ORIGINAL ARTICLE

Genomics-based higher classification of the species-rich hairstreaks (Lepidoptera: Lycaenidae: Eumaeini)

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Abstract

We propose a higher classification of the lycaenid hairstreak tribe Eumaeini – one of the youngest and most species-rich butterfly tribes – based on autosome, Lepidopteran Z sex chromosome and mitochondrial protein-coding genes. The subtribe Neolycaenina Korb is a *synonym* of Callophryidina Tutt and subtribe Tmolusina Bálint is a *synonym* of Strephonotina K. Johnson, Austin, Le Crom, & Salazar. Proposed names are Rhammina Prieto & Busby, *new subtribe*; Timaetina Busby & Prieto, *new subtribe*; Atlidina Martins & Duarte, *new subtribe*; Evenina Faynel & Grishin, *new subtribe*; Jantheclina Robbins & Faynel, *new subtribe*; Paiwarriina Lamas & Robbins, *new subtribe*; Cupatheclina Lamas & Grishin, *new subtribe*; Parrhasiina Busby & Robbins, *new subtribe*; Ipideclina Martins & Grishin, *new subtribe*; and Trichonidina Duarte & Faynel, *new subtribe*. Phylogenetic results from the autosome and Z sex chromosome analyses are similar. Future analyses of datasets with hundreds of terminal taxa may be more practical time-wise by focussing on the smaller number of sex chromosome sequences (2.6% of nuclear protein-coding sequences). The phylogenetic classification and biological summaries for each subtribe suggest that a variety of factors affected Eumaeini diversification. About a dozen kinds of male secondary sexual organs with frequent evolutionary gains and losses occur in Atlidina, Evenina and Jantheclina (141 species combined). Females have been shown to use these organs to discriminate between conspecific and nonconspecific males, facilitating sympatry among close relatives. Eumaeina, Rhammina and Timaetina (140 species combined) are overwhelmingly montane with some evidence for a higher incidence of sympatric diversification. Seven Neotropical lineages in five subtribes invaded the temperate parts of the Nearctic Region with a diversification increase in the Callophryidina (262 species). North American *Satyrium* and *Callophrys* then invaded the Palearctic at least once each, with a major species-richness increase in *Satyrium*. The evolution of litter-feeding detritivores within Calycopidina (172 species) resulted in an increase in diversification rate compared with its flower-feeding sister lineage. Atlidina, Strephonotina, Parrhasiina and Strymonina (562 species combined) each contain a mixture of genera that specialize on one or two caterpillar food plant families and genera that are polyphagous. These would be appropriate subtribes to assess how the breadth of caterpillar food plants and the frequency of host shifts affected diversification.

INTRODUCTION

The tribe Eumaeini (Lepidoptera: Lycaenidae) is biologically notable for being a rapidly diversifying clade. With an estimated age of approximately 30 million years, it is one of the youngest recognized tribes of butterflies (Espeland et al., 2018; Valencia-Montoya et al., 2021). With about 1200 New World and 100+ Palearctic species (Robbins, 2004a; Weidenhoffer, Bozano, & Churkin, 2004), it is also one of the most species-rich with 7%–8% of the world's diurnal butterfly species (Lamas, 2008).

The higher classification of Eumaeini has been unsettled. Many proposed lineages based on morphology were poorly characterized (Robbins, 2004a), and those that were readily recognized, such as the *Atlides* Section and the *Lamprospilus* Section (later named Calycopidina), were based on homoplastic characters (Duarte & Robbins, 2010; Martins, Duarte, & Robbins, 2019a). A molecular analysis based upon 187 eumaeines recognized eight lineages, but no taxonomic changes were proposed (Valencia-Montoya et al., 2021). Congruence between morphological and molecular groupings was limited.

Eumaeines are evolutionarily notable for a variety of male secondary sexual organs that have been associated with diversification (Valencia-Montoya et al., 2021). For example, males of the Neotropical *Arcas cypria* (Geyer) have scent pads, scent patches, scent pouches and abdominal brush organs (Martins, Duarte, & Robbins, 2019b; Robbins, Martins, Busby, & Duarte, 2012). Over 90% of eumaeine species possess at least one male secondary sexual organ (Valencia-Montoya et al., 2021). The seven male secondary sexual organs in one clade (*Atlides* Section) were gained or lost within the lineage, often multiple times (Martins et al., 2019b). Females in the *Atlides* Section use these organs to identify conspecific males (Martins et al., 2019b). In this sense, the evolutionary gain of male secondary sexual organs might have facilitated sympatric diversification.

Eumaeines occur in a wide range of habitats. They inhabit areas with negligible rainfall, such as the Atacama Desert, to forests with 800 cm annual precipitation (Lamas, McInnis, Busby, & Robbins, 2021; Vargas & Duarte, 2016). They occur in areas up to 4000 m elevation (Bálint, Katona, & Kertész, 2019). They are widespread in the Palearctic, whereas in the New World, they occur in almost all areas with plants from the subarctic to the central valley of Chile (Robbins, 2004a). One lineage of Eumaeini (*Callophrys* Westwood and relatives) is distributed in the Palearctic, Nearctic and Neotropical Regions. It was suggested that geography played a central role in the early divergence of *Callophrys* and relatives (Valencia-Montoya et al., 2021).

Eumaeines are ecologically notable for the diverse array of plants eaten by its caterpillars (e.g., Beccaloni, Viloria, Hall, &

Robinson, 2008; Fiedler, 1991; Silva, Duarte, Diniz, & Morais, 2011). Species in genera such as *Rekoa* Kaye, *Strymon* Hübner, *Pseudolycaena* Wallengren and *Panthiades* Hübner feed on plants in more than a dozen families (e.g., Austin, Miller, & Miller, 2007; Janzen & Hallwachs, 2021; Monteiro, 1991; Robbins, 1991a; Robbins & Nicolay, 2002). The genus *Callophrys* is recorded from Gymnosperms, Monocotyledons and Dicotyledons (Ehrlich & Raven, 1965). Calycopidina are leaf-litter detritivores (Duarte & Robbins, 2010; Robbins et al., 2010), including seeds and mushrooms (Basset et al., 2018; Gripenberg et al., 2019; Nishida & Robbins, 2020). In contrast, the caterpillars of some genera specialize primarily on one plant family. Examples include *Eumaeus* Hübner on Zamiaceae (Robbins et al., 2021), *Evenus* Hübner on new leaves of Sapotaceae (Janzen & Hallwachs, 2021; Robbins, 2004a), a lineage of *Strymon* Hübner on Bromeliaceae (Robbins, 2010a), *Arawacus* Kaye on Solanaceae (Robbins, 2000) and *Thereus* Hübner on Loranthaceae (Heredia & Robbins, 2016). The concept that caterpillar food plant associations, such as specialization, generalization and the frequency of host shifts, shape diversification has been widely supported (e.g., Braga, Guimarães, Wheat, Nylin, & Janz, 2018; Fordyce, 2010; Hardy & Otto, 2014; Janz, 2011; Janz, Nylin, & Wahlberg, 2006; St Laurent, Carvalho, Earl, & Kawahara, 2021). However, without a classification to use as a foundation, patterns of Eumaeini caterpillar food plant utilization have not been assessed.

Mutualistic interactions between caterpillars and ants occur widely among Lycaenidae and have been implicated in rapid diversification in Old World lineages (i.e., Eastwood, Pierce, Kitching, & Hughes, 2006; Pierce, 1984). In Eumaeini, ants may provide enemy-free space for caterpillars (Kaminski, Freitas, & Oliveira, 2010; Kaminski, Rodrigues, & Freitas, 2012), which may be facultatively myrmecophilous (DeVries, 1990, 1991), but obligate mutualism is unrecorded. Whether myrmecophily is an important factor in the diversification of Eumaeini is largely unexplored.

Sequencing complete genomes of Eumaeini butterflies using museum specimens provides a prodigious quantity of phylogenetic data (Cong et al., 2016, 2017; Robbins et al., 2021). In this paper, we infer phylogenetic relationships using three datasets of protein-coding genes. The first dataset contains autosome sequences with 'diploid' inheritance. The second is the Lepidopteran Z sex chromosome genes with 'haplo-diploid' inheritance and the third contains mitochondrial loci with 'maternal' inheritance.

There are additional reasons for focussing on Z sex chromosome loci. Sex chromosome loci outperform autosomal ones in resolving some species trees (Corl & Ellegren, 2013). Sex linked genes have been implicated in reproductive isolation because they have a disproportionately large effect on hybrid sterility and viability (Coyne & Orr, 1989; Payseur, Presgraves, & Filatov, 2018; Presgraves, 2018).

There is an elevated differentiation of the sex chromosomes compared to autosomes among closely related taxa, as shown in the Z sex chromosome of *Heliconius* Kluk butterflies (e.g., Kronforst et al., 2013; Martin et al., 2013; Van Belleghem et al., 2018). These findings suggest that the sex chromosome might be useful for resolving phylogenetic relations in a rapidly diverging clade such as Eumaeini.

Here we propose a comprehensive subtribal classification based on a phylogenetic analysis of 202 eumaeine species representing almost every available generic name. Second, we summarize conspicuous biological and biogeographic characteristics in each subtribe. Integrating the proposed classification with the summary datasets, we then seek to identify taxa and characteristics that are associated with fast or slow diversification. The goal is to advance the hypothesis that a variety of factors are likely to have affected diversification of Eumaeini.

MATERIALS AND METHODS

Terminal taxa

The 266 Eumaeini generic names are listed in Data S1. Of these, two are suppressed by the International Commission on Zoological Nomenclature (ICZN), 16 are homonyms, three are incorrect original spellings, 12 are subsequent misspellings and 12 are nomina nuda. Another eight are objective synonyms (the same type species as another generic name), and nine have a type species that is a subjective synonym of a type species of another genus. We sequenced representatives of 202 of the remaining 204 generic names (Data S2). For each generic name, we sequenced a specimen of the type species or a closely related species based on morphological traits. We were unable to sequence specimens representing *Variegata* K. Johnson and *Semonina* Robbins. Representatives of four species in other tribes of Theclinae were used as outgroups. Taxonomic authors for generic names in the text below are given in Data S1.

Generation of sequence alignments

DNA was extracted and genomic libraries were prepared either from freshly collected specimens stored in RNAlater or from abdomens/legs of dry pinned specimens in museum collections according to established protocols (Li et al., 2019; Zhang, Cong, Shen, Brockmann, & Grishin, 2019). All libraries were sequenced for 150 bp from both ends targeting with ×5 to ×10 coverage using Illumina HiSeq X10.

We used the *Calycopis cecrops* (Fabricius) genome (Cong et al., 2016) as a reference to assemble genomic sequences. We focussed on coding sequences and aligned the sequencing reads of these samples with the amino acid sequences of exons in the *Calycopis* reference. For more distantly related samples, alignment based on protein sequences increases accuracy and sensitivity (Pearson, 2013), reducing the chance of aligning nonorthologous

reads or failure in alignment due to low similarity in the DNA sequences. Reference exons were filtered to remove short exons less than 12 amino acids or redundant exons with identity greater than 95%.

To remove adapter sequences and low-quality bases at the end of reads, NGS reads were processed by Trimmomatic–0.39 (Bolger, Lohse, & Usadel, 2014) with parameters *seedmismatches 3, palindromeClipThreshold 25* and *simpleClipThreshold 10*. We searched each reference exon against sequence reads of samples using DIAMOND (Buchfink, Xie, & Huson, 2015) with *parameters l 1, comp-based-stats 1, masking 0* and *evalue 0.01*. We computed the cumulative sequencing depth for each reference exon among all samples. We discarded the exons that have sequencing depth more than 2.5 times the median depth because they may arise from repeats in the genome.

From the DIAMOND results of exons in the *Calycopis* reference, we kept the reads that could be unambiguously mapped to one locus by both E-value (<$1e^{-5}$ × E-value for other loci) and sequence identity (> identity for other loci +10). We further filtered the alignments by requiring at least 75% coverage over the reads of each reference exon and sequence identity higher than that between the reference and the sample. Because we used a number of old, dry museum specimens that can be contaminated by DNA from fungi, bacteria and surrounding specimens, we applied the following two protocols to detect and remove contaminants.

First, we set the identity cutoff of mapped reads to each reference exon using the reference genome of *Calephelis nemesis* (W.H. Edwards) in Riodinidae (Cong et al., 2017). Lycaenidae samples are more closely related to *C. cecrops* than to Riodinidae (Espeland et al., 2018). We mapped *Calycopis* reference exons to the *C. nemesis* genome and calculated the identity between them as the identity cutoff for each exon. We kept sample reads with identity higher than the cutoff for each exon.

Second, for each 30 bp sliding window applied to the alignment between the *Calycopis* reference and the sample reads, we clustered the reads into groups of similar sequences using the following procedure. We ranked reads by their sequence identity to the reference exons from high to low. The first read initiated a cluster. Starting from the second read, a new read was compared to the first sequence of each cluster and assigned to the first cluster when the first sequence had no more than one mismatch from the current sequence. If a new read could not be assigned to existing clusters, a new cluster was initiated. For each cluster, we computed its size and the average number of mismatches to the reference exon, and we considered a cluster to be good if its size was at least half of the largest cluster size and the number of mismatches was no larger than the minimal mismatches among all clusters. If the number of good clusters was no more than 2 (diploid genome), we discarded the reads not included in the good clusters. Alignments of mitochondrial genes were constructed using a similar pipeline, except that we allowed only 1 good cluster per window because the mitogenome is haploid.

After this cleaning procedure, the dominant nucleotide (frequency > 0.6) at each position in the sequence alignment was used

to generate the exon sequences of a sample. The exon sequences were further translated to amino acid sequences and sequences of different exons of a protein were concatenated to obtain the protein sequence of a sample. Taxon information and sequencing data can be accessed through NCBI Bioproject ID PRJNA778531.

Construction of phylogenetic trees

We constructed phylogenetic trees for autosomes, Z chromosome and mitogenome, respectively. Gene content of the Lepidoptera Z chromosome is highly conserved (Fraïsse, Picard, & Vicoso, 2017), therefore we aligned *Calycopis cecrops* exons using TBLASTN (evalue 0.001, seg no) (Altschul, Gish, Miller, Myers, & Lipman, 1990) with reference to the *Heliconius melpomene* genome where the Z chromosome sequence is known. We identified *Calycopis cecrops* exons as Z-linked if their best TBLASTN hit was on the *Heliconius* Z chromosome. Genes with more than 80% exons mapped to the Z chromosome were considered Z-linked.

We removed positions from the alignments that are present in less than 40% of the samples, and the 13.87 million remaining positions in the alignment were used for phylogenetic analysis. Analysing almost 14 million bp poses practical difficulties, for which reason we generated 50 samples consisting of 100,000 codons each using a "random.sample" function (//docs.python.org/3/library/random.html). In this random sampling procedure, each autosomal position is expected to be represented in one of the 50 trees ($300,000 \times 50/13,870,000 = 1.08$). We used IQ-TREE (Nguyen, Schmidt, von Haeseler, & Minh, 2015) (version 1.6.10) with the GTR + GAMMA model to construct a maximum-likelihood phylogenetic tree for each of the 50 sampled alignments. The resulting trees were used to generate a consensus tree with sumtrees.py in the dendropy package (Sukumaran & Holder, 2010). A similar procedure was used to derive the Z chromosome-based phylogeny. Bootstrap support values may not be appropriate for large datasets (Lemoine et al., 2018). The large number of base pairs in this study almost always resulted in 100% values. Instead, we calculated the proportion of times that a node was present in each of the 50 trees. For mitogenomes, a maximum-likelihood tree was constructed from the 13 mitochondrial protein-coding genes with IQ-TREE. The best model was automatically selected by a Bayesian information criterion implemented in IQ-TREE. The ultrafast bootstrap (bb 1000) in IQ-TREE was used to estimate the confidence of the phylogenetic tree of mitogenomes.

Taxonomy

We partitioned Eumaeini into subtribes based on monophyly in analyses of both autosome and Z sex chromosome protein-coding DNA base pair sequences (Table 1). Among monophyletic lineages, we chose those that we considered to be most useful for communicating biological and biogeographic information. In the discussion, we note

other possible subtribal circumscriptions and give the reasons for the options that we chose. In a few cases, subtribes were not monophyletic in an analysis of mitochondrial sequences or in a previous molecular phylogeny (Valencia-Montoya et al., 2021). These results are summarized (Table 1), and we discuss possible reasons for them.

For each subtribe, we present a diagnosis that includes conspicuous morphological traits that are characteristic of that subtribe. To satisfy ICZN Code Articles 13.1 and 13.2, we differentiate each subtribe with molecular sequence synapomorphies (Table 2). Nomenclatural issues are addressed in Data S1, where we modify those currently recognized genera that were not monophyletic in the phylogenetic results based on autosomal, Z sex chromosome and mitochondrial sequences (with one exception noted below). Provisionally included genera are also listed in each subtribe account to facilitate communication.

The taxonomic composition of each subtribe is summarized. The number of included genera that we provisionally list in Data S1 is given. The number of species is presented as a range. The lower bound is the number of species with scientific names. The upper bound adds an estimate, based on our research, of the number of species in museum collections that lack scientific names.

Biological traits

We summarize the occurrence of male secondary sexual organs in each subtribe and note instances in which the morphology of these organs needs better documentation. Terminology for these organs follows Martins et al. (2019b).

All Eumaeini subtribes inhabit the American tropics, but we point out those subtribes that also occur elsewhere. We note subtribes that are primarily restricted to montane or wet habitats. We present information, when available, on the incidence of sympatry among closely related species. For genera that have not been revised, distributional and habitat information is primarily taken from large faunal works (e.g., Godman & Salvin, 1887; Draudt 1919–1920), augmented with information from the museum collections with which we work. Biogeographic region for each generic type species is recorded in Data S4.

We summarize patterns of caterpillar food plant specificity and myrmecophily for each subtribe. Published caterpillar food plant records are yet scanty. Misidentifications and a lack of vouchers have been problematic (i.e., Cajé et al., 2021). For these reasons, we cite original published records in which adults were illustrated or in which the identifications were verified by museum vouchers, such as the food plant records reported in Guagliumi (1965) and Zikán and Zikán (1968). We also add data from reared vouchers in public institutions that we examined and identified. These food plant records are intended to point out major patterns of specialization, generalization and host shifts, but they are not exhaustive. Obligate myrmecophily is unreported in Eumaeini, but some species are facultatively myrmecophilous (DeVries, 1990, 1991). Myrmecophily is not noted in most publications on food plants. When noted, the remarks are usually anecdotal.

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TABLE 1 Monophyly of subtribes from analyses of autosomes, Z sex chromosomes, mitochondrial DNA and a variety of DNA sequences (Valencia-Montoya et al., 2021)

Subtribe	Dataset autosomes	Dataset Z sex chromosome	Dataset mitochondria	Valencia-Montoya et al. (2021)
Eumaeina	monophyletic	monophyletic	monophyletic	*Thestius* does not cluster
Rhammina	monophyletic	monophyletic	*Balintus* does not cluster	*Balintus* does not cluster
Timaetina	monophyletic	monophyletic	*Busbiina* does not cluster	monophyletic
Atlidina	monophyletic	monophyletic	monophyletic	monophyletic
Evenina	monophyletic	monophyletic	monophyletic	monophyletic
Jantheclina	monophyletic	monophyletic	Paraphyletic with respect to Evenina	*Allosmaitia* and *Aveexcrenota* do not cluster
Paiwarriina	monophyletic	monophyletic	monophyletic	paraphyletic with *Thestius*
Cupatheclina	monophyletic	monophyletic	monophyletic	monophyletic
Parrhasiina	monophyletic	monophyletic	monophyletic	monophyletic
Ipideclina	monophyletic	monophyletic	monophyletic	not sequenced
Calycopidina	monophyletic	monophyletic	monophyletic	monophyletic
Strymonina	monophyletic	monophyletic	monophyletic	monophyletic
Strephonotina	monophyletic	monophyletic	monophyletic	monophyletic
Trichonidina	monophyletic	monophyletic	*Megathecla* does not cluster	monophyletic
Callophryidina	monophyletic	monophyletic	monophyletic	monophyletic

Note: The placements of six of 202 generic names – *Thestius*, *Busbiina*, *Balintus*, *Allosmaitia*, *Aveexcrenota* and *Megathecla* – are variable and account for virtually all the nonmonophyletic results at the subtribal level.

