Butterfly classification and species discovery using genomics

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ABSTRACT. Genomic sequencing of worldwide butterfly fauna followed by phylogenetic analysis of protein-coding genes informs butterfly classification throughout the taxonomic hierarchy, from families to species. As a rule, we attribute the same taxonomic rank to more prominent clades of comparable divergence (i.e., at the same level in the tree). For species delimitation, we use criteria based on relative genetic differentiation and the extent of gene exchange between populations. We analyze the current taxonomic classification of butterflies in the light of genomic phylogenies and encounter clades that correspond to yet unnamed taxa. As a result, 11 tribes, 33 subtribes, 2 genera, 11 subgenera, and 12 species are proposed as new. New tribes are: in family Nymphalidae Rafinesque, 1815: in subfamily Heliconiinae Swainson, 1822: Vindulini Grishin, **trib. n.** (type genus *Vindula* Hemming, 1934) and Algiini Grishin, **trib. n.** (type genus *Algia* Herrich-Schäffer, 1864), Lebadeini Grishin, **trib. n.** (type genus *Lebadea* C. Felder, 1861, in subfamily Limenitidinae Behr, 1864), and Amnosiini Grishin, **trib. n.** (type genus *Amnosia* E. Doubleday, 1849, in subfamily Pseudergolinae Jordan, 1898) and in family Lycaenidae [Leach], [1815]: in subfamily Aphnaeinae Distant, 1884: Cigaritini Grishin, **trib. n.** (type genus *Cigaritis* Donzel, 1848) and Axiocersini Grishin, **trib. n.** (type genus *Axiocerses* Hübner, [1819]) and in subfamily Theclinae: Drinini Grishin, **trib. n.** (type genus *Drina* Nicéville, 1890), Hypochrysopini Grishin, **trib. n.** (type genus *Hypochrysops* C. Felder & R. Felder, 1860), Jalmenini Grishin, **trib. n.** (type genus *Jalmenus* Hübner, 1818), Pseudalmenini Grishin, **trib. n.** (type genus *Pseudalmenus* H. H. Druce, 1902), and Rapalini Grishin, **trib. n.** (type genus *Rapala* F. Moore, 1881). New subtribes are: in Papilionidae Latreille, [1802], Meandrusina Grishin, **subtrib. n.** (type genus *Meandrusa* F. Moore, 1888, in Papilionini Latreille, [1802]); in Pieridae Swainson, 1820: Gandacina Grishin, **subtrib. n.** (type genus *Gandaca* F. Moore, 1906, in Coliadini Swainson, 1821), Hebomoiina Grishin, **subtrib. n.** (type genus *Hebomoia* Hübner, [1819], in Anthocharidini Scudder, 1889), and Pseudopierina Grishin, **subtrib. n.** (type genus *Pseudopieris* Godman & Salvin, 1890, in Dismorphiini Schatz, 1886); in Nymphalidae: Lachnopterina Grishin, **subtrib. n.** (type genus *Lachnoptera* E. Doubleday, 1847, in Algiini Grishin, trib. n.), in Vagrantini Pinratana & Eliot, 1996: Terinosina Grishin, **subtrib. n.** (type genus *Terinos* Boisduval, 1836) and Smerinina Grishin, **subtrib. n.** (type genus *Smerina* Hewitson, 1874), in Adoliadini Doubleday, 1845: Evenaina Grishin, **subtrib. n.** (type genus *Evena* Westwood, 1850) and Pseudathymina Grishin, **subtrib. n.** (type genus *Pseudathyma* Staudinger, 1891), and Kumothalina Grishin, **subtrib. n.** (type genus *Kumothales* Overlaet, 1940, in Cymothoini Dhungel & Wahlberg, 2018); in Riodinidae Grote, 1895 (1827): Teratophthalmina Grishin, **subtrib. n.** (type genus *Teratophthalma* Stichel, 1909, in Mesosemiini Bates, 1859), Argyrogrammanina Grishin, **subtrib. n.** (type genus *Argyrogrammana* Strand, 1932, in Symmachiini Reuter, 1896), in the tribe Calydnini Seraphim, Freitas & Kaminski, 2018: Echenaidina Grishin, **subtrib. n.** (type genus *Echenais* Hübner, [1819]) and Echydnina Grishin, **subtrib. n.** (type genus *Echydna* J. Hall, 2002), and Cariina Grishin, **subtrib. n.** (type genus *Caria* Hübner, 1823, in Riodinini Grote, 1895 (1827); in Lycaenidae: Megalopalpina Grishin, **subtrib. n.** (type genus *Megalopalpus* Röber, 1886, in Miletini Reuter, 1896), Pseudaletidina Grishin, **subtrib. n.** (type genus *Pseudaletis* H. H. Druce, 1888, in Cigaritini Grishin, trib. n.), in Aphnaeini Distant, 1884: Aloeidina Grishin, **subtrib. n.** (type genus *Aloeides* Hübner, [1819]) and Phasisina Grishin, **subtrib. n.** (type genus *Phasis* Hübner, [1819]), Pilodeudorigina Grishin, **subtrib. n.** (type genus *Pilodeudorix* H. H. Druce, 1891, in Rapalini Grishin, trib. n.), Hemiolaina Grishin, **subtrib. n.** (type genus *Hemiolaus* Aurivillius, 1922, in Oxylidini Eliot, 1973), Cupidopsina Grishin, **subtrib. n.** (type genus *Cupidopsis* Karsch, 1895, in Hypotheclini Eliot, 1973), and in tribe Polyommatini Swainson, 1827: Theclinesthina Grishin, **subtrib. n.** (type genus *Theclinesthes* Röber, 1891), Azanina Grishin, **subtrib. n.** (type genus *Azanus* F. Moore, 1881), Unina Grishin, **subtrib. n.** (type genus *Una* Nicéville, 1890), Ionolycina Grishin, **subtrib. n.** (type genus *Ionolyce* Toxopeus, 1929), Pithecopina Grishin, **subtrib. n.** (type genus *Pithecops* Horsfield, 1828), Zizulina Grishin, **subtrib. n.** (type genus *Zizula* Chapman, 1910), Jamidina Grishin, **subtrib. n.** (type genus *Jamides* Hübner, [1819]), Fameganina Grishin, **subtrib. n.** (type genus *Famegana* Eliot, 1973), Oboroniina Grishin, **subtrib. n.** (type genus *Oboronia* Karsch, 1893), and Uranothaumatina Grishin, **subtrib. n.** (type genus *Uranothauma* Butler, 1895); and in Hesperiidae Latreille, 1809, Cupithina Grishin, **subtrib. n.** (type genus *Cupitha* F. Moore, 1884, in Astictopterini Swinhoe, 1912). The new genera are *Balenga* Grishin, **gen. n.** (type

species *Proteides balenge* Holland, 1891, in Gretnini Grishin, 2019) and *Tulsia* Grishin, **gen. n.** (type species *Parnara tulsi* Nicéville, 1884, in Baorini Doherty, 1886). New subgenera are: in Pieridae, *Lirinia* Grishin, **subgen. n.** (type species *Terias lirina* H. Bates, 1861, in genus *Pyrisitia* A. Butler, 1870); in Nymphalidae: *Hyperanartia* Grishin, **subgen. n.** (type species *Vanessa dione* Latreille, [1813], in genus *Hypanartia* Hübner, [1821]) and *Paranartia* Grishin, **subgen. n.** (type species *Hypanartia hippomene* Hübner, [1823], in genus *Vanessa* [Fabricius], 1807); in Lycaenidae, *Auricirrus* Grishin, **subgen. n.** (type species *Papilio thysbe* Linnaeus, 1764, in genus *Chrysoritis* Butler, 1898); and in Hesperiidae: *Isocleros* Grishin, **subgen. n.** (type species *Pamphila* (?) *mackenii* Trimen, 1868, in genus *Acleros* Mabille, 1885), *Mesna* Grishin, **subgen. n.** (type species *Parnara leucophaea* Holland, 1894, in genus *Fresna* Evans, 1937), *Lippina* Grishin, **subgen. n.** (type species *Carystus telesinus* Mabille, 1878, in genus *Xanthoneura* Eliot, 1978), *Ganda* Grishin, **subgen. n.** (type species *Zophopetes ganda* Evans, 1937, in genus *Leona* Evans, 1937), *Zarida* Grishin, **subgen. n.** (type species *Hesperia lacida* Hewitson, 1876, in genus *Gretna* Evans, 1937), and in genus *Gegenes* Hübner, 1819: *Flanga* Grishin, **subgen. n.** (type species *Parnara perobscura* H. H. Druce, 1912), and *Havea* Grishin, **subgen. n.** (type species *Hesperia havei* Boisduval, 1833). New species are: in Nymphalidae: *Microtia elvira* Grishin, **sp. n.** (type locality in the USA: AZ, Pima/Santa Cruz Cos.) and *Cyllopsis brocki* **sp. n.** (type locality in Mexico: Sonora, Yécora), in Riodinidae, *Argyrogrammana astuta* Grishin, **sp. n.** (type locality in Peru: Madre de Dios), in Hesperiidae: *Cecropterus* (*Thorybes*) *rockiensis* Grishin, **sp. n.** (type locality in USA: CO, Jefferson Co.), *Cecropterus* (*Thorybes*) *floridianus* Grishin, **sp. n.** (type locality in USA: FL, Volusia Co.), *Cecropterus* (*Thorybes*) *oaxacensis* Grishin, **sp. n.** (type locality in Mexico: Oaxaca), *Nascus* (*Bron*) *lux* Grishin, **sp. n.** (type locality in Brazil: Amapá), *Cogia chiagua* Grishin, **sp. n.** (type locality in Guatemala), *Celotes sabinus* Grishin, **sp. n.** (type locality in USA: AZ, Pima Co.), *Acleros togo* Grishin, **sp. n.** (type locality in Togo), *Ceratrichia notata* Grishin, **sp. n.** (type locality in Central African Republic), and *Semalea malawi* Grishin, **sp. n.** (type locality in Malawi). Furthermore, we elevate a tribe to subfamily, resurrect 3 tribes, 3 subtribes, 5 genera (and confirm 1), 3 subgenera, change the rank of 5 currently recognized tribes to subtribes (and confirm 1), 10 genera to subgenera, synonymize 4 genera, and present evidence to support 21 taxa as species instead of subspecies and 3 taxa as subspecies instead of synonyms. Namely, we reinstate Liphyrinae Doherty, 1889 as a subfamily (was a tribe of Miletinae Reuter, 1896), treat the following as tribes: Leptidiini Grote,1897 (in Dismorphiinae Schatz, 1886) and in Theclinae Swainson, 1830: Surendrini Koçak & Seven, 1997 (not a subtribe of Arhopalini Bingham, 1907) and Myrinini Toxopeus, 1929 (not a synonym of Amblypodiini Doherty, 1886), and subtribes: Callidryina Kirby, 1896 and Gonepterygina Verity, 1920 (in Coliadini Swainson, 1821), Abrotina Hemming, 1960 and Bebeariina Hemming, 1960 (in Adoliadini Doubleday, 1845), and Sarotina Bridges, 1988 (in Helicopini Stichel, 1928). We confirm *Libytheana* Michener, 1943 as a valid genus, not a junior subjective synonym of *Prolibythea* Scudder, 1889 and resurrect from synonymy the following genera: *Pseudanaphaeis* Bernardi, 1953 (not *Belenois* Hübner, [1819]), *Charmion* Nicéville, 1894 (not *Celaenorrhinus* Hübner, [1819]), *Sape* Mabille, 1891 (not *Sarangesa* F. Moore, [1881]), *Milena* Evans, 1912 (not *Caltoris* Swinhoe, 1893) and subgenera: *Neofieldia* Özdikmen, 2008 and *Bassaris* Hübner, [1821] of *Vanessa* [Fabricius], 1807 and *Spindasis* Wallengren, 1857 of *Cigaritis* Donzel, 1848. We change the status of the following taxa from tribes to subtribes: Nathalina Bálint, 2022 and Kricogonina Bálint, 2022 of Euremini Grote, 1898, Tarakina Eliot, 1973 of Spalgini, 1929, Horagina Swinhoe, 1910 and Loxurina Swinhoe, 1910 of Cheritrini Swinhoe, 1910, and Niphandina Sibatani & Ito, 1942 of Polyommatini; from genus to subgenus: *Leucidia* E. Doubleday, 1847 of *Abaeis* Hübner, [1819], *Cesa* Seven, 1997 of *Crudaria* Wallengren, 1875, *Paralycaeides* Nabokov, 1945 of *Itylos* Draudt, 1921, *Eldoradina* Balletto, 1993 of *Nabokovia* Hemming, 1960, *Pyrrhochalcia* Mabille, 1904 of *Coeliades* Hübner, 1818, *Paracleros* Berger, 1978 of *Acleros* Mabille, 1885, *Mopala* Evans, 1937 of *Leona* Evans, 1937, *Afrogegenes* Jong & Coutsis, 2017 and *Torbenlarsenia* Kemal & Koçak, 2020 of *Gegenes* Hübner, 1819, and *Zenonoida* Fan & Chiba, 2016 of *Zenonia* Evans, 1935; and from genus to junior subjective synonym: *Vansomerenia* Heath, 1997 of *Chloroselas* Butler, 1886, *Ceratricula* Larsen, 2013 of *Paronymus* Aurivillius, 1925, *Xanthodisca* Aurivillius, 1925 of *Semalea* Holland, 1896, *Perrotia* Oberthür, 1916 of *Galerga* Mabille, 1898. The following taxa are species, not subspecies or synonyms: *Pyrisitia mayobanex* (M. Bates, 1939), **stat. nov.** and *Pyrisitia memulus* (A. Butler, 1871), **stat. rest.** (not *Pyrisitia dina* (Poey, 1832)), *Abaeis gratiosa* (E. Doubleday, 1847), **stat. rest.** and *Abaeis angulata* (Wallengren, 1860), **stat. rest.** (not *Abaeis arbela* (Geyer, 1832)), *Teriocolias doris* (Röber, 1909), **stat. rest.** (not *Teriocolias deva* (E. Doubleday, 1847)), *Vanessa madegassorum* (Aurivillius, 1899), **stat. nov.** (not *Vanessa hippomene* (Hübner, 1823)), *Eresia* (*Anthanassa*) *seminole* Skinner, 1911, **stat. rev.** (not *Eresia* (*Anthanassa*) *texana* (W. H. Edwards, 1863)), *Cecropterus* (*Thorybes*) *albosuffusa* (H. Freeman, 1943), **stat. nov.** and *Cecropterus* (*Thorybes*) *indistinctus* (Austin & J. Emmel, 1998), **stat. nov.** (not *Cecropterus* (*Thorybes*) *pylades* (Scudder, 1870)), *Cogia hiska* Evans, 1953, **stat. nov.** (not *Cogia hippalus* (W. H. Edwards, 1882)), *Cogia moschus* (W. H. Edwards, 1882), **stat. rest.** (not *Cogia caicus* (Herrich-Schäffer, 1869)), *Pholisora albicirrus* Glassberg 2023, **stat. nov.** (not *Pholisora catullus* (Fabricius, 1793)), *Acleros* (*Isocleros*) *instabilis* Mabille, 1889, **stat. rest.** and *Acleros* (*Isocleros*) *olaus* (Plötz, 1884), **stat. rest.** (not *Acleros* (*Isocleros*) *mackenii* (Trimen, 1868)), *Fresna* (*Mesna*) *bassa* (Lindsey & L. Miller, 1965), **stat. nov., comb. nov.** (not *Meza leucophaea* (Holland, 1894)), *Paronymus volta* (L. Miller, 1971), **stat. nov., comb. nov.** (not *Meza cybeutes* (Holland, 1894)), *Paronymus indeterminabilis* (Strand, 1912), **stat. rest., comb. nov.** and *Paronymus congdoni* (Larsen, 2013), **stat. nov., comb. nov.** (not *Ceratricula semilutea* (Mabille, 1891)), *Semalea corvinus* (Mabille, 1890), **stat. rest.** (not *Semalea sextilis* (Plötz, 1886)), *Xanthoneura patmapana* (Fruhstorfer, 1911), **stat. nov.** (not *Xanthoneura corissa* (Hewitson, 1876)), *Gretna capra* Evans, 1937, **stat. nov.** (not *Gretna carmen* Evans, 1937), and *Lerodea dysaules* Godman, 1900, **stat. rest.** (not a synonym of *Lerodea arabus* (W. H. Edwards, 1882)), while *Vernia verna sequoyah* (H. Freeman, 1942), **stat. rest.** (not a synonym of *Vernia verna* W. H. Edwards, 1862) and *Euphyes vestris osceola* (Lintner, 1878), **stat. rev.** (not a synonym of *Euphyes vestris vestris* (Boisduval, 1852)) are subspecies. In addition, we propose new genus-species combinations: *Pyrisitia amelia* (Poey, [1852]), *Pyrisitia lirina* (H. Bates, 1861), *Abaeis paulina* (H. Bates,

1861), *Abaeis xantochlora* (Kollar, 1850), *Abaeis fabiola* (C. Felder & R. Felder, 1861), *Abaeis tupuntenem* (Lichy, 1976), and *Abaeis adamsi* (Lathy, 1898) (not *Eurema* Hübner, [1819]), *Shijimia potanini* (Alphéraky, 1889) (not *Tongeia* Tutt, 1908), *Fresna* (*Mesna*) *larea* (Neave, 1910), *Fresna* (*Mesna*) *leucophaea* (Holland, 1894), *Fresna* (*Mesna*) *mabea* (Holland, 1894), *Paronymus banda* (Evans, 1937), *Paronymus cybeutes* (Holland, 1894), *Paronymus elba* (Evans, 1937), *Paronymus gardineri* (Collins & Larsen, 2008), *Paronymus indusiate* (Mabille, 1891), and *Paronymus mabillei* (Holland, 1893) (not *Meza* Hemming, 1939), *Paronymus punctata* (Holland, 1896) (not *Ceratrichia* Butler, 1870), *Galerga ariel* (Mabille, 1878) (not *Xanthodisca* Aurivillius, 1925), *Isoteinon anomoeus* (Plötz, 1879), *Isoteinon bruno* (Evans, 1937), *Isoteinon inornatus* (Trimen, 1864), and *Isoteinon punctulata* (A. Butler, 1895) (not *Astictopterus* C. Felder & R. Felder, 1860), *Borbo gemella* (Mabille, 1884) (not *Torbenlarsenia* Kemal & Koçak, 2020), and *Gegenes* (*Torbenlarsenia*) *cottrelli* (Larsen, 2013), *Gegenes* (*Torbenlarsenia*) *fallax* (Gaede, 1916), *Gegenes* (*Torbenlarsenia*) *fanta* (Evans, 1937), *Gegenes* (*Torbenlarsenia*) *micans* (Holland, 1896), and *Gegenes* (*Torbenlarsenia*) *sirena* (Evans, 1937) (not *Borbo* Evans, 1949); and a new species-subspecies combination *Cogia hiska hester* Evans, 1953 (not *Cogia hippalus*). *Acleros nyassicola* Strand, 1921 is a junior subjective synonym of *Acleros* (*Isocleros*) *olaus* (Plötz, 1884), not of *Acleros* (*Isocleros*) *mackenii* (Trimen, 1868). We transferred the tribes Oxylidini Eliot, 1973, Remelanini Eliot, 1973, and Hypolycaenini Swinhoe, 1910 from Theclinae Swainson, 1831 to Polyommatinae Swainson, 1827. We conclude that [No genus] *osibius* Draudt, 1924 is an unavailable name. The **lectotype** is designated for *Eudamus caicus* Herrich-Schäffer, 1869 (type locality likely in Mexico: Oaxaca, as deduced by sequence comparison), and the **neotype** is designated for *Telemiades solon* Plötz, 1882 (type locality becomes Brazil: Bahia). The type localities of *Ceratrichia punctata* Holland, 1896 and *Osmodes staudingeri* Holland, 1896 are Sierra Leone: Freetown and Cameroon: Efoulan, respectively, as determined from the locality labels of primary type specimens. Finally, we provide taxonomic lists for Euremini (to worldwide subgenera and American species) and Lycaenidae (to subtribes).

INTRODUCTION, CONCEPTS, AND METHODS

This work continues a series of studies derived from genomic sequencing of butterflies and uses the same principles and methods (Cong et al. 2019a, b; Li et al. 2019; Zhang et al. 2019a–d; Cong et al. 2020; Zhang et al. 2020; Cong et al. 2021; Zhang et al. 2021; Robbins et al. 2022; Zhang et al. 2022b, c; Zhang et al. 2023c, e). The goal is to improve butterfly classification through genomic data analyses. The approach is that of screening. Specimens of various taxa throughout the butterfly phylogeny worldwide are selected. The emphasis is placed on species recorded from the United States, and specimens across the range are taken for each species. Most specimens come from collections, both museum and private (see acknowledgments section for their list); specimen age varies from ~250 years to recently collected. Whenever possible, we sequence primary type specimens to have an objective reference for the name (Zhang et al. 2022a). Primarily, legs are used for DNA extraction. Our protocol is non-destructive, and legs are preserved. Extracted DNA is fragmented (unless a specimen is old and its DNA is already short) and sequenced at 150 bp on Illumina next-generation sequencing platform. 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.

Sequence data (i.e., sequence segments of 150 bp or shorter) of each specimen are used to assemble exons of protein-coding genes as guided by a reference genome available for the phylogenetically closest species. These protein-coding genes are used for phylogeny reconstruction. Three trees are constructed using IQtree v1.6.12 under the GTR+GAMMA model (Nguyen et al. 2015): from autosomes in the nuclear genome, the gene predicted to be in the Z chromosome, and the mitochondrial genome. To decrease computational load, 100,000 codons (resulting in 300,000 base pairs, about 2% of the total) are randomly selected from the entire dataset to use for the nuclear trees. Statistical support for branches is estimated from 100 replicates of 10,000 codons each, sampled from the total set of codons, and trees are constructed from each replicate. Statistical support value (from 0 to 100) is simply the number of replicates with a particular bipartition identical to the one in the 100,000-codon tree. For further methods details, see our previous publications (Li et al. 2019; Zhang et al. 2022b).

The resulting trees were visualized, rotated, and colored in FigTree (Rambaut 2018). The current taxonomic classification was overlaid on the trees to find non-monophyletic taxa and clades corresponding to taxa without names. Genomic trees frequently reveal "levels," i.e., timepoints when diversification occurred in several lineages independently (Zhang et al. 2021). These "synchronized"

diversifications result from geological events affecting all major lineages at the same time, offering an opportunity to match taxonomic ranks (tribe, subtribe, genus, subgenus) to the levels in genomic trees, which leads to a more objective and internally consistent classification tied to both genetic differentiation and paleontological history. In classification decisions, we strongly rely on 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, in a way that the organism balances it in its genome (we select random codons from all protein-coding genes), to deduce phylogenetically sound taxonomic classification.

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 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) 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.

Tribes are defined as a prominent level in genomic trees between subfamilies and genera that supports most tribes as they are currently circumscribed in each subfamily. Subtribes correspond to a notable tree level between tribes and genera. Genera are defined as the most prominent level in genomic trees between tribes and species that largely corresponds to the current classification into genera. Subgenera correspond to a rather prominent level between genera and species. 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) frequently introgress between species (Bachtrog et al. 2006; Cong et al. 2017a), 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.

Sections below are arranged in the taxonomic order deduced from genome-scale phylogeny complemented by phenotypic considerations. For most new taxa, in addition to brief phenotypic diagnoses (genitalia terminology follows Carneiro et al. (2013), we use "harpe" for Evans' "cuiller" (Evans 1949)) frequently accompanied by references that discuss and illustrate morphological characters

in greater detail, we provide diagnostic DNA characters in the nuclear genome and/or (when meaningful) in 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 described in Cong et al. (2019b) and is aimed at finding more robust characters likely to stand when additional specimens and species are sequenced.

The character states are given in species diagnoses as abbreviations for one of the six reference genomes: *Pterourus glaucus* (Linnaeus, 1758) (pg) (Cong et al. 2015), *Pieris rapae* (Linnaeus, 1758) (pra) (Shen et al. 2016), *Heliconius melpomene* (Linnaeus, 1758) (hm) (Davey et al. 2016), *Calephelis nemesis* (W. H. Edwards, 1871) (cne) (Cong et al. 2017b), *Calycopis cecrops* (Fabricius, 1793) (cce) (Cong et al. 2016), or *Cecropterus lyciades* (Geyer, 1832) (aly, because this species was formerly in the genus *Achalarus* Scudder, 1872) (Shen et al. 2017). E.g., aly728.44.1:G672C means position 672 in exon 1 of gene 44 from scaffold 728 of the *Cecropterus lyciades* (Geyer, 1832) (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 in the supplemental file deposited at < https://osf.io/7tnqy/ >. This link to the DNA sequences accessible from this publication ensures that DNA characters given in the diagnoses can be readily associated with actual sequences.

Whole genome shotgun datasets we obtained and used in this work are available from the NCBI database < https://www.ncbi.nlm.nih.gov/ > as BioProject PRJNA1022154 and BioSample entries of the project contain the locality and other collection data of the sequenced specimens shown in the trees. For each specimen in tree figures, the following information is provided (separated by "|"): taxon name with comments in square brackets, DNA sample code, type status, general locality, and year of collection ("old" if not dated and likely collected 100–150 years ago). Type status abbreviations are: HT holotype, LT lectotype, ST syntype, T type (could be ST, LT, paralectotype, or HT, status not investigated), PT paratype; and if a synonym name is given (in parenthesis, preceded by "=", and in addition by "‡" for unavailable names), type status refers to the synonym. COI barcode sequences reported here have been deposited in GenBank with accessions OR578710–OR578722 and OR589636–OR589640. Several photographs shown in this work were taken from iNaturalist (2023). Links to observations by observation number reported in figure legends are < https://www.inaturalist.org/observations/xxx >, where xxx is the observation number. Abbreviations or acronyms for collections are listed in the acknowledgments section.

Family Papilionidae Latreille, [1802]

Meandrusina Grishin, new subtribe
http://zoobank.org/72E085A2-EA04-4D25-8124-04A86D17F26B

Type genus. *Meandrusa* F. Moore, 1888.

Definition. *Meandrusa* (type species *Papilio evan* E. Doubleday, 1845 currently treated as a subspecies of *Papilio payeni* Boisduval, 1836) was placed in the subtribe Teinopalpini Grote, 1899, but our genomic trees show that it is not monophyletic with *Teinopalpus* Hope, 1843 (type species *Teinopalpus imperialis* Hope, 1843) and instead is sister to Papilionini Latreille, [1802] with 100% support (Fig. 1). Genetic differentiation of *Meandrusa* from Papilionini is approximately the same as of *Battus* Scopoli, 1777 (type species *Papilio polydamas* Linnaeus, 1758) from other Troidini Talbot, 1939 (comparable distance from the root, Fig. 1). Therefore, we consider that *Meandrusa* belongs to the tribe Papilionini. However, the tree shows that *Meandrusa* is prominently separated from the rest of Papilionini and, therefore, belongs to a distinct subtribe analogously to *Battus*. This subtribe does not have a name and is proposed as new. As detailed by Miller (1987) for *Meandrusa*, the new subtribe is characterized by bifid tarsal claws and differs from the rest of Papilionini by strongly incurved middle discocellular vein on the forewing, shorter
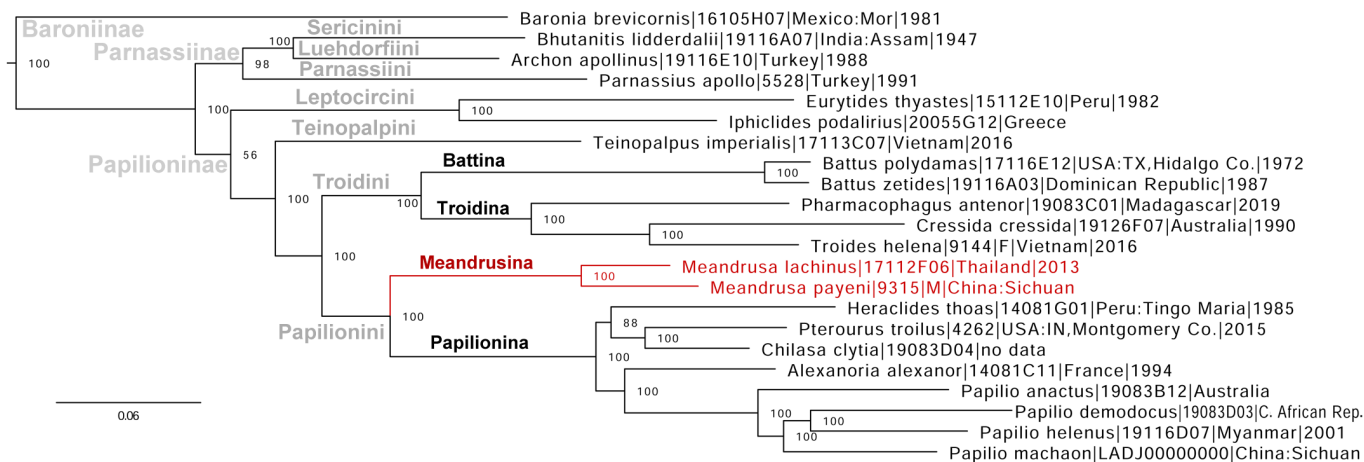
Fig. 1. The phylogenetic tree of selected Papilionidae inferred from protein-coding regions of the nuclear genome (autosomes). Family-group names are shown above or below the corresponding branches. A new subtribe proposed in this work is shown in red. Names of other subtribes are shown in black, and names of subfamilies and tribes are shown in shades of gray.

forewing discal cell (less than half of the wing), and scaled tibiae and tarsi, and from Teinopalpini by scaled antennae and prodiscrimen (equivalent to the prosternum of other insects) with a spine. Visually, species in the new subtribe are recognized by the distinct shape of curved forewings (especially in males) with produced and somewhat hooked apex narrowing to a point (less prominently in *Meandrusa sciron* (Leech, 1890)). A combination of the following nuclear genomic base pairs is diagnostic: pgl2854.3.1: A400G, pgl827.10.7:G122A, pgl827.10.7:G138A, pgl1898.30.3:G202A, pgl1397.11.1: G1138A.

Genera included. Only the type genus.

Parent Taxon. Tribe Papilionini Latreille, [1802].

Family Pieridae Swainson, 1820

Lirinia Grishin, new subgenus
http://zoobank.org/A59BC65A-CEE7-4380-8D40-877A90B74CFD

Type species. *Terias lirina* H. Bates, 1861.

Definition. Our genomic tree reveals that the *T. lirina* (type locality in Brazil: Pará) lineage is monophyletic with neither *Abaeis* Hübner, [1819] (type species *Papilio nicippe* Cramer, 1779) nor *Eurema* Hübner, [1819] (type species *Papilio delia* Cramer, 1780, a junior homonym, valid name for this species is *Pieris daira* Godart, 1819), and instead is a confident sister to all other *Pyrisitia* A. Butler, 1870 (type species *Papilio proterpia* Fabricius, 1775), but is genetically differentiated from them at the level of a subgenus (Fig. 2). Therefore, we transfer *T. lirina* to *Pyrisitia* forming a **new combination** *Pyrisitia lirina* (H. Bates, 1861) and propose that its lineage represents a distinct subgenus of *Pyrisitia*. This new subgenus differs from its relatives by the characters given and illustrated for *Eurema furtadoi* Casagrande & O. Mielke, 1979 in its original description (Casagrade and Mielke 1979). In brief, wings rounded, mostly white with black forewing apex, reminiscent of *Abaeis albula* (Cramer, 1775) (type locality in Suriname), with which it was lumped in the past (Klots 1929), but with very different genitalia: in males, uncus broader, with two shot side processes (absent in *A. albula*); saccus shorter, about the same length as tegumen with uncus; aedeagus bow-shaped, broader and shorter, twice as long as saccus; valva shaped as a half-circle, harpe with robust ventral tooth and much smaller vestigial dorsal tooth; in females, corpus bursae smaller with much smaller signum and a small bubble-shaped appendix (instead of the appendix as long as corpus). A combination of the following nuclear genomic base pairs is diagnostic: pse1181.9.1: G68A, pse988.17.1:A57G, pse6193.9.1:G135T, pse5030.21.1:A392T, pse5030.21.1:T376G, pse907.3.2: A270C, pse1899.1.7:G805A, pse1899.1.7:T806C, pse2087.5.1:C260T, pse102.3.4:C1026G.

6

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

**Species included.** Only the type species.

Parent taxon. Genus *Pyrisitia* A. Butler, 1870.
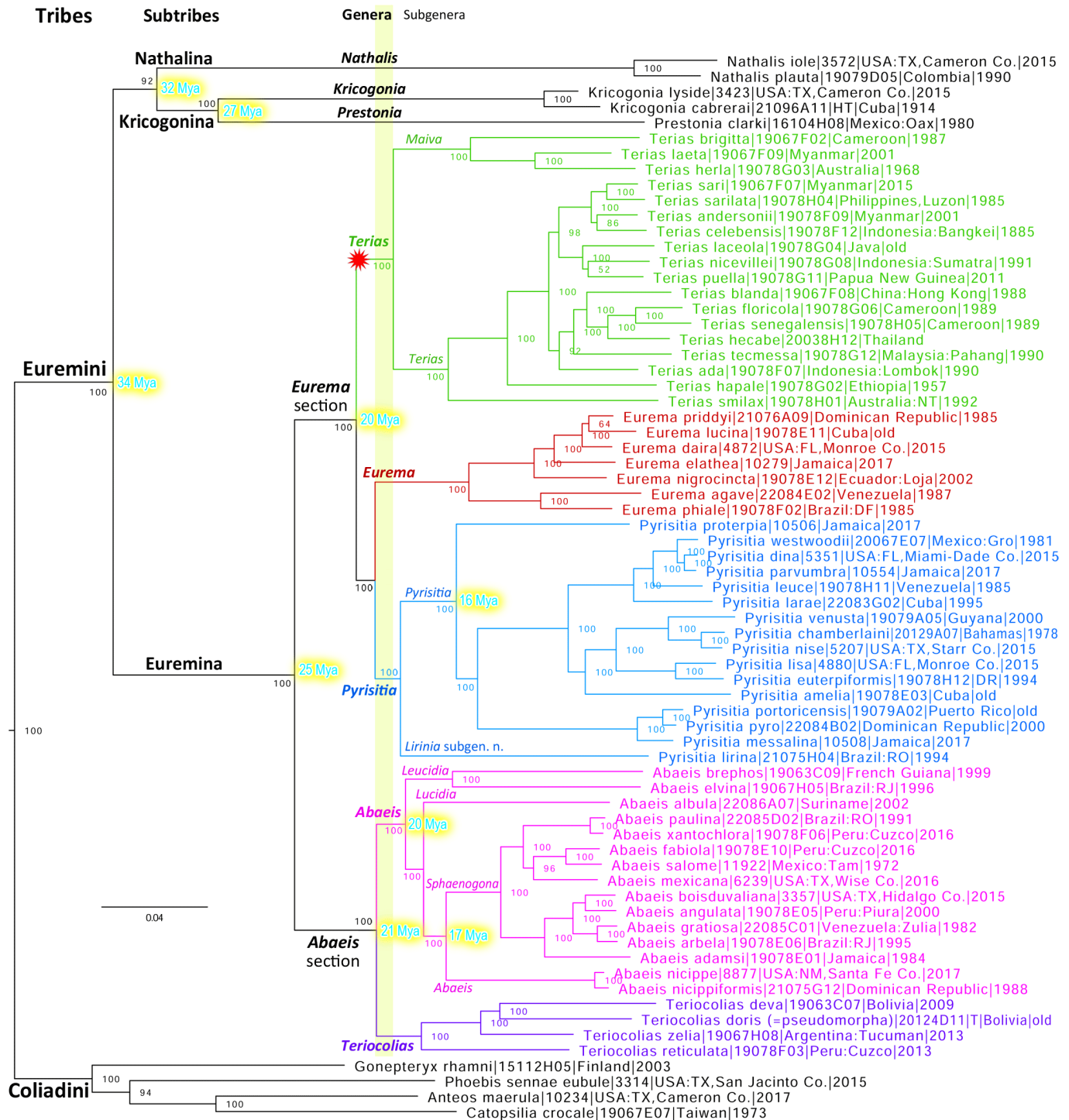
Fig. 2. The phylogenetic tree of Euremini inferred from protein-coding regions of the nuclear genome (autosomes). Levels in the tree that correspond to the taxonomic hierarchy are marked above as Tribes, Subtribes, Genera, and Subgenera. The translucent vertical lime bar denotes the level approximately corresponding to genera. Family-group names (roman font) and genus-group names (genera in bold italics and subgenera in italics) are shown by corresponding branches. Different genera of Euremini are shown in different colors. Numbers in cyan on a yellow background followed by "Mya" placed on the right of several tree nodes indicate the approximate ages of these nodes in million years (rounded) as estimated by Kawahara et al. (2023); smaller numbers are statistical support values of the tree branches (in %, most are 100% implying high confidence). The red asterisk denotes Euremini's arrival in the Old World from the New World, and the genus *Terias* originated as a result.

7

Pyrisitia mayobanex (M. Bates, 1939) and *Pyrisitia memulus* (A. Butler, 1871) are species-level taxa

As we previously concluded, *Pyrisitia westwoodii* (Boisduval, 1836) (type locality in Mexico) is a distinct species, not a subspecies of *Pyrisitia dina* (Poey, 1832) (type locality in Cuba) (Zhang et al. 2021). Sequencing of additional specimens that included the nominal *P. dina* (Fig. 3 blue) confirms this conclusion, also confirming *Pyrisitia parvumbra* (Kaye, 1925) (type locality in Jamaica) (Fig. 3 magenta) as a distinct species (Turner and Turland 2017): F_{st}/G_{min} between *P. parvumbra* and *P. dina dina* of 0.59/0.002 and the COI barcode difference of 2.7% (18 bp). Furthermore, we find prominent genetic differentiation between *P. dina* and the taxon originally proposed as *Eurema helios mayobanex* M. Bates, 1939 (type locality in Haiti): F_{st}/G_{min} of 0.39/0.00, COI difference of 1.8% (12 bp). Therefore, we propose that *Pyrisitia mayobanex* (M. Bates, 1939), **stat. nov.** is a species-level taxon. Inspecting the genomic trees, we see that *Terias memulus* Butler, 1871 (type locality in Haiti), currently regarded as a subspecies of *Pyrisitia leuce* (Boisduval, 1836) (type locality in Brazil: Rio Grande do Sul), is most strongly differentiated from it genetically: F_{st}/G_{min} 0.60/0.00 and the COI barcode difference of 7.3% (48 bp) (Fig. 3 orange), while other *P. leuce* subspecies cluster closely together in the tree (Fig. 3 violet). Therefore, we reinstate *Pyrisitia memulus* (A. Butler, 1871), **stat. rest.** as a species.
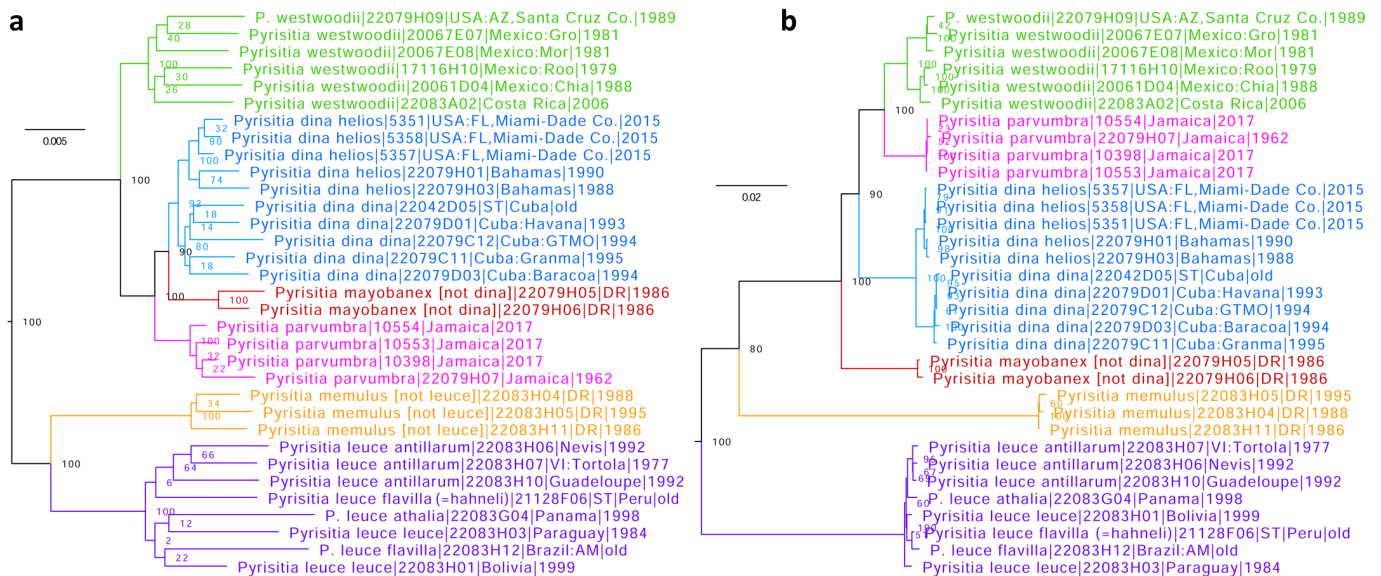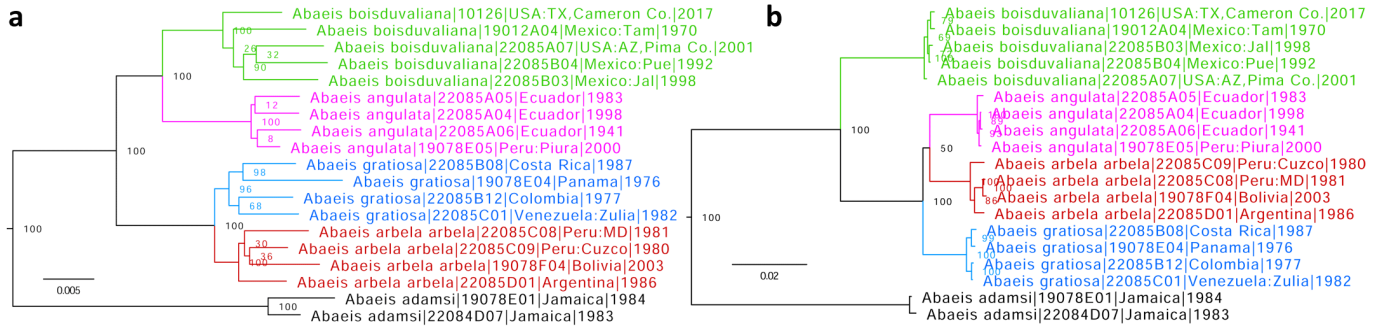

Fig. 3. Phylogenetic trees of *Pyrisitia dina* relatives inferred from protein-coding regions of **a)** the nuclear (autosomes) and **b)** the mitochondrial genomes. Different species are shown in different colors: *P. westwoodii* (green), *P. dina* (blue), *P. mayobanex* **stat. nov.** (red), *P. parvumbra* (magenta), *P. memulus* **stat. rest.** (orange), and *P. leuce* (violet).

Abaeis gratiosa (E. Doubleday, 1847) and *Abaeis angulata* (Wallengren, 1860) are species-level taxa, not subspecies of *Abaeis arbela* (Geyer, 1832)

Genomic sequencing of taxa treated as subspecies of *Eurema arbela* Geyer, 1832 (type locality in "Java", possibly southern Brazil) in Lamas (2004), currently in the genus *Abaeis* Hübner, [1819] (type species *Papilio nicippe* Cramer, 1779) (Zhang et al. 2019b), confirms that *Abaeis boisduvaliana* (C. Felder & R. Felder, 1865) (type locality in Mexico) is a distinct species due to its genetic differentiation from *A. arbela* (Fig. 4 green and red). E.g., its COI barcode is 3.3% (22 bp) different. Moreover, we find that *Abaeis gratiosa* (E. Doubleday, 1847), **stat. rest.** (type locality in Venezuela) and *Abaeis angulata* (Wallengren, 1860), **stat. rest.** (type locality not given, likely in Ecuador) are prominently differentiated genetically from *A. arbela*, *A. boisduvaliana*, and each other both in nuclear and mitochondrial genomes (Fig. 4) and, therefore, are best treated as distinct species. F_{st}/G_{min}/COI difference for the pairs of closest (in nuclear genome) relatives are: *A. gratiosa* and *A. arbela*: 0.21/0.01/3.5% (23 bp) and *A. angulata* and *A. boisduvaliana*: 0.64/0.001/3.6% (24 bp).

Fig. 4. Phylogenetic trees of *Abaeis arbela* species group (rooted with *Abaeis adamsi* **comb. nov.**) inferred from protein-coding regions of **a)** the nuclear (autosomes) and **b)** the mitochondrial genomes. Different species are shown in different colors: *A. boisduvaliana* (green), *A. angulata* (magenta), *A. gratiosa* (blue), and *A. arbela* (red).

Classification of the tribe Euremini Grote, 1898

The phylogenetic tree of the tribe Euremini Grote, 1898 (type genus *Eurema* Hübner, [1819]) inferred from protein-coding regions in the nuclear genome (autosomes only) reveals strong statistical support (100% for most branches) and noticeable tree levels (resulting from coinciding diversifications in different clades at about the same distance from the root) to aid its higher classification (Fig. 2). The level closest to the origin of the tribe consists of three prominent clades that we treat as subtribes: Nathalina Bálint, 2022, **stat. nov.** (type genus *Nathalis* Boisduval, 1836), Kricogonina Bálint, 2022, **stat. nov.** (type genus *Kricogonia* Reakirt, 1864) and the nominotypical, Euremina. The former two were originally proposed as tribes, but the early split of the subfamily Coliadinae Swainson, 1821 (type genus *Colias* [Fabricius], 1807) into two prominent clades argues for treating these clades as tribes (Euremini and Coliadini) rather than dividing them further. Therefore, further divisions would correspond to the subtribal level. The monotypic genus *Prestonia* Schaus, 1920 (type species *Prestonia clarki* Schaus, 1920) placed in Euremini by Zhang et al. (2021) is sister to *Kricogonia* and diverged from it approximately 27 million years ago (Mya), as estimated in Kawahara et al. (2023), which is close to the split of the subtribe Euremina into two clades (25 Mya). Due to this similar level of genetic differentiation between *Kricogonia* and *Prestonia* and between the two first clades of Euremina, *Prestonia* is placed in the subtribe Kricogonina rather than in a subtribe of its own. Such classification emphasizes the sister relationship of the two genera (*Kricogonia* and *Prestonia*) rather than the distinction between them.

While there is little doubt that the five known species in Nathalina and Kricogonina are best classified into the three genera corresponding to the most prominent clades in the tree (Fig. 2), the taxonomy of the subtribe Euremina is more complex. Traditionally, the entire subtribe has been treated as a single genus *Eurema* Hübner, [1819] (type species *Papilio delia* Cramer, 1780, a junior homonym, valid name for this species is *Pieris daira* Godart, 1819) (Klots 1933). However, early DNA work suggested strong genetic differentiation within the subtribe (Pollock et al. 1998), formalized by Opler and Warren (2002), who partitioned the US species into three genera: *Eurema*, *Pyrisitia* A. Butler, 1870 (type species *Papilio proterpia* Fabricius, 1775), and *Abaeis* Hübner, [1819] (type species *Papilio nicippe* Cramer, 1779). This split has been largely followed (Lamas 2004; Pelham 2008), although some species have been reassigned between these genera (Zhang et al. 2019b). Our work (Zhang et al. 2019c; Zhang et al. 2019b) and more recent publications (Kawahara et al. 2023) support the notion of strong genetic differentiation within Euremina and date its diversification to approximately 25 Mya (Fig. 2). This level of differentiation and age are too large for placing all Euremina in the single genus *Eurema*.

The subtribe Euremina splits into two prominent clades at approximately 25 Mya, as estimated by Kawahara et al. (2023). These two clades can be taken to represent genera, and the subtribe can be divided into two genera: *Eurema* and *Abaeis*. However, even this level of genetic differentiation and age would be larger than for most genera of butterflies (Talavera et al. 2012; Li et al. 2019; Zhang et al. 2019a, c), and the ages between 15 and 20 Mya would be more consistent with the genus level. Even if absolute values of age estimates are not particularly accurate due to various errors, their relative values

and the fact they are all estimated mainly with the same method and on similar datasets argue for the validity of such comparisons of estimated ages between nodes. For these reasons, we regard the two clades of Euremina as "sections": the *Eurema* section and the *Abaeis* section, and take the next level in the tree to define genera.

