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A taxonomic overview of the *Apodemia mormo* complex from a genomic perspective

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ABSTRACT. Genomic analysis of the *Apodemia mormo* group (Riodinidae Grote, 1895 (1827)) specimens across the range from southwestern Canada through much of the western USA and northwestern Mexico, complemented by phenotypic examination and photographs of live individuals to inspect eye color, partitions the complex into eight species, one of which is proposed as new: *Apodemia* (*Apodemia*) *apache* Grishin, **sp. n.** (type locality in USA: Arizona, Apache Co.), and three elevated from subspecies of *A. mejicanus*: *Apodemia* (*Apodemia*) *maxima* (Weeks, 1891), **stat. rest.**, *Apodemia* (*Apodemia*) *deserti* W. Barnes & McDunnough, 1918, **stat. nov.**, and *Apodemia* (*Apodemia*) *pueblo* J. Scott, 1998, **stat. nov.**, in addition to four others confirmed as species-level taxa: *Apodemia* (*Apodemia*) *virgulti* (Behr, 1865), *Apodemia* (*Apodemia*) *mormo* (C. Felder & R. Felder, 1859), *Apodemia* (*Apodemia*) *duryi* (W. H. Edwards, 1882), and *Apodemia* (*Apodemia*) *mejicanus* (Behr, 1865). Geographic variation, both genetic and phenotypic, is interpreted as subspecies, 12 of which are described as new (type localities are listed in parentheses): *Apodemia* (*Apodemia*) *maxima bajanor* Grishin, **ssp. n.** (Mexico: BC, San Quintín Mpio.), *Apodemia* (*Apodemia*) *mormo nordesta* Grishin, **ssp. n.** (Canada: SK, vic. Val Marie), *Apodemia* (*Apodemia*) *mormo centralis* Grishin, **ssp. n.** (USA: UT, San Juan Co.), *Apodemia* (*Apodemia*) *mormo sudesta* Grishin, **ssp. n.** (USA: CO, Costilla Co.), *Apodemia* (*Apodemia*) *mormo confusa* Grishin, **ssp. n.** (USA: AZ, Coconino Co.), *Apodemia* (*Apodemia*) *mormo arizatra* Grishin, **ssp. n.** (USA: AZ, Cochise Co.), *Apodemia* (*Apodemia*) *deserti keni* Grishin, **ssp. n.** (USA: CA, Kern Co.), *Apodemia* (*Apodemia*) *deserti megawhy* Grishin, **ssp. n.** (USA: AZ, Pima Co.), *Apodemia* (*Apodemia*) *apache rufa* Grishin, **ssp. n.** (USA: AZ, Cochise Co., Huachuca Mts.), *Apodemia* (*Apodemia*) *apache riftoria* Grishin, **ssp. n.** (USA: NM, Sandoval Co., Sandia Mts.), *Apodemia* (*Apodemia*) *apache texana* Grishin, **ssp. n.** (USA: TX, Brewster Co., Del Norte Mts.), and *Apodemia* (*Apodemia*) *pueblo mescalero* Grishin, **ssp. n.** (USA: NM, Lincoln Co., Sacramento Mts.). Populations from the Coastal Ranges in Southern California are identified as *Apodemia* (*Apodemia*) *mormo arenaria* J. Emmel, T. Emmel & Pratt, 1998, which we treat as a subspecies of *A. mormo*, distinct from and possibly sympatric with *A. virgulti* in that area. *Apodemia* (*Apodemia*) *mormo langei* J. A. Comstock, 1939 is found to occupy a broad range in central coastal California (Contra Costa to Kern Cos.), with the federally endangered "species" restricted to the population at and around the type locality. A **neotype** is designated for *Nemeobius mejicanus* Behr, 1865 (Mexico: Sonora, Guaymas Mpio.) and a **lectotype** is designated for *Apodemia mormo deserti* W. Barnes & McDunnough, 1918 (USA: California, San Diego Co.).

Key words: taxonomy, genomics, phylogeny, biodiversity, conservation, *Eriogonum*, *Krameria*.

ZooBank registration: https://zoobank.org/B03D72FF-880C-4A7C-8B6B-21BF78E70FE1

INTRODUCTION

The Mormon Metalmarks (*Apodemia mormo* species group) constitute a bewildering species complex characterized by a mosaic of isolated colonies and variable populations across western North America (Opler and Powell 1962; Forbes 1981; Pratt and Ballmer 1991; Emmel and Emmel 1998; Emmel et al. 1998b; Scott 1998, 2017). These butterflies typically inhabit dry, arid regions from Canada to Mexico, and display notable differences in wing color and pattern both between and within populations. Currently,

the complex consists of 20 valid taxa grouped into four species, with 16 additional subspecies (Warren et al. 2024). This arrangement synthesizes literature, unpublished opinions, and personal observations. No single reference provides an overview of all these taxa.

Some members of the complex have conservation significance, which has attracted attention to this group in recent works (Proshek et al. 2013, 2015). Most notably, Lange's Metalmark, *A. mormo langei* J. A. Comstock, 1939, is a federally listed endangered butterfly currently restricted to the Antioch Dunes in California. DNA data suggest that this colony is no more divergent than other isolated populations, underscoring the uncertainty of its taxonomic status (Proshek et al. 2015). Likewise, the two disjoint populations of *A. mormo* in Canada are of conservation concern (Proshek et al. 2013). Accurate delimitation of species and subspecies in the *A. mormo* group is therefore critical for conservation management.

Species delimitation involves careful studies combining morphology, field observations, and life history work. Such comprehensive research is exemplified by Pratt and Ballmer (1991), who documented three distinct "biotypes" of *A. mormo* in the Mojave Desert. They concluded that these "biotypes" may represent three distinct species, as they currently are treated in several works (Pelham 2008; Pelham 2023; Warren et al. 2024). DNA-based studies have been instructive, providing the first insight into the genetic structure of *A. mormo* group populations (Proshek et al. 2013, 2015). However, they are yet to result in a taxonomic breakthrough.

The most transformative recent advance was made by Cary (2022) and Cary and Toliver (2022, last updated in 2025), and involves a meticulous synthesis of existing observations and photographs, integrating data on wing patterns, distributions, and caterpillar foodplants while broadly utilizing online resources, such as iNaturalist (2026). The major milestone with significant implications for *Apodemia* taxonomy is the observation that the eye color of live adults can be diagnostic and can potentially aid species delimitation. Focusing on the study area east of Las Cruces (Doña Ana Co., New Mexico), Cary (2022) convincingly demonstrated that *Apodemia duryi* (W. H. Edwards, 1882) can be confidently distinguished from a parapatric (or narrowly sympatric) taxon — which, for the lack of a better option, he called *Apodemia mejicanus* (Behr, 1865) — by the eye color: "chartreuse" (greenish-yellow) vs. "gray" (greenish-gray).

Here, we extend this integrative approach over the entire *A. mormo* species group and utilize whole-genome shotgun sequence data that we obtained for representative populations across the range. Our goals are to probe species limits in the *A. mormo* group and to lay a genomic foundation for a revised classification and informed conservation decisions. We apply the same methods within the same 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, c, 2023b–d, 2024a–c, 2025a–d). As a result, we partition the *A. mormo* group into eight species, one of which is new, and 25 additional subspecies (12 new).

MATERIALS AND METHODS

The material used in this study derives from museum and private collections (see Acknowledgments for a list) and spans a temporal range from freshly collected specimens to those preserved for over a century. We strive to obtain whole-genome shotgun datasets of primary type specimens, thereby establishing an objective reference for species names (Cong et al. 2021; Zhang et al. 2022a). A leg is typically used for DNA extraction, performed non-destructively to allow for subsequent morphological examination. If DNA is not already degraded due to age, it is fragmented prior to genomic library construction. Sequencing is carried out on the Illumina platform, generating 150-base-pair (bp) reads. The procedure does not rely on targeted gene amplification; instead, it sequences all recovered DNA. Consequently, the method is suitable for old specimens with highly fragmented DNA, often around 30–50 bp in length.

For each specimen, we use all sequencing reads, both full-length 150 bp and shorter fragments, to assemble exons of protein-coding genes. Assembly is guided by a reference genome of a closely related

species for which a high-quality complete genomic assembly exists. These reconstructed genes form the dataset used for phylogenetic analyses. We infer three phylogenetic trees using IQ-TREE v1.6.12 under the GTR+GAMMA model (Nguyen et al. 2015): one based on autosomal (nuclear) loci, a second based on genes inferred to reside on the Z chromosome, and a third derived from mitochondrial DNA. For each specimen, all well-covered codons are included in an alignment that is generated dynamically and not saved, and the total number of sites used in each nuclear genome analysis (ranging from several hundred thousand to several million) is reported in the corresponding figure legends. Mitochondrial genomes are ~15,000 bp in length. Statistical support relies on ultrafast bootstrap: support > 97% is regarded as strong, whereas values < 90% are considered weak and indicate unresolved relationships (Hoang et al. 2018). Further technical details can be found in our earlier publications (Li et al. 2019; Zhang et al. 2022b).

Phylogenetic trees are displayed, colored, and rotated in FigTree (Rambaut 2018). Our taxonomic conclusions rely strongly on genomic phylogenies, with morphological evidence used for further support. This approach reflects the greater breadth of information contained in genomes, which capture not only characters expressed in adult morphology traditionally used in butterfly taxonomy, but also genetic signals related to life history, ecology, reproductive biology, and diet. Although it is not yet possible to predict phenotypes directly from genomic sequences, combined protein-coding DNA data serve as pivotal proxies, and reliable phylogenies guide classification. Together, these components support a taxonomic system that is consistent with both evolutionary history and genomic data.

The present study focuses on taxa at the species and subspecies ranks. Species limits are assessed using multiple lines of evidence, including differentiation on the Z chromosome with F_{st} values > 0.20 (generally indicative of species-level divergence), G_{min} values < 0.05 (suggesting restricted gene flow) (Cong et al. 2019a), COI barcode divergence of approximately > 2% (Hebert et al. 2003) in conjunction with phenotypic differentiation (Lukhtanov et al. 2016), and the presence of distinct, strongly supported clades in phylogenetic trees (Zhang et al. 2022c). We also recognize that mitochondrial markers such as COI frequently introgress across species (Bachtrog et al. 2006; Cong et al. 2017a); consequently, species may share identical barcode sequences (Burns et al. 2008; Zhang et al. 2023a). Additional review of these criteria is provided by Zhang et al. (2022a) in the section "Species, subspecies, and genomics."

Traditionally, subspecies are defined as geographically separated populations displaying consistent phenotypic differences (i.e., approximately 70% of individuals can be distinguished by appearance alone, irrespective of locality) while still potentially capable of interbreeding (Mayr 1982; Monroe 1982). Practically, reproductive compatibility is rarely demonstrable, and butterfly subspecies are most commonly recognized based solely on differences in wing pattern. It is often unclear whether such differences reflect underlying genetic divergence or environmentally induced variation. In this work, we also describe new subspecies that correspond to genomic clades — defined as distinct groups recovered in at least one phylogenetic tree — that are genetically differentiated and strongly supported (approximately 100% bootstrap) but do not meet the criteria for recognition as separate species. These subspecies represent early stages in the speciation process of diverging populations that have not yet developed sufficient reproductive isolation. Once such clades are identified, wing pattern characters are examined to identify diagnostic phenotypic traits. As is typical for subspecies, these traits are statistical rather than absolute and show varying degrees of overlap. Because our subspecies delimitation is grounded in genomic evidence, the DNA characters for subspecies are stronger than morphological characters and apply to nearly all specimens. Accordingly, we provide DNA-based diagnoses for each newly described taxon.

For all newly established taxa, we give a brief description of diagnostic morphological characters and accompanying illustrations, together with diagnostic DNA characters from the nuclear genome and, where available, from the COI barcode. DNA characters are derived from protein-coding genes using our previously developed workflow (see SI Appendix in Li et al. 2019). The strategy for selecting robust diagnostic DNA characters, outlined in Cong et al. (2019b), is intended to provide diagnoses that are expected to remain stable as additional specimens and species are added to genomic datasets.

DNA character states are reported relative to the reference genome of *Calephelis nemesis* (W. H. Edwards, 1871) (cne) (Cong et al. 2017b). The notation used is as follows: cne1547.7.2:T197C means

position 197 in exon 2 of gene 7 from scaffold 1547 of the *C. nemesis* reference genome (cne) is C, having changed from T in the ancestor. When characters are given for the sister clade of the diagnosed taxon, the following notation is used: cne630.5.7:C93C (not T), which means 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 follow the same format but lack a prefix ending in ':' and in some cases lack the ancestral base pair (where unclear). Full exon sequences from the reference genome, with diagnostic positions for newly described taxa highlighted in green, are provided in the supplementary file https://osf.io/ajtnm. Providing this link ensures that all diagnostic characters can be directly traced to their underlying sequences. Links to iNaturalist (2026) observations cited in figure legends are formed as https://www.inaturalist.org/observations/xxx (where xxx is the observation number) or https://www.inaturalist.org/photos/xxx (where xxx is the photo number). iNaturalist photographs were identified by us to the best of our ability based solely on phenotype, without DNA sequencing of these specimens; therefore, some identifications may be erroneous.

Whole-genome shotgun datasets generated and analyzed in this study will be deposited in the NCBI database (https://www.ncbi.nlm.nih.gov) under BioProject PRJNA1422253. Associated BioSample records provide locality information and additional collection details for all sequenced specimens included in the phylogenetic trees. Tree figures show the following information for each specimen, separated by vertical bars "|": taxon name, DNA sample code, type status, locality, and year of collection ("old" if not dated and likely collected 100–150 years ago). Type status abbreviations are: HT holotype, LT lectotype, NT neotype, PT paratype, AT allotype, and TT topotype (not a true type, but a specimen from the general area of the type locality of a taxon). When a synonym name is given (in parentheses, preceded by "=", and in addition by "‡" for all but junior subjective synonyms), the type status refers to the synonym. COI barcode sequences reported here have been submitted to GenBank under accessions PX971407–PX971421. Abbreviations or acronyms for collections are listed in the Acknowledgments.

RESULTS AND DISCUSSION

Our genomic analysis complemented by phenotypic and biogeographic considerations revealed 13 new taxa in the *Apodemia mormo* group. In the following sections, we first address the nomenclature, such as the designation of primary type specimens and the formal description of new taxa accompanied by a brief justification of their status. Taxonomic sections dealing with status changes from subspecies to species, and genomics-based identification of *A. mormo* group populations are interspersed according to the phylogenetic order of the taxa. After the 13 new names are introduced, a dedicated section addresses the details of the logic behind our species delimitation in this group that we partition into eight species. Finally, a taxonomic list of the *Apodemia mormo* group resulting from this study is provided.

Neotype designation for *Nemeobius mejicanus* Behr, 1865

The name *Nemeobius mejicanus* Behr, 1865 was proposed based on an unstated number of specimens provided by Dr. Dinklage and claimed to be "from the Sierra Madre, in the neighborhood of Mazatlán" (Sinaloa, Mexico) (Behr 1865). We searched for *N. mejicanus* syntypes or any specimens from southern Sinaloa among Riodinidae holdings in all major collections listed in the Acknowledgments section, particularly in CAS, FMNH, and CMNH, where such historical material is most likely to reside. We failed to find any syntypes (or other specimens), a result that agrees with the published evidence that they were likely destroyed in the 1906 San Francisco earthquake and fire (Emmel et al. 1998a).

Scott (2017) discussed the taxonomic identity of *N. mejicanus*, translated its original description, and cited accompanying comparisons with other species. He concurred that the current application of this name to the populations in Sonora and southeastern Mexico agrees with the original description. He did not designate a neotype but suggested that a specimen from the Huachuca Mountains in southeastern Arizona, USA (Cochise Co.), should be designated as the neotype, citing the stability of nomenclature.

However, such a designation would be in conflict with ICZN Art. 75.3.6, which requires "evidence that the neotype came as nearly as practicable from the original type locality," and the Huachuca Mountains do not qualify, because specimens of this species are known from the localities closer to the original type locality in Mexico. Moreover, the name *mejicanus* implies that Behr intended to highlight the Mexican origin of the type series. Therefore, selecting a specimen from the Huachuca Mountains as a neotype of *N. mejicanus* may be in violation of the ICZN Code and would be inconsistent with the intent of the original author. Thus, we opted to designate a neotype from Mexico, closer to the original type locality. However, according to our genomic analysis, the species represented by this neotype is found in southeastern Arizona, including the Huachuca Mountains.

There is an exceptional need for a neotype of *N. mejicanus* to define this taxon objectively and thus stabilize nomenclature due to the presence of phenotypically similar new taxa and a possibly incorrect type locality as given in the original description. Hereby, N.V.G. designates the specimen in the CSUC illustrated in Fig. 1a (DNA sample NVG-17066A10) as the **neotype** of *Nemeobius mejicanus* Behr, 1865. This neotype stabilizes the current usage of this name as traditionally applied to *Apodemia mormo* group populations from northwestern Mexico and southeastern Arizona.

This neotype satisfies all requirements set forth by the ICZN Article 75.3, namely: **75.3.1.** It is designated to clarify the taxonomic identity of *N. mejicanus*, which is necessary because a new species that may barely enter Mexico near the USA border is present among its relatives, and the name *mejicanus* has also been incorrectly applied to it, thus creating a potential instability; and to define the type locality that was possibly incorrect in the original description; **75.3.2.** The characters to differentiate this taxon from others are given in the original description by Behr (1865), which we translate from Latin as: "wings above tawny, brown towards the margin, with all the usual bands and spots, white [and] edged with black; beneath, the forewings tawny, at the apex and margin grayish, with bands and spots as above; the hindwings grayish, irregularly variegated with white spots edged with black and merging with the ground color;" and complemented by the comparative section in English: "all wings are occupied with ... [a fulvous coloration on the upperside], till beyond the second band, where the brownish coloration of the margin begins; bands and spots perfectly white" (Behr 1865); to which we add that the eyes of live adults are greenish-yellow and the brown bar in the middle of cell M_3-CuA_1 on the dorsal hindwing is more strongly offset distad from the brown postdiscal line and its bar in cell M_2-M_3; **75.3.3.** The neotype specimen is a male bearing the following four rectangular labels (2nd handwritten, others printed; 3rd yellow, others white): [MEX: Sonora | Nacopuli Canyon | 5 mi. N San Carlos | III-23-2004 Oplers], [SC5], [Barcode of Life | DNA voucher specimen | CSU-CPG-LEP001291 | BOLD ID ABLCU291-09], [DNA sample ID: | NVG-17066A10 | c/o Nick V. Grishin], and is illustrated in Fig. 1a; the neotype was collected by Paul A. Opler and Evi M. Buckner-Opler; it is a well-preserved and perfectly spread specimen with a slight damage to the apex of the right forewing; **75.3.4.** We failed to find syntypes of *N. mejicanus* among Riodinidae holdings in all collections we visited (see Acknowledgments for the list) and, considering published evidence that they were destroyed in the 1906 San Francisco earthquake and fire (Emmel et al. 1998a), believe that they were lost; **75.3.5.** The neotype closely agrees with the original description in all characters, as evidenced by comparing the neotype illustrated in Fig. 1a with the characters given for this taxon in the original description, translated above (75.3.2.); **75.3.6.** The neotype is from near the coast of Sonora, Mexico, and the original type locality given as "the Sierra Madre, in the neighborhood of Mazatlán", Sinaloa, agrees with it in the sense that they are both localities in western Mexico near the coast, although no *Apodemia mormo* group specimens are known as far south into Mexico as Mazatlán; **75.3.7.** The neotype is deposited in the Colorado State University Collection, Fort Collins, CO, USA (CSUC). As a result of the neotype designation, the type locality of *N. mejicanus* becomes Mexico: Sonora, 5 mi north of San Carlos Nuevo Guaymas, Nacapule Canyon. The COI barcode sequence of the neotype, sample NVG-17066A10, GenBank PX971407, 658 base pairs, is:

AACATTATATTTTATTTTTGGAATTTGAGCAGGAATAGTTGGAACCTCATTAAGATTATTAATTCGAATAGAATTAGGAACATCAGGATCTTTAATTGGTGATGATCAAATTTATAATACT
ATTGTTACAGCTCATGCTTTTATTATAATTTTTTTTATAGTTATACCTATTATAATTGGAGGATTTGGTAATTGATTAGTACCATTAATACTTGGAGCTCCGGATATAGCTTTTCCACGAA
TAAATAATATAAGATTTTGACTTTTACCCCCCTCATTATTCTTATTAATTTCTAGAAGAATTGTAGAAAATGGAGCAGGAACAGGATGAACAGTTTATCCCCCACTTTCATCTAATATTGC
CCATGGAGGAGCTTCAGTTGATTTAGCTATTTTTTCTTTACATTTAGCTGGTATTTCTTCAATTTTAGGTGCAATTAATTTTATTACAACTATTATTAATATACGTGTTAATAATATATCT
TTTGATCAAATACCTTTATTTGTATGATCGGTAGGAATTACAGCTTTATTATTATTACTCTCATTACCTGTTTTAGCTGGAGCTATTACCATATTATTAACTGATCGTAATTTAAACACAT
CATTTTTTGATCCAGCAGGTGGAGGAGATCCAATTTTATATCAACATTTATTT

Fig. 1 (legend continues on the next page). *Apodemia mejicanus* specimens in dorsal (left or above) and ventral (right or below) views: **a) neotype** ♂ NVG-17066A10 Mexico: Sonora, 5 mi N of San Carlos, Nacapule Cyn., 23-Mar-2004, P. & E. Opler

leg. [CSUC] and non-types: **b)** ♂ NVG-16101A05 USA: "TX, Davis Mts. nr. Ft. Davis" (probably SE AZ), 1–15-Jun-1928, O. Poling leg. [AMNH]; **c)** ♀ 11-BOA-13383BrockC10 AZ, Santa Cruz Co., Atascosa Mts., Peck Canyon, 22-Jul-1990, J. P. Brock leg. [JPBC]; **d)** topotype ♀ 11-BOA-13383BrockC08, 25–26-Mar-2003, J. P. Brock leg. [JPBC]; **e)** ♂ 11-BOA-13383BrockC11 AZ, Santa Cruz Co., Pajarito Mtns., California Gulch, 8-Oct-1992, J. P. Brock leg. [JPBC]; **f)** ♂ NVG-24066F11 AZ, Pima Co., 6.7 mi W of SH83, Ridge N of Box Canyon Dam, 10-Mar-1995, J. & F. Preston leg. [MGCL]. Gray "F" indicates flipped (left-right inverted) images.

Apodemia (*Apodemia*) *maxima* (Weeks, 1891) is a species-level taxon distinct from *Apodemia* (*Apodemia*) *mejicanus* (Behr, 1865) and closely related to *Apodemia* (*Apodemia*) *virgulti* (Behr, 1865)

Initially proposed as a species, *Lemonias maxima* Weeks, 1891 (type locality in Mexico: Baja California Sur, vic. San José del Cabo), is currently treated as a subspecies of *Apodemia* (*Apodemia*) *mejicanus* (Behr, 1865) (type locality Mexico: Sonora, 5 mi N of San Carlos). This is probably because both are from Mexico, tend to be larger in size than other relatives, and look superficially similar, having generally larger white spots and more extensive orange coloration on the wings above, particularly in the basal half (Figs. 1, 3e–h), which is frequently dark brown in other species. Having designated the neotype of *A. mejicanus*, we objectively define the taxonomic identity of this species and find that *A. mejicanus maxima* is not in the same clade as *Apodemia* (*Apodemia*) *mejicanus* (Fig. 2a, b); instead, it is closely related to *Apodemia* (*Apodemia*) *virgulti* (Behr, 1865) (type locality in USA: California, Los Angeles Co., Verdugo Mts., La Tuna Canyon). Together, they form a clade sister to all other *A. mormo* group species in the Z chromosome tree (Fig. 2a). Therefore, *L. maxima* is not a subspecies of *A. mejicanus*, because they are not closely related, as revealed by their genomic DNA. However, it is conceivable that *L. maxima* may be a subspecies of *A. virgulti* instead. Indeed, *L. maxima* from Baja California Sur is sister to all subspecies of *A. virgulti*, including *Apodemia* (*Apodemia*) *virgulti dialeuca* Opler & Powell, 1962 from Baja California (Norte). Nevertheless, *L. maxima* and *A. virgulti* are genetically differentiated at the species level in both nuclear (Fig. 2a, b) and mitochondrial (Fig. 2c) genomes, e.g., the COI barcodes of the *A. virgulti virgulti* neotype (sequenced as NVG-15105E04) and *A. maxima* from the type locality differ by 2% (13 bp). Moreover, *L. maxima* is not monophyletic with *A. virgulti* in the nuclear genome tree, forming a clade sister to all other *A mormo* group species (Fig. 2b). Therefore, we propose that *Apodemia* (*Apodemia*) *maxima* (Weeks, 1891) **stat. rest.** is a species-level taxon distinct from both *Apodemia* (*Apodemia*) *mejicanus* (Behr, 1865) and *Apodemia* (*Apodemia*) *virgulti* (Behr, 1865).

Apodemia (*Apodemia*) *maxima bajanor* Grishin, new subspecies

https://zoobank.org/3FCE2677-02BB-4FF3-8887-59D94639146A

(Figs. 2 part, 3c–d)

Definition and diagnosis. Genomic analysis reveals that a specimen from central Baja California, Mexico, is sister to *Apodemia* (*Apodemia*) *maxima* (Weeks, 1891) **stat. rest.** (type locality in Mexico: Baja California Sur, vic. San José del Cabo) with 100% ultrafast bootstrap support in both nuclear genome trees (Fig. 2a, b) and shares the mitochondrial genome with its more northern populations (Fig. 2c), while being more distant from and not monophyletic with *Apodemia* (*Apodemia*) *virgulti* (Behr, 1865) (type locality in USA: California, Los Angeles Co.) (Fig. 2 blue) or *Apodemia* (*Apodemia*) *mormo* (C. Felder & R. Felder, 1859) (type locality in USA: likely in NV, Washoe Co.) (Fig. 2 black). Therefore, we identify this specimen as *A. maxima*, despite its more pronounced wing pattern similarity with *A. virgulti* and *A. mormo* than with *A. maxima*. However, the *A. mormo*-looking specimen is genetically differentiated from *A. maxima* at the subspecies level in the nuclear genome (Fig. 2a, b) and is phenotypically different, being smaller and darker. Therefore, this specimen represents a new subspecies. This new subspecies (Figs. 2d, 3c, d) differs from its relatives, in particular the geographically closest *A. maxima maxima* (Fig. 3e–h) and *Apodemia* (*Apodemia*) *virgulti dialeuca* Opler & Powell, 1962 (type

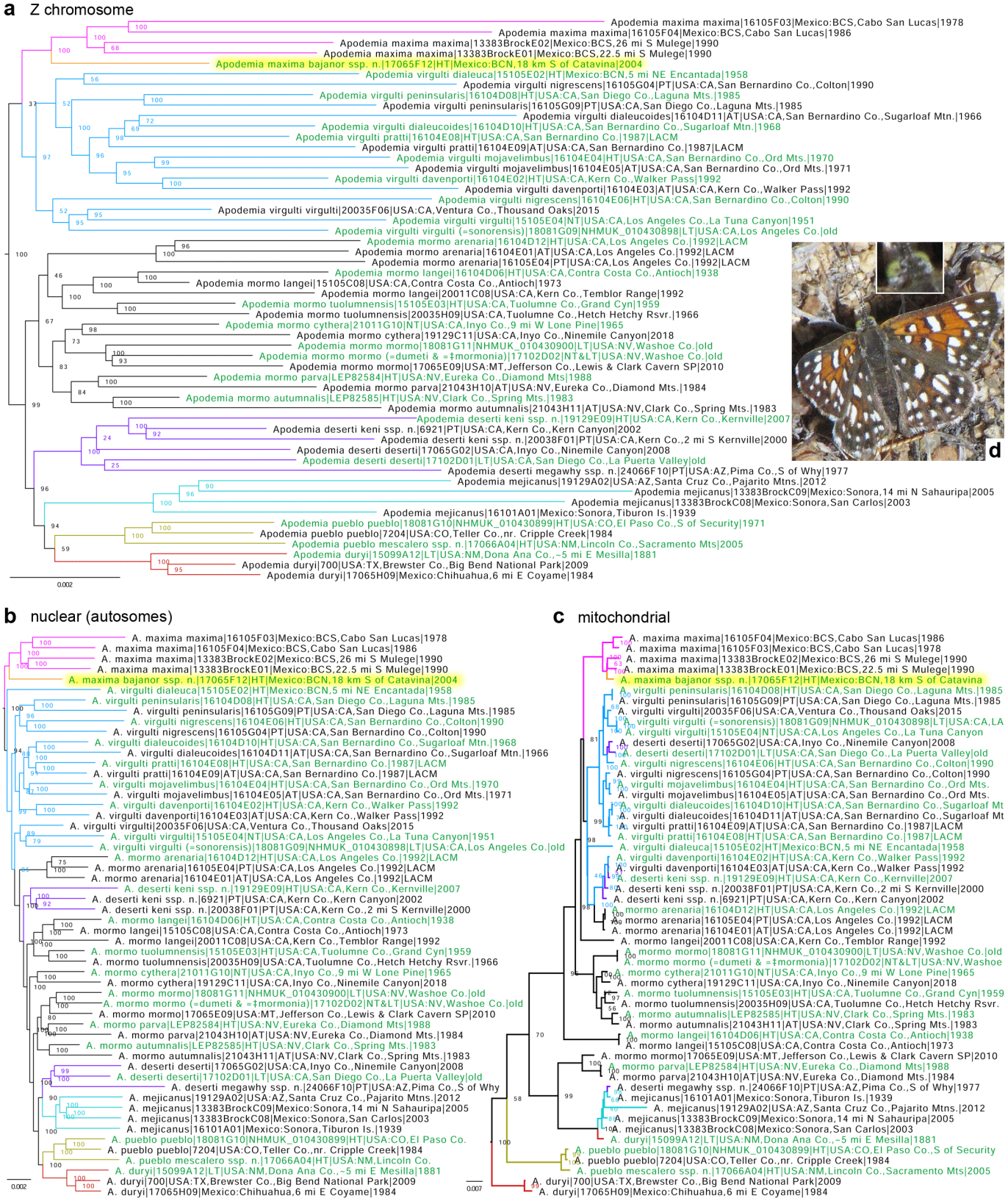

Fig. 2. Phylogenetic trees of *A. mormo* group taxa, constructed from protein-coding regions in: **a)** the Z chromosome, based on 392,565 positions, **b)** the nuclear genome (autosomes), based on 4,529,118 positions, and **c)** the mitochondrial genome; and **d)** *A. maxima bajanor* **ssp. n.**, iNaturalist observation No. 75722779 Mexico: Baja California (Norte), Ensenada, GPS 29.30, −114.07, 21-Apr-2021 © Jorge H. Valdez; color-corrected, brightened, rotated, flipped (left-right inverted), and cropped, CC BY-NC 4.0 https://creativecommons.org/licenses/by-nc/4.0/; inset shows a magnified view of the head. Clades of different species are colored differently: *A. maxima* **stat. rest.** (magenta, with *A. maxima bajanor* **ssp. n.** in orange, the name highlighted in yellow), *A. virgulti* (blue), *A. mormo* (black), *A. deserti* **stat. nov.** (violet), *A. mejicanus* (cyan), *A. pueblo* **stat. nov.** (olive), and *A. duryi* (red). Primary type specimens are labeled in green font. Ultrafast bootstrap (Hoang et al. 2018) values are shown.