TABLE 2 Differentiating gene sequences for Eumaeini subtribes

Subtribe	Distinguishing genetic sequences
Eumaeina	cce.2894.13.5:G2312A, cce.117602.1.3:T503A, cce.117602.1.3:C514G, cce.1920.4.2:A1922G
Rhammina	cce.3413.13.1:T337A, cce.3413.13.1:G338T, cce.2784.3.6:A1508G, cce.3516.7.1:G692A
Timaetina	cce.4657.1.3:C1418A, cce.6475.2.1:A4115T, cce.6475.2.1:A4115T, cce.2595.1.2:G1441A
Atlidina	cce.6475.2.1:T3586A, cce4260.2.3:T859A, cce.694.7.7:G2008A, cce6475.2.1:G2620A
Evenina	cce.179145.1.1:A511C, cce.5263.2.1:T2410A, cce.302667.2.2:T2894C, cce.72976.7.4:A4403T
Jantheclina	cce.165326.13.1:C221A, cce957.9.4:A9254C, cce.621.3.3:T164C, cce.621.3.3:C142T
Paiwarriina	cce.13174.19.5:T139A, cce.3074.1.4:G226C, cce.13686.1.3:T231C, cce.483.7.2:A10C
Cupatheclina	cce.1467.11.2:A1126C, cce.2790.1.3:A67G, cce.5392.4.1:T200C, cce.3034.5.1:G97C
Parrhasiina	cce.1806.8.2:A344G, cce.993.29.4:A43C, cce.1546.4.5:T827A, cce.3911.8.16:C119T
Ipideclina	cce.557.5.1:A1330T, cce.1546.6.3:C158G, cce.557.5.1:A602C, cce2207.3.1:A712G and not cce.4319.10.3:943C, not cce.4260.2.3:2090G, not cce.7187.5.1:G862A, not cce4319.10.3:294A
Calycopidina	cce.312.2.3:A598G, cce.8343.11.4:C4475A, cce.2805.8.6:T109G, cce.2805.8.6:C110A
Strymonina	cce.1367.1.1:A437T, cce.2423.1.2:T4300A, cce.9657.10.14:C25A, cce.2070.8.17:G251C
Strephonotina	cce.663.6.2:A610G, cce.419.10.2:G433A, cce.2423.1.2:A2467C, cce.2041.8.30:A584G
Trichonidina	cce.1162.12.1:A3868C, cce.3869.2.3:A106C, cce.3869.2.3:A110G, cce.1162.12.1:G6708C
Callophryidina	cce.7057.16.1:A193C, cce.303173.8.11:T185C, cce.7057.16.1:A310G, cce.6582.6.9:C2185A

Note: Character states are given as abbreviations, such as cce.2894.13.5:G2312A. The "cce" refers to the *Calycopis cecrops* reference genome (Cong et al., 2016). To satisfy ICZN code articles 13.1 and 13.2, the character "cce.2894.13.5:G2312A" in words is "position 2312 of gene 13 and exon 5 in scaffold 2894 in the annotated *Calycopis cecrops* genome has nucleotide G in the coding strand (5' to 3' direction), which is differentiated from other lineages, which have nucleotide A in the coding strand".

We discuss diversification in each subtribe by briefly assessing the evolution of morphological, biogeographic and ecological traits using the phylogenetic results as a framework. The dataset in this paper was selected for taxonomic reasons, not with the purpose of doing a quantitative analysis of diversification. Rather, as noted, the intention is to point those subtribes where different factors were likely to have influenced diversification.

Museum acronyms

CPAC (Brazil, Distrito Federal, Planaltina, EMBRAPA, Centro de Pesquisas Agropecuárias do Cerrado); *DZUP* (Brazil, Paraná, Curitiba, Universidade Federal do Paraná, Coleção de Entomologia Pe. Jesus Santiago Moure); *FIOC* (Brazil, Rio de Janeiro, Rio de Janeiro, Fundação Instituto Oswaldo Cruz); *MCZ* (USA, Massachusetts, Harvard University, Museum of Comparative Zoology); *MGCL* (USA, Florida, Gainesville, University of Florida, Florida Museum of Natural History, McGuire Center for Lepidoptera and Biodiversity); *MIZA* (Venezuela, Maracay, Museo del Instituto de Zoología Agrícola); *MNCR* (Costa Rica, San Jose, Museo Nacional de Costa Rica); *TAMU* (USA, Texas, College Station, Texas A & M University); *UCRC* (USA, California, Riverside, University of California, Department of Entomology,

Entomology Research Museum); *USNM* (USA, Washington D.C., Smithsonian Institution, National Museum of Natural History); and *UWIZM* (Trinidad and Tobago, St. Augustine, University of the West Indies Zoological Museum).

RESULTS

Phylogenetic analyses

We illustrate maximum likelihood phylogenetic trees for 202 genera (sequenced specimens listed in Data S2) based on analyses of autosomal (Figure 1), Z sex chromosome (Figure 2) and mitochondrial (Figure 3) protein-coding sequences, with relative node support values
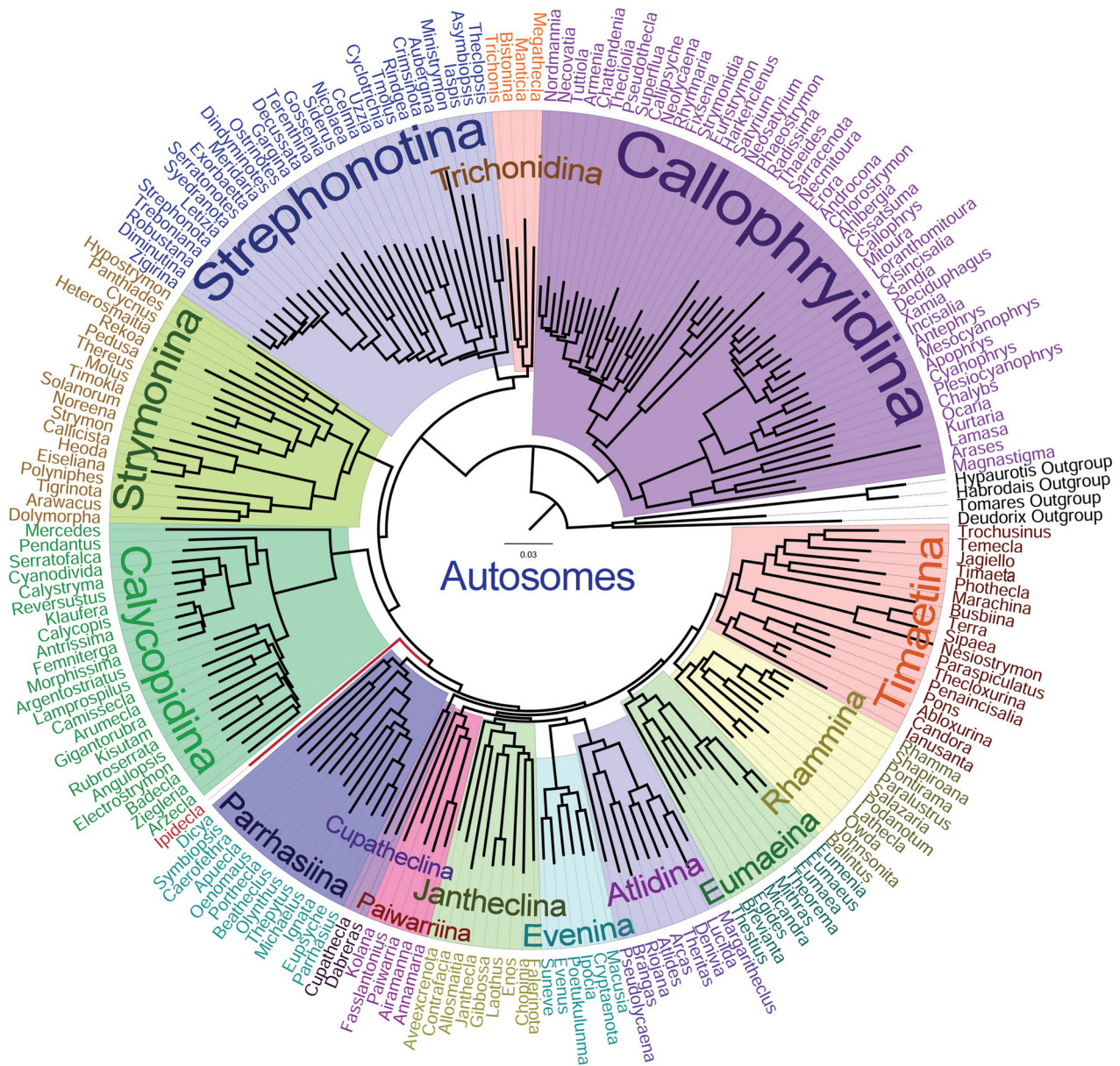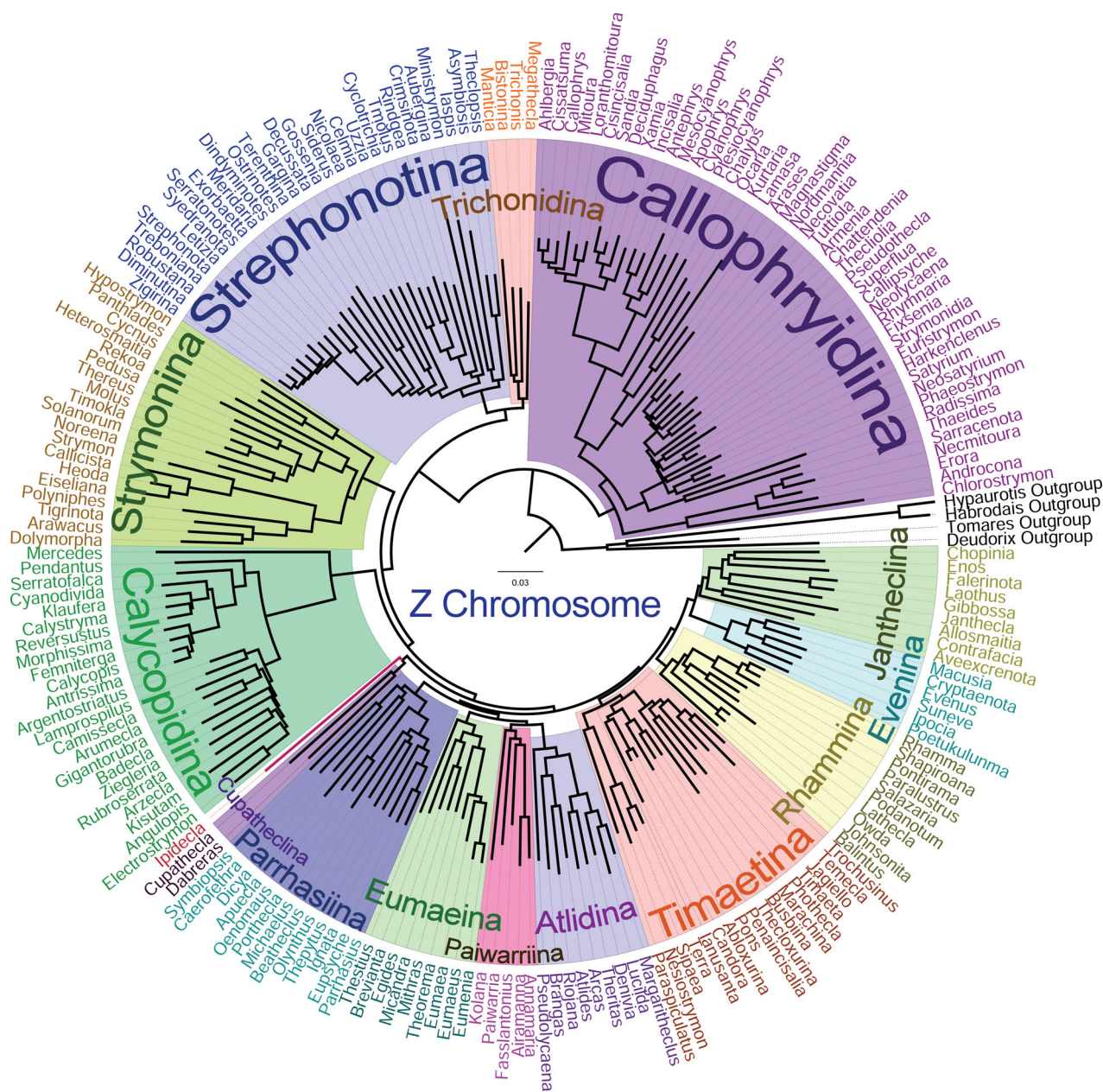

FIGURE 1 Maximum likelihood phylogenetic relationships of Eumaeini based on 13.5 million autosome protein-coding base pairs. Ipideclina contains only the genus *Ipidecla* (red)

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in a more traditional format in Data S3. Sequencing resulted in 13.87 million autosomal bp and 368 thousand Z sex chromosome bp (2.6% of the sequenced nuclear genome). The 13 mitochondrial protein-coding genes were composed of 11,130 bp (less than 0.1% of the nuclear genome).

The fifteen subtribes that we recognize are monophyletic in analyses of both the autosome and Z sex chromosome sequences. Eleven subtribes are monophyletic in the analysis of mitochondrial sequences, and the other four subtribes are monophyletic except for one genus in each that does not cluster or one case of paraphyly (Table 1). Ten subtribes are monophyletic in the illustrated tree in Valencia-Montoya et al. (2021), one subtribe was not sequenced and the other four subtribes are monophyletic except for one or two genera in each that do

not cluster (Table 1). Topology of the autosome and Z sex chromosome trees (Figures 1 and 2) is highly congruent from Callophryidina (purple upper right) to Calycopidina (green lower left). Relationships among Eumaeina + Timaetina + Rhammina + Atlidina + Evenina + Jantheclina + Paiwarriina + Cupatheclina + Parrhasiina differ, and some lineages have short branch lengths (little genomic change). Although topology of the mitochondria tree (Figure 3) is generally similar to those of the autosome and Z sex chromosome trees, there are many differences. Biogeographic region for each of the 202 generic type species is recorded in Data S4. In sum, 169 generic type species are Neotropical, 18 are primarily Nearctic and 15 are Palearctic.

FIGURE 2 Maximum likelihood phylogenetic relationships of Eumaeini based on 368 thousand Z sex chromosome protein-coding base pairs. Ipideclina contains only the *Ipidecla* (red)
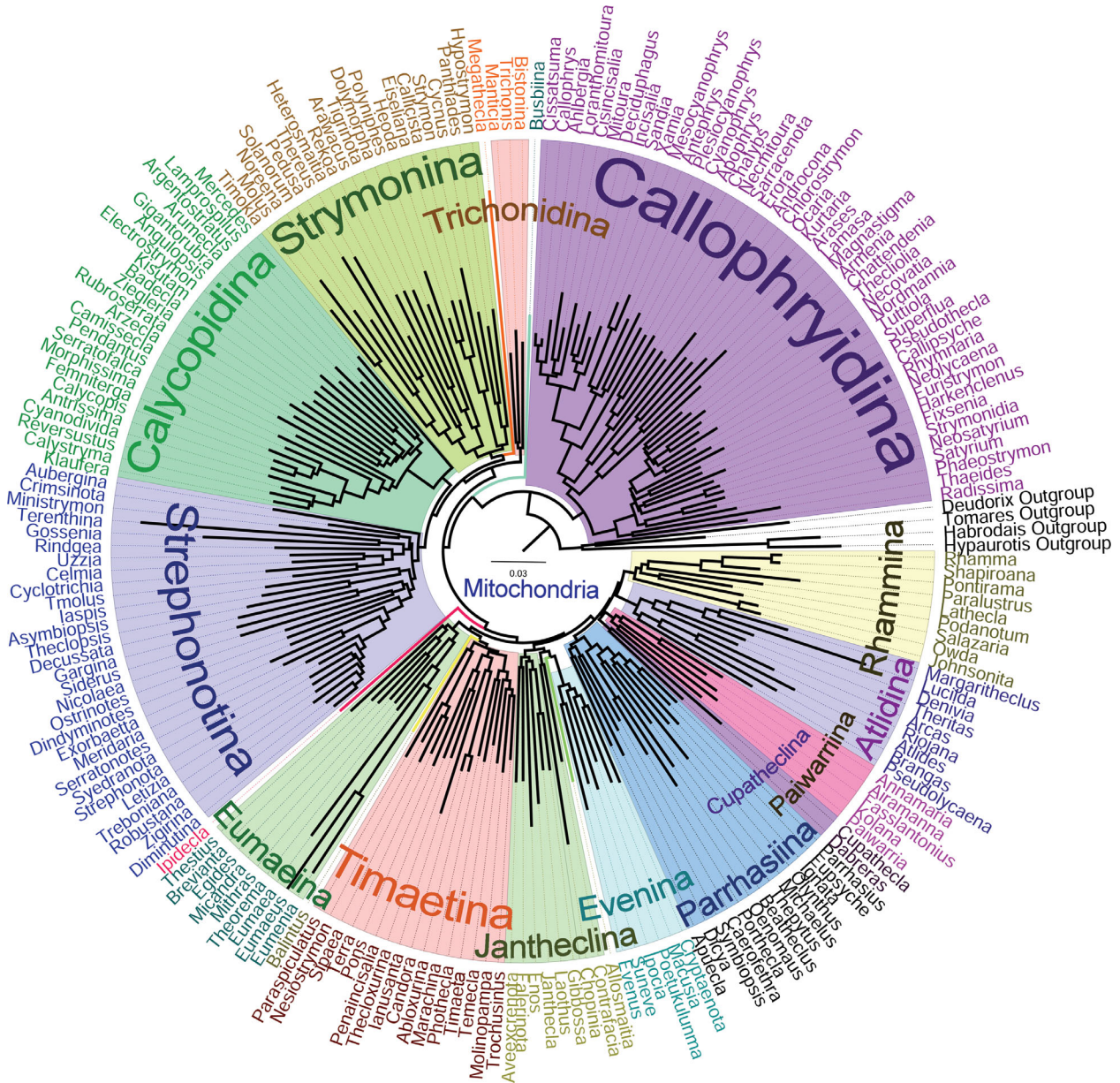
FIGURE 3 Maximum likelihood phylogenetic relationships of Eumaeini based on 11,130 mitochondrial protein-coding base pairs. Ipideclina contains only the genus *Ipidecla* (red). The subtribes Timaetina, Rhammina, Jantheclina, and Trichonidina are not monophyletic

Currently recognized genera that were not monophyletic in the autosome, Z sex chromosome and mitochondria trees (with the exception of *Enos*, discussed below) were modified. For example, the former characterization of *Thepytus* (Robbins, Busby, & Duarte, 2010) was not monophyletic in the autosome and Z chromosome analyses, thus we provisionally split it into *Thepytus* and *Beatheclus*. As another example, *Timaeta* was paraphyletic in terms of *Temecla* (Robbins & Busby, 2008) in all analyses, so we combined them. We tried to minimize the number of changes, but the large genera *Calycopis* (Calycopidina) and *Nicolaea* (Strephonotina) as previously recognized were not monophyletic, resulting in the provisional listing of more genera. Phylogenetic analyses of species within each subtribe, especially Calycopidina and Strephonotina, will be needed to propose a more stable generic classification.

Systematics and biology

EUMAEINA DOUBLEDAY

Included Genera. Eumaeus Hübner, *Theorema* Hewitson, *Mithras* Hübner, *Micandra* Staudinger, *Brevianta* K. Johnson, Kruse & Kroenlein, *Thestius* Hübner.

Diagnosis

Eumaeina here is equivalent to the *Eumaeus* Section of Robbins (2004-b), which had been characterized primarily by brush organ traits, plus

FIGURE 4 Legend on next page.

Micandra, *Brevianta* and *Thestius* sensu stricto, but without *Paiwarria* and *Paraspiculatus*. A possible morphological synapomorphy for Eumaeina is the poor development of forewing veins mdc and ldc, as noted for *Eumaeus* by Bates (1861). Subsequently, this character has been used rarely, probably because development of these forewing veins is variable and difficult to score. Eumaeina is monophyletic in the analyses of autosomal, Z sex chromosome and mitochondrial DNA sequences, but not in Valencia-Montoya et al. (2021) as *Thestius s.s.* was embedded in the sister lineage to Eumaeina (Table 1). Eumaeina is distinguished from other subtribes based on DNA sequence data only (Table 2).

Male secondary sexual organs

Semi-hemispherical abdominal brush organs are unique to species of *Eumaeus*, *Theorema* and *Mithras* (Robbins et al., 2021). Piliform scales on the dorsal hindwing of male *Eumaeus childrenae* (Grey) are absent in females and may be androconia (Robbins et al., 2021). A dorsal forewing scent pad occurs in all species of *Mithras*, *Micandra* and *Brevianta*, but in some species of the latter two, there are additional complex androconial structures that have not been detailed morphologically. A dorsal hindwing scent patch occurs in *Thestius*, but is often absent in small individuals.

Biogeography, habitat and larval food plants

The genera of Eumaeina occur in most of the forested Neotropics (Data S4), including the northern Antilles. Some are primarily lowland (*Mithras*, *Theorema*, *Thestius*) whereas others are primarily montane (*Micandra*, *Brevianta*). *Eumaeus* is a caterpillar food plant specialist on Zamiaceae (Robbins et al., 2021), but the other genera are recorded from Fabaceae and a variety of other Angiosperm families (Robbins et al., 2021). Caterpillars of *Micandra* are myrmecophilous whereas those of *Eumaeus* are not (DeVries, 1991).