The next tree level, dating to approximately 20 Mya, consists of five clades, one of which is entirely from the Old Word, the only Old Word group in the entire tribe Euremina (Fig. 2 marked with red asterisk). We propose that these five clades represent genera in Euremina: *Terias* W. Swainson, 1821 (type species *Papilio hecabe* Linnaeus, 1758) and *Eurema* with its sister *Pyrisitia* A. Butler, 1870 (type species *Papilio proterpia* Fabricius, 1775) belong to the *Eurema* section, and *Abaeis* with *Teriocolias* Röber, 1909 (type species *Terias atinas* Hewitson, 1874, a junior subjective synonym of *Terias zelia* Lucas, 1852) belong to the *Abaeis* section. This partitioning into genera is biogeographically significant because it reflects the invasion of the only Euremini lineage from the New World, where the tribe likely originated, into the Old World, giving rise to the genus *Terias*, followed by its extensive diversification. Genera of Euremina defined this way are analogous to *Codatractus* Lindsey, 1921 vs. *Lobocla* Moore, 1884, *Heliopetes* Billberg, 1820 vs. *Pyrgus* Hübner, [1819], and *Oarisma* Scudder, 1872 vs. *Thymelicus* Hübner, [1819] (in the latter two, pairs some species from the Old World genus returned to the New World at a later time) and correspond to similar geological time-frame of the mid-Miocene climatic optimum characterized by elevated biotic movement from America to Asia (Jiang et al. 2019).

The phylogenetic tree (Fig. 2) guides the assignment of species to genera, and we restore the monophyly by proposing new genus-species combinations: *Pyrisitia amelia* (Poey, [1852]), **comb. nov.**, *Pyrisitia lirina* (H. Bates, 1861), **comb. nov.**, *Abaeis paulina* (H. Bates, 1861), **comb. nov.**, *Abaeis xantochlora* (Kollar, 1850), **comb. nov.**, *Abaeis fabiola* (C. Felder & R. Felder, 1861), **comb. nov.**, *Abaeis tupuntenem* (Lichy, 1976), **comb. nov.**, *Abaeis adamsi* (Lathy, 1898), **comb. nov.**, *Abaeis brephos* (Hübner, [1809]), **comb. nov.**, and *Abaeis elvina* (Godart, 1819), **comb. nov**. The latter two combinations reflect our treatment of *Leucidia* E. Doubleday, 1847, **stat. nov.** (type species *Pieris elvina* Godart, 1819) as a subgenus of *Abaeis* despite its unique phenotype. Such treatment results in a more internally consistent classification because an *Abaeis* that includes *Leucidia* corresponds to a more prominent clade in the tree, and the *Leucidia* clade has split from the rest of *Abaeis* at the tree level corresponding to subgenera (Fig. 2). This level allows us to define five subgenera in Euremina in addition to the five genera (Fig. 2 and listed below). Finally, we note that *Teriocolias doris* (Röber, 1909), **stat. rest.** (type locality in Bolivia), currently regarded as a subspecies of *Teriocolias deva* (E. Doubleday, 1847) (type locality in French Guiana), is genetically very distant from it: e.g., COI barcodes differ by 7.6% (50 bp) and is a distinct species.

Below is a proposed classification of the tribe Euremini. Only available genus-group names are listed; subspecies names are not given and can be found on the Butterflies of America website (Warren et al. 2023), and the Old Word species are not provided (all belong to the genus *Terias*, which consists only of Old World species). Type genus (for family-group names) or type species (for genus-group names) names are given in parenthesis; synonyms are preceded by = and all but subjective synonyms also by ‡ with a valid name of this species following the colon. New taxa and status changes are shown in red font.

Tribe **Euremini** Grote, 1898 (*Eurema* Hübner, [1819])

Subtribe **Nathalina** Bálint, 2022, **stat. nov.** (*Nathalis* Boisduval, 1836)

Genus ***Nathalis*** Boisduval, 1836 (*Nathalis iole* Boisduval, 1836)
Nathalis iole Boisduval, 1836
Nathalis plauta E. Doubleday, 1847

Subtribe **Kricogonina** Bálint, 2022, **stat. nov.** (*Kricogonia* Reakirt, 1864)

Genus ***Kricogonia*** Reakirt, 1863 (*Colias lyside* Godart, 1819)
Kricogonia lyside (Godart, 1819)
Kricogonia cabrerai Ramsden, 1920

Genus ***Prestonia*** Schaus, 1920 (*Prestonia clarki* Schaus, 1920)
Prestonia clarki Schaus, 1920

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

  Eurema section

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

        Consists of all Old World species of *Euremini*

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

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

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

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

    Genus **Eurema** Hübner, [1819] (=‡*Papilio delia* Cramer, 1780: *Pieris daira* Godart, 1819)

      Eurema priddyi (Lathy, 1898)
      Eurema lucina (Poey, [1852])
      Eurema daira (Godart, 1819)
      Eurema elathea (Cramer, 1777)
      Eurema nigrocincta Dognin, 1889
      Eurema agave (Cramer, 1775)
      Eurema phiale (Cramer, 1775)

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

      Subgenus *Pyrisitia* A. Butler, 1870 (*Papilio proterpia* Fabricius, 1775)

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

      Subgenus *Lirinia* Grishin, **subgen. n.**

        Pyrisitia lirina (H. Bates, 1861), **comb. nov.**

  Abaeis section

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

      Subgenus *Leucidia* E. Doubleday, 1847 (*Pieris elvina* Godart, 1819), **stat. nov.**

        Abaeis brephos (Hübner, [1809]), **comb. nov.**
        Abaeis elvina (Godart, 1819), **comb. nov.**

      Subgenus *Lucidia* Lacordaire, 1833 (*Papilio albula* Cramer, 1775)

        Abaeis albula (Cramer, 1775)

      Subgenus *Sphaenogona* Butler, 1870 (*Terias bogotana* C. & R. Felder, 1861: a ssp. of *T. mexicana* Boisduval)

        Abaeis paulina (H. Bates, 1861), **comb. nov.**
        Abaeis xantochlora (Kollar, 1850), **comb. nov.**
        Abaeis fabiola (C. Felder & R. Felder, 1861), **comb. nov.**
        Abaeis tupuntenem (Lichy, 1976), **comb. nov.**
        Abaeis salome (C. Felder & R. Felder, 1861)
        Abaeis mexicana (Boisduval, 1836)
        Abaeis boisduvaliana (C. Felder & R. Felder, 1865)
        Abaeis angulata (Wallengren, 1860), **stat. rest.**
        Abaeis gratiosa (E. Doubleday, 1847), **stat. rest.**
        Abaeis arbela (Geyer, 1832)
        Abaeis adamsi (Lathy, 1898), **comb. nov.**

      Subgenus *Abaeis* Hübner, [1819] (*Papilio nicippe* Cramer, 1779)

        Abaeis nicippe (Cramer, 1779)
        Abaeis nicippiformis (Munroe, 1947)

    Genus **Teriocolias** Röber, 1909 (=*Terias atinas* Hewitson, 1874: *Terias zelia* Lucas, 1852)

      Teriocolias deva (E. Doubleday, 1847)
      Teriocolias doris (Röber, 1909), **stat. rest.**
      Teriocolias zelia (Lucas, 1852)
      Teriocolias reticulata (A. Butler, 1871)

# Subtribes in Coliadini Swainson, 1821

The genomic tree reveals four prominent clades in the tribe Coliadini Swainson, 1821 that are at approximately the same distance from the root (Fig. 5). We propose treating these clades as subtribes. Three of these subtribes have names: the nominotypical one, Callidryina Kirby, 1896, **stat. nov.**, and Gonepterygina Verity, 1920, **stat. nov**. The name Callidryina is formed from the genus *Callidryas* Boisduval & Le Conte, 1830 (type species *Papilio eubule* Linnaeus, 1767), which is currently treated as a junior subjective synonym of *Phoebis* Hübner, [1819] (type species *Phoebis cypris* Hübner, [1819], which is an unjustified emendation of *Papilio cipris* Cramer, 1777, which is a junior subjective synonym of *Papilio argante* Fabricius, 1775). Callidryina consists of two closely related genera, *Phoebis* (that includes *Rhabdodryas* Godman & Salvin, 1889) and *Aphrissa* Butler, 1873. In addition to the type genus *Gonepteryx* Leach, 1815, we place *Dercas* E. Doubleday, 1847 in Gonepterygina. The fourth subtribe does not have a name. It is described below.

Gandacina Grishin, new subtribe
http://zoobank.org/EF448D21-E251-4ABA-9A22-22EBD93A8303

Type genus. *Gandaca* F. Moore, 1906.

Definition. *Gandaca* (type species *Terias harina* Horsfield, 1829) is sister to Gonepterygina Verity, 1920,
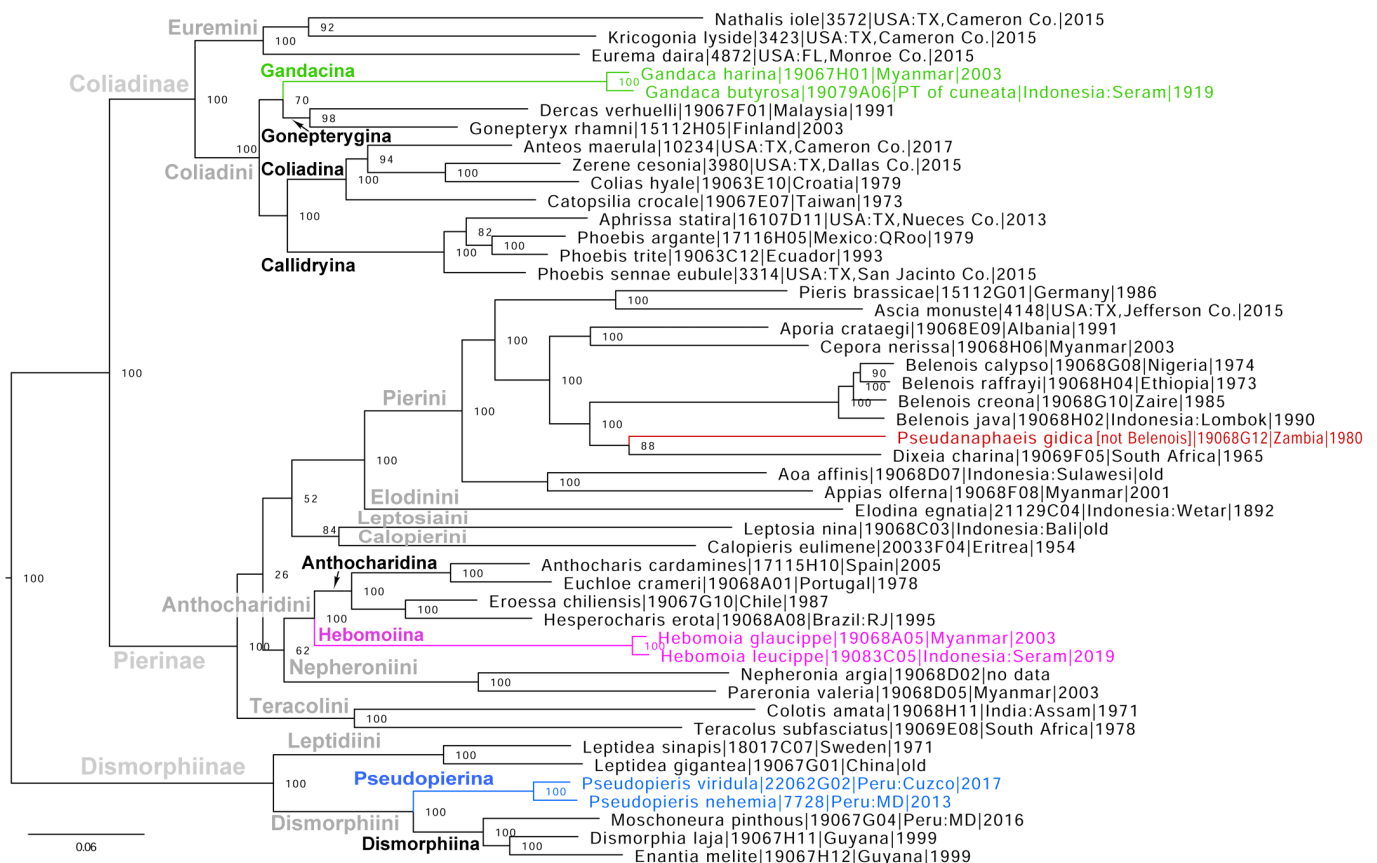
Fig. 5. The phylogenetic tree of selected Pieridae inferred from protein-coding regions of the nuclear genome (autosomes). Family-group names are shown by corresponding branches, or an arrow points to the branch. Names, clades, and species of new subtribes proposed in this work are shown in color, except that red indicates a reinstated genus *Pseudanaphaeis* (not a synonym of *Belenois*). Names of other subtribes are shown in black, and names of subfamilies and tribes are shown in shades of gray. Note the extreme variation of base-pair substitution rate in Pieridae, where DNA of some taxa (e.g., *Gonepteryx*) changes at least two times slower than others (e.g., *Belenois*), as evidenced by the distance from the root to these leaves. Therefore, no vertical bars or lines can demarcate tribes and subtribes in this tree, where branch length corresponds to the estimated number of base pair changes along the branch.

stat. nov. but is more distant from the members of this subtribe both genetically and phenotypically. Furthermore, the statistical support for Gonepterygina to include *Gandaca* is lower than for most other clades in the tree (88%) (Fig. 5). Therefore, the clade with *Gandaca* is defined as a subtribe. This new subtribe is diagnosed by the following characters: in male genitalia, uncus pointed dorsad at the base, with dorsal margin strongly arched and finely serrated, uncus shorter than in relatives and broader towards its distal end in dorsal view; in female genitalia, corpus bursae nearly spherical with a ring-shaped signum at its base and an appendix that is larger than the corpus itself; in facies, is more similar to *Eurema* Hübner, [1819] and relatives (tribe Euremini Grote, 1898) than to Gonepterygina: lemon-yellow wings without central spots, hindwings plain or with dark margin by the apex and forewings with dark apex continuing into thin marginal border. See Kaur et al. (2022) for illustrations. A combination of the following nuclear genomic base pairs is diagnostic: pse19182.2.2:A3375G, pse1982.1.2:A51T, pse200.39.1:T1209C, pse1378.26.1:G839A, pse200.29.1:C1534G.

Genera included. Only the type genus.

Parent Taxon. Tribe Coliadini Swainson, 1821.

Pseudanaphaeis Bernardi, 1953 is a genus distinct from *Belenois* Hübner, [1819]

Currently considered a junior subjective synonym of *Belenois* Hübner, [1819] (type species *Papilio calypso* Drury, 1773, sequenced as NVG-19068G08), *Pseudanaphaeis* Bernardi, 1953 (type species *Pieris gidica* Godart, 1819, sequenced as NVG-19068G12), is not monophyletic with it, and instead is sister to *Dixeia* Talbot, 1932 (type species *Pieris charina* Boisduval, 1836, sequenced as NVG-19069F05) (Fig. 5). Extensive genetic differentiation between *Dixeia* and *Belenois* precludes from considering them congeneric. Therefore, we propose to treat *Pseudanaphaeis* Bernardi, 1953, **stat. rest.** as a distinct genus.

Hebomoiina Grishin, new subtribe
http://zoobank.org/71C79ADE-4BBF-4CC8-86B6-331BCD38863B

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

Definition. *Hebomoia* (type species *Papilio glaucippe* Linnaeus, 1758) belongs to the tribe Anthocharidini Scudder, 1889, but is genetically differentiated from its other genera (Fig. 5). Phenotypically, species in this lineage are characterized by a more robust appearance that the rest of the tribe. Therefore, we propose that the clade with *Hebomoia* corresponds to a subtribe. This new subtribe is diagnosed by a bifurcate uncus and bifurcate valva, forewing with five radial veins, two of which and M_1 (not stalked with R) originate at the discal cell, larger size (forewing longer than 40 mm), and pointed broadly orange apex of the forewing. See Klots (1933) for additional discussion and illustrations of these characters given for *Hebomoia*. A combination of the following nuclear genomic base pairs is diagnostic: pse123.37.1:A2228G, pse123.37.1:T1285A, pse9809.2.1:G1812A, pse657.5.2:A89G, pse5906.8.2:G3017A.

Genera included. Only the type genus.

Parent Taxon. Tribe Anthocharidini Scudder, 1889.

Tribes and subtribes in Dismorphiinae Schatz, 1886

The subfamily Dismorphiinae Schatz, 1886 splits into two prominent clades that we propose to treat as tribes: the nominotypical and Leptidiini Grote,1897, **stat. rev.**, which is monotypic (Fig. 5). The two tribes are well-defined morphologically (Klots 1933) and biogeographically, with Leptidiini being the Old World tribe and Dismorphiini restricted to the New World.

Pseudopierina Grishin, new subtribe

http://zoobank.org/25317F65-DA92-4FD1-88BB-ED275C6B46A1

Type genus. *Pseudopieris* Godman & Salvin, 1890.

Definition. *Pseudopieris* (type species *Pieris nehemia* Boisduval, 1836) is sister to and is stronger differentiated genetically from the rest of Dismorphiini Schatz, 1886 (Fig. 5). Therefore, combined with phenotypic differences, we propose that the lineage with *Pseudopieris* corresponds to a subtribe. This new subtribe is distinguished from the rest of Dismorphiini (and Dismorphiinae, for that matter) by much broader wings that are more like in *Pieris* Schrank, 1801, rather than the elongated wings of Dismorphiinae, the last abdominal segment with rounded lobes and a cleft, and M_1 stalked with R stem on the forewing. See Klots (1933) for details and illustrations given for *Pseudopieris*. A combination of the following base pairs in the nuclear genome is diagnostic: pse7986.9.2:A4048G, pse19182.2.2:T3830C, pse165.20.1:A803T, pse578.3.2:C31A, pse578.3.2:A12G.

Genera included. Only the type genus.

Parent Taxon. Tribe Dismorphiini Schatz, 1886.

Family Nymphalidae Rafinesque, 1815

Libytheana Michener, 1943 is a genus distinct from *Prolibythea* Scudder, 1889

Considered synonyms in some publications (Kawahara 2009; Sohn et al. 2012), fossil *Prolibythea* Scudder, 1889 (type species *Prolibythea vagabunda* Scudder, 1889) and contemporary *Libytheana* Michener, 1943 (type species *Libythea bachmanii* Kirtland, 1851, which is regarded as a subspecies of *Papilio carinenta* Cramer, 1777), both American, are separated by at least 30 million years according to the age estimate of the fossil as late Priabonian (Sohn et al. 2012). The typical age of congeners is not larger than 20 million years. Furthermore, the divergence between *Libytheana* and the Old World genus *Libythea* [Fabricius], 1807 (type species *Papilio celtis* Laicharting, 1782) was dated to about 12 Mya (Kawahara et al. 2023), which is more recent than 30 Mya. Thus, it is most likely that *Prolibythea* lived before the divergence between *Libytheana* and *Libythea*. Therefore, if *Libytheana* and *Libythea* are treated as separate genera, then *Prolibythea* is not congeneric with *Libytheana* to avoid paraphyly.

The tribe *Vagrantini* Pinratana & Eliot, 1996 as currently defined is paraphyletic

Currently, the tribe Vagrantini Pinratana & Eliot, 1996 consists of ten genera: *Vagrans* Hemming, 1934, *Cupha* Billberg, 1820, *Phalanta* Horsfield, 1829, *Smerina* Hewitson, 1874, *Terinos* Boisduval, 1836, *Algia* Herrich-Schäffer, 1864), *Algiachroa* Parsons, 1989, *Cirrochroa* E. Doubleday, 1847, *Lachnoptera* E. Doubleday, 1847, and *Vindula* Hemming, 1934 (Wahlberg 2019). However, our genomic tree reveals that Vagrantini, defined to include all ten genera, is paraphyletic with respect to Argynnini Swainson, 1833 with the highest support (Fig. 6). The first five genera listed above form a clade sister to Argynnini. This clade includes *Vagrans*, which is the type genus of Vagrantini. Therefore, to restore monophyly, we restrict Vagrantini to include only these five genera: *Vagrans*, *Cupha*, *Phalanta*, *Smerina*, and *Terinos*. The remaining five genera previously included in Vagrantini form a clade sister to both Vagrantini and Argynnini (Fig. 6) and, therefore, belong to other tribes. No published family-group names have been formed from any of these five genera; hence, these other tribes are new. They are described below.

Vindulini Grishin, new tribe

http://zoobank.org/151AC163-E036-49BE-A49C-48D7B9F0108F

Type genus. *Vindula* Hemming, 1934.
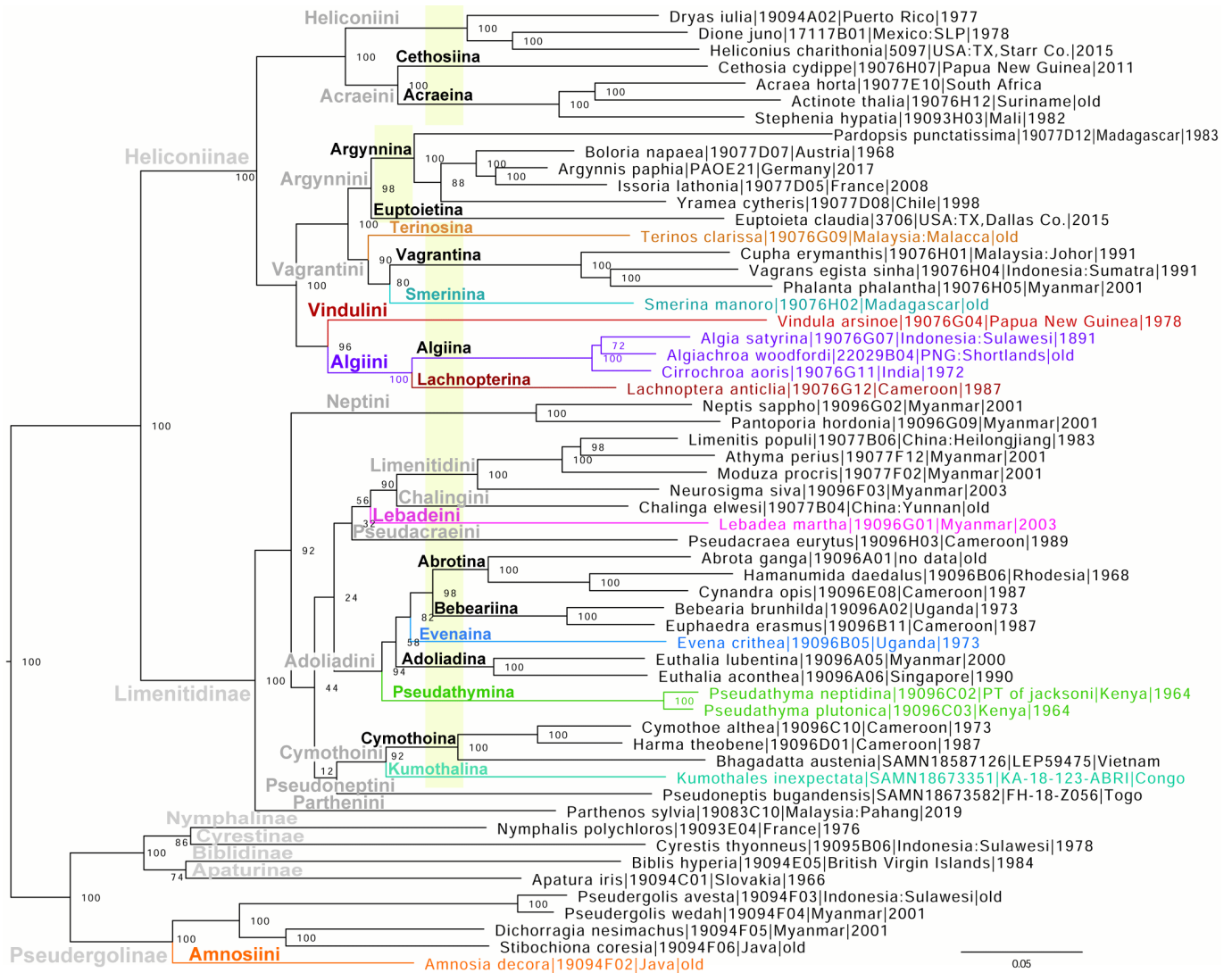
Fig. 6. The phylogenetic tree of selected Nymphalidae inferred from protein-coding regions of the nuclear genome (autosomes). Sequences of the three samples with numbers starting with "SAMN" were taken from the alignment provided in Supplementary materials to Kawahara et al. (2023). Family-group names are shown above or below the corresponding branches. Names, clades, and species of new tribes and subtribes proposed in this work are shown in color. Names of other subtribes are shown in black, and names of subfamilies and tribes are shown in shades of gray. The translucent vertical lime bar denotes a level in the tree approximately corresponding to subtribes; however, due to variation in base pair substitution rates (i.e., not all tree leaves are at the same level), the correspondence may not be exact. E.g., DNA changes in Argynnini are slower than in most other groups (many Argynnini leaves are closer to the left compared to most others); hence, the level is shifted to the left, which also preserves the originally proposed (Simonsen 2006) division into two and not three subtribes.

Definition. *Vindula* (type species *Papilio arsinoe* Cramer, 1777) constitutes a lineage sister to four other genera that were previously included in Vagrantini Pinratana & Eliot, 1996 but did not belong to this tribe (see above). This lineage diverged from these other genera at about the same level as (if not earlier than) Vagrantini from Argynnini Swainson, 1833, and therefore corresponds to a tribe (Fig. 6). This new tribe is distinguished from its relatives by sclerotized subpapillary glands in females and forked humeral vein (Penz and Peggie 2003). A combination of the following nuclear genomic base pairs is diagnostic: hm2013347-RA.4:T162C, hm2013540-RA.5:G265A, hm2015146-RA.7:G80A, hm2015146-RA.7:G79A, hm2013347-RA.4:A220C.

Genera included. Only the type genus.

Parent Taxon. Subfamily Heliconiinae Swainson, 1822.

Algiini Grishin, new tribe
http://zoobank.org/AE49C6E7-8E51-4E4E-9947-151B37A467E8

Type genus. *Algia* Herrich-Schäffer, 1864.

Definition. This tribe corresponds to the second major subclade in the clade that is sister to both Argynnini Swainson, 1833 and Vagrantini Pinratana & Eliot, 1996. This subclade is sister to Vindulini **trib. n.**, diverging from it at about the same level as (if not earlier than) Argynnini from Vagrantini (Fig. 6). Due to this prominent genetic differentiation, it is defined as a tribe. This new tribe is distinguished from its relatives by unsclerotized subpapillary glands in females, forked humeral vein, and/or smooth eyes and undifferentiated androconial scales, or by an oval patch of androconial scales in males in the apical area of dorsal hindwing covering 1/7–1/6 of its surface (Penz and Peggie 2003). A combination of the following nuclear genomic base pairs is diagnostic: hm2000037-RA.1:C698G, hm2008858-RA.12:T1021C, hm2008858-RA.12:C1022T, hm2016824-RA.4:C154A, hm2017493-RA.1:A2480G.

Genera included. The type genus (i.e., *Algia* Herrich-Schäffer, 1864), *Algiachroa* Parsons, 1989, *Cirrochroa* E. Doubleday, 1847, and *Lachnoptera* E. Doubleday, 1847.

Parent Taxon. Subfamily Heliconiinae Swainson, 1822.

Lachnopterina Grishin, new subtribe
http://zoobank.org/8BBABF1F-145B-4A67-94F5-F498130FB857

Type genus. *Lachnoptera* E. Doubleday, 1847.

Definition. *Lachnoptera* (type species *Papilio iole* Fabricius, 1781) forms a lineage that splits from all other Algiini **trib. n.** at the tree level of subtribes (Fig. 6), therefore representing a subtribe. This new subtribe is distinguished from its relatives by unsclerotized subpapillary glands in females (Penz and Peggie 2003) and an oval patch of androconial scales in males in the apical area of dorsal hindwing covering 1/7–1/6 of its surface. A combination of the following nuclear genomic base pairs is diagnostic: hm2008958-RA.5:T118G, hm2008958-RA.5:G119T, hm2006642-RA.2:A2275C, hm2006706-RA.1:A709T, hm2006706-RA.1:A748T, hm2015589-RA.1:A1852A (not C), hm2014529-RA.4:A139A (not G), hm2012118-RA.6:A79A (not G), hm2016492-RA.5:A1813A (not G), hm2016492-RA.5:C1831C (not A).

Genera included. Only the type genus.

Parent Taxon. Tribe Algiini Grishin, **trib. n.**

Terinosina Grishin, new subtribe
http://zoobank.org/31DFAAA5-EA63-431B-AC9D-BF686549FEC8

Type genus. *Terinos* Boisduval, 1836.

Definition. *Terinos* (type species *Terinos clarissa* Boisduval, 1836) forms a deep-diverging lineage in the tribe Vagrantini Pinratana & Eliot, 1996 at about the tree level corresponding to subtribes (Fig. 6) and, therefore, represents a subtribe. This new subtribe is distinguished from its relatives by a combination of the following characters: larval head with scoli, hindwing cell closed, a fold across the forewing between R and M veins, vein R_2 arising from discal cell, vein R_4 arising at about the end of R_2, humeral vein simple and straight, gnathos arms not ventrally fused, valva with a long (about 2/3 of valva length) projection off its base inside (Penz and Peggie 2003). A combination of the following base pairs in the nuclear genome is diagnostic: hm2007153-RA.3:A305G, hm2014625-RA.4:T887A, hm2012596-RA.1:C853G, hm2011273-RA.1:T484G, hm2011273-RA.1:G486A.

Genera included. Only the type genus.

Parent Taxon. Tribe Vagrantini Pinratana & Eliot, 1996.

Smerinina Grishin, new subtribe
http://zoobank.org/06DF6620-9B17-4522-9E4B-BD5342AC8DF5

Type genus. *Smerina* Hewitson, 1874.

Definition. *Smerina* (type species *Smerina vindonissa* Hewitson, 1874) forms a deep-diverging lineage in the tribe Vagrantini Pinratana & Eliot, 1996 at about the tree level corresponding to subtribes (Fig. 6) and therefore represents a subtribe. This new subtribe is distinguished from its relatives by a combination of the following characters: papilla anales moderately retracted (not deeply) inside the body, aedeagus not broadened at the tip in ventral view, costa of valva with one spiny process (Penz and Peggie 2003), forewing apex more produced and hindwing margin evenly curved (not wavy, no tails). A combination of the following base pairs in the nuclear genome is diagnostic: hm2015462-RA.1:T360C, hm2015689-RA. 5:T57C, hm2009280-RA.3:T94G, hm2010526-RA.2:A67G, hm2017391-RA.1:A139C.

Genera included. Only the type genus.

Parent Taxon. Tribe Vagrantini Pinratana & Eliot, 1996.

Lebadeini Grishin, new tribe
http://zoobank.org/F26F931E-9141-4329-92B6-6E86A9F369E9

Type genus. *Lebadea* C. Felder, 1861.

Definition. *Lebadea* (type species *Limenitis ismene* E. Doubleday, 1848, which is a junior subjective synonym of *Papilio martha* Fabricius, 1787), currently in Neptini Newman, 1870 (Dhungel and Wahlberg 2018; Wahlberg 2019) is not monophyletic with it and instead is placed as sister to the clade of Chalingini Hemming, 1960 and Limenitidini Behr, 1864 but with weak support; therefore, it is distinct from them (Fig. 6). Thus, this lineage, currently consisting only of *Lebadea*, represents a tribe that does not have a name. This new tribe is diagnosed by a combination of the following characters: tegumen and uncus are smaller than typical for Limenitidini, uncus is more gracile, thus more similar to *Neptis* [Fabricius], 1807, and differs from *Neptis* in having a well-defined and projecting anteriad lobe (not just a hump) on the dorsal side of the segment A2 in the pupa (Willmott 2003). A combination of the following nuclear genomic base pairs is diagnostic: hm2005025-RA.3:C373A, hm2006832-RA.2:C97A, hm2004700-RA.1: C590A, hm2004700-RA.1:G351T, hm2005025-RA.3:G319A.

Genera included. Only the type genus.

Parent Taxon. Subfamily Limenitidinae Behr, 1864.

Comment. Using morphological analysis, Willmott (2003) has placed *Lebadea* in the "*Limenitis* group" of genera away from *Neptis*, which seems to agree more with our genomic results.

Subtribes in Adoliadini Doubleday, 1845

Currently, no subtribes are in use for Adoliadini (Wahlberg 2019). However, our genomic tree reveals five prominent clades in this tribe (Fig. 6), confirming the results reported by Dhungel and Wahlberg (2018). We propose to treat these clades as subtribes. This subtribal arrangement will bring additional order to the species-rich tribe Adoliadini. Three of these subtribes have names: the nominotypical one, Abrotina Hemming, 1960, **stat. nov.**, and Bebeariina Hemming, 1960, **stat. nov.** (the last two were originally proposed as tribes), and two do not. They are described below.

Evenaina Grishin, new subtribe
http://zoobank.org/AB51B17D-4CB5-4909-8C7C-C76C81E84C4B

Type genus. *Evena* Westwood, 1850.

Definition. *Evena* (type species *Papilio crithea* Drury, 1773) forms a prominent phylogenetic lineage within Adoliadini Doubleday, 1845 on par with other subtribes (Fig. 6) and therefore represents a new subtribe. The new subtribe is diagnosed by genitalia and venation as described in detail and illustrated by Chermock (1950) for the genus *Catuna* W. F. Kirby, 1871 (a junior objective synonym of *Evena*). In brief, uniquely long and narrow saccus nearly as long as valva and R_1 vein arising before the end of the discal cell, then fusing with Sc for some distance and diverging to meet costal margin are diagnostic. Furthermore, the subtribe is recognized by the unique appearance of its species, somewhat resembling Heliconiinae Swainson, 1822: with elongated forewings and shorter, rounded hindwings, spider-web forewing pattern, and a pale frequently triangular area across the hindwing toward the apex, hidden from view when the butterfly is sitting. A combination of the following nuclear genomic base pairs is diagnostic: hm2005164-RA.2:C119T, hm2017194-RA.1:C92T, hm2017194-RA.1:G298A, hm2005515-RA.6: C97G, hm2016751-RA.4:C44T, hm2007706-RA.6:G759G (not T), hm2009397-RA.1:A367A (not T), hm2020285-RA.1:C553C (not A), hm2020285-RA.1:A554A (not G), hm2004293-RA.6:A149A (not G).

Genera included. Only the type genus.

Parent Taxon. Tribe Adoliadini Doubleday, 1845.

Comment. The name for the subtribe is formed by taking the entire name of the type genus as a root to avoid homonymy with Evenina Faynel & Grishin, 2022 (type genus *Evenus* Hübner, [1819], in Eumaeini E. Doubleday, 1847).

Pseudathymina Grishin, new subtribe
http://zoobank.org/55581E3A-18C6-492F-BD1A-3B3F205896AF

Type genus. *Pseudathyma* Staudinger, 1891.

Definition. *Pseudathyma* (type species *Pseudacraea sibyllina* Staudinger, 1890) forms a prominent phylogenetic lineage within Adoliadini Doubleday, 1845 on par with other subtribes (Fig. 6) and, therefore, represents a new subtribe. This new subtribe is diagnosed by open discal cells of both wings, R_2 that originates slightly beyond, instead of before, the end of the discal cell, and the absence of the anal lobe on the hindwing, per Chermock (1950), who gave these characters for *Pseudathyma*. In wing patterns, members of this subtribe are more similar to *Neptis* [Fabricius], 1807 in having four generally pale areas on the forewing (by the middle of the inner margin, in the discal area distad of the discal cell, by the apex, and in the discal cell) than to most Adoliadini. A combination of the following nuclear genomic base pairs is diagnostic: hm2007185-RA.1:A1149G, hm2007185-RA.1:C1150T, hm2017262-RA.1: A935G, hm2018054-RA.1:T155C, hm2017807-RA.2:A68T.

Genera included. Only the type genus.

Parent Taxon. Tribe Adoliadini Doubleday, 1845.

Kumothalina Grishin, new subtribe
http://zoobank.org/101F0041-F957-4CD5-92F7-079A780A043D

Type genus. *Kumothales* Overlaet, 1940.

Definition. Wahlberg et al. (2020) placed *Kumothales* (type species *Kumothales inexpectata* Overlaet, 1940) in the tribe Cymothoini Dhungel & Wahlberg, 2018. Our analysis confirms this conclusion and previously published phylogenies (Wahlberg et al. 2020; Kawahara et al. 2023) and places the *Kumothales* lineage as sister to all other Cymothoini that diverged from them before the divergence of Adoliadini Doubleday, 1845 into subtribes (Fig. 6). This substantial genetic differentiation of *Kumothales* is also the reason for the difficulty in finding the place for this genus in taxonomic hierarchy without DNA analysis. Therefore, this lineage represents a subtribe. This new subtribe is distinguished from its relatives by the details of wing venation as described for *Kumothales* by Overlaet (1940) and a

combination of the following characters: wings less rounded, forewing apex lobed, hindwing margin wavy, wings without bands, with a unique submarginal wavy pattern consisting of dark inverted deep U with a sharp tooth (narrow V) inserted into it in every cell. A combination of the following nuclear genomic base pairs is diagnostic: hm2008200-RA.1:A517C, hm2006358-RA.1:C1151A, hm2009464-RA.1:C128T, hm2010867-RA.7:G38C, hm2012380-RA.2:A48G, hm2012713-RA.1:T428T (not C), hm2012713-RA.1:G946G (not A), hm2007718-RA.2:C205C (not A), hm2006845-RA.2:T1311T (not A), hm2006845-RA.2:A1314A (not G).

Genera included. Only the type genus.

Parent Taxon. Tribe Cymothoini Dhungel & Wahlberg, 2018.

Amnosiini Grishin, new tribe
http://zoobank.org/AD32BD0A-6755-4650-AB24-3FD7A43DFA06

Type genus. *Amnosia* E. Doubleday, 1849.

Definition. *Amnosia* (type species *Amnosia decora* E. Doubleday, 1849) belongs to the subfamily Pseudergolinae Jordan, 1898, but is more distant from and sister to the rest of the subfamily (Fig. 6). Genetic differentiation of the *Amnosia* lineage from other Pseudergolinae is at the level of a tribe. Therefore, we propose that the *Amnosia* lineage corresponds to a tribe. This new tribe is diagnosed by a combination of the following characters: wings mostly dark in males, forewing with a pale stripe from mid-costa to tornus, and hindwing with two pairs of larger submarginal eyespots beneath that are better defined than in other Pseudergolinae. A combination of the following nuclear genomic base pairs is diagnostic: hm2002290-RA.3:A49G, hm2013678-RA.4:A234C, hm2013678-RA.4:G246A, hm2013678-RA.4: T294C, hm2006306-RA.3:G107C, hm2013835-RA.2:G178G (not A), hm2014102-RA.2:C115C (not T), hm2014102-RA.2:A117A (not T), hm2009568-RA.1:T184T (not A), hm2009568-RA.1:C185C (not A).

Genera included. Only the type genus.

Parent Taxon. Subfamily Pseudergolinae Jordan, 1898.

Hyperanartia Grishin, new subgenus
http://zoobank.org/D264019C-2106-4F29-9F1F-7830321FAD68

**Type species.** *Vanessa dione* Latreille, [1813].

Definition. The genus *Hypanartia* Hübner, [1821] (type species *Hypanartia demonica* Hübner, [1821], which is a junior subjective synonym of *Papilio lethe* Fabricius, 1793) has been divided into two species groups: the *paullus* group (includes the type species of *Hypanartia*) and the *dione* group (Willmott et al. 2001; Llorente et al. 2023). Our genomic tree shows this split (Fig. 7) and is consistent with the cladogram constructed using morphological characters (Willmott et al. 2001). Here, the division of *Hypanartia* into two clades is formalized, and the new subgenus is proposed to encompass the *dione* group. This new subgenus is distinguished from the nominotypical subgenus by male genitalia: nearly triangular in lateral view valvae, separated at the base in ventral view; vinculum broader near the base of succus in lateral view; saccus with narrower anterior part (at least in lateral view); and gnathos continuously sclerotized, joined. See Willmott, Hall, and Lamas (2001) for additional information and illustrations. A combination of the following nuclear genomic base pairs is diagnostic: hm2021257-RA.1: A261G, hm2002154-RA.32:T1114A, hm2013826-RA.2:G702A, hm2006214-RA.3:T888C, hm2005917-RA. 1:C3222G.

Etymology. The Latin prefix *hypo-* means "below", "beneath", and sometimes "less than". Species of the new subgenus are clearly more than that, and this prefix is replaced with *hyper-* (i.e., "above", "high", "beyond", "excessive") for an exaggerated look of some of these butterflies: typically with more angular wings, longer tails, and bolder white spots. The name is a feminine noun in the nominative singular.

Species included. The type species (i.e., *Vanessa dione* Latreille, [1813]), *Hypanartia celestia* Lamas, Willmott & J. Hall, 2001, *Eurema charon* Hewitson, 1878, *Hypanartia christophori* Jasinski, 1998, *Hypanartia cinderella* Lamas, Willmott & J. Hall, 2001, *Hypanartia fassli* Willmott, J. Hall & Lamas, 2001, *Eurema kefersteini* Doubleday, [1847], *Eurema lindigii* C. Felder & R. Felder, 1862, *Hypanartia splendida* Rothschild, 1903, and *Hypanartia trimaculata* Willmott, J. Hall & Lamas, 2001 (including their subspecies and synonyms).

Parent taxon. Genus *Hypanartia* Hübner, [1821].

Comments. In their genetic differentiation (Fig. 7), the two subgenera of *Hypanartia* are approximately the same as some subgenera in *Nymphalis* Kluk, 1780 (type species *Papilio polychloros* Linnaeus, 1758). Therefore, they are phylogenetically equivalent to the two subgenera *Nymphalis* and *Aglais* Dalman, 1816 (type species *Papilio urticae* Linnaeus, 1758) (i.e., the same level in the tree), and are stronger differentiated genetically than *Nymphalis* from *Polygonia* Hübner, [1819] (type species *Papilio c-aureum* Linnaeus, 1758).
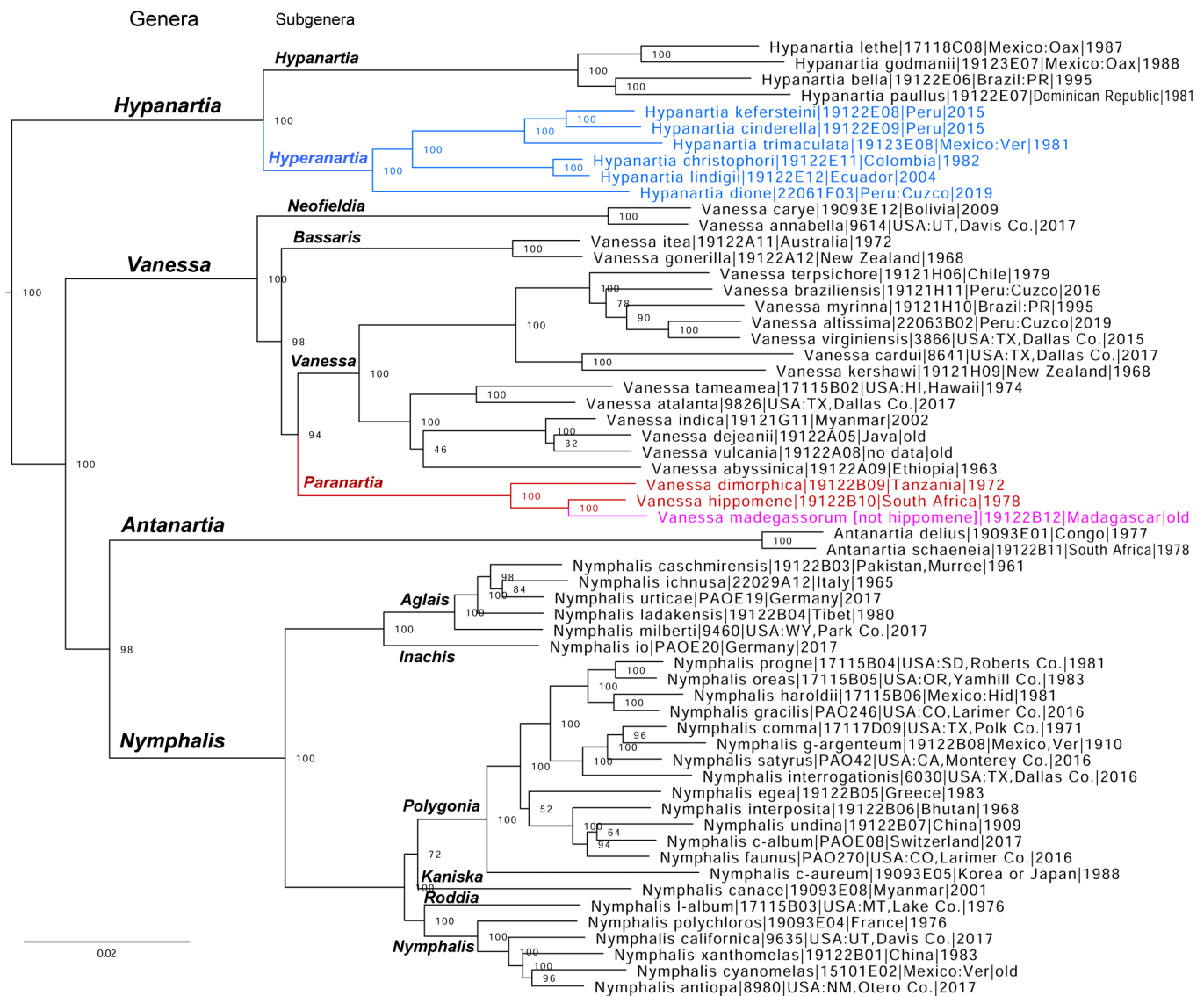
Fig. 7. The phylogenetic tree of *Nymphalis* relatives inferred from protein-coding regions of the nuclear genome (autosomes). Genus-group names are shown above or below corresponding branches. Names of genera are shown on the left and in a larger font than names of subgenera. Names, clades, and species of new subgenera proposed in this work are shown in color, except that magenta indicates a new status of *Vanessa madegassorum* (species, not a subspecies of *Vanessa hippomene*).

Vanessa madegassorum (Aurivillius, 1899) is a species distinct from *Vanessa hippomene* (Hübner, 1823)

Genomic sequencing reveals notable genetic differentiation between the nominotypical *Vanessa hippomene* (Hübner, 1823) (type locality not given, deduced by wing shape and patterns of a specimen shown in the original illustration to be in South Africa) and *Vanessa hippomene madegassorum* (Aurivillius, 1899) (type locality in Madagascar) (Fig. 7). The COI barcodes of the two taxa differ by 2.9% (19 bp). Phenotypically, *V. h. madegassorum* is characterized by more prominently scalloped (even toothed at veins) wing margins, a longer and thinner major hindwing tail at the end of vein M_3, a second, shorter tail at the end of vein CuA_2 (absent in the nominotypical *V. hippomene*), orange (rather than yellower) forewing band, green scaling by the forewing apex beneath, and reduced pale scaling and spot by mid-costa on the ventral hindwing (Fig. 8). Taken together, these observations suggest that *Vanessa madegassorum* (Aurivillius, 1899), **stat. nov.** is a species distinct from *Vanessa hippomene* (Hübner, 1823). *Vanessa madegassorum* **stat. nov.** is known only from Madagascar, with the last reported record from 1976 (Lees et al. 2003), and may be of conservation concern, if not already extinct. The COI barcode sequence of *V. madegassorum* **stat. nov.**, sample NVG-19122B12, GenBank accession OR578710, 658 base pairs, is:

```
TACTTTATATTTTATTTTCGGAATTTGAGCAGGAATAGTTGGAACTTCACTTAGTTTATTAATTCGAACTGAATTAGGAAATCCAGGATCTTTAATTGGAGATGATCAAATTTATAATACA
ATTGTTACAGCTCATGCTTTTATTATAATTTTCTTTATAGTTATACCTATTATAATTGGAGGTTTTGGTAATTGATTAATTCCACTTATATTAGGAGCCCCTGATATAGCTTTTCCACGTA
TAAATAATATAAGATTTTGACTTTTACCCCCTTCATTAATATTATTAATTTCTAGTAGAATTGTTGAAAATGGAGCAGGAACAGGATGAACAGTTTACCCCCCACTTTCATCTAATATTGC
TCATAGAGGATCTTCTGTAGATCTAGCAATTTTTTCATTACATTTAGCTGGAATTTCCTCTATTTTAGGAGCAATTAATTTTATTACTACTATTATTAATATACGAATTAATAGAATATCT
TTTGATCAAATACCTTTATTTGTTTGAGCTGTAGGTATTACAGCTTTACTTTTATTAATCTCTCTTCCTGTTTTAGCTGGAGCTATTACTATACTTCTAACAGATCGAAATATTAATACAT
CATTTTTTGATCCTGCGGGAGGAGGAGACCCAATTCTTTATCAACATTTATTT
```


Fig. 8. *Vanessa madegassorum* **stat. nov.** male (dorsal: left, ventral: right) in USNM collection sequenced as NVG-19122B12 with its labels. All images are to scale.

