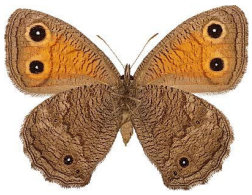
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Genomic analysis reveals new subspecies of *Cercyonis* Scudder, 1875 (Nymphalidae: Satyrinae: Satyrini)

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ABSTRACT. Genomic analysis of *Cercyonis* (*Cercyonis*) Scudder, 1875 (Nymphalidae Rafinesque, 1815) partitions the subgenus into three species groups and reveals five new subspecies from the USA (type localities in parentheses): *Cercyonis* (*Cercyonis*) *pegala koosharem* Stout and Grishin, **ssp. n.** (Utah, Sevier Co.), *Cercyonis* (*Cercyonis*) *pegala lasala* Grishin, M. Fisher, and Hannawacker **ssp. n.** (Utah, Grand Co.), *Cercyonis* (*Cercyonis*) *pegala hortoni* Grishin, **ssp. n.** (Arizona, Gila Co.), *Cercyonis* (*Cercyonis*) *meadii maculana* Grishin, **ssp. n.** (Colorado, Montezuma Co.), and *Cercyonis* (*Cercyonis*) *meadii rimana* Grishin, **ssp. n.** (Arizona, Yavapai Co.). A neotype is designated for *Satyrus boopis* Behr, 1864 (USA, California, Contra Costa Co.). The neotype of *Satyrus behrii* F. Grinnell, 1905 is invalid and not warranted. A provisional ordered taxonomic list of the subgenus *Cercyonis* is provided, recognizing six species and 35 subspecies (excluding the nominotypical subspecies).

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

ZooBank registration: https://zoobank.org/6BE874B6-F532-407E-83E8-42C1BAEB5077

INTRODUCTION

The genus *Cercyonis* Scudder, 1875 (Nymphalidae: Satyrinae: Satyrini) comprises three subgenera (Zhang et al. 2020, 2021). The nominotypical subgenus, *Cercyonis* (*Cercyonis*), which is the subject of the present study, is restricted to the New World and ranges from southern Canada throughout much of the United States into northern Mexico (Emmel 1969, 1975; iNaturalist 2026). The remaining two subgenera occur in the Palearctic region.

Species of *Cercyonis* (*Cercyonis*) are medium- to large-sized butterflies inhabiting a wide range of open habitats, including prairies, grasslands, shrublands, open woodlands, and montane meadows. Caterpillars feed on grasses (Poaceae Barnhart (1895)) (Scott 1986) and possibly sedges (Cyperaceae Juss. (1789)). Adults are characterized by their predominantly brown to gray dorsal and ventral wing coloration, usually bearing one or more eyespots on the forewing and hindwing. Considerable geographic variation in wing pattern, coloration, and eyespot development has contributed to a complex taxonomic history and the description of many subspecies (Brown [1966]; Emmel 1969, 1975; Austin 1992; Sourakov 1995; Pelham 2008; Emmel et al. 2012).

The taxonomy of *Cercyonis* has been a challenge due to wing pattern similarities between species and variability within species, resulting in a number of misidentifications (Brown [1966]). The latest

treatment, based on integrating genomic analysis with phenotypic considerations, includes six species (Zhang et al. 2022c, 2023c, 2025d; Warren et al. 2024). The most recent changes subsequent to Pelham (2008) include the analysis of eastern subspecies by Calhoun (2016), leading to the synonymization of some names; the discovery (through genomic sequencing of the lectotype) that *Cercyonis silvestris* (W. H. Edwards, 1861) is a species-level taxon closely related to *Cercyonis oetus* (Boisduval, 1869), with *Cercyonis silvestris incognita* J. Emmel, T. Emmel & Mattoon, 2012 representing a subspecies (instead of a species); the elevation of *Cercyonis hypoleuca* Hawks & J. Emmel, 1998 to species; the placement of *Cercyonis damei* W. Barnes & Benjamin, 1926 as a subspecies of *Cercyonis sthenele* (Boisduval, 1852) rather than a subspecies of *Cercyonis meadii* (W. H. Edwards, 1872); and the corresponding recognition of *Cercyonis meadii mexicana* R. Chermock, 1949 as a valid subspecies (not a junior synonym).

Here, we apply our integrative approach and utilize whole-genome shotgun sequence data that we obtained for all valid taxa of the subgenus *Cercyonis*. Our goals are to infer a genome-based phylogeny of the subgenus and to assess the taxonomic status of several unique groups of populations, five of which are described here as new subspecies. We apply the same methods and conceptual framework as in our previous studies (Cong et al. 2019a, b; Li et al. 2019; Zhang et al. 2019a–d; Cong et al. 2020; Zhang et al. 2020; Cong et al. 2021; Zhang et al. 2021; Robbins et al. 2022; Zhang et al. 2022b, d; Zhang et al. 2023b–d; Zhang et al. 2024a–c; Zhang et al. 2025a–g; Cong et al. 2026a, b; Zhang et al. 2026a, b). As a result, we recognize *Cercyonis* (*Cercyonis*) as comprising six species and 35 additional subspecies (excluding the nominotypical subspecies), including five that are new.

MATERIALS AND METHODS

The specimens examined in this study come primarily from museum and private collections (see Acknowledgments for details) and range in age from recently collected material to specimens preserved for more than a century. Whenever possible, we obtain whole-genome shotgun data from name-bearing type specimens to establish an objective genomic reference for species names (Cong et al. 2021; Zhang et al. 2022a). DNA is usually extracted non-destructively from a single leg, so that it remains available for subsequent morphological study. When DNA has not already been degraded because of specimen age, it is fragmented before genomic library preparation. Sequencing is performed on the Illumina platform, producing 150-base pair (bp) reads. Rather than relying on targeted amplification of particular genes or fragments, the protocol sequences all DNA recovered from the specimen. As a result, it is equally applicable to old specimens with highly fragmented DNA, which is often only about 30–50 bp long.

For each specimen, all sequencing reads are used to reconstruct exons of protein-coding genes, including not only complete 150 bp reads but also shorter fragments. Gene assembly is guided by the reference genome of a closely related species with a high-quality complete genome assembly. The reconstructed protein-coding genes are then used for phylogenetic inference. We infer three phylogenetic trees with IQ-TREE v1.6.12 under the GTR+GAMMA model (Nguyen et al. 2015): one from the nuclear genome (autosomes), and one from mitochondrial DNA. For each specimen, all well-covered codons are incorporated into an alignment generated "on the fly" and not retained, and the number of positions included in each nuclear genome tree is reported in the corresponding figure legend. Complete mitochondrial genomes are approximately 15,000 base pairs in length. Statistical support is assessed using ultrafast bootstrap, with values greater than 97% regarded as more reliable, whereas values below 90% indicate weak support and leave the relationship unresolved (Hoang et al. 2018). Further methodological details are available in our previous publications (Li et al. 2019; Zhang et al. 2022b).

Phylogenetic trees are displayed, colored, and clades rotated using FigTree (Rambaut 2018). Our taxonomic decisions are based primarily on genomic phylogenies, while morphology is used as corroborating evidence. This approach reflects the fact that genomes contain information extending beyond characters expressed in adult phenotype, the traditional basis of butterfly taxonomy, to include signatures associated with life history, ecology, reproduction, and diet. Although phenotypic traits cannot yet be inferred directly from genomic sequences, combined protein-coding DNA data provide reliable genetic proxies, and well-supported phylogenetic hypotheses serve as the principal guide for

classification. Together, these sources of evidence yield a taxonomic framework that is consistent with both genomic data and evolutionary relationships.

In this study, the main emphasis is on the subspecies levels, because the species level arrangement of *Cercyonis* (*Cercyonis*) has been previously established (Zhang et al. 2022c, 2023c, 2025d). In the cited works, species were delimited from multiple lines of evidence: differentiation in the Z chromosome with $F_{st} > 0.20$ (species-level divergence) and $G_{min} < 0.05$ (limited gene flow) (Cong et al. 2019a, 2026), COI barcode divergence of approximately 2% or greater (Hebert et al. 2003) together with its correspondence to phenotypic differentiation (Lukhtanov et al. 2016), and the presence of distinct, strongly supported clades in phylogenetic trees (Zhang et al. 2022d). We recognize that mitochondrial markers such as COI often introgress across species boundaries (Bachtrog et al. 2006; Cong et al. 2017), and therefore different species may occasionally possess identical barcode sequences (Burns et al. 2008; Zhang et al. 2023a).

Conventionally, subspecies are geographically distinct superpopulations that exhibit consistent phenotypic differences (when ~70% of individuals can be identified by appearance alone, regardless of locality) while remaining potentially capable of interbreeding (Mayr 1982; Monroe 1982). In practice, however, reproductive compatibility is rarely tested, and in butterflies, subspecies are usually recognized solely by differences in wing pattern. Whether these differences are genetically determined or environmentally induced is often unknown. Genomic analyses make it possible to compare populations directly at the genetic level. In this study, we describe new subspecies that correspond to distinct genomic clades that are genetically differentiated but not sufficiently divergent to warrant recognition as separate species. These subspecies represent early stages of speciation, corresponding to populations that have begun to diverge but may not yet have evolved substantial reproductive isolation. After identifying these genomic clades, we examine wing patterns to establish diagnostic phenotypic characters. As expected for subspecies, these diagnostic features are statistical rather than absolute and show individual variation. Because our subspecies concepts are founded on genomic clades, the diagnostic DNA characters are more dependable than morphological traits and are applicable to nearly all specimens. Therefore, DNA-based diagnoses are presented for every new subspecies described in this study.

For every new subspecies, we provide brief descriptions of diagnostic morphological characters and illustrations together with diagnostic DNA characters from the nuclear genome and, whenever possible, the COI barcode. These diagnostic DNA characters, obtained from protein-coding genes, were identified using our established protocol (see SI Appendix in Li et al. (2019)). The method for selecting robust diagnostic characters, described by Cong et al. (2019b), is intended to identify characters that are expected to remain informative as additional specimens and species are added to genomic datasets.

DNA character states are reported relative to the reference genome of *Heliconius melpomene* (Linnaeus, 1758) (hm) (Davey et al. 2016). The notation is: hm1547.7.2:T197C meaning position 197 in exon 2 of gene 7 from scaffold 1547 of the *H. melpomene* reference genome (hm) is C, having changed from T in the ancestor. When a character is specified for the sister clade of the diagnosed taxon, the notation is: hm630.5.7:C93C (not T) meaning that position 93 in exon 7 of gene 5 on scaffold 630 is occupied by the ancestral base pair C, which was changed to T in the sister clade (so it is not T in the diagnosed taxon). COI barcode characters are written in the same format but without a prefix ending in ':' and the ancestral nucleotide may be omitted when it cannot be inferred confidently. Complete exon sequences from the reference genome, with diagnostic positions highlighted in green, are available in the supplementary file https://osf.io/fc6gn. This file allows diagnostic characters used in the descriptions to be traced directly to corresponding sequences. Links to iNaturalist (2026) observations cited by observation number in the figure legends follow the format https://www.inaturalist.org/observations/n, where n represents the observation number. The iNaturalist photographs were identified by us to the best of our ability using wing patterns alone, without DNA sequencing of the depicted specimens (except for one photograph of a paratype); consequently, some identifications may prove to be incorrect.

The whole-genome shotgun datasets generated in this study will be deposited in the NCBI database (https://www.ncbi.nlm.nih.gov/) under BioProject PRJNA1521434. Corresponding BioSample records contain locality information and other collection data for these specimens. For each specimen, the

tree figures report the following information, separated by "|": taxon name with comments in square brackets, DNA sample code, type status, general locality, and year of collection ("old" if not dated and likely collected more than 100 years ago). Type status abbreviations are: HT holotype, LT lectotype, NT neotype, ST syntype, PT paratype, AT allotype, PLT paralectotype; if a synonym is listed (in parentheses, preceded by "="), the indicated type status refers to that synonym. The COI barcode sequences reported in this study have been deposited in GenBank under accession numbers PZ783659–PZ783664. Abbreviations and acronyms for collections are provided in the Acknowledgments.

RESULTS AND DISCUSSION

We inferred a genome-based phylogeny of the subgenus *Cercyonis* using all protein-coding genes from the nuclear genome (autosomes) and the mitochondrial genome, and placed the subgenus in the phylogenetic context of related genus-group taxa. Our genomic analysis, complemented by phenotypic and biogeographic considerations, revealed five new subspecies of the subgenus *Cercyonis*. The following sections deal with the formal descriptions of the new taxa accompanied by brief justifications of their status. We also clarify the status of two neotypes and discuss several taxa involved in the most recent taxonomic changes, illustrate these taxa and their relatives and describe differences between them to aid identification. Finally, a taxonomic list of the subgenus *Cercyonis* resulting from this study is provided.

Cercyonis (*Cercyonis*) *pegala koosharem* Stout and Grishin, new subspecies

https://zoobank.org/F5A11FB0-355E-481A-B799-8327A92AACB1

(Figs. 1 part, 2a–b, 16a–b part, 16c, 17 part)

Definition and diagnosis. Genomic analysis reveals that a pair of specimens from south-central Utah forms a clade sister to *Cercyonis* (*Cercyonis*) *pegala utahensis* Austin, 1992 (type locality USA: Utah, Utah Co., Benjamin) and is genetically differentiated from it at the subspecies level (Fig. 1); e.g., their COI barcodes differ by 1.7% (11 bp), and therefore these specimens represent a new subspecies. While the close relationship of the new subspecies with *C. pegala utahensis* makes sense geographically, the two subspecies are markedly different in their wing patterns (Fig. 2a–b vs. c–d and Fig. 5a–c). The new subspecies is darker than *C. pegala utahensis* and has reduced eyespots, both in size and number. The forewing eyespots are more weakly defined on the dorsal side in the male and are not surrounded by a sharply outlined beige patch in the female as in *C. pegala utahensis*. The dorsal hindwing is typically has one or two small eyespots near the tornus [frequently three or more eyespots in *C. pegala utahensis*, with at least one being larger]. The ventral hindwing of the female usually has no more than two or three small eyespots near the tornus [six prominent eyespots in both sexes of *C. pegala utahensis*]. Mottling and darker bands and lines on the ventral side of wings are less conspicuous and less contrasty than in *C. pegala utahensis*, and are paler, while the ground color is darker. The difference in the ground color of the ventral side of wings is especially pronounced in the female, which is brown in the new subspecies and tan in *C. pegala utahensis*. The new subspecies is more similar in wing patterns to phylogenetically distant subspecies *Cercyonis* (*Cercyonis*) *pegala pluvialis* Austin, 1992 (type locality in USA: Nevada, White Pine Co., White River Valley) (Fig. 3c–d) and in particular to *Cercyonis* (*Cercyonis*) *pegala paludum* Austin, 1992 (type locality in USA: Nevada, Elko Co., Pleasant Valley) (Fig. 3a–b). Even from these less spotted subspecies, the new subspecies differs by the darker ventral side and less contrasty mottling, and in females by absent or much-reduced tan coloring around and between the forewing eyespots. In its darker aspect, the new subspecies is reminiscent of some eastern subspecies, such as *Cercyonis* (*Cercyonis*) *pegala nephele* (W. Kirby, 1837) (type locality in Canada, Ontario) (Fig. 6c–e), but differs from them by typically more developed and better outlined (at least ventrally) yellow rings around the black eyespots on the forewings and more uniformly colored ventral side [frequently two-toned, with the distal half being paler in the eastern subspecies] and more weakly expressed, narrow discal dark band. Due to poorly understood individual variation, this subspecies is best identified by DNA, with diagnostic base pairs in the nuclear genome: hm2005400-RA.3:G372A, hm2005400-RA.3:T384A,

hm2004513-RA.9:G39A, hm2004513-RA.9:G57A, hm2015614-RA.6:A108G; and the COI barcode: G38A, 169T, C287T, G470G, C574T, T619A.