Diversification

Subtribe Eumaeina consists of six genera containing 34–38 species. No more than two species of the primarily lowland genera *Theorema*, *Mithras*, *Eumaeus* and *Thestius s.s.* occur at a locality (13 species combined). In contrast, the incidence of sympatry is higher in the primarily montane *Micandra* and *Brevianta* (25 species combined). For example, five *Micandra* species are sympatric at 1600–1800 m elevation in eastern Ecuador, and five *Brevianta* species are sympatric in the mountains of Panama (unpublished data). Although the switch to eating cycads

in the aposematically coloured *Eumaeus* (Figure 4a) increased diversification rate, subsequent amplified rates of gene changes were arguably more biologically significant (Robbins et al., 2021).

RHAMMINA PRIETO & BUSBY, NEW SUBTRIBE

http://zoobank.org/ urn:lsid:zoobank.org:act:C9735B7D-DEF7-480C-8D10-46B0F53D2532.

Type Genus. Rhamma K. Johnson.

Other Included Genera. Balintus D'Abrera, *Johnsonita* Salazar & Constantino, *Lathecla* Robbins, *Podanotum* Torres & K. Johnson, *Salazaria* D'Abrera & Bálint.

Diagnosis

Rhammina represents part of the *Micandra* Section of Robbins (2004b) with the addition of *Lathecla* (Robbins & Busby, 2015). A "fan-shaped" signa of the female genitalia occurs in all genera other than *Salazaria*, but also occurs in some species of *Micandra* (Eumaeina), in some genera of Timaetina, and in most genera of Calycopidina, where this structure was detailed morphologically (Duarte & Robbins, 2010). Rhammina is monophyletic in the analyses of autosome and Z sex chromosome sequences. Except for the monotypic *Balintus*, it is also monophyletic in the mitochondrial tree and in the results in Valencia-Montoya et al. (2021) (Table 1). Rhammina is distinguished from other subtribes based on DNA sequence data (Table 2).

Male secondary sexual organs

Rhammina contains a variety of male secondary sexual organs on the wings. Unique organs occur on the wings of *Lathecla* and *Johnsonita* (Bálint et al., 2021; Robbins & Busby, 2015). *Podanotum* lacks male secondary sexual organs (Busby, Faynel, Moser, & Robbins, 2017). Scent pads are universal in *Rhamma*, the most species-rich genus, except for species such as *R. anosma* (Draudt). Abdominal brush organs are unrecorded in Rhammina.

Biogeography, habitat and larval food plants

The genera of Rhammina are Andean endemics (Figure 4b) except for *Lathecla*, which occurs from Mexico to southern Brazil in lowland and montane habitats (Robbins & Busby, 2015). *Johnsonita* was reported from

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FIGURE 4 (a) warningly coloured adult of *Eumaeus atala* (Poey) (Eumaeina); (b),(c) Andean *Rhamma* (Rhammina) (top) and *Penaincisalia* (Timaetina), representative montane species; (d),(e) *Arcas cypria* (Geyer) (Atlidina) dorsal forewing (left) with a discal cell brown scent pad and a grey scent patch, and ventral hindwing with scent pouch opening; (f),(g) *Evenus regalis* (Cramer) (left) and *E. temathea* (Hewitson) (Evenina). The latter resembles the wing pattern of satyrine Nymphalidae; (h),(i) *Annamaria rhaptissima* (K. Johnson) (Paiwarriina) with male (left) and female sexually dimorphic ventral wing patterns; (j) *Dabreras teucria* with a scent patch on the dorsal hindwing costa (Cupatheclina); (k) *Oenomaus ortygnus* (Cramer) (Parrhasiina), a commercial crop pest of Annonaceae. Scale refers to set specimens

Panama (Draudt, 1919–1920), but there are no vouchers. A photograph taken in Ecuador was incorrectly attributed to Panama (Bálint et al., 2021). Efforts to sample high elevation habitats more broadly have improved the ability to assess intraspecific geographic variation in *Rhamma* (Prieto, Núñez, & Hausmann, 2018; Prieto & Vargas, 2016). *Rhamma* has been reared from Fabaceae and Melastomataceae (Arregui & Onore, 1989; Callaghan, 2008). There are no records of myrmecophily.

Diversification

The subtribe Rhammina consists of 6 genera containing 58–74 species. With the exception of *Lathecla*, this subtribe is endemic to the Andes.

TIMAETINA BUSBY & PRIETO, NEW SUBTRIBE

http://zoobank.org/ urn:lsid:zoobank.org:act:C5D9818A-ABA9-4891-926A-1ADD3D304ACE

Type Genus. *Timaeta* K. Johnson, Kruse & Kroenlein.

Other Included Genera. *Penaincisalia* K. Johnson, *Busbiina* Robbins, *Phothecla* Robbins, *Marachina* Robbins, *Nesiostrymon* Clench, *Paraspiculatus* K. Johnson & Constantino.

Diagnosis

Timaetina represents part of the *Micandra* Section of Robbins (2004b) with the addition of *Marachina* and *Paraspiculatus*. "Fan-shaped" signa (see Rhammina) are present in all genera except *Paraspiculatus* and some *Penaincisalia* (Busby et al., 2017; Prieto, Bálint, Boyer, & Micó, 2008; Prieto, Grishin, Hausmann, & Lorenc-Brudecka, 2016). Timaetina is monophyletic in the analyses of autosome and Z sex chromosome sequences and in the results of Valencia-Montoya et al. (2021). It was monophyletic in the mitochondria tree except for *Busbiina* (Table 1). Timaetina is distinguished from other subtribes based on DNA sequence data only (Table 2).

Male secondary sexual organs

A variety of male secondary sexual organs on the wings occur in this subtribe. Although scent pads are a characteristic of most species of *Penaincisalia*, unique organs occur in *Timaeta* and *Phothecla* (Robbins & Busby, 2008; Robbins & Duarte, 2004). The male secondary sexual organs on the forewings of *Marachina* need better documentation. *Paraspiculatus* lacks male secondary sexual organs (Busby et al., 2017). Abdominal brush organs are not reported in Timaetina.

Biogeography, habitat and larval food plants

The genera of Timaetina are primarily montane. The species-rich *Penaincisalia* (Figure 4c) is endemic to the Andes, where species may

occur in habitats at 4000 m elevation (Bálint et al., 2019). *Timaeta* was reared from Melastomataceae (Badenes-Pérez, Alfaro-Alpízar, & Johnson, 2010) under the generic name *Temecla*, but there are no records for myrmecophily.

Diversification

The subtribe Timaetina consists of seven genera containing 102–128 species, with the vast majority of the species with a montane distribution. Phylogenetic revisions of *Timaeta* and *Paraspiculatus* showed a high incidence of sympatric diversification (Busby et al., 2017; Robbins & Busby, 2008).

ATLIDINA MARTINS & DUARTE, NEW SUBTRIBE

http://zoobank.org/ lsid:zoobank.org:act:D67CA146-F37A-46FB-8DDB-2E754E0F57EF

Type Genus. *Atlides* Hübner.

Other Included Genera. *Brangas* Hübner, *Denivia* K. Johnson, *Arcas* Swainson, *Theritas* Hübner, *Pseudolycaena* Wallengren.

Diagnosis

Atlidina represents the *Atlides* Section of Martins et al. (2019a, 2019b) with *Dabreras* transferred to Cupatheclina. A phylogeny based on morphology (Martins et al., 2019a, 2019b) differed from the phylogeny in this paper primarily by the location of the root. Notable morphological features of Atlidina are homoplastic. A cleft hindwing anal lobe (Godman & Salvin, 1887; illustrated in Martins et al., 2019a) occurs in all Atlidina (Martins et al., 2019a, 2019b), but also in *Dabreras* (Cupatheclina) and some species of *Panthiades* (Strymonina). A process of the male genitalia vinculum lying under the brush organs occurs in all Atlidina that possess brush organs, but also in *Evenus* (Evenina), *Aveexcrenota* (Jantheclina) and *Dabreras* (Cupatheclina). Atlidina is monophyletic in analyses of autosome, Z sex chromosome and mitochondrial sequences and is congruent with results presented by Valencia-Montoya et al. (2021). Atlidina is distinguished from other subtribes based on DNA sequence data only (Table 2).

Male secondary sexual organs

Martins et al. (2019a, 2019b) documented seven different kinds of male secondary sexual organs in Atlidina (Figure 4d,e). They found that evolutionary gains of these organs occurred primarily when species were sympatric with their sister lineage and their loss when species were not sympatric with their sister lineage. Many males in this subtribe produce scents that are perceptible to people (Robbins et al., 2012).

Biogeography, habitat and larval food plants

Atlidina is a widespread Neotropical subtribe with one species in temperate areas of North America (*Atlides halesus* [Cramer], Data S4) and one in the subtropical areas in South America (*Atlides thargelia* [Burmeister]). Although primarily denizens of wet forest, a few species, such as *Atlides gaumeri* (Godman) and *Pseudolycaena dorcas* (H. H. Druce), occur most frequently in drier, sparsely-forested habitats. Caterpillars of *Denivia* are generalists on Bombacaceae, Chrysobalanaceae, Euphorbiaceae, Fabaceae, Lecythidaceae, Meliaceae and Sterculiaceae (Müller, 1878; Guppy, 1904; Hoffmann, 1930, 1933; Monte, 1934; Kirkpatrick, 1954; Zikán, 1956; Guagliumi, 1967; Muyshondt, 1973; Robbins & Aiello, 1982; reared adults in MIZA and USNM). Similarly, the larvae of *Pseudolycaena* are generalists on Anacardiaceae, Celastraceae, Combretaceae, Myrtaceae, Rosaceae, Ulmaceae, Urticaceae, Annonaceae, Fabaceae, Malpighiaceae, Meliaceae, Euphorbiaceae and Sapotaceae (summarized in Austin et al., 2007). In contrast, the caterpillars of *Atlides* and *Brangas* specialize on mistletoe plant families Loranthaceae and Viscaceae (Sepp, 1829–1852; Hoffmann, 1937; Zikán, 1956; Whittaker, 1984; Janzen & Hallwachs, 2021; reared vouchers in USNM). Myrmecophily does not occur in *Denivia* and *Pseudolycaena* (DeVries, 1990, 1991).

Diversification

This subtribe consists of six genera containing 74–81 species. Atlidina is likely an appropriate subtribe for investigating the evolution of male secondary sexual organs because of the variety of these organs and the frequency with which they were gained and lost (Martins et al., 2019a, 2019b).

EVENINA FAYNEL & GRISHIN, NEW SUBTRIBE

http://zoobank.org/ urn:lsid:zoobank.org:act:276DA02D-7331-4EC1-BE6A-7F488329DA2F

Type Genus. *Evenus* Hübner.

Diagnosis

Evenina contains the relatively autapomorphic genus *Evenus*. Upturned scales on the enlarged frons of males (Godman & Salvin, 1887; Robbins & Busby, 2009) occur in most species, but also in species of *Janthecla* and *Laothus* (Jantheclina). "Longitudinal" androconia on the dorsal forewing costa (Godman & Salvin, 1887; Neild & Bálint, 2014) occur in most species of *Evenus*, but also in some *Laothus* (Jantheclina). Evenina is monophyletic and strongly supported in all molecular analyses (Table 1), but its phylogenetic placement is inconsistent. It is the phylogenetic sister of Atlidina in the autosomal tree, of Jantheclina in the Z sex chromosome tree, of *Allosmaitia* (Jantheclina) in the mitochondria tree, and of part of the Jantheclina in

Valencia-Montoya et al. (2021). Evenina is distinguished from other subtribes based on DNA sequence data only (Table 2).

Male secondary sexual organs

As noted, upturned scales on an enlarged frons of the male head occur in some species of *Evenus* as well as *Janthecla* and *Laothus* (Jantheclina) and are usually associated with short "longitudinal" scales along the forewing costa. Some *Evenus*, such as *E. coronata* (Hewitson), also have androconia on the costa of the dorsal hindwing, on the inner margin of the ventral forewing, and at the base of the cubital ventral forewing vein. *Evenus regalis* (Cramer) lacks androconia on the wings. Paired dorsal brush organs are associated with a process of the vinculum, much as they are in the Atlidina and in *Aveexcrenota* (Jantheclina).

Biogeography, habitat, and larval food plants

Evenus is Neotropical with one species in the subtropical areas in South America (*Evenus latreillii* (Hewitson)). Most species occur in lowland wet forest, but the *E. coronata* clade (three species) is strictly montane. Caterpillars of *Evenus* eat the new growth of Sapotaceae (summarized in Robbins, 2004a; Sermeño, Robbins, Lamas, & Gámez, 2013). Flowering and new growth for some Sapotaceae trees is seasonal, so that there appears to be one adult brood a year (Janzen & Hallwachs, 2021; Schultze-Rhonhof, 1938; Terra-Araújo, Faria, Ribeiro, & Swenson, 2012). There are no records of myrmecophily in the Evenina.

Diversification

This subtribe currently consists of one genus and 16–18 species. The montane *E. coronata* and relatives appear to be elevationally parapatric with the lowland *E. regalis*. The former has at least four kinds of male secondary sexual organs on the head and wings whereas the latter lacks these organs. For this reason, Godman and Salvin (1887) did not consider them to be closely related. *Evenus* adults are large, conspicuous blue and green butterflies (Figure 4f). In three species in one lineage of *Evenus*, however, the females resemble brown satyrine butterflies (Nymphalidae) (Figure 4g). The only possible difference other than wing pattern in this "satyrine resembling" lineage is that adults do not seem to be seasonally single-brooded.

JANTHECLINA ROBBINS & FAYNEL, NEW SUBTRIBE

http://zoobank.org/ urn:lsid:zoobank.org:act:CC454EE6-F45B-4C6B-A708-7B1B66C3EEF8.

Type Genus. *Janthecla* Robbins & Venables.

Other Included Genera. *Aveexcrenota* Salazar & K. Johnson; *Contrafacia* K. Johnson; *Allosmaitia* Clench; *Enos* K. Johnson, Kruse & Kroenlein; *Laothus* K. Johnson, Kruse & Kroenlein.

HAIRSTREAK SUBTRIBE CLASSIFICATION

Systematic
Entomology

Royal
Entomological
Society

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Diagnosis

Jantheclina is equivalent to the *Allosmaitia* Section of Robbins (2004b), which was characterized by overall genitalic similarity, with the addition of *Contrafacia*, *Enos* and *Aveexcrenota*. The homoplastic occurrence of male secondary sexual organs is noted in the accounts of Atlidina and Evenina. Jantheclina is monophyletic in analyses of autosome and Z sex chromosome sequences, but paraphyletic with respect to Evenina in the mitochondria tree. It is monophyletic in Valencia-Montoya et al. (2021) except for *Allosmaitia* and *Aveexcrenota*. Jantheclina are distinguished from other subtribes based on DNA sequence data only (Table 2).

Male secondary sexual organs

Male secondary sexual organs in Jantheclina may be located on the head, legs, forewings, hindwings or abdomen. According to these phylogenetic results, each of these organs was gained or lost at least once in the subtribe. The following is a brief overview of some of the diversity of male secondary sexual organs in Jantheclina. Upturned scales on an enlarged frons of the male head occur in some species of *Janthecla* and *Laothus* (as well as in the Evenina) and are often associated with short "longitudinal" scales along the forewing costa, as already noted. *Laothus gibberosa* (Hewitson) has a unique forewing costal "hump" associated with these scales (Draudt, 1919–1920). A "scale brush" is located on the enlarged foreleg femur of one species of *Janthecla* (Robbins & Venables, 1991). Forewing scent pads occur in *Allosmaitia* and many species of *Janthecla*. An additional dorsal forewing scent patch also occurs in *Allosmaitia* and *Enos myrtusa* (Hewitson) in which the androconia are interspersed with regular wing scales (Robbins, 1987). Varied androconial structures occur on the costa of the dorsal hindwing in some species *Janthecla*, *Laothus* and *Allosmaitia*. In some *Enos*, the hindwing costal area lacks scales. The inner margin of the ventral forewings may have a scent patch, sometimes accompanied by an enlarged hindwing costa, in *Laothus*, *Enos* and *Janthecla*, which is superficially similar to structures in *Strephonota* (Strephonotina). Brush organs in *Aveexcrenota* resemble those of Atlidina and Evenina. Brush organs in *Contrafacia* resemble those in *Kolana* (Paiwarriina) and some genera of Strymonina (Robbins, 1991a). Some species such as *Janthecla leea* Venables & Robbins and *Laothus viridicans* (C. Felder & R. Felder) lack male secondary sexual organs.

Biogeography, habitat and larval food plants

The genera of Jantheclina are strictly Neotropical (Data S4). Two genera appear to be food plant specialists as larvae: *Laothus* specialize on Asteraceae (Hoffmann, 1935, 1937, Zikán, 1956; vouchers in USNM), whereas *Allosmaitia* feed on Malpighiaceae (Armas, 2004; Dewitz, 1879; Gundlach, 1881; Kaminski & Freitas, 2010; Silva et al., 2011; Silva, Duarte, Araújo, & Morais, 2014). Larvae of *Laothus* and *Allosmaitia* are not myrmecophilous (DeVries, 1990, 1991; Kaminski & Freitas, 2010).

Diversification

Jantheclina consists of six genera containing 38–39 species. The phylogenetically inconsistent occurrence of male secondary sexual organs, as noted, suggests a high incidence of evolutionary gains and losses.

PAIWARRIINA LAMAS & ROBBINS, NEW SUBTRIBE

http://zoobank.org/ urn:lsid:zoobank.org:act:02D4B672-34AA-4DC2-A3CC-8471458B1A1D

Type Genus. *Paiwarria* Kaye.

Other Included Genera. *Annamaria* D'Abrera & Bálint, *Fasslantonius* Bálint & Salazar, *Kolana* Robbins.

Diagnosis

Paiwarriina consists of the *Kolana* and *Paiwarria* clades. Some species in each lineage have a conspicuous oval scent pad at the distal end of the forewing discal cell, which may be a morphological synapomorphy for the subtribe, albeit superficially similar scent pads occur elsewhere, such as *Arcas splendor* (H. H. Druce) (Atlidina) (Robbins et al., 2012). Paiwarriina is monophyletic in analyses of autosome, Z sex chromosome and mitochondrial sequences (Table 1), but is paraphyletic in Valencia-Montoya et al. (2021) in terms of *Thestius* (Eumaeina). Paiwarriina is distinguished from other subtribes based on DNA sequence data only (Table 2).

Male secondary sexual organs

All described species have a dorsal forewing scent pad. Males of *Annamaria* have up to four male secondary sexual organs on the wings (Robbins & Lamas, 2008, as *Lamasina*). All have a dorsal forewing scent pad and a scent patch, which is often covered by regular wing scales. Some males have a patch of presumed androconia at the tornus of the dorsal forewing and/or a black androconial patch at the base of the ventral forewing. Paired dorsal brush organs abut a process of the male genitalia dorsal vinculum in all genera except *Annamaria*. In *Paiwarria* and *Fasslantonius*, these structures are similar to those in *Radissima* (Callophryidina). In *Kolana*, they are similar to those in *Contrafacia* (Jantheclina), *Thereus*, *Rekoa*, *Heterosmaitia* and *Arawacus* (Strymonina).

Biogeography, habitat and larval food plants

The genera of Paiwarriina are Neotropical with most species in wet forest. A few, such as *K. buccina* (H. H. Druce) and *P. aphaca* (Hewitson), may occur in drier forested habitats. Caterpillar food plant

records for *Kolana* are Araliaceae, Connaraceae, Erythroxylaceae, Lythraceae, Malpighiaceae, Melastomataceae, Ochnaceae and Vochysiaceae (Silva et al., 2011, 2014; voucher in MNCR). *Paiwarria* may specialize on Celastraceae (Diniz, Morais, & Camargo, 2001; Silva et al., 2014), but data are scant. There are no records of myrmecophily.

Diversification

Paiwarriina consists of four genera containing 15–16 species. The ventral wing patterns of most species in the *Paiwarria* clade are conspicuously sexually dimorphic (Figure 4h,i) whereas those of the *Kolana* lineage are not. The former clade has almost twice as many species as the latter.

CUPATHECLINA LAMAS & GRISHIN, NEW SUBTRIBE

http://zoobank.org/ urn:lsid:zoobank.org:act:ABE3BF4E-8E83-4C14-8CA4-705EEFCA8D50

Type Genus. Cupathecla Bálint.
Other Included Genus. Dabreras Bálint.

Diagnosis

The original descriptions of *Cupathecla* and *Dabreras* did not note a relationship between them (Bálint, 2005; Bálint & Faynel, 2008) and the latter genus was not sequenced in Valencia-Montoya et al. (2021). Cupatheclina is distinguished from other subtribes based on DNA sequence data only (Table 2).

Male secondary sexual organs

Cupathecla has a dorsal forewing scent pad in the discal cell extending across the disco-cellular veins, a characteristic that otherwise occurs in *Megathecla* (Trichonidina). *Dabreras* has a dorsal scent patch on the hindwing costa (Figure 4j) and a ventral scent patch on the forewing inner margin, analogous to those found in some *Thereus* (Robbins, Heredia, & Busby, 2015). *Dabreras* has abdominal brush organs. A process of the vinculum/tegumen abuts the ventral and inner surface of the brush organs, a structure that otherwise occurs in *Brangas* (Atlidina).

