2:T139G.

Etymology. The name is a feminine noun in the nominative singular, given for the dark appearance of these species, with "o" to derive from the type species name and to avoid homonymy with *Ebena* Schumacher, 1817 (in Mollusca); from the genus *Ebenus*, commonly known as ebony plants. Ebony wood is known for its dark, brown, and often nearly black colors.

Species included. *Pythonides juxta* Bell, 1934, *Quadrus eboneus* E. Bell, 1947, *Ouleus negrus* Nicolay, 1980, *Ouleus negrus cristatus* Steinhauser, 1989 (see below), and *Pythonides pescada* Bell, 1956.

Parent taxon. Genus *Quadrus* Lindsey, 1925.

Quadrus (*Ebona*) *cristatus* (Steinhauser, 1989) is a species distinct from *Quadrus* (*Ebona*) *negrus* (Nicolay, 1980)

The genomic tree reveals that the holotype of *Ouleus negrus cristatus* Steinhauser, 1989 (type locality Colombia: Valle del Cauca, Rio Anchicayá, sequenced as NVG-15038D08, GenBank barcode OR665721) and a topotypical paratype of *Ouleus negrus* Nicolay, 1980 (type locality Panama: Veraguas Prov., Santa Fe, sequenced as NVG-19076D07, GenBank barcode OR665722) are not monophyletic and belong to different, albeit closely related, clades in the subgenus *Ebona* **new subgenus** of *Quadrus* Lindsey, 1925 (type species *Papilio cerialis* Stoll, 1782) (Fig. 1). Furthermore, they are genetically differentiated from each other, e.g., COI barcode difference of 4.3% (28 bp). Therefore, we propose that *Quadrus* (*Ebona*) *cristatus* (Steinhauser, 1989), **new status,** is a species distinct from *Quadrus* (*Ebona*) *negrus* (Nicolay, 1980). We note that *Q. cristatus* is closely related to (conspecific with?) *Pythonides pescada* E. Bell, 1956 (type locality in Ecuador: Río Pescado) (Fig. 1) and is phenotypically similar to it in having a distal part of ventral hindwing white. However, *O. negrus* is closely related to (but distinct from!) *Zera eboneus* E. Bell, 1947 (type locality in Mexico: Veracruz) and is phenotypically similar to it in largely uniform dark-brown, unspotted appearance on both sides of wings. These close relationships were overlooked, likely because species in the two pairs were incorrectly placed in different genera before (*Ouleus* and *Pythonides*, and *Ouleus* and *Zera*). If they were classified correctly, each pair's more recently proposed species might have never been described due to phenotypic similarities with its previously named counterpart. Analysis of additional specimens, including their genomic sequencing, may lead to conclusion that *Q. pescada* and *Q. cristatus* are conspecific because they are more similar to each other genetically (0.3%, 2 bp COI barcode difference) than *O. eboneus* to *O. negrus*, the latter pair being sufficiently different from each other for us to be confident about their specie-level status (COI barcode difference of 2.6%, 17 bp).

Noctis Grishin, new subgenus

http://zoobank.org/628D6182-4F0F-4953-83CB-7781E5AFBC99

Type species. *Achlyodes accedens* Mabille, 1895.

Definition. The newly expanded genus *Quadrus* Lindsey, 1925 (type species *Papilio cerialis* Stoll, 1782) can be divided into eight clades at the subgenus level in the tree (Fig. 1). In addition to the nominotypical subgenus, two of these clades correspond to traditional subgenera, previously treated as genera: *Ouleus* Lindsey, 1925 (type species *Achlyodes fridericus* Geyer, 1832) and *Zera* Evans, 1953 (type species *Achlyodes zera* Butler, 1870), and five clades represent new subgenera. One of these new subgenera keys to E.37.6a in Evans (1953) and is distinguished from its relatives by mostly dark wings without blue, uncus tip with a small stalked triangle, and slender ampulla process. In DNA, a combination of the following nuclear genomic base pairs is diagnostic: aly1139.36.2:G59A, aly1838.6.2:A63G, aly529.46.1:A354G, aly451.31.2:T72A, aly2487.16.4:A87G.

Etymology. The name is a masculine noun in the nominative singular, given for the black appearance of these species: *noctis* is Latin for "of the night" or "nighttime."

Species included. *Ouleus dilla* Evans, 1953 and *Achlyodes accedens* Mabille, 1895.

Parent taxon. Genus *Quadrus* Lindsey, 1925.

Cyrna Grishin, new subgenus

http://zoobank.org/1E1041B3-4CDC-4C7C-ACF3-522D4ED3233A

Type species. *Achlyodes cyrna* Mabille, 1895.

Definition. The newly expanded genus *Quadrus* Lindsey, 1925 (type species *Papilio cerialis* Stoll, 1782) can be divided into eight clades at the subgenus level in the tree (Fig. 1). In addition to the nominotypical subgenus, two of these clades correspond to traditional subgenera, previously treated as genera: *Ouleus* Lindsey, 1925 (type species *Achlyodes fridericus* Geyer, 1832) and *Zera* Evans, 1953 (type species *Achlyodes zera* Butler, 1870), and five clades represent new subgenera. One of these new subgenera keys to E.37.1c in Evans (1953) and is distinguished from its relatives by mostly dark wings without blue, no tibial tuft in males, hind-tibiae with two pairs of spurs, and uncus tip tapered to a point. In DNA, a combination of the following nuclear genomic base pairs is diagnostic: aly84.28.1:T2136A, aly84.28.1:G2577A, aly203.14.2:T24C, aly203.14.2:T54C, aly1656.40.1:A1276G.

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

Species included. *Achlyodes bubaris* Godman and Salvin, 1895, *Achlyodes calavius* Godman and Salvin, 1895, *Ouleus candidus* Steinhauser, 1989, *Bolla zora* Evans, 1953 (see below), and *Achlyodes cyrna* Mabille, 1895.

Parent taxon. Genus *Quadrus* Lindsey, 1925.

Quadrus (*Cyrna*) *zora* (Evans, 1953), new combination

Inspection of the holotype of *Bolla zora* Evans, 1953 (type locality in Ecuador), which is a female, reveals that it does not belong to *Bolla* Mabille, 1903 (type species *Bolla pullata* Mabille, 1903, treated as a junior subjective synonym of *Staphylus imbras* Godman and Salvin, 1896), but instead is a species of *Quadrus* Lindsey, 1925 (type species *Papilio cerialis* Stoll, 1782) similar to *Quadrus* (*Cyrna*) *calavius* Godman and Salvin, 1895. On the dark-brown forewing, it possesses three subapical white dots in an arc, the middle dot smallest (the shape, size, and location of these dots suggest *Quadrus*), and two faint bands from costa to inner margin, postdiscal and subapical. Therefore, we propose a new combination *Quadrus* (*Cyrna*) *zora* (Evans, 1953).

Quadrus (*Quadrus*) *ophia* (A. Butler, 1870) is a species distinct from *Quadrus* (*Quadrus*) *lugubris* (R. Felder, 1869)

The genomic tree reveals that *Achlyodes ophia* Butler, 1870 (type locality in Venezuela), currently treated as a subspecies of *Quadrus lugubris* (R. Felder, 1869) (type locality in Mexico: Veracruz), is not monophyletic with it and instead is sister to *Quadrus truncata* (Hewitson, 1870) (type locality in Ecuador) (Fig. 1). Moreover, genetic differentiation between *Q. lugubris ophia* and *Q. lugubris lugubris* is at the level characteristic of distinct species, e.g., their COI barcodes differ by 3.5% (23 bp). Therefore, we propose that *Quadrus* (*Quadrus*) *ophia* (A. Butler, 1870), **restored status**, is a species distinct from *Quadrus* (*Quadrus*) *lugubris* (R. Felder, 1869).

Lectotype designation for *Achlyodes servius* Plötz, 1884

Achlyodes servius Plötz, 1884 (type locality in Brazil), treated above as a valid species in the subgenus *Zera* Evans, 1953 (type species *Achlyodes zera* Butler, 1870) of the genus *Quadrus* Lindsey, 1925 (type species *Papilio cerialis* Stoll, 1782), was described from an unstated number of specimens and the name "servius" was attributed to a letter or a manuscript by Herrich-Schäffer (Plötz 1884). A detailed search in the MFNB collection yielded two specimens we believe are syntypes of *A. servius*, sequenced as NVG-21115E08 (Fig. 2b) and NVG-21115E10. The first one, a male, agrees with the original description and bears an identification label crediting Herrich-Schäffer for the manuscript name "sergius" (similar enough to "servius" to assume the difference resulting from some trivial error), as mentioned by Plötz in the original description. The second specimen, a female, bears a label in Plötz's handwriting, "Brasilia / Nov Frib." but has two hyaline spots by the forewing apex, not three as mentioned in the original description (it was probably not the specimen drawn, and Plötz wrote descriptions from his drawings). The two specimens were near each other in the same drawer, were collected in the Brazilian state of Rio de Janeiro, and are conspecific judging from our genomic sequencing results (Fig. 2a). Because one of these specimens was labeled by Plötz himself, and the other one bears a label attributing its name to the manuscript by Herrich-Schäffer (as in the original description of *A. servius*) and also bears a specimen number label (5908) identifying it as a part of Hesperiidae collection inspected (and at times references in publications using these numbers) by Plötz, these specimens are syntypes. To stabilize nomenclature, N.V.G. hereby designates the syntype in the MFNB collection, a male shown in Fig. 2b, bearing three labels (2nd green, others white): [5908], [Sergius | HSch. ms | Rio v. Lgsdf], [DNA sample ID: | NVG-21115E08 | c/o Nick V. Grishin], as the **lectotype** of *Achlyodes servius* Plötz, 1884. The lectotype was missing an abdomen when inspected. According to its large green label in the handwriting of Carl Heinrich Hopffer (1810–1876), who was the curator of the collection in Berlin until his death, this specimen was collected in Brazil: Rio de Janeiro by Georg Heinrich von Langsdorff (1774–1852) and identified by the name "sergius" in an unpublished manuscript by Herrich-Schäffer. The number on the first label, "5908", is the entry in the collection Catalog by Hopffer. In addition to confirming the information repeated on the green label, the Catalog reveals that there were three specimens with this number. All these details increase our confidence that the lectotype was indeed a syntype. The COI barcode sequence of *A. servius* lectotype, sample NVG-21115E08, GenBank OR665723, 658 base pairs, is:

AACTTTATATTTTATTTTTGGAATTTGAGCAGGAATAGTAGGAACTTCATTAAGTTTATTAATTCGAACTGAATTAGGAAATCC
TGGATCCTTAATTGGAGATGATCAAATTTATAATACTATTGTAACTGCTCATGCTTTTATTATAATTTTTTTTATAGTTATACCAA
TTATAATTGGAGGATTTGGGAATTGACTAGTACCCCTTATACTAGGAGCCCCTGATATAGCTTTTCCTCGAATAAATAATATAAG
TTTTTGATTATTACCTCCCTCTTTAATATTATTAATTTCAAGTAGTGTTGTAGAAAATGGAGCCGGTACAGGTTGAACCGTATA
CCCTCCTCTTTCTGCTAATATTGCTCATCAAGGCTCATCAGTAGATTTAGCAATCTTTTCTCTTCATTTAGCAGGAATTTCATC
AATTTTAGGAGCTATTAATTTTATTACTACAATTATTAATATACGAATTAATAATCTTTCCTTAGATCAAATACCCCTATTTGTTT
GATCTGTTGGAATTACAGCATTACTTTTACTATTATCTTTACCTGTTTTAGCTGGAGCTATTACTATATTATTAACTGACCGAAA
TTTAAATACATCATTTTTTGATCCTGCTGGAGGAGGAGATCCAATTTTATATCAACATTTATTT

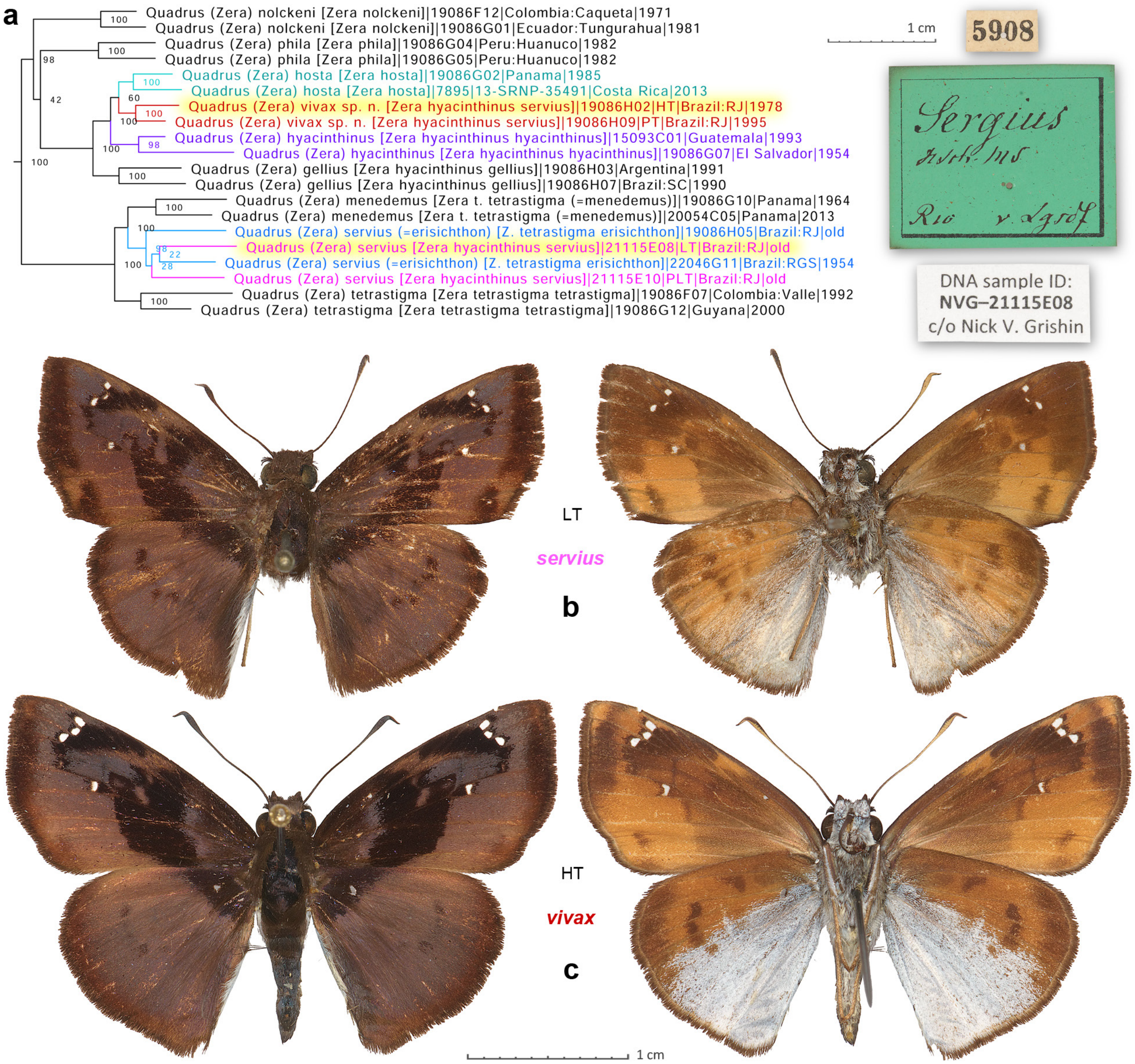

Figure 2. *Quadrus* (*Zera*) nuclear genome-based phylogeny and type specimens. **a)** The nuclear genome-based phylogeny of selected species: *Q. vivax* **sp. n.** (red), *Q. hyacinthinus* (purple), *Q. hosta* (cyan), *Q. servius* **stat. rest.** (blue and magenta, with its synonym *Achlyodes erisichthon* labeled in blue) rooted with the remaining *Zera* species (not shown; see Fig. 1). Specimens shown below are highlighted in yellow; see Fig. 1 for other notations. **b)** Lectotype of *Quadrus* (*Zera*) *servius* designated herein, with its labels shown above on the right. **c)** Holotype of *Quadrus* (*Zera*) *vivax* **sp. n**. Specimens are in dorsal (left) and ventral (right) views, data in text. The scale bar at the bottom refers to specimens; the scale bar at the top refers to labels reduced by 1/3 compared to specimens.