Fig. 3. *Apodemia mormo* group taxa from the Baja California peninsula, Mexico, in dorsal (left of the panel letter) and ventral (right of the panel letter) views: **a–b)** *A. virgulti dialeuca*, **c–d)** *A. maxima bajanor* **ssp. n.**, and **e–h)** *A. maxima maxima* **stat. rest**. Specimens: **a) holotype** ♂ NVG-15105E02 BCN, Sierra San Pedro Martir, 5 mi NE of Encantada, 31-May-1958, J. Powell leg. [CAS]; **c) holotype** ♂ NVG-17065F12 BCN, 18 km S of Cataviña, 8-Apr-2004, E. B. Runquist leg. [CSUC]; **e)** non-type ♂ 11-BOA-13383BrockE02 BCS, 26 mi S of Mulegé, 20-Mar-1990, J. P. Brock leg. [JPBC]. iNaturalist observations: **b)** 158474028 BCN, Ensenada, 31.7293, −116.1034, 30-Apr-2023 © Erik Meling; **d)** 15495930 BCN, Ensenada, 30.058, −115.321, 28-Oct-2013 © Jeff Harding; **f)** 101786794 BCS, Los Cabos, 23.0118, −109.7280, 23-Nov-2021 © Bill Levine; **g)** 328009172 BCS, La Paz, 23.7553, −109.7211, 20-Nov-2025 © Amelia Ryan; **h)** 320589989 BCS, La Paz, 24.2450, −110.1505, 12-Oct-2025 © Diana Laura G López. iNaturalist images are color-corrected, brightened, rotated, cropped, and some are flipped (left-right inverted); CC BY-NC 4.0 https://creativecommons.org/licenses/by-nc/4.0/. The scale bar refers to pinned specimens only; live adults are not to scale and are reduced by ~¼ compared to specimens. Insets in b), d), and h) show a magnified view of the eye.

locality Mexico: Baja California, 5 mi NE of Encantada) (Fig. 3a, b) by the following combination of characters: dorsally, extensive orange-red (ochraceous, yellowish-brown) is present on the forewing from the costal margin to the postdiscal band of white spots framed with brown and through the discal cell to CuA_2 or slightly beyond towards the inner margin [less orange in *A. virgulti dialeuca*, which is mostly brown with orange patches]; but the orange is nearly absent on the hindwing [A. *virgulti dialeuca* has a narrow postdiscal orange band, and *A. maxima maxima* is mostly orange except for the outer margin and brown framing of the white spots and along the veins], and may be present in the discal cell as isolated spots and between the white spots in the postdiscal band; overall smaller than *A. maxima maxima* and about the size of *A. virgulti dialeuca*, sharing with the latter the hue of orange coloration, which is more yellowish than red, while *A. maxima maxima* is typically redder and more rusty in color (fulvous, reddish-orange-brown); white spots are complete (i.e., present in every cell in every band) and well developed, but not particularly larger than in *A. virgulti dialeuca* [*A. maxima maxima* has larger white spots, which are more prominent due to brown framing and largely reddish-orange wings]; the ventral side is darker than in *A. virgulti dialeuca* due to less developed whitish overscaling, thus being similar to *A. maxima maxima*; and the eyes are greenish-yellow as in both *A. virgulti dialeuca* and *A. maxima maxima*. This subspecies is not cryptic, but due to unexplored individual variation, it is most confidently identified by DNA, with diagnostic base pairs in the nuclear genome: cne10499.1.2:A454T, cne10499.1.2:C455T, cne10499.1.2:C662A, cne7676.18.3:T105A, cne7676.18.3:G172A, cne630.5.7:G54G (not C), cne630.5.7:C93C (not T), cne23345.2.2:G42G (not A), cne4618.8.1:A138A (not G), cne4618.8.1:A204A (not C); while the COI barcode does not distinguish it from the nominotypical subspecies.

Barcode sequence of the holotype. Sample NVG-17065F12, GenBank PX971408, 658 base pairs:

AACATTATATTTTATTTTTGGAATTTGAGCAGGAATAGTTGGAACTTCACTAAGATTATTAATTCGTATAGAATTAGGAACATCCGGATCTTTAATTGGTGATGATCAAATTTATAATACT
ATTGTAACAGCTCATGCTTTTATTATAATTTTTTTTATAGTTATACCTATTATAATTGGAGGATTTGGTAATTGATTAGTACCATTAATACTTGGAGCTCCAGATATAGCTTTTCCACGAA
TAAATAATATAAGATTTTGACTTTTACCCCCCCTCATTATTTTTATTAATTTCTAGAAGAATTGTAGAAAATGGAGCAGGAACAGGATGAACAGTTTATCCCCCACTTTCATCCAATATTGC
TCATGGAGGAGCTTCTGTTGATTTAGCTATTTTTTCCTTACATTTAGCTGGTATCTCTTCAATTTTAGGTGCAATTAATTTTATTACAACTATTATTAACATACGTGTCAATAACATATCT
TTTGATCAAATACCTTTATTTGTATGATCAGTAGGAATTACAGCTTTATTACTCCTACTTTCATTACCTGTTTTAGCTGGAGCTATTACTATATTATTAACTGATCGTAATCTAAATACAT
CATTTTTTGACCCAGCGGGTGGAGGAGATCCAATTTTATATCAACATTTATTT

Type material. Holotype: ♂ deposited in the Colorado State University Collection, Fort Collins, CO, USA (CSUC), illustrated in Fig. 3c, bears the following three printed rectangular labels, two white: [MEX: Baaja Calif. | Sur, 18 km. S | Catavina IV-8-04 | Erik B. Runquist], [DNA sample ID: | NVG-17065F12 | c/o Nick V. Grishin], and one red [HOLOTYPE ♂ | Apodemia (Apodemia) | maxima bajanor Grishin].

Type locality. Mexico: Baja California (Norte), 18 km south of Cataviña.

Etymology. The name is derived from the type locality in *Baja*[California]*Nor*[te] and is treated as a noun in apposition.

Distribution. Currently confirmed only from the holotype collected in central Baja California (Norte), Mexico (Fig. 31), but iNaturalist photographs suggest its wider distribution in the region.

Remark. Although we have not sequenced it yet from Mexico, in addition to the three taxa discussed above, *Apodemia virgulti peninsularis* J. Emmel, T. Emmel & Pratt, 1998 (type locality in USA: California, San Diego Co., Laguna Mts.) is expected to enter northern parts of Baja California. iNaturalist (2026) photographs from that region are consistent with the phenotype of this subspecies, which is similar to *A. virgulti dialeuca* but has more extensive fulvous areas on the dorsal side of both wings.

Apodemia mormo langei is widely distributed in west-central California

Genomic analysis of populations of *Apodemia* (*Apodemia*) *mormo* (C. Felder & R. Felder, 1859) (type locality in USA: likely Nevada, Washoe Co.) reveals that *Apodemia* (*Apodemia*) *mormo langei* J. A. Comstock, 1939 (type locality USA: California, Contra Costa Co., vic. Antioch), a subspecies currently restricted to a single population at the type locality, forms a subclade in the nuclear genome trees (Fig. 4a, b red) within a larger and confidently supported clade (Fig. 4a, b blue) of phenotypically similar specimens from central coastal California, which are currently considered "nr. *langei*". This clade (both

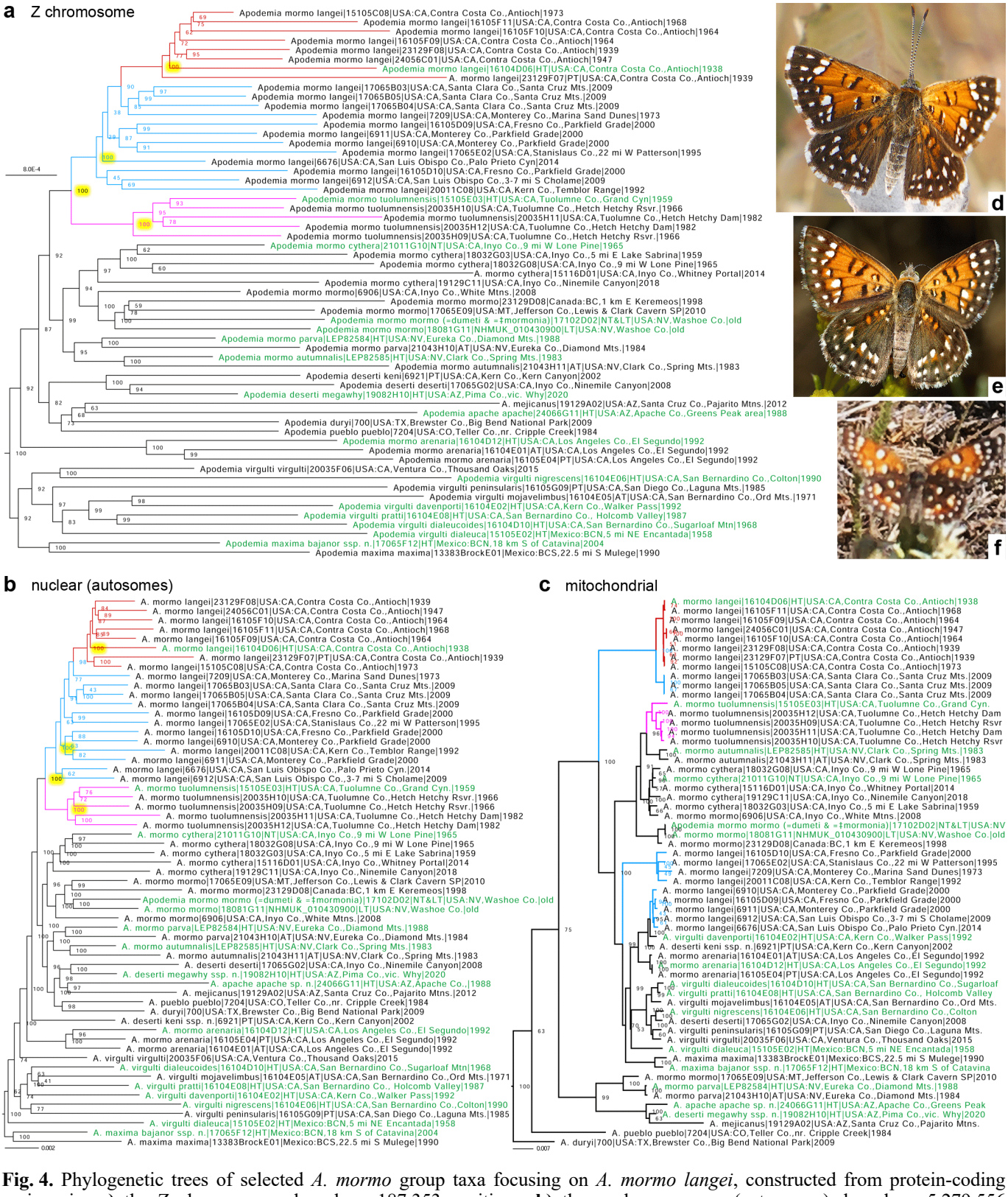

Fig. 4. Phylogenetic trees of selected *A. mormo* group taxa focusing on *A. mormo langei*, constructed from protein-coding regions in: **a)** the Z chromosome, based on 187,353 positions, **b)** the nuclear genome (autosomes), based on 5,279,556 positions, and **c)** the mitochondrial genome; and **d–f)** iNaturalist observations, males from USA: California: **d)** *A. mormo langei* topotype, observation No. 94983809, Contra Costa Co., vicinity of Antioch, Aug-2023 (data obscured) © Bill Nownes; **e)** likely *A. mormo langei* from San Luis Obispo Co., observation No. 200791503, GPS 35.7019, −120.2474, 14-Sep-2011 © fiddletunes; **f)** *A. mormo tuolumnensis*, observation No. 93922466, Tuolumne Co., vic. Hetch Hetchy Dam, GPS 37.8979, −119.8303, 5-Sep-2021 © Clark Black; images are color-corrected, brightened, rotated, cropped, and (d) flipped, CC BY-NC 4.0 https://creativecommons.org/licenses/by-nc/4.0/. Primary type specimens are labeled in green font. Clades of focus are colored: *A. mormo langei* in blue with the topotypical population in red and *A. mormo tuolumnensis* in magenta. Ultrafast bootstrap support values (Hoang et al. 2018) of 100% for the relevant branches are highlighted in yellow in the nuclear genome trees.

Fig. 5. *Apodemia mormo langei* from USA: California in dorsal (right or above) and ventral (left or below) views: **a–d)** from the type locality, Contra Costa Co., Antioch: **a) holotype** ♂ NVG-16104D06, 14-Aug-1938, W. H. Lange leg. [LACM]; **b)** non-type ♂ NVG-15105C08 10-Aug-1973, Rosser W. Garrison leg. [CAS]; **c)** iNaturalist observation No. 150789490, Aug-2021 (c) John Hibbard, color-corrected, brightened, cropped, and flipped, CC-BY (https://creativecommons.org/licenses/by/4.0/); **d)** allotype ♀ NVG-16104D07 data as for the holotype; and **e–h)** from more southern localities, not previously included in this subspecies, K. Davenport leg.: **e)** ♂ NVG-20011C08 Kern Co., Temblor Range, Annette Rd., 7-Oct-1992; **f)** ♂ NVG-6912 San Luis Obispo Co., 3–7 mi S of Cholame, Palo Prieto Cyn., 18-Sep-2009; **g)** ♀ NVG-20011D01 San Luis Obispo Co., Cottonwood Pass, 7-Sep-1992; **h)** ♂ NVG-16105D09 Fresno Co., Parkfield Grade, 30-Aug-2000, on *Eriogonum indictum* [LACM].

topotypical *langei* and "nr. *langei*") is sister to *Apodemia* (*Apodemia*) *mormo tuolumnensis* Opler & Powell, 1962 (type locality USA: California, Tuolumne Co., Yosemite National Park, Grand Canyon of the Tuolumne) with 100% ultrafast bootstrap support (Fig. 4a, b magenta). These populations together form a clade sister to all other specimens currently included in *A. mormo* thus confirming their placement as subspecies or phenotypic segregates of *A. mormo* rather than belonging to other species in the *A. mormo* group. We note that the mitochondrial genome analysis reveals a complex picture of multiple introgressions and/or incomplete lineage sorting, with several haplotypes representing these populations (Fig. 4c) The topotypical *A. mormo langei* together with several specimens from the nearby Santa Cruz Mountains, possess a prominently distinct haplotype.

Wing patterns agree with the nuclear genome analysis in several aspects. First, topotypical *A. mormo langei* (Figs. 4d, 5a–d) is similar to many specimens of "nr. *langei*" (Figs. 4e, 5e–h) in the characteristic absence (or reduction) of white scaling between the brown bars near the end of the discal cell on the dorsal forewing, generally more extensive reddish-orange coloration, and a mostly dark brown, white-spotted dorsal hindwing lacking a postdiscal reddish-orange band. Second, *A. mormo tuolumnensis* (Fig. 4f), while also having a largely orange dorsal forewing, is more different from *A. mormo langei* due to the presence of the end-of-cell white bar on the dorsal forewing and a postdiscal orange band on the dorsal hindwing. Third, the topotypical *A. mormo langei* is more uniform phenotypically, consistent with it being a single, highly inbred population of lower genetic diversity (Fig. 4a, b red; note the longer branch grouping these specimens with generally shorter terminal branches), while "nr. *langei*" is more diverse phenotypically (e.g., some specimens have a well-developed white bar in the forewing discal cell, Fig. 5h) and genetically (Fig. 4a, b blue; longer terminal branches, paraphyletic with respect to the topotypical *A. mormo langei*). While there is an overlap in variation, the topotypical *A. mormo langei* specimens tend to have more developed reddish-orange patches and scaling in the basal half of the dorsal hindwing and usually slightly larger dorsal white spots, particularly noticeable on the hindwing and in the middle of cell M_1-CuA_1 on the forewing.

As a consequence of this analysis, we propose to include all these genetically similar populations that form a confidently supported clade in the nuclear genome trees (Fig. 4a, b blue with red) in *A. mormo langei*, a subspecies sister to *A. mormo tuolumnensis*. We believe that a subspecies concept should apply to major groups of geographically proximate populations rather than to individual populations. "Blue" specimens together with "red" specimens in Fig. 4a, b form a monophyletic group of such neighboring populations (Fig. 31 pale yellow-green circles) and correspond better to this subspecies concept than "red" specimens taken out from them. Therefore, we treat *A. mormo langei* as a subspecies of *A. mormo* that is widely distributed in west-central California. Thus, the federally endangered "species" refers only to the single, and northernmost, population of *A. mormo langei* at near the type locality, because other populations to the south of it are not endangered more than any other butterfly taxon in the region; and extending any special protection to them is counterproductive.

Apodemia (*Apodemia*) *mormo arenaria* J. Emmel, T. Emmel & Pratt, 1998 is not a subspecies of *Apodemia* (*Apodemia*) *virgulti* (Behr, 1865)

Currently, *Apodemia* (*Apodemia*) *mormo arenaria* J. Emmel, T. Emmel & Pratt, 1998 (type locality USA: California, Los Angeles Co., El Segundo sand dunes) is treated as a subspecies of *Apodemia* (*Apodemia*) *virgulti* (Behr, 1865) (type locality in USA: California, Los Angeles Co., Verdugo Mts., La Tuna Canyon), due to a superficial similarity in wing patterns and the proximity of their ranges. However, phylogenetic analysis using the Z-chromosome protein-coding genes places it within *Apodemia* (*Apodemia*) *mormo* (C. Felder & R. Felder, 1859) (type locality in USA: likely Nevada, Washoe Co.) and among its populations from the Coastal Ranges of southern California, together with *Apodemia* (*Apodemia*) *mormo langei* J. A. Comstock, 1939 (type locality USA: California, Contra Costa Co., vic. Antioch) and *Apodemia* (*Apodemia*) *mormo tuolumnensis* Opler & Powell, 1962 (type locality USA: California, Tuolumne Co., Yosemite National Park, Grand Canyon of the Tuolumne) (Fig. 6a). The

phenotypically similar *Apodemia* (*Apodemia*) *mormo cythera* (W. H. Edwards, 1873) (type locality USA: California, Inyo Co., 9 mi W of Lone Pine) is recovered as the clade sister to all these taxa (Fig. 6a). Autosome gene analysis yields a generally similar phylogeny, although it is somewhat obscured by gene

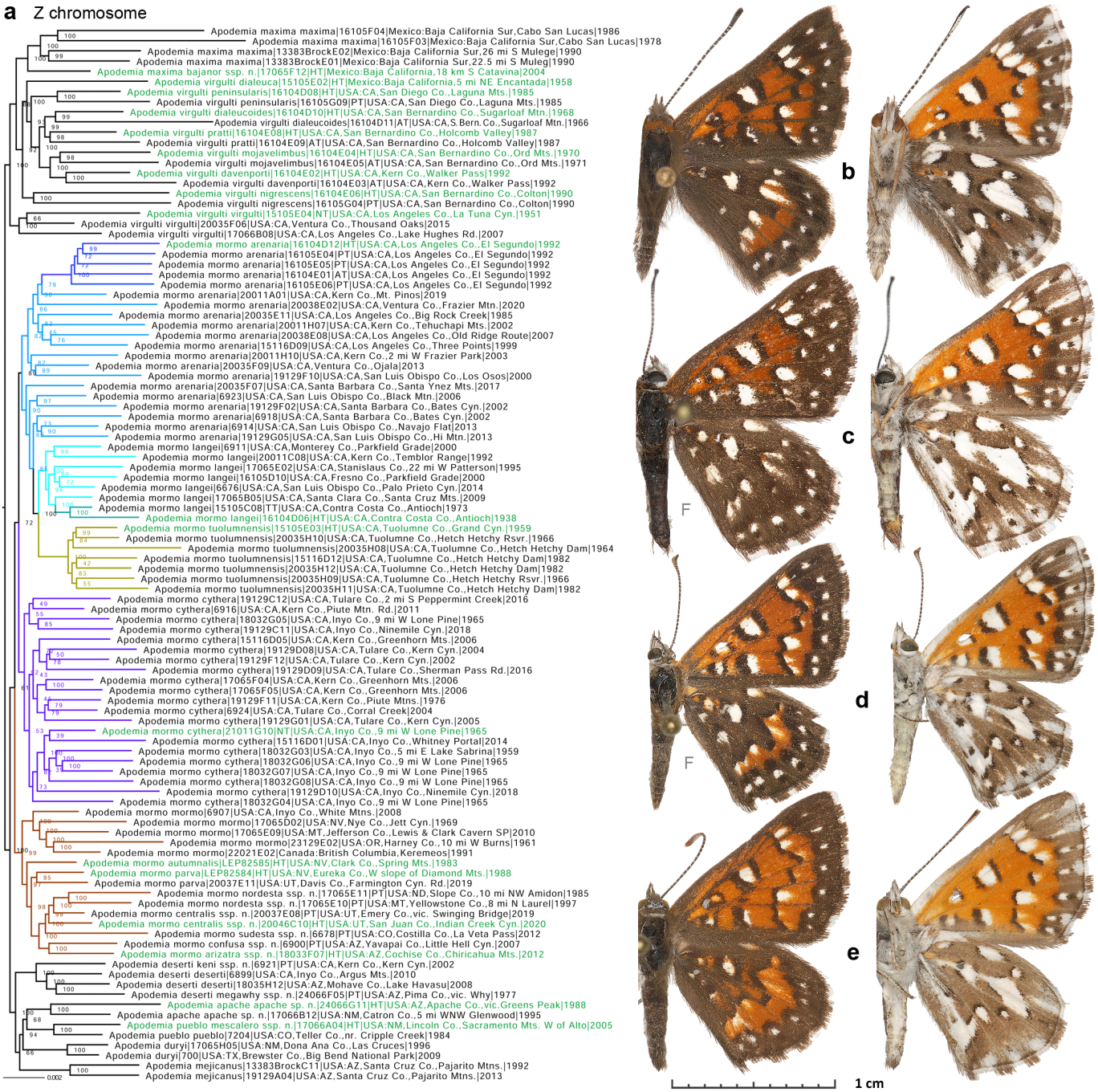

Fig. 6. *Apodemia mormo* group taxa focusing on *A. mormo arenaria* **comb. rest**. **a)** Phylogenetic tree of selected specimens constructed from protein-coding regions in the Z chromosome, based on 256,133 positions. Primary type specimens are labeled in green font. Clades of focus are colored: *A. mormo arenaria* (blue, with type specimens [all from the same locality] in dark blue), *A. mormo langei* (cyan, with the topotypical specimens in dark cyan), *A. mormo tuolumnensis* (olive, all from the same canyon), *A. mormo cythera* (violet), and other subspecies of *A. mormo* (brown, including the nominotypical). Ultrafast bootstrap (Hoang et al. 2018) values are shown at nodes. **b–e)** *Apodemia mormo arenaria* males from USA: California: **b) holotype** NVG-16104D12 Los Angeles Co., El Segundo sand dunes, eclosed 13-Apr-1992, J. F. Emmel, T. C. Emmel, & R. H. T. Mattoni leg., larva collected (12-Mar-1992) and reared on *Eriogonum parvifolium*; and non-types from the Coastal Ranges, K. Davenport leg.: **c)** less orange phenotype NVG-6908 San Luis Obispo Co., Navajo Creek, 28-Aug-2006; **d)** phenotype similar to topotypical *A. mormo arenaria* NVG-20011B11 San Luis Obispo Co., Syncline Hill W of Simmler, 27-Aug-2013; and **e)** more orange phenotype NVG- 20011H10 Kern Co., 2 mi W of Frazier Park, 12-Jul-2003. Gray "F" indicates flipped (left-right inverted) images.

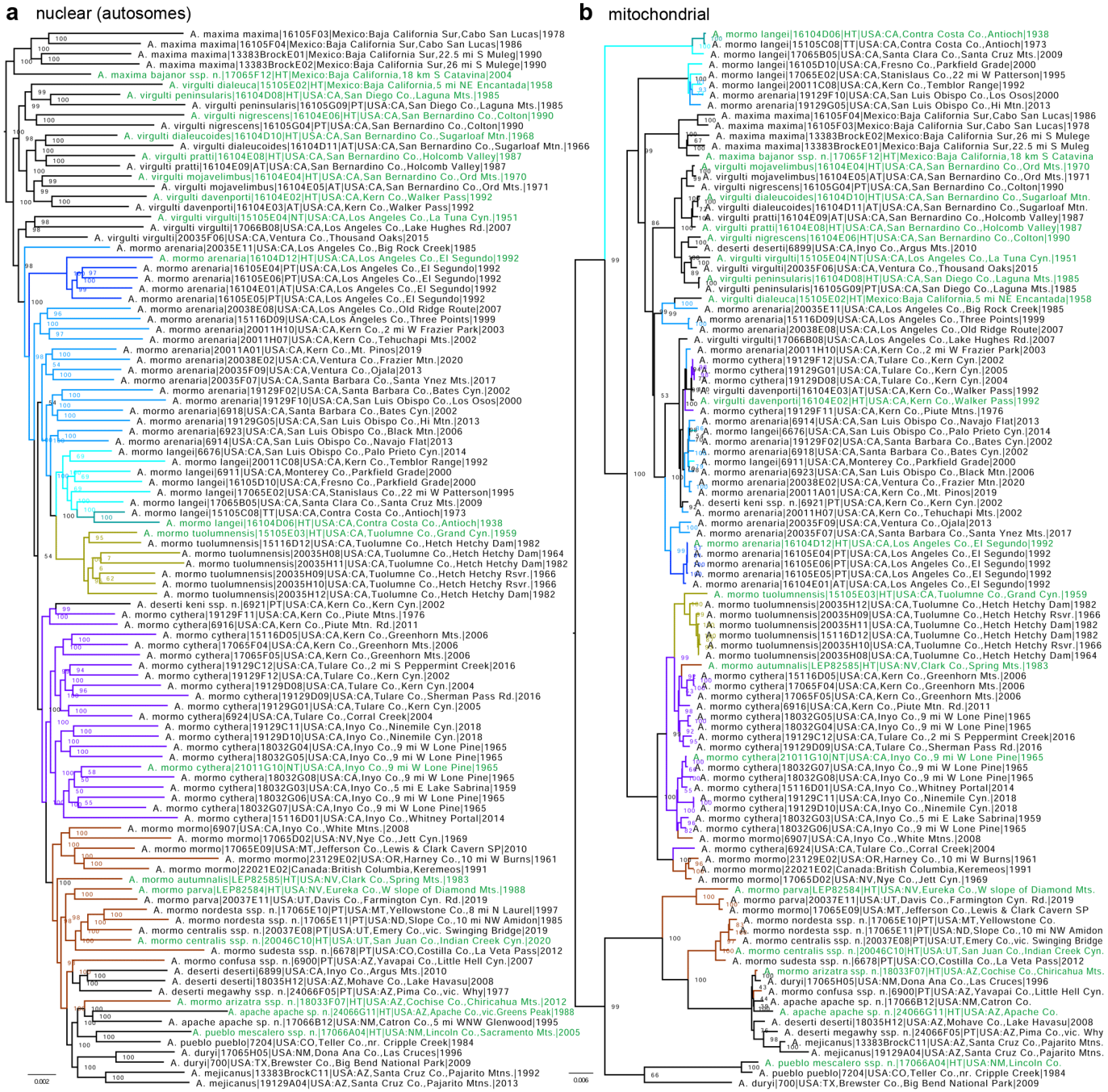

Fig. 7. Phylogenetic trees of selected *A. mormo* group taxa focusing on *A. mormo arenaria* **comb. rest.** constructed from protein-coding regions in: **a)** the nuclear genome (autosomes), based on 8,756,466 positions, and **b)** the mitochondrial genome. Primary type specimens are labeled in green font. Clades of focus are colored: *A. mormo arenaria* (blue, with type specimens [all from the same locality] in dark blue), *A. mormo langei* (cyan, with the topotypical specimens in dark cyan), *A. mormo tuolumnensis* (olive, all from the same canyon), *A. mormo cythera* (violet), and other subspecies of *A. mormo* (brown, including the nominotypical). Ultrafast bootstrap (Hoang et al. 2018) values are shown at nodes.

exchange and introgression (Fig. 7a). The mitochondrial genome tree is more challenging to rationalize due to evolutionary irregularities, but the type series of *A. mormo arenaria* is sister to specimens from the Coastal Ranges in Ventura and Santa Barbara counties, California (Fig. 7b).

The situation we observe with *A. mormo arenaria* is similar to that with *A. mormo langei* (see above). The topotypical population of *A. mormo langei* originates within more genetically diverse coastal populations, being at the northern limit of their ranges (Figs. 4a, b, 6a, 7a, 31). The topotypical population of *A. mormo arenaria* also originates within genetically diverse coastal populations, being at the southern

limit of their ranges (Figs. 6a, 7a, 31). These Coastal Ranges populations are genetically and phenotypically more diverse and, taken together, form a cline between the type localities of *A. mormo langei* and *A. mormo arenaria* (Fig. 31). Pending more detailed studies, we assign the South Coast Range populations to *A. mormo arenaria*, and "break" the cline between it and *A. mormo langei* by the monophyly with *A. mormo tuolumnensis*: specimens in the clade sister to *A. mormo tuolumnensis* in the Z chromosome tree are assigned to *A. mormo langei*, and those outside the clade formed by both *A. mormo langei* and *A. mormo tuolumnensis* are assigned to *A. mormo arenaria*.

Defined this way, *A. mormo arenaria* is even more genetically diverse than *A. mormo langei*, and this is also reflected in its phenotypic diversity (Fig. 6b–e). The phenotypic variation spans a wide range. The typical *A. mormo arenaria* (Fig. 6b, d) is characterized by the dark dorsal hindwing with a reddish-orange postdiscal band and well-developed white spots (even within this band) and is intermediate in phenotype among other forms. The darker phenotype (Fig. 6c) has a reduced reddish-orange patch on the dorsal forewing and lacks the orange hindwing band. The orange phenotype (Fig. 6e) has reduced brown ground color and smaller white spots, sometimes lacking those inside the postdiscal orange band on the hindwing. The topotypical population of *A. mormo arenaria* (Fig. 6b) generally differs from others by a slightly darker reddish-orange color (tending toward crimson) and stronger brown overscaling along the veins inside reddish areas. These phenotypes represent individual variation rather than geographic variation because they are present across the range of the subspecies. Such genetic diversity underpinning the phenotypic diversity within these populations in the Coastal Ranges north and northwest of Los Angeles may imply that they were ancestral for this group of subspecies (*A. mormo arenaria*, *A. mormo langei*, and *A. mormo tuolumnensis*).

In summary, we treat *Apodemia* (*Apodemia*) *mormo arenaria* J. Emmel, T. Emmel & Pratt, 1998, **comb. rest.** as a subspecies of *A. mormo* as originally proposed. We note that our use of "comb. rest." (meaning restored combination) is a taxonomical notation, not nomenclatural, because it refers to a species-subspecies combination, not an association of a species or subspecies epithet with a genus name, defined as a "combination" by the ICZN Code (see Glossary) (ICZN, 1999). Furthermore, we tentatively identify *A. mormo* group populations from the Coastal Ranges in Southern California as *A. mormo arenaria* that transition into *A. mormo langei* in the vicinity of Pozo in San Luis Obispo County.

Subspecies of *Apodemia* (*Apodemia*) *mormo* (C. Felder & R. Felder, 1859)

Apodemia (*Apodemia*) *mormo* (C. Felder & R. Felder, 1859) (type locality in USA: likely Nevada, Washoe Co.) is the most widely distributed species in the group, known from southern Canada to southern Arizona and from the California coast to the Rocky Mountains of Colorado and New Mexico (Fig. 30 circles). Phenotypically, *A. mormo* is more diverse in California, where some populations and subspecies are extensively reddish-orange, including the hindwing with a well-developed postdiscal orangish band (see their analysis above), while others are dark with a mostly blackish-brown dorsal hindwing and a smaller orange patch on the dorsal forewing. This dark form is constant throughout the rest of the range, giving the appearance of phenotypic uniformity.