Barcode sequence of the holotype. Sample NVG-21113F10, GenBank PZ783659, 658 base pairs:

AACTTTATATTTTATTTTTGGAATTTGAGCAGGTATAATAGGAACATCTCTTAGTCTAATTATTCGAACAGAATTAGGTAATCCCGGATCTTTAATTGGAGATGATCAAATTTATAATACT
ATTGTCACAGCTCATGCTTTTATTATAATTTTTTTTATAGTTATACCTATTATAATTGGAGGATTCGGTAATTGACTTGTCCCCCTTATACTAGGAGCCCCTGATATAGCTTTCCCCCGAA
TAAATAATATAAGATTTTGACTTTTACCCCCTTCCTTAATCCTCTTAATTTCAAGAAGTATTGTAGAAAATGGAGCAGGTACTGGATGAACTGTTTATCCCCCCTTATCCTCAAATATTGC
CCATGGAGGAGCTTCTGTAGATTTAGCTATTTTTTCTTTACACTTAGCTGGTATTTCCTCAATTTTAGGAGCTATTAATTTTATTACAACAATTATCAATATACGAGTCAATAGCATATCT
TATGATCAAATACCTTTATTTGTCTGAGCAGTTGGTATTACAGCTTTACTATTACTACTATCTTTACCTGTCTTAGCTGGAGCTATTACTATACTTCTCACAGACCGAAATTTAAATACTT
CATTTTTTGATCCAGCAGGAGGAGGAGACCCAATCTTATACCAACATTTATTT

Type material. Holotype: ♂ deposited in the McGuire Center for Lepidoptera and Biodiversity collection, Gainesville, FL, USA (MGCL), illustrated in Fig. 2a, bears the following five printed rectangular labels, four white: [UT: Sevier Co. 6966' | Otter Creek 38° 33' | 49.1"N, 111° 50' 59.2" W | July 20, 2014 | Leg: W. Dempwolf], [Cercyonis pegala | ♂ | Coll of: W R Dempwolf], [DNA sample ID: | NVG-21113F10 | c/o Nick V. Grishin], [WRD 8824], and one red [HOLOTYPE ♂ | Cercyonis (Cercyonis) | pegala koosharem | Stout and Grishin]. The coordinates on the label place the locality on the road, though the holotype and paratypes were collected off the road. **Paratypes:** 15♂♂ and 8♀♀ from the type locality: with the same data as the holotype: 2♂♂ WRD 8825 and WRD 8826, 2♀♀ WRD 8827 and WRD 8828, and 1♀ NVG-21113F11, WRD 8829 [WRDC]; 20-Jul-2014: 10♂♂ WRD from 10357 to 10366, and 2♀♀ WRD 10367 and WRD 10368 [WRDC]; and others (3♂♂ and 3♀♀) GPS 38.5642, −111.8481, 6-Aug-2004, T. L. Stout leg., except 1♂ collected 20-Jul-2006 [MGCL] (Fig. 2b).

Type locality. USA: Utah, Sevier Co., Otter Creek at UT-62, ca. 2 mi south of Koosharem Reservoir, elevation 6931 ft, approx. GPS 38.5642, −111.8481.

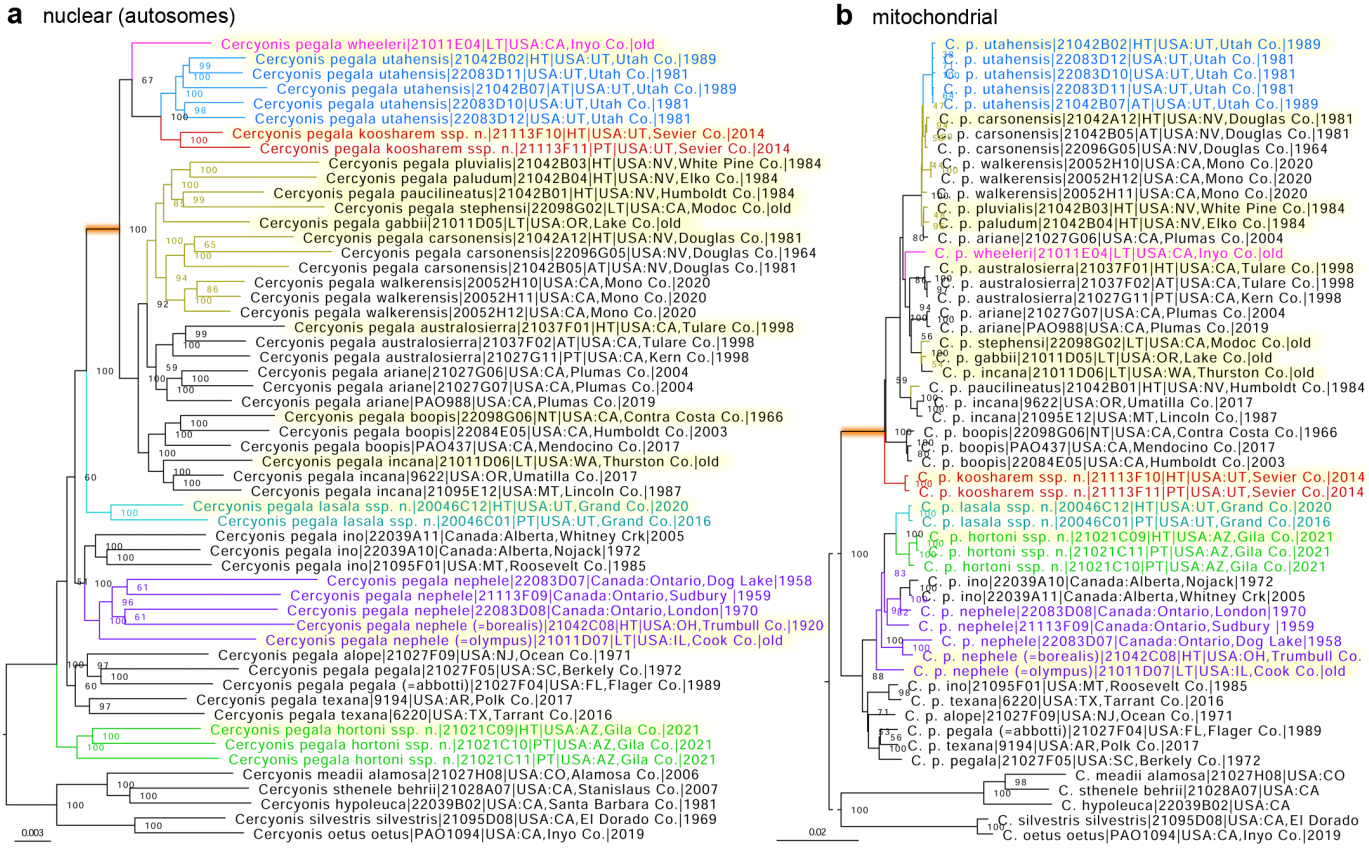


Fig. 1. Phylogenetic trees of all valid *Cercyonis* (*Cercyonis*) *pegala* subspecies constructed from protein-coding regions in: **a)** the nuclear genome (autosomes), based on 2,149,974 positions, and **b)** the mitochondrial genome. Primary type specimens are highlighted in yellow, the stem branch of the clade of western subspecies is highlighted in orange, the clade of subspecies from the southern intermountain region is shown in olive, and selected subspecies are colored: *C. pegala wheeleri* (magenta), *C. pegala utahensis* (blue), *C. pegala koosharem* **ssp. n.** (red), *C. pegala lasala* **ssp. n.** (cyan), *C. pegala hortoni* **ssp. n.** (green), and *C. pegala nephele* (violet). Ultrafast bootstrap (Hoang et al. 2018) values are shown at nodes. Gaps in two branches in the mitochondrial tree indicate where a vertical slice of the tree was removed to reduce its horizontal dimension (to allow an increase in the font size), i.e., branches with gaps are longer than shown. See Fig. 16b for complete branches.

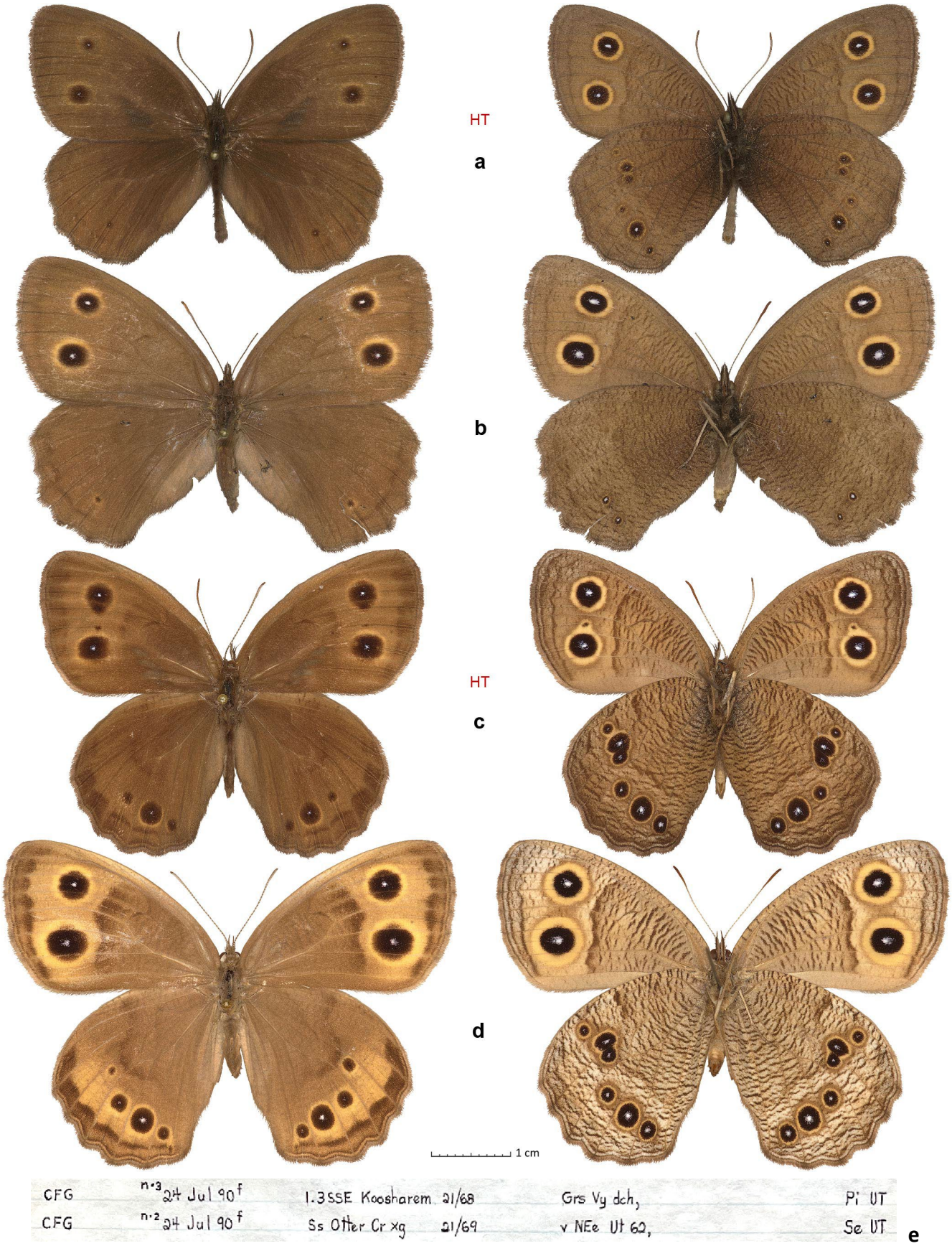


Fig. 2. Type specimens of *Cercyonis* (*Cercyonis*) *pegala* subspecies from USA, Utah, in dorsal (left) and ventral (right) views: **a–b)** *C. pegala koosharem* **ssp. n.** Sevier Co., Otter Creek at UT-62, 6966 ft, 20-Jul-2014, W. R. Dempwolf leg.: **a)** **holotype** ♂ NVG-21113F10 [MGCL] and **b)** paratype ♀ NVG-21113F11 [WRDC]; and **c–d)** *C. pegala utahensis* Utah Co., Benjamin, 1390 m, 6-Jul-1989, G. T. Austin leg.: **c)** **holotype** ♂ NVG-21042B02 and **d)** allotype ♀ NVG-21042B07; and **e)** an excerpt from Col. Clyde F. Gillette's notebook with localities for *C. pegala koosharem* **ssp. n.** that he or his associates discovered.