Quadrus (*Zera*) *gellius* (Mabille, 1903) and *Quadrus* (*Zera*) *servius* (Plötz, 1884) are species distinct from *Quadrus* (*Zera*) *hyacinthinus* (Mabille, 1877)

Genomic sequencing of the lectotype of *Achlyodes servius* Plötz, 1884 (type locality in Brazil, sequenced as NVG-21115E08) from “Rio” in MFNB currently treated as a subspecies of *Quadrus* (*Zera*) *hyacinthinus* (Mabille, 1877) (type locality not specified, likely in Central America) reveals that it is in a clade different from it and instead is closer to *Quadrus* (*Zera*) *tetrastigma* (Sepp, [1847]) (type locality in Suriname) while being genetically differentiated from the latter as well (Fig. 1, 2a), e.g., COI barcode difference of 0.9% (6 bp) while showing consistent separation in the Z chromosome with F_{st}/G_{min} of 0.51/0.002. Furthermore, *Pythonides gellius* Mabille, 1903 (type locality in "Ecuador", likely in SE South America), currently another subspecies of *Q. hyacinthinus*, while being closer related to it than *A. servius*, is also non-monophyletic with it and shows notable genetic differentiation from it (Fig. 1, 2a), e.g., COI barcode difference of 3.8% (25 bp). Therefore, we propose that *Quadrus* (*Zera*) *gellius* (Mabille, 1903), **restored status**, and *Quadrus* (*Zera*) *servius* (Plötz, 1884), **restored status**, are species distinct from *Quadrus* (*Zera*) *hyacinthinus* (Mabille, 1877) and from *Quadrus* (*Zera*) *tetrastigma* (Sepp, [1847]).

Quadrus (*Zera*) *vivax* Grishin, new species

http://zoobank.org/6B5F54D9-0706-4CDC-9811-05E1A9414155

Definition and diagnosis. Evans misidentified (at least some) *Achlyodes servius* Plötz, 1884 (type locality in Brazil), which he treated as a subspecies of *Zera hyacinthinus* (Mabille, 1877) (type locality not specified, likely in Central America). Above, we placed *Zera* Evans, 1953 (type species *Achlyodes zera* Butler, 1870) in the genus *Quadrus* Lindsey, 1925 (type species *Papilio cerialis* Stoll, 1782) as a subgenus. Also, as shown above, *A. servius* is not closely related to *Q. hyacinthinus* but instead is a distinct species closer to *Quadrus* (*Zera*) *tetrastigma* (Sepp, [1847]) (type locality in Suriname). However, the species that keys to Evans' "*Zera hyacinthinus servius*" and indeed is closer related to *Q. hyacinthinus* does not have a name and is described here. It is a species-level taxon, not a subspecies of *Q. hyacinthinus*, due to genetic differentiation (Fig. 2a), e.g., their COI barcodes differ by 2% (13 bp) in the presence of consistent phenotypic differences described below. Furthermore, while this species is in the same clade as *Q. hyacinthinus*, it is sister to *Quadrus* (*Zera*) *hosta* (Evans, 1953) (type locality in Costa Rica), differing from it by 3.8% (25 bp) in the COI barcode. This new species keys to E.38.5b in Evans (1953) and is distinguished from its relatives by the following combination of characters: dorsal forewing without a hyaline spot in cell CuA_1-CuA_2, dark central area extending neither to the wing base nor the end of discal cell, wing base violaceous, dark area in discal cell more extensive than in relatives and without prominent, continuous pale bar crossing it, but with one or two small, pale, sometimes narrowly connected spots; ventral forewing with a conspicuous tawny spot by the apex and tornal area broadly tawny, could be extending to and reaching costal margin, mostly unmarked, but sometimes with submarginal dark spot(s); dark discal band absent or vestigial on dorsal hindwing; tornal half of ventral hindwing bluish-white, contrasting with the tawny area and not gradually merging into it as in *Q. servius*.

Barcode sequence of the holotype. Sample NVG-19086H02, GenBank OR721875, 658 base pairs:

AACCTTATATTTTATTTTTGGAATTTGAGCAGGAATAGTTGGAACTTCTTTAAGTTTGTTAATTCGAACTGAATTAGGAAATCC
TGGATCTTTAATTGGAGATGATCAAATTTATAATACTATCGTAACTGCTCATGCTTTTATTATAATTTTTTTTATAGTTATACCAA
TTATAATTGGAGGATTTGGAAATTGACTAGTACCCCTTATACTAGGAGCACCTGATATAGCTTTCCCCCGAATAAATAATATAA
GTTTTTGGTTATTACCCCCTTCTTTAATATTATTAATCTCAAGTAGTATTGTAGAAAATGGAGCTGGTACAGGTTGAACAGTTT
ACCCACCTCTTTCAGCTAATATTGCCCATCAAGGATCATCTGTAGATTTAGCAATTTTTTCTCTTCATTTAGCAGGAATTTCTT
CAATTCTAGGAGCTATTAATTTTATTACTACAATTATTAATATACGAGTCAATAATCTTTCCTTAGATCAAATACCCCTTTTTGTT
TGATCCGTAGGAATTACAGCATTACTTTTATTATTATCTTTACCTGTTTTAGCTGGAGCTATTACTATACTATTAACTGATCGAA
ATTTAAATACATCATTTTTTGATCCTGCTGGAGGAGGAGATCCAATTTTATATCAACATTTATTT

Type material. Holotype: ♂ currently deposited in the National Museum of Natural History, Smithsonian Institution, Washington, DC, USA [USNM], illustrated in Fig. 2c, bears four printed (date handwritten) labels: three white [BRAZIL: RJ | Petropolis 900m | 6 Aug.'78 | S. S. Nicolay], [DNA sample ID: | NVG-19086H02 | c/o Nick V. Grishin], [USNMENT | {QR Code} | 01588802] and one red [HOLOTYPE ♂ | Quadrus (Zera) | vivax Grishin]. **Paratypes:** 1♂ 1♀ from Brazil: 1♂ Rio de Janeiro, Teresópolis, elevation 1000 m, GPS −22.4500, −42.9833, 17-Feb-1995, Robbins and Caldas leg. (NVG-19086H09, USNMENT 01588809) [USNM]; 1♀ Santa Catarina, Sao Bento do Sul, Feb-1984, Rank leg., from D. and J. Jenkins collection (NVG-15093C04) [MGCL].

Type locality. Brazil: Rio de Janeiro, Petrópolis.

Etymology. In Latin, *vivax* means lively or vibrant, given for the contrasty and more vivid appearance of this species compared to its relatives: ventral side of wings with more conspicuous tawny patches and spots and brighter, whiter, better defined pale area on the hindwing. The name is an adjective.

Distribution. Southeast and South Brazil.

Achlyodes erisichthon Plötz, 1884 is a junior subjective synonym of *Quadrus* (*Zera*) *servius* (Plötz, 1884), not a subspecies of *Quadrus* (*Zera*) *tetrastigma* (Sepp, [1847])

Genomic comparison of the lectotype of *Achlyodes servius* Plötz, 1884 (type locality in Brazil, sequenced as NVG-21115E08) from "Rio" in MFNB (white ventral hindwing by inner margin) with specimens identified by us as *Quadrus* (*Zera*) *tetrastigma erisichthon* (Plötz, 1884) (type locality not stated, syntypes not located, specimens from SE Brazil with ventral hindwing largely pale-orange, yellower by inner margin but not white) reveals the lack of genetic differentiation between them (Fig. 1, 2a), i.e., their COI barcodes are identical. Therefore, these taxa are different color morphs of the same species, and we propose that *Achlyodes erisichthon* Plötz, 1884 is a junior subjective **new synonym** of *Quadrus* (*Zera*) *servius* (Plötz, 1884), not a subspecies of *Quadrus* (*Zera*) *tetrastigma* (Sepp, [1847]). We note that *A. servius* and *A. erisichthon* were proposed in the same work (on the same page) issued on the same date, and we give precedence to the name *A. servius* acting as First Revisers (ICZN Code Art. 24.2.2.).

Furthermore, in the absence of extant type specimens, the identity of *A. erisichthon* remains somewhat uncertain, and we use this name for the taxon identified as such by Evans (1953). Judging from the original description (Plötz 1884) and copies (in BMNH and USNM) of the unpublished and lost illustration t[afel]. 982 by Plötz (Godman 1907), we believe that Evans identified this species correctly. Moreover, due to the extensive tawny coloration of the ventral forewing, prominent forewing subapical spots, and other wing pattern details as illustrated in the drawings, *A. erisichthon* is not conspecific with *Q. tetrastigma*, a conclusion that would hold even if Evans misidentified *A. erisichthon*. However, two characters of the *A. erisichthon* drawing reveal an unusual specimen, i.e., four—instead of the usual three—forewing subapical spots (also mentioned in the original description) and the absence of a dark cross-bar in the forewing discal cell, which is mostly violaceous—instead of dark-brown in the middle—cast certain doubt on the identification of this taxon and even its attribution to *Quadrus* (*Zera*).

Nevertheless, out of all Hesperiidae species known to us worldwide (the type locality of *A. erisichthon* was not stated), *Quadrus* (*Zera*) is the best match to the drawing due to this violaceous coloration, s-shaped placement of the forewing subapical spots, and other details of wing pattern, in particular, on the ventral side. While we have seen *Quadrus* (*Zera*) specimens with a vestigial 4th subapical forewing spot, none was suitable for the neotype of *A. erisichthon* because these specimens did not agree with the drawing and the original description in other characters. In its largely tawny hindwing, *A. erisichthon* is also similar to *Quadrus* (*Zera*) *gellius* (Mabille, 1903) (type locality in "Ecuador", likely in SE South America). However, the hindwing is more uniformly tawny in the latter species, but the original description of *A. erisichthon* specifically mentions greenish-gray overscaling by the inner margin (Plötz 1884). This overscaling is typical of *Q. servius* form lacking extensive white area on the ventral hindwing and is the manifestation of this white overscaling, but much reduced.

Finally, Plötz studied *Q. servius* specimens from SE Brazil (at least four, see above), proposing this name for the white-overscaled form. It is likely that he also encountered the tawny hindwing form from the same area and, additionally noticing four (not three) subapical spots on an unusual specimen, considered it to be a closely related but distinct species he called *A. erisichthon*, which he placed in the key next to *Q. servius* and, therefore, these two species were likely quite close to each other in appearance. We suggest the synonymy proposed above for all these reasons, and will be looking for a specimen suitable for *A. erisichthon* neotype designation, keeping in mind that it could be not yet re-discovered species different from all others currently known.

Quadrus (*Zera*) *menedemus* (Godman and Salvin, 1894) is a valid species, not a synonym of *Quadrus* (*Zera*) *tetrastigma* (Sepp, [1847])

The genomic tree reveals that *Pythonides menedemus* Godman and Salvin, 1894 (type locality in Panama: Chiriqui) currently treated as a junior subjective synonym of *Quadrus* (*Zera*) *tetrastigma* (Sepp, [1847]) (type locality in Suriname) is not monophyletic with it and instead is sister to *Quadrus* (*Zera*) *servius* (Plötz, 1884) (type locality in Brazil) (Fig. 1, 2a). Moreover, genetic differentiation between *P. menedemus* and *Q. tetrastigma* is at the level characteristic of distinct species, e.g., their COI barcodes differ by 1.8% (12 bp). Therefore, we propose that *Quadrus* (*Zera*) *menedemus* (Godman and Salvin, 1894), **restored status**, is a valid species, not a synonym of *Quadrus* (*Zera*) *tetrastigma* (Sepp, [1847]). We note that while the name *Q. menedemus* is defined by its extant syntypes, the identity of *Q. tetrastigma* could be questioned, because it is identified from the original description and illustrations only; its syntypes likely lost. However, this name has been stably applied to the populations in the Guianas, and we do not have a compelling reason to challenge this interretation. Currently, there is no exceptional need to define *Q. tetrastigma* by a neotype.

Atarnes Godman and Salvin, 1897 and *Eburuncus* Grishin, 2012 are subgenera of *Milanion* Godman and Salvin, 1895

Inspection of the genomic tree reveals close clustering of the three genera: *Atarnes* Godman and Salvin, 1897 (type species *Leucochitonea sallei* C. Felder and R. Felder, 1867), *Eburuncus* Grishin, 2012 (type species *Leucochitonea unifasciata* C. Felder and R. Felder, 1867), and *Milanion* Godman and Salvin, 1895 (type species *Papilio hemes* Cramer, 1777) that taken together are prominently distinct from their relatives (Fig. 1). The tree taxa share a number of phenotypical features and some species in them were misclassified before (Grishin 2012). Therefore, to simplify the taxonomic classification and reflect all these similarities, we propose to treat *Atarnes* Godman and Salvin, 1897, **new status,** and *Eburuncus* Grishin, 2012, **new status,** as subgenera of *Milanion* Godman and Salvin, 1895.