Among the dark populations, three subspecies are currently recognized. In addition to the western nominotypical subspecies, the name *Apodemia* (*Apodemia*) *mormo autumnalis* Austin, 1998 (type locality USA: Nevada, Clark Co., Spring Mts.) was applied to specimens from the southeastern parts of the range, while specimens from the northeastern parts have been identified as *Apodemia* (*Apodemia*) *mormo parva* Austin, 1998 (type locality USA: Nevada, Eureka Co., Diamond Mts.). Having sequenced the holotypes of both of these subspecies described by Austin along with the lectotype of *A. mormo*, we find that this tripartite treatment oversimplifies the picture (Fig. 8a–c). First, genomic comparison suggests that both *A. mormo autumnalis* and *A. mormo parva* are restricted to the regions west of the Colorado Plateau, and form two prominent clades in the nuclear genome trees (Fig. 8a, b), supporting their status as distinct subspecies. All other *A. mormo* populations from the eastern parts of the range form a strongly supported clade (100% ultrafast bootstrap) sister to *A. mormo parva* and are therefore neither *A. mormo parva* nor *A.*


a Z chromosome
Apodemia maxima maxima|13383BrockE02|Mexico:Baja California Sur,26 mi S Mulege|1990
Apodemia maxima maxima|13383BrockE01|Mexico:Baja California Sur,22.5 mi S Mulege|1990
Apodemia maxima bajanor ssp. n.|17065F12|HT|Mexico:Baja California,18 km S Catavina|2004
Apodemia virgulti dialeucoides|20035F01|USA:CA,San Bernardino,Wildhorse Meadow|1990
Apodemia virgulti davenporti|6926|USA:CA,Kern Co.,E side Piute Mts.|2010
Apodemia virgulti virgulti|17066B10|USA:CA,Los Angeles Co.,Lake Hughes Rd.|2007
Apodemia mormo arenaria|16104D12|HT|USA:CA,Los Angeles Co.,El Segundo|1992
Apodemia mormo arenaria|16104E01|AT|USA:CA,Los Angeles Co.,El Segundo|1992
Apodemia mormo langei|15105C08|USA:CA,Contra Costa Co.,Antioch|1973
Apodemia mormo langei|17065B05|USA:CA,Santa Clara Co.,Santa Cruz Mts., vic. Mt Thayer|2009
Apodemia mormo tuolumnensis|20035H09|USA:CA,Tuolumne Co.,Hetch Hetchy Rsvr.|1966
Apodemia mormo tuolumnensis|20035H12|USA:CA,Tuolumne Co.,Hetch Hetchy Dam|1982
Apodemia mormo cythera|21011G10|NT|USA:CA,Inyo Co.,9 mi W Lone Pine|1965
Apodemia mormo cythera|18032G07|USA:CA,Inyo Co.,9 mi W Lone Pine|1965
Apodemia mormo cythera|18032G06|USA:CA,Inyo Co.,9 mi W Lone Pine|1965
Apodemia mormo mormo|6907|USA:CA,Inyo Co.,White Mtns.|2008
Apodemia mormo mormo|17065D02|USA:NV,Nye Co.,Jett Cyn.|1969
Apodemia mormo mormo|18081G11|NHMUK_010430900|LT|USA:NV,Washoe Co.|old
Apodemia mormo mormo|17107E05|USA:OR,Sheman Co.,Spanish Hollow|1973
Apodemia mormo mormo|22021E02|Canada:British Columbia,Keremeos|1991
Apodemia mormo mormo|23129E02|USA:OR,Harney Co.,10 mi W Burns|1961
Apodemia mormo mormo|7208|USA:WA,Yakima Co.,Tampico|1960
Apodemia mormo mormo|17065E09|USA:MT,Jefferson Co.,Lewis & Clark Cavern SP|2010
Apodemia mormo autumnalis|3244|USA:CA,San Bernardino Co.,Providence Mtns.|1972
Apodemia mormo autumnalis|LEP82585|HT|USA:NV,Clark Co.,Spring Mts.|1983
Apodemia mormo autumnalis|21043H11|AT|USA:NV,Clark Co.,Spring Mts.|1983
Apodemia mormo parva|LEP82584|HT|USA:NV,Eureka Co.,Diamond Mts.|1988
Apodemia mormo parva|21043H10|AT|USA:NV,Eureka Co.,Diamond Mts.|1984
Apodemia mormo parva|16105F01|USA:UT,Salt Lake Co.,Wasatch Mts.|1963
Apodemia mormo parva|23129F01|USA:UT,Cache Co.,Logan Cyn., Spring Hollow|1965
Apodemia mormo parva|20037E11|USA:UT,Davis Co.,Farmington Cyn. Rd.|2019
Apodemia mormo parva|20047B02|USA:ID,Bear Lake Co.,Georgetown Cyn.|2012
Apodemia mormo parva|19067C11|USA:UT,Sevier Co.,Rpahvant Range, Clear Creek|1996
Apodemia mormo parva|19067C12|USA:UT,Sevier Co.,Rpahvant Range, Clear Creek|1996
Apodemia mormo nordesta ssp. n.|23129D07|HT|Canada:Saskatchewan,Val Marie|1983
Apodemia mormo nordesta ssp. n.|16101A09|PT|USA:MT,Phillips Co.,1.5 mi S Saco|1951
Apodemia mormo nordesta ssp. n.|17065E11|PT|USA:ND,Slope Co.,10 mi NW Amidon|1985
Apodemia mormo nordesta ssp. n.|17065E10|PT|USA:MT,Yellowstone Co.,8 mi N Laurel|1997
Apodemia mormo centralis ssp. n.|16105E03|USA:UT,Uintah Co.,Asphalt Ridge|1965
Apodemia mormo centralis ssp. n.|17065C12|USA:UT,Wasatch Co.,10 mi W Fruitland|1966
Apodemia mormo centralis ssp. n.|16105E01|USA:UT,Wasatch Co.,10 mi W Fruitland|1966
Apodemia mormo centralis ssp. n.|16105E02|USA:UT,Wasatch Co.,Currant Creek|1961
Apodemia mormo centralis ssp. n.|16105E12|USA:UT,Wasatch Co.,10 mi W Fruitland|1966
Apodemia mormo centralis ssp. n.|16105D12|PT|USA:CO,Delta Co.,Leroux Creek|1969
Apodemia mormo centralis ssp. n.|17065E08|PT|USA:UT,Sevier Co.,IH70 Ivie Creek Rest Area|2012
Apodemia mormo centralis ssp. n.|20037E09|PT|USA:UT,Emery Co.,vic. Swinging Bridge|2019
Apodemia mormo centralis ssp. n.|17065D10|PT|USA:UT,San Juan Co.,Pack Creek|1978
Apodemia mormo centralis ssp. n.|PAO563|PT|USA:CO,Mesa Co.,E of Gateway|2017
Apodemia mormo centralis ssp. n.|20046C10|HT|USA:UT,San Juan Co.,Indian Creek Cyn.|2020
Apodemia mormo centralis ssp. n.|20046C09|PT|USA:UT,San Juan Co.,Indian Creek Cyn.|2019
Apodemia mormo centralis ssp. n.|7212|PT|USA:UT,Emery Co.,Little Gilson Butte|1986
Apodemia mormo centralis ssp. n.|7302|PT|USA:UT,San Juan Co.,vic. Newspaper Rock|1994
Apodemia mormo centralis ssp. n.|24066H05|USA:AZ,Navajo Co.,Winslow|1980
Apodemia mormo centralis ssp. n.|17065D12|USA:NM,San Juan Co.,SW Farmington|1973
Apodemia mormo centralis ssp. n.|17065E05|USA:NM,McKinley Co.,S of Gallup|1997
Apodemia mormo centralis ssp. n.|17065D07|USA:NM,Sandoval Co.,18 mi NW San Ysidro|1983
Apodemia mormo centralis ssp. n.|17065E06|USA:NM,Rio Arriba Co.,SH96 2 mi E SH112|1985
Apodemia mormo sudesta ssp. n.|17065E12|USA:NM,Taos Co.,Rio Grande Gorge|1985
Apodemia mormo sudesta ssp. n.|6678|PT|USA:CO,Costilla Co.,La Veta Pass|2012
Apodemia mormo centralis ssp. n.|24066H11|USA:AZ,Coconino Co.,32 mi SE Page|1986
Apodemia mormo centralis ssp. n.|19067C10|USA:AZ,Mohave Co.,~2 mi E Pipe Springs|1987
Apodemia mormo centralis ssp. n.|20037E07|USA:AZ,Coconino Co.,Nail or Hail Cyn.|2006
Apodemia mormo confusa ssp. n.|6902|PT|USA:AZ,Mohave Co.,Hualapai Mts.|2004
Apodemia mormo confusa ssp. n.|6901|PT|USA:AZ,Mohave Co.,lower Hualapai Mts.|2013
Apodemia mormo confusa ssp. n.|17068F05|PT|USA:AZ,Mohave Co.,Hualapai Mts.|1988
Apodemia mormo confusa ssp. n.|17068F06|PT|USA:AZ,Mohave Co.,Hualapai Mts.|1991
Apodemia mormo confusa ssp. n.|16105E11|PT|USA:AZ,Mohave Co.,Hualapai Mts.|1990
Apodemia mormo confusa ssp. n.|6900|PT|USA:AZ,Yavapai Co.,Little Hell Cyn.|2007
Apodemia mormo confusa ssp. n.|19129A06|PT|USA:AZ,Yavapai Co.,SR260 at mi 237|2009
Apodemia mormo confusa ssp. n.|17065D06|HT|USA:AZ,Coconino Co.,Buffalo Park|2005
Apodemia mormo confusa ssp. n.|24066H09|USA:AZ,Gila Co.,W McFadden Peak|1988
Apodemia mormo arizatra ssp. n.|24066H07|USA:AZ,Santa Cruz Co.,Mt. Hopkins|1979
Apodemia mormo arizatra ssp. n.|18033F07|HT|USA:AZ,Cochise Co.,Chiricahua Mts.|2012
A. mormo arizatra ssp. n.|18033F05|PT|USA:AZ,Cochise Co.,Chiricahua Mts.|2012
Apodemia mormo arizatra ssp. n.|7207|PT|USA:AZ,Pima Co.,Santa Catalina Mts.|old
Apodemia mormo arizatra ssp. n.|7206|PT|USA:AZ,Pima Co.,Santa Rita Mts.|old
Apodemia mormo arizatra ssp. n.|16101B01|USA:AZ,Pinal Co.,nr. Oracle|1965
0.002
d
e
f
g

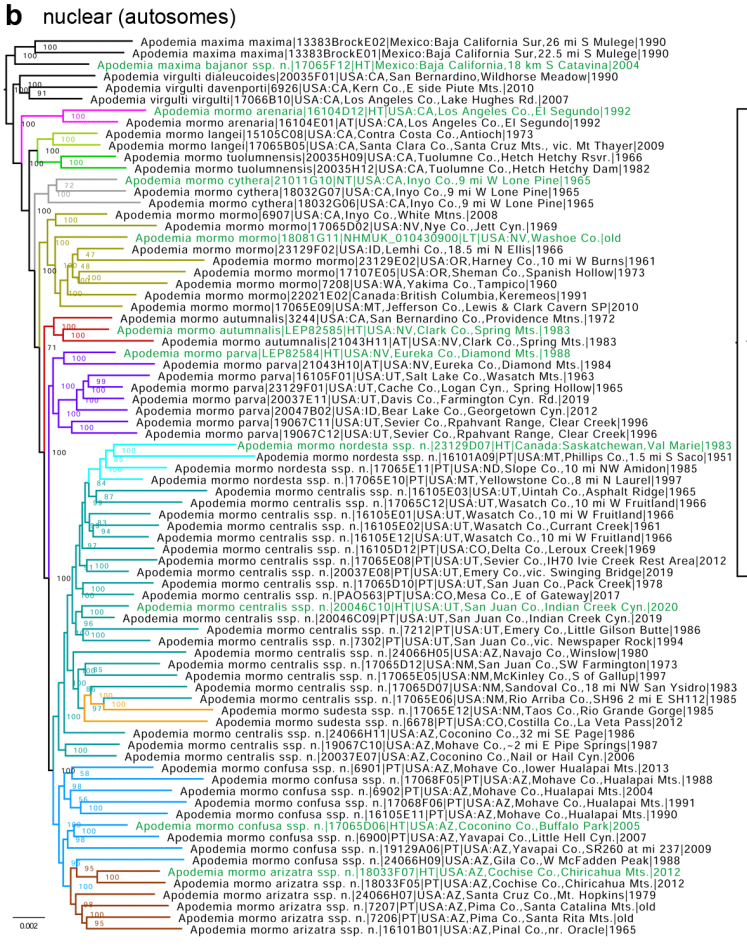
b nuclear (autosomes)
Apodemia maxima maxima|13383BrockE02|Mexico:Baja California Sur,26 mi S Mulege|1990
Apodemia maxima maxima|13383BrockE01|Mexico:Baja California Sur,22.5 mi S Mulege|1990
Apodemia maxima bajanor ssp. n.|17065F12|HT|Mexico:Baja California,18 km S Catavina|2004
Apodemia virgulti dialeucoides|20035F01|USA:CA,San Bernardino,Wildhorse Meadow|1990
Apodemia virgulti davenporti|6926|USA:CA,Kern Co.,E side Piute Mts.|2010
Apodemia virgulti virgulti|17066B10|USA:CA,Los Angeles Co.,Lake Hughes Rd.|2007
Apodemia mormo arenaria|16104D12|HT|USA:CA,Los Angeles Co.,El Segundo|1992
Apodemia mormo arenaria|16104E01|AT|USA:CA,Los Angeles Co.,El Segundo|1992
Apodemia mormo langei|15105C08|USA:CA,Contra Costa Co.,Antioch|1973
Apodemia mormo langei|17065B05|USA:CA,Santa Clara Co.,Santa Cruz Mts., vic. Mt Thayer|2009
Apodemia mormo tuolumnensis|20035H09|USA:CA,Tuolumne Co.,Hetch Hetchy Rsvr.|1966
Apodemia mormo tuolumnensis|20035H12|USA:CA,Tuolumne Co.,Hetch Hetchy Dam|1982
Apodemia mormo cythera|21011G10|NT|USA:CA,Inyo Co.,9 mi W Lone Pine|1965
Apodemia mormo cythera|18032G07|USA:CA,Inyo Co.,9 mi W Lone Pine|1965
Apodemia mormo cythera|18032G06|USA:CA,Inyo Co.,9 mi W Lone Pine|1965
Apodemia mormo mormo|6907|USA:CA,Inyo Co.,White Mtns.|2008
Apodemia mormo mormo|17065D02|USA:NV,Nye Co.,Jett Cyn.|1969
Apodemia mormo mormo|18081G11|NHMUK_010430900|LT|USA:NV,Washoe Co.|old
Apodemia mormo mormo|23129E02|USA:ID,Lemhi Co.,18.5 mi N Ellis|1966
Apodemia mormo mormo|23129E02|USA:OR,Harney Co.,10 mi W Burns|1961
Apodemia mormo mormo|17107E05|USA:OR,Sheman Co.,Spanish Hollow|1973
Apodemia mormo mormo|7208|USA:WA,Yakima Co.,Tampico|1960
Apodemia mormo mormo|22021E02|Canada:British Columbia,Keremeos|1991
Apodemia mormo mormo|17065E09|USA:MT,Jefferson Co.,Lewis & Clark Cavern SP|2010
Apodemia mormo autumnalis|3244|USA:CA,San Bernardino Co.,Providence Mtns.|1972
Apodemia mormo autumnalis|LEP82585|HT|USA:NV,Clark Co.,Spring Mts.|1983
Apodemia mormo autumnalis|21043H11|AT|USA:NV,Clark Co.,Spring Mts.|1983
Apodemia mormo parva|LEP82584|HT|USA:NV,Eureka Co.,Diamond Mts.|1988
Apodemia mormo parva|21043H10|AT|USA:NV,Eureka Co.,Diamond Mts.|1984
Apodemia mormo parva|16105F01|USA:UT,Salt Lake Co.,Wasatch Mts.|1963
Apodemia mormo parva|23129F01|USA:UT,Cache Co.,Logan Cyn., Spring Hollow|1965
Apodemia mormo parva|20037E11|USA:UT,Davis Co.,Farmington Cyn. Rd.|2019
Apodemia mormo parva|20047B02|USA:ID,Bear Lake Co.,Georgetown Cyn.|2012
Apodemia mormo parva|19067C11|USA:UT,Sevier Co.,Rpahvant Range, Clear Creek|1996
Apodemia mormo parva|19067C12|USA:UT,Sevier Co.,Rpahvant Range, Clear Creek|1996
Apodemia mormo nordesta ssp. n.|23129D07|HT|Canada:Saskatchewan,Val Marie|1983
Apodemia mormo nordesta ssp. n.|16101A09|PT|USA:MT,Phillips Co.,1.5 mi S Saco|1951
Apodemia mormo nordesta ssp. n.|17065E11|PT|USA:ND,Slope Co.,10 mi NW Amidon|1985
Apodemia mormo nordesta ssp. n.|17065E10|PT|USA:MT,Yellowstone Co.,8 mi N Laurel|1997
Apodemia mormo centralis ssp. n.|16105E03|USA:UT,Uintah Co.,Asphalt Ridge|1965
Apodemia mormo centralis ssp. n.|17065C12|USA:UT,Wasatch Co.,10 mi W Fruitland|1966
Apodemia mormo centralis ssp. n.|16105E01|USA:UT,Wasatch Co.,10 mi W Fruitland|1966
Apodemia mormo centralis ssp. n.|16105E02|USA:UT,Wasatch Co.,Currant Creek|1961
Apodemia mormo centralis ssp. n.|16105E12|USA:UT,Wasatch Co.,10 mi W Fruitland|1966
Apodemia mormo centralis ssp. n.|16105D12|PT|USA:CO,Delta Co.,Leroux Creek|1969
Apodemia mormo centralis ssp. n.|17065E08|PT|USA:UT,Sevier Co.,IH70 Ivie Creek Rest Area|2012
Apodemia mormo centralis ssp. n.|20037E09|PT|USA:UT,Emery Co.,vic. Swinging Bridge|2019
Apodemia mormo centralis ssp. n.|17065D10|PT|USA:UT,San Juan Co.,Pack Creek|1978
Apodemia mormo centralis ssp. n.|PAO563|PT|USA:CO,Mesa Co.,E of Gateway|2017
Apodemia mormo centralis ssp. n.|20046C10|HT|USA:UT,San Juan Co.,Indian Creek Cyn.|2020
Apodemia mormo centralis ssp. n.|20046C09|PT|USA:UT,San Juan Co.,Indian Creek Cyn.|2019
Apodemia mormo centralis ssp. n.|7212|PT|USA:UT,Emery Co.,Little Gilson Butte|1986
Apodemia mormo centralis ssp. n.|7302|PT|USA:UT,San Juan Co.,vic. Newspaper Rock|1994
Apodemia mormo centralis ssp. n.|24066H05|USA:AZ,Navajo Co.,Winslow|1980
Apodemia mormo centralis ssp. n.|17065D12|USA:NM,San Juan Co.,SW Farmington|1973
Apodemia mormo centralis ssp. n.|17065E05|USA:NM,McKinley Co.,S of Gallup|1997
Apodemia mormo centralis ssp. n.|17065D07|USA:NM,Sandoval Co.,18 mi NW San Ysidro|1983
Apodemia mormo centralis ssp. n.|17065E06|USA:NM,Rio Arriba Co.,SH96 2 mi E SH112|1985
Apodemia mormo sudesta ssp. n.|17065E12|USA:NM,Taos Co.,Rio Grande Gorge|1985
Apodemia mormo sudesta ssp. n.|6678|PT|USA:CO,Costilla Co.,La Veta Pass|2012
Apodemia mormo centralis ssp. n.|24066H11|USA:AZ,Coconino Co.,32 mi SE Page|1986
Apodemia mormo centralis ssp. n.|19067C10|USA:AZ,Mohave Co.,~2 mi E Pipe Springs|1987
Apodemia mormo centralis ssp. n.|20037E07|USA:AZ,Coconino Co.,Nail or Hail Cyn.|2006
Apodemia mormo confusa ssp. n.|6901|PT|USA:AZ,Mohave Co.,lower Hualapai Mts.|2013
Apodemia mormo confusa ssp. n.|17068F05|PT|USA:AZ,Mohave Co.,Hualapai Mts.|1988
Apodemia mormo confusa ssp. n.|6902|PT|USA:AZ,Mohave Co.,Hualapai Mts.|2004
Apodemia mormo confusa ssp. n.|17068F06|PT|USA:AZ,Mohave Co.,Hualapai Mts.|1991
Apodemia mormo confusa ssp. n.|16105E11|PT|USA:AZ,Mohave Co.,Hualapai Mts.|1990
Apodemia mormo confusa ssp. n.|17065D06|HT|USA:AZ,Coconino Co.,Buffalo Park|2005
Apodemia mormo confusa ssp. n.|6900|PT|USA:AZ,Yavapai Co.,Little Hell Cyn.|2007
Apodemia mormo confusa ssp. n.|19129A06|PT|USA:AZ,Yavapai Co.,SR260 at mi 237|2009
Apodemia mormo confusa ssp. n.|24066H09|USA:AZ,Gila Co.,W McFadden Peak|1988
Apodemia mormo arizatra ssp. n.|18033F07|HT|USA:AZ,Cochise Co.,Chiricahua Mts.|2012
Apodemia mormo arizatra ssp. n.|18033F05|PT|USA:AZ,Cochise Co.,Chiricahua Mts.|2012
Apodemia mormo arizatra ssp. n.|24066H07|USA:AZ,Santa Cruz Co.,Mt. Hopkins|1979
Apodemia mormo arizatra ssp. n.|7207|PT|USA:AZ,Pima Co.,Santa Catalina Mts.|old
Apodemia mormo arizatra ssp. n.|7206|PT|USA:AZ,Pima Co.,Santa Rita Mts.|old
Apodemia mormo arizatra ssp. n.|16101B01|USA:AZ,Pinal Co.,nr. Oracle|1965
0.002
c mitochondrial
A. mormo langei|17065B05|USA:CA,Santa Clara Co.,Santa Cruz Mts., vic. Mt Thayer
A. maxima maxima|13383BrockE02|Mexico:Baja California Sur,26 mi S Mulege|1990
A. maxima maxima|13383BrockE01|Mexico:Baja California Sur,22.5 mi S Mulege
A. maxima bajanor ssp. n.|17065F12|HT|Mexico:Baja California,18 km S Catavina
A. virgulti virgulti|17066B10|USA:CA,Los Angeles Co.,Lake Hughes Rd.|2007
A. virgulti dialeucoides|20035F01|USA:CA,San Bernardino,Wildhorse Meadow|1990
A. virgulti davenporti|6926|USA:CA,Kern Co.,E side Piute Mts.|2010
A. mormo arenaria|16104E01|AT|USA:CA,Los Angeles Co.,El Segundo|1992
A. mormo arenaria|16104D12|HT|USA:CA,Los Angeles Co.,El Segundo|1992
A. mormo autumnalis|LEP82585|HT|USA:NV,Clark Co.,Spring Mts.|1983
A. mormo autumnalis|21043H11|AT|USA:NV,Clark Co.,Spring Mts.|1983
A. mormo tuolumnensis|20035H12|USA:CA,Tuolumne Co.,Hetch Hetchy Dam|1982
A. mormo tuolumnensis|20035H09|USA:CA,Tuolumne Co.,Hetch Hetchy Rsvr.|1966
A. mormo cythera|18032G07|USA:CA,Inyo Co.,9 mi W Lone Pine|1965
A. mormo cythera|21011G10|NT|USA:CA,Inyo Co.,9 mi W Lone Pine|1965
A. mormo mormo|6907|USA:CA,Inyo Co.,White Mtns.|2008
A. mormo cythera|18032G06|USA:CA,Inyo Co.,9 mi W Lone Pine|1965
A. mormo mormo|7208|USA:WA,Yakima Co.,Tampico|1960
A. mormo mormo|17107E05|USA:OR,Sheman Co.,Spanish Hollow|1973
A. mormo mormo|23129F02|USA:ID,Lemhi Co.,18.5 mi N Ellis|1966
A. mormo mormo|23129E02|USA:OR,Harney Co.,10 mi W Burns|1961
A. mormo mormo|22021E02|Canada:British Columbia,Keremeos|1991
A. mormo mormo|18081G11|NHMUK_010430900|LT|USA:NV,Washoe Co.|old
A. mormo mormo|17065D02|USA:NV,Nye Co.,Jett Cyn.|1969
A. mormo parva|LEP82584|HT|USA:NV,Eureka Co.,Diamond Mts.|1988
A. mormo parva|21043H10|AT|USA:NV,Eureka Co.,Diamond Mts.|1984
A. mormo parva|19067C12|USA:UT,Sevier Co.,Rpahvant Range, Clear Creek|1996
A. mormo mormo|17065E09|USA:MT,Jefferson Co.,Lewis & Clark Cavern SP|2010
A. mormo parva|23129F01|USA:UT,Cache Co.,Logan Cyn., Spring Hollow|1965
A. mormo parva|20047B02|USA:ID,Bear Lake Co.,Georgetown Cyn.|2012
A. mormo parva|20037E11|USA:UT,Davis Co.,Farmington Cyn. Rd.|2019
A. mormo centralis ssp. n.|16105E03|USA:UT,Uintah Co.,Asphalt Ridge|1965
A. mormo parva|16105F01|USA:UT,Salt Lake Co.,Wasatch Mts.|1963
A. mormo parva|19067C11|USA:UT,Sevier Co.,Rpahvant Range, Clear Creek|1996
A. mormo centralis ssp. n.|19067C10|USA:AZ,Mohave Co.,~2 mi E Pipe Springs|1987
A. mormo centralis ssp. n.|20037E07|USA:AZ,Coconino Co.,Nail or Hail Cyn.|2006
A. mormo centralis ssp. n.|24066H11|USA:AZ,Coconino Co.,32 mi SE Page|1986
A. mormo nordesta ssp. n.|23129D07|HT|Canada:Saskatchewan,Val Marie|1983
A. mormo nordesta ssp. n.|16101A09|PT|USA:MT,Phillips Co.,1.5 mi S Saco|1951
A. mormo nordesta ssp. n.|17065E11|PT|USA:ND,Slope Co.,10 mi NW Amidon|1985
A. mormo nordesta ssp. n.|17065E10|PT|USA:MT,Yellowstone Co.,8 mi N Laurel|1997
A. mormo centralis ssp. n.|16105E02|USA:UT,Wasatch Co.,Currant Creek|1961
A. mormo centralis ssp. n.|17065C12|USA:UT,Wasatch Co.,10 mi W Fruitland|1966
A. mormo centralis ssp. n.|7212|PT|USA:UT,Emery Co.,Little Gilson Butte|1986
A. mormo centralis ssp. n.|20037E08|PT|USA:UT,Emery Co.,vic. Swinging Bridge|2019
A. mormo centralis ssp. n.|16105E12|USA:UT,Wasatch Co.,10 mi W Fruitland|1966
A. mormo centralis ssp. n.|16105E01|USA:UT,Wasatch Co.,10 mi W Fruitland|1966
A. mormo centralis ssp. n.|17065D10|PT|USA:UT,San Juan Co.,Pack Creek|1978
A. mormo centralis ssp. n.|20046C09|PT|USA:UT,San Juan Co.,Indian Creek Cyn.|2019
A. mormo centralis ssp. n.|20046C10|HT|USA:UT,San Juan Co.,Indian Creek Cyn.|2020
A. mormo centralis ssp. n.|17065E08|PT|USA:UT,Sevier Co.,IH70 Ivie Creek Rest Area
A. mormo centralis ssp. n.|16105D12|PT|USA:CO,Delta Co.,Leroux Creek|1969
A. mormo centralis ssp. n.|PAO563|PT|USA:CO,Mesa Co.,E of Gateway|2017
A. mormo centralis ssp. n.|17065E05|USA:NM,McKinley Co.,S of Gallup|1997
A. mormo centralis ssp. n.|17065E06|USA:NM,Rio Arriba Co.,SH96 2 mi E SH112|1985
A. mormo sudesta ssp. n.|17065E12|USA:NM,Taos Co.,Rio Grande Gorge|1985
A. mormo sudesta ssp. n.|6678|PT|USA:CO,Costilla Co.,La Veta Pass|2012
A. mormo centralis ssp. n.|24066H05|USA:AZ,Navajo Co.,Winslow|1980
A. mormo centralis ssp. n.|17065D07|USA:NM,Sandoval Co.,18 mi NW San Ysidro
A. mormo centralis ssp. n.|17065D12|USA:NM,San Juan Co.,SW Farmington|1973
A. mormo centralis ssp. n.|7302|PT|USA:UT,San Juan Co.,vic. Newspaper Rock|1994
A. mormo autumnalis|3244|USA:CA,San Bernardino Co.,Providence Mtns.|1972
A. mormo confusa ssp. n.|24066H09|USA:AZ,Gila Co.,W McFadden Peak|1988
A. mormo confusa ssp. n.|17065D06|HT|USA:AZ,Coconino Co.,Buffalo Park|2005
A. mormo confusa ssp. n.|17068F05|PT|USA:AZ,Mohave Co.,Hualapai Mts.|1988
A. mormo confusa ssp. n.|6901|PT|USA:AZ,Mohave Co.,lower Hualapai Mts.|2013
A. mormo confusa ssp. n.|17068F06|PT|USA:AZ,Mohave Co.,Hualapai Mts.|1991
A. mormo confusa ssp. n.|16105E11|PT|USA:AZ,Mohave Co.,Hualapai Mts.|1990
A. mormo confusa ssp. n.|6902|PT|USA:AZ,Mohave Co.,Hualapai Mts.|2004
A. mormo confusa ssp. n.|6900|PT|USA:AZ,Yavapai Co.,Little Hell Cyn.|2007
A. mormo confusa ssp. n.|19129A06|PT|USA:AZ,Yavapai Co.,SR260 at mi 237
A. mormo arizatra ssp. n.|18033F07|HT|USA:AZ,Cochise Co.,Chiricahua Mts.|2012
A. mormo arizatra ssp. n.|18033F05|PT|USA:AZ,Cochise Co.,Chiricahua Mts.|2012
A. mormo arizatra ssp. n.|24066H07|USA:AZ,Santa Cruz Co.,Mt. Hopkins|1979
A. mormo arizatra ssp. n.|7207|PT|USA:AZ,Pima Co.,Santa Catalina Mts.|old
A. mormo arizatra ssp. n.|16101B01|USA:AZ,Pinal Co.,nr. Oracle|1965
A. mormo arizatra ssp. n.|7206|PT|USA:AZ,Pima Co.,Santa Rita Mts.|old
0.005

Fig. 8 (see the previous page). Phylogenetic trees of selected *A. mormo* group taxa focusing on the populations of *A. mormo* ssp. from the eastern part of the range, constructed from protein-coding regions in: **a)** the Z chromosome, based on 493,419 positions, **b)** the nuclear genome (autosomes), based on 7,060,605 positions, and **c)** the mitochondrial genome; and **d–g)** iNaturalist observations, males (color of the dot in the lower left of each image corresponds to the color of this taxon in the trees): **d)** *A. mormo nordesta* **ssp. n.**, observation No. 173717488 (photo 301712425, inset 301714853) Canada: Saskatchewan, Grasslands National Park, Killdeer Badlands, GPS 49.0202, −106.5698, 21-Aug-2015 © alchem30 (inset shows a magnified view of the eye of the same individual, photo 301714853); **e)** *A. mormo centralis* **ssp. n.**, observation No. 98669807, USA: Utah, San Juan Co., Canyonlands National Park, GPS 38.1100, −109.8158, 16-Oct-2021 © sacjackson; **f)** *A. mormo confusa* **ssp. n.**, observation No. 323364021, USA: Arizona, Yavapai Co., vic. Mingus Mtn., GPS 34.7140, −112.1534, 1-Oct-2025 © datrinite; **g)** *A. mormo arizatra* **ssp. n.**, observation No. 103908464, USA: Arizona, Cochise Co., Chiricahua Mts., nr Rustler Park, 5-Jul-2013 © Ken Kertell; images are color-corrected, brightened, rotated, cropped, and (g) is flipped, CC BY-NC 4.0 https://creativecommons.org/licenses/by-nc/4.0/. In the trees, primary type specimens are labeled in green font and clades of focus are colored: *A. mormo arenaria* (magenta), *A. mormo langei* (lime), *A. mormo tuolumnensis* (green), *A. mormo cythera* (gray), *A. mormo mormo* (olive), *A. mormo autumnalis* (red), *A. mormo parva* (violet), *A. mormo nordesta* **ssp. n.** (cyan), *A. mormo centralis* **ssp. n.** (teal), *A. mormo sudesta* **ssp. n.** (orange), *A. mormo confusa* **ssp. n.** (blue), and *A. mormo arizatra* **ssp. n.** (brown). Ultrafast bootstrap (Hoang et al. 2018) values are shown at nodes.

mormo autumnalis. This clade does not have available names associated with it and thus represents at least one new subspecies.

The Madrean "Sky Islands" of southwestern Arizona are inhabited by dark populations, frequently nearly black with white spots and lacking reddish-orange coloration. Due to their phenotypic distinction and a certain level of genetic differentiation (Fig. 8 brown), they warrant recognition as a distinct subspecies from the southern part of the range. Similarly, southeastern populations from the southern San Luis Valley in Colorado and northern New Mexico, sometimes incorrectly assigned to *A. mejicanus* instead of *A. mormo* (Warren et al. 2024), are also distinct phenotypically in being typically darker with more strongly developed black overscaling along the veins in the reddish-orange forewing patch. These specimens form a clade in the nuclear genomic trees (Fig. 8a, b orange) and they comprise another distinct subspecies. Northeastern populations found to the north of the Colorado Plateau frequently have larger white spots and are genetically distinct (Fig. 8a, b cyan), thus representing another subspecies. Finally, the populations from the Colorado Plateau are genetically diverse, but are in a clade (Fig. 8a–c teal) distinct and sister to the clade with the populations from the western spine of the Transition Zone in Arizona (Fig. 8a–c blue). The difference between them is present in the mitochondrial genome as well. Therefore, these two groups of populations are recognized as two additional subspecies. These five subspecies (southern, southeastern, northeastern, central, and transitional) are described as new below.

