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Genomics-guided refinement of butterfly taxonomy

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ABSTRACT. Continuing with comparative genomic exploration of worldwide butterfly fauna, we use all protein-coding genes as they are retrieved from the whole genome shotgun sequences for phylogeny construction. Analysis of these genome-scale phylogenies projected onto the taxonomic classification and the knowledge about butterfly phenotypes suggests further refinements of butterfly taxonomy that are presented here. As a general rule, we assign most prominent clades of similar genetic differentiation to the same taxonomic rank, and use criteria based on relative population diversification and the extent of gene exchange for species delimitation. As a result, 7 tribes, 4 subtribes, 14 genera, and 9 subgenera are proposed as new, i.e., in subfamily Pierinae Swainson, 1820: Calopierini Grishin, **trib. n.** (type genus *Calopieris* Aurivillius, 1898); in subfamily Riodininae Grote, 1895: Callistiumini Grishin, **trib. n.** (type genus *Callistium* Stichel, 1911); in subfamily Nymphalinae Rafinesque, 1815: Pycinini Grishin, **trib. n.** (type genus *Pycina* Doubleday 1849), Rhinopalpini Grishin, **trib. n.** (type genus *Rhinopalpa* C. & R. Felder 1860), Kallimoidini Grishin, **trib. n.** (type genus *Kallimoides* Shirôzu & Nakanishi 1984), Vanessulini Grishin, **trib. n.** (type genus *Vanessula* Dewitz 1887), and Doleschalliaini Grishin, **trib. n.** (type genus *Doleschallia* C. & R. Felder 1860); in tribe Mesosemiini Bates, 1859: *Eunogyrina* Grishin, **subtrib. n.** (type genus *Eunogyra* Westwood, 1851); in tribe Satyrini Boisduval, 1833: Callerebiina Grishin, **subtrib. n.** (type genus *Callerebia* Butler, 1867), Gyrocheilina Grishin, **subtrib. n.** (type genus *Gyrocheilus* Butler, 1867), and Calistina Grishin, **subtrib. n.** (type genus *Calisto* Hübner, [1823]); in subfamily Euselasiinae Kirby, 1871: *Pelolasia* Grishin, **gen. n.** (type species *Eurygona pelor* Hewitson, [1853]), *Myselasia* Grishin, **gen. n.** (type species *Eurygona mys* Herrich-Schäffer, [1853]), *Eurylasia* Grishin, **gen. n.** (type species *Eurygona euryone* Hewitson, 1856), *Maculasia* Grishin, **gen. n.** (type species *Euselasia albomaculiga* Callaghan, 1999), and *Eugelasia* Grishin, **gen. n.** (type species *Eurygona eugeon* Hewitson, 1856); in subtribe Mesosemiina Bates, 1859: *Ectosemia* Grishin, **gen. n.** (type species *Papilio eumene* Cramer, 1776) and *Endosemia* Grishin, **gen. n.** (type species *Papilio ulrica* Cramer, 1777); in tribe Symmachiini Reuter, 1896: *Tigria* Grishin, **gen. n.** (type species *Mesene xypete* Hewitson, 1870) and *Asymma* Grishin, **gen. n.** (type species *Symmachia virgatula* Stichel, 1910); in tribe Riodinini Grote, 1895: *Putridivora* Grishin, **gen. n.** (type species *Charis argyrea* Bates, 1868), *Chadia* Grishin, **gen. n.** (type species *Charis cadytis* Hewitson, 1866), *Inkana* Grishin, **gen. n.** (type species *Charis incoides* Schaus, 1902), and *Oco* Grishin, **gen. n.** (type species *Symmachia ocellata* Hewitson, 1867); in subtribe Zabuellina Seraphim, Freitas & Kaminski, 2018: *Teenie* Grishin, **gen. n.** (type species *Calydna tinea* Bates, 1868); *Boreographium* Grishin, **subgen. n.** (type species *Papilio marcellus* Cramer, 1777, parent genus *Eurytides* Hübner, [1821]), *Esperourus* Grishin, **subgen. n.** (type species *Papilio esperanza* Beutelspacher, 1975, parent genus *Pterourus* Scopoli, 1777), *Hyppasonia* Grishin, **subgen. n.** (type species *Papilio hyppason* Cramer, 1775, parent genus *Heraclides* Hübner, [1819]), *Sisymbria* Grishin, **subgen. n.** (type species *Pieris sisymbrii* Boisduval, 1852, parent genus *Pontia* [Fabricius], 1807), *Greenie* Grishin, **subgen. n.** (type species *Thecla sheridonii* [sic] Edwards, 1877, parent genus *Callophrys* Billberg, 1820), *Magda* Grishin, **subgen. n.** (type species *Erebia magdalena* Strecker, 1880, parent genus *Erebia* Dalman, 1816), and in genus *Eresia* Boisduval, 1836: *Notilia* Grishin, **subgen. n.** (type species *Eresia orthia* Hewitson, 1864), *Levinata* Grishin, **subgen. n.** (type species *Eresia levina* Hewitson, 1872), and *Ithra* Grishin, **subgen. n.** (type species *Phyciodes ithra* Kirby, 1900). Furthermore, we resurrect 6 genera, change the rank of 36 currently used genera to subgenus, synonymize 3 subtribes, 42 genera or subgenera, assign 3 genera to tribes and subtribes, and transfer 34 additional species to genera different from those these taxa are presently assigned to, present evidence to support 7 taxa as species instead of subspecies, and 1 taxon as a subspecies instead of species. Namely, the following taxa are valid genera: *Terias* Swainson, 1821 (not in *Eurema* Hübner, [1819]), *Erythia* Hübner, [1819] and *Marmessus* Hübner, [1819] (not in *Euselasia* Hübner, [1819]), *Eucorna* Strand, 1932 (not in *Voltinia* Stichel, 1910), *Cremna* Doubleday, 1847 (not in *Napaea* Hübner, [1819]), and *Hallonympha* Penz & DeVries, 2006 (not in *Zabuella* Stichel, 1911). The following taxa are best treated as subgenera: *Zegris* Boisduval, 1836 of *Anthocharis* Boisduval, Rambur, [Duménil] & Graslin, [1833]; *Baltia* Moore, 1878 and *Pontieuchloia* Verity, 1929 of *Pontia* [Fabricius], 1807; *Phrissura* Butler, 1870 of *Appias* Hübner, [1819]; *Saletara* Distant, 1885 of *Catophaga* Hübner, 1819; *Leodonta* Butler, 1870 of *Pereute* Herrich-Schäffer, 1867; *Takashia* M. Okano & T. Okano, 1985 of *Polycaena* Staudinger, 1886; *Corrachia* Schaus, 1913 of *Styx* Staudinger, 1876; *Ionotus* Hall, 2005 and *Voltinia* Stichel, 1910 of *Cremna* Doubleday, 1847; *Hermathena* Hewitson, 1874 of *Ithomiola* C. & R. Felder, 1865; *Lucillella* Strand, 1932 of *Esthemopsis* C. & R. Felder, 1865; *Mesenopsis* Godman & Salvin, 1886 and *Xenandra* C. & R. Felder, 1865 of *Symmachia* Hübner, [1819]; *Pirascca* J. Hall & Willmott, 1996 of *Pterographium* Stichel, 1910; *Imelda* Hewitson, 1870 of *Echenais* Hübner, [1819]; *Calicosama* J. Hall & Harvey, 2001 of *Behemothia* Hall, 2000; *Polygrapha* Staudinger, 1887 and *Fountainea* Rydon, 1971 of *Anaea* Hübner, [1819]; *Siderone* Hübner, [1823] and *Phantos* Dias, 2018 of *Zaretis* Hübner, [1819]; *Harsiesis* Fruhstorfer, 1911 of *Platypthima* Rothschild & Jordan, 1905; *Vila* Kirby, 1871 of *Biblis* Fabricius, 1807; *Diaethria* Billberg, 1820 and *Perisama* Doubleday, 1849 of *Callicore* Hübner, [1819]; *Antigonis* C. Felder, 1861 of *Haematera* Doubleday, 1849; *Asterope* Hübner, [1819], *Nica* Hübner, [1826], *Peria* Kirby, 1871, and *Callicorina* Smart, 1976 of *Temenis* Hübner, [1819]; *Anthanassa* Scudder, 1875, *Castilia* Higgins, 1981, *Telenassa* Higgins, 1981, *Dagon* Higgins, 1981, and *Janatella* Higgins, 1981 of *Eresia* Boisduval, 1836; and *Wallengrenia* Berg, 1897 of *Polites* Scudder, 1872. The following taxa are junior subjective synonyms: Maniolina Grote, 1897 of Erebiina Tutt, 1896; Melanargiina Wheeler, 1903 of Satyrina Boisduval, 1833; Phyciodina Higgins, 1981 of Melitaeina Herrich-Schäffer, 1843; *Cunizza* Grote, 1900 of *Hesperocharis* C. Felder, 1862; *Reliquia* Ackery, 1975 of *Pontia* [Fabricius], 1807; *Tatochila* A. Butler, 1870, *Piercolias* Staudinger, 1894, *Hypsochila* Ureta, 1955, *Theochila* W. D. Field, 1958, *Pierphulia* W. D. Field, 1958, and *Infraphulia* W. D. Field, 1958 of *Phulia* Herrich-Schäffer, 1867; *Mesapia* Gray, 1856 of *Aporia* Hübner, [1819]; *Catasticta* Butler, 1870 of *Archonias* Hübner, 1827; *Sandia* Clench & P. Ehrlich, 1960 and *Xamia* Clench, 1961 of *Incisalia* Scudder, 1872; *Hades* Westwood, 1851 of *Methone* Doubleday, 1847; *Semomesia* Westwood, 1851, *Mesophthalma* Westwood, 1851, *Perophthalma* Westwood, 1851 and *Leucochimona* Stichel, 1909 of *Mesosemia* Hübner, [1819], *Xynias* Hewitson, 1874 of *Mesenopsis* Godman & Salvin, 1886; *Stichelia* J. Zikán, 1949 of *Symmachia* Hübner, [1819]; *Chimastrum* Godman & Salvin, 1886 of *Mesene* Doubleday, 1847; *Alethea* Nielsen & Salazar, [2018] of *Pirascca* J. Hall & Willmott, 1996; *Panaropsis* J. Hall, 2002 of *Pterographium* Stichel, 1910; *Comphotis* Stichel, 1910 of *Phaenochitonia* Stichel, 1910; *Colaciticus* Stichel, 1910 of *Baeotis* Hübner, [1819]; *Nahida* Kirby, 1871 of *Ithomeis* Bates, 1862; *Machaya* Hall & Willmott, 1995 of *Pachythone* Bates, 1868; *Percnodaimon* Butler, 1876 and *Erebiola* Fereday, 1879 of *Argyrophenga* Doubleday, 1845; *Hestinalis* Bryk, 1938 of *Mimathyma* Moore, 1896; *Catacore* Dillon, 1948 of *Diaethria* Billberg, 1820; *Mesotaenia* Kirby, 1871 and *Orophila* Staudinger, 1886 of *Perisama* Doubleday, 1849; *Paulogramma* Dillon, 1948 of *Catagramma* Boisduval, 1836; *Panacea* Godman & Salvin, 1883 of *Batesia* C. Felder & R. Felder, 1862; *Napeocles* Bates, 1864 of *Siproeta* Hübner, [1823]; *Texola* Higgins, 1959 and *Dymasia* Higgins, 1960 of *Microtia* H. Bates, 1864; *Tisona* Higgins, 1981 of *Ortilia* Higgins, 1981; *Abananote* Potts, 1943 and *Altinote* Potts, 1943 of *Actinote* Hübner, [1819]; *Episcada* Godman & Salvin, 1879 of *Ceratinia* Hübner, 1816; and *Appia* Evans, 1955 of *Pompeius* Evans, 1955. The following genera are placed in taxonomic hierarchy: *Prestonia* Schaus, 1920 belongs to Euremini Grote, 1898; *Petrocerus* Callaghan, 1979 belongs to Theopina Clench, 1955; and *Paralasa* Moore, 1893 belongs to Ypthimina Reuter, 1896. The following taxa are distinct species rather than subspecies (of species shown in parenthesis): *Pyrisitia westwoodii* (Boisduval, 1836) (not *Pyrisitia dina* (Poey, 1832)), *Biblis aganisa* Boisduval, 1836 (not *Biblis hyperia* (Cramer, 1779)), *Phystis variegata* (Röber, 1913) and *Phystis pratti* (A. Hall, 1935) (not *Phystis simois* (Hewitson, 1864)), *Phocides batabano* (Lucas, 1857) and *Phocides bicolora* (Boddaert, 1783) (not *Phocides pigmalion* (Cramer, 1779)), *Lobotractus mysie* (Dyar, 1904) (not *Lobotractus valeriana* (Plötz, 1881)). *Nahida coenoides* (Hewitson, 1870) is conspecific with *Ithomeis aurantiaca* H. Bates, 1862. Additional new and revised combinations are: *Teriocolias deva* (E. Doubleday, 1847), *Teriocolias reticulata* (A. Butler, 1871), *Hesperocharis leucothea* (Molina, 1782), *Methone euploea* (Hewitson, [1855]), *Methone eucerus* (Hewitson, 1872), *Methone hypophaea* (Godman & Salvin, 1878), *Methone eubule* (R. Felder, 1869), *Methone onorata* (Hewitson, 1869), *Methone authe* (Godman, 1903), *Methone dolichos* (Staudinger, [1887]), *Methone baucis* (Stichel, 1919), *Methone eucrates* (Hewitson, 1872), *Napaea danforthi* A. Warren & Opler, 1999, *Napaea dramba* (J. Hall, Robbins & Harvey, 2004), *Napaea sanarita* (Schaus, 1902), *Napaea agroeca* Stichel, 1910, *Napaea tumbesia* J. Hall & Lamas, 2001, *Napaea umbra* (Boisduval, 1870), *Napaea phryxe* (C. & R. Felder, 1865), *Napaea cebrenia* (Hewitson, [1873]), *Napaea loxicha* (R.G. Maza & J. Maza, 2016), *Napaea maya* (J. Maza & Lamas, 2016), *Napaea necaxa* (R.G. Maza & J. Maza, 2018), *Napaea totonaca* (R.G. Maza & J. Maza, 2016), *Mesene aeolia* (Bates, 1868), *Pterographium hypochloris* (Bates, 1868), *Phaenochitonia florus* (Fabricius, 1793), *Ourocnemis carausius* (Westwood, 1851), *Ourocnemis principalis* (Hopffer, 1874), *Ourocnemis renaldus* (Stoll, 1790), and *Ourocnemis aerosus* (Stichel, 1924), *Hallonympha maculosa* (Bates, 1868), *Exoplisia aphanis* (Stichel, 1910), *Phystis fontus* (A. Hall, 1928), *Phocides batabano okeechobee* (Worthington, 1881), and *Phocides batabano batabanoides* (W. Holland, 1902). Finally, we confirm the combination *Zabuella castanea* (Prittwitz, 1865) and find *Pyrgus centaureae dzekh* Gorbunov, 2007 as a new subspecies for North America.

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

ZooBank registration: http://zoobank.org/5027ADA7-E67E-415E-AE9C-D8E282AF942D

INTRODUCTION: METHODS AND CONCEPTS

Genome-scale DNA analysis opens a new dimension in exploration of butterfly taxonomy and offers a promise of more objective and internally consistent classification firmly grounded in evolutionary considerations and reliable phylogenies (Allio et al. 2019; Li et al. 2019; Zhang et al. 2019a; Zhang et al. 2019b; Zhang et al. 2020). Many conclusions we arrive at challenge current taxonomy based largely on phenotypes: phylogenomic analysis shows that some taxa are not monophyletic, while others are either too broad or too narrow in terms of genetic diversification compared to taxa of the same rank. Here, the resultant taxonomic hypotheses are formalized and corresponding name changes are proposed.

Classification concepts and methods employed in this work do not differ from those in our previous studies, where they were explained in more detail (Zhang et al. 2019c; Zhang et al. 2020). Here, they are simply applied to additional taxonomic groups of butterflies. In brief, we do not amplify any specific gene markers, but instead sequence all DNA molecules in a specimen that pass the procedure of genomic library construction (Li et al. 2019; Zhang et al. 2019a). Therefore, all genes of a butterfly are sequenced together. On the one hand, this approach allows us to obtain complete genomes of butterflies. On the other hand, it enables DNA sequencing of century-old specimens with degraded DNA that may be too short for the amplification procedure of standard gene markers (Cong et al. 2021). For fresher specimens, the method produces nearly 99% of all genes, but for older specimens it could be only 10% due to DNA degradation. Nevertheless, even 10% of about 15,000 total genes that constitute the gene set of most butterflies (Zhang et al. 2019d) provides more information than a study based on amplification of several genes. As a result, genome-scale phylogenetic trees are not biased by gene marker selection, but represent the entire organism, and therefore enable us to judge more accurately about its evolution.

For phylogenetic analysis, all sequences are aligned to the closest reference genome and from this alignment, we select positions in exons with a gap fraction less than 0.4: i.e., such position in the alignment is not a gap in more than 40% of specimens. We then compute a reference tree using IQ-TREE version 1.6.8 with model GTR+G (Minh et al. 2020) from an alignment with 300K such positions randomly sampled. Then, 100 partitions consisting of 30K randomly sampled such positions are generated to construct 100 trees for estimating the confidence of each node in the reference tree. The support values are assigned to each node (and shown in the trees below) by mapping trees from 100 partitions to the reference tree using sumtrees.py script from the DendroPy package (Sukumaran and Holder 2010). The same procedure is repeated for the Z chromosome tree, which is only composed of Z-linked positions. The Z-linked exons are inferred by aligning exons of the closest genome reference to known *Heliconius melpomene* Z chromosome (Davey et al. 2016) using tBLASTn (Gertz et al. 2006). Mitogenome tree is based on all protein-coding regions and inferred by IQ-TREE with automatic model estimation and 1000 ultrafast bootstrap replicates. COI dendrograms are constructed with BioNJ (Gascuel 1997) using Phylogeny.fr website (Dereeper et al. 2008) with the default model and 200 bootstrap replicates. DNA characters are obtained using the approach we developed to increase their robustness to missing species as described in our previous work (Cong et al. 2019b; Zhang et al. 2019e). The character states are given as abbreviations: e.g., cne703.2.8:A1414C means position 1414 in exon 8 of gene 2 from scaffold 703 of *Calephelis nemesis* (cne) reference genome (Cong et al. 2017) is C, changed from A in the ancestor; or cne5129.1.5:A833A (not G), which means that position 833 in exon 5 of gene 1 on scaffold 5129 is occupied by the ancestral base pair A, which was changed to G in the sister clade (it is not G in the diagnosed taxon). We also use *Calycopis cecrops* (cce) (Cong et al. 2016) and *Heliconius melpomene* (hm) (Davey et al. 2016) genomes as references. For *H. melpomene*, the abbreviation is like hm2009277-RA.13:T2076C, where hm2009277-RA is the protein ID and 13 is exon number.

The resulting phylogenetic trees are inspected visually and compared with the current butterfly classification. Close attention is paid to family-group and genus-group taxa that are not monophyletic in the trees, i.e., are not the groups of species that consists of all descendants of their common ancestor. First, identification is checked for specimens that disrupt monophyly of higher level taxa by inspection of sequenced specimens, their photographs or genitalia when necessary. Then, the quality of sequence datasets is analyzed in detail for the possibility of insufficient coverage and contamination, both from other butterfly specimens or bacteria and fungi. When we are convinced about the identifications and appropriate data quality, suggestions are made as how to restore monophyly of these taxa, either by combining a number of taxa into one that is monophyletic, by transferring species between the taxa, or by splitting the non-monophyletic taxon into several monophyletic taxa. The names of these taxa follow the placement of their type genera or species: the clade with the type species carries its genus name. Clades that do not contain type genera or type species for any of the available names are named as new taxa.

In decisions about taxa and their ranks we rely on their prominence in phylogenetic trees and internal consistency of definition based on genetic diversification. The discussion below uses **genus** rank as an example, but similar logic applies to other ranks. Our criteria for genera were explained previously (Li et al. 2019; Zhang et al. 2020). Traditionally, genera were defined using arbitrary and subjective criteria based on prominent phenotypic characters that make a certain group of species stand out from other similar groups of species. We attempt to define genera more objectively based on the patterns of branch lengths in genome-scale phylogenetic trees, while keeping in mind agreement with the current classification. Most prominent tree branches near the origin of tribes and subtribes are typically defined as genera. By "prominent", we mean that the branch is comparatively longer among neighboring branches (Fig. 1), and therefore is more likely to define a better supported and more reliable clade in the tree. Also, longer branches (branch length is proportional to the number of accepted mutations along the branch) are expected to contain more phenotypic mutations and correlate with larger phenotypic differences, which indeed may be the case due to generally good agreement between current mostly phenotypic classification and our tree-based definition of genera. We note that these prominent branches frequently "line up" under each other forming a level of classification (Fig. 1 green highlight, Figs. 13–18) and naturally define genus level clades. This level dates to about 15-20 Mya (Chazot et al. 2019).

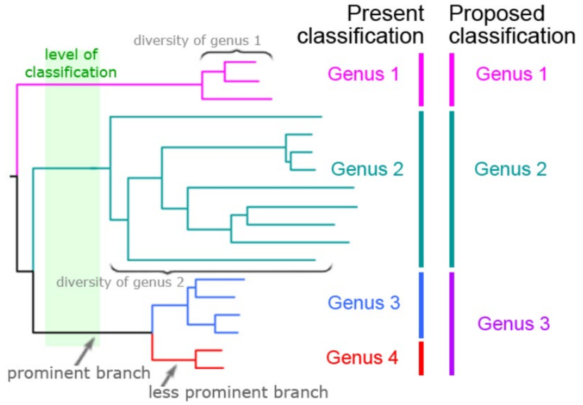

Fig. 1. Prominence, consistency and diversity.

We note that, similar to species, genera can vary in genetic diversification. E.g., Genus 1 (Fig. 1 magenta) is genetically compact, while Genus 2 (Fig. 1 cyan) is genetically diverse. But both are supported by prominent branches. However, Genus 3 and Genus 4 (Fig. 1 blue and red) are both compact and not separated from each other by prominent branches. From genetic perspective, their definition appears arbitrary and inconsistent with how Genus 2 is defined: they do not form the same level in the classification. The level that defines Genus 3 and 4 is closer to the leaves, and therefore should not have the same rank and the level that defines Genus 1 and 2. Thus, to achieve better consistency of the classification, we propose to combine Genus 3 and 4 into one, emphasizing evolutionary relationships and not subjective preferences of the authors who defined Genus 3 and 4. The next prominent level is defined as **subgenus**. For **species**, we largely rely on Fst (relative genetic diversification) and Gmin (measure of gene exchange) as detailed in Cong et al. (2019a). As a rough guide, but not a decisive criterion (Trujano-Ortega et al. 2020), we frequently provide percent difference in COI barcodes: 2% is usual for different species (Hebert et al. 2003), 10% for different genera, and about 7-8% for different congeneric subgenera.

The taxonomic rearrangements presented below follow the standardized format. Taxonomic act is the title of each section. For cited genera and subgenera, type species are given, and if the type species are synonyms, valid names are provided. When the species are listed with their originally proposed genus name, author names are given without parenthesis. For each species and subspecies with changed rank, type locality is specified. Most sections are illustrated by a segment of a nuclear genomic tree (or Z chromosome tree when specified) with species minimally necessary to support the conclusion. Presently employed genus-species combinations (Callaghan and Lamas 2004; Lamas 2004; Mielke 2005; Pelham 2008; Hall 2018) are used in the figures, including recently proposed changes (Pelham 2019; Zhang et al. 2019c; Pelham 2020; Zhang et al. 2020). New combinations and taxonomic changes are given in the text. Colors highlight phylogenetic groups and inconsistencies within the present classification that require attention and changes proposed here. The section ends with a conclusion and, if necessary, with a list of species with revised genus-species names combinations. The sections are ordered by family and generally in their taxonomic order deduced from genome-scale phylogeny complemented by phenotypic considerations. 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 PRJNA731937, and BioSample entries of the project contain the locality and collection data of the sequenced specimens shown in the trees. Exon sequences with diagnostic characters highlighted are also available from <https://osf.io/kj4es/>.

Family Papilionidae Latreille, [1802]

Boreographium Grishin, new subgenus

http://zoobank.org/32D82A5D-2DEB-4685-8179-D5FF9E5F2225

Type species. *Papilio marcellus* Cramer, 1777.

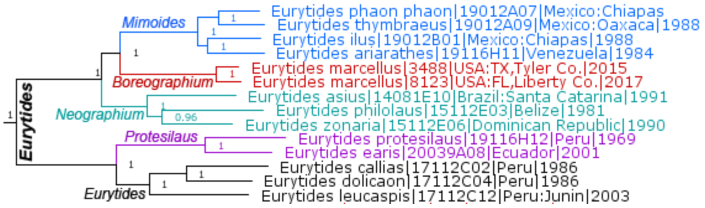

Fig. 2. Genus *Eurytides* with subgenera *Boreographium* subgen. n. (red), *Mimoides* (blue), *Neographium* (cyan), *Protesilaus* (purple) and *Eurytides* (black).

Definition. As revealed by genome-scale phylogenetic trees (Zhang et al. 2019d; Zhang et al. 2019c), the type species of this new subgenus is in the same clade with the subgenus *Mimoides* K. Brown, 1991 (type species *Papilio ariarathes* Esper, 1788) (Fig. 2). However, its wing patterns and shapes are more similar to subgenus *Neographium* Möhn, 2002 (type species *Papilio philolaus* Boisduval, 1836). This phenotypic distinction and early divergence from the common ancestor with *Mimoides* suggest that the *marcellus* clade should be defined as a subgenus of its own. This new subgenus is diagnosed by male genitalia: a unique broadly rounded ear-shaped harpe with a dorsal narrow keel projecting ventrad as a tooth for half of its length, and with two prominent narrow teeth: dorsal tooth directed anteriad, ventral tooth directed caudad, as illustrated on plate 66 in Tyler et al (1994). In other subgenera, the harpe is either narrower, or the keel is broader or not projecting beyond harpe, or the teeth are smaller or directed differently.

Etymology. The name is a masculine noun in the nominative singular, formed from *Boreo*[tis] (Latin for northern) + *Graphium* in reference to the northernmost representatives of the "Graphium" complex of taxa in America distributed up to northern Minnesota (Lotts and Naberhaus 2021).

Species included. Only the type species.

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

Esperourus Grishin, new subgenus

http://zoobank.org/DC085A9A-4391-49F3-B3AE-F2F57B0BB76C

Type species. *Papilio esperanza* Beutelspacher, 1975.

Fig. 3. Genus *Pterourus* with subgenera *Esperourus* subgen. n. (red), *Pterourus* (blue), *Jasoniades* (cyan), *Pyrrhosticta* (purple), and *Agehana* (green).

Definition. Confidently placed by Zakharov et al. (2004) as sister to the nominal subgenus of *Pterourus* Scopoli, 1777 (type species *Papilio troilus* Linnaeus, 1758) this new subgenus shows prominent genetic differentiation from the three species of the nominal subgenus (Fig. 3) and has diverged from them prior to the diversification of all other species of the genus *Pterourus*. Due to its ancient (comparatively to other *Pterourus* species) origin, the clade with *Pterourus esperanza* represents a valid subgenus. This new subgenus is diagnosed by a unique serrated lobe near the distal end of harpe in male genitalia, as illustrated on plate 100 in Tyler et al. (1994); and may be distinguished from other *Pterourus* species by its ventral forewing discal cell with 4 yellow longitudinal rays in the basal half, and from the three species in the subgenus *Pterourus* by its basal edge of the postdiscal band on the ventral hindwing that are closer to the outer margin than to the discal cell.

Etymology. The name is a masculine noun in the nominative singular, formed as a fusion of the type species name with its genus name: *Esper*[anza] + [Pter]*ourus*.

