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Lepidoptera from the Pantepui. Part XVIII. A new subspecies of *Laothus* and description of the hitherto unknown male of *Cyanophrys roraimiensis* (Lepidoptera: Lycaenidae)

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Abstract – A new subspecies of *Laothus numen* (Druce, 1907) (Lycaenidae: Theclinae: Eumaeini) is described from the highlands of the Guiana Shield: *Laothus numen keylae* Costa, Grishin & Bálint, ssp. nov. Additionally, the male of *Cyanophrys roraimiensis* Johnson & Smith, 1993, previously known exclusively from the female holotype, is described and illustrated for the first time. Finally, we discuss the evolutionary implications of these taxa, contrasting the phenotypic stability of *C. roraimiensis* across isolated tepui massifs with the allopatric divergence exhibited by *L. numen keylae* ssp. nov. With 12 original figures.

Key words – Auyán Tepui, Cerro Duida, endemism, Eumaeini, Guiana Highlands, Roraima, Serranía del Cuao, subspecific divergence

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Resumen – Lepidoptera del Pantepui. Parte XVIII. Una nueva subespecie de *Laothus* y descripción del macho hasta ahora desconocido de *Cyanophrys roraimiensis* (Lepidoptera: Lycaenidae). Se describe una nueva subespecie de *Laothus numen* (Druce, 1907) (Lycaenidae: Theclinae: Eumaeini) de las tierras altas del Escudo Guayanés: *Laothus numen keylae* Costa, Grishin & Bálint, ssp. nov. Adicionalmente, se describe e ilustra por primera vez el macho de *Cyanophrys roraimiensis* Johnson & Smith, 1993, previamente conocido exclusivamente a partir del holotipo hembra. Por último, se discuten las implicaciones evolutivas de estos taxones, contrastando la estabilidad fenotípica de *C. roraimiensis* a lo largo de serranías aisladas con la divergencia alopátrica exhibida por *L. numen keylae* ssp. nov. Con 12 figuras originales.

Palabras clave – Auyán Tepui, Cerro Duida, divergencia subespecífica, endemismo, Eumaeini, Roraima, Serranía del Cuao, Tierras altas de Guayana.

INTRODUCTION

The Pantepui Biogeographical Province (Costa *et al.* 2014, Viloria & Costa 2019) harbours exceptionally high levels of endemism, not only on the tepui summits but also in the cloud forests on their slopes (~1,000 – 2,200 m a.s.l.). For taxa inhabiting the latter zone, endemism is thought to have arisen primarily through the repeated vertical displacement of vegetation belts during Quaternary glacial–interglacial cycles, which would have allowed intermittent biotic exchange among massifs that are isolated today (Rull *et al.* 2019). Among butterflies, some Pantepui endemics have differentiated into distinct taxa on separate massifs, as documented in several Dismorphiini and Pierini (Costa *et al.* 2021*a*, *b*, 2024*b*), whereas others appear morphologically uniform across their entire range. Pantepui endemics may therefore follow markedly different evolutionary trajectories, and comparing taxa that share the same distribution offers a way to explore this diversity.

The Serranía del Cuao (Amazonas State, Venezuela), located at the western extreme of Pantepui, is one of the three mountain ranges that make up the Cuao–Sipapo–Marieta system to the south and south-east of Puerto Ayacucho (Figs. 5, 12). The Cuao Massif consists of sandstones and quartzites of the Roraima Group and reaches a maximum plateau altitude of about 2,000 m a.s.l. It lies on the same parallel as Mount Roraima (~5°N), approximately 750 km away. This range is strongly isolated from eastern Pantepui (Gran Sabana, Auyán Tepui, Mount Roraima, Mount Ayanganna) by the extensive valleys of the Caroní and Caura watersheds (Figs. 5, 11).

Owing to this isolation, several endemic taxa, at both species and subspecies level, have been discovered in this range (*Stevenaria yutajensis* Viloria & Costa, 2016, *Eretris cuaoensis* Viloria & Attal, 2019, *Pedaliodes parakana* Viloria & Costa, 2019, *Euptychia woroina* Viloria & Benmesbah, 2020, *Pseudopieris viridula autana* Costa & Viloria, 2021, and *Dismorphia zathoe hernandi*

Costa & Neild, 2021, among other taxa). During recent expeditions to western Pantepui (2016–2024), we were fortunate to find two lycaenid species previously thought to be endemic to eastern Pantepui: *Laothus numen* (Druce, 1907) and *Cyanophrys roraimiensis* Johnson & Smith, 1993. The three female specimens of the former showed constant characters that distinguish them from females of *L. numen* from eastern Pantepui. As no males were available, we carried out a comprehensive genomic analysis to determine their taxonomic status. For the latter, we obtained the previously unknown male, allowing its morphology to be evaluated for the first time. Because both species occur at the eastern and western extremes of Pantepui, are separated by the same lowland barriers and inhabit similar montane forests, they provide a natural comparison. Here we show that *L. numen* has diverged across this gap, whereas *C. roraimiensis* has remained uniform in both morphology and mitochondrial DNA. We then discuss what these contrasting patterns suggest about the processes shaping the Pantepui butterfly fauna.

MATERIALS AND METHODS

After capture, specimens were placed in glassine envelopes and then transferred to the laboratory, where they were set, labelled, digitized, and inventoried with serial numbers from the Lycaenidae Pantepui Database (LPD), managed by MC with identifications by ZB. For morphological studies, we used standard lepidopterological techniques (Winter 2000). One male of *Cyanophrys roraimiensis* (specimen LPD #372) was dissected (HNHM Bálint genitalia preparation No. 1743), and the preparation is kept with the relevant specimen in a plastic microvial filled with glycerol. Specimen anatomy was examined at HNHM using an Olympus SZX12 optical stereomicroscope; digital images were captured with an attached Olympus DP70 digital camera. Adult specimens were photographed at the MC collection using a Nikon D7000 digital camera equipped with an AF-S VR Micro-Nikkor 105mm f/2.8G IF-ED lens.

The terminology of wing venation follows the Comstock-Needham nomenclature system (Miller 1970).

Molecular analysis: DNA processing (CCDB protocol). DNA extraction, amplification, and sequencing were carried out at the Canadian Centre for DNA Barcoding (CCDB, University of Guelph) following standard high-throughput protocols (Ivanova *et al.* 2006). Genomic DNA was isolated using the automated Glass Fiber Plate (GFP) extraction method. For specimens with well-preserved DNA, the standard Sanger sequencing pipeline was employed to amplify the 658 base-pair (bp) barcode region of the mitochondrial cytochrome *c* oxidase subunit I (COI) gene. For older historical collection specimens or samples displaying degraded DNA, target fragments were recovered

using the CCDB Next-Generation Sequencing (NGS) protocol. Sequence assembly and initial quality control were performed through the Barcode of Life Data Systems (BOLD) workflow.

Genomic sequencing and phylogenetic analysis (Nick V. Grishin laboratory protocol): genomic processing followed established procedures (Li *et al.* 2019; Zhang *et al.* 2019). In brief, genomic DNA was extracted from a single leg per specimen. Shotgun libraries were constructed and sequenced as 150 bp paired-end reads on an Illumina platform. Protein-coding sequences were assembled from the resulting reads using DIAMOND (Buchfink *et al.* 2015) with a reference protein dataset from *Calycopis cecrops* (Fabricius, 1793) (Cong *et al.* 2016). Maximum likelihood phylogenetic trees were constructed using IQ-TREE v1.6.12 (Nguyen *et al.* 2015) under the GTR+G model for three separate datasets: (1) nuclear autosomes, (2) genes predicted to be located on the Z chromosome, and (3) the mitochondrial genome. Nodal support was evaluated using ultrafast bootstrap approximation with 1000 replicates (Minh *et al.* 2013). The whole-genome shotgun datasets generated in this study will be deposited in the NCBI database (https://www.ncbi.nlm.nih.gov/) under BioProject PRJNA1517279. The COI barcode sequences received GenBank accession numbers PZ877611–PZ877616. Sequence data for the Brazilian specimen *Cyanophrys bertha* (DRD1078) were provided by Diego R. Dolibaina and registered at SISGEN with the code R299D41.

Abbreviations – a.s.l.= above sea level; COI = Cytochrome c Oxidase Subunit I; DFW (VFW) = dorsal (ventral) forewing; DHW (VHW) = dorsal (ventral) hindwing; HT = holotype; LNU = *Laothus numen* specimen; LPD = Lycaenidae Pantepui Database; MC = Mauro Costa; NVG = Nick V. Grishin; ZB = Zsolt Bálint.