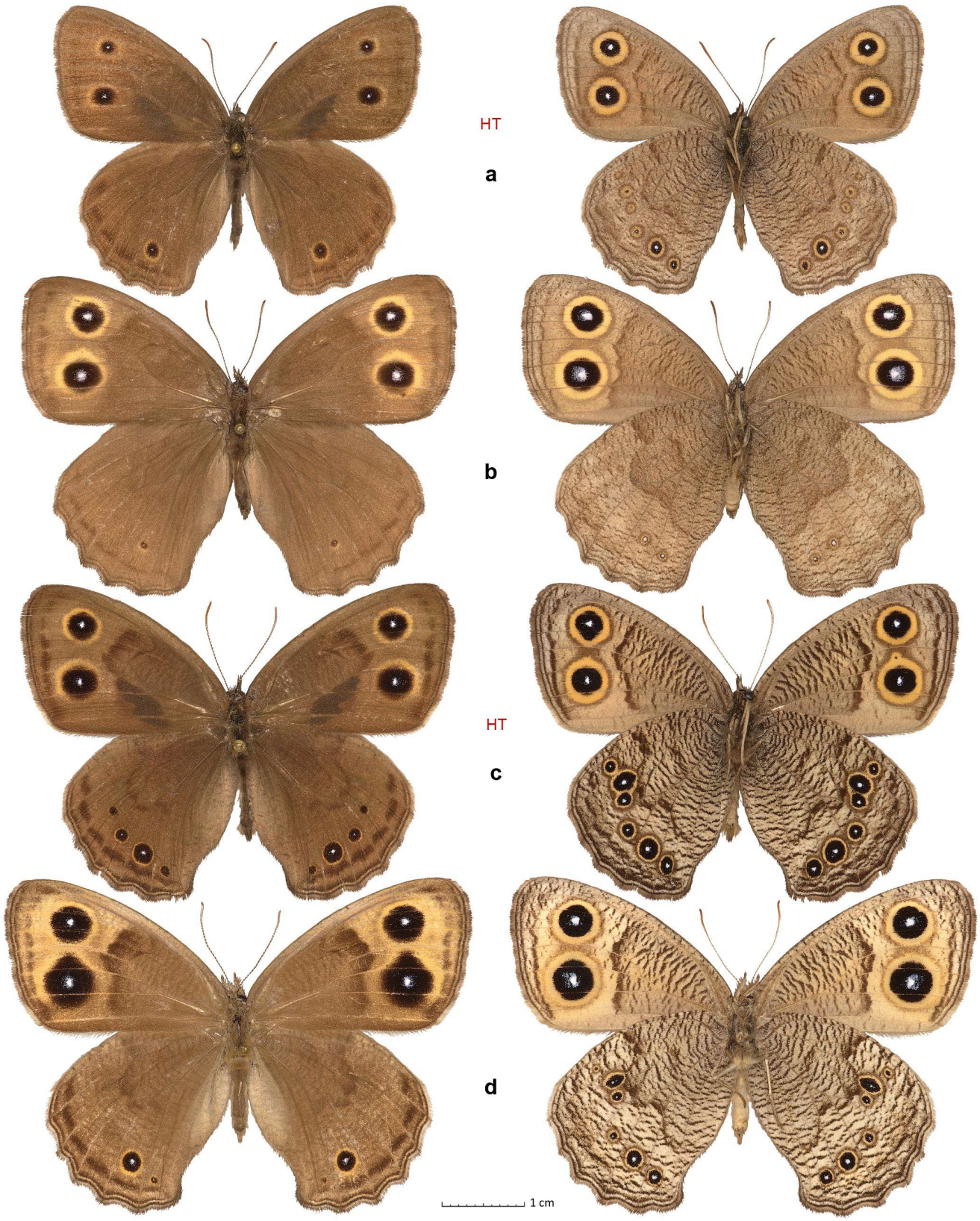


Fig. 3. Type specimens of *Cercyonis* (*Cercyonis*) *pegala* subspecies from USA, Nevada, G. T. Austin leg. [MGCL], in dorsal (left) and ventral (right) views: **a–b)** *C. pegala paludum* Elko Co., Pleasant Valley, NV-227, 3.7 mi W of Lamoille Canyon Rd., 21-Jul-1984: **a)** **holotype** ♂ NVG-21042B04 and **b)** allotype ♀ NVG-21042B09; and **c–d)** *C. pegala pluvialis* White Pine Co., White River Valley, 1 mi N of Nye Co. line, 15-Jul-1984: **c)** **holotype** ♂ NVG-21042B03 and **d)** allotype ♀ NVG-21042B08.

Etymology. The name, a noun in apposition, refers to the type locality of this new subspecies between Koosharem Reservoir and the town of Koosharem. The name itself, usually pronounced KOO-shuh-rum, comes from the Southern Paiute word Kuu'sharem, which refers to a type of edible root or red clover native to Grass valley around Otter Creek.

Distribution. Currently known only from the vicinity of the type locality in the Grass Valley along the Otter Creek south of Koosharem Reservoir, Sevier and Piute Cos., Utah.

Remarks. Dale Nielson and T.L.S. have inherited the notes from what many consider the most productive Utah lepidopterist ever, Colonel Clyde F. Gillette. He was intensely dedicated to his research on Utah butterflies (state records, county records, early records, late records, low- and high-elevation records, larval host plants, nectar sources, etc.) from the mid-1900s to the early 21st century. After meeting Gillette in 1986, T.L.S. frequently sought him for information, especially on Utah butterfly life histories. They even spent some time together in the field in the late 1980s. In Gillette's notes, T.L.S. found the records of *C. pegala* in Utah, where either Clyde or someone before him had found this new subspecies on July 24, 1990 (Fig. 2e). He was equally relentless about abbreviating as much as possible on his data labels and field notes to provide the most concise and precise data possible. In Fig. 2e, the first line translates as 1.3 miles SSE of Koosharem in a grass valley ditch, Piute County, UT. The second line translates to south side of the Otter Creek crossing; vicinity of the NE end of UT Hwy 62; adjacent to UT Hwy 24. n·3 indicates sample size. 21/68 indicates elevation in meters and feet; i.e., 2100 meters/6800 feet. Clyde always rounded meter and feet equivalents to the nearest hundred. Se UT means Sevier County, UT. Pi UT means Piute County, UT. Although we currently do not have photographs of the immature stages of the new subspecies, we illustrate fifth instar caterpillars of its relatives (Fig. 4).

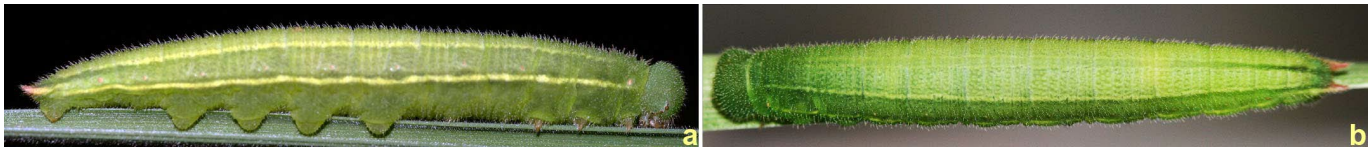


Fig. 4. Fifth instar caterpillars of *Cercyonis* (*Cercyonis*) *pegala* from USA, T. L. Stout leg.: **a)** *C. pegala utahensis* ♀ Utah, Utah Co., Lindon, Wasatch Race Park, 4600 ft, GPS 40.339, −111.7678, ex ovum ex ♀ collected on 27-Jul-2007, eclosed on 29-Dec-2007; **b)** *C. pegala paludum* ♂ Idaho, Bannock Co., Goodenough Creek, GPS 42.6548, −112.2796, ex ovum ex ♀ collected on 2-Aug-2007, eclosed on 11-Apr-2008.

Phylogenetic position of *Cercyonis* (*Cercyonis*) *pegala wheeleri* (W. H. Edwards, 1873)

Cercyonis (*Cercyonis*) *pegala wheeleri* (W. H. Edwards, 1873), together with its junior subjective synonym *Satyrus hoffmani* Strecker, 1873, was described from the same specimen lot (collected around the same time and at the same place, possibly by the same person), although different specimens, originating from the Camp Independence – Owens Lake region in Inyo Co. California, USA (Brown 1964; Austin 1992). This subspecies is uniquely characterized by a twinned anterior eyespot on the forewing, though this phenotype may also occur in other populations (Sourakov 1995). The subspecies is currently presumed extinct and 20 remaining specimens are preserved in several collections (Austin 1992). Genomic phylogeny (Figs. 1a, 16a) based on all concatenated autosomal genes (nuclear genome) places the lectotype of *C. pegala wheeleri* (Fig. 5d) (the only specimen of this subspecies that we sequenced) as sister to the clade of specimens from Utah: *Cercyonis* (*Cercyonis*) *pegala utahensis* Austin, 1992 (type locality Utah Co., Benjamin) (Figs. 2c–d, 5a–c) and *Cercyonis* (*Cercyonis*) *pegala koosharem* **ssp. n.** (type locality Sevier Co., vic. Koosharem) (Figs. 2a–b).

This phylogenetic position is unexpected because the existing specimens were collected in California at a locality that is geographically much closer to Californian subspecies *Cercyonis* (*Cercyonis*) *pegala walkerensis* Austin, 1992 (type locality Mono Co., Huntoon Valley) and *Cercyonis* (*Cercyonis*) *pegala australosierra* J. Emmel, T. Emmel & K. Davenport, 2008 (type locality in Tulare Co., Poso Creek drainage; this subspecies may be extinct as well). Despite this, *C. pegala wheeleri* is not closely



Fig. 5. Specimens of *Cercyonis* (*Cercyonis*) *pegala* from USA in dorsal (left) and ventral (right) views: **a–c)** *C. pegala utahensis* Utah, Utah Co., J. & F. Preston leg. [MGCL]: **a)** ♂ NVG-22083D11 Benjamin, 6-Jul-1981, and ♀♀ from Jordan River at UT-73, 10-Jul-1981: **b)** NVG-22083D12 and **c)** NVG-22083D10; and **d)** *C. pegala wheeleri* **lectotype** ♀ NVG-21011E04 California, Inyo Co., Camp Independence – Owens Lake region, 1871 [CMNH].

related to them. While *C. pegala wheeleri* shares several wing pattern traits with *C. pegala utahensis* (Fig. 5), and could indeed be more closely related to this unique subspecies (which is phylogenetically set apart from others in the southern intermountain region; Figs. 1a, 16a), it is also possible that the grouping between *C. pegala wheeleri* and the *C. pegala utahensis* clade is artifactual, to be tested by sequencing additional *C. pegala wheeleri* specimens. Regardless of the exact phylogenetic affinity, our genomic analysis reveals that *C. pegala wheeleri* belongs to the *ariane* subspecies group (orange-highlighted clade in Fig. 1). It is unique among all taxa in both nuclear (Figs. 1a, 16a) and mitochondrial (Figs. 1b, 16b) DNA, because the lectotype of *C. pegala wheeleri* (Figs. 1, 16 magenta) is positioned deep in the phylogeny, closer to the root of the tree than the clades of most of the other western subspecies.

Cercyonis (*Cercyonis*) *pegala lasala* Grishin, M. Fisher, and Hannawacker new subspecies

https://zoobank.org/B1A1F130-B758-4250-AB9C-BF483059A915

(Figs. 1 part, 6a–b, 7, 16a–b part, 16d, 17 part)

Definition and diagnosis. Genomic analysis reveals that specimens from southeastern Utah belong to the eastern subspecies group and are genetically differentiated from all known taxa at the subspecies level (Fig. 1); e.g., their COI barcodes differ by 1.1% (7 bp) from both *Cercyonis* (*Cercyonis*) *pegala nephele* (W. Kirby, 1837) (type locality in Canada, Ontario) and *Cercyonis* (*Cercyonis*) *pegala ino* G. Hall, 1924 (type locality Canada: Alberta, Calgary); therefore these specimens represent a new subspecies. These Utah specimens and similar western Colorado populations have been discussed by Hannawacker (2020) and Fisher (2005), respectively. This new subspecies is most similar to *C. pegala nephele* (Fig. 6c–e) and *C. pegala ino* in its darker aspect and less conspicuous yellow rings around the black forewing eyespots in males [males of western subspecies of *C. pegala* have more prominent and sharply defined yellow rings at least ventrally], but differs from them by a greater difference in size between the ventral forewing and hindwing eyespots in males: forewing eyespots are much larger than the hindwing eyespots [in males of other dark-colored eastern subspecies ventral hindwing eyespots are usually only a little smaller than the forewing eyespots]; typically larger forewing eyespots in females: yellow rings around the two ventral forewing eyespots nearly joining in many specimens, and beige rings around black eyespots are better defined dorsally; and reduced number and size of ventral hindwing eyespots in females, usually two or fewer near the tornus. Due to its cryptic nature and poorly explored individual variation, this subspecies is best identified by DNA, with diagnostic base pairs in the nuclear genome: hm2007546-RA.19:T96A, hm2007546-RA.19:C105T, hm2013248-RB.28:G63A, hm2013335-RA.1:T594C, hm2013335-RA.1:G693A; and the COI barcode: G38G, C212C, T347C, T553C, A631A.

Barcode sequence of the holotype. Sample NVG-20046C12, GenBank PZ783660, 658 base pairs:

AACTTTATATTTTATTTTTGGAATTTGAGCAGGTATAGTAGGAACATCTCTTAGTCTAATTATTCGAACAGAATTAGGTAACCCCGGATCTTTAATTGGAGATGATCAAATTTATAATACT
ATTGTCACAGCCCATGCTTTTATTATAATTTTTTTTATAGTTATACCCATTATAATTGGAGGATTCGGTAATTGACTTGTCCCTCTTATACTAGGAGCCCCTGATATAGCTTTCCCCCGAA
TAAATAATATAAGATTTTGACTTTTACCCCCTTCCTTAATCCTCCTAATTTCAAGAAGTATTGTAGAAAATGGAGCAGGTACTGGATGAACTGTTTATCCCCCCCTATCCTCAAATATTGC
CCATGGAGGAGCTTCTGTAGATTTAGCTATTTTTTCTTTACACTTAGCTGGTATTTCCTCAATTTTAGGAGCTATTAATTTTTATTACAACGATTATTAATATACGAGTCAATAATATATCT
TATGATCAAATACCTTTATTTGTTTGAGCAGTTGGTATTACAGCTTTACTATTACTACTCTCTTTACCCGTCTTAGCTGGAGCTATTACAATACTTCTCACAGACCGAAATTTAAATACTT
CATTTTTTGATCCTGCAGGAGGAGGAGACCCAATTTTATATCAACATTTATTT

Type material. Holotype: ♂ deposited in the McGuire Center for Lepidoptera and Biodiversity collection, Gainesville, FL, USA (MGCL), illustrated in Fig. 6a, bears the following three printed rectangular labels, two white: [Castle Creek 6400' | Grand County, Utah | 1 July 2020 | Robb Hannawacker], [DNA sample ID: | NVG-20046C12 | c/o Nick V. Grishin], and one red [HOLOTYPE ♂ | Cercyonis (Cercyonis) | pegala lasala Grishin, | M. Fisher, and Hannawacker]. **Paratypes:** 11♂♂ and 6♀♀ from USA, Utah, Grand Co., R. Hannawacker leg.: 1♀ NVG-20046C01 Matheson Wetlands, GPS 38.579, −109.574, 2-Jul-2016 (Fig. 6b, 7a) and 1♀ NVG-20047D11 the same data as the holotype, GPS 38.599, −109.293 (Fig. 7b); and Colorado [M. S. F. research collection]: Mesa Co., M. S. Fisher leg.: 2♀♀ Unaweep Canyon, SR141 E of Gateway, 5500 ft, 19-Aug-1967; 2♂♂ John Brown Canyon, SW of Gateway on CR4.4, 7000 ft, 17-Jul-1973; and 6♂♂ 15 air mi up Escalante Creek, 6648 ft, GPS 38.6283, −108.4480, 11-Jun-2026; and 3♂♂ & 2♀♀ Garfield Co., SR139 S of Douglas Pass, 7400 ft, GPS: 39.5894, −108.8217, 11-Jul-2016, R. L. Patterson leg.


HT
a
b
LT
c
d
LT
e
1 cm

Fig. 6 (see previous page). *Cercyonis* (*Cercyonis*) *pegala* subspecies in dorsal (left) and ventral (right) views: **a–b)** *C. pegala lasala* **ssp. n.** from USA, Utah, Grand Co., R. Hannawacker leg. [MGCL]: **a)** **holotype** ♂ NVG-20046C12 Castle Creek, 6300 ft, 1-Jul-2020 and **b)** paratype ♀ NVG-20046C01 Matheson Wetlands, 2-Jul-2016; **c–d)** *Cercyonis pegala nephele*: **c)** **lectotype** of *Satyrus nephele* variety *olympus* (a junior subjective synonym) ♂ NVG-21011D07 USA, Illinois, Cook Co., Chicago, Jun-1879, ex ovum, C. E. Worthington leg. (Brown 1964) [CMNH]; **d)** non-type ♀ NVG-22083E10 Canada, Ontario, Northwest District, Georgian Bay, 9-Jul-1941 [MGCL]; and **e)** *Cercyonis pegala incana* **lectotype** ♂ NVG-21011D06 USA, Washington, Thurston Co., Olympia, old, H. K. Morrison leg. [CMNH].