Species included. Only the type species.

Parent taxon. Genus *Pterourus* Scopoli, 1777.

Hyppasonia Grishin, new subgenus

http://zoobank.org/B37D0541-CD40-4824-AE21-BD6E37D37CB7

Type species. *Papilio hyppason* Cramer, 1775.

Fig. 4. Genus *Heraclides* with subgenera *Hyppasonia* subgen. n. (red), *Heraclides* (blue), *Calaides* (cyan) and *Priamides* (purple).

Definition. Previously, we noted this unnamed subgenus in the COI barcode dendrogram (Shiraiwa et al. 2014). Here, its definition is formalized. While the COI barcodes demonstrate its distinction from other subgenera of *Heraclides* Hübner, [1819] (type species *Papilio thoas* Linnaeus, 1771), its unexpected sister relationship with the nominal subgenus *Heraclides*—instead of with *Priamides* Hübner, [1819] (type species *Priamides hipponous* Hübner, [1819], which is a junior objective synonym of *Heraclides anchisiades* (Esper, 1788)) as hinted by similarities in wing shape and patterns—was discovered by Lewis et. al. (2015). Our genomic tree confirms this placement, and at the same time reveals prominent genetic differentiation from the nominal subgenus (Fig. 4). Curiously, the long branch in the tree that defines this subgenus suggests accelerated evolution that may explain its phenotypic differences from the nominal subgenus and likely mimetic wing patterns. This new subgenus is distinguished from others by a bilobed, crab-claw harpe with strongly unequal lobes: one lobe broad, rounded and serrated distad, and the other lobe shorter, narrow, tooth-like (for illustration see plate 83 in Tyler et al. (1994)). In other species with a bilobed harpe, the two lobes are nearly equal or at least the larger lobe is narrower and prominently constricted before the serrated end.

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 *Heraclides* Hübner, [1819].

Family Pieridae Swainson, 1820

Prestonia Schaus, 1920 belongs to Euremini Grote, 1898

The monotypic genus *Prestonia* Schaus, 1920 (type and the only species *Prestonia clarki* Schaus, 1920) has been tentatively placed near *Phoebis* Hübner, [1819] (type species *Phoebis cypris* Hübner, [1819], a junior subjective synonym of *Papilio argante* Fabricius, 1775) due to phenotypic similarity and no DNA sequences available for it. The genomic tree reveals that subfamily Coliadinae Swainson, 1821 splits into two clades that we treat as **tribes**: Coliadini Swainson, 1821 (includes *Phoebis*) and Euremini Grote, 1898 (Fig. 5). Genomic-scale phylogeny confidently places *Prestonia* as sister to *Kricogonia* Reakirt, 1863 (type species *Colias lyside* Godart, 1819) and therefore *Prestonia* belongs to Euremini Grote, 1898 (the clade that does not include *Phoebis*) and not to Coliadini.

Teriocolias deva (E. Doubleday, 1847) and *Teriocolias reticulata* (A. Butler, 1871) new combinations

Currently placed in *Eurema* Hübner, [1819] (type species *Papilio delia* Cramer, 1780, a junior homonym: valid name for this species is *Pieris daira* Godart, 1819), two species *Terias deva* Doubleday, 1847 and *Terias reticulata* Butler, 1871 are not monophyletic with *E. daira*, and instead are in the same clade with *Teriocolias zelia* (Lucas, 1852), which is a valid name of *Terias atinas* Hewitson, 1874, the type species of *Teriocolias* Röber, 1909 (Fig. 5). Therefore, these two species do not belong to *Eurema* and instead can be placed in *Teriocolias* implying *Teriocolias deva* (E. Doubleday, 1847) **comb. n.** and *Teriocolias reticulata* (A. Butler, 1871) **comb. n.**

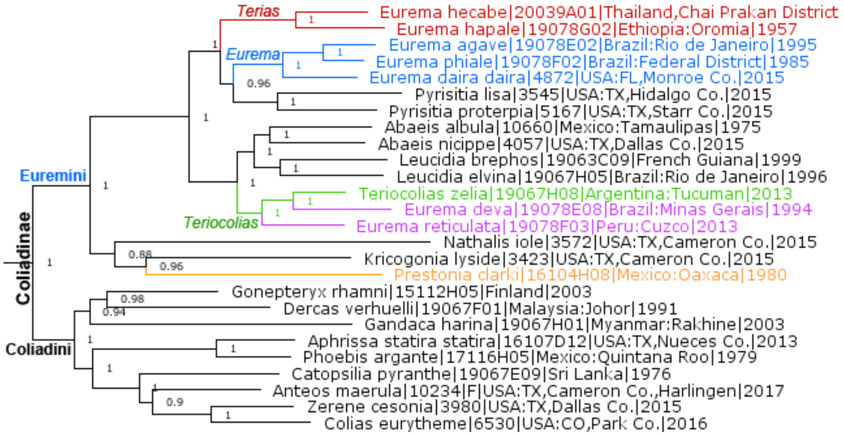

Fig. 5. Coliadinae and its two tribes: Coliadini and Euremini. *Eurema* (blue), *Terias* (red), and *Teriocolias* (green and magenta).

Terias Swainson, 1821 is a valid genus

Our genomic tree reveals that *Eurema* Hübner, [1819] (type species *Papilio delia* Cramer, 1780, a junior homonym: valid name is *Pieris daira* Godart, 1819) is paraphyletic with respect to *Pyrisitia* Butler, 1870 (type species *Papilio proterpia* Fabricius, 1775) (Fig. 5). To restore monophyly, we choose to keep *Pyrisitia* as a genus and therefore treat the Old World clade currently placed in *Eurema* as a distinct valid genus. *Terias* Swainson, 1821 (type species *Papilio hecabe* Linnaeus, 1758) is its oldest available name.

Pyrisitia westwoodii (Boisduval, 1836) is a species distinct from *Pyrisitia dina* (Poey, 1832)

Currently considered a subspecies of *Pyrisitia dina* (Poey, 1832) (type locality Cuba), *Terias westwoodii* Boisduval, 1836 (type locality Mexico) is prominently separated genetically from the insular taxa (Fig. 6). Compared to *Pyrisitia dina helios* (M. Bates, 1934) (type locality Bahamas) the Fst/Gmin statistics are 0.46/0.03 and their COI barcodes are 2.7% (18 bp) different. Therefore, we propose that *Pyrisitia westwoodii* (Boisduval, 1836), **reinstated status** is a species-level taxon and employ *Pyrisitia westwoodii gabriela* Le Crom & Llorente, 2004 **comb. nov.** We also confirm *Pyrisitia parvumbra* (Kaye, 1925) as a species (Fig. 6; 2.6%, 17 bp barcode difference).

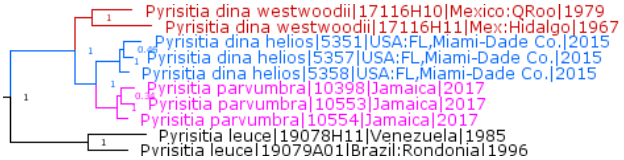

Fig. 6. *Pyrisitia westwoodii* (red), and *dina* (blue) and *parvumbra* (Jamaica).

Zegris Boisduval, 1836 is a subgenus of *Anthocharis* Boisduval, Rambur, [Duménil] & Graslin, [1833]

Zegris Boisduval, 1836 (type species *Papilio eupheme* Esper, [1804]) originates within *Anthocharis* Boisduval, Rambur, [Duménil] & Graslin, [1833] (type species *Papilio cardamines* Linnaeus, 1758), rendering it paraphyletic, and is confidently placed as a sister to subgenus *Paramidea* Kuznetsov, 1929 (type species: *Anthocharis scolymus* Butler, 1866) (Fig. 7). Subgenera of *Anthocharis* are genetically close to each other and even to the sister genus *Euchloe* (type species *Euchloe ausonia* var. *esperi* W. F.

Kirby, 1871, which is *Euchloe crameri* Butler (1869)) (Fig. 7). To restore the monophyly, instead of elevating subgenera of *Anthocharis* to genus status, we propose to treat *Zegris* Boisduval, 1836 as a subgenus of *Anthocharis* Boisduval, Rambur, [Duménil] & Graslin, [1833], along with its other two subgenera *Tetracharis* Grote, 1898 (type species *Anthocharis cethura* C. & R. Felder, 1865) and *Paramidea*.

Fig. 7. *Anthocharis* (blue and red) and *Euchloe* (magenta).

Cunizza Grote, 1900 is a junior subjective synonym of *Hesperocharis* C. Felder, 1862

Despite differing wing patterns, a monotypic genus *Cunizza* Grote, 1900 (type and the only species *Papilio hirlanda* Stoll, 1790) originates within *Hesperocharis* Felder, 1862 (type species *Pieris erota* Lucas, 1852) rendering it paraphyletic (Fig. 8). To restore monophyly, we propose that *Cunizza* Grote, 1900 is a junior subjective synonym of *Hesperocharis* C. Felder, 1862.

Fig. 8. *Hesperocharis* (blue, red and magenta) and *Mathania* (green).

Hesperocharis leucothea (Molina, 1782) new combination

Papilio leucothea Molina, 1782 (type locality Chile), currently placed in the genus *Mathania* Oberthür, 1890, originates within *Hesperocharis* Felder, 1862 (type species *Pieris erota* Lucas, 1852) according to the genome-scale tree (Fig. 8), which implies *Hesperocharis leucothea* (Molina, 1782) **comb. n.**

Reliquia Ackery, 1975 is a junior subjective synonym of *Pontia* [Fabricius], 1807

A monotypic genus *Reliquia* Ackery, 1975 (type and the only species *Reliquia santamarta* Ackery, 1975) originates within *Pontia* [Fabricius], 1807 (type species *Papilio daplidice* Linnaeus, 1758), rendering *Pontia* paraphyletic (Fig. 9). The tree shows that *Reliquia* is a close sister to the clade of three closely related species: *Pontia callidice* Hübner, [1800] (the type species of *Synchloe* Hübner, 1818, currently a junior subjective synonym of *Pontia*), *Pontia callidice* (Boisduval & Le Conte, [1830]) and *Pontia occidentalis* (Reakirt, 1866). E.g., COI barcodes of *R. santamarta* and *P. callidice* differ by 4.7% (31 bp). Therefore, *Reliquia* is a junior subjective synonym of *Synchloe*. Because we do not have sufficient evidence to raise *Synchloe* from synonymy with *Pontia*, we propose that *Reliquia* Ackery, 1975 is also a junior subjective synonym of *Pontia* [Fabricius], 1807.

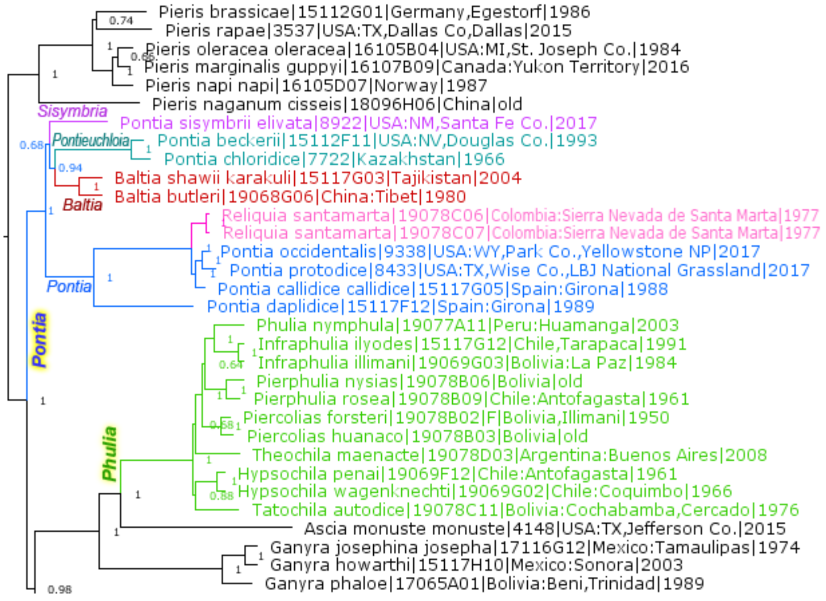

Fig. 9. Genera *Phulia* (green) and *Pontia*, colored non-green, with subgenera *Pontia* (blue), *Baltia* (red), *Pontieuchloia* (cyan), and *Sisymbria* subgen. n. (magenta). Former genus *Reliquia* is shown in pink.

Baltia Moore, 1878 and *Pontieuchloia* Verity, 1929 are subgenera of *Pontia* [Fabricius], 1807

A small genus *Baltia* Moore, 1878 (type species *Mesapia shawii* Bates, 1873) originates within *Pontia* [Fabricius], 1807 (type species *Papilio daplidice* Linnaeus, 1758), rendering *Pontia* paraphyletic (Fig. 9). *Baltia* is a confident but comparatively distant sister to the clade of two closely related species *Pontia chloridice* Hübner, [1813] (the type species of *Pontieuchloia* Verity, 1929, currently a junior subjective synonym of *Pontia*) and *Pontia beckerii* (W. H. Edwards, 1871). E.g., COI barcodes of *B. shawii* and *P. chloridice* differ by 8.5% (51 bp). To restore monophyly of *Pontia* and, at the same time, keep the relative distinction of *Baltia*, we propose that *Baltia* Moore, 1878 is a subgenus of *Pontia* [Fabricius], 1807. If *Baltia* is a subgenus and not a synonym, clades comparable to it in prominence should be defined as subgenera. In addition to the nominal subgenus (Fig. 9 blue and pink), of which *Synchloe* Hübner, 1818 (type species *Papilio callidice* Hübner, [1800]) is kept as a junior subjective synonym, we propose that *Pontieuchloia* Verity, 1929 is a valid subgenus (Fig. 9 cyan). For these subgenera to be monophyletic, a new subgenus is proposed next for the clade with *Pontia sisymbrii* (Boisduval, 1852) (Fig. 9 magenta).

Sisymbria Grishin, new subgenus

http://zoobank.org/28C486B5-3F65-4CDD-AC44-3FE386B58D0B

Type species. *Pieris sisymbrii* Boisduval, 1852.

Definition. This new subgenus differs from other subgenera of *Pontia* by the following combination of characters: forewing vein R_3 longer than in other subgenera, about half of vein R_{4+5} length; androconia present in the forewing discal cell spot in males, this spot is narrower than in other subgenera, with a notch on the outer edge (smoothly curved of straight in *Baltia*) and without a line of white scales along the discal cross-vein that is curved less strongly than in most other subgenera towards the wing base; dorsal hindwing without prominent bar at the end of discal cell; aedeagus shorter and relatively broader than in other subgenera, prominently curved at phallobase; hindwing below with gray or brown (not green or yellow) scaling along yellowish veins; full-grown caterpillar with orange-yellow framed with black rings on grayish segments; univoltine in spring. See Chang (1963) for elaboration on and illustrations of some of these characters as they are given for *P. sisymbrii*.

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 *Pontia* [Fabricius], 1807.

Comments. The genomic tree reveals markedly uneven rates of evolution within *Pontia* (Fig. 9): the nominotypical subgenus evolves about 2 times faster than other subgenera. This observation combined with rather substantial genetic differentiation among *Pontia*, including the COI barcode, which in *P. (Sisymbria) sisymbrii* and *P. (Pontia) daplidice* differs by 8.7% (57 bp), and close similarity in phenotypes of *Pontia* species creates a unique situation. On the one hand, *Pontia* (including *Baltia*) is a morphologically compact genus. On the other hand, strong genetic diversification behind this apparent phenotypic similarity may suggest elevating subgenera of *Pontia* to genera (which will return *Baltia* to the genus status), a step that we refrain from.

Tatochila A. Butler, 1870, *Piercolias* Staudinger, 1894, *Hypsochila* Ureta, 1955, *Theochila* W. D. Field, 1958, *Pierphulia* W. D. Field, 1958, and *Infraphulia* W. D. Field, 1958 are junior subjective synonyms of *Phulia* Herrich-Schäffer, 1867

Phulia Herrich-Schäffer, 1867 (type species *Pieris nymphula* Blanchard, 1852), *Tatochila* A. Butler, 1870 (type species *Synchloe autodice* Hübner, [1818]), *Piercolias* Staudinger, 1894 (type species *Trifurcula* *huanaco* Staudinger, 1894), *Hypsochila* Ureta, 1955 (type species *Tatochila microdice* f. *wagenknechti* Ureta, 1938), *Theochila* W. D. Field, 1958 (type species *Pieris maenacte* Boisduval, 1836), *Pierphulia* W. D. Field, 1958 (type species *Phulia nysias* Weymer, 1890), and *Infraphulia* W. D. Field, 1958 (type species *Phulia nymphula* var. *illimani* Weymer, 1890) cluster closely in the genomic tree without obvious separation into groups (Fig. 9 green). E.g., COI barcodes of *P. nymphula* and *T. autodice* differ by 4.0% (26 bp). However, being combined into one, all these genera together represent a prominently distinct genetic group that is sister to *Ascia* Scopoli, 1777 (type species *Papilio monuste* Linnaeus, 1764) and more distantly related to *Ganyra* Billberg, 1820 (type species *Papilio amaryllis* Fabricius, 1793, a junior homonym: valid name for this species is *Pieris josephina* Godart, 1819). With genetic similarity between these taxa being at the level of a species group, it may not be meaningful to consider these names as denoting valid subgenera, and therefore we propose that *Tatochila* A. Butler, 1870, *Piercolias* Staudinger, 1894, *Hypsochila* Ureta, 1955, *Theochila* W. D. Field, 1958, *Pierphulia* W. D. Field, 1958, and *Infraphulia* W. D. Field, 1958 are junior subjective synonyms of *Phulia* Herrich-Schäffer, 1867.

Calopierini Grishin, new tribe

http://zoobank.org/B7717ECE-C015-48AA-A57D-B7A6A3CCE4F6

Type genus. *Calopieris* Aurivillius, 1898.

Definition. In the genomic tree, this taxon is confidently placed as sister to the tribe Leptosiaini Braby, 2014 (Fig. 10, a monotypic tribe consisting of *Leptosia* Hübner, 1818) and shares veins M_1 and M_2 being connate with the hindwing discal cell, but genetically and phenotypically distant from it otherwise. Most notably, the wings are not rounded as in *Leptosia* and venation differs: forewing veins R_3 and R_{4+5} stalked for less than half of their lengths and M_1 stalked with their stalk, resembling Coliadinae Swainson, 1821 (e.g., *Phoebis* Hübner, [1819]). In general appearance reminds more of *Colotis*, where it was formerly included as a subgenus (Klots 1933), but is distinguished from it by very short and slender palpi that do not protrude beyond the front of the head and are not visible from above. Antennae are short (about half of forewing discal cell length) with large and flattened clubs. The combination of the abovementioned characters of palpi, antennae and wing venation uniquely defines this new tribe.

Genera included. Only the type genus.

Parent Taxon. Subfamily Pierinae Swainson, 1820.

Comments. Although grammatically correct formation of this tribe name calls for insertion of "id" before "ini", these letters have been elided from the stem to agree with Pierini, under Art. 29.3.1.1 (ICZN 1999).

Phrissura Butler, 1870 is a subgenus of *Appias* Hübner, [1819]

Frequently treated as a separate and monotypic genus, *Phrissura* Butler, 1870 (type species *Pieris illana* C. & R. Felder, 1862, currently a subspecies of *Pieris aegis* C. & R. Felder, 1861), is rather closely allied to *Appias* Hübner, [1819] (type species *Papilio zelmira* Stoll, 1780, currently a subspecies of *Papilio libythea* Fabricius, 1775) (Fig. 10 magenta and orange). E.g., COI barcodes of *P. illana* and *Appias olferna* Swinhoe, 1890 differ by 9.9% (65 bp). To emphasize the relationship between *Appias* and monotypic *Phrissura*, we propose treating the latter as a subgenus of the former, as already adopted in some publications (Wahlberg et al. 2014).

Fig. 10. *Calopierini* trib. n. (green), *Appias* (magenta and orange) with its subgenus *Phrissura* (orange) and *Catophaga* (blue and red) with its subgenus *Saletara* (red).

Saletara Distant, 1885 is a subgenus of *Catophaga* Hübner, 1819

Frequently treated as a subgenus of *Appias* Hübner, [1819] (type species *Papilio zelmira* Stoll, 1780, currently a subspecies of *Papilio libythea* Fabricius, 1775), *Catophaga* Hübner, [1819] (type species *Papilio paulina* Cramer, [1777]) is not monophyletic with it and instead, together with *Saletara* Distant, 1885 (type species *Pieris nathalia* C. & R. Felder, 1862, currently a subspecies of *Papilio liberia* Cramer, [1779]), is sister to *Aoa* de Nicéville, 1898 (type and the only species *Pieris affinis* Vollenhoven, 1865) (Fig. 10). Therefore, in agreement with Wahlberg et al. (2014), we treat *Catophaga* as a valid genus distinct from *Appias*. Our genomic tree reveals close clustering of *Saletara* (Fig. 10 red) with *Catophaga* (Fig. 10 blue) at the level consistent with congeners, hence we propose that *Saletara* is a subgenus of *Catophaga*.

Mesapia Gray, 1856 is a junior subjective synonym of *Aporia* Hübner, [1819]

A monotypic genus *Mesapia* Gray, 1856 (type and the only species *Pieris peloria* Hewitson, 1853) originates within *Aporia* Hübner, [1819] (type species *Papilio crataegi* Linnaeus, 1758) rendering it paraphyletic (Fig. 11). Due to the close relationship of these taxa, it is not desirable to restore monophyly by breaking *Aporia* into at least 3 genera. Therefore, agreeing with previous studies (Ding and Zhang 2016; Todisco et al. 2020), genomic-scale phylogeny provides the ultimate evidence that *Mesapia* Gray, 1856 is a junior subjective synonym of *Aporia* Hübner, [1819].

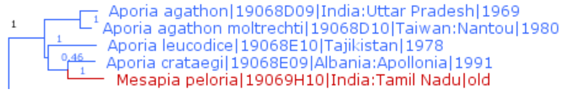

Fig. 11. *Aporia* (blue and red).

Leodonta Butler, 1870 is a subgenus of *Pereute* Herrich-Schäffer, 1867

Despite its nearly extreme difference in appearance, *Leodonta* Butler, 1870 (type species *Euterpe dysoni* Doubleday, 1847) and *Pereute* Herrich-Schäffer, 1867 (type species *Euterpe callinice* C. & R. Felder, 1861) are genetically close sisters (Fig. 12). Genetic diversification between them is smaller than that in a related genus *Mylothris* Hübner, [1819] (Fig. 12). Disparate phenotypes are frequently placed in the same genus, e.g. *Pterourus euterpinus* (Salvin & Godman, 1868) and *Pterourus eurymedon* (Lucas, 1852) to some extent resemble *Pereute* and *Leodonta*, respectively. Therefore, we propose adopting a more internally consistent classification when groups of similar divergence are assigned similar taxonomic rank, and treat *Leodonta* Butler, 1870 as a subgenus of *Pereute* Herrich-Schäffer, 1867 despite their wing pattern differences.

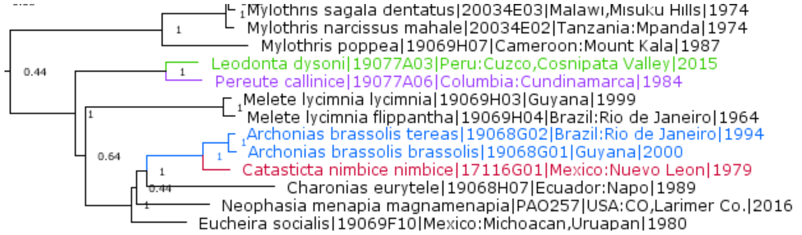

Fig. 12. *Pereute* (purple and green) with its subgenus *Leodonta* (green) and *Archonias* (blue and red) with its synonym *Catasticta* (red).

Catasticta Butler, 1870 is a junior subjective synonym of *Archonias* Hübner, 1827

Catasticta Butler, 1870 (type species *Euterpe nimbice* Boisduval, 1836) clusters closely with *Archonias* Hübner, [1829] (type species *Archonias marcias* Hübner, 1825 which is currently treated as a subspecies of *Papilio brassolis* Fabricius, 1777 from Brazil: Bahia) in the genomic tree (Fig. 12). Genetic diversification between these genera is within the norm for most Pieridae genera, e.g., *Mylothris* shown in the same tree. Moreover, previously published phylogenetic trees reveal that *Catasticta* is not monophyletic (Padrón 2014; Wahlberg et al. 2014), although sometimes with low support. Furthermore, Padrón (2014) discussed this issue at length and suggested synonymy between *Catasticta* and *Archonias*.

We agree with these conclusions, also supported by our genome-scale results. Although further studies are required to develop a meaningful classification within this very large genus, three independent studies provide phylogenetic data suggesting that *Catasticta* Butler, 1870 is a junior subjective synonym of *Archonias* Hübner, 1827. This name change may not be welcomed by those used to the name *Catasticta*, but it will be necessary to accept at one point. While some may consider breaking this large genus into several genera, the genomic tree indicates that other relatives of *Catasticta*, such as *Charonias* Röber, 1908 (type species *Euterpe eurytele* Hewitson, 1853), *Neophasia* Behr, 1869 (type species *Pieris menapia* C. & R. Felder, 1859), and *Eucheira* Westwood, 1834 (type and the only species *Eucheira socialis* Westwood, 1834) are all closely allied to each other and may be treated as subgenera of *Archonias*, along with some others currently placed in *Catasticta*. However, details of such classification will be revealed after genomic-scale sequencing of all major species groups in this complex is completed.

Family Lycaenidae [Leach], [1815]

***Sandia* Clench & P. Ehrlich, 1960 and *Xamia* Clench, 1961 are junior subjective synonyms of *Incisalia* Scudder, 1872**

Appearance could be misleading, especially if unusual. Despite unique wing patterns, we find from the genomic analysis that *Sandia* Clench & P. Ehrlich, 1960 (type and the only species *Callophrys* (*Sandia*) *mcfarlandi* P. Ehrlich & Clench, 1960) originates within *Deciduphagus* K. Johnson, 1992 (type species *Thecla augustinus* Westwood, 1852), and is sister to *Callophrys fotis* (Strecker, [1878]) (Fig. 13). Because *Deciduphagus* is currently a junior subjective synonym of *Incisalia* Scudder, 1872 (type species *Lycus niphon* Hübner, [1819]) (Pelham 2008; Pelham 2020) due to evolutionary closeness, and because *Sandia* renders both *Deciduphagus* and *Incisalia* paraphyletic, we propose that *Sandia* is a junior subjective synonym of *Incisalia*. Furthermore, uniquely patterned *Xamia* Clench, 1961 (type species *Thecla xami* Reakirt, [1867]) also originates within *Deciduphagus* and is sister to the *Deciduphagus* core group that contains the type species. Although *Xamia* is more distant from other congeners than *Sandia*, it still falls within the prominent *Incisalia* clade. Thus leaving it as a valid subgenus would require a new name for at least *Callophrys polios* (Cook & F. Watson, 1907), which is sister to the clade consisting of *Xamia* and the core *Deciduphagus* species, but is not prominently distinct from its relatives. Therefore, we propose to treat *Xamia* as a junior subjective synonym of *Incisalia*. Finally, we note that *Deciduphagus* as originally defined (Fig. 13 cyan) (Johnson 1992) is also paraphyletic with respect to *Incisalia* (Fig. 13 green), and *Callophrys henrici* (Grote & Robinson, 1867) with *Callophrys irus* (Godart, [1824]) should be attributed to *Incisalia sensu stricto* instead of to *Deciduphagus*. As a result of this analysis (Fig. 13), we conclude that the genus *Callophrys* diversified into 5 prominent clades that correspond to the level of subgenus: *Callophrys*, *Incisalia*, *Cisincisalia* K. Johnson, 1992 (type species *Cisincisalia moecki* K. Johnson, 1992, a junior subjective synonym of *Callophrys guatemalena* Clench, 1981), *Mitoura* Scudder, 1872 (type species *Thecla smilacis* Boisduval & Le Conte, [1835]) and the fifth subgenus that includes Nearctic species superficially similar to Palearctic *Callophrys*, but instead is a confidently supported sister to *Incisalia* (Fig. 13 red) (ten Hagen and Miller 2010). This subgenus does not have a name available for it and therefore is new.