Subgenera in *Vanessa* [Fabricius], 1807

The genus *Vanessa* [Fabricius], 1807 (type species *Papilio atalanta* Linnaeus, 1758) has been divided into five species groups: the *atalanta* group (includes the type species of *Vanessa*), the *cardui* group (*Papilio cardui* Linnaeus, 1758 is the type species of *Cynthia* [Fabricius], 1807), the *carye* group (*Hamadryas carye* Hübner, 1812 is the type species of *Neofieldia* Özdikmen, 2008), the *itea* group

(*Papilio itea* Fabricius, 1775 is the type species of *Bassaris* Hübner, [1821]), and the *hippomene* group (Wahlberg and Rubinoff 2011). Because four of these groups are characterized by notable genetic differentiation (Fig. 7), we propose to treat the two names as subgenera: *Neofieldia* Özdikmen, 2008, **stat. rest.** and *Bassaris* Hübner, [1821], **stat. rev**. and leave *Cynthia* as a junior subjective synonym of *Vanessa*. The *hippomene* species group does not have a name. It is described below.

Paranartia Grishin, new subgenus

http://zoobank.org/5760367D-44F8-48AF-B592-2B1AEE4CC755

Type species. *Hypanartia hippomene* Hübner, [1823].

Definition. Comprises the *hippomene* species group in *Vanessa* [Fabricius], 1807, as proposed by Wahlberg and Rubinoff (2011), who inferred a comprehensive phylogeny of *Vanessa* and its relatives and discovered the phylogenetic position of the *hippomene* group within *Vanessa*. This group is unusual because its constituent species have been previously placed in *Antanartia* Rothschild & Jordan, 1903 (type species *Papilio delius* Drury, 1782) due to phenotypic similarities. We treat the *hippomene* group as a new subgenus (Fig. 7). This subgenus is distinguished from *Antanartia* by genitalia: in males, aedeagus without spines and projections (does not end in a "barb" like a fish hook end structure) and valva without projections off costa, which is nearly straight; and in females, with developed signa in corpus bursae (Howarth 1966), and from *Vanessa* by a sharp tooth-like tail at the vein M_3 on hindwing. A combination of the following nuclear genomic base pairs is diagnostic: hm2005743-RA.6:T48C, hm2002542-RA.3: A237G, hm2017019-RA.1:T160C, hm2002154-RA.32:A1116G, hm2021745-RA.5: C862A.

Etymology. The prefix *para*- means "beside", "beyond", or "similar to". Species of the new subgenus are similar to and were previously placed in *Antanartia*, and the prefix *para*- is fused with the latter genus name to form the new name. The name is a feminine noun in the nominative singular.

Species included. The type species (i.e., *Hypanartia hippomene* Hübner, [1823]), *Antanartia dimorphica* Howarth, 1966, and *Hypanartia hippomene* var. *madegassorum* Aurivillius, 1899, **stat. nov.** (including their subspecies and synonyms).

Parent taxon. Genus *Vanessa* [Fabricius], 1807.

Comments. The four subgenera of *Vanessa* are more genetically distinct from each other than some subgenera within *Nymphalis* Kluk, 1780 (type species *Papilio polychloros* Linnaeus, 1758) (Fig. 7), and several of such *Nymphalis* subgenera are commonly treated as genera, e.g., *Polygonia* Hübner, [1819] (type species *Papilio c-aureum* Linnaeus, 1758).

Eresia (*Anthanassa*) *seminole* Skinner, 1911 is a species distinct from *Eresia* (*Anthanassa*) *texana* (W. H. Edwards, 1863)

Currently in the subgenus *Anthanassa* Scudder, 1875 (of *Eresia* Boisduval, 1836) and treated as a subspecies of its type species *Melitaea texana* W. H. Edwards, 1863 (type locality USA: Texas, probably Comal Co., New Braunfels), *Eresia texana seminole* Skinner, 1911 (type locality USA: Georgia, Decatur Co., Bainbridge), is genetically differentiated from it (Fig. 9 blue vs. red), showing F_{st}/G_{min} in the Z chromosome of

Fig. 9. Nuclear genome tree (autosomes) of *Eresia texana* (blue) and *Eresia seminole* **stat. rest.** (red). Primary types are in magenta.

0.39/0.01 and COI barcode difference of 3.6% (24 bp). Therefore, in agreement with Calhoun (1997), we regard *Eresia* (*Anthanassa*) *seminole* Skinner, 1911, **stat. rev.** as a species-level taxon.
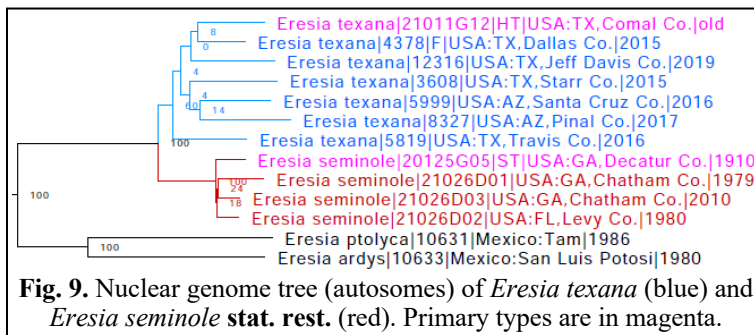
## *Microtia elvira* Grishin, new species

(Figs. 10 part, 11, 12a, b)

Definition and diagnosis. Genomic sequencing of *Microtia* H. Bates, 1864 (type species *Microtia elva* H. Bates, 1864) specimens reveals a deep split within its type species (Fig. 10). The western clade (Fig. 10 red) is profoundly differentiated from the eastern clade (Fig. 10 blue) with the Z chromosome F_{st}/G_{min} of 0.60/0.006 and COI barcode difference of 4.7% (31 bp), which is more than expected from phenotypic similarity. This scenario parallels that of *Microtia perse* (W. H. Edwards, 1882) (type locality in USA: AZ, Graham Co.) vs. *Microtia elada* (Hewitson, 1868) (type locality in Mexico) (Fig. 10 green vs. violet). Therefore, the two clades represent distinct species. Specimens from around the type locality (Guatemala) belong to the eastern clade. Curiously, *Microtia elva horni* Rebel, 1906 (type locality in Mexico: Oaxaca) and its junior subjective synonym *Microtia elva* form *draudti* Röber, [1914] (type locality in Mexico, "Coatepec" on the label of a syntype) (Fig. 10 teal colored), which are also in the eastern clade but are visually rather distinct in their much broader orange-yellow markings and nearly half of dorsal hindwing orange-yellow, are not particularly different genetically from the nominotypical *M. elva*. Thus, the western clade does not have available names associated with it and represents a new species. This new species is most similar to *M. elva*, with which it was previously combined. Distinguished from *M. elva* by largely yellow or orange-yellow tibiae and frequently other leg parts (legs in *M. elva* are back). Additionally, characterized by narrower orange-yellow bands and thinner, bar-like (particularly in males) orange-yellow mark by the middle of the inner forewing margin (Figs. 11, 12a). In *M. elva*, this bar is more rounded, larger, and can be nearly triangular and much broader at the base, widening both distad and basad (Fig. 12c). The outer edge of the hindwing discal band (on both dorsal and ventral sides) is more angled in the middle (Figs. 11, 12b), instead of straighter and more rounded edge in *M. elva* (Fig. 11d). Due to variation in colors and patterns, most confident identification is provided by DNA. The following combination of characters is diagnostic in the nuclear genome: hm2014195-RA.2:C190T, hm2014195-RA.2:T201A, hm2016592-RA.17:G261A, hm2017493-RA.1:G240A, hm2008057-RA.6:T171C and COI barcode: G38A, C238C, 421C, A583T, T637C.

Barcode sequence of the holotype: Sample NVG-22096H10, GenBank OR578711, 658 base pairs:

```
TACTTTATATTTTATTTTTGGAATTTGAGCAGGAATAATTGGAACATCTTTAAGACTTTTAATTCGAACTGAATTAGGAAACCCAGGATCATTAATTGGAGATGATCAAATTTATAATACT
ATTGTTACAGCTCATGCTTTTATTATAATTTTTTTTTATAGTTATACCTATTATAATTGGAGGATTTGGTAATTGATTAATTCCATTAATATTAGGAGCTCCTGATATAGCTTTCCCCCGAA
TAAATAATATAAGATTTTGACTACTACCCCCATCACTTATATTATTAATTTCTAGAAGAATTGTAGAAAATGGAGCAGGAACAGGATGAACAGTGTACCCCCCACTTTCTTCTAATATTGC
TCATAGAGGATCATCTGTTGATTTAGCAATTTTTTCACTACATCTAGCAGGAATTTCCTCAATTCTAGGAGCTATTAATTTTATTACTACAATTATTAATATACGAATTAATAATATATCA
TTTGATCAAATACCTTTATTTGTTTGAGCAGTTGGTATTACAGCTCTTTTATTATTATTATCTTTACCAGTATTAGCAGGAGCTATTACTATACTCCTTACTGATCGAAATATTAATACAT
CATTTTTTGACCCAGCTGGAGGAGGGGATCCCATTTTATATCAACATCTATTT
```
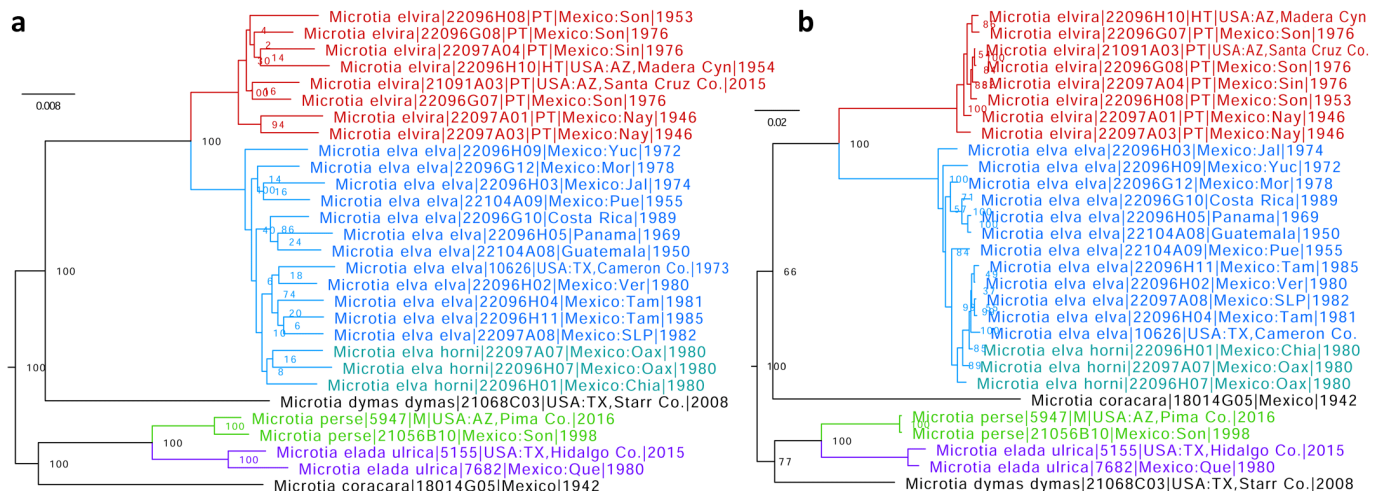

Fig. 10. Phylogenetic trees of *Microtia* inferred from protein-coding regions of **a)** nuclear (autosomes) and **b)** mitochondrial genomes: *Microtia elvira* **sp. n.** (red), *M. elva* (blue with *M. e. horni* labeled in teal), *M. perse* (green), and *M. elada* (violet).

Fig. 11. Holotype of *Microtia elvira* **sp. n.** in dorsal (left) and ventral (right) views, data in text.

Fig. 12. *Microtia elvira* **sp. n.** (**a**, **b**) and *Microtia elva* (**c**, **d**) iNaturalist observations: USA: AZ, Santa Cruz Co.: **a**) 144668453 Montosa Canyon, GPS 31.6727, −110.9406, 19-Aug-2016 © jmbearce; **b**) 141491956 Atascosa Mts., California Gulch, GPS 31.4220, −111.2404, 3-Oct-2014 © Ken Kertell; and Mexico: Nuevo Leon, Monterrey: **c**) 4292755 Parque la Estanzuela, GPS 25.5507, −100.2707, 7-Oct-2016 © Roberto González; **d**) 171257635 Guadalupe, Contry Sol, GPS 25.6505, −100.2648, 5-Jul-2023 © Rodolfo Salinas Villarreal. Arrows in b) and d) point at the legs to draw attention to their color difference. Images are color-corrected and rotated. CC BY-NC 4.0 https://creativecommons.org/licenses/by-nc/4.0/

Type material. Holotype: ♂ deposited in the Los Angeles County Museum of Natural History, Los Angeles, CA, USA [LACM], illustrated in Fig. 11, bears three printed (number "12" handwritten) labels: two white [October 12, 1954 | Madera Canyon, Santa Rita Mt's. | Southern Arizona. | W. Rees & H. Reid], [DNA sample ID: | NVG-22096H10 | c/o Nick V. Grishin], and one red [HOLOTYPE ♂ | Microtia elvira | Grishin]. **Paratypes:** 5♂♂ 2♀♀: 1♂ USA, <u>Arizona</u>, Santa Cruz Co., Sycamore canyon, GPS 31.4213, −111.1942, 25-Sep-2015, Brian Banker leg. (NVG-21091A03); others at LACM, Mexico: <u>Sonora</u>: 2♂♂ Rio Cuchujaqui, 8 rd. mi E of Alamos, el. 1000', 30-Aug-1976, J. P. & K. E. Donahue leg. (NVG-22096G07 & G08); 1♀ Alamos, 25-Jul-7-Aug-1953, Fred S. Truxal leg. (NVG-22096H08); 1♂ <u>Sinaloa</u>, 27.8 km S Culiacán, 30-Aug-1976, C. D. George & R. K. Snelling leg. (NVG-22097A04); 1♂ 1♀ <u>Nayarit</u>, 5–10 mi N of Tepic, 2500'-3000', 13-Dec-1946 (NVG-22097A03 & A01).

Type locality. USA: Arizona, Pima/Santa Cruz Cos., Santa Rita Mountains, Madera Canyon.

Etymology. The meaning of the name Elvira is typically associated with traits such as truthful, trustworthy, or pure, and also noble or elf-like. Formed from the name of its sister species, *elva*, it signifies our high confidence that this is a "trustworthy" species, i.e., strongly differentiated from *M. elva* but is *elva*- or elf-like. The name of this western counterpart of *M. elva* is longer to mean that it takes a long day from sunrise in the east to sunset in the west. The name is a feminine noun in apposition.

English name. Elfoid.

Distribution. Southeastern Arizona and western Mexico (confirmed from Sonora, Sinaloa, and Nayarit).

Comment. Both *M. elvira* **sp. n.** and *M. elva* occur in the USA. *Microtia elva* strays into the lower Rio Grande Valley of Texas, e.g., a male from Brownsville in Cameron County collected by William W. & Nadine McGuire on 20-Jul-1971 [TAMU] that we sequenced as NVG-10626 (Fig. 10).
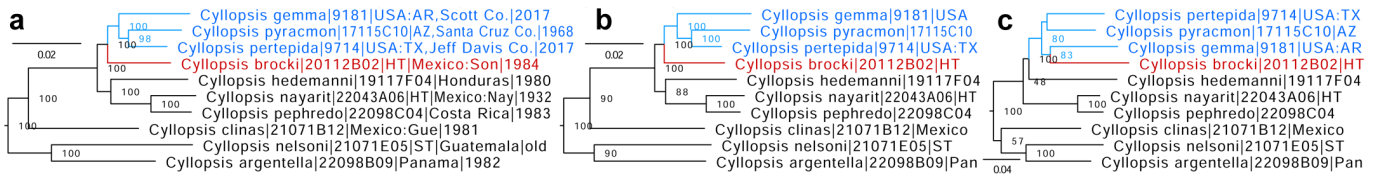
Cyllopsis brocki Grishin, new species
(Figs. 13 part, 14–16)

Definition and diagnosis. Inspection of nuclear genomic trees reveals that a single specimen from Mexico, Sonora, initially identified as "*Cyllopsis pertepida*", is confidently placed as sister to the clade

Fig. 13. Phylogenetic trees of selected *Cyllopsis* species inferred from protein-coding regions of **a)** the nuclear genome (autosomes), **b)** the Z chromosome, and **c)** the mitochondrial genome: *C. brocki* **sp. n.** (red) and its sister group (blue).

Fig. 14. Holotype of *Cyllopsis brocki* **sp. n.** in dorsal (left) and ventral (right) views, data in text.

of three species: *Cyllopsis gemma* (Hübner, 1808), *Cyllopsis pertepida* (Dyar, 1912), and *Cyllopsis pyracmon* (A. Butler, 1867) (Fig. 13a, b, red and blue), and therefore represents a species distinct from them. In the mitochondrial genome tree, which has lower statistical support, this species is also in the same clade with the three others but is sister to *C. gemma* (Fig. 13c). Because all other described species of *Cyllopsis* R. Felder, 1869 (type species *Cyllopsis hedemanni* R. Felder, 1869) belong to other clades (Fig. 13) and are phenotypically different (Miller 1974), this species is new. It differs from its relatives by a combination of larger size (forewing length about 20 mm, while typically less than 18 mm in *C. gemma*), a large androconial patch (cut by veins) in the discal area of the dorsal forewing (absent in *C. gemma*), postdiscal brown line strongly toothed towards the margin at vein M_1 and not reaching the costal margin (as in *C. gemma* and some *C. pertepida*,

Fig. 15. *Cyllopsis brocki* **sp. n.** (possible), iNaturalist observation 142409312 Mexico: Sonora, Yécora, GPS 28.3783, −108.8370, 3-Sep-2018, © jmbearce. Brightened and color-corrected. CC BY-NC 4.0 https://creativecommons.org/licenses/by-nc/4.0/

but not in *C. pyracmon*), more extensive and coarse mottling on the ventral side of wings, especially in the basal part of the hindwing (as in some *C. pyracmon* but not in other species), and reduced rusty overscaling dorsally: wings appear more brown than reddish (Figs. 14, 15). In male genitalia (Fig. 16), diagnosed by broader valva with more convex costa-ampulla, valva more distinctively narrowing into harpe in lateral view, harpe with broader and more angular distal end in dorsal view shaped like a triangular plate rather than ending in a point. In DNA, a combination of the following characters is

diagnostic in the nuclear genome: hm2006469-RA.2:C61T, hm2003322-RA.2:G69A, hm2003322-RA.2:T106C, hm2009012-RA.1:T408C, hm2009012-RA.1:G885T, hm2009732-RA.2:G72G (not A), hm2009355-RA.1:A261A (not G), hm2009355-RA.1:G270G (not A), hm2013443-RA.4:T606T (not C), hm2013443-RA.4:T702T (not A) and COI barcode:

T235C, T283C, T379A, T451A, T544C, A631G. Due to pronounced and frequently seasonal wing pattern variation in *Cyllopsis* that is unexplored in the new species, definitive identification is possible by genitalia or DNA.

Barcode sequence of the holotype: Sample NVG-20112B02, GenBank OR578712, 658 base pairs:

```
AACTTTATATTTTATTTTTGGAATTTGAGCAGGTATAGTTGGAACCTCCCTTAGTCT
TATTATTCGAATAGAATTAGGTAATCCAGGATTTTTAATTGGAGATGATCAAATTTA
TAATACTATTGTAACAGCTCATGCTTTTATTATAATTTTTTTTATAGTTATACCTAT
TATAATTGGTGGATTTGGGAACTGATTAGTTCCCCTTATATTAGGGGCCCCCGATAT
AGCTTTCCCCCGAATAAATAATATAAGATTTTGACTACTTCCCCCCTCATTAGTCCT
TTTAATTTCAAGAAGTATTGTAGAAAATGGAGCTGGRACAGGATGAACAGTTTACCC
CCCTCTTTCTTCTAATATTGCCCACAGAGGATCTTCAGTCGATTTAGCAATTTTTTC
TTTACATTTAGCTGGGATTTCATCAATTTTAGGAGCTATTAATTTTATTACAACAAT
TATTAACATACGAATTAATAATATAACGTATGATCAAATACCTCTATTTGTTTGAGC
AGTTGGAATTACAGCATTATTATTATTACTCTCTTTACCAGTATTAGCTGGAGCTAT
TACTATACTTTTAACTGATCGAAATTTAAATACTTCATTTTTTGATCCTGCTGGAGG
AGGGGACCCTATTTTATACCAACATTTATTT
```

Type material. Holotype: ♂ deposited in the McGuire Center for Lepidoptera and Biodiversity, Gainesville, FL, USA [MGCL], illustrated in Fig. 14, bears four printed labels: three white [31 July 1984 | Trinidad-Yecora Rd. | 1-5 mi. e. Trinidad | Mine, Son., Mexico | leg. Jim P. Brock], [DNA sample ID: | NVG-20112B02| c/o Nick V. Grishin], [genitalia vial | NVG230917-02 | Nick V. Grishin], and one red [HOLOTYPE ♂ | Cyllopsis brocki | Grishin].

Fig. 16. Genitalia of *Cyllopsis brocki* **sp. n.** holotype (data in text) in left lateral (top left), dorsal (right) and left ventrolateral (bottom left) views.

Type locality. Mexico: Sonora, Yécora, E of Santa Rosa, Trinidad-Yecora Rd., 3–5mi E of Trinidad mine.

Etymology. The name honors Jim P. Brock, the collector of the holotype and one of the finest and most knowledgeable Lepidopterists with a sixth sense for butterflies and caterpillars, finding them effortlessly (or so it seems) where others fail. Jim's significant contributions to butterfly knowledge delivered through his many books, presentations, and nature tours can only be matched by his contagious excitement, passion for sharing his expertise, and unsurpassed kindness. We deeply appreciate Jim's extensive support of our projects throughout the years. The name is a singular noun in the genitive case.

Distribution. Known only from the holotype collected in Mexico: Sonora.

Comment. The type locality of this new species is near the type locality of *Amblyscirtes brocki* H. Freeman, 1992 (Hesperiidae), with its two paratypes collected on the same date and at approximately the same place as the holotype of *Cyllopsis brocki* **sp. n**.


Family Riodinidae Grote, 1895 (1827)

Teratophthalmina Grishin, new subtribe
http://zoobank.org/8C350BD8-8094-472C-9C17-70A9C2023D20

Type genus. *Teratophthalma* Stichel, 1909.

Definition. Currently placed in the subtribe Eunogyrina Grishin, 2021, *Teratophthalma* (type species *Mesosemia phelina* C. Felder & R. Felder, 1862) is indeed sister to its type genus *Eunogyra* Westwood, 1851, but is rather distant from it both genetically (Fig. 17) and phenotypically, and therefore represents a subtribe of its own. The description and diagnostic characters of this new subtribe are as those given for *Teratophthalma* on pages 76–77 (illustrated in Fig. 11) by Stichel (1910). In brief, the subtribe belongs to Mesosemiini (see Hall (2003) for *Teratophthalma*) and is diagnosed by the following combination of characters: wings without multiple narrow bands, eyespots at the end of the forewing discal cell but not along wing margins; genitalic valvae short (as long as tegumen) and triangular, simple with pointed apex,
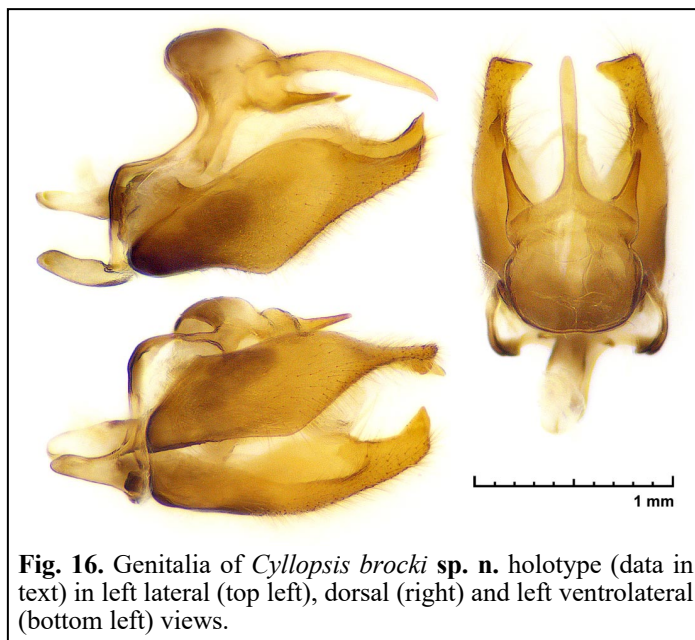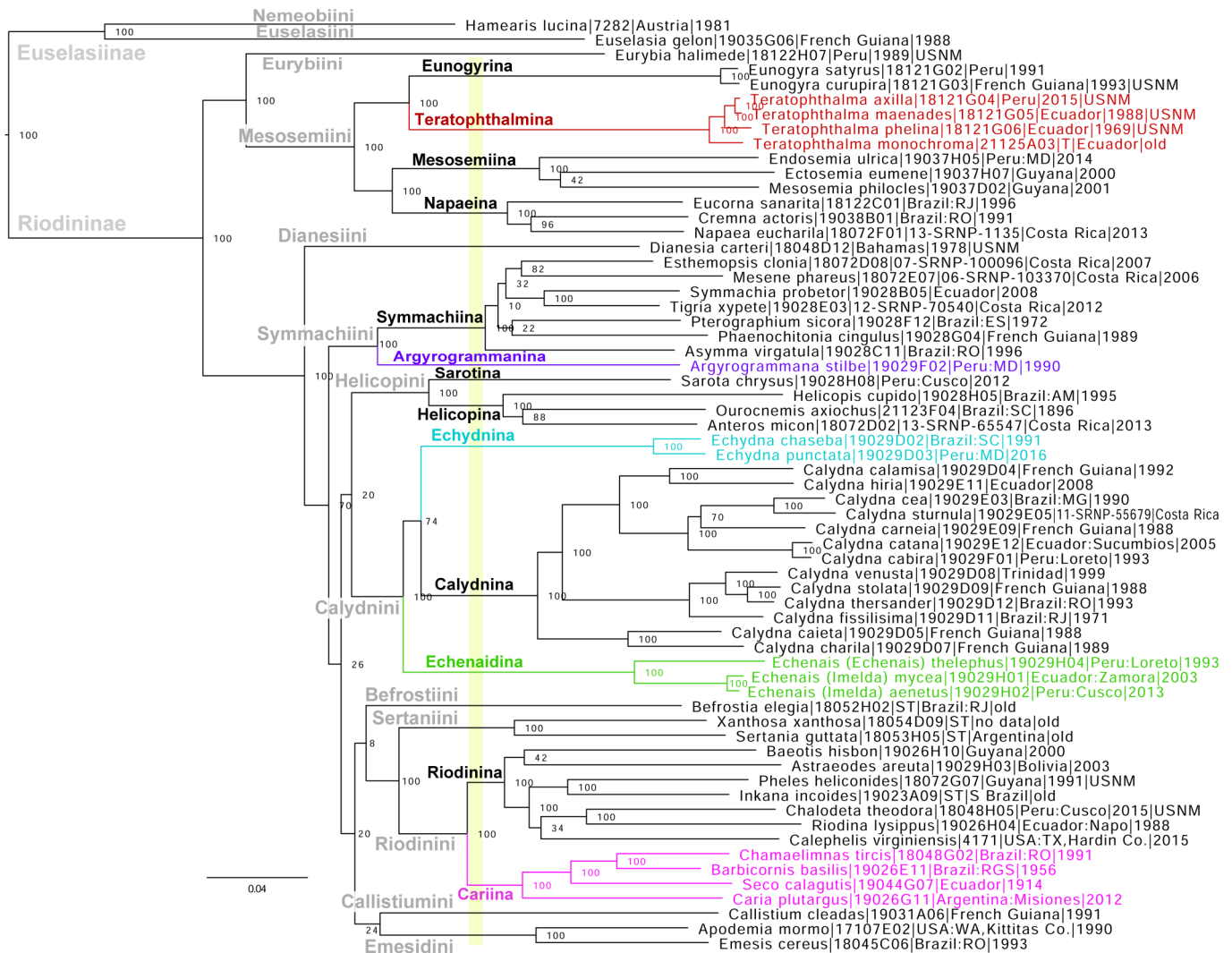
pedicel unsclerotized in the middle or ventrally split (or both). A combination of the following nuclear genomic base pairs is diagnostic: cne1792.4.2:T805C, cne11317.11.9:A512G, cne12569.1.1:T2145C, cne599.10.1:A4814T, cne1398.1.1:C838G.

Genera included. Only the type genus.

Parent Taxon. Tribe Mesosemiini Bates, 1859.

Fig. 17. The phylogenetic tree of selected Riodinidae inferred from protein-coding regions of the nuclear genome (autosomes). Family-group names are shown above or below the corresponding branches. Names, clades, and species of new subtribes proposed in this work are shown in color. Names of other subtribes are shown in black, and names of subfamilies and tribes are shown in shades of gray. Note the relatively constant rate of DNA change in Riodininae (i.e., molecular clock), as evidenced by approximately the same distance from the root to each leaf. The translucent vertical lime bar denotes a level in the tree approximately corresponding to subtribes.

Argyrogrammanina Grishin, new subtribe
http://zoobank.org/FA7881EE-0382-4796-9C6B-A10B4C08B0A1

Type genus. *Argyrogrammana* Strand, 1932.

Definition. *Argyrogrammana* (type species *Erycina stilbe* Godart, 1824) is prominently differentiated genetically from the rest of Symmachiini Reuter, 1896 (Fig. 17), and we propose that the lineage containing *Argyrogrammana* is a subtribe. This new subtribe differs from other Symmachiini by a thin submarginal line of (sometimes fused) metallic (golden or silvery-blue) spots on both wings above and beneath and a dark medial stripe across the eyes (Hall and Willmott 1996). A combination of the

27

following nuclear genomic base pairs is diagnostic: cne3461.2.10:G397A, cne2040.8.2:A100G, cne3461. 2.10:G382A, cne2478.7.10:C607A, cne6674.8.2:G397C.

Genera included. Only the type genus.

Parent Taxon. Tribe Symmachiini Reuter, 1896.

Argyrogrammana astuta Grishin, new species
http://zoobank.org/C3B104C6-18F0-4FAE-8506-DD345ED63531
(Figs. 18, 19)

Definition and diagnosis. Genomic sequencing of the holotype of *Argyrogrammana praestigiosa* (Stichel, 1929) (type locality not specified, likely the Guianas) (in MFNB, NVG-18077D12) reveals that a sequenced specimen identified as *A. praestigiosa* from southeastern Peru (illustrated in Fig. 11 in Hall et al. (2023)) is genetically distant from it with COI barcodes differing by 2.6% (17 bp). In the presence of phenotypic differences, such as those in wing patterns discussed in detail by Hall et al. (2023), the observed genetic differentiation suggests that the specimen from Peru is not *A. praestigiosa* but a distinct species. This species is new, and its males (female is unknown) differ from superficially most similar *A. praestigiosa* by the characters described for "west Amazonian males" in Hall et al. (2023), such as more extensive orange coloration of dorsal wings, i.e., basal area of forewing with three orange bands and in some specimens an orange marginal streak near tornus, hindwing with more orange scaling by its apex,

Fig. 18. Holotype of *Argyrogrammana astuta* **sp. n.** in dorsal (left) and ventral (right) views, data in text.

Fig. 19. *Argyrogrammana astuta* **sp. n.** iNaturalist observations from Peru: Madre de Dios, Tambopata: **a**) 175878841 GPS −12.6060, −69.0324, 27-Jul-2023 © danielblanco521; **b**) 67719625 Tambopata, GPS −12.0467, −69.6766, 29-Sep-2017, © Ken Kertell; **c**) 94229584 ventral of b) © David Geale. Images are color-corrected and rotated. CC BY-NC 4.0 https://creativecommons.org/licenses/by-nc/4.0/

e.g., an orange band may cut through the brown patch to reach the costa (the apical area is mostly brown in *A. praestigiosa*). Beneath, brown scaling is less extensive, pale bands are wider, with more orange scales in them (particularly toward wing margins), and with sharper edges, especially towards the outer margin; submarginal dark spots are more even, e.g., on hindwing spots in cells M_1-M_2 and M_2-M_3 are not particularly larger than others (they are larger and more pointed in *A. praestigiosa*). The dorsal side of the abdomen with a brown central spot at the base of each segment (entirely orange in *A. praestigiosa*). Other species of *Argyrogrammana* are more distant and different, e.g., the next closest species is *A. glaucopis* (H. Bates, 1868), which is characterized by much less extensive orange coloration and additional blue spots on the forewing, and *A. caerulea* J. Hall, 2023 has even more extensive blue forewing patches.

Barcode sequence of the holotype: Sample NVG-19029F11, GenBank [OR578713](#), 658 base pairs:

```
AACTTTATATTTTATTTTTGGAATTTGAGCTGGAATAATTGGAACTTCTTTAAGTTTATTAATTCGTATAGAATTAGGTAATCCAAACTCATTAATTGGTAATGACCAAATTTATAATACA
ATTGTAACTGCTCATGCTTTTATTATAATTTTTTTTATAGTTATACCTATTATAATTGGAGGGTTTGGAAATTGATTAATTCCTTTAATATTAGGGGCTCCTGATATAGCATTTCCACGAA
TAAATAACATAAGTTTTTGATTATTACCCCCCTCCTTAATTCTTTTAATTTCAAGAAGTATTGTTGAAAATGGAGCAGGAACAGGATGAACAGTTTATCCCCCTCTTTCTTCTAATATTGC
TCATAGAGGCTCATCCGTTGATTTAGCCATTTTTTCTCTTCATTTAGCTGGGATTTCTTCCATTCTAGGAGCTATTAATTTTATTACTACAATTATTAATATACGTATTAATAATATAGCT
TTTGATCAAATACCTTTATTTGTTTGATCTGTAGGAATTACAGCTCTTCTTTTATTATTATCATTACCAGTTTTAGCTGGAGCTATTACCATATTATTAACAGATCGTAATTTAAATACAT
CATTTTTTGATCCTGCTGGAGGTGGAGATCCTATTTTATACCAACATTTATTT
```

Type material. Holotype: ♂ deposited in the National Museum of Natural History, Washington, DC, USA [USNM], illustrated in Fig. 18 (and Fig. 11 in Hall et al. (2023) left-right inverted—i.e., mirror image of the specimen—and with imperfections edited out), bears four printed labels: three white [PERU, Madre de Dios | Tambopata Reserve | 12° 50'S 69° 17'W, 300m | 28 Oct 1991 | Leg. R. Robbins], [DNA sample ID: | NVG-19029F11 | c/o Nick V. Grishin], [USNMENT | {QR Code} | 01544363], and one red [HOLOTYPE ♂ | Argyrogrammana | astuta Grishin].

Type locality. Peru: Madre de Dios, Tambopata National Reserve, elevation 300 m, GPS −12.83, −69.28.

Etymology. In Latin, *astutus* is astute, cunning, clever, sly, and artful, and *praestigiosus* is deceptive and misleading. This new species was skillfully hiding among the deceitful *A. praestigiosa* until genomic sequencing revealed its distinction. The name is a feminine adjective.

Distribution. This species is genetically confirmed only from the holotype collected in southeastern Peru; however, it is expected at least in the southwestern Amazonian Basin (Fig. 19).

Comments. Hall et al. (2023) described in detail wing pattern differences between populations of *A. praestigiosa*, concluding that they represent intraspecific variation due to the lack of apparent differences in genitalia and citing phenotypic intermediates. *Argyrogrammana astuta* **sp. n.** corresponds to the "west Amazonian" *A. praestigiosa* of Hall et al. (2023). It is possible that *A. praestigiosa* is even more deceitful, and additional variation described by Hall et al. (2023) may refer to additional species in this complex.

Subtribes in Helicopini Stichel, 1928

Inspection of the genomic tree reveals that *Sarota* Westwood, 1851 (type species *Papilio chrysus* Stoll, 1782), which is confidently placed in the tribe Helicopini Stichel, 1928 (Fig. 17), diverges from other members of the tribe at the tree level corresponding to subtribes (left of the lime bar in Fig. 17). Therefore, this lineage represents a valid subtribe. As a result, we propose to split Helicopini into two subtribes: the nominotypical and Sarotina Bridges, 1988, **stat. rest**.

Echenaidina Grishin, new subtribe
http://zoobank.org/3BAD20C2-92C3-4F44-A713-583D7B3932E2

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

Definition. Two subgenera, *Echenais* (type species *Lemonias alphaea* Hübner, 1808, which is a junior subjective synonym of *Papilio thelephus* Cramer, 1775) and *Imelda* Hewitson, 1870 (type species *Imelda glaucosmia* Hewitson, 1870), show prominent genetic differentiation from other taxa in the tribe Calydnini Seraphim, Freitas & Kaminski, 2018 and, therefore, constitute a subtribe (Fig. 17). This new subtribe differs from other Calydnini by a submarginal (not marginal) continuous yellow, blue, or metallic

line or band on dorsal sides of both wings and/or largely white, yellow, orange, or blue (but not mostly black or dark brown) hindwing above, or orange patch in the middle of the hindwing. A combination of the following nuclear genomic base pairs is diagnostic: cne2872.1.1:A361C, cne12666.5.7:A497G, cne2222.10.1:A431T, cne2483.2.1:A1667G, cne254274.1.1:T198C.

Genera included. Only the type genus (including subgenus *Imelda* Hewitson, 1870).

Parent Taxon. Tribe Calydnini Seraphim, Freitas & Kaminski, 2018.

Echydnina Grishin, new subtribe
http://zoobank.org/7E98DF54-98E3-41D7-BC19-3528A548CD96

Type genus. *Echydna* J. Hall, 2002.

Definition. *Echydna* (type species *Calydna chaseba* Hewitson, 1854) is genetically differentiated from other Calydnini genera at the tree level similar to that of Echenaidina **subtrib. n.** and therefore represents a distinct subtribe (Fig. 17). Diagnostic characters for this subtribe are as those given in detail and illustrated by Hall (2002) for *Echydna*. In brief, it is diagnosed by a combination of setose eyes and black frons; in male genitalia, unique cornuti of three elements: a narrow unspined plate anteriad of an unsclerotized sack with small spines and sclerotized ovoid with larger spines; and in female genitalia, small signa without surface sculpturing. A combination of the following nuclear genomic base pairs is diagnostic: cne2156.9.5:A3355G, cne5645.4.3:G360A, cne16213.4.1:A205G, cne16034.2.1:T643G, cne5785. 9.3:G454A.

Genera included. Only the type genus.

Parent Taxon. Tribe Calydnini Seraphim, Freitas & Kaminski, 2018.

Cariina Grishin, new subtribe
http://zoobank.org/6D9F6CE6-E393-4484-8124-963E2C60DE55

Type genus. *Caria* Hübner, 1823.

Definition. The tribe Riodinini Grote, 1895 (1827) splits into two prominent clades: the larger includes the type genus, and the smaller consists of genera not previously used for family-group names (Fig. 17). We propose that these two clades represent two subtribes, one of which is new. This new subtribe is diagnosed by a combination of the following characters: eyes bare, palpi short, not visible above, both sides of all wings either with submarginal row of metallic (silver, green) spots usually connected into a band, or dark and with yellow bands or spots, or pale veins. In *Barbicornis*, hindwings unique, shovel-shaped with a tail in the middle nearly equal to the hindwing length; in *Chamaelimnas*, forewings elongated and with a yellow band, either diagonal (from mid-costa to tornus) or longitudinal (from base towards outer margin); in *Caria* and *Seco*, forewing costal margin typically at least slightly convex. Male genitalia with terminally bilobed valvae; in *Chamaelimnas*, boomerang-shaped, ventral lobe vestigial. Best identified by DNA, and a combination of the following nuclear genomic base pairs is diagnostic: cne1302.2.1:A1473G, cne1302.2.1:A2614C, cne1143.5.1:A883G, cne1143.5.1:A884C, cne8241.4.4:A67C.

Genera included. The type genus (*Caria* Hübner, 1823), *Barbicornis* Godart, 1824, *Chamaelimnas* C. Felder & R. Felder, 1865, and *Seco* J. Hall & Harvey, 2002.

Parent Taxon. Tribe Riodinini Grote, 1895 (1827).

Family Lycaenidae [Leach], [1815]

Liphyrinae Doherty, 1889 is a subfamily

Currently treated as a tribe within subfamily Miletinae Reuter, 1896, Liphyrini Doherty, 1889 show

prominent genetic differentiation from the rest of Miletinae and are at the level in the genomic tree that corresponds to subfamilies (Fig. 20). Therefore, we return this morphologically unique group to the status of a subfamily as originally proposed: Liphyrinae Doherty, 1889, **stat. rest**.

Megalopalpina Grishin, new subtribe
http://zoobank.org/2A22AFFB-346D-4DCF-B256-C59DA7FCEFB1

Type genus. *Megalopalpus* Röber, 1886.

Definition. *Megalopalpus* Röber, 1886 (type species *Megalopalpus simplex* Röber, 1886) forms a lineage sister to all other Miletini Reuter, 1896 and is more prominently separated from them than they are from each other (Figs. 20, 21). Therefore, we propose that this lineage represents a subtribe. This new subtribe is diagnosed by a combination of the following characters, as given for the *Megalopalpus* section by Eliot (1973): uncus with tegumen plates triangular, with a unique for this group broad lobe-like triangular ventrally-pointed process, falces strongly curved, males lack secondary sexual characters, hindwing with precostal vein. A combination of the following nuclear genomic base pairs is diagnostic: cce64.1.4:G152C, cce5960.3.7:A41T, cce7884.1.3:A388A (not C), cce28693.2.4:G109G (not A), cce9880.2.2:A83A (not C), cce49.4.1:C595C (not T), cce16970.13.7:T187T (not G).

Genera included. Only the type genus.

Parent Taxon. Tribe Miletini Reuter, 1896.

## Tarakina Eliot, 1973 is a subtribe

Currently treated as a tribe in the subfamily Miletinae Reuter, 1896, Tarakini Eliot, 1973 is sister to Spalgini Toxopeus, 1929 and shows less extensive genetic differentiation from them than typical for the tribal level (Fig. 21). The *Taraka* Doherty, 1889 lineage has split from Spalgini at the same tree level as Megalopalpina **subtrib. n.** has split from Miletina Reuter, 1896. Therefore, we place Tarakina Eliot, 1973, **stat. rev**. as a subtribe in the tribe Spalgini, 1929.

Cesa Seven, 1997 is a subgenus of *Crudaria* Wallengren, 1875

The monotypic genus *Cesa* Seven, 1997 (type species *Spindasis waggae* Sharpe, 1898) is closely related to *Crudaria* Wallengren, 1875 (type species *Arhopala ? leroma* Wallengren, 1857): the COI barcodes of the type and the only species of *Cesa* (GenBank JN286116) and the type species of *Crudaria* (NVG-22012H12) differ by 5.5% (36 bp). For comparison, the COI barcode difference between the type species of sister genera (according to Boyle et al. (2015)) *Crudaria* and *Cigaritis* Donzel, 1848 (type species *Cigaritis zohra* Donzel, 1848, NVG-22012H05) is 9.6% (63 bp), which is nearly twice as large and does not preclude genus-level genetic differentiation between *Crudaria* and *Cigaritis*. Therefore, *Cesa* does not represent a significant deviation from *Crudaria* to warrant its monotypic status as a genus and may be placed in this genus with its close relatives. Acknowledging some morphological distinction of *Spindasis waggae*, we propose to treat *Cesa* Seven, 1997, **stat. nov.** as a subgenus of *Crudaria* Wallengren, 1875.