Depositories and collection codens – AFN = Andrew F. Neild collection (London, UK); CF = Christophe Faynel collection (Montaud, France); HNHM = Hungarian Natural History Museum (Budapest, Hungary); MCC = Mauro Costa collection (Caracas, Venezuela); MIZA = Museo del Instituto de Zoología Agrícola, Facultad de Agronomía, Universidad Central de Venezuela (Maracay, Venezuela); NHMUK = The Natural History Museum (London, UK); NP = Nino Page collection (Cayenne, French Guiana); SISGEN = Sistema Nacional de Gestão do Patrimônio Genético e do Conhecimento Tradicional Associado, Brasil; USNM = National Museum of Natural History, Smithsonian Institution (Washington DC, USA).

RESULTS

Family: LYCAENIDAE Leech, 1815
Subfamily THECLINAE Swainson, 1831
Tribe: Eumaeini Doubleday, 1847
Genus *Laothus* Johnson, Kruse & Kroenlein, 1997

The genus *Laothus* (type species: *Thecla barajo* Reakirt, [1867]) currently comprises nine species as has been monographed by Prieto *et al*. (2025). These species, predominantly adapted to montane habitats, are distributed from Mexico and Central America to Argentina along the Andean arc. Representatives of this genus inhabit other mountain ranges isolated from the Andes, such as south-eastern Brazil and Pantepui; among these, *Laothus numen* (Druce, 1907) stands out: a showy and rare hairstreak butterfly, characterised by a marked sexual dimorphism (Fig. 2 d, e, f, h) and, until now, known exclusively from eastern Pantepui.

Laothus numen (Druce, 1907)
(Figure 1)

This beautiful lycaenid was discovered by Henry Whitely, a British ornithologist and explorer, who was probably the first naturalist to reach the montane levels (1,000–2,000 m a.s.l.) of a tepui during his pioneering expeditions to Mount Roraima and Kukenán Tepui between 1881 and 1883 (Whitely 1884). During these expeditions, Whitely collected mainly birds, but also insects (Coleoptera and Lepidoptera); it was precisely from these travels that he obtained the type specimens (one male and one female) of *Laothus numen* along with other butterflies, several of which were later described as new taxa (such as *Dismorphia crisia roraimae* Hall, 1939, and *Heliconius elevatus roraima* Turner, 1966). The syntypes of *Laothus numen* are currently preserved at the NHMUK [see illustrations in the original description by Druce (1907: plate XXXII, figs. 4 male, 5 female) and photos in D'abrera (1995: 1258)].

During our recent expeditions to western Pantepui (2016–2024), particularly to the Serranía del Cuao (Amazonas State, Venezuela) and Cerro Duida, we collected four female specimens similar in habitus to *Laothus numen*, yet possessing consistent differences from all known females of this species.

Material examined (n=11; all from eastern Pantepui: six males, five females) – BRITISH GUIANA: Roraima, Whitely // B.M. TYPE No. Rh 555 (NHMUK: male syntype); Roraima, Whitely (NHMUK: female syntype); VENEZUELA: Bolívar, Auyán Tepui, Guayaraca, 1100 m, 16. IV. 1956. (MIZA,on loan USNM: male); Bolívar, Gran Sabana, S. Fco de Yuruaní – Peraitepui, km 7, 1200 m, 27. III. 1986, leg. M. Costa (MCC: male, LPD # 314); Region 7, Mt. Ayanganna,

24. IV. 1999, leg. Fratello, DNA: NVG-18107E11, GenBank PZ877616 (USNM: female); Bolívar, Gran Sabana, Sta. Elena-Icabarú, Km 24.6, 1050 m, 07. II. 1999, leg. A. Neild (AFN: female, LPD # 348); Bolívar, Gran Sabana, San Francisco de Yuruaní – Peraitepui, km 7, 1200 m, 12. IX. 2003, leg. M. Costa, DNA: NVG-23031F03, GenBank PZ877615 (MCC: male, LPD # 284); Bolívar, Sierra de Lema, La Escalera, 1400 m, 23. II. 2004, leg. M. Costa, DNA: NVG-23031F04, GenBank PZ877614 (MCC: female, LPD # 285); Bolívar, Gran Sabana, Río Karuay, 1000 m, 02. I. 2010, leg. M. Costa (MCC: male, LPD # 288); Bolívar, Gran Sabana, Sororopán Tepui, 1700 m, 16. XII. 2015, leg. M. Costa (MCC: female, LPD # 287); Bolívar, Auyán Tepui, Guayaraca-El Danto, 1400 m, 27. I. 2019 leg. M. Costa and M. Benmesbah (CF: male, LPD # 313).

Laothus numen keylae Costa, Grishin & Bálint, **ssp. nov.**
(Figures 1–2)

Type material (all from western Pantepui) – Holotype female, set dorsally, in good condition; forewing costa length = 20.4 mm; labelled as: (1) VENEZUELA [/] Amazonas [/] Serranía del Cuao [/] Valle del Caño Negro [/] 1360 m [/] 15-II-2016 [/] 05°05'07"N – 67°26'26"W [/] *M. Costa* (square label, paper white, letters and numbers black printed); (2) LPD # 286 (3) DNA sample: NVG-23031F06, COI barcode GenBank PZ877612. To be deposited in MIZA (Fig. 2). Paratypes (n = 2): VENEZUELA: Amazonas, Serranía del Cuao, Cerro Paraka, 1500 m, 22. III. 2016, leg. M. Costa, DNA sample: NVG-23031F05, COI barcode GenBank PZ877613 (MCC: female, LPD # 283); VENEZUELA, Amazonas, Serranía del Cuao, Valle del Caño Negro, 12. III. 2024, 1400 m, 05°05'14"N-67°26'19"W, leg. N. Page (NP: feamle, LPD # 398).

Barcode sequence of the holotype. Sample NVG-23031F06, 658 base pairs. GenBank PZ877612

AACTTTATATTTTATCTTTGGTATTTGAGCAGGTATATTAGGAACTTCTTTA-
AGAATTTTAATTCGAATAGAACTAGGTACACCAGGATCTTTAATTGGTGATGAT-
CAAATTTATAATACTATTGTTACAGCTCATGCTTTTATTATAATTTTTTTTATAGT-
TATACCTATTATAATTGGAGGATTTGGAAATTGATTAGTACCCCTAATATT-
AGGAGCCCCTGATATAGCATTTCCACGAATAAATAATATAAGATTTTGAT-
TATTACCTCCTTCATTAATATTATTAGTTTCAAGAAGAATTGTAGAAAATG-
GAGCAGGAACAGGATGAACAGTTTATCCCCCACTTTCATCTAATATTGCT-
CATGGAGGATCCTCAGTTGATTTAGCTATTTTTTCCTTACATTTAGCAG-
GAATTTCTTCAATTTTAGGAGCTATTAATTTTATTACAACTATTATTAATATAC-
GAGTTAATAATTTATCATTTGATCAAATATCATTATTTATTTGAGCTGTAGGAAT-
TACAGCATTATTATTATTATTATCTTTACCAGTTTTAGCTGGAGCTATTACTATAT-
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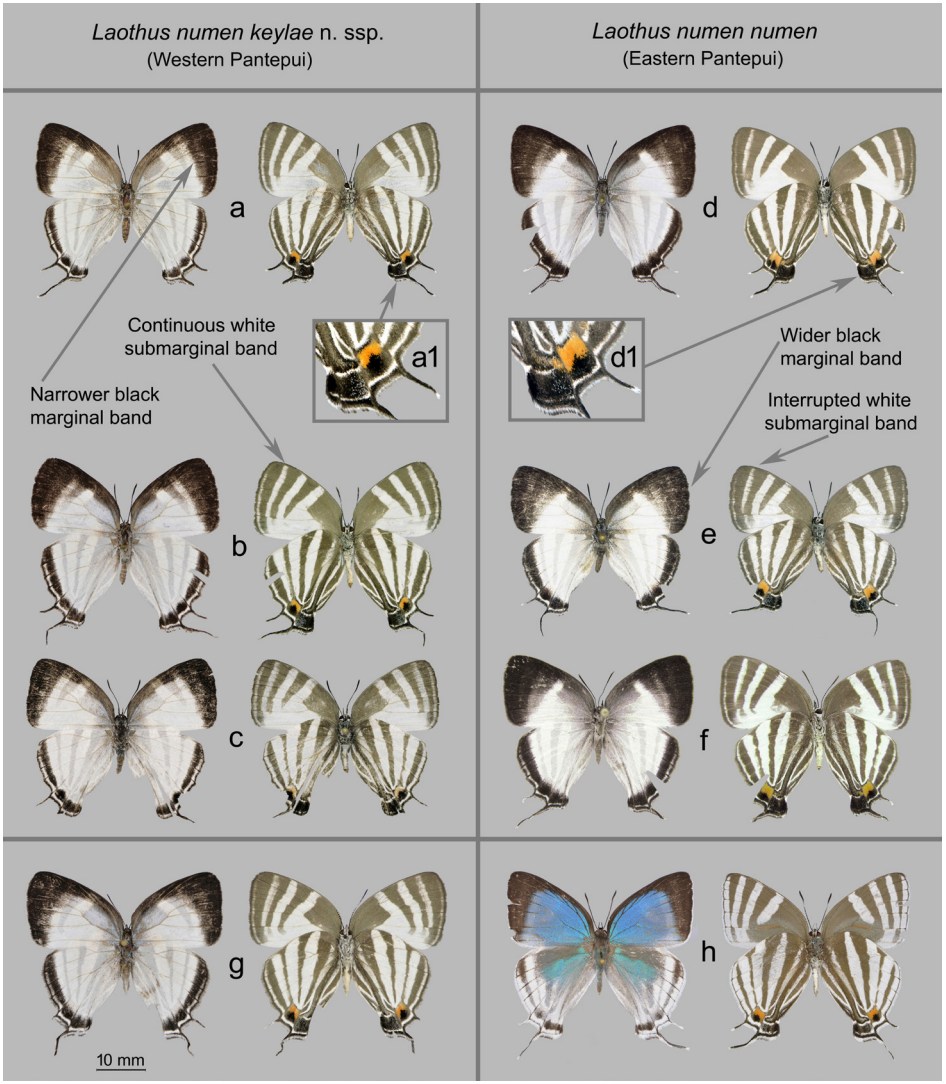