Biogeography, habitat and larval food plants

Cupathecla occurs in most of the forested Neotropics, including montane habitats in the eastern Andes, whereas *Dabreras* is restricted to the Amazonian Region. Larval food plant records for

Cupathecla are Flacourtiaceae and Meliaceae (vouchers in MIZA and USNM).

Diversification

Cupatheclina consists of two genera containing three species. No known aspects of morphology or biology support a relationship between these two genera.

PARRHASIINA BUSBY & ROBBINS, NEW SUBTRIBE

http://zoobank.org/ urn:lsid:zoobank.org:act:4B69E55B-49BC-493A-A0F4-145C27B3BE61

Type Genus. Parrhasius Hübner.
Other Included Genera. Ignata K. Johnson, *Michaelus* Nicolay, *Thepytus* Robbins, *Olynthus* Hübner, *Beatheclus* Bálint & Dahners, *Oenomaus* Hübner, *Apuecla* Robbins, *Dicya* K. Johnson, *Caerofethra* K. Johnson, *Symbiopsis* Nicolay.

Diagnosis

Nicolay (1976, 1979, 1982) suggested a relationship among many of the included genera on account of their robust male genitalia capsules, but this trait also occurs in *Panthiades* (Strymonina). Although the male genitalia capsules of *Apuecla*, *Dicya* and *Symbiopsis* are somewhat robust, the relationship with the other genera is novel. Parrhasiina are monophyletic in all molecular analyses (Table 1). Parrhasiina is distinguished from other subtribes based on DNA sequence data only (Table 2).

Male secondary sexual organs

Dorsal forewing scent pads are universal except for *Symbiopsis* and *Caerofethra*. A dorsal forewing scent patch additionally occurs in some species of *Parrhasius* and *Michaelus* (Nicolay, 1979). Paired abdominal brush organs occur in *Caerofethra*, *Thepytus thyrea* (Hewitson) and *T. epytus* (Godman & Salvin) (Robbins, Busby, & Duarte, 2010). A unique single median brush organ occurs in *Symbiopsis* (Robbins, 2004a).

Biogeography, habitat and larval food plants

This subtribe occurs widely throughout the forested Neotropics with one species in temperate North America (*Parrhasius m-album* [Boisduval & Le Conte], Data S4). As far as is known most genera feed on only one or two plant families. *Olynthus* is recorded from Lecythidaceae and Caryocaraceae (Nicolay, 1982; Silva et al., 2011; reared adults in USNM), *Oenomaus* (Figure 4k, including *Porthecla*) from Annonaceae (Fennah, 1937; Ballou, 1945; Guagliumi, 1965, 1967; Silva et al., 1967–1968;

Kendall, 1975; Kaminski et al., 2012; reared adults in CPAC, MIZA, and USNM), *Thepytus* from Vochysiaceae (Silva et al., 2011), *Beatheclus* from Loranthaceae (Janzen & Hallwachs, 2021; Silva et al., 2011; Uchôa, Caires, Nicácio, & Duarte, 2012), *Michaelus* from Bignoniaceae and Fabaceae (summarized in Robbins, 2010b; Kaminski et al., 2010; Silva et al., 2011) and *Symbiopsis* from Fabaceae (Janzen & Hallwachs, 2021; reared vouchers in USNM). In contrast, *Parrhasius* is polyphagous on Araliaceae, Asteraceae, Bignoniaceae, Euphorbiaceae, Fabaceae, Fagaceae, Malpighiaceae and Malvaceae (Zikán, 1956; Clench, 1961b; Zikán & Zikán, 1968; Maes, Hellebuyck, & Gantier, 1999; Rodrigues, Kaminski, Freitas, & Oliveira, 2010; Janzen & Hallwachs, 2021; vouchers in CPAC, FIOC). Caterpillars of *Parrhasius* and *Olynthus* are myrmecophilous, but those of *Symbiopsis* are not (DeVries, 1990, 1991; Rodrigues et al., 2010).

Diversification

Parrhasiina currently consists of 11 genera containing 102–112 species. Apparent caterpillar food plant specialization in most genera is contrasted with polyphagy in *Parrhasius* highlights the need for more rearing data.

IPIDECLINA MARTINS & GRISHIN, NEW SUBTRIBE

http://zoobank.org/ urn:lsid:zoobank.org:act:C0DFF57C-5974-478B-9758-A6924D3124D7

Type Genus. Ipidecla Dyar.

Diagnosis

Ipidecla was proposed in Riodinidae even though some included species had previously been treated as lycaenids (Druce, 1909; Godman & Salvin, 1887). The genitalia are phenotypically similar to those of *Penaincisalia* (Robbins, 2004a), but this similarity is homoplastic according to the phylogeny. Ipideclina is distinguished from other subtribes based on DNA sequence data only (Table 2).

Male secondary sexual organs

All species have a complex androconial cluster on the dorsal forewings that has not been characterized morphologically, but appears to be a scent pad.

Biogeography, habitat and larval food plants

Ipidecla is Neotropical from Mexico to southern Brazil, most commonly in deciduous forest. Larval food plant records are Anacardiaceae, Combretaceae and Fabaceae (Kaye, 1940; vouchers in UCRC, MIZA). Myrmecophily is unknown.

Diversification

A single genus containing three species. Adults superficially resemble adults of Riodinidae (Figure 5a), but there are no other evident differences from other subtribes.

CALYCOPIDINA DUARTE & ROBBINS

Included Genera. Calycopis Scudder, *Serratofalca* K. Johnson, *Pendantus* K. Johnson & Kroenlein, *Camissecla* Robbins & Duarte, *Gigantorubra* K. Johnson, *Electrostrymon* Clench, *Rubroserrata* K. Johnson & Kroenlein, *Ziegleria* K. Johnson, *Arzecla* Duarte & Robbins, *Badecla* Duarte & Robbins, *Kisutam* K. Johnson & Kroenlein, *Lamprospilus* Geyer, *Argentostriatus* K. Johnson, *Mercedes* K. Johnson.

Diagnosis

Perhaps the most conspicuous morphological synapomorphy for Calycopidina is a thickened lateral edge of the female 8th abdominal tergum, but this trait is homoplastic in its occurrence (Duarte & Robbins, 2010) and is absent in *Pendantus* and *Ziegleria*. Fan-shaped signa of the female genitalia is another widespread character in Calycopidina (Duarte & Robbins, 2010), but also occurs in some Rhammina, Timaetina and Eumaeina. A lack of male secondary sexual organs on the wings is another widespread trait of Calycopidina (Duarte & Robbins, 2010), but also occurs in many other subtribes. Duarte and Robbins (2010) inferred phylogenetic relationships among the genera based on morphology. The primary difference in the molecular phylogeny herein is that the subtribe is rooted within *Calycopis*, rendering the previous concept of *Calycopis* not monophyletic. Calycopidina is monophyletic in all molecular analyses (Table 1) and is distinguished from other subtribes based on DNA sequence data only (Table 2).

Male secondary sexual organs

No male secondary sexual organs occur on the wings of Calycopidina. However, most species possess abdominal paired brush organs (Duarte & Robbins, 2010).

Biogeography, habitat and larval food plants

This subtribe occurs in virtually all habitats below 3000 m elevation from the temperate United States (*C. cecrops*) to subtropical parts of southern South America (e.g., *Calycopis caulonia* (Hewitson), *Badecla clarissa* (Draudt)). Caterpillars of Calycopidina are leaf-litter detritivores (Duarte & Robbins, 2010; Robbins, Aiello, et al., 2010), including seeds and mushrooms (Gripenberg et al., 2019; Nishida &

Robbins, 2020). Females lay eggs in the leaf litter where caterpillars feed (Duarte & Robbins, 2010). The only exception is *Mercedes* (previously a part of *Calycopis*), in which caterpillars eat flowers on the plant (Silva et al., 2011; vouchers in USNM, UWIZM). *Mercedes* is sister to the remainder of the subtribe in the phylogenetic results. The caterpillars of *Camissecla* are not myrmecophilous (DeVries, 1990, 1991).

Diversification

Calycopidina currently consists of 14 genera containing 131–172 species. An evolutionary switch from phytophagy to detritivory usually inhibits diversification (Mitter, Farrell, & Wiegmann, 1988), but Calycopidina appears to be an exception. Some species appear to oviposit only on fallen flowers/seeds and others on fallen leaves. The number of species without scientific names in this subfamily is large, and the 172 species upper limit is conservative. The relatively nondescript wing patterns and lack of male secondary sexual organs on the wings make it difficult to recognize specific differences. Wing pattern sexual dimorphism in some genera, such as *Lamprospilus* (Figure 5b), also contributes to difficulties with species recognition.

STRYMONINA TUTT

Included Genera. *Thereus* Hübner, *Rekoa* Kaye, *Heterosmaitia* Clench, *Arawacus* Kaye, *Strymon* Hübner, *Hypostrymon* Clench, *Panthiades* Hübner.

Diagnosis

This subtribe was not predicted in classifications based on morphology. Despite the lack of supporting morphological evidence, Strymonina is monophyletic in all analyses (Table 1) and is distinguished from other subtribes based on DNA sequence data only (Table 2).

Male secondary sexual organs

The typical organs in this subtribe are a scent patch in the dorsal forewing discal cell and a scent pad on the radial/disco-cellular veins, as documented in *Rekoa* (Robbins, 1991a). One or both may be absent. In *Strymon*, the discal cell scent patch is covered with regular wing

scales, in much the same way that it is in *Tmolus*, *Ministrymon* and some *Nicolaea* (Strephonotina) (Robbins & Nicolay, 2002). In *Panthiades*, the scent pad is surrounded by a circle of scales that are firmly embedded in the wing membrane (Robbins, 2005). The dorsal forewing androconial cluster in two *Thereus* species was originally described as an "oblique ovular sac-like brand occupying most of the cell of the forewing, but not distinctly apparent, with a longitudinal opening and enclosing large whitish scales" (Druce, 1907: page 591). It is a distinctive structure that has not been documented further.

Other kinds of scent patches in the Strymonina are not restricted to the forewing discal cell. In *Thereus*, some species have a scent patch on the costa of the dorsal hindwing, sometimes with associated hair-like androconia, and a second one on the ventral forewing (Robbins et al., 2015). In two species, there are erect hair-like androconia on the inner margin of the ventral forewing (Robbins et al., 2015). In *Arawacus*, a dorsal forewing scent patch occurs either in the discal cell or distal of it. In some species, a second scent patch is located on the dorsal surface of the hindwing (Robbins, 2010b). In *Panthiades*, a dorsal forewing scent patch is located distal of the discal cell (Robbins, 2005).

Paired abdominal brush organs are associated with dorsal processes of the vinculum in *Thereus* and *Rekoa* and in some species of *Arawacus* (Robbins, 1991a, 2000; Robbins et al., 2015). Robbins (1991a) detailed their structure, which is indistinguishable from those in *Contrafacia* (Jantheclina) and *Kolana* (Paiwarriina). Paired dorsal and ventral brush organs occur in *Thereus* (Robbins et al., 2015), which otherwise only occur in some *Chalybs* (Callophryidina) (Faynel, 2019). Most *Strymon* have brush organs (Robbins & Nicolay, 2002), but the vinculum is unmodified. There are no brush organs in *Panthiades* and *Hypostrymon* (Clench, 1975; Nicolay, 1976).

Biogeography, habitat and larval food plants

Strymonina has the broadest geographic range of the subtribes in the New World, extending from Canada to the central valley of Chile in virtually all vegetated habitats. Strymonina contains many widespread and common species, especially members of *Heterosmaitia*, *Strymon* and *Panthiades*, noted for larval feeding on at least a dozen plant families (Janzen & Hallwachs, 2021; Monteiro, 1991; Robbins, 1991a; Robbins & Nicolay, 2002). Alternatively, some lineages primarily specialize on Loranthaceae (about 35 *Thereus* species), Solanaceae (about 16 *Arawacus* species) or Bromeliaceae (about 16 *Strymon* species) (Heredia & Robbins, 2016; Robbins, 1991a, 2000, 2010a). There are numerous records of myrmecophilous behaviour (i.e., DeVries, 1990,

FIGURE 5   (a), *Ipidecla schausi* (Godman & Salvin) (Ipideclina) superficially resembles some Riodinidae; (b) *Lamprospilus genius* Geyer (Calycopidina) male (left) and female with wing pattern sexual dimorphism; (c),(d) ventral "false head" wing patterns in *Panthiades phaleros* (Linnaeus) (left) and *Arawacus aetolus* (Sulzer) (Strymonina); (e) *Ostrinotes tarena* (Hewitson) with a wing pattern representative of many Strephonotina; (f),(g) male *Trichonis hyacinthus* (Cramer) (left) and male *Bistonina bactriana* (Hewitson) (Trichonidina) with little similarity in wing pattern or male secondary sexual organs; (h),(i),(j), *Chalybs janias* (Cramer) (left), *Erora badeta* (Hewitson) (right, top) and *Chlorostrymon simaethis* (Drury) (Callophryidina) with ventral green wings. Scale refers to set specimens

1991; Robbins, 1991b). Conspicuous false head wing patterns (characterized in Robbins, 1981) occur in some species of *Thereus*, *Panthiades* and *Arawacus* (Figure 5c,d).

Diversification

Strymonina currently consists of seven genera containing 123–138 species. Repeated caterpillar food plant specialization and/or generalization, as noted above, as well as the variety of male secondary sexual organs suggest that each of these factors may have affected diversification.

STREPHONOTINA K. JOHNSON, AUSTIN, LE CROM & SALAZAR

Included Genera. Theclopsis Godman & Salvin, *Ministrymon* Clench, *Iaspis* Kaye, *Crimsinota* K. Johnson, *Aubergina* K. Johnson, *Tmolus* Hübner, *Celmia* K. Johnson, *Rindgea* K. Johnson, *Nicolaea* K. Johnson, *Terenthina* Robbins, *Siderus* Kaye, *Gossenia* Bálint, *Gargina* Robbins, *Decussata* K. Johnson, Austin, Le Crom & Salazar, *Ostrinotes* K. Johnson, Austin, Le Crom & Salazar, *Strephonota* K. Johnson, Austin, Le Crom & Salazar.

Diagnosis

Strephonotina represents the *Tmolus* Section of Robbins (2004b) with four genera added from the *Hypostrymon* Section. Many species in Strephonotina have the female genitalia corpus bursae constricted medially (Faynel & Robbins, 2014; Robbins & Duarte, 2004). Many also have sexually dimorphic forewing venation in which vein M_2 arises closer to vein M_1 in males than it does in females (Robbins & Duarte, 2004). Strephonotina was found monophyletic in all molecular analyses (Table 1) and is distinguished from other subtribes based on DNA sequence data only (Table 2).

Male secondary sexual organs

Dorsal forewing scent pads and patches occur widely in the Strephonotina, but not all. In *Tmolus*, *Ministrymon* and some *Nicolaea*, a discal cell dorsal forewing scent patch is covered by regular wing scales (Robbins & Glassberg, 2013), as in the genus *Strymon* (Strymonina). A conspicuous ventral forewing scent patch occurs in *Strephonota strephon* (Fabricius) and relatives accompanied by an enlarged hindwing costa. Scattered androconia on the ventral surface of the hindwing occur in *S. jactator* (H.H. Druce) and relatives (unpublished data). Abdominal brush organs are absent except for *Siderus nouraguensis* Faynel & Robbins (Faynel & Robbins, 2014).

Biogeography, habitat and larval food plants

Strephonotina is Neotropical except for the subtropical part of the distribution of *Ministrymon leda* (W.H. Edwards) in North America and the subtropical parts of the distributions of *M. gamma* (H.H. Druce) and *M. sanguinalis* (Burmeister) in South America. Caterpillar food plant usage in Strephonotina is variable. For example, *Tmolus* has been reared from Acanthaceae, Anacardiaceae, Boraginaceae, Campanulaceae, Celastraceae, Combretaceae, Connaraceae, Fabaceae, Gesneriaceae, Lecythidaceae, Malpighiaceae, Melastomataceae, Ochnaceae, Simaroubaceae, Solanaceae, Verbenaceae and Vochysiaceae (Perkins & Swezey, 1924; Lima, 1936; Zimmerman, 1958; Robbins & Aiello, 1982; Silva et al., 2011; vouchers in CPAC, MIZA and USNM). In contrast, *Ministrymon* appears to specialize on Fabaceae (Comstock & Dammers, 1935; Ballmer & Pratt, 1989; Silva et al., 2011; Janzen & Hallwachs, 2021; vouchers in DZUP, MIZA, TAMU, UCRC, USNM and UWIZM). Myrmecophilous behaviour is recorded in *Tmolus* and *Gargina* (DeVries, 1990, 1991).

Diversification

Strephonotina currently consists of 16 genera containing 148–228 species. Perhaps the most notable trait of Strephonotina is that a majority of the species have a relatively nondescript grey ventral wing pattern with a postmedian line (Figure 5e). Compared with Atlidina and Evenina (Figure 4d–g), for example, the adults are less colourful and have fewer types of male secondary sexual organs. As with Calycopidina, there are many undescribed species.

TRICHONIDINA DUARTE & FAYNEL, NEW SUBTRIBE

http://zoobank.org/ urn:lsid:zoobank.org:act:36D5508F-9355-418C-92B5-E5AE45951D36

Type Genus. Trichonis Hewitson.

Other Included Genera. Bistonina Robbins, *Manticia* Bálint, *Megathecla* Robbins.

Diagnosis

This subtribe includes genera with strikingly different wing patterns, genitalia and androconia (Figure 5f,g). *Trichonis* contains two sexually dimorphic species that are conspicuously different from all other eumaeines (Robbins, 1987). Eliot (1973) placed *Trichonis* and *Micandra* (Eumaeina) in the *Trichonis* section, but the morphological basis for this action was disputed (Robbins, 1987). Trichonidina was recognized in Valencia-Montoya et al. (2021) and is monophyletic in all analyses based on molecular sequences except *Megathecla* in the mitochondrial tree (Table 1); it is distinguished from other subtribes based on DNA sequence data only (Table 2).

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Male secondary sexual organs

All species of Trichonidina have dorsal forewing scent pads except for the two species of *Trichonis*. *Megathecla* has a scent pad that extends from the discal cell to forewing cells M_1-M_3, which also occurs in *Cupathecla* (Cupatheclina). Some *Bistonina* have dorsal forewing scent patches. The overlapping dorsal hindwing and ventral forewing scent patches in *Trichonis* are distinctive (Robbins, 1987). Abdominal brush organs are not recorded in Trichonidina.

Biogeography, habitat and larval food plants

Most species of Trichonidina are restricted to the Amazonian Region. No members of this subtribe appear to have been reared.

Diversification

Trichonidina consists of four genera containing 10–14 species. As with Cupatheclina, no known aspects of morphology or biology support a relationship among these genera.

CALLOPHRYIDINA TUTT

Included Genera. Callophrys Billberg, *Cyanophrys* Clench, *Chalybs* Hübner, *Ocaria* Clench, *Magnastigma* Nicolay, *Satyrium* Scudder, *Thaeides* K. Johnson, Kruse & Kroenlein, *Radissima* K. Johnson, *Erora* Scudder, *Semonina* Robbins, *Chlorostrymon* Clench.

Diagnosis

Widespread conspicuous morphological traits in Callophryidina are homoplastic in their occurrence. *Chalybs*, *Callophrys*, *Cyanophrys*, *Erora*, *Semonina* and *Chlorostrymon* have species with a green ventral ground colour (Figure 5h–j), but based on the autosome and Z sex chromosome results, the occurrence of this trait is homoplastic. A serrate keel on the ventral tip of the penis (Clench, 1961a) occurs in genera *Phaeostrymon*, *Magnastigma*, *Chlorostrymon*, *Ocaria* and most species of *Satyrium*. It is homoplastic in our phylogeny, and also occurs in *Podanotum* in Rhammina (Robbins, 2004a). The structure of the male abdominal brush organs and the associated modification of the vinculum in *Radissima* is almost identical to that in *Paiwarria* (Paiwarriina). The female genitalia ductus seminalis arises at the dorsal anterior edge of the ductus bursae with a posterior lobe of the corpus bursae dorsal of it (Nicolay, 1980) in *Magnastigma*, *Chlorostrymon*, *Ocaria* and *Satyrium alcestis* (W.H. Edwards). This trait does not occur elsewhere in Eumaeini, but its occurrence is homoplastic. The species in this subtribe tend to have more beta-trichoid sensilla (see Chun & Schoonhoven, 1973) at the distal end of the mid- and hind tibia than other Eumaeini, but variability makes this trait unlikely

synapomorphic. As noted in Robbins and Duarte (2004), the posteriorly developed male genitalia labides and the female genitalia ductus seminalis arising from the middle of the ductus bursae in *Erora* (Field, 1941) superficially resemble the genitalia of the Old World *Hypochrysops* C. & R. Felder (Sands, 1986) of the tribe Luciini (Australian Region). Callophryidina is monophyletic in Valencia-Montoya et al. (2021) and in all analyses herein (Table 1); it is distinguished from other subtribes based on DNA sequence data only (Table 2).