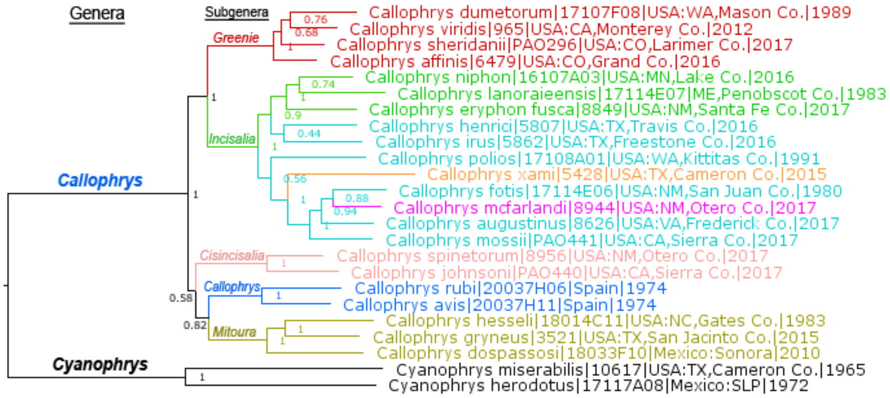

Fig. 13. *Callophrys* subgenera: *Greenie* subgen. n. (red), *Cisincisalia* (pink), *Callophrys* (blue), *Mitoura* (olive), and *Incisalia* (green) with its synonyms *Deciduphagus* (cyan), *Xamia* (orange), and *Sandia* (magenta).

Greenie Grishin, new subgenus

http://zoobank.org/733681D0-34AF-4884-9396-BE415705E783

Type species. *Thecla sheridonii* [sic] Edwards, 1877, presently *Callophrys sheridanii* (Edwards, 1877).

Definition. Previously placed in the subgenus *Callophrys* Billberg, 1820 (type species *Papilio rubi* Linnaeus, 1758) but is not monophyletic with it, forming a prominent lineage of its own within the genus *Callophrys* (Fig. 13). In appearance, remarkably similar to some species (including the type) from the subgenus *Callophrys* in: wings rounded without tails, slightly lobed hindwings at anal angle, and green color of ventral surface with postdiscal variously complete to absent row of white markings. Distinguished from *Callophrys* by hindwing tornal area: less developed lobe and less crenulate outer margin, and generally smaller and rounder forewing androconial patch. Diagnosed among the genus *Callophrys* by a combination of the following characters in the nuclear genome: cce2400.8.3:T366C, cce8426.17.3:C4290T, cce10587.6.6:G181C, cce925.9.4:C351T, and cce2041.25.2:T1572A; and the COI barcode: 479C (not T) and 610C (not T), differing from the subgenus *Callophrys* in 202T (not A), 512G (not T), and 556T (not A). See <https://osf.io/kj4es/> for the sequences with these characters.

Etymology. The name is a feminine noun in the nominative singular, Latinized verbatim from the affectionate English name of this butterfly group.

Species included. The type species, *Thecla viridis* W. H. Edwards, 1862, *Thecla dumetorum* Boisduval, 1852, and *Thecla affinis* W. H. Edwards, 1862.

Parent taxon. Genus *Callophrys* Billberg, 1820.

Family Riodinidae Grote, 1895

Takashia M. Okano & T. Okano, 1985 is a subgenus of *Polycaena* Staudinger, 1886

Monotypic genus *Takashia* M. Okano & T. Okano, 1985 (type and the only species *Timelaea nana* Leech, 1892) is a close sister to *Polycaena* Staudinger, 1886 (type species *Polycaena tamerlana* Staudinger, 1886) (Fig. 14 magenta and blue). To avoid yet another not truly distinct monotypic genus, we propose to place *Takashia* M. Okano & T Okano, 1985 as a subgenus of *Polycaena* Staudinger, 1886.

Corrachia Schaus, 1913 is a subgenus of *Styx* Staudinger, 1876

Two monotypic genera *Styx* Staudinger, 1876 (type and the only species *Styx infernalis* Staudinger, 1875) and *Corrachia* Schaus, 1913 (type and the only species *Corrachia leucoplaga* Schaus, 1913) are close sisters (Fig. 14 red and green). Hindered by substantial difference in appearance, their close kinship has been revealed by DNA sequencing and discussed in detail (Espeland et al. 2015). Their COI barcodes differ by only 7.4% (49 bp). Here, we take the next step and eliminate the two monotypic genera by proposing that *Corrachia* Schaus, 1913 is a subgenus of *Styx* Staudinger, 1876. Considering these two close relatives to be congeneric is more revealing about their evolutionary relationship than keeping them in two not prominently distinct monotypic genera.

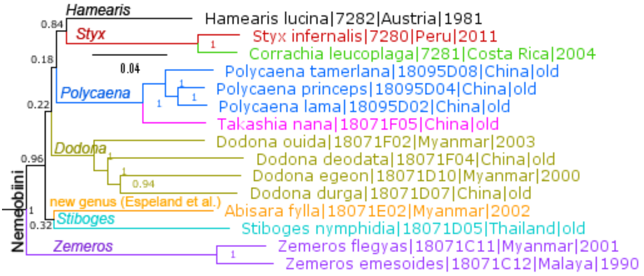

Fig. 14. Nemeobiini genera: *Hamearis* (black), *Styx* (red and green), *Polycaena* (blue and magenta), *Dodona* (olive), new genus (Espeland et al. 2015), *Stiboges* (cyan) and *Zemeros* (purple).

Hades Westwood, 1851 is a junior subjective synonym of *Methone* Doubleday, 1847

Despite their difference in appearance, monotypic genus *Methone* Doubleday, 1847 (type and the only species *Papilio cecilia* Cramer, 1777) is genetically close to *Hades* Westwood, 1851 (type species *Hades noctula* Westwood, 1851) (Fig. 15 brown and gray). Therefore, we propose that *Hades* is a junior subjective synonym of *Methone* and deduce that the phenotypic difference between *Hades* and *Methone* was caused by rapid evolution possibly driven by selection for mimetic appearance of their type species, each in a different mimetic complex.

Methone Doubleday, 1847 receives 9 species from *Euselasia* Hübner, [1819]

We find that *Euselasia* Hübner, [1819] (type species *Euselasia gelaena* Hübner, [1819], which is *Papilio gelon* Stoll, 1787) as currently defined is paraphyletic with respect to *Methone* Doubleday, 1847 (type species *Papilio cecilia* Cramer, 1777), and a number of *Euselasia* species belong to the clade with *Methone cecilia* (Fig. 15 red and brown). The type species of *Euselasia* and *Methone* are genetically distant from each other, e.g., their COI barcodes differ by 11.5% (76 bp), which is typical for species in different genera. Therefore, to restore the monophyly, instead of placing *Methone* in *Euselasia*, we transfer *Methone*-clade species (Fig. 15 red) and their phenotypically close relatives from *Euselasia* to *Methone* to form the following **new combinations**: *Methone euploea* (Hewitson, [1855]), *Methone eucerus* (Hewitson, 1872), *Methone hypophaea* (Godman & Salvin, 1878), *Methone eubule* (R. Felder, 1869), *Methone onorata* (Hewitson, 1869), *Methone authe* (Godman, 1903), *Methone dolichos* (Staudinger, [1887]), *Methone baucis* (Stichel, 1919), and *Methone eucrates* (Hewitson, 1872).

Erythia Hübner, [1819] and *Marmessus* Hübner, [1819] are valid genera

Considered junior subjective synonyms of *Euselasia* Hübner, [1819] (type species *Euselasia gelaena* Hübner, [1819], which is *Papilio gelon* Stoll, 1787), *Erythia* Hübner, [1819] (type species *Papilio labdacus* Stoll, 1780) (Fig. 15 olive) and *Marmessus* Hübner, [1819] (type species *Papilio lisias* Cramer, 1777) (Fig. 15 cyan) are genetically distant from *Euselasia* (Fig. 15 blue) and form two prominent clades in the tree that should be assigned a genus rank (Fig. 15). Therefore, we reinstate *Erythia* and *Marmessus* as valid genera. As a result, we split *Euselasia* as it is currently circumscribed into 4 genera. Indeed, *Euselasia sensu lato* is a tribe rank taxon by its genetic divergence comparable to the divergence between *Taxila* Doubleday, 1847 (in the subtribe Abisarina Stichel, 1928) and *Hamearis* Hübner, 1819 (in the subtribe Nemeobiina Bates, 1868) (Fig. 15 black). However, after this split, species remaining in *Euselasia* are not monophyletic (all named *Euselasia* in Fig. 15) and there are other prominent clades in the tree. The level in the tree with these clades is visually obvious, because they diversified at about the same time (Fig. 15 different colors, with names along branches). These nine clades supported by prominent branches of about the same length correspond to genera. The type species of *Psalidopteris* Hübner, 1823, *P. nycha*

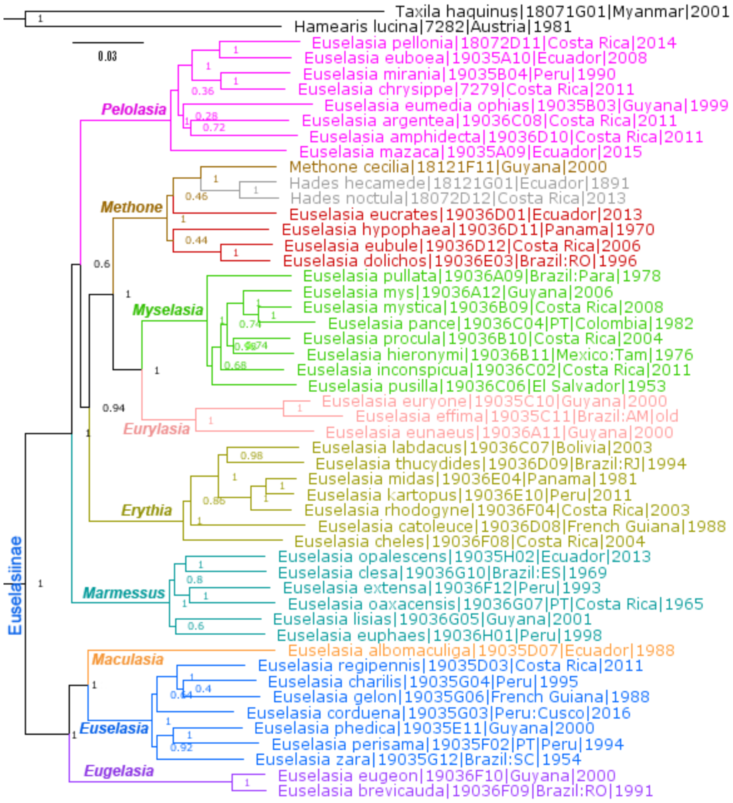

Fig. 15. Euselasiinae genera: *Pelolasia* gen. n. (magenta), *Methone* (brown, gray, and red), *Myselasia* gen. n. (green), *Eurylasia* gen. n. (pink), *Erythia* (olive), *Marmessus* (cyan), *Maculasia* gen. n. (orange), *Euselasia* (blue), *Eugelasia* gen. n. (purple). Compare Euselasiinae divergence to that of *Taxila* and *Hamearis* (black).

Hübner, 1823, which is a junior subjective synonym of *Hesperia thucydides* Fabricius, 1793, is in the *Erythia* clade, making *Psalidopteris* a junior subjective synonym of *Erythia*. Thus, four of these major clades have names and five do not, corresponding to five new genera that are proposed next.

Pelolasia Grishin, new genus

http://zoobank.org/A9AC96C6-B5D0-416D-9C5E-0853B7BD8339

Type species. *Eurygona pelor* Hewitson, [1853].

Definition. Currently within *Euselasia* Hübner, [1819] (type species *Euselasia gelaena* Hübner, [1819], which is *Papilio gelon* Stoll, 1787) but is not monophyletic with it (Fig. 15 magenta). Instead, an independent prominent lineage originating in the early radiation of Euselasiini Kirby, 1871 and a poorly supported sister to the clade that includes *Methone* Doubleday, 1847 (type species *Papilio cecilia* Cramer, 1777) (Fig. 15 brown, gray and red) and *Erythia* Hübner, [1819] (type species *Papilio labdacus* Stoll, 1780) (Fig. 15 olive). Therefore, it constitutes a new genus. Union of Stichel (1928) groups Peloriformes, Eusepiformes, Melaphaeoformes, Argenteoformes and Eubuliformes (in part). Characterized by wings rounder than in relatives, hindwing with undulate outer margin and checkered fringes, ventrally with postdiscal reddish line and a row of marginal black dots framed with white, reddish, or both; or nearly immaculate wings below, silvery to golden, may be with marginal black dots on hindwing and brown postdiscal line; or with 3–5 brown narrow bands over broader than bands pale background, lacking isolated large eyespots or dotted discal pattern, or with a row of small eyespots along hindwing margin. The following combination of nuclear genome characters is diagnostic: cne2559.1.3:T87C, cne3355.8.1:T362C, cne1314.4.1:A351G, cne2022.5.2:C448A, and cne599.10.1:T5841A.

Etymology. The name is a feminine noun in the nominative singular formed as a fusion of the type species name and its former genus name: *Pelo*[r] + [Euse]*lasia* to keep the word at 9 letters, which is the number of letters in *Euselasia* and the number of genera *Euselasia* is being split into.

Species included. The type species, *Eurygona amphidecta* Godman & Salvin, 1878, *Eurygona argentea* Hewitson, 1871, *Eurygona artos* Herrich-Schäffer, [1853], *Eurygona aurantia* Butler & Druce, 1872, *Eurygona bettina* Hewitson, 1869, *Eurygona candaria* Druce, 1904, *Eurygona cataleuca* R. Felder, 1869, *Eurygona chrysippe* Bates, 1866, *Eurygona euboea* Hewitson, [1853], *Eurygona eumedia* Hewitson, 1853, *Eurygona eumenes* Hewitson, 1853, *Euselasia eupatra* Seitz, 1916, *Eurygona eusepus* Hewitson, 1853, *Eurygona fervida* Butler, 1874, *Euselasia hahneli* Staudinger, [1887], *Euselasia ignitus* Stichel, 1924, *Eurygona mazaca* Hewitson, 1860, *Erythia melaphaea* Hübner, 1823, *Eurygona mirania* Bates, 1868, *Euselasia misteriosa* Salazar & J. Vargas, 2019, *Euselasia nytua* J. Hall & Willmott, 2009, *Euselasia pellonia* Stichel, 1919, *Euselasia rubrocilia* Lathy, 1926, and *Euselasia seitzi* Lathy, 1926.

Parent taxon. Subfamily Euselasiinae Kirby, 1871.

Myselasia Grishin, new genus

http://zoobank.org/61CDF024-ADCB-49D0-82FA-9956EA9E5553

Type species. *Eurygona mys* Herrich-Schäffer, [1853].

Definition. Currently within *Euselasia* Hübner, [1819] (type species *Euselasia gelaena* Hübner, [1819], which is *Papilio gelon* Stoll, 1787) but is not monophyletic with it (Fig. 15 green). Instead, an independent prominent lineage in the same clade with and of the same rank as *Methone* Doubleday, 1847 (type species *Papilio cecilia* Cramer, 1777) (Fig. 15 brown, gray and red), thus is a new genus. Largely, the Hygeniiformes group of Stichel (1928), sharing its diagnostic characters. Hindwing rounded, below with a kinked-L-shaped central reddish band and an eyespot in the middle by the margin, but without well-developed marginal longitudinal dashes; forewing without eyespots and with 1-2 narrow reddish bands. The following combination of nuclear genome characters is diagnostic: cne23605.2.5:C468T, cne13338.5.3: A334C, cne123.2.3:C1009T, cne18035.2.1:C172A, and cne81.14.5:A756G.

Etymology. The name is a feminine noun in the nominative singular formed as a fusion of the type species name and its former genus name: *Mys* + [Eus]*elasia* to keep the word at 9 letters, which is the number of letters in *Euselasia* and the number of genera *Euselasia* is being split into.

Species included. The type species, *Eurygona alcmena* Druce, 1878, *Eurygona athena* Hewitson, 1869, *Eurygona cafusa* Bates, 1868, *Euselasia crinon* Stichel, 1919, *Euselasia cucuta* (Schaus, 1902), *Euselasia cyanofusa* J. Hall & Willmott, 1998, *Euselasia eberti* Callaghan, 1999, *Euselasia ella* Seitz, 1916, *Eurygona eulione* Hewitson, 1856, *Euselasia eustola* Stichel, 1919, *Euselasia gradata* Stichel, 1927, *Eurygona hieronymi* Salvin & Godman, 1868, *Papilio hygenius* Stoll, 1787, *Euselasia illarina* J. Hall, Willmott & R. Busby, 1998, *Eurygona inconspicua* Godman & Salvin, 1878, *Euselasia janigena* Stichel, 1919, *Euselasia jigginsi* J. Hall & Willmott, 1998, *Eurygona leucon* Schaus, 1913, *Euselasia mapatayna* J. Hall & Willmott, 1998, *Euselasia marica* Stichel, 1919, *Eurygona mystica* Schaus, 1913, *Euselasia nauca* J. Hall & Willmott, 1998, *Euselasia pance* Callaghan, 1999, *Eurygona procula* Godman & Salvin, 1885, *Euselasia pseudomys* Callaghan, 1999, *Euselasia pullata* Stichel, 1927, *Eurygona pusilla* R. Felder, 1869, *Euselasia rhodon* Seitz, 1913, and *Eurygona sergia* Godman & Salvin, 1885.

Parent taxon. Subfamily Euselasiinae Kirby, 1871.

Eurylasia Grishin, new genus

http://zoobank.org/44399705-A1CF-43AF-B35E-F510E964BDE0

Type species. *Eurygona euryone* Hewitson, 1856.

Definition. Currently within *Euselasia* Hübner, [1819] (type species *Euselasia gelaena* Hübner, [1819], which is *Papilio gelon* Stoll, 1787) but is not monophyletic with it (Fig. 15 pink). Instead, an independent prominent lineage in the same clade with and of the same rank as *Methone* Doubleday, 1847 (type species *Papilio cecilia* Cramer, 1777) (Fig. 15 brown, gray and red), hence is a new genus. It is diagnosed by its distal ⅖ of hindwing dusted pale-yellow below, large round marginal eyespot in the middle of it, and either large eyespot in the middle by forewing margin below or diagonal orange patch on forewing above. The hindwing tornus is pale above in some species. The following combination of nuclear genomic characters is diagnostic: cne9878.8.1:C146A, cne178.3.20:C595T, cne178.3.20:T596C, cne7676.26.2: T31C, and cne5931.2.1:A478G.

Etymology. The name is a feminine noun in the nominative singular formed as a fusion of the type species name and its former genus name: *Eury*[one] + [Euse]*lasia* to keep the word at 9 letters, which is the number of letters in *Euselasia* and the number of genera *Euselasia* is being split into.

Species included. The type species, *Eurygona effima* Hewitson, 1869, *Euselasia thusnelda* Möschler, 1883, and *Eurygona eunaeus* Hewitson, 1855.

Parent taxon. Subfamily Euselasiinae Kirby, 1871.

Maculasia Grishin, new genus

http://zoobank.org/20121C52-93F8-4540-9070-FF2971B2D960

Type species. *Euselasia albomaculiga* Callaghan, 1999.

Definition. The genus is sister to *Euselasia* Hübner, [1819] (*Euselasia gelaena* Hübner, [1819], which is *Papilio gelon* Stoll, 1787) and is prominently distinct from it genetically (Fig. 15 orange). Therefore, it constitutes a new genus. Distinguished from its relatives by the characters given on pages 1047–1048 and illustrated in Figs. 3–6, 46–47 for *Euselasia albomaculiga* by Callaghan (1999). In brief, its wings are rounded, without blue scaling, its forewings are with a large pale spot, and its ventral hindwing submarginal black spots are surrounded by grayish-white (not at the end of orange rays, except the central large one that is framed by yellow basad), and have yellow streaks along the veins not between them; valvae narrowing to a point, not bilobed, as long as tegumen with uncus, slightly wider than aedeagus, vinculum angled in lateral view, with spurs in the middle directed caudad. Additionally, the following combination of nuclear genomic characters is diagnostic: cne2298.2.2:A2104A (not C), cne5129.1.5: A833A (not G), cne2685.14.3:A934A (not T), cne1095.7.22:G1463G (not A), cne4870.1.18:T552T (not A), cne2885.9.10:A4270C, cne1547.14.4:A2756G, cne1696.1.1:A2529T, cne7231.10.9:T567C, and cne1036.6.11:G3200C.

Etymology. The name is a feminine noun in the nominative singular formed as a fusion of the type species name and its former genus name: [albo]*Macu*[liga] + [Euse]*lasia* to keep the word at 9 letters, which is the number of letters in *Euselasia* and the number of genera *Euselasia* is being split into.

Species included. Only the type species.

Parent taxon. Subfamily Euselasiinae Kirby, 1871.

Eugelasia Grishin, new genus

http://zoobank.org/36F889D1-2E27-40BB-95B9-7619031A223E

Type species. *Eurygona eugeon* Hewitson, 1856.

Definition. This taxon is sister to the clade formed by *Euselasia* Hübner, [1819] (*Euselasia gelaena* Hübner, [1819], which is *Papilio gelon* Stoll, 1787) and *Maculasia* gen. n. and is prominently distinct from it genetically (Fig. 15 purple); hence it is a new genus. It is distinguished from its relatives by its inverted-drop shaped hindwing with extended anal lobe, as well as by its solid-brown color above and lack of eyespots below, fringes dark, legs yellow; and the following combination of nuclear genomic characters: cne1999.2.1:C203A, cne1015.3.2:T555C, cne2803.19.1:G88A, cne5471.1.1:T261C, and cne703.2.8:A1414C.

Etymology. The name is a feminine noun in the nominative singular formed as a fusion of the type species name and its former genus name: *Euge*[on] + [Euse]*lasia* to keep the word at 9 letters, which is the number of letters in *Euselasia* and the number of genera *Euselasia* is being split into.

Species included. The type species and *Euselasia brevicauda* Lathy, 1926.

Parent taxon. Subfamily Euselasiinae Kirby, 1871.

Eunogyrina Grishin, new subtribe

http://zoobank.org/CB55411C-D989-4F77-87C6-9E2E2023C608

Type genus. *Eunogyra* Westwood, 1851.

Definition. Placed in Mesosemiina Bates, 1859 on the basis of phenotypic assessment (Hall 2003), the two genera *Eunogyra* Westwood, 1851 (type species *Eunogyra satyrus* Westwood, 1851) and *Teratophthalma* Stichel, 1909 (type species *Mesosemia phelina* C. & R. Felder, 1862) form a clade that is sister to the clade formed by Mesosemiina and Napaeina Hall, 2003 (Figs. 16, 27), and therefore *Eunogyra* taken together with *Teratophthalma* constitute a substribe. The description and diagnostic characters of this new subtribe are as those given for *Eunogyra* on page 463 by Westwood (1851) and page 90 (illustrated in Fig. 16) by Stichel (1910), and for *Teratophthalma* on pages 76–77 (illustrated in Fig. 11) by Stichel (1910). In brief, the subtribe belongs to Mesosemiini (see Hall (2003) for genera *Eunogyra* and *Teratophthalma*), and is diagnosed by the following combination of characters: wings without multiple narrow bands, eyespots either at the end of forewing discal cell or along wing margins;

genitalic valvae short (as long as tegumen) and triangular, simple with rounded or pointed apex, but without two separated posterior projections with narrow intervening section, pedicel unsclerotized in the middle or ventrally split (or both).

Genera included. The type genus and *Teratophthalma* Stichel, 1909.

Parent Taxon. Tribe Mesosemiini Bates, 1859.

Semomesia Westwood, 1851, *Mesophthalma* Westwood, 1851, *Perophthalma* Westwood, 1851 and *Leucochimona* Stichel, 1909 are junior subjective synonyms of *Mesosemia* Hübner, [1819]

The following four genera render *Mesosemia* Hübner, [1819] (type species *Mesosemia phicoclessa* Hübner, [1819], which is *Papilio philocles* Linnaeus, 1758) paraphyletic, in agreement with Seraphim (2018): *Semomesia* Westwood, 1851 (type species *Papilio croesus* Fabricius, 1777), *Mesophthalma* Westwood, 1851 (type species *Mesophthalma idotea* Westwood, 1851), *Perophthalma* Westwood, 1851 (type species *Mesosemia tenera* Westwood, 1851 which is *Papilio tullius* Fabricius, 1787) and *Leucochimona* Stichel, 1909 (type species *Papilio philemon* Cramer, 1775, homonym, current name *Mesosemia icare* Hübner, [1819]) (Fig. 16). Our genomic phylogeny indicates that all these genera (Fig. 16 green, purple, orange, and olive) and a number of other lineages currently placed in *Mesosemia* (Fig. 16 blue) diversified rapidly around the same time, leading to the comb-like structure of the tree rather than a well-resolved dichotomous phylogeny. This situation is commonly encountered in genomic analyses of butterflies (Li et al. 2019; Zhang et al. 2019a; Zhang et al. 2019d) and suggests existence of levels in diversification that can be used for classification. This radiation of *Mesosemia* and related genera was dated to about 15 Mya (Seraphim et al. 2018) and therefore corresponds to the diversification of a genus. All these *Mesosemia*-like genera are close to each other both genetically (Fig. 16) and phenotypically, and we propose to treat *Semomesia* Westwood, 1851, *Mesophthalma* Westwood, 1851, *Perophthalma* Westwood, 1851 and *Leucochimona* Stichel, 1909 as junior subjective synonyms of *Mesosemia* Hübner, [1819].

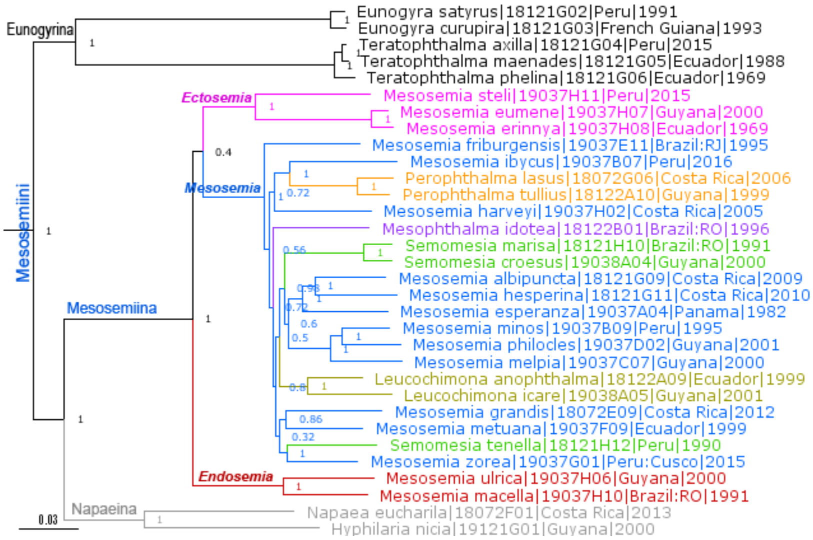

Fig. 16. Mesosemiini subtribes: Eunogyrina subtrib. n. (black), Napaeina (gray) and Mesosemiina with genera: *Ectosemia* gen. n. (magenta), *Endosemia* gen. n. (red), and *Mesosemia* (blue and other colors) with its synonyms *Semomesia* (green), *Mesophthalma* (purple), *Perophthalma* (orange) and *Leucochimona* (olive).