Apodemia (*Apodemia*) *mormo arizatra* Grishin, new subspecies

https://zoobank.org/5874B5D1-1CCB-4E96-A8C0-943E7D1926AC

(Figs. 8a–c part, 8g, 9, 10a, 30–31 part)

Definition and diagnosis. This is the southern subspecies of *Apodemia* (*Apodemia*) *mormo* (C. Felder & R. Felder, 1859) (type locality in USA: likely Nevada, Washoe Co.). It is similar to *Apodemia* (*Apodemia*) *mormo autumnalis* Austin, 1998 (type locality USA: Nevada, Clark Co., Spring Mts.) in its somewhat larger size, but differs from it and other subspecies of *A. mormo* by being darker and having much reduced or nearly absent orange patches on the dorsal forewing, especially distad of the discal cell (some females may be almost black with white spots, nearly lacking any orange scales dorsally); the dorsal hindwing lacks orange scales between the two white spots in cells M_1-M_2 and M_2-M_3, being just black, but some orange coloration may be present towards the base of the discal cell as small spots. The longitudinal orange streak at the base of the ventral hindwing is well-developed, as is also the large orange patch on the ventral forewing with orange scales extending between the white postdiscal spots along the veins, but not prominently distad of this band, except possibly on the veins. Due to relatively unexplored individual variation, especially at the periphery of the range, this subspecies is best identified by DNA, with diagnostic base pairs in the nuclear genome: cne1894.1.2:T24C, cne1894.1.2:C51T,

Fig. 9. *Apodemia mormo arizatra* **ssp. n.** types from USA: Arizona in dorsal (left) and ventral (right) views: **a) holotype** ♂ NVG-18033F07 Cochise Co., Chiricahua Mts., Rustler Park, 4-Aug-2012, M. Walker leg. and paratypes: **b)** ♀ NVG-18033F05 same data as the holotype; **c)** ♂ NVG-7206 Pima Co., Sta. Rita Mts., old; **d)** ♂ NVG-7207 Pima Co., Sta. Catalina Mts., old.

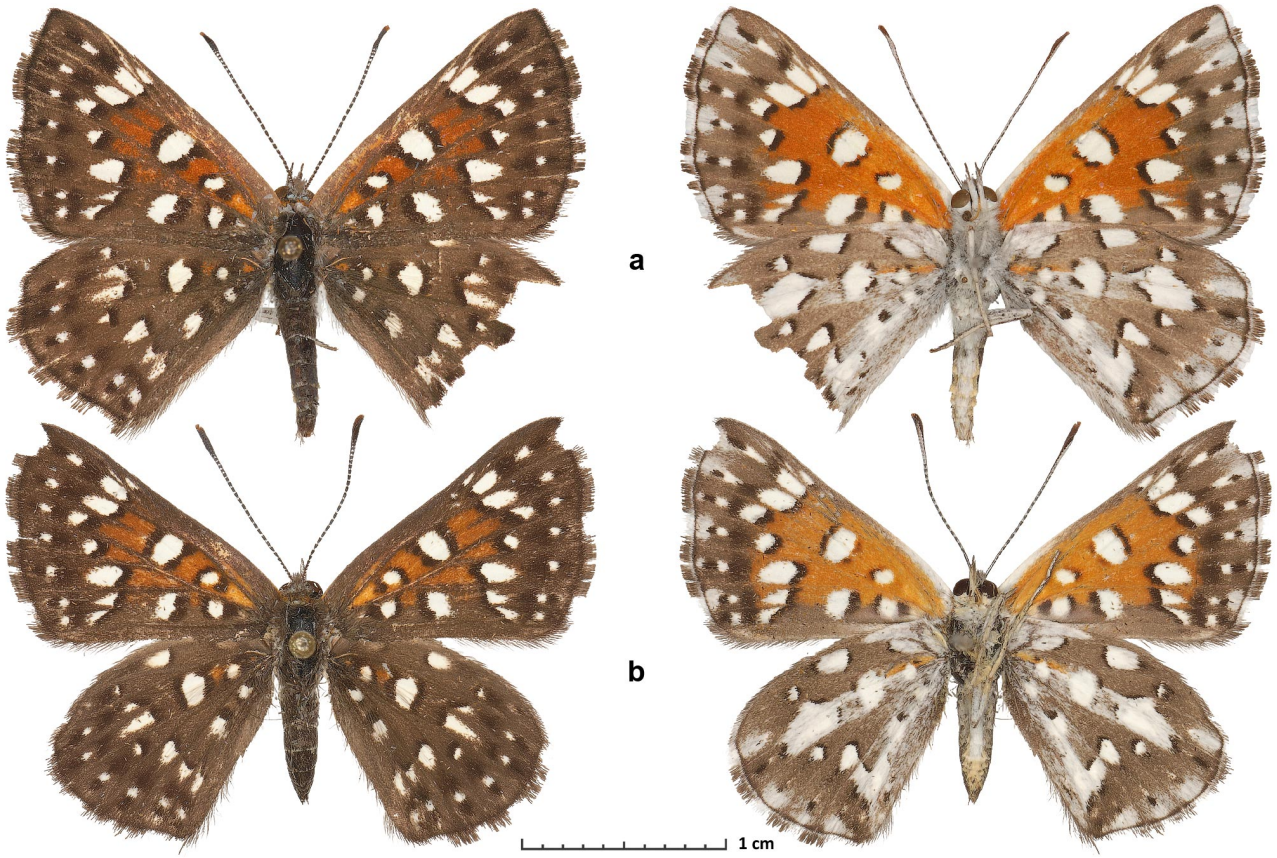

Fig. 10. *Apodemia mormo* ssp. non-type specimens genetically similar to *A. mormo arizatra* **ssp. n.** but with a more strongly developed fulvous scaling on the dorsal forewing, from USA: Arizona, in dorsal (left) and ventral (right) views: **a)** *Apodemia mormo arizatra* **ssp. n.** ♂ NVG-16101B01 Pinal Co., Peppersauce Canyon, 12-Sep-1965, J. H. Hessel leg. [AMNH] and **b)** *Apodemia mormo confusa* **ssp. n.** ♂ NVG-24066H09 Gila Co., Salome Creek, W of McFadden Peak, nr. J. R. Ranch, 24–25-Sep-1988, J. P. Brock leg. [MGCL].

cne6600.13.5:T126G, cne6600.13.5:T132G, cne6600.13.5:C135T; while the COI barcode may not distinguish all specimens of this subspecies from others, likely due to introgression.

Barcode sequence of the holotype. Sample NVG-18033F07, GenBank PX971409, 658 base pairs:

AACATTATATTTTATTTTTGGAATTTGAGCAGGAATAGTTGGAACCTCATTAAGATTATTAATTCGAATAGAATTAGGAACATCAGGATCTTTAATTGGTGATGATCAAATTTATAATACT
ATTGTTACAGCTCATGCTTTCATTATAATTTTTTTTATAGTTATACCTATTATAATTGGAGGATTTGGTAATTGATTAGTACCATTAATACTTGGAGCTCCGGATATAGCTTTTCCACGAA
TAAATAATATAAGATTTTGACTTTTACCCCCCTCATTATTCTTATTAATTTCTAGAAGAATTGTAGAAAATGGAGCAGGAACAGGATGAACAGTTTATCCCCCACTTTCATCTAATATTGC
CCATGGAGGAGCTTCAGTTGATTTAGCTATTTTTTCTTTACATTTAGCTGGTATTTCTTCAATTTTAGGTGCAATTAATTTTATTACAACTATTATTAATATACGTGTTAATAATATATCT
TTTGATCAAATACCTTTATTTGTATGATCAGTAGGAATTACAGCTTTATTATTATTACTCTCATTACCTGTTTTAGCTGGAGCTATTACCATATTATTAACTGATCGTAATTTAAACACAT
CATTTTTTGATCCAGCAGGTGGAGGAGATCCAATTTTATATCAACATTTATTT

Type material. Holotype: ♂ currently in the research collection of Mark Walker (Oceanside, CA, USA), to be deposited in the McGuire Center for Lepidoptera and Biodiversity collection, Gainesville, FL, USA (MGCL), illustrated in Fig. 9a, bears the following three printed rectangular labels, two white: [Rustler Park | 04-VIII-12 AZ | Cochise Co. | Lat 31 54' 42" N | Long 109 15' 54"W | Mark Walker leg.], [DNA sample ID: | NVG-18033F07 | c/o Nick V. Grishin], and one red [HOLOTYPE ♂ | Apodemia (Apodemia) | mormo arizatra Grishin]. **Paratypes:** 3♂♂ and 2♀♀: USA, Arizona: 1♂ (NVG-18033F08) and 2♀♀ (NVG-18033F05 (Fig. 9b), NVG-18033F06) data as the holotype; and Pima Co., old, Barnes collection [USNM]: 1♂ NVG-7206 Santa Rita Mts., genitalia NVG161005-33 (Fig. 9c); and 1♂ NVG-7207 Santa Catalina Mts., genitalia NVG161005-34 (Fig. 9d).

Type locality. USA: Arizona, Cochise Co., Chiricahua Mountains, Rustler Park, 8100 ft, GPS 31.9117, −109.2650.

Etymology. In Latin, *ater* (feminine: *atra*) means black. The name reflects the darker aspect of this subspecies from Arizona and is treated as a feminine adjective.

Distribution. Higher elevations in the mountains of southeastern Arizona (Santa Rita, Santa Catalina, and Chiricahua Mts.) (Fig. 31).

Remarks. A male NVG-16101B01 from Arizona, Pinal Co., Santa Catalina Mts., Peppersauce Canyon, 12-Sep-1965, J. H. Hessel leg. [AMNH] (Fig. 10a) is at the northern boundary of the range, is genomically similar to this new subspecies, and we tentatively identify it as such. However, this specimen has more extensive reddish coloration on the forewings above; therefore, we exclude it from the type series. Likewise, a male with better developed dorsal forewing reddish-orange patches and some reddish coloration distad of the postdiscal white spots on the dorsal hindwing, NVG-24066H07 from Arizona, Santa Cruz Co., Mt. Hopkins, Observatory Rd., 8000 ft, 29-Sep-1979, R. A. Bailowitz leg. [MGCL], is also excluded from the type series.

Apodemia (*Apodemia*) *mormo sudesta* Grishin, new subspecies

https://zoobank.org/195EB71F-3C92-497E-BB1B-4C01497CC055

(Figs. 8a–c part, 11a–c, 30–31 part)

Definition and diagnosis. This is the southeastern subspecies of *Apodemia* (*Apodemia*) *mormo* (C. Felder & R. Felder, 1859) (type locality in USA: likely Nevada, Washoe Co.). It is similar to the nominotypical subspecies but averages somewhat larger and is darker, with reduced, but still developed orange patches on the dorsal forewing, expressed distad of the discal cell, but narrower, and transected by darker veins that are typically more prominent than in other subspecies; the dorsal hindwing is usually without orange scales between the two white spots in cells M_1-M_2 and M_2-M_3, being just black, and the orange spots and patches are present towards the base of the discal cell. The white spots are smaller, which is best seen by the size of the spot in the middle of the forewing cell M_3-CuA_1 (compare within each sex, as females tend to have larger spots). The longitudinal orange streak at the base of the ventral hindwing is developed, and the orange patch on the ventral forewing ends basad of the postdiscal white spots, not penetrating between them. Due to relatively unexplored individual variation and intergradation with other subspecies westward, this subspecies is best identified by DNA, with diagnostic base pairs in the nuclear genome: cne109.6.6:A333G, cne109.6.6:A378T, cne8269.2.2:C152T, cne8269.2.2:G153C, cne8269.2.2:A154C; while the COI barcode may not distinguish all specimens of this subspecies from others, likely due to introgression.

Barcode sequence of a topotypical paratype. Sample NVG-6678, GenBank PX971410, 658 base pairs:

AACATTATATTTTATTTTTGGAATTTGAGCAGGAATAGTTGGAACCTCATTAAGATTATTAATTCGAATAGAATTAGGAACATCAGGATCTTTAATTGGTGATGATCAAATTTATAATACT
ATTGTTACAGCTCATGCTTTTATTATAATTTTTTTTATAGTTATACCTATTATAATTGGAGGATTTGGTAATTGATTAGTACCATTAATACTTGGAGCTCCAGATATAGCTTTTCCACGAA
TAAATAATATAAGATTTTGACTTTTACCCCCCTCATTATTCTTATTAATTTCTAGAAGAATTGTAGAAAATGGAGCAGGAACAGGATGAACAGTTTATCCCCCACTTTCATCTAATATTGC
CCATGGAGGAGCTTCAGTTGATTTAGCTATTTTTTCTTTACATTTAGCTGGTATTTCTTCAATTTTAGGTGCAATTAATTTTATTACAACTATTATTAATATACGTGTTAATAATATATCT
TTTGATCAAATACCTTTATTTGTATGATCAGTAGGAATTACAGCTTTATTATTATTACTTTCATTACCTGTTTTAGCTGGAGCTATTACTATATTATTAACTGATCGTAATTTAAATACAT
CATTTTTTGACCCAGCAGGTGGAGGAGATCCTATTTTATATCAACATTTATTT

Type material. Holotype: ♂ currently in the research collection of Mark Walker (Oceanside, CA, USA), to be deposited in the McGuire Center for Lepidoptera and Biodiversity collection, Gainesville, FL, USA (MGCL), illustrated in Fig. 11a, bears the following three printed rectangular labels, two white: [La Veta Pass | 02-VIII-12 CO | Costilla Co. | Lat 37 33' 39" N | Long 107 17' 15" W | Mark Walker leg.], [DNA sample ID: | NVG-25047A12 | c/o Nick V. Grishin], and one red [HOLOTYPE ♂ | Apodemia (Apodemia) | mormo sudesta Grishin]. **Paratypes:** 2♂♂ and 1♀: USA, Colorado: 1♂ NVG-6678 data as the holotype; 1♀ NVG-20047B03 Costilla Co., Rd. H 0.5 mi W of CO-159, 23-Aug-2015, M. Hofmann leg. [MHC]; and 1♂ NVG-17065C04 Conejos Co., 12 mi E of Manassa, Rd. 142 at Rio Grande River, 7480 ft, 37.1802, −105.7304, 5-Aug-2013, C. E. Harp leg. [CSUC] (Fig. 11c).

Type locality. USA: Colorado, Costilla Co., Sangre de Cristo Mountains, La Veta Pass, GPS 37.5608, −105.2875.

Etymology. In Spanish, *sudeste* means southeast. The name reflects the southeastern range of this subspecies and is treated as a noun in apposition.

Distribution. Currently known from the southern San Luis Valley and vicinity in south-central Colorado and north-central New Mexico, USA (Fig. 31).

Fig. 11. *Apodemia mormo sudesta* **ssp. n.** specimens from USA in dorsal (left) and ventral (right) views: **a) holotype** ♂ NVG-25047A12 Colorado, Costilla Co., La Veta Pass, 37.5608, −105.2875, 2-Aug-2012, M. Walker leg.; **b)** non-type ♀ NVG-17065E12 New Mexico, Taos Co., Rio Grande Gorge, E side of Chawa Lama Overlook, 7000 ft, 24-Aug-1985, R. W. Holland leg. [CSUC]; and **c)** paratype ♂ NVG-17065C04 Colorado, Conejos Co., 12 mi E of Manassa, Rd. 142 at Rio Grande River, 7480 ft, 5-Aug-2013, C. Harp leg. [CSUC]; compared with **d)** *Apodemia mormo centralis* **ssp. n.** non-type ♂ NVG-17065E05 New Mexico, McKinley Co., S of Gallup, 5.5 mi S of I-40 on NM-602, 9500 ft, 30-Aug-1997, R. W. Holland leg. [CSUC].

Remark. A female NVG-17065E12 from New Mexico, Taos Co., Rio Grande Gorge, E side of Chawa Lama Overlook, 7000 ft, 24-Aug-1985, R. W. Holland leg. [CSUC] (Fig. 11b) is geographically close to the type locality, is phenotypically similar to this new subspecies, and we tentatively identify it as such. However, this specimen is genomically more similar to a specimen from the Jemez Mountains, and therefore, we exclude it from the type series.

Apodemia (*Apodemia*) *mormo nordesta* Grishin, new subspecies

https://zoobank.org/34215762-9446-4970-8941-D15C8301F305

(Figs. 8a–c part, 8d, 12a–b, 30–31 part)

Definition and diagnosis. This is the northeastern subspecies of *Apodemia* (*Apodemia*) *mormo* (C. Felder & R. Felder, 1859) (type locality in USA: likely Nevada, Washoe Co.). It is similar to the nominotypical subspecies (Fig. 12c, d), and the orange patches on the dorsal forewing are prominent but constrained to the middle of the wing; dark overscaling along the veins inside these patches is more diffuse or weak; the dorsal hindwing is usually with orange scales between the two white spots in cells M_1-M_2 and M_2-M_3 and at the base of the discal cell. The white spots are frequently larger than in other subspecies (e.g., Fig. 8d), The longitudinal orange streak at the base of the ventral hindwing is absent or weak, but the orange patch on the ventral forewing penetrates between the postdiscal white spots along the veins. Due to relatively unexplored individual variation and intergradation with other subspecies southward, this subspecies is best identified by DNA, with diagnostic base pairs in the nuclear genome: cne1547.7.2:C150T, cne1547.7.2:T197C, cne8392.2.1:G450T, cne8392.2.1:T492A, cne148.15.1:A1068G; while the COI barcode may not distinguish all specimens of this subspecies from others, likely due to introgression.

Barcode sequence of the holotype. Sample NVG-23129D07, GenBank PX971411, 658 base pairs:

AACATTATATTTTATTTTTGGAATTTGAGCAGGAATAGTTGGAACCTCATTAAGATTATTAATTCGAATAGAATTAGGAACATCAGGATCTTTAATTGGTGATGATCAAATTTATAATACT
ATTGTTACAGCTCATGCTTTTATTATAATTTTTTTTATAGTTATACCTATTATAATTGGAGGATTTGGTAATTGATTAGTACCATTAATACTTGGAGCTCCAGATATAGCTTTTCCACGAA
TAAATAATATAAGATTTTGACTTTTACCCCCCTCATTATTCTTATTAATTTCTAGAAGAATTGTAGAAAATGGAGCAGGAACAGGATGAACAGTTTATCCCCCACTTTCATCTAATATTGC
CCATGGAGGAGCTTCAGTTGATTTAGCTATTTTTTCTTTACATTTAGCTGGTATTTCTTCAATTTTAGGTGCAATTAATTTTATTACAACTATTATTAATATACGTATTAATAATATATCT
TTTGATCAAATACCTTTATTTGTATGATCAGTAGGAATTACAGCTTTATTATTATTACTTTCATTACCTGTTTTAGCTGGAGCTATTACTATATTATTAACTGATCGTAATTTAAACACAT
CATTTTTTGATCCAGCAGGTGGAGGAGATCCTATTTTATATCAACATTTATTT

Type material. Holotype: ♂ deposited in the Canadian National Collection of Insects, Arachnids and Nematodes, Ottawa, Ontario, Canada (CNC), illustrated in Fig. 12a, bears the following eight rectangular labels (2nd, 3rd handprinted, others printed with handwritten text in italics; 4th green, 6th yellow, and 8th red): [Val Marie | Sask. *11* | *VIII* 1*983* | R. Hooper], [IN | BADLANDS], [Databased for | The Butterflies of | Canada Project | 1998–1999], [Specimen ID | CNCLEP | 00118230], [Barcode of Life | DNA voucher specimen | Sample ID | CCDB-24271-G12 | BOLD Proc. ID: | CNCBF654-14], [DNA sample ID: | NVG-23129D07 | c/o Nick V. Grishin], and [HOLOTYPE ♂ | Apodemia (Apodemia) | mormo nordesta Grishin]. **Paratypes:** 4♂♂ and 2♀♀: USA: 1♀ NVG-17065E11 North Dakota, Slope Co., 10 mi NW Amidon, Burning Coal Vein Campground, 12-Sep-1985, J. R. Powers leg. [CSUC] and Montana: Phillips Co., 1.5 mi S of Saco, W. Wheaton leg. [AMNH]: 2♂♂ 11-Aug-1951 (NVG-16101A10 and NVG-16101A11) and 2♂♂ 20-Aug-1951 (NVG-16101A08 and NVG-16101A09) and 1♀ NVG-17065E10 Yellowstone Co., 8 mi N of Laurel, MT-532 below south-facing slopes, 3380 ft, 17-Aug-1997, C. E. Harp leg. [CSUC] (Fig. 12b).

Type locality. Canada: Saskatchewan, southeast of Val Marie, approx. GPS 49.2059, −107.6628.

Etymology. In Spanish, *nordeste* means southeast. The spelling with the letter *d* is used to prevent confusion with "no rest". The name reflects the northwestern distribution of this subspecies and is treated as a noun in apposition.

Distribution. Currently known from extreme south-central Canada (Saskatchewan) and north-central USA: Montana (except western) and North Dakota (Fig. 31).

Remark. The topotypical population of this new subspecies, termed the "Mormon Metalmark, Prairie Population," is of special conservation concern in Canada; and similarly to Proshek et al. (2013), we identified its (taken together with populations in USA: MT & ND) notable genetic differentiation from the nominotypical populations in the west, thus justifying conservation efforts for this unique subspecies.

Fig. 12. *Apodemia mormo nordesta* **ssp. n.** type specimens in dorsal (left) and ventral (right) views: **a) holotype** ♂ NVG-23129D07 Canada: Saskatchewan, vic. Val Marie, 11-Aug-1983, R. Hooper leg. [CNC] and **b)** paratype ♀ NVG-17065E10 USA: Montana, Yellowstone Co., 8 mi N of Laurel, Hwy 532 below S facing slopes, 3380 ft, 17-Aug-1997, C. Harp leg. [CSUC]; compared with *Apodemia mormo mormo* non-types from nearby localities: **c)** ♂ NVG-23129F02 USA: Idaho, Lemhi Co., 18.5 mi N of Ellis on Hwy 93, 22-Aug-1966 [CNC] and **d)** ♀ NVG-17065E09 USA: Montana, Jefferson Co., Lewis & Clark Cavern State Park, return trail, 29-Sep-2010, P. A. & E. M. Opler leg. [CSUC].

Apodemia (*Apodemia*) *mormo centralis* Grishin, new subspecies

https://zoobank.org/D36FE067-F1AA-4AEE-BCBA-54C7329F0E4F

(Figs. 8a–c part, 8e, 13a–b, 15d, 30–31 part)

Definition and diagnosis. This is the subspecies of *Apodemia* (*Apodemia*) *mormo* (C. Felder & R. Felder, 1859) (type locality in USA: likely Nevada, Washoe Co.) from the Colorado Plateau. It is similar to *Apodemia* (*Apodemia*) *mormo parva* Austin, 1998 (type locality USA: Nevada, Eureka Co., Diamond Mts.) (Fig. 13c, d) in having larger reddish-orange patches on the dorsal forewing, but is larger overall in size and has smaller dorsal white spots, especially in the submarginal row on the hindwing. It is more strongly overscaled with diffuse brown scales at the distal margins, and the brown inner dash of the white spot in the postdiscal band on the ventral forewing in cell M_3-CuA_1 is typically midway between the dashes in cells M_2-M_3 and CuA_1-CuA_2 (or at least more strongly offset from the dash in M_2-M_3) [closer to the dash in cell M_2-M_3 in *A. mormo parva*]. The longitudinal orange streak at the base of the ventral hindwing is well developed, and the orange patch on the ventral forewing penetrates between and frequently distad of the white spots in the postdiscal band. Due to relatively unexplored individual variation and intergradation with other subspecies at the periphery of its range, this subspecies is best identified by DNA, with diagnostic base pairs in the nuclear genome: cne3991.4.5:A96C, cne3991.4.5:G115T, cne3991.4.5:C116T, cne2798.3.1:C489A, cne6946.3.3:G141A, cne1547.7.2:C150C (not T), cne1547.7.2:T197T (not C), cne8392.2.1:G450G (not T), cne8392.2.1:T492T (not A), cne148.15.1:A1068A (not G), cne109.6.6:A333A (not G), cne109.6.6:A378A (not T), cne8269.2.2:C152C (not T), cne8269.2.2:G153G (not C), cne8269.2.2:A154A (not C); while the COI barcode may not distinguish all specimens of this subspecies from others, likely due to introgression.

Barcode sequence of the holotype. Sample NVG-20046C10, GenBank PX971412, 658 base pairs:

AACATTATATTTTATTTTTGGAATTTGAGCAGGAATAGTTGGAACCTCATTAAGATTATTAATTCGAATAGAATTAGGAACATCAGGATCTTTAATTGGTGATGATCAAATTTATAATACT
ATTGTTACAGCTCATGCTTTTATTATAATTTTTTTTATAGTTATACCTATTATAATTGGAGGATTTGGTAATTGATTAGTACCATTAATACTTGGGGCTCCCGATATAGCTTTTCCACGAA
TAAATAATATAAGATTTTGACTTTTACCCCCCTCATTATTCTTATTAATTTCTAGAAGAATTGTAGAAAATGGAGCAGGAACAGGATGAACAGTTTATCCCCCACTTTCATCTAATATTGC
CCATGGAGGAGCTTCAGTTGATTTAGCTATTTTTTCTTTACATTTAGCTGGTATTTCTTCAATTTTAGGTGCAATTAATTTTATTACAACTATTATTAATATACGTGTTAATAATATATCT
TTTGATCAAATACCTTTATTTGTATGATCAGTAGGAATTACAGCTTTATTATTATTACTCTCATTACCTGTTTTAGCTGGAGCTATTACTATATTATTAACTGATCGTAATTTAAATACAT
CATTTTTTGATCCAGCAGGTGGAGGAGATCCTATTTTATATCAACATTTATTT

Type material. Holotype: ♂ deposited in the McGuire Center for Lepidoptera and Biodiversity collection, Gainesville, FL, USA (MGCL), illustrated in Fig. 13a, bears the following four printed rectangular labels, three white: [Indian Creek Canyon | Bear's Ears NM, UT | 21 August 2020 | Robb Hannawacker], [Mormon Metalmark | Apodemia mormo], [DNA sample ID: | NVG-20046C10 | c/o Nick V. Grishin], and one red [HOLOTYPE ♂ | Apodemia (Apodemia) | mormo centralis Grishin]. **Paratypes:** 7♂♂ and 4♀♀: USA, Utah: 1♀ NVG-20046C09 data as the holotype but 6-Sep-2019 (Fig. 13b); San Juan Co.: 1♂ NVG-17065D10 La Sal Mts., Pack Creek, 6700 ft, 4-Sep-1978, J. A. Scott leg. [CSUC] and 1♂ NVG-7302 vic. of Newspaper Rock, 18-Aug-1994, A. S. & N. Menke leg., genitalia NVG161007-29 [USNM]; Emery Co.: Little Gilson Butte, 29-Aug-1986, A. S. Menke leg. [USNM]: 1♂ NVG-7211, genitalia NVG161005-38 and 1♂ NVG-7212, genitalia NVG161005-39; and 1♂ NVG-20037E08 2 mi S of San Rafael River Swinging Bridge, 3000 ft, 39.0608, −110.6722, 17-Aug-2019, T. L. Stout leg.; and 1♂ NVG-17065E08 Sevier Co., rest stop area off I-70, 12-Jul-2012, K. Davenport leg. [CSUC]; and Colorado: Mesa Co., E of Gateway: 1♂ PAO-563 West Creek Picnic Area, 10-Sep-2017, P. A. Opler & E. M. Buckner-Opler leg. and 1♀ NVG-23129E10 Unaweep Canyon, West Creek, 6000 ft, 23-Jun-1972, M. Fisher leg. [CNC]; and 2♀♀ (NVG-16105D11 and NVG-16105D12) Delta Co., Leroux Creek, 31-Aug-1969, S. Ellis leg. [LACM]. Only the specimens mentioned above are included as paratypes, because they are more close genomically to the holotype and are from the central slice of the range; other sequenced specimens identified as this subspecies are not included in the type series.

Type locality. USA: Utah, San Juan Co., Bears Ears National Monument, Indian Creek Canyon.

Etymology. In Latin, *centralis* (feminine *centralis*) means central, middle, or pertaining to the center. The name reflects the central distribution of this subspecies among others and is a feminine adjective.

Distribution. This is the subspecies of the Colorado Plateau, with the range almost exactly matching the Plateau limits, i.e., southeastern half of Utah, western Colorado, northern Arizona and northwestern New Mexico (Fig. 31).

Fig. 13. *Apodemia mormo centralis* **ssp. n.** type specimens in dorsal (above) and ventral (below) views: **a) holotype** ♂ NVG-20046C10 USA: Utah, San Juan Co., Bears Ears NM, Indian Creek Cyn., 21-Aug-2020, R. Hannawacker leg. [MGCL] and **b)** paratype ♀ NVG-20046C09 with the same data but 6-Sep-2019; compared with *A. mormo parva*: **c)** topotypical paratype ♂ NVG-21043H10 USA: Nevada, Eureka Co., Diamond Mts., 0.7 mi N of Eureka, 28-Aug-1984, G. T. Austin leg. [MGCL] and **d)** non-type ♀ NVG-19067C12 Utah, Sevier Co., Clear Creek Cyn., ~4 mi W of I-70 exit 17, 12-Aug-1996, M. Smith leg. [UCDC].

Apodemia (*Apodemia*) *mormo confusa* Grishin, new subspecies

https://zoobank.org/E47AF4BE-CD5E-44BD-A77F-2755FAFE294F

(Figs. 8a–c part, 8f, 10b, 14d–e, 15a–c, 26g, 30–31 part)

Definition and diagnosis. This is the subspecies of *Apodemia* (*Apodemia*) *mormo* (C. Felder & R. Felder, 1859) (type locality in USA: likely Nevada, Washoe Co.) from the western spine of the Transition Zone in Arizona. Starting this analysis, we were confused (hence the name) regarding the subspecific identity of these populations. Previously, they have been identified as *Apodemia* (*Apodemia*) *mormo autumnalis* Austin, 1998 (type locality USA: Nevada, Clark Co., Spring Mts.) (Fig. 14a–c) due to the larger size of these specimens and their fall-flying phenology. However, as discussed above, these populations are genetically distinct from *A. mormo autumnalis* and are not monophyletic with it, instead being in the clade sister to *Apodemia* (*Apodemia*) *mormo parva* Austin, 1998 (type locality USA: Nevada, Eureka Co., Diamond Mts.) in the nuclear genome trees (Fig. 8a, b). Initially, we attempted to place these populations under *A. mormo centralis* **ssp. n.** described above, but they are more similar genetically to the southeastern Arizona subspecies from the higher elevations, *A. mormo arizatra* **ssp. n.**, and are not monophyletic with *A. mormo centralis* **ssp. n**. from the Colorado Plateau. Therefore, the genetic and biogeographic evidence supports the treatment of these Transition Zone populations as a separate subspecies. This new subspecies is most similar to *A. mormo autumnalis* but differs from it by a better developed longitudinal orange streak at the base of the ventral hindwing and typically larger white spots. In females, the reddish-orange patch penetrates between and distad of the white postdiscal band on the ventral forewing, but in males, this patch terminates basad of the band. Due to its partly cryptic nature and unexplored individual variation, this subspecies is best identified by DNA, with diagnostic base pairs in the nuclear genome: cne3452.1.2:C741T, cne2409.3.10:G1329A, cne200.3.13:T45C, cne1027.1.3:A183T, cne1027.1.3:A190T, cne1894.1.2:T24T (not C), cne1894.1.2:C51C (not T), cne6600.13.5:T126T (not G), cne6600.13.5:T132T (not G), cne6600.13.5: C135C (not T); while the COI barcode may not distinguish all specimens of this subspecies from others, likely due to introgression.