Male secondary sexual organs

Dorsal forewing scent pads occur widely in Callophryidina. The scent pad in some species of *Ocaria* is a complex structure in need of further study. A dorsal hindwing scent patch occurs in several species of *Erora*. Paired abdominal dorsal brush organs occur widely in the Callophryidina. In *Erora* and *Semonina*, some species have paired dorsal brush organs that do not touch the vinculum (Robbins & Duarte, 2004). *Callophrys henrici* (Grote & Robinson) lacks male secondary sexual organs.

Biogeography, habitat and larval food plants

Callophryidina occurs in the Palearctic, Nearctic and Neotropical Regions (Data S4). All Palearctic Eumaeini belong to *Callophrys* or *Satyrium*, as delimited for over half a century (Ziegler, 1960). Classifications, such as those in Clench (1978) and Weidenhoffer et al. (2004), in which *Satyrium* is partitioned into smaller genera, are not supported by the results.

With few exceptions, the eumaeine species that inhabit areas with freezing temperatures belong to this subtribe. As noted, caterpillars of *Callophrys* eat Gymnosperms, Monocotyledons and Dicotyledons (Ehrlich & Raven, 1965). More generally, a vast array of larval food plants, as well as myrmecophilous behaviour, have been recorded for Callophryidina in multiple regions. The species of Holarctic *Satyrium* appear to be obligately univoltine but many of Holarctic *Callophrys* are multivoltine.

Diversification

Callophryidina consists of 11 genera containing 112–131 Neotropical and Nearctic species and a similar number of Palearctic species. It is the only subtribe with Palearctic species. Valencia-Montoya et al. (2021) concluded that geography played a central role in the early divergence of Callophryidina.

DISCUSSION

Subtribal classification

Eumaeini is divided into 15 subtribes, each of which is monophyletic in the tree based on autosome protein-coding genes (Figure 1) and in

the tree based on Z sex chromosome protein-coding genes (Figure 2). Subtribal nomenclature is addressed in Data S1. The classification of 102 generic names in Data S1 is provisional until most species in each subtribe can be sequenced and analysed. Eumaeini currently contains 1074–1323 species.

Using non-eumaeine fossils, the ancestor where Callophryidina split from the remainder of Eumaeini was estimated at 13.8–18.8 Ma (Chazot et al., 2019) and at 23.8–33.5 Ma (Espeland et al., 2018; Valencia-Montoya et al., 2021). Given these nonoverlapping ranges and the lack of fossils of eumaeines or closely related tribes (Valencia-Montoya et al., 2021), dating divergence times of eumaeine lineages is premature.

The differences between the results presented here and those of Valencia-Montoya et al. (2021) (Table 1) may be due, in part, to their smaller dataset. The analysis in Valencia-Montoya et al. (2021) was based upon 187 eumaeines with between five and 374 sequenced loci. The species that varied in placement – *Thestius meridionalis* (Draudt), *Balintus tityrus* (C. Felder & R. Felder), *Allosmaitia* sp. and *Aveexcrenota anna* (H. H. Druce) – were among the taxa with five sequenced loci.

Relationships in the clade comprising subtribes Eumaeina + Rhammina + Timaetina + Atlidina + Evenina + Jantheclina + Paiwarriina + Cupatheclina + Parrhasiina were not strongly resolved in our results, nor in Valencia-Montoya et al. (2021). We considered lumping these clades into one large subtribe of about 500 species even though it was not monophyletic in the mitochondrial results (e.g., *Busbiina*). An advantage of this action would be a simpler classification. A disadvantage is that it would be a classificatory taxon that conveyed little information because of morphological, biogeographical and ecological heterogeneity. For that reason, we instead chose a classification that was intended to better communicate biological information. For example, Rhammina is primarily Andean endemics, Atlidina is renowned for its variety of male secondary sexual organs and Paiwarriina has a stark contrast among wing pattern sexually monomorphic and dimorphic sister clades.

Callophryidina is the most species-rich subtribe and is sister to the remainder of the Eumaeini. We considered splitting this clade in two, but there was no partition in which each clade was monophyletic in all the molecular analyses.

The classification of Eumaeini presented herein contains 102 genera. However, *Enos* + *Chopinia* + *Falerinota* is not monophyletic in analysis of mitochondrial sequences (Data S3). We recognize the monophyly of *Enos* based upon monophyly in the autosome and Z sex chromosome analyses herein, and based on results by Valencia-Montoya et al. (2021) (see Robbins, 1987).

The two proposed generic names that we did not sequence are placed in Callophryidina. The type species of *Variegatta* has a complex cornutus in the male genitalia penis that is unique among eumaeines to *Ocaria*, for which reason it was treated as a junior synonym of *Ocaria* (Robbins, 2004a, 2004b). The type species of *Semonina* and some species of *Erora* have a pair of male abdominal brush organs that do not touch the vinculum – a unique structure in Eumaeini – for which reason they were treated as close relatives (Robbins & Duarte, 2004).

Lepidopteran Z sex chromosome

The maximum likelihood tree based on Z sex chromosome loci is similar to that based on autosome sequences (Figures 1 and 2). The topology among subtribes is the same with respect to Callophryidina to Strymonina. The similarities allow us to propose a classification in which subtribes are monophyletic in both trees (Figures 1 and 2). When analysing hundreds of taxa, the analysis of the small number of Z sex chromosome sequences (2.6% of nuclear base pairs) may be more practical as far as time and expense. Moreover, sex chromosomes disproportionately affect hybrid sterility/nonviability and show elevated differences among related taxa (e.g., Kronforst et al., 2013; Martin et al., 2013; Payseur et al., 2018), suggesting some utility for their use in phylogenetic analyses. On the other hand, divergence patterns in sex chromosomes are influenced by changes in population size (Pool & Nielsen, 2007; Van Belleghem et al., 2018), indicating that caution be exercised when interpreting phylogenetic signal in sex chromosome sequences.

Diversification and morphological homoplasy

Although rapidly diversifying clades may be accompanied by relatively little morphological evolution (Adams, Berns, Kozak, & Wiens, 2009), our phylogenetic results show that Eumaeini suggest many instances of conspicuous morphological homoplasy. Male secondary sexual organs represent many proposed synapomorphies of a previous classification (Robbins, 2004a, 2004b). The homoplastic occurrence of these traits in the Lepidoptera has long been known, based on phylogenetic incongruence with other morphological structures (summarized in Robbins et al., 2012). The molecular phylogenetic results confirm this pattern; Atlidina, Jantheclina and Evenina provide many examples. Primary sexual structures in Eumaeini are also homoplastic. For example, a dorsal process of the fused male genitalia vinculum/tegumen in which the vinculum groove is flush with the posterior margin of the process (see Robbins, 1991a) is present in Atlidina, Jantheclina and Paiwarriina. As another example, a "fan-shaped" signa (sensu Duarte & Robbins, 2010) occur in many genera of Eumaeina, Rhammina, Timaetina and Calycopidina, and based on these molecular results, they have been gained or lost in each subtribe.

Homoplasy of conspicuous morphological traits in Eumaeini is not restricted to sexual organs. For example, our results indicate that a "cleft" anal lobe (Martins et al., 2019a) likely evolved three times; once in the ancestor of Atlidina, within the genus *Panthiades* (Strymonina) and in the ancestor of *Dabreras* (Cupatheclina). As another example, a thickened ridge on the lateral edge of the female 8th abdominal tergum (see Duarte & Robbins, 2010) is absent in *Pendantus* and *Ziegleria*. Similarly, males and females in some genera, such as *Lamprospilus* (Calycopidina) and *Annamaria* (Paiwarriina), have sexually dimorphic ventral wing patterns (Figures 4h,i and 5b); related genera, such as *Arzecla* (Calycopidina) and *Kolana* (Paiwarriina) respectively, have monomorphic ventral wing patterns.

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Diversification and biogeography

About 85% of the species in subtribes Eumaeina, Rhammina and Timaetina (240 species combined) occur in the Andes (Figure 4b,c). Although stratification in narrow elevational zones has been implicated in the diversification of some Andean butterflies (e.g., Adams, 1985; Pyrcz & Wojtusiak, 2002), such patterns do not occur in Eumaeini (Lamas et al., 2021). On the contrary, the incidence of sympatry between sister lineages in Timaetina may be high (Busby et al., 2017; Robbins & Busby, 2008). The subtribes Eumaeina, Rhammina and Timaetina may be appropriate taxa to study the apparent higher incidence of sympatry in montane habitats on diversification.

The Neotropical Eumaeini likely invaded Nearctic areas with freezing weather seven times, according to our results (Data S4). Atlidina (e.g., *Atlides halesus*), Parrhasiina (e.g., *Parrhasius m-album*), Calycopidina (e.g., *Calycopis cecrops*) and Strymonina (e.g., *Strymon melinus* [Hübner]) each appear to have colonized the Nearctic once. In contrast, the Neotropical Callophryidina invaded the temperate parts of the Nearctic, including the mountains of Mexico and Guatemala, three times (*Callophrys*, *Satyrium* and within *Erora*). The Nearctic *Callophrys* and *Satyrium* each invaded the Palearctic at least once. Although more sequenced taxa are needed, it appears that colonization of the Palearctic by *Satyrium* led to a vastly increased rate of diversification.

Diversification and larval food plants

Two relationships between diversification and caterpillar food plants are evident despite the caveat that caterpillar food plant records are still not well documented. Calycopidina (172 species) (Figure 5b) consists of leaf-litter detritus feeding caterpillars except for *Mercedes* (14 species), which eat flowers. *Mercedes* is sister to the remainder of the subtribe, which provides an example of a detritivorous lineage that is more species-rich than its flower-feeding sister clade. This result is evolutionarily unusual (Mitter et al., 1988).

Atlidina, Strephonotina, Parrhasiina and Strymonina (562 species combined) each contain genera that specialize on one or two plant families as well as genera that are generalists on many plant families. For example, in Atlidina, *Atlides* and *Brangas* are specialists on mistletoes (Loranthaceae and Viscaceae) whereas *Denivia* is a generalist. In the Strephonotina, *Ministrymon* is a specialist on Fabaceae whereas *Tmolus* is a generalist. In the Parrhasiina, *Oenomaus* (including *Porthecla*) is a specialist on Annonaceae whereas *Parrhasius* is a generalist. In the Strymonina, *Thereus* is a specialist on Loranthaceae whereas *Panthiades* is a generalist. Although none of these examples are sister genera, food plant specialization and generalization appear to be highly labile; further study is needed to understand the evolutionary significance of these patterns of host feeding.

CONFLICT OF INTEREST

The authors declare that there is no conflict of interest.

DATA AVAILABILITY STATEMENT

Data that support the findings of this study are available in the supporting information and in NCBI Bioproject ID PRJNA778531.

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REFERENCES

Adams, M.J. (1985) Speciation in the pronophiline butterflies (Satyridae) of the northern Andes. *Journal of Research on the Lepidoptera*, (S1), 33–49.

Adams, D.C., Berns, C.M., Kozak, K.H. & Wiens, J.J. (2009) Are rates of species diversification correlated with rates of morphological evolution? *Proceedings of the Royal Society of London B*, 276(1668), 2729–2738. https://doi.org/10.1098/rspb.2009.0543

Altschul, S.F., Gish, W., Miller, W., Myers, E.W. & Lipman, D.J. (1990) Basic local alignment search tool. *Journal of Molecular Biology*, 215(3), 403–410. https://doi.org/10.1016/S0022-2836(05)80360-2

Armas, L.F. (2004) *Malpighia punicifolia* (Malpighiaceae), nueva planta hospedera de *Allosmaitia c. coelebs* (Lepidoptera: Lycaenidae). *Cocuyo*, 14, 14.

Arregui, T. & Onore, G. (1989) Estudio preliminar sobre la entomofauna asociada a *Lupinus mutabilis* Sweet, en el Ecuador. *Memorias. VI Congreso Internacional sobre Cultivos Andinos (Quito)*, 185–188.

Austin, G.T., Miller, L.D. & Miller, J.Y. (2007) Taxonomic comments on *Pseudolycaena* Wallengren (Lepidoptera: Lycaenidae: Theclinae: Eumaeini). *Bulletin of the Allyn Museum*, 149, 1–22.

Badenes-Pérez, F.R., Alfaro-Alpízar, M.A. & Johnson, M.T. (2010) Diversity, ecology and herbivory of hairstreak butterflies (Theclinae) associated with the velvet tree, *Miconia calvescens* in Costa Rica. *Journal of Insect Science*, 10(209), 1–9.

Bálint, Z. (2005) Systematics and taxonomic notes on Neotropical hairstreak lycaenids in connection to the genus *Megathecla* (Lycaenidae:

Theclinae: Eumaeini). *Boletín científico Museo de Historia natural. Universidad de Caldas*, 9, 278–294.

Bálint, Z., Boyer, P., Cerdeña, J., Farfán Larico, J., Lorenc-Brudecka, J., Prieto, C. et al. (2021) Contributions to the knowledge of Neotropical Lycaenidae: taxonomy of *Johnsonita* Salazar & Constantino, 1995 with descriptions of seven new species (Theclinae: Eumaeini). *Zootaxa*, 4963(1), 11–57. https://doi.org/10.11646/zootaxa.4963.1.2

Bálint, Z. & Faynel, C. (2008) Review of the genus Brangas [sic] Hübner, 1819 (Lepidoptera: Lycaenidae) with description of a new genus. *Annales Historico-Naturales Musei Nationalis Hungarici*, 100, 271–306.

Bálint, Z., Katona, G. & Kertész, K. (2019) A new species of *Penaincisalia* (Lepidoptera: Lycaenidae) from Peru. *Opuscula Zoologica (Budapest)*, 50(2), 137–144.

Ballmer, G.R. & Pratt, G.F. (1989) A survey of the last instar larvae of the Lycaenidae of California. *Journal of Research on the Lepidoptera*, 27(1), 1–81.

Ballou, C.H. (1945) Notas sobre insectos dañinos observados en Venezuela 1938–1943. *Tercera Conferencia interamericana de Agricultura (Caracas)*, 34, 1–151.

Basset, Y., Dahl, C., Ctvrtecka, R., Gripenberg, S., Lewis, O.T., Segar, S.T. et al. (2018) A cross-continental comparison of assemblages of seed- and fruit-feeding insects in tropical rainforests: faunal composition and rates of attack. *Journal of Biogeography*, 45(6), 1395–1407. https://doi.org/10.1111/jbi.13211

Bates, H.W. (1861) Contributions to an insect fauna of the Amazon Valley–Lepidoptera–Papilionidae. *Journal of Entomology*, 1(4), 218–245.

Beccaloni, G.W., Viloria, A.L., Hall, S.K. & Robinson, G.S. (2008) Catalogue of the hostplants of the Neotropical butterflies. Catálogo de las plantas huésped de las mariposas neotropicales. *Zaragoza, Sociedad Entomológica Aragonesa. (Monografías del Tercer Milenio)*, 8, 536.

Bolger, A.M., Lohse, M. & Usadel, B. (2014) Trimmomatic: a flexible trimmer for Illumina sequence data. *Bioinformatics*, 30, 2114–2120. https://doi.org/10.1093/bioinformatics/btu170

Braga, M.P., Guimarães, P.R., Wheat, C.W., Nylin, S. & Janz, N. (2018) Unifying host-associated diversification processes using butterfly-plant networks. *Nature Communications*, 9(5155), 1–10. https://doi.org/10.1038/s41467-018-07677-x|

Buchfink, B., Xie, C. & Huson, D. (2015) Fast and sensitive protein alignment using DIAMOND. *Nature Methods*, 12, 59–60. https://doi.org/10.1038/nmeth.3176

Busby, R.C., Faynel, C., Moser, A. & Robbins, R.K. (2017) Sympatric diversification in the upper Amazon: a revision of the Eumaeine genus *Paraspiculatus* (Lepidoptera: Lycaenidae). *Smithsonian Contributions to Zoology*, 649, 1–65. https://doi.org/10.5479/si.1943–6696.649

Cajé, S.O.S., Melo, J.D., Santos, K.L.A., Bastos, A.S., Robbins, R.K. & Lima, I.M.M. (2021) Natural history and parasitoids of *Arawacus ellida* (Lycaenidae: Eumaeini) in Brazil. *Journal of the Lepidopterists' Society*, 75(4), 235–240. https://doi.org/10.18473/lepi.75i4.a2

Callaghan, C.J. (2008) The biology of *Rhamma arria* in Colombia (Lepidoptera: Lycaenidae). *Tropical Lepidoptera*, 18(1), 60–61.

Chazot, N., Wahlberg, N., Freitas, A.V.L., Mitter, C., Labandeira, C., Sohn, J.-C. et al. (2019) Priors and posteriors in Bayesian timing of divergence analyses: the age of butterflies revisited. *Systematic Biology*, 68, 797–813. https://doi.org/10.1093/sysbio/syz002

Chun, M.W. & Schoonhoven, L.M. (1973) Tarsal contact chemosensory hairs of the large white butterfly *Pieris brassicae* and their possible role in oviposition behaviour. *Entomologia Experimentalis et Applicata*, 16(3), 343–357. https://doi.org/10.1111/j.1570-7458.1973.tb00283.x

Clench, H.K. (1961a) Tribe Theclini. In: Ehrlich, P.R. & Ehrlich, A.H. (Eds.) *How to know the butterflies*. Dubuque, Iowa: Brown Co., pp. 177, 262–220 525 figs.

Clench, H.K. (1961b) *Panthiades m-album* (Lycaenidae): remarks on its early stages and on its occurrence in Pennsylvania. *Journal of the Lepidopterists' Society*, 15(4), 226–232.

Clench, H.K. (1975) A review of the genus *Hypostrymon* (Lepidoptera: Lycaenidae). *Bulletin of the Allyn Museum*, 25, 1–7.

Clench, H.K. (1978) The names of certain Holarctic hairstreak genera (Lycaenidae). *Journal of the Lepidopterists' Society*, 32(4), 277–281.

Comstock, J.A. & Dammers, C.M. (1935) Notes on the early stages of three butterflies and six moths from California. *Bulletin of the Southern California Academy of Sciences*, 34(2), 120–142.

Cong, Q., Shen, J., Borek, D., Robbins, R.K., Opler, P.A., Otwinowski, Z. et al. (2017) When COI barcodes deceive, complete genomes reveal introgression in hairstreaks. *Proceedings of the Royal Society of London B*, 284(1848), 20161735. https://doi.org/10.1098/rspb.2016.1735

Cong, Q., Shen, J., Borek, D., Robbins, R.K., Otwinowski, Z. & Grishin, N.V. (2016) Complete genomes of hairstreak butterflies, their speciation, and nucleo–mitochondrial incongruence. *Scientific Reports*, 6(24863), 1–15. https://doi.org/10.1038/srep24863

Cong, Q., Shen, J., Li, W., Borek, D., Otwinowski, Z. & Grishin, N.V. (2017) The first complete genomes of metalmarks and the classification of butterfly families. *Genomics*, 109(5–6), 485–493. https://doi.org/10.1016/j.ygeno.2017.07.006

Corl, A. & Ellegren, H. (2013) Sampling strategies for species trees: the effects on phylogenetic inference of the number of genes, number of individuals, and whether loci are mitochondrial, sex-linked, or autosomal. *Molecular Phylogenetics and Evolution*, 67(2), 358–366. https://doi.org/10.1016/j.ympev.2013.02.002

Coyne, J.A. & Orr, H.A. (1989) Patterns of speciation in drosophila. *Evolution*, 43(2), 362–381.

DeVries, P. (1990) Enhancement of symbioses between butterfly caterpillars and ants by vibrational communication. *Science*, 248(4959), 1104–1106.

DeVries, P. (1991) Call production by myrmecophilous riodinid and lycaenid butterfly caterpillars (Lepidoptera): morphological, acoustical, functional, and evolutionary patterns. *American Museum Novitates*, 3025, 1–23.

Dewitz, H. (1879) Naturgeschichte cubanischer Schmetterlinge. Nach Beobachtungen des Herrn Dr. Gundlach bearbeitet. *Zeitschrift für die gesammten Naturwissenschaften*, 52(2), 155–174.

Diniz, I.R., Morais, H.C. & Camargo, A.J.A. (2001) Host plants of lepidopterous caterpillars in the cerrado of the Distrito Federal, Brazil. *Revista Brasileira de Entomologia (São Paulo)*, 45(2), 107–122.

Draudt, M. (1919–1920) In: Theclini, F. & Seitz, A. (Eds.) *Die Amerikanischen Tagfalter*, Vol. 5. Stuttgart, Alfred Kernen: Die Gross-Schmetterlinge der Erde, pp. 744–812.

Druce, H.H. (1907) On Neotropical Lycaenidae, with descriptions of new species. *Proceedings of the Zoological Society of London*, 3, 566–632.

Druce, H.H. (1909) On some new and little-known Neotropical Lycaenidae. *Transactions of the Entomological Society of London*, 3, 431–438.

Duarte, M. & Robbins, R.K. (2010) Description and phylogenetic analysis of the Calycopidina (Lycaenidae, Theclinae, Eumaeini): a subtribe of detritivores. *Revista Brasileira de Entomología*, 54(1), 45–65.