Inspection of the branching pattern in the tree (Fig. 16) reveals the next level: i.e., diversification of the subtribe Mesosemiina Bates, 1859 into 3 lineages. Their exact bifurcation order is not resolved (support 0.4) due to closeness of these events in time (=rapid radiation) and possible incomplete lineage sorting or introgression early in their origins. These 3 lineages correspond to genera, although currently these species are included in the paraphyletic genus *Mesosemia*. One of these lineages is the genus *Mesosemia* (*sensu lato*) that includes all available names in the group as synonyms (as detailed above), together with *Diophtalma* Boisduval, 1836 (type species *Diophtalma telegone* Boisduval, 1836), which is already considered to be its synonym. Therefore, the other two lineages do not have names and represent new genera that are defined below. Furthermore, a possibility of additional new genera in Mesosemiina has been suggested, although not yet formalized (Seraphim et al. 2018).

Ectosemia Grishin, new genus

http://zoobank.org/8AB8B269-CAE8-417D-BF0D-E46043B20CBE

Type species. *Papilio eumene* Cramer, 1776.

Definition. Species in this clade are currently in *Mesosemia* Hübner, [1819] (type species *Mesosemia phicoclessa* Hübner, [1819], which is *Papilio philocles* Linnaeus, 1758), but are quite distant from it falling much outside of the *Mesosemia* radiation and originating during the earlier round of radiation (Fig. 16). Therefore this clade is a taxon of the same rank, a genus. This new genus differs from *Mesosemia* by the following combination of characters: hindwing not lobed in the middle, each wing with 2 broad and straight parallel bands: discal and postdiscal, bands do not encircle forewing eyespot as in most *Mesosemia*, but discal forewing band bends distad at costa, no striations, discal cell eyespots developed ventrally on both wings, elongated along the cell, with 3 white spots inside (sometimes 2 on hindwing). Furthermore, the following combination of nuclear genomic characters is diagnostic: cne7048.1.3: T2251C, cne3658.2.1:A638T, cne2957.11.4:A952G, cne3658.2.1:A608C, and cne3461.2.10:C1462A.

Etymology. The name is a feminine noun in the nominative singular formed by replacing prefix "Meso-" with "Ecto-" in the name of the former genus for these species.

Species included. The type species, *Mesosemia decolorata* Lathy, 1932, *Mesosemia erinnya* Stichel, 1910, and *Mesosemia steli* Hewitson, 1858.

Parent taxon. Subtribe Mesosemiina Bates, 1859.

Endosemia Grishin, new genus

http://zoobank.org/AA1AC39C-2696-46A8-9927-2A8CDBB14D28

Type species. *Papilio ulrica* Cramer, 1777.

Definition. Species in this clade are currently in *Mesosemia* Hübner, [1819] (type species *Mesosemia phicoclessa* Hübner, [1819], which is *Papilio philocles* Linnaeus, 1758), but are quite distant from it falling much outside of the *Mesosemia* radiation and originating during the earlier round of radiation (Fig. 16). Therefore this clade is a taxon of the same rank, a genus. This new genus differs from both *Mesosemia* and *Ectosemia* gen. n. by the following combination of characters: hindwing not lobed in the middle, forewing eyespot not elongated along discal cell, discal band (if developed) narrow, bands do not encircle forewing eyespot, or bands diffuse and poorly formed. Furthermore, the following combination of nuclear genomic characters is diagnostic: cne703.2.8:T903C, cne1411.6.4:T1025A, cne2651.14.5: A4602G, cne12205.6.2: G835A, and cne8028.2.1:T1787A.

Etymology. The name is a feminine noun in the nominative singular formed by replacing prefix "Meso-" with "Endo-" in the name of the former genus for these species.

Species included. The type species and *Mesosemia macella* Hewitson, 1859.

Parent taxon. Subtribe Mesosemiina Bates, 1859.

Eucorna Strand, 1932 is a valid genus

Presently, *Eucorna* Strand, 1932 (type species *Voltinia sanarita* (Schaus, 1902)) is a junior subjective synonym of *Voltinia* Stichel, 1910 (type species *Esthemopsis* (?) *radiata* Godman & Salvin, 1886), but is not monophyletic with it, and is sister to all other Napaeina Hall, 2003 except *Hyphilaria* Hübner, [1819] (type species *Hyphilaria nicia* Hübner, [1819]) (Fig. 17). Hence, *Eucorna* is a valid genus.

Reassessment of *Voltinia* Stichel, 1910 and *Napaea* Hübner, [1819]

Our genome-level phylogeny combined with phenotypic assessment of species missing from the tree reveals that *Voltinia* Stichel, 1910 (type species *Esthemopsis* (?) *radiata* Godman & Salvin, 1886) consists of only two species: the type and *Voltinia theata* Stichel, 1910 (Fig. 17 gray). Based on this phylogeny, we transfer all other species presently in *Voltinia* to *Napaea* Hübner, [1819] (type species *Cremna eucharila* Bates, 1867) (Fig. 17 red to blue). The following revised combinations are proposed for them: *Napaea danforthi* A. Warren & Opler, 1999 (as originally proposed!), *Napaea dramba* (J. Hall, Robbins & Harvey, 2004), *Napaea sanarita* (Schaus, 1902), *Napaea agroeca* Stichel, 1910, *Napaea tumbesia* J. Hall & Lamas, 2001 (as originally proposed!), *Napaea umbra* (Boisduval, 1870), *Napaea phryxe* (C. & R. Felder, 1865), *Napaea cebrenia* (Hewitson, [1873]), *Napaea loxicha* (R. G. Maza & J. Maza, 2016), *Napaea maya* (J. Maza & Lamas, 2016), *Napaea necaxa* (R. G. Maza & J. Maza, 2018), *Napaea totonaca* (R. G. Maza & J. Maza, 2016).

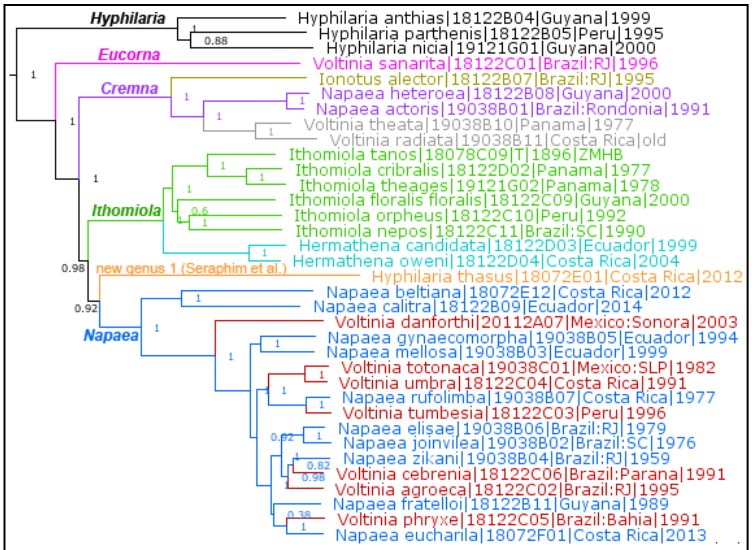

Fig. 17. Napaeina genera: *Hyphilaria* (black), *Eucorna* (magenta), *Cremna* (purple, olive and gray), *Ithomiola* (green and cyan), new genus 1 (Seraphim et al. 2018) (orange) and *Napaea* (blue and red).

Ionotus Hall, 2005 and *Voltinia* Stichel, 1910 are subgenera of *Cremna* Doubleday, 1847, which is a valid genus

A genus comprised of two species, *Voltinia* Stichel, 1910 (type species *Esthemopsis* (?) *radiata* Godman & Salvin, 1886) (Fig. 17 gray) is a close sister to *Cremna* Doubleday, 1847 (type species *Papilio actoris* Cramer, 1776), which also consists of only two species: the type and *Cremna heteroea* Bates, 1867 (Fig. 17 purple); and *Ionotus* Hall, 2005 (type and the only species *Hamanumida alector* Geyer, 1837) (Fig. 17 olive) is sister to them combined. Hence, we reinstate *Cremna* as a valid genus (not a synonym of *Napaea*), and due to genetic similarities place *Ionotus* Hall, 2005 and *Voltinia* Stichel, 1910 as its subgenera.

Hermathena Hewitson, 1874 is a subgenus of *Ithomiola* C. & R. Felder, 1865

Despite its mostly white coloration, much different from its relatives, *Hermathena* Hewitson, 1874 (type species *Hermathena candidata* Hewitson, 1874) (Fig. 17 cyan) clusters closely with *Ithomiola* C. & R. Felder, 1865 (type species *Ithomiola floralis* C. & R. Felder, 1865) (Fig. 17 green), which even now includes species considerably different in appearance (Hall 2005). The male genitalia of these taxa are rather similar as illustrated by Hall (2005). To achieve a more internally consistent classification, we place *Hermathena* Hewitson, 1874 as a subgenus of *Ithomiola* C. & R. Felder, 1865.

Lucillella Strand, 1932 is a subgenus of *Esthemopsis* C. & R. Felder, 1865

Lucillella Strand, 1932 (type species *Lucilla camissa* Hewitson, 1870) (Fig. 18 pale blue) and *Esthemopsis* C. & R. Felder, 1865 (type species *Esthemopsis clonia* C. & R. Felder, 1865) (Fig. 18 gray) are closely related sisters that form a clade prominently separated from others (Fig. 18) and sister to

Mesene Doubleday, 1847 (type species *Papilio phareus* Cramer, 1777) (Fig. 18 olive). Because *Mesene* is already more diverse than *Lucillella* and *Esthemopsis* combined, to achieve better consistency of classification, we propose treating *Lucillella* Strand, 1932 as a subgenus of *Esthemopsis* C. & R. Felder, 1865.

Xynias Hewitson, 1874 is a junior subjective synonym of *Mesenopsis* Godman & Salvin, 1886, which along with *Xenandra* C. & R. Felder, 1865 are subgenera of *Symmachia* Hübner, [1819], that contains *Stichelia* J. Zikán, 1949 as its junior subjective synonym

First, *Xynias* Hewitson, 1874 (type species *Xynias cynosema* Hewitson, 1874, which is a subspecies of *Esthemopsis lithosina* Bates, 1868) (Fig. 18 bright green) is in the same clade with *Mesenopsis* Godman & Salvin, 1886 (type species *Limnas* (?) *bryaxis* Hewitson, 1870) (Fig. 18 purple) and is closely related to the type species of *Mesenopsis* genetically and possesses, similar to it, elongated wing shape. Therefore, we place *Xynias* as a junior subjective synonym of *Mesenopsis*. Dissimilar wing patterns in these species are caused by their involvement in different mimicry complexes.

Second, *Stichelia* J. Zikán, 1949 (type species *Amarynthia bocchoris* Hewitson, 1876) (Fig. 18 bright orange) originates within *Symmachia* Hübner, [1819] (type species *Symmachia probetrix* Hübner, [1819], which is *Papilio probetor* Stoll, 1782) *sensu stricto* (Fig. 18 blue). To restore monophyly of *Symmachia sensu stricto* and considering genetic closeness, we propose treating *Stichelia* J. Zikán, 1949 as a junior subjective synonym of *Symmachia* Hübner, [1819].

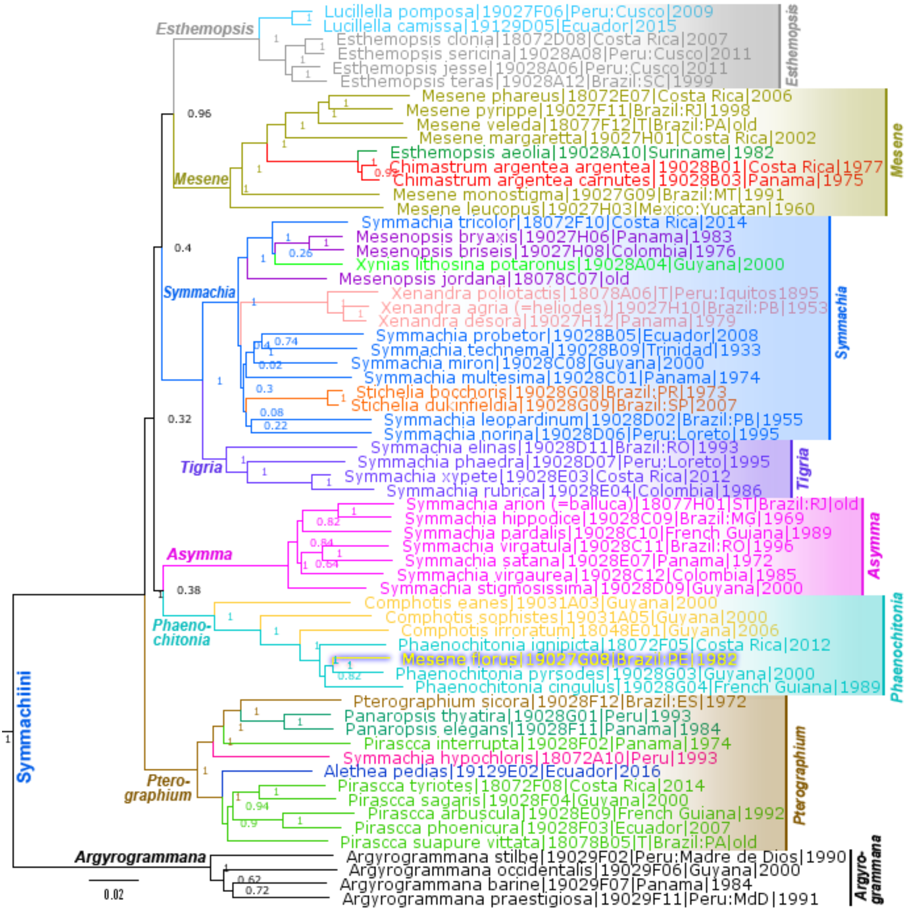

Fig. 18. Symmachiini genera marked on the tree, including *Tigria* gen. n. (violet) and *Asymma* gen. n. (magenta). Different colors denote different genera and inconsistencies with the current classification.

Third, *Xenandra* C. & R. Felder, 1865 (type species *Xenandra heliodes* C. & R. Felder, 1865, which is currently a junior subjective synonym of *Limnas agria* Hewitson, 1853) (Fig. 18 pale pink), falls within a rapid radiation that dates past the diversification of most Symmachiini Reuter, 1896 genera. We consider the radiation that led to the origin of *Xenandra* to represent the diversification within the genus *Symmachia*, (Fig. 18 blue clade labeled with the name) and therefore propose treating *Xenandra* C. & R. Felder, 1865 as a subgenus of *Symmachia* Hübner, [1819] because it forms a prominent clade within it.

Lastly, the clade with *Mesenopsis* (includes *Xynias* and *Symmachia tricolor* Hewitson, 1867) originates early in the radiation of *Symmachia* and is not prominently distinct from it. Therefore, we treat *Mesenopsis* Godman & Salvin, 1886 as a subgenus of *Symmachia* Hübner, [1819]. As a result, genus *Symmachia* (Fig. 18 blue, purple, bright green, pale pink, bright orange) consists of 3 subgenera:

Symmachia, *Xenandra*, and *Mesenopsis*. Finally, some species currently in *Symmachia* fall outside this genus (e.g., Fig. 18 violet and magenta clades). Two of such major clades do not have names and are proposed as new genera here.

Tigria Grishin, new genus

http://zoobank.org/1665C4A1-7AF7-4426-855A-1799CC9F59E4

Type species. *Mesene xypete* Hewitson, 1870.

Definition. A sister clade to other *Symmachia* Hübner, [1819] (type species *Symmachia probetrix* Hübner, [1819], which is *Papilio probetor* Stoll, 1782), but prominently distinct from it, more so than *Symmachia sensu stricto* species are from each other (Fig. 18 blue), and genetically distant from them at a level where other Symmachiini genera are defined (Fig. 18), is therefore a genus. It is similar to *Symmachia* and distinguished from it by the following combination of characters (at least in males): forewing costa rather straight, not concave, apex produced, hindwing typically with angular tornus; antennae long, about ¾ of forewing length; eyes bare; wings red-orange, bordered and partly striped at least along forewing costa with black or dark-brown, dark areas could take half of wings, no pale spot mid-costa. The following combination of nuclear genome characters is diagnostic: cne1935.6.1:A2889G, cne3461.1.14: G922C, cne3437.1.9:A1260G, cne3461.1.14:A846G, and cne2170.2.1:T2751C.

Etymology. The name is a feminine noun in the nominative singular given for the red-orange tiger-striped appearance of these species.

Species included. The type species, *Polystichtis rubrica* Stichel, 1929, *Cricosoma phaedra* Bates, 1868 and *Metacharis elinas* Rebillard, 1958.

Parent taxon. Tribe Symmachiini Reuter, 1896.

Asymma Grishin, new genus

http://zoobank.org/901035D7-E6D1-4F16-A1FD-BA85C48AAC50

Type species. *Symmachia virgatula* Stichel, 1910.

Definition. This group of species is currently placed in *Symmachia* Hübner, [1819] (type species *Symmachia probetrix* Hübner, [1819], which is *Papilio probetor* Stoll, 1782) but is not monophyletic with it (Fig. 18). It originates early in the radiation of the Symmachiini core group, a possible, but weakly supported sister to *Phaenochitonia* Stichel, 1910 (type species *Papilio cingulus* Stoll, 1790) *sensu lato* (see below), and therefore is a genus. Similar to *Symmachia* and *Tigria* gen. n. and is distinguished from them by the following combination of characters (at least in males): forewing costa concave in the middle, as in most *Symmachia* but different from *Tigria* gen. n., wings red-orange to yellow, bordered and partly striped or spotted at least along forewing costa with black or dark-brown, without white spots by the forewing apex. The following combination of nuclear genome characters is diagnostic: cne4291.7.6: A1077G, cne4291.7.6:A1064G, cne4291.7.6:A1051G, cne3461.2.5:A1310G, and cne3461.1.15:A3342C.

Etymology. The name is a feminine noun in the nominative singular, formed from the beginning of the former genus name of these species, prefixing it with "a" for "not", because these species cannot possibly belong to *Symmachia*: *A* + *symma*[chia].

Species included. The type species, *Synapta arion* C. & R. Felder, 1865, *Symmachia giffordi* P. Jauffret & J. Jauffret, 2010, *Symmachia hippodice* Godman, 1903, *Symmachia pardalis* Hewitson, 1867, *Symmachia satana* J. Hall & Harvey, 2007, *Symmachia stigmosissima* Stichel, 1910, and *Symmachia virgaurea* Stichel, 1910.

Parent taxon. Tribe Symmachiini Reuter, 1896.

Chimastrum Godman & Salvin, 1886 is a junior subjective synonym of *Mesene* Doubleday, 1847

Chimastrum Godman & Salvin, 1886 (type species *Mesene argentea* Bates, 1866) (Fig. 18 red) originates within *Mesene* Doubleday, 1847 (type species *Papilio phareus* Cramer, 1777) (Fig. 18 olive), thus rendering it paraphyletic. To restore the monophyly, instead of breaking *Mesene* (that is currently already assembled from close relatives) into several genus-group taxa, we treat *Chimastrum* as a junior subjective synonym of *Mesene*.

Mesene aeolia (Bates, 1868), new combination

Kept in *Esthemopsis* C. & R. Felder, 1865 (type species *Esthemopsis clonia* C. & R. Felder, 1865) since its description, *E. aeolia* Bates, 1868 (type locality Brazil: Para) is not monophyletic with it, and instead is sister to *Mesene argentea* Bates, 1866, the type species of *Chimastrum* Godman & Salvin, 1886 that originates within *Mesene* Doubleday, 1847 (type species *Papilio phareus* Cramer, 1777) (Fig. 18, sequenced specimen in Fig. 19), implying *Mesene aeolia* (Bates, 1868) **comb. nov.**

Fig. 19. *Esthemopsis aeolia*

Alethea Nielsen & Salazar, [2018] is a junior subjective synonym of *Pirascca* J. Hall & Willmott, 1996, which is a subgenus of *Pterographium* Stichel, 1910, that contains *Panaropsis* J. Hall, 2002 as its junior subjective synonym

The monotypic *Alethea* Nielsen & Salazar, [2018] (type and the only species *Siseme pedias* Godman, 1903) (Fig. 18 dark blue), *Panaropsis* J. Hall, 2002 (type species *Panara elegans* Schaus, 1920) (Fig. 18 cyan-green), *Pirascca* J. Hall & Willmott, 1996 (type species *Papilio sagaris* Cramer, 1775) (Fig. 18 green) and monotypic *Pterographium* Stichel, 1910 (type and the only species *Pterographium aphaniodes* Stichel, 1910, which is *Panara sicora* Hewitson, 1875) (Fig. 18 brown) taken together form a prominent clade in the tree that originated early in the diversification of Symmachiini Reuter, 1896 into genera and therefore corresponds to genus rank. This genus gets the name *Pterographium* as the oldest available for its species. This species-rich *Pterographium sensu lato* splits into 2 well-defined and strongly supported but not very prominent clades (100% support for each clade, Fig. 18) that we treat as subgenera. The nominal subgenus (upper clade in Fig. 18) contains *Panaropsis* as sister to its type species, and therefore *Panaropsis* becomes a junior subjective synonym of *Pterographium*, along with some other species such as *Phaenochitona* [sic] *interrupta* Lathy, 1932 (currently in *Pirascca*). The second subgenus of *Pterographium* (lower clade in Fig. 18) is *Pirascca*, a close sister to monotypic and unusually patterned *Alethea*, which we place as junior subjective synonym of *Pirascca* due to genetic similarities. We reason that considerable phenotypic differences of *Pterographium (Pirascca) pedias* (Godman, 1903) **comb. nov.** from other *Pirascca* are caused by rapid evolution towards a different mimicry complex.

Pterographium hypochloris (Bates, 1868), new combination

Currently in *Symmachia* Hübner, [1819] (type species *Symmachia probetrix* Hübner, [1819], which is *Papilio probetor* Stoll, 1782), *Emesis hypochloris* Bates, 1868 (type locality Brazil: Amazonas) is not monophyletic with it and instead originates within *Pterographium* Stichel, 1910 (type species *Pterographium aphaniodes* Stichel, 1910, which is *Panara sicora* Hewitson, 1875) *sensu lato* as it is defined above (Fig. 18, sequenced specimen shown in Fig. 20), hence *Pterographium hypochloris* (Bates, 1868) **comb. nov.**

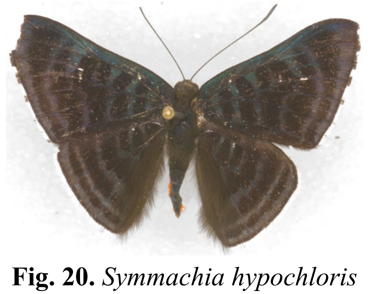

Fig. 20. *Symmachia hypochloris*

Comphotis Stichel, 1910 is a junior subjective synonym of *Phaenochitonia* Stichel, 1910

Comphotis Stichel, 1910 (type species *Cricosoma irroratum* Godman, 1903) (Fig. 18 pale orange) is paraphyletic with respect to *Phaenochitonia* Stichel, 1910 (type species *Papilio cingulus* Stoll, 1790) (Fig. 18 bright cyan), but taken together, they form a prominent lineage consistent with other Symmachiini Reuter, 1896 genera. Therefore we place *Comphotis* Stichel, 1910-XII-31 as a junior subjective synonym of *Phaenochitonia* Stichel, 1910-IX.

Phaenochitonia florus (Fabricius, 1793), new combination

Fig. 21. *Mesene florus*

Currently in *Mesene* Doubleday, 1847 (type species *Papilio phareus* Cramer, 1777), *Hesperia florus* Fabricius, 1793 (type locality "Indiis", likely SE Brazil) is not monophyletic with it and originates within *Phaenochitonia* Stichel, 1910 (type species *Papilio cingulus* Stoll, 1790) (Fig. 18 yellow, highlighted in violet, sequenced specimen shown in Fig. 21), implying *Phaenochitonia florus* (Fabricius, 1793) **comb. nov.** Distinctness of this species from *Mesene* came as a surprise considering how well it was fitting in that genus on the basis of wing colors, patterns and shape, even reminding of *Mesene* type species.

Reassessment of *Ourocnemis* Bethune-Baker, 1887 and *Anteros* Hübner, [1819]

The tree of Helicopini Stichel, 1928 revealed a distribution of species between the two genera *Ourocnemis* Bethune-Baker, 1887 (type species *Anteros axiochus* Hewitson, 1867) and *Anteros* Hübner, [1819] (type species *Papilio formosus* Cramer, 1777) not as presently attributed (Fig. 22). A number of species placed in *Anteros* were in the same clade with *Ourocnemis*, confirming the suspicion of Hall (1998) that *Anteros* may be paraphyletic. Using this phylogenetic result and phenotypic similarities (cream vs. dark background of wings below) for species with missing DNA data, we transfer four species from *Anteros* to *Ourocnemis* to form the following **new combinations**: *Ourocnemis carausius* (Westwood, 1851), *Ourocnemis principalis* (Hopffer, 1874), *Ourocnemis renaldus* (Stoll, 1790), and *Ourocnemis aerosus* (Stichel, 1924).

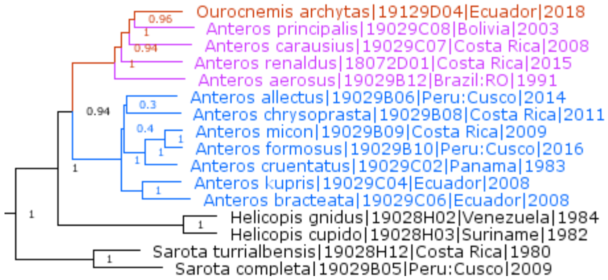

Fig. 22. Helicopini genera with *Ourocnemis* (red and magenta) and *Anteros* (blue).

Imelda Hewitson, 1870 is a subgenus of *Echenais* Hübner, [1819]

Despite the differences in appearance, monotypic genus *Echenais* Hübner, [1819] (type species *Lemonias alphaea* Hübner, [1808], which is *Papilio thelephus* Cramer, 1775) is genetically close to *Imelda* Hewitson, 1870 (type species *Imelda glaucosmia* Hewitson, 1870, which is a subspecies of *Nymphidium mycea* Hewitson, 1865) (Fig. 23). E.g., COI barcodes of their type species differ by 8.4% (55 bp). Therefore we propose treating *Imelda* Hewitson, 1870 as a subgenus of *Echenais* Hübner, [1819].

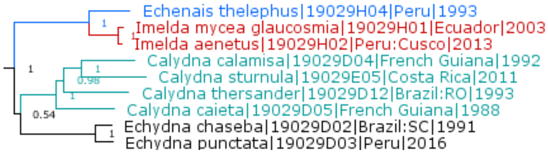

Fig. 23. *Echenais* (blue) subgenus *Imelda* (red).

Colaciticus Stichel, 1910 is junior subjective synonym of *Baeotis* Hübner, [1819]

Despite different coloration and wing shape, which are probably due to mimicry, *Colaciticus* Stichel, 1910 (type species *Monethe johnstoni* Dannatt, 1904) originates deep within *Baeotis* Hübner, [1819] (type species *Baeotis hisbaena* Hübner, [1819] which is *Papilio hisbon* Cramer, 1775) (Fig. 24). *Baeotis* is a well-defined prominent genus that we do not wish to split. Therefore, to restore the monophyly, we propose that *Colaciticus* Stichel, 1910 is a junior subjective synonym of *Baeotis* Hübner, [1819].

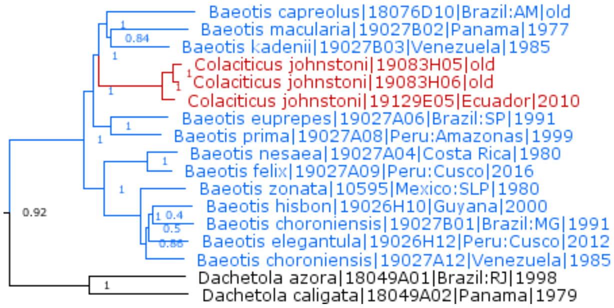

Fig. 24. *Baeotis* (blue and red).