Barcode sequence of the holotype. Sample NVG-17065D06, GenBank PX971413, 658 base pairs:

AACATTATATTTTATTTTTGGAATTTGAGCAGGAATAGTTGGAACCTCATTAAGATTATTAATTCGAATAGAATTAGGAACATCAGGATCTTTAATTGGTGATGATCAAATTTATAATACT
ATTGTTACAGCTCATGCTTTTATTATAATTTTTTTTATAGTTATACCTATTATAATTGGAGGATTTGGTAATTGATTAGTACCATTAATACTTGGAGCTCCGGATATAGCTTTTCCACGAA
TAAATAATATAAGATTTTGACTTTTACCCCCCTCATTATTCTTGTTAATTTCTAGAAGAATTGTAGAAAATGGAGCAGGAACAGGATGAACAGTTTATCCCCCACTTTCATCTAATATTGC
CCATGGAGGAGCTTCAGTTGATTTAGCTATTTTTTCTTTACATTTAGCTGGTATTTCTTCAATTTTAGGTGCAATTAATTTTATTACAACTATTATTAATATACGTGTTAATAATATATCT
TTTGATCAAATACCTTTATTTGTATGATCAGTAGGAATTACAGCTTTATTATTATTACTTTCATTACCTGTTTTAGCTGGAGCTATTACCATATTATTAACTGATCGTAATTTAAACACAT
CATTTTTTGATCCAGCAGGTGGAGGAGATCCAATTTTATATCAACATTTATTT

Type material. Holotype: ♂ deposited in the Colorado State University Collection, Fort Collins, CO, USA (CSUC), illustrated in Fig. 14d, bears the following four rectangular labels (first two handwritten, others printed), three white: [Ariz: | Coconino Co. | Buffalo Park | nr. Flagstaff | 21 July 2005 | R. A. Bailowitz], [on yellow | flowering | Eriogonum], [DNA sample ID: | NVG-17065D06 | c/o Nick V. Grishin], and one red [HOLOTYPE ♂ | Apodemia (Apodemia) | mormo confusa Grishin]. **Paratypes:** 8♂♂ and 1♀: USA, Arizona: Mohave Co., Hualapai Mts., K. Davenport leg.: 1♂ NVG-17068F05, 2-Oct-1988 [CSUC] (Fig. 15b); 1♂ NVG-16105E11, 17-Sep-1990 [LACM]; 1♂ NVG-17068F06, 4-Oct-1991 [CSUC] (Fig. 15c); 1♀ NVG-6902, 18-Sep-2004 (Fig. 14e); and 1♂ NVG-6901, 1-Oct-2013 and Yavapai Co.: 1♂ NVG-25025E01, 5-10 mi S of Ash Fork, 12-Sep-1975, R. Wielgus leg., on *Eriogonum wrightii* [ASUHIC]; 1♂ NVG-6900, Little Hell Canyon, 8-Sep-2007, K. Davenport leg. (Fig. 15a); and 2♂♂ (NVG-19129A05 & NVG-19129A06) AZ-260 at mi post 237, 34.5017, −111.6346, 18-Sep-2009, T. Horton leg. [THC].

Type locality. USA: Arizona, Coconino Co., Flagstaff, Buffalo Park.

Etymology. In Latin, *confusus* (feminine: *confusa*) means confused, mixed up, indistinct, or blurred; and perfectly describes the nature of this subspecies and the process of its discovery. The species epithet means easily confused with similar taxa, previously misidentified, and not clearly separable. The name is a feminine perfect passive participle in the nominative singular used as an adjective.

Distribution. This is the subspecies from the western spine of the Transition Zone in Arizona: Kingman to Globe and Flagstaff to Phoenix (Fig. 31).

Fig. 14. *Apodemia mormo autumnalis* in dorsal (left) and ventral (right) views: **a) holotype** ♂ LEP82585 USA: Nevada, Clark Co., Spring Mts., 2 rd. mi N of Red Cloud Mine, 1829 m, 31-Aug-1983, G. T. Austin leg. [MGCL]; **b)** non-type ♂ NVG-3244 USA: California, San Bernardino Co., Providence Mtns., Bonanza King Mine, 19-Sep-1972, J. Hafernik leg., genitalia NVG15011-60, [TAMU]; **c)** paratype (allotype) ♀ NVG-21043H11 with the same data as the holotype; compared with *Apodemia mormo confusa* **ssp. n.** type specimens from USA: Arizona: **d) holotype** ♂ NVG-17065D06 Coconino Co., Flagstaff, Buffalo Park, 21-Jul-2005, R. A. Bailowitz leg. [CSUC] and **e)** paratype ♀ NVG-6902 Mohave Co., Hualapai Mts., 18-Sep-2004, K. Davenport leg. Gray "F" indicates a flipped (left-right inverted) image.

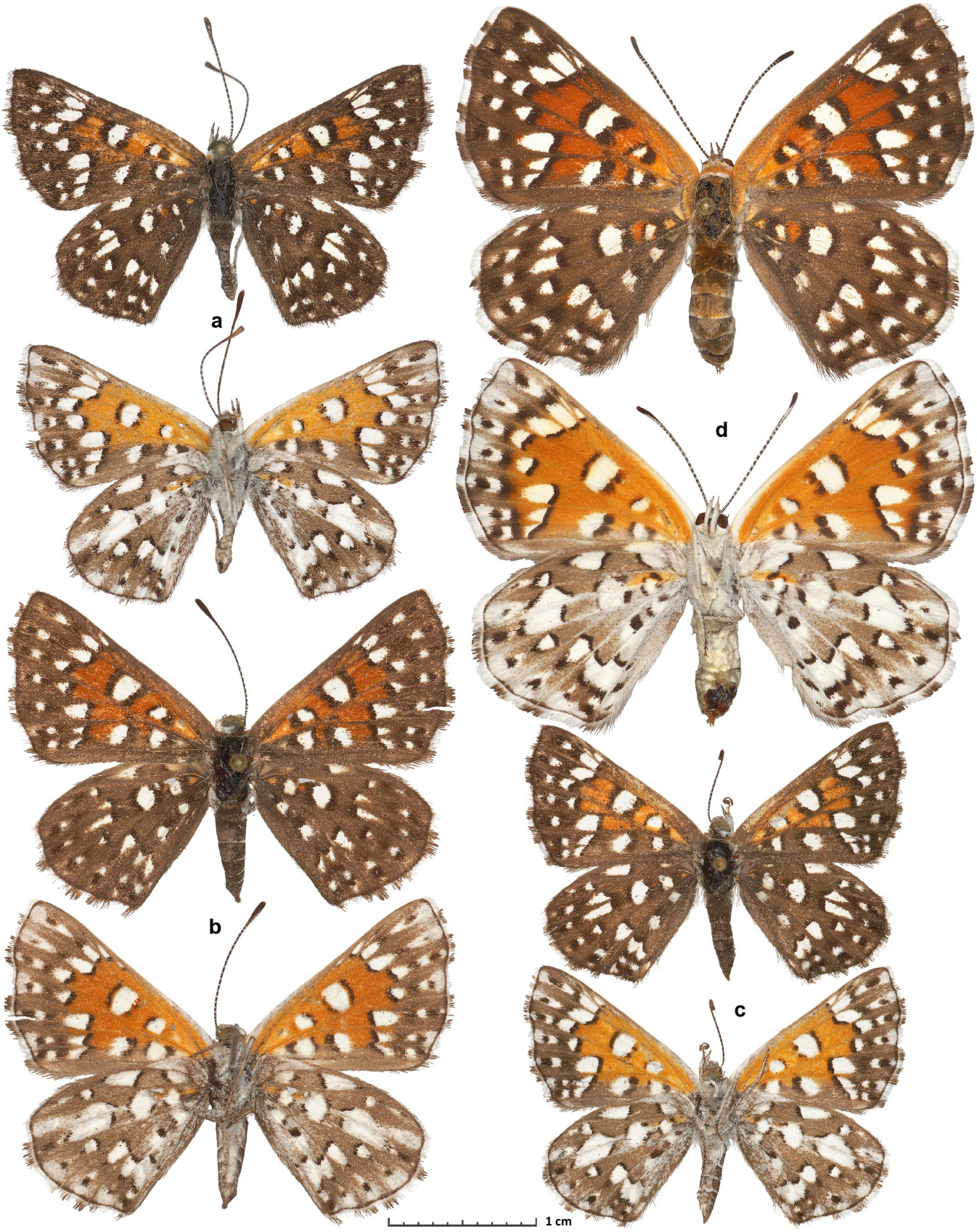

Fig. 15. *Apodemia mormo confusa* **ssp. n.** paratypes from USA: Arizona, K. Davenport leg. in dorsal (above) and ventral (below) views: **a)** ♂ NVG-6900 Yavapai Co., Little Hell Canyon, 8-Sep-2007 and **b–c)** Mohave Co., Hualapai Mts., [CSUC]: **b)** ♂ NVG-17068F05, 2-Oct-1988 and **c)** ♂ NVG-17068F06, 4-Oct-1991; compared with **d)** *Apodemia mormo centralis* **ssp. n.** non-type ♀ NVG-19067C10 USA: Arizona, Mohave Co., AZ-389, 1.7 mi E of Pipe Springs, 15-Aug-1987, M. Smith leg. [UCDC].

Remarks. A male NVG-24066H09 from Arizona, Gila Co., Salome Creek, W of McFadden Peak, nr. J. R. Ranch, 24–25-Sep-1988, J. P. Brock leg. [MGCL] (Fig. 10b) is phenotypically similar to this new subspecies, and we tentatively identify it as such. However, this specimen is genomically similar to *A. mormo arizatra* **ssp. n.**, and therefore, we exclude it from the type series. Furthermore, we note that the Hualapai Mountains population (Mohave Co., Arizona) belongs to this new subspecies and not to *A. mormo autumnalis* despite its geographic proximity to the type locality of the latter.

Lectotype designation for *Apodemia mormo deserti* W. Barnes & McDunnough, 1918

Apodemia mormo deserti W. Barnes & McDunnough, 1918, previously treated as a valid subspecies of *Apodemia mejicanus* (Behr, 1865) (type locality Mexico: Sinaloa, Sierra Madre, nr. Mazatlán, possibly in error) and which we here propose to regard as a species-level taxon, was described from three [syn]"types" (1♂ and 2♀♀) collected by G. Field in La Puerta Valley, southern California, on July 11th (Barnes and McDunnough 1918). We located the only male syntype in the USNM collection. It matches the original description, is the specimen shown on Plate XII, Fig. 1 [photograph in Barnes and McDunnough (1918)], and agrees with the current usage of this name. To define this prevailing-usage taxonomic identity of the name *A. mormo deserti* objectively, N.V.G. hereby designates this syntype in the USNM collection, a male with the following three rectangular labels (1st white, 2nd white with red frames and lines, 3rd green; 2nd handwritten, others printed with handwritten text shown in italics): [Geo. H. Field | LaPuerta Valley | *July '11* Cal.], [A. mormo | v. deserti | Type ♂ B&M^{c}D], and [Photograph | Pl. *12* No. *1*], as the **lectotype** of *Apodemia mormo deserti* W. Barnes & McDunnough, 1918. The lectotype is missing its abdomen, left antenna, the anterior part of the left forewing from about the mid-costa to apex, and the right forewing apex; its head is tilted to the left and the left hindwing is torn near its middle. Images of this specimen photographed by Gerardo Lamas before most of this damage occurred (with abdomen, left forewing, and left antenna intact) are shown on the Butterflies of America website (Warren et al. 2024). According to the label of the lectotype, the type locality of *A. mormo deserti* is USA: California, San Diego Co., La Puerta Valley, which is a historical name for what is currently called Mason Valley to the east of the Cuyamaca Mountains. The lectotype was possibly collected on the old Mason's ranch, which was approximately 5 mi west of the historical Vallecito (Stage) Station, around GPS 32.98, −116.43. The COI barcode sequence of the lectotype, sample NVG-17102D01, GenBank PX971414, 658 base pairs is:

AACATTATATTTTATTTTTGGAATTTGAGCAGGAATAGTTGGAACTTCACTAAGATTATTAATTCGAATAGAATTAGGAACATCTGGATCTTTAATTGGTGATGATCAAATTTATAATACT
ATTGTAACAGCTCATGCTTTTATTATAATTTTTTTTATAGTTATACCTATTATAATTGGAGGATTTGGTAATTGATTAGTACCATTAATACTTGGAGCCCCAGATATAGCTTTTCCACGAA
TAAATAATATAAGATTTTGACTTTTACCCCCCTCATTATTTTTATTAATTTCTAGAAGAATTGTGGAAAATGGAGCAGGAACAGGATGAACAGTTTATCCCCCACTTTCATCCAATATTGC
CCATGGAGGAGCTTCTGTTGATTTAGCTATTTTTTCTTTACATTTAGCTGGTATTTCTTCAATTTTAGGTGCAATTAATTTTATTACAACTATTATTAATATACGTGTCAATAACATATCT
TTTGATCAAATACCTTTATTTGTATGATCAGTAGGAATTACAGCCTTATTACTCTTACTTTCATTACCTGTTTTAGCTGGAGCTATTACTATATTATTAACTGATCGTAATTTAAATACAT
CATTTTTTGACCCAGCAGGTGGAGGAGATCCAATTTTATATCAACATTTATTT

Apodemia (*Apodemia*) *deserti* W. Barnes & McDunnough, 1918, stat. nov. and *Apodemia* (*Apodemia*) *pueblo* J. Scott, 1998, stat. nov. are species distinct from *Apodemia* (*Apodemia*) *mejicanus* (Behr, 1865)

Currently regarded as subspecies of *Apodemia* (*Apodemia*) *mejicanus* (Behr, 1865) (type locality Mexico: Sonora, 5 mi N of San Carlos), and originally proposed as *Apodemia mormo deserti* W. Barnes & McDunnough, 1918 (type locality in USA: California, San Diego Co., Mason Valley) and *Apodemia mormo pueblo* J. Scott, 1998 (type locality in USA: Colorado, El Paso Co., S of Security), the latter two taxa are genetically differentiated from the former and each other at the species level (Fig. 30), forming distinct and strongly supported clades in the nuclear genome tree. F_{st}/G_{min} values computed on the Z chromosome genes for pairs of these taxa are: 0.29/0.8% (*mejicanus* vs. *deserti*); 0.34/0.3% (*mejicanus* vs. *pueblo*); and 0.35/1.1% (*deserti* vs. *pueblo*), suggesting their distinction at the species level. When combined, the three taxa are likely paraphyletic with respect to *Apodemia* (*Apodemia*) *duryi* (W. H. Edwards, 1882) (type locality USA: New Mexico, Doña Ana Co., ca. 5 mi E of Mesilla), which is similar to *A. mejicanus* in having greenish-yellow eyes, while the other two taxa possess greenish-gray eyes

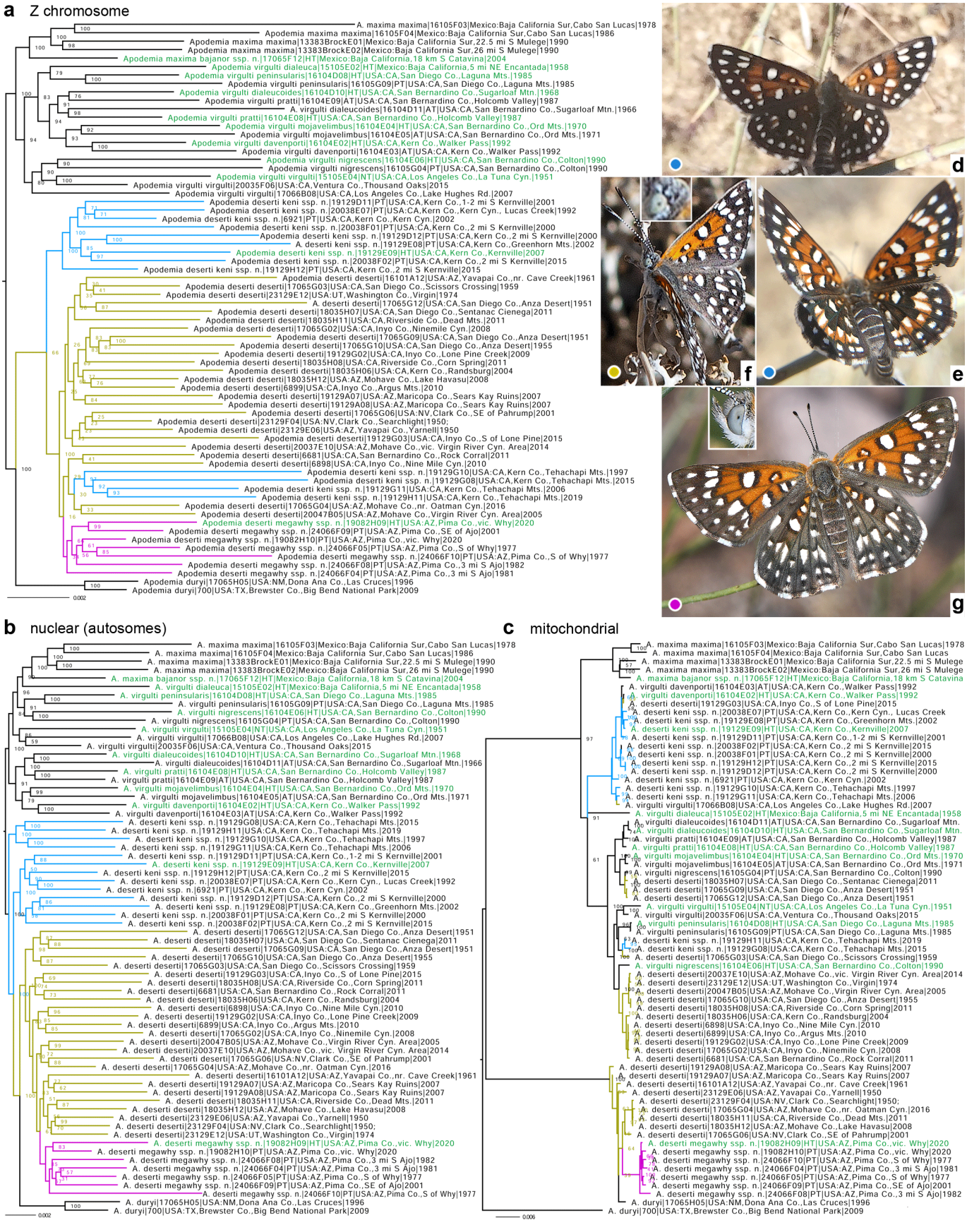

Fig. 16 (legend continues on the next page). Phylogenetic trees of selected *A. mormo* group taxa focusing on *A. deserti* **stat. nov.** constructed from protein-coding regions in: **a)** the Z chromosome, based on 322,803 positions, **b)** the nuclear genome (autosomes), based on 4,622,655 positions, and **c)** the mitochondrial genome; and **d–g)** iNaturalist observations (color of the dot in the lower left of each image corresponds to the color of this taxon in the trees): **d–e)** *A. deserti keni* **ssp. n.** (possible), in

copula, observation No. 15149493 USA: California, Kern Co., Tehachapi Mts. NW of Rosamond, GPS 34.9778, −118.3871, 7-May-2018, photographed by Marcus Tamura (no rights reserved), photos: **d)** 22646119 ♂ and **e)** 22646070 ♀; **f)** *A. deserti deserti* **stat. nov.** observation No. 85865959 (magnified view of the head in inset), USA: California, Kern Co., Red Rock Canyon State Park, GPS 35.3734, −117.9888, 16-Apr-2021 © Jeremiah Degenhardt; **g)** *A. deserti megawhy* **ssp. n.**, observation No. 140682836 USA Arizona, Pima Co., Organ Pipe Cactus NM, Alamo Canyon, 26-Oct-2022 © Ken Kertell; inset shows a magnified view of the head, observation No. 140683068, with the same data, but may not be the same individual; images are color-corrected, brightened, rotated, and cropped, CC BY-NC 4.0 https://creativecommons.org/licenses/by-nc/4.0/. In the trees, primary type specimens are labeled in green font and clades of focus are colored: *A. deserti keni* **ssp. n.** (blue), *A. deserti deserti* **stat. nov.** (olive), and *A. deserti megawhy* **ssp. n.** (dark magenta). Other clades are shown in black. Ultrafast bootstrap (Hoang et al. 2018) values are placed at nodes.

(Fig. 29). Furthermore, *Krameria* spp. are likely caterpillar foodplants of *A. mejicanus* (Jim P. Brock, pers. comm.), while *deserti* and *pueblo* use *Eriogonum* spp. (Pratt and Ballmer 1991; Scott 1998, 2017). Therefore, we propose to treat *Apodemia* (*Apodemia*) *deserti* W. Barnes & McDunnough, 1918, **stat. nov.** and *Apodemia* (*Apodemia*) *pueblo* J. Scott, 1998, **stat. nov.** as species-level taxa distinct from *A. mejicanus*. For additional discussion, see the section dealing with species delimitation below.

Apodemia (*Apodemia*) *deserti megawhy* Grishin, new subspecies

https://zoobank.org/CE3E6A6B-5CE1-4FFA-90B3-54BD866B23AE

(Figs. 16a–c part, 16g, 17a–b, 21 part, 30–31 part)

Definition and diagnosis. Genomic analysis reveals that specimens from south-central Arizona identified as *Apodemia* (*Apodemia*) *deserti* W. Barnes & McDunnough, 1918, **stat. nov.** (type locality in USA: California, San Diego Co., Mason Valley) indeed fall within this species but are genetically differentiated from the nominotypical populations at the subspecies level, forming a distinct clade in the nuclear genome tree (Fig. 16a, b magenta), and possessing a unique mitochondrial genome haplotype (Fig. 16c magenta). Therefore, these populations represent a new subspecies. This new subspecies (Fig. 16g) is most similar to *A. deserti* (Figs. 16f) in having greenish-gray eyes (Fig. 29d), but differs from it by being larger and darker [nominotypical populations have a grayish-brown rather than blackish ground color] (Fig. 17a, b vs. c, d), thus resembling *Apodemia* (*Apodemia*) *mormo* (C. Felder & R. Felder, 1859) (type locality in USA: likely Nevada, Washoe Co.), which differs by its greenish-yellow eyes (Fig. 29c). Due to relatively unexplored individual variation, this subspecies is best identified by DNA, with diagnostic base pairs in the nuclear genome: cne4618.8.1:T117G, cne4618.8.1:T294C, cne4618.5.4:T10G, cne4618.5.4:A33T, cne555.4.2:A510G; but the COI barcode may not distinguish it from other taxa.

Barcode sequence of the holotype. Sample NVG-19082H09, GenBank PX971415, 658 base pairs:

AACATTATATTTTATTTTTGGAATTTGAGCAGGAATAGTTGGAACCTCATTAAGATTATTAATTCGAATAGAATTAGGAACATCAGGATCTTTAATTGGTGATGATCAAATTTATAATACT
ATTGTTACAGCTCATGCTTTTATTATAATTTTTTTTTATAGTTATACCTATTATAATTGGAGGATTTGGTAATTGATTAGTACCATTAATACTTGGAGCTCCGGATATAGCTTTTCCACGAA
TAAATAATATAAGATTTTGACTTTTACCCCCCTCATTATTCTTATTAATTTCTAGAAGAATTGTAGAAAATGGAGCAGGAACAGGATGAACAGTTTATCCCCCACTTTCATCTAATATTGC
CCATGGAGGAGCTTCAGTTGATTTAGCTATTTTTTCTTTACATTTAGCTGGTATTTCTTCAATTTTAGGTGCAATTAATTTTATTACAACTATTATTAATATACGTGTTAATAATATATCT
TTTGATCAAATACCTTTATTTGTATGATCAGTAGGAATTACAGCTTTATTATTATTACTCTCATTACCTGTTTTAGCTGGAGCTATTACCATATTATTAACTGATCGTAATTTAAACACAT
CATTTTTTGACCCAGCAGGTGGAGGAGATCCAATTTTATATCAACATTTATTT

Type material. Holotype: ♂ deposited in the McGuire Center for Lepidoptera and Biodiversity collection, Gainesville, FL, USA (MGCL), illustrated in Fig. 17a, bears the following three printed rectangular labels, two white: [Sells | 04-V-20 AZ | Pima Co. | Lat 32 10' 35" N | Long 112 11' 37" W | Mark Walker leg.], [DNA sample ID: | NVG-19082H09 | c/o Nick V. Grishin], and one red [HOLOTYPE ♂ | Apodemia (Apodemia) | deserti megawhy Grishin]. **Paratypes:** 4♂♂ and 5♀♀: USA, Arizona, Pima Co. [MGCL]: 1♀ NVG-19082H10 the same data as the holotype (Fig. 17b); 3 mi S of Ajo, Locomotive Peak, 10-Apr-1982, C. Hageman leg.: 1♂ NVG-24066F08 and 1♀ NVG-24066F04; SE of Ajo, Bates Well Rd., 1-May-2001, K. Hansen leg.: 2♂♂ (NVG-24066F07 & NVG-24066F09) and 2♀♀ (NVG-24066F02 & NVG-24066F03); and S of Why on AZ-85, 21-Sep-1977, D. L. Bauer leg.: 1♂ NVG-24066F10 and 1♀ NVG-24066F05.

Type locality. USA: Arizona, Pima Co., between Sells and Why, just west of Maish Vaya, near mile post 87 on AZ-86, GPS 32.1764, −112.1936. This is our southeasternmost record of *A. deserti* **stat. nov**.

Fig. 17. *Apodemia deserti megawhy* **ssp. n.** type specimens from USA: Arizona, Pima Co., between Sells and Why, just west of Maish Vaya, nr. mile post 87 on AZ-86, 32.1764, −112.1936, M. Walker leg., 4-May-2020, in dorsal (above) and ventral (below) views: **a) holotype** ♂ NVG-19082H09 and **b)** paratype ♀ NVG-19082H10; compared with *A. deserti deserti* **stat. nov.** non-type specimens from the general vicinity of the type locality in USA: California, San Diego Co., Anza Desert, R. E. Stanford leg. [CSUC]: **c)** ♂ NVG-23129F02 Sentenac Canyon, 14-Oct-1951 and **d)** ♀ NVG-17065G03 Scissors Crossing, 19-Sep-1959.

Etymology. The name reflects the large size (*mega*-) of this subspecies and its type locality near the town of Why, Arizona. It also implies "a huge unanswered why" or "big questions" about this subspecies. Why *A. deserti* and not *A. mormo*? Why there, around Why? Why is it geographically isolated from other populations of *Apodemia*? The name is treated as a noun in apposition.

Distribution. Currently known from south-central Arizona (western Pima Co.) in and around Organ Pipe Cactus National Monument, in the vicinity and south of Ajo and Why (Figs. 21, 31).

Apodemia (*Apodemia*) *deserti keni* Grishin, new subspecies

https://zoobank.org/6E7D5CA6-F81F-44D5-B98E-C2D47B1F957A

(Figs. 16a–c part, 16d–e, 18, 19a, 21 part, 30–31 part)

Definition and diagnosis. Ken Davenport discovered double-brooded populations of the *Apodemia mormo* group taxon in the mountains to the east of Bakersfield in Kern Co., California, that he was tentatively associating with *Apodemia* (*Apodemia*) *virgulti* (Behr, 1865) (type locality in USA: California, Los Angeles Co., Verdugo Mts., La Tuna Canyon) due to similarities in wing patterns. This double-brooded taxon is found around *Eriogonum wrightii* Torr. ex Benth. and *Eriogonum nudum* Dougl. ex Benth., which are its likely caterpillar foodplants. The subspecies of *A. virgulti* in this region, *Apodemia* (*Apodemia*) *virgulti davenporti* J. Emmel, T. Emmel & Pratt, 1998 (type locality USA: California, Kern Co., Walker Pass), is single brooded, flying in spring. Genomic analysis of the double-brooded entity reveals that it is not *A. virgulti* but is closely related to *Apodemia* (*Apodemia*) *deserti* W. Barnes & McDunnough, 1918, **stat. nov.** (type locality in USA: California, San Diego Co., Mason Valley) in the Z chromosome (Fig. 16a blue and olive). However, it might have received introgression from *A. virgulti*, because it is positioned closer toward *A. virgulti* ("pulled away" from *A. deserti* toward the base of the tree) in the nuclear genome tree (Fig. 16b). Due to its phenotypic and genetic distinction, we regard this double-brooded taxon as a new subspecies and place it in *A. deserti* due to the phylogenetic affinity in the Z chromosome. Being a species distinct from *A. virgulti*, possible sympatry between this new subspecies of *A. deserti* and *A. virgulti davenporti* can thus be explained.

The new subspecies (Figs. 16d, e, 18, 19a) differs from other taxa in the region in the following ways. From the nominotypical *A. deserti* (Figs. 16f, 19b, c), by frequently having more extensive reddish-orange coloration on the dorsal side of wings, in particular the postdiscal reddish band on the hindwing (Fig. 18a, c) that other populations of *A. deserti* lack; darker individuals of the new subspecies (Figs. 18b, d, 19a) are more similar to typical *A. deserti*, but they have a darker-brown ground color, less into gray tones typical of *A. deserti*, redder patches compared to yellower in *A. deserti*, and usually lack a well-developed longitudinal orange streak at the base of the ventral hindwing, which is prominently developed in *A. deserti*. From *Apodemia* (*Apodemia*) *mormo cythera* (W. H. Edwards, 1873) (type locality USA: California, Inyo Co., 9 mi W of Lone Pine), by browner-red tones compared to the more orange of *A. mormo cythera* (Fig. 28b), by prominent white spots in the postdiscal forewing band in cells M_2-M_3 and M_3-CuA_1, which *A. mormo cythera* usually lacks (or has smaller spots), and by developed pale spots inside the reddish band in the dorsal hindwing cells M_1-M_2 and M_2-M_3, which *A. mormo cythera* lacks (or has diffuse spots). From *A. virgulti davenporti* (Fig. 19d, 28a), by less saturated reddish-orange coloration; typically less diffuse white spots in the orange postdiscal band on the dorsal hindwing; in specimens with the orange hindwing band, by more extensive orange patches in cell CuA_2-1A+2A on the dorsal forewing; and likely caterpillar foodplant being *E. wrightii* and *E. nudum* [*E. fasciculatum* Benth. for *A. virgulti davenporti*]. The darker individuals of the new subspecies with uniformly blackish-brown white-spotted hindwing can be confused with neither *A. mormo cythera* nor *A. virgulti davenporti*, both of which have a reddish-orange band on the dorsal hindwing (except rare melanic forms that are darker overall, even on the forewing). Eye color of live individuals of the new subspecies remains unknown. Due to extensive individual variation, this subspecies can be unambiguously identified by DNA, with diagnostic base pairs in the nuclear genome: cne7419.2.7:C60T, cne7419.2.7:A135G, cne1095.9.8:T114C, cne3423.1.13:T98A, cne1493.15.3:T126A; while the COI barcode may not distinguish all specimens of this subspecies from others, likely due to introgression.

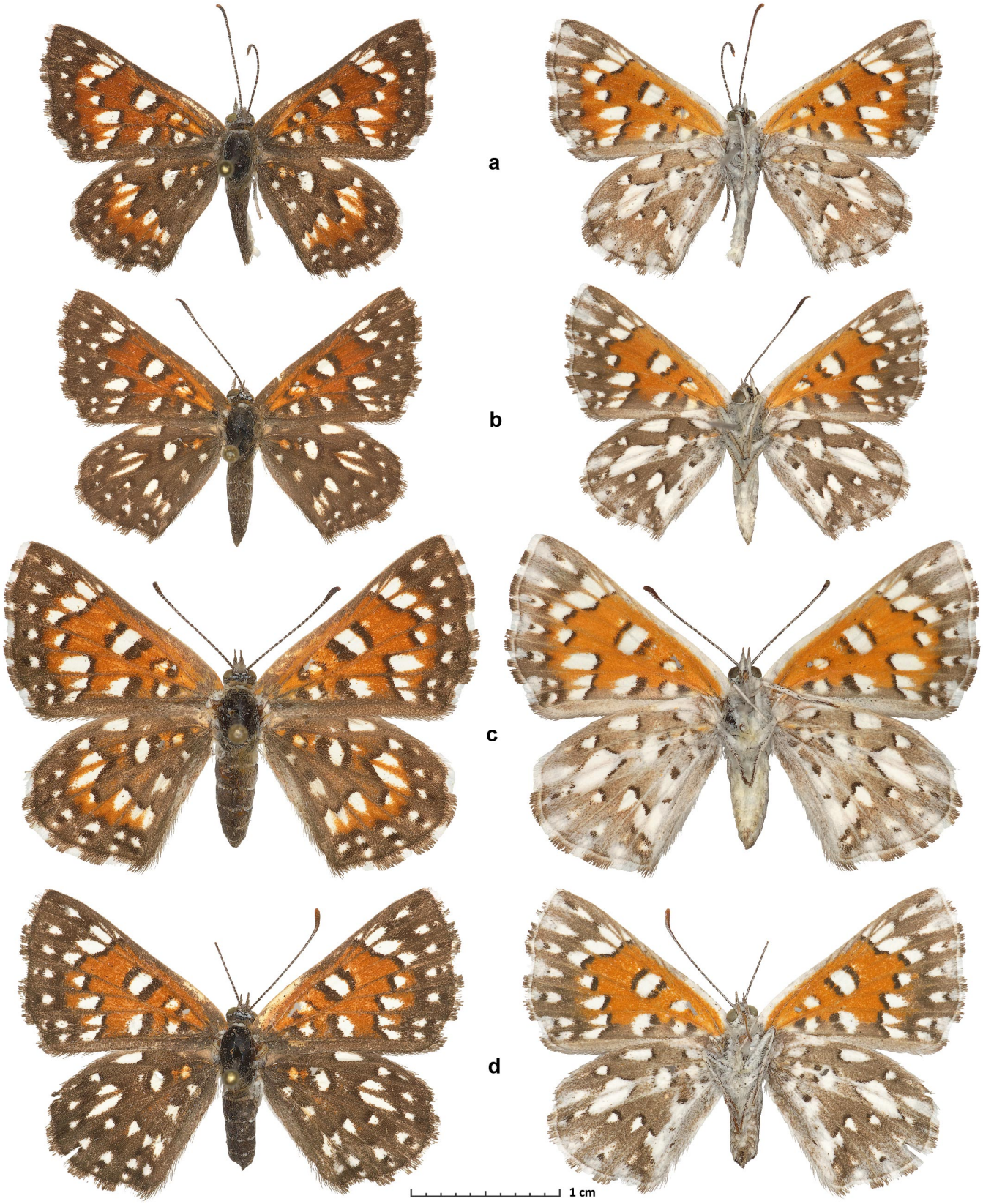

Fig. 18. *Apodemia deserti keni* **ssp. n.** type specimens from USA: California, Kern Co., K. Davenport leg. in dorsal (left) and ventral (right) views: **a) holotype** ♂ NVG-19129E09 Kernville, 11-Jun-2007 [MGCL] and paratypes: **b)** ♂ NVG-19129E11 SE of Kernville, E of Lake Isabella, May-2000 (assoc. *Eriogonum wrightii*); **c)** ♀ NVG-19129D12, 2 mi S of Kernville, 27-May-2000 and **d)** ♀ NVG-19129H12, 2 mi S of Kernville, 14-May-2015.