Tribe Achlyodini Burmeister, 1878, subtribe Achlyodina Burmeister, 1878

Eurypterus later Mabille, 1891 and *Eurypterus haber* Mabille, 1891 belong to the genus *Eantis* Boisduval, 1836, not *Aethilla* Hewitson, 1868

Eurypterus later Mabille, 1891 (type locality likely in Peru) and *Eurypterus haber* Mabille, 1891 (type locality probably in Peru) are currently in the genus *Aethilla* Hewitson, 1868 (type species *Aethilla eleusinia* Hewitson, 1868),

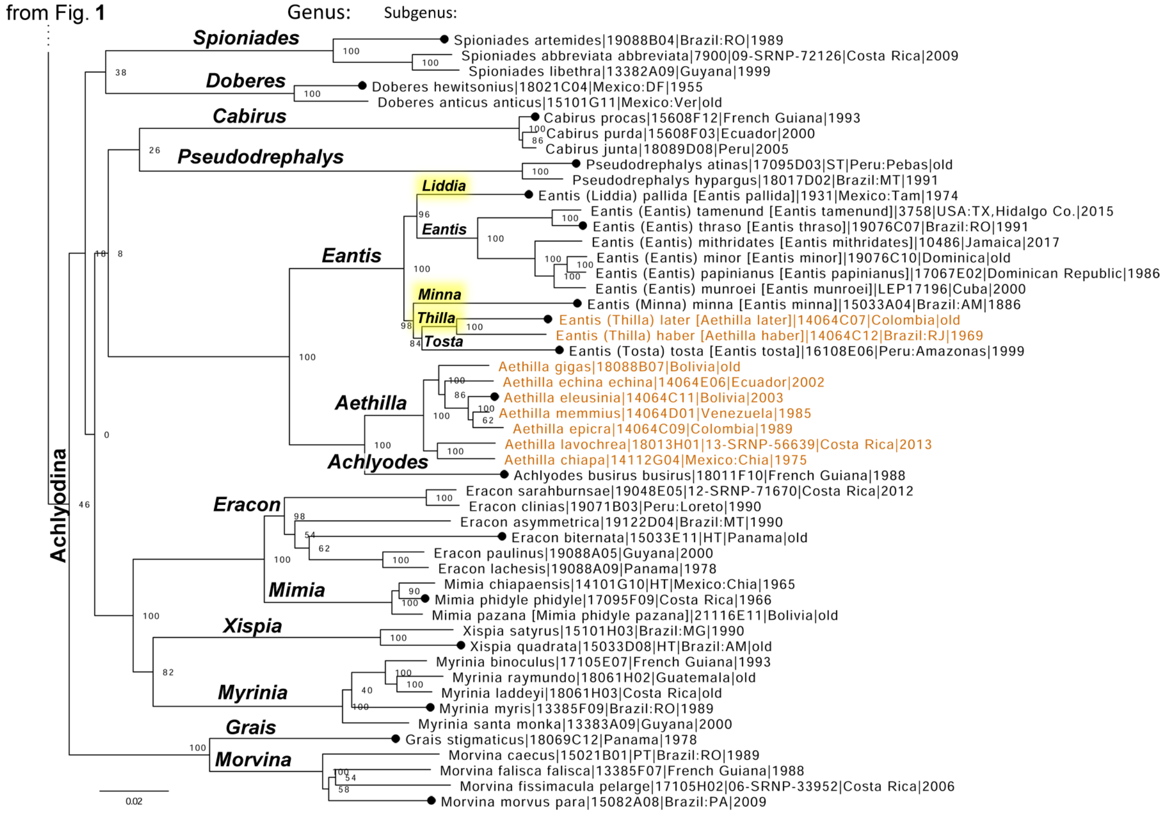

Figure 3. The nuclear genome-based phylogeny of Achlyodini (continued from Fig. 1). A segment corresponding to the subtribe Achlyodinia is shown. The top segment of the tree (subtribe Pythonidina) is replaced with four dots and is shown in Fig. 1. See Fig. 1 for notations. The names of taxa that before this work were placed in the genus *Aethilla* are shown in orange to illustrate the lack of monophyly.

because of their general appearance and visual similarities with *Aethilla*. However, the genomic tree reveals that they are not monophyletic with *Aethilla*, which is sister to *Achlyodes* Hübner, 1819 (type species *Papilio busirus* Cramer, 1779), but instead originate within *Eantis* Boisduval, 1836 (type species *Urbanus thraso* Hübner, 1807) (Fig. 3). Therefore, we transfer them from *Aethilla* to *Eantis* forming **new combinations**: *Eantis later* (Mabille, 1891) and *Eantis haber* (Mabille, 1891).

Liddia Grishin, new subgenus

http://zoobank.org/BEF8C41C-DD78-426C-BB39-91BDA3210A75

Type species. *Helias pallida* R. Felder, 1869.

Definition. The genomic tree shows that the genus *Eantis* Boisduval, 1836 (type species *Urbanus thraso* Hübner, 1807) splits into five lineages at the subgenus level, and we regard these lineages as representing five subgenera (Fig. 3). Out of these subgenera, in addition to the nominotypical, only one has a name: *Tosta* Evans, 1953 (type species *Tosta tosta* Evans, 1953), while three others are new. One of these new subgenera keys to F.2.4 in Evans (1953) and is distinguished from its relatives by the following characters: forewing only slightly falcate, wings paler brown above; valvae asymmetric, left with a process from the ampulla, right without, harpe with convex dorsal margin without a process at its base by ampulla, aedeagus not strongly bent in the middle. In DNA, a combination of the following nuclear genomic base pairs is diagnostic: aly1249.23.2:T82G, aly322.13.2:A64C, aly2612.12.4:A232C, aly2612.12.4:G284C, aly619.2.4:A36T.

Etymology. The name is a feminine noun in the nominative singular, formed from the type species name: [pal] *Lid*{*di*}*a*.

Species included. Only the type species.

Parent taxon. Genus *Eantis* Boisduval, 1836.

Minna Grishin, new subgenus

http://zoobank.org/BAE6E4C1-284A-401C-99CD-2F51DB4A382B

Type species. *Achlyodes minna* Evans, 1953.

Definition. The genomic tree shows that the genus *Eantis* Boisduval, 1836 (type species *Urbanus thraso* Hübner, 1807) splits into five lineages at the subgenus level, and we regard these lineages as representing five subgenera (Fig. 3). Out of these subgenera, in addition to the nominotypical, only one has a name: *Tosta* Evans, 1953 (type species *Tosta tosta* Evans, 1953), while three others are new. One of these new subgenera keys to F.2.3. in Evans (1953) and is distinguished from its relatives by the following characters: forewing only slightly falcate, wings dark-brown above; process from ampulla is longer and thinner than in others, and there is no process from the base of harpe near ampulla, aedeagus not strongly bent in the middle. In DNA, a combination of the following nuclear genomic base pairs is diagnostic: aly4333.9.1:C37T, aly822.26.1:T192C, aly127.21.4:T198G, aly1313.7.1:G322T, aly481.7.1:A380C.

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

Species included. Only the type species.

Parent taxon. Genus *Eantis* Boisduval, 1836.

Thilla Grishin, new subgenus

http://zoobank.org/ADF9A522-9D1D-466B-8A62-65A40F9E70F2

Type species. *Eurypterus later* Mabille, 1891.

Definition. The genomic tree shows that the genus *Eantis* Boisduval, 1836 (type species *Urbanus thraso* Hübner, 1807) splits into five lineages at the subgenus level, and we regard these lineages as representing five subgenera (Fig. 3). Out of these subgenera, in addition to the nominotypical, only one has a name: *Tosta* Evans, 1953 (type species *Tosta tosta* Evans, 1953), while three others are new. One of these new subgenera consists of species previously placed in *Aethilla* Hewitson, 1868 (type species *Aethilla eleusinia* Hewitson, 1868) and keys to F.1.8 or F.1.4a (in part, as incorrect synonymy) in Evans (1953) and is distinguished from its relatives by the following characters: forewing more pointed or even slightly falcate at the apex, hindwing less produced or more rounded at the tornus; ampulla with a long terminally serrated process directed dorsoposterad and extending over harpe, harpe with process-like expansion at its base by ampulla. In DNA, a combination of the following nuclear genomic base pairs is diagnostic: aly577.14.5:A210G, aly728.5.4:G78A, aly461.13.3:T129C, aly2012.59.3:A90G, aly2012.59.3:T100C.

Etymology. The name is a feminine noun in the nominative singular, formed from the previous genus name for these species: [Ae]*Thilla*.

Species included. *Eurypterus later* Mabille, 1891 and *Eurypterus haber* Mabille, 1891.

Parent taxon. Genus *Eantis* Boisduval, 1836.

Mimia pazana Evans, 1953 is a species distinct from *Mimia phidyle* (Godman and Salvin, 1894)

The genomic tree reveals that *Mimia phidyle* (Godman and Salvin, 1894) (type locality in Panama: Chiriqui) is paraphyletic with respect to *Mimia chiapaensis* Freeman, 1969 (type locality in Mexico: Chiapas), with *Mimia phidyle pazana* Evans,1953 (type locality in Bolivia) being sister to the clade of the former two taxa (Fig. 3). The two subspecies of *M. phidyle* are genetically differentiated at the level typical for distinct, and not even very closely related, species (e.g., their COI barcodes differ by 4.9%, 32 bp) and are phenotypically different (Evans 1953). Therefore, we propose that *Mimia pazana* Evans,1953, **new status,** is a species distinct from *Mimia phidyle* (Godman and Salvin, 1894).

Tribe Carcharodini Verity, 1940

Genomic analysis of the tribe Carcharodini Verity, 1940 reveals six prominent clades at the subtribe tree level (Fig. 4–6). Therefore, we partition the tribe into six subtribes corresponding to these clades. Only one of these subtribes, the nominotypical, has a name, and others are new. These five subtribes are described below.

Cyclosemiina Grishin, new subtribe

http://zoobank.org/C9F6823E-F97F-4C0B-8C9A-BF1E09CC49BE

Type genus. *Cyclosemia* Mabille, 1878.

Definition. This new subtribe corresponds to one of the six major clades in the tribe Carcharodini Verity, 1940 (Fig. 4–6). It keys to E.27 in Evans (1953) and is diagnosed by the following combination of characters: uncus undivided, gracile, valvae symmetrical, typically with a style; palpi with short 2nd and long 3rd segments, males without costal fold, dorsal forewing at the end of discal cell with an eyespot, usually bi-pupiled, and both wings with dark bands from costa to inner margin. In DNA, a combination of the following nuclear genomic base pairs is diagnostic: aly1294.6.1:T204G, aly1264.5.2:G47C, aly1264.5.2:A130C, aly838.12.1:T458A, aly838.12.1:A427C..

Genera included. Only the type genus.

Parent taxon. Tribe Carcharodini Verity, 1940.

Ilianina Grishin, new subtribe

http://zoobank.org/AE693F6C-DD1E-4F25-9D8B-15E1AC97A09A

Type genus. *Iliana* E. Bell, 1937.

Definition. This new subtribe corresponds to one of the six major clades in the tribe Carcharodini Verity, 1940 (Fig. 4–6). It keys to E.16.3a, E.13.6a, or F.7.2, 3, or 4 in Evans (1953) and is diagnosed by the following combination of characters: both wings are semi-triangular in males; uncus frequently with flanges at its base (one on each side) either divided (arms are usually widely separated) or aedeagus unusually flared, trumpet-shaped and juxta large (longer than a third of aedeagus), or aedeagus very thin (narrower than uncus in lateral view); ampulla modified with lobes or processes, and/or expanded in many species, harpe either narrow and upturned, wrapping around distal margin of valva, or broad and protruding posteriad, diamond-shaped to nearly triangular with serrated dorsoposterior margin. Most reliably identified by DNA, and a combination of the following nuclear genomic base pairs is diagnostic: aly276665.25.1:G295A, aly594.12.19:T108A, aly594.12.19:C131T, aly3241.2.5:C191G, aly3241.2.5:C235G.

Genera included. *Cornuphallus* Austin, 1997, *Iliana* E. Bell, 1937, and *Tiana* Grishin, 2019.

Parent taxon. Tribe Carcharodini Verity, 1940.

Nisoniadina Grishin, new subtribe

http://zoobank.org/06559DF6-FAB5-41D4-B86D-397F658ED67F

Type genus. *Nisoniades* Hübner, [1819].

Definition. This new subtribe corresponds to one of the six major clades in the tribe Carcharodini Verity, 1940 (Fig. 4–6). Approximately corresponds to the *Nisoniades* sub-group of Evans (1953) (with several exceptions, but generally agrees with his description) and is diagnosed by the following combination of characters: antennae usually not shorter than half of costa, apiculus hooked and gracile, shorter than the rest of the club; forewing without lower median veinlet, hindwing inner margin produced and usually longer than forewing costal margin, dorsal hindwing in males frequently with a tuft of scales at the base of cell Sc+R$_1$-RS; uncus undivided, aedeagus usually bent and wider at the bent, valvae asymmetrical, broad, oval to nearly circular, harpe narrow, frequently framing the valva or slightly protruding distad. Most reliably identified by DNA, and a combination of the following nuclear genomic base pairs is diagnostic: aly1259.30.2:T226A, aly127.55.5:G122C, aly9181.1.1:A400T, aly9181.1.1:G401C, aly2101.3.2:T247A.

Genera included. *Arteurotia* A. Butler and H. Druce, 1872, *Conognathus* C. Felder and R. Felder, 1862, *Ocella* Evans, 1953, *Sophista* Plötz, 1879 (includes *Austinus* O. Mielke and Casagrande, 2016 and *Pachyneuria* Mabille, 1888, see below), *Polyctor* Evans, 1953, *Pellicia* Herrich-Schäffer, 1870 (includes *Mictris* Evans, 1955, see below), *Nisoniades* Hübner, [1819], *Viola* Evans, 1953, and *Viuria* Grishin, 2019.

Parent taxon. Tribe Carcharodini Verity, 1940.

Burcina Grishin, new subtribe

http://zoobank.org/4E6C387B-AD5F-41C2-BBD3-7DEC415A315C

Type genus. *Burca* E. Bell and W. Comstock, 1948.