Nahida coenoides (Hewitson, 1870) is conspecific with *Ithomeis aurantiaca* H. Bates, 1862 and *Nahida* Kirby, 1871 is a junior subjective synonym of *Ithomeis* Bates, 1862

Monotypic genus *Nahida* Kirby, 1871 (type and the only species *Threnodes coenoides* Hewitson, 1870) originates within *Ithomeis aurantiaca* H. Bates, 1862 (type locality Brazil: Amazonas), which is the type species of *Ithomeis* Bates, 1862 (Fig. 25) implying that *Nahida* is a junior subjective synonym of *Ithomeis*. Moreover, *Ithomeis coenoides* (Hewitson, 1870) **comb. nov.** and various subspecies of *I. aurantiaca* are very close to each other genetically, e.g., their COI barcodes are mostly 0.15% (1 bp) different, at maximum 0.9% (6 bp) with *Ithomeis aurantiaca satellites* H. Bates, 1862 (type locality Brazil: Para). Therefore, we consider *I. coenoides* to be conspecific with *I. aurantiaca*, and propose the following **new** species-subspecies **combinations**: *Ithomeis aurantiaca coenoides* (Hewitson, 1870), *Ithomeis aurantiaca ecuadorica* (Strand, 1911), *Ithomeis aurantiaca trochois* (Hewitson, 1877).

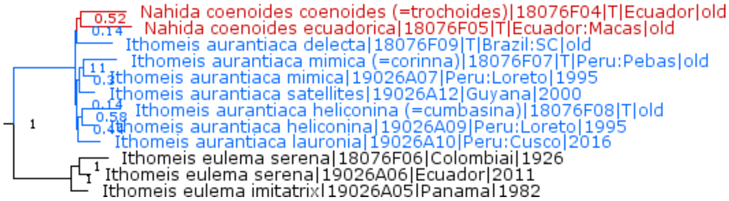

Fig. 25. *Nahida coenoides* (red) is *Ithomeis aurantiaca* (blue).

Putridivora Grishin, new genus

http://zoobank.org/AD6A1874-503C-4A07-B079-79A326060635

Type species. *Charis argyrea* Bates, 1868.

Definition. Currently within *Detritivora* Hall & Harvey, 2002 (type species *Charis matic* Harvey & Hall, 2002), but is not monophyletic with it, and instead is sister to the clade that includes *Detritivora* with a number of other genera such as *Charis* Hübner, [1819] (type species *Charis ania* Hübner, [1819], which is *Papilio anius* Cramer, 1776) and *Calephelis* Grote & Robinson, 1869 (type species *Erycina virginiensis* Guérin-Méneville, [1832]) (Fig. 26), hence a new genus. Similar to *Detritivora* as described by Hall and Harvey (2002), and distinguished from it by 3 (not 4) dark marks in discal cell and signa markedly elongate along corpus bursae wall, as described by Hall and Harvey (2001), see their Fig. 6a.

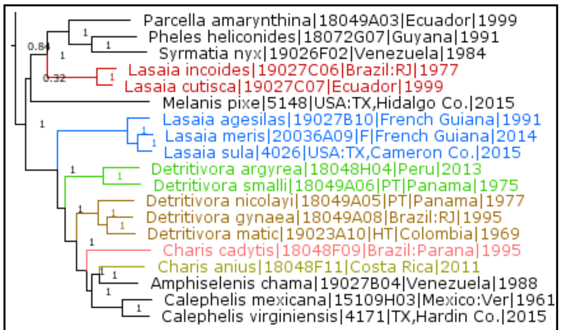

Fig. 26. *Putridivora* gen. n. (green), *Detritivora* (brown), *Chadia* (pink), *Charis* (olive), *Inkana* gen. n. (red), and *Lasaia* (blue).

Etymology. The name is a feminine noun in the nominative singular formed by replacing prefix "Detriti-" with "Putridi-" in the name of the former genus for these species, but keeping the meaning.

Species included. The type species and *Charis smalli* Hall & Harvey, 2001.

Parent taxon. Tribe Riodinini Grote, 1895.

Chadia Grishin, new genus

http://zoobank.org/10295164-45F5-4C4E-8323-FBC0D37E802D

Type species. *Charis cadytis* Hewitson, 1866.

Definition. Currently one of the two species of *Charis* Hübner, [1819] (type species *Charis ania* Hübner, [1819], which is *Papilio anius* Cramer, 1776), but is not monophyletic with the second (and the type) species, and instead sister to the clade that includes a number of other genera such as *Charis* and *Calephelis* Grote & Robinson, 1869 (type species *Erycina virginiensis* Guérin-Méneville, [1832]) (Fig. 26). Therefore, it constitutes a new genus. Distinguished from its relatives by atypical for the group more elongated wings (without pointed apex), orange band at forewing apex, prominent silver wing margins in males below; exceptionally curved, earlobe-shaped aedeagus and very broad valvae, as broad as long.

Etymology. The name is a feminine noun in the nominative singular formed from the beginning of the type species name with insertion of h for *Charis*.

Species included. Only the type species.

Parent taxon. Tribe Riodinini Grote, 1895.

Inkana Grishin, new genus

http://zoobank.org/4FEC8FF0-3B35-4B6A-BEC4-5CF06240CA5C

Type species. *Charis incoides* Schaus, 1902.

Definition. Currently in the genus *Lasaia* Bates, 1868 (type species *Papilio meris* Stoll, 1781) but is not monophyletic with it and is far removed from it in the tree, being sister to the clade with several genera such as *Pheles* Herrich-Schäffer, [1858] (type species *Pheles heliconides* Herrich-Schäffer, [1853]) and *Parcella* Stichel, 1910 (type and the only species *Amblygonia amarynthina* C. & R. Felder, 1865) (Fig. 26) and therefore is a genus of its own. Similar to *Lasaia* in wing shape and color and male genitalia. Description and diagnostic characters for this new genus are as given for *Lasaia cutisca* Hall & Willmott, 1998 and *Lasaia incoides* on pages 23–24 and illustrated in Figs. 3–4, 9–10 by Hall & Willmott (1998). In brief, brown above and lacks blue or green scaling of *Lasaia* males, wings below uniform in background without paler patches and bands of most *Lasaia* species, hindwing outer margin lacks prominent concavity of *Lasaia* at vein M_2 (manifested also as a "tooth" at M_1); eyes setose; genitalic valvae narrow, about 3 times longer than broad, *processus superior* with rounded projection from ventral margin, *processus inferior* long and narrow, with a pointed tip.

Etymology. The name is a feminine noun in the nominative singular formed from the type species name with k for c to avoid a homonym.

Species included. The type species and *Lasaia cutisca* Hall & Willmott, 1998.

Parent taxon. Tribe Riodinini Grote, 1895.

Callistiumini Grishin, new tribe

http://zoobank.org/3BFAAAD2-83E4-48EF-9952-CA85DA8DEB9E

Type genus. *Callistium* Stichel, 1911.

Definition. Presently, *Callistium* (type species *Charis cleadas* Hewitson, 1866) is kept in *incertae sedis* (Seraphim et al. 2018). Genomic analysis reveals that the type species of *Callistium* may be sister to Calydnini Seraphim, Freitas & Kaminski, 2018, albeit with very weak support (Fig. 27), while other species currently placed in *Callistium* belong to other genera (see below). Therefore, the *Callistium* lineage is of ancient origin, not confidently associated with any Riodinidae tribes and thus is a distinct tribe. Description and diagnostic characters of this new tribe are as those given for *Callistium* on page 258 and illustrated in Fig. 68 by Stichel (1911). Briefly, thorax bulky, head large, eyes setose, antennae longer than ⅔ of forewing, venation similar to *Anteros*, uncus with tegumen large, about the same length as vinculum height in lateral view, hood-shaped, well separated from each other, uncus hooked at the tip, falces curved and short, not reaching middle of uncus, vinculum bent caudad in the middle, valvae twice as long as broad, slightly longer than tegumen, rounded, fused together, with small lobes on dorsal and ventral margins, aedeagus long, slightly curved and terminally pointed.

Genera included. Only the type genus.

Parent Taxon. Subfamily Riodininae Grote, 1895.

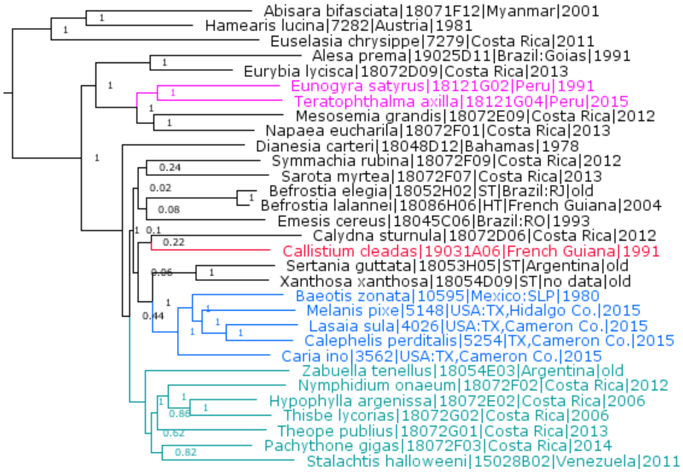

Fig. 27. Callistiumini trib. n. (red) among Riodinidae tribes and subtribes, including Riodinini (blue), Nymphidiini (cyan) and Eunogyrina subtrib. n. (magenta).

Comments. *Callistus* Bonelli, 1810 (Coleoptera: Carabidae) is the type genus of Callistini. According to Art. 55.4. of the ICZN Code (ICZN 1999), one letter difference, which in this case would be an extra "i" from the suffix "-ini", avoids homonymy. However, it does not avoid confusion, including internet search engines that correct possible spelling errors. Therefore, the choice was to form the name as Callistiumini using the entire word as a stem (Art. 29.1.), instead of Callistiini.

Zabuella castanea (Prittwitz, 1865), confirmed combination

Placed in *Callistium* (type species *Charis cleadas* Hewitson, 1866) by Hall (2018), *Calydna castanea* Prittwitz, 1865 is not monophyletic with its type species, but instead is sister to the type species of *Zabuella* Stichel, 1911, which is *Lemonias tenellus* Burmeister, 1878 (Fig. 28), and is genetically close to it. Therefore, we agree with Seraphim et al. (2018) who reached the same conclusion, and confirm the combination *Zabuella castanea* (Prittwitz, 1865).

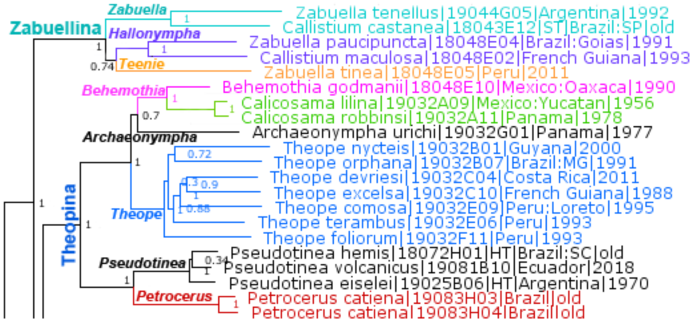

Fig. 28. Zabuellina genera: *Zabuella* (cyan), *Hallonympha* (magenta), and *Teenie* gen. n. (orange); and Theopina genera: *Behemothia* (magenta with subgenus *Calicosama* in cyan), *Archaeonympha* (black), *Theope* (blue), *Pseudotinea* (black), and *Petrocerus* (red).

Hallonympha Penz & DeVries, 2006, valid genus, and *Hallonympha maculosa* (Bates, 1868), new combination

Although synonymized with *Zabuella* Stichel, 1911 (type species *Lemonias tenellus* Burmeister, 1878) by Hall (2018), *Hallonympha* Penz & DeVries, 2006 (type species *Apodemia paucipuncta* Spitz, 1930) is genetically distant from it (Fig. 28), in agreement with Seraphim et al. (2018). E.g., COI barcodes of the type species of these genera differ by 9.1% (60 bp) and their divergence dates to about 20 Mya (Seraphim et al. 2018). Therefore, we reinstate *Hallonympha* as a valid genus. Currently in *Callistium* (type species *Charis cleadas* Hewitson, 1866), *Calydna maculosa* Bates, 1868 (type locality Brazil: Amazonas) is not monophyletic with its type species and instead is sister to the type species of *Hallonympha* (Fig. 28). Their COI barcodes are only 7.4% (49 bp) different. Hence, we propose *Hallonympha maculosa* (Bates, 1868) **comb. nov.**

Teenie Grishin, new genus

http://zoobank.org/BDF61309-B594-4355-B2ED-306025A2E8D9

Type species. *Calydna tinea* Bates, 1868.

Definition. Currently in the genus *Zabuella* Stichel, 1911 (type species *Lemonias tenellus* Burmeister, 1878) as suggested by Hall (2018), this group is not monophyletic with it and is sister to *Hallonympha* Penz & DeVries, 2006 (type species *Apodemia paucipuncta* Spitz, 1930), but prominently differs from it genetically and thus constitutes a genus (Fig. 28). Diagnostic characters for the new genus are as those detailed for *Z. tinea* and *Z. argiella* in Hall (2018). Briefly, similar to *Zabuella* and *Hallonympha* in wing patterns and genitalia, but aedeagus narrower, and signa highly asymmetrical both in position and size.

Etymology. The name is a feminine noun in the nominative singular inspired by the type species name.

Species included. The type species (including *Lemonias eudocia* Godman & Salvin, 1897 as it synonym) and *Calydna argiella* Bates, 1868.

Parent taxon. Subtribe Zabuellina Seraphim, Freitas & Kaminski, 2018.

Petrocerus Callaghan, 1979 belongs to Theopina Clench, 1955

Currently in *incertae sedis*, *Petrocerus* Callaghan, 1979 (type species *Calydna catiena* Hewitson, 1875) is a confident sister to *Pseudotinea* Hall & Callaghan, 2003 (type species *Calydna volcanicus* Callaghan & Salazar, 1997) (Fig. 28). Together they are sister to the clade with *Theope* Doubleday, 1847 (type species *Polyommatus terambus* Godart, [1824]), and therefore, *Petrocerus* belongs to Theopina Clench, 1955.

Calicosama J. Hall & Harvey, 2001 is a subgenus of *Behemothia* Hall, 2000

Monotypic genus *Behemothia* Hall, 2000 (type and the only species *Pandemos godmanii* Dewitz, 1877) is closely related to nearly monotypic *Calicosama* J. Hall & Harvey, 2001 (type species *Nymphidium lilina* Butler, 1870) (Fig. 28). Both genera are mostly Central American. To highlight their close kinship and reduce the number of unnecessarily monotypic genera we propose that *Calicosama* J. Hall & Harvey, 2001 is a subgenus of *Behemothia* Hall, 2000.

Exoplisia aphanis (Stichel, 1910), new combination

Placed in *Seco* Hall & Harvey, 2002 (type species *Charis calagutis* Hewitson, 1871), *Charmona aphanis* Stichel, 1910 is not monophyletic with its type species, but is sister to *Exoplisia* Godman & Salvin, 1886 (type species *Amarynthis hypochalybe* C. & R. Felder, 1861) and is not prominently distinct from it (Fig. 29). Therefore, we place it in this genus to form *Exoplisia aphanis* (Stichel, 1910) **comb. nov.**

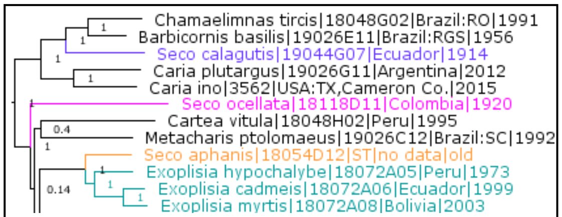

Fig. 29. *Seco* (purple), *Oco* gen. n. (magenta), *Exoplisia* (cyan and orange).

Oco Grishin, new genus

http://zoobank.org/1D2F2454-EFC9-473A-A91D-17097BB3DB03

Type species. *Symmachia ocellata* Hewitson, 1867.

Definition. Currently in the genus *Seco* Hall & Harvey, 2002 (type species *Charis calagutis* Hewitson, 1871), but is not monophyletic with its type species, and instead forms an independent lineage in early radiation of the core Riodinini group (Fig. 29). Diagnostic characters for this new genus are as those given for *Seco* (except the characters specific to either *Seco calagutis* (Hewitson, 1871) or *Exoplisia aphanis*

(Stichel, 1910) comb. nov. [then placed in *Seco*]) on pages 415-417 in Hall and Harvey (2002). Readily distinguished from its relatives by a black yellow-bordered eyespot at forewing apex.

Etymology. The name is a feminine noun in the nominative singular formed as a fusion of the type species name with the name of the genus it was formerly placed in: *O*[cellata] + [Se]*co* for its eyespots.

Species included. Only the type species.

Parent taxon. Tribe Riodinini Grote, 1895.

Machaya Hall & Willmott, 1995 is a junior subjective synonym of *Pachythone* Bates, 1868

Despite the difference in appearance, *Machaya* Hall & Willmott, 1995 (type species *Machaya obstinata* Hall & Willmott, 1995) originates deep within *Pachythone* Bates, 1868 (type species *Pachythone erebia* Bates, 1868) at the time of rapid diversification of its crown group (Fig. 30). Therefore, to restore the monophyly, we propose that *Machaya* is a junior subjective synonym of *Pachythone.*

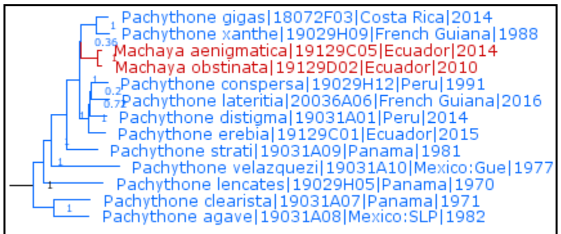

Fig. 30. *Pachythone* (blue and red).

Family Nymphalidae Rafinesque, 1815

Polygrapha Staudinger, 1887 and *Fountainea* Rydon, 1971 are subgenera of *Anaea* Hübner, [1819]

Our genomic phylogeny of Anaeini Reuter, 1896 is fully consistent with that of Toussaint et al. (2019) in identifying major clades in the tribe and re-aligning species of the former *Polygrapha* Staudinger, 1887 (type species *Paphia cyanea* Salvin & Godman, 1868) (Fig. 31). We note that relative branch lengths also agree between the two phylogenies. Assigning all species in one of the sister clades to the single genus *Memphis* Hübner, [1819] (type species *Papilio odilia* Stoll, 1780, which is a junior subjective synonym of *Papilio polycarmes* Fabricius, 1775), but dividing its sister clade of equal diversification into 3 genera: *Polygrapha*, *Fountainea* Rydon, 1971 (type species *Anaea phidile* Geyer, 1837, a subspecies of *Papilio ryphea* Cramer, 1775) and *Anaea* Hübner, [1819] (type species *Papilio troglodyta* Fabricius, 1775) is internally inconsistent. Not willing to break *Memphis* into several genera, we propose treating *Polygrapha* and *Fountainea* as subgenera of *Anaea*. This generic realignment results in two large and equally diversified sister genera: *Anaea* and *Memphis*, with *Consul* Hübner, [1807] (type species *Papilio fabius* Cramer, 1776) being their sister.

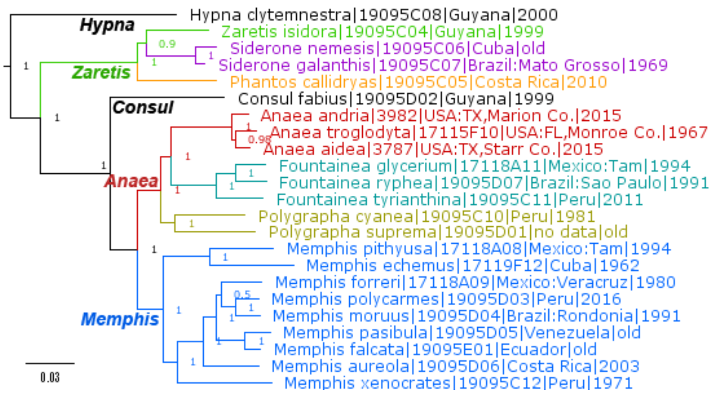

Fig. 31. Anaeini genera: *Anaea* (red, cyan and olive), *Memphis* (blue), *Zaretis* (green, purple and orange), *Consul*, and *Hypna*.

Siderone Hübner, [1823] and *Phantos* Dias, 2018 are subgenera of *Zaretis* Hübner, [1819]

Genetic differentiation within the clade of three genera: *Siderone* Hübner, [1823] (type species *Siderone ide* Hübner, [1823], a junior subjective synonym of *Papilio nemesis* Illiger, 1801), *Phantos* Dias, 2018 (type species *Nymphalis callidryas* R. Felder, 1869) and *Zaretis* Hübner, [1819] (type species *Papilio* *isidora* Cramer, 1779) is less than that of *Memphis* and *Anaea* (*sensu lato*, as above) (Fig. 31), suggesting that *Siderone* and *Phantos* are subgenera of *Zaretis* to restore internal consistency of the classification. According to Fig. 3 in Toussaint et al. (2019), all non-monotypic genera of Anaeini as we define them (*Anaea*, *Memphis*, *Consul* and *Zaretis*) diversified around the same time 17-20 Mya, indicating internal consistency of our definition; and monotypic genera *Coenophlebia* C. & R. Felder, 1862 (type and the only species *Siderone archidona* Hewitson, 1860, we have not sequenced this species yet) and *Hypna* Hübner, [1819] (type species *Papilio clytemnestra* Cramer, 1777) are more distant from others to maintain their distinction.

Maniolina Grote, 1897 and Melanargiina Wheeler, 1903 are junior subjective synonyms of Erebiina Tutt, 1896 and Satyrina Boisduval, 1833, respectively

The nuclear genomic tree of Satyrini Boisduval, 1833 reveals a confidently supported clade that contains a number of subtribes as they are currently defined (Peña et al. 2006; Wahlberg 2019a), including the nominotypical subtribe Satyrina. We call this clade the Satyrini crown group (Fig. 32). The tree confidently groups the monotypic subtribes Erebiina Tutt, 1896 and Melanargiina Wheeler, 1903 (Wahlberg 2019a) with Maniolina Grote, 1897 and Satyrina Boisduval, 1833, respectively (Fig. 32). Subtribes in each pair are more closely related to each other compared to other pairs of subtribes in Satyrini Boisduval, 1833, e.g., Euptychiina Reuter, 1896 and Pronophilina Reuter, 1896. Therefore, to simplify subtribal classification and avoid indistinct monotypic subtribes, we propose that Maniolina Grote, 1897 is a junior subjective synonym of Erebiina Tutt, 1896 and Melanargiina Wheeler, 1903 is a junior subjective synonym of Satyrina Boisduval, 1833. The Satyrini crown group first splits into two most distinct sister clades (Fig. 32). One is the subtribe Satyrina. The other contains all other subtribes and has undergone rapid radiation that largely obscures the order of bifurcations near its origin thus creating obstacles for its classification. It is possible to consider this entire group as a single subtribe, because it is the most prominent and well-supported large clade in the tree. However, we refrain from this unification because of the number of species involved and the practicality of partitioning them into phylogenetically meaningful smaller groups of ICZN-administered rank (ICZN 1999). Therefore we keep the current classification of the group essentially as proposed by Peña et al. (2006) with the two exceptions mentioned above. However, as a consequence, several lineages borne out of that rapid radiation, and therefore consistent with the Peña et al. (2006) definition, do not have available names and need to be named as subtribes, which is accomplished below. The following acts also eliminate "Subtribe uncertain" group of available genus-group names as listed by Wahlberg (2019a).

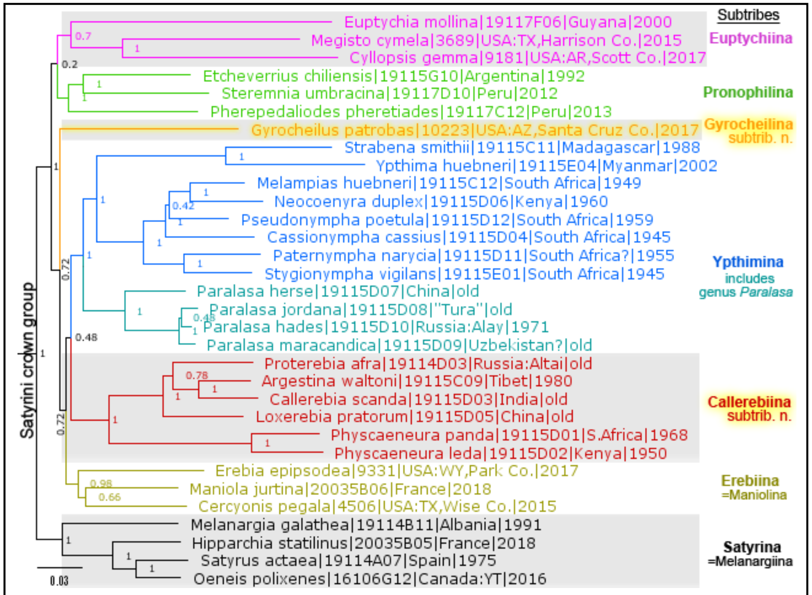

Fig. 32. Subtribes in the Satyrini crown group, each in its own color, except Ypthimina is blue + cyan. Subtribe names are listed on the right.

Paralasa Moore, 1893 belongs to Ypthimina Reuter, 1896

Listed among the "Subtribe uncertain" genera by Wahlberg (2019a), *Paralasa* Moore, 1893 (type species *Erebia kalinda* Moore, 1865) is a confident sister to Ypthimina Reuter, 1896 (Fig. 32). Therefore, instead of proposing a monotypic subtribe for this genus, we include *Paralasa* in the subtribe Ypthimina.

Callerebiina Grishin, new subtribe

http://zoobank.org/46A68C99-BBC2-4F6C-BB06-4CA2AD2343B8

Type genus. *Callerebia* Butler, 1867.

Definition. Several genera of uncertain tribal placement (Wahlberg 2019a) confidently grouped with others sometimes placed in Ypthimina Reuter, 1896 (Fig. 32 red). Close relationship of *Callerebia*, *Loxerebia* and *Argestina* that are in the red clade has been reported before (Yang and Zhang 2015). This prominent red clade is indeed a weakly supported sister to Ypthimina (Fig. 32 blue and cyan). However, due to the weak statistical support (therefore possibly erroneous sister relationship with Ypthimina) and the origin of both clades near the rapid radiation of many Satyrini subtribes, this clade is proposed as a new subtribe. A phenotypically diverse assembly of species, generally characterized by *Erebia*-like appearance, typically with a row of orange black-centered eyespots on each wing, but these could be reduced to a couple of eyespots, similar to Ypthimina, or wings could be unspotted brown or even mostly white above (with brown borders) in some species; gnathos developed (absent in many Ypthimina), but arms shorter than uncus, saccus reduced, valva rather stout, flattened and rounded or excavated near the apex, aedeagus rather short, shorter than valva, typically bent and twisted, boomerang-shaped differentiating the subtribe from *Erebia* Dalman, 1816. Due to phenotypic diversity, best diagnosed by the DNA characters in the nuclear genome: hm2009277-RA.13:T2076C, hm2009277-RA.13:A130C, hm2015715-RA.2:C2137T, hm2009379-RA.4:T1915C, ahm2002906-RA.2:A128G, where the part before the first dot (e.g. hm2009277-RA) is the protein ID, next number (e.g. 13) is exon of the *Heliconius melpomene* genome assembly (Davey et al. 2016), and combination like A130C means base pair C at position 130, changed from A in the ancestor. See <https://osf.io/kj4es/> for the sequences of these exons.

Genera included. The type genus, *Proterebia* Roos & Arnscheid, 1980, *Argestina* Riley, 1923, *Loxerebia* Watkins, 1925, and *Physcaeneura* Wallengren, 1857.

Parent Taxon. Tribe Satyrini Boisduval, 1833.