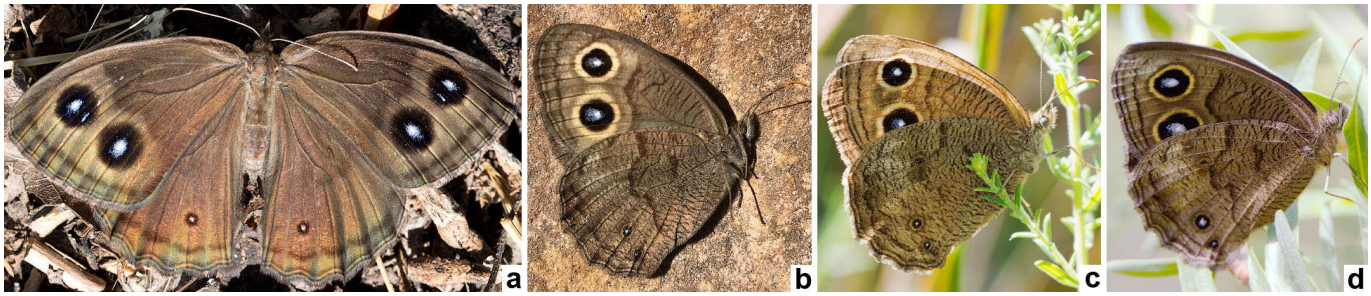


Fig. 7. *Cercyonis* (*Cercyonis*) *pegala lasala* females from USA, Utah, Grand Co.; iNaturalist observations, photographs by R. Hannawacker, unless indicated: **a–b)** paratypes freshly captured in the field and **c–d)** live adults: **a)** observation No. 3597534, NVG-20046C01 Matheson Wetlands, GPS 38.579, −109.574, 2-Jul-2016; **b)** observation No. 51628918, NVG-20047D11 Castle Creek, Rock Castle Campground, 6400 ft, GPS 38.599, −109.293 (the type locality), 1-Jul-2020; **c)** observation No. 236021074, Onion Creek, GPS 38.696, −109.254, 15-Aug-2024; and **d)** observation No. 85673419, the type locality, 3-Jul-2021 © Chris Quirin; color-corrected, brightened, rotated, and cropped, CC BY 4.0 https://creativecommons.org/licenses/by/4.0/.

Type locality. USA: Utah, Grand Co., Castle Creek, Rock Castle Campground, elevation 6400 ft, GPS 38.599, −109.293.

Etymology. The name is derived from the La Sal Mountains, a landmark of the region this subspecies inhabits. The name is treated as a noun in apposition.

Distribution. Currently known from the region centered around the La Sal Mountains in eastern Utah and western Colorado. Genomic sequencing of specimens collected eastward from the type locality across western Colorado is pending to establish the true range of this subspecies, specifically whether it occurs broadly across the region or remains restricted to the area where the Colorado paratypes were collected.

Remarks. This new subspecies exhibits phenotypic variation among populations in southeastern Utah. Rock Castle/Castle Creek individuals from and near the type locality tend to be relatively small and dark and occur particularly in shaded, old-growth riparian habitat. Matheson Wetlands individuals are uncommon, strongly associated with deep shade beneath large cottonwoods, and tend to be larger and somewhat lighter; the female paratype NVG-20046C01 was especially striking in life and showed dorsal iridescence. Monticello Mill site (San Juan Co.) individuals tend to be lighter. These are field observations by R. Hannawacker rather than quantified characters, and it remains unclear whether the differences reflect genetic population structure, developmental environment, or both.

Cercyonis (*Cercyonis*) *pegala hortoni* Grishin, new subspecies

https://zoobank.org/A5B87F8F-3329-4B4A-A838-8E7FAF3D048C

(Figs. 1 part, 8, 16a–b part, 16e, 17 part)

Definition and diagnosis. Genomic analysis reveals that several specimens from the Transitional Zone in central Arizona belong to the eastern subspecies group and are genetically differentiated from all known taxa at the subspecies level (Fig. 1); e.g., their COI barcodes differ by 1.2% (8 bp) and 1.5% (10 bp) from *Cercyonis* (*Cercyonis*) *pegala nephele* (W. Kirby, 1837) (type locality in Canada, Ontario) and *Cercyonis* (*Cercyonis*) *pegala ino* G. Hall, 1924 (type locality Canada: Alberta, Calgary), respectively, and by 1.4% (9 bp) from *Cercyonis* (*Cercyonis*) *pegala lasala* **ssp. n.** described right above, and therefore these specimens represent a new subspecies. This new subspecies is most similar to *C. pegala nephele* (Fig. 6c–e), *C. pegala ino*, and *C. pegala lasala* **ssp. n.** in its darker aspect and less conspicuous yellow rings



Fig. 8. *Cercyonis* (*Cercyonis*) *pegala hortoni* **ssp. n.** from USA, Arizona: **a–c)** Gila Co., Colonel Devin Trail, GPS 34.4302, −111.2608, 14-Jul-2021: **a)** **holotype** ♂ NVG-21021C09 T. Horton leg., in dorsal (left) and ventral (right) views; and iNaturalist observations © Tom Horton: **b)** ♀ observation No. 87363729 and **c)** ♂ observation No. 87363703; and **d–e)** Coconino Co., Oak Creek Canyon, N of Sedona: **d)** ♂ observation No. 373639376, 12240 AZ-89A, GPS 35.0120, −111.7385, 18-Jun-2026 © Jay and Shauna Dempsey and **e)** ♀ observation No. 248886084, vic. Manzanita Campground, GPS 34.9350, −111.7417, 31-Jul-2022 © jmbearce; iNaturalist photographs are color-corrected, brightened, rotated, cropped, and flipped in (d), CC BY-NC 4.0 https://creativecommons.org/licenses/by-nc/4.0/.

around the black forewing eyespots in males [males of western subspecies of *C. pegala* have more prominent and sharply defined yellow rings at least ventrally], but differs from them by a greater difference in size between the ventral forewing and hindwing eyespots in males: forewing eyespots are much larger than the hindwing eyespots [in males of other dark-colored eastern subspecies ventral hindwing eyespots are usually only a little smaller than the forewing eyespots]; typically large forewing eyespots in females [smaller than in *C. pegala lasala* **ssp. n.**]: yellow rings around the two ventral forewing eyespots come close but do not touch, and beige rings around black eyespots are usually inconspicuous; the costal triplet of eyespots (usually small) is present on the ventral hindwing [usually lacking in females of *C. pegala lasala* **ssp. n.**]; and the ventral side mottling is particularly conspicuous in the basal half of the wings (extending to the margin on the hindwing, which is only slightly paler in the distal half), with dark-brown streaks and dashes being longer, complete, uniformly colored, and sharply defined. Due to its cryptic nature and poorly explored individual variation, this subspecies is best identified by DNA, with diagnostic base pairs in the nuclear genome: hm2014574-RA.10:C72T, hm2014574-RA.10:A75C, hm2018037-RA.5:C99T, hm2005332-RA.3:G81A, hm2005332-RA.3:G165A; and the COI barcode: G38G, C212T, T557C, A631G, T646T.

Barcode sequence of the holotype. Sample NVG-21021C09, GenBank PZ783661, 658 base pairs:

AACTTTATATTTTATTTTTGGAATTTGAGCAGGTATAGTAGGAACATCTCTTAGTCTAATTATTCGAACAGAATTAGGTAACCCCGGATCTTTAATTGGAGATGATCAAATTTATAATACT
ATTGTCACAGCCCATGCTTTTATTATAATTTTTTTTATAGTTATACCCATTATAATTGGAGGATTCGGTAATTGACTTGTCCCTCTTATATTAGGAGCCCCTGATATAGCTTTCCCCCGAA
TAAATAATATAAGATTTTGACTTTTACCCCCTTCCTTAATCCTCCTAATTTCAAGAAGTATTGTAGAAAATGGAGCAGGTACTGGATGAACTGTTTACCCCCCCTTATCCTCAAATATTGC
CCATGGAGGAGCTTCTGTAGATTTAGCTATTTTTTCTTTACACTTAGCTGGTATTTCCTCAATTTTAGGAGCTATTAATTTTATTACAACAATTATTAATATACGAGTCAATAGCATATCT
TATGATCAAATACCTTTATTTGTTTGAGCAGTTGGTATTACAGCTTTACTATTACTACTCTCTTTACCTGTCCTAGCTGGAGCTATTACAATACTTCTCACAGACCGAAATTTAAATACTT
CATTTTTTGATCCTGCAGGAGGAGGGGACCCAATTTTATATCAACATTTATTT

Type material. Holotype: ♂ deposited in the McGuire Center for Lepidoptera and Biodiversity collection, Gainesville, FL, USA (MGCL), illustrated in Fig. 8a, bears the following three printed rectangular labels (text in italics handwritten), two white: [USA: ARIZONA: Gila Co. | Colonel Devin Trail | GPS 34.43020, -111.26077 | 14-July-2021, T. B. Horton Jr.], [DNA sample ID: | NVG-21021C09 | c/o Nick V. Grishin], and one red [HOLOTYPE ♂ | Cercyonis (Cercyonis) | pegala hortoni Grishin]. GPS coordinates on the label point to the parking lot, not the exact collecting locality. **Paratypes:** 2♂♂ (NVG-21021C10 and NVG-21021C11) with the same data as the holotype [TBHJC].

Type locality. USA: Arizona, Gila Co., Colonel Devin Trail, approx. GPS 34.4302, −111.2608.

Etymology. The subspecies is named in honor of Tom B. Horton Jr. (Arizona, USA), the collector of the type series, who encountered a strong flight on July 14, 2021, at what becomes the type locality of this taxon and was interested in the trinomial of this butterfly. To address his question, he kindly mailed us a specimen and leg samples for DNA sequencing, which revealed the taxonomic distinction of these populations. As a result, Tom has the trinomial now. Tom's keen interest in nature, frequently focused on butterflies, has resulted in many notable finds and discoveries shared through his beautiful photography. Several of his photographs are used in this work (Figs. 8b–e, 16e, g, i). We are grateful to Tom for supporting our genomic projects with butterfly specimens and samples. The name is a noun in the genitive case.

Distribution. Transitional Zone northeast of Phoenix, Arizona, from around Sedona to Globe.

Neotype designation for *Satyrus boopis* Behr, 1864

Emmel et al. (1998b) published a neotype designation for *Satyrus boopis* Behr, 1864 (type locality USA: California, Contra Costa Co., Point Richmond), currently a valid subspecies of *Cercyonis pegala* (Fabricius, 1775) (type locality USA: South Carolina, vic. Charleston). This designation falls in a gray area between satisfying and failing Art. 75.3 of the ICZN Code (1999). While the designation fulfills Art. 75.3.3–75.3.7, the situation with Arts. 75.3.1 and 75.3.2 is less clear. There are two ways to approach this designation. The first approach is the most charitable, and we look for any evidence to satisfy the ICZN Code requirements. One can accept that the parent Art. 75.3 ("exceptional need") and the subordinate Art. 75.3.1 ("it is designated with the express purpose of clarifying the taxonomic status …") are satisfied because Emmel et al. (1998b) cited Brown ([1966]), and Brown provided a justification for the neotype designation. Art. 75.3.2 ("characters … differentiating from other taxa … or a bibliographic reference to such a statement") may be considered satisfied, because although neither Emmel et al. (1998b) nor Brown ([1966]) provided the differential diagnosis, Emmel et al. (1998b) cited Behr's original publication, which described the taxon (Behr 1864). According to this more permissive interpretation, the neotype of *S. boopis* is validly designated by Emmel et al. (1998b).

The second approach is to interpret ICZN requirements more literally. Although Art. 75.3.2 mentions a "bibliographic reference," this is not among the conditions of the parent Art. 75.3 and the subordinate Art. 75.3.1. These sections of Art. 75.3 require the conditions to be "stated expressly" and "a statement … with the express purpose … ." Such statements are missing from the *S. boopis* neotype designation by Emmel et al. (1998b). Moreover, Emmel et al. (1998b) merely cite the original description of *S. boopis*, but do not explicitly cite it to give "a statement of the characters," thus possibly failing Art. 75.3.2. A more generous interpretation of the citation requirement (i.e., any citation of the original publication would satisfy) erodes the intent of Art. 75.3.2 to explain the differences of the taxon from others: nearly every attempted neotype designation would cite the original work at least as part of the name of the taxon. Therefore, according to this more restrictive interpretation, the neotype of *S. boopis* is invalid as designated by Emmel et al. (1998b).

The two interpretations create potential for the instability of nomenclature if someone follows the second, more restrictive, interpretation and designates a specimen of a different taxon as the neotype of *S. boopis*. We believe that Emmel et al. (1998b) satisfied all the requirements of Art. 75.3.3–75.3.7, and their designated neotype represents the nominal taxon as intended by Behr (1864), which agrees with the

current application of the name. However, in the interest of nomenclatural stability, we also adopt a more restrictive approach and consider that the designation of Emmel et al. (1998b) failed the parent Art. 75.3 and the subordinate Art. 75.3.1–75.3.2, and therefore is invalid.

There is an exceptional need for a neotype of *S. boopis* to define this taxon objectively because it has been historically confused with similar taxa, several of which were misidentified, as discussed by Brown ([1966]), such as Californian taxa frequently with uncertain type localities known currently as *Cercyonis oetus* (Boisduval, 1869) (type locality in USA: California, hypothesized to be in Placer Co. by Emmel et al. (1998a)), *Cercyonis silvestris* (W. H. Edwards, 1861) (type locality in USA: California, hypothesized to be in Butte Co. by Emmel et al. (1998d)), *Cercyonis sthenele* (Boisduval, 1852) (type locality USA: California, San Francisco), *Cercyonis pegala ariane* (Boisduval, 1852) (type locality in USA: California, hypothesized to be in Plumas Co. by Emmel et al. (1998a)), and *C. pegala boopis* (Behr, 1864). Note that for most of these taxa the type localities were not detailed in the original descriptions beyond "California" and are only hypothetical. The superficial similarity between some of these taxa is notorious, and the identity of several was confused until very recently. For instance, *C. silvestris* was regarded as a subspecies of *C. sthenele* (Pelham 2008) until its identity as a species more distant from *C. sthenele* and closely related to *C. oetus* was revealed by the genomic sequence comparison involving the lectotype (Zhang et al. 2022c; Zhang et al. 2025d). In the light of these confusions, contradicting opinions in the literature (Brown [1966]), and wing pattern similarities between some of these taxa, a neotype of *S. boopis*, the only name among the abovementioned similar taxa not objectively defined by a single name-bearing type specimen, is exceptionally needed.