Definition. This new subtribe corresponds to one of the six major clades in the tribe Carcharodini Verity, 1940 (Fig. 4–6). It keys to E.30 in Evans (1953) and is diagnosed by the following combination of characters: unusual for the subfamily secondary sexual characters in males: either a costal fold that covers a long hair-pencil, or brands in the middle of forewing, no tibial tufts; uncus undivided, valvae mostly symmetrical, ampulla modified, frequently with process(es), protrudes beyond harpe posteriad; palpi short and porrect, forewing not produced, hindwing quadrate, angled at apex and vein M$_3$, and rounded at tornus. In DNA, a combination of the following nuclear genomic base pairs is diagnostic: aly481.18.1:G1591A, aly318.41.3:A82C, aly671.39.1:C130A, aly671.39.1:A1039G, aly291.11.14:C85A.

Genera included. Only the type genus.

Parent taxon. Tribe Carcharodini Verity, 1940.

Pholisorina Grishin, new subtribe

http://zoobank.org/9FEFDDB5-1BE4-4377-861F-B40047521F9C

Type genus. *Pholisora* Scudder, 1872.

Definition. This new subtribe corresponds to one of the six major clades in the tribe Carcharodini Verity, 1940 (Fig. 4–6). Approximately corresponds to the *Staphylus* sub-group of Evans (1953) (with many exceptions, but generally agrees with his description) and is diagnosed by the following combination of characters: antennae usually not shorter than half of costa, apiculus obtuse, shorter than the rest of the club; forewing without lower median veinlet, hindwing quadrate, longest at vein CuA$_1$, inner margin not produced and approximately the same length as forewing costal margin, no tufts of scales on hindwing; uncus typically undivided and thinning toward distal end, aedeagus narrower, not bent, valvae almost always symmetrical (if asymmetrical then elongated and rectangular, not rounded), valva mostly rectangular, harpe protruding distad, variable in shape from narrow, almost needle-like to broad and wide, nearly the same length and height as valva. Most reliably identified by DNA, and combination of the following nuclear genomic base pairs is diagnostic: aly1139.42.2:C42T, aly1139.42.2:G63A, aly1107.9.6:G214A, aly1107.9.6:G215A, aly1107.9.6:C922A.

Genera included. *Gorgopas* Godman and Salvin, 1894, *Incisus* Grishin, 2019, *Clytius* Grishin, 2019, *Perus* Grishin, 2019, *Bolla* Mabille, 1903, *Staphylus* Godman and Salvin, 1896 (includes *Hesperopsis* Dyar, 1905 as a subgenus, see below), and *Pholisora* Scudder, 1872.

Parent taxon. Tribe Carcharodini Verity, 1940.

Torgus Grishin, new subgenus

http://zoobank.org/324B2041-EFAA-41BE-9403-70E49EF66BB9

Type species. *Ouleus gorgus* E. Bell, 1937.

Definition. Instead of originating within the genus *Eantis* Boisduval, 1836 (type species *Urbanus thraso* Hübner, 1807) as previously assumed, members of this new subgenus form a lineage sister to all other *Iliana* E. Bell, 1937 (type species *Iliana romulus* Bell, 1937), but are separated from them by prominent genetic differentiation at the subgenus level (Fig. 4). Therefore, they are placed in *Iliana* and a new subgenus is proposed for them. It keys to F.7.2 or F.7.5. in Evans (1953) and is distinguished from its relatives by the following characters: tegumen with longer side processes, harpe forked, not simply directed dorsal as in the subgenus *Iliana*, and ampulla not expanded. In DNA, a combination of the following nuclear genomic base pairs is diagnostic: aly315.4.2:A178C, aly1249.27.3:C34A, aly1249.27.3:A35C, aly806.12.1:C2122T, aly806.12.1:A1482G.

Etymology. The name is a masculine noun in the nominative singular, a fusion of the names of the two species placed in the genus: *T*[aurus]+[g]*orgus*.

Species included. *Ouleus gorgus* E. Bell, 1937 and *Tosta taurus* Evans, 1953, for which we therefore propose new genus-species combinations: *Iliana* (*Torgus*) *gorgus* and *Iliana* (*Torgus*) *taurus*.

Parent taxon. Genus *Iliana* E. Bell, 1937.

Fenops Grishin, new subgenus

http://zoobank.org/FF4C0769-80D2-4BCC-8906-DA6D7B852FC6

Type species. *Cabares enops* Godman and Salvin, 1894.

Definition. The genomic tree reveals that the genus *Polyctor* Evans, 1953 (type species *Pirgus* [sic!] *polyctor* Prittwitz, 1868) splits into two prominent clades at the tree level of subgenera (Fig. 4). A subgenus represented by one of the clades does not have a name. Species of this new subgenus key to E.18.2a in Evans (1953) and are distinguished from the relatives by the following characters: absent white bands and spots on dorsal side of wings, hindwing outer margin strongly humped or angled in the middle, terminal projection of harpe on the right valva strongly upturned and reaches costa. In DNA, a combination of the following nuclear genomic base pairs is diagnostic: aly7032.3.4:A46C, aly798.5.3:T760G, aly798.5.3:A794C, aly16.3.1:T537A, aly16.3.1:T825C.

Etymology. The name is a masculine noun in the nominative singular, a fusion of the names of the two species placed in the genus: *Fe*[ra]+[e]*nops*.

Species included. *Cabares enops* Godman and Salvin, 1894, *Achlyodes fera* Weeks, 1901, and *Polyctor tensa* Evans, 1953.

Parent taxon. Genus *Polyctor* Evans, 1953.

Polyctor (*Polyctor*) *dagua* Evans, 1953 is a species distinct from *Polyctor* (*Polyctor*) *polyctor* (Prittwitz, 1868)

Sequencing of the holotype of *Polyctor* (*Polyctor*) *polyctor* (Prittwitz, 1868) (type locality in Brazil: Rio de Janeiro) and its comparison with present-day specimens reveals distinction of *Polyctor polyctor dagua* Evans, 1953 (type

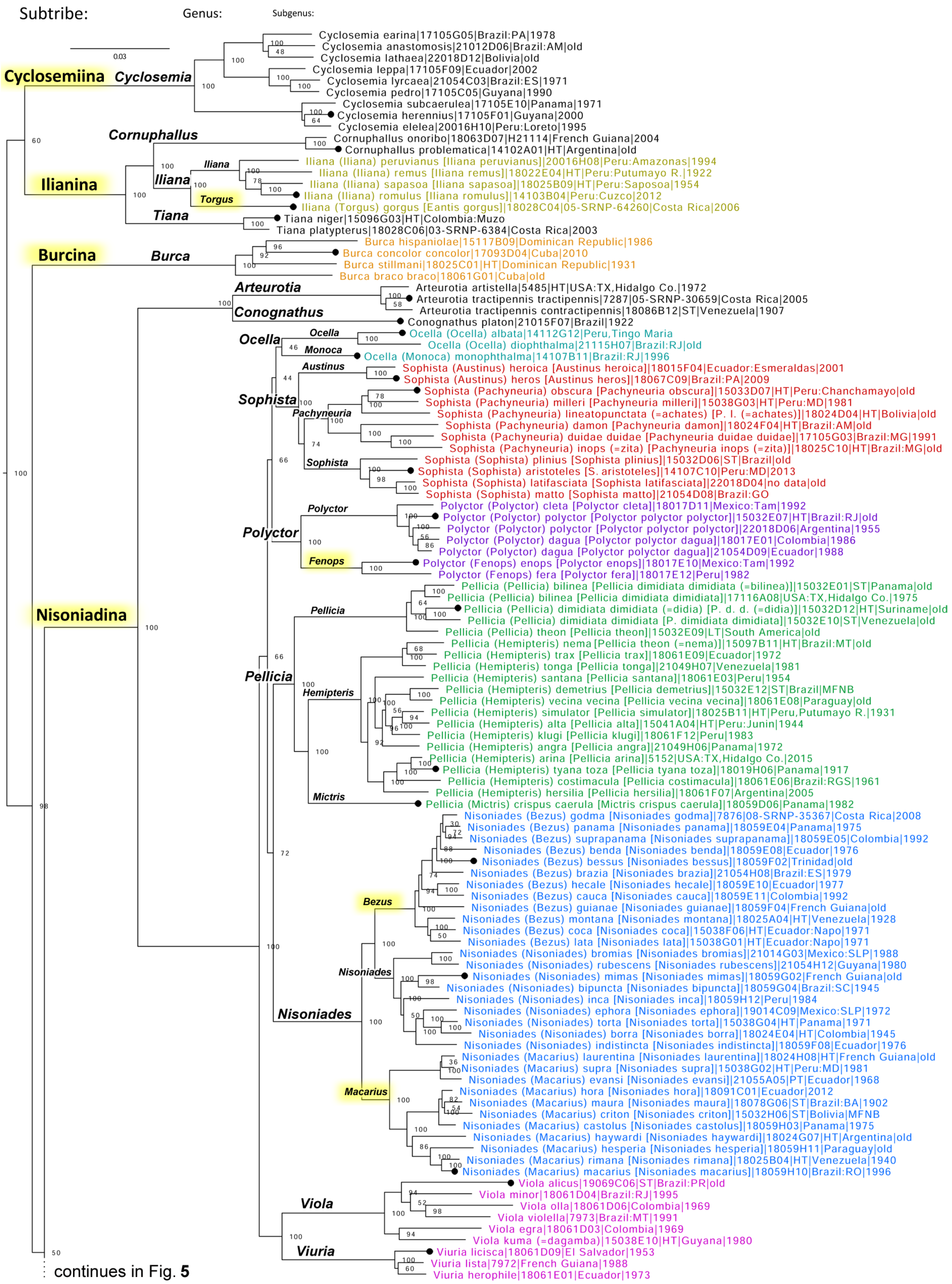

Figure 4. The nuclear genome-based phylogeny of Carcharodini, first segment (continues in Fig. 5, 6). See Fig. 1 for notations.

locality Colombia: Dagua), phenotypically unique taxon in its darker aspect and yellower white bands. E.g., the Z chromosome F_{st}/G_{min} between them is 0.39/0.00. Therefore, we propose that *Polyctor* (*Polyctor*) *dagua* Evans, 1953 **new status,** is a species distinct from *Polyctor* (*Polyctor*) *polyctor* (Prittwitz, 1868).

Pachyneuria Mabille, 1888 and *Austinus* O. Mielke and Casagrande, 2016 are subgenera of *Sophista* Plötz, 1879

Genomic tree places three current recognized genera, *Sophista* Plötz, 1879 (type species *Thracides aristoteles* Westwood, 1852), *Pachyneuria* Mabille, 1888 (type species *Pachyneuria obscura* Mabille, 1888) and *Austinus* O. Mielke and Casagrande, 2016 (type species *Echelatus heros* Mabille and Boullet, 1917) at the subgenus level (Fig. 4). E.g., the COI barcode difference of *Pachyneuria obscura* and *Austinus heros* from *Sophista aristoteles* is 7.2% (48 bp) and 6.4% (4 bp), respectively. Furthermore, all these species possess similar wing shape and male genitalia in the shape of valvae rounder than in their relatives, harpe folded along the inner surface of the right valva, and lanceolate in dorsal view undivided uncus. Differences between these three genera are confined mainly to wing patterns. Therefore, we propose that *Pachyneuria* Mabille, 1888 and *Austinus* O. Mielke and Casagrande, 2016 are subgenera of *Sophista* Plötz, 1879.

Pellicia (*Pellicia*) *bilinea* Mabille, 1889 is a species distinct from *Pellicia* (*Pellicia*) *dimidiata* Herrich-Schäffer, 1870

Genomic sequencing of *Pellicia bilinea* Mabille, 1889 (type locality in Panama: Chiriqui) syntype (NVG-15032E01, GenBank barcode OR665724) and a possible syntype of *Pellicia dimidiata* Herrich-Schäffer, 1870 (type locality Mexico and La Guaira, [Venezuela]), names currently regarded as subjective synonyms, and their comparison with additional specimens suggests that they belong to distinct species (Fig. 4): e.g., their F_{st}/G_{min}/COI differences are 0.31/0.00/2.3% (15 bp). The only possible syntype of *P. dimidiata* we found (NVG-15032E10 in MFNB, GenBank barcode OR665725) was from Venezuela: La Guaira, from the Weymer's collection, with identification label in Plötz's handwriting "Pellicia (157.) / Dimidiata HS." This is likely the specimen illustrated by Plötz in his unpublished drawings as t[afel]. 199 (Godman 1907) that also corresponds to an unnecessary replacement name *Pellicia corinna* Plötz, 1882, as mentioned by Godman (1907) and by Weymer on another label of this specimen: "Corinna Plötz i. l. / Dimidiata HS / non Feld. / Laguayra". The remark "non Feld." refers to *Carterocephalus dimidiatus* C. Felder and R. Felder, 1867, currently a valid species of *Dalla* Mabille, 1904 (type species *Cyclopides eryonas* Hewitson, 1877), a possible reason behind the replacement name *P. corinna*. The taxonomic identity of this syntype is consistent with the current application of the name *P. dimidiata*. However, exercising caution, we do not yet designate this specimen as a lectotype (or neotype if it is not a syntype). We will continue searching for Mexican syntypes and further investigating Weymer's specimen. We suspect that the identification label by Plötz was the earliest label on this specimen, also accompanied by a small label "H S / 66 / Weymer", probably meaning that this might have been a Herrich-Schäffer specimen in Weymer's possession. The identification label by Weymer was added later when Plötz decided (incorrectly) that the name needed a replacement and suggested the name *corinna*, yet unpublished (therefore "i. l.", for "in litteris", on this label). For these reasons, it is possible that this specimen is sufficiently old and may indeed be a syntype of *P. dimidiata* as labeled. Regardless of its status as a syntype, South American populations represent a species distinct from the Central American species. Therefore, we propose that *Pellicia* (*Pellicia*) *bilinea* Mabille, 1889, **restored status**, is a species distinct from *Pellicia* (*Pellicia*) *dimidiata* Herrich-Schäffer, 1870, assuming that *P. dimidiata* is a South American species, pending further research. We note that only *P. bilinea* Mabille, 1889 was recorded from the US (Fig. 4).