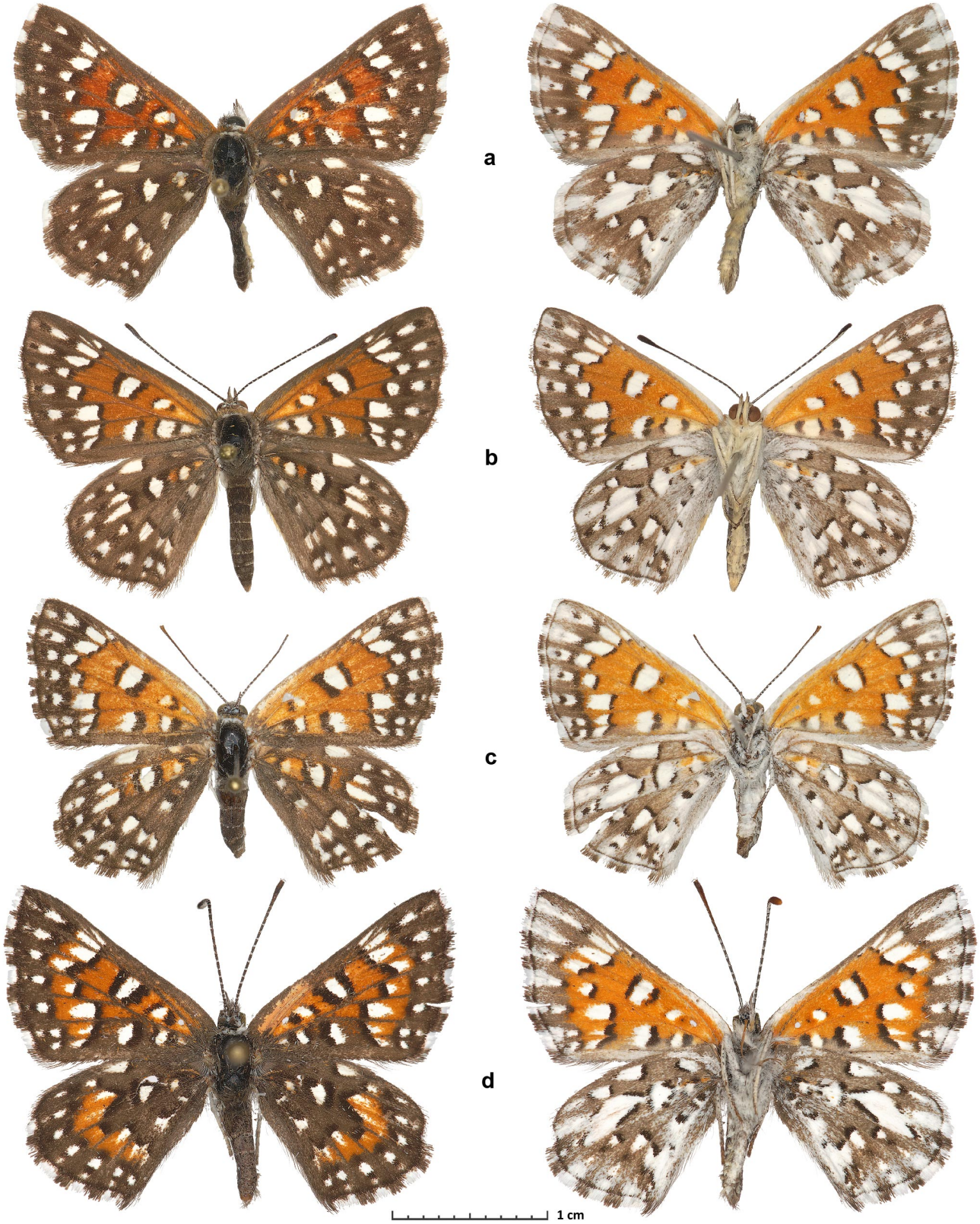

Fig. 19. Comparison of *Apodemia mormo* group spring-flying taxa from USA: California, Southern Sierra Nevada region, in dorsal (left) and ventral (right) views: **a)** *A. deserti keni* **ssp. n.** paratype ♂ NVG-19129D11, Kern Co., 1–2 mi S of Kernville, 20-May-2001, K. Davenport leg. and non-type specimens: **b–c)** *A. deserti deserti* **stat. nov.**: **b)** ♂ NVG-18035H06 Kern Co., Randsburg, 19-Apr-2004, M. Walker leg. and **c)** ♀ NVG-19129G03 Inyo Co., S of Lone Pine, Lubken Canyon, 22-Apr-2015, K. Davenport leg. and **d)** *A. virgulti davenporti* ♂ NVG-6926 Kern Co., E side Piute Mts., 3 mi W of Sageland, 16-Apr-2010, K. Davenport leg.

Barcode sequence of the holotype. Sample NVG-19129E09, GenBank PX971416, 658 base pairs:

AACATTATATTTTATTTTTGGAATTTGAGCAGGAATAGTTGGAACTTCACTAAGATTATTAATTCGAATAGAATTAGGAACATCTGGATCTTTAATTGGTGATGATCAAATTTATAATACT
ATTGTAACAGCTCATGCTTTTATTATAATTTTTTTTATAGTTATACCTATTATAATTGGAGGATTTGGTAATTGATTAGTACCATTAATACTTGGAGCCCCAGATATAGCTTTTCCACGAA
TAAATAATATAAGATTTTGACTTTTACCCCCTTCATTATTTTTATTAATTTCTAGAAGAATTGTGGAAAATGGAGCAGGAACAGGATGAACAGTTTATCCCCCACTTTCATCCAATATTGC
CCATGGAGGAGCTTCTGTTGATTTAGCTATTTTTTCTTTACATTTAGCTGGTATTTCTTCAATTTTAGGTGCAATTAATTTTATTACAACTATTATTAATATACGTGTCAATAACATATCT
TTTGATCAAATACCTTTATTTGTGTGATCAGTAGGAATTACAGCCTTATTACTATTACTTTCATTACCTGTTTTAGCTGGAGCTATTACTATATTATTAACTGATCGTAATTTAAATACAT
CATTTTTTGATCCAGCAGGTGGAGGAGATCCAATTTTATATCAACATTTATTT

Type material. Holotype: ♂ deposited in the McGuire Center for Lepidoptera and Biodiversity collection, Gainesville, FL, USA (MGCL), illustrated in Fig. 18a, bears the following four rectangular labels (first three handprinted, others printed), three white: [KERNVILLE | KERN CO, CALIF | 11 JUNE 2007], [leg. KEN | DAVENPORT], [DNA sample ID: | NVG-19129E09 | c/o Nick V. Grishin], and one red [HOLOTYPE ♂ | Apodemia (Apodemia) | deserti keni Grishin]. **Paratypes:** 14♂♂ and 9♀♀: USA, California, Kern Co., K. Davenport leg.: 1♂ NVG-20011B01 Kernville, 6-Jun-1999; 1♂ NVG-20011A12 S of Kernville, 28-May-2019; 1♂ NVG-20011C05 SE of Kernville, Sierra Way, 20-May-2001; 4♂♂ (NVG-20011A08, NVG-20011A10, NVG-20011A11 & NVG-20011C04) 1–2 mi S of Kernville, 20-May-2000; 2♂♂ (NVG-19129D11 (Fig. 19a) & NVG-19129E07) 1–2 mi S of Kernville, 20-May-2001; 2 mi S of Kernville: 1♀ NVG-19129E12, 6-Jun-1999; 3♀♀ (NVG-19129E10, NVG-19129D12 (Fig. 18c) & NVG-20038F01) 27-May-2000; 1♀ NVG-20011C07, 22-May-2002; 1♀ NVG-19129H12 (Fig. 18d), 14-May-2015; and 2♀♀ (NVG-20011C03 & NVG-20038F02) 14-May-2015; 1♂ NVG-20011A09 Lake Isabella, Sierra Way, 20-Sep-2008; 1♂ NVG-20011C06 3 mi S Kernville, E side of Lake Isabella, 20-May-2001; 1♂ NVG-19129E11 SE of Kernville, E of Lake Isabella, May-2000 (Fig. 18b); 1♀ NVG-19129E08 Greenhorn Mts., Sawmill Rd., 2–3 mi W of CA-155, 3500–4000 ft, 2-Jun-2002; and Kern Canyon, Lucas Creek: 1♂ NVG-20038E07 9-Sep-1992 and 1♂ NVG-6921, 31-May-2002. Although we currently identify *A. deserti* specimens from the eastern parts of Tehachapi Mountains (Kern Co., CA) as this subspecies, we do not include them in the type series, because they differ genomically from the population in the vicinity of the type locality and are not monophyletic with them in the nuclear genome trees (Fig. 16a, b).

Type locality. USA: California, Kern Co., Kernville.

Etymology. The name honors Ken Davenport (Bakersfield, CA), collector of the type series, who has conducted extensive field research on *Apodemia* in California and beyond. The name is a noun in the genitive case. Due to Ken's keen interest in *Apodemia* and dedicated studies of its species, subspecies, and populations, there is already an *Apodemia* subspecies named after him with the epithet derived from his last name: *A. virgulti davenporti*, also with the type locality in Kern County, CA. Curiously, the new subspecies *keni* (Fig. 18a) may be most similar in appearance to *davenporti* in having more strongly developed white spots, a character particularly noticeable on the dorsal hindwing (Fig. 19d).

A mnemonic for the two names is that the type locality of *keni* **ssp. n.** is to the west of *davenporti*, ordering them west to east, left to right, as in Ken Davenport. Also, *deserti* is alphabetically before *virgulti*, and ordering these subspecies by the species name we get *keni* **ssp. n.** (*deserti*) before *davenporti* (*virgulti*), which conversely offers an association mnemonic between subspecies and corresponding species names: Ken(*i*) Davenport(*i*) → *deserti* then *virgulti*. Ken discovered that the new subspecies is double-brooded in contrast to the single-brooded and sympatric *A. virgulti davenporti*. The double-brooded taxon is *deserti*, starting with the same letter, and its name *keni* contains two consonants and two vowels. The single-brooded *davenporti* is a subspecies of *virgulti*, and *virg-* is also the root of the Latin word *virgo*, originally meaning unmarried, i.e., single (although some other subspecies of *A. virgulti*, including the nominotypical, are multi-brooded). Finally, the similarity of the word *keni* with the word Kern hints at the type locality of *A. deserti keni* **ssp. n.** in Kernville, Kern County.

Ken's meticulous and sustained studies of Californian butterflies, together with his comprehensive compilation of butterfly records, have profoundly enriched our knowledge. Among his many contributions, Ken, together with James A. Scott, discovered a new species of *Pholisora* Scudder, 1872, *Pholisora crestar* J. Scott & Davenport, 2017, and, together with John and Thomas Emmel, a new subspecies of *Cercyonis* Scudder, 1875, *C. pegala australosierra* J. Emmel, T. Emmel & K. Davenport, 2008. He generously and openly shares his extensive knowledge with everyone and regularly donates numerous specimens from his research collection to several museums across the United States. These specimens are

of excellent DNA quality and have facilitated a number of research projects, including those in our laboratory. Ken guided us through the complexities of Californian butterfly diversity, highlighting key questions and problems that merit further investigation, and he contributed many significant specimens specifically for genomic sequencing in our lab. We are deeply grateful to Ken for his kindness, generosity, and wisdom, and we take pleasure in naming this new subspecies after him.

Distribution. Currently known from the mountain region to the east of Bakersfield in Kern Co., California: from Kernville to south of Tehachapi (Figs. 21, 31).

Apodemia (*Apodemia*) *apache* Grishin, new species

https://zoobank.org/95BFD8F5-3AF6-4C7F-823D-444A7DA2D6AF

(Figs. 20a–c part, 20e, 21 part, 22a–b, 26b, 29e, 30–31 part)

Definition and diagnosis. Genomic analysis reveals that specimens from the White Mountains in Arizona, together with the surrounding populations in the region that we initially associated with *Apodemia* (*Apodemia*) *deserti* W. Barnes & McDunnough, 1918, **stat. nov.** (type locality in USA: California, San Diego Co., Mason Valley) are not monophyletic with it and instead form a prominent nuclear genome clade in the neighborhood of *Apodemia* (*Apodemia*) *pueblo* J. Scott, 1998, **stat. nov.** (type locality in USA: Colorado, El Paso Co., S of Security) and *Apodemia* (*Apodemia*) *duryi* (W. H. Edwards, 1882) (type locality USA: New Mexico, Doña Ana Co., ca. 5 mi E of Mesilla) (Fig. 20a, b), and therefore represent a new species. The range of this new species, together with *A. pueblo* **stat. nov.** overlaps with the range of its possible caterpillar foodplant *Eriogonum jamesii* Benth. (Scott 1998, 2017), while the range of phenotypically similar *A. deserti* **stat. nov.** overlaps with the range of its foodplant *Eriogonum inflatum* Torr. (Pratt and Ballmer 1991) (Fig. 21), agreeing with our genomic identification of these specimens and distinction of this new species from *A. deserti* **stat. nov.** (although species of the *A. mormo* group may not be as strictly foodplant-specific). This new species differs from its relatives by the following combination of characters: typically with a dark brown white-spotted dorsal hindwing, which has reddish scales between the white postdiscal spots in cells M_1-M_2 and M_2-M_3 and could develop a reddish-orange postdiscal band in some specimens; dorsal forewing with a reddish-orange central patch cut by dark-brown veins; ventrally with a more weakly developed and narrower longitudinal orange ray near the base of the ventral hindwing [usually broader and more prominent in *A. deserti* **stat. nov.**]; orange scaling on the ventral forewing protrudes between and distad of the postdiscal white spots and typically fully surrounds the white spot in cell CuA_1-CuA_2 [usually brown distad in *A. deserti* **stat. nov.**]; and the eyes are greenish-gray. Due to its cryptic nature and poorly known individual variation, this species is best identified by DNA, with diagnostic base pairs in the nuclear genome: cne1153.6.1:G306T, cne1738.1.6:A465G, cne1738.1.2:A174G, cne911.5.2:C872T, cne911.5.2:T875C, cne21.1.4:T60T (not C), cne6257.6.7:C147C (not T), cne6528.4.4:G264G (not A), cne1172.14.9:G45G (not T), cne2604.1.4:C36C (not T), cne3772.13.1:C39C (not A), cne254675.12.8:A78A (not T), cne254675.12.8:G421G (not A), cne85.8.8:T141T (not G), cne85.8.8:C177C (not T); while the COI barcode may not distinguish all specimens of this subspecies from others, likely due to introgression.

Barcode sequence of the holotype. Sample NVG-24066G11, GenBank PX971417, 658 base pairs:

AACATTATATTTTATTTTTGGAATTTGAGCAGGAATAGTTGGAACCTCATTAAGATTATTAATTCGAATAGAATTAGGAACATCAGGATCTTTAATTGGTGATGATCAAATTTATAATACT
ATTGTTACAGCTCATGCTTTCATTATAATTTTTTTTATAGTTATACCTATTATAATTGGAGGATTTGGTAATTGATTAGTGCCATTAATACTTGGAGCTCCGGATATAGCTTTTCCACGAA
TAAATAATATAAGATTTTGACTTTTACCCCCCCTCATTATTCTTATTAATTTCTAGAAGAATTGTAGAAAATGGAGCGGGAACAGGATGAACAGTTTATCCCCCACTTTCATCTAATATTGC
CCATGGAGGAGCTTCAGTTGATTTAGCTATTTTTTCTTTACATTTAGCTGGTATTTCTTCAATTTTAGGTGCAATTAATTTTATTACAACTATTATTAATATACGTGTTAATAATATATCT
TTTGATCAAATACCTTTATTTGTATGATCAGTAGGAATTACAGCTTTATTATTATTACTCTCATTACCTGTTTTAGCTGGAGCTATTACCATATTATTAACTGATCGTAATTTAAACACAT
CATTTTTTGATCCAGCAGGTGGAGGAGATCCAATTTTATATCAACATTTATTT

Type material. Holotype: ♂ deposited in the McGuire Center for Lepidoptera and Biodiversity collection, Gainesville, FL, USA (MGCL), illustrated in Fig. 22a, bears the following five labels (1st handwritten, others printed; 3rd circular, others rectangular; 3rd yellow, 5th red, others white): [Az Apach. Co. | rte 60, 8 mi W | Greens Peak | rd. 4 VI 88 | DDM], [G T Austin colln | MGCL Acc. | 2004-5], ( ) no text on this label, [DNA sample ID: | NVG-24066G11 | c/o Nick V. Grishin], and [HOLOTYPE ♂ | Apodemia (Apodemia) | apache Grishin]. The holotype was collected by Doug D. Mullins. **Paratypes:** 3♂♂ and 2♀♀: USA, Arizona, Apache Co. [MGCL]: 1♂ NVG-24066G10 & 1♀ NVG-24066G12 the same