Hereby, N.V.G. designates a male in the CAS collection illustrated in Fig. 9a (DNA sample NVG-22098G06) as the **neotype** of *Satyrus boopis* Behr, 1864. This neotype is the same specimen as that

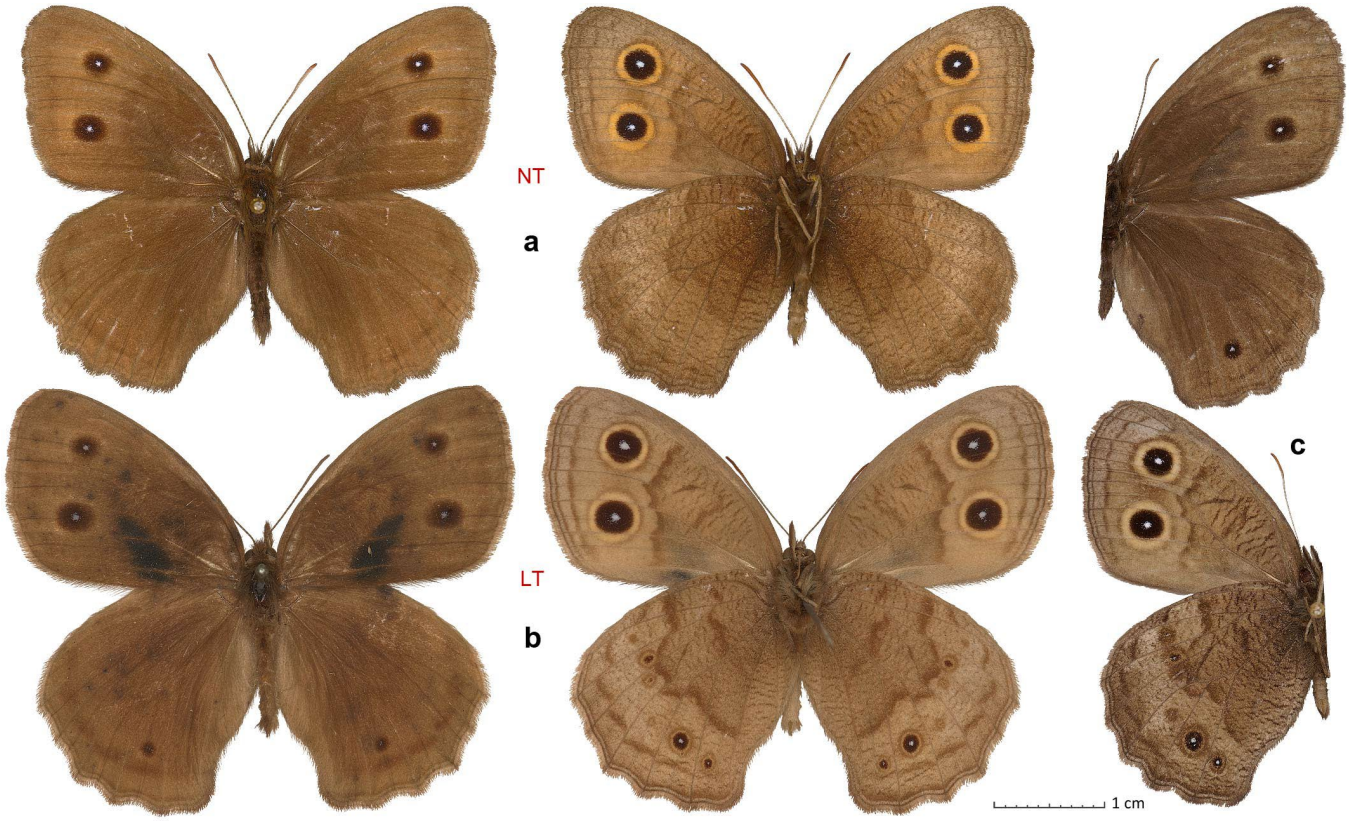


Fig. 9. *Cercyonis* (*Cercyonis*) *pegala boopis* males from USA, California in dorsal (left or above) and ventral (right or below) views: **a) neotype** NVG-22098G06 Contra Costa Co., Point Richmond, 30-May-1966, R. L. Langston leg. [CAS]; **b) lectotype** of *Satyrus ariane baroni* W. H. Edwards, 1880 (a junior subjective synonym) NVG-21011C12 northern California, O. T. Baron leg., suggested by Brown (1964) to be Mendocino Co. [CMNH]; and **c)** non-type NVG-22084E05 Humboldt Co., Redwood National Park, Bald Hills Rd., 9.0 mi SE US-101 jct., 2250–2300 ft, J. F. Emmel leg., 30-Jul-2003 [MGCL].

selected as the neotype of *S. boopis* by Emmel et al. (1998b) and it further stabilizes the current usage of this name. The neotype satisfies all requirements set forth by the ICZN Article 75.3, as detailed below.

75.3.1. It is designated to clarify the taxonomic identity of *S. boopis*, which is necessary because this taxon has been confused with several others (see above), in particular with *C. pegala ariane* (see Comstock (1924) and Brown ([1966])).

75.3.2. The characters to differentiate this taxon from others are given by Behr (1864) in the original description, which we translate from Latin as "Similar to Sthenele, but the wing margin is not checkered; instead, it is distinctly marked by a transverse line, and in the female the eyespots of the upper wings are located within a paler band. Beneath, the wings are divided into two halves: the basal portion is brown, the marginal portion gray, becoming brownish toward the margin. Both surfaces are marbled, except that the halo surrounding the eyespots on the forewings alone is paler and of a uniform color." To these characters, we add the following: *S. boopis* is most similar to *C. pegala ariane* and differs from it by being grayer beneath [*C. pegala ariane* is generally warmer brown], with a narrower, less contrasting discal dark band on the ventral hindwing; more uniform and less distinctly mottled marginal area of the ventral side of wings; and absent or smaller and less developed eyespots on the ventral hindwing. We note that while many specimens of *S. boopis*, such as the neotype, completely lack the ventral hindwing eyespot, other specimens may have them; for comparison, we also illustrate the lectotype of *Satyrus ariane baroni* W. H. Edwards, 1880 (type locality in northern California, USA, suggested by Brown (1964) to be in Mendocino Co.) (Fig. 9b), the name currently treated as a junior subjective synonym of *S. boopis*, and a non-type sequenced specimen from Humboldt Co., California (Fig. 9c), which is in the clade with the *S. boopis* neotype (Fig. 1) and thus is identified as this taxon by us.

75.3.3. The neotype specimen is a male bearing the following five rectangular printed (text in italics handwritten) labels (3rd red, others white): [Point Richmond, | Contra Costa Co., | Calif. *MAY 30, 1966* ♂], [R. L. Langston | Collector], [NEOTYPE | Satyrus boopis Behr | Designated by J. F. | Emmel, T. C. Emmel, | & S. O. Mattoon, 1998], [California Academy | of Sciences | Type | No. *17857*], [DNA sample ID: | NVG-22098G06 | c/o Nick V. Grishin], and illustrated in Fig. 9a; it is a well-preserved and perfectly spread specimen with a line-like scratch in the costal area of the dorsal hindwing (both wings).

75.3.4. We failed to find syntypes of *S. boopis* in all collections we visited (see Acknowledgments for their list) and, considering published evidence that they were destroyed in the 1906 San Francisco earthquake and fire (Emmel et al. 1998b), believe that they were lost.

75.3.5. The neotype closely agrees with everything that is known about the former name-bearing type, as evidenced by comparing the neotype illustrated in Fig. 9a with the characters given for this taxon in the original description (Behr 1864) and detailed above (75.3.2), for instance, the ventral side of both wings is bicolored, being paler in the outer half, and the ventral hindwing lacks eyespots ("*S. Boopis* being only distinguished by the absence of the series of eyes on the under side of the hind wings" (Behr 1864)).

75.3.6. The neotype is from Contra Costa Co., California, USA, and the original type locality is given as "Contra Costa" in the text and "Californian" in the title of the work with the original description (Behr 1864), thus agreeing with each other. As a result of the neotype designation, the type locality of *S. boopis* remains USA: California, Contra Costa Co., Point Richmond.

75.3.7. The neotype is deposited in the collection of the California Academy of Sciences, San Francisco, CA, USA (CAS).

This neotype designation is unconditional. As a result of this designation and in any interpretation, the specimen selected as the neotype of *S. boopis* by Emmel et al. (1998b) is the neotype of this taxon. For those who prefer a more permissive interpretation of Art. 75.3, this specimen is the neotype designated by Emmel et al. (1998b), but the designation by Grishin is invalid according to Art. 75.4. For those who prefer a more restrictive interpretation of Art. 75.3, this specimen is the neotype designated by Grishin, but the designation of Emmel et al. (1998b) is invalid because it failed at least some sections of Art. 75.3, such as the parent Art. 75.3 and Art. 75.3.1, and possibly Art. 75.3.2. Finally, the COI barcode sequence of the neotype, sample NVG-22098G06, GenBank PZ783662, 658 base pairs, is:

AACTTTATATTTTATTTTTGGAATTTGAGCAGGTATAATAGGAACATCTCTTAGTCTAATTATTCGAACAGAATTAGGTAATCCCGGATCTTTAATTGGAGATGATCAAATTTATAATACT
ATTGTCACAGCTCATGCTTTTATTATAATTTTTTTTATAGTTATACCTATTATAATTGGAGGATTCGGTAATTGACTTGTCCCCCTTATACTAGGAGCCCCTGATATAGCTTTCCCCCGAA
TAAATAATATAAGATTTTGACTTTTACCCCCTTCCTTAATCCTCCTAATTTCAAGAAGTATTGTAGAAAATGGAGCAGGTACTGGATGAACTGTTTATCCCCCCTTATCCTCAAATATTGC
CCATGGAGGAGCTTCTGTAGATTTAGCTATTTTTTCTTTACACTTAGCTGGTATTTCCTCAATTTTAGGAGCTATTAATTTTATTACAACAATTATCAATATACGAATCAATAGCATATCT
TATGATCAAATACCTTTATTTGTCTGAGCAGTTGGTATTACAGCTTTACTATTACTACTATCTTTACCTGTCTTAGCTGGAGCTATTACTATACTTCTCACAGACCGAAATTTAAATACTT
CATTTTTTGACCCTGCAGGAGGAGGAGACCCAATCTTATACCAACATTTATTT

Cercyonis (*Cercyonis*) *meadii maculana* Grishin, new subspecies

https://zoobank.org/073159D9-45E5-4560-8711-CC983C7441EA

(Figs. 10 part, 11a–b, 16a–b part, 16f, 17 part)

Definition and diagnosis. Genomic analysis reveals that two females of *Cercyonis* (*Cercyonis*) *meadii* (W. H. Edwards, 1872) (type locality in USA: Colorado, Park Co., South Park) from southeastern Utah and southwestern Colorado form a separate clade that is genetically differentiated from others at the subspecies level in the nuclear genome (Fig. 10a magenta), although their COI barcodes do not differ; they therefore represent a new subspecies. This new subspecies is most similar to the nominotypical subspecies (Fig. 11f–h) in being darker ventrally than *Cercyonis* (*Cercyonis*) *meadii alamosa* T. Emmel & J. Emmel, 1969 (type locality in USA: Colorado, Saguache Co., San Luis Valley) (Fig. 11c–e) with

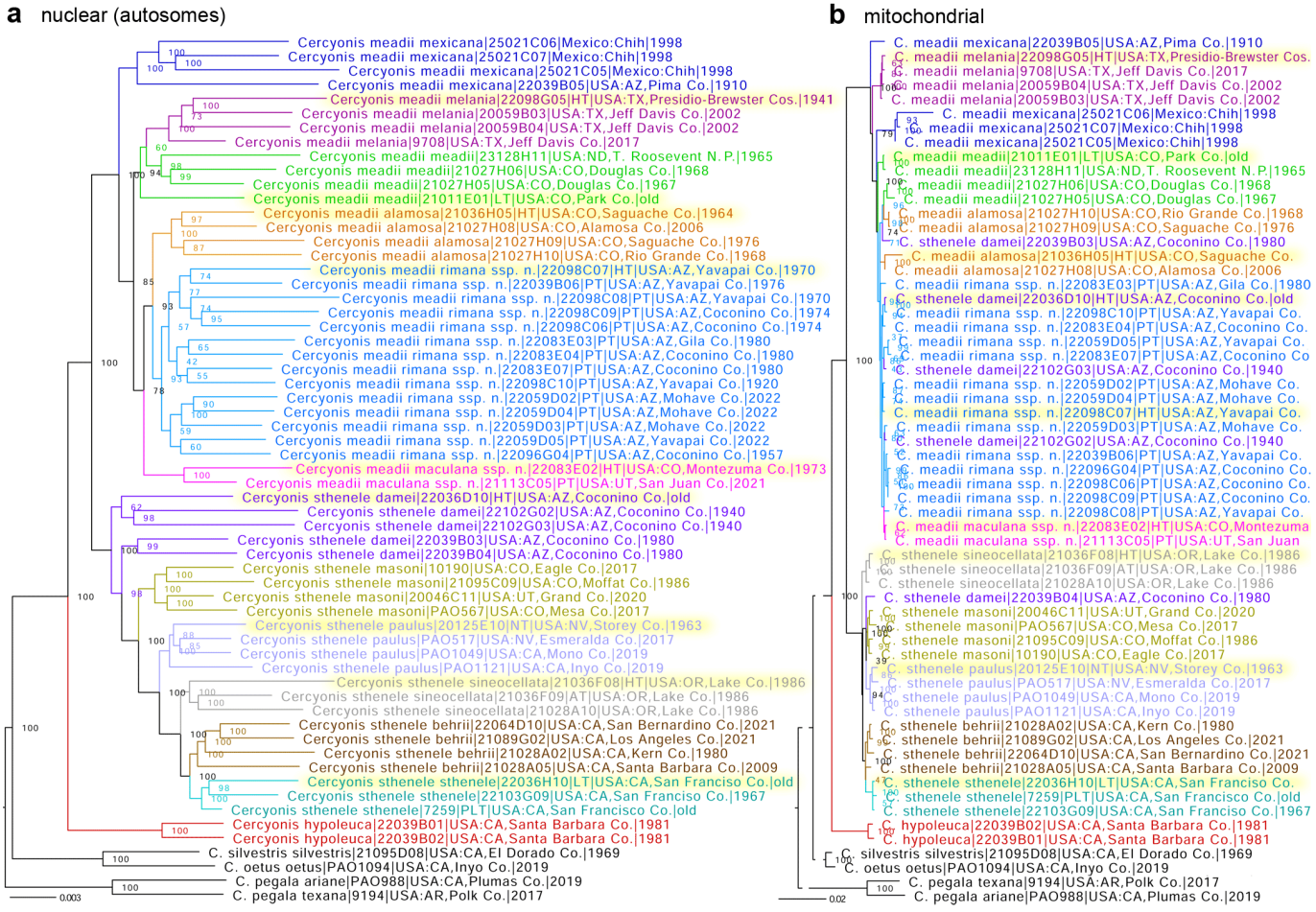


Fig. 10. Phylogenetic trees of all valid taxa in the *Cercyonis* (*Cercyonis*) *sthenele* group constructed from protein-coding regions in: **a)** the nuclear genome (autosomes), based on 6,268,179 positions, and **b)** the mitochondrial genome. Primary type specimens are highlighted in yellow, and taxa of the group are shown in different colors: *C. meadii mexicana* (dark blue), *C. meadii melania* (purple), *C. meadii meadii* (green), *C. meadii alamosa* (orange), *C. meadii rimana* **ssp. n.** (blue), *C. meadii maculana* **ssp. n.** (magenta), *C. sthenele damei* (violet), *C. sthenele masoni* (olive), *C. sthenele paulus* (lavender), *C. sthenele sineocellata* (gray), *C. sthenele behrii* (brown), *C. sthenele sthenele* (cyan), and *C. hypoleuca* (red). Ultrafast bootstrap (Hoang et al. 2018) values are shown at nodes. Gaps in branches of the mitochondrial tree indicate where a vertical slice of the tree was removed to reduce its horizontal dimension (to allow an increase in the font size), i.e., branches with gaps are longer than depicted. See Fig. 16b for complete branches.