Vansomerenia Heath, 1997 is a junior subjective synonym of *Chloroselas* Butler, 1886

The monotypic genus *Vansomerenia* Heath, 1997 (type species *Desmolycaena rogersi* Riley, 1932) originates within the genus *Chloroselas* Butler, 1886 (type species *Chloroselas esmeralda* Butler, 1886), rendering it paraphyletic (Fig. 21). The difference between their COI barcodes is 6.2% (41 bp), which is typical for congeners. To restore monophyly and place close relatives in a single genus, we propose that *Vansomerenia* Heath, 1997, **syn. nov.** is a junior subjective synonym of *Chloroselas* Butler, 1886.
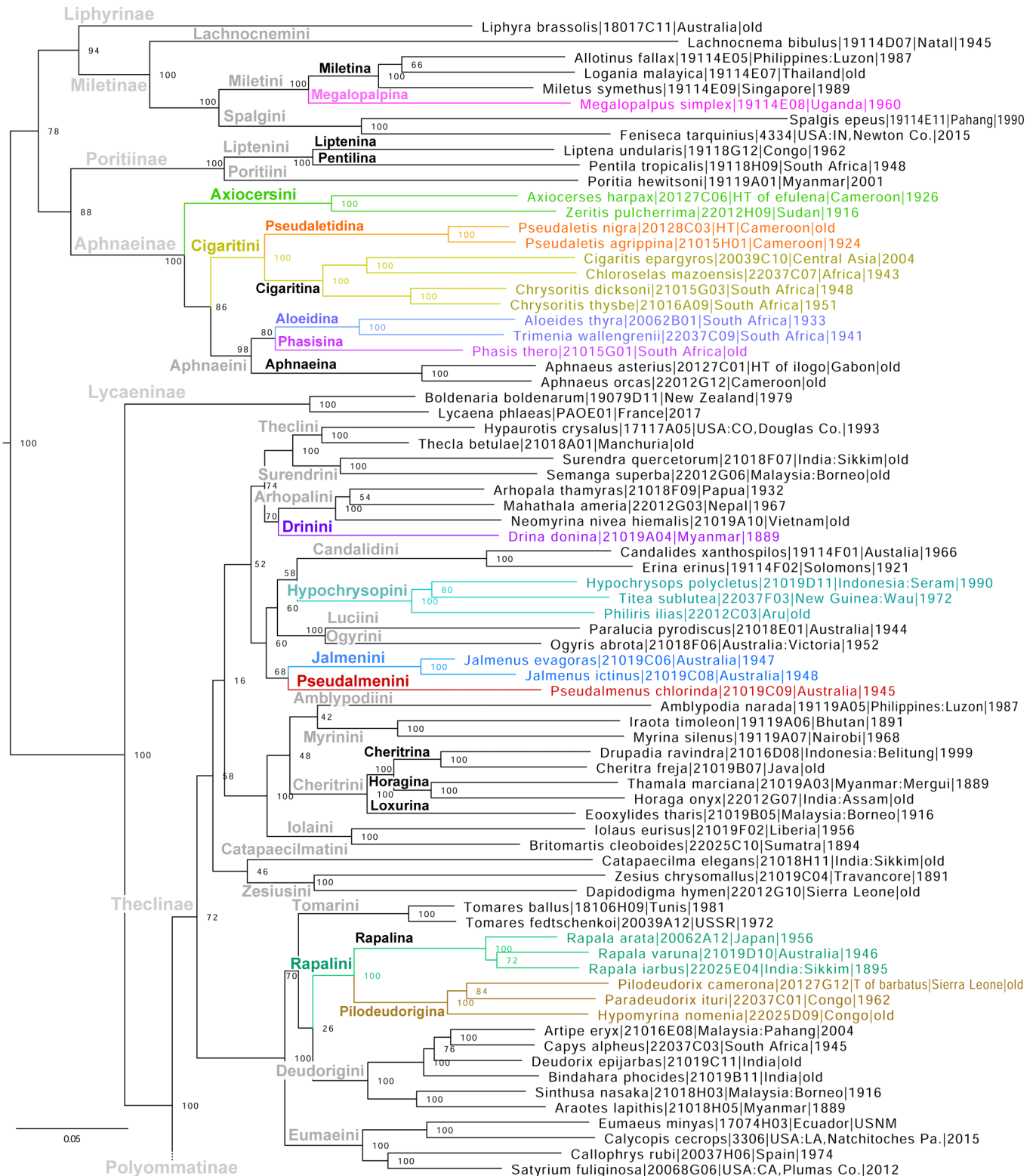
Fig. 20. The phylogenetic tree of selected Lycaenidae (Polyommatinae are shown in Fig. 22 below) inferred from protein-coding regions of the nuclear genome (autosomes). Family-group names are shown above or below the corresponding branches. Not all subtribes are shown and/or labeled (see the subtribal classification list of Lycaenidae below). Names, clades, and species of new tribes and subtribes proposed in this work are shown in color. Names of other subtribes are shown in black, and names of subfamilies and tribes are shown in shades of gray.
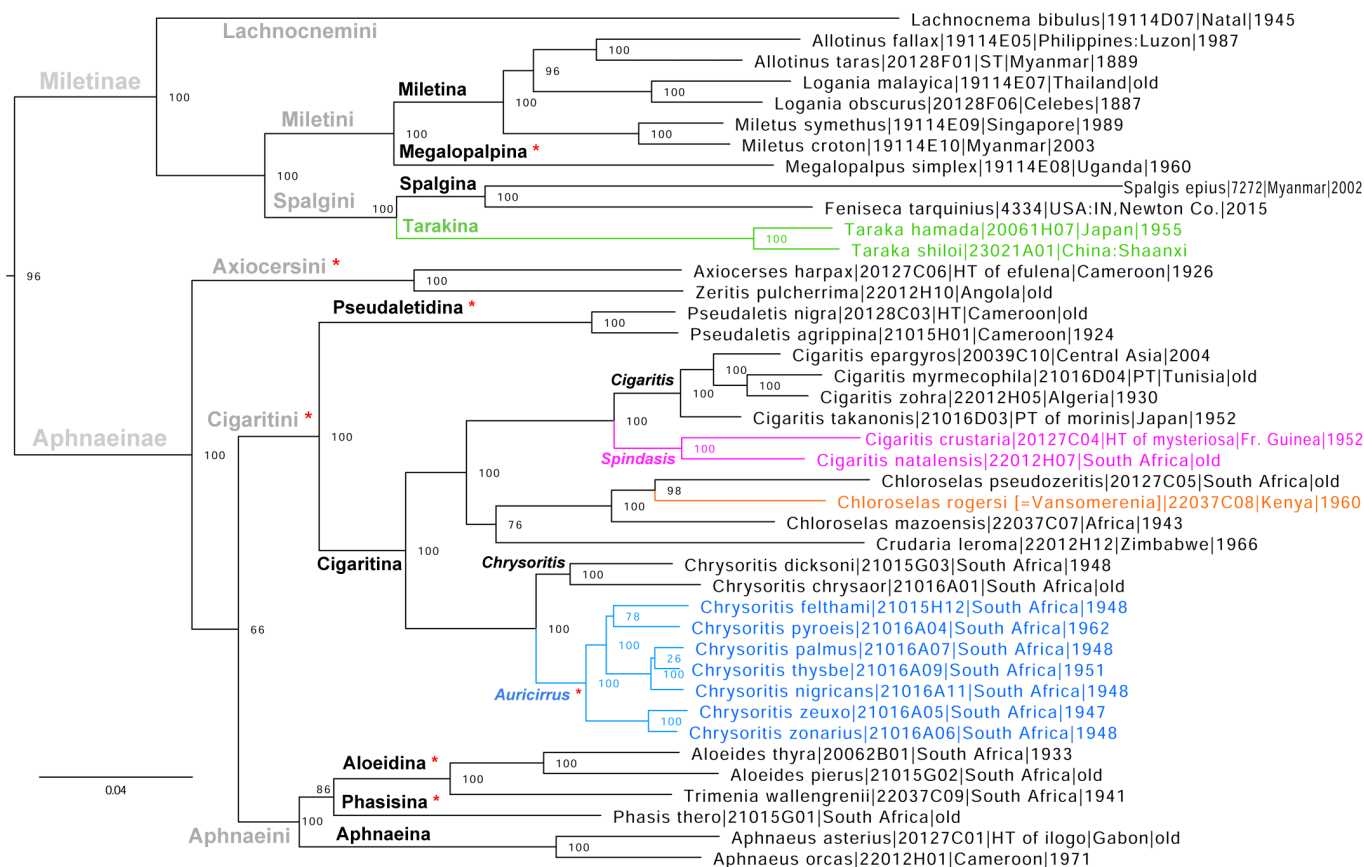
Fig. 21. The phylogenetic tree of Miletinae and Aphnaeinae inferred from protein-coding regions of the nuclear genome (autosomes). Names are shown by corresponding branches: family-group in roman font and subgenera in italics. Names proposed in this work are marked with red asterisks. Names, clades, and species of taxa referring to this figure from the text are colored: Tarakina **stat. nov.** (green), *Spindasis* **stat. rest.** (magenta), *Vansomerenia* **syn. nov.** (orange), and *Auricirrus* **subgen. n.** (blue). Other names of subtribes are shown in black, and names of subfamilies and tribes are shown in shades of gray.

Auricirrus Grishin, new subgenus
http://zoobank.org/B527E473-8675-489E-B979-EAFF56996F4B

Type species. *Papilio thysbe* Linnaeus, 1764.

Definition. African genus *Chrysoritis* Butler, 1898 (type species *Zeritis oreas* Trimen, 1891) has been divided into two clades: the eastern (*chrysaor* clade) and the western (includes the *thysbe* clade) (Talavera et al. 2020) (Fig. 21). Strong genetic differentiation between these clades warrants their recognition at least as subgenera: estimated divergence time between them is about 17 Mya (Talavera et al. 2020), comparable to that of some genera. Among all *Chrysoritis* species, the type species of available genus-group names belong to the eastern clade (Talavera et al. 2020): *Zeritis oreas* Trimen, 1891 (of *Chrysoritis*), *Zeritis lycegenes* Trimen, 1874, which is a subspecies of *Zeritis lyncurium* Trimen, 1868 (of *Poecilmitis* Butler, 1899), *Zeritis phosphor* Trimen, 1864 (of *Bowkeria* Quickelberge, 1972), and *Phasis dicksoni* Gabriel, 1947 (of *Oxychaeta* Tite & Dickson, 1973). This eastern clade represents the nominotypical subgenus. However, the western clade remains without a name and represents a new subgenus. This subgenus differs from the nominal by the absence of tibial spicules (Heath 1997), produced (but not tailed) hindwing tornus and/or blue or violet scaling on dorsal surface of wings in some species (lacking in the nominotypical subgenus), and in species with more rounded tornus, spots on ventral forewing—especially at the end of discal cell—are with more extensive silvery scaling. A combination of the following nuclear genomic base pairs is diagnostic: cce3229.3.2:A633G, cce2784.3.3: C85G, cce2423.1.2:A2767T, cce7537.1.5:C57T, cce5689.1.7:A744G.

Etymology. The name *Chrysoritis* may have been derived from the Greek "chryso" (gold) and "ritis" (hair or curl). Their Latin equivalents are "aurum" (gold) and "cirrus" (lock or curl of hair), connected with a

vowel *i* to form the name of the subgenus. The name is a masculine noun in the nominative singular.

Species included. The type species (i.e., *Papilio thysbe* Linnaeus, 1764) and 41 others, names given in their original combinations: *Poecilmitis adonis* Pennington, 1962, *Poecilmitis turneri amatola* Dickson & McMaster, 1967, *Chrysoritis adonis aridimontis* Heath & Pringle, 2007, *Poecilmitis aridus* Pennington, 1953, *Poecilmitis azurius* Swanepoel, 1975, *Poecilmitis beaufortia* Dickson, 1966, *Poecilmitis beulah* Quickelberge, 1966, *Poecilmitis blencathrae* Heath & Ball, 1992, *Poecilmitis braueri* Pennington, 1967, *Poecilmitis thysbe brooksi* Riley, 1938, *Zeritis chrysantas* Trimen, 1868, *Poecilmitis* (*Poecilmitis*) *daphne* Dickson, 1975, *Poecilmitis endymion* Pennington, 1962, *Zeritis felthami* Trimen, 1904, *Poecilmitis irene* Pennington, 1968, *Poecilmitis lyndseyae* Henning, 1979, *Poecilmitis lysander* Pennington, 1962, *Poecilmitis mithras* Pringle, 1994, *Phasis thysbe* var. *nigricans* Aurivillius, 1924, *Poecilmitis orientalis* Swanepoel, 1976, *Papilio palmus* Stoll, 1781, *Poecilmitis pan* Pennington, 1962, *Poecilmitis pelion* Pennington, 1953, *Poecilmitis penningtoni* Riley, 1938, *Poecilmitis perseus* Henning, 1977, *Poecilmitis plutus* Pennington, 1967, *Poecilmitis pyramus* Pennington, 1953, *Zeritis pyroeis* Trimen, 1864, *Poecilmitis rileyi* Dickson, 1966, *Poecilmitis stepheni* Dickson, 1978, *Poecilmitis swanepoeli* Dickson, 1965, *Poecilmitis thysbe trimeni* Riley, 1938, *Poecilmitis turneri* Riley, 1938, *Poecilmitis uranus* Pennington, 1962, *Poecilmitis violescens* Dickson, 1971, *Poecilmitis whitei* Dickson, 1994, *Poecilmitis williami* Heath, 1997, *Poecilmitis wykehami* Dickson, 1980, *Papilio zeuxo* Linnaeus, 1764, *Phasis zeuxo zonarius* Riley, 1938, *Poecilmitis nigricans zwartbergae* Dickson, 1982 (including their subspecies and synonyms). Species taxonomy follows Heath (2023) and Williams (2023c).

Parent taxon. Genus *Chrysoritis* Butler, 1898.

Spindasis Wallengren, 1857 is a subgenus of *Cigaritis* Donzel, 1848

Phylogenetic analysis of Aphnaeinae Distant, 1884 revealed that the genus *Cigaritis* Donzel, 1848 (type species *Cigaritis zohra* Donzel, 1848) splits into two prominent clades: mostly Oriental (hindwing tornal lobe not well developed or lacking, at least one hindwing tail short, < 2 mm) and African (hindwing tornal lobe well developed, both hindwing tails long) (Riley 1925) with genetic differentiation between them similar to that of the two subgenera in *Chrysoritis* Butler, 1898 (type species *Zeritis oreas* Trimen, 1891) (Boyle et al. 2015) (Fig. 21). Therefore, the two clades of *Cigaritis* correspond to subgenera. The (mostly) Oriental clade is the nominal subgenus because the type species of *Cigaritis* (from NW Africa) belongs to this clade. Two additional genus-group names have type species currently placed in *Cigaritis*: *Spindasis* Wallengren, 1857 (type species *Spindasis masilikazi* Wallengren, 1857, which is a junior subjective synonym of *Aphnaeus natalensis* Westwood, [1851]) and *Apharitis* Riley, 1925 (type species *Polyommatus epargyros* Eversmann, 1855). The latter is in the Asian clade and, therefore, remains a junior subjective synonym of *Cigaritis*. The former belongs to the African clade and, therefore, this clade corresponds to the subgenus *Spindasis* Wallengren, 1857, **stat. rest.**, which we propose to treat as a valid subgenus instead of a synonym.

Tribes in Aphnaeinae Distant, 1884

Inspection of the genomic tree reveals three strongly supported clades in the subfamily Aphnaeinae Distant, 1884 that we define as tribes (Figs. 20, 21): nominotypical, "Apharitini" Chou et al., 1994, and the third one that does not have a name and is described below. The name "Apharitini" was published in Chou et al. (1994) in an informal way without description, definition, or references to them (fails ICZN Art. 13.) and is a *nomen nudum*. The name for this tribe that satisfies the requirements of the ICZN Code is proposed below. We define three tribes and not two because the phylogenetic affinities of the unnamed tribes with the nominotypical one are not particularly strong (86%), and combining their clades may not result in a monophyletic taxon if this topology is incorrect. The three clades are the same in the recently published large-scale tree (Kawahara et al. 2023), but the topology is different in a tree based on a more limited set of gene markers (but a larger set of taxa) (Boyle et al. 2015).

Cigaritini Grishin, new tribe

http://zoobank.org/E44D9831-7137-4120-86CB-700DBCC8D752

Type genus. *Cigaritis* Donzel, 1848.

Definition. The clade with *Cigaritis* (type species *Cigaritis zohra* Donzel, 1848) and related genera is genetically differentiated from other clades and is at the tree level of a tribe (Figs. 20, 21). This new tribe is morphologically diverse and can be distinguished from other members of the subfamily Aphnaeinae Distant, 1884 by the shape of uncus, which is highly variable, but nevertheless bilobed or divided, with centrally concave distal margin (see Stempffer (1967) for illustrations and more detailed descriptions): in *Lipaphnaeus* Aurivillius, 1916, subtriangular uncus is deeply divided with narrow, tooth-like pointed lobes; in *Chloroselas* Butler, 1886, the lobes are small and subtriangular uncus is with a central notch separating finely serrated lobes; in *Cigaritis* Donzel, 1848, uncus is broader than long, nearly rectangular or trapezoidal in dorsal view (sometimes nearly vestigial), lobes widely separated, uncus mostly concave (may be with irregularities) between the lobes; in *Chrysoritis* Butler, 1898 and *Crudaria* Wallengren, 1875, uncus is similar, trapezoidal or heart-shaped, but less broad, with rounded lobes and convex margin between them; in *Pseudaletis* H. H. Druce, 1888, uncus is divided for nearly its entire length with finger-like terminally rounded lobes. In other Aphnaeinae tribes, uncus in undivided and not strongly bilobed: typically, from almost square to broadly rectangular, with nearly flat (with some irregularities) distal margin, or dome-shaped with convex distal margin, which is only slightly concave in *Trimenia* Tite & Dickson, 1973 (type species *Zeritis wallengrenii* Trimen, 1887), thus resembling *Chrysoritis*, but uncus is narrower and without clearly defined lobes expanded laterally (as in *Chrysoritis* and *Crudaria*). Furthermore, *Trimenia* has saccus, which is not developed in *Chrysoritis*. A combination of the following nuclear genomic base pairs is diagnostic: cce332.12.5:A61T, cce1232.20.1:A596G, cce1351.40.3:A349T, cce5072.9.1:A67C, cce2368.14.7:G95T.

Genera included. The type genus (i.e., *Cigaritis* Donzel, 1848), *Chloroselas* Butler, 1886, *Chrysoritis* Butler, 1898, *Crudaria* Wallengren, 1875, *Lipaphnaeus* Aurivillius, 1916, and *Pseudaletis* H. H. Druce, 1888, including their subgenera and synonyms (e.g., *Cesa* Seven, 1997, *Vansomerenia* Heath, 1997, and *Apharitis* Riley, 1925).

Parent Taxon. Subfamily Aphnaeinae Distant, 1884.

Comment. This tribe corresponds to "Apharitini" of Chou et al. (1994), published without description, definition, or references to them: a *nomen nudum* (fails ICZN Art. 13.). *Apharitis* Riley, 1925 (type species *Polyommatus epargyros* Eversmann, 1855) is a junior subjective synonym of *Cigaritis*.

Pseudaletidina Grishin, new subtribe

http://zoobank.org/D8A065B1-F0CF-4A7F-BADA-F06FDEECA919

Type genus. *Pseudaletis* H. H. Druce, 1888.

Definition. *Pseudaletis* (type species *Pseudaletis agrippina* H. H. Druce, 1888) is in the lineage that is sister to all other Cigaritini Grishin, **trib. n.** and is genetically differentiated from them at the subtribal level (Figs. 20, 21). Therefore, we propose to treat this lineage as a subtribe. This new subtribe is diagnosed by a combination of the following characters, as given for the *Pseudaletis* section by Eliot (1973): palpi short—much less than half of the head length—covered in appressed scales, proboscis very short (but functional), forewing appears disproportionately large comparatively to hindwing; uncus divided for nearly its entire length with finger-like terminally rounded lobes, falces rudimentary, pointed processes inflexibly fused to tegumen; female abdomen with a prominent tuft of specialized scales, which are spoon-shaped with long "handles". A combination of the following nuclear genomic base pairs is diagnostic: cce1853.23.8:T1384A, cce133.4.1:A287G, cce4260.4.1:G34A, cce1367.9.3:G1252A, cce17940.6.2:C71A.

Genera included. Only the type genus.

Parent Taxon. Tribe Cigaritini Grishin, **trib. n.**

Axiocersini Grishin, new tribe

http://zoobank.org/1BBFE9EC-AB8B-4709-A250-4DA082ED2B4E

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

Definition. *Axiocerses* (type species *Papilio perion* Stoll, 1782, which is a junior subjective synonym of *Papilio harpax* Fabricius, 1775) and *Zeritis* Boisduval, 1836 (type species *Zeritis neriene* Boisduval, 1836) are confident sisters in the genomic tree (Figs. 20, 21), consistently with similarities in their morphology reported previously (Stempffer 1967). The two genera form a clade that originates early in the radiation of the subfamily Aphnaeinae Distant, 1884, and, therefore, it corresponds to a tribe. This new tribe is distinguished from the relatives by a combination of the following characters: uncus very broad and short, distal margin straight or convex, lobes nearly triangular or rounded, falces thick at the base, then strongly angled with free branch long and slender, ventral side with apophysis, tegumen with uncus hood-shaped, tegumen with convex anterior margin; palpi short, not extending or slightly extending beyond the fronts, 2nd segment of palpi with long scales and hairs; tarsus unsegmented, with spines below; forewing with only 10 veins (Stempffer 1967; Henning and Henning 1996). The similarity in uncus, falces, and tegumen unifies *Axiocerses* and *Zeritis* Boisduval, 1836 (Stempffer 1967). A combination of the following nuclear genomic base pairs is diagnostic: cce243.9.9:A1417C, cce15587.11.3:G103A, cce127.4.3:A149T, cce980.22.7:C902T, cce2423.1.2:T2315C.

Genera included. The type genus (i.e., *Axiocerses* Hübner, [1819]) and *Zeritis* Boisduval, 1836.

Parent Taxon. Subfamily Aphnaeinae Distant, 1884.

Aloeidina Grishin, new subtribe

http://zoobank.org/A32E1EE2-A06D-4100-AFD9-3214F38A2C93

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

Definition. Within Aphnaeini Distant, 1884, the clade of several genera that includes *Aloeides* (type species *Papilio pierus* Cramer, 1779) corresponds to the subtribal level in the tree (Figs. 20, 21). This new subtribe is distinguished from its relatives by a combination of these characters, as discussed and illustrated by Stempffer (1967), Tite & Dickson (1973), and Eliot (1973): foreleg and midleg tibiae with apical spurs, palpi smooth, with equal length scales (in several species with some scattered long ribbon-shaped blunt scales), or with uniquely long and bristly white scales (in *Erikssonia* Trimen, 1891), forewing vein R_{4+5} originates at or beyond the junction of the discocellular vein and vein M_1, vein R_2 originates next to the origin of vein R_{4+5}. A combination of the following nuclear genomic base pairs is diagnostic: cce5760.10.2:C484T, cce2790.13.2:T63C, cce2790.13.2:A183G, cce1354.3.7:A61T, cce1354.3.7:T1903A.

Genera included. The type genus (i.e., *Aloeides* Hübner, [1819]), *Argyraspodes* Tite & Dickson, 1973, *Erikssonia* Trimen, 1891, and *Trimenia* Tite & Dickson, 1973.

Parent Taxon. Tribe Aphnaeini Distant, 1884.

Phasisina Grishin, new subtribe

http://zoobank.org/B6D8239D-DAF0-4865-9F3E-18677ABDEA6F

Type genus. *Phasis* Hübner, [1819].

Definition. Within Aphnaeini Distant, 1884, the clade of several genera that includes *Phasis* (type species *Papilio salmoneus* Stoll, 1781, which is a junior subjective synonym of *Papilio thero* Linnaeus, 1764) corresponds to the subtribal level in the tree (Figs. 20, 21). This new subtribe is distinguished from its relatives by a combination of the following characters, as discussed and illustrated by Tite & Dickson (1973): tibia of all legs without apical spurs, forewing vein M_2 originates much closer to the origin of vein

M_1 than to the origin of vein M_3, vein R_2 originates at a distance from vein R_{4+5}, size larger with forewing longer than 16 mm. A combination of the following nuclear genomic base pairs is diagnostic: cce288.3.2: A79C, cce33.3.3:A234G, cce2859.6.1:T729C, cce511.6.1:A54G, cce14215.5.1:T850C, cce33280.1.7:T944T (not A), cce3467.4.4:A374A (not G), cce7428.5.1:G156G (not A), cce4435.12.1:C616C (not A), cce1239.1. 3:T235T (not G).

Genera included. The type genus (i.e., *Phasis* Hübner, [1819]) and *Tylopaedia* Tite & Dickson, 1973.

Parent Taxon. Tribe Aphnaeini Distant, 1884.

Surendrini Koçak & Seven, 1997 is a tribe

Currently placed in the tribe Arhopalini Bingham, 1907, Surendrina Koçak & Seven, 1997 is not monophyletic with it and instead is sister to Theclini Swainson, 1830 (Fig. 20). It is conceivable to place Surendrina in Theclini, but the two groups are more distinct from each other than subtribes and are at the tree level of tribes. Therefore, we propose to treat the former taxon as a tribe Surendrini Koçak & Seven, 1997, **stat. nov**.

Drinini Grishin, new tribe
http://zoobank.org/2001E28A-4C8C-45D9-B228-E34D99B26E85

Type genus. *Drina* Nicéville, 1890.

Definition. Currently in Loxurini Swinhoe, 1910, *Drina* (type species *Myrina donina* Hewitson, 1865) is not monophyletic with it and is not closely related to that tribe, instead forming a separate lineage originating early in the diversification of Theclinae Swainson, 1831 (Fig. 20). Therefore, we propose that this lineage corresponds to a tribe. This new tribe is diagnosed by a combination of the following characters, as given for the *Drina* section by Eliot (1973): male genitalia with significantly reduced (nearly vestigial) tegumen (not wider than valva in lateral view), uncus, and falces, and long and narrow vinculum; forewing with 11 veins, the three M veins are nearly at the same distance from each other, hindwing with a single tail at vein CuA_2. A combination of the following nuclear genomic base pairs is diagnostic: cce305.14.6:G130A, cce305.14.6:T131C, cce1105.7.5:G93A, cce144.8.2:G223A, cce204.17.10: C49A, cce3081.9.2:G97G (not T), cce2598.5.13:G484G (not C), cce2598.5.13:C485C (not A), cce948.2.2: T73T (not A), cce948.2.2: A139A (not G).

Genera included. Only the type genus.

Parent Taxon. Subfamily Theclinae Swainson, 1831.

Hypochrysopini Grishin, new tribe
http://zoobank.org/71317481-C0FE-4839-97E2-341444327DD7

Type genus. *Hypochrysops* C. Felder & R. Felder, 1860.

Definition. Currently placed in Luciini Waterhouse & Lyell, 1914, *Hypochrysops* (type species *Papilio polycletus* Linnaeus, 1758) and related genera are not monophyletic with it and instead form a distinct clade within Theclinae Swainson, 1831 not confidently associated with any other subtribe (Fig. 20). Therefore, this clade represents a subtribe. This new tribe is diagnosed by a combination of the following characters, as given for the *Hypochrysops* section by Eliot (1973): uncus not produced, rounded, falces prominent, strongly curved, juxta absent or vestigial, aedeagus very thick, just slightly narrower than valva, valva rhomboidal, saccus not developed; ventral wing surface typically with obsolete or distorted patterns with metallic silver or green spots and bands and red blotches. A combination of the following nuclear genomic base pairs is diagnostic: cce3313.6.1:G1784C, cce3313.6.1:G2131C, cce67043.1.6:C55G, cce67043.1.6:A56T, cce1184.15.22:G142C.

Genera included. The type genus (i.e., *Hypochrysops* C. Felder & R. Felder, 1860), *Philiris* Röber, 1891, and *Titea* Eliot, 1973.

Parent Taxon. Subfamily Theclinae Swainson, 1831.

Jalmenini Grishin, new tribe
http://zoobank.org/D58D0D0A-382D-4E6D-B879-75D3DE7A3670

Type genus. *Jalmenus* Hübner, 1818.

Definition. Currently in Zesiusinae Swinhoe, 1912, *Jalmenus* (type species *Jalmenus evagoras* Hübner, 1818, which is a junior homonym of *Papilio evagoras* Donovan, 1805) is far removed from the genus *Zesius* Hübner, [1819] (type species *Zesius chrysomallus* Hübner, 1823) in the genomic tree, and instead forms a distinct lineage within Theclinae Swainson, 1831 not confidently associated with other genera (Fig. 20). Therefore, this lineage represents a tribe. This new tribe is diagnosed by a combination of the following characters, as given for the *Jalmenus* section (excluding *Pseudalmenus* H. H. Druce, 1902) by Eliot (1973): uncus and tegumen narrower in lateral view, longer than in relatives, ventral side not expanded, falces smaller, tegumen not expanded anteriad, valva without costal process, simple and rounded; palpi with 3rd segment very long, 2nd segment with bristle-like scales. A combination of the following nuclear genomic base pairs is diagnostic: cce9330.11.2:G69A, cce7486.3.3:T58G, cce9657.10.14:T3166C, cce10680.1.1:T28C, cce4529.2.2:A67G.

Genera included. Only the type genus.

Parent Taxon. Subfamily Theclinae Swainson, 1831.

Pseudalmenini Grishin, new tribe
http://zoobank.org/BB6B6C59-EAD7-42B4-B7E6-CA95E94A419D

Type genus. *Pseudalmenus* H. H. Druce, 1902.

Definition. In the genomic tree, *Pseudalmenus* (type species *Ialmenus myrsilus* Westwood, 1851, which is a subspecies of *Thecla chlorinda* Blanchard, 1848) is a weakly supported (54%) sister of *Jalmenus* Hübner, 1818, and therefore may not be monophyletic with it (Fig. 20). Hence, we propose that this lineage represents a tribe. This new tribe was included in the *Jalmenus* section by Eliot (1973) and is diagnosed by a combination of the following characters: 3rd segment of palpi shorter than in Jalmenini **trib. n.**, 2nd segment hairy; uncus with ventral portion expanded, protruding posteriad of the dorsal margin, falces long and strongly curved, tegumen well-developed, expanded anteriad, valva with the curved costal process giving it a crab claw-like appearance. A combination of the following nuclear genomic base pairs is diagnostic: cce10780.3.1:G247A, cce1122.11.2:C1079G, cce11670.2.2:C750T, cce24738.4.8:A1793G, cce10780.2.2:A2954G.

Genera included. Only the type genus.

Parent Taxon. Subfamily Theclinae Swainson, 1831.

Myrinini Toxopeus, 1929 is a tribe

Currently in Amblypodiini Doherty, 1886, close relatives *Myrina* [Fabricius], 1807 (type species *Papilio alcides* Cramer, 1776) and *Iraota* F. Moore, 1881 (type species *Hesperia maecenas* Fabricius, 1793) are distantly related to *Amblypodia* Horsfield, 1829 (type species *Thecla narada* Horsfield, 1828). The clade of these three genera is not strongly supported (42%) in our tree (Fig. 20), and their union is not monophyletic in a global phylogeny of butterflies (Kawahara et al. 2023). Therefore, we propose a status of a tribe for Myrinini Toxopeus, 1929, **stat. nov**., which consists of two genera (*Myrina* and *Iraota*).

Horagina Swinhoe, 1910 and Loxurina Swinhoe, 1910 are subtribes of Cheritrini Swinhoe, 1910

Currently regarded as distinct tribes, Cheritrini Swinhoe, 1910, Horagini Swinhoe, 1910, and Loxurini Swinhoe, 1910 (Eliot 1973) are closely related to each other and are at the tree level of subtribes (Fig. 20). Being combined, all three constitute one tribe. The priority of these names could not be determined because they were proposed (as subfamilies) on the same page of the same work (i.e., issued on the same date). As the first revisers, we give priority to Cheritrini Swinhoe, 1910, because this group includes more genera and species than the other two. As a result, we propose that Horagina Swinhoe, 1910, **stat. nov.** and Loxurina Swinhoe, 1910, **stat. nov.** are subtribes of Cheritrini Swinhoe, 1910.

Rapalini Grishin, new tribe
http://zoobank.org/6B76C64C-1C57-4CC8-BBA2-925D4AFBCF7D

Type genus. *Rapala* F. Moore, 1881.

Definition. Currently, in Deudorigini Doherty, 1886, several genera, including *Rapala* (type species *Thecla varuna* Horsfield, 1829), form a clade that is not confidently monophyletic with it: only 26% partitions in the genomic tree support their grouping with Deudorigini. Low support values indicate a more distant relationship and a possibility of incomplete lineage sorting or gene exchange around the time of origin of these clades. The clade consisting of *Rapala* (mostly Oriental) and three Afrotropical genera closely related to *Pilodeudorix* H. H. Druce, 1891 (type species *Pilodeudorix barbatus* H. H. Druce, 1891) is most confidently supported (100%) and corresponds to the level of a tribe in the tree (Fig. 20). This new tribe differs from relatives by male genitalia having conjoined valvae that evenly taper to narrow rounded or pointed apices, uncus and tegumen broad, two lobes of uncus with a concave margin between them, hood-shaped; secondary sexual characters in males: an oval brand of small androconia near the base of cell $Sc+R_1$-RS (at least in non-African species), and typically a hair tuft on ventral forewing near inner margin to complement the brand, sometimes with other brands, including those on abdomen; hindwing tailed, forewing veins R_{4+5} and M_1 originate separately, although may be very narrowly separated at their origins (Eliot 1973). Most confidently distinguished by DNA and a combination of the following base pairs in the nuclear genome is diagnostic: cce303273.1.1:G197A, cce1093.2.1:A4672C, cce3516.7.1:A173T, cce12299.7.3:G134A, cce4160.2.2:A207G.

Genera included. The type genus (i.e., *Rapala* F. Moore, 1881), *Pilodeudorix* H. H. Druce, 1891, *Hypomyrina* H. H. Druce, 1891, and *Paradeudorix* Libert, 2004.

Parent Taxon. Subfamily Theclinae Swainson, 1831.

Pilodeudorigina Grishin, new subtribe
http://zoobank.org/5826F9A8-6834-487C-B207-DC883CE19307

Type genus. *Pilodeudorix* H. H. Druce, 1891.

Definition. Afrotropical clade of Rapalini **trib. n.** that includes *Pilodeudorix* (type species *Pilodeudorix barbatus* H. H. Druce, 1891, which is a junior subjective synonym of *Sithon camerona* Plötz, 1880) is genetically differentiated from non-Arican (mostly Oriental) species at the tree level of a subtribe (Fig. 20). This new subtribe is diagnosed by a combination of the following characters: abdomen frequently with scent brands and hindwings with hair tufts; aedeagus shorter and less gracile that in the nominotypical tribe, frequently expanded terminally, vesica with many small cornuti and usually with large cuneus; basally fused valvae with a rectangular gap between them in many species, in others, each valva with a process, hook-like in ventral view, uncus lobes are frequently less separated from each other than in the nominotypical subtribe (Stempffer 1967). Best distinguished by DNA and a combination of
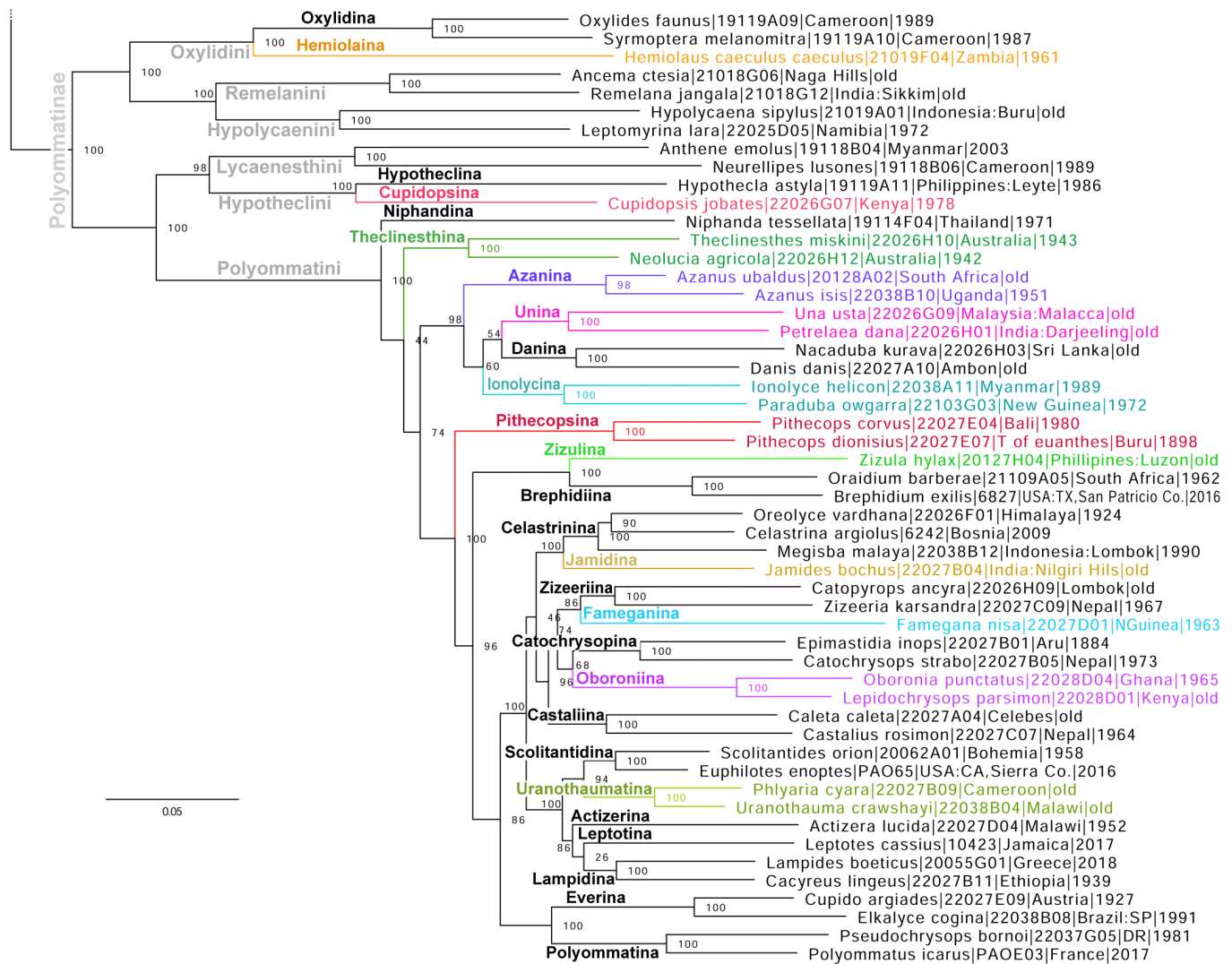
Fig. 22. The phylogenetic tree of selected Polyommatinae (other Lycaenidae are shown in Fig. 20) inferred from protein-coding regions of the nuclear genome (autosomes). Family-group names are shown above or below the corresponding branches. Not all subtribes are shown and/or labeled (see the subtribal classification list of Lycaenidae below). Names, clades, and species of new subtribes proposed in this work are shown in color. Names of other subtribes are shown in black, and names of subfamilies and tribes are shown in shades of gray.

the following nuclear genomic base pairs is diagnostic: cce303351.9.14:A88G, cce303351.9.14:A89G, cce14215.8.1:C143T, cce881.1.6:A79G, cce462.24.2:C89G.

Genera included. The type genus (i.e., *Pilodeudorix* H. H. Druce, 1891), *Hypomyrina* H. H. Druce, 1891, and *Paradeudorix* Libert, 2004.

Parent Taxon. Tribe Rapalini Grishin, **trib. n**.

Oxylidini Eliot, 1973, Remelanini Eliot, 1973, and Hypolycaenini Swinhoe, 1910 belong to Polyommatinae Swainson, 1827, not to Theclinae Swainson, 1831

Traditionally placed among hairstreaks (Theclinae Swainson, 1831) due to their appearance (frequently with very long hindwing tails), species from the tribes Oxylidini Eliot, 1973, Remelanini Eliot, 1973, and Hypolycaenini Swinhoe, 1910 are confidently placed as a sister clade to "Blues" and are not monophyletic with the subfamily Theclinae (Figs. 20, 22). Therefore, they do not belong to Theclinae. Their genetic differentiation from the clade that consists of traditional Polyommatinae Swainson, 1827

(tribes Lycaenesthini Toxopeus, 1929, Hypotheclini Eliot, 1973, and Polyommatini Swainson, 1827) is smaller than that for other subfamilies of Lycaenidae. Insufficient differentiation argues against treating Oxylidini, Remelanini, and Hypolycaenini as a subfamily of their own. Therefore, we place them in the subfamily Polyommatinae. We see that the three subfamilies, Lycaeninae, Theclinae, and Polyommatinae, are closely related to each other (Figs. 20, 22), as expected and evidenced by morphology (Eliot 1973). The genetic distinction of Lycaeninae from the two other subfamilies is more pronounced, and the tree branches separating them are more prominent (Fig. 20). However, Theclinae and Polyommatinae are less distinct from each other, and "blues" originate from within "hairstreaks", not next to them, like butterflies originate from within moths, birds from within reptiles, and tetrapods from within fishes. Furthermore, due to their close relationship, it is conceivable to unify Theclinae and Polyommatinae into one subfamily (Polyommatinae). We are not taking this step here and continue with the traditional tri-subfamily arrangement for now, simply rearranging tribes among Theclinae and Polyommatinae to restore monophyly. See our proposed subtribal classification of Lycaenidae below.

Hemiolaina Grishin, new subtribe

http://zoobank.org/45FFC7EB-6CFA-49A6-A688-EC98E721BA62

Type genus. *Hemiolaus* Aurivillius, 1922.

Definition. *Hemiolaus* (type species *Jolaus caeculus* Hopffer, 1855) forms a lineage sister to other Oxylidini Eliot, 1973, but is genetically differentiated from them at the subtribal level, and therefore represents a subtribe (Fig. 22). This new subtribe is diagnosed by a combination of the following characters, as given for the *Hemiolaus* section by Eliot (1973): juxta enlarged, longer than half of valva, shaped as the end of a nail puller with a deep cleft; ventral hindwing of males with a scent patch beneath a hair brush; antennal club short, nudum confined to the club, about 32 segments, palpi with 3rd segment slightly less than half of the 2nd, tarsus of male foreleg terminally tapered and downturned. A combination of the following nuclear genomic base pairs is diagnostic: cce54422.3.2:C373T, cce993.15.2:A922T, cce303329.2.7:A2399C, cce2502.15.1:A320C, cce5483.2.11:T370A.

Genera included. Only the type genus.

Parent Taxon. Tribe Oxylidini Eliot, 1973.

Cupidopsina Grishin, new subtribe

http://zoobank.org/8AFD9453-3743-4ECB-BA87-4DAC0A3297FB

Type genus. *Cupidopsis* Karsch, 1895.

Definition. Confidently placed in the tribe Hypotheclini Eliot, 1973, the lineage with *Cupidopsis* (type species *Lycaena jobates* Hopffer, 1855) is genetically differentiated from the *Hypothecla* Semper, 1890 lineage at the tree level of subtribes (Fig. 22) and therefore represents a subtribe. This new subtribe is diagnosed by a combination of the following characters as given for the *Cupidopsis* section by Eliot (1973): only 10 veins on the forewing, secondary sexual characters absent, aedeagus with developed coecum and ductus entrance on dorsal side, saccus smaller than in relatives, nearly vestigial, tegumen with uncus comparatively massive, the same length as valva in lateral view. A combination of the following nuclear genomic base pairs is diagnostic: cce9377.2.3:A136T, cce4053.12.2:A3235C, cce332.21. 2:G117T, cce199. 20.2:A244C, cce3203.9.2:A172C.

Genera included. Only the type genus.

Parent Taxon. Tribe Hypotheclini Eliot, 1973.

Comments. A family-group name formed from the same genus was proposed as a *nomen nudum* (fails ICZN Art. 13.) by Koçak (1996). The genomic tree demonstrates that this subtribe (as other Hypotheclini) belongs to Polyommatinae Swainson, 1827 (Figs. 20, 22), contrary to the hypothesis of Stradomsky

(2016), who nevertheless correctly associated *Cupidopsis* with *Hypothecla*.

Niphandina Sibatani & Ito, 1942 is a subtribe

In agreement with Stradomsky (2016), we find that Niphandini Sibatani & Ito, 1942 clusters closely with Polyommatini Swainson, 1827, being at the tree level with subtribes (Fig. 22). Therefore, we confirm its treatment as a subtribe Niphandina Sibatani & Ito, 1942, **stat. conf**.

Theclinesthina Grishin, new subtribe
http://zoobank.org/32E65131-DDFB-4EBC-BE37-4F42E8F5F6D3

Type genus. *Theclinesthes* Röber, 1891.

Definition. The clade with *Theclinesthes* (type species *Plebeius* (*Theclinesthes*) *eremicola* Röber, 1891, which is a junior subjective synonym of *Nacaduba miskini gaura* Doherty, 1891) originates near the base of Polyommatini Swainson, 1827 (Fig. 22) and therefore represents a subtribe. This new subtribe is diagnosed by a combination of the following characters, as given for the *Theclinesthes* section by Eliot (1973) and Stradomsky (2016): uncus lobes and (vestigial) falces directed ventrad, vinculum in lateral view much broader than in relatives, as broad as valva, aedeagus basally bulbous and apically tapered, ductus enters at anterior end, valva constricted in the middle. A combination of the following nuclear genomic base pairs is diagnostic: cce2737.15.2:A259G, cce3516.7.8:A98T, cce10374.3.2:A67C, cce2234.8.11:G1960A, cce2399.18.8:A86G.

Genera included. The type genus (i.e., *Theclinesthes* Röber, 1891), *Neolucia* G. Waterhouse & Turner, 1905, and *Sahulana* Hirowatari, 1992.

Parent Taxon. Tribe Polyommatini Swainson, 1827.

Comment. The same name was published in a pioneering study by Stradomsky (2016) without explicitly indicating that the name was intentionally new (fails ICZN Art. 16.1.) and not stating what the type genus of this taxon was (fails ICZN Art. 16.2.). This name for the subtribe already discovered by Stradomsky and confirmed by our genomic analysis is simply formalized here to comply with the ICZN Code (ICZN [International Commission on Zoological Nomenclature] 1999).

Azanina Grishin, new subtribe
http://zoobank.org/DF55B888-23ED-4B2E-94F9-B1B6685CBDA3

Type genus. *Azanus* F. Moore, 1881.

Definition. *Azanus* (type species *Papilio ubaldus* Stoll, 1782) is confidently placed in a clade of Polyommatini Swainson, 1827 containing several subtribes, not confidently grouping with any of them (Fig. 22). Therefore, the lineage with *Azanus* represents a subtribe. This new subtribe is diagnosed by a combination of the following characters, as given for the *Azanus* section by Eliot (1973): male genitalia elongated and flattened, uncus narrowly divided into separate lobes, forewings veins SC and R_1 come together and then diverge, androconia of two unusual types: nearly rectangular scales with concave bases and long padded scales, eyes hairy, ventral forewing with a dark streak below SC vein. A combination of the following nuclear genomic base pairs is diagnostic: cce9549.2.2:A815G, cce302383.7.1:T1153A, cce302383.7.1:C1154G, cce2510.1.2:A686G, cce178.15.6:A356G.

Genera included. Only the type genus.

Parent Taxon. Tribe Polyommatini Swainson, 1827.

Comment. The same name was proposed as a *nomen nudum* (fails ICZN Art. 13.) by Koçak (1996) and then published in a pioneering study by Stradomsky (2016) without explicitly indicating that the name was intentionally new (fails ICZN Art. 16.1.) and not stating what the type genus of this taxon was (fails

ICZN Art. 16.2.). This name for the subtribe already discovered by Koçak and Stradomsky and confirmed by our genomic analysis is simply formalized here to comply with the ICZN Code (ICZN [International Commission on Zoological Nomenclature] 1999).

Unina Grishin, new subtribe
http://zoobank.org/2FD670E6-5ECD-404E-A1F7-842AEF97335C

Type genus. *Una* Nicéville, 1890.

Definition. *Una* (type species *Zizera*? *usta* Distant, 1886) is confidently placed in the clade of Polyommatini Swainson, 1827 with several subtribes, not confidently grouping with any of them (Fig. 22). Therefore, the lineage with *Ionolyce* represents a subtribe. This new subtribe is a union of the *Una* and *Petrelaea* sections of Eliot (1973), who listed characters for them, and is diagnosed as follows: male genitalia elongated and appear flattened, with gracile and long aedeagus and prominent saccus (absent in close relatives); forewings with 11 veins, veins SC and R_1 fuse at least for some distance. A combination of the following nuclear genomic base pairs is diagnostic: cce10730.5.6:A179T, cce7658.4.3:A184G, cce4822.3.3:A98T, cce5018.4.1:A78G, cce870.7.1:G452A.

Genera included. The type genus (i.e., *Una* Nicéville, 1890), *Orthomiella* Nicéville, 1890, *Petrelaea* Toxopeus, 1929, and *Pseudonacaduba* Stempffer, 1942.

Parent Taxon. Tribe Polyommatini Swainson, 1827.

Comment. The same name was proposed as a *nomen nudum* (fails ICZN Art. 13.) by Koçak & Seven (1997).

Ionolycina Grishin, new subtribe
http://zoobank.org/77081BED-FF23-424A-98B3-541E04BA53E5

Type genus. *Ionolyce* Toxopeus, 1929.

Definition. *Ionolyce* (type species *Ionolyce helicon javanica* Toxopeus, 1929) is confidently placed in the clade of Polyommatini Swainson, 1827 with several subtribes, not confidently grouping with any of them (Fig. 22). Therefore, the lineage with *Ionolyce* represents a subtribe. This new subtribe is diagnosed by a combination of the following characters, as given for *Ionolyce* by Tite (1963): cornuti in aedeagus are large and spine-like, ribs in androconial scales are ribbon-like with nodular irregularities mainly in the posterior third of the scale; fused part of veins SC and R_1 is typically longer than in relatives, and the free end of vein SC is faint. A combination of the following nuclear genomic base pairs is diagnostic: cce437.15.1:A182G, cce303334.4.2:C106G, cce3111.1.6:A86G, cce3368.2.2:T241A, cce29649.12.1:A151G.

Genera included. The type genus (i.e., *Ionolyce* Toxopeus, 1929) and *Paraduba* Bethune-Baker, 1906.

Parent Taxon. Tribe Polyommatini Swainson, 1827.

Pithecopina Grishin, new subtribe
http://zoobank.org/3E5E4A9A-64A9-4AFC-85DD-81B13BE53FBF

Type genus. *Pithecops* Horsfield, 1828.

Definition. The clade with *Pithecops* (type species *Pithecops hylax corax* Fruhstorfer, 1919, which is a subspecies of *Pithecops corvus* Fruhstorfer, 1919) is confidently placed as sister to the "crown group" of Polyommatini Swainson, 1827 that undergoes extensive diversification (Fig. 22), and we include it in the "crown group" despite its unusual wing patterns. The *Pithecops* clade does not have close relatives within Polyommatini and, therefore, represents a subtribe. This new subtribe is diagnosed by a combination of the following characters, as given for the *Pithecops* section by Eliot (1973): male genitalia elongated and

appear flattened, uncus broadly divided nearly to its base, secondary sexual characters absent, veins SC and R_1 fuse at least for some distance, eyes not hairy, palpi hairy. A combination of the following nuclear genomic base pairs is diagnostic: cce59502.1.2:A118G, cce1246.19.3:A71G, cce9990.6.1:G740A, cce1317.1.1:C772T, cce3516.4.2:G83T.

Genera included. Only the type genus.

Parent Taxon. Tribe Polyommatini Swainson, 1827.