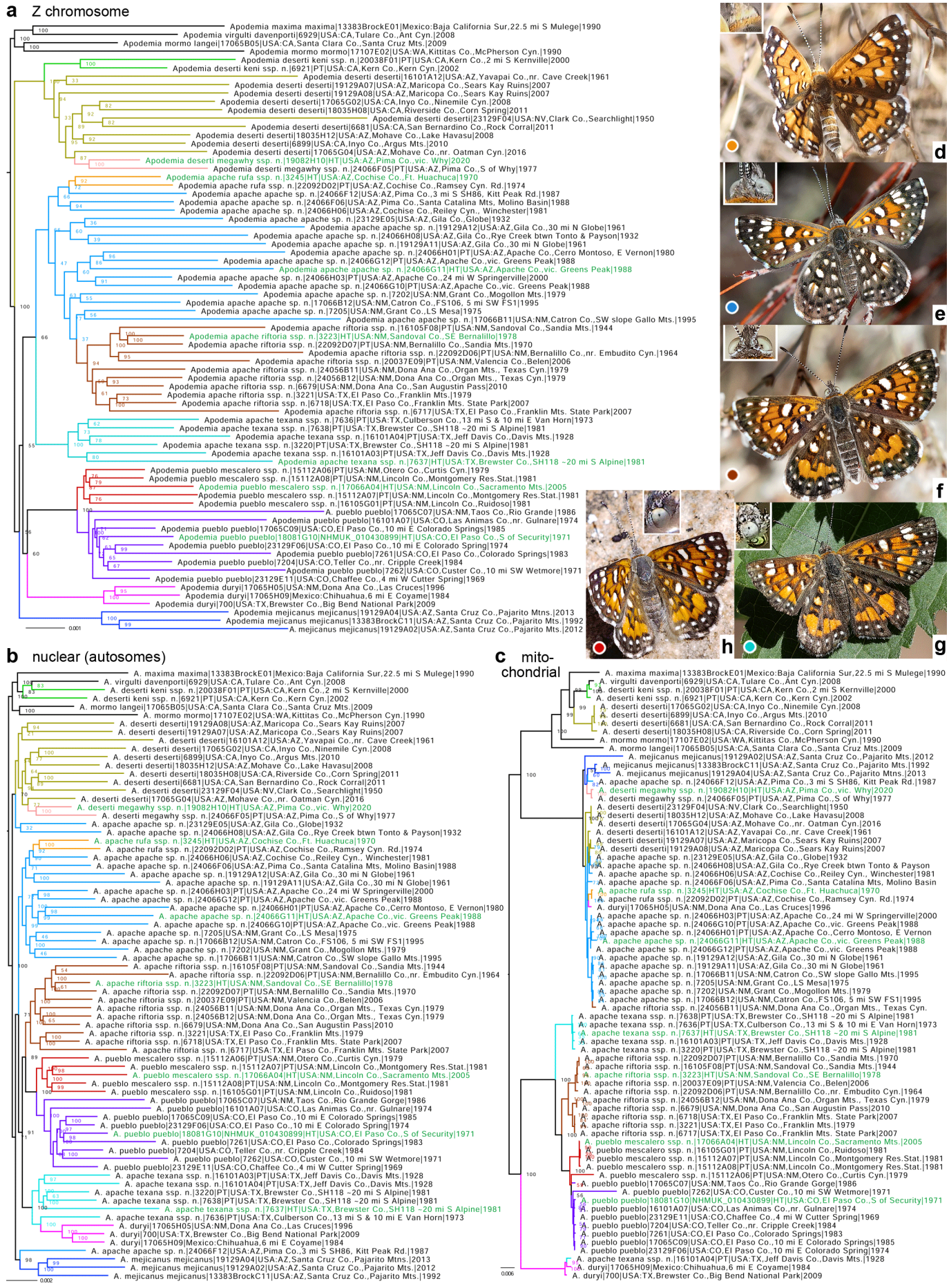
a Z chromosome
Apodemia maxima maxima|13383BrockE01|Mexico:Baja California Sur,22.5 mi S Mulege|1990
Apodemia virgulti davenporti|6929|USA:CA,Tulare Co.,Ant Cyn.|2008
Apodemia mormo langei|17065B05|USA:CA,Santa Clara Co.,Santa Cruz Mts.|2009
Apodemia mormo mormo|17107E02|USA:WA,Kittitas Co.,McPherson Cyn.|1990
Apodemia deserti keni ssp. n.|20038F01|PT|USA:CA,Kern Co.,2 mi S Kernville|2000
Apodemia deserti keni ssp. n.|6921|PT|USA:CA,Kern Co.,Kern Cyn.|2002
Apodemia deserti deserti|16101A12|USA:AZ,Yavapai Co.,nr. Cave Creek|1961
Apodemia deserti deserti|19129A07|USA:AZ,Maricopa Co.,Sears Kay Ruins|2007
Apodemia deserti deserti|19129A08|USA:AZ,Maricopa Co.,Sears Kay Ruins|2007
Apodemia deserti deserti|17065G02|USA:CA,Inyo Co.,Ninemile Cyn.|2008
Apodemia deserti deserti|18035H08|USA:CA,Riverside Co.,Corn Spring|2011
Apodemia deserti deserti|23129F04|USA:NV,Clark Co.,Searchlight|1950
Apodemia deserti deserti|6681|USA:CA,San Bernardino Co.,Rock Corral|2011
Apodemia deserti deserti|18035H12|USA:AZ,Mohave Co.,Lake Havasu|2008
Apodemia deserti deserti|6899|USA:CA,Inyo Co.,Argus Mts.|2010
Apodemia deserti deserti|17065G04|USA:AZ,Mohave Co.,nr. Oatman Cyn.|2016
Apodemia deserti megawhy ssp. n.|19082H10|HT|USA:AZ,Pima Co.,vic. Why|2020
Apodemia deserti megawhy ssp. n.|24066F05|PT|USA:AZ,Pima Co.,S of Why|1977
Apodemia apache rufa ssp. n.|3245|HT|USA:AZ,Cochise Co.,Ft. Huachuca|1970
Apodemia apache rufa ssp. n.|22092D02|PT|USA:AZ,Cochise Co.,Ramsey Cyn. Rd.|1974
Apodemia apache apache ssp. n.|24066F12|USA:AZ,Pima Co.,3 mi S SH86, Kitt Peak Rd.|1987
Apodemia apache apache ssp. n.|24066F06|USA:AZ,Pima Co.,Santa Catalina Mts, Molino Basin|1988
Apodemia apache apache ssp. n.|24066H06|USA:AZ,Cochise Co.,Reiley Cyn., Winchester|1981
Apodemia apache apache ssp. n.|23129E05|USA:AZ,Gila Co.,Globe|1932
Apodemia apache apache ssp. n.|19129A12|USA:AZ,Gila Co.,30 mi N Globe|1961
Apodemia apache apache ssp. n.|24066H08|USA:AZ,Gila Co.,Rye Creek btwn Tonto & Payson|1932
Apodemia apache apache ssp. n.|19129A11|USA:AZ,Gila Co.,30 mi N Globe|1961
Apodemia apache apache ssp. n.|24066H01|PT|USA:AZ,Apache Co.,Cerro Montoso, E Vernon|1980
Apodemia apache apache ssp. n.|24066G12|PT|USA:AZ,Apache Co.,vic. Greens Peak|1988
Apodemia apache apache ssp. n.|24066G11|HT|USA:AZ,Apache Co.,vic. Greens Peak|1988
Apodemia apache apache ssp. n.|24066H03|PT|USA:AZ,Apache Co.,24 mi W Springerville|2000
Apodemia apache apache ssp. n.|24066G10|PT|USA:AZ,Apache Co.,vic. Greens Peak|1988
Apodemia apache apache ssp. n.|7202|USA:NM,Grant Co.,Mogollon Mts.|1979
Apodemia apache apache ssp. n.|17066B12|USA:NM,Catron Co.,FS106, 5 mi SW FS1|1995
Apodemia apache apache ssp. n.|7205|USA:NM,Grant Co.,LS Mesa|1975
Apodemia apache apache ssp. n.|17066B11|USA:NM,Catron Co.,SW slope Gallo Mts.|1995
Apodemia apache riftoria ssp. n.|16105F08|PT|USA:NM,Sandoval Co.,Sandia Mts.|1944
Apodemia apache riftoria ssp. n.|3223|HT|USA:NM,Sandoval Co.,SE Bernalillo|1978
Apodemia apache riftoria ssp. n.|22092D07|PT|USA:NM,Bernalillo Co.,Sandia Mts.|1970
Apodemia apache riftoria ssp. n.|22092D06|PT|USA:NM,Bernalillo Co.,nr. Embudito Cyn.|1964
Apodemia apache riftoria ssp. n.|20037E09|PT|USA:NM,Valencia Co.,Belen|2006
Apodemia apache riftoria ssp. n.|24056B11|USA:NM,Dona Ana Co.,Organ Mts., Texas Cyn.|1979
Apodemia apache riftoria ssp. n.|24056B12|USA:NM,Dona Ana Co.,Organ Mts., Texas Cyn.|1979
Apodemia apache riftoria ssp. n.|6679|USA:NM,Dona Ana Co.,San Augustin Pass|2010
Apodemia apache riftoria ssp. n.|3221|USA:TX,El Paso Co.,Franklin Mts.|1979
Apodemia apache riftoria ssp. n.|6718|USA:TX,El Paso Co.,Franklin Mts. State Park|2007
Apodemia apache riftoria ssp. n.|6717|USA:TX,El Paso Co.,Franklin Mts. State Park|2007
Apodemia apache texana ssp. n.|7636|PT|USA:TX,Culberson Co.,13 mi S & 10 mi E Van Horn|1973
Apodemia apache texana ssp. n.|7638|PT|USA:TX,Brewster Co.,SH118 ~20 mi S Alpine|1981
Apodemia apache texana ssp. n.|16101A04|PT|USA:TX,Jeff Davis Co.,Davis Mts.|1928
Apodemia apache texana ssp. n.|3220|PT|USA:TX,Brewster Co.,SH118 ~20 mi S Alpine|1981
Apodemia apache texana ssp. n.|16101A03|PT|USA:TX,Jeff Davis Co.,Davis Mts.|1928
Apodemia apache texana ssp. n.|7637|HT|USA:TX,Brewster Co.,SH118 ~20 mi S Alpine|1981
Apodemia pueblo mescalero ssp. n.|15112A06|PT|USA:NM,Otero Co.,Curtis Cyn.|1979
Apodemia pueblo mescalero ssp. n.|15112A08|PT|USA:NM,Lincoln Co.,Montgomery Res.Stat.|1981
Apodemia pueblo mescalero ssp. n.|17066A04|HT|USA:NM,Lincoln Co.,Sacramento Mts.|2005
Apodemia pueblo mescalero ssp. n.|15112A07|PT|USA:NM,Lincoln Co.,Montgomery Res.Stat.|1981
Apodemia pueblo mescalero ssp. n.|16105G01|PT|USA:NM,Lincoln Co.,Ruidoso|1981
A. pueblo pueblo|17065C07|USA:NM,Taos Co.,Rio Grande|1986
Apodemia pueblo pueblo|16101A07|USA:CO,Las Animas Co.,nr. Gulnare|1974
Apodemia pueblo pueblo|17065C09|USA:CO,El Paso Co.,10 mi E Colorado Springs|1985
Apodemia pueblo pueblo|18081G10|NHMUK_010430899|HT|USA:CO,El Paso Co.,S of Security|1971
Apodemia pueblo pueblo|23129F06|USA:CO,El Paso Co.,10 mi E Colorado Spring|1974
Apodemia pueblo pueblo|7261|USA:CO,El Paso Co.,Colorado Springs|1983
Apodemia pueblo pueblo|7204|USA:CO,Teller Co.,nr. Cripple Creek|1984
Apodemia pueblo pueblo|7262|USA:CO,Custer Co.,10 mi SW Wetmore|1971
Apodemia pueblo pueblo|23129E11|USA:CO,Chaffee Co.,4 mi W Cutter Spring|1969
Apodemia duryi|17065H05|USA:NM,Dona Ana Co.,Las Cruces|1996
Apodemia duryi|17065H09|Mexico:Chihuahua,6 mi E Coyame|1984
Apodemia duryi|700|USA:TX,Brewster Co.,Big Bend National Park|2009
Apodemia mejicanus mejicanus|19129A04|USA:AZ,Santa Cruz Co.,Pajarito Mts.|2013
Apodemia mejicanus mejicanus|13383BrockC11|USA:AZ,Santa Cruz Co.,Pajarito Mts.|1992
A. mejicanus mejicanus|19129A02|USA:AZ,Santa Cruz Co.,Pajarito Mts.|2012
0.001
b nuclear (autosomes)
A. maxima maxima|13383BrockE01|Mexico:Baja California Sur,22.5 mi S Mulege|1990
A. virgulti davenporti|6929|USA:CA,Tulare Co.,Ant Cyn.|2008
A. deserti keni ssp. n.|20037E09|PT|USA:CA,Kern Co.,2 mi S Kernville|2000
A. deserti keni ssp. n.|6921|PT|USA:CA,Kern Co.,Kern Cyn.|2002
A. mormo langei|17065B05|USA:CA,Santa Clara Co.,Santa Cruz Mts.|2009
A. mormo mormo|17107E02|USA:WA,Kittitas Co.,McPherson Cyn.|1990
A. deserti deserti|19129A08|USA:AZ,Maricopa Co.,Sears Kay Ruins|2007
A. deserti deserti|19129A07|USA:AZ,Maricopa Co.,Sears Kay Ruins|2007
A. deserti deserti|16101A12|USA:AZ,Yavapai Co.,nr. Cave Creek|1961
A. deserti deserti|17065G02|USA:CA,Inyo Co.,Ninemile Cyn.|2008
A. deserti deserti|6899|USA:CA,Inyo Co.,Argus Mts.|2010
A. deserti deserti|18035H12|USA:AZ,Mohave Co.,Lake Havasu|2008
A. deserti deserti|18035H08|USA:CA,Riverside Co.,Corn Spring|2011
A. deserti deserti|6681|USA:CA,San Bernardino Co.,Rock Corral|2011
A. deserti deserti|23129F04|USA:NV,Clark Co.,Searchlight|1950
A. deserti deserti|17065G04|USA:AZ,Mohave Co.,nr. Oatman Cyn.|2016
A. deserti megawhy ssp. n.|19082H10|HT|USA:AZ,Pima Co.,vic. Why|2020
A. deserti megawhy ssp. n.|24066F05|PT|USA:AZ,Pima Co.,S of Why|1977
A. apache apache sp. n.|23129E05|USA:AZ,Gila Co.,Globe|1932
A. apache apache ssp. n.|24066H08|USA:AZ,Gila Co.,Rye Creek btwn Tonto & Payson|1932
A. apache rufa ssp. n.|3245|HT|USA:AZ,Cochise Co.,Ft. Huachuca|1970
A. apache rufa ssp. n.|22092D02|PT|USA:AZ,Cochise Co.,Ramsey Cyn. Rd.|1974
A. apache apache sp. n.|24066H06|USA:AZ,Cochise Co.,Reiley Cyn., Winchester|1981
A. apache apache ssp. n.|24066F06|USA:AZ,Pima Co.,Santa Catalina Mts, Molino Basin|1988
A. apache apache ssp. n.|19129A12|USA:AZ,Gila Co.,30 mi N Globe|1961
A. apache apache ssp. n.|19129A11|USA:AZ,Gila Co.,30 mi N Globe|1961
A. apache apache ssp. n.|24066H03|PT|USA:AZ,Apache Co.,24 mi W Springerville|2000
A. apache apache sp. n.|24066G12|PT|USA:AZ,Apache Co.,vic. Greens Peak|1988
A. apache apache ssp. n.|24066H01|PT|USA:AZ,Apache Co.,Cerro Montoso, E Vernon|1980
A. apache apache ssp. n.|24066G11|HT|USA:AZ,Apache Co.,vic. Greens Peak|1988
A. apache apache ssp. n.|24066G10|PT|USA:AZ,Apache Co.,vic. Greens Peak|1988
A. apache apache ssp. n.|7205|USA:NM,Grant Co.,LS Mesa|1975
A. apache apache sp. n.|17066B12|USA:NM,Catron Co.,FS106, 5 mi SW FS1|1995
A. apache apache ssp. n.|7202|USA:NM,Grant Co.,Mogollon Mts.|1979
A. apache apache sp. n.|17066B11|USA:NM,Catron Co.,SW slope Gallo Mts.|1995
A. apache riftoria ssp. n.|16105F08|PT|USA:NM,Sandoval Co.,Sandia Mts.|1944
A. apache riftoria ssp. n.|22092D06|PT|USA:NM,Bernalillo Co.,nr. Embudito Cyn.|1964
A. apache riftoria ssp. n.|3223|HT|USA:NM,Sandoval Co.,SE Bernalillo|1978
A. apache riftoria ssp. n.|22092D07|PT|USA:NM,Bernalillo Co.,Sandia Mts.|1970
A. apache riftoria ssp. n.|20037E09|PT|USA:NM,Valencia Co.,Belen|2006
A. apache riftoria ssp. n.|24056B11|USA:NM,Dona Ana Co.,Organ Mts., Texas Cyn.|1979
A. apache riftoria ssp. n.|24056B12|USA:NM,Dona Ana Co.,Organ Mts., Texas Cyn.|1979
A. apache riftoria ssp. n.|6679|USA:NM,Dona Ana Co.,San Augustin Pass|2010
A. apache riftoria ssp. n.|3221|USA:TX,El Paso Co.,Franklin Mts.|1979
A. apache riftoria ssp. n.|6718|USA:TX,El Paso Co.,Franklin Mts. State Park|2007
A. apache riftoria ssp. n.|6717|USA:TX,El Paso Co.,Franklin Mts. State Park|2007
A. pueblo mescalero ssp. n.|15112A06|PT|USA:NM,Otero Co.,Curtis Cyn.|1979
A. pueblo mescalero ssp. n.|15112A07|PT|USA:NM,Lincoln Co.,Montgomery Res.Stat.|1981
A. pueblo mescalero ssp. n.|17066A04|HT|USA:NM,Lincoln Co.,Sacramento Mts.|2005
A. pueblo mescalero ssp. n.|15112A08|PT|USA:NM,Lincoln Co.,Montgomery Res.Stat.|1981
A. pueblo mescalero ssp. n.|16105G01|PT|USA:NM,Lincoln Co.,Ruidoso|1981
A. pueblo pueblo|17065C07|USA:NM,Taos Co.,Rio Grande Gorge|1986
A. pueblo pueblo|16101A07|USA:CO,Las Animas Co.,nr. Gulnare|1974
A. pueblo pueblo|17065C09|USA:CO,El Paso Co.,10 mi E Colorado Springs|1985
A. pueblo pueblo|23129F06|USA:CO,El Paso Co.,10 mi E Colorado Spring|1974
A. pueblo pueblo|18081G10|NHMUK_010430899|HT|USA:CO,El Paso Co.,S of Security|1971
A. pueblo pueblo|7261|USA:CO,El Paso Co.,Colorado Springs|1983
A. pueblo pueblo|7204|USA:CO,Teller Co.,nr. Cripple Creek|1984
A. pueblo pueblo|7262|USA:CO,Custer Co.,10 mi SW Wetmore|1971
A. pueblo pueblo|23129E11|USA:CO,Chaffee Co.,4 mi W Cutter Spring|1969
A. apache texana ssp. n.|16101A03|PT|USA:TX,Jeff Davis Co.,Davis Mts.|1928
A. apache texana ssp. n.|16101A04|PT|USA:TX,Jeff Davis Co.,Davis Mts.|1928
A. apache texana ssp. n.|3220|PT|USA:TX,Brewster Co.,SH118 ~20 mi S Alpine|1981
A. apache texana ssp. n.|7638|PT|USA:TX,Brewster Co.,SH118 ~20 mi S Alpine|1981
A. apache texana ssp. n.|7637|HT|USA:TX,Brewster Co.,SH118 ~20 mi S Alpine|1981
A. apache texana ssp. n.|7636|PT|USA:TX,Culberson Co.,13 mi S & 10 mi E Van Horn|1973
A. duryi|17065H05|USA:NM,Dona Ana Co.,Las Cruces|1996
A. duryi|700|USA:TX,Brewster Co.,Big Bend National Park|2009
A. duryi|17065H09|Mexico:Chihuahua,6 mi E Coyame|1984
A. apache apache sp. n.|24066F12|USA:AZ,Pima Co.,3 mi S SH86, Kitt Peak Rd.|1987
A. mejicanus mejicanus|19129A04|USA:AZ,Santa Cruz Co.,Pajarito Mts.|2013
A. mejicanus mejicanus|19129A02|USA:AZ,Santa Cruz Co.,Pajarito Mts.|2012
A. mejicanus mejicanus|13383BrockC11|USA:AZ,Santa Cruz Co.,Pajarito Mts.|1992
0.002
c mito-chondrial
A. maxima maxima|13383BrockE01|Mexico:Baja California Sur,22.5 mi S Mulege|1990
A. virgulti davenporti|6929|USA:CA,Tulare Co.,Ant Cyn.|2008
A. deserti keni ssp. n.|20038F01|PT|USA:CA,Kern Co.,2 mi S Kernville|2000
A. deserti keni ssp. n.|6921|PT|USA:CA,Kern Co.,Kern Cyn.|2002
A. deserti deserti|17065G02|USA:CA,Inyo Co.,Ninemile Cyn.|2008
A. deserti deserti|6899|USA:CA,Inyo Co.,Argus Mts.|2010
A. deserti deserti|6681|USA:CA,San Bernardino Co.,Rock Corral|2011
A. deserti deserti|18035H08|USA:CA,Riverside Co.,Corn Spring|2011
A. mormo mormo|17107E02|USA:WA,Kittitas Co.,McPherson Cyn.|1990
A. mormo langei|17065B05|USA:CA,Santa Clara Co.,Santa Cruz Mts.|2009
A. mejicanus mejicanus|19129A02|USA:AZ,Santa Cruz Co.,Pajarito Mts.|2012
A. mejicanus mejicanus|13383BrockC11|USA:AZ,Santa Cruz Co.,Pajarito Mts.|1992
A. mejicanus mejicanus|19129A04|USA:AZ,Santa Cruz Co.,Pajarito Mts.|2013
A. apache apache sp. n.|24066F12|USA:AZ,Pima Co.,3 mi S SH86, Kitt Peak Rd.|1987
A. deserti megawhy ssp. n.|19082H10|HT|USA:AZ,Pima Co.,vic. Why|2020
A. deserti megawhy ssp. n.|24066F05|PT|USA:AZ,Pima Co.,S of Why|1977
A. deserti deserti|23129F04|USA:NV,Clark Co.,Searchlight|1950
A. deserti deserti|18035H12|USA:AZ,Mohave Co.,Lake Havasu|2008
A. deserti deserti|17065G04|USA:AZ,Mohave Co.,nr. Oatman Cyn.|2016
A. deserti deserti|16101A12|USA:AZ,Yavapai Co.,nr. Cave Creek|1961
A. deserti deserti|19129A07|USA:AZ,Maricopa Co.,Sears Kay Ruins|2007
A. deserti deserti|19129A08|USA:AZ,Maricopa Co.,Sears Kay Ruins|2007
A. apache apache sp. n.|23129E05|USA:AZ,Gila Co.,Globe|1932
A. apache apache ssp. n.|24066H08|USA:AZ,Gila Co.,Rye Creek btwn Tonto & Payson
A. apache apache sp. n.|24066H06|USA:AZ,Cochise Co.,Reiley Cyn., Winchester|1981
A. apache apache ssp. n.|24066F06|USA:AZ,Pima Co.,Santa Catalina Mts, Molino Basin
A. apache rufa ssp. n.|3245|HT|USA:AZ,Cochise Co.,Ft. Huachuca|1970
A. apache rufa ssp. n.|22092D02|PT|USA:AZ,Cochise Co.,Ramsey Cyn. Rd.|1974
A. duryi|17065H05|USA:NM,Dona Ana Co.,Las Cruces|1996
A. apache apache sp. n.|24066H03|PT|USA:AZ,Apache Co.,24 mi W Springerville|2000
A. apache apache sp. n.|24066G10|PT|USA:AZ,Apache Co.,vic. Greens Peak|1988
A. apache apache sp. n.|24066H01|PT|USA:AZ,Apache Co.,Cerro Montoso, E Vernon
A. apache apache sp. n.|24066G11|HT|USA:AZ,Apache Co.,vic. Greens Peak|1988
A. apache apache sp. n.|24066G12|PT|USA:AZ,Apache Co.,vic. Greens Peak|1988
A. apache apache sp. n.|19129A12|USA:AZ,Gila Co.,30 mi N Globe|1961
A. apache apache ssp. n.|19129A11|USA:AZ,Gila Co.,30 mi N Globe|1961
A. apache apache sp. n.|17066B11|USA:NM,Catron Co.,SW slope Gallo Mts.|1995
A. apache apache ssp. n.|7205|USA:NM,Grant Co.,LS Mesa|1975
A. apache apache sp. n.|7202|USA:NM,Grant Co.,Mogollon Mts.|1979
A. apache apache sp. n.|17066B12|USA:NM,Catron Co.,FS106, 5 mi SW FS1|1995
A. apache riftoria ssp. n.|24056B11|USA:NM,Dona Ana Co.,Organ Mts., Texas Cyn.
A. apache texana ssp. n.|7638|PT|USA:TX,Brewster Co.,SH118 ~20 mi S Alpine|1981
A. apache texana ssp. n.|7636|PT|USA:TX,Culberson Co.,13 mi S & 10 mi E Van Horn|1973
A. apache texana ssp. n.|7637|HT|USA:TX,Brewster Co.,SH118 ~20 mi S Alpine|1981
A. apache texana ssp. n.|16101A03|PT|USA:TX,Jeff Davis Co.,Davis Mts.|1928
A. apache texana ssp. n.|3220|PT|USA:TX,Brewster Co.,SH118 ~20 mi S Alpine|1981
A. apache riftoria ssp. n.|16105F08|PT|USA:NM,Sandoval Co.,Sandia Mts.|1944
A. apache riftoria ssp. n.|3223|HT|USA:NM,Sandoval Co.,SE Bernalillo|1978
A. apache riftoria ssp. n.|22092D07|PT|USA:NM,Bernalillo Co.,Sandia Mts.|1970
A. apache riftoria ssp. n.|20037E09|PT|USA:NM,Valencia Co.,Belen|2006
A. apache riftoria ssp. n.|22092D06|PT|USA:NM,Bernalillo Co.,nr. Embudito Cyn.|1964
A. apache riftoria ssp. n.|24056B12|USA:NM,Dona Ana Co.,Organ Mts., Texas Cyn.|1979
A. apache riftoria ssp. n.|6679|USA:NM,Dona Ana Co.,San Augustin Pass|2010
A. apache riftoria ssp. n.|6718|USA:TX,El Paso Co.,Franklin Mts. State Park|2007
A. apache riftoria ssp. n.|3221|USA:TX,El Paso Co.,Franklin Mts.|1979
A. apache riftoria ssp. n.|6717|USA:TX,El Paso Co.,Franklin Mts. State Park|2007
A. pueblo mescalero ssp. n.|17066A04|HT|USA:NM,Lincoln Co.,Sacramento Mts.|2005
A. pueblo mescalero ssp. n.|16105G01|PT|USA:NM,Lincoln Co.,Ruidoso|1981
A. pueblo mescalero ssp. n.|15112A07|PT|USA:NM,Lincoln Co.,Montgomery Res.Stat.|1981
A. pueblo mescalero ssp. n.|15112A08|PT|USA:NM,Lincoln Co.,Montgomery Res.Stat.|1981
A. pueblo mescalero ssp. n.|15112A06|PT|USA:NM,Otero Co.,Curtis Cyn.|1979
A. pueblo pueblo|17065C07|USA:NM,Taos Co.,Rio Grande Gorge|1986
A. pueblo pueblo|7262|USA:CO,Custer Co.,10 mi SW Wetmore|1971
A. pueblo pueblo|18081G10|NHMUK_010430899|HT|USA:CO,El Paso Co.,S of Security|1971
A. pueblo pueblo|16101A07|USA:CO,Las Animas Co.,nr. Gulnare|1974
A. pueblo pueblo|23129E11|USA:CO,Chaffee Co.,4 mi W Cutter Spring|1969
A. pueblo pueblo|7204|USA:CO,Teller Co.,nr. Cripple Creek|1984
A. pueblo pueblo|7261|USA:CO,El Paso Co.,Colorado Springs|1983
A. pueblo pueblo|17065C09|USA:CO,El Paso Co.,10 mi E Colorado Springs|1985
A. pueblo pueblo|23129F06|USA:CO,El Paso Co.,10 mi E Colorado Spring|1974
A. apache texana ssp. n.|16101A04|PT|USA:TX,Jeff Davis Co.,Davis Mts.|1928
A. duryi|17065H09|Mexico:Chihuahua,6 mi E Coyame|1984
A. duryi|700|USA:TX,Brewster Co.,Big Bend National Park|2009
0.006
d
e
f
g
h

Fig. 20 (see the previous page). Phylogenetic trees of selected *A. mormo* group taxa focusing on the gray-eyed taxa constructed from protein-coding regions in: **a)** the Z chromosome, based on 375,822 positions, **b)** the nuclear genome (autosomes), based on 3,926,517 positions, and **c)** the mitochondrial genome; and **d–g)** iNaturalist observations (color of the dot in the lower left of each image corresponds to the color of this taxon in the trees): **d)** *A. apache rufa* **ssp. n.**, observation No. 278247017 USA: Arizona, Santa Cruz Co., San Rafael Valley, GPS 31.3491, −110.5803, 3-May-2025 © Ethan; **e)** *A. apache apache* **sp. n.**, observation No. 98669807, USA: Arizona, Apache Co., Greens Peak Rd. W of Springerville, 4-May-2011 © Ken Kertell; **f)** *A. apache riftoria* **ssp. n.**, observation No. 93221338 (photo 154473522), USA: New Mexico, Bernalillo Co., vic. Sandia Heights, GPS 35.1772, −106.4667, 27-Aug-2021 © Mike Andersen; **g)** *A. apache texana* **ssp. n.**, observation No. 130990471 (photo 222846452, inset 222846486), USA: Texas, Jeff Davis Co., Mt. Livermore, GPS 30.6398, −104.1851, 13-Aug-2022 © Arman Moreno; **h)** *A. pueblo mescalero* **ssp. n.**, observation No. 210415181 (photo 372112633, inset 372112615), USA: New Mexico, Lincoln Co., Valley of Fires, GPS 33.6826, −105.9239, 14-Apr-2024 © John Sullivan; insets show a magnified view of the head of the same specimen (may be in a different pose); images are color-corrected, brightened, rotated, cropped, and some are flipped, CC BY-NC 4.0 https://creativecommons.org/licenses/by-nc/4.0/. In the trees, primary type specimens are labeled in green font and clades of focus are colored: *A. deserti keni* **ssp. n.** (green), *A. deserti deserti* **stat. nov.** (olive), *A. deserti megawhy* **ssp. n.** (pink), *A. apache rufa* **ssp. n.** (orange), *A. apache apache* **sp. n.** (blue), *A. apache riftoria* **ssp. n.** (brown), *A. apache texana* **ssp. n.** (cyan), *A. pueblo mescalero* **ssp. n.** (red), *A. pueblo pueblo* **stat. nov.** (violet), *A. duryi* (magenta), and *A. mejicanus* (dark blue). Ultrafast bootstrap (Hoang et al. 2018) values are shown.

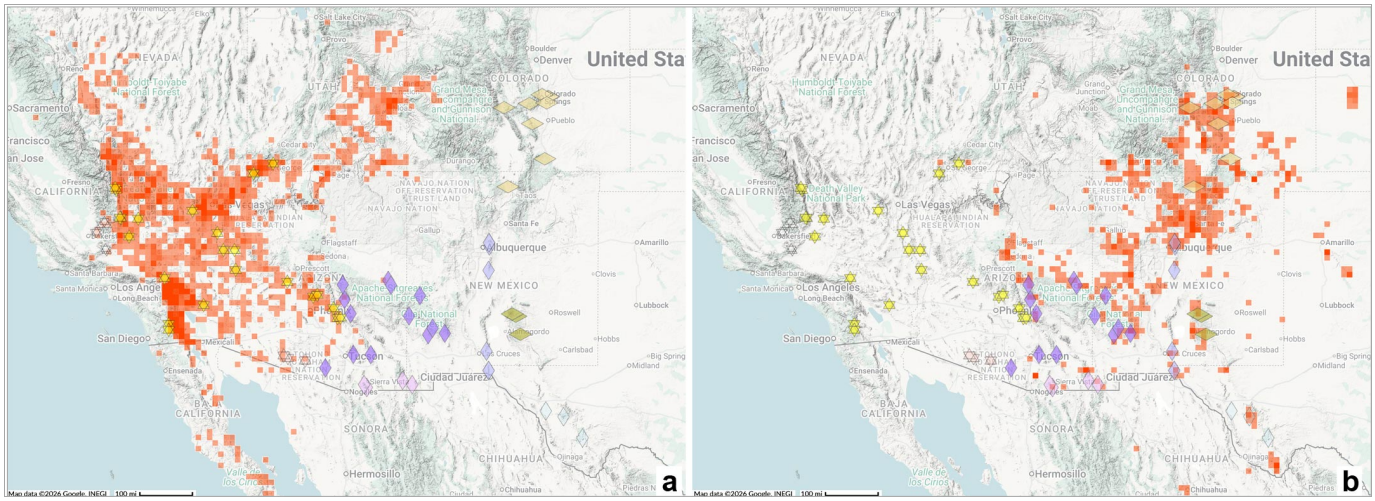

Fig. 21. Map of *Eriogonum* observations taken from iNaturalist (2026): **a)** *E. inflatum* (caterpillar foodplant of *A. deserti* **stat. nov.**) and **b)** *E. jamesii* (caterpillar foodplant of *A. pueblo* **stat. nov.**). *Eriogonum* localities are shown as small red squares, unmodified (CC BY-NC 4.0; https://creativecommons.org/licenses/by-nc/4.0/). These records were not checked, and some may be misidentifications. Semi-transparent symbols marking the localities of sequenced specimens of the *Apodemia* (*Apodemia*) *deserti* subgroup are overlaid onto the iNaturalist map. *Apodemia s*pecies are indicated by shape; subspecies by color as shown in the legend within Fig. 31: *A. deserti* **stat. nov.** (stars): *A. deserti keni* **ssp. n.** (white, smaller), *A. deserti deserti* (yellow), and *A. deserti megawhy* **ssp. n.** (pink); *A. apache* **sp. n.** (vertical diamonds): *A. apache apache* (violet), *A. apache rufa* **ssp. n.** (pale lavender), *A. apache riftoria* **ssp. n.** (periwinkle), and *A. apache texana* **ssp. n.** (pale blue); *A. pueblo* **stat. nov.** (horizontal diamonds): *A. pueblo mescalero* **ssp. n.** (olive) and *A. pueblo pueblo* (tan).

data as the holotype but 28-May-1988, J. B. Walsh leg.; 1♂ NVG-24066H01 Cerro Montoso, E of Vernon, 3-Jun-1980, R. A. Bailowitz leg.; and 1♂ NVG-24066H02 &1♀ NVG-24066H03 (Fig. 22b), US-60, 24 mi W of Springerville, ex ova 16-May-2000, Ken Hansen leg. Only the specimens mentioned above are included as paratypes because they are closer genomically to the holotype and are from the vicinity of the type locality; other sequenced specimens identified as this subspecies are not included in the type series.

Type locality. USA: Arizona, Apache Co., Greens Peak Road 8 mi west of US-60, elevation 7000 ft.

Etymology. The name refers to Apache County, which includes the type locality, and more broadly to the Apache region and the Apache Nation historically associated with this area; it is a noun in apposition.

Suggested English name. Apache Metalmark.

Distribution. The nominotypical subspecies inhabits the northern half of the Madrean Sky Island region: southeastern quarter of Arizona and southwestern New Mexico, USA (except the segment near the Mexican border) (Figs. 21, 31). For other subspecies see below.

Apodemia (*Apodemia*) *apache rufa* Grishin, new subspecies

https://zoobank.org/3EA00763-A2EF-46C4-B9B6-C83952E19ABB

(Figs. 20a–c part, 20d, 21 part, 22c–d, 30–31 part)

Definition and diagnosis. Specimens from the very southern parts of southeastern Arizona and southwestern New Mexico, USA, identified as *Apodemia* (*Apodemia*) *apache* **sp. n.** by the genomic analysis (Fig. 20a, c orange) are largely orange on both sides of the wings (Figs. 20d, 22c, d) and differ markedly from the darker nominotypical specimens (Figs. 20e, 22a, b). Therefore, these orange specimens represent a new subspecies, which stands out among others by both sexes having orange (instead of dark brown) ground color, even on the ventral side of the wing: the ventral forewing is largely orange with brown spots and dashes, and the hindwing is mostly pale-whitish with orange (not brown) between the white spots (dark brown is confined to the framing of the white spots). Specimens of *Apodemia* (*Apodemia*) *duryi* (W. H. Edwards, 1882) (type locality USA: New Mexico, Doña Ana Co., ca. 5 mi E of Mesilla) can also be largely orange above (Fig. 23); however, they have olive brown (not orange) ground color between whitish spots on the ventral hindwing and greenish-yellow eyes, not grayish as in this new subspecies. Due to largely unexplored individual variation, this subspecies is best identified by DNA, with diagnostic base pairs in the nuclear genome: cne21.1.4:T60C, cne6257.6.7:C147T, cne6528.4.4:G264A, cne1172.14.9:G45T, cne2604.1.4:C36T; while the COI barcode may not distinguish all specimens of this subspecies from others, likely due to introgression, and its mitochondrial genomes fall into the clade containing four different *Apodemia* species that are not strongly differentiated from each other in their mitogenomes (Fig. 20c).

Barcode sequence of the holotype. Sample NVG-3245, GenBank PX971418, 658 base pairs:

AACATTATATTTTATTTTTGGAATTTGAGCAGGAATAGTTGGAACCTCATTAAGATTATTAATTCGAATAGAATTAGGAACATCAGGATCTTTAATTGGTGATGATCAAATTTATAATACT
ATTGTTACAGCTCATGCTTTCATTATAATTTTTTTTATAGTTATACCTATTATAATTGGAGGATTTGGTAATTGATTAGTACCATTAATACTTGGAGCTCCGGATATAGCTTTTCCACGAA
TAAATAATATAAGATTTTGACTTTTACCCCCCTCATTATTCTTATTAATTTCTAGAAGAATTGTAGAAAATGGAGCAGGAACAGGATGAACAGTTTATCCCCCACTTTCATCTAATATTGC
CCATGGAGGAGCTTCAGTTGATTTAGCTATTTTTTCTTTACATTTAGCTGGTATTTCTTCAATTTTAGGTGCAATTAATTTTATTACAACTATTATTAATATACGTGTTAATAATATATCT
TTTGATCAAATACCTTTATTTGTATGATCAGTAGGAATTACAGCTTTATTATTATTACTCTCATTACCTGTTTTAGCTGGAGCTATTACCATATTATTAACTGATCGTAATTTAAACACAT
CATTTTTTGATCCAGCAGGTGGAGGAGATCCAATTTTATATCAACATTTATTT

Type material. Holotype: ♂ deposited in the Texas A&M University Insect Collection, College Station, TX, USA (TAMU), illustrated in Fig. 22c, bears the following six rectangular labels (1st and 2nd handprinted, others printed), five white: [Ft. Huachuca | Cochise Co. Ariz | IX-13-1970 | J. E. Hafernik], [Apodemia | mormo | mejicanus | (Behr) | det. J. Hafernik' 70], [ex. J. A. Hafernik Collection | 1997-1999, Texas A&M | University Insect Collection], [DNA sample ID: | NVG-3245 | c/o Nick V. Grishin], [genitalia | NVG150111-61 | Nick V. Grishin], and one red [HOLOTYPE ♂ | Apodemia (Apodemia) | apache rufa Grishin]. **Paratypes:** 2♂♂ and 2♀♀: USA, Arizona, Cochise Co.: Ramsey Canyon Rd. 1 mi W of AZ-92, 29-Apr-1974, G. S. Forbes leg.: 1♂ NVG-17066A02 [CSUC] and 1♀ NVG-22092D02, INHS#3142 [INHS] and US-80, 30 mi NE of Douglas, 20-Sep-1987, J. Kemner leg. [CSUC]: 1♂ NVG-17066B02, BOLD sample CSU-CPG-LEP002127 and 1♀ NVG-17066B01, BOLD sample CSU-CPG-LEP002126 (Fig. 22d).

Type locality. USA: Arizona, Cochise Co., Fort Huachuca.

Etymology. In Latin, *rufus* (feminine: *rufa*) means red, reddish, ginger, or ruddy. The name reflects the rufous aspect of this species compared to its blacker relatives and is an adjective.

Distribution. Currently known from the southern parts of southeastern Arizona and southwestern New Mexico, USA (Figs. 21, 31).

Remarks. A female NVG-17066A01 from New Mexico, Hidalgo Co., Gray Ranch, N slope of Animas Mts., 0.7 mi S of Double Adobe Camp & 0.5 mi N of Buck Tank, 5200 ft, 26-Sep-1993, R. W. Holland & S. J. Cary leg. [CSUC] (Fig. 10b) is genomically similar to this new subspecies, and we tentatively identify it as such. However, this specimen is darker and phenotypically intermediate toward the nominotypical subspecies, and therefore we exclude it from the type series. More generally, *Apodemia apache rufa* **ssp. n.** illustrates that a monophyletic subspecies at the periphery of a species' range can arise within another subspecies, rendering the latter paraphyletic (Fig. 20, orange within blue), as expected when subspecies are traditionally delimited by geography and phenotype rather than strict monophyly. Reciprocally monophyletic subspecies may be less common (see the next one for an example).

Fig. 22. *Apodemia apache* **sp. n.** type specimens from USA: Arizona, in dorsal (left) and ventral (right) views: **a–b)** *A. apache apache* from Apache Co. [MGCL]: **a) holotype** ♂ NVG-24066G11 Greens Peak Rd. 8 mi W of US-60, 4-Jun-1988, D. D. Mullins leg. and **b)** paratype ♀ NVG-24066H03 US-60, 24 mi W of Springerville, *ex ovum*, 16-May-2000, K. Hansen leg.; and **c–d)** *A. apache rufa* **ssp. n.** from Cochise Co.: **c) holotype** ♂ NVG-3245 Fort Huachuca, 13-Sep-1970, J. A. Hafernik leg. [TAMU] and **d)** paratype ♀ NVG-17066B01 US-80 30 mi NE of Douglas, 20-Sep-1987, J. Kemner leg. [CSUC].

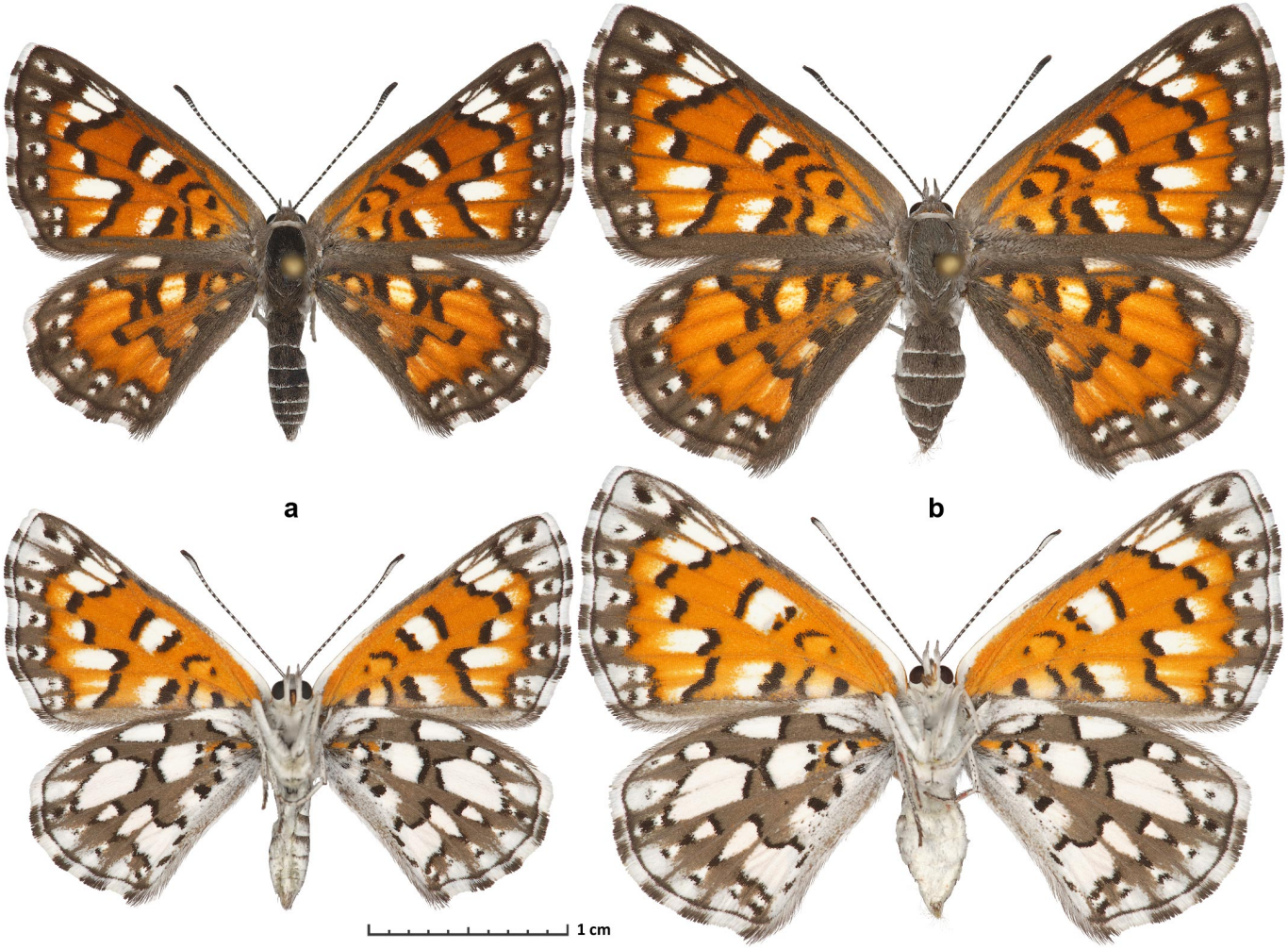

Fig. 23. *Apodemia duryi* from USA: Texas, Brewster Co., Big Bend National Park, along the road to Rio Grande Village, vic. Dugout Wells, N. V. Grishin leg., *ex ova ex* ♀, reared on *Krameria* sp., in dorsal (above) and ventral (below) views, eclosed: **a)** ♂ 8-Aug-2005 and **b)** ♀ 25-Aug-2005.