Eastwood, R.G., Pierce, N.E., Kitching, R.L. & Hughes, J.M. (2006) Do ants enhance diversification in lycaenid butterflies? Phylogenetic evidence from a model myrmecophile. *Jalmenus evagoras. Evolution*, 60(2), 315–327.

Ehrlich, P.R. & Raven, P.H. (1965) Butterflies and plants: a study in coevolution. *Evolution*, 18(4), 586–608.

Eliot, J.N. (1973) The higher classification of the Lycaenidae (Lepidoptera): a tentative arrangement. *Bulletin of the British Museum (Natural History) Entomology*, 28(6), 371–505.

Espeland, M., Breinholt, J., Willmott, K.R., Warren, A.D., Vila, R., Toussaint, E.F.A. et al. (2018) A comprehensive and dated phylogenomic analysis of butterflies. *Current Biology*, 28(5), 770–778. https://doi.org/10.1016/j.cub.2018.01.061

Faynel, C. (2019) Le genre *Chalybs* Hübner, [1819] avec la description d'une nouvelle espèce du plateau des Guyanes (Lepidoptera, Lycaenidae, Theclinae). *Lambillionea*, 119(S3), 1–34.

HAIRSTREAK SUBTRIBE CLASSIFICATION

Systematic
Entomology

Royal
Entomological
Society

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Faynel, C. & Robbins, R.K. (2014) Description d'un nouveau Lycaenidae de l'inselberg des Nouragues et de deux autres espèces inédites provenant de la forêt de la Montagne de Kaw en Guyane (Lepidoptera: Theclinae: Eumaeini). *Annales de la Société entomologique de France (N.S.)*, 50(2), 191–201. https://doi.org/10.1080/00379271.2014.934040

Fennah, R.G. (1937) Lepidopterous pests of the sour–sop in Trinidad. (2) *Thecla ortygnus* Cramer. *Tropical Agriculture*, 14(8), 244–245.

Fiedler, K. (1991) Systematic, evolutionary, and ecological implications of myrmecophily within the Lycaenidae (Insecta: Lepidoptera: Papilionoidea). *Bonner Zoologische Monographien*, 31, 1–210.

Field, W.D. (1941) Notes on *Erora laeta* (Edwards) and *Erora quaderna* (Hewitson) (Lepidoptera, Lycaenidae). *Annals of the Entomological Society of America*, 34(2), 303–316.

Fordyce, J.A. (2010) Host shifts and evolutionary radiations of butterflies. *Proceedings of the Royal Society of London B*, 277(1701), 3735–3743. https://doi.org/10.1098/rspb.2010.0211

Fraïsse, C., Picard, M.A.L. & Vicoso, B. (2017) The deep conservation of the Lepidoptera Z chromosome suggests a non-canonical origin of the W. *Nature Communications*, 8, 1486. https://doi.org/10.1038/s41467-017-01663-5

Godman, F.D. & Salvin, O. (1887–1901) *Biologia Centrali–Americana. Insecta. Lepidoptera–Rhopalocera*. Published by authors, Vol. 2, London: Dulau & Co., Bernard Quaritch, p. 782.

Gripenberg, S., Basset, Y., Lewis, O.T., Terry, J.C.D., Wright, S.J., Simón, I. et al. (2019) A highly–resolved food web for insect seed predators in a species–rich tropical forest. *Ecology Letters*, 22(10), 1638–1649. https://doi.org/10.1111/ele.13359

Guagliumi, P. (1965) Contributo ala conoscenza dell'entomofauna nociva del Venezuela. *Rivista di Agricoltura subtropicale e tropicale*, 59(7/9), 376–408.

Guagliumi, P. (1967) Insetti e arachnidi delle piante comuni del Venezuela segnalati nel periodo 1938–1963. *Relazioni e Monografia agrarie subtropicale e tropicale (N.S.)*, 86, 391.

Gundlach, J. (1881) Contribución a la Entomología Cubana. Parte primera. In: Montiel, G. (Ed.) *Lepidópteros*. La Habana, p. 480.

Guppy, J. (1904) Notes on the habits and early stages of some Trinidad butterflies. *Transactions of the Entomological Society of London*, 2, 225–228.

Hardy, N.B. & Otto, S.P. (2014) Specialization and generalization in the diversification of phytophagous insects: tests of the musical chairs and oscillation hypotheses. *Proceedings of the Royal Society of London B*, 281(1795), 20132960.

Heredia, M.D. & Robbins, R.K. (2016) Natural history of the mistletoe–feeding *Thereus lomalarga* (Lepidoptera, Lycaenidae, Eumaeini) in Colombia. *Zootaxa*, 4117(3), 301–320. https://doi.org/10.11646/zootaxa.4117.3.1

Hoffmann, F. (1930) Beiträge zur Naturgeschichte brasilianischer Schmetterlinge. I. *Zeitschrift für wissenschaftliche Insektenbiologie*. I, 25(6/7), 93–112.

Hoffmann, F. (1933) Beiträge zur Naturgeschichte brasilianischer Schmetterlinge. *Deutsche entomologische Zeitschrift*, 1932(2/3), 97–148.

Hoffmann, F. (1935) Futterpflanzen der Raupen brasilianischer Schmetterlinge. *Entomologischer Anzeiger*, 15(16/17), 117–120.

Hoffmann, F. (1937) Beiträge zur Naturgeschichte brasilianischer Schmetterlinge. II. *Internationale entomologische Zeitschrift*, 51(23), 231–232.

Janz, N. (2011) Ehrlich and Raven revisited: mechanisms underlying codiversification of plants and enemies. *Annual Review of Ecology, Evolution, and Systematics*, 42, 71–89.

Janz, N., Nylin, S. & Wahlberg, N. (2006) Diversity begets diversity: host expansions and the diversification of plant-feeding insects. *BMC Evolutionary Biology*, 6(4), 1–10. https://doi.org/10.1186/1471-2148-6-4

Janzen, D.H. & Hallwachs, W. (2021) Dynamic database for an inventory of the macrocaterpillar fauna, and its food plants and parasitoids, of Area de Conservacion Guanacaste (ACG), northwestern Costa Rica. http://janzen.sas.upenn.edu. Accessed 15 January 2021.

Kaminski, L.A. & Freitas, A.V.L. (2010) Natural history and morphology of immature stages of the butterfly *Allosmaitia strophius* (Godart) (Lepidoptera: Lycaenidae) on flower buds of Malpighiaceae. *Studies on Neotropical Fauna and Environment*, 45(1), 11–19.

Kaminski, L.A., Freitas, A.V.L. & Oliveira, P.S. (2010) Interaction between mutualisms: ant-tended butterflies exploit enemy-free space provided by ant-treehopper associations. *American Naturalist*, 176(3), 332–334.

Kaminski, L.A., Rodrigues, D. & Freitas, A.V.L. (2012) Immature stages of *Parrhasius polibetes* (Lepidoptera: Lycaenidae): host plants, tending ants, natural enemies and morphology. *Journal of Natural History*, 46(11/12), 645–667.

Kaye, W.J. (1940) Additions and corrections to the recorded species of Trinidad butterflies (Lepid. Rhop.). *Transactions of the Royal Entomological Society of London*, 90(21), 551–573.

Kendall, R.O. (1975) Larval foodplants for seven species of hairstreaks (Lycaenidae) from Mexico. *Bulletin of the Allyn Museum*, 24, 1–4.

Kirkpatrick, T.W. (1954) Notes on minor insect pests of cacao in Trinidad. Part2. Lepidoptera (butterflies and moths). *Reports on Cacao Research*, 1953, 67–72.

Kronforst, M.R., Hansen, E.B.M., Crawford, N.G., Gallant, J.R., Zhang, W., Kulathinal, R.J. et al. (2013) Hybridization reveals the evolving genomic architecture of speciation. *Cell Reports*, 5(3), 666–677.

Lamas, G. (2008) La sistemática sobre mariposas (Lepidoptera: Hesperioidea y Papilionoidea) en el mundo: Estado actual y perspectivas futuras. In: Llorente, J.E. & Lanteri, A. (Eds.) *Contribuciones taxonómicas en órdenes de insectos hiperdiversos*. México: D.F., Universidad Nacional Autónoma de México, pp. 57–70.

Lamas, G., McInnis, M.L., Busby, R.C. & Robbins, R.K. (2021) The lycaenid butterfly fauna (Lepidoptera) of Cosñipata, Peru: annotated checklist, elevational patterns, and rarity. *Insecta Mundi*, 0861, 1–34.

Lemoine, F., Domelevo Entfellner, J.B., Wilkinson, E., Correia, D., Dávila Felipe, M., Oliveira, T. et al. (2018) Renewing Felsenstein's phylogenetic bootstrap in the era of big data. *Nature*, 556, 452–456. https://doi.org/10.1038/s41586-018-0043-0

Li, W., Cong, Q., Shen, J., Zhang, J., Hallwachs, W., Janzen, D.H. et al. (2019) Genomes of skipper butterflies reveal extensive convergence of wing patterns. *Proceedings of the National Academy of Sciences*, 116(13), 6232–6237. https://doi.org/10.1073/pnas.1821304116

Lima, A.M.C. (1936) *Terceiro catalogo dos insectos que vivem nas plantas do Brasil*. Rio de Janeiro, Ministerio da. *Agricultura*, 2, 460.

Maes, J., Hellebuyck, M.V.J. & Gantier, J.C. (1999) Superfamilia Papilionoidea. In: Maes, J.-M. (Ed.) *Catálogo de los insectos y artrópodos terrestres de Nicaragua*, Vol. III. León, pp. 1245–1395.

Martin, S.H., Dasmahapatra, K.K., Nadeau, N.J., Salazar, C., Walters, J.R., Simpson, F. et al. (2013) Genome-wide evidence for speciation with gene flow in *Heliconius* butterflies. *Genome Research*, 23(11), 1817–1828.

Martins, A.R.P., Duarte, M. & Robbins, R.K. (2019a) Phylogenetic classification of the *Atlides* section of the Eumaeini (Lepidoptera, Lycaenidae). *Zootaxa*, 4563(1), 119–134. https://doi.org/10.11646/zootaxa.4563.1.6

Martins, A.R.P., Duarte, M. & Robbins, R.K. (2019b) Hairstreak butterflies (Lepidoptera, Lycaenidae) and evolution of their male secondary sexual organs. *Cladistics*, 35(2), 173–197. https://doi.org/10.1111/cla.12355

Mitter, C., Farrell, B. & Wiegmann, B. (1988) The phylogenetic study of adaptive zones: has phytophagy promoted insect diversification? *American Naturalist*, 132(1), 107–128.

Monte, O. (1934) Borboletas que vivem em plantas cultivadas. Publicações. Secretaria da Agricultura. *Estado de Minas-Gerais (Serie. agricola)*, 21, 221.

Monteiro, R.F. (1991) Cryptic larval polychromatism in *Rekoa marius* Lucas and *R. palegon* Cramer (Lycaenidae: Theclinae). *Journal of Research on the Lepidoptera*, 29(1/2), 77–84.

Müller, J.F.T. (1878) Pflanzengattungen, an denen mir bekannte Tagfalter–Raupen leben. *Stettiner entomologische Zeitung*, 39(7/9), 296.

Muyshondt, A. (1973) Notes on the life cycle and natural history of butterflies of El Salvador. I. *Prepona omphale octavia* (Nymphalidae). *Journal of the Lepidopterists Society*, 27(3), 210–219.

Neild, A.F.E. & Bálint, Z. (2014) Notes on the identity of *Evenus coronata* (Hewitson, 1865) (Lepidoptera: Lycaenidae: Theclinae: Eumaeini) with the description of a remarkable overlooked sibling species. *Tropical Lepidoptera Research*, 24(2), 105–120.

Nguyen, L., Schmidt, H.A., von Haeseler, A. & Minh, B.Q. (2015) IQ-TREE: a fast and effective stochastic algorithm for estimating maximum-likelihood phylogenies. *Molecular Biology and Evolution*, 32(1), 268–274. https://doi.org/10.1093/molbev/msu300

Nicolay, S.S. (1976) A review of the Hübnerian genera *Panthiades* and *Cycnus* (Lycaenidae: Eumaeini). *Bulletin of the Allyn Museum*, 35, 1–30.

Nicolay, S.S. (1979) Studies in the genera of American hairstreaks. 5. A review of the Hübnerian genus *Parrhasius* and description of a new genus *Michaelus* (Lycaenidae: Eumaeini). *Bulletin of the Allyn Museum*, 56, 1–52.

Nicolay, S.S. (1980) The genus *Chlorostrymon* and a new subspecies of *C. simaethis*. *Journal of the Lepidopterists' Society*, 34(2), 253–256.

Nicolay, S.S. (1982) Studies in the genera of American hairstreaks. 6. A review of the Hübnerian genus *Olynthus* (Lycaenidae: Eumaeini). *Bulletin of the Allyn Museum*, 74, 1–30.

Nishida, K. & Robbins, R.K. (2020) One side makes you taller: a mushroom–eating butterfly caterpillar (Lycaenidae) in Costa Rica. *Neotropical Biology and Conservation*, 15(4), 463–470. https://doi.org/10.3897/neotropical.15.e57998

Payseur, B.A., Presgraves, D.C. & Filatov, D.A. (2018) Introduction: sex chromosomes and speciation. *Molecular Ecology*, 27(19), 3745–3748. https://doi.org/10.1111/mec.14828

Pearson, W.R. (2013) An introduction to sequence similarity ("homology") searching. *Current Protocols in Bioinformatics*, 42, 3.1.1–3.1.8. https://doi.org/10.1002/0471250953.bi0301s42

Perkins, R.C.L. & Swezey, O.H. (1924) The introduction into Hawaii of insects that attack *lantana*. *Bulletin of the Experiment Station of the Hawaiian Sugar Planters' Association (Entomological Series)*, 16, 1–83.

Pierce, N.E. (1984) Amplified species diversity: a case study of an Australian lycaenid butterfly and its attendant ants. In: Vane-Wright, R.I. & Ackery, P.R. (Eds.) *The biology of butterflies*. London: Academic Press, pp. 197–200.

Pool, J.E. & Nielsen, R. (2007) Population size changes reshape genomic patterns of diversity. *Evolution*, 61(12), 3001–3006. https://doi.org/10.1111/j.1558–5646.2007.00238.x

Presgraves, D.C. (2018) Evaluating genomic signatures of "the large X–effect" during complex speciation. *Molecular Ecology*, 27(19), 3822–3830. https://doi.org/10.1111/mec.14777

Prieto, C., Bálint, Z., Boyer, P. & Micó, E. (2008) A review of the "browni group" of *Penaincisalia* with notes on their distribution and variability (Lepidoptera: Lycaenidae). *Zootaxa*, 1941, 1–24.

Prieto, C., Grishin, N., Hausmann, A. & Lorenc-Brudecka, J. (2016) The *Penaincisalia amatista* species–group (Lepidoptera: Lycaenidae, Eumaeini) in Colombia, insights from mtDNA barcodes and the description of a new species. *Systematics and Biodiversity*, 14(2), 171–183.

Prieto, C., Núñez, R. & Hausmann, A. (2018) Molecular species delimitation in the genus *Rhamma* Johnson, 1992 (Lepidoptera: Lycaenidae, Theclinae). *Mitochondrial DNA (A)*, 30(1), 1–17.

Prieto, C. & Vargas, M.A. (2016) Elfin butterflies of the genus *Rhamma* Johnson (Lepidoptera: Lycaenidae: Theclinae): a review of the Colombian species. *Zootaxa*, 4093(3), 323–342.

Pyrcz, T.W. & Wojtusiak, J. (2002) The vertical distribution of pronophiline butterflies (Nymphalidae, Satyrinae) along an elevational transect in Monte Zerpa (cordillera de Mérida, Venezuela) with remarks on their diversity and parapatric distribution. *Global Ecology and Biogeography*, 11(3), 211–221.

Robbins, R.K. (1981) The "false head" hypothesis: predation and wing pattern variation of lycaenid butterflies. *American Naturalist*, 118(5), 770–775.

Robbins, R.K. (1987) Evolution and identification of the New World hairstreak butterflies (Lycaenidae: Eumaeini): Eliot's *Trichonis* section and *Trichonis* Hewitson. *Journal of the Lepidopterists' Society*, 40(3), 138–157.

Robbins, R.K. (1991a) Evolution, comparative morphology, and identification of the eumaeine butterfly genus *Rekoa* Kaye (Lycaenidae: Theclinae). *Smithsonian Contributions to Zoology*, 498, 1–64.

Robbins, R.K. (1991b) Cost and evolution of a facultative mutualism between ants and lycaenid larvae (Lepidoptera). *Oikos*, 62(3), 363–369.

Robbins, R.K. (2000) The New World hairstreak genus *Arawacus* Kaye (Lepidoptera: Lycaenidae: Theclinae: Eumaeini). *Proceedings of the Entomological Society of Washington*, 102(1), 162–169.

Robbins, R.K. (2004a) Introduction to the checklist of Eumaeini (Lycaenidae). In: Lamas, G. (Ed.) *Checklist: part 4A. Hesperioidea – Papilionoidea*. In: Heppner, J. B. (Ed.), *Atlas of Neotropical Lepidoptera*, Vol. 5A. Gainesville: Association for Tropical Lepidoptera; Scientific Publishers, pp. xxiv–xxx.

Robbins, R.K. (2004b) Lycaenidae. Theclinae. Tribe Eumaeini. In: Lamas, G. (Ed.) *Checklist: part 4A. Hesperioidea – Papilionoidea*. In: Heppner, J. B. (Ed.), *Atlas of Neotropical Lepidoptera*, Vol. 5A. Gainesville: Association for Tropical Lepidoptera; Scientific Publishers, pp. 118–137.

Robbins, R.K. (2005) Phylogenetic relationships among the species of *Panthiades* Hübner (Lycaenidae: Theclinae: Eumaeini). *Proceedings of the Entomological Society of Washington*, 107(3), 501–509.

Robbins, R.K. (2010a) The "upside down" systematics of hairstreak butterflies (Lycaenidae) that eat pineapple and other Bromeliaceae. *Studies on Neotropical Fauna and Environment*, 45(1), 21–37.

Robbins, R.K. (2010b) Four commonly confused hairstreaks (Lycaenidae, Theclinae, Eumaeini): three need names, one does not. *Journal of the Lepidopterists' Society*, 64(1), 1–13.

Robbins, R.K. & Aiello, A. (1982) Foodplant and oviposition records for Panamanian Lycaenidae and Riodinidae. *Journal of the Lepidopterists' Society*, 36(2), 65–75.

Robbins, R.K., Aiello, A., Feinstein, J., Berkov, A., Caldas, A., Busby, R.C. et al. (2010) A tale of two species: detritivory, parapatry, and sexual dimorphism in *Lamprospilus collucia* and *L. orcidia* (Lycaenidae: Theclinae: Eumaeini). *Journal of Research on the Lepidoptera*, 42, 64–73.

Robbins, R.K. & Busby, R.C. (2008) Phylogeny, taxonomy, and sympatry of *Timaeta* (Lycaenidae: Theclinae: Eumaeini): an Andean montane Forest endemic. *Tijdschrift voor Entomologie*, 151(2), 205–233.

Robbins, R.K. & Busby, R.C. (2009) Updated phylogeny, taxonomy, and diversification of *Janthecla* Robbins & Venables (Lycaenidae: Theclinae: Eumaeini). *Journal of Research on the Lepidoptera*, 41, 5–13.

Robbins, R.K. & Busby, R.C. (2015) Evolutionary gain of male secondary sexual structures in the widespread Neotropical montane genus *Lathecla* (Lepidoptera, Lycaenidae, Eumaeini). *Insect Systematics and Evolution*, 46(1), 47–78.

Robbins, R.K., Busby, R.C. & Duarte, M. (2010) Phylogeny and taxonomy of *Thepytus* (Lycaenidae, Theclinae, Eumaeini). *Arthropod Systematics & Phylogeny*, 68(1), 35–52.

Robbins, R.K, Cong, Q., Zhang, J., Shenc, J., Rierac, J.Q., Murray, D., Busby, R.C., Faynel, C., Hallwachs, W., Janzen, D.H., Grishin, N.V. (2021) A switch to feeding on cycads generates parallel accelerated evolution of toxin tolerance in two clades of *Eumaeus* caterpillars (Lepidoptera: Lycaenidae). *Proceedings of the National Academy of Sciences*, 118(7)(e2018965118), 1–6. https://doi.org/10.1073/pnas.2018965118

Robbins, R.K. & Duarte, M. (2004) Descriptions of new butterfly genera. Lycaenidae, Eumaeini. In: Lamas, G. (Ed.) *Checklist: part 4A.*

Hesperioidea – Papilionoidea. In: Heppner, J. B. (Ed.), *Atlas of Neotropical Lepidoptera*, Vol. 5A. Gainesville: Association for Tropical Lepidoptera; Scientific Publishers, pp. 275–282.