Fig. 11 (legend continues on the next page). *Cercyonis* (*Cercyonis*) *meadii* from USA in dorsal (left or above) and ventral (right or below) views: **a–b)** *C. meadii maculana* **ssp. n.** ♀♀ from Colorado, Montezuma Co.: **a)** **holotype** NVG-22083E02 vic. Mesa Verde National Park, 25-Jul-1973, L. Harris leg., and **b)** iNaturalist observation No. 301557034 Cortez, GPS 37.3268, −108.7174, 27-Jul-2025 © colocritters; rotated, brightened, and cropped, CC BY-NC 4.0 https://creativecommons.org/licenses/by-nc/4.0/; **c–e)** *C. meadii alamosa* from Colorado: **c)** **holotype** ♂ NVG-21036H05 Saguache Co., San Luis Valley, CO-17, 7.0

mi N of jct. CO-112, 7537 ft, 17-Aug-1964, T. C. Emmel leg.; **d)** allotype ♀ NVG-21036H06 the same data as the holotype, except 20-Aug-1965; and **e)** non-type ♂ NVG-21027H08 Alamosa Co., N side of CO-150 SW of Great Sand Dunes National Park, 7658 ft, 10-Aug-2006, C. Harp leg. [CSUC]; and **f–h)** *C. meadii meadii*: **f–g)** Colorado, Douglas Co., Deckers, 3-Aug-1968, R. E. Stanford leg. [CSUC]: **f)** ♂ NVG-21027H06 and **g)** ♀ NVG-21027H07; and **h)** ♂ NVG-23128H10 North Dakota, Slope Co., Badlands, 20-Jul-1961 [CNC].



Fig. 12. *Cercyonis* (*Cercyonis*) *meadii* in dorsal (left or above) and ventral (right or below) views: **a–c)** *C. meadii melania* from USA, Texas: **a)** **holotype** ♂ NVG-22098G05 Presidio Co., Marfa – Brewster Co., Alpine, 17-Jul-1941, A. & E. Smith leg. [CAS], and **b)** allotype ♀ not sampled, Brewster Co., Chisos Mts., 19-Jul-1941, A. & E. Smith leg. [CAS]; and **c)** ♂ NVG-22083F02 Jeff Davis Co., nr. Fort Davis, 4-Jul-1972, B. Weber leg. [MGCL]; **d–f)** *C. meadii mexicana*: **d)** ♀ NVG-25021C06, Mexico, Chihuahua, 30 km SW of Colonia Juarez, 12-Aug-1998, J. P. Brock leg. [JPBC]; **e)** ♀ NVG-25021C07, same data as (d); and **f)** ♀ NVG-22039B05 Arizona, Pima Co., Santa Catalina Mts., Green Spring, 7200 ft [CHGC].

some frosting mostly confined to the subapical portion of the ventral hindwing [frosting is more uniformly distributed from the costal to the inner margin, almost forming a diffuse pale band in *C. meadii alamosa*, which also has a marbled basal part of the hindwing], but the female is larger, with a darker, tawny-reddish forewing patch gradually merging into brown ground color [typically more distinctly bordered and brighter, orange-reddish in females of the nominotypical subspecies], and with conspicuously larger eyespots, both on the forewing and hindwing: the hindwing has two larger eyespots near the tornus and up to four additional ones in a row towards the costal margin; the forewing has two large eyespots, each with a dark protuberance on the dorsal side directed towards the apex and tornus for the apical and tornal eyespots, respectively. *Cercyonis* (*Cercyonis*) *meadii melania* (Wind, 1946) (type locality in USA: Texas, Marfa to Alpine) (Fig. 12a–c) can be equally large, with a darker, diffuse reddish patch, but the eyespots are smaller, especially on the forewing, and the mottling in the posterior part of the ventral forewing is less developed. The final described subspecies, *Cercyonis* (*Cercyonis*) *meadii mexicana* (R. Chermock, 1949) (type locality in Mexico: Chihuahua) (Fig. 12d–f), is similar to *C. meadii melania*, but is smaller and frequently has larger eyespots approaching those in the new subspecies, but the reddish patch on the forewing is smaller and the ventral mottling within the patch is less developed; the ventral hindwing is darker and more uniformly colored, nearly without frosting that is present in the new subspecies. Due to poorly explored individual variation, this subspecies is best identified by DNA, with diagnostic base pairs in the nuclear genome: hm2006455-RA.1:C273T, hm2013926-RA.26:C24T, hm2006296-RA.2:C33T, hm2014388-RA.1:C3435T, hm2011330-RA.2:A154G; but the COI barcode does not distinguish this subspecies from several others.

Barcode sequence of the holotype. Sample NVG-22083E02, GenBank PZ783663, 658 base pairs:

AACTTTATATTTTATTTTTGGAATTTGAGCAGGTATAGTAGGAACCTCCCTTAGTCTTATTATTCGAACAGAATTAGGTACCCCAGGATCTTTAATTGGAGATGATCAAATTTATAATACT
ATTGTTACAGCCCATGCTTTTATTATAATTTTTTTTATAGTAATGCCTATTATAATTGGAGGATTTGGTAATTGACTTGTCCCCCTCATATTAGGAGCCCCTGATATAGCTTTCCCCCGAA
TAAATAATATAAGATTTTGACTTTTACCCCCTTCATTAATACTATTGATTTCAAGTAGTATCGTAGAAAATGGAGCAGGAACTGGATGAACAGTTTACCCCCCCTTATCCTCAAATATTGC
CCATAGAGGTGCCTCTGTTGATTTAGCTATTTTCTCTTTACATTTAGCTGGTATCTCTTCAATTCTAGGAGCTATTAATTTTATTACCACAATTATCAATATGCGAGTTAATAGTATATCT
TATGATCAAATGCCCCTATTTGTCTGAGCTGTCGGAATTACAGCCTTATTATTATTACTCTCTTTACCTGTCTTAGCTGGAGCTATTACTATACTTCTTACTGATCGAAATCTAAATACTT
CTTTTTTTGACCCAGCAGGAGGAGGAGATCCAATCCTATATCAACATTTATTT

Type material. Holotype: ♀ deposited in the McGuire Center for Lepidoptera and Biodiversity collection, Gainesville, FL, USA (MGCL), illustrated in Fig. 11a, bears the following five rectangular labels (2nd handwritten, others printed), four white: [USA: COLORADO | Montezuma Co; | vic. Mesa Verde N.P. | 25-VII-1973 | Lowell Harris], [mesa verde | 7/25/73], [MGCL Accession | #2009-32 | Lowell Harris], [DNA sample ID: | NVG-22083E02 | c/o Nick V. Grishin], and one red [HOLOTYPE ♀ | Cercyonis (Cercyonis) | meadii maculana Grishin]. **Paratype:** 1♀ from USA, Utah, San Juan Co., Monticello Mill Site, GPS 37.8629, −109.3292, 14-Aug-2021, Robb Hannawacker leg. (Fig. 16f, left-right inverted from the original live photograph).

Type locality. USA: Colorado, Montezuma Co., vic. Mesa Verde National Park.

Etymology. The name refers to the atypically large and irregular maculation (Latin *macula*, spot) in females of this subspecies and is treated as a noun in apposition.

Distribution. The Great Sage Plain in southeastern Utah and southwestern Colorado.

Cercyonis (*Cercyonis*) *meadii rimana* Grishin, new subspecies

https://zoobank.org/FA6C2544-9E9D-4C3E-8A49-3C3AAB478FE0

(Figs. 10 part, 13, 16a–b part, 16g–h, 17 part)

Definition and diagnosis. Genomic analysis reveals that specimens of *Cercyonis* (*Cercyonis*) *meadii* (W. H. Edwards, 1872) (type locality in USA: Colorado, Park Co., South Park) from the southwestern rim of the Colorado Plateau (south-central Utah and north-to-central Arizona) form a separate clade in the nuclear genome that is sister to *Cercyonis* (*Cercyonis*) *meadii alamosa* T. Emmel & J. Emmel, 1969 (type locality in USA: Colorado, Saguache Co., San Luis Valley) but genetically differentiated from it at the subspecies level (Fig. 10a blue vs. orange), although their COI barcodes do not differ; these specimens therefore represent a new subspecies. This new subspecies is most similar to *C. meadii alamosa* (Fig. 11c–e), frequently exhibiting more or less developed frosting on the ventral hindwing, especially in the distal third, but the frosting is usually more limited (especially in males) and in females typically


HT
a
b
c
d
e
f
g
h
F
1 cm

Fig. 13 (see previous page). Type specimens of *Cercyonis* (*Cercyonis*) *meadii rimana* **ssp. n.** from USA, Arizona in dorsal (left or above) and ventral (right or below) views: **a) holotype** ♂ NVG-22098C07 Yavapai Co., 4 mi N of Prescott, Granite Dells, 18-Aug-1970, L. M. Martin leg. [LACM]; and paratypes: **b)** ♂ NVG-22096G04 Coconino Co., nr. Flagstaff, 26-Aug-1957, A. O. Shields & D. J. Dirks leg. [LACM]; **c)** ♂ NVG-22083E04 Coconino Co., Leupp Rd., 2.2 mi N and 5.4 mi E of Winona, 28-Aug-1980, G. T. Austin leg. [MGCL]; **d)** ♀ NVG-22098C08, data as the holotype, except 28-Aug-1970; **e)** ♀ NVG-22098C06 Coconino Co., nr. Williams, Kaibab Lake Campground, 2-Sep-1974, B. Iwahashi leg. [LACM]; **f)** ♀ NVG-22083E07, same data as (c); **g)** ♀ NVG-22083E03 Gila Co., White Mts., AZ-73 3 mi W of Geronimo Pass, 2-Sep-1980, G. T. Austin leg. [MGCL]; and **h)** ♀ NVG-22059D02 Mohave Co., Hualapai Mountain Park, 6690 ft, 8-Sep-2022, W. R. Dempwolf leg. [WRDC]. Gray F indicates a flipped (left-right inverted) image.

confined to the apical area [frosting is more uniformly distributed from the costal to the inner margin, almost forming a diffuse pale band in *C. meadii alamosa*, which also has a marbled basal part of the hindwing]. Darker specimens of the new subspecies may resemble the nominotypical *C. meadii* (Fig. 11f–h), but they have a larger and frequently paler, more yellow, tawny-reddish patch on the forewing. The new subspecies differs from *Cercyonis* (*Cercyonis*) *meadii melania* (Wind, 1946) (type locality in USA: Texas, Marfa to Alpine) (Fig. 12a–c) by finer and less developed mottling at least within the reddish patch on the ventral forewing; from *Cercyonis* (*Cercyonis*) *meadii mexicana* (R. Chermock, 1949) (type locality in Mexico: Chihuahua) (Fig. 12d–f) by less uniformly colored ventral hindwing with at least some traces of frosting; and from *Cercyonis* (*Cercyonis*) *meadii maculana* **ssp. n.** (type locality USA: Colorado, Montezuma Co., vic. Mesa Verde National Park) described right above by smaller eyespots usually lacking protuberances and usually less developed mottling in the reddish patch on the ventral forewing. This subspecies can be confidently identified by DNA, with diagnostic base pairs in the nuclear genome: hm2016317-RA.14:C36A, hm2010732-RA.1:C792T, hm2010732-RA.1:T795A, hm2012721-RA.11:G87A, hm2005871-RA.1:C504T; but the COI barcode does not distinguish this subspecies from several others.

Barcode sequence of the holotype. Sample NVG-22098C07, GenBank PZ783664, 658 base pairs:

AACTTTATATTTTATTTTTGGAATTTGAGCAGGTATAGTAGGAACCTCCCTTAGTCTTATTATTCGAACAGAATTAGGTACCCCAGGATCTTTAATTGGAGATGATCAAATTTATAATACT
ATTGTTACAGCCCATGCTTTTATTATAATTTTTTTTATAGTAATGCCTATTATAATTGGAGGATTTGGTAATTGACTTGTCCCCCTCATATTAGGAGCCCCTGATATAGCTTTCCCCCGAA
TAAATAATATAAGATTTTGACTTTTACCCCCTTCATTAATACTATTGATTTCAAGTAGTATCGTAGAAAATGGAGCAGGAACTGGATGAACAGTTTACCCCCCCTTATCCTCAAATATTGC
CCATAGAGGTGCCTCTGTTGATTTAGCTATTTTCTCTTTACATTTAGCTGGTATCTCTTCAATTCTAGGAGCTATTAATTTTATTACCACAATTATCAATATGCGAGTTAATAGTATATCT
TATGATCAAATGCCCCTATTTGTTTGAGCTGTCGGAATTACAGCCTTATTATTATTACTCTCTTTACCTGTCTTAGCTGGAGCTATTACTATACTTCTTACTGATCGAAATCTAAATACTT
sCTTTTTTTGACCCAGCAGGAGGAGGAGATCCAATCCTATATCAACATTTATTT

Type material. Holotype: ♂ deposited in the Los Angeles County Museum of Natural History, Los Angeles, CA, USA (LACM), illustrated in Fig. 13a, bears the following four printed rectangular labels, three white: [Granite Dells | 4 mi. N. of], [Prescott, Yavapai | County, Arizona | August 18 1970 | collected by | Lloyd M. Martin], [DNA sample ID: | NVG-22098C07 | c/o Nick V. Grishin], and one red [HOLOTYPE ♂ | Cercyonis (Cercyonis) | meadii rimana Grishin]. **Paratypes:** 7♂♂ and 6♀♀: USA, Arizona: Mohave Co. 8-Sep-2022, W. R. Dempwolf leg. [WRDC]: 1♂ NVG-22059D03 CR-147 S of Pinion Pines, 5200 ft, GPS 35.1277, −113.9168 and 1♂ NVG-22059D04 and 1♀ NVG-22059D02 (Fig. 13h) Hualapai Mountain Park, 6690 ft, GPS 35.0959, −113.8874; Coconino Co.: 2♀♀ (NVG-22098C06 (Fig. 13e) and NVG-22098C09) nr. Williams, Kaibab Lake Campground, 2-Sep-1974, B. Iwahashi leg. [LACM]; 1♂ NVG-22096G04, nr. Flagstaff, 26-Aug-1957, A. O. Shields & D. J. Dirks leg. [LACM] (Fig. 13b); and 1♂ NVG-22083E04 (Fig. 13c) and 1♀ NVG-22083E07 (Fig. 13f) Leupp Rd., 2.2 mi N and 5.4 mi E of Winona, 28-Aug-1980, G. T. Austin leg. [MGCL]; Yavapai Co.: 1♂ NVG-22059D05 AZ-89A, Mingus Mountain, 6379 ft, GPS 34.6944, −112.1682, 4-Sep-2022, W. R. Dempwolf leg. [WRDC]; 1♂ NVG-22039B06 NW of Prescott, 7-Aug-1976 [CHGC]; and data as the holotype (4 mi N of Prescott, Granite Dells, L. M. Martin leg. [LACM]): 1♂ NVG-22098C10 26-27-Aug-1920 and 1♀ NVG-22098C08 28-Aug-1970 (Fig. 13d); and 1♀ NVG-22083E03 Gila Co., White Mts., AZ-73 3 mi W of Geronimo Pass, 2-Sep-1980, G. T. Austin leg. [MGCL] (Fig. 13g).