Comment. The same name was published in a pioneering study by Stradomsky (2016) without explicitly indicating that the name was intentionally new (fails ICZN Art. 16.1.) and not stating what the type genus of this taxon was (fails ICZN Art. 16.2.). This name for the taxon already discovered by Stradomsky and confirmed by our genomic analysis is simply formalized here to comply with the ICZN Code (ICZN [International Commission on Zoological Nomenclature] 1999).

Zizulina Grishin, new subtribe
http://zoobank.org/A230CCD1-B083-4025-8B78-A31A89478932

Type genus. *Zizula* Chapman, 1910.

Definition. The lineage with *Zizula* (type species *Lycaena gaika* Trimen, 1862, which is a junior subjective synonym of *Papilio hylax* Fabricius, 1775) is a confident sister to Brephidiina Stempffer, 1957, but is at the tree level that corresponds to subtribes in the "crown group" of Polyommatini Swainson, 1827 (Fig. 22) and therefore represents a subtribe. This new subtribe is diagnosed by a combination of the following characters, as given for the *Zizula* section by Eliot (1973): male genitalia unusual, aedeagus stout and terminally divided into two processes of about half of its length, dorsal and ventral, together resembling a beak, valva with a rod-like process of about the same length as genitalia and long bristles twice of valval length, veins SC and R_1 fused towards costa, secondary sexual characters absent. A combination of the following nuclear genomic base pairs is diagnostic: cce993.15.2:A161G, cce993.15.2:T162C, cce811.10.3:A2207G, cce811.10.3:T2197C, cce1162.15.2:T151A.

Genera included. Only the type genus.

Parent Taxon. Tribe Polyommatini Swainson, 1827.

Comment. The same name was proposed as a *nomen nudum* (fails ICZN Art. 13.) by Koçak (1996) and then published in a pioneering study by Stradomsky (2016) without explicitly indicating that the name was intentionally new (fails ICZN Art. 16.1.) and not stating what the type genus of this taxon was (fails ICZN Art. 16.2.). This name for the subtribe already discovered by Koçak and Stradomsky and confirmed by our genomic analysis is simply formalized here to comply with the ICZN Code (ICZN [International Commission on Zoological Nomenclature] 1999).

Jamidina Grishin, new subtribe
http://zoobank.org/F3E26669-CDF0-4EFC-9539-F88A3D47B1F7

Type genus. *Jamides* Hübner, [1819].

Definition. The lineage with *Jamides* (type species *Papilio bochus* Stoll, 1782) is a confident sister to Celastrinina Tutt, 1907, but splits from the latter at the tree level of subtribes (Fig. 22), thus representing a subtribe. This new subtribe is diagnosed by a combination of the following characters, as given for the *Jamides* section by Eliot (1973): male genitalia with vinculum lacking cephalad expansion, uncus directed ventrad, falces very long (nearly half of valva length), aedeagus longer than valva (usually by a third or more), valva deeply bilobed; forewing veins SC and R_1 are not fused for any distance, but connected with a short cross-vein. A combination of the following nuclear genomic base pairs is diagnostic: cce23510.3.2:T93C, cce23510.3.2:A432G, cce1568.2.4:A5519G, cce1568.2.4:A6856C, cce10823.2.3:T258C.

Genera included. Only the type genus.

Parent Taxon. Tribe Polyommatini Swainson, 1827.

Comment. The same name was proposed as a *nomen nudum* (fails ICZN Art. 13.) by Koçak (1996) and then published in a pioneering study by Stradomsky (2016) without explicitly indicating that the name was intentionally new (fails ICZN Art. 16.1.) and not stating what the type genus of this taxon was (fails ICZN Art. 16.2.). This name for the subtribe already discovered by Koçak and Stradomsky and confirmed by our genomic analysis is simply formalized here to comply with the ICZN Code (ICZN [International Commission on Zoological Nomenclature] 1999).

Fameganina Grishin, new subtribe
http://zoobank.org/07D24435-1EAD-4C80-9350-0A1FA6003972

Type genus. *Famegana* Eliot, 1973.

Definition. The lineage with *Famegana* (type species *Lycaena alsulus* Herrich-Schäffer, 1869, which is a junior subjective synonym of *Lycaena nisa* Wallace, 1866) is sister to Zizeeriina Chapman, 1910 with moderate confidence (Fig. 22). Because the confidence of this grouping is not the highest and because this lineage originates at the tree level of subtribes, it represents a subtribe. This new subtribe is diagnosed by a combination of the following characters, as given for the *Famegana* section by Eliot (1973): in male genitalia, tegumen and uncus bulky, falces stout and nearly rigidly connected, uncus lobes terminally pointed and slightly downturned; veins SC and R_1 touch each other over a short distance, eyes not hairy, palpi with bristles. A combination of the following nuclear genomic base pairs is diagnostic: cce1088.12. 3:A100T, cce1088.12.3:G102A, cce18.45.4:G1256T, cce18.45.4:G1255A, cce10490.1.2:T1933A.

Genera included. Only the type genus.

Parent Taxon. Tribe Polyommatini Swainson, 1827.

Comment. The same name was proposed as a *nomen nudum* (fails ICZN Art. 13.) by Koçak & Seven (1997) and then published in a pioneering study by Stradomsky (2016) without explicitly indicating that the name was intentionally new (fails ICZN Art. 16.1.) and not stating what the type genus of this taxon was (fails ICZN Art. 16.2.). This name for the subtribe already discovered by Koçak& Seven and Stradomsky and confirmed by our genomic analysis is simply formalized here to comply with the ICZN Code (ICZN [International Commission on Zoological Nomenclature] 1999).

Oboroniina Grishin, new subtribe
http://zoobank.org/FB96541D-672A-41A6-9C47-2EDAADEC0D60

Type genus. *Oboronia* Karsch, 1893.

Definition. The clade with *Oboronia* (type species *Oboronia staudingeri* Hemming, 1960, which is a junior subjective synonym of *Plebeius punctatus* Dewitz, 1879) is placed within the "crown group" of Polyommatini Swainson, 1827 without strongly supported phylogenetic affinity to any subtribe (Fig. 22) and therefore represents a subtribe of its own. This new subtribe is diagnosed by a combination of the following characters, as given for the *Euchrysops* section by Eliot (1973): male genitalia with long falces, vinculum broadening in the middle in lateral view, long and narrow valva, massive rod-shaped aedeagus with anterior ductus entrance; veins SC and R_1 not fused. A combination of the following nuclear genomic base pairs is diagnostic: cce349.2.1:C166A, cce349.2.1:A167T, cce935.8.2:A66G, cce2073.8.1: A230G, cce178.15.6:A190G.

Genera included. The type genus (i.e., *Oboronia* Karsch, 1893), *Euchrysops* Butler, 1900, *Lepidochrysops* Hedicke, 1923, *Orachrysops* Vári, 1986, and *Thermoniphas* Karsch, 1895.

Parent Taxon. Tribe Polyommatini Swainson, 1827.

Comment. The same name was published in a pioneering study by Stradomsky (2016) without explicitly indicating that the name was intentionally new (fails ICZN Art. 16.1.) and not stating what the type genus of this taxon was (fails ICZN Art. 16.2.). This name for the subtribe already discovered by Stradomsky and confirmed by our genomic analysis is simply formalized here to comply with the ICZN Code (ICZN [International Commission on Zoological Nomenclature] 1999).

Uranothaumatina Grishin, new subtribe

http://zoobank.org/57D2B8F3-36FA-4457-88B2-FC99DADC2EF8

Type genus. *Uranothauma* Butler, 1895.

Definition. The lineage with *Uranothauma* (type species *Uranothauma crawshayi* Butler, 1895) is confidently placed as sister to Scolitantidina Tutt, 1907 (Fig. 22), but it was not traditionally included in the latter subtribe. Additionally, because it originates at the tree level corresponding to subtribes, it represents a subtribe. This new subtribe is a union of the *Uranothauma* and *Phlyaria* sections of Eliot (1973), who listed characters for them, and is diagnosed as follows (see also Stradomsky (2016) for genitalia illustrations): in male genitalia, saccus absent, falces developed, as long as tegumen with uncus, vinculum expanded in the middle in lateral view, aedeagus shorter than valva, rod-shaped with ductus entrance dorso-cephalad, valva elongated, undivided; veins SC and R_1 touch each other or fuse at least for some distance, eyes hairy, palpi hairy or bristly. A combination of the following nuclear genomic base pairs is diagnostic: cce993.29.2:A515G, cce103.22.12:A47G, cce462.35.1:G193T, cce912.1.1:C56A, cce1162.12.1:G739A.

Genera included. The type genus (i.e., *Uranothauma* Butler, 1895) and *Phlyaria* Karsch, 1895.

Parent Taxon. Tribe Polyommatini Swainson, 1827.

Comment. The same name was published in a pioneering study by Stradomsky (2016) without explicitly indicating that the name was intentionally new (fails ICZN Art. 16.1.) and not stating what the type genus of this taxon was (fails ICZN Art. 16.2.). This name for the subtribe already discovered by Stradomsky and confirmed by our genomic analysis is simply formalized here to comply with the ICZN Code (ICZN [International Commission on Zoological Nomenclature] 1999).

Higher classification of Lycaenidae to the subtribal level

Based on our genome-scale phylogeny (Figs. 20–22) complemented with other studies (Talavera et al. 2012; Boyle et al. 2015; Robbins et al. 2022; Boyle et al. 2023; Kawahara et al. 2023), we propose the following provisional classification of Lycaenidae into subfamilies, tribes, and subtribes. We partition the family into eight subfamilies. If no tribes and subtribes are listed for a subfamily, we consider that subfamily to be monotypic. If no subtribes are listed for a tribe, we consider that tribe to be monotypic. The type genus name for each taxon is given in parentheses. New taxa and status changes are shown in red font. Synonymy is not provided.

Family **Lycaenidae** [Leach], [1815] (*Lycaena* [Fabricius], 1807)

Subfamily **Curetinae** Distant, 1884 (*Curetis* Hübner, [1819])

Subfamily **Liphyrinae** Doherty, 1889 (*Liphyra* Westwood, [1864]), **stat. rest.**

Subfamily **Miletinae** Reuter, 1896 (*Miletus* Hübner, [1819])

    Tribe **Lachnocnemini** Clench, 1955 (*Lachnocnema* Trimen, 1887)

    Tribe **Miletini** Reuter, 1896 (*Miletus* Hübner, [1819])

        Subtribe Miletina Reuter, 1896 (*Miletus* Hübner, [1819])

        Subtribe Megalopalpina Grishin, **subtrib. n.** (*Megalopalpus* Röber, 1886)

    Tribe **Spalgini** Toxopeus, 1929 (*Spalgis* F. Moore, 1879)

        Subtribe Spalgina Toxopeus, 1929 (*Spalgis* F. Moore, 1879)

        Subtribe Tarakina Eliot, 1973, **stat. rev.** (*Taraka* Doherty, 1889)

Subfamily **Poritiinae** Doherty, 1886 (*Poritia* F. Moore, [1866])

    Tribe **Liptenini** Röber, 1892 (*Liptena* Westwood, [1851])

        Subtribe Durbaniina Clench, 1955 (*Durbania* Trimen, 1862)
        Subtribe Pentilina Aurivillius, 1914 (*Pentila* Westwood, [1851])
        Subtribe Liptenina Röber, 1892 (*Liptena* Westwood, [1851]); includes Mimacraeina Stempffer, 1961
        Subtribe Iridanina Clench, 1965 (*Iridana* Aurivillius, 1920)
        Subtribe Epitolina Jackson, 1962 (*Epitola* Westwood, [1851])
        Subtribe Cooksoniina Sáfián, Boyle & Pierce, 2023 (*Cooksonia* H. H. Druce, 1905)

    Tribe **Poritiini** Doherty, 1886 (*Poritia* F. Moore, [1866])

Subfamily **Aphnaeinae** Distant, 1884 (*Aphnaeus* Hübner, [1819]); not monophyletic with Theclinae!

    Tribe **Axiocersini** Grishin, **trib. n.** (*Axiocerses* Hübner, [1819])

    Tribe **Cigaritini** Grishin, **trib. n.** (*Cigaritis* Donzel, 1848)

        Subtribe Pseudaletidina Grishin, **subtrib. n.** (*Pseudaletis* H. H. Druce, 1888)
        Subtribe Cigaritina Grishin (*Cigaritis* Donzel, 1848)

    Tribe **Aphnaeini** Distant, 1884 (*Aphnaeus* Hübner, [1819])

        Subtribe Aloeidina Grishin, **subtrib. n.** (*Aloeides* Hübner, [1819])
        Subtribe Phasisina Grishin, **subtrib. n.** (*Phasis* Hübner, [1819])
        Subtribe Aphnaeina Distant, 1884 (*Aphnaeus* Hübner, [1819])

Subfamily **Lycaeninae** [Leach], [1815] (*Lycaena* [Fabricius], 1807)

Subfamily **Theclinae** Swainson, 1830 (*Thecla* [Fabricius], 1807)

    Tribe **Theclini** Swainson, 1830 (*Thecla* [Fabricius], 1807)

    Tribe **Surendrini** Koçak & Seven, 1997, **stat. nov.** (*Surendra* F. Moore, 1879)

    Tribe **Arhopalini** Bingham, 1907 (*Arhopala* Boisduval, 1832)

    Tribe **Drinini** Grishin, **trib. n.** (*Drina* Nicéville, 1890)

    Tribe **Candalidini** Eliot, 1973 (*Candalides* Hübner, [1819])

    Tribe **Hypochrysopini** Grishin, **trib. n.** (*Hypochrysops* C. Felder & R. Felder, 1860)

    Tribe **Luciini** Waterhouse & Lyell, 1914 (*Lucia* W. Swainson, 1833)

    Tribe **Ogyrini** Waterhouse & Lyell, 1914 (*Ogyris* Angas, 1847)

    Tribe **Jalmenini** Grishin, **trib. n.** (*Jalmenus* Hübner, 1818)

    Tribe **Pseudalmenini** Grishin, **trib. n.** (*Pseudalmenus* H. H. Druce, 1902)

    Tribe **Amblypodiini** Doherty, 1886 (*Amblypodia* Horsfield, 1829)

    Tribe **Myrinini** Toxopeus, 1929, **stat. nov.** (*Myrina* [Fabricius], 1807)

    Tribe **Cheritrini** Swinhoe, 1910 (*Cheritra* F. Moore, 1881)

        Subtribe Cheritrina Swinhoe, 1910 (*Cheritra* F. Moore, 1881)
        Subtribe Horagina Swinhoe, 1910, **stat. nov.** (*Horaga* F. Moore, 1881)
        Subtribe Loxurina Swinhoe, 1910, **stat. nov.** (*Loxura* Horsfield, [1829])

    Tribe **Iolaini** Riley, 1958 (*Iolaus* Hübner, [1819])

    Tribe **Catapaecilmatini** Eliot, 1973 (*Catapaecilma* Butler, 1879)

    Tribe **Zesiusini** Swinhoe, 1912 (*Zesius* Hübner, [1819])

    Tribe **Tomarini** Eliot, 1973 (*Tomares* Rambur, 1840)

    Tribe **Rapalini** Grishin, **trib. n.** (*Rapala* F. Moore, 1881)

        Subtribe Rapalina Grishin (*Rapala* F. Moore, 1881)
        Subtribe Pilodeudorigina Grishin, **subtrib. n.** (*Pilodeudorix* H. H. Druce, 1891)

    Tribe **Deudorigini** Doherty, 1886 (*Deudorix* Hewitson, 1863)

    Tribe **Eumaeini** Doubleday, 1847 (*Eumaeus* Hübner, [1819])

        Subtribe Eumaeina Doubleday, 1847 (*Eumaeus* Hübner, [1819])
        Subtribe Rhammina Prieto & Busby, 2022 (*Rhamma* K. Johnson, 1992)
        Subtribe Timaetina Busby & Prieto, 2022 (*Timaeta* K. Johnson, Kruse & Kroenlein, 1997)
        Subtribe Atlidina Martins & Duarte, 2022 (*Atlides* Hübner, [1819])
        Subtribe Evenina Faynel & Grishin, 2022 (*Evenus* Hübner, [1819])
        Subtribe Jantheclina Robbins & Faynel, 2022 (*Janthecla* Robbins & Venables, 1991)
        Subtribe Paiwarriina Lamas & Robbins, 2022 (*Paiwarria* Kaye, 1904)
        Subtribe Cupatheclina Lamas & Grishin, 2022 (*Cupathecla* Bálint, 2005)
        Subtribe Parrhasiina Busby & Robbins, 2022 (*Parrhasius* Hübner, [1819])
        Subtribe Ipideclina Martins & Grishin, 2022 (*Ipidecla* Dyar, 1916)
        Subtribe Calycopidina Duarte & Robbins, 2010 (*Calycopis* Scudder, 1876)
        Subtribe Strymonina Tutt, 1907 (*Strymon* Hübner, 1818)
        Subtribe Strephonotina K. Johnson, Austin, Le Crom & Salazar, 1997 (*Strephonota* K. Johnson et al., 1997)
        Subtribe Trichonidina Duarte & Faynel, 2022 (*Trichonis* Hewitson, 1865)

Subtribe Callophryidina Tutt, 1907 (*Callophrys* Billberg, 1820)

Subfamily **Polyommatinae** Swainson, 1827 (*Polyommatus* Latreille, 1804)
Tribe **Oxylidini** Eliot, 1973 (*Oxylides* Hübner, [1819])
Subtribe Oxylidina Eliot, 1973 (*Oxylides* Hübner, [1819])
Subtribe Hemiolaina Grishin, **subtrib. n.** (*Hemiolaus* Aurivillius, 1922)
Tribe **Remelanini** Eliot, 1973 (*Remelana* F. Moore, 1884)
Tribe **Hypolycaenini** Swinhoe, 1910 (*Hypolycaena* C. Felder & R. Felder, 1862)
Tribe **Lycaenesthini** Toxopeus, 1929 (*Lycaenesthes* F. Moore, 1866)
Tribe **Hypotheclini** Eliot, 1973 (*Hypothecla* G. Semper, 1890)
Subtribe Hypotheclina Eliot, 1973 (*Hypothecla* G. Semper, 1890)
Subtribe Cupidopsina Grishin, **subtrib. n.** (*Cupidopsis* Karsch, 1895)
Tribe **Polyommatini** Swainson, 1827 (*Polyommatus* Latreille, 1804)
Subtribe Niphandina Sibatani & Ito, 1942, **stat. conf.** (*Niphanda* F. Moore, 1875)
Subtribe Theclinesthina Grishin, **subtrib. n.** (*Theclinesthes* Röber, 1891)
Subtribe Azanina Grishin, **subtrib. n.** (*Azanus* F. Moore, 1881)
Subtribe Unina Grishin, **subtrib. n.** (*Una* Nicéville, 1890)
Subtribe Danina Koçak & Seven, 1997 (*Danis* [Fabricius], 1807)
Subtribe Ionolycina Grishin, **subtrib. n.** (*Ionolyce* Toxopeus, 1929)
Subtribe Pithecopina Grishin, **subtrib. n.** (*Pithecops* Horsfield, 1828)
Subtribe Zizulina Grishin, **subtrib. n.** (*Zizula* Chapman, 1910)
Subtribe Brephidiina Stempffer, 1957 (*Brephidium* Scudder, 1876)
Subtribe Celastrinina Tutt, 1907 (*Celastrina* Tutt, 1906)
Subtribe Jamidina Grishin, **subtrib. n.** (*Jamides* Hübner, [1819])
Subtribe Zizeeriina Chapman, 1910 (*Zizeeria* Chapman, 1910)
Subtribe Fameganina Grishin, **subtrib. n.** (*Famegana* Eliot, 1973)
Subtribe Catochrysopina Toxopeus, 1929 (*Catochrysops* Boisduval, 1832)
Subtribe Oboroniina Grishin, **subtrib. n.** (*Oboronia* Karsch, 1893)
Subtribe Castaliina Distant, 1884 (*Castalius* Hübner, [1819])
Subtribe Scolitantidina Tutt, 1907 (*Scolitantides* Hübner, [1819])
Subtribe Uranothaumatina Grishin, **subtrib. n.** (*Uranothauma* Butler, 1895)
Subtribe Actizerina Koçak, 1996 (*Actizera* Chapman, 1910)
Subtribe Leptotina Wagener, 1995 (*Leptotes* Scudder, 1876)
Subtribe Lampidina Tutt, 1907 (*Lampides* Hübner, [1819])
Subtribe Everina Tutt, 1907 (*Everes* Hübner, [1819])
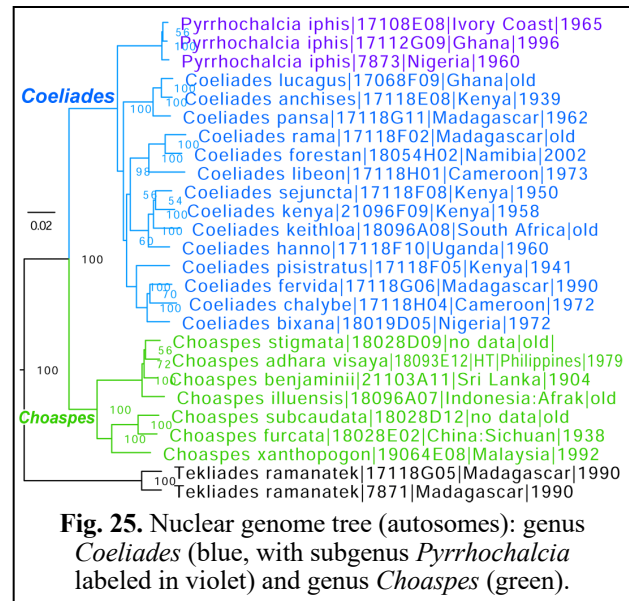Subtribe Polyommatina Swainson, 1827 (*Polyommatus* Latreille, 1804)

Our classification of Polyommatini Swainson, 1827 compared to that by Stradomsky (2016)

In his pioneering work based on limited DNA sequence data and careful genitalic comparison, Stradomsky (2016) proposed to partition the tribe Polyommatini into 22 subtribes. Stradomsky's classification fares well compared to our genomic results (see above), and his study is impressive in its insight. Out of our 23 subtribes, 20 match Stradomsky's in names, and one, Celastrinina Tutt, 1907, was referred to by its junior subjective synonym, Lycaenopsina Swinhoe, 1910. The remaining two subtribes, Ionolycina **subtrib. n.** and Unina **subtrib. n.**, were placed by Stradomsky into his Danina Koçak & Seven, 1997 and "Azanina," respectively. *Una* Nicéville, 1890 cannot belong to "Azanina," because it is in the clade with *Danis* [Fabricius], 1807 and not with *Azanus* F. Moore, 1881 (see Fig. 22 and Kawahara et al. (2023)). While it is indeed possible to unify these four groups into a single subtribe, Danina, genetic differentiation within this subtribe would be larger than in other subtribes in Polyommatini (Fig. 22). Therefore, dividing the group into four subtribes brings the classification in line with the genetic differentiation within other Polyommatini subtribes. Finally, Stradomsky's "Cacyreina" is merged into our Lampidina Tutt, 1907 due to genetic similarities, and Stradomsky's phylogeny based on a small number of gene markers is poorly supported around these taxa. We put names of subtribes used by Stradomsky in quotes because they were proposed somewhat informally: authorship of previously published names was not indicated, and for the names we could not find in previous publications, Stradomsky did not explicitly indicate that they were intentionally new (fails ICZN Art. 16.1.) and did not specify what their type genera were (fails ICZN Art. 16.2.). Moreover, it remains unclear from the text of
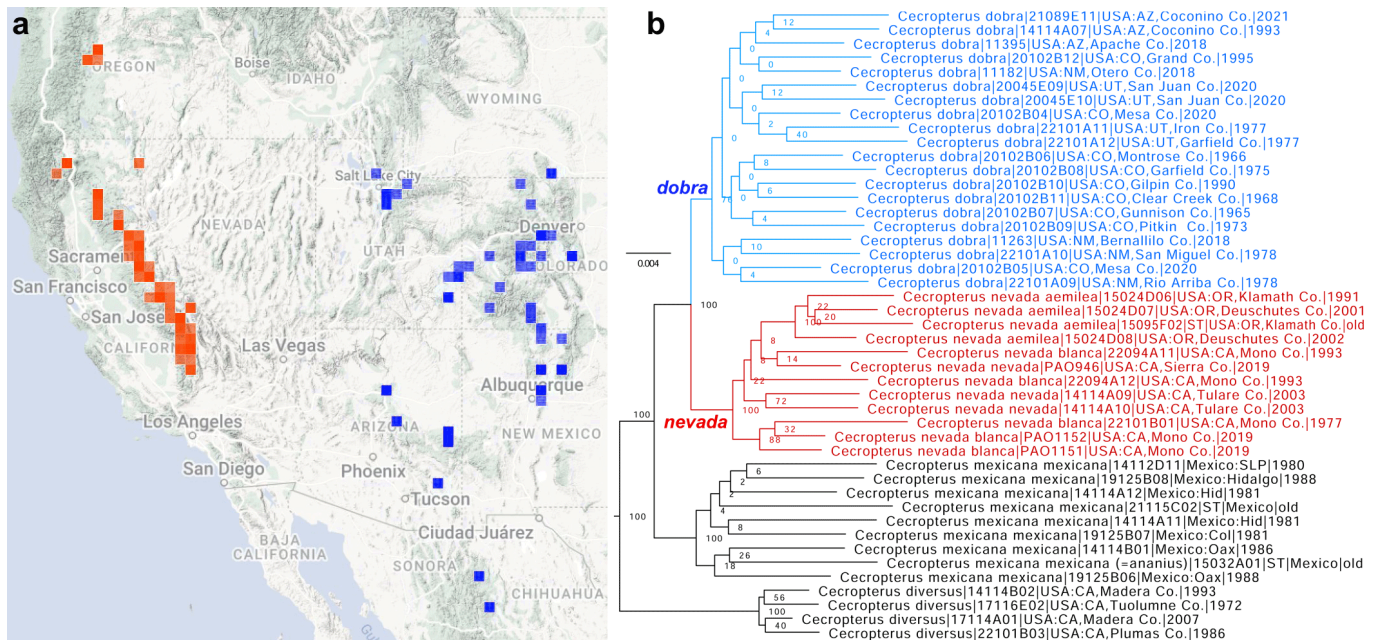
his article which names Stradomsky considered new in the sense of the ICZN Code (if any) and if he intended to propose new ICZN-compliant names in his work.

Paralycaeides Nabokov, 1945 is a subgenus of *Itylos* Draudt, 1921 and *Eldoradina* Balletto, 1993 of *Nabokovia* Hemming, 1960

Inspection of genomic trees reveals that two pairs of genera: (1) *Itylos* Draudt, 1921 (type species *Cupido speciosa* Staudinger, 1894, which is a junior subjective synonym of *Lycaena titicaca* Weymer, 1890) and *Paralycaeides* Nabokov, 1945 (type species *Itylos inconspicua* Draudt, 1921) and (2) *Nabokovia* Hemming, 1960 (type species *Thecla faga* Dognin, 1895 and *Eldoradina* Balletto, 1993 (type species *Nabokovia* (*Eldoradina*) *cyanea* Balletto, 1993) are closely related to each other in each pair (Fig. 23): COI barcode difference of 5.9%–6% (39–40 bp) in each pair. Furthermore, at least one genus in each pair consists of a small number of species.

Fig. 23. Nuclear genome tree (autosomes): genus *Itylos* (red, subgenus *Paralycaeides* in magenta) and genus *Nabokovia* (blue, subgenus *Eldoradina* in violet color).

Therefore, we propose to treat the junior name in each pair as a subgenus name: *Paralycaeides* Nabokov, 1945 of *Itylos* Draudt, 1921 and *Eldoradina* Balletto, 1993 of *Nabokovia* Hemming, 1960.

Shijimia Matsumura, 1919 is confirmed as a valid genus with *Shijimia potanini* Alphéraky, 1889, new combination

Genomic sequencing and analysis of representatives of the subtribe Everina Tutt, 1907 (type genus *Everes* Hübner, [1819])) reveals that *Shijimia* Matsumura, 1919 (type species *Lycaena moorei* Leech, 1889) may not be monophyletic with *Cupido* Schrank, 1801 (type species *Papilio minimus* Fuessly, 1775) and

instead may be sister to *Bothrinia* Chapman, 1909 (type species *Cyaniris chennellii* de Nicéville, [1884]) (Fig. 24), confirming that it is meaningful to treat *Shijimia* as a valid genus. We sequenced one of the two syntypes of *Everes umbriel* Doherty, 1889 (type locality Tenasserim Valley) currently treated as a junior subjective synonym (or subspecies) of *Lycaena potanini* Alphéraky, 1889 (type locality in China: Gansu Province) in the genus *Tongeia* Tutt, 1908 (type species *Lycaena fischeri* Eversmann, 1843), and found that it is not monophyletic with *Tongeia fischeri*, but is closely related to *Shijimia*

Fig. 24. Nuclear genome tree (autosomes) of Everina representatives: genera *Cupido* (green), *Shijimia* (red), *Bothrinia* (violet), and *Tongeia* (blue).

Matsumura, 1919 (type species *Lycaena moorei* Leech, 1889) (Fig. 24). Therefore, we propose a new combination: *Shijimia potanini* (Alphéraky, 1889), **comb. nov**.

Family Hesperiidae Latreille, 1809

Pyrrhochalcia Mabille, 1904 is a subgenus of *Coeliades* Hübner, 1818

Although immediately distinguishable by its much larger size, black wings with metallic-green shine (and broad green streaks in females) above, and shiny cyan-green-olive hindwings beneath, *Pyrrhochalcia* Mabille, 1904 (type and the only species *Papilio iphis* Drury, 1773) was recognized as a close relative of *Coeliades* Hübner, 1818 (type species *Papilio forestan* Stoll, 1782) by Evans (1937) and placed next to *Pyrrhiades* Lindsey & Miller, 1965 (type species *Papilio lucagus* Cramer, 1777)—currently within

Coeliades—by Chiba (2009) in his key, differing by the relative positions of vein origins on hindwing. Moreover, some species of *Coeliades* are patterned similarly, although without extensive green coloration on ventral hindwing: *C. lucagus* (Cramer, 1777) and *C. aeschylus* (Plötz, 1884) (both formerly in *Pyrrhiades*). Our genomic tree and recently published phylogeny (Toussaint et al. 2021) support this close relationship between *Pyrrhochalcia* and *Coeliades* by placing the former as a close sister of the latter without prominent separation between them (Fig. 25). Genetic differentiation within *Coeliades* even after including *Pyrrhochalcia* is approximately the same as that within the genus *Choaspes* F. Moore, 1881 (type species *Hesperia* (*Thymele*) *benjaminii* Guérin-Méneville, 1843) (Fig. 25 blue vs. green). Therefore, we propose that *Pyrrhochalcia* Mabille, 1904, **stat. nov.** is a subgenus of *Coeliades* Hübner, 1818.

Fig. 25. Nuclear genome tree (autosomes): genus *Coeliades* (blue, with subgenus *Pyrrhochalcia* labeled in violet) and genus *Choaspes* (green).

Cecropterus (*Thorybes*) *nevada* (Scudder, 1872) is restricted to OR, CA, and NV and *Cecropterus* (*Thorybes*) *dobra* (Evans, 1952) is found eastward in the US

Genomic sequencing of specimens from the northeastern part of the range of the *Cecropterus* (*Thorybes*) *mexicana* species group that consists of three species: *Cecropterus* (*Thorybes*) *nevada* (Scudder, 1872), *Cecropterus* (*Thorybes*) *dobra* (Evans, 1952), and *Cecropterus* (*Thorybes*) *mexicana* (Herrich-Schäffer, 1869) reveals that all of them are *C. dobra*, which is genetically uniform throughout its range (Fig. 26). Therefore, *C. nevada* is restricted to the westernmost part of the USA (Oregon, California, and Nevada) and is separated from *C. dobra* by a wide gap in its distribution, according to iNaturalist observations (2023) (Fig. 26).

Fig. 26. *Cecropterus* (*Thorybes*) *dobra* (blue) and *Cecropterus* (*Thorybes*) *nevada* (red): **a)** a distribution map made on the basis of iNaturalist (2023) observations: iNaturalist maps for *C. dobra* and *C. nevada* were superimposed and merged in Photoshop and re-colored (CC BY-NC 4.0 https://creativecommons.org/licenses/by-nc/4.0/), the map does not refer to sequenced specimens, records were not checked and some may be misidentifications; **b)** nuclear genome tree (autosomes) showing that specimens we sequenced from several localities in Utah, Colorado, New Mexico, and Arizona are *C. dobra*.

Fig. 27. Phylogenetic trees of *Cecropterus* (*Thorybes*) *pylades* species group inferred from protein-coding regions of **a)** the Z chromosome (best for species delimitation) and **b)** the mitochondrial genome. Different species are shown in different colors: *C. floridianus* **sp. n.** (red), *C. pylades* (green), *C. indistinctus* **stat. nov.** (cyan), *C. rockiensis* **sp. n.** (purple), *C. albosuffusa* **stat. nov.** (blue), *C. oaxacensis* **sp. n.** (orange), and *C. drusius* (black). Primary type specimens are labeled in magenta (except that *C. oaxacensis* is left in orange as the sole representative of its species).

Cecropterus albosuffusa (H. Freeman, 1943) and *Cecropterus indistinctus* (Austin & J. Emmel, 1998) are species distinct from *Cecropterus pylades* (Scudder, 1870)

Genomic comparison of *Cecropterus* Herrich-Schäffer, 1869 (type species *Cecrops zarex* Hübner, 1818) reveals close relationship between *Cecropterus* (*Thorybes*) *pylades* (Scudder, 1870) (type locality in USA: Massachusetts) and *Cecropterus* (*Thorybes*) *drusius* (W. H. Edwards, [1884]) (type locality in southern Arizona) that are unified by the presence of costal fold in males (Evans 1955). We regard them as the *C. pylades* species group (Fig. 27). Genomic trees (the Z chromosome and the mitogenome) confirm that *C. drusius* with its distinctive genitalia (Fig. 30q) is sister to all others but reveal that the entity currently treated as a single species *C. pylades* consists of several genetically differentiated clades (Fig. 27). The Z chromosome (Fig. 27a) and the mitochondrial genome (Fig. 27b) trees show identical strongly supported topology between the clades (but not within clades, where the subtrees are comb-like

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due to genetic similarity and gene exchange) and placement of specimens into them, thus increasing the confidence in the results due to this uncommon congruence between nuclear and mitochondrial trees.

The extent of genetic differentiation suggests that the clades within *C. pylades* represent distinct species (Cong et al. 2019a). We find that *Cecropterus pylades albosuffusa* (H. Freeman, 1943) (type locality USA: Texas, Ft. Davis) forms a clade distant from the nominotypical *C. pylades* with F_{st}/G_{min} of 0.39/0.001 and COI barcode difference of 2.1% (14 bp). Similarly, the westernmost *Cecropterus pylades indistinctus* (Austin & J. Emmel, 1998) (type locality in USA: California: San Diego Co.) is separated from the nominotypical *C. pylades* with F_{st}/G_{min} of 0.41/0.002 and COI barcode difference of 1.7% (11 bp). Therefore, we propose treating *Cecropterus* (*Thorybes*) *albosuffusa* (H. Freeman, 1943), **stat. nov.** and *Cecropterus* (*Thorybes*) *indistinctus* (Austin & J. Emmel, 1998), **stat. nov.** as species-level taxa, not subspecies of *C. pylades*. Hence, no subspecies are recognized in the *C. pylades* species group. Furthermore, three additional clades with strong genetic differentiation do not have names and represent new species. These three new species are described below. Finally, we note that the speciation scenario in the "crown" subgroup of the *C. pylades* group consisting of four USA species: Floridian, eastern, west-coastal, and central (Fig. 27 red, green, cyan, and purple) parallels that of the *Erynnis brizo* (Boisduval & Le Conte, [1837]) species group as laid out by Burns (2020).

Cecropterus (*Thorybes*) *rockiensis* Grishin, new species
http://zoobank.org/7CC2D85B-497D-4A81-9486-82434CCBE143
(Figs. 27 part, 28, 29 part, 30k, l)

Definition and diagnosis. Both the Z chromosome and the mitogenome trees reveal partitioning of western US populations previously assigned to *Cecropterus* (*Thorybes*) *pylades* (Scudder, 1870) (type locality in USA: Massachusetts) into two clades: *Cecropterus* (*Thorybes*) *indistinctus* (Austin & J. Emmel, 1998), **stat. nov.** (type locality in the USA: California: San Diego Co., holotype sequenced as NVG-17109A08) and a clade consisting of specimens from and around the Rocky Mountains region in the US, not associated with any available names (Fig. 27 cyan and purple). The F_{st}/G_{min} between the two clades are 0.37/0.004, and their COI barcodes differ by 1.1% (7 bp). Therefore, the Rocky Mountains clade represents a species-level taxon. This new species is generally similar in appearance to its closest relative, *C. indistinctus*, in the following combination of characters: stronger checkered fringes (especially on the forewing), ventral wing surface distally paler gray-brown, but not strongly overscaled with white, on average smaller hyaline spots, and less rounded forewings; and differs from it by more prominently checkered fringes, paler ground color, stronger expressed darker framing around (or in place of) hyaline forewing spots, better defined ventral hindwing bands, typically larger hyaline spots and specimen size. In male genitalia, uncus arms are thicker and not as widely separated as in *C.* (*Thorybes*) *albosuffusa* (H. Freeman, 1943), **stat. nov.** (type locality USA: Texas, Ft. Davis), more angled than rounded at the base between them; similar to *C. pylades* and *C. indistinctus* and differ from them by somewhat wider

Fig. 28. Holotype of *Cecropterus* (*Thorybes*) *rockiensis* **sp. n.** in dorsal (left) and ventral (right) views, data in text.

separation of uncus arms, rather parallel than slightly converging distad and usually longer compared to tegumen than in the other two species, a notch between ampulla and harpe is typically shallower and wider, harpe is longer, more upcurved. Definitive identification is provided by DNA, and a combination of the following characters is diagnostic in nuclear genome: aly5196.9.2:C915T, aly536.8.1:C750T, aly1259.10.2:A1122G, aly276561.5.1:G2469A, aly5021.6.4:A1940G and in the COI barcode: A217G, T460C, T596C, A637A.

Barcode sequence of the holotype: Sample NVG-22099H03, GenBank OR578714, 658 base pairs:

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AACTTTATATTTTATTTTCGGAATTTGAGCAGGATTAATTGGAACTTCTTTAAG
TTTACTTATTCGAACTGAATTAGGAACTCCAGGATCTTTAATTGGAGATGATCA
AATTTATAATACTATTGTCACAGCTCATGCTTTTATTATAATTTTCTTTATAGT
TATACCTATTATAATTGGAGGATTTGGAAATTGATTAATTCCCCCTTATACTAGG
GGCTCCTGACATAGCTTTTCCTCGTATAAATAATATAAGATTTTGATTATTACC
TCCATCTTTAACTCTTTTAATTTCAAGAAGTATTGTTGAAAATGGAGCAGGTAC
TGGATGAACTATTTACCCCCCCTTTATCTTCTAATATTGCTCATCAAGGAGCTTC
AGTAGATTTAGCAATTTTTTCTTTACATCTTGCTGGAATTTCTTCAATTTTAGG
AGCTATTAATTTTATTACAACTATTATCAATATACGAATTAATAATTTATCATT
TGATCAAATACCATTATTTATTTGAGCTGTTGGAATTACAGCTTTATTACTTTTT
ACTTTCATTACCTGTTTTAGCTGGAGCTATTACTATATTATTAACTGATCGAAA
CCTAAATACTTCATTTTTTGATCCAGCAGGTGGAGGAGATCCAATTTTATATCA
ACATTTATTT
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Type material. Holotype: ♂ deposited in the California Academy of Sciences, San Francisco, CA, USA [CAS], illustrated in Fig. 28, bears six printed (other text but "COLO" on the first label is handwritten) labels: five white [COLO. V-24-79 | Jefferson Co. | Clear Cr. Cyn.], [Ray E. Stanford | collector], [Collection of | C.D.MacNeill], [DNA

Fig. 29. A map of sequenced specimens from the *Cecropterus* (*Thorybes*) *pylades* group. Different species are shown in different symbols of different colors: *C. floridianus* **sp. n.** (larger red circles), *C. pylades* (smaller green circles), *C. indistinctus* **stat. nov.** (cyan diamonds), *C. rockiensis* **sp. n.** (purple squares), *C. albosuffusa* **stat. nov.** (smaller dark blue downturned triangles), and *C. oaxacensis* **sp. n.** (larger orange upturned triangle) and labeled on the map near their type localities. Type localities for valid names are indicated by tiny circles placed inside symbols, or (if no specimens from these localities were sequenced) by a small circle framed with the color of the taxon (for *C. pylades* only).

sample ID: | NVG-22099H03 | c/o Nick V. Grishin], [{QR Code} CASENT | 8566837], and one red [HOLOTYPE ♂ | Cecropterus (Thorybes) | rockiensis Grishin]. **Paratypes:** 20♂♂ 7♀♀: 1♀ Montana, Yellowstone Co., Billings, 5-Jun-1948, Neil Euting leg. (NVG-22099H04, CASENT8566838) [CAS]; 2♂♂ Nebraska, Sioux Co., Monroe Cyn., 6 mi. N of Harrison, 25-Jun-1983, S. M. Spomer leg. (NVG-22064H01 & H02); Utah: Salt Lake Co.: 1♂ Mill Creek Canyon, 28-Jun-1967, C. J. Callaghan leg. (NVG-22099H07, CASENT8566841) [CAS]; Salt Lake, City Creek Canyon: 1♂ 15-Jun-1930, Lloyd M. Martin leg. (NVG-22094A09) [LACM]; 1♂ 9-Jun-1946, L. I. Hewes leg. (NVG-22099H08, CASENT 8566842) [CAS]; Utah Co.: 1♂ Provo Canyon, 14-Jun-1947, William A. Hammer leg. (NVG-22099G12, CASENT8566834) [CAS]; 1♂ Mt. Timpanogos, 5.6 mi W of Jct. Hwy 189 & 92 on 92, 22-Jul-1946, C. D. MacNeill leg. (NVG-22099H09, CASENT8566843) [CAS]; 1♂ Beaver Co., East Fork Baker Canyon, SH153, Tushar Mts, N side of Beaver Canyon, larva collected on 1-Jul-2022, eclosed 7-Dec-2022, Todd Stout leg. (NVG-22068D07); 1♀ Washington Co., 11-May-1977, D. F. Shillingburg leg. (NVG-22099H06, CASENT8566840) [CAS]; 1♀ Zion National Park, 15-Jun-1928, T. Craig leg. (NVG-22099H10, CASENT8566844) [CAS]; San Juan Co.: 1♀ La Sal Mts., Pack Creek day use area, 31-May-2016, Robb Hannawacker leg. (NVG-20045E07); 1♂ Abajo Mts., Indian Creek trail, el. 6400'-7400', 8-May-2020, Robb Hannawacker leg. (NVG-20045E08); Colorado: 1♂ Garfield Co., Glenwood Cyn, el. 6200', 8-Jun-1977, Ray E. Stanford leg. (NVG-22099H02, CASENT8566836) [CAS]; 1♂ Eagle Co., Fryingpan River, 10-Jun-1976, Ray E. Stanford leg. (NVG-22099H05, CASENT8566839) [CAS]; Boulder Co.: 1♀ Lefthand Canyon, 16-May-1954, Donald Eff leg. (NVG-22099H01, CASENT8566835) [CAS]; 1♂ Flagstaff Mtn., 15-Jun-1953, Donald Eff leg. (NVG-22094A08) [LACM]; New Mexico: 1♂

Fig. 30. Male genitalia of *Cecropterus* (*Thorybes*) *pylades* species group: **a–d)** *C. floridianus* **sp. n.** from USA, FL: **a)** NVG-22101A01, paratype, genitalia slide J. W. T. 25-34, data in text [CAS]; **b)** holotype, data in text; **c)** and **d)** from genitalia slides G11 and G14, respectively, by E. L. Bell, only valvae shown [AMNH]; **e–i)** *C. pylades* from USA: **e–g)** left valva in situ, N. V. Grishin, leg.: **e)** TX, Wise Co., LBJ National Grassland, 4-May-2008 and **f**, **g)** OK: Murray Co., 5 mi S of Davis, 23-Apr-2008; **h)** NVG-9288, AR, Montgomery Co., Ouachita National Forest, 6.5 air mi WNW of Oden, 6-Jul-2017, N. V. Grishin leg.; **i)** NJ, from genitalia slide G13 by E. L. Bell, only valvae shown [AMNH]; **j)** *C. indistinctus* **stat. nov.**, USA: CA, San Diego Co., El Cajon, 28-Apr-1934, Ray Hulbirt leg., genitalia slide J. W. T. 25-36 by J. W. Tilden [CAS]; **k, l)** *C. rockiensis* **sp. n.** paratypes from USA: **k)** NVG-11465 from AZ: Apache Co. and **l)** NVG-8970 from NM: Otero Co., data in text; **m–o)** *C. albosuffusa* **stat. nov.**: **m**, **n)** Mexico [TMMC]: **m)** NVG-22056A08, Coahuila, Zaragosa, C. J. Durden leg., 11-Apr-1976, genitalia vial NVG-22056A09 and **n)** NVG-22056A04, Nuevo Leon: Galeana, Cerro Potosi, C. J. Durden leg., 25-Jul-1981, genitalia vial NVG-22056A05; **o)** USA: AZ, Santa Rita Mts., 10-Jul-1941, J. W. Tilden leg. and genitalia slide J. W. T. 25-13 [CAS]; **p)** *C. oaxacensis* **sp. n.** holotype from Mexico: Oaxaca, data in text; **q)** *C. drusius* USA: AZ, from genitalia slide G47 by E. L. Bell, aedeagus (left) and valva (right) [AMNH]. Panels **b**, **h**, **k**, **l**, **n**, **p)** show complete genitalia in dorsal (above) and left lateral (below) views, and **m)** only left lateral view. Panels **a**, **j**, **o)** assemble genitalia parts from slides to display aedeagus (if detached, top left), detached valva (left), and the rest of the genital capsule in lateral view (right). All images are to scale.

Sandoval Co., Cibola National Forest, SH165 4.2 mi S of Placitas, GPS 35.2502, −106.4104, 14-May-2017, Qian Cong, Jing Zhang & Nick V. Grishin leg. (NVG-8800); 1♂ 1♀ Lincoln Co.,1.5 mi E of Capitan Gap Rd N water course, el.7000', 10-May-1981, J. McCaffrey leg. (NVG-15099H08 & H09) [FMNH]; 2♂♂ Otero Co., Lincoln National Forest, La Luz Canyon Rd., 4.8 air mi NE of High Rolls, GPS 32.9992, −105.7759, 21-May-2017, Qian Cong, Jing Zhang & Nick V. Grishin leg. (NVG-8970, Fig. 30l

& NVG-9057); <u>Arizona</u>: Coconino Co.: 1♂ 1♀ S rim of Grand Cyn, 10-Jun-1942, J. S. Garth leg. (NVG-22094A02 & A03) [LACM]; 1♂ Lockett Meadow, GPS 35.3605, −111.6208, 24-May-2021, Brian Banker leg. (NVG-21089E12); 1♂ Apache Co., Greens Peak area, Pipeline Spring at Fs117, GPS 34.1413, −109.5809, 25-May-2018, Jing Zhang & Nick V. Grishin leg. (NVG-11465, Fig. 30k); 1♂ Graham Co., Adam's Flat, GPS 32.6508, −109.8125, 23-Apr-2009, Mark Walker leg. (NVG-18037D10).

Type locality. USA: Colorado, Jefferson Co., Clear Creek Canyon.

Etymology. The name is given for the general area of the distribution of this species, which is in and around the Rocky Mountains (the Rockies), by fusing the Latin suffix -*ensis* (meaning "from place" or "of place") with the word "Rockies". The name is a masculine adjective in the nominative case.

English name. Rocky Mountains Cloudywing.

Distribution. Across the Rocky Mountains and neighboring states: confirmed from Montana, Nebraska, Utah, Colorado, New Mexico, and Arizona.