Robbins, R.K. & Glassberg, J. (2013) A butterfly with olive green eyes discovered in the United States and the Neotropics (Lepidoptera, Lycaenidae, Eumaeini). *ZooKeys*, 305, 1–20. https://doi.org/10.3897/zookeys.301.5081ZooKeys

Robbins, R.K., Heredia, M.D. & Busby, R.C. (2015) Male secondary sexual structures and the systematics of the *Thereus oppia* species group (Lepidoptera, Lycaenidae, Eumaeini). *ZooKeys*, 520, 109–130. https://doi.org/10.3897/zookeys.520.10134

Robbins, R.K. & Lamas, G. (2008) Nomenclature, variation, and the biological species concept in *Lamasina* (Lycaenidae: Theclinae: Eumaeini). *Revista Brasileira de Zoologia*, 25(1), 116–127.

Robbins, R.K., Martins, A.R., Busby, R.C. & Duarte, M. (2012) Loss of male secondary sexual structures in allopatry in the Neotropical butterfly genus *Arcas* (Lycaenidae: Theclinae: Eumaeini). *Insect Systematics & Evolution*, 43(1), 35–65. https://doi.org/10.1163/187631212X626195

Robbins, R.K. & Nicolay, S.S. (2002) An overview of *Strymon* Hübner (Lycaenidae: Theclinae: Eumaeini). *Journal of the Lepidopterists' Society*, 55(3), 85–100.

Robbins, R.K. & Venables, B.A.B. (1991) Synopsis of a new neotropical hairstreak genus, *Janthecla*, and description of a new species (Lycaenidae). *Journal of the Lepidopterists' Society*, 45(1), 11–33.

Rodrigues, D., Kaminski, L.A., Freitas, A.V.L. & Oliveira, P.S. (2010) Trade-offs underlying polyphagy in a facultative ant–tended florivorous butterfly: the role of host plant quality and enemy–free space. *Oecologia*, 163(3), 719–728.

Sands, D.P.A. (1986) A revision of the genus *Hypochrysops* C. & R. Felder (Lepidoptera: Lycaenidae). *Entomon*, 7, 1–116.

Schultze-Rhonhof, A. (1938) Ueber die ersten Stände zweier Rhopaloceren aus Ecuador. *Deutsche entomologische Zeitschrift "Iris"*, 52(1), 36–43.

Sepp, J. (1829–1852) *Natuurlijke Historie van Surinaamsche Vlinders, naar het leven geteekend*. [Afterwards entitled:] *Surinaamsche Vlinders. Papillons de Surinam*. Amsterdam, J. C. Sepp en Zoon. 3 Deel. pp. viii, iv, viii, 1–328, 152 pls.

Sermeño, J.M., Robbins, R.K., Lamas, G. & Gámez, J.A. (2013) Cría en laboratorio de las "joyas vivientes" de El Salvador, *Evenus regalis* (Cramer) y *Evenus batesii* (Hewitson) (Lepidoptera, Lycaenidae). *Bioma (San Salvador)*, 1(3), 4–9 44–48.

Silva, N.A.P., Duarte, M., Araújo, E.B. & Morais, H.C. (2014) Larval biology of anthophagous Eumaeini (Lepidoptera: Lycaenidae, Theclinae) in the Cerrado of Central Brazil. *Journal of Insect Science*, 14(184), 1–17.

Silva, N.A.P., Duarte, M., Diniz, I.R. & Morais, H.C. (2011) Host plants of Lycaenidae on inflorescences in central Brazilian cerrado. *Journal of Research on the Lepidoptera*, 44, 95–105.

Silva, A. G. A., Gonçalves, C. R., Galvão, D. M., Gonçalves, A. J. L., Gomes, J., Silva, M.N. & Simoni L. (1967–1968) *Quarto catalogo dos insetos que vivem nas plantas do Brasil. Ministerio da Agricultura, Rio de Janeiro*, Part I, Vol. 1, 422 pp., Vol. 2, 906 pp., Part II, Vol.1, 622 pp., Vol. 2, 265 pp.

St Laurent, R.A., Carvalho, A.P.S., Earl, C. & Kawahara, A.Y. (2021) Food plant shifts drive the diversification of sack-bearer moths. *The American Naturalist*, 198(5), E170–E184. https://doi.org/10.1086/716661

Sukumaran, J. & Holder, M.T. (2010) DendroPy: a python library for phylogenetic computing. *Bioinformatics*, 26(12), 1569–1571. https://doi.org/10.1093/bioinformatics/btq228

Terra-Araújo, M.H., Faria, A.D., Ribeiro, J.E.L.S. & Swenson, U. (2012) Flower biology and subspecies concepts in *Micropholis guyanensis* (Sapotaceae): evidence of ephemeral flowers in the family. *Australian Systematic Botany*, 25(5), 295–303.

Uchôa, M.A., Caires, C.S., Nicácio, J. & Duarte, M. (2012) Frugivory of *Neosilba* species (Diptera: Lonchaeidae) and *Thepytus echelta* (Lepidoptera: Lycaenidae) on *Psittacanthus* (Santalales: Loranthaceae) in ecotonal Cerrado–south Pantanal, Brazil. *Florida Entomologist*, 95(3), 630–640.

Valencia-Montoya, W.A., Quental, T.B., Tonini, J.F.R., Talavera, G., Crall, J. D., Lamas, G. et al. (2021) Evolutionary trade-offs between male secondary sexual traits revealed by a comprehensive phylogeny of the hyperdiverse tribe Eumaeini (Lepidoptera: Lycaenidae). *Proceedings of the Royal Society of London B*, 288(1950), 20202512. https://doi.org/10.1098/rspb.2020.2512

Van Belleghem, S.M., Baquero, M., Papa, R., Salazar, C., McMillan, W.O., Counterman, B.A. et al. (2018) Patterns of Z chromosome divergence among *Heliconius* species highlight the importance of historical demography. *Molecular Ecology*, 27, 3852–3872. https://doi.org/10.1111/mec.14560

Vargas, H.A. & Duarte, M. (2016) First host plant record for *Strymon davara* (Hewitson) (Lepidoptera, Lycaenidae) in the highly human-modified coastal valleys of the Atacama Desert. *Revista Brasileira de Entomologia*, 60(4), 352–355.

Weidenhoffer, Z., Bozano, G.C. & Churkin, S. (2004) *Guide to the butterflies of the Palearctic region*. Omnes Artes, Milano: Lycaenidae part II.

Whittaker, P.L. (1984) Population biology of the great purple hairstreak, *Atlides halesus*, in Texas (Lycaenidae). *Journal of the Lepidopterists' Society*, 38(3), 179–185.

Zhang, J., Cong, Q., Shen, J., Brockmann, E. & Grishin, N.V. (2019) Genomes reveal drastic and recurrent phenotypic divergence in Firetip skipper butterflies (Hesperiidae: Pyrrhopyginae). *Proceedings of the Royal Society of London B*, 286(1903), 20190609.

Ziegler, J.B. (1960) Preliminary contribution to a redefinition of the genera of north American hairstreaks (Lycaenidae) north of Mexico. *Journal of the Lepidopterists' Society*, 14(1), 19–23.

Zikán, J.F. (1956) Beiträge zur Biologie von 12 Theclinen–arten. *Dusenia*, 7, 139–148.

Zikán, J.F. & Zikán, W. (1968) Inseto–fauna do Itatiaia e da Mantiqueira. III. Lepidoptera. *Pesquisa agropecuária Brasileira (Agronomia)*, 3, 45–109.

Zimmerman, E.C. (1958) *Insects of Hawaii*, Vol. 7. Honolulu: Macrolepidoptera. Univ. Hawaii Press, p. 542.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

Data S1. Subtribe and provisional generic classification of the Eumaeini.

Data S2. List of specimens sequenced.

Data S3. Phylogenetic trees for the autosome, sex chromosome and mitochondrial sequences.

Data S4. Colour-coded primary geographic distribution of the type species of each generic name on the autosome cladogram.

Eumaeina Doubleday, 1847
Type Genus *Eumaeus* Hübner, [1819]
= Eumenides Boisduval, 1836 [type genus *Eumenia* Godart, [1824]]
Invalid under ICZN Article 55 because Eumenides is a junior homonym of the family-group name Eumenida Leach,
1812 (Hymenoptera), based on the wasp genus *Eumenes* Latreille, 1802.

Eumaeus Hübner, [1819], type species: *Rusticus minyas* Hübner, [1809]
    Eumenia Godart, [1824], type species: *Eumenia toxea* Godart, [1824]
    Eumaea Geyer, [1834], type species: *Eumaea debora* Geyer, [1834]
    Epula Gistel, 1848, repl. name for *Eumenia.*, ICZN art. 67.8, type species: *Eumenia toxea* Godart, [1824]
Theorema Hewitson, 1865, type species: *Theorema eumenia* Hewitson, 1865
Mithras Hübner, [1819], subsequent designation, Scudder, 1875, type species: *Papilio nautes* Cramer, 1779
Micandra Staudinger, 1888, cf. Prieto (2011) for authorship, type species designation, type species: *Pseudolycaena*
    platyptera C. Felder & R. Felder, 1865
    Egides Salazar, 1995, not available, nom. nud.
    Egides K. Johnson, Kruse & Kroenlein, 1997, type species: *Pseudolycaena aegides* C. Felder & R. Felder,
    1865
Brevianta K. Johnson, Kruse & Kroenlein, 1997, type species: *Thecla undulata* Hewitson, 1867
    Bussa K. Johnson, Kruse & Kroenlein, 1997, not available, preocc. (Ragonot 1888), type species: *Thecla busa*
    Godman & Salvin, 1887
Thestius Hübner, [1819], subsequent designation, Scudder, 1875, type species: *Papilio pholeus* Cramer, 1777

Rhammina Prieto & Busby, **new subtribe**
Type Genus *Rhamma* K. Johnson, 1992

Balintus D'Abrera, 2001, ICZN Opinion 2358 (2015), type species: *Pseudolycaena tityrus* C. Felder & R. Felder,
    1865
Johnsonita Salazar & Constantino, 1995, type species: *Johnsonita johnsoni* Salazar & Constantino, 1995
    Owda K. Johnson, Kruse & Kroenlein, 1997, type species: *Thecla auda* Hewitson, 1867
Rhamma K. Johnson, 1992, type species: *Thecla oxida* Hewitson, 1870
    Pontirama K. Johnson, 1992, (Robbins 2004, first reviser, ICZN art. 24.2), type species: *Pontirama brunea* K.
    Johnson, 1992
    Shapiroana K. Johnson, 1992, (Robbins 2004, first reviser, ICZN art. 24.2), type species: *Shapiroana shapiroi*
    K. Johnson, 1992
    Paralustrus K. Johnson, 1992, (Robbins 2004, first reviser, ICZN art. 24.2), type species: *Thecla commodus* C.
    Felder & R. Felder, 1865
Lathecla Robbins, 2004, type species: *Thecla latagus* Godman & Salvin, 1887
Podanotum Torres & K. Johnson, 1996, type species: *Podanotum clarissimus* Hall, Willmott & K. Johnson, 1996
Salazaria D'Abrera & Bálint, 2001, ICZN Opinion 2358 (2015), type species: *Thecla sala* Hewitson, 1867

Timaetina Busby & Prieto, **new subtribe**
Type Genus *Timaeta* K. Johnson, Kruse & Kroenlein, 1997
= Thecloxurina K. Johnson, 1992 [type genus *Thecloxurina* K. Johnson, 1992].
Unavailable under ICZN Articles 13.1 and 13.2 because Thecloxurina is a family-group name proposed after 1930
without "a description or definition that states in words characters that are purported to differentiate the taxon."

Penaincisalia K. Johnson, 1990, type species: *Thecla ? culminicola* Staudinger, 1894
    Thecloxurina K. Johnson, 1992, type species: *Thecla loxurina* C. Felder & R. Felder, 1865
    Pons K. Johnson, 1992, type species: *Pons magnifica* K. Johnson, 1992
    Abloxurina K. Johnson, 1992, subsequent designation, Prieto & Lorenc-Brudecka, 2014, type species:

Penaincisalia ismaeli Busby & Hall, 2005
   Candora K. Johnson, 1992, type species: *Candora fallacandor* K. Johnson, 1992
   Ianusanta Bálint, 2011, type species: *Ianusanta ianusi* Bálint, 2011
Busbiina Robbins, 2004, type species: *Thecla bosora* Hewitson, 1870
Timaeta K. Johnson, Kruse & Kroenlein, 1997, type species: *Pseudolycaena timaeus* C. Felder & R. Felder, 1865
   Trochusinus K. Johnson, Salazar & Vélez, 1997, (Robbins 2004, first reviser, ICZN art. 24.2), type species: *Thecla trochus* H.H. Druce, 1907
   Jagiello Bálint & Wojtusiak, 2000, type species: *Jagiello molinopampa* Bálint & Wojtusiak, 2000
   Temecla Robbins, 2004, type species: *Thecla tema* Hewitson, 1867
Phothecla Robbins, 2004, type species: *Thecla photismos* H.H. Druce, 1907
Marachina Robbins, 2004, type species: *Thecla maraches* H.H. Druce, 1912
Nesiostrymon Clench, [1964], type species: *Thecla celida shoumatoffi* Comstock & Huntington, 1943
   Terra K. Johnson & Matusik, 1988, type species: *Thecla tera* Hewitson, 1878
   Sipaea K. Johnson, 1991, type species: *Thecla hyccara* Hewitson, 1868
Paraspiculatus K. Johnson & Constantino, 1997, type species: *Paraspiculatus colombiensis* K. Johnson & Constantino, 1997

Atlidina Martins & Duarte, **new subtribe**
Type Genus *Atlides* Hübner, [1819]

Atlides Hübner, [1819], subsequent designation, Scudder, 1875, type species: *Papilio halesus* Cramer, 1777
   Riojana D'Abrera & Bálint, 2001, ICZN Opinion 2358 (2015), type species: *Thecla thargelia* Burmeister, 1878
Brangas Hübner, [1819], subsequent designation, Scudder, 1875, type species: *Papilio caranus* Stoll, 1780
Denivia K. Johnson, 1992, type species: *Thecla deniva* Hewitson, 1874
   Lucilda D'Abrera & Bálint, 2001, ICZN Opinion 2358 (2015), type species: *Thecla crines* H.H. Druce, 1907
   Margaritheclus Bálint, 2002, type species: *Pseudolycaena danaus* C. Felder & R. Felder, 1865
Arcas Swainson, 1832, type species: *Papilio imperialis* Cramer, 1775
Theritas Hübner, 1818, subsequent designation, Scudder, 1875, type species: *Theritas mavors* Hübner, 1818
Pseudolycaena Wallengren, 1858, type species: *Papilio marsyas* Linnaeus, 1758

Evenina Faynel & Grishin, **new subtribe**
Type Genus *Evenus* Hübner, [1819]
= Macusiina K. Johnson, Kruse & Kroenlein, 1997 [type genus *Macusia* Kaye]
Unavailable under ICZN Articles 13.1 and 13.2 because Macusiina is a family-group name proposed after 1930 without "a description or definition that states in words characters that are purported to differentiate the taxon."

Evenus Hübner, [1819], subsequent designation, Scudder, 1875, type species: *Papilio regalis* Cramer, 1775
   Euenus Hübner, [1826], not available, missp.
   Endymion Swainson, 1831, type species: *Papilio regalis* Cramer, 1775
   Macusia Kaye, 1904, type species: *Thecla satyroides* Hewitson, 1865
   Cryptaenota K. Johnson, 1992, type species: *Thecla latreillii* Hewitson, 1865
   Ipocia Brévignon, 2000, type species: *Papilio gabriela* Cramer, 1775
   Poetukulunma Brévignon, 2002, type species: *Thecla sponsa* Möschler, 1877
   Poetuculunma Brévignon, 2002, not available, incorrect original spelling, type species: *Thecla sponsa* Möschler, 1877
   Suneve Bálint, 2006, type species: *Thecla coronata* Hewitson, 1865

Jantheclina Robbins & Faynel, **new subtribe**
Type Genus *Janthecla* Robbins & Venables, 1991

Aveexcrenota Salazar & K. Johnson, 1997, type species: *Thecla anna* H.H. Druce, 1907
Contrafacia K. Johnson, 1989, type species: *Contrafacia mexicana* K. Johnson, 1989
   Orcya K. Johnson, 1990, type species: *Thecla orcynia* Hewitson, 1868
Allosmaitia Clench, [1964], type species: *Thecla coelebs* Herrich-Schäffer, 1862

Enos K. Johnson, Kruse & Kroenlein, 1997, type species: *Thecla thara* Hewitson, 1867

    Falerinota K. Johnson, Austin, Le Crom & Salazar, 1997, (Robbins 2004, first reviser, ICZN art. 24.2), type species: *Thecla falerina* Hewitson, 1867

    Chopinia D'Abrera, 2001, ICZN Opinion 2358 (2015), type species: *Thecla mazurka* Hewitson, 1867

    Ricuchallo Piñas, 2006, not available, nom. nud.

Janthecla Robbins & Venables, 1991, type species: *Thecla janthina* Hewitson, 1867

Laothus K. Johnson, Kruse & Kroenlein, 1997, type species: *Thecla barajo* Reakirt, [1867]

    Gibbonota Salazar & López, 1996, not available, preocc. (Heinrich, 1937), type species: *Thecla gibberosa* Hewitson, 1867

    Gibbossa Salazar & López, 2001, repl. name for *Gibbonota*, (ICZN art. 67.8), type species: *Thecla gibberosa* Hewitson, 1867

    Runalatus Piñas, 2006, not available, nom. nud.

Paiwarriina Lamas & Robbins, **new subtribe**
Type Genus *Paiwarria* Kaye, 1904

Paiwarria Kaye, 1904, type species: *Papilio venulius* Cramer, 1779

Annamaria D'Abrera & Bálint, 2001, ICZN Opinion 2358 (2015), type species: *Thecla draudti* Lathy, 1926

    Eucharia Boisduval, 1870, not available, subsequent designation, Kirby, 1871; preocc. (Hübner, [1820]), type species: *Papilio ganimedes* Cramer, 1775

    Lamasina Robbins, 2002, repl. name for *Eucharia*, (ICZN art. 67.8), type species: *Papilio ganimedes* Cramer, 1775

    Airamanna Bálint, 2009, type species: *Annamaria columbia* Bálint, 2005

Fasslantonius Bálint & Salazar, 2003, type species: *Thecla episcopalis* Fassl, 1912

Kolana Robbins, 2004, type species: *Thecla ligurina* Hewitson, 1874

Cupatheclina Lamas & Grishin, **new subtribe**
Type Genus *Cupathecla* Bálint, 2005

Cupathecla Bálint, 2005, type species: *Papilio cupentus* Stoll, 1781

Dabreras Bálint, 2008, type species: *Thecla teucria* Hewitson, 1868

Parrhasiina Busby & Robbins, **new subtribe**
Type Genus *Parrhasius* Hübner, [1819]

Parrhasius Hübner, [1819], subsequent designation, Scudder, 1875, type species: *Papilio polibetes* Stoll, 1781

    Eupsyche Scudder, 1876, type species: *Thecla m-album* Boisduval & Le Conte, 1833

    Sumapanda Piñas, 2006, not available, nom. nud.

Ignata K. Johnson, 1992, type species: *Ignata ignobilis* K. Johnson, 1992

Michaelus Nicolay, 1979, type species: *Thecla vibidia* Hewitson, 1869

Thepytus Robbins, 2004, type species: *Thecla epytus* Godman & Salvin, 1887

Olynthus Hübner, [1819], subsequent designation, Scudder, 1875, type species: *Papilio narbal* Stoll, 1790

Beatheclus Bálint & Dahners, 2006, type species: *Beatheclus beatrizae* Bálint & Dahners, 2006

Oenomaus Hübner, [1819], subsequent designation, Scudder, 1875, type species: *Papilio ortygnus* Cramer, 1779

    Draudtiana Kesselring & Ebert, [1982], not available, nom. nud.

    Porthecla Robbins, 2004, type species: *Thecla porthura* H.H. Druce, 1907

Apuecla Robbins, 2004, type species: *Thecla upupa* H.H. Druce, 1907

Dicya K. Johnson, 1991, type species: *Thecla dicaea* Hewitson, 1874

Caerofethra K. Johnson, 1991, type species: *Thecla emendatus* H.H. Druce, 1907

Symbiopsis Nicolay, 1971, type species: *Thecla strenua* Hewitson, 1877

Ipideclina Martins & Grishin, **new subtribe**
Type Genus *Ipidecla* Dyar, 1916

Ipidecla Dyar, 1916, type species: *Ipidecla miadora* Dyar, 1916

Calycopidina Duarte & Robbins, 2010

Type Genus *Calycopis* Scudder, 1876

= Calycopina K. Johnson & Kroenlein, 1993 [type genus *Calycopis* Scudder, 1876]

= Angulopina K. Johnson & Kroenlein, 1993 [type genus *Angulopis* K. Johnson, 1991]

Unavailable under ICZN Articles 13.1 and 13.2 because Calycopina and Angulopina are family-group names proposed after 1930 without "a description or definition that states in words characters that are purported to differentiate the taxon."