Hemipteris Mabille, 1889 and *Mictris* Evans, 1955 are subgenera of *Pellicia* Herrich-Schäffer, 1870

The genomic tree reveals that *Pellicia* Herrich-Schäffer, 1870 (type species *Pellicia dimidiata* Herrich-Schäffer, 1870) as currently circumscribed is paraphyletic with respect to *Mictris* Evans, 1955 (type species *Mycteris caerula* Mabille, 1877) with the highest statistical support (Fig. 4). The third prominent clade in the group corresponds to an available name *Hemipteris* Mabille, 1889 (type species *Hemipteris fumida* Mabille, 1889, a junior subjective synonym of *Pellicia tyana* Plötz, 1882), currently a junior subjective synonym of *Pellicia*. Because the diversification of the three clades (*Pellicia*, *Mictris*, and *Hemipteris*) corresponds to a subgenus level in the tree, and all these species are similar in appearance, it seems that placing them into a single genus is a better choice for restoring monophyly instead of elevating *Hemipteris* to genus. Therefore, we propose that *Hemipteris* Mabille, 1889, **restored status**, and *Mictris* Evans, 1955, **new status**, are subgenera of *Pellicia* Herrich-Schäffer, 1870. As a result, only *Pellicia bilinea* Mabille, 1889, **restored status**, *Pellicia dimidiata* Herrich-Schäffer, 1870 and *Pellicia theon* Plötz, 1882 (as judged by their primary type specimens) belong to the nominotypical subgenus (Fig. 4). All other species currently placed in *Pellicia* belong to the subgenus *Hemipteris*. The subgenus *Mictris* is monotypic.

Lectotype designation for *Pellicia theon* Plötz, 1882

Pellicia theon Plötz, 1882 (type locality in South America) currently treated as a valid species in its original genus was described from unstated number of specimens (Plötz 1882). A single syntype is curated as such in the MFNB collection. It agrees with the original description and is likely the specimen illustrated by Plötz in his unpublished drawings as t[afel]. 200 (Godman 1907), copies in BMNH and USNM, because the details of the illustration match the details of the specimen. For instance, it appears that a glue patch in the middle of ventral hindwing along vein CuA_2 applied to secure the tear in the syntype is depicted as a pair of gray streaks. There are no natural markings at this spot in *Pellicia*. To stabilize nomenclature, N.V.G. hereby designates the syntype in the MFNB collection, a male bearing nine labels (1st red, others white): [typus], [53 |Weymer], [Pellicia (156$^{\underline{i.}}$) | Theon Pl.], [Hesperia], [26:17], [Coll. Weymer], [Theon Plötz i l. | Amer. Mer.], [DNA sample ID: | NVG-15032E09 | c/o Nick V. Grishin], and [{QR Code} http://coll.mfn-berlin.de/u/ | 940b9e], as the **lectotype** of *Pellicia theon* Plötz, 1882. The third label, matching Plötz's handwriting, adds to our confidence that the lectotype was indeed one of the syntypes. The fifth label is the number (genus:species) of *P. theon* in the Mabille catalog (1903). The COI barcode sequence of *P. theon* lectotype, sample NVG-15032E09, GenBank OR721877, 658 base pairs, is:

AACTTTATATTTTATTTTTGGTATTTGATCTGGAATAGTAGGAACATCATTAAGTTTAATTATTCGATCCGAATTAGGTACCCCT
AGATCTTTTATTGGAGATGATCAAATTTATAATACCATTGTAACAGCTCATGCCTTTATTATAATTTTTTTATAGTTATACCTAT
TATAATTGGAGGATTCGGAAATTGATTAGTACCCCTTATATTAGGAGCTCCTGATATAGCTTTTCCCCGAATAAATAATATAAGA
TTTTGACTTTTACCTCCTTCTATTACTTTACTAATTTCAAGAAGTTTTGTAGAAAATGGTGTTGGTACAGGTTGAACTGTTTAT
CCCCCTTTATCTGCTAATATTGCTCACCAAGGTTCTTCTGTAGATTTAGCAATTTTTTCTTTACATTTAGCTGGTATTTCATCTA
TTTTAGGTGCTATTAATTTTATTACAACCATTATTAATATACGTATTAACAATTTATTATTTGATCAAATACCTTTATTTATTTGA
GCTGTTGGAATTACAGCTTTACTTTTATTATTATCTCTACCAGTTTTAGCTGGAGCTATTACCATACTATTAACTGATCGAAATT
TAAATACATCTTTTTTTGACCCTGCGGGAGGAGGAGATCCAATTTTATATCAACATTTATTT

Pellicia (*Hemipteris*) *nema* R. Williams and E. Bell, 1939 is a species distinct from *Pellicia* (*Pellicia*) *theon* Plötz, 1882

Genomic sequencing of the holotype of *Pellicia nema* Williams and Bell (type locality in Brazil: Mato Grosso, sequenced as NVG-15097B11, GenBank barcode OR721876) and the lectotype of *Pellicia theon* Plötz, 1882 (type locality in South America, sequenced as NVG-15032E09, GenBank barcode OR721877) currently considered conspecific reveals that they belong to different subgenera, *Hemipteris* Mabille, 1889 (type species *Hemipteris fumida* Mabille, 1889, a junior subjective synonym of *Pellicia tyana* Plötz, 1882) and *Pellicia* Herrich-Schäffer, 1870 (type species *Pellicia dimidiata* Herrich-Schäffer, 1870), respectively (Fig. 4). Not finding other species with older names that are justifiably conspecific with either of the two, we propose that *Pellicia* (*Hemipteris*) *nema* Williams and Bell, 1939, **restored status**, is a species distinct from *Pellicia* (*Pellicia*) *theon* Plötz, 1882. We hypothesize that the two species were confused with each other because Evans (1953) misidentified *P. theon*. What he identified as *P. theon* was probably *P. nema*. As identified by its lectotype, labeled as "theon Pl." in Plötz's writing, *P. theon* is a species closely related to *Pellicia dimidiata* Herrich-Schäffer, 1870 (type locality Mexico and La Guaira [Venezuela]) (Fig. 4). Evans treated the former within his concept of the latter species, but their COI barcodes differ by 1.4% (9 bp).

Bezus Grishin, new subgenus

http://zoobank.org/F70C2876-F6A2-4633-8938-B52917E75CF9

Type species. *Pellicia bessus* Möschler, 1877.

Definition. The genus *Nisoniades* Hübner, 1819 (type species *Papilio bromius* Stoll, 1787, a junior subjective synonym of *Papilio mimas* Cramer, 1775) splits into three prominent clades at the subgenus level (Fig. 4). Because no available genus-group names have been associated with *Nisoniades*, two of three subgenera are new. This new subgenus keys to E.19.1c in Evans (1953) and is distinguished from its relatives by the following characters: vein RS on ventral hindwing in males does not run along vein M_1 but diverges from it at its origin, which is around the middle between the base and end of the discal cell, and is swollen until the end of cell, not much beyond, and harpe of right valva is not divided. In DNA, a combination of the following nuclear genomic base pairs is diagnostic: aly84.3.1:T55C, aly84.3.1:C101T, aly37338.21.1:A1627T, aly37338.21.1:G1861T, aly3486.1.4:T485A.

Etymology. The name is a masculine noun in the nominative singular formed from the type species name to keep it short and avoid a homonym.

Species included. *Nisoniades godma* Evans, 1953, *Nisoniades panama* Evans, 1953, *Nisoniades suprapanama* Steinhauser, 1989, *Nisoniades benda* Evans, 1953, *Pellicia bessus* Möschler, 1877, *Nisoniades brazia* Evans, 1953, *Pellicia hecale* Hayward, 1940, *Nisoniades cauca* Evans, 1953, *Nisoniades remo* Evans, 1953, *Pellicia guianae* R. Williams and E. Bell, 1939, *Pellicia montana* R. Williams and E. Bell, 1939, *Nisoniades coca* Steinhauser, 1989, and *Nisoniades lata* Steinhauser, 1989.

Parent taxon. Genus *Nisoniades* Hübner, [1819].

Macarius Grishin, new subgenus

http://zoobank.org/3C0E9973-A2BA-4F62-8B65-C9DA18692468

Type species. *Pellicia macarius* Herrich-Schäffer, 1870.

Definition. The genus *Nisoniades* Hübner, 1819 (type species *Papilio bromius* Stoll, 1787, a junior subjective synonym of *Papilio mimas* Cramer, 1775) splits into three prominent clades at the subgenus level (Fig. 4). Because no available genus-group names have been associated with *Nisoniades*, two of three subgenera are new. This new subgenus keys to E.19.3, E19.4, or E.19.12a in Evans (1953) and is distinguished from its relatives by the following characters: vein RS on ventral hindwing in males usually runs parallel to vein M_1 from its origin to the end of the swollen portion, if divergent then right harpe is bifid or vein RS origin is closer to the end of cell than to the wing base and dorsal hindwing tuft in males is inconspicuous, harpe of right valva is frequently bifid, hindwing is frequently quadrate and angled at vein CuA_1, harper of left valva frequently does not extend past ampulla. In DNA, a combination of the following nuclear genomic base pairs is diagnostic: aly6517.5.2:T1476C, aly6517.5.2:G1699T, aly4975.2.1:C43T, aly4975.2.1:T73G, aly23605.23.23:A145G.

Etymology. The name is a masculine noun in the nominative singular, tautonymous with the type species name.

Species included. *Pellicia laurentina* R. Williams and E. Bell, 1939, *Nisoniades evansi* Steinhauser, 1989, *Nisoniades supra* Steinhauser, 1989, *Pellicia maura* Mabille and Boullet, 1917, *Pellicia hora* Hayward, 1939, *Pellicia criton* Mabille, 1898, *Pellicia hesperia* Hayward, 1939, *Arteurotia castolus* Hewitson, 1878, *Pellicia haywardi* R. Williams and E. Bell, 1939, *Pellicia rimana* E. Bell, 1942, *Pellicia macarius* Herrich-Schäffer, 1870, and *Achlyodes nyctineme* A. Butler, 1877.

Parent taxon. Genus *Nisoniades* Hübner, [1819].

Quadralis Grishin, new subgenus

http://zoobank.org/C859F739-AC31-4F2E-9A2A-14778E4FC67B

Type species. *Pterygospidea extensa* Mabille, 1891.

Definition. Sister to the rest of the genus *Gorgopas* Godman and Salvin, 1894 (type species *Achlyodes viridiceps* Butler & H. Druce, 1872, which is currently regarded as a junior subjective synonym of *Pellicia chlorocephala* Herrich-Schäffer, 1870) and sufficiently distinct from it (Fig. 5), resembling in appearance some species of *Polyctor* Evans, 1953 (type species *Pirgus* [sic!] *polyctor* Prittwitz, 1868). Keys to E.18.4 in Evans (1953) and distinguished from its relatives by nearly square hindwing due to a blunt tooth at the vein CuA_1 and hyaline spots in forewing cells between veins M_1 to 1A+2A. In DNA, a combination of the following nuclear genomic base pairs is diagnostic: aly770.25.10:A48C, aly451.25.1:G1816A, aly3686.9.6:G137C, aly1656.12.3:G757C, aly5196.9.2:C832T.

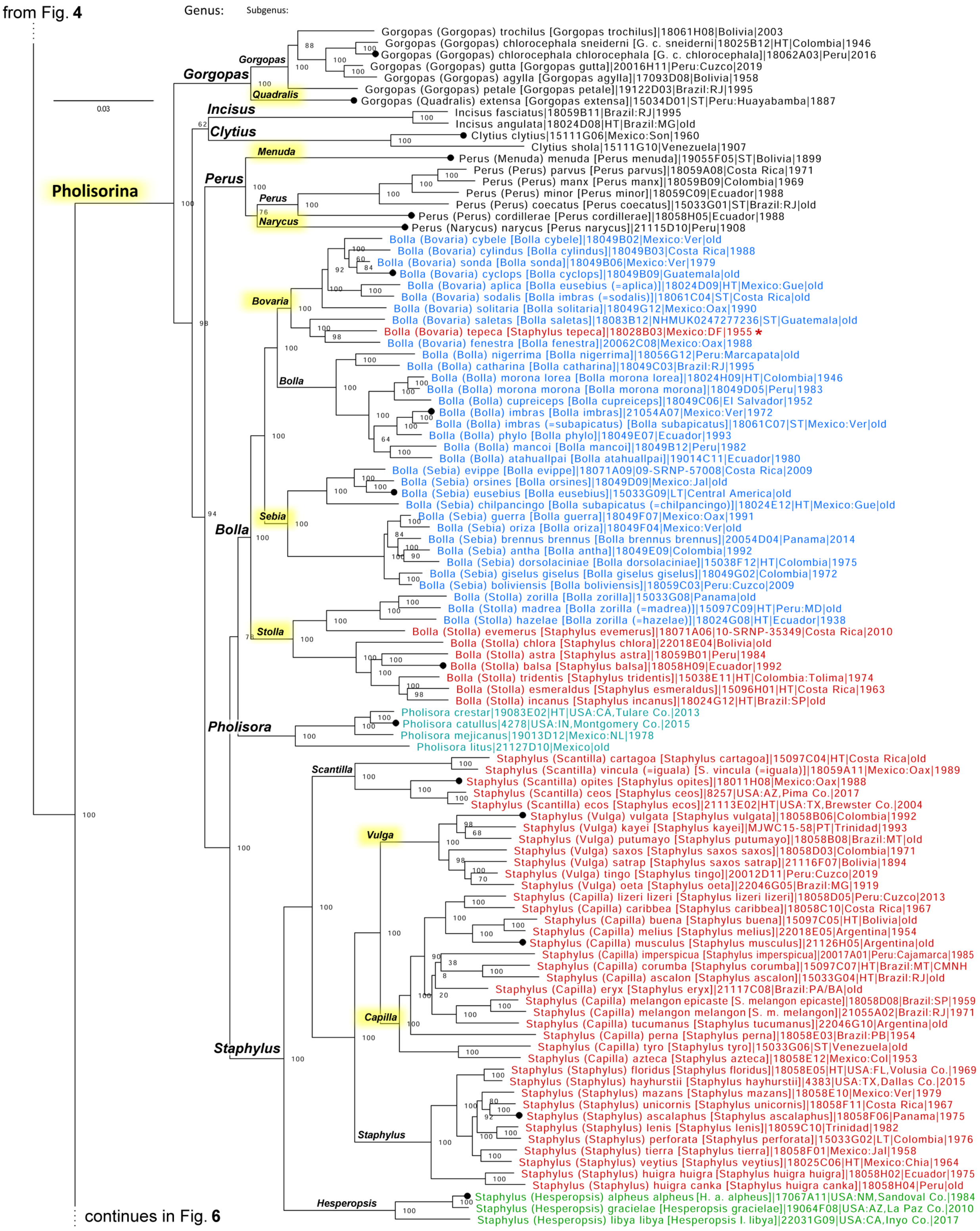

Figure 5. The nuclear genome-based phylogeny of Carcharodini, middle segment (continues in 6, see Fig. 4 for the first segment) showing Pholisorina **subtrib. n**. Species formerly placed in *Staphylus* are labeled in red. Asterisk marks a species with a dedicated study (Lemes et al. 2023) that already assigned it to *Bolla*. See Fig. 1 for notations.