Cecropterus (*Thorybes*) *floridianus* Grishin, new species
http://zoobank.org/EA537AE1-E4FB-4C72-8615-D9BE2DE7336A
(Figs. 27 & 29 parts, 30a–d, 31)

Definition and diagnosis. Both the Z chromosome and the mitogenome trees reveal that eastern US populations previously assigned to *Cecropterus* (*Thorybes*) *pylades* (Scudder, 1870) (type locality in USA: Massachusetts) are not monophyletic, and populations from Florida form a clade sister to three species combined (*C. pylades*, *C. indistinctus*, and *C. rockiensis* **sp. n.**) (Fig. 27). Genetic differentiation between *C. pylades* and the Floridian populations is notable: F_{st}/G_{min} between the two clades are 0.24/0.003 and the COI barcode difference is 2.3%–2.4% (15–16 bp). Therefore, the Floridian clade represents a distinct species. This new species is similar in appearance to *C. pylades* in darker ground color, weaker checkered fringes (especially on forewing), weaker developed marginal pale overscaling on wings beneath, larger size, and rounder wings; and differs from it by darker appearance and generally smaller hyaline spots. In the male genitalia, most similar to *C. pylades*, e.g., uncus arms slightly converge distad, but valva is usually broader, the central bump on its costa is typically less pronounced (in lateral view), harpe is relatively shorter, broader, and straighter, less angled along the ventral margin, and uncus arms are usually shorter compared to tegumen (Fig. 30a–d). Definitive identification is provided by DNA and a combination of the following characters is diagnostic in nuclear genome: aly1409.4.2:G1779A, aly383.20.2:T1131A, aly3507.12.1:G3947C, aly383.21.1:A1654G, aly1409.4.2:A1477C and in COI barcode: T91A, T232C, T355C, T478C, T514A.

Barcode sequence of the holotype: Sample NVG-22032A09, GenBank OR578715, 658 base pairs:

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AACTTTATATTTTATTTTCGGAATTTGAGCAGGATTAATTGGAACTTCTTTAAGTTTACTTATTCGAACTGAATTAGGAACTCCAGGATCATTAATTGGAGATGACCAAATTTATAATACT
ATTGTCACAGCTCATGCTTTTATTATAATTTTCTTTATAGTTATACCTATTATAATTGGAGGATTTGGAAATTGATTAATTCCTCTTATACTAGGAGCTCCTGATATAGCCTTTCCTCGTA
TAAATAATATAAGATTTTGATTATTACCCCCATCTTTAACTCTTTTAATTTCAAGAAGTATTGTTGAAAATGGAGCAGGTACTGGATGAACTGTTTATCCCCCATTATCTTCCAATATTGC
TCACCAAGGAGCTTCAGTAGATTTAGCAATTTTTTCTTTACATCTTGCAGGAATTTCTTCAATTTTAGGAGCTATTAATTTTATTACAACTATTATTAATATACGAATTAATAACTTATCA
TTTGATCAAATACCATTATTTATTTGAGCAGTTGGAATTACAGCTTTATTACTTTTACTTTCACTACCTGTTTTAGCTGGAGCTATTACTATATTATTAACTGATCGAAATTTAAATACTT
CATTTTTTGATCCAGCAGGTGGAGGAGATCCTATTTTATATCAACATTTATTT
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Type material. Holotype: ♂ deposited in the National Museum of Natural History, Smithsonian Institution, Washington, DC, USA [USNM], illustrated in Fig. 31, bears four printed labels: three white [USA:FLA: Volusia Co. | New Smyrna Beach | 3 April 1969 | Leg. G. Rawson], [DNA sample ID: | NVG-22032A09 | c/o Nick V. Grishin], [genitalia vial | NVG230917-01 | Nick V. Grishin], and one red [HOLOTYPE ♂ | Cecropterus (Thorybes) | floridianus Grishin]. **Paratypes:** 4♂♂ 3♀♀ from USA, <u>Florida</u>: 1♂ Franklin Co., USH98 0.4 mi. S of junction with Co. Rd. 370, 3 air mi N of Alligator Point, GPS 29.9378, −84.3907, 29-Mar-1988, J. M. Burns leg., (NVG-22032A08) [USNM]; 1♀ Dixie Co., 16 km S Steinhatchee, end of Rt. 361, 4-Apr-1988, Scott W. Gross leg. (NVG-22032A07) [USNM]; 1♂ Levy Co., Cedar Key, 25-Jul-1963, C. J. Durden leg. (NVG-20062C06) [TMMC]; 1♀ Alachua Co., Gainesville, 20-Apr-1973, E. C. Knudson leg. (NVG-22032A10) [USNM]; 1♂ Marion Co., Ocala National Forest nr. Juniper Springs, 15-May-1988, Scott W. Gross leg. (NVG-22032A12) [USNM]; 1♀ Volusia Co., New Smyrna Beach, G. W. Rawson leg. 10-Mar-1969 (NVG-22032A11) [USNM]; 1♂ Martin Co., Port Sewall, 16-Mar-1939, genitalia 25-34 J. W. Tilden (NVG-22101A01, Fig. 30a) [CAS].

Fig. 31. Holotype of *Cecropterus* (*Thorybes*) *floridianus* **sp. n.** in dorsal (left) and ventral (right) views, data in text.

Type locality. USA: Florida, Volusia Co., New Smyrna Beach.

Etymology. The name for this Floridian species is formed by adding "-*us*" and is a masculine adjective.

English name. Florida Cloudywing.

Distribution. Confirmed only from the USA: Florida, but is likely to be found at least in Georgia.

Cecropterus (*Thorybes*) *oaxacensis* Grishin, new species
http://zoobank.org/5638F005-DC60-47A2-BB6F-6D9B0650F399
(Figs. 27 & 29 parts, 30p, 32, 33)

Definition and diagnosis. Inspection of genomic trees reveals that a single specimen from Mexico, Oaxaca, initially identified by us as "*Cecropterus albosuffusa*" (curated with "*Cecropterus drusius*" in the collection), is not placed among *Cecropterus* (*Thorybes*) *albosuffusa* (H. Freeman, 1943) (type locality USA: Texas, Ft. Davis) specimens we sequenced from across the range (Fig. 27). This specimen is sister to all analyzed *C. albosuffusa*, some from Puebla and DF in Mexico. This consistent placement of the specimen in the trees constructed from protein-coding regions in autosomes, Z chromosome, and mitochondrial genome, where all sequenced *C. albosuffusa* specimens across the range from Arizona and Texas to Pueblo cluster closely together, and its distinction in the COI barcode of 1.2% (8 bp, while *C. albosuffusa* did not show variation in the barcode) suggest that it represents a distinct species. This new species is diagnosed by white hindwing fringe from vein M_2 to tornus, similar to *Cecropterus* (*Thorybes*) *drusius* (W. H. Edwards, [1884]) (type locality in southern Arizona) but has *C. albosuffusa*-like genitalia with rounded (Fig. 30p), not claw-shaped (Fig. 30q) harpe, rounder hindwings in males (in *C. drusius* males, hindwings are slightly extended at tornus, almost lobed), broad paler "frosty" submarginal area on ventral hindwing, which *C. drusius* typically lacks (some specimens with narrower pale overscaling), and broader forewing subapical spots in a straight line, each spot is nearly square. In male genitalia (Fig. 30p), it is most similar to *C. albosuffusa* (Fig. 30m–o) but differs in thicker and shorter relative to tegumen uncus arms, broader and more rounded in lateral view tegumen, and broader, rounder and more upturned harpe. In DNA, a combination of the following characters is diagnostic in nuclear genome: aly638.13.2: A120C, aly638.13.2:C165T, aly4592.3.6:T120C, aly4592.3.6:A159T, aly727.34.3:C417T, aly596.8.8:G120G (not A), aly596.8.8:G618G (not A), aly767.17.3:A273A (not G), aly767.17.3:T941T (not G), aly1432.13.4: C50C (not T) and COI barcode: A181G, A421A, T574C, C595C, T604C.

Barcode sequence of the holotype: Sample NVG-19125B09, GenBank OR578716, 658 base pairs:

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AACTTTATATTTTATTTTTGGAATTTGAGCAGGATTAATTGGAACTTCTTTAAGTTTACTTATTCGAACTGAATTAGGAACTCCAGGATCTTTAATTGGAGATGATCAAATTTATAATACT
ATTGTCACAGCTCATGCTTTTATTATAATTTTCTTTATAGTTATACCTATTATAATTGGGGGATTTGGAAATTGATTAATTCCTCTTATATTAGGAGCTCCTGATATAGCTTTTCCTCGTA
TAAATAATATAAGATTTTGATTATTACCCCCATCTTTAACTCTTTTAATTTCAAGAAGTATTGTTGAAAACGGAGCAGGTACTGGATGAACTGTTTATCCCCCTTTATCTTCTAATATTGC
TCATCAAGGAGCTTCAGTAGATTTAGCAATTTTTTCTTTACATCTTGCAGGAATTTCATCAATTTTAGGAGCTATTAATTTTATTACAACTATTATTAATATACGAATTAATAATTTATCA
TTTGATCAAATACCATTATTTATTTGAGCTGTTGGAATTACAGCCTTATTACTTTTACTTTCATTACCTGTTTTAGCTGGAGCTATTACCATATTATTAACTGATCGAAACTTAAATACCT
CATTTTTTGATCCTGCAGGTGGAGGAGATCCTATTTTATATCAACATTTATTT
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Fig. 32. Holotype of *Cecropterus* (*Thorybes*) *oaxacensis* **sp. n.** pinned through its side (to be spread later), data in text.

Fig. 33. *Cecropterus* (*Thorybes*) *oaxacensis* **sp. n.** female, iNaturalist observation 110602850 from Mexico: Oaxaca, San Miguel Tequixtepec, 17-Jun-2014, © John Kemner; photographs show the same individual. Images are color-corrected, and the rightmost is rotated approximately 90° clockwise. CC BY-NC 4.0 https://creativecommons.org/licenses/by-nc/4.0/

Type material. Holotype: ♂ deposited in the University of Texas Biodiversity Center collection, Austin, TX, USA [TMMC], illustrated in Fig. 32, bears four printed labels: three white [OA.Tlalixtac.002 | 5 mi N Oaxaca | KemnerJ 88138A02], [DNA sample ID: | NVG-19125B09 | c/o Nick V. Grishin], [DNA sample ID: | NVG-22056A03 | c/o Nick V. Grishin], and one red [HOLOTYPE ♂ | Cecropterus (Thorybes) | oaxacensis Grishin], collected by John Kemner on 17-May-1988 (i.e., "88138": day 138 of 1988).

Type locality. Mexico: Oaxaca, Tlalixtac de Cabrera, Hwy 175, ca. 5 mi north of Oaxaca City.

Etymology. The name is given for the type locality and is a masculine adjective in the nominative case.

English name. Oaxaca Cloudywing.

Distribution. Known only from Mexico: Oaxaca. Specimens from phenotypically similar (but mostly darker-fringed) populations to the north (e.g., Puebla and Ciudad de México) are *Cecropterus* (*Thorybes*) *albosuffusa* (H. Freeman, 1943) as identified by genomic sequencing (Fig. 27).

Telemiades solon Plötz, 1882 is a junior subjective synonym of *Nascus* (*Bron*) *broteas* (Cramer, 1780)

The name *Telemiades solon* Plötz, 1882 (type locality in South America), currently applied to a valid species of *Nascus* Watson, 1893 (type species *Papilio phocus* Cramer, 1777), was proposed in a key with a specimen number 4874 in Berlin collection (MFNB) mentioned and the drawing "t. 154" referenced

(Plötz 1882). Neither the specimen nor the illustration or its copy could be found. Godman (1907) skipped the numbers t. 149 to t. 159 in his analysis of unpublished illustrations of American Hesperiidae by Plötz, and none of these drawings were copied. The fate of the original Plötz's illustrations is still unknown (Zhang et al. 2023d). A search of the Hesperiidae holdings in MFNB did not yield the specimen with the number 4874. However, the catalog of the old Hesperiidae collection in MFNB handwritten by Hopffer (Zhang et al. 2023d) has a record for No. 4874: two specimens collected in "Rio" [Brazil: Rio de Janeiro]. Initially, they were listed as "*sp.*" (i.e., unidentified), but subsequently, "*sp.*" was crossed out, and "*Pherenice Hew.*" was written instead. *Eudamus pherenice* Hewitson, 1867 (type locality in Brazil) is currently regarded as a junior subjective synonym of *Nascus* (*Nascus*) *phocus* (type locality in Suriname). Thus, the appearance of these two specimens No. 4874 was likely that of *Nascus*, even if they were misidentified by Hopffer (i.e., they were not *pherenice* but some other similar species), and thus, if they were *T. solon*, consistent with the placement of *T. solon* in Plötz's key among species currently in *Nascus*. Therefore, it is possible that the specimen(s) referred to by Plötz as "4874" was (were) listed in the Hopffer catalog for that entry and collected in Southeast Brazil (Rio de Janeiro), a detail not given in the original description of *T. solon*.

Evans (1952) applied the name "*Nascus solon*" to an Amazonian species not known from Southeast Brazil. This discrepancy found after an inspection of the Berlin collection catalog prompted us to study the original description of *T. solon* more closely. We concluded that Evans misidentified *T. solon* because the species Evans identified as "*N. solon*" does not agree with the original description of *T. solon*. Most significantly, Plötz mentions a brown "hair pencil" (a tuft of long hair-like scales) at the base of cell 1^b [i.e., 1A+2A-3A] on ventral hindwing in *T. solon*, but this tuft is pale, mostly yellow, in Evans' "*N. solon*." Then, in *T. solon*, pale spots in the middle of the forewing are close together and "only separated by veins" (Plötz 1882); but in "*N. solon*", the spot in cell M_3-CuA_1 does not reach the cell origin, which is filled with the ground color (yellow-brown) for at least half of the width of the pale spot in cell CuA_1-CuA_2 along vein CuA_1. Furthermore, in *T. solon*, the hyaline spot in forewing cell M_1-M_2 is small, a pale spot by the costa in the middle of the forewing is mentioned only as "beneath, costal margin is also spotted with pale", and the ventral hindwing is with brown "crossbar in cell 7 [$Sc+R_1$-RS] and in the discal cell". In contrast, in "*N. solon*", the spot in the forewing cell M_1-M_2 is nearly the same size as the spot in the cell R_5-M_1, forewing is with a well-developed hyaline spot by mid-costa, which is seen from the dorsal side as well (hyaline!), hindwing is with weakly developed or missing cental brown spot in the discal cell, and the spot in the cell $Sc+R_1$-RS is small, not a "crossbar". Therefore, Evans' "*N. solon*" is not conspecific with the true *T. solon*.

Next, we searched for specimens that agree with the original description of *T. solon*. The specimen we found to match the description closely was No. 4865 in MFNB. This specimen was previously curated as a type of *Netrocoryne seneca* Plötz, 1882 (type locality Brazil) because No. 4865 was mentioned by Plötz (1882) in the original description of *N. seneca*. However, this specimen is a pseudotype because it agrees neither with the original description nor with a copy of Plötz's unpublished illustration of *N. seneca* (Zhang et al. 2023d). It is possible that due to some mistakes in referencing the MFNB specimen numbers, this specimen No. 4865 was instead (or in addition) a syntype of *T. solon*. However, we do not have defendable evidence to support this hypothesis. Therefore, we proceeded with the neotype designation because there is an exceptional need to clarify both the taxonomic identity and the type locality of *T. solon*. This taxon has been misidentified by Evans (1952), who applied this name to a species that does not agree with the original description of *T. solon*. This mistake creates inconsistencies in the literature and the potential for further destabilization of nomenclature due to the existence of additional species in this group unless the name *T. solon* is objectively defined by the neotype. Therefore, N.V.G. designates the specimen No. 4865 in MFNB illustrated in Fig. 1a–c in Zhang et al. (2023d) (DNA sample NVG-15031F11) as the **neotype** of *Telemiades solon* Plötz, 1882.

Our neotype of *T. solon* satisfies all requirements set forth by the ICZN Article 75.3, namely: **75.3.1.** It is designated to clarify the taxonomic identity of *Telemiades solon* Plötz, 1882, which has been misinterpreted and attributed to a different species that does not agree with the original description of *T. solon*, and to detail its type locality that was given only generally (as "South America") in the original

description; **75.3.2.** The characters to differentiate this taxon from others were specified by Plötz (1882), and we regard them as follows: forewing with a hyaline spot in cell CuA_2-$1A$+$2A$, hyaline spots in the middle of the forewing are crowded together and separated only by veins, hyaline spots in cells M_1-M_2 and M_2-M_3 are small, and the former is merged with the apical spots that together form an oval-shaped hyaline patch separated by veins, a hyaline spot in cell R_2-R_3 is merged with this patch and not offset basad, the hyaline spot is absent by the costal margin near its middle, but the costal margin with a pale spot in the middle beneath; ground color of wings olive-brown, the base of ventral hindwing and most of ventral hindwing are clay-yellow, ventral hindwing with brown crossbars in cell Sc+R_1-RS and the discal cell, and, in addition to the broadly brown outer margin area, with a postdiscal brown band and a brown tuft of hair-like scales at the base of cell $1A$+$2A$-$3A$; **75.3.3.** The neotype specimen is a male bearing eight labels (1st red, 3rd bluish-greenish, the last orange, and others white): [typus], [4865], [Bahia Sello], [GEN.PREP., | MIELKE | 1996], [seneca | Pl. | type], [DNA sample ID: | NVG-15031F11 | c/o Nick V. Grishin], [{QR Code} http://coll.mfn-berlin.de/u/ | 940b3c], [not a type specimen of | Netrocoryne seneca | Plötz, 1882 | determined by Zhang, | Cong et al. 2023] and illustrated in Fig. 1a–c (without the last label, which was added later) in Zhang et al. (2023d); the neotype has a chipped off tornus on both hindwings; **75.3.4.** We searched for syntypes of *T. solon* in the MFNB collection because the original description specified specimen(s) with the number 4874 in Berlin. While there was an entry in the old collection catalog with No. 4874 listing two specimens, we could not find them among Hesperiidae holdings, and therefore, we believe that syntypes were lost; **75.3.5.** The neotype closely agrees with the original description of *T. solon* in all (but one) characters, as evidenced by comparing the neotype illustrated in Fig. 1a–c in Zhang et al. (2023d) with the characters for this taxon given in the original description (Plötz 1882) and listed above (75.3.2.); the only discrepancy is that palpi are nearly white beneath, not clay-yellow (could have been discolored) as stated by Plötz (1882); **75.3.6.** The neotype is from Brazil: Bahia, which is within the original type locality given as "South America"; **75.3.7.** The neotype is in the collection of the Museum für Naturkunde, Berlin, Germany (MFNB).

Genomic sequencing confirms the phenotypic assessment of the *T. solon* neotype as a specimen of *Nascus* (*Bron*) *broteas* (Cramer, 1780) (type locality in Suriname) (Zhang et al. 2023d) because it groups with specimens of the latter species in the tree (Fig. 34). Notably, Draudt (1922) has already placed *T. solon* within his *Nascus cous* (Möschler, 1879) (listing *Nascus eugamon* Godman & Salvin, 1893 as a synonym of the latter), and expressed an opinion that these may be males of *N. broteas*, which was then known only by females. Therefore, as a result of the neotype designation, *Telemiades solon* Plötz, 1882, **syn. nov.** becomes a junior subjective synonym of *Nascus* (*Bron*) *broteas* (Cramer, 1780). The COI barcode sequence of *T. solon* neotype, sample NVG-15031F11, GenBank OR578717, 658 base pairs, is:

```
AACATTATATTTTATTTTTGGAATTTGAGCTGGAATAATTGGAACTTCTCTTAGATTACTAATTCGAACTGAATTAGGAACCCCCGGATCTTTAATTGGAGATGATCAAATTTATAATACT
ATCGTAACAGCTCATGCTTTCATTATAATTTTTTTTTATAGTAATACCTATTATAATTGGAGGATTTGGAAATTGATTAGTACCTCTTATACTAGGAGCTCCTGATATAGCATTTCCACGAA
TAAATAACATAAGATTTTGATTATTACCTCCATCATTAACATTATTAATTTCAAGAAGAATTGTCGAAAATGGTGCTGGTACTGGATGAACAGTTTACCCCCCTTTATCAGCAAATATTGC
TCACCAAGGTTCTTCCGTAGATTTAGCAATCTTTTCTTTACATTTAGCTGGAATTTCTTCTATTTTAGGAGCTATTAACTTTATTACAACAATTATTAATATACGAATTAGAAATTTATCT
TTTGATCAAATACCATTATTTATTTGAGCTGTAGGAATTACAGCATTATTATTACTACTTTCTTTACCTGTTTTAGCAGGAGCTATTACTATATTACTTACTGATCGAAATTTAAATACAT
CTTTCTTTGACCCAGCTGGAGGAGGAGATCCTATTCTTTATCAACATTTATTT
```

Nascus (*Bron*) *corilla* Evans, 1952 is a species-level taxon

Nascus solon corilla Evans, 1952 (type locality in Venezuela) was proposed as a subspecies of a species
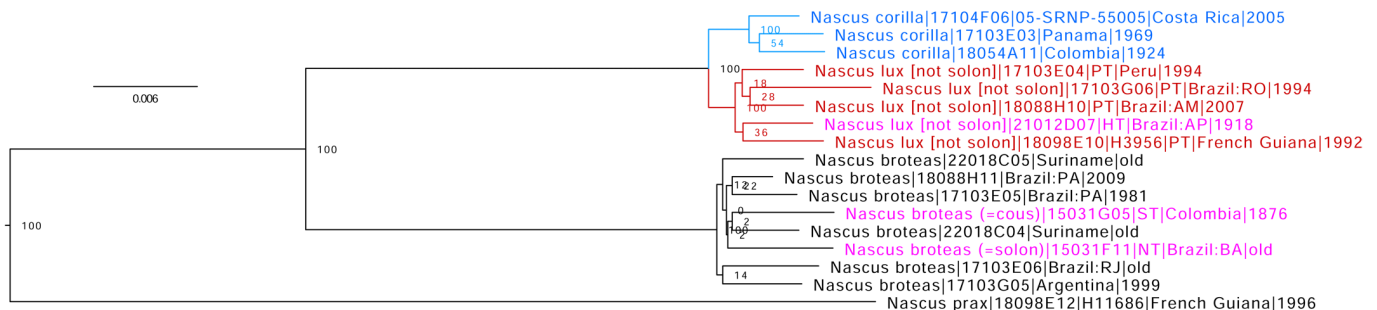
Fig. 34. The phylogenetic tree of *Nascus* (*Bron*) inferred from nuclear genome protein-coding regions (autosomes): *N.* (*B.*) *corilla* **stat. nov.** (blue), *N.* (*B.*) *lux* **sp. n.** (red), and *N.* (*B.*) *broteas* (black). Primary type specimens are labeled in magenta.

that Evans misidentified as "*N. solon*". We argue above that the true *Telemiades solon* Plötz, 1882 (type locality in Brazil: Bahia) is conspecific with *Nascus broteas* (Cramer, 1780) (type locality in Suriname). Because a species that Evans considered to be "*N. solon*" is distinct from *N. broteas*, it is not conspecific with the true *T. solon* and should not be identified by this name. Because no other available name applies to Evans' "*N. solon*", *Nascus corilla* Evans, 1952, **stat. nov.** becomes a species-level taxon.

Nascus (*Bron*) *lux* Grishin, new species

http://zoobank.org/4B4097CE-A43D-4ABB-A5E5-1EAE4FD5C049

(Figs. 34 part, 35)

Definition and diagnosis. Inspection of genomic trees reveals that Amazonian populations, which Evans (1952) considered to be conspecific with *Nascus corilla* Evans, 1952, **stat. nov.** (type locality in Venezuela) and misidentified as *Telemiades solon* Plötz, 1882 (type locality in Brazil: Bahia) as determined above, are genetically differentiated from *N. corilla* with F_{st}/G_{min} of 0.48/0.003 (although their COI barcodes do not reveal differences but in 1 or 2 base pairs) and therefore represent a distinct species (Fig. 34). This species does not have a name. This new species keys to "*Nascus solon solon*" D.5.3(b) in Evans (1952) and is distinguished from its closest relative, *N. corilla*, **stat. nov.** (see above), by pale-yellow to orange-yellow patches of scales, variable in their expression, dividing the brown outer marginal area on the ventral hindwing (that is solid dark brown in *N. corilla*) into narrow postdiscal and broad submarginal bands in males, and usually having five (not four) subapical hyaline spots in females; and from other species of *Nascus* by the following combination of characters: forewing apical spot in cell R_2-R_3 is in line with others, not offset basad; yellow or pale brown tuft of long scales at the base of cell 1A+2A-3A on ventral hindwing; palpi beneath and cheeks are white; prominent hyaline spot in the middle of forewing by costal margin in males; forewing typically larger than 28 mm in males and 30 mm in females. A combination of the following nuclear genomic characters is diagnostic: aly525.35.1:C54T, aly214.21.1:C303T, aly214.21.1:G312A, aly26.5.3:C294T, aly50.27.2:A51G.

Fig. 35. Holotype of *Nascus lux* **sp. n.** in dorsal (left) and ventral (right) views, data in text.

Barcode sequence of the holotype: Sample NVG-21012D07, GenBank OR578718, 658 base pairs:

```
AACTTTATATTTTATTTTTGGAATTTGAGCTGGAATAATTGGAACTTCTCTTAGATTATTAATTCGAACTGAATTAGGCACCCCTGGATCTTTAATTGGAGATGATCAAATTTATAATACA
ATTGTAACAGCTCATGCTTTTATTATAATTTTTTTTATAGTTATACCTATTATAATTGGAGGATTCGGAAATTGACTAGTACCTCTTATATTAGGAGCTCCTGATATAGCATTTCCACGAA
TAAATAATATAAGATTTTGATTATTACCTCCATCATTAACATTATTAATTTCAAGAAGAATTGTAGAAAATGGTGCTGGTACTGGTTGAACAGTTTACCCCCCTTTATCAGCAAATATTGC
TCACCAAGGATCTTCTGTAGATTTAGCAATTTTTTCATTACATTTAGCAGGAATTCCTCAATTTTAGGAGCTATTAACTTTATTACAACAATTATTAATATACGAATTAGAAATTTATCT
TTTGATCAAATACCATTATTTATTTGAGCTGTAGGTATTACAGCTTTATTATTATTACTTTCTTTACCTGTTTTAGCAGGAGCTATTACTATATTACTTACTGATCGAAATTTAAATACAT
CTTTTTTTGATCCTGCAGGAGGAGGTGATCCAATTCTTTATCAACATTTATTT
```

Type material. Holotype: ♂ deposited in the Carnegie Museum of Natural History, Pittsburgh, PA, USA [CMNH], illustrated in Fig. 35, bears four printed (last two digits of the year handwritten) labels: three

white [Uassa Island, | Uassa Swamp. | S. M. Klages, C. M. Acc. 6176], [May | 1918], [DNA sample ID: | NVG-21012D07 | c/o Nick V. Grishin], and one red [HOLOTYPE ♂ | Nascus (Bron) | lux Grishin]. **Paratypes**: 4♂♂, one from each locality <u>Peru</u>: Huanuco, Tingo Maria, 800m, May-Jun-1994, genitalia X-5174 J. M. Burns 2002 (NVG-17103E04, USNMENT00913776); <u>Brazil</u>: Rondônia, 62 km S Ariquemes, Fazenda Rancho Grande, elevation 165m, GPS −10.53, −63.80, 27-Aug-8-Sep-1994, Ron Leuschner leg. (NVG-17103G06, USNMENT00913805); Amazonas, Maues, Rio Preto, 15-25-Nov-2007 (NVG-18088H10); and <u>French Guiana</u>: Roura, Coralie, GPS 4.5083, −52.3750, L. Sénécaux & A. Docquin leg. 24-Jul-1992 (NVG-18098E10, H3956).

Type locality. Brazil: Amapá, Rio Uaçá region ("Uassa Swamp"), which is by the border between Brazil and French Guyana.

Etymology. In Latin, *lux* means "light" and refers to the lighter (i.e., paler) overall appearance of this sunny species, light—instead of brown—tuft of scales on the hindwing (a beam of light), and a sprinkle of light scales between the postdiscal and submarginal brown bands on the ventral hindwing (a phenotypic character that typically separates this species from its closest relative). The name is a noun in apposition.

Distribution. Generally, in and around the Amazonian region in South America. This species has been recorded from French Guiana, Peru, Ecuador, and Brazil (Amapá, Amazonas, Rondônia).

Comment. This name is proposed for Evans' concept of "*Nascus solon solon*" (Evans misidentified *Telemiades solon* Plötz, 1882), and due to genetic differentiation, the two taxa Evans considered to be subspecies: "*Nascus solon corilla*" and "*Nascus solon solon*" are distinct species: *Nascus corilla* and *Nascus lux* **sp. n.**, respectively.

Cogia hiska Evans, 1953 (with its subspecies *Cogia hippalus hester* Evans, 1953) is a species distinct from *Cogia hippalus* (W. H. Edwards, 1882)

Genomic sequencing of *Cogia hippalus* (W. H. Edwards, 1882) (type locality USA: AZ, Pima Co. Tucson, lectotype sequenced as NVG-15101B12) specimens across the range reveals their partitioning into two clades with genetic differentiation at the species level: F_{st}/G_{min} and COI barcode difference of 0.49/0.004/2.9% (19 bp) (Fig. 36). Therefore, the two clades represent two distinct species. One clade contains specimens from the northwestern part of the range northeast to South Texas, USA, and south to Oaxaca, Mexico: the nominotypical *C. hippalus* and its close relative *Cogia hippalus peninsularis* L. Miller & MacNeill, 1969 (type locality Mexico: Baja California Sur, Arroyo San Bartolo, holotype sequenced as NVG-15095C07). The other clade consists of specimens from the southeastern part of the range from Mexico: Tamaulipas to Venezuela: *Cogia hippalus hiska* Evans, 1953 (type locality Costa Rica: Puerto Carrillo) and *Cogia hippalus hester* Evans, 1953 (type locality Venezuela: Merida). Our methods of analysis do not find species-level genetic differences between *C. h. hiska* and *C. h. hester*. The names *hiska* and *hester* were proposed in the same work issued on the same date. As the first revisers, we
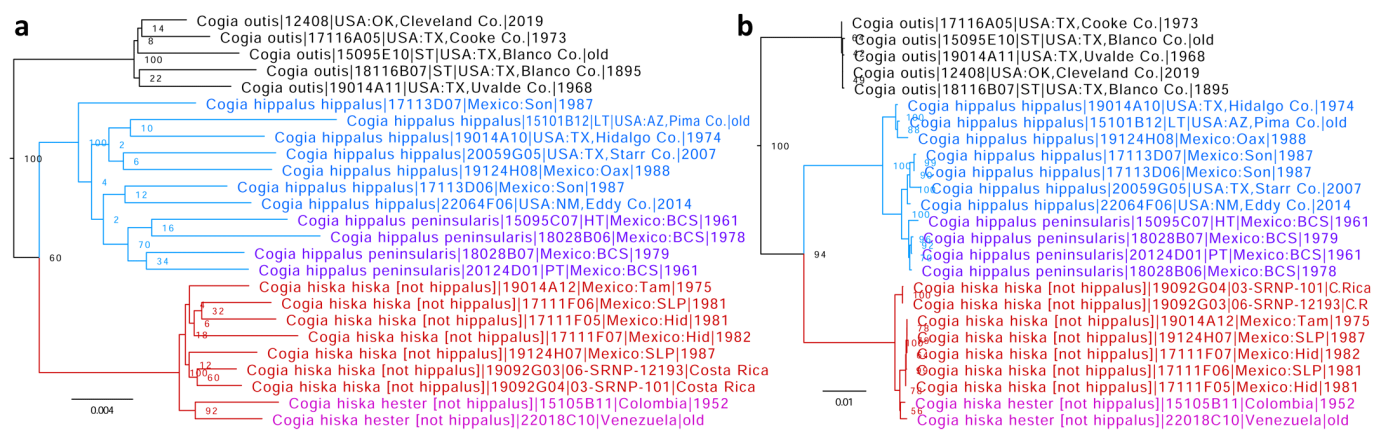
Fig. 36. Phylogenetic trees of selected *Cogia* inferred from protein-coding regions of **a)** the nuclear (autosomes) and **b)** the mitochondrial genomes. Different species are shown in different colors: *C. hippalus* (blue with its subspecies *C. h. peninsularis* labeled in violet), *C. hiska* (red, with its subspecies *C. h. hester* labeled in magenta), and *C. outis* (black).

give precedence to *hiska* due to its larger distribution. Thus, we propose that *Cogia hiska* Evans, 1953, **stat. nov.** is a species and *Cogia hiska hester* Evans, 1953, **comb. nov.** is its subspecies.

Lectotype designation for *Eudamus caicus* Herrich-Schäffer, 1869 with the type locality likely in Mexico: Oaxaca

Eudamus caicus Herrich-Schäffer, 1869 (type locality Tropical America, possibly into southern USA), currently a valid species in the genus *Cogia* Butler, 1870 (type species *Cogia hassan* Butler, 1870) was described from an unstated number of specimens without details about their localities (Herrich-Schäffer 1869). One specimen without a locality label is curated in the MFNB collection as a syntype of *E. caicus*. We determine that this specimen is indeed a syntype because it agrees with the original description and matches closely in wing patterns a specimen BMNH(E) 1236437 (a male, in BMNH) that Godman selected as the most similar in his collection to the unpublished drawing by Plötz of *Eudamus schaefferi* Plötz, 1881 (a replacement name for *E. caicus* Herrich-Schäffer, 1869, erroneously deemed preoccupied), and labeled as "Compared with | Plotz's drawing of | schaefferi, | Plötz | caicus, | HS." Godman placed such similar-styled labels on specimens that, in his opinion, closely resembled the originals of Plötz's drawings that he inspected (Godman 1907), and we use this specimen as a "proxy" for the drawing. We note that *E. schaefferi* (Plötz's t[afel]. 129, which is *E. caicus* H.-S.) was not mentioned in Godman's publication (1907), which might be because that work dealt with American species, but the locality for *E. schaefferi* was not explicitly stated in the original description and, due to the lack of locality labels on the syntype, likely not appearing on the Plötz's drawing numbered 129. This Godman's specimen from "N. Sonora, | Mexico" is actually *Cogia caicus moschus* (W. H. Edwards, 1882), but is similar in wing pattern to the nominotypical *C. caicus*; its photographs are shown on the Butterflies of America website (Warren et al. 2023). To stabilize nomenclature, N.V.G. hereby designates the syntype in the MFNB collection, a female with the following seven printed labels, the 1st purple and others white: [Origin], [Coll. H.—Sch.], [Daunus Cr.], [Caicus | HS. | Achlyodes], [Caicus | H-Sch.], [{QR Code} http://coll.mfn-berlin.de/u/ | 940b5d], and [DNA sample ID: | NVG-15032A02 | c/o Nick V. Grishin] as the **lectotype** of *Eudamus caicus* Herrich-Schäffer, 1869. Genomic trees place the lectotype among specimens from Mexico, Oaxaca (Fig. 37), suggesting that it was collected there because it is genetically within this metapopulation. Therefore, we infer that the type locality of *Cogia caicus* (Herrich-Schäffer, 1869) may be in Oaxaca and will test this hypothesis further by sequencing specimens from other localities.
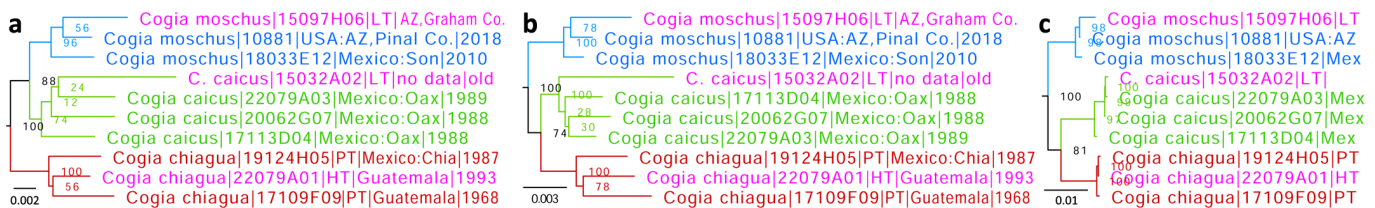
Fig. 37. Phylogenetic trees of selected *Cogia* species inferred from protein-coding regions of **a)** the nuclear genome (autosomes), **b)** the Z chromosome, and **c)** the mitochondrial genome. Different species are shown in different colors: *C. moschus* **stat. rest.** (blue), *C. caicus* (green), and *C. chiagua* **sp. n.** (red). Primary type specimens are labeled in magenta.

Cogia moschus (W. H. Edwards, 1882) is a species distinct from *Cogia caicus* (Herrich-Schäffer, 1869)

We find the genetic differentiation between *Cogia caicus* (Herrich-Schäffer, 1869) (type locality likely in Mexico: Oaxaca, as deduced above, lectotype sequenced as NVG-15032A02, in MFNB) and *Cogia caicus moschus* (W. H. Edwards, 1882) (type locality in USA: AZ, Graham Co., lectotype sequenced as NVG-15097H06, in CMNH) to be of a magnitude suggestive of distinct species: F_{st}/G_{min}/COI differences are 0.50/0.003/0.9% (6 bp) (Fig. 37). Therefore, we propose that *Cogia moschus* (W. H. Edwards, 1882), **stat. rest.** is a species-level taxon.

Cogia chiagua Grishin, new species

(Figs. 37 part, 38, 39a)

Fig. 38. Holotype of *Cogia chiagua* **sp. n.** in dorsal (left) and ventral (right) views, data in text.

Definition and diagnosis. In addition to *Cogia moschus* (W. H. Edwards, 1882) (type locality in USA: AZ, Graham Co.) and *Cogia caicus* (Herrich-Schäffer, 1869) (type locality likely in Mexico: Oaxaca), genomic trees reveal a third lineage of similar genetic differentiation (Fig. 37 red) with F_{st}/G_{min}/COI differences from the former and the latter, respectively: 0.49/0.009/0.9% (6 bp) and 0.4/0.006/0.5% (3 bp) that represents a species. This new species differs from its two close relatives by being darker overall, smaller (or lacking) hyaline spots, and darker palpi beneath. Male genitalia are variable, but the harpe typically is broader, rounder, and dorsally with more robust teeth on a shorter ridge near the ampulla; aedeagus with a smaller number of cornuti (Fig. 39). A combination of the following characters in the COI barcode is diagnostic: A40A, C343C, T349T, T386T, A481G, T556A.

Barcode sequence of the holotype: Sample NVG-22079A01, GenBank OR578719, 658 base pairs:

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AACATTATATTTTATTTTTGGAATTTGAGCAGGAATAGTTGGAACTTCTTTAAGTTTATTAATTCGTACTGAATTAG
GAACTCCAGGATCATTAATTGGAGATGATCAAATTTATAATACTATTGTAACAGCTCATGCTTTTATTATAATTTTT
TTTATAGTTATACCTATTATAATTGGAGGATTTGGAAATTGATTAGTTCCCTTAATATTAGGAGCTCCTGATATAGC
TTTTCCTCGTATAAATAATATAAGATTTTGATTACTTCCCCCATCATTAACATTATTAATTTCTAGAAGTATTGTAG
AAAATGGTGCTGGTACTGGATGAACAGTATATCCCCCCCTTTCATCAAATATTGCACATCAAGGTTCATCAGTAGAT
TTAGCTATTTTTTCTTTACATTTAGCTGGTATTTCATCTATTTTAGGTGCTATTAATTTTATTACTACAATTATTAA
TATACGAATTAGAAATTTGTCATTTGATCAAATACCTTTATTTGTATGAGCAGTAGGAATTACAGCTTTATTACTTT
TACTTTCTTTACCTGTATTAGCTGGTGCTATTACTATACTTTTAACAGATCGAAATCTTAATACATCATTTTTTGAT
CCTGCTGGAGGAGGAGACCCTATTTTATATCAACATTTATTT
```

Type material. Holotype: ♂ deposited in the McGuire Center for Lepidoptera and Biodiversity, Gainesville, FL, USA [MGCL], illustrated in Fig. 38, bears five printed labels: four white [Antigua, Sacatepequez | Guatemala | September 16, 1993 | D.L.Lindsley], [Cogia Butler | caicus (Herrich-Schäffer) | caicus (Herrich-Schäffer)], [D.L. Lindsley colln. | MGCL Accession | # 2008-20], [DNA sample ID: | NVG-22079A01 | c/o Nick V. Grishin], and one red [HOLOTYPE ♂ | Cogia chiagua | Grishin]. **Paratypes**: 3♂♂, 1♀: 1♂ Mexico, Chiapas, Comitán, Laguna Chamula, 7100', 13-May-1987, C.J. Durden leg. (NVG-19124H05) [TMMC] and Guatemala: 1♂ Panajachel, 2-Jun-1968, Beals leg. (NVG-17109F09) [LACM] and Duenas, G.C. Champion leg. [BMNH]: 1♂ (BMNH(E) 1236437, genitalia mini-slide 153, Fig. 39a) and 1♀.

Fig. 39. Male genitalia of *Cogia* in lateral view (left valva separated and rotated 180°). **a)** *C. chiagua* **sp. n.** paratype, mini-slide 153, data in text. **b)** *C. moschus* **stat. rest.**, Mexico: N Sonora, Morrison leg., BMNH(E) 1236437, mini-slide 151. Photographs by N. V. G. © The Trustees of the Natural History Museum London and are made available under Creative Commons License 4.0 (https://creativecommons.org/licenses/by/4.0/).

Type locality. Guatemala: Sacatepéquez Department, Antigua.

Etymology. The name is a fusion of *Chia*[pas] + *Gua*[temala] for the known distribution of this species and is a feminine noun in apposition.

Distribution. Currently known from Mexico: Chiapas and from Guatemala.

Pholisora albicirrus Glassberg, 2023 is a species distinct from *Pholisora catullus* (Fabricius, 1793)

We find the genetic differentiation between *Pholisora catullus* (Fabricius, 1793) (type locality "Indiis," probably eastern USA) and *Pholisora catullus albicirrus* Glassberg 2023 (type locality in USA: AZ, Santa Rita Mts.) to be of a magnitude suggestive of distinct species: F_{st}/COI differences are 0.46/2.3% (15 bp) (Fig. 40), similar to that for *Pholisora crestar* J. Scott & Davenport, 2017 (type locality in USA: CA, Tulare Co.) (Zhang et al. 2020). Therefore, we propose that *Pholisora albicirrus* Glassberg 2023, **stat. nov.** is a species-level taxon in agreement with phenotypic differences mentioned in the original description (Glassberg 2023), which, from our experience with other Hesperiidae, also suggest species, and not subspecies, status.
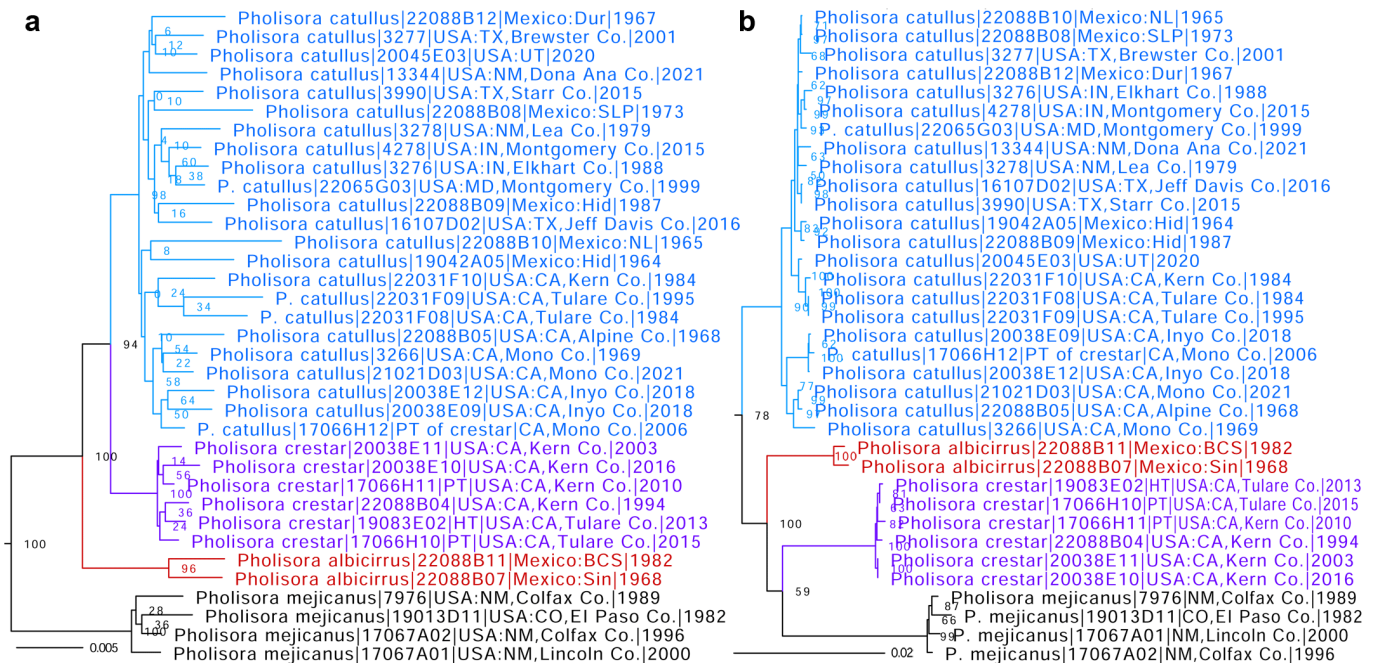
Fig. 40. Phylogenetic trees of *Pholisora* species recorded from the USA inferred from protein-coding regions of **a)** the Z chromosome (best for species delimitation) and **b)** the mitochondrial genome. Different species are shown in different colors: *P. catullus* (blue), *P. crestar* (violet), and *P. albicirrus* **stat. nov.** (red).

Celotes sabinus Grishin, new species
http://zoobank.org/085EAF93-91A9-4F81-886C-0E77073C8B0E
(Figs. 41 part, 42, 43a)

Definition and diagnosis. Inspection of genomic trees reveals that *Celotes nessus* (W. H. Edwards, 1877) (type locality USA: Texas, Bexar Co., San Antonio; lectotype sequenced as NVG-15097F12) as currently circumscribed (Fig. 41 blue and red) is not monophyletic, and populations from the eastern part of the range (Fig. 41 blue) are sister to *Celotes spurcus* A. Warren, Steinhauser, Hernandez-Mejía & Grishin, 2008 (type locality in Mexico: Querétaro) (Fig. 41 green). While species, in general, do not have to be monophyletic, populations currently identified as *C. nessus* from the western part of the range (Fig. 41 red) are genetically differentiated from the eastern populations (which include nominotypical) at the level characteristic of distinct species, with Z chromosome F_{st}/G_{min} of 0.32/0.008 and COI barcode difference

of ~2.0% (13 bp, but barcodes introgress between these species). Therefore, these western populations are a species distinct from *C. nessus*. This western species does not have a name because the only two junior synonyms of *C. nessus*: *Spilothyrus notabilis* Strecker, [1878] (type locality in the USA: Texas, vicinity of New Braunfels and San Antonio; two syntypes sequenced as NVG-15039C06 and NVG-15039C07) and *Carcharodus radiatus* Plötz, 1884 (type locality in USA: Texas, syntypes not located, attributed to a species by locality), are conspecific with the eastern species. This new species is distinguished from *C. spurcus* by approximately two times shorter process of valva (from the base of ampulla), which is similar in length to *C. nessus*, and from *C. nessus* by terminally broader harpe, wider separation between harpe and ampulla (broader gap between them), wider process of valva, broader valva narrowing less towards vinculum, and two small teeth on aedeagus shaft: by its bend and halfway between the bend and distal end (Fig. 43). A combination of the following nuclear genomic characters is diagnostic: aly2284.30.1: G1323A, aly40182.1.2:C154A, aly40182.1.2:C171T, aly1445.3.1:G246A, aly1445.3.1:A195G.
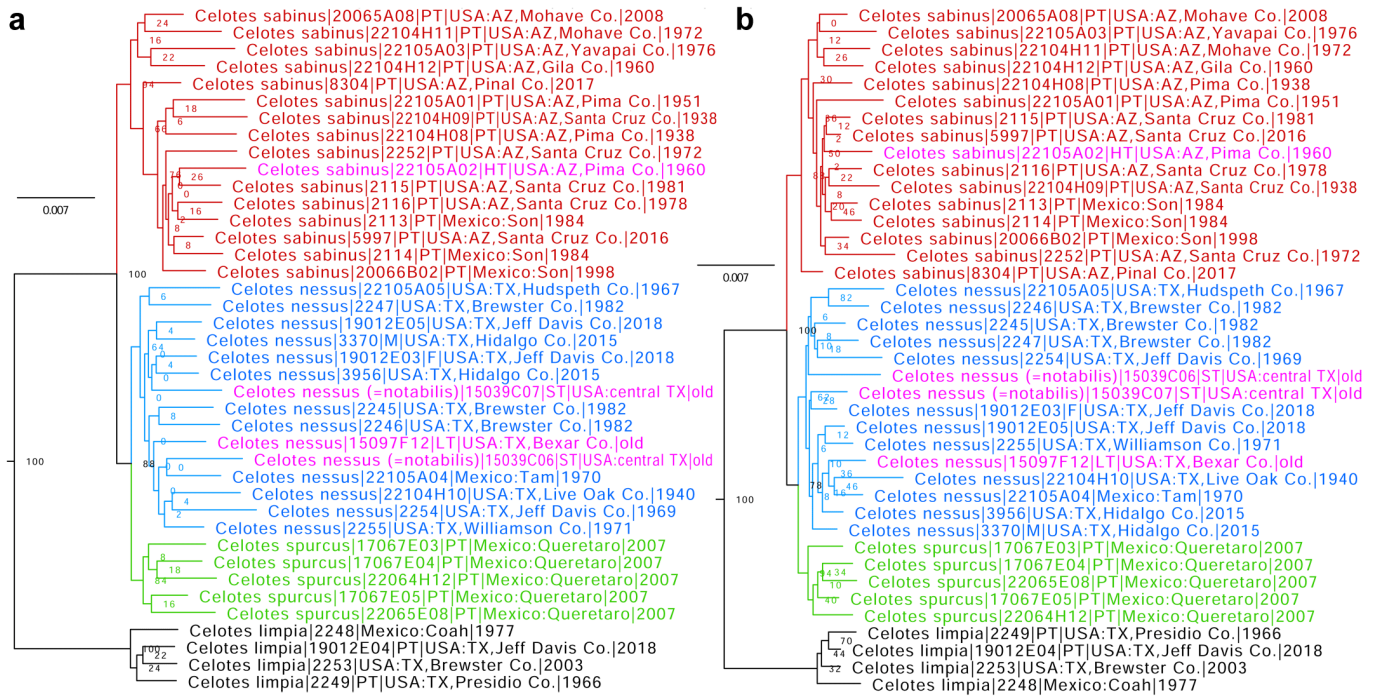
Fig. 41. Phylogenetic trees of *Celotes* inferred from protein-coding regions of **a)** the nuclear genome (autosomes) and **b)** the Z chromosome. Different species are shown in different colors: *C. sabinus* **sp. n.** (red), *C. nessus* (blue), and *C. spurcus* (green). Primary type specimens are labeled in magenta.

Barcode sequence of the holotype: Sample NVG-22105A02, GenBank OR578720, 658 base pairs:

```
AACTTTATATTTCATTTTTGGAATTTGAGCAGGCATAGTAGGTACTTCTCTAAGTTTATTAATTCGAACTGAATTAGGAAATCCAGGATCTCTAATTGGGGATGATCAAATTTATAATACT
ATTGTAACAGCACATGCCTTCATTATAATTTTTTTTATGGTAATGCCTATTATAATTGGAGGATTTGGAAATTGATTAGTACCTTTAATACTAGGAGCTCCTGATATAGCATTCCCACGTA
TAAATAATATAAGATTTTGATTATTACCTCCTTCTTTAACACTTCTTATTTCAAGAAGTATTGTAGAAAATGGAGCAGGAACAGGATGAACAGTTTACCCCCCTCTATCATCTAATATTGC
TCATCAAGGTTCATCTGTTGACTTAGCTATCTTTTCTTTACATCTAGCAGGAATTTCATCAATCTTAGGAGCAATTAACTTCATTACAACTATTATTAATATACGAATTAGAAATTTATCA
TTTGATCAAATACCTTTATTTGTATGAGCTGTAGGAATTACAGCATTACTTTTATTATTATCTTTACCTGTTTTAGCTGGAGCTATTACAATATTATTAACTGATCGAAATTTAAATACAT
CTTTCTTTGATCCTGCTGGAGGAGGAGATCCAATTTTATATCAACACTTATTT
```

Type material. Holotype: ♂ deposited in the California Academy of Sciences, San Francisco, CA, USA [CAS], illustrated in Fig. 42, bears seven printed labels (date on the first label handwritten): six white [Sabino Cany. | Santa Catalina Mts. | Pima Co. Arizona | 1. IV. 60], [collected by | Kilian Roever], [Collection of | J. W. Tilden], [JAMES W. TILDEN | COLLECTION – 1985 | Gift to the California | Academy of Sciences], [DNA sample ID: | NVG-22105A02 | c/o Nick V. Grishin], [{QR Code} CASENT | 8568344], and one red [HOLOTYPE ♂ | Celotes sabinus | Grishin]. **Paratypes**: 13♂♂, 4♀♀: USA, <u>Arizona</u>: Mohave Co., 1♀ Hualapai Mts., lower el., 16-Apr-2008, Ken Davenport leg. (NVG-20065A08, CSU_ENT1024696) [CSUC]; 1♂ nr. Wickieup, 30-Mar-1972, J. W. Tilden leg. (NVG-22104H11, CASENT8568341) [CAS]; 1♀ Yavapai Co., 8 mi SW of Prescott, 21-Apr-1976, James W. "Bill" Tilden leg. (NVG-22105A03, CASENT8568345) [CAS]; 1♂ Maricopa Co., Camp Creek on Cave

Fig. 42. Holotype of *Celotes sabinus* **sp. n.** in dorsal (left) and ventral (right) views, data in text.

Creek Rd., 12 mi NE of Jct. of Cave Creek and Scottsdale Rds., 8-Apr-1968, J. A. Miller leg., genitalia NVG140320-91 (NVG-2250) [TAMU]; 1♂ Gila Co., Sevenmile wash, 22-Aug-1960, P. A. Opler leg. (NVG-22104H12, CASENT 8568342) [CAS]; 1♂ Pinal Co., Coronado National Forest, Santa Catalina Mts., Peppersauce Canyon, 26-Mar-2017, Q. Cong, J. Zhang, and N. V. Grishin leg. (NVG-8304); Pima Co.: 1♂ Baboquivari Mts., Brown Canyon, 21-Mar-1938, J. W. Tilden leg., genitalia J.W.T. 25-15 (NVG-22104H08, CASENT8568338) [CAS] (Fig. 43a); 1♂ Santa Catalina Mts., Molino Basin, 7-Sep-1951, C. D. MacNeill leg. (NVG-22105A01, CASENT8568343) [CAS]; Santa Cruz Co.: 1♂ Pena Blanca Canyon, 11-Jul-1981, Jim P. Brock leg. (NVG-2115); 2♂♂ Walker Canyon nr. Pena Blanca Lake, 16-Aug-1972, John Hafernik leg., genitalia NVG140320-92 & -93 (NVG-2251 & NVG-2252) [TAMU]; 1♂ Pajarito Mtns., California Gulch, 30-Mar-2016, N. Grishin leg. (NVG-

Fig. 43. Male genitalia of *Celotes* from USA, in lateral view. **a)** *Celotes sabinus* **sp. n.** paratype, slide J. W. T. 25-15, AZ: Baboquivari Mts., Brown Canyon, 21-Mar-1938, DNA sample NVG-22104H08. **b)** *Celotes nessus*, slide 25-16, TX: George West, 12-Jun-1940, DNA sample NVG-22104H10. Specimens are in CAS, collected and genitalia prepared by J. W. Tilden. Genital capsule is shown on the right, separated valva is on the left with aedeagus above it. Aedeagus of *C. sabinus* is shown in ventrolateral view as mounted on the slide.

5997); 1♂ Patagonia, 24-Mar-1938, J. W. Tilden leg. (NVG-22104H09, CASENT8568339) [CAS]; 1♀ 3.5mi SW of Patagonia, 6-Aug-1978, Jim P. Brock leg. (NVG-2116); Mexico: Sonora: 1♂ 16 mi E of Tecoripa, 15-Mar-1984, Jim P. Brock leg. (NVG-2114); 1♀ 8 mi W of Rio Yaqui, 16-Mar-1984, Jim P. Brock leg. (NVG-2113); 1♂ ca. 8 mi NE of Bavispe, elevation ca. 4000', 25-Mar-1998, Richard W. Holland leg. (NVG-20066B02, CSU_ENT1024701) [CSUC].

Type locality. USA: Arizona, Pima Co., Santa Catalina Mountains, Sabino Canyon.

Etymology. The name is formed from the type locality of this species, Sabino Canyon, a place familiar to many naturalists, which is just northeast of Tucson at the foothills of the Santa Catalina Mountains in southeastern Arizona, where this species is common. The name is a masculine adjective.

English name. Arizona streaky-skipper.

Distribution. Currently known from USA: Arizona and Mexico: Sonora and is likely present in southwestern New Mexico.

Comment. We were surprised to learn that *C. sabinus* **sp. n.** is more distant from *C. nessus* than morphologically distinct *C. spurcus*, which is rather close to *C. nessus* genetically.

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Charmion Nicéville, 1894 is a genus distinct from *Celaenorrhinus* Hübner, [1819]

Genomic tree reveals that *Hesperia ficulnea* Hewitson, 1868, the type species of the genus *Charmion* Nicéville, 1894 currently regarded as a junior subjective synonym of the genus *Celaenorrhinus* Hübner, [1819] (type species *Papilio eligius* Stoll, 1781) is not monophyletic with it (Fig. 44 red). We find that *Bettonula* Libert & Larsen, 2014 (type species *Celaenorrhinus bettoni* Butler, 1902) renders *Celaenorrhinus* paraphyletic. Therefore, to restore the monophyly, we

Fig. 44. Nuclear genome tree (autosomes): *Charmion* (red) and *Celaenorrhinus* (blue), *Sape* (magenta) and *Sarangesa* (green).

propose that *Charmion* Nicéville, 1894, **stat. rest.** is a genus distinct from *Celaenorrhinus* Hübner, [1819].
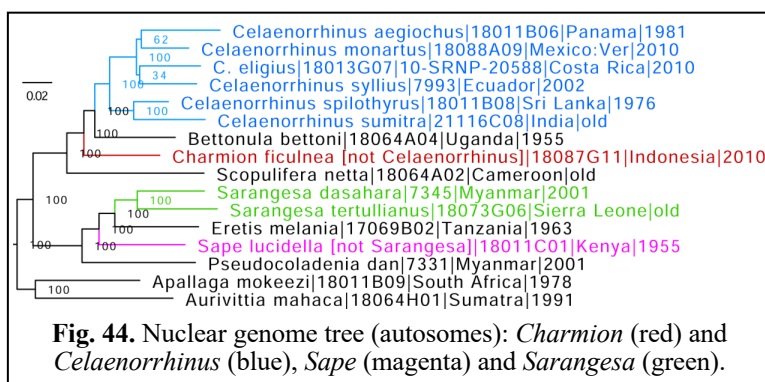
Sape Mabille, 1891 is a genus distinct from *Sarangesa* F. Moore, [1881]

Genomic tree reveals that *Sape lucidella* Mabille, 1891, the type species of the genus *Sape* Mabille, 1891 currently treated as a junior subjective synonym of the genus *Sarangesa* F. Moore, [1881] (type species *Sarangesa albicilia* F. Moore, [1881]) is not monophyletic with it (Fig. 44 magenta). We find that *Eretis* Mabille, 1891 (type species *Eretis melania* Mabille, 1891) renders *Sarangesa* paraphyletic. Therefore, to restore the monophyly, we propose that *Sape* Mabille, 1891, **stat. rest.** is a genus distinct from *Sarangesa* F. Moore, [1881].

Cupithina Grishin, new subtribe
http://zoobank.org/905E8110-34EC-4CB3-A0C0-3F9002414D3E

Type genus. *Cupitha* F. Moore, 1884.

Definition. The tribe Astictopterini Swinhoe, 1912 splits into two clades containing approximately the same number of genera, each supported by 100% of partitions (see Fig. 1 in Zhang et al. (2023b) and Figs. 45, 46). Although neither clade is very prominent (branches separating them are not particularly long), both are most strongly supported. Therefore, to bring order to the genera in Astictopterini, we divide the tribe into two subtribes. The clade with the type species of the tribe contains generally larger species with more robust bodies and corresponds to the nominotypical subtribe. The second clade, with *Cupitha* (type species *Cupitha tympanifera* F. Moore, 1884, which is a junior subjective synonym of *Pamphila purreea* Moore, 1877), consists of smaller and frequently brighter patterned species and corresponds to the subtribe without an available name. This new and mostly Afrotropical subtribe is distinguished from its relatives by a combination of the following characters (Evans 1937; Evans 1949): palpi either porrect with convergent 3rd segment or erect with thin and erect 3rd segment; antennal club with pointed apiculus, either obtuse or hooked; caudal angle of hindwing discal cell not bent up: median vein and vein M_3 collinear, end of cell relatively straight, and vein 3A usually shorter than vein CuA_2; thorax not shaggy beneath; coxae and tibiae of hindlegs not densely fringed; valvae symmetrical, uncus typically narrowing to a point, ovate, terminal part narrow, frequently needle-like, uncus usually not expanded terminally and not hourglass-shaped. Most confidently identified by DNA and a combination of the following nuclear genomic base pairs is diagnostic: aly1775.3.2:A50G, aly27.16.1:A638C, aly27.16.1:C644G, aly1603.20.3:G76C, aly1651.28.7:A167G.

Genera included. The type genus (i.e., *Cupitha* F. Moore, 1884), *Acada* Evans, 1937, *Acleros* Mabille, 1885, *Andronymus* Holland, 1896, *Caenides* Holland, 1896, *Ceratricula* Larsen, 2013, *Fresna* Evans, 1937, *Gorgyra* Holland, 1896, *Gyrogra* Lindsey & Miller, 1965, *Hollandus* Larsen & Collins, 2015, *Hypoleucis* Mabille, 1891, *Melphina* Evans, 1937, *Melphinyet* Larsen, 2012, *Noctulana* Larsen, 2012,
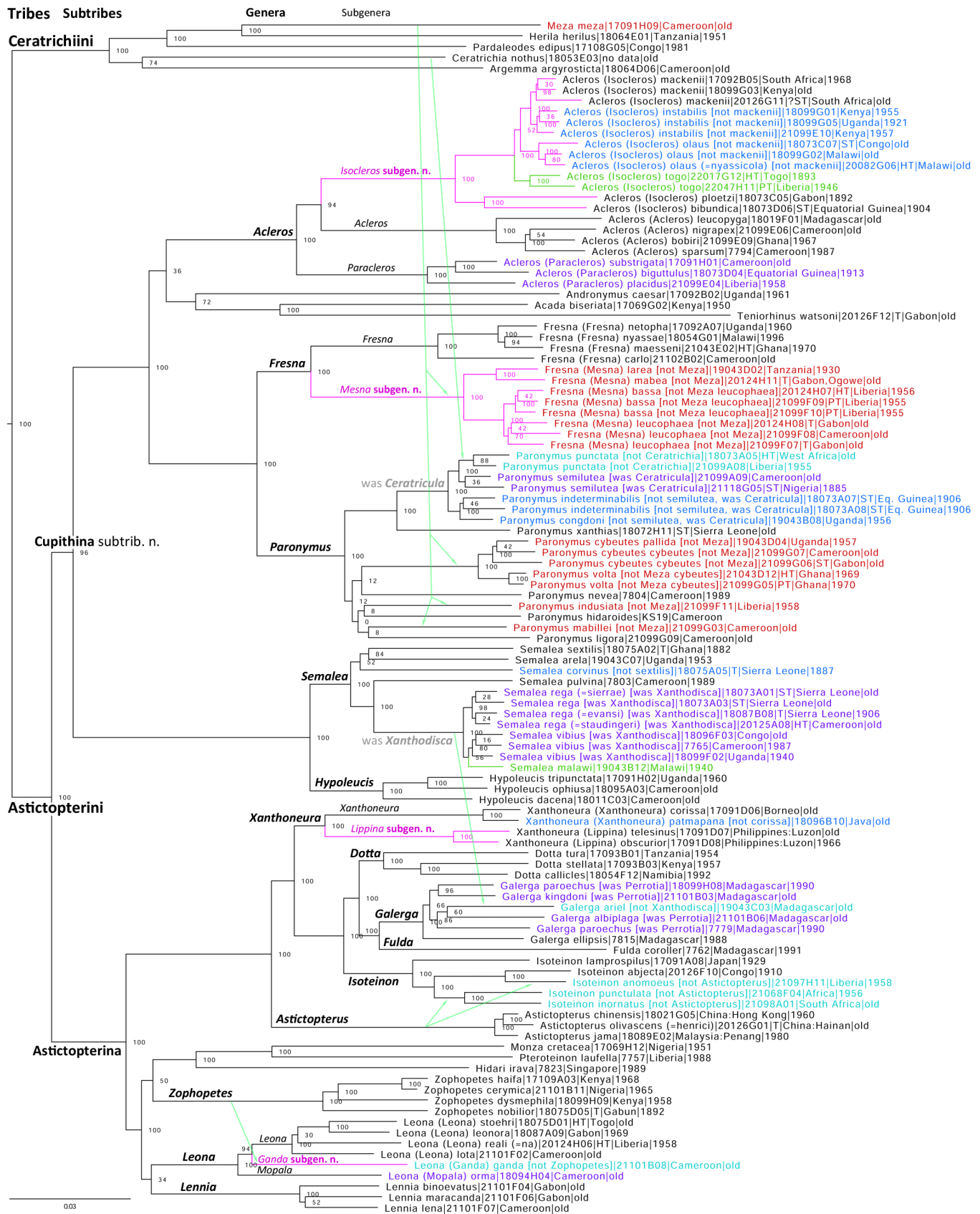
Fig. 45. The phylogenetic tree of selected Ceratrichiini and Astictopterini inferred from protein-coding regions of the nuclear genome (autosomes). Levels in the tree that approximately correspond to the taxonomic hierarchy are marked above as Tribes, Subtribes, Genera, and Subgenera. Family-group names (roman font) and relevant genus-group names (genera in bold italics and subgenera in italics) are shown by corresponding branches. New species are in green, clades of new subgenera are in magenta, labels of taxa previously in *Meza* are in red, and others are colored as follows: elevated to species (blue), transferred between genera (cyan; green arrows show the transfer), and included into other genera as subgenera or synonyms (violet).
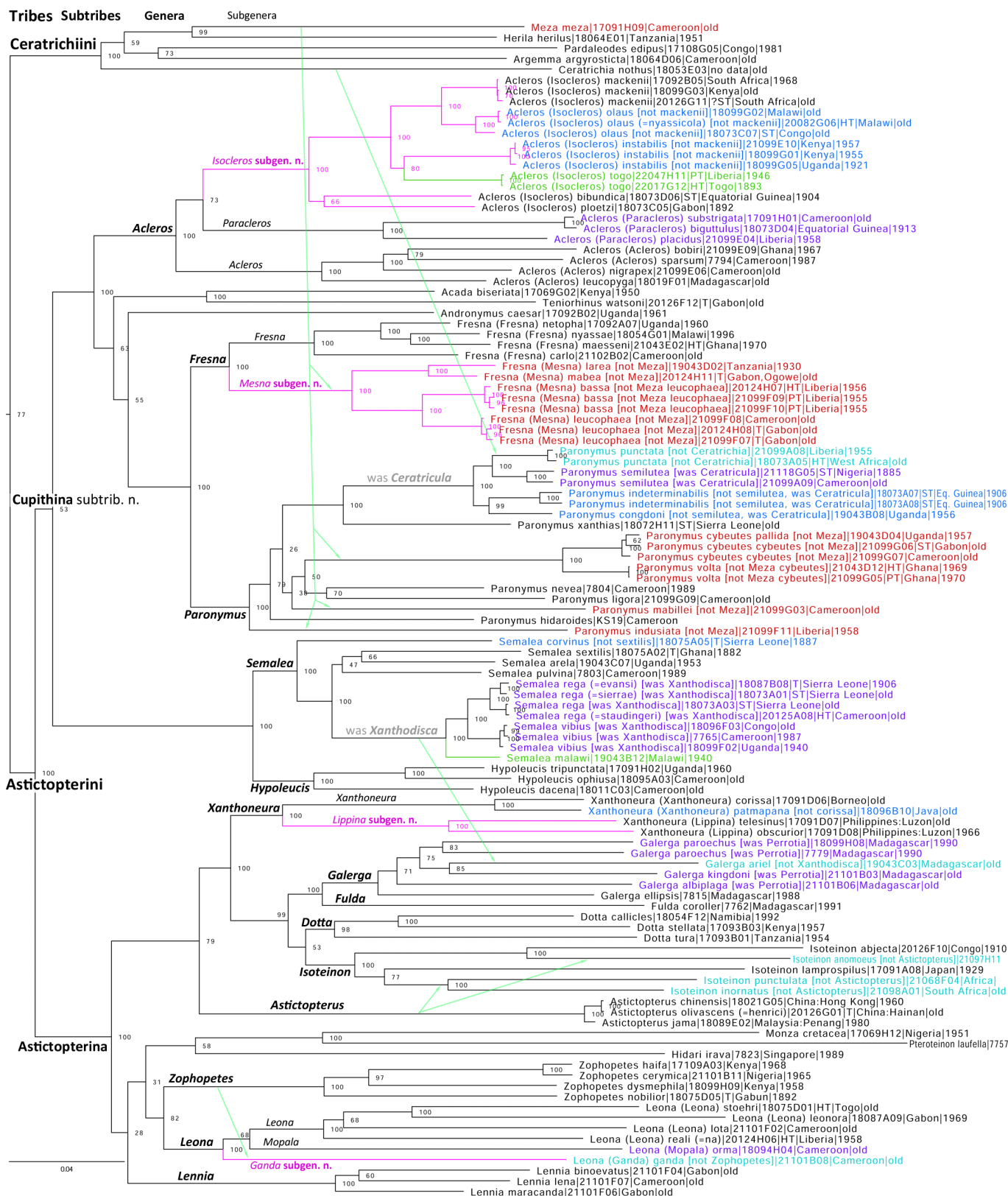
Fig. 46. The phylogenetic tree of selected Ceratrichiini and Astictopterini inferred from protein-coding regions of the mitochondrial genome. See Fig. 45 for notations.

Osmodes Holland, 1892, *Osphantes* Holland, 1896, *Paracleros* Berger, 1978 (see below), *Paronymus* Aurivillius, 1925, *Parosmodes* Holland, 1896, *Platylesches* Holland, 1896, *Rhabdomantis* Holland, 1896, *Semalea* Holland, 1896, *Teniorhinus* Holland, 1892, *Xanthodisca* Aurivillius, 1925 (see below),

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Xanthonymus Grishin, 2019, and *Zographetus* Watson, 1893. All other genera placed in Astictopterini by Zhang et al. (2023b) belong to the nominotypical subtribe Astictopterina.

Parent Taxon. Tribe Astictopterini Swinhoe, 1912.

Paracleros Berger, 1978 is a subgenus of *Acleros* Mabille, 1885

Acleros Mabille, 1885 (type species *Cyclopides leucopyga* Mabille, 1877) and *Paracleros* Berger, 1978 (type species *Acleros biguttulus* Mabille, 1889) are two phenotypically similar sister genera, which, taken together, are prominently separated from others (Figs. 45, 46). COI barcode difference between their type species is 9.1% (60 bp), which is borderline for distinct genera in many butterfly groups. Moreover, *Acleros*, as currently circumscribed, is not a genetically prominent group and splits into two such groups in the nuclear genome tree (Fig. 45): the nominotypical *Acleros* and the other one, which is proposed as a new subgenus below. In the mitochondrial genome tree, *Acleros* is not even monophyletic, albeit with a weaker support (Fig. 46). On the one hand, we see that *Acleros* and *Paracleros* taken together form a prominent clade. On the other hand, *Acleros* and *Paracleros* are not prominently separated from each other, and there is a third clade of nearly the same rank. This clade is currently included in *Acleros* but is sister to *Paracleros* in the mitochondrial genome tree. Neither of these three groups consists of a large number of species. For all these reasons, we propose to treat *Paracleros* Berger, 1978, **stat. nov.** as a subgenus of *Acleros* Mabille, 1885.

Isocleros Grishin, new subgenus
http://zoobank.org/1109E9E2-43A8-422D-BF56-967608087687

Type species. *Pamphila* (?) *mackenii* Trimen, 1868.

Definition. As discussed in the previous section, *Acleros* Mabille, 1885 (type species *Cyclopides leucopyga* Mabille, 1877) that includes *Paracleros* Berger, 1978 (type species *Acleros biguttulus* Mabille, 1889) splits into three prominent clades: the nominotypical *Acleros*, *Paracleros*, and the third clade not associated with any available genus-group names (Figs. 45, 46). The third clade represents a new subgenus that keys to 41.B.(a) (excluding a^2) or 41.B.(b)(b^1) in Evans (1937) and is distinguished from its relatives by darker distal half of ventral hindwing or if hindwing is more uniform in color then dorsal forewing is with broadly white inner margin; tegumen with uncus are narrow in lateral view, uncus in dorsal view is either bulb-shaped or continuously narrows to a point. A combination of the following nuclear genomic base pairs is diagnostic: aly2627.4.1:T63A, aly2627.4.1:C69T, aly116.29.1:T2049A, aly116.29.1:G2814A, aly9673.4.1:A480G.

Etymology. The name of the other subgenus was formed by adding the prefix *par-* (i.e., besides, alongside) to the genus name. Similarly, we fuse the prefix *iso-* (i.e., similar, equal, the same) to the genus name. The name is a masculine noun in the nominative singular.

Species included. The type species (i.e., *Pamphila* (?) *mackenii* Trimen, 1868), *Acleros bibundica* Strand, 1913, *Acleros instabilis* Mabille, 1889, *Apaustus olaus* Plötz, 1884, *Acleros ploetzi* Mabille, 1889, and a new species described below.

Parent taxon. Genus *Acleros* Mabille, 1885.

Acleros (*Isocleros*) *instabilis* Mabille, 1889 and *Acleros* (*Isocleros*) *olaus* (Plötz, 1884) are species distinct from *Acleros* (*Isocleros*) *mackenii* (Trimen, 1868)

Inspection of genomic trees (Figs. 45, 46) and analysis of genetic differentiation reveals that *Acleros instabilis* Mabille, 1889 (type locality in Tanzania) and *Apaustus olaus* Plötz, 1884 (type locality in Congo, syntype sequenced as NVG-18073C07) currently treated as subspecies of *Acleros* (*Isocleros*) *mackenii* (Trimen, 1868), (type locality in South Africa, possible syntype sequenced as NVG-20126G11)

are genetically differentiated from it with F_{st}/COI barcode difference of 0.23/4% (26 bp) and 0.49/2.6% (17 bp), respectively, and from each other with 0.39/4.7% (31 bp). Therefore, we propose to reinstate these two taxa as species: *Acleros* (*Isocleros*) *instabilis* Mabille, 1889, **stat. rest.** and *Acleros* (*Isocleros*) *olaus* (Plötz, 1884), **stat. rest**.

Acleros nyassicola Strand, 1921 is a junior subjective synonym of *Acleros* (*Isocleros*) *olaus* (Plötz, 1884), not of *Acleros* (*Isocleros*) *mackenii* (Trimen, 1868)

In the genomic trees, the holotype of *Acleros nyassicola* Strand, 1921 (type locality in Malawi, sequenced as NVG-20082G06, in SDEI) reveals that it is not conspecific with *Acleros* (*Isocleros*) *mackenii* (Trimen, 1868), (type locality in South Africa, possible syntype sequenced as NVG-20126G11) and instead groups with *Acleros* (*Isocleros*) *olaus* (Plötz, 1884), **stat. rest.** (type locality in Congo, syntype sequenced as NVG-18073C07) (Figs. 45, 46). Therefore, we propose to treat *Acleros nyassicola* Strand, 1921 as a junior subjective synonym of *Acleros* (*Isocleros*) *olaus* (Plötz, 1884).

Acleros (*Isocleros*) *togo* Grishin, new species
http://zoobank.org/10245D25-D8E1-4342-A2AA-0104A185EA97
(Figs. 45–46 part, 47)

Definition and diagnosis. Genomic trees reveal that two specimens from Western Africa identified as *Acleros olaus* (Plötz, 1884), **stat. rest.** (type locality in Congo, syntype sequenced as NVG-18073C07) are not monophyletic with *A. olaus* and form a clade approximately equidistant from it and *Acleros mackenii* (Trimen, 1868) (type locality in South Africa, possible syntype sequenced as NVG-20126G11) with *Acleros instabilis* Mabille, 1889, **stat. rest.** (type locality in Tanzania) (Figs. 45, 46), suggesting that these two specimens belong to a distinct species. Its genetic differentiation measured by F_{st}/COI barcode difference is: 0.31/5.5% (36 bp) from *A. olaus*, 0.31/4.7% (31 bp) from *A. mackenii*, and 0.41/5.3% (35 bp from *A. instabilis*, which is substantial and provides strong support for these two specimens as
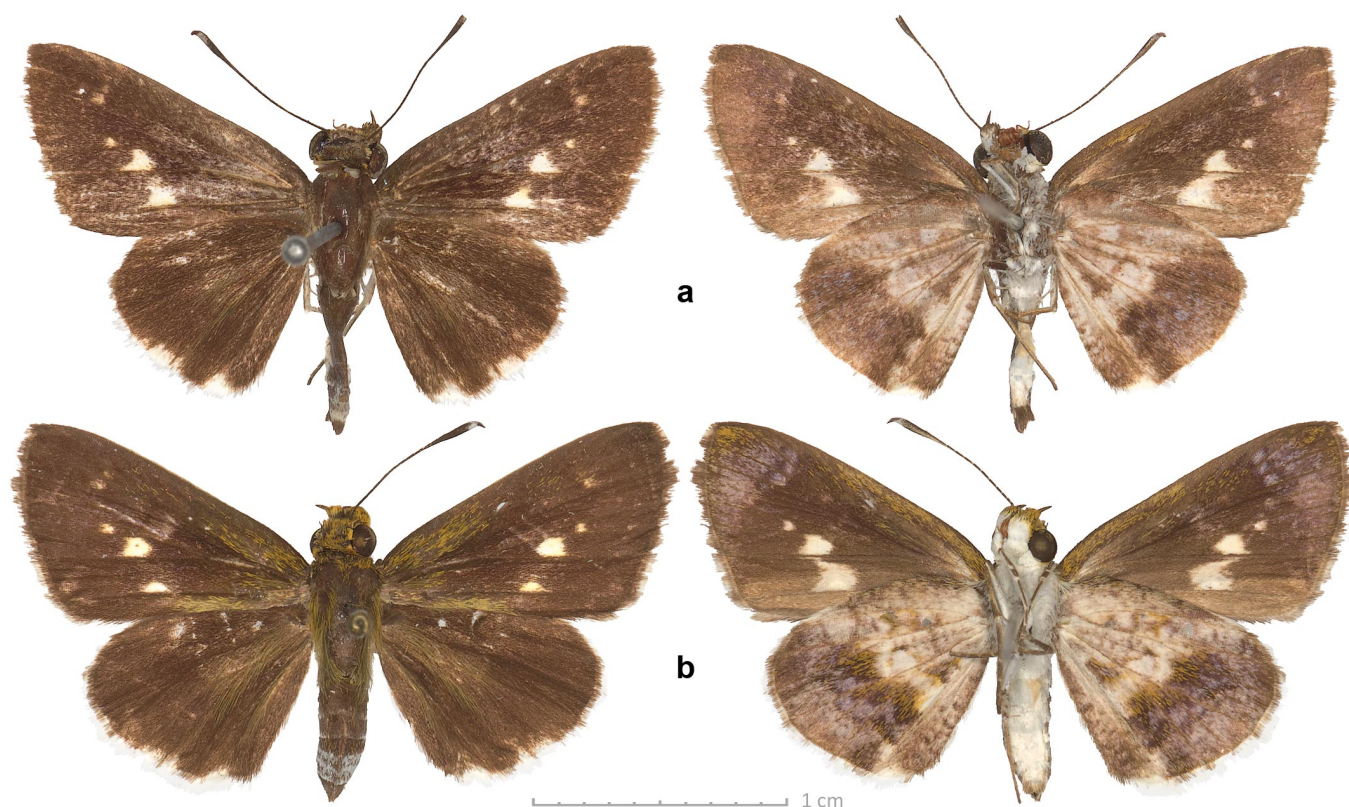
Fig. 47. Holotype ♂ (**a**) and paratype ♀ (**b**) of *Acleros togo* **sp. n.** in dorsal (left) and ventral (right) views, data in text.

representatives of a new species. This species is distinguished from its relatives by the following combination of characters: forewing subapical spots are present, yellowish above and purplish beneath (not white in the specimens of the type series), diffuse, nearly in line (spot by costa is not strongly offset distad from others), other forewing spots are crisper, with sharper defined edges, the spot in cell CuA_2-$1A+2A$ on ventral forewing is with equally sharp edges (not more diffuse and disappearing towards the outer margin), forewing spot in cell CuA_1-CuA_2 is closer to the spot in cell CuA_2-$1A+2A$ than in *A. olaus*. Due to variability in phenotype, this rather cryptic species is confidently identified by DNA: in the nuclear genome: aly164.2.2:C73A, aly173.7.6:A182T, aly8937.5.1:A305G, aly1260.26.1:A247G, aly24.4.2: G63T and in the COI barcode: T38A, T91C, T376A, G380A, A514C, T571C.

Barcode sequence of the holotype: Sample NVG-22017G12, GenBank OR589638, 658 base pairs:

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AACTTTATATTTTATTTTTGGTATTTGAGCAGGTATAATAGGATCATCTTTAAGATTATTAATTCGTACAGAATTAGGTAACCCTGGATCCTTAATCGGAGATGATCAAATTTATAATACA
ATTGTTACAGCTCATGCTTTTATTATAATTTTTTTTATAGTAATACCTATTATAATTGGAGGATTTGGTAATTGATTAGTTCCTCTTATATTAGGAGCTCCTGATATAGCTTTCCCCCGAA
TAAATAATATAAGATTTTGAATACTTCCCCCATCTTTAACATTATTAATTTCAAGAAGAATTGTAGAAAATGGTGCTGGAACTGGCTGAACTGTTTACCCCCCTCTTTCTTCTAATATTGC
ACATCAAGGATCATCAATTGATTTAGCTATTTTTTCTTTACATTTAGCCGGAATTTCATCTATTTTAGGAGCTATTAATTTTATTACAACTATTATTAATATACGAATTAAAAATATATCA
TTTGATCAATTACCTTTATTTATTTGATCCGTAGGTATTACTGCTTTACTTTTACTTTTATCTCTACCTGTTTTAGCAGGTGCTATCACAATACTTCTTACTGACCGAAACTTAAATACTT
CTTTTTTCGATCCTGCCGGAGGAGGAGATCCTATTTTATATCAACATTTATTT
```

Type material. Holotype: ♂ deposited in the Zoologische Staatssammlung München, Germany [ZSMC], illustrated in Fig. 47a, bears six labels: 2nd blue, last red, and others white [43390], [Togo | Misahöhe | 1893 | E. Baumann S.], [363 | 7.XII.93 | A. olaus], [olaus | Plötz], [DNA sample ID: | NVG-22017G12 | c/o Nick V. Grishin], and [HOLOTYPE ♂ | *Acleros* (*Isocleros*) | *togo* Grishin]. **Paratype:** ♀ Liberia: Monrovia, Firestone Plantation, Dec-1946, Harry A. Beatty leg. (NVG-22047H11) [CUIC] (Fig. 47b).

Type locality. Togo: Misahöhe.

Etymology. The name is given for the country with the type locality. The name is a noun in apposition.

Distribution. Western Africa, recorded from Togo and Liberia.

Taxonomic rearrangement of species currently in the genus *Meza* Hemming, 1939

The genus *Meza* Hemming, 1939 (type species *Hesperia meza* Hewitson, 1877) currently consists of 10 species. Genomic trees reveal that the genus is not monophyletic (Figs. 45, 46) and partitions according to the three sections of the identification key provided by Evans (1937): (i) no secondary sexual characters; (ii) male dorsal hindwing with a hair tuft that overlays bases of veins CuA_1 and CuA_2 and (iii) hair tuft enters a pouch either at the end of discal cell or along the median vein. The type species *M. meza*— section (i), no tuft—belongs to the tribe Ceratrichiini Grishin, 2019 and other species (with tuft) belong to two clades in the tribe Astictopterini Swinhoe, 1912. Section (ii) consists of three species and is sister to the genus *Fresna* Evans, 1937 (type species *Hesperia netopha* Hewitson, 1878). Although this clade is prominent, it is at the tree level of a subgenus (Figs. 45, 46). We include these species in *Fresna*, forming the following new combinations: *Fresna larea* (Neave, 1910), **comb. nov.**, *Fresna leucophaea* (Holland, 1894), **comb. nov.**, and *Fresna mabea* (Holland, 1894), **comb. nov**. All the remaining species are from section (iii) and are dispersed within the clade corresponding to the genus *Paronymus* Aurivillius, 1925 (type species *Hesperia ligora* Hewitson, 1876) (Figs. 45, 46). We assign them to this genus, forming new combinations: *Paronymus banda* (Evans, 1937), **comb. nov.**, *Paronymus cybeutes* (Holland, 1894), **comb. nov.**, *Paronymus elba* (Evans, 1937), **comb. nov.**, *Paronymus gardineri* (Collins & Larsen, 2008), **comb. nov.**, *Paronymus indusiate* (Mabille, 1891), **comb. nov.**, *Paronymus mabillei* (Holland, 1893), **comb. nov**. As a result, *Meza* becomes monotypic to consist of only the type species *M. meza*, while other species currently in *Meza* are transferred to *Fresna* or *Paronymus*.

Mesna Grishin, new subgenus
http://zoobank.org/A3DDA72C-3E34-42E8-82FF-457715B8E65E

Type species. *Parnara leucophaea* Holland, 1894.

Definition. As discussed above, *Meza* Hemming, 1939 (type species *Hesperia meza* Hewitson, 1877) was not monophyletic, and some of its species formed a clade sister to *Fresna* Evans, 1937 (type species

Hesperia netopha Hewitson, 1878) (Figs. 45, 46). To restore the monophyly, we placed these species in *Fresna*. However, they are genetically and morphologically distinct from other *Fresna* and constitute a new subgenus. Species of this new subgenus key to 44.B. in Evans (1937) and are distinguished from similar-looking species (e.g., *Meza* and *Paronymus*) by the following characters: male dorsal hindwing with a hair tuft that overlays bases of veins CuA_1 and CuA_2 (does not enter a pouch either at the end of discal cell or along the median vein as in *Paronymus*; *Meza* lacks the tuft) and uncus narrowly squared at the tip in dorsal view, not terminating in a sharp point (as in *Paronymus*), and not bulb-shaped (as in *Meza*). A combination of the following nuclear genomic base pairs is diagnostic: aly1249.14.7:T1966C, aly1249.14.7:C2004T, aly536.106.2:A3984G, aly1656.5.1:A135C, aly8937.7.1:A198C.

Etymology. The name indicates that these species started in the genus *Me*[za] and ended in [Fre]*sna*. The name is a feminine noun in the nominative singular.

Species included. The type species (i.e., *Parnara leucophaea* Holland, 1894), *Meza leucophaea bassa* Lindsey & L. Miller, 1965 (see below), *Parnara larea* Neave, 1910, and *Parnara mabea* Holland, 1894.

Parent taxon. Genus *Fresna* Evans, 1937.

Fresna (*Mesna*) *bassa* (Lindsey & L. Miller, 1965) is a species distinct from *Fresna* (*Mesna*) *leucophaea* (Holland, 1894)

Genetic differentiation between *Meza leucophaea bassa* Lindsey & L. Miller, 1965 (type locality in Liberia, holotype sequenced as NVG-20124H07) that we placed in the genus *Fresna* Evans, 1937 (type species *Hesperia netopha* Hewitson, 1878) and *Fresna leucophaea leucophaea* (Holland, 1894) (type locality in Gabon, syntypes sequenced as NVG-21099F07 and NVG-21099F08) is notable, e.g., COI barcode differ by 3.3% (22 bp) and the two taxa form separate clades in genomic trees (Figs. 45, 46). Therefore, we propose that *Fresna* (*Mesna*) *bassa* (Lindsey & L. Miller, 1965), **stat. nov.** is a species distinct from *Fresna* (*Mesna*) *leucophaea* (Holland, 1894).

Paronymus volta (L. Miller, 1971) is a species distinct from *Paronymus cybeutes* (Holland, 1894)

Genetic differentiation as measured by F_{st}/COI barcode difference between *Meza cybeutes volta* Miller, 1971 (type locality in Ghana, holotype sequenced as NVG-21043D12) that we placed in the genus *Paronymus* Aurivillius, 1925 (type species *Hesperia ligora* Hewitson, 1876) and *Paronymus leucophaea leucophaea* (Holland, 1894) (type locality in Gabon, syntype sequenced as NVG-21099G06) is: 0.43/3.8% (25 bp) and the two taxa form separate clades in genomic trees (Figs. 45, 46). Therefore, we propose that *Paronymus volta* (L. Miller, 1971), **stat. nov.** is a species distinct from *Paronymus cybeutes* (Holland, 1894). *Paronymus cybeutes pallida* (Holland, 1896) (type locality in Congo) does not differ prominently from the nominotypical subspecies, and we retain it as a subspecies of *P. cybeutes*.

Ceratricula Larsen, 2013 is a junior subjective synonym of *Paronymus* Aurivillius, 1925

The genus *Ceratricula* Larsen, 2013 (type species *Ceratrichia semilutea* Mabille, 1891) forms a tight clade within *Paronymus* Aurivillius, 1925 (type species *Hesperia ligora* Hewitson, 1876) that is a confident sister to *Paronymus xanthias* (Mabille, 1891) (type locality in Nigeria) (Figs. 45, 46) rendering *Paronymus* paraphyletic. To restore the monophyly, we propose that *Ceratricula* Larsen, 2013, **syn. nov.** is a junior subjective synonym of *Paronymus* Aurivillius, 1925.

Paronymus punctata (Holland, 1896), new combination; its type locality is Sierra Leone: Freetown

The name *Ceratrichia punctata* (type locality in "Tropical West Africa") was published by Holland (1896) in synonymy with *Ceratrichia phocion* (Fabricius, 1781) (type locality in South Africa) and attributed to Mabille as a "MS. name", with the holotype specimen ("another male … has been designated as the type") from the Staudinger collection, now in MFNB. A short description was provided: "primaries more spotted than is quite usual." Evans (1937) used the name "*Ceratrichia punctata* Holland" as valid, attributing it to Holland's publication and citing the same "type" specimen in Berlin. Therefore, under Articles 11.6.1 and 50.7 of the ICZN Code (1999), the name *Ceratrichia punctata* Holland 1896 is currently both available and valid and is based on the holotype in Berlin. N.V.G. found the holotype, which bears a purple "Origin." label, an identification label in Mabille's handwriting, "C. punctata / Mab. ♂", and an identification label in Holland's handwriting, "Ceratrichia / phocion, / ♂", among several others. The locality label on the holotype is "Frtn. / Pr." meaning that it was collected by Preuss in Freetown, Serra Leone. German botanist Paul Rudolph Preuss collected in Sierra Leone in 1886–1888 (Barnhart 1965), giving a possible range of dates when the holotype was captured.

Genomic sequencing of the holotype (NVG-18073A05) places it as sister to *Paronymus semilutea* (Mabille, 1891) (type locality in Nigeria, syntype sequenced as NVG-21118G05) (Figs. 45, 46), being distinct from it due to genetic differentiation, e.g., COI barcode difference of 2.1% (14 bp). Therefore, we propose *Paronymus punctata* (Holland, 1896), **comb. nov**. The holotype of *P. punctata* is not conspecific with the species Evans (1937) identified as *C. punctata*: e.g., the holotype has ventral forewing nearly uniformly brown without pale areas by the inner margin characteristic of Evans' *C. punctata*; smaller forewing and ventral hindwing spots, and brownish tuft of hair-like scales by the base of dorsal hindwing. Evans' *C. punctata* lacks androconia and is a species of *Ceratrichia* Butler, 1870 (type species *Papilio nothus* Fabricius, 1787); it does not have a name. This new species is described below.

Ceratrichia notata Grishin, new species
http://zoobank.org/3BD674EC-B100-4309-8181-393A29D4EE03

Definition and diagnosis. As shown above, Evans misidentified *Paronymus punctata* Holland, 1896, **comb. nov**. The distinctive species he considered "*Ceratrichia punctata*" does not have a name and is new. This new species keys to 31.A.(b)(b^2)(a^3) in Evans (1937) and is identified by a combination of brown dorsal forewing with white dots, single (upper) dot in discal cell, ventrally with pale-yellow area by inner margin; most of dorsal hindwing is yellow with costal third brown, ventrally pale yellow, not white, broadly brown at the outer margin and with submarginal dots encircled with brown, such dot in the discal cell, and (frequently replaced with brown spots) 3–4 additional dots around.

Type material. Holotype: ♂ deposited in the African Butterfly Research Institute, Nairobi, Kenya [ABRI], collected in Central African Republic: Zomea, Oct-1982, ABRI-2019-2412, and its photographs can be found in Williams (2023a), as the male "*Ceratrichia punctata*" (misidentification). **Paratypes:** 2♂♂ 2♀♀: 1♀ with the same data as the holotype but Sep-1996 and ABRI-2019-2413; others in BMNH: 1♂ 1♀ from Cameroon and 1♂ from Angola.

Type locality. Central African Republic: Zomea.

Etymology. This species was previously misidentified as "*punctata*", which means "dotted" in Latin. A Latin synonym of "punctata" is "notata", which is adopted as the name of this species. The name "notata" can also be translated as "noted", and this species is noted for its larger white dots and bright colors and for the confusion about its name due to misidentification that genomic analysis of primary type specimens helped to resolve. The name is a feminine adjective.

Distribution. Western Africa, recorded from Cameroon, Central African Republic, and Angola.

Paronymus indeterminabilis (Strand, 1912) and *Paronymus congdoni* (Larsen, 2013) are species distinct from *Paronymus semilutea* (Mabille, 1891)

Genomic trees reveal that sister taxa *Ceratrichia indeterminabilis* Strand, 1912 (type locality Equatorial Guinea [not Cameroon!]: Benito [river] area, Monte Alen, syntypes sequenced as NVG-18073A07 and NVG-18073A08) and *Ceratricula semilutea congdoni* Larsen, 2013 (type locality in Uganda) prior to this publication treated as subspecies of *Ceratricula semilutea* (Mabille, 1891) (type locality Nigeria: Lagos, syntype sequenced as NVG-21118G05) that we placed in *Paronymus* Aurivillius, 1925 (type species *Hesperia ligora* Hewitson, 1876) (see above), are not monophyletic with *C. semilutea* (Figs. 45, 46) and are well differentiated from it genetically with COI barcode difference of 3.0% (20 bp) and 3.6% (24 bp), respectively, and from each other of 3.3% (22 bp). Therefore, we propose to treat them as species-level taxa: *Paronymus indeterminabilis* (Strand, 1912), **stat. rest.** and *Paronymus congdoni* (Larsen, 2013), **stat. nov**.

Semalea corvinus (Mabille, 1890) is a species distinct from *Semalea sextilis* (Plötz, 1886)

Genomic sequencing of *Cobalus corvinus* Mabille, 1890 (type locality in Sierra Leone, type sequenced as NVG-18075A05) currently treated as a junior subjective synonym of *Semalea sextilis* (Plötz, 1886) (type locality in Ghana) reveals that it is not monophyletic with it and instead originates deep in the radiation of *Semalea* Holland, 1896 (type species *Hesperia pulvina* Plötz, 1879) (Figs. 45, 46). Therefore, we reinstate *Semalea corvinus* (Mabille, 1890), **stat. rest.** as a species-level taxon.

Xanthodisca Aurivillius, 1925 is a junior subjective synonym of *Semalea* Holland, 1896

Genomic trees reveal that *Semalea* Holland, 1896 (type species *Hesperia pulvina* Plötz, 1879) in paraphyletic with respect to *Xanthodisca* Aurivillius, 1925 (type species *Astictopterus vibius* Hewitson, 1878) (Figs. 45, 46). Restoring monophyly, we propose that *Xanthodisca* Aurivillius, 1925, **syn. nov.** is a junior subjective synonym of *Semalea* Holland, 1896 due to genetic similarity.