Calycopis Scudder, 1876, type species: *Rusticus poeas* Hübner, [1811]

    Calystryma Field, 1967, type species: *Calystryma blora* Field, 1967

    Femniterga K. Johnson, 1988, type species: *Femniterga notacastanea* K. Johnson, 1988

    Tergissima K. Johnson, 1988, type species: *Tergissima mosconiensis* K. Johnson, 1988

    Morphissima K. Johnson, 1991, type species: *Morphissima scalpera* K. Johnson, 1991

    Antrissima K. Johnson, 1991, type species: *Antrissima varicolor* K. Johnson, 1991

    Fieldia K. Johnson, 1991, not available, preocc. (Walcott, 1912), type species: *Fieldia yungas* K. Johnson, 1991

    Cyanodivida K. Johnson, 1991, type species: *Cyanodivida fornoi* K. Johnson, 1991

    Gigantofalca K. Johnson, 1991, type species: *Gigantofalca stacya* K. Johnson, 1991

    Kroenleina K. Johnson, 1991, type species: *Kroenleina panornata* K. Johnson, 1991

    Serratoterga K. Johnson, 1991, type species: *Serratoterga larsoni* K. Johnson, 1991

    Klaufera K. Johnson, 1991, type species: *Thecla pisis* Godman & Salvin, 1887

    Distissima K. Johnson, 1991, type species: *Distissima spenceri* K. Johnson, 1991

    Terminospinissima K. Johnson, 1991, type species: *Terminospinissima serratissima* K. Johnson, 1991

    Furcovalva K. Johnson, 1991, type species: *Furcovalva extensa* K. Johnson, 1991

    Reversustus K. Johnson, 1991, type species: *Thecla puppius* Godman & Salvin, 1887

    Profieldia K. Johnson, 1992, repl. name for *Fieldia*, (ICZN art. 67.8), type species: *Fieldia yungas* K. Johnson, 1991

Serratofalca K. Johnson, 1991, type species: *Thecla cerata* Hewitson, 1877

Pendantus K. Johnson & Kroenlein, 1993, type species: *Thecla plusios* Godman & Salvin, 1887

Camissecla Robbins & Duarte, 2004, type species: *Thecla camissa* Hewitson, 1870

Gigantorubra K. Johnson, 1993, type species: *Thecla collucia* Hewitson, 1877

    Arumecla Robbins & Duarte, 2004, type species: *Thecla aruma* Hewitson, 1877

Electrostrymon Clench, 1961, type species: *Papilio endymion* Fabricius, 1781

    Angulopis K. Johnson, 1991, type species: *Thecla autoclea* Hewitson, 1877

Rubroserrata K. Johnson & Kroenlein, 1993, type species: *Thecla mathewi* Hewitson, 1874

Ziegleria K. Johnson, 1993, type species: *Ziegleria bernardi* K. Johnson, 1993

Arzecla Duarte & Robbins, 2010, type species: *Thecla arza* Hewitson, 1874

Badecla Duarte & Robbins, 2010, type species: *Thecla badaca* Hewitson, 1868

Kisutam K. Johnson & Kroenlein, 1993, type species: *Thecla syllis* Godman & Salvin, 1887

Lamprospilus Geyer, 1832, type species: *Lamprospilus genius* Geyer, 1832

Argentostriatus K. Johnson, 1991, type species: *Thecla tamos* Godman & Salvin, 1887

Mercedes K. Johnson, 1991, type species: *Thecla demonassa* Hewitson, 1868

Strymonina Tutt, 1907

Type Genus *Strymon* Hübner, 1818

Strymonini Tutt was placed on the Official List of Family-Group Names in Opinion 541 (ICZN, 1959).

= Thereusina K. Johnson & Kroenlein, 1993 [type genus *Thereus* Hübner, [1819]].

Unavailable under ICZN Articles 13.1 and 13.2 because Thereusina is a family-group name proposed after 1930 without "a description or definition that states in words characters that are purported to differentiate the taxon."

Thereus Hübner, [1819], type species: *Papilio lausus* Cramer, 1779

    Molus Hübner, [1819], subsequent designation, Scudder, 1875 (Robbins 2004, first reviser, ICZN art. 24.2), type species: *Papilio phalanthus* Stoll, 1780

    Noreena K. Johnson, MacPherson & Ingraham, 1986, type species: *Noreena maria* K. Johnson, MacPherson

       & Ingraham, 1986

      Solanorum K. Johnson, 1992, type species: *Solanorum gentilii* K. Johnson, 1992

      Timokla K. Johnson, Kruse & Kroenlein, 1997, type species: *Papilio erix* Cramer, 1775

      Pedusa D'Abrera, 2001, ICZN Opinion 2358 (2015), type species: *Thecla pedusa* Hewitson, 1867

Rekoa Kaye, 1904, type species: *Papilio meton* Cramer, 1779

Heterosmaitia Clench, [1964], type species: *Thecla bourkei* Kaye, 1925

Arawacus Kaye, 1904, type species: *Papilio aetolus* Sulzer, 1776

      Polyniphes Kaye, 1904, (Robbins 1991, first reviser, ICZN art. 24.2), type species: *Polyommatus dumenilii* Godart, [1824]

      Dolymorpha Holland, 1931, type species: *Thecla jada* Hewitson, 1867

      Tigrinota K. Johnson, 1992, type species: *Thecla ellida* Hewitson, 1867

Strymon Hübner, 1818, subsequent designation, Riley, 1922, type species: *Strymon melinus* Hübner, 1818

      Callipareus Scudder, 1872, type species: *Strymon melinus* Hübner, 1818

      Calliparus Hemming, 1967, not available, missp.

      Callicista Grote, 1873, type species: *Callicista ocellifera* Grote, 1873

      Uranotes Scudder, 1876, repl. name for *Callipareus*, (ICZN art. 67.8), type species: *Strymon melinus* Hübner, 1818

      Eiseliana Ajmat, 1978, type species: *Eiseliana koehleri* Ajmat, 1978

      Heoda K. Johnson, Miller & Herrera, 1992, type species: *Thecla heodes* H.H. Druce, 1909

Hypostrymon Clench, 1961, type species: *Thecla critola* Hewitson, 1874

Panthiades Hübner, [1819], subsequent designation, Scudder, 1875, type species: *Papilio pelion* Cramer, 1775

      Cycnus Hübner, [1819], subsequent designation, Scudder, 1875 (Robbins 2004, first reviser, ICZN art. 24.2), type species: *Papilio phaleros* Linnaeus, 1767

      Laotisama Piñas, 2006, not available, nom. nud.

Strephonotina K. Johnson, Austin, Le Crom & Salazar, 1997
type genus *Strephonota* K. Johnson, Austin, Le Crom & Salazar, 1997
Emended under ICZN Articles 19.2, 29, and 32.5.3 from Strephonina K. Johnson, Austin, Le Crom & Salazar, 1997
= Tmolusina Bálint, 2014 [type genus *Tmolus* Hübner, [1819]] **new synonym**

Theclopsis Godman & Salvin, 1887, type species: *Thecla lebena* Hewitson, 1868

      Asymbiopsis K. Johnson & Le Crom, 1997, type species: *Asymbiopsis designarus* K. Johnson & Le Crom, 1997

Ministrymon Clench, 1961, type species: *Thecla leda* W.H. Edwards, 1882

Iaspis Kaye, 1904, subsequent designation, ICZN, 1967, type species: *Thecla temesa* Hewitson, 1868

Crimsinota K. Johnson, 1993, type species: *Thecla socia* Hewitson, 1868

Aubergina K. Johnson, 1991, type species: *Thecla alda* Hewitson, 1868

Tmolus Hübner, [1819], subsequent designation, Scudder, 1875, type species: *Papilio echion* Linnaeus, 1767

      Cyclotrichia K. Johnson, Austin, Le Crom & Salazar, 1997, type species: *Thecla wickhami* Riley, 1919

      Jahuaima Piñas, 2006, not available, nom. nud.

Celmia K. Johnson, 1991, type species: *Papilio celmus* Cramer, 1775

      Uzzia K. Johnson, 1991, (Robbins 2004, first reviser, ICZN art. 24.2), type species: *Thecla uzza* Hewitson, 1873

Rindgea K. Johnson, 1993, senior homonym of *Rindgea* Ferguson 2008 in Geometridae, type species: *Rindgea umuarama* K. Johnson, 1993

Nicolaea K. Johnson, 1993, type species: *Thecla cauter* H.H. Druce, 1907

      Nicolea D'Abrera, 2001, not available, missp.

Terenthina Robbins, 2004, type species: *Thecla terentia* Hewitson, 1868

Siderus Kaye, 1904, type species: *Siderus parvinotus* Kaye, 1904

      Bithys Hübner, 1818, not available, subsequent designation, Riley, 1922; suppr. (ICZN, Opinion 541), type species: *Bithys leucophaeus* Hübner, 1818

      Bythis Hübner, [1831], not available, missp.

Gossenia Bálint, [2019], type species: *Papilio lycabas,* 1777 Cramer

Gargina Robbins, 2004, type species: *Thecla gargophia* Hewitson, 1877

Decussata K. Johnson, Austin, Le Crom & Salazar, 1997, type species: *Decussata colombiana* K. Johnson, Austin, Le Crom & Salazar, 1997

Ostrinotes K. Johnson, Austin, Le Crom & Salazar, 1997, type species: *Thecla ostrinus* H.H. Druce, 1907

Strephonota K. Johnson, Austin, Le Crom & Salazar, 1997, type species: *Thecla strephon occidentalis* Lathy, 1926

    Strephonota Salazar, 1995, not available, nom. nud.

    Zigirina K. Johnson, Austin, Le Crom & Salazar, 1997, (Robbins 2004, first reviser, ICZN art. 24.2), type species: *Thecla zigira* Hewitson, 1869

    Syedranota K. Johnson, Austin, Le Crom & Salazar, 1997, (Robbins 2004, first reviser, ICZN art. 24.2), type species: *Thecla syedra* Hewitson, 1867

    Treboniana K. Johnson, Austin, Le Crom & Salazar, 1997, (Robbins 2004, first reviser, ICZN art. 24.2), type species: *Thecla trebonia* Hewitson, 1870

    Serratonotes K. Johnson, Austin, Le Crom & Salazar, 1997, (Robbins 2004, first reviser, ICZN art. 24.2), type species: *Thecla porphyritis* H.H. Druce, 1907

    Letizia K. Johnson, Austin, Le Crom & Salazar, 1997, (Robbins 2004, first reviser, ICZN art. 24.2), type species: *Thecla phoster* H.H. Druce, 1907

    Robustana K. Johnson, Austin, Le Crom & Salazar, 1997, (Robbins 2004, first reviser, ICZN art. 24.2), type species: *Robustina prima* K. Johnson, Austin, Le Crom & Salazar, 1997

    Diminutina K. Johnson, Austin, Le Crom & Salazar, 1997, (Robbins 2004, first reviser, ICZN art. 24.2), type species: *Thecla tyriam* H.H. Druce, 1907

    Dindyminotes K. Johnson, Austin, Le Crom & Salazar, 1997, (Robbins 2004, first reviser, ICZN art. 24.2), type species: *Papilio dindymus* Cramer, 1775

    Exorbaetta K. Johnson, Austin, Le Crom & Salazar, 1997, type species: *Thecla metanira* Hewitson, 1867

    Meridaria Bálint, 2014, type species: *Meridaria hightoni* Bálint, 2014

Trichonidina Duarte & Faynel, **new subtribe**
Type Genus *Trichonis* Hewitson, 1865

Bistonina Robbins, 2004, type species: *Thecla biston* Möschler, 1877

Trichonis Hewitson, 1865, type species: *Papilio theanus* Cramer, 1777

Manticia Bálint, 2019, type species: *Thecla mantica* H.H. Druce, 1907

Megathecla Robbins, 2002, repl. name for *Gullivera*, (ICZN art. 67.8), type species: *Thecla gigantea* Hewitson, 1867

    Gulliveria D'Abrera & Bálint, 2001, not available, preocc. (Castelnau, 1878)., type species: *Thecla gigantea* Hewitson, 1867

    Gullivera D'Abrera, 2001, not available, incorrect original spelling, type species: *Thecla gigantea* Hewitson, 1867

    Gullicaena Bálint, 2002, repl. name for *Gulliveria*. (ICZN art. 67.8), type species: *Thecla gigantea* Hewitson, 1867

Callophryidina Tutt, 1907
Type Genus *Callophrys* Billberg, 1820
Emended under Articles 19.2, 29, and 32.5.3 from Callophryidi Tutt, 1907
= Neolycaenina Korb, 1997 [Type Genus *Neolycaena* de Nicéville, 1890], **new synonym**
= Satyriumina Bálint & Costa, 2012 [Type Genus *Satyrium* Scudder, 1876]
Unavailable under ICZN Article 16.1 because Satyriumina was introduced after 1999 without being "explicitly indicated as intentionally new."

Callophrys Billberg, 1820, subsequent designation, Scudder, 1875, type species: *Papilio rubi* Linnaeus, 1758

    Lycus Hübner, [1819], not available, preocc. (Fabricius, 1787), type species: *Papilio rubi* Linnaeus, 1758

    Licus Hübner, 1823, not available, missp.

    Mitoura Scudder, 1872, type species: *Thecla smilacis* Boisduval & Le Conte, [1835]

    Mitouri Scudder, 1872, not available, incorrect original spelling, type species: *Thecla smilacis* Boisduval & Le Conte, [1835]

    Mitura Butler, 1875, not available, missp.

    Incisalia Scudder, 1872, type species: *Lycus niphon* Hübner, [1819]

    Satsuma Murray, 1874, not available, preocc. (Adams, 1868), type species: *Lycaena ferrea* Butler, 1866

    Ahlbergia Bryk, 1946, repl. name for *Satsuma*. (ICZN art. 67.8), type species: *Lycaena ferrea* Butler, 1866

Ginzia Okano, 1947, repl. name for *Satsuma*. (ICZN art. 67.8); Hemming (1967) gave the year as 1941, type species: *Lycaena ferrea* Butler, 1866

Calophrys Barragué, 1954, not available, missp.

Sandia Clench & Ehrlich, 1960, type species: *Callophrys (Sandia) mcfarlandi* Ehrlich & Clench, 1960

Xamia Clench, 1961, type species: *Thecla xami* Reakirt, [1867]

Cisincisalia K. Johnson, 1992, type species: *Cisincisalia moecki* K. Johnson, 1992

Novosatsuma K. Johnson, 1992, type species: *Novosatsuma monstrabila* K. Johnson, 1992

Deciduphagus K. Johnson, 1992, type species: *Thecla augustinus* Westwood, 1852

Cissatsuma K. Johnson, 1992, type species: *Satsuma albilinea* Riley, 1939

Loranthomitoura Ballmer & Pratt, 1992, type species: *Thecla spinetorum* Hewitson, 1867

Cyanophrys Clench, 1961, type species: *Strymon agricolor* Butler & H. Druce, 1872

Plesiocyanophrys K. Johnson, Eisele & MacPherson, 1993, type species: *Thecla goodsoni* Clench, 1946

Antephrys K. Johnson, Eisele & MacPherson, 1993, type species: *Antephrys prestoni* K. Johnson, Eisele & MacPherson, 1993

Mesocyanophrys D'Abrera, 1995, not available, nom. nud.

Paracyanophrys D'Abrera, 1995, not available, nom. nud.

Mesacyanophrys D'Abrera, 1995, not available, nom. nud.

Mesocyanophrys K. Johnson, 1997, type species: *Thecla lycimna* Hewitson, 1868

Apophrys K. Johnson & Le Crom, 1997, type species: *Hesperia herodotus* Fabricius, 1793

Chalybs Hübner, [1819], subsequent designation, Scudder, 1875, type species: *Papilio janias* Cramer, 1779

Chalyps Hübner, [1826], not available, missp.

Ocaria Clench, 1970, type species: *Thecla ocrisia* Hewitson, 1868

Arases K. Johnson, 1992, type species: *Arases clenchi* K. Johnson, 1992

Galba K. Johnson, 1992, not available, preocc. (Schrank 1803)., type species: *Galba elvira* K. Johnson, 1992

Lamasa K. Johnson, 1992, type species: *Thecla calesia* Hewitson, 1870

Variegatta K. Johnson, 1992, type species: *Thecla elongata* Hewitson, 1870

Ocacuni Piñas, 2006, not available, nom. nud.

Kurtaria Bálint, 2019, repl. name for *Galba*. (ICZN art. 67.8), type species: *Galba elvira* K. Johnson, 1992

Magnastigma Nicolay, 1977, type species: *Thecla tegula* Hewitson, 1868

Satyrium Scudder, 1876, type species: *Lycaena fuliginosa* W.H. Edwards, 1861

Chrysophanus Hübner, 1818, not available, subsequent designation, Riley, 1922; suppr. (ICZN, Opinion 541), type species: *Chrysophanus mopsus* Hübner, 1818

Chrysophanes Weidemeyer, 1864, not available, missp.

Argus Gerhard, 1850, not available, preocc. (Bohadsch, 1761), type species: *Lycaena ledereri* Boisduval, 1848

Callipsyche Scudder, 1876, (Ziegler 1960, first reviser, ICZN art. 24.2), type species: *Thecla behrii* W.H. Edwards, 1870

Neolycaena Nicéville, 1890, type species: *Lycaena sinensis* Alphéraky, 1881

Nordmannia Tutt, 1907, type species: *Lycaena myrtale* Klug, 1834

Edwardsia Tutt, 1907, not available, preocc. (Costa, 1838), type species: *Papilio w-album* Knoch, 1782

Klugia Tutt, 1907, not available, preocc. (Robineau-Desvoidy, 1863), type species: *Papilio spini* Fabricius, 1775

Kollaria Tutt, 1907, not available, preocc. (Pictet, 1841), type species: *Thecla sassanides* Kollar, 1849

Felderia Tutt, 1907, not available, preocc. (Walsingham, 1887), type species: Thecla w-album var. *eximia* Fixsen, 1887

Erschoffia Tutt, 1907, not available, preocc. (Swinhoe, 1900), type species: *Thecla lunulata* Erschoff, 1874

Fixsenia Tutt, 1907, type species: *Thecla herzi* Fixsen, 1887

Leechia Tutt, 1907, not available, preocc. (South, 1901), type species: *Thecla thalia* Leech, 1893

Bakeria Tutt, 1907, not available, preocc. (Kieffer, 1905), type species: *Lycaena ledereri* Boisduval, 1848

Chattendenia Tutt, 1908, repl. name for *Edwardsia*. (ICZN art. 67.8), type species: *Papilio w-album* Knoch, 1782

Strymonidia Tutt, 1908, repl. name for *Leechia* (ICZN art. 67.8), precedence over *Chattendenia*, type species: *Thecla thalia* Leech, 1893

Strymonidea Dunk, 1952, not available, missp.

Pseudothecla Strand, 1910, repl. name for *Erschoffia*. (ICZN art. 67.8), type species: *Thecla lunulata* Erschoff, 1874

Superflua Strand, 1910, repl. name for *Kollaria*. (ICZN art. 67.8), type species: *Thecla sassanides* Kollar, 1849

Thecliolia Strand, 1910, repl. name for *Felderia*. (ICZN art. 67.8), type species: Thecla w-album var. *eximia* Fixsen, 1887

Thecliola Waterhouse, 1912, not available, missp.

Tuttiolia Strand, 1910, repl. name for *Klugia*. (ICZN art. 67.8), type species: *Papilio spini* Fabricius, 1775

Tuttiola Hemming, 1967, not available, missp.

Necovatia Verity, 1951, type species: *Papilio acaciae* Fabricius, 1787

Euristrymon Clench, 1961, type species: *Papilio favonius* J.E. Smith, 1797

Phaeostrymon Clench, 1961, type species: *Thecla alcestis* W.H. Edwards, 1871

Harkenclenus dos Passos, 1970, repl. name for *Chrysophanus*. (ICZN art. 67.8), type species: *Chrysophanus mopsus* Hübner, 1818

Rhymnaria Zhdanko, 1983, type species: *Lycaena rhymnus* Eversmann, [1832]

Armenia Dubatolov & Korshunov, 1984, repl. name for *Argus* and *Bakeria* (ICZN art. 67.8), type species: *Lycaena ledereri* Boisduval, 1848

Neosatyrium Fisher, 2009, type species: *Rusticus calanus* Hübner, [1809]

Thaeides K. Johnson, Kruse & Kroenlein, 1997, type species: *Thecla theia* Hewitson, 1870

Radissima K. Johnson, 1992, type species: *Sithon umbratus* Geyer, 1837

Erora Scudder, 1872, type species: *Thecla laeta* W.H. Edwards, 1862

Androcona K. Johnson, Eisele & MacPherson, 1993, type species: *Thecla muridosca* Dyar, 1918

Sarracenota K. Johnson, Eisele & MacPherson, 1993, type species: *Thecla opisena* H.H. Druce, 1912

Necmitoura K. Johnson, Eisele & MacPherson, 1993, type species: *Necmitoura marcusa* K. Johnson, Eisele & MacPherson, 1993

Semonina Robbins, 2004, type species: *Thecla semones* Godman & Salvin, 1887

Chlorostrymon Clench, 1961, type species: *Thecla telea* Hewitson, 1868