Gyrocheilina Grishin, new subtribe

http://zoobank.org/EF7C543A-88B9-4DCC-9847-139CC7763B84

Type genus. *Gyrocheilus* Butler, 1867.

Definition. Previously placed in Pronophilina Reuter, 1896 (Wahlberg 2019a), but is not monophyletic with it. Instead, it originates in early radiation of the clade that is sister to Satyrina Boisduval, 1833 (Figs. 32, 33 orange), likely prior to divergence of subtribes Ypthimina Reuter, 1896 and Erebiina Tutt, 1896, and therefore is a subtribe. Diagnosed by the combination of the following characters: most prominently, female foreleg is much reduced, with 2 tarsal subsegment, not spined; then forewings apically rounded with somewhat undulate outer margin, hindwing with strongly undulate, almost toothed outer margins; forewing discal cell short and broad: slightly longer than half of wing, width ⅓–½ of its length; forewing vein R_1 starts at distal ¼ of discal cell, R_2 very near discal cell apex (only slightly stalked), R_3 and R_4 stalked for ⅓ of their length, R_4 and R_5 stalked for about half of their length, recurrent vein in discal cell from the middle of discocellular vein for ¼ of discal cell length, discocellular vein straight between R_2 and M_1 and between M_2 and M_3 origins, but V-shaped between M_1 and M_2 origins; forewing with 4 (rarely 3) white-centered round eyespots, hindwing without such eyespots but frequently with several cream-colored ovals or crescents; palpi long and porrect, scales on the second segment long, up to 5 times the width of the segment, eyes bare, antennae shorter than half of forewing; pupa suspended, spindle-shaped, smooth, head capsule apically extended similar to cremaster, forked at the tip.

Genera included. Only the type genus.

Parent Taxon. Tribe Satyrini Boisduval, 1833.

Calistina Grishin, new subtribe

http://zoobank.org/F1D9A7DC-F549-4EC9-8C68-D8032DC4FB95

Type genus. *Calisto* Hübner, [1823].

Definition. The phylogenetic position of *Calisto* Hübner, [1823] (type species *Papilio zangis* Fabricius, 1775) remains uncertain (Peña et al. 2006; Wahlberg 2019a). Previously it was placed in Pronophilina Reuter, 1896 (Miller 1968), but is not monophyletic with it (Fig. 33). Apparently, it is an ancient phylogenetic lineage (Matos-Maravi et al. 2014) dating to the rapid radiation of the clade sister to Satyrina Boisduval, 1833 (Fig. 33) restricted to Caribbean Islands and not closely associated with any group of Satyrini, therefore is a subtribe. This new subtribe is distinguished from other Satyrini by venation: forewing vein R_1 originates at or beyond (but not before) the end of discal cell, all other R veins stalked, discocellular vein irregular, veins M_1 and M_2 invade more into the discal cell, bases of Sc and Cu, but not A, are inflated; humeral vein weak, short, curved parallel to Sc. Further details about these diagnostic venation characters for the subtribe are as given for *Calisto* on page 104 by Brown and Heineman (1972).

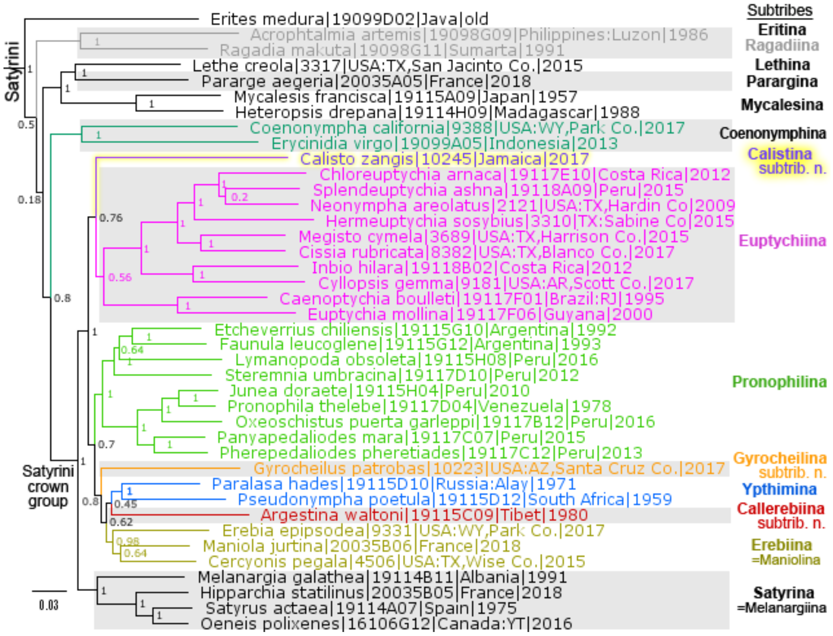

Fig. 33. Satyrini subtribes marked with alternating shading, names listed on the right. All Z chromosome protein-coding genes are used for this tree.

Genera included. Only the type genus.

Parent Taxon. Tribe Satyrini Boisduval, 1833.

Comments. The phylogenetic tree constructed from all protein-coding regions predicted to be on the Z chromosome (Fig. 33) reveals some affinity of *Calisto* to Euptychiina Reuter, 1896. Although this relationship seems possible, it is not obvious from morphology, and only 76% out of 100 selections of positions from the genomic alignment support this placement (0.76 value at the node in Fig. 33). In our experience, this value is too low for confident classification. Therefore, placing *Calisto* in Euptychiina could be incorrect. Also, it is clearly incorrect to keep *Calisto* in Pronophilina, because as our tree shows, support for the Pronophilina clade that includes a diverse sample of genera is very strong, at 100% (Fig. 33 green), and *Calisto* is placed outside of this clade. Therefore, the solution was to propose a new substribe for the *Calisto* clade. Another curious observation is that the *Euptychia* Hübner, 1818 (type species *Oreas mollina* Hübner, [1813]) clade (i.e., *Euptychia sensu lato*) is quite removed from the rest of Euptychiina, and their association is only weakly supported (0.56, Fig. 33). This sister to *Euptychia sensu lato* clade is more prominent than Euptychiina as currently defined, and may deserve subtribal status: a question that could be answered in future studies.

Harsiesis Fruhstorfer, 1911 is a subgenus of *Platypthima* Rothschild & Jordan, 1905

Harsiesis Fruhstorfer, 1911 (type species *Hypocista* [sic] *hygea* Hewitson, 1863) and *Platypthima* Rothschild & Jordan, 1905 (type species *Platypthima ornata* Rothschild & Jordan, 1905) are characterized by an elevated evolutionary rate as revealed by their longer branches (Fig. 34). Despite their faster evolution, the two are more genetically similar to each other than other pairs of sister genera, e.g., COI barcodes between their type species (GenBank accession GQ357203 for *P. ornata*) differ by 9.4% (62 bp). Therefore *Harsiesis* Fruhstorfer, 1911 is a subgenus of *Platypthima* Rothschild & Jordan, 1905.

Percnodaimon Butler, 1876 and *Erebiola* Fereday, 1879 are junior subjective synonyms of *Argyrophenga* Doubleday, 1845

Two monotypic genera *Erebiola* Fereday, 1879 (type and the only species *Erebiola butleri* Fereday, 1879) and *Percnodaimon* Butler, 1876 (type and the only species *Percnodaimon pluto* Butler, 1876, homonym, valid name *Erebia merula* Hewitson, 1875) cluster closely with *Argyrophenga* Doubleday, 1845 (type species *Argyrophenga antipodum* Doubleday, 1845) (Fig. 34), all being from New Zealand and phenotypically similar. Therefore, *Percnodaimon* Butler, 1876 and *Erebiola* Fereday, 1879 are junior subjective synonyms of *Argyrophenga* Doubleday, 1845.

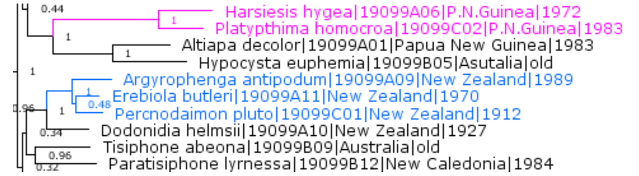

Fig. 34. *Platypthima* (magenta) and *Argyrophenga* (blue).

Magda Grishin, new subgenus

http://zoobank.org/4AF74BDC-1FCD-42B6-8BFB-A316F0F09D93

Type species. *Erebia magdalena* Strecker, 1880.

Definition. Forms a rather prominent clade within *Erebia* Dalman, 1816 (type species type species *Papilio ligea* Linnaeus, 1758) sister to the clade with subgenera *Atercoloratus* Bang-Haas, 1938 (type species *Coenonympha alini* Bang-Haas, 1937) and *Boeberia* Prout, 1901 (type species *Papilio parmenio* Böber, 1809), thus is not monophyletic with the subgenus *Erebia* (Figs. 35, 36). A COI barcode dendrogram constructed for the type species of all 11 available genus-group names associated with *Erebia* reveals that this clade does not contain any of them, and therefore is a new taxon (Fig. 35). To maintain a broadly defined genus *Erebia*, this taxon is assigned a subgenus rank. This new subgenus consists of the *magdalena* and *embla* groups of Peña et al. (2015). Phenotypically, a diverse assembly of species previously placed in different species groups (Warren 1936; Pelham 2008) and strongly associated together only from DNA sequence data be it gene markers (Peña et al. 2015), COI barcodes (Fig. 35), or all genomic protein-coding regions (Fig. 36). Morphologically, diagnosed either by a very short gnathos: shorter than third of uncus in lateral view (the *magdalena* group except *E. discoidalis* (W. Kirby, 1837)); or in species with longer gnathos (the *embla* group and *E. discoidalis*) arms directed posterior-ventrad in lateral view, rounded and inflated at the tips; or if upturned at the tips then only slightly and arms more parallel to uncus in lateral view than in other subgenera due to a strong kink at their origin, so they bend to position their axes parallel to the uncus near their origin (instead of being directed more ventrad), distance between gnathos and vinculum along tegumen shorter than tegumen height in lateral view and valva simple, without heel-like expansion, tip rounded, valva either short, about 3 times as long as

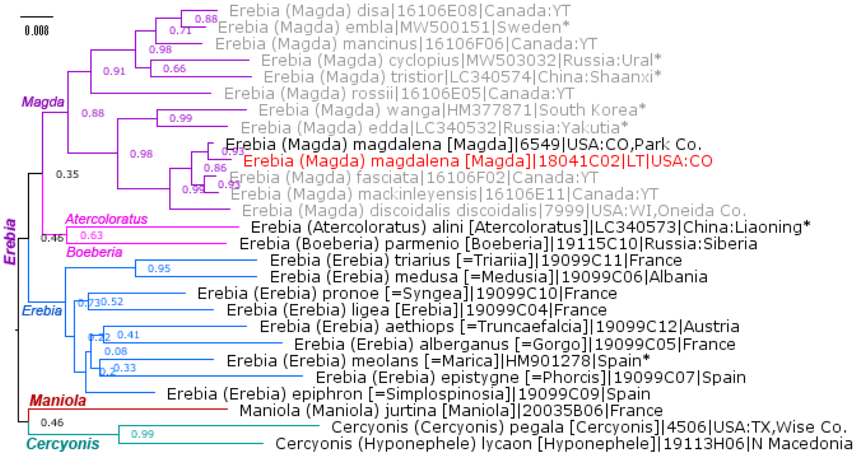

Fig. 35. COI barcode dendrogram of *Erebia* (blue, purple, and magenta) with its subgenera *Magda* subgen. n. (purple), *Atercoloratus* and *Boeberia* (magenta). Non-type species of available genus-group names are in gray, the lectotype of the type species of *Magda* is in red, genus-group names each species is the type of are given in brackets (= for synonyms), Accession numbers are given for GenBank sequences, which are marked with an asterisk.

broad with many small teeth in distal half (*E. discoidalis*), or long, more than 4 times longer than wide and with a broad-W-shaped dorsal margin (*E. rossii* (J. Curtis, 1835)). The following combination of characters in the COI barcode region is diagnostic: 271C (not T), 274C (not T), 421T or C (not A), 424T (not A), 451T or C (not A), 484not T, and 622T (not A).

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

Species included. The type species, *Hipparchia cyclopius* Eversmann, 1844, *Papilio disa* Thunberg, 1791, *Hipparchia discoidalis* Kirby, 1837, *Erebia edda* Ménétriés, 1851, *Papilio embla* Thunberg, 1791, *Erebia erinnyn* Warren, 1932, *Erebia fasciata* Butler, 1868, *Erebia mackinleyensis* Gunder, 1932, *Erebia mancinus* Doubleday, 1849, *Hipparchia rossii* Curtis, 1835, *Erebia magdalena sachaensis* Dubatolov, 1992, *Erebia tristis tristior* Goltz, 1937, and *Erebia wanga* Bremer, 1864.

Parent taxon. Genus *Erebia* Dalman, 1816.

Additional genomic support for the broadly defined genera *Cercyonis* Scudder, 1875, *Maniola* Schrank, 1801 and *Erebia* Dalman, 1816

Due to the pattern of diversification in the genomic tree, we proposed to place *Hyponephele* Muschamp, 1915 (type species *Papilio lycaon* Rottemburg, 1775) as a subgenus of *Cercyonis* Scudder, 1875 (type species *Papilio alope* Fabricius, 1793, currently a subspecies of *Papilio pegala* Fabricius, 1775) and *Pyronia* Hübner, [1819] (type species *Papilio tithonus* Linnaeus, 1771) with *Aphantopus* Wallengren, 1853 (type species *Papilio hyperantus* Linnaeus, 1758) as subgenera of *Maniola* Schrank, 1801 (type species *Maniola lemur* Schrank, 1801, which is a junior subjective synonym of *Papilio jurtina* Linnaeus, 1758) (Zhang et al. 2020). Although the three genus-level names (*Hyponephele*, *Pyronia*, and *Aphantopus*) have been in wide historical use, we have prioritized internal consistency of the classification and selection of the most prominent clades in the genomic tree as genera, as argued by Zhang et al. (2020) in the Introduction and Discussion sections. Internal consistency allows us to apply more objective and reproducible criteria and relate ranks (genus or subgenus) to comparable evolutionary events. Here, we expand the genomic tree with additional taxa (Fig. 36). The results strengthen our conclusion and agree with the recently published comprehensive phylogeny of European butterflies (Wiemers et al. 2020). The three clades that we consider genera: *Erebia* Dalman, 1816 (type species *Papilio ligea* Linnaeus, 1758), *Cercyonis sensu lato* and *Maniola sensu lato* that we unified into the subtribe Erebiina Tutt, 1896, prominently stand out (i.e., tree branches leading to them are the longest internal branches in the tree) and diversified around the same time (i.e. distances from the last common ancestors of these genera to the leaves are approximately the same for all three). Moreover, more divergent taxa that have been at times treated as genera (listed as subgenera here): *Cercyonis* (*Ereminephele*) *huebneri* Koçak, 1980 (formerly *Hyponephele*) and *Erebia* (*Boeberia*) *parmenio* Böber, 1809 originate near the last common ancestors of their genera, further supporting evolutionary significance of this time point. It does not seem accidental that 3 distinct but

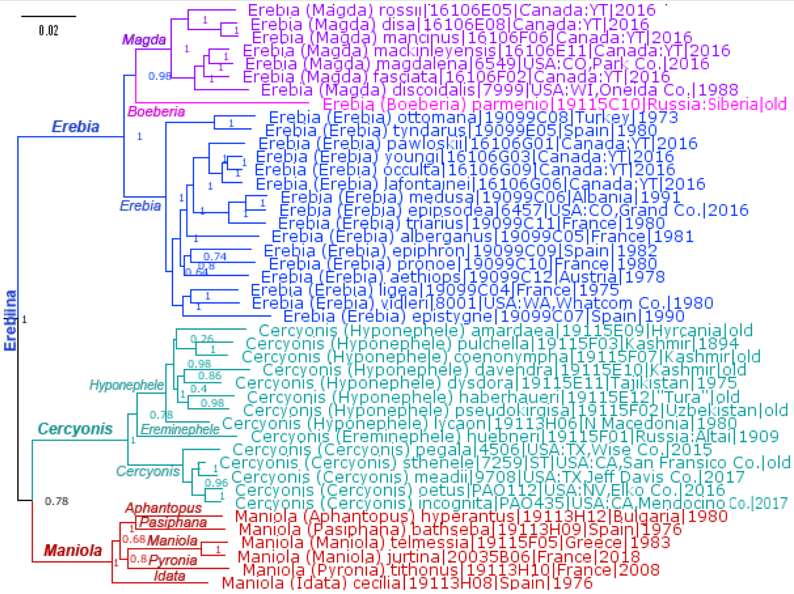

Fig. 36. *Erebiina* genera: *Erebia* (blue, purple, and magenta) with its subgenera *Magda* subgen. n. (purple) and *Boeberia* (magenta), *Cercyonis* (cyan) with its subgenera *Hyponephele* and *Ereminephele*, and *Maniola* (red) with its subgenera *Aphantopus*, *Pasiphana*, *Pyronia*, and *Idata*.

related phylogenetic lineages diversified around the same time, and if we chose the names of genera to reflect the pivotal common point in their evolution, the three-genus classification fits it best. As an alternative, we would be left with many small lineages as genera, and for internal consistency (i.e. taxonomic category represents a level in the classification), would need to split *Erebia* into at least 3 distinct genera, and *Maniola* into at least 5 (Fig. 36). We prefer to treat these smaller lineages as subgenera, as they do not represent the most prominent level of diversification, but the next one to it.

Hestinalis Bryk, 1938 is a junior subjective synonym of *Mimathyma* Moore, 1896

In the genomic tree *Hestinalis* Bryk, 1938 (type species *Hestina mimetica* Butler, 1874) originates within *Mimathyma* Moore, 1896 (type species *Athyma chevana* Moore, 1866) rendering it paraphyletic (Fig. 37). To restore monophyly and considering genetic closeness of these species, we propose that *Hestinalis* Bryk, 1938 is a junior subjective synonym of *Mimathyma* Moore, 1896. Curiously, *Hestina* Westwood, 1850 (type species *Papilio assimilis* Linnaeus, 1758) is in a different clade and thus is not synonymous with *Hestinalis*.

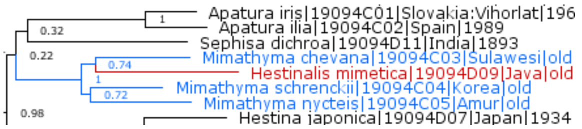

Fig. 37. *Mimathyma* (blue and red).

Vila Kirby, 1871 is a subgenus of *Biblis* Fabricius, 1807

A monotypic genus *Biblis* Fabricius, 1807 (type species *Papilio biblis* Fabricius, 1775, a junior homonym, valid name for this species is *Papilio hyperia* Cramer, 1779) is a close relative of *Vila* Kirby, 1871 (type species *Olina azeca* Doubleday, [1848]) (Fig. 38, compare with diversification in *Dynamine* Hübner, [1819]). The COI barcodes of the type species of these two genera differ by 7% (46 bp). Due to genetic similarities, we propose treating *Vila* as a subgenus of *Biblis*. The wing pattern differences between all these species are likely caused by different mimetic complexes they take part in.

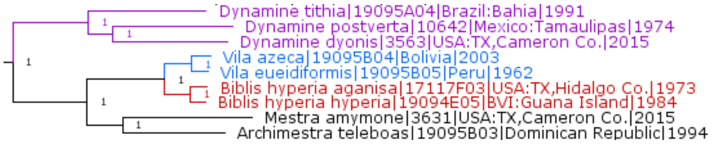

Fig. 38. *Vila* (blue), *Biblis* (red) and *Dynamine* (purple).

Biblis aganisa Boisduval, 1836 is a species distinct from *Biblis hyperia* (Cramer, 1779)

Genetic diversification between the nominotypical *Biblis (Biblis) hyperia* (Cramer, 1779) (type locality St. Thomas) and *Biblis (Biblis) hyperia aganisa* Boisduval, 1836 (type locality inferred as Mexico) is at the level of that between two species from the subgenus *Vila*: *Biblis (Vila) azeca* (Doubleday, [1848]) and *Biblis (Vila) eueidiformis* (Joicey & Talbot, 1918) (Fig. 38). The COI barcodes of the two taxa differ by 4.6% (30 bp). The nominotypical *B. hyperia* is characterized by more prominent dorsal forewing marginal bands than *B. b. aganisa*. Taken together, these arguments suggest that *Biblis aganisa* Boisduval, 1836 **reinstated status** is a species distinct from *Biblis hyperia* (Cramer, 1779).

The following taxa are junior subjective synonyms: *Catacore* Dillon, 1948 of *Diaethria* Billberg, 1820; *Mesotaenia* Kirby, 1871 with *Orophila* Staudinger, 1886 of *Perisama* Doubleday, 1849; and *Paulogramma* Dillon, 1948 of *Catagramma* Boisduval, 1836

Genomic sequencing and analysis of the type species of available genus-group names of the subtribe Callicorina Orfila, 1952 resulted in a fully resolved confident phylogeny (Fig. 39) that revealed close relationships between some of them. For instance, even the most distinctive of the type species for available genus-group names in the *Diaethria* Billberg, 1820 (type species *Papilio clymena* Cramer, 1775) clade sometimes separated in the monotypic genus *Catacore* Dillon, 1948 (type and the only species *Catagramma kolyma* Hewitson, 1851) clusters closely with *Diaethria*. The COI barcodes of *Diaethria* and *Catacore* type species are only 6.7% (44 bp) different. In agreements with Wahlberg (2019a), we treat *Catacore* Dillon, 1948 as a junior subjective synonym of *Diaethria* Billberg, 1820. Next, the three genera *Perisama* Doubleday, 1849 (type species *Catagramma bomplandii* Guérin-Méneville, [1844]), *Mesotaenia* Kirby, 1871 (type species *Callitaenia doris* C. & R. Felder, 1861, a subspecies of *Catagramma vaninka* Hewitson, 1855) and *Orophila* Staudinger, 1886 (type species *Cybelis campaspe* Hewitson, 1869, a subspecies of *Cybdelis cardases* Hewitson, 1869) cluster closely together (Fig. 39). Their COI barcodes also indicate a close relationship, e.g., the type species of *Mesotaenia* and *Perisama* are only 6.2% (41 bp) different. Therefore, we agree with Wahlberg (2019a) and confirm that *Mesotaenia* Kirby, 1871 and *Orophila* Staudinger, 1886 are junior subjective synonyms of *Perisama* Doubleday, 1849. Furthermore, the genomic tree confirms the close relationship between *Paulogramma* Dillon, 1948 (type species *Nymphalis pyracmon* Godart, [1824]) and *Catagramma* Boisduval, 1836 (type species *Catagramma hydaspes* Boisduval, 1836, which is a junior subjective synonym of *Nymphalis pygas* Godart, [1824]). The reasons why Freitas et al. (2014) resurrected *Paulogramma* in favor of the older name *Catagramma* that they did not use are unclear. Their tree (Freitas et al. 2014: Fig. 3) shows "*Callicore pygas*", the current name for the type species of *Catagramma*, inside *Paulogramma* as they define it. Furthermore, Wahlberg (2019a) lists *Paulogramma* in synonymy with *Catagramma*. Therefore, we confirm that *Paulogramma* Dillon, 1948 is a junior subjective synonym of *Catagramma* Boisduval, 1836. Finally, we confirm that *Lucinia* Hübner, [1823] belongs to Callicorina (Fig. 39).

Fig. 39. Callicorina genera: *Lucinia* (black), *Haematera* (red: subgenus *Antigonis*, and cyan), *Catagramma* (olive & pink), and *Callicore* (purple & yellow: subgenus *Diaethria*, magenta & green: subgenus *Perisama*, and blue).

Diaethria Billberg, 1820 and *Perisama* Doubleday, 1849 are subgenera of *Callicore* Hübner, [1819]

Inspection of genetic diversification and prominence of tree branches, we find that, contrary to their wing pattern similarity, *Catagramma* Boisduval, 1836 (type species *Catagramma hydaspes* Boisduval, 1836, which is a junior subjective synonym of *Nymphalis pygas* Godart, [1824]) is a prominent genus strongly separated from others in the *Callicore* group, in agreement with Freitas et al. (2014) who called this genus by its junior synonym *Paulogramma* Dillon, 1948 (type species *Nymphalis pyracmon* Godart, [1824]) (Fig. 39). Therefore, we retain *Catagramma* as a genus. However, the other three taxa: *Callicore* Hübner, [1819] (type species *Papilio astarte* Cramer, 1779), *Diaethria* Billberg, 1820 (type species *Papilio clymena* Cramer, 1775) and *Perisama* Doubleday, 1849 (type species *Catagramma bomplandii* Guérin-Méneville, [1844]) cluster more closely and are less prominently separated from each other in the tree (Fig. 39), e.g., COI barcodes of the type species of differ by 8.8% (58 bp). Therefore, we propose that *Diaethria* Billberg, 1820 and *Perisama* Doubleday, 1849 are subgenera of *Callicore* Hübner, [1819]. This adjustment of status (from genus to subgenus) makes their classification more internally consistent, and this newly broader *Callicore* becomes similar in genetic divergence to its relatives *Eunica* Hübner, [1819], *Hamadryas* Hübner, [1806], and *Dynamine* Hübner, [1819]. In wing patterns and shapes, the currently proposed subgenera of *Callicore* are rather similar to each other, and a number of erroneous attributions to former genera have been made in classifying these species (Freitas et al. 2014).

Antigonis C. Felder, 1861 is a subgenus of *Haematera* Doubleday, 1849

A monotypic genus *Antigonis* C. Felder, 1861 (type and the only species *Cybdelis pharsalia* Hewitson, 1852) is rather closely related to another monotypic genus *Haematera* Doubleday, 1849 (type species *Haematera thysbe* Doubleday, 1849, which is a subspecies of *Callidula pyrame* Hübner, [1819]) (Fig.

39), e.g., their COI barcodes differ by 9.3% (61 bp), suggesting that *Antigonis* C. Felder, 1861 is a subgenus of *Haematera* Doubleday, 1849, thus eliminating two not truly distinctive monotypic genera.

Asterope Hübner, [1819], *Nica* Hübner, [1826], *Peria* Kirby, 1871, and *Callicorina* Smart, 1976 are subgenera of *Temenis* Hübner, [1819]

We obtained and analyzed genomic data for the type species of all 10 available genus-group names of the subtribe Epiphilina Jenkins, 1987 that resulted in a well-resolved phylogeny (Fig. 40). We find that *Temenis* Hübner, [1819] (type species *Papilio merione* Fabricius, 1781, which is *Papilio laothoe* Cramer, 1777) may not be monophyletic, with its type species being sister to *Asterope* Hübner, [1819] (type species *Oreas sapphira* Hübner, [1816]) with medium support, and *Temenis pulchra* Hewitson, 1861, the type species of *Callicorina* Smart, 1976 possibly originating among other related genera, two of which are monotypic: *Nica* Hübner, [1826] (type and the only species *Nymphalis flavilla* Godart, [1824]) and *Peria* Kirby, 1871 (type and the only species *Papilio lamis* Cramer, 1779). Species of this group are close to each other, e.g., COI barcodes of the type species of *Peria* and *Temenis* differ by only 6.8% (45 bp) and taken together prominently separate from the rest of the subtribe. Even if *Temenis* is monophyletic (i.e., if the topology in Fig. 40 is incorrect), it is not prominently distinct from its relatives, and therefore we propose that they all are congeneric. Thus, *Asterope* Hübner, [1819], *Nica* Hübner, [1826], *Peria* Kirby, 1871, and *Callicorina* Smart, 1976 are subgenera of *Temenis* Hübner, [1819]. Curiously, the subgenus *Callicorina* does not belong to the subtribe Callicorina.

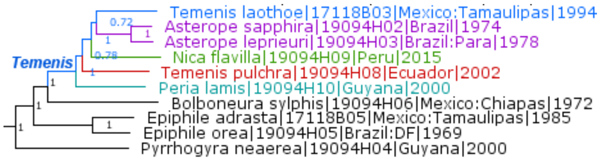

Fig. 40. *Temenis* (colored) with its subgenera *Asterope* (purple), *Nica* (green), *Callicorina* (red), *Peria* (cyan).