Semalea malawi Grishin, new species
http://zoobank.org/A1AA303B-9ABF-4F7C-B84B-2ABD765583DF
(Figs. 45–46 part, 48)

Definition and diagnosis. The mitochondrial genome tree reveals that a specimen from Malawi identified as *Semalea vibius* (Hewitson, 1878), **comb. nov.** (type locality in Gabon) is sister to both *S. vibius* and *Semalea rega* (Mabille, 1889), **comb. nov.** (type locality in Sierra Leone) (Fig. 46), suggesting that it is a third species distinct from them. We sequenced primary type specimens of all four names associated with *S. rega* and confirmed their synonymy (Figs. 45, 46). Specimens from western Africa (Cameroon, Congo) serve as references for *S. vibius*. Therefore, the third species is new. In the COI barcode, it differs from *S. vibius* by 1.1% (7 bp), which is larger than the difference between *S. vibius* and *S. rega* of 0.6% (4 bp). Despite this moderate difference in the barcode, F_{st}/G_{min} of 0.35/0.008 for *S. vibius* and *S. rega* indicate that they are distinct species, in agreement with phenotypic distinction. However, we could not compute these statistics for the new species because it is known from a single specimen (at least two specimens are needed). This new species is distinguished from its relatives by the lack of subapical spots on the forewing, larger forewing orange patch that reaches closer to the outer margin, palpi beneath and cheeks more orange than yellow in color, and largely brown ventral hindwing, which is unspotted, and sparsely overscaled with orange. Due to variability in phenotype, confidently identified by DNA: in the nuclear genome: aly281.6.2:A130G, aly281.6.2:C131T, aly1249.8.1:T514C, aly1603.31.1:A370C, aly37338.23.1:C264T, aly54.4.1:T1461T (not A), aly6648.1.2:A161A (not C), aly5294.20.2:T630T (not C), aly386.8.2:A506A (not T), aly393.3.1:A492A (not G) and in the COI barcode: T88C, T118C, T139A, T202C, T547T, T610T, T646T.

Fig. 48. Holotype of *Semalea malawi* **sp. n.** in dorsal (left) and ventral (right) views, data in text.

Barcode sequence of the holotype: Sample NVG-19043B12, GenBank OR589640, 658 base pairs:

AACTTTATATTTTATTTTTGGTATTTGAGCAGGTATATTAGGAACATCTTTAAGTTTATTAATTCGAACTGAATTAGGTAATCCTGGCTCATTAATTGGAGATGATCAAATTTATAACACA
ATTGTAACAGCTCATGCATTTATTATAATTTTTTTTATAGTTATACCTATTATAATTGGAGGATTTGGAAATTGATTAGTCCCTTTAATATTAGGAGCTCCTGATATAGCTTTCCCACGAA
TAAATAATATAAGATTTTGATTACTTCCCCCCTCCCTTACCTTATTAATCTCAAGAAGAATTGTAGAAAATGGAGCTGGAACTGGATGAACTGTCTATCCCCCCCTTTCATCTAATATTGC
TCACCAAGGTTCTTCTGTTGATTTAGCAATCTTTTCTTTACATTTAGCAGGAATTTCTTCTATTTTAGGAGCTATTAATTTTATTACTACAATTATTAATATACGAATTAAAAATTTATCT
TTTGATCAACTACCTTTATTTGTTTGATCTGTTGGTATTACTGCTTTACTTCTTCTTCTTTCTTTACCTGTTTTAGCTGGAGCTATTACAATATTATTAACTGATCGTAATCTTAATACTTT
CTTTTTTTGACCCTGCTGGAGGAGGAGACCCTATTCTTTATCAACATTTATTT

Type material. Holotype: ♂ deposited in the American Museum of Natural History, New York, NY, USA [AMNH], illustrated in Fig. 48, bears five labels: four white [11-viii-40. | ♂ | Vizara | 2600'. | Nyasaland | R. C. Wood], [vibius | vibius | ♂], [DNA sample ID: | NVG-19043B12 | c/o Nick V. Grishin], [{QR Code} | AMNH_IZC 00337937], and one red [HOLOTYPE ♂ | *Semalea malawi* | Grishin].

Type locality. Malawi: ca. 9 mi E of Nkhata Bay, Vizara Rubber Plantation, elevation 2600'.

Etymology. The name is given for the country with the type locality. The name is a noun in apposition.

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

The type locality of *Osmodes staudingeri* Holland, 1896 is Cameroon: Efoulan

The type locality of *Osmodes staudingeri* Holland, 1896, currently treated as a junior subjective synonym of *Semalea rega* (Mabille, 1889), **comb. nov.** (type locality in Sierra Leone) was given in the original description as "Valley of the Ogové" (Holland 1896), which is in Gabon, frequently spelled as Ogooué River Valley. This species was described from the female holotype in Holland's collection, which is in CMNH: "Type [not types] in my collection" and "I do not know the male of this species. The solitary female in my collection …," which was illustrated (Holland 1896). N.V.G. found a female in CMNH with the following five labels, white, but the 4th (without any text) red: [Efulen, | Kamerun, | A. I. Good | C. M. Acc. 4454], [Osmodes | staudingeri | ♀ type Holl.], [unknown | to Mabille], [ ], [DNA sample ID: | NVG-20125A08 | c/o Nick V. Grishin]. The female matches the original description perfectly and agrees with the illustration rather closely. Provided that it carries its identification label (2nd label) in Holland's handwriting, it is the holotype of *O. staudingeri*. However, the locality label does not mention "Valley of the Ogové," but points to Cameroon: Efoulan (in current spelling). This is a more likely locality because this species is not otherwise known from Gabon but recorded from Cameroon (Williams 2023b). Therefore, we hypothesize that the locality in the original description is erroneous, and the locality label on the holotype points to its provenance. Hence, the type locality of *O. staudingeri* is Cameroon: Efoulan, and genomic sequencing of the holotype confirms this taxon as a junior subjective synonym of *S. rega* (syntype in MFNB sequenced as NVG-18073A03) (Figs. 45, 46).

Xanthoneura patmapana (Fruhstorfer, 1911) is a species distinct from *Xanthoneura corissa* (Hewitson, 1876)

Two phenotypically different subspecies, *Xanthoneura corissa corissa* (Hewitson, 1876) (type locality in Kalimantan) and *Xanthoneura corissa patmapana* (Fruhstorfer, 1911) (type locality in Java), are genetically differentiated (Figs. 45, 46) and differ by 4.1% (27 bp) in their barcodes. Therefore, we propose treating *Xanthoneura patmapana* (Fruhstorfer, 1911), **stat. nov.** as a species distinct from *Xanthoneura corissa* (Hewitson, 1876).

Lippina Grishin, new subgenus
http://zoobank.org/22B4014B-4B5D-45D4-8283-6C65583887B7

Type species. *Carystus telesinus* Mabille, 1878.

Definition. Genomic trees reveal that while *Xanthoneura* Eliot, 1978 (type species *Hesperia corissa* Hewitson, 1876) is monophyletic (and we keep it as a single genus), it deeply splits into two clades: the nominotypical and unnamed that represents a new subgenus. Members of this new subgenus key to J.10.23. in Evans (1949) and are distinguished from their relatives by the 3rd segment of palpi stout and bent forward, ventral hindwing largely unmarked (or with a central spot), veins not yellower, forewing with a spot in cell M_2-M_3 right above the spot in cell M_3-CuA_1, these two spots together give an appearance of a single larger spot; uncus in dorsal view much narrower than long, narrowing in the middle, divided, arms small knob-like, not widely separated. A combination of the following nuclear genomic base pairs is diagnostic: aly577.16.2:T174C, aly577.16.2:T198A, aly577.16.2:A216G, aly1591.7.3: A333C, aly1222.40.2:A15G.

Etymology. The species of this subgenus are from [Phi]*lippin*[es]+a. The name is a feminine noun in the nominative singular.

Species included. The type species (i.e., *Carystus telesinus* Mabille, 1878) and *Xanthoneura obscurior* de Jong & Treadaway, 2007.

Parent taxon. Genus *Xanthoneura* Eliot, 1978.

Perrotia Oberthür, 1916 is a junior subjective synonym of *Galerga* Mabille, 1898

Genomic trees reveal a tight clade of Malagasy species sister to a Malagasy genus *Fulda* Evans, 1937 (type species *Hesperia coroller* Boisduval, 1833) (Fig. 45, 46). Currently, these species are placed in two genera: *Perrotia* Oberthür, 1916 (type species *Perrotia albiplaga* Oberthür, 1916) and *Galerga* Mabille, 1898 (type species *Galerga hyposticta* Mabille, 1898). However, the two genera are genetically close, e.g., the COI barcode difference between their type species is 7.3% (48 bp), and not distinctly differentiated from each other. Therefore, we propose to treat *Perrotia* Oberthür, 1916, **syn. nov.** is a junior subjective synonym of *Galerga* Mabille, 1898.

Galerga ariel (Mabille, 1878), new combination

Currently in *Xanthodisca* Aurivillius, 1925 (type species *Astictopterus vibius* Hewitson, 1878), *Pamphila ariel* Mabille, 1878 (type locality in Madagascar) is not monophyletic with it and instead originates deep within *Galerga* Mabille, 1898 (type species *Galerga hyposticta* Mabille, 1898) (Figs. 45, 46), where we place it as *Galerga ariel* (Mabille, 1878), **comb. nov.**

Afrotropical species of *Astictopterus* C. Felder & R. Felder, 1890 belong to *Isoteinon* C. Felder & R. Felder, 1862

Genomic trees reveal that Afrotropical species currently placed in *Astictopterus* C. Felder & R. Felder, 1860 (type species *Astictopterus jama* C. Felder & R. Felder, 1860) are not monophyletic with it and

instead originate within *Isoteinon* C. Felder & R. Felder, 1862 (type species *Isoteinon lamprospilus* C. Felder & R. Felder, 1862) (Fig. 45, 46). Therefore, to restore monophyly, we transfer these species from *Astictopterus* to *Isoteinon*, forming the following new combinations: *Isoteinon anomoeus* (Plötz, 1879), **comb. nov.** (type locality in Ghana), *Isoteinon bruno* (Evans, 1937), **comb. nov.** (type locality in Tanzania), *Isoteinon inornatus* (Trimen, 1864), **comb. nov.** (type locality in South Africa), and *Isoteinon punctulata* (A. Butler, 1895), **comb. nov.** (type locality in Tanzania).

Mopala Evans, 1937 is a subgenus of *Leona* Evans, 1937

The monotypic genus *Mopala* Evans, 1937 (type species *Ismene ? orma* Plötz, 1879), which stands out by the large white patch on ventral hindwing and otherwise unspotted wings, is genetically close to *Leona* Evans, 1937 (type species *Hesperia leonora* Plötz, 1879) in our genomic trees (Fig. 45, 46), while they both are distant from other genera that are their closest relatives. Male genitalia in both genera are similar in the shape of uncus and valva, and all these species could be accommodated within one genus. Because *Mopala* and *Leona* were described in the same work published on the same date, as the first revisers, we give priority to *Leona* due to it being a larger genus, and propose that *Mopala* Evans, 1937 **stat. nov.** is a subgenus of *Leona* Evans, 1937.

Ganda Grishin, new subgenus
http://zoobank.org/9A4C7BA6-2C42-47E6-B619-E54A20FF850E

Type species. *Zophopetes ganda* Evans, 1937.

Definition. Described by Evans (1937) in the genus *Zophopetes* Mabille, 1904 (type species *Pamphila dysmephila* Trimen, 1868) and kept in it since, *Z. ganda* (type locality in Ivory Coast) is not monophyletic with *Zophopetes* and instead is in the same clade with *Leona* Evans, 1937 (type species *Hesperia leonora* Plötz, 1879) and its subgenus *Mopala* Evans, 1937 (type species *Ismene ? orma* Plötz, 1879): sister to the subgenus *Leona* in the nuclear genome tree (Fig. 45) and sister to both *Leona* and *Mopala*, but less confidently, in the mitochondrial genome tree (Fig. 46). In either case, it is closely related to them both and yet genetically differentiated from them at approximately the same level as they are from each other. Therefore, similarly to *Mopala*, the lineage with *Z. ganda* represents a subgenus of *Leona*. This new subgenus keys to 53.A. in Evans (1937) and is distinguished from its relatives by males with a brand (from the base of vein CuA_1 to near vein 1A+2A) and an apical spot on dorsal forewing (both absent in *Zophopetes*), ventral hindwing uniformly pale-brown with small dark-brown-framed spots (not like *Leona* and *Mopala*); upturned harpe, uncus in dorsal view narrower than in *Zophopetes*, especially in the middle, with smaller knob-shaped arms. A combination of the following nuclear genomic base pairs is diagnostic: aly1038.19.1:T165C, aly1405.10.1:T456C, aly925.11.3:A69G, aly587.17.1:T205A, aly2127.3.3:A24G, aly1838.61.1:T618T (not C), aly1838.61.1:T675T (not A), aly4305.26.4:C31C (not G), aly27.16.1:C354C (not A), aly614.16.1:A1098A (not G).

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 *Leona* Evans, 1937.

Balenga Grishin, new genus
http://zoobank.org/21C6F5FF-4E85-4D88-AD3B-D010B1F11F7B

Type species. *Proteides balenge* Holland, 1891.

Definition. Currently, Gretnini Grishin, 2019 is a monotypic tribe consisting of a single genus *Gretna* Evans, 1937 (type species *Hesperia cylinda* Hewitson, 1876). Inspection of genomic trees reveals that *Grenta balenge* (Holland, 1891) (type locality in Gabon) is strongly differentiated genetically from the

rest of the genus (e.g., COI barcode difference of 10.9%, 72 bp), at least to the same extent as *Isma* Distant, 1886 (type species *Isma obscura* Distant, 1886) from *Iambrix* Watson, 1893 (type species *Nisoniades salsala* F. Moore, 1866) or *Hyarotis* F. Moore, 1881 (type species *Papilio adrastus* Stoll, 1780) from *Quedara* Swinhoe, 1919 (type species *Quedara comoplea* Swinhoe, 1919) and is at the tree level corresponding to genera. Therefore, the lineage with *G. balenge* represents a genus-level taxon (Fig. 49). This new genus keys to 57.B. in Evans (1937) and is distinguished from its relatives by the subapical forewing spot in cell R_5-M_1 being offset distad from others, uncus with processes at its base directed sideways (one on each side, no processes in *Gretna*), and deeper separation between harpe and ampulla that is more expanded than in *Gretna*. A combination of the following COI barcode base pairs is diagnostic: T206C, A494T, A520C, A562C, A586T.

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

Species included. Only the type species.

Parent taxon. Tribe Gretnini Grishin, 2019.
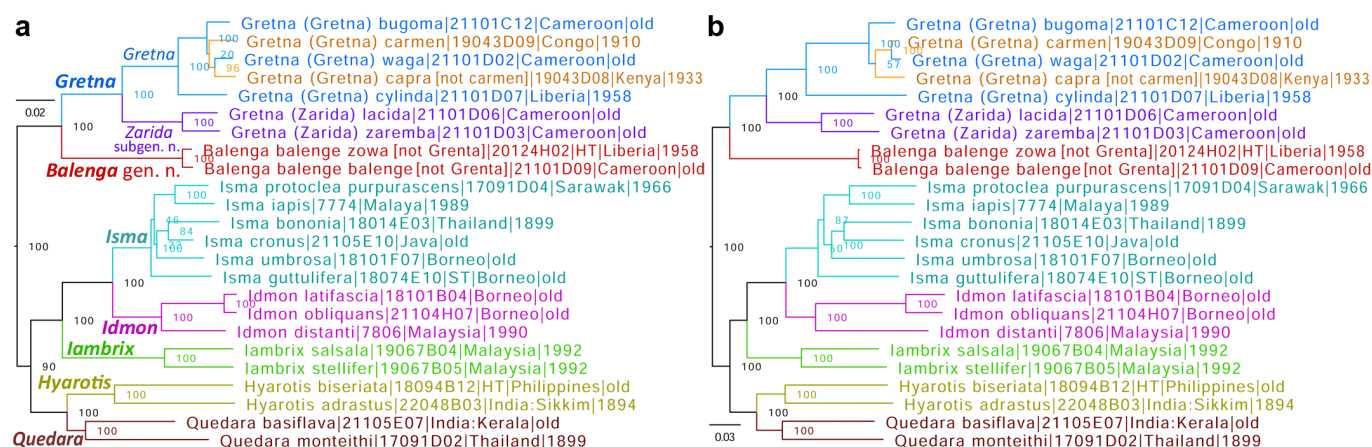
Fig. 49. Phylogenetic trees of selected Gretnini species and ingroups inferred from protein-coding regions of **a)** the nuclear (autosomes) and **b)** the mitochondrial genomes. Different genera are shown in different colors: *Gretna* (blue with subgenus *Zarida* **subgen. n.** in violet and *Gretna capra* **stat. nov.** with *Gretna carmen* in orange), *Balenga* **gen. n.**, *Isma* (cyan), *Idmon* (magenta), *Iambrix* (green), *Hyarotis* (olive), and *Quedara* (brown).

Zarida Grishin, new subgenus

http://zoobank.org/699B2792-5716-45FF-B4D9-477760251BD8

Type species. *Hesperia lacida* Hewitson, 1876.

Definition. Within a smaller genus *Gretna* Evans, 1937 (type species *Hesperia cylinda* Hewitson, 1876) due to removal of *Balenga balenge* Holland, 1891, **comb. nov.** (type locality in Gabon), we note the genetic differentiation of a clade sister to that with the type species (Fig. 49). This clade diverges from other *Gretna* at least at the tree level corresponding to subgenera (if not genera), i.e., approximately the same as *Isma* Distant, 1886 (type species *Isma obscura* Distant, 1886) from *Idmon* Nicéville, 1895 (type species *Baoris unicolor* Distant, 1886, a junior homonym, available name for this species is *Iambrix distanti* Shepard, 1937) (Fig. 49), and we regard it as representing a subgenus. This new subgenus keys to 53.A.(a)(b[1]) in Evans (1937) and is distinguished from its relatives by an undivided and much narrower uncus, almost spike-shaped in dorsal view; better developed (and hyaline) spot in the middle of dorsal hindwing, prominent spot in forewing cell CuA_2-1A+2A, and clearly defined whitish bands or area on ventral hindwing. A combination of the following COI barcode base pairs is diagnostic: T56C, T154C, T379A, T553A, T556A.

Etymology. The name is a feminine noun in the nominative singular and is a fusion of species names in this subgenus: *Zar*[emba]+[lac]*ida*.

Species included. The type species (i.e., *Hesperia lacida* Hewitson, 1876) and *Telesto zaremba* Plötz, 1884.

Parent taxon. Genus *Gretna* Evans, 1937.

Gretna capra Evans, 1937 is a species distinct from *Gretna carmen* Evans, 1937

Originally proposed as a subspecies, *Gretna carmen capra* Evans, 1937 (type locality in Kenya) is not monophyletic with *Gretna carmen* Evans, 1937 (type locality in Cameroon) in genomic trees (Fig. 49) and is strongly differentiated from it genetically, e.g., COI barcode difference of 3.6% (24 bp). Therefore, we propose that *Gretna capra* Evans, 1937, **stat. nov.** is a species distinct from *Gretna carmen* Evans, 1937, as hinted by Larsen (1991).

Milena Evans, 1912 is a genus distinct from *Caltoris* Swinhoe, 1893

Genomic trees reveal that *Caltoris* Swinhoe, 1893 (type species *Hesperia kumara* F. Moore, 1878) as currently circumscribed is not monophyletic, and phylogenetic positions of some species differ between trees not being strongly supported in any of them (Fig. 50). One of such lineages is *Caltoris plebeia* (Nicéville, 1887) (type locality in India): it is sister to the clade of *Caltoris* with its type species in the Z chromosome tree (with weak support: 46% partitions), and sister to *Prusiana* Evans, 1937 (type species *Pamphila prusias* C. Felder, 1861) in the nuclear genome tree from autosomes (58% of partitions) and mitogenome (70% of partitions), indicating complex evolutionary history of this lineage. Recognizing the uniqueness of *C. plebeia*, it has been chosen as the type species of the available genus-group name *Milena* Evans, 1912, which is currently regarded as a synonym of *Caltoris*. Presently, we have decided to keep *Prusiana* as a genus (instead of placing it as a subgenus in *Caltoris*) due to its genetic differentiation and phenotypic differences. Therefore, to ensure monophyly of all the taxa, we propose that *Milena* Evans, 1912, **stat. rest.** is a genus distinct from *Caltoris* Swinhoe, 1893.

Tulsia Grishin, new genus
http://zoobank.org/52B76DE3-029E-4623-B87F-578013E5C53F

Type species. *Parnara tulsi* Nicéville, 1884.

Definition. Genomic trees reveal that the lineage of *Caltoris tulsi* (Nicéville, 1884) (type locality in India) originates in rapid radiation and is not strongly grouped with any other single genus. Complemented with its strong genetic differentiation from others (Fig. 50), it represents a genus-level taxon. This new genus keys to M.7.12. in Evans (1949) and is distinguished from its relatives by forewing without tuft of scales beneath and spots in discal cell, ventral hindwing in its basal half and ventral forewing along costal margin overscaled with pale purplish (not ocherous) scales; uncus rounded at its distal end, only slightly knobbed on the sides, ampulla expanded and pointed dorsad (not rounded at its apex). A combination of the following nuclear genomic base pairs is diagnostic: aly2643.5.1:T192C, aly2613.4.2:G2377C, aly1877.13.1:A892T, aly1877.13.1:T938C, aly1877.13.1:A1195T.

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

Species included. Only the type species.

Parent taxon. Tribe Baorini Doherty, 1886.

Afrogegenes Jong & Coutsis, 2017 and *Torbenlarsenia* Kemal & Koçak, 2020 are subgenera of *Gegenes* Hübner, 1819

Nuclear genome trees point to a strongly supported clade that is sister to *Borbo* Evans, 1949 (type species *Hesperia borbonica* Boisduval, 1833) and includes type species of three genera: *Gegenes* Hübner, 1819

Fig. 50. Phylogenetic trees of selected Baorini species inferred from protein-coding regions of **a**, **b)** the nuclear genome (autosomes), **b)** proportionally rescaled to bring leaves to the same level, **c)** the Z chromosome, and **d)** the mitochondrial genome. *Parnara* is genetically removed from the rest, and the corresponding tree branches were truncated (as indicated by dots) to save space. The translucent vertical lime bar in (b) denotes the level approximately corresponding to genera. Shown by branches they refer to, names of genera are in bold italics, and subgenera are in italics: *Gegenes* (blue with *Havea* **subgen. n.** red and *Flanga* **subgen. n.** aquamarine), *Borbo* (olive), *Baoris* (gray), *Tulsia* **gen. n.** (magenta), *Caltoris* (violet), *Milena* **stat. rest.** (bright green), *Prusiana* (brown), *Zenonia* (cyan with subgenus *Zenonoida* **stat. nov.** orange), and *Zinaida* (purple).

(type species *Papilio pumilio* Hoffmansegg, 1804), *Afrogegenes* Jong & Coutsis, 2017 (type species *Hesperia hottentota* Latreille, 1824), and *Torbenlarsenia* Kemal & Koçak, 2020 (type species *Hesperia holtzi* Plötz, 1882) in addition to several species currently in *Borbo* Evans, 1949 (type species *Hesperia borbonica* Boisduval, 1833) (Fig. 50). However, within this clade, strongly supported major subclades are absent, and *Torbenlarsenia* as currently circumscribed (Fan et al. 2016) is not monophyletic. Moreover, *Torbenlarsenia gemella* (Mabille, 1884) (type locality in Madagascar) is not in this clade but belongs to *Borbo*, where we transfer it as *Borbo gemella* (Mabille, 1884), **stat. rev**. This whole clade with *Gegenes* is at the genus level in the tree and splits into five confident subclades, three of which represent named genus-group taxa: we propose to treat *Afrogegenes* Jong & Coutsis, 2017, **stat. rev.** and *Torbenlarsenia* Kemal & Koçak, 2020, **stat. rev.** as subgenera of *Gegenes* Hübner, 1819. The remaining two subclades do not have names and are described as new subgenera below. Finally, to restore the monophyly of *Borbo*, we transfer several species to the subgenus *Torbenlarsenia*, forming new combinations: *Gegenes* (*Torbenlarsenia*) *cottrelli* (Larsen, 2013), **comb. nov.**, *Gegenes* (*Torbenlarsenia*) *fallax* (Gaede, 1916), **comb. nov.**, *Gegenes* (*Torbenlarsenia*) *fanta* (Evans, 1937), **comb. nov.**, *Gegenes* (*Torbenlarsenia*) *micans* (Holland, 1896), **comb. nov.**, and *Gegenes* (*Torbenlarsenia*) *sirena* (Evans, 1937), **comb. nov**.

Flanga Grishin, new subgenus
http://zoobank.org/894F0986-7046-4A95-8D78-731C61C881A0

Type species. *Parnara perobscura* H. H. Druce, 1912.

Definition. As discussed above and shown in the trees (Fig. 50), the newly expanded genus *Gegenes* Hübner, 1819 (type species *Papilio pumilio* Hoffmansegg, 1804) can be partitioned into five subgenera. The species previously called *Torbenlarsenia perobscura* (H. H. Druce, 1912) (type locality in Ghana) is not monophyletic with *Hesperia holtzi* Plötz, 1882 (type locality in Angola), which is the type species of *Torbenlarsenia* Kemal & Koçak, 2020, and belongs to a distinct clade that we define as one of the five subgenera. It does not have a name. This new subgenus keys to 68.B.(b)(a^1)(a^2)(a^3) in Evans (1937) and is distinguished from its relatives by long, finger-like flanges at the base of uncus and thinner, more terminally rounded tooth of harpe projecting anteriad. A combination of the following nuclear genomic base pairs is diagnostic: aly151.39.1:A351T, aly1139.20.2:A245C, aly1412.8.1:G430C, aly1412.8.1:C431A, aly1349.7.9:G58T.

Etymology. The name is a feminine noun in the nominative singular and refers to long flanges from the base of uncus that identify this subgenus.

Species included. The type species (i.e., *Parnara perobscura* H. H. Druce, 1912) and *Pamphila detecta* Trimen, 1893.

Parent taxon. Genus *Gegenes* Hübner, 1819.

Havea Grishin, new subgenus
http://zoobank.org/4816F043-591A-46E9-B19C-5C9761CD7AD9

Type species. *Hesperia havei* Boisduval, 1833.

Definition. As discussed above and shown in the trees (Fig. 50), the newly expanded genus *Gegenes* Hübner, 1819 (type species *Papilio pumilio* Hoffmansegg, 1804) can be partitioned into five subgenera. The lineage with the species currently called *Borbo havei* (Boisduval, 1833) (type locality in Madagascar) corresponds to the last one (others discussed above). This new subgenus keys to 68.B.(b)(b^1)(c^2) in Evans (1937) and is distinguished from its relatives by narrower uncus terminally rounded in dorsal view with approximately parallel sides (not concave, and not gradually narrowing distad) and ampulla expanded distad and rounded, nearly reaching the distal end of harpe, which is with a sharp, tooth-like process directed anterodorsad at its base. A combination of the following nuclear genomic base pairs is diagnostic: aly1952.2.12:C46T, aly1952.2.12:T48A, aly310.6.1:G1542C, aly4196.3.1:T1023C, aly4196.3.1: G1039T, aly127.59.2:T289T (not C), aly6209.2.1:T1095T (not G), aly813.4.5:A855A (not C), aly275211.12.

5:A60A (not G), aly7600.1.6:T103T (not A).

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

Species included. Only the type species.

Parent taxon. Genus *Gegenes* Hübner, 1819.

Zenonoida Fan & Chiba, 2016 is a subgenus of *Zenonia* Evans, 1935

Genomic trees reveal that genetic differentiation between *Zenonia* Evans, 1935 (type species *Pamphila zeno* Trimen, 1864) and *Zenonoida* Fan & Chiba, 2016 (type species *Hesperia eltola* Hewitson, 1869) is smaller than that within their sister genus *Zinaida* Evans, 1937 (type species *Parnara nascens* Leech, 1893) and places the former two at the subgenus tree level (Fig. 50). COI barcodes of their type species differ by 8.8% (58 bp). Furthermore, these genera are phenotypically close, and neither of them includes a large number of species. Therefore, we propose that *Zenonoida* Fan & Chiba, 2016, **stat. nov.** is a subgenus of *Zenonia* Evans, 1935.

On the distribution of *Euphyes vestris* (Boisduval, 1852) and *Euphyes kiowah* (Reakirt, 1866)

On the basis of genetic differences, *Euphyes kiowah* (Reakirt, 1866) (type locality in the USA: Colorado, Rocky Mountains) was regarded by Zhang et al. (2022b) as a species distinct from *Euphyes vestris* (Boisduval, 1852) (type locality in USA: California, Plumas Co.). Here, we investigate the distribution of these two species using genomic sequencing and analysis. Specimens from across the range were selected for sequencing (Fig. 51), and genomic trees are shown in Fig. 52. Both autosome and Z chromosome trees confirm prominent genetic differentiation between the two species (*E. vestris* and *E. kiowah*). In the US, *Euphyes kiowah* is confined to the south-central area, confirmed from Colorado, Arizona, New Mexico, and Texas (excluding northeastern, eastern, and coastal regions) (Fig. 51 squares), and *E. vestris* occurs everywhere else (Fig. 51 circles). Interestingly, the entire central Texas (Edwards Plateau region) is inhabited by *E. kiowah*, but *E. vestris* is found immediately to the south of it in more coastal regions. The eastern boundary between these two parapatric species is relatively straight

Fig. 51. A map of sequenced specimens: *Euphyes vestris* (circles, purple and shades of blue) and *Euphyes kiowah* (squares, shades of red) with their subspecies: *E. vestris osceola* (purple), *E. vestris vestris* (darker blue), *E. vestris harbisoni* (paler blue), *E. vestris metacomet* (sky blue), *E. kiowah kiowah* (red), and *E. kiowah chamuli* (maroon).

in the northwest-to-southeast direction and likely goes through northeastern Colorado, Oklahoma, and Texas panhandles and towards the Texas coast, where the boundary turns southwest to circumvent coastal areas. Studies of specimens along this boundary may bring insights into the speciation process and isolation mechanisms of these two species. On the western side, *E. kiowah* and *E. vestris* are separated by the Great Basin, in which neither species seems to be present. As a result, we see that the distribution of *E. vestris* engulfs that of *E. kiowah*, the latter being restricted to more arid areas.
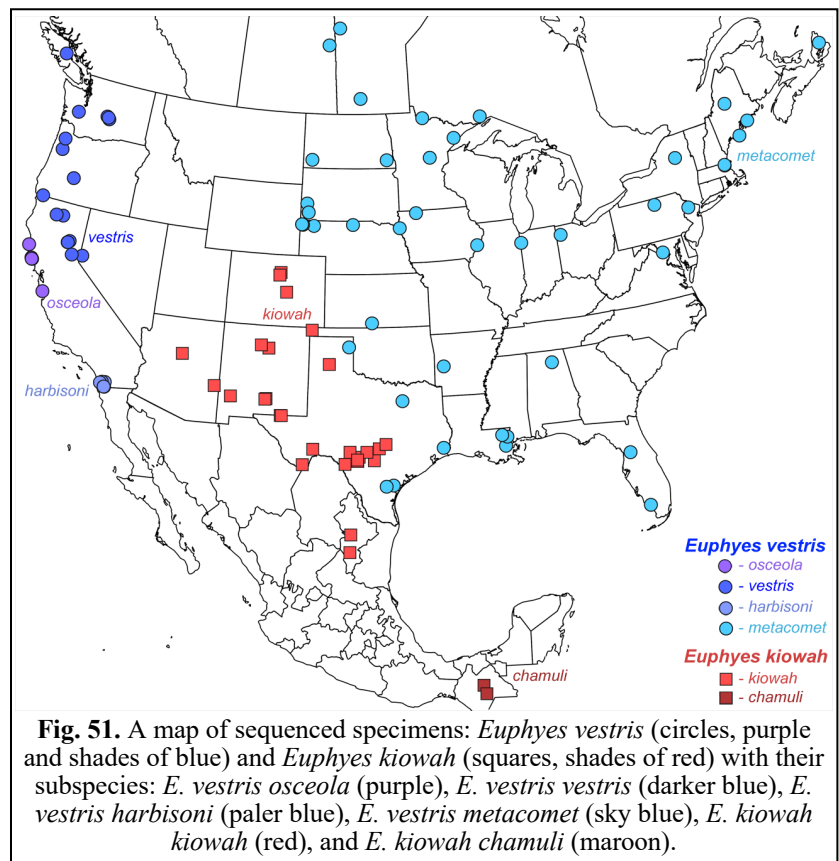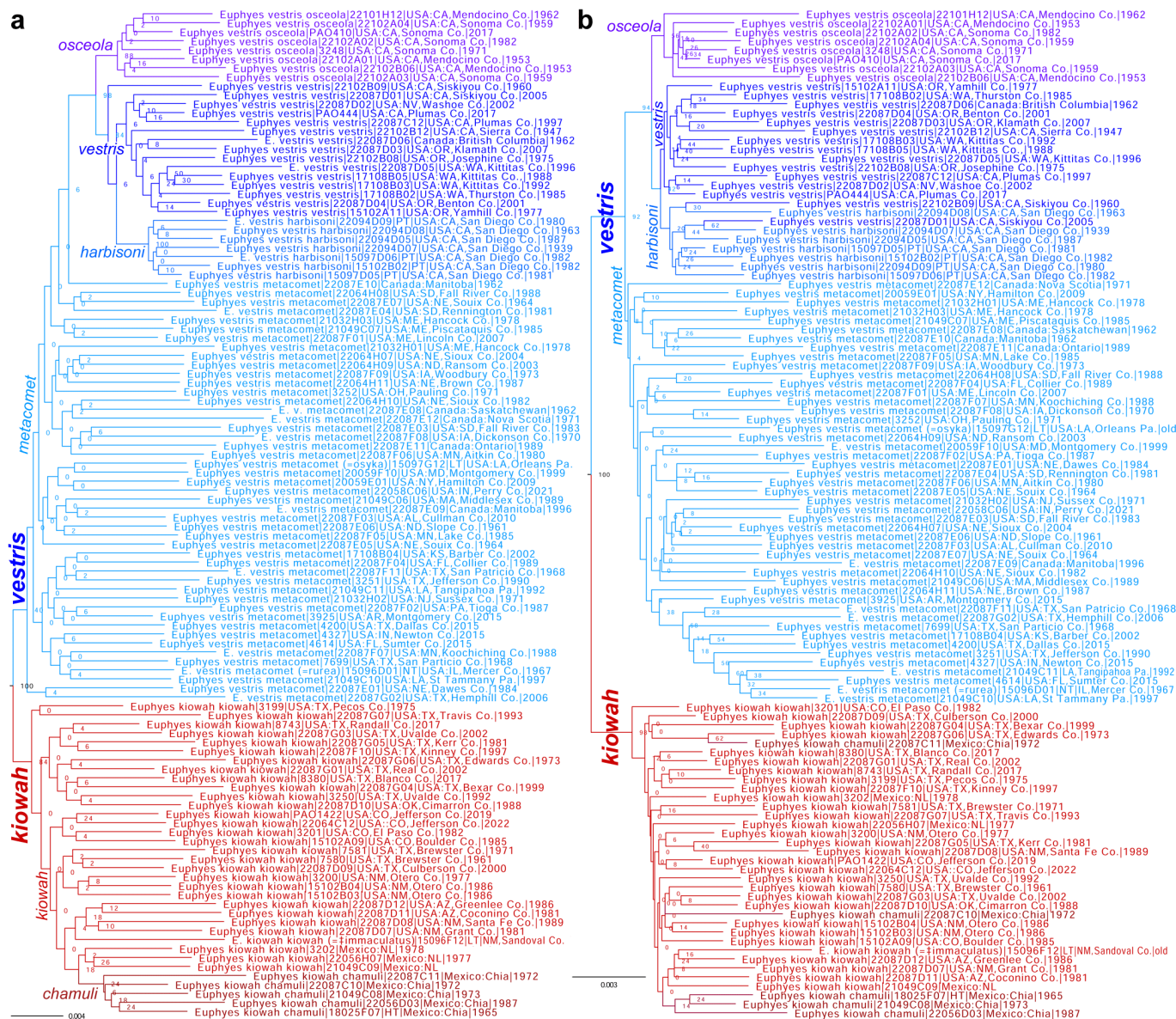
Fig. 52. Phylogenetic trees of *Euphyes vestris* (purple and shades of blue) and *Euphyes kiowah* (red) inferred from protein-coding regions of **a)** the nuclear genome (autosomes) and **b)** the Z chromosome. Different subspecies are shown in different shades of colors and labeled in smaller font by their clades or regions (if not monophyletic) in the tree.

Euphyes vestris osceola (Lintner, 1878) is a valid subspecies

Currently placed as a junior subjective synonym of *Euphyes vestris vestris* (Boisduval, 1852) (type locality in the USA: California, Plumas Co.), *Pamphila osceola* Lintner, 1878 (type locality in the USA: California, Mendocino Co.) shows genetic differentiation from it and forms a distinct clade in genomic trees (Fig. 52). Due to this genetic differentiation, coastal north-central California populations of *E. vestris* are best treated as a separate subspecies, even more distant genetically from the nominotypical subspecies than southern Californian *Euphyes vestris harbisoni* J. Brown & McGuire, 1983 (type locality in USA: California, San Diego Co.) (Fig. 52). Therefore, in agreement with Emmel et al. (1998), we consider *Euphyes vestris osceola* (Lintner, 1878), **stat. rev.** to be a valid subspecies.

Vernia verna sequoyah (H. Freeman, 1942) is a valid subspecies

Polites verna sequoyah H. Freeman, 1942 (type locality USA: Arkansas, Little Rock) was placed by Evans (1955) as a junior subjective synonym of *Pamphila verna* W. H. Edwards, 1862 (type locality in
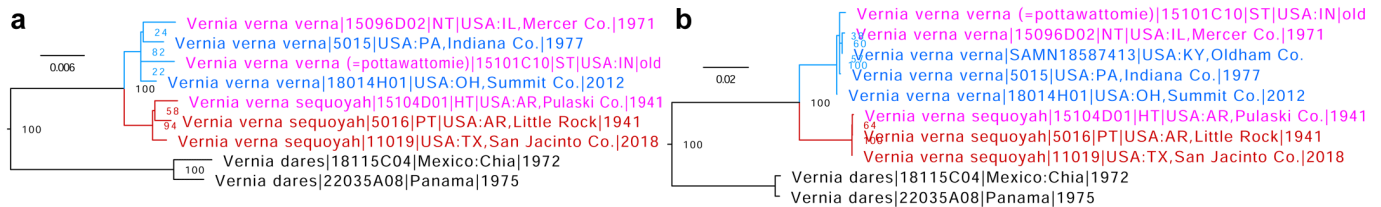
Fig. 53. Phylogenetic trees inferred from protein-coding regions in: **a)** the Z chromosome and **b)** the mitochondrial genome with *Vernia verna verna* (blue) and *V. verna sequoyah* (red). Primary type specimens are labeled in magenta. The sequence of SAMN18587413 is taken from the alignment provided in Kawahara et al. (2023).

USA: Mercer Co.), the type species of and currently in the genus *Vernia* Grishin, 2019. The genomic tree reveals that sequenced specimens of *Vernia verna* partition into two clades (Fig. 53). The clades are characterized by close genetic similarity of specimens within each clade and a certain level of genetic differentiation between the clades. Therefore, populations assigned to these clades can be treated as two distinct subspecies. The neotype of *V. verna* and a syntype of *Pamphila pottawattomie* Worthington, 1880 from "N. Ind." (type locality in USA: IL, Cook Co., and IN, Lake Co.) belong to one clade, and the holotype of *P. v. sequoyah* belongs to the other. We propose that the two clades represent two subspecies and reinstate *Vernia verna sequoyah* (H. Freeman, 1942), **stat. rest.** as a valid subspecies. Moreover, due to genetic differentiation, future studies of additional specimens may determine that it is a species-level taxon.

Lerodea dysaules Godman, 1900 is a valid species distinct from *Lerodea arabus* (W. H. Edwards, 1882)

Originally proposed as a species and treated (with some reservations) as such by Evans (1955), *Lerodea dysaules* Godman, 1900 (type locality Mexico: Guerrero, Venta de Zopilote) was later synonymized with *Lerodea arabus* (W. H. Edwards, 1882) (type locality USA: Arizona, Pima Co., Sabino Canyon), because no appreciable differences in genitalia were observed, and wing pattern differences given by Evans (1955) do not hold up in a larger series of specimens (Warren and Mielke 2005). Genomic sequencing of *L. arabus* from across its range reveals a deep split into two clades (Fig. 54a, b), unexpected from phenotypic assessment. The two clades are most strongly differentiated genetically with F_{st}/G_{min} statistics 0.70/0.00 and COI barcode difference of 8.2% (54 bp), typical for species from different subgenera and remarkably large for close relatives. Therefore, the two clades represent two distinct species.

The distribution of *L. arabus* as recorded on iNaturalist (2023) is disjoint, showing a cluster of observations in southeastern Arizona and the major range from Sinaloa – Durango – Coahuila – Nuevo Leon – south Texas southwards (Fig. 54c). These two disjoint areas in the distribution correspond perfectly to the two distinct species revealed by genomic sequencing (plus specimens from both clades in Sonora, Mexico where no iNaturalist observations existed) (Fig. 54). Sequenced specimens from near the type locality of *L. arabus* provide the name for the southeastern Arizona and Sonora (except southernmost) cluster (Fig. 54 blue). The type locality of *Lerodea dysaules* falls well within the major range, and the sequenced specimen from Guerrero belongs to the second species along with other specimens across the major range (Fig. 54 red), providing an available name for this species. Therefore, we reinstate *Lerodea dysaules* Godman, 1900, **stat. rest.** as a species-level taxon. In conclusion, *L. arabus* is the northwestern species, and *L. dysaules* is the southeastern species. The two species may meet in southern Sonora, Mexico, and the westernmost record of *L. dysaules* is from Alamos, Sonora (sequenced as NVG-21056A02) (Fig. 54 red). Curiously, genomic sequencing suggests that populations from Mexico Baja California Sur are *L. arabus* (Fig. 54).

As for the phenotypic assessment, both species are variable in wing patterns, and if identification is possible, it should be done within each pattern form, comparing specimens with similar patterns between species. Generally, ventral overscaling in *L. dysaules* is more mottled in appearance, especially

in a form with a well-developed brown discal patch on the ventral hindwing; this patch is smaller, not extending towards the apex but turning towards mid-costa and is bordered by more diffuse small pale spots (if the spots are present at all), these spots are also diffuse and frequently connected into a band even if the central brown patch is absent. In *L. arabus*, pale ventral overscaling is more uniform, without apparent mottling, the hindwing brown patch (if expressed) is larger and frequently extending towards the apex (at least the area between the patch and the apex is darker than the central submarginal area), giving the patch a more triangular appearance; if postdiscal small pale spots are expressed, their edges are better defined, and the spots are more contrasty on the background, better separated from each other, especially in specimens lacking the patch, and the spot in cell Sc+R$_1$-RS may be particularly prominent. To aid in the identification of these species, we provide COI barcodes of specimens from near the type localities:

Lerodea arabus from USA: AZ, Pima Co. [LACM], sample NVG-22094F10, GenBank <u>OR578721</u>:

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AACTTTATATTTTATTTTTGGAATTTGAGCAGGAATATTAGGAACATCATTAAGTCTTTTAATTCGAACAGAATTAGGTAATCCTGGATCTTTAATTGGAGATGATCAAATTTACAATACT
ATTGTGACAGCTCACGCTTTTATTATAATTTTTTTCATGGTAATACCTATTATAATTGGTGGATTTGGTAATTGATTAGTTCCTCTAATATTAGGTGCCCCAGATATAGCTTTCCCACGAA
TAAATAATATAAGATTTTGAATACTGCCACCTTCCTTAATATTATTAATTTCAAGTAGAATTGTAGAAATGGTGCAGGAACAGGTTGAACTGTATATCCTCCTCTTTCTTCTAATATTGC
CCACCAAGGAGCCTCAGTTGACTTAGCGATTTTTTCATTACATTTAGCAGGTATTTCATCTATTTTAGGAGCTATTAACTTTATTACTACTATTAATAATAATACGAATTAAAAATTTATCA
TTTGATCAAATACCTTTATTTGTTTGATCAGTAGGAATTACAGCATTATTATTACTTTTATCTCTACCTGTTTTAGCAGGTGCTATTACCATACTTTTAACTGACCGAAATTTAAACACTT
CATTTTTTGATCCTGCTGGAGGAGGAGATCCTATTTTATATCAACATTTATTT
```

Lerodea dysaules from Mexico: Guerrero [MGCL], sample NVG-21085D09, GenBank <u>OR578722</u>:

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AACTTTATACTTTATTTTTGGAATTTGAGCAGGAATATTAGGAACATCTTTAAGTCTTTTAATTCGAACAGAATTAGGCAATCCTGGATCTTTAATTGGAGATGATCAAATTTATAATACT
ATTGTAACAGCCCATGCCTTTATTATAATTTTTTTTATAGTTATGCCTATTATAATTGGAGGATTTGGTAATTGACTAGTTCCTTTAATATTAGGAGCACCTGACATAGCATTCCCACGAA
ACATCAAGGAGCCTCAGTTGACCTTGCAATTTTTTCTCTTCATTTAGCTGGTATTTCATCCATTTTAGGAGCTATTAATTTTATTACTACTATTATTAACATACGAATTAAAAATTTATCA
TTCGATCAAATACCTTTATTTGTCTGATCTGTAGGAATTACAGCATTATTATTACTTTTTATCTTTACCTGTCTTAGCAGGAGCTATTACTATACTTTTAACCGATCGAAACCTTAATACTT
CATTCTTTGATCCTGCTGGAGGAGGAGATCCTATTTTATATCAACATTTATTT
```


Fig. 54. *Lerodea arabus* (blue) and *Lerodea dysaules* **stat. rest.** (red): phylogenetic trees inferred from protein-coding regions in: **a)** the nuclear genome (autosomes) and **b)** the mitochondrial genome; **c)** a distribution map made from iNaturalist (2023) observations: some points in the iNaturalist map *L. arabus* were re-colored in Photoshop and the two points corresponding to sequenced specimens from Mexico: Sonora were added (CC BY-NC 4.0 https://creativecommons.org/licenses/by-nc/4.0/), other points do not refer to sequenced specimens, records were not checked, and some may be misidentifications.

[No genus] *osibius* Draudt, 1924 is an unavailable name

The name "osibius" was published by Draudt (1921–1924) below a specimen illustration on the plate 113B entitled "AGRIAS-ERYNNIS", row c image 4 from the left, out of 7. No other mention of the name

is found in this work. The species illustrated first (i.e., top left: row a image [1]) on plate 113B was placed in the genus *Agrias*, and the species illustrated last (i.e., bottom right: row c image [7], current name *Hesperia colorado* (Scudder, 1874)) was placed by Draudt (1923b) in the genus *Erynnis*. The species illustrated next to last (row c, images [5] and [6], current name *Turesis complanula* (Herrich-Schäffer, 1869), misidentified as "*lucasi*") was placed by Draudt (1923a) in the genus *Turesis*. Only two genera are mentioned in the title of this plate (*Agrias* and *Erynnis*), but at least three are illustrated. Therefore, it remains unclear which genus "osibius" was placed in (*Agrias*, *Turesis* [not mentioned on the plate], *Erynnis*, or some other genus). Mielke (1993) listed "osibius" (as "osybius") in combination with the genus *Turesis* Godman, 1901 (type species *Hesperia lucas* Fabricius, 1793) and treated it as a valid species (Mielke 2004; Mielke 2005). However, the name "osibius" by Draudt is unavailable because it was not proposed "in unambiguous combination with a generic name" as demonstrated above (fails ICZN Code Art. 11.9.3) and therefore cannot be used as a valid name for any species. Finally, we were not able to unambiguously determine the identity of the specimen illustrated by Draudt (1921–1924) (among others, it might have been *Rhinthon* Godman, 1900 or *Niconiades* Hübner, [1821]), but it does not seem to belong to *Turesis* due to details in its wing pattern, such as a postdiscal arc of increasing in size pale spots on ventral hindwing, that are not characteristic of *Turesis*.

ACKNOWLEDGMENTS

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