Etymology. The name is a masculine noun (to agree in gender with the names of species in this subgenus) in the nominative singular, given for the square-shaped hindwing: in Latin, *quadratum* is square, and *alis* is wing.

Species included. Only the type species.

Parent taxon. Genus *Gorgopas* Godman and Salvin, 1894.

Menuda Grishin, new subgenus

http://zoobank.org/61EF142F-EE57-49AF-A475-041DBC620ED4

Type species. *Nisoniades menuda* Weeks, 1902.

Definition. The genus *Perus* Grishin, 2019 (type species *Pholisora cordillerae* Lindsey, 1925) splits into three prominent lineages at the subgenus level in the tree (Fig. 5), two of which correspond to currently monotypic and unnamed subgenera. One of these new subgenera keys to E.32.16 in Evans (1953) and is distinguished from its relatives by undivided and narrow, nearly needle-shaped and somewhat upturned in lateral view uncus without projections at its base and harpe nearly as long as valva, with a beak-like tooth on its dorsal margin and projection off ampulla reaching the "beak". In DNA, a combination of the following nuclear genomic base pairs is diagnostic: aly686.40.2:T38C, aly686.40.2:T99C, aly671.7.4:T75C, aly2811.5.5:A489G, aly171.6.1:G5424C.

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

Species included. Only the type species.

Parent taxon. Genus *Perus* Grishin, 2019.

Narycus Grishin, new subgenus

http://zoobank.org/7D5FD1DE-9860-48E2-AB25-D0B6F00C7CAB

Type species. *Pythonides narycus* Mabille, 1889.

Definition. The genus *Perus* Grishin, 2019 (type species *Pholisora cordillerae* Lindsey, 1925) splits into three prominent lineages at the subgenus level in the tree (Fig. 5), two of which correspond to currently monotypic and unnamed subgenera. One of these new subgenera keys to E.37.8 in Evans (1953) and is distinguished from its relatives by undivided and semi-triangular in dorsal view, narrowing to a point, and downturned in lateral view uncus without projections at its base and harpe only slightly shorter than valva, with a broad beak-like tooth on its dorsal margin projecting dorsad beyond costa-ampulla in lateral view. In DNA, a combination of the following nuclear genomic base pairs is diagnostic: aly736.3.1:G100T, aly736.3.1:C101T, aly214.18.3:A37C, aly214.18.3:C38T, aly173.28.7:A73T.

Etymology. The name is a masculine noun in the nominative singular, tautonymous with the type species name.

Species included. Only the type species.

Parent taxon. Genus *Perus* Grishin, 2019.

Bovaria Grishin, new subgenus

http://zoobank.org/86413A71-3528-4B5A-BB4D-9C7C43667518

Type species. *Achlyodes cyclops* Mabille, 1876.

Definition. The nuclear genomic tree reveals that *Bolla* Mabille, 1903 (type species *Bolla pullata* Mabille, 1903, treated as a junior subjective synonym of *Staphylus imbras* Godman and Salvin, 1896) splits into four clades at the subgenus level (Fig. 5). The subgenera corresponding to three of these clades do not have available names and are new. One of these new subgenera keys to E.31.1b or E.31.18a in Evans (1953) and is distinguished from its relatives by the following characters: at least around tornus of ventral hindwing with gray or ocherous overscaling, distal third of ventral forewing paler than the rest, if not then forewing cell CuA_1-CuA_2 with a prominent hyaline spot (at least in females) and/or wings ocherous-brown with conspicuous darker spots somewhat connected into bands, antenna nudum with about 13 segments; tegumen in dorsal view rounded, wider at the base, without processes near uncus (but could be with small "knobs"), uncus lanceolate to narrowly triangular, valva more square than rectangular, or rounded on the sides, ampulla with a bulge or a bulbous process, harpe usually extended posteriad, could be claw-like and upturned or relatively short and overlapping with valva and with inner dorsal margin serrated and/or expanded. Confident identification is provided by DNA, and a combination of the following base pairs is diagnostic: in the nuclear genome: aly537.31.1:G611A, aly1139.42.5:C79A, aly1139.42.5:A27T, aly84.37.1:T1180C, aly84.37.1:T1395C, and in the COI barcode: A181A, 263C, A265T, A424A, 592A, T652T, T653T.

Etymology. The name is a feminine noun in the nominative singular, unifying a number of *Bolla* species with variable superficial appearance: *Bo*[lla] + *varia*[ble].

Species included. *Bolla cybele* Evans, 1953, *Staphylus cylindus* Godman and Salvin, 1896, *Bolla sonda* Evans, 1953, *Achlyodes cyclops* Mabille, 1877, *Pholisora aplica* E. Bell, 1937, **restored status** (see below), *Bolla sodalis* Schaus, 1913, **restored status** (see below), *Bolla solitaria* Steinhauser, 1991, *Staphylus saletas* Godman and Salvin, 1896, *Pholisora tepeca* E. Bell, 1942, and *Bolla fenestra* Steinhauser, 1991.

Parent taxon. Genus *Bolla* Mabille, 1903.

Sebia Grishin, new subgenus

http://zoobank.org/D31D04CF-D4BF-4D85-BE43-D68B7FB57421

Type species. *Nisoniades eusebius* Plötz, 1884.

Definition. The nuclear genomic tree reveals that *Bolla* Mabille, 1903 (type species *Bolla pullata* Mabille, 1903, treated as a junior subjective synonym of *Staphylus imbras* Godman and Salvin, 1896) splits into four clades at the subgenus level (Fig. 5). The subgenera corresponding to three of these clades do not have available names and are new. One of these new subgenera keys to E.31.10 or 11c (except 18a) in Evans (1953) and is distinguished from its relatives by the following characters: at least around tornus of ventral hindwing with gray or ocherous overscaling, distal third of ventral forewing not paler than the rest, forewing typically broader, more pointed at the apex, discal cell without white or hyaline spots, antenna nudum with about 13 segments; tegumen in dorsal view notched, but not lobed, in the middle on its sides, with projections at the base of uncus in some species, uncus bulbous at the base, narrowing to a sharp or more rounded point, valva approximately rectangular (at least more so than in relatives), ampulla small, indistinct, harpe usually long, could also be rectangular and not shorted than valva, bilobed, or short and upturned, in which case tegumen with short processes at the base of uncus. Confident identification is provided by DNA, and a combination of the following base pairs is diagnostic: in the nuclear genome: aly594.10.2:A96T, aly594.10.2:T117G, aly84.89.2:C467G, aly84.89.2:T480C, aly84.99.2:A925T, and in the COI barcode: A40T, C81(mostly T), 82R, T652C, or if 652T then T653C.

Etymology. The name is a masculine noun in the nominative singular, formed from the type species name: [eu] *Sebi*[us] + *a*.

Species included. *Staphylus evippe* Godman and Salvin, 1896, *Staphylus orsines* Godman and Salvin, 1896, *Nisoniades eusebius* Plötz, 1884, *Pholisora chilpancingo* E. Bell, 1937, **restored status** (see below), *Bolla tetra guerra* Evans, 1953, *Bolla tetra oriza* Evans, 1953, *Staphylus brennus* Godman and Salvin, 1896, *Bolla antha* Evans, 1953, *Bolla dorsolaciniae* Steinhauser, 1989, *Hesperia giselus* Mabille, 1883, and *Pholisora giselus* race *boliviensis* E. Bell, 1937.

Parent taxon. Genus *Bolla* Mabille, 1903.

Stolla Grishin, new subgenus

http://zoobank.org/CA87FEC7-A5E2-413D-96D0-9E0CE260713B

Type species. *Pholisora balsa* E. Bell, 1937.

Definition. The nuclear genomic tree reveals that *Bolla* Mabille, 1903 (type species *Bolla pullata* Mabille, 1903, treated as a junior subjective synonym of *Staphylus imbras* Godman and Salvin, 1896) splits into four clades at the subgenus level (Fig. 5). The subgenera corresponding to three of these clades do not have available names and are new. One of these new subgenera includes many species previously placed in *Staphylus* Godman and Salvin, 1896 (type species *Helias ascalaphus* Staudinger, 1876). Species in this subgenus key to E.31.21, E.32.1b, 9, 27, 32, or 37 in Evans (1953) and are distinguished from its relatives by the following characters: ventral hindwing even around tornus frequently without gray or ocherous overscaling, distal third of ventral forewing not paler than the rest, forewing usually narrower, more rounded at the apex, discal cell with white or hyaline spot(s) in some species, antenna nudum with 10–11 segments in most species; tegumen in dorsal view not notched and not lobed in the middle on its sides, and could be with projections (sometimes long) at the base of uncus, uncus undivided, terminally narrowing, usually separated from tegumen by a notch (or a concavity) in lateral view, harpe may be elongated, extending posteriad, or broader and upturned, ampulla with a process, projection, or a hump. Confident identification is provided by DNA, and a combination of the following base pairs is diagnostic: in the nuclear genome: aly291.13.2:C57T, aly1720.4.1:A1080G, aly1720.4.1:A837G, aly1720.4.1:A1147C, aly728.40.3:T120C, and in the COI barcode: C81C, 82Y, T284C, A286T, A298A, T652T, T653T.

Etymology. The name is a feminine noun in the nominative singular, meaning that the genus includes a large number of species that were transferred from *Staphylus* to *Bolla*: *St*[aphylus] + [B]*olla*.

Species included. *Antigonus zorilla* Plötz, 1886, *Pholisora madrea* R. Williams and E. Bell, 1940, **restored status** (see below), *Pholisora hazelae* Hayward, 1940, **restored status** (see below), *Staphylus evemerus* Godman and Salvin, 1896, *Staphylus chlora* Evans, 1953, *Pholisora astra* R. Williams and E. Bell, 1940, *Pholisora balsa* E. Bell, 1937, *Staphylus tridentis* Steinhauser, 1989, *Staphylus esmeraldus* L. Miller, 1966, *Hesperia chlorocephala* Latreille, [1824], and *Staphylus incanus* E. Bell, 1932.

Parent taxon. Genus *Bolla* Mabille, 1903.

Lectotype designation for *Nisoniades eusebius* Plötz, 1884

Nisoniades eusebius Plötz, 1884 (type locality in Central America), currently a valid species in the genus *Bolla* Mabille, 1903 (type species *Bolla pullata* Mabille, 1903, treated as a junior subjective synonym of *Staphylus imbras* Godman and Salvin, 1896) and the type species of the subgenus *Sebia*, **new subgenus**, was described from an unstated number of specimens (Plötz 1884). One specimen is curated in the MFNB collection as a syntype of *N. eusebius*. It agrees with the original description and was sequenced as NVG-15033G09. To stabilize nomenclature, N.V.G. hereby designates the syntype in the MFNB collection, a male bearing eight labels (1st red, others white): [typus], [Centr Amer.], [Parna Plötz | n. 151 best. v. Plötz.], [Eusebius Plötz | Plötz taf 1053], [Coll. Weymer], [Eusebius Plötz i. l. | Parna Plötz i. l. | olim | Amer centr.], [DNA sample ID: | NVG-15033G09 | c/o Nick V. Grishin], [{QR Code} http://coll.mfn-berlin.de/u/ | 80a659] as the **lectotype** of *Nisoniades eusebius* Plötz, 1884. According to its labels, this specimen was identified by Plötz ("best[immt]. v[on]. Plötz") as "parna", which was initially suggested ("olim", Latin for 'formerly', 'once', or 'formerly known as'), and unpublished, the name for this species that was later changed to "Eusebius", and this label with the name was added to the specimen prior to publication ("i[n] l[itteris]"). Furthermore, per the dedicated label, this specimen is from Central America, exactly as stated in the original description. These data on the labels increase our confidence in this specimen, originally from the Weymer collection, being a syntype. The COI barcode sequence of *N. eusebius* lectotype, sample NVG-15033G09, GenBank OR665726, 658 base pairs, is:

AACTTTATACTTTATTTTTGGTATTTGATCTGGAATAGTTGGAACTTCTTTAAGTATTCTTATTCGTTCTGAACTAGGAATGCCT
GGATCTTTAATTGGAGATGATCAAATTTATAATACTATTGTAACAGCTCATGCTTTTATTATAATTTTTTTTATAGTAATACCTAT
TATAATTGGAGGATTTGGAAATTGATTGGTGCCCCTTATATTAGGAGCTCCTGATATAGCTTTTCCTCGAATAAATAATATAAG
ATTTTGACTTTTACCTCCTTCTCTAATATTATTAATTTCTAGTAGTATTGTAGAAAGTGGGGCAGGTACAGGATGAACAGTATAT
CCCCCACTTTCAGCTAATATTGCCCATCAAGGTTCTTCTGTAGATTTAGCTATTTTTTCTCTTCATTTAGCTGGTATTTCTTCAA
TTTTAGGTGCTATTAATTTCATTACAACTATTATCAATATACGAATTAATAACTTATCCTTTGATCAAATACCTTTATTTGTTTGA
GCAGTAGGTATTACTGCATTACTTTTATTATTATCTTTACCAGTATTAGCAGGAGCTATTACTATACTTCTAACTGATCGTAATTT
AAATACATCATTCTTTGATCCAGCAGGTGGAGGAGATCCTATTTTATACCAACATCTATTT

Bolla (*Bovaria*) *sodalis* (Schaus, 1913) is a species distinct from *Bolla* (*Bolla*) *imbras* (Godman and Salvin, 1896)

Evans (1953) apparently misinterpreted *Bolla sodalis* Schaus, 1913 (type locality Costa Rica: El Alto) in treating it as a junior subjective synonym of *Bolla* (*Bolla*) *imbras* (Godman and Salvin, 1896) (type locality in Mexico: Veracruz and Tabasco, and Guatemala). We suggest Evan's mistake, because the original description and illustration of *B. sodalis* show a species that is "Nearest [to] *B. cylindus* G. & S." (Schaus 1913), if not for any other reason than the pattern of forewing hyaline spots, which *B. imbras* lacks. Genomic sequencing of a syntype of *Bolla sodalis*

(NVG-18061C04, GenBank barcode OR665727) places it away from *B. imbras* (currently a valid name for the type species of *Bolla* Mabille, 1903) and indeed in the subgenus *Bovaria* **new subgenus** Consideraing only species with names more senior than *B. sodalis*, it is sister to the clade of *Bolla cylindus* Godman and Salvin, 1896) (type locality in Mexico: Veracruz and Costa Rica) and *Bolla cyclops* (Mabille, 1877) (type locality in Guatemala and Colombia) (Fig. 5). Therefore, we propose that *Bolla* (*Bovaria*) *sodalis* (Schaus, 1913), **restored status,** is a species distinct from *Bolla* (*Bolla*) *imbras* (Godman and Salvin, 1896).