Apodemia (*Apodemia*) *apache texana* Grishin, new subspecies

https://zoobank.org/71B22B63-D109-4CD4-AAFE-625CA6A3B0C1

(Figs. 20a–c part, 20g, 21 part, 24a–b, 30–31 part)

Definition and diagnosis. Genomic analysis reveals that specimens of *Apodemia* (*Apodemia*) *apache* **sp. n.** from Texas form a prominent clade in the nuclear genome trees genetically differentiated from the nominotypical populations at least at the subspecies level (Fig. 20a, b) and have a distinctive mitochondrial genome haplotype (Fig. 20c cyan); therefore, these specimens represent a new subspecies. This new subspecies differs from its relatives by the following combination of characters: extensive orange coloration on the dorsal side of the wings, which also have brownish areas intermixed with orange patches and white spots; the brown bar near the middle of cell M_3-CuA_1 on the dorsal forewing is more strongly offset distad from the discal brown band [similar to *A. duryi*, and could be due to introgression with it]; no whitish longitudinal ray or white overscaling in the middle of the ventral hindwing connecting the discal and postdiscal white spots; and the eyes are greenish-gray. Due to its cryptic nature and unexplored individual variation, this subspecies is best identified by DNA, with diagnostic base pairs in the nuclear genome: cne1493.10.2:T84C, cne1493.10.2:G114A, cne23874.13.1:A43G, cne23874.13.1:G51A, cne2323.3.4:C208T; and in the COI barcode: T385C, A451C, A508G, T571C, A619T (although one sequenced specimen had a barcode introgressed from *Apodemia duryi* and thus different from this one).

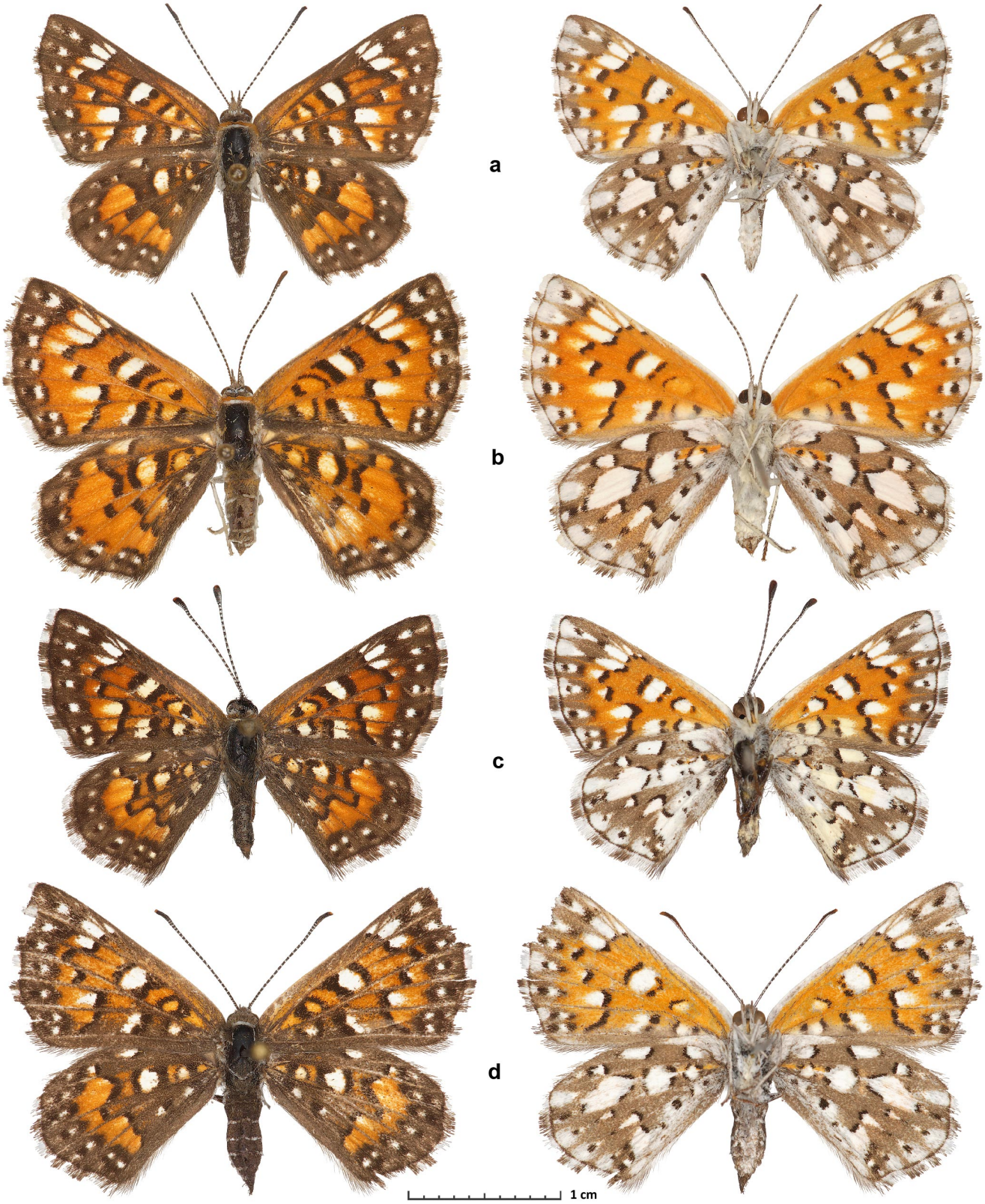

Fig. 24. *Apodemia apache* **sp. n.** specimens from USA in dorsal (left) and ventral (right) views: **a–b)** *Apodemia apache texana* **ssp. n.** from Texas [TAMU]: **a) holotype** ♂ NVG-7637 Brewster Co., TX-118, ca. 20 mi S of Alpine and **b)** paratype ♀ NVG-7636 Culberson Co., 13 mi S & 10 mi E of Van Horn, 21-Apr-1973, Jack L. Harry leg.; and **c–d)** *Apodemia apache riftoria* **ssp. n.**: **c) holotype** ♂ NVG-3223 New Mexico, Sandoval Co., SE of Bernalillo, Sandia Mts. at Juan Tabo, 6850 ft, 29-Apr-1978, R. E. Acciavatti leg. [TAMU] and **d)** non-type ♀ NVG-6718 Texas, El Paso Co., Franklin Mountains State Park, vic. Cottonwood Springs, 31.9139, −106.4979, 16-Apr-2007, N. V. Grishin leg.

Barcode sequence of the holotype. Sample NVG-7637, GenBank PX971419, 658 base pairs:

AACATTATATTTTATTTTTGGAATTTGAGCAGGAATAGTTGGAACTTCATTAAGATTATTAATTCGAATAGAACTAGGAACATCAGGATCTTTAATTGGTGACGATCAAATTTATAATACT
ATTGTCACAGCTCATGCTTTTATTATAATTTTTTTCATAGTTATACCTATTATAATTGGAGGATTTGGTAATTGATTAGTACCATTAATACTTGGAGCTCCAGATATAGCTTTTCCACGAA
TAAATAATATAAGATTTTGACTTCTACCTCCCTCATTATTTTTATTAATTTCTAGAAGAATTGTAGAAAATGGAGCAGGAACAGGATGAACAGTTTATCCCCCACTTTCATCTAATATTGC
CCATGGAGGAGCTTCAGTTGACTTAGCTATTTTTTCATTACATTTAGCTGGTATTTCTTCAATTTTAGGTGCAATTAATTTTATTACCACTATTATTAATATACGTGTTAATAATATATCT
TTTGATCAAATACCCCTATTTGTGTGATCAGTAGGAATTACAGCTTTATTACTTTTACTTTCACTGCCTGTTTTAGCTGGAGCTATCACTATATTATTAACTGATCGTAATTTAAATACAT
CATTTTTTGATCCTGCAGGTGGGGGAGACCCAATTTTATATCAACATTTATTT

Type material. Holotype: ♂ deposited in the Texas A&M University Insect Collection, College Station, TX, USA (TAMU), illustrated in Fig. 24a, bears the following six printed rectangular labels (text in italics handwritten), five white: [TEXAS: | Brewster County | Tx Hwy 118 ca. *20* | miles south of Alpine], [coll. | 19 APR 198*1* | Roy O. Kendall | and C. A. Kendall], [RIODINIDAE: | Apodemia mormo mexicana | (Behr, 1865) | ♂ det. Roy O. Kendall | M. & B. No. 544e], [DNA sample ID: | NVG-7637 | c/o Nick V. Grishin], [genitalia | NVG170107-68 | Nick V. Grishin], and one red [HOLOTYPE ♂ | Apodemia (Apodemia) | apache texana Grishin]. **Paratypes:** 2♂♂ and 3♀♀: USA, Texas: 1♂ (NVG-7638, genitalia NVG170107-69) & 1♀ (NVG-3220, genitalia NVG15011-36) with the same data as the holotype; 1♂ (NVG-16101A04) & 1♀ (NVG-16101A03) Jeff Davis Co., Davis Mts., nr. Fort Davis, 5000 ft, 1–10-May-1928, O. Poling leg. [AMNH]; and 1♀ NVG-7636 Culberson Co., 13 mi S & 10 mi E of Van Horn, 21-Apr-1973, J. L. Harry leg., genitalia NVG170107-67 [TAMU] (Fig. 24b).

Type locality. USA: Texas, Brewster Co., Texas State Highway 118 ca. 20 mi south of Alpine.

Etymology. The name is derived from the state with the type locality and is treated as a feminine adjective.

Distribution. Known only from Texas, USA (Culberson, Jeff Davis, and Brewster Cos.) (Figs. 21, 31).

Apodemia (*Apodemia*) *apache riftoria* Grishin, new subspecies

https://zoobank.org/90327D65-9B1F-44F1-BD64-B0BBD44BCBD6

(Figs. 20a–c part, 20f, 21 part, 24c–d, 26f, 30–31 part)

Definition and diagnosis. Genomic analysis reveals that specimens of *Apodemia* (*Apodemia*) *apache* **sp. n.** from the Rio Grande Rift in New Mexico and Texas form a prominent clade in the nuclear genome trees genetically differentiated from other populations at the subspecies level (Fig. 20a, b) and therefore these specimens represent a new subspecies. This new subspecies differs from its relatives by the following combination of characters: less extensive than in *A. apache texana* **ssp. n.** (especially in females) but still prominent orange coloration on the dorsal side of the wings, which also have brownish areas intermixed with orange patches and white spots; the brown bar near the middle of cell M_3-CuA_1 on the dorsal forewing is not as prominently offset distad from the discal brown band; developed (sometimes weak) whitish longitudinal ray and white overscaling in the middle of the ventral hindwing connecting the discal and postdiscal white spots; and greenish-gray eyes. Due to its somewhat cryptic nature and poorly explored individual variation, this subspecies is best identified by DNA, with diagnostic base pairs in the nuclear genome: cne3772.13.1:C39A, cne254675.12.8:A78T, cne254675.12.8:G421A, cne85.8.8:T141G, cne85.8.8:C177T; while the COI barcode may not distinguish all specimens of this subspecies from others, likely due to introgression.

Barcode sequence of the holotype. Sample NVG-3223, GenBank PX971420, 658 base pairs:

AACATTATACTTTATTTTTGGAATTTGAGCAGGAATAGTTGGAACTTCATTAAGATTATTAATTCGAATAGAACTAGGAACATCAGGATCTTTAATTGGTGACGATCAAATTTATAATACT
ATTGTCACAGCTCATGCTTTTATTATAATTTTTTTCATAGTTATACCTATTATAATTGGAGGATTTGGTAATTGATTAGTACCATTAATACTTGGAGCTCCAGATATAGCTTTTCCACGAA
TAAATAATATAAGATTTTGACTTCTACCCCCCTCATTATTTTTATTAATTTCTAGAAGAATTGTAGAAAATGGAGCAGGAACAGGATGAACAGTTTATCCCCCACTTTCATCTAATATTGC
CCATGGAGGAGCTTCAGTTGATTTAGCTATTTTTTCATTACATTTAGCTGGTATTTCTTCAATTTTAGGTGCAATTAATTTTATTACTACTATTATTAATATACGTGTTAACAATATATCT
TTTGATCAAATACCCCTATTTGTATGATCAGTAGGAATTACAGCTTTATTACTTTTACTTTCACTGCCTGTTTTAGCTGGAGCTATTACTATATTATTAACTGATCGTAATTTAAATACAT
CATTTTTTGACCCAGCAGGTGGAGGAGACCCAATTTTATATCAACATTTATTT

Type material. Holotype: ♂ deposited in the Texas A&M University Insect Collection, College Station, TX, USA (TAMU), illustrated in Fig. 24c, bears the following six printed rectangular labels (text in italics handwritten), five white: [NEW MEXICO: | Sandoval County | SE of Bernalillo | Sandia Mountains | at Juan Tabo 6850 ft.], [Coll. | *29 APR 1978* | Robert E. Acciavatti], [RIODINIDAE: | Apodemia mormo mexicana | (Behr, 1865) | ♂ det. Roy O. Kendall | M. & B. No. 544e], [DNA sample ID: | NVG-3223 | c/o Nick V. Grishin], [genitalia | NVG150111-39 | Nick V. Grishin], and one red [HOLOTYPE ♂ | Apodemia (Apodemia) | apache riftoria Grishin]. **Paratypes:** 3♂♂ and 2♀♀: USA, New Mexico: 1♂

NVG-16105F08 from the type locality, 1-Aug-1944, W. O. Griesel leg. [LACM]; Bernalillo Co.: 1♂ NVG-22092D07 Sandia Mts., lower La Luz Trail, 7-May-1970, M. Toliver leg. [INHS]; 1♂ NVG-22092D06 Sandia Mts., vic. Embudito Canyon, 6200 ft, 26-Apr-1964, M. Toliver leg. [INHS]; and 1♀ NVG-17066A03 Manzano Mts., south rim of Tijeras Canyon, 6200 ft, 23-Sep-1980, R. W. Holland leg. [CSUC]; and 1♀ NVG-20037E09 Valencia Co., Manzano Range, Belen, 6053 ft, 21-Apr-2006, T. L. Stout leg. Only the specimens from the Sandia and Manzano Mountains (central New Mexico) listed above are included as paratypes, because they are closer genomically to the holotype and are from the vicinity of the type locality; other sequenced specimens identified as this subspecies are not included in the type series.

Type locality. USA: New Mexico, Sandoval Co., southeast of Bernalillo, Sandia Mountains at Juan Tabo, 6850 ft.

Etymology. The name is a fusion: *rift* + *ori*[ent]*a*[l] and reflects the range of this subspecies along the central to southern part of the Rio Grande Rift on the eastern side of the Rio Grande valley, from the Sandia Mountains (New Mexico) south to the Franklin Mountains (Texas). The name is treated as a noun in apposition.

Distribution. Currently known from the central and southern parts of the Rio Grande Rift in New Mexico and Texas, from east of Albuquerque to El Paso (Figs. 21, 31).

Apodemia (*Apodemia*) *pueblo mescalero* Grishin, new subspecies

https://zoobank.org/DFA1D260-D6B3-4FE6-941E-B977AA5B10A7

(Figs. 20a–c part, 20h, 21 part, 25c–e, 30–31 part)

Definition and diagnosis. Genomic analysis reveals that populations in the Sacramento Mountains, New Mexico belong to *Apodemia* (*Apodemia*) *pueblo* J. Scott, 1998, **stat. nov.** (type locality in USA: Colorado, El Paso Co., S of Security) because they form a clade sister to this species, not being very strongly differentiated from it genetically (Fig. 20a, b). However, this clade is sufficiently prominent and these populations are monophyletic; thus, we regard them as a distinct and new subspecies of *A. pueblo*. This new subspecies (Figs. 30h, 25c–e) differs from the nominotypical subspecies (Fig. 25a, b) by having more extensive orange areas of a more saturated color above; more prominent white overscaling on the ventral hindwing connecting the discal cell white spot with the postdiscal (larger) white spot, nearly forming a continuous longitudinal ray through the middle of the wing; and reduced submarginal white spots on the dorsal hindwing. The eyes are greenish-gray. Due to largely unexplored individual variation, this subspecies is best identified by DNA, with diagnostic base pairs in the nuclear genome: cne555.2.3: C276T, cne555.2.3:G300A, cne18828.1.3:A60C, cne1150.1.3:T36C, cne1150.1.3:A42T; while the COI barcode may not distinguish all specimens of this subspecies from others, likely due to introgression.

Barcode sequence of the holotype. Sample NVG-17066A04, GenBank PX971421, 658 base pairs:

AACATTATATTTTATTTTTGGAATTTGAGCAGGAATAGTTGGAACTTCATTAAGATTATTAATTCGAATAGAACTAGGAACATCAGGATCCTTAATTGGTGATGATCAAATTTATAATACT
ATTGTCACAGCTCATGCTTTTATTATAATTTTTTTCATAGTTATACCTATTATAATTGGAGGATTTGGTAATTGATTAGTGCCATTAATACTTGGAGCTCCAGATATAGCTTTTCCACGAA
TAAATAATATAAGATTTTGACTTCTACCCCCCTCATTATTTTTATTAATTTCTAGAAGAATTGTAGAAAATGGAGCAGGAACAGGATGAACAGTTTATCCCCCACTTTCATCTAATATTGC
CCATGGAGGAGCTTCAGTTGATTTAGCTATTTTTTCATTACATTTAGCTGGTATCTCTTCAATTTTAGGTGCAATTAATTTTATTACCACTATTATTAATATACGTATTAACAATATATCT
TTTGATCAAATACCCTTATTTGTATGATCAGTAGGAATTACAGCTTTATTACTTTTACTTTCACTGCCTGTTTTAGCTGGAGCTATTACTATATTATTAACTGATCGTAATTTAAATACAT
CATTTTTCGATCCAGCAGGTGGAGGAGACCCAATTTTATATCAACATTTATTT

Type material. Holotype: ♂ deposited in the Colorado State University Collection, Fort Collins, CO, USA (CSUC), illustrated in Fig. 25c, bears the following three printed rectangular labels, two white: [NM: Lincoln Co. | Lincoln N. For. | Sacramento Mts. | Hwy. 352, W of Alto, | 9600' VIII-9-2005 | P. and E. Opler], [DNA sample ID: | NVG-17066A04 | c/o Nick V. Grishin], and one red [HOLOTYPE ♂ | Apodemia (Apodemia) | pueblo mescalero Grishin]. **Paratypes:** 5♂♂: USA, New Mexico: Lincoln Co.: 6 mi N of Ruidoso, Montgomery Biol. Res. Station, 7000 ft, G. A. Gorelick leg.: 1♂ NVG-15112A08, 6-Jul-1981 [FMNH] and 2♂♂ (NVG-16105F12 & NVG-16105G01) 7-Jul-1981 [LACM] and 1♂ NVG-15112A07 Rd. to Montgomery Biol. Res. Station, 10-Jul-1981, J. McCaffrey leg. [FMNH] (Fig. 25d) and 1♂ NVG-15112A06 Otero Co., Curtis Canyon, Sta. No. 7, 7250 ft, 32.8667, −105.6333 15-Jul-1979 [FMNH] (Fig. 25e).

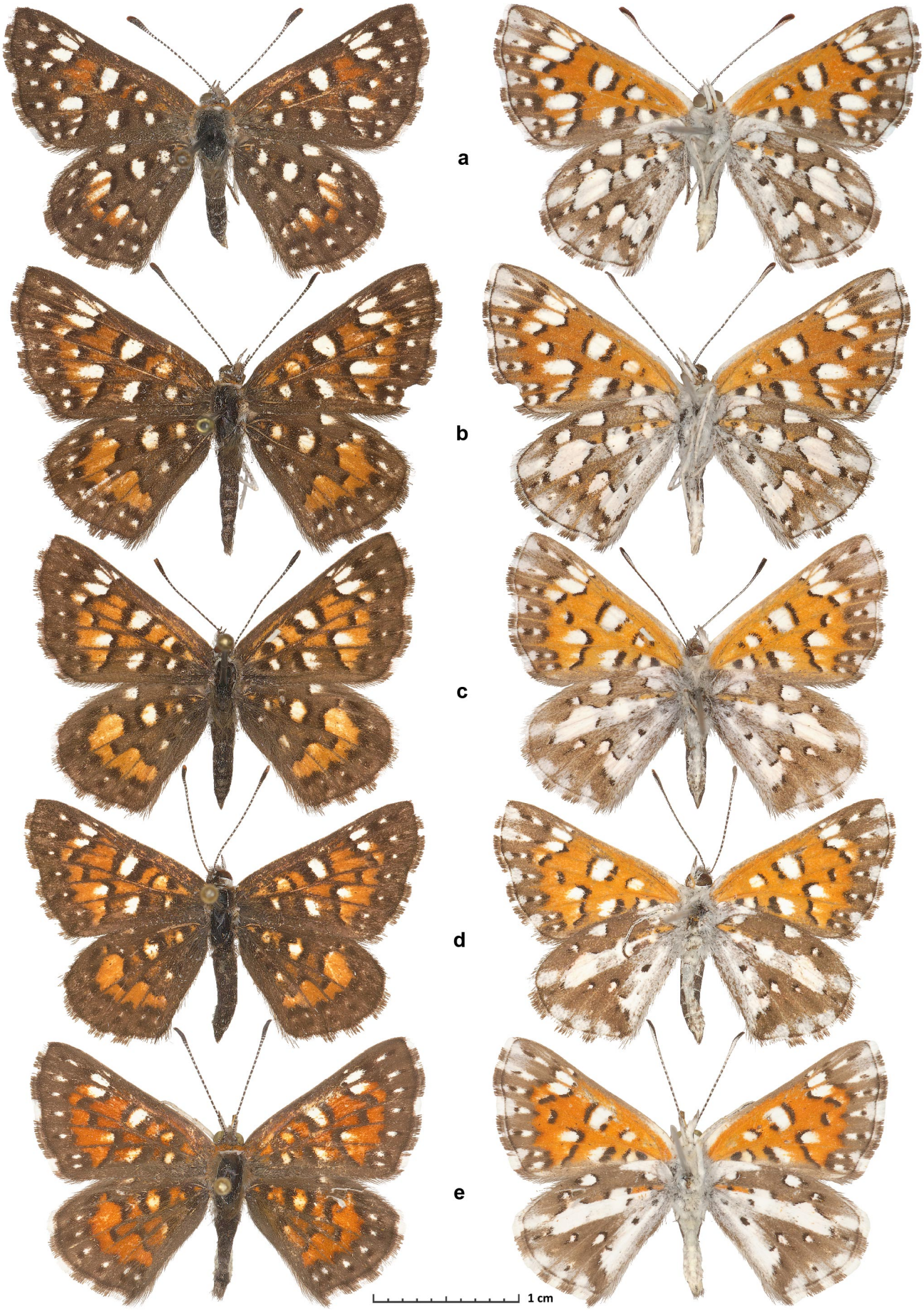

Fig. 25 (legend continues on the next page). *Apodemia pueblo* **stat. nov.** males from USA: Colorado and New Mexico in dorsal (left) and ventral (right) views: **a–b)** *A. pueblo pueblo* from Colorado: **a) holotype** NHMUK_010430899 El Paso Co.,

S of Security, 11-Aug-1971, James A. Scott leg. [BMNH] and **b)** non-type NVG-23129E11 Chaffee Co., 4 mi W of Cutter Spring, 29-Jul-1969 [CNC]; and **c–e)** *A. pueblo mescalero* **ssp. n.** from New Mexico: **c) holotype** NVG-17066A04 Lincoln Co., Lincoln N. F., Sacramento Mts., NM-352, W of Alto, 9600 ft, 9-Aug-2005, P. & E. Opler [CSUC]; and paratypes [FMNH]: **d)** NVG-15112A07 Lincoln Co., Rd. to Montgomery Field Sta., 10-Jul-1981, J. McCaffrey leg. and **e)** NVG-15112A06 Otero Co., Curtis Canyon, Sta. No. 7, 7250 ft, 15-Jul-1979. Photographs in (a) taken by N.V.G. are ©The Trustees of the Natural History Museum, London, and are made available under Creative Commons License 4.0 (https://creativecommons.org/licenses/by/4.0/).

Type locality. USA: New Mexico, Lincoln Co., Lincoln National Forest, Sacramento Mountains, NM-352 west of Alto, elevation 9600 ft.

Etymology. The name reflects the distribution of this subspecies in the Mescalero region centered around the Mescalero Apache Tribal land and the Sacramento Mountains, and is treated as a noun in apposition.

Distribution. Currently known only from the Sacramento Mountains and their vicinity in New Mexico, USA (Lincoln and Otero Cos.) (Figs. 21, 31).

On possible sympatry of *Apodemia mormo* group taxa

For species delimitation, it is essential to probe the regions of their sympatry. Scott (2017) argued that it may be reasonable to treat the *A. mormo* complex as a single species "because evidently nowhere do two

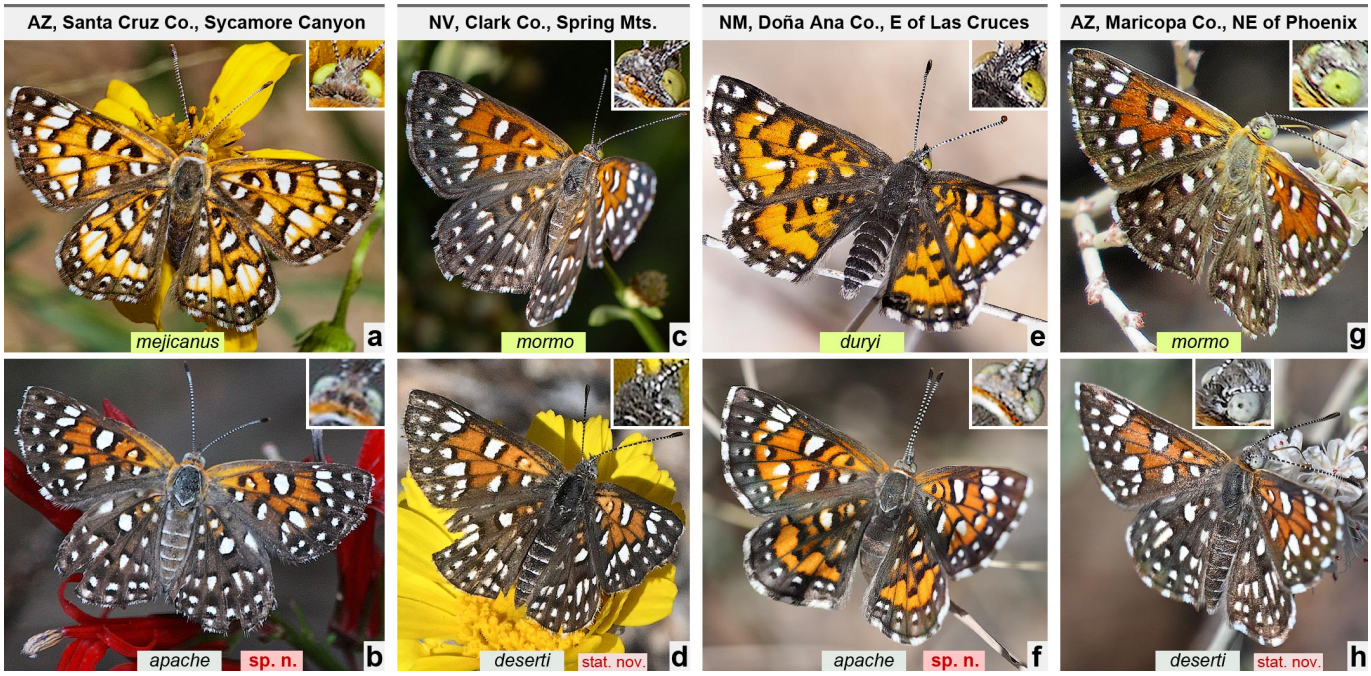

Fig. 26. Examples of sympatric or nearby occurrences of *A. mormo* group species (green-eyed are in the first row and gray-eyed are in the second row), iNaturalist observations from the USA: **a–b)** Arizona, Santa Cruz Co., Sycamore Canyon: **a)** *A. mejicanus*, observation No. 247271862, 31.4320, −111.1885, 10-Oct-2024 © Tom Horton and **b)** *A. apache apache* **sp. n.**, observation No. 144698442, 31.4322, −111.1889, 16-Sep-2017 © jmbearce; **c–d)** Nevada, Clark Co., Spring Mts.: **c)** *A. mormo autumnalis*, observation No. 243876527 Pine Creek trail, 36.1234, −115.4847, 24-Sep-2024 © Kirstyn Eckhardt and **d)** *A. deserti deserti* **stat. nov.**, observation No. 139085470 (photo 375426443) Late Night trail, 36.0115, −115.4326, 30-Apr-2024 © lonnyholmes; **e–f)** New Mexico, Doña Ana Co., E of Las Cruces: **e)** *A. duryi*, observation No. 153658853 (photo 265421645) at the base of Tortugas Mountain, 4300 ft, Apr-2023 (data obscured) © Mike Andersen and **f)** *A. apache riftoria* **ssp. n.**, observation No. 12670207 Organ Mts., Sep-2017 (data obscured) © Andrew Meeds; **g–h)** Arizona, Maricopa Co., NE of Phoenix: **g)** *A. mormo confusa* **ssp. n.**, observation No. 60135561 (photo 96132762) North Scottsdale, 33.6911, −111.7904, 23-Sep-2017 © larivera and **h)** *A. deserti deserti* **stat. nov.**, observation No. 323120891 (photo 584641955) Seven Springs, 33.9485, −111.8295, 16-Oct-2022 © Arthur Yang; images are color-corrected, brightened, rotated, cropped, and some flipped; CC BY-NC 4.0 https://creativecommons.org/licenses/by-nc/4.0/. Insets show a magnified view of the head of the same specimen. Names of species are shown on a background of their typical eye color. Photographs were taken with different cameras under different lighting and white balance settings; therefore, colors may not be fully comparable between images. Nevertheless, the greenish-yellow tint of the eyes in the first row, versus more grayish eyes in the second row, is conveyed.

"*mormo*" group taxa fly together at the same time and place." Inspection of iNaturalist (2026) observations reveals at least one case of nearly perfect sympatry between two taxa, both photographed in the fall, with the distance between their reported GPS coordinates being 45 meters (with the caveat that one of the GPS readings refers to a vehicle in a parking lot) (Fig. 26a, b). From these observations, *A. mejicanus* and *A. apache* **sp. n.** are sympatric and synchronic in Sycamore Canyon, Santa Cruz Co., Arizona. They are confidently distinguished by eye color (greenish vs. grayish) and superficially appear profoundly different: the latter is mostly orange with larger white spots (Fig. 26a), and the former is largely grayish-brown with a reddish forewing patch and smaller white spots (Fig. 26b).

Other examples of green- vs. gray-eyed taxa photographed near each other are: *A. mormo autumnalis* (Fig. 26c) and *A. deserti deserti* **stat. nov.** (Fig. 26d) in the Spring Mountains, Clark Co., Nevada; *A. duryi* (Fig. 26e) and *A. apache riftoria* **ssp. n.** (Fig. 26f) east of Las Cruces in Doña Ana Co., New Mexico — see also Cary (2022) for a detailed map of *A. mormo* group records at this general locality, minding that Cary unavoidably misidentified *A. apache riftoria* **ssp. n.** as *A. mejicanus*; and *A. mormo confusa* **ssp. n.** (Fig. 26g) and *A. deserti deserti* **stat. nov.** (Fig. 26h) northeast of Phoenix, Maricopa Co., Arizona. As in Cary (2022), we interpret these nearby occurrences of phenotypically and genetically distinct synchronic taxa (even if they are not fully sympatric) as evidence that they represent distinct species. The argument is that if they were conspecific, they would hybridize more extensively, and the differences between them would be leveled out in the region of parapatry or partial sympatry.

Three *Apodemia mormo* group species in one canyon

Among sequenced specimens, we found a case, already suggested based on phenotypic comparison by Ken Davenport, the collector of these specimens, in which three distinct species are found along the same canyon. Sequencing *Apodemia mormo* group specimens from USA: California, Inyo Co., Ninemile Canyon