Panacea Godman & Salvin, 1883 is a junior subjective synonym of *Batesia* C. Felder & R. Felder, 1862

A monotypic genus *Batesia* C. Felder & R. Felder, 1862 (type species *Batesia hypochlora* C. & R. Felder, 1862) is closely related to *Panacea prola* (Doubleday, [1848]), the type species of *Panacea* Godman & Salvin, [1883] (Fig. 41), suggesting that the two genera are subjective synonyms, thus eliminating the need for yet another indistinct monotypic genus. The wing shape and general patterns of these species are quite similar as well, *Batesia* differing in the absence of black striations characteristic of *Panacea*, giving *Batesia* a more distinctive "cleaner" appearance otherwise not much different from *Panacea*, but clearly distinct from their relatives: sister genera *Ectima* Doubleday, [1848] and *Hamadryas* Hübner, [1806].

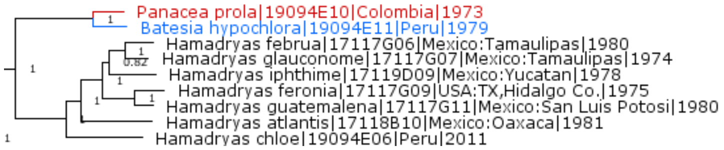

Fig. 41. *Panacea* (red), *Batesia* (blue) and *Hamadryas*.

Introductory comments on Nymphalinae

Five genera from the subfamily Nymphalinae Rafinesque, 1815 were placed as *incertae sedis* by Wahlberg (2019a): *Pycina* Doubleday 1849 (type and the only species *Pycina zamba* Doubleday, [1849]), *Rhinopalpa* C. & R. Felder 1860 (type and the only species *Rhinopalpa fulva* C. & R. Felder, 1860, a junior subjective synonym of *Vanessa eudoxia* Guérin-Méneville, 1840, with is a subspecies of *Papilio polynice* Cramer, 1779)), *Kallimoides* Shirôzu & Nakanishi 1984 (type and the only species *Kallima rumia* Doubleday, 1849), *Vanessula* Dewitz 1887 (type and the only species *Vanessula buchneri* Dewitz, 1887, a junior subjective synonym of *Liptena milca* Hewitson, 1873), and *Doleschallia* C. & R. Felder 1860 (type species *Papilio bisaltide* Cramer, 1777). The reasons behind the *incertae sedis* placement, such as ancient origin of these taxa forming long branches in the trees, were given by Wahlberg (2019b), who concluded: "Clearly more data are needed for these ancient taxa." To shed light on their classification, we obtained whole genome shotgun for the type species of these five genera and placed them in the phylogenetic context of other Nymphalinae. The tree constructed from protein-coding genes of the Z chromosome is illustrated (Fig. 42). In this mostly well-supported phylogeny, all currently defined tribes receive 100% statistical support. The five taxa in question are found in deeper radiation near the origins of Nymphalinae and are not closely associated with any of the currently defined tribes. *Pycina zamba* and *Rhinopalpa polynice* are confidently placed prior to divergence of other tribes such as Victorinini Scudder, 1893 and Junoniini Reuter, 1896 (Fig. 42). *Doleschallia bisaltide* is a confident sister to Melitaeini Herrich-Schäffer, 1843, but is prominently separated from them, originating well prior to radiation of Melitaeini into subtribes. Notably, Melitaeini are characterized by an elevated evolutionary rate reflected in much longer branches within the tribe compared to those of most other Nymphalinae, including *Doleschallia*. Finally, although *Kallimoides rumia* and *Vanessula milca* are confidently placed in the clade consisting of Victorinini, Junoniini, Melitaeini and *Doleschallia*, their exact phylogenetic position remains weakly supported because they originated during a rapid radiation event near the last common ancestor of this clade. It is likely that *K. rumia* is a distant sister of Victorinini. However, the association of *V. milca* with Junoniini is questionable. It is not likely that the lack of confidence in this phylogenic placement is caused by the shortage of sequence data. It is plausible that these taxa are of hybrid origin, or their evolution involved incomplete lineage sorting resulting in phylogenetic incongruence among different genes. Regardless of their exact phylogenetic origins, and exactly due to this phylogenetic uncertainty, these taxa do not belong to any existing tribes. For all the reasons stated above, each of these five lineages represents a tribe of Nymphalinae, as named below.

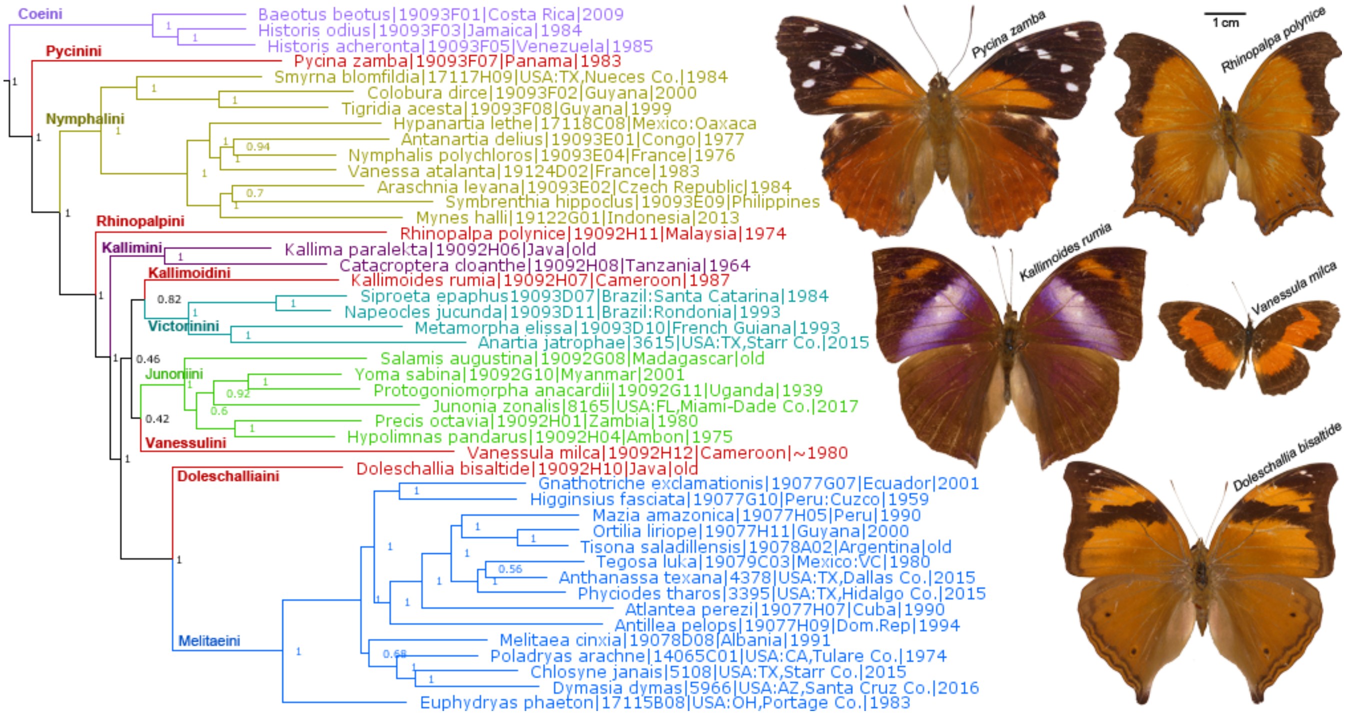

Fig. 42. Nymphalinae tribes. New tribes are colored in red. Specimens shown are actual specimens sequenced.

Pycinini Grishin, new tribe

http://zoobank.org/D5C0AE41-2615-4852-9B59-8533C27E4798

Type genus. *Pycina* Doubleday 1849.

Definition. Formerly placed within the tribe Coeini Scudder, 1893, this tribe is not monophyletic with it and instead is sister to all other Nymphalinae Rafinesque, 1815 excluding Coeini (Fig. 42), which justifies its status as a new tribe. The tribe is diagnosed by the characters given for *Pycina* on pages 305–306 by Westwood (1850) and on page 330 by Godman & Salvin (1884). In brief, diagnosed by densely hairy eyes, relatively small and thin palpi not extending beyond middle of eyes in lateral view, long slender antennae more than half of forewing length, elongated forewings, more so than in similarly patterned *Smyrna* Hübner, [1823], and undulating costal margin of hindwing: i.e., prominently concave near the middle instead of evenly convex throughout as in its relatives.

Genera included. Only the type genus.

Parent Taxon. Subfamily Nymphalinae Rafinesque, 1815.

Rhinopalpini Grishin, new tribe

http://zoobank.org/4A3ACC99-A761-49B9-BA00-00F83FF443DE

Type genus. *Rhinopalpa* C. & R. Felder 1860.

Definition. Originates early in the Nymphalinae radiation and is sister to the clade consisting of several tribes, e.g., Kallimini Doherty, 1886 and Melitaeini Herrich-Schäffer, 1843 among others (Fig. 42), indicating that this new taxon is a tribe. Diagnosed by long and densely scaled stout palpi (as suggested by the name, but not longer than the head as in Libytheinae Boisduval, 1833), discal cells short on both wings, about ⅓ of wing length, all forewing R veins run very close together and R_3, R_4 and R_5 stalked for most of their length, forewings produced into apical and tornal lobes, hindwings with stubby tail in the middle of outer margin; below with a row of 6 eyespots along the margin of both wings; caterpillar with long scoli turned anteriad at tips past thoracic segments; pupa unusually shaped somewhat resembling a dead leaf, with 3 pairs of horn-like protuberances, first pair very prominent, directed posteriad.

Genera included. Only the type genus.

Parent Taxon. Subfamily Nymphalinae Rafinesque, 1815.

Comments. The name Rhinopalpini as published by Teshirogi (2016) appears to be a nomen nudum: Referred to Wahlberg et al. (2005), a work that does not mention the name, and the name is not "explicitly indicated as intentionally new" in Teshirogi (2016), thus failing Art. 16.1. of the ICZN Code (ICZN 1999).

Kallimoidini Grishin, new tribe

http://zoobank.org/22C74A4F-6B24-4502-99BB-B8E3C66AFABE

Type genus. *Kallimoides* Shirôzu & Nakanishi 1984.

Definition. This tribe is a distant sister of Victorinini Scudder, 1893 with moderate support (Fig. 42). Being an ancient lineage as indicated by its phylogenetic placement and only moderate statistical support for association with Victorinini, it is assigned the status of a tribe. Diagnostic characters for this tribe are those given in detail for the genus *Kallimoides* on pages 107-108 and wing venation and genitalia are illustrated in Figs. 5 and 40-45, respectively, by Shirôzu & Nakanishi (1984). Most notably, the new tribe is diagnosed by S-shaped vein R_1 on forewing, partially coalescing with Sc and then with R_2; prominently reduced tegumen and large S-shaped aedeagus terminally thinning into a hook in male genitalia; and the absence of genital plate in females.

Genera included. Only the type genus.

Parent Taxon. Subfamily Nymphalinae Rafinesque, 1815.

Vanessulini Grishin, new tribe

http://zoobank.org/D584B74C-8DC8-479A-AD25-9197A03A843B

Type genus. *Vanessula* Dewitz 1887.

Definition. Belongs to the same clade with Victorinini, Junoniini, Melitaeini and *Doleschallia*, but not closely allied to any of them as judged by its ancient origin and poor statistical support for its placement within this clade, justifying its status of a tribe (Fig. 42). The tribe is diagnosed by the characters given for *Vanessula* on pages 145–146 by Dewitz (1887). In brief, forewing vein R_1 near its origin partly coalescent with Sc, vein R_2 stalked with R_3, R_3 with R_4 and R_4 with R_5 for at least half of their lengths each, discal cell closed, short, about 1/3 of forewing; eyes bare, palpi long and thin, slightly longer than head, antennae half of forewing length; wings moderately elongated, wing shape similar to Melitaeini.

Genera included. Only the type genus.

Parent Taxon. Subfamily Nymphalinae Rafinesque, 1815.

Doleschalliaini Grishin, new tribe

http://zoobank.org/88D32044-DB8E-486F-8C09-0D188E5CDC93

Type genus. *Doleschallia* C. & R. Felder 1860.

Definition. Formerly included in Kallimini Doherty, 1886 due to extensive superficial similarity. In the genomic tree, confidently placed as sister to Melitaeini Newman, [1870], but more distant from them than they are from each other, and is of an ancient origin estimated nearly 70 Mya (Su et al. 2017), which justifies its status of a tribe (Fig. 42). Similar to *Kallima* Doubleday 1849 in wing shape and coloration, apparently due to convergence. Diagnosed by its produced forewing apex and hindwing tornus extended in a short tail, below colored as a dead brown leaf with mid-rib (as in Kallimini), with several eyespots along the wing margins; discal cells open on both wings (closed in Kallimini), all forewing R veins close together, R_4 and R_5 stalked for 2/3 of their length, hindwing humeral vein simple (branches into 2 in Kallimini); eyes bare, pupa smooth and rounded, abdomen segments without protuberances that are present in Kallimini.

Genera included. Only the type genus.

Parent Taxon. Subfamily Nymphalinae Rafinesque, 1815.

Comments. *Doleschalla* Walker 1861 (Diptera: Tachinidae) is the type genus of Doleschallini. According to Art. 55.4. of the ICZN Code (ICZN 1999), one letter difference, which in this case would be an extra "i" from the suffix "-ina", avoids homonymy. However, it does not avoid confusion, including internet search engines that correct possible spelling errors, especially in this case, because it is a duplication of a letter in the suffix formation from the correctly determined stem. The Code gives a choice to alleviate the problem: Art. 29.4. (original stem formation to be maintained) and Recommendation 29A are followed here, and the entire name of the type genus is taken as a stem with hopes to diminish confusions. The choice of being ridiculed for grammatically incorrect stem formation is a "lesser evil" compared to increased confusion of those who use the name.

Additional genomic support to partition *Nymphalis* genus group into 4 genera: *Hypanartia* Hübner, [1821], *Vanessa* [Fabricius], 1807, *Antanartia* Rothschild & Jordan, 1903, and *Nymphalis* Kluk, 1780

To achieve a more objective, internally consistent and eventually stable classification, we have placed *Aglais* Dalman, 1816 (type species *Papilio urticae* Linnaeus, 1758) and *Polygonia* Hübner, [1819] (type species *Papilio c-aureum* Linnaeus, 1758) as subgenera of *Nymphalis* Kluk, 1780 (type species *Papilio polychloros* Linnaeus, 1758) on the basis of genomic evidence (Zhang et al. 2020). Here, we obtained and analyzed whole genome shotgun sequences of additional taxa from the *Nymphalis* group, defined as a moderately prominent clade formed by *Hypanartia* Hübner, [1821] (type species *Hypanartia demonica* Hübner, [1821], which is a junior subjective synonym of *Papilio lethe* Fabricius, 1793) and its sister taxa that include *Vanessa* [Fabricius], 1807 (type species *Papilio atalanta* Linnaeus, 1758), *Antanartia* Rothschild & Jordan, 1903 (type species *Papilio delius* Drury, 1782) and *Nymphalis* (Fig. 42). The resulting phylogeny is in agreement with previous studies (Wahlberg and Nylin 2003; Wahlberg and Rubinoff 2011) (Fig. 43). Notably, (1) *Kaniska* Moore, [1899] (type and the only species *Papilio canace* Linnaeus, 1763) is placed within *Nymphalis* as a subgenus, sister to subgenus *Polygonia* with moderate support; (2) *Roddia* Korshunov, 1995 (type and the only species *Papilio l-album* Esper, 1781) is situated at a distance from and thus is a valid subgenus sister to subgenus *Nymphalis*; (3) *Inachis* Hübner, [1819] (type and the only species *Papilio io* Linnaeus, 1758) is similarly distanced from *Aglais* as *Roddia* from *Nymphalis sensu stricto* and therefore is a valid subgenus; (4) the genus *Antanartia* is sister to *Nymphalis*, is prominently distinct from it, and forms a long branch in the tree indicating accelerated evolution, which resulted in its relatively unusual wing shape and pattern, likely due to convergence more similar to the two *Vanessa* species formerly placed in *Antanartia* (*Vanessa hippomene* (Hübner, [1823] and *Vanessa dimorphica* Howarth, 1966) rather than to *Nymphalis*. Overall, the *Vanessa* group has split over a relatively narrow time period into 4 most prominent clades, which (except *Antanartia*) diversified around the same time, indicating evolutionary significance of that time point. Therefore, it is meaningful to define genera as these 4 clades, assigning more recent diversifications to subgenera. This study completes genomic coverage of all distinct lineages in the *Nymphalis* group, and the results are unlikely to change after inclusion of the remaining species.

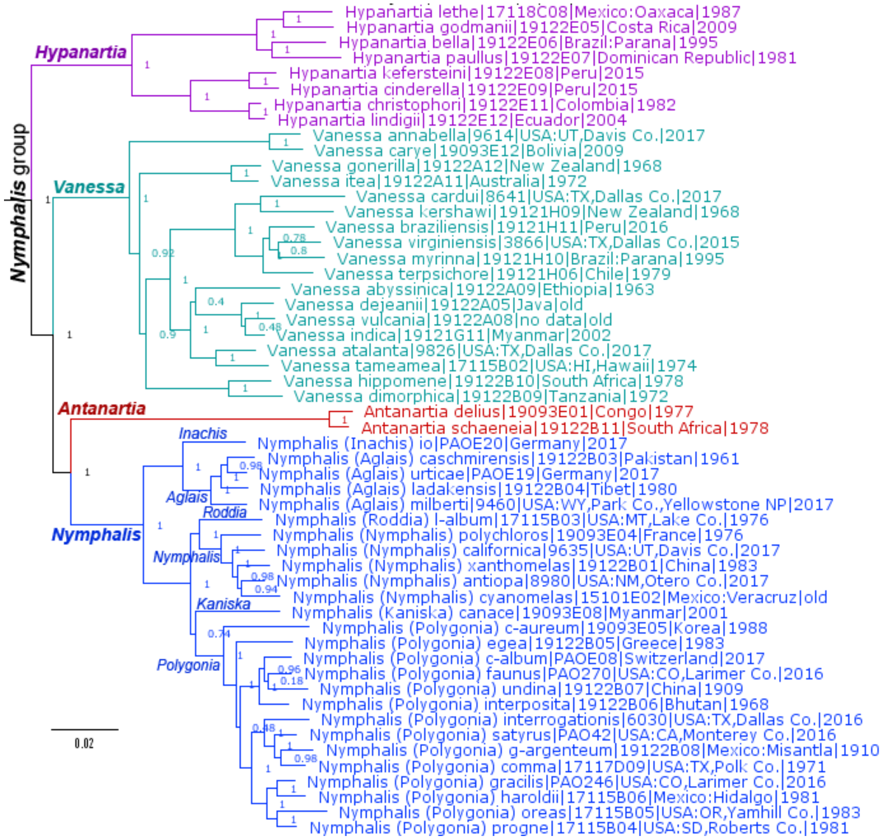

Fig. 43. *Vanessa* group genera: *Hypanartia* (purple), *Vanessa* (cyan), *Antanartia* (red), and *Nymphalis* (blue, subgenera labeled at their clades).

Napeocles Bates, 1864 is a junior subjective synonym of *Siproeta* Hübner, [1823]

We obtained genomic data for all 10 known species of Victorinini Scudder, 1893, and the resulting phylogenetic tree revealed that the monotypic genus *Napeocles* Bates, 1864 (type species *Hamadryas jucunda* Hübner, [1808]) clusters very closely with *Siproeta* Hübner, [1823] (type species *Siproeta trayja* Hübner, [1823], currently a subspecies of *Siproeta epaphus* (Latreille, [1813])) (Fig. 44). The 4 species in this clade clump together, suggesting that *Napeocles* Bates, 1864 is a junior subjective synonym of *Siproeta* Hübner, [1823] despite profound differences in wing shape and patterns, a result of apparently convergent similarity with dead leaf mimics.

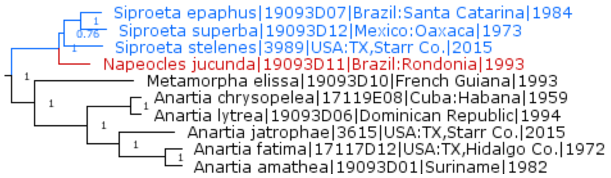

Fig. 44. *Siproeta* (blue and red) among Victorinini.

Tribe Melitaeini Herrich-Schäffer, 1843 consists of two subtribes

We sequenced and analyzed genomic data for all valid genera and nearly all available genus-group names of the tribe Melitaeini Herrich-Schäffer, 1843. The resulting nuclear all-gene phylogeny of selected most distinct taxa agrees with previous studies based on gene markers (Wahlberg et al. 2005; Wahlberg and Freitas 2007; Long et al. 2014) (Fig. 45). The genome-based phylogeny reveals nearly extreme evolutionary rate heterogeneity among different clades of *Melitaeini*, as much as 3-fold difference: with *Euphydryas* Scudder, 1872 (type species *Papilio phaeton* Drury, 1773) having the lowest rate (=shortest distance in horizontal dimension from the root on the left to the tree leaves on the right) and insular taxa such as *Atlantea* Higgins, 1959 (type species *Synchloe perezi* Herrich-Schäffer, 18620) having the highest rate (=longest distances: branches for these taxa are sticking out to the right from the rest). This heterogeneity is likely connected to the high diversification rate in the tribe (species richness) and leads to the difficulties with its classification. From its last common ancestor, the tribe divides into two most prominent clades: *Euphydryas* evolving with the speed typical for Nymphalidae (Fig. 42) and its sister that includes all other taxa that evolve at progressively elevated rates. Despite the elevated rates, the internal branches in this sister to *Euphydryas* clade are shorter than the branch leading to it, suggesting that the taxa within this clade are closely related to each other and are not as prominently distinct so to define as subtribes compared to the whole clade itself. Therefore, instead of dividing this clade into additional subtribes, we propose that the Melitaeini consists of only two subtribes: Euphydryina Higgins, 1976 and Melitaeina Herrich-Schäffer, 1843, which is the major and unquestionable division of the tribe. The most prominent (i.e. the longest compared to their surrounding) internal branches within Melitaeina are defined here as genera (Fig. 45). Many of these genera correspond to those in use today, i.e., *Melitaea* Fabricius, 1807 (type species *Papilio cinxia* Linnaeus, 1758), *Poladryas* Bauer, 1975 (type species *Melitaea arachne* W. H. Edwards, 1869), *Chlosyne* Butler, 1870 (type species *Papilio janais* Drury, 1782), *Gnathotriche* C. & R. Felder, 1862 (type species *Euterpe exclamationis* Kollar, 1849), *Higginsius* Hemming, 1964 (type species *Melitaea fasciata* Hopffer, 1874), *Antillea* Higgins, 1959 (type species *Papilio pelops* Drury, 1773), and *Atlantea* are traditionally used genera that are prominent clades in the genomic tree (Fig. 45). Other cases suggest adjustment to ranks and names that are detailed below.

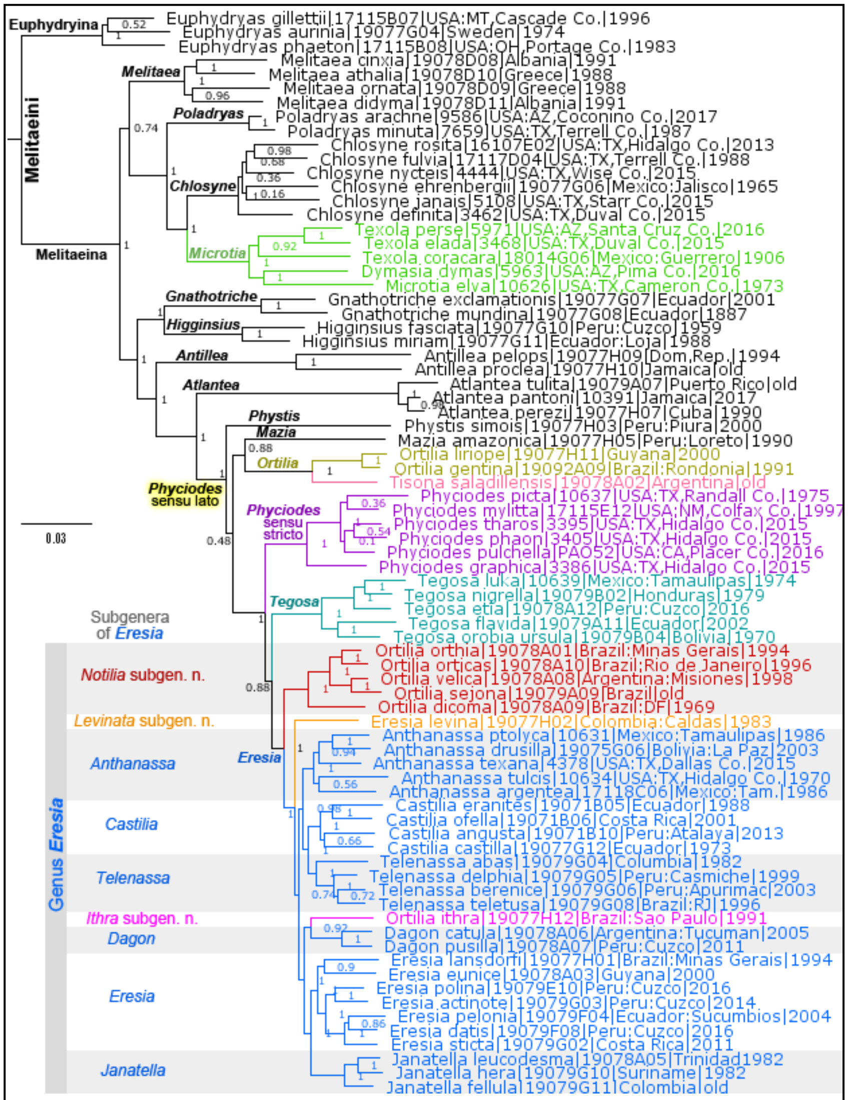

Fig. 45. Melitaeini subtribes Euphydryina and Melitaeina, and genera, including *Microtia* (green), *Ortilia* (olive and pink), *Phyciodes* (purple), *Tegosa* (cyan) and *Eresia* (red, orange, blue, and magenta).

Texola Higgins, 1959 and *Dymasia* Higgins, 1960 are junior subjective synonyms of *Microtia* H. Bates, 1864

Microtia H. Bates, 1864 (type and the only species *Microtia elva* H. Bates, 1864), *Dymasia* Higgins, 1960 (type and the only species *Melitaea dymas* W. H. Edwards, 1877) and *Texola* Higgins, 1959 (type species *Eresia elada* Hewitson, 1868) cluster closely in the genomic tree (Fig. 45). Our result agrees with the previous assessment based on gene markers (Wahlberg et al. 2005; Wahlberg and Freitas 2007; Long et al. 2014) and morphological study by Kons (2000), who already synonymized *Texola* and *Dymasia* with *Microtia*, a suggestion cited by Wahlberg et al. (2005) five years later but not followed either in that work (Wahlberg et al. 2005) or in subsequent publications (Pelham 2008; Long et al. 2014) and many on-line resources (Warren et al. 2016; North American Butterfly Association 2018; Wahlberg 2019a; Pelham 2020). Finally, more than two decades after these studies, we reach the same conclusion on a much larger DNA dataset: *Texola* Higgins, 1959 and *Dymasia* Higgins, 1960 are junior subjective synonyms of *Microtia* H. Bates, 1864. A curious observation is that *Microtia* [=*Texola*] *coracara* (Dyar, 1912) appears to be more distant from other *Texola* than *Dymasia* from *Microtia* (Fig. 45), further supporting unification of these species. The unification is a more meaningful solution, because this clade actually consists of four semi-equal lineages, which are (1) *M. elada* (Hewitson, 1868) species group; (2) *M. anomalus* (Godman & Salvin, 1897) species group that includes *M. coracara*; (3) *M. dymas*; and (4) *M. elva*; rather than the traditional three (*Texola*, *Dymasia* and *Microtia*). An alternative could be to split the group into these 4, rather than 3, evolutionary lineages, but each of these 4 groups is nearly monotypic (or monotypic under some species concepts) and is a species group rather than a genus or even subgenus. Finally, *Microtia sensu lato* is characterized by an elevated evolutionary rate compared to its sister *Chlosyne* Butler, 1870 (type species *Papilio janais* Drury, 1782): in Fig. 45, branches of *Microtia* (green) are longer (i.e., stick out to the right more) than branches of *Chlosyne* (black). This elevated rate may be behind more pronounced phenotypic differences between *Microtia* species compared to *Chlosyne* that resulted in the oversplit classification of *Microtia* into genera.