Type locality. USA: Arizona, Yavapai Co., 4 mi north of Prescott, Granite Dells.

Etymology. The name is derived from the English word rim to reflect the range of this subspecies along the southwestern rim of the Colorado Plateau. The name is treated as a noun in apposition.

Distribution. Southwestern rim of the Colorado Plateau from around Koosharem in Utah through the Grand Canyon, Prescott, and to Whiteriver in Arizona, mostly in the Transitional Zone.



Fig. 14 (legend continues on the next page). *Cercyonis* (*Cercyonis*) *sthenele* subspecies from the eastern part of the range, USA, in dorsal (left or above) and ventral (right or below) views: **a–d)** *C. sthenele damei* from Arizona, Coconino Co., Grand

Canyon, Kaibab Plateau, Cape Royal, unless otherwise specified: **a)** ♂ NVG-22102G02, CASENT_8567016, 26-Jul-1940, L. I. Hewes [CAS]; **b)** ♂ NVG-22039B03 17-Aug-1980, J. A. Scott leg. [CHGC]; **c)** ♀ NVG-22102G03, CASENT_8567017 S Rim, 27-Jun-1940, L. I. Hewes [CAS]; **d)** ♀ NVG-22039B04, data as (b); **e)** *C. sthenele masoni* ♂ NVG-20047D12 Utah, Grand Co., Castle Creek, 6400 ft, 1-Jul-2020, Robb Hannawacker leg.; and **f–h)** *C. sthenele paulus*: **f)** ♂ NVG-22084E08 Nevada, Clark Co., E side of Sheep Range, nr. mouth of Sawmill Canyon, ca. 3 air mi NNW of Mormon Well, 6000-6500 ft, 1-Jul-1969, J. Emmel & O. Shields leg. [MGCL]; **g)** **neotype** ♂ NVG-20125E10 Nevada, Storey Co., vic. Virginia City, 1-Aug-1963, P. & B. Herlan leg. [CMNH] and **h)** ♀ NVG-22096F04 California, Mono Co., Mono Lake, 22-Jul-1946, M. L. Walton leg. [LACM].

Cercyonis (*Cercyonis*) *sthenele damei* (W. Barnes & Benjamin, 1926)

The taxonomic identity of *Cercyonis* (*Cercyonis*) *sthenele damei* (W. Barnes & Benjamin, 1926) (type locality in USA: Arizona, Coconino Co., Grand Canyon) has been a source of confusion (Miller and Brown 1981; Pelham 2008). Genomic sequencing of the holotype revealed that it represents a subspecies of *Cercyonis* (*Cercyonis*) *sthenele* (Boisduval, 1852) (type locality USA: California, San Francisco) most closely related to *Cercyonis* (*Cercyonis*) *sthenele masoni* Cross, 1937 (type locality in USA: Colorado, Mesa Co., Black Ridge Breaks) and *Cercyonis* (*Cercyonis*) *sthenele paulus* (W. H. Edwards, 1879) (type locality in USA: Nevada, Storey Co., vic. Virginia City) (Zhang et al. 2023c). We sequenced additional specimens of *C. sthenele damei* (Fig. 10 violet), and illustrate two males (Fig. 14a, b), two females (Fig. 14c, d), and a live individual (Fig. 16i) of this subspecies compared with *C. sthenele masoni* (Fig. 14e, 16j) and *C. sthenele paulus* (Fig. 14f–h). Sequenced specimens of *C. sthenele damei* lack the reddish patches of *Cercyonis* (*Cercyonis*) *meadii* (W. H. Edwards, 1872) (type locality in USA: Colorado, Park Co., South Park) and are similar to the two other more eastern subspecies of *C. sthenele*, but differ from them in a more uniformly colored ventral hindwing that has more weakly defined brown bands and lines, especially in males. Females of *C. sthenele damei* are usually less contrasty on the ventral side, with less prominent paler areas in the marginal half of the hindwing and towards the forewing apex than females of *C. sthenele masoni* and *C. sthenele paulus*, and are more similar to males of the latter two subspecies in the expression of the variegated ventral wing pattern.

Neotype of *Satyrus behrii* F. Grinnell, 1905 is invalid and not warranted

Emmel et al. (1998c) published a neotype designation for *Satyrus behrii* F. Grinnell, 1905 (type locality USA: California, Marin Co., Mt. Tamalpais), currently a valid subspecies of *Cercyonis sthenele* (Boisduval, 1852) (type locality USA: California, San Francisco). Although their designation satisfied Articles 75.3.3–75.3.7 of the ICZN Code (1999) and the specimen they selected most likely represents the species described by Grinnell (1905), the designation fails the parent Art. 75.3 ("exceptional need" must be "stated expressly") and the subordinate Art. 75.3.1 ("a statement that it is designated with the express purpose of clarifying the taxonomic status or the type locality of a nominal taxon" is not included). Therefore, the neotype is invalid. Moreover, the taxonomic identity of *S. behrii* has not been questioned, and at its type locality there is only one taxon that agrees with the original description, which is rather detailed and unambiguous. Therefore, according to Art. 75.2 and the corresponding example (ICZN, 1999), there is no need to designate a neotype of *S. behrii*. The need is neither stated by Emmel et al. (1998c) nor currently present. If it is later determined that cryptic species may be confused with *S. behrii*, then the specimen selected as the neotype by Emmel et al. (1998c) may be validly designated at that time.

Mapping wing patterns onto the phylogeny of the *Cercyonis sthenele* group

Cercyonis (*Cercyonis*) *hypoleuca* Hawks & J. Emmel, 1998 (type locality USA: California, Santa Barbara Co., Santa Cruz Is.) (Fig. 15g–h) was originally described as a subspecies of *Cercyonis* (*Cercyonis*) *sthenele* (Boisduval, 1852) (type locality USA: California, San Francisco) (Fig. 15d–f) due to the similarity in wing patterns and resemblance in male genitalia (Hawks and Emmel 1998), but it was subsequently shown to be a genetically differentiated species by Zhang et al. (2023c). First, we confirm the species-level distinction of *C. hypoleuca*, which forms a clade sister to both *C. sthenele* and *Cercyonis*



Fig. 15. *Cercyonis* (*Cercyonis*) taxa from USA, California in dorsal (left or above) and ventral (right or below) views: **a–c)** *C. sthenele behrii* [CSUC]: **a)** ♂ NVG-21028A07 Stanislaus Co., Del Puerto Canyon, 18-Jun-2007, P. & E. Opler leg.; **b)** ♂ NVG-21028A04 Tulare Co., Kennedy Meadows, 30-Jun-1988, K. Davenport leg.; and **c)** ♀ NVG-21028A06 Santa Barbara Co., 3000 ft, 12-Jun-1966, R. W. Holland leg.; **d–f)** *C. sthenele sthenele* types from San Francisco Co., San Francisco, old: **d)** **lectotype** ♂ NVG-22036H10 [USNM] and paralectotypes ♀♀: **e)** NVG-26035F11 [USNM] and **f)** NVG-22103G09, CASENT 8567119 [CAS]; and **g–h)** *C. hypoleuca* Santa Barbara Co., Santa Cruz Island, Jul-1981, R. C. Priestaf leg. [CHGC]: **g)** ♂ NVG-22039B01 and **h)** ♀ NVG-22039B02.

(*Cercyonis*) *meadii* (W. H. Edwards, 1872) (type locality USA: Colorado, Park Co., South Park) in all genomic trees (Figs. 10, 16).

Second, despite prominent differences in wing pattern and shape, the nominotypical *C. sthenele* is most closely related to geographically proximal *Cercyonis* (*Cercyonis*) *sthenele behrii* (F. Grinnell, 1905) (type locality USA: California, Marin Co., Mt. Tamalpais) (Fig. 15a–c), also in all trees (Figs. 10 cyan vs. brown, 16). More distantly related taxa *C. hypoleuca* and *C. sthenele sthenele* are more similar to each other in wing patterns, both having a variegated appearance beneath, with well-defined paler areas in equivalent portions of the wings. Conversely, close relatives *C. sthenele sthenele* and *C. sthenele behrii* differ strongly, with the latter being more uniformly colored without prominent frosty patches on the ventral side of the wings. This example shows that wing patterns do not necessarily correlate with phylogenetic relatedness.

Third, despite superficial similarities between *C. hypoleuca* and *C. sthenele sthenele*, details of their wing patterns differ, as described by Hawks and Emmel (1998). Most conspicuously, the ventral hindwing discal brown area (a broad band) is wider in *C. hypoleuca*, and the band increases in width from the costal to the inner margin (Fig. 15g–h), while this band is narrower in *C. sthenele sthenele* and approximately the same width throughout, not wider near the inner margin than at the costal margin (Fig. 15d–f).

A provisional ordered taxonomic list of *Cercyonis* (*Cercyonis*) Scudder, 1875

The results of this work are summarized as a provisional taxonomic list of species, subspecies, and synonyms in the subgenus *Cercyonis*. The initial list is taken from Pelham (2008) and modified according to Calhoun (2016) and our genomic results (Figs. 1, 10, 16a–b). First, we place the New World subgenus *Cercyonis* in the phylogenetic context of its relatives, including all valid genera and subgenera in the subtribe Erebiina Tutt, 1896 (type genus *Erebia* Dalman, 1816) (Fig. 16a–b). We confirm our previous results about the higher classification of this subtribe (Zhang et al. 2020; Zhang et al. 2021; Zhang et al. 2026b): considering genetic differentiation in the universally accepted genus *Erebia*, we assign the genus rank to the corresponding prominent level in the phylogenetic trees, resulting in two additional genera in this subtribe: *Cercyonis* and *Maniola* Schrank, 1801 (type species *Maniola lemur* Schrank, 1801, which is a junior subjective synonym of *Papilio jurtina* Linnaeus, 1758), which are sister genera. The next tree level (closer to the leaves) corresponds to subgenera. Consistently with our previous results, *Erebia* and *Maniola* partition into four and five subgenera, respectively (Fig. 16a–b), and *Cercyonis* consists of three subgenera: *Hyponephele* Muschamp, 1915 (type species *Papilio lycaon* Rottemburg, 1775) and *Ereminephele* Koçak & Kemal, 2001 (type species *Hyponephele huebneri* Koçak, 1980) in the Old World in addition to the nominotypical subgenus.

Second, we arrange species of the subgenus *Cercyonis* into three groups forming distinct clades below the subgenus level (Fig. 16a–b): the *pegala* group consisting of a single homonymous species, the *sthenele* group of three species (*C. meadii*, *C. sthenele*, and *C. hypoleuca*), and the *silvestris* group of two closely related species (*C. silvestris* and *C. oetus*). Third, we order taxa to maximize phenotypic similarity and geographic proximity of the list neighbors without disrupting the confidently supported phylogenetic order in the nuclear genome trees (Figs. 1a, 10a, 16a) (i.e., a strongly supported clade in the tree is a contiguous segment in the list). We start the list from *C. pegala*, a species with the largest range, and because *C. sthenele* and *C. silvestris* can most easily be confused with each other, place them in close proximity in the list. Due to superficial similarity between *C. sthenele sthenele* and *C. hypoleuca*, they are placed as adjacent taxa, with *C. hypoleuca* necessarily between *C. sthenele* and *C. silvestris* due to the tree topology constraints. Under all these constraints, placing *C. meadii* instead of *C. oetus* adjacent to *C. pegala*, due to both species having reddish to yellowish patches on the wings, completes the order of species groups and species as: *pegala* - *meadii* - *sthenele* - *hypoleuca* - *silvestris* - *oetus*.

To elaborate on the species order, *meadii* - *sthenele* - *hypoleuca* form a strongly supported clade (the *C. sthenele* species group) (Fig. 16a–b) and this trio must not be interrupted by other taxa. However, considering that *meadii* - *sthenele* are confidently sister taxa, the trio can alternatively be placed into any of



Fig. 16 (legend continues on the next page). Phylogenetic trees of all valid *Cercyonis* (*Cercyonis*) taxa and representatives of all valid genera and subgenera in the subtribe Erebiina Tutt, 1896, constructed from protein-coding regions in: **a)** the nuclear genome (autosomes), based on 2,648,655 positions, and **b)** the mitochondrial genome; and **c–j)** iNaturalist observations from USA: **c)** *C. pegala koosharem* **ssp. n.** observation No. 55088769, Utah, Sevier Co., Otter Creek at UT-62, GPS 38.5649,

−111.8480, 19-Aug-2017 © jmklodzen; **d)** *C. pegala lasala* **ssp. n.** observation No. 176063528, Utah, Grand Co., Moab, GPS 38.5915, −109.2646, 13-Jul-2020 © Amanda Barth; **e)** *C. pegala hortoni* **ssp. n.** observation No. 40866564, Arizona, Gila Co., Colonel Devin Trail, GPS 34.4305, −111.2610, 19-Aug-2011 © Tom Horton; **f)** *C. meadii maculana* **ssp. n.** paratype, observation No. 91168101, Utah, San Juan Co., Monticello, GPS 37.8629, −109.3292, 14-Aug-2021, photographed by R. Hannawacker; **g–h)** *C. meadii rimana* **ssp. n.** from Arizona, Coconino Co.: **g)** observation No. 89805465, nr. the Grand Canyon North Rim, GPS 36.4605, −112.3398, 1-Aug-2021 © Tom Horton, and **h)** observation No. 39121701, Grand Canyon Village (South Rim), GPS 36.0576, −112.1426, 21-Jul-2009 © Jessee J. Smith; **i)** *C. sthenele damei* observation No. 26888066, Arizona, Coconino Co., Cape Final Trail, GPS 36.1458, −111.9354, 1-Aug-2011 © Tom Horton; **j)** *C. sthenele masoni* observation No. 59491802, Colorado, Mesa Co., Colorado National Monument, GPS 39.0308, −108.6863, 27-Aug-2019 © Joey Bom; images are color-corrected, brightened, rotated, cropped, and some flipped, CC BY-NC 4.0 https://creativecommons.org/licenses/by-nc/4.0/. In the trees, names of valid genera and subgenera are specified by their clades, along with species and subspecies groups proposed in this work; corresponding ranks (genus, subgenus, species group, subspecies group; highlighted in peach color) are indicated at their tree levels, and different species of the subgenus *Cercyonis* are colored differently: *C. pegala* (blue, with the *ariane* clade shown in lighter blue), *C. meadii* (red), *C. sthenele* (green), *C. hypoleuca* (magenta), *C. silvestris* (cyan), and *C. oetus* (violet). Ultrafast bootstrap (Hoang et al. 2018) values are shown at nodes.