Bolla **(*Bovaria*)** ***aplica*** **(E. Bell, 1937) is a species distinct from** ***Bolla*** **(*Sebia*)** ***eusebius*** **(Plötz, 1884)**

Genomic sequencing of the holotype of *Pholisora aplica* E. Bell, 1937 (type locality in Mexico: Guerrero, NVG-18024D09, GenBank barcode OR665728) and the lectotype of *Nisoniades eusebius* Plötz, 1884 (type locality in Central America, NVG-15033G09) regarded by Evans (1953) as conspecific in the genus *Bolla* Mabille, 1903 (type species *Bolla pullata* Mabille, 1903, treated as a junior subjective synonym of *Staphylus imbras* Godman and Salvin, 1896) reveals that they belong to different subgenera: *Bovaria* **new subgenus** (type species *Achlyodes cyclops* Mabille, 1876) and *Sebia* **new subgenus** (type species *Nisoniades eusebius* Plötz, 1884), respectively (Fig. 5). This problem arose because Evans (1953) misidentified *N. eusebius*, e.g., its syntype has costal fold, but according to Evans' key, his "*eusebius*" lacks costal fold. The phylogenetic tree shows that *N. eusebius* is sister to *Bolla* (*Sebia*) *orsines* (Godman and Salvin, 1896) (type locality in Mexico: Jalisco) and *P. aplica* is sister to *Bolla* (*Bovaria*) *sodalis* (Schaus, 1913) (type locality Costa Rica: El Alto), **restored status,** Thus, although we have not sequenced specimens identified by Evans as "*eusebius*", we hypothesize that they were *B. sodalis*. We find that while *P. aplica* is closely related to *B. sodalis*, they show some genetic differentiation, e.g., their COI barcodes differ by 0.6% (4 bp) and come from different biogeographic areas. Therefore, to attract attention to the problem and due to confusion in the literature, we propose that *Bolla* (*Bovaria*) *aplica* (E. Bell, 1937), **restored status,** is a species-level taxon distinct from both *Bolla* (*Sebia*) *eusebius* (Plötz, 1884) (definitively) and *Bolla* (*Bovaria*) *sodalis* (Schaus, 1913) (tentatively), and leave it for future studies to determine whether it is best treated as a subspecies of the latter.

Bolla **(*Sebia*)** ***chilpancingo*** **(E. Bell, 1937) is a species distinct from** ***Bolla*** **(*Bolla*)** ***subapicatus*** **(Schaus, 1902); the latter is a junior subjective synonym of** ***Bolla*** **(*Bolla*)** ***imbras*** **(Godman and Salvin, 1896)**

Genomic sequencing of the holotype of *Pholisora chilpancingo* Bell, 1937 (type locality in Mexico: Guerrero, NVG-18024E12, GenBank barcode OR665729) and a syntype of *Staphylus subapicatus* Schaus, 1902 (type locality in Mexico: Veracruz, NVG-18061C07, GenBank barcode OR665730) regarded by Evans (1953) as conspecific in the genus *Bolla* Mabille, 1903 (type species *Bolla pullata* Mabille, 1903, treated as a junior subjective synonym of *Staphylus imbras* Godman and Salvin, 1896) reveals that they belong to different subgenera: *Sebia* **new subgenus** (type species *Nisoniades eusebius* Plötz, 1884) and the nominotypical subgenus, respectively (Fig. 5). This problem arose because Evans (1953) misidentified *S. subapicatus*. Indeed, *P. chilpancingo* forms a distinct lineage in the tree and keys to the "*subapicatus*" of Evans. However, *S. subapicatus* falls within the genetic variation of *Bolla* (*Bolla*) *imbras* (Godman and Salvin, 1896) (type locality in Mexico: Veracruz and Tabasco, and Guatemala) (Fig. 5), e.g., the COI barcodes of the specimens we sequenced differ by 1 bp. Therefore, we propose that *Bolla* (*Sebia*) *chilpancingo* (E. Bell, 1937), **restored status**, is a valid species distinct from *Bolla* (*Bolla*) *subapicatus* (Schaus, 1902), but the latter taxon is a new junior subjective synonym of *Bolla* (*Bolla*) *imbras* (Godman and Salvin, 1896).

Bolla **(*Stolla*)** ***madrea*** **(R. Williams and E. Bell, 1940) and** ***Bolla*** **(*Stolla*)** ***hazelae*** **(Hayward, 1940) are species distinct from** ***Bolla*** **(*Stolla*)** ***zorilla*** **(Plötz, 1886)**

Genomic sequencing of the holotypes of *Pholisora madrea* R. Williams and E. Bell, 1940 (type locality in Peru: Madre de Dios, NVG-15097C09, GenBank barcode OR665731) and *Pholisora hazelae* Hayward, 1940 (type locality in Ecuador, NVG-18024G08, GenBank barcode OR665732) and a syntype of *Antigonus zorilla* Plötz, 1886 (type locality in Panama, NVG-18056H01, GenBank barcode OR665733), currently treated as conspecific in the genus *Bolla* Mabille, 1903 (type species *Bolla pullata* Mabille, 1903, considered a junior subjective synonym of *Staphylus imbras* Godman and Salvin, 1896) reveals that while all three are in the same clade, they are genetically differentiated at the level not unprecedented even for subgenera (Fig. 5), e.g., COI barcode differences are: 8.2% (54 bp) for *P. madrea* and *P. hazelae*, 7.1% (47 bp) for *P. madrea* and *A. zorilla*, and 7.6% (50 bp) for *P. hazelae* and *A. zorilla*. Therefore, we propose that *Bolla* (*Stolla*) *madrea* (R. Williams and E. Bell, 1940), **restored status**, and *Bolla* (*Stolla*) *hazelae* (Hayward, 1940), **restored status**, are species distinct from *Bolla* (*Stolla*) *zorilla* (Plötz, 1886).

Hesperopsis Dyar, 1905 is a subgenus of *Staphylus* Godman and Salvin, 1896

The phylogenetic tree did not reveal a prominent separation between *Staphylus* Godman and Salvin, 1896 (type species *Helias ascalaphus* Staudinger, 1876) and *Hesperopsis* Dyar, 1905 (type species *Thanaos alpheus* W. H. Edwards, 1876), quite the opposite, it illustrates their closeness (Fig. 5), which is equally reflected in the similarity of their wing shapes and patterns. *Staphylus* and *Hesperopsis* are closer related than some species of *Bolla* to each other. While *Staphylus* is a large genus, *Hesperopsis* is a small group of three North American species. Including them in *Staphylus* is not expected to cause confusion but would highlight their close relationships. Therefore, we proposed to treat *Hesperopsis* Dyar, 1905 as a subgenus of *Staphylus* Godman and Salvin, 1896.

Scantilla Godman and Salvin, 1896 is a subgenus of *Staphylus* Godman and Salvin, 1896

The nuclear genomic tree reveals that *Staphylus* Godman and Salvin, 1896 (type species *Helias ascalaphus* Staudinger, 1876) splits into five clades at the subgenus level (Fig. 5). The subgenus *Hesperopsis* Dyar, 1905 (type species *Thanaos alpheus* W. H. Edwards, 1876) is sister to all others. The next prominent clade is sister to the clade with the type species of *Staphylus* and contains the type species of the available genus-group name *Scantilla* Godman and Salvin, 1896, *Scantilla opites* Godman and Salvin, 1896. Therefore, this clade corresponds to the subgenus *Scantilla*, **new status**, resurrected from synonymy. In addition to the type species, the following species belong to this subgenus: *Pholisora cartagoa* R. Williams & E. Bell, 1940, *Tagiades vincula* Plötz, 1886, *Pholisora ceos* W. H. Edwards, 1882, and *Staphylus ecos* Grishin, 2022. Curiously, the two subgenera (*Hesperopsis* and *Scantilla*) are characterized by a slower substitution rate than others: tree distance from the last common ancestor of *Staphylus* to the leaves is smaller for species in these two subgenera than for others.

Vulga Grishin, new subgenus

http://zoobank.org/DA9638E7-54AF-4B18-B4B8-D6E275D4977B

Type species. *Achlyodes vulgata* Möschler, 1879.

Definition. The nuclear genomic tree reveals that *Staphylus* Godman and Salvin, 1896 (type species *Helias ascalaphus* Staudinger, 1876) splits into five clades at the subgenus level (Fig. 5). The subgenera corresponding to two of these clades, which are sister to each other, do not have available names and are new. One of these new subgenera keys to E.32.5c, 7, or 9c in Evans (1953) and is distinguished from its relatives by the following characters: spots on wings rather inconspicuous, head without green scales but is golden in some species; ampulla of valva frequently expanded, overlaps harpe from inside (if not then harpe and valva of approximately equal size, and ampulla expansion reaches the end of harpe), vinculum brushes absent, uncus undivided, narrowing to a point, lanceolate and semi-triangular towards the tip, typically broader than in relatives, and not strongly concave in lateral view, tegumen typically not broader than uncus. Confident identification is provided by DNA, and a combination of the following base pairs is diagnostic: in the nuclear genome: aly3824.12.4:A540G, aly3824.12.4:A595C, aly259.26.2:T1260A, aly259.26.2:A590C, aly390.10.14:G2931A and the COI barcode: T29G, A241A, A334T, T337A, T346A, T412T, T578C, A580T.

Etymology. The name is a feminine noun in the nominative singular formed from the type species name: *Vulga*[ta].

Species included. *Achlyodes vulgata* Möschler, 1879, *Pholisora melaina* Hayward, 1947, *Staphylus kayei* Cock, 1996, *Staphylus putumayo sambo* Evans, 1953, *Pholisora putumayo* E. Bell, 1937, *Staphylus saxos* Evans, 1953, *Staphylus saxos satrap* Evans, 1953 (see below), *Staphylus tingo* Steinhauser, 1989, *Nisoniades oeta* Plötz, 1884, and *Staphylus punctiseparatus* Hayward, 1933.

Parent taxon. Genus *Staphylus* Godman and Salvin, 1896.

Staphylus (*Vulga*) *satrap* Evans, 1953 is a species distinct from *Staphylus* (*Vulga*) *saxos* Evans, 1953

Described as a subspecies of *Staphylus saxos* Evans, 1953 (type locality in Colombia: Cali), *S. s. satrap* Evans, 1953 (type locality in Bolivia) is not monophyletic with it and is genetically differentiated from it at the level characteristic of distinct species (Fig. 5), e.g., their COI barcodes differ by 4.4% (29 bp). Moreover, Evans (1953) mentions and illustrates differences in genitalia that suggest species level of these taxa. Therefore, we propose that *Staphylus* (*Vulga*) *satrap* Evans, 1953, **new status**, is a species distinct from *Staphylus* (*Vulga*) *saxos* Evans, 1953, and the latter becomes monotypic.

Capilla Grishin, new subgenus

http://zoobank.org/942D19CE-7B9C-47E7-9650-1721B9A18AB4

Type species. *Helias aurocapilla* Staudinger, 1876, currently a junior subjective synonym of *Hesperia musculus* Burmeister, 1875.

Definition. The nuclear genomic tree reveals that *Staphylus* Godman and Salvin, 1896 (type species *Helias ascalaphus* Staudinger, 1876) splits into five clades at the subgenus level (Fig. 5). The subgenera corresponding to two of these clades, which are sister to each other, do not have available names and are new. One of these new subgenera is phenotypically diverse, keying to E.32.3, 8, 10a, 11a, 13d, 19, 21, or 22 in Evans (1953) and is distinguished from its relatives by the following characters: wings typically narrower than in relatives, several species with more extensive white/hyaline forewing spots; the only subgenus that includes species with divided, rounded (except the very tip), or bulbous at the tip uncus, but uncus undivided and narrow, nearly needle-like in some species, and not strongly concave in lateral view, tegumen usually broader than uncus, vinculum relatively straight in lateral view, harpe mostly broad, with rounded or truncate distal margin, overlays ampulla from the inside (at least in species with lanceolate uncus), ampulla frequently expanded and projects to the end of harper in some species, aedeagus frequently shorter and broader than in relatives. Confident identification is provided by DNA, and a combination of the following base pairs is diagnostic: in the nuclear genome: aly1405.20.35:T489C, aly1405.20.35:T444C, aly1405.20.35:G452C, aly1370.7.2:A2191G, aly1370.7.2:T804G, and the COI barcode T29(mostly T), A130Y, A241(mostly T), A256T, T412(mostly A), T578(mostly T), A580(mostly A).

Etymology. The name is a feminine noun in the nominative singular, formed from the type species name: [auro] *Capilla*.

Species included. *Pholisora lizeri* Hayward, 1938, *Pholisora caribbea* R. Williams and E. Bell, 1940, *Pholisora buena* R. Williams and E. Bell, 1940, *Staphylus melius* Steinhauser, 1989, *Hesperia musculus* Burmeister, 1875, *Pholisora imperspicua* Hayward, 1940, *Pholisora corumba* R. Williams and E. Bell, 1940, *Helias ascalon* Staudinger, 1876, *Staphylus eryx* Evans, 1953, *Hesperia melangon* Mabille, 1883, *Nisoniades tucumanus* Plötz, 1884, *Staphylus perna* Evans, 1953, *Staphylus insignis* O. Mielke, 1980, *Helias tyro* Mabille, 1878, and *Pholisora azteca* Scudder, 1872.

Parent taxon. Genus *Staphylus* Godman and Salvin, 1896.