Tisona Higgins, 1981 is a junior subjective synonym of *Ortilia* Higgins, 1981

The monotypic genus *Tisona* Higgins, 1981 (type and the only species *Phyciodes saladillensis* Giacomelli, 1911) was proposed on the basis of genitalic differences, most significantly "penis apex with crossing ostium-folds" (Higgins 1981), i.e., with two twisted finger-like processes at the tip. Higgins likened *Tisona* to *Tegosa* Higgins, 1981 (type species *Acraea claudina* Eschscholtz, 1821). To better understand its phylogenetic affinities, we sequenced the only available although century-old specimen of *Tisona saladillensis* in the National Museum of Natural History collection (USNM) (Fig. 46). It lacks the right hindwing, and one of its labels, probably written by William Schaus, reads || Argentina | Giacomelli ||, suggesting that this specimen may have been part of the type series. In the genomic tree, it clusters closely and confidently with *Ortilia* Higgins, 1981 (type species *Papilio liriope* Cramer, 1775), away from *Tegosa* (Fig. 45). COI barcodes of *O. liriope* and *T. saladillensis* differ by 5.5% (36 bp). This small difference strongly suggests that the two species are congeneric, and we place *Tisona* Higgins, 1981 as a junior subjective synonym of *Ortilia* Higgins, 1981. Although the unusual genitalia of this species revealed its uniqueness despite the common *Phyciodes*-like wing patterns, DNA analysis was necessary to understand its origins and classification.

Fig. 46. Sequenced specimen of *Ortilia saladillensis*. Labels reduced 2 times compared to the specimen.

Anthanassa Scudder, 1875, *Castilia* Higgins, 1981, *Telenassa* Higgins, 1981, *Dagon* Higgins, 1981, and *Janatella* Higgins, 1981 are subgenera of *Eresia* Boisduval, 1836

The most inclusive prominent clade that contains *Phyciodes* Hübner, [1819] (type species *Papilio cocyta* Cramer, 1777) and is consistent in genetic diversification (corrected for its higher evolutionary rate) with how other Melitaeina genera are defined is labeled "*Phyciodes* sensu lato" in Fig. 45. It includes the majority of Melitaeina genera and species as they are presently defined. This current classification that remains largely unchanged since the Higgins revision (1981), represents the other extreme and appears to be oversplit, because many genera defined by Higgins are too close genetically and do not stand out as prominent clades in the tree (Fig. 45, first word in species names). Most notably, *Anthanassa* Scudder, 1875 (type species *Melitaea texana* Edwards, 1863), *Castilia* Higgins, 1981 (type species *Eresia castilla* C. & R. Felder, 1862), *Telenassa* Higgins, 1981 (type species *Argynnis teletusa* Godart, [1824]), *Dagon* Higgins, 1981 (type species *Eresia catula* Hopffer, 1874), *Janatella* Higgins, 1981 (type species *Eresia leucodesma* C. & R. Felder, 1861), and *Eresia* Boisduval, 1836 (type species *Nereis eunice* Hübner, [1807]) cluster closely together, and the internal branches separating them are short and indistinct. While most of Higgins genera are indeed monophyletic, with some exceptions noted in the tree by colors (Fig. 45) and discussed below, the lack of their distinctiveness and low divergence is more consistent with that of subgenera. E.g., COI barcodes of the type species of *Eresia* and *Anthanassa* differ by only 6.5% (43 bp), without any correction for the generally elevated evolutionary rate of these lineages. Moreover, even *Phyciodes* is not particularly removed from this cluster of closely related "genera": COI barcodes of *Phyciodes tharos* (Drury, 1773) and *Anthanassa texana* (W. H. Edwards, 1863) differ by only 7.3% (48 bp). Therefore, we would generally favor broader defined genera and could propose "*Phyciodes* sensu lato" (Fig. 45) as a genus to combine most of these Higgins genera. However, looking for a compromise to meaningfully classify this species-rich lineage, we opt for a centrist solution. We note that *Phyciodes sensu stricto* and *Tegosa* Higgins, 1981 (type species *Acraea claudina* Eschscholtz, 1821) do form somewhat prominent clades in the tree, and we keep them as genera. As a result, clades split prior to them also keep their genus rank: *Phystis* Higgins, 1981 (type and the only species *Eresia simois* Hewitson, 1864), *Mazia* Higgins, 1981 (type and the only species *Melitaea amazonica* Bates, 1864) and *Ortilia* Higgins, 1981 (type species *Papilio liriope* Cramer, 1775). All others: *Anthanassa* Scudder, 1875, *Castilia* Higgins, 1981, *Telenassa* Higgins, 1981, *Dagon* Higgins, 1981, and *Janatella* Higgins, 1981 are placed as subgenera of *Eresia* Boisduval, 1836. Finally, we note several clades in the tree that disrupt monophyly of the genera as defined by Higgins (Fig. 45: red and magenta "*Ortilia*" and orange "*Eresia*"). These clades also appear in the phylogenetic studies based on gene markers, although their exact positions relative to the other clades varied (Wahlberg and Freitas 2007; Long et al. 2014). To remove ambiguity about their status, these clades are named as subgenera of *Eresia* below.

Notilia Grishin, new subgenus

http://zoobank.org/3A8FA139-BE8C-444A-A212-6108DA6D3EAB

Type species. *Eresia orthia* Hewitson, 1864.

Definition. Previously placed in *Ortilia* Higgins, 1981 (type species *Papilio liriope* Cramer, 1775), this group is not monophyletic with it. Instead it is sister to all other *Eresia sensu lato*, and is close to them (Fig. 45). Previously discovered and defined as the Brazilian "Ortilia" clade by Wahlberg and Freitas (2007), this phylogenetic group was also confirmed and discussed in a more recent study suggesting "that this clade requires a new name" (Long et al. 2014). Due to its genetic closeness to *Eresia sensu lato*, this distinctive lineage is named as a subgenus of *Eresia* rather than a separate genus pending further analysis. It keys out to *Ortilia* in Higgins (1981) sharing the following diagnostic combination of characters with it: antennal club pyriform, aedeagus end without a pair of twisted processes, tegumen reduced, scaphial extensions small, without hooks and spines at angles, saccus single, narrow, finger-like, not expanding terminally, without a cleft. Differs from *Ortilia* in shorter and straighter harpe projecting directly caudodorsad (not arched at its origin changing direction from cephalodorsad) and less extensive or absent fulvous markings on wings above.

Etymology. The name is a feminine noun in the nominative singular, formed as a fusion *Not* + [Ort]*ilia* to indicate distinction from *Ortilia*.

Species included. The type species, *Phyciodes orticas* Schaus, 1902, *Phyciodes sejona* Schaus, 1902, *Eresia velica* Hewitson, 1864, *Eresia dicoma* Hewitson, 1864, and *Phyciodes polinella* Hall, 1928.

Parent taxon. Genus *Eresia* Boisduval, 1836.

Levinata Grishin, new subgenus

http://zoobank.org/5C69C6A2-7ADD-4E42-8818-23CCB9A042CE

Type species. *Eresia levina* Hewitson, 1872.

Definition. Previously placed in *Eresia* Boisduval, 1836 (type species *Nereis eunice* Hübner, [1807]), this group is not monophyletic with it. Instead it is sister to all other *Eresia sensu lato* but *Notilia* subgen. n. (Fig. 45). It is a phenotypically distinctive subgenus diagnosed by wings rounder than *Eresia* with broad discal band across forewing, blue in the type species. Its male genitalia are distinctive, with diagnostic characters for this new subgenus as described for *Eresia levina* on page 150 and illustrated in Figs. 430–431 in Higgins (1981): i.e., genital capsule larger than in other *Eresia*, tegumen sclerotized, shoulders well-developed, scaphial extension expanded, sclerotized and terminally with many small teeth, valvae with fine teeth on inner sides near apex, aedeagus terminally rounded, without ostium keel.

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 *Eresia* Boisduval, 1836.

Ithra Grishin, new subgenus

http://zoobank.org/BADF7F37-1CFB-4846-AC56-6B125E8B6708

Type species. *Phyciodes ithra* Kirby, 1900.

Definition. Previously placed in *Ortilia* Higgins, 1981 (type species *Papilio liriope* Cramer, 1775), this group is not monophyletic with it. Instead it is sister to *Dagon* Higgins, 1981 (type species *Eresia catula* Hopffer, 1874), but not with decisive statistical support (Fig. 45), and therefore is a distinctive lineage of the same rank, i.e., subgenus. Diagnosed by male genitalia and the characters for this subgenus are as those given for *Ortilia ithra* on page 120 and illustrated in Figs. 318–320 in Higgins (1981). Keys out to *Ortilia* in Higgins (1981) due to the following combination of characters this new subgenus shares with *Ortilia* and *Notilia* subgen. n.: pear-shaped (not extended) antennal club, no elongated processes at aedeagus end, reduced tegumen with small scaphial extensions not armed with hooks or spines, saccus single, terminally narrower, without a cleft. Differs from *Ortilia* and *Notilia* subgen. n. in having larger genital capsule, longer and bulkier saccus, prominent but short in dorsal view tegumen with very short scaphial extensions, short apical sections of valvae with thicker and rather straight harpes directed caudodorsad, aedeagus narrowing from phallobase caudad in basal half.

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

Species included. Only the type species.

Parent taxon. Genus *Eresia* Boisduval, 1836.

Phystis fontus (A. Hall, 1928), new combination

To our initial surprise, the distinctive species *Telenassa fontus* (A. Hall, 1928) (type locality Guyana, Fig. 47 middle) was placed among subspecies of *Phystis simois* (Hewitson, 1864) (type locality Brazil, Fig. 47 left and right) in the genomic tree, rendering *P. simois* paraphyletic (Fig. 48). Suspecting contamination from the specimens of *P. simois* that were sampled next to it, we initially removed this otherwise excellent sample (NVG-19077H04) from the analysis pending DNA re-extraction and re-sequencing. However, *T. fontus* and *P. simois* were found to be sisters based of gene markers (Wahlberg and Freitas 2007; Long et al. 2014) supporting the validity of our genomic results. Due to this genetic similarity, we place *T. fontus* in *Phystis* to form *Phystis fontus* (A. Hall, 1928), **comb. n.** and marvel about evolutionary plasticity leading to distinctly different wing shapes in this small genus.

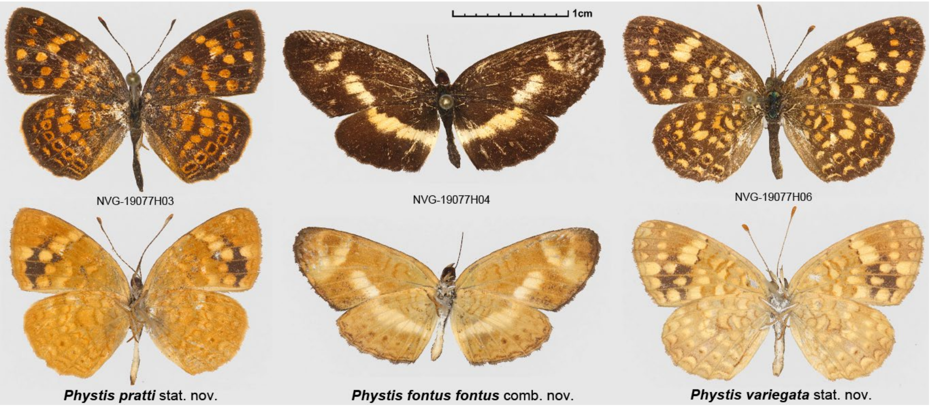

Fig. 47. Phenotypic diversity in *Phystis*. Sequenced specimens are shown.

Phystis variegata (Röber, 1913) and *Phystis pratti* (A. Hall, 1935) are species distinct from *Phystis simois* (Hewitson, 1864)

Confident paraphyly of the species *Phystis simois* (Hewitson, 1864) (type locality Brazil, Fig. 47 left and right) with respect to *Phystis fontus* (A. Hall, 1928), comb. n. was one of the more unsettling results in this project (Fig. 48). However, COI barcodes of the two subspecies *Phystis simois pratti* (A. Hall, 1935) (type locality North Peru, Fig. 47 left) and *Phystis simois variegata* (Röber, 1913) (type locality Argentina, Fig. 47 right) differ by 6.4% (42 bp), which is more than the difference between some of the Higgins genera (Higgins 1981), see above. Inspection of specimens (Fig. 47 left and right) reveals marked difference in wing shapes of the two subspecies, not commonly found within species. Therefore, these two subspecies are species that are also distinct from the nominotypical *Phystis simois* (Hewitson, 1864) (type locality Brazil) due to phenotypic differences and COI barcode differences (7.1% & 8.1%) between our specimens and *P. simois* available from GenBank (accession EF493956) (Wahlberg and Freitas 2007). Hence, the names for these species are *Phystis variegata* (Röber, 1913) **stat. nov.** and *Phystis pratti* (A. Hall, 1935) **stat. nov**. We have not studied *Phyciodes chinchipensis* Hayward, 1964 (type locality Peru: Rio Chinchipe) currently treated as a subspecies of *P. simois*. Nevertheless, examination of the holotype photographs (Warren et al. 2016) suggests that it is not *P. simois*. Due to wing pattern resemblance and locality (both are from North Peru), we tentatively place it as a subspecies of *P. pratti* instead, keeping in mind that it may be a distinct species and not a mere color variation.

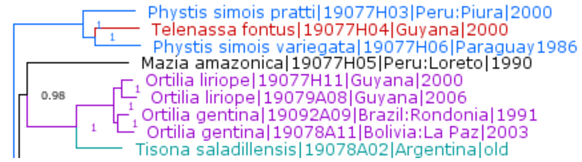

Fig. 48. *Phystis* (blue, red) and *Ortilia* (purple, cyan).

Abananote Potts, 1943 and *Altinote* Potts, 1943 are junior subjective synonyms of *Actinote* Hübner, [1819]

In agreement with previous studies (Silva-Brandao et al. 2008; Carvalho et al. 2020), we find that genera *Actinote* Hübner, [1819] (type species *Papilio thalia* Linnaeus, 1758), *Abananote* Potts, 1943 (type species *Acraea abana* Hewitson, 1868) and *Altinote* Potts, 1943 (type species *Heliconius neleus* Latreille, [1813]) are closely related and some of them are not monophyletic as currently circumscribed (Fig. 49). The type species of *Abananote* and *Altinote* are quite closely related: e.g. their COI barcodes differ by 6.4% (42 bp), the same divergence as between the two former subspecies of *Phystis simois* (see above), and therefore are congeneric. The *Actinote* clade is separated from them by a prominent gap (Carvalho et al. 2020), and the barcodes of *A. thalia* and *A. neleus* differ by 8.5% (56 bp), which would suggest their attribution to different subgenera. However, species phylogeny is at odds with intuitive phenotypic assessment (Lamas 2004): there is an additional third clade unexpected from phenotypes (Silva-Brandao et al. 2008; Carvalho et al. 2020). Therefore, until these inconsistencies between phenotypic and genetic classifications of this group are sorted out, we propose placing *Abananote* Potts, 1943 and *Altinote* Potts, 1943 as junior subjective synonyms of *Actinote* Hübner, [1819]. This treatment is consistent with the unified, and more genetically diverse, Old World genus *Telchinia* Hübner, [1819] (type species *Papilio serena* Fabricius, 1775) that is sister to *Actinote sensu lato* (Fig. 49).

Fig. 49. *Actinote* (blue, magenta and orange).

Episcada Godman & Salvin, 1879 is a junior subjective synonym of *Ceratinia* Hübner, 1816

Genome-level phylogeny confirms problems with the current classification of *Episcada* Godman & Salvin, 1879 (type species *Ithomia salvinia* Bates, 1864) and *Ceratinia* Hübner, 1816 (type species *Nerëis neso* Hübner, [1806]) (Willmott and Freitas 2006): the two genera are closely related and *Episcada* renders *Ceratinia* paraphyletic (Fig. 50), in agreement with other studies (Chazot et al. 2020). COI barcodes of the *Episcada* and *Ceratinia* type species differ by only 4.4% (29 bp), less than between the two former subspecies of *Phystis simois* (6.4%, see above). Therefore, we propose treating *Episcada* Godman & Salvin, 1879 as a junior subjective synonym of *Ceratinia* Hübner, 1816.

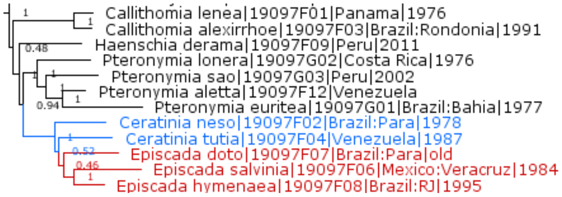

Fig. 50. *Ceratinia* (blue and red).

Family Hesperiidae Latreille, 1809

Phocides batabano (Lucas, 1857) and *Phocides bicolora* (Boddaert, 1783) are species distinct from *Phocides pigmalion* (Cramer, 1779)

In his key, Evans (1952) stated that uncus flanges in genitalia of continental subspecies of *Phocides pigmalion* (Cramer, 1779) (type locality Suriname) are as long as the uncus, but are shorter in the island subspecies, being similar to other *Phocides* Hübner, [1819] (type species *Phocides cruentus* Hübner, [1819], which is *Hesperia polybius* Fabricius, 1793). Consistently with this notable genitalic difference, the genomic tree partitions *P. pigmalion* into several groups (Fig. 51) rendering it paraphyletic with respect to *Phocides belus* Godman & Salvin, 1893 (type locality Mexico) and *Phocides lincea* (Herrich-Schäffer, 1869) (type locality not stated, probably the Guianas), and suggesting that *P. pigmalion* is a complex of several species. While the inclusion of *P. belus* in the *pigmalion* group is expected because

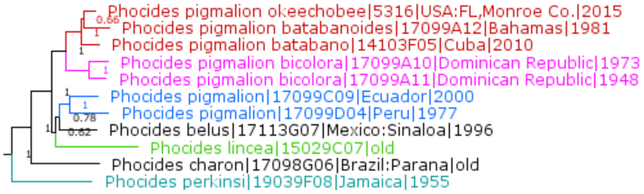

Fig. 51. *Phocides batabano* (red), *bicolora* (magenta), *pigmalion* (blue), *lincea* (green) and *perkinsi* (cyan).

Evans (1952) treated it as a subspecies of *P. pigmalion*, *P. lincea* was a surprise. Linked by Evans (1952) with *Phocides perkinsi* (Kaye, 1931) (type locality Jamaica) as its subspecies that was elevated to species only recently (Turner and Turland 2017), and placed at the end of Evans' key, *P. lincea* has not been associated with the *pigmalion* group before. Our genomic results definitively confirm *P. perkinsi* (Fig. 51 cyan) as a species-level taxon, because it is far removed from *P. lincea* (Fig. 51 green). Furthermore, due to genetic and genitalic differences, we reinstate *Phocides batabano* (Lucas, 1857) (type locality Cuba) and *Phocides bicolora* (Boddaert, 1783) (type locality not stated, likely Haiti) as species. The COI barcodes of *P. batabano* and *P. bicolora* differ by 2% (13 bp), and *P. pigmalion* (from Ecuador) and *P. batabano* by 3.3% (22 bp). Wing patterns agree with this partitioning of *P. pigmalion* as it was defined by Mielke (2005) previously, into at least three species: forewing hyaline spots absent (*P. batabano*), present but narrow and wings green-striped (*P. bicolora*), and present and broader, wings blue-striped (*P. pigmalion*). To accommodate this treatment, we revise species-subspecies combinations as: *Phocides batabano okeechobee* (Worthington, 1881) and *Phocides batabano batabanoides* (W. Holland, 1902).

Lobotractus mysie (Dyar, 1904) is a species distinct from *Lobotractus valeriana* (Plötz, 1881)

Correctly associating then "*Codatractus*" *mysie* (Dyar, 1904) with "*Codatractus*" *valeriana* (Plötz, 1881) as close relatives by visual inspection of photographs of their primary type specimens, Mielke and Warren (2004) concluded that "*valeriana* ... is clearly conspecific with *T. mysie*." We sequenced the lectotypes of *L. valeriana* and *L. mysie* and found that their COI barcodes differ by 2.1% (14 bp). Furthermore, the genomic tree of *L. valeriana* specimens from across the range revealed their partitioning into two clades, each clade with its type specimen: *mysie* from the US (Fig. 52 purple), and *valeriana* from various localities in Mexico (Fig. 52 blue). Fst/Gmin statistics for these clades were 0.41/0.04, suggesting that they represent distinct species (Cong et al. 2019a; Zhang et al. 2020). Therefore, we reinstate *Lobotractus mysie* (Dyar, 1904) as a species different from *Lobotractus valeriana* (Plötz, 1881), and consequently exclude *L. valeriana* from the US fauna. Curiously, Burns (1996) and (2001) reached similar conclusion as far as the US fauna is concerned, but likely for incorrect reasons.

Fig. 52. *Lobotractus valeriana* (blue), and *mysie* (purple).

Pyrgus centaureae dzekh Gorbunov, 2007 is a new subspecies for North America

The genomic tree of *Pyrgus centaureae* (Rambur, 1839) (type locality Sweden) taxa reveals that a specimen collected by J. L. Harry west of Galbraith Lake around Dalton Hwy mi. 274 in Alaska is not monophyletic with North American populations, but instead belongs to the Old World lineage (Fig. 53). Therefore, it is not *Pyrgus centaureae freija* (B. Warren, 1924) (type locality Labrador), but *Pyrgus centaureae dzekh* Gorbunov, 2007 (type locality Russia: Chukotka). Hence, we add this subspecies to North American fauna. The tree reveals partitioning of *P. centaureae* into two clades: mostly Palearctic lineage (Fig. 53 blue) and Nearctic lineage (Fig. 53 magenta). However, COI barcodes of specimens from different lineages (e.g. Sweden vs. USA: WV) differ by only 0.15% (1 bp) and Fst/Gmin statistics of the two lineages are 0.21/0.08, suggesting rather limited genetic differentiation and continuing gene exchange between them. On the basis of statistics from this small sample of specimens we sequenced, we cannot yet support the two lineages as distinct species, and the Nearctic assemblage of subspecies may be conceptualized as a semi-species instead.

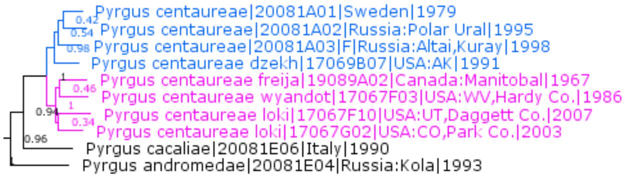

Fig. 53. *Pyrgus centaureae*: Palearctic lineage (blue) and Nearctic lineage (magenta).

Appia Evans, 1955 is a junior subjective synonym of *Pompeius* Evans, 1955

The monotypic genus *Appia* Evans, 1955 (type and the only species *Appia appia* Evans, 1955) originates within *Pompeius* Evans, 1955 (type species *Hesperia pompeius* Latreille, [1824]) being sister to *Pompeius amblyspila* (Mabille, 1897) and rendering *Pompeius* paraphyletic (Fig. 54). All of these species are genetically close, e.g., COI barcodes of the type species of *Appia* and *Pompeius* differ by only 5% (33 bp). Therefore, to restore the monophyly, we treat *Appia* Evans, 1955 as a junior subjective synonym of *Pompeius* Evans, 1955. Both taxa were proposed in the same work issued on the same date (Evans 1955), and using ICZN Code Art. 24, we give priority to *Pompeius*, because this name was used more frequently in the literature and the genus is not monotypic as *Appia*.

Wallengrenia Berg, 1897 is a subgenus of *Polites* Scudder, 1872

We sequenced all major phenotypically distinct taxa from the *Hylephila* Billberg, 1820 (type species *Papilio phyleus* Drury, 1773) group of genera (Fig. 54, rooted with *Hesperia* Fabricius, 1793). Confirming our previous assessment (Zhang et al. 2019c), we see that *Polites* Scudder, 1872 (type species *Hesperia peckius* W. Kirby, 1837) is genetically close to *Wallengrenia* Berg, 1897 (type species *Hesperia premnas* Wallengren, 1860) and is not separated from it by a long internal branch (Fig. 54). Both branches that are labeled "*Polites*" in Fig. 54 are longer than the branch between them and therefore assigning a taxonomic rank to them seems more appropriate than to the shorter branch between them. Moreover, COI barcodes of *W. otho* and *P. peckius* differ by 5.2% (34bp) further confirming their close relationship. Therefore, we propose treating *Wallengrenia* Berg, 1897 as a subgenus of *Polites* Scudder, 1872. The resulting classification of the *Hylephila* Billberg, 1820 (type species *Papilio phyleus* Drury, 1773) group is marked on the tree rooted with *Hesperia comma* (Linnaeus, 1758) (Fig. 54). *Hylephila* is sister to all others in the group. Then, there are two major levels in the tree. First, the genus *Polites* that includes *Wallengrenia* originates at about the same level as other three genera in the group: *Pompeius* Evans, 1955 (type species *Hesperia pompeius* Latreille, [1824]), *Hedone* Scudder, 1872 (type species *Hesperia brettus* Boisduval & Le Conte, [1837], a junior subjective synonym of *Thymelicus vibex* Geyer, 1832), and *Limochores* Scudder, 1872 (type species *Hesperia manataaqua* Scudder, 1863, which is a junior subjective synonym of *Hesperia origenes* Fabricius, 1793). This diversification event dates to about 15 Mya (Zhang et al. 2019d) and therefore corresponds to genera. Second, *Polites* diversifies into 4 prominent lineages: *Polites*, *Yvretta* Hemming, 1935 *Coa* Grishin, 2019 and *Wallengrenia* Berg, 1897. This more recent diversification (~10 Mya) corresponds to subgenera.

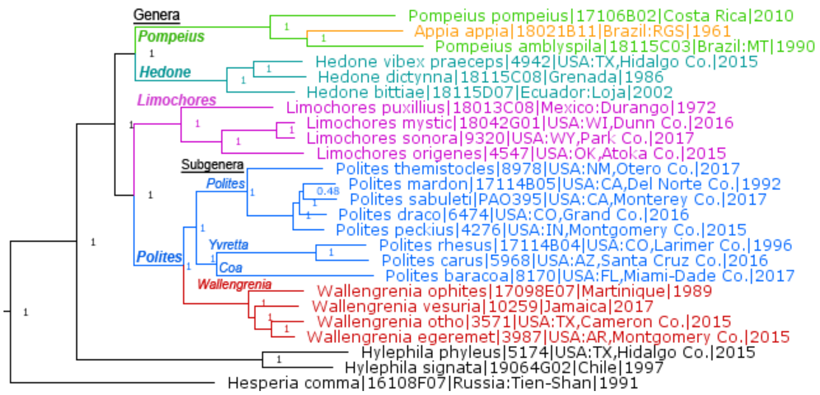

Fig. 54. Genera: *Pompeius* (green and orange), *Hedone* (cyan), *Limochores* (magenta) and *Polites* (blue and red) with subgenus *Wallengrenia* (red).

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