Figure 1. Comparison of *Laothus numen* females from western Pantepui (left half) and eastern Pantepui (right half): a–c = *Laothus numen keylae* ssp. nov., female holotype and paratypes (LPD # 283 and # 398); d–f = *Laothus n. numen* female specimens LPD # 285, # 287 and specimen from British Guyana (USNM); a1, d1 = details of the "thecla-spot"; g = *Laothus numen* female from Duida Massif (LPD # 367); h = *Laothus numen numen,* male specimen from south-eastern Venezuela, Bolívar State, Gran Sabana (LPD # 288). Scale bar (10 mm) applies to all specimens except enlarged details (×2.4). Compiled by M. Costa.

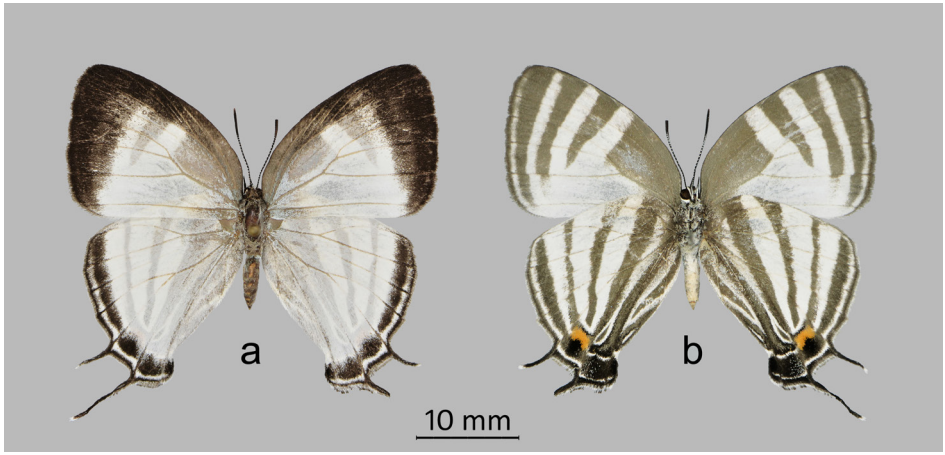


Figure 2. *Laothus numen keylae* ssp. nov. Holotype female: a = dorsal view; b = ventral view. Scale as indicated. Compiled by M. Costa.

Additional material examined (from southwestern Pantepui) – VENEZUELA, Amazonas, Cerro Duida, 1500 m, 15. XII. 2021, leg. H. Camico (MCC: female LPD # 367), DNA: NVG-23031F07. This single specimen may represent a variation or an undescribed subspecies and for this reason is not included in the type series.

Diagnosis – Females of *Laothus numen* can be recognized by the white dorsal colouration with dark margins, a characteristic shared exclusively with both *L. gibberosa* and *L. phydela* (Hewitson, 1867); *L. numen* is distinguished from *L. gibberosa* by the lack of a white spot near the subcostal vein at the base of the VFW and from *L. phydela* by the lack of scattered white scales in the median and post median dark bands of the VFW and by the presence of a black marginal band on the DHW (Prieto *et al*. 2025).

Description – Female: mean forewing length along costa: 20.3 mm (n = 3). The three available females of *Laothus numen keylae* ssp. nov. are in most respects similar to those of *L. numen numen*; however, they differ consistently from the nominate subspecies in the following characters (Fig. 1): (1) Dorsal forewings surfaces: narrower marginal dark band. In *Laothus numen keylae* ssp. nov. this band extends from the outer margin inward only as far as the level of the ventral premarginal dark line (Fig. 1a–c); in *L. n. numen* it is broader, extending proximally up to the postdiscal band (Fig. 1d–f). (2) Ventral forewing surfaces: continuous white submarginal band. In *Laothus numen keylae* ssp. nov. this band is uninterrupted from the costa down to where it merges with the broad white area along the inner margin (Fig. 1a–c); in *L. n. numen* it is disjunct, being interrupted in space Cu1-Cu2, near vein Cu2 (Fig. 1d–f). (3) "*Thecla-spot*": narrower orange spot, approximately half as wide as that of *L. n. numen* (Fig. 1a1, d1). Note that the size of the *Thecla*-spot is constant in both sexes of the nominate subspecies.

Habitat (Figs 3–4) – The habitat of *L. numen keylae* ssp. nov. in the Cuao Range is the montane cloud forest on the slope of Cerro Paraka (Fig. 3), where one of the paratypes was collected at 1,500 m a.s.l. The other two type specimens were found on the Cuao Range plateau, in the Caño Negro valley between 1,360 and 1,400 m a.s.l., within the narrow riparian forest bordering the watercourse (Fig. 4).

This habitat should not be confused with a typical lowland gallery forest, a term usually associated with drier, seasonally arid climates where narrow corridors of forest along riverbanks are sustained by the proximity to the water table. On the summit plateaus of the tepuis, the situation is distinct: rainfall is exceptionally high, but the substrate is predominantly quartzitic sandstone, preventing the development of tall, dense cloud forests like those found on the slopes between 1,000 and 1,500 m a.s.l. A thin layer of organic matter or peat forms on the sandstone slabs, supporting low-growing endemic plants such as *Brocchinia*, *Stegolepis*, *Heliamphora*, and other shrubby or herbaceous taxa. However, along the watercourses, continuous erosion and sedimentation have generated over time a deeper soil profile suitable for the development of a 'high tepui riparian forest', supporting evergreen trees 6 to 12 m in height.



Figure 3. Cloud forest on the western slope of Cerro Paraka (Serranía del Cuao, Amazonas State, Venezuela). In the background, cliffs of nearby Cerro Woroi. Photo: M. Costa.



Figure 4. The Caño Negro valley (1,300 -1,400 m a.s.l.) on the Cuao Range plateau. Photo: M. Costa.

Distribution – *Laothus numen* is a very rare butterfly, previously known from only a few specimens from eastern Pantepui, where it has been collected between 1,000 and 1,700 m a.s.l. (Fig. 5). The first records are those of Whitely, based on which Druce (1907) described the species stating "Roraima, British Guiana" as the type locality. Whitely did not specify the exact collection locality or capture date for the male and female type specimens. However, as deduced from Whitely's route depicted on his map (Whitely 1884), which lies entirely west of Kukenán Tepui and Mt. Roraima, the specimens were actually collected in Venezuelan territory on the western slopes of these mountains during his 1881–1883 expeditions.

Figure 5 shows the known collection localities of *L. n. numen* (green circles): in Venezuela, Auyán Tepui and several localities in the Gran Sabana (Sierra de Lema, Ptarí Tepui and Sororopán Tepui, Mt. Roraima and surrounding areas); and in Guyana, Mt. Ayanganna. All these sites are situated within the eastern Pantepui. The Serranía del Cuao, where the three types of *Laothus numen keylae* ssp. nov. were collected, is located in the extreme western Pantepui. This region is strongly isolated from eastern Pantepui by the vast lowland and river valleys of the Caroní and Caura watersheds. Further south, also isolated, lies the Duida Massif, part of southern Pantepui. The single female specimen (LPD #367, Fig. 1g) from Cerro Duida may represent another undescribed subspecies of *L. numen*; however, additional specimens (and ideally males) will be necessary before it can be formally described.

Etymology – The subspecific epithet is dedicated to Keyla Arana, wife of Hernando Camico (both from the Piaroa community of Raudal del Danto, Amazonas), who accompanied and guided us on seven expeditions to the highlands of the Cuao Range. The name is a noun in the genitive case.

Discussion – Subspecies are rarely described within Neotropical Lycaenidae, largely because the region's immense diversity remains morphologically and biogeographically understudied, and phenotypically distinct taxa are usually proposed as species, later frequently synonymized. Conversely, in better-studied regions with far lower species richness, such as North America north of Mexico, subspecific taxa are routinely recognized.

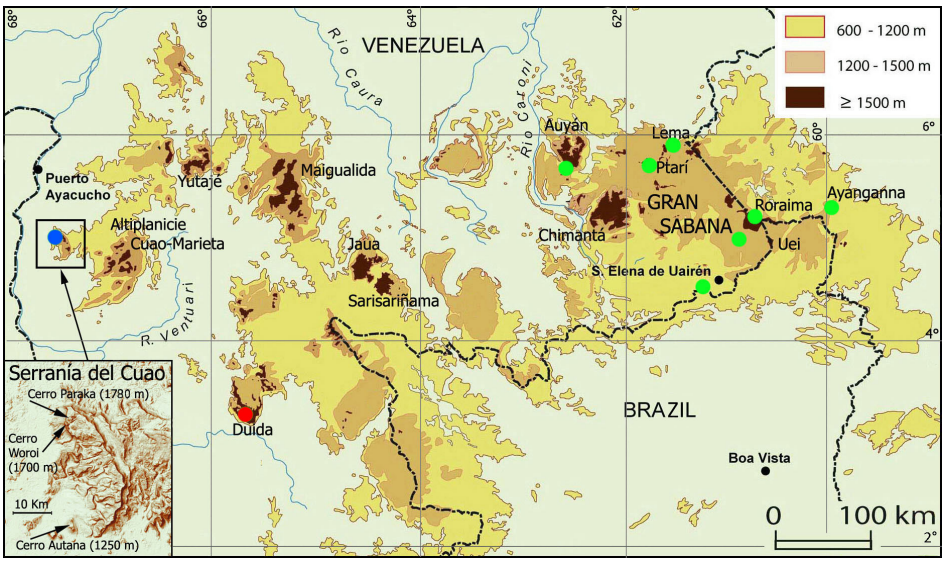


Figure 5. Distribution of *Laothus numen numen* (green circles) in eastern Pantepui and *Laothus numen keylae* ssp. nov. (blue circle) in western Pantepui. The red circle represents the collection locality (Duida Massif) of a single female specimen (LPD # 367, Fig. 1g), which may represent an undescribed subspecies (though, current evidence is insufficient to support this conclusion). Compiled by Gilles Séraphin and M. Costa.

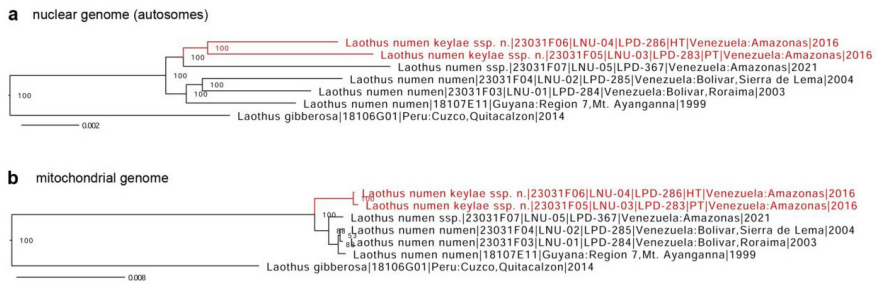


Figure 6. Phylogenetic trees of *Laothus numen* (rooted with *Laothus gibberosa*) constructed from protein-coding regions in: a = the nuclear genome (autosomes), based on 8,489,166 positions; b = the mitochondrial genome. Ultrafast bootstrap (Hoang *et al.* 2018) values are shown at nodes. For each specimen, its species or subspecies name is followed by DNA sample number and other collection numbers, type status (HT: holotype; PT: paratype), locality, and the year of collection; *L. numen keylae* ssp. nov. is shown in red. Compiled by Nick V. Grishin.

With regard to *Laothus numen keylae* ssp. nov., due to the absence of males, a genomic analysis was conducted to evaluate its phylogenetic position (Fig. 6). Analyses of the protein-coding regions of the nuclear genome (autosomes) as well as the mitogenome (Fig. 6a–b) demonstrate that the specimens from Serranía del Cuao (*L. numen keylae* ssp. nov.) form a distinct, well-supported clade. Although the shallow divergence in the COI barcode (approximately 0.6%, 4 bp) indicates that this population is best treated at the subspecific level, this conclusion does not rely on COI alone. Single-locus COI barcodes frequently fail to resolve recent or incipient radiation events in butterflies. When analysing thousands of protein-coding loci across the nuclear genome, specimens from Serranía del Cuao form a confidently supported clade distinct from typical *L. numen*, although closely related to it (Fig. 6a). Therefore, these specimens represent a distinct taxon. The specimens of *L. numen* we sequenced do not segregate into two prominent clades that would represent two species, but instead internal branches within the *L. numen* clade are approximately the same length. Therefore, this taxon is proposed as a subspecies. The hypothesis that this population is a distinct subspecies is further supported by biogeographical factors alongside the corresponding adaptation of this species to montane environments, notably the geographic isolation between the eastern and extreme western limits of Pantepui (Fig. 5). This is what distinguishes the Pantepui from the Andes, where there is forest continuity across a vast belt spanning thousands of kilometres, and where, for instance, *Laothus gibberosa*, the species most closely related to *L. numen*, can exhibit gradual phenotypic variations across its vast range of distribution (Colombia, Ecuador, and Peru). The populations across the Pantepui represent a system of high-altitude biogeographical islands driven by vicariant isolation, rather than a continuous clinal distribution like that observed in the Andes. In conclusion, the combination of (1) diagnostic morphological differences in the female wing pattern, (2) genetic differentiation in both nuclear and mitochondrial genomes, and (3) extreme geographic isolation in the westernmost Pantepui strongly supports treating this population as a distinct subspecies, reflecting an ongoing process of vicariant lineage divergence.

The Duida specimen of *L. numen* (LNU-05) reveals nuclear-mitochondrial incongruence: while it is sister to *L. n. keylae* ssp. nov. in the nuclear genome tree (Fig. 6a), it clusters within the *L. numen numen* clade in the mitochondrial genome tree (Fig. 6b). This incongruence likely reflects historical introgression or incomplete lineage sorting (ILS) among these isolated tepuyan populations. Due to its different phylogenetic position in the mitochondrial genome tree and genetic differentiation from both subspecies of *L. numen*, we have excluded the Duida specimen from the type series of *L. numen keylae* ssp. nov., pending the discovery and comparative analysis of additional material.

Genus *Cyanophrys* Clench, 1961

The genus *Cyanophrys* (type species *Strymon agricolor* Butler & Druce, 1872) was originally established as a subgenus of *Callophrys* Billberg, 1820 by Clench (1961), diagnosed by the following key characters: (1) ventral wings green, (2) male scent pad present but very small, and (3) tips of valvae not capped. Subsequently, Eliot (1973), Riley (1975) and Brown (1993a) treated *Cyanophrys* at generic rank without explicit justification. Johnson *et al.* (1993) also applied *Cyanophrys* at the generic level and provided a diagnosis. D'Abrera (1995) followed this treatment when documenting the unpublished nomenclature left by Johnson in the NHMUK collections, thereby introducing several *nomina nuda*. Finally, Robbins (2004a) retained this generic status, and the genus was later formally diagnosed and revised by Robbins and Duarte (2005).

Currently, the genus comprises 17 species (Butterflies of America; Warren *et al*. 2026), some with broad trans-American distributions from Mexico to Argentina, and others with restricted geographical ranges and high conservation concern (Brown 1993b).

Robbins and Duarte (2005) diagnosed *Cyanophrys* on the basis of two key characters: (1) an anal lobe posteriorly produced beyond the outer margin of cell Cu_2-2A, and (2) the presence of a dorsal male genital brush organ. These characters define the genus only in relation to other eumaeines placed by Robbins (2004) in his *Callophrys* Section, but not to other genera within Callophryidina (Robbins *et al.* 2022). However, when combined with non-iridescent (dull) green ventral wing surface (see Kertész *et al.* 2006b), these three characters together unambiguously diagnose the genus (ZB unpubl. data).

Cyanophrys roraimiensis Johnson & Smith, 1993
(Figures 7–10)

Material examined (n = 10; 2 males and 8 females all from Venezuela) – Bolívar, Auyán Tepui, El Peñón, 1850 m, 26. XII. 2012, leg. M. Costa (MCC: female, LPD # 131); Bolívar, Auyán Tepui, entre Libertador y El Oso, 2200 m, 23. XII. 2012, leg. M. Costa (MCC: female, LPD # 132); Bolívar, Sierra de Lema, La Escalera, Km 123 sur El Dorado, 1400 m, 09. IV. 2001, leg. M. Costa (HNHM: female, LPD # 166); Bolívar, Auyán Tepui, El Dragón, 1750 m, 04. II. 2019, leg. M. Costa and M. Benmesbah (MCC: female, LPD # 259); same, 06. II. 2019. (MCC: female, LPD # 307); Bolívar, Sierra de Lema, vía El Dorado-S. Elena, km 131,7, 1400 m, 11–14. II. 1999, leg. A. F. Neild (AFN: female, LPD # 349); Amazonas, Serranía del Cuao, Cerro Paraka, 1500 m, 05–15. I. 2024, leg. M. Costa and H. Camico, (MCC: male, LPD # 372; HNHM: male, LPD # 373, Bálint gen. prep. No. 1743); Amazonas, Serranía del Cuao, Cerro Paraka, 1500 m, 26. XII. 2024, leg. M. Costa and H. Camico (MCC: female, LPD # 393; HNHM: female; LPD # 394).

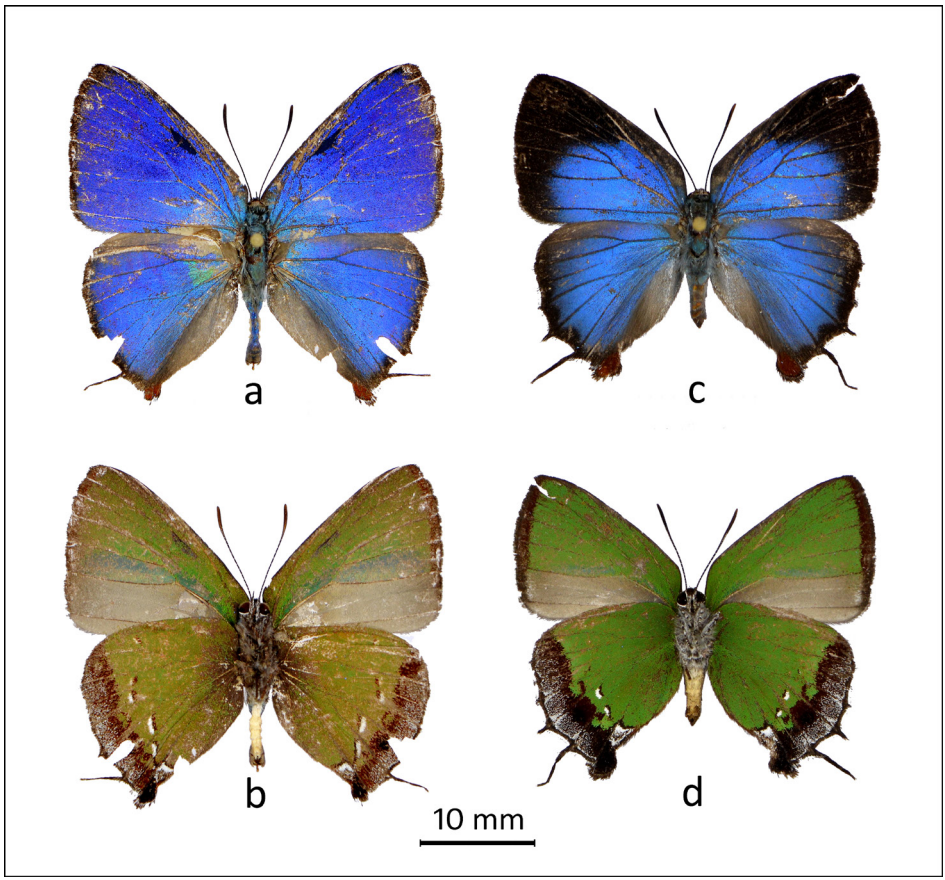


Figure 7. *Cyanophrys roraimiensis* specimens in dorsal and ventral views: a = male (LPD # 372) dorsal; b = ditto, ventral; c = female (LPD # 393) dorsal; d = ditto, ventral. Scale as indicated. Compiled by M. Costa

Discovery and subsequent records – Johnson and Smith (1993) described *Cyanophrys roraimiensis* based on a single female specimen previously reported by Huntington (1933) and later by Comstock and Huntington (1943) as "*Thecla crethona*" (labelled "Arabupu, Brazil, 26 December 1927"), collected by G. H. H. Tate during the Mount Roraima-Mount Duida expeditions of 1927-1929. Contrary to the assumption of Johnson and Smith (1993), according to which Comstock and Huntington (1943) had mentioned additional specimens of *C. roraimiensis*, they in fact cited no other specimens beyond the one later designated as the holotype, from neither Mount Roraima nor Mount Duida. As stated by Robbins and Duarte (2005), a second specimen (also a female) was collected "in the adjoining *tepui* region of Venezuela"; this likely refers to the specimen collected by Andrew Neild in 1999 (Gran Sabana, Sierra de Lema, LPD # 349), which they did not have the opportunity to examine.

Consequently, Robbins and Duarte (2005) did not include *C. roraimiensis* in their analysis, as no specimens were available for study and no male was known to provide the richer set of diagnostic characters required for their work. Later, several female specimens were found during our research in the eastern Pantepui (*cf.* Bálint & Costa 2012), though the male remained unknown. Recently, four specimens of *C. roraimiensis* (two males and two females) were surprisingly collected during two separate expeditions to the western Pantepui (Serranía del Cuao, Amazonas, Venezuela; January and December 2024). Finding no morphological differences between the eastern and western females, and given that mitochondrial analysis of the four western specimens (Cuao Range) and five eastern ones (Gran Sabana) placed them all within a single, undifferentiated clade, we concluded that they belong to the same species, *Cyanophrys roraimiensis*. Here, we redescribe the species (including the male for the first time), confirm its generic placement, and discuss additional aspects of its biology and distribution.

Redescription – Male (Fig. 7a–b): Forewing costa length 16 mm. Head frons with brown scales, thorax and abdomen dorsally blue, abdomen cream white ventrally; dorsal forewing surface bright blue with an absorber observable at a shallow angle, hindwing also bright blue; ventral forewing surface ground colour above cubital vein green and below grey, no pattern; ventral hindwing surface ground colour green with scattered white postmedian spot-pattern, submargin ash-grey with maroon *Thecla*-spot and margin, tornus black, minute tail (1 mm) at vein Cu_1 terminus and longer tail (3 mm) at vein Cu_2 terminus. Scent pad composed by an elongate triangular shaped cluster of androconial scales at the base of veins R_2, R_3 and M_1 and filling the apical corner of the discal cell (Fig. 8), male genitalia with brush organ less developed (Fig. 9).

Female (Fig. 7c–d): Forewing costa length 17–18 mm. Similar to male, but with deeper blue ground colour without dorsal forewing scent organ, and dorsal wing surface with black margin, extremely widened in forewing apical area.

Habitat and distribution – The habitat of *Cyanophrys roraimiensis* in the Cuao Range (western Pantepui) is the same as that of *Laothus numen keylae* ssp. nov. (see above). In eastern Pantepui, *C. roraimiensis* has been collected in the cloud forests along the slopes of Mount Roraima, Sierra de Lema, and Auyán Tepui (Costa *et al.* 2024a: 283–284). On the latter, it has also been found on the summit plateau near El Dragón Camp area (Fig. 10; *cf.* Costa *et al.* 2020: 34–35).

The elevational range of *C. roraimiensis*, between 1,400 and 2,200 m, confirms its status as a species adapted to montane environments. To date, records of *C. roraimiensis* remain strictly confined to the Gran Sabana and Auyán Tepui in eastern Pantepui, and the Serranía del Cuao in western Pantepui (Fig. 11). However, field sampling across the region remains vastly incomplete; it is therefore highly probable that the species occurs across additional massifs throughout the region.

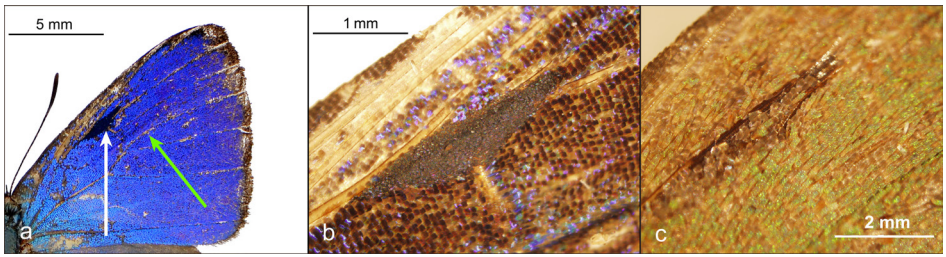


Figure 8. *Cyanophrys roraimiensis* male dorsal forewing scent organ: a = forewing of specimen LPD # 372, showing the androconial cluster (scent pad) located at the bases of the veins R_2, R_3 and M_1 (indicated by the white arrow), and the absorber, best viewed obliquely, composed of cover scales heavily packed with pigment (indicated by the green arrow in its central area); b = forewing of specimen LPD # 373 under higher magnification, showing the scent pad, also visible on the ventral wing surface; c = male ventral forewing (specimen LPD # 373): the apical area of the discal cell on the surface of the ventral forewing without androconia, showing physical alteration of the wing membrane caused by a clearly visible scent pad at the corresponding location on the dorsal wing surface. Scales as indicated. Compiled by Zs. Bálint.

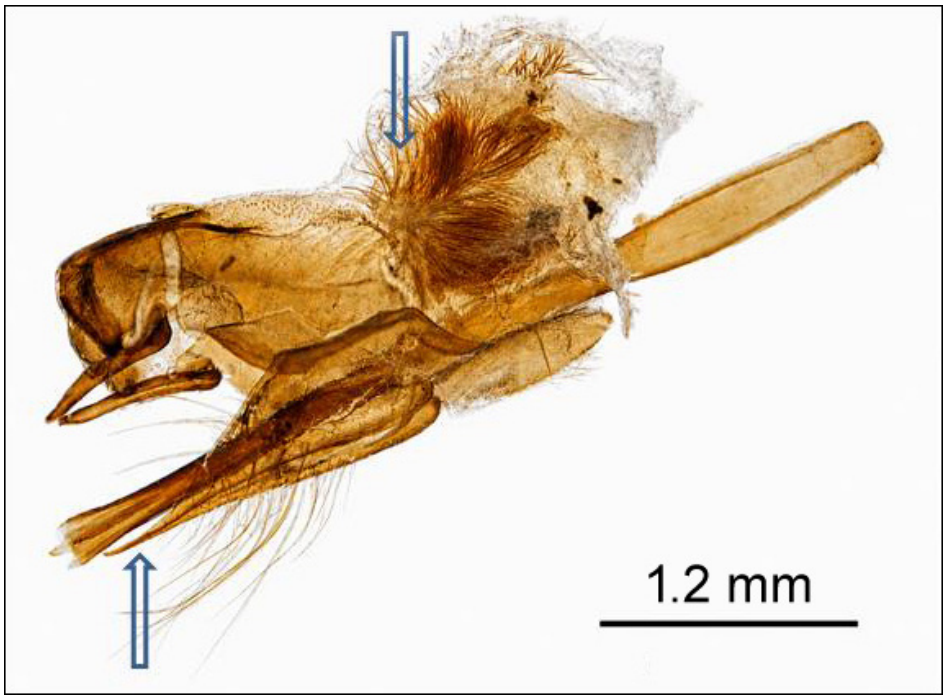


Figure 9. *Cyanophrys roraimiensis* (specimen LPD # 372): male genitalia in lateral and aedeagus in dorsal views with relatively less developed brush organ situated on the anterior end of the vinculum dorsal surface (marked by an arrow pointing from top to bottom) and valve (marked with an arrow pointing up from bottom to top) with a terminal thickening (in ventral view). HNHM Bálint genitalia preparation No. 1743. Scale as indicated. Compiled by Zs. Bálint.



Figure 10. Auyán Tepui plateau, near El Dragón Camp, 1,750 m a.s.l., habitat of *Cyanophrys roraimiensis*. Photo: P. Costa.

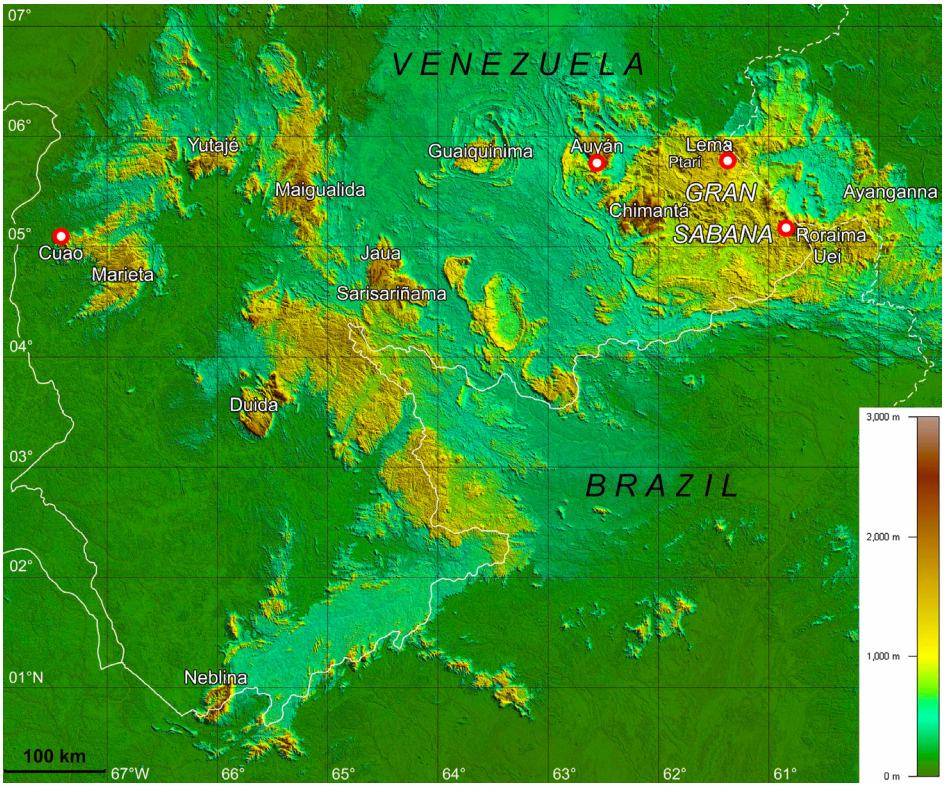


Figure 11. Distribution map of *Cyanophrys roraimiensis* in eastern Pantepui (Gran Sabana, Auyán Tepui) and western Pantepui (Serranía del Cuao). Red circles with white centers indicate locations where *C. roraimiensis* has been recorded. Compiled by C. Brewer-Carías and M. Costa.

Generic placement and intergeneric relationships – The species *C. roraimiensis* perfectly fits within *Cyanophrys,* as its ventral wing surface is dull green, the male dorsal forewing possesses a typical scent pad (see above), and the male genitalia feature a brush organ. Robbins and Duarte (2005) suspected that the species belonged to the *C. crethona –C. miserabilis –C. velezi* species group – recovered as monophyletic in their hypothesized phylogeny – because all these species share a brown frons and a "thin, stringy" brush organ. In contrast, other *Cyanophrys* species possess a green frons and a thicker, chunkier brush organ. However, the male dorsal forewing androconia appear to be differently arranged or absent in those taxa compared to *C. roraimiensis*; furthermore, wing shape, ventral wing pattern, and certain male genitalia traits also differ. Based on our molecular analysis, the clade [*C. remus* + (*C. pseudolongula* + *C. roraimiensis*)] is strongly supported. All taxa within this group share a male dorsal wing surface with a gleaming blue ground colour, as well as a forewing with a black absorber (Fig. 8a; *cf.* Faynel & Bálint, 2012) associated with a long triangular scent pad at the base of veins R_2, R_3 and M_1 (Fig. 8a). This pad leaves a visible imprint on the ventral wing surface (Fig. 8c), which shows that this cluster is a true scent pad (*cf.* Robbins 1991). Moreover, all species within this group possess a male genital dorsal brush organ with the anterior ends of the setae oriented horizontally (Character 11 of Robbins & Duarte 2005), which in lateral view arises primarily above the origin of the vinculum strut (Fig. 9: Character 14 of Robbins & Duarte 2005). The valva of the male genitalia exhibits a thickened terminus, but is not capped as documented for the "Brown-frons Complex of *Cyanophrys sensu lato*" by Johnson and Le Crom (1997) (Character 9 of Robbins & Duarte 2005).

Molecular divergence and population conspecificity – The uncorrected pairwise nucleotide divergence (p-distance) calculated for the cytochrome c oxidase subunit I (COI) barcode region between the *Cyanophrys roraimiensis* populations from south-eastern Venezuela (Gran Sabana, Bolívar State) and from the isolated western Serranía del Cuao (Amazonas State) ranged from 0.15 to 0.31%. This remarkably low genetic distance falls strictly within the expected limits for intraspecific variation in Neotropical Lycaenidae, thereby suggesting that these geographically isolated populations are conspecific. Furthermore, the molecular data, combined with a high degree of morphological stasis, suggest that historical isolation across these discrete tepui systems has not triggered allopatric speciation. However, because this assessment relies solely on mitochondrial data, nuclear genomic markers will be necessary to further test lineage sorting and evaluate potential nuclear gene flow or deeper divergence between these populations (Fig. 12).

Discovery of the unknown male – Historically, *Cyanophrys roraimiensis* was known exclusively from female specimens collected in the eastern portion of Pantepui (Gran Sabana). Given that the newly sampled population from Amazonas State comprises two females and two males, and that their genetic profiles exhibit negligible divergence from the eastern specimens, we confidently

report the discovery and characterization of the hitherto unknown male of *C. roraimiensis*. The integration of molecular tools definitively associates the sexes, providing further insight into the taxonomy of the genus.

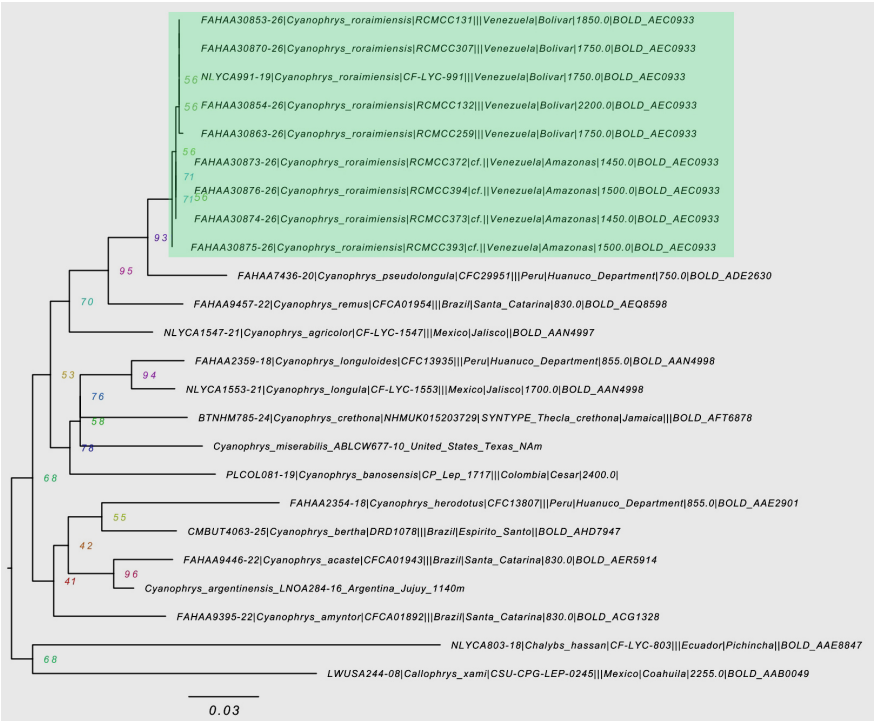


Figure 12. Maximum likelihood phylogenetic tree of *Cyanophrys* species with outgroup from the two closest genera *Chalybs* and *Callophrys*. The tree is based on COI barcode sequences (24 aligned sequences, 658 bp), generated using IQ-TREE with automatic model selection (ModelFinder) and one partition per codon position. Node support values correspond to 2,000 Ultrafast Bootstrap (UFBoot) replicates. The scale bar indicates the number of substitutions per site averaged across partitions in an edge-proportional model. The nine *C. roraimiensis* specimens (five from the eastern and four from the western Pantepui massifs) form the clade highlighted in green. Compiled by C. Fåhraeus.

DISCUSSION

Biogeographical patterns and divergent evolutionary trajectories – The comparative analysis of *Laothus numen* and *Cyanophrys roraimiensis* reveals two contrasting evolutionary trajectories among endemic Lycaenidae across Pantepui. Both species inhabit montane environments and occur at both the eastern and western extremes of this highland system. However, their patterns

of intraspecific variation differ substantially: while *L. numen* exhibits evidence of vicariant isolation and genetic differentiation between disjunct massifs, *C. roraimiensis* displays remarkable phenotypic stability across its entire range.

This contrast highlights key processes governing speciation in the Guiana Highlands; the incipient vicariance observed in *L. numen* mirrors the deeply established divergence of other Pantepui endemics, such as *Pereute lindemannae* Reissinger, 1970 (Pieridae), which has differentiated into distinct subspecific lineages across isolated massifs: *P. l. lindemannae* in the south, and *P. l. pemona* and *P. l. piaroa,* both described by De Marmels, Clavijo & Chacín, 2003, in eastern and western Pantepui, respectively. Similar patterns of montane slope fragmentation are well documented across several Dismorphiini and Pierini lineages (Costa *et al.* 2021*a, b,* 2024*b*). In these cases, deep lowland valleys act as impassable ecological barriers, permanently restricting gene flow and allowing genetic drift and local adaptation to drive morphological and genomic divergence.

Conversely, the phenotypic uniformity of *C. roraimiensis* is shared by several other Pantepui endemics, including *Lamprospilus ayawi* Bálint, Fratello, Costa & Benmesbah 2019, *Thaeides hyperion* Bálint, Costa & Grishin 2024, *Marpesia pantepuiana* Costa, Attal & Viloria 2016, *Greta clavijoi* Neild, 2008, *Caligo suzanna weidmanni* Blandin, Attal, Orellana, Neild, Lamas & Costa 2025, among many more taxa.

Three primary biological mechanisms may account for this morphological stasis across disjunct tepui slopes:

(1) *Dispersal capacity and habitat continuity*: *C. roraimiensis* occupies an elevational range spanning 1,400–2,200 m, inhabiting cloud forest slopes and submontane ecotones (Berry *et al.* 1995, Huber 1995). This ecological flexibility may facilitate episodic gene flow across intermediate elevation corridors, preventing the fixation of distinct phenotypic characters (Rull *et al.* 2019).

(2) *Lineage age and recent range expansion***:** the lack of marked morphological differentiation may reflect a more recent colonization event during Quaternary glacial cycles, when cooler climates caused montane vegetation zones to descend by several hundred metres, establishing temporary ecological connections between now-isolated massifs (Rull *et al.* 2019).

(3) *Stabilizing selection*: strong stabilizing selection may maintain morphological stasis despite ongoing neutral genomic divergence (Futuyma 2009).

Taxonomic implications for Pantepui Lycaenidae – These findings demonstrate that geographic isolation across Pantepui does not necessarily trigger allopatric speciation or visible phenotypic divergence. While genomic data (such as thousands of nuclear loci) confirm that western populations from the Cuao Range form a monophyletic lineage distinct from typical *L. numen*, such nuclear genomic evidence is not yet available for *C. roraimiensis*, leaving its population structure to be inferred solely from its uniform external morphology.

Recognizing both vicariant differentiation and morphological stasis is essential for accurately estimating endemic diversity across the Pantepui Biogeographical Province. Future comparative phylogeographic studies incorporating multi-locus genomic screening will further refine our understanding of whether phenotypically uniform species harbour cryptic genomic divergence or represent genuinely homogeneous, widespread endemic taxa across the Guiana Highlands.

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Authorship contributions. Conceptualisation: Zs. Bálint, M. Costa, A. L. Viloria; Methodology: Zs. Bálint, M. Costa, N. V. Grishin, C. Fåhraeus; Resources: M. Costa, Zs. Bálint, C. Faynel, ; Genomics: N. V. Grishin, C. Fåhraeus, A. M. Schomann; Writing – original draft: M. Costa, Zs. Bálint; Writing – review & editing: all authors. All authors have read and approved the final version of the manuscript.

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A Pántepui lepkéi, XVIII. rész: Egy új *Laothus* alfaj és a *Cyanophrys roraimiensis* eddig ismeretlen hímjének leírása (Lepidoptera: Lycaenidae)

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Összefoglalás –A szerzők a *Laothus numen* (Druce, 1907) (Lángszinérfélék: Farkröpérformák: Farkincás-rokonúak) egy új alfaját írják le a dél-amerikai Guyana-pajzs felföldjeiről: *Laothus numen keylae* Costa, Grishin & Bálint, ssp. nov. néven. Ezenkívül a *Cyanophrys roraimiensis* Johnson & Smith, 1993 hímjét, amelyet korábban kizárólag a nőstény holotípus alapján ismertek, most először írják le és dokumentálják. Végül megvitatják a taxonok rokonsági vonatkozásait, szembeállítva a *C. roraimiensis* fenotípusos stabilitását az izolált tepui-hegységekben a *L. numen keylae* ssp. nov. által mutatott allopatrikus divergenciával.12 eredeti ábrával.

Kulcsszavak –Auyán Tepui, Cerro Duida, endemizmus, Eumaeini, Guayana-felföld, Roraima, Serranía del Cuao, szubspecifikus eltérés.

ÁBRAMAGYARÁZATOK

1. ábra. *Laothus numen* nőstények összehasonlítása a Pantepui régió nyugati (bal hasáb) és keleti (jobb hasáb) részéből: a–c = *Laothus n. keylae* ssp. nov., holotípus és paratípusok (LPD #283 és #398); d–f: *Laothus n. numen* példányok (LPD #285, #287) és példány Brit Guyanából (USNM); a1, d1 = a *Thecla*-folt részletei; g = *Laothus numen* nőstény a Duida-hegységből (LPD #367); h = *Laothus n. numen*, hím példány a Gran Sabanáról (Bolívár állam, Délkelet-Venezuela) (LPD #288). A jelzett méretarány (10 mm) minden példányra vonatkozik, kivéve a nagyított részleteket (×2,4). Készítette: M. Costa.

2. ábra. *Laothus numen keylae* ssp. nov. holotípus nőstény: a = felül nézet, b = fonák nézet; méretarány jelezve. Készítette M. Costa.

3. ábra. Köderdő a Cerro Paraka nyugati lejtőjén (Serranía del Cuao, Amazonas állam, Venezuela). A háttérben a közeli Cerro Woroi sziklái. Fotó: M. Costa.

4. ábra. A Caño Negro völgye (1300-1400 m t.sz.f.) a Cuao-hegység fennsíkján. Fotó: M. Costa.

5. ábra. A *Laothus numen numen* (zöld körök) elterjedése Kelet-Pantepuiban és a *Laothus numen keylae* ssp. nov. (kék kör) elterjedése Nyugat-Pantepuiban. A piros kör egyetlen nőstény példány (LPD # 367, 1g. ábra) gyűjtési helyét (Duida-hegység) jelöli, amely egy leíratlan alfajt képviselhet (bár a jelenlegi bizonyítékok nem elegendőek ennek a következtetésnek az alátámasztására). Összeállította: Gilles Séraphin és M. Costa.

6. ábra. A *Laothus numen* filogenetikai fái (*Laothus gibberosa* gyökerekkel), fehérjét kódoló régiókból felépítve: a = a nukleáris genom (autoszómák), 8 489 166 pozíció alapján; b = a mitokondriális genom. Az ultragyors bootstrap (HOANG *et al.* 2018) értékek a csomópontokban láthatók. Minden példány esetében a faj vagy alfaj nevét a DNS-minta száma és egyéb gyűjtési adatok jelzik, a típusstátusz (HT = holotípus; PT = paratípus), ezt a lelőhely és a gyűjtés éve követi; az *L. numen keylae* ssp. n. piros színnel kiemelve . Összeállította: Nick V. Grishin.

7. ábra. *Cyanophrys roraimiensis* példányok felül és alul nézetben: a = hím (LPD # 372) felülről; b = ugyanaz, alulól; c = nőstény (LPD # 393) felülről; d = ugyanaz, alulról. Méretarány a jelölés szerint. Összeállította: M. Costa.

8. ábra. A *Cyanophrys roraimiensis* hím elülső szárnyának felszínén levő illatszerv: a = az LPD #372 példány szárnya az androkóniális folttal (illatpárna), amely az R2, R3 és M1 erek tövénél található (fehér nyíllal jelölve), és a pigmenttel erősen telített fedőpikkelyekből áll hőelnyelő pikkelyfolt, amely lapos szögből nézve a legjobban látható (a középső területén található zöld nyíllal jelölve); b = az LPD #373 példány elülső szárnyának felszíne, nagyobb nagyításban, amelyen látható az illatpárna, amely a fonákon is látható; c = a fonákon található sejt apikális területe androkónia nélkül, a szárnyhártya fizikai elváltozását mutatva, amelyet a felszín megfelelő helyén levő látható illatpárna okoz (LPD #373. számú példány):. Összeállította: Bálint Zs.

9. ábra. *Cyanophrys roraimiensis* (LPD #372. számú példány) hímivarszerv fogókészüléke oldal-, és az aedeagusban felülnézetben, viszonylag kevésbé fejlett corematával a vinculum háti felszínének elülső végén (felülről lefelé mutató nyíl jelöli) és az elkeskenyedő valvával (alulról felfelé mutató nyíl jelöli). MTM Bálint gen. prep. No. 1743. Összeállította: Bálint Zs.

10. ábra. Az Auyán Tepui-fennsík, El Dragón tábor közelében, 1750 m tengerszint feletti magasságban, a *Cyanophrys roraimiensis* élőhelye. Fotó: P. Costa.

11. ábra. A *Cyanophrys roraimiensis* elterjedési térképe Pantepui keleti részén (Gran Sabana, Auyán Tepui) és Pantepui nyugati részén (Serranía del Cuao). A fehér középű piros körök jelzik azokat a helyeket, ahonan a *C. roraimiensis*-t jelezték. Összeállította: C. Brewer-Carías és M. Costa.. Összeállította: C-B. Carías és M. Costa.

12. ábra. *Cyanophrys* fajok a legnagyobb valószínűség elv (maximum likelihood módszer) alapján készített filogenetikai fája a két legközelebbi génuszból (*Chalybs* és *Callophrys*) vett külcsoport fajokkal. A fa COI vonalkód-szekvenciákon (24 illesztett szekvencia, 658 bp) alapul, amelyeket IQ-TREE segítségével generáltak automatikus modellkiválasztással (ModelFinder) és kodononként egy partícióval. A csomópont-támogatási értékek 2000 Ultrafast Bootstrap (UFBoot) ismétlésnek felelnek meg. A skálasáv a helyenkénti helyettesítések számát jelzi, átlagolva a partíciókon egy célarányos modellben. A kilenc *C. roraimiensis* példány (öt a keleti és négy a nyugati Pantepui régióból) alkotja a zölddel kiemelt kládot. Összeállította: C. Fåhraeus.