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the following three additional arrangements: *sthenele* - *meadii* - *hypoleuca*, *hypoleuca* - *meadii* - *sthenele*, and *hypoleuca* - *sthenele* - *meadii*. The same consideration applies to *silvestris* - *oetus* (the *C. silvestris* species group), and it can be listed as *oetus* - *silvestris*. Because the *C. sthenele* and *C. silvestris* species groups are sisters with 100% ultrafast bootstrap support (Hoang et al. 2018) (Fig. 16a–b), they must be adjacent in the list. Therefore, the following orders of the species groups are possible (gr. means group): *pegala* gr. - *sthenele* gr. - *silvestris* gr. (as used here), *pegala* gr. - *silvestris* gr. - *sthenele* gr., *sthenele* gr. - *silvestris* gr. - *pegala* gr., and *silvestris* gr. - *sthenele* gr. - *pegala* gr. Because *C. pegala* and *C. meadii* have reddish or orangish forewing patches, we place them consecutively in the list. Because *C. hypoleuca* is most similar to the nominotypical *C. sthenele*, they are consecutive in the list. Because *C. silvestris* is most similar to *C. sthenele*, we place them close to each other (but necessarily with *C. hypoleuca* between them due to the constraints explained above). Because *C. pegala* has the largest geographic range, it is placed first. These considerations lead to the species order adopted in the list.

Similar considerations are used to order subspecies within species. An additional caveat is that while the species-level phylogeny is most strongly supported and congruent between the nuclear and mitochondrial genome (note that *C. silvestris* and *C. oetus* share similar mitogenome haplotypes) (Fig. 16a vs. b), the subspecies "phylogeny" is more ambiguous, and may not be easy to infer due to the continuing gene flow between them. At the population level, genetic identity is defined by allele frequencies rather than uniquely sorted diagnostic alleles, making strict phylogenetic tree-thinking insufficient for describing relationships between subspecies. Therefore, for the ambiguous subspecies-level bifurcations in the nuclear genome tree, we hypothesize the order on the list based on geographic proximity, phenotypic similarity, and the mitochondrial genome tree (Fig. 16b) if it is more confident.

In *C. pegala*, the clade of western subspecies prominently stands out (highlighted in orange in Fig. 1). We define this clade as the *ariane* subspecies group (Fig. 16a–b). More eastern subspecies of *C. pegala* form a clade in the mitochondrial genome tree (Fig. 16b), but not in the nuclear genome tree (Fig. 16a), in which statistical support for the bifurcations among the eastern subspecies is weak. These eastern subspecies are referred to as the *pegala* subspecies group. Within each subspecies group, subspecies are ordered by the phylogeny and geographic proximity (preference given to the arrangement from north to south and west to east) for instance, *C. pegala boopis* and *C. pegala incana* from the western group are placed next to the subspecies in the eastern group, starting from the southwestern subspecies *C. pegala lasala* **ssp. n.** and *C. pegala hortoni* **ssp. n**. To allow this adjacency within the phylogenetic constraints, the western group starts with *C. pegala utahensis* and relatives: *C. pegala wheeleri* placed first to allow adjacency of superficially similar and geographically more proximal *C. pegala koosharem* **ssp. n.** and *C. pegala pluvialis*. In *C. meadii*, *C. meadii rimana* **ssp. n.** is placed last to be adjacent to sympatric *C. sthenele damei*, which is placed first among *C. sthenele*. To accommodate this adjacency, we start subspecies of *C. meadii* from *C. meadii mexicana*, the southernmost taxon, thus inverting the default north-south order. The *C. meadii* subspecies are thus ordered south-to-north and then back to mid-range (*C. meadii alamosa*) and east-to-west. The subspecies of *C. oetus* are arranged from

north to south and west to east. Further refinement of the suggested tentative order below is warranted.

In the taxonomic list, new subspecies are shown in red font. Comments follow a vertical bar | after the type locality; an equal sign = precedes junior subjective synonyms given in their original genus combinations. The list covers 41 valid taxa (with 11 junior subjective synonyms) comprising 6 species and 35 subspecies (excluding the nominotypical subspecies, 5 new). Type localities of valid taxa are shown on the map (Fig. 17).

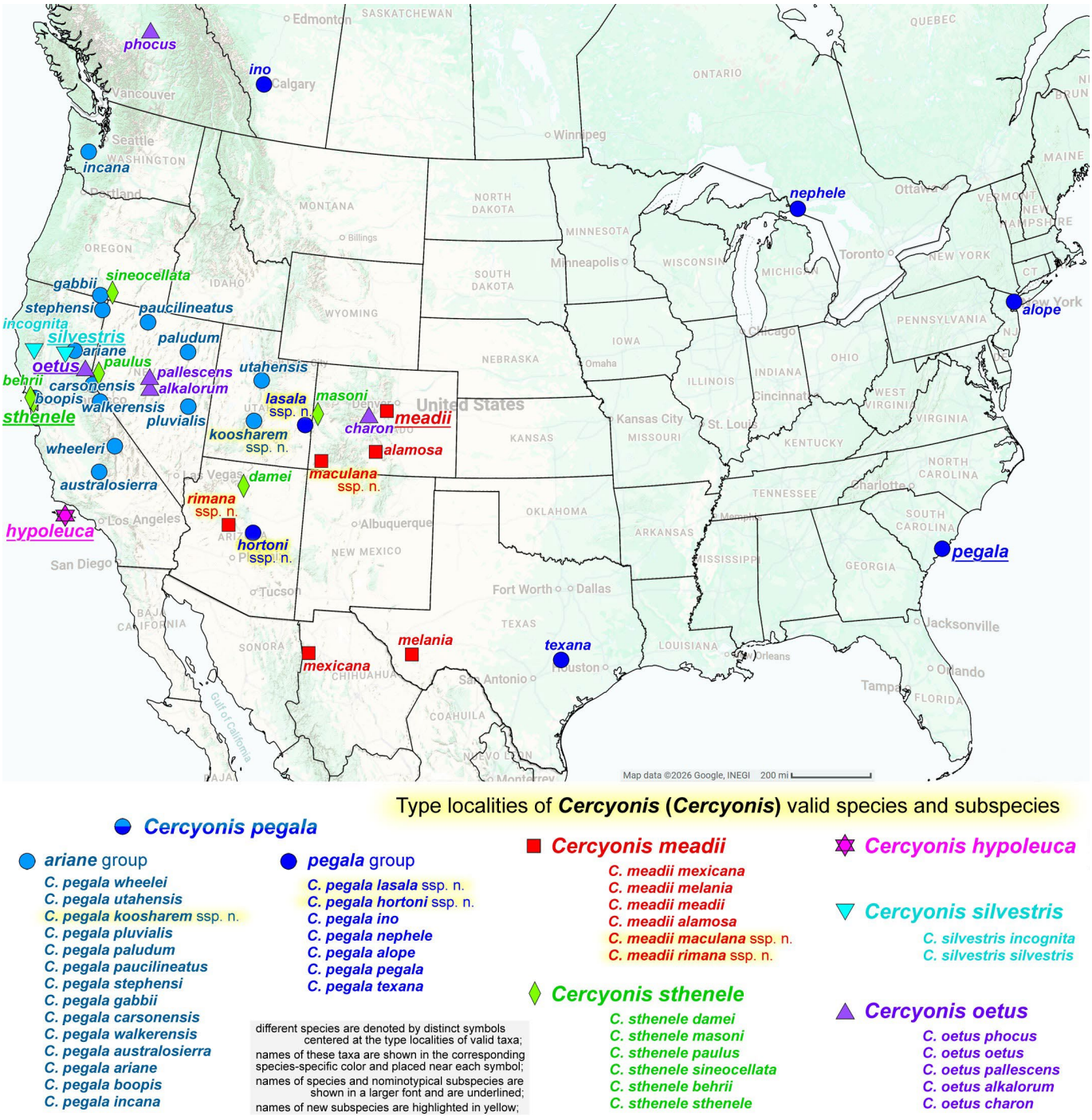


Fig. 17. Type localities of all valid taxa in the subgenus *Cercyonis*. Different species are denoted by distinct shape- and color-coded symbols (color scheme from Fig. 16) centered at the type localities of valid taxa: *C. pegala* (blue circles ●, with the *ariane* subspecies group in lighter blue ●), *C. meadii* (red squares ■), *C. sthenele* (green diamonds ♦), *C. hypoleuca* (magenta star ✶), *C. silvestris* (cyan inverted triangles ▼), and *C. oetus* (violet upright triangles ▲). The names of taxa are shown in the corresponding species-specific colors and placed near each symbol, sometimes overlapping it (e.g., *C. pegala carsonensis*, *walkerensis*, and *boopis*). Names of species and nominotypical subspecies are shown in a larger font and are underlined.

Genus ***Cercyonis*** Scudder, 1875; type species *Papilio alope* Fabricius, 1793, currently *C. pegala alope*
Subgenus ***Cercyonis*** Scudder, 1875; type species *Papilio alope*, currently *C. pegala alope*

pegala species group

Cercyonis pegala (Fabricius, 1775); USA: SC, vic. Charleston

ariane subspecies group | western

Cercyonis pegala wheeleri (W. H. Edwards, 1873); USA: CA, Inyo Co., vic. Owens Lake
= *Satyrus hoffmani* Strecker, 1873; USA: CA, Inyo Co., vic. Owens Lake | junior subjective synonym
Cercyonis pegala utahensis Austin, 1992; USA: UT, Utah Co., Benjamin
Cercyonis pegala koosharem Stout & Grishin, **ssp. n.**; USA: UT, Sevier Co., Otter Creek at UT-62
Cercyonis pegala pluvialis Austin, 1992; USA: NV, White Pine Co., White River Valley
Cercyonis pegala paludum Austin, 1992; USA: NV, Elko Co., Pleasant Valley
Cercyonis pegala paucilineatus Austin, 1992; USA: NV, Humboldt Co., Quin River Valley
Cercyonis pegala stephensi (W. G. Wright, 1905); USA: CA, Modoc Co., Surprise Valley
= *Cercyonis pegala blanca* T. Emmel & Mattoon, 1972; USA: NV, Humboldt Co. | junior subjective synonym
Cercyonis pegala gabbii (W. H. Edwards, 1870); USA: OR, Lake Co., Goose Lake
Cercyonis pegala carsonensis Austin, 1992; USA: NV, Douglas Co., Carson River Valley
Cercyonis pegala walkerensis Austin, 1992; USA: CA, Mono Co., Huntoon Valley
Cercyonis pegala australosierra J. Emmel, T. Emmel & K. Davenport, 2008; USA: CA, Tulare Co.
Cercyonis pegala ariane (Boisduval, 1852); USA: CA, Plumas Co.
Cercyonis pegala boopis (Behr, 1864); USA: CA, Contra Costa Co., Point Richmond
= *Satyrus ariane baroni* W. H. Edwards, 1880; USA: CA, Mendocino Co. | junior subjective synonym
Cercyonis pegala incana (W. H. Edwards, 1880); USA: WA, Thurston Co., Olympia

pegala subspecies group | eastern

Cercyonis pegala lasala Grishin, M. Fisher, & Hannawacker **ssp. n.**; USA: UT, Grand Co., Castle Creek
Cercyonis pegala hortoni Grishin, **ssp. n.**; USA: AZ, Gila Co., Colonel Devin Trail
Cercyonis pegala ino G. Hall, 1924; Canada: Alberta, Calgary
Cercyonis pegala nephele (W. Kirby, 1837); Canada: Ontario, nr. Lake Huron
= *Satyrus nephele olympus* W. H. Edwards, 1880; USA: IL, Cook Co. | junior subjective synonym
= *Cercyonis* (*Satyrus*) *pegala borealis* F. Chermock, 1929; USA: OH, Trumbull Co. | junior subjective synonym
Cercyonis pegala alope (Fabricius, 1793); USA: NY, vic. New York City
= *Satyrus alope maritima* W. H. Edwards, 1880; USA: MA, Dukes Co. | junior subjective synonym
= *Cercyonis alope ochracea* F. Chermock & R. Chermock, 1942; USA: RI, Providence Co. | jun. subj. syn.
= *Cercyonis pegala agawamensis* Arey & Grkovich, 2014; USA: MA, Essex Co. | junior subjective synonym
Cercyonis pegala pegala (Fabricius, 1775); USA: SC, vic. Charleston
= *Cercyonis alope carolina* F. Chermock & R. Chermock, 1942; USA: NC, Transylvania Co. | jun. subj. syn.
= *Cercyonis pegala abbotti* F. Brown, 1969; USA: FL, Washington Co., Chipley | junior subjective synonym
Cercyonis pegala texana (W. H. Edwards, 1880); USA: TX, Bastrop Co., Bastrop

sthenele species group

Cercyonis meadii (W. H. Edwards, 1872); USA: CO, Park Co., South Park
Cercyonis meadii mexicana (R. Chermock, 1949); Mexico: Chihuahua, head of Rio Piedras Verdes
Cercyonis meadii melania (Wind, 1946); USA: TX, Presidio Co., Marfa – Brewster Co., Alpine
Cercyonis meadii meadii (W. H. Edwards, 1872); USA: CO, Park Co., South Park
Cercyonis meadii alamosa T. Emmel & J. Emmel, 1969; USA: CO, Saguache Co., San Luis Valley
Cercyonis meadii maculana Grishin, **ssp. n.**; USA: CO, Montezuma Co., vic. Mesa Verde Nat. Park
Cercyonis meadii rimana Grishin, **ssp. n.**; USA: AZ, Yavapai Co., 4 mi N of Prescott, Granite Dells

Cercyonis sthenele (Boisduval, 1852); USA: CA, San Francisco Co., San Francisco
Cercyonis sthenele damei (W. Barnes & Benjamin, 1926); USA: AZ, Coconino Co., Grand Canyon
Cercyonis sthenele masoni Cross, 1937; USA: CO, Mesa Co., Black Ridge Breaks
Cercyonis sthenele paulus (W. H. Edwards, 1879); USA: NV, Storey Co., vic. Virginia City
Cercyonis sthenele sineocellata Austin & J. Emmel, 1998; USA: OR, Lake Co., W of Crump Lake
Cercyonis sthenele behrii (F. Grinnell, 1905); USA: CA, Marin Co., Mt. Tamalpais
Cercyonis sthenele sthenele (Boisduval, 1852); USA: CA, San Francisco Co., San Francisco

Cercyonis hypoleuca Hawks & J. Emmel, 1998; USA: CA, Santa Barbara Co., Santa Cruz Is.

silvestris species group

Cercyonis silvestris (W. H. Edwards, 1861); USA: CA, Butte Co.

Cercyonis silvestris incognita J. Emmel, T. Emmel & Mattoon, 2012; USA: CA, Mendocino Co.

Cercyonis silvestris silvestris (W. H. Edwards, 1861); USA: CA, Butte Co.

= *Satyrus ariane okius* Oberthür, 1914; USA: CA | tentatively a junior subjective synonym; possibly *C. sthenele*

Cercyonis oetus (Boisduval, 1869); USA: CA, Placer Co., SSE of Donner Pass

Cercyonis oetus phocus (W. H. Edwards, 1874); Canada: British Columbia, Lake La Hache

Cercyonis oetus oetus (Boisduval, 1869); USA: CA, Placer Co., SSE of Donner Pass

Cercyonis oetus pallescens T. Emmel & J. Emmel, 1971; USA: NV, Lander Co., Reese River Valley

Cercyonis oetus alkalorum Austin, 1998; USA: NV, Nye Co., Big Smoky Valley

Cercyonis oetus charon (W. H. Edwards, 1872); USA: CO, Upper Arkansas River Valley

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