Composition of Carcharodina Verity, 1940 with comments on nomenclature

The subtribe Carcharodina Verity, 1940 consists of the following genera: *Noctuana* E. Bell, 1937, *Windia* H. Freeman, 1969, *Carcharodus* Hübner, [1819], *Muschampia* Tutt, 1906 (the senior name for this genus is *Sloperia* Tutt, 1906, see below), *Favria* Tutt, 1906, *Gomalia* Moore, 1879, *Agyllia* Grishin, 2019, *Ernsta* Grishin, 2019, and *Spialia* Swinhoe, 1912 (Fig. 6). We phylogenetically arrange genera in the subtribe to start with the New World representatives, because they would follow all the rest of Carcharodini that are from the New World, thus not disrupting the geographic arrangement. The ordering ends with the strongly checkered in wing pattern members of the subtribe, such as *Spialia,* because the next tribe to follow in the taxonomic list would be Pyrginae Burmeister, 1878. To link the two tribes by phenotypic similarity of their constituent species, Pyrginae could start from the Old World checkered skippers in the genus *Pyrgus* Hübner, [1819]), which are superficially similar to *Spialia* and many *Muschampia*, and are the only representatives of Pyrginae in the Old Word. Furthermore, genera in the two pairs (*Favria*, *Muschampia*) and (*Carcharodus*, *Muschampia*) best be next to each other due to phenotypic similarity between some species in each pair, and the phylogeny additionally constrains the pairing (*Favria*,

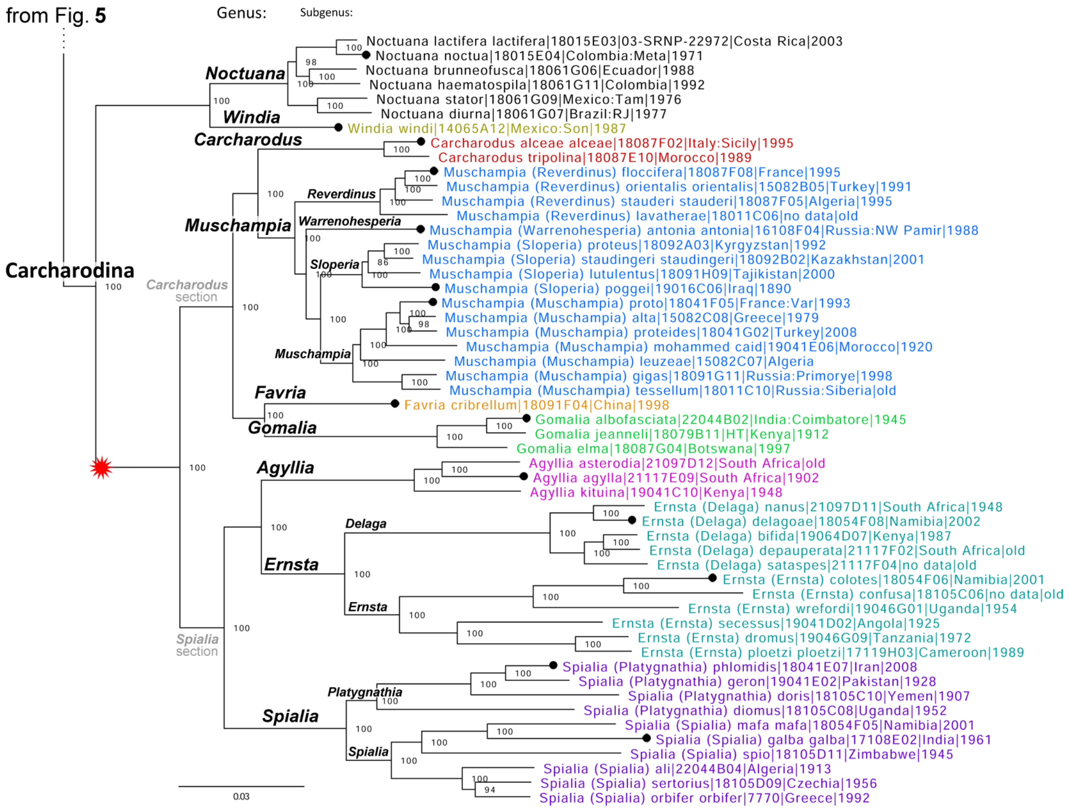

Figure 6. The nuclear genome-based phylogeny of Carcharodini, the last segment (continues from Fig. 4 and 5) showing Carcharodina. Different genera are shown in different colors. See Fig. 1 for notations. The red asterisk on a tree branch denotes the arrival of Carcharodina in the Old World from the New World. See the discussion about *Muschampia* (a junior name) vs. *Sloperia* (should have priority) in the text.

Gomalia). We choose to place *Carcharodus* first due to some wing pattern similarity with *Windia*, and because this order results in a continuous placement of African members (in *Gomalia*, *Agyllia*, and *Ernsta*), ending with mostly Palearctic *Spialia* to follow with Palearctic and similar-looking *Pyrgus*.

In agreement with the ICZN Code, the name *Sloperia* Tutt, 1906 takes precedence over *Muschampia* Tutt, 1906, as selected by the first reviser (Warren 1926) and should be the correct name to use instead of *Muschampia*, as pointed out by Hemming (1967). However, judging by the literature (Wiemers et al. 2018; Wiemers et al. 2020) and discussions with colleagues, the prevailing usage of *Muschampia* is preferred by most of them. We do not have a solution to this problem, and it joins the list of similar problems when there is a disagreement between the articles of the ICZN Code and the community opinion (e.g., gender agreement ICZN Code articles vs. the community of Lepidopterists is an example of a more significant, but similar in spirit, issue). We see the advantages of both treatments in this specific case. Indeed, *Muschampia* has been a widely used name familiar to many people, and it seems that the community opinion should outweigh the priority of a semi-random decision made by the first reviser. Conversely, the rules are universal, clearly spelled out, and long-term, but the community opinions are subject to change, especially with generational changes. Furthermore, the name *Sloperia* is shorter and may be easier for newcomers to learn, fitting the array of other names in the subtribe, such as *Spialia*, *Gomalia*, and *Favria*. Whatever the decision, it is not a question to be solved by scientific tools. It is possible that after some period of deliberation, the community might embrace *Sloperia* (it is not a bad option at all), or the community would be more ready to make a stronger case for ICZN to issue an opinion. However, whichever path is taken, we strongly oppose solving this (and other) nomenclatural problem by fiddling with taxonomy just so that the name *Muschampia* is still in use (e.g., with the sole purpose of accommodating the use of *Muschampia*, treating both *Muschampia* and *Sloperia* as valid genera).

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Literature Cited

Bachtrog D, Thornton K, Clark A, Andolfatto P. 2006. Extensive introgression of mitochondrial DNA relative to nuclear genes in the *Drosophila yakuba* species group. Evolution 60(2): 292–302.

Buchfink B, Xie C, Huson DH. 2015. Fast and sensitive protein alignment using DIAMOND. Nature Methods 12(1): 59–60.

Burns JM, Janzen DH, Hajibabaei M, Hallwachs W, Hebert PD. 2008. DNA barcodes and cryptic species of skipper butterflies in the genus *Perichares* in Area de Conservacion Guanacaste, Costa Rica. Proceedings of the National Academy of Sciences of the United States of America 105(17): 6350–6355.

Cong Q, Shen J, Borek D, Robbins RK, Opler PA, Otwinowski Z, Grishin NV. 2017. 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, Zhang J, Li W, Kinch LN, Calhoun JV, Warren AD, Grishin NV. 2021. Genomics reveals the origins of historical specimens. Molecular Biology and Evolution 38(5): 2166–2176.

Cong Q, Zhang J, Grishin NV. 2019a. Genomic determinants of speciation [Preprint]. bioRxiv BIORXIV/2019/837666. Available at https://www.biorxiv.org/content/10.1101/837666v1 (Last accessed November 2023.)

Cong Q, Zhang J, Shen J, Grishin NV. 2019b. Fifty new genera of Hesperiidae (Lepidoptera). Insecta Mundi 0731: 1–56.

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. The Trustees of the British Museum (Natural History); London. v + 246 p., pls. 26–53.

Fan X, Chiba H, Huang Z, Fei W, Wang M, Safian S. 2016. Clarification of the phylogenetic framework of the tribe Baorini (Lepidoptera: Hesperiidae: Hesperiinae) inferred from multiple gene sequences. PLoS One 11(7): e0156861.

Godman FD. 1907. Notes on the American species of Hesperiidae described by Plötz. Annals and Magazine of Natural History (7)20(16): 132–155.

Grishin NV. 2012. Uncus shaped akin to elephant tusks defines a new genus for two very different-in-appearance Neotropical skippers (Hesperiidae: Pyrginae). The Journal of Research on the Lepidoptera 45: 101–112.

Hebert PD, Cywinska A, Ball SL, deWaard JR. 2003. Biological identifications through DNA barcodes. Proceedings of the Royal Society B: Biological Sciences 270(1512): 313–321.

Hemming AF. 1967. The generic names of the butterflies and their type-species (Lepidoptera: Rhopalocera). Bulletin of the British Museum (Natural History). Entomology Suppl. 9: 1–509.

Huang Z-F, Chiba H, Jin J, Kizhakke AG, Wang M, Kunte K, Fan X-L. 2019. A multilocus phylogenetic framework of the tribe Aeromachini (Lepidoptera: Hesperiidae: Hesperiinae), with implications for taxonomy and biogeography. Systematic Entomology 44(1): 163–178.

ICZN [International Commission on Zoological Nomenclature]. 1999. International code of zoological nomenclature. Fourth edition. International Trust for Zoological Nomenclature; London. xxx + 306 p.

Lemes JRA, Siewert RR, Mielke OHH, Casagrade MM, Warren AD. 2023. Taxonomic and distributional notes on *Bolla tepeca* (Bell, 1942), new combination (Lepidoptera: Hesperiidae: Pyrginae). Tropical Lepidoptera Research 33(2): 102–110.

Li W, Cong Q, Shen J, Zhang J, Hallwachs W, Janzen DH, 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.

Lukhtanov VA, Sourakov A, Zakharov E. 2016. DNA barcodes as a tool in biodiversity research: testing pre-existing taxonomic hypotheses in Delphic Apollo butterflies (Lepidoptera, Papilionidae). Systematics and Biodiversity 14: 599–613.

Mabille P. 1903. Lepidoptera Rhopalocera. Fam. Hesperidae. Genera Insectorum 17a: 1–78.

Nguyen LT, Schmidt HA, von Haeseler A, Minh BQ. 2015. IQ-TREE: a fast and effective stochastic algorithm for estimating maximum-likelihood phylogenies. Molecular Biology and Evolution 32(1): 268–274.

Plötz C. 1882. Einige Hesperiinen-Gattungen und deren Arten. Berliner entomologische Zeitschrift 26(2): 253–266.

Plötz C. 1884. Die Hesperiinen-Gruppe der Achlyoden. Jahrbücher des nassauischen Vereins für Naturkunde 37: 1–55.

Rambaut A. 2018. FigTree, version 1.4.4. Available at http://tree.bio.ed.ac.uk/software/figtree/ (Last accessed November 2023.)

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

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

Schaus W. 1913. New species of Rhopalocera from Costa Rica. Proceedings of the Zoological Society of London 1913(3): 339–367.

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

Toussaint EFA, Braby MF, Müller CJ, Petrie EA, Kawahara AY. 2022. Molecular phylogeny, systematics and generic classification of the butterfly subfamily Trapezitinae (Lepidoptera: Papilionoidea: Hesperiidae). Zoological Journal of the Linnean Society 195: 1407–1421.

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

Toussaint EFA, Chiba H, Yago M, Dexter KM, Warren AD, Storer C, Lohman DJ, Kawahara AY. 2021a. Afrotropics on the wing: phylogenomics and historical biogeography of awl and policeman skippers. Systematic Entomology 46(1): 172–185.

Toussaint EFA, Ellis EA, Gott RJ, Warren AD, Dexter KM, Storer C, Lohman DJ, Kawahara AY. 2021b. Historical biogeography of Heteropterinae skippers via Beringian and post-Tethyan corridors. Zoologica Scripta 50(1): 100–111.

Toussaint EFA, Vila R, Yago M, Chiba H, Warren AD, Aduse-Poku K, Storer C, Dexter KM, Maruyama K, Lohman DJ, Kawahara AY. 2019. Out of the Orient: Post-Tethyan transoceanic and trans-Arabian routes fostered the spread of Baorini skippers in the Afrotropics. Systematic Entomology 44(4): 926–938.

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

Warren BCS. 1926. Monograph of the tribe Hesperiidi (European species) with revised classification of the subfamily Hesperiinae (Palaearctic species) based on the genital armature of the males. Transactions of the entomological Society of London 74: 1–170.

Wiemers M, Balletto E, Dincă V, Fric ZF, Lamas G, Lukhtanov V, Munguira ML, van Swaay CAM, Vila R, Vliegenthart A, Wahlberg N, Verovnik R. 2018. An updated checklist of the European Butterflies (Lepidoptera, Papilionoidea). ZooKeys 811: 9-45.

Wiemers M, Chazot N, Wheat CW, Schweiger O, Wahlberg N. 2020. A complete time-calibrated multi-gene phylogeny of the European butterflies. ZooKeys 938: 97–124.

Zhang J, Cong Q, Burns JM, Grishin NV. 2022a. Checking the checkered taxonomy of Plötz's checkered skippers (Hesperiidae: Pyrgini). The Taxonomic Report of the International Lepidoptera Survey 10(5): 1–31.

Zhang J, Cong Q, Grishin NV. 2023a. Thirteen new species of butterflies (Lepidoptera: Hesperiidae) from Texas. Insecta Mundi 0969: 1–58.

Zhang J, Cong Q, Shen J, Brockmann E, 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, Grishin NV. 2019b. Three new subfamilies of skipper butterflies (Lepidoptera, Hesperiidae). ZooKeys 861: 91–105.

Zhang J, Cong Q, Shen J, Grishin NV. 2022b. Taxonomic changes suggested by the genomic analysis of Hesperiidae (Lepidoptera). Insecta Mundi 0921: 1–135.

Zhang J, Cong Q, Shen J, Opler PA, Grishin NV. 2021. Genomics-guided refinement of butterfly taxonomy. The Taxonomic Report of the International Lepidoptera Survey 9(3): 1–54.

Zhang J, Cong Q, Shen J, Song L, Grishin NV. 2022c. Genomic DNA sequencing reveals two new North American species of *Staphylus* (Hesperiidae: Pyrginae: Carcharodini). The Taxonomic Report of the International Lepidoptera Survey 10(4): 1–13.

Zhang J, Cong Q, Shen J, Song L, Grishin NV. 2023b. Butterfly classification and species discovery using genomics. The Taxonomic Report of the International Lepidoptera Survey 11(3): 1–93.

Zhang J, Cong Q, Shen J, Song L, Grishin NV. 2023c. A taxonomic list of the Old World genera in the subfamily Hesperiinae (Hesperiidae) arranged into tribes. The Taxonomic Report of the International Lepidoptera Survey 11(2): 1–6.

Zhang J, Cong Q, Shen J, Song L, Grishin NV. 2023d. Supplementary information to "Genomics-based taxonomic rearrangement of Achlyodini and Carcharodini (Lepidoptera: Hesperiidae: Pyrginae)." Table S1, Table S2, and DNA sequences of exons with diagnostic characters. Available at https://osf.io//8be5h/ (Last accessed November 2023.)

Zhang J, Dolibaina DR, Cong Q, Shen J, Song L, Mielke CGC, Casagrade MM, Mielke OHH, Grishin NV. 2023d. Taxonomic notes on Neotropical Hesperiidae (Lepidoptera). Zootaxa 5271(1): 91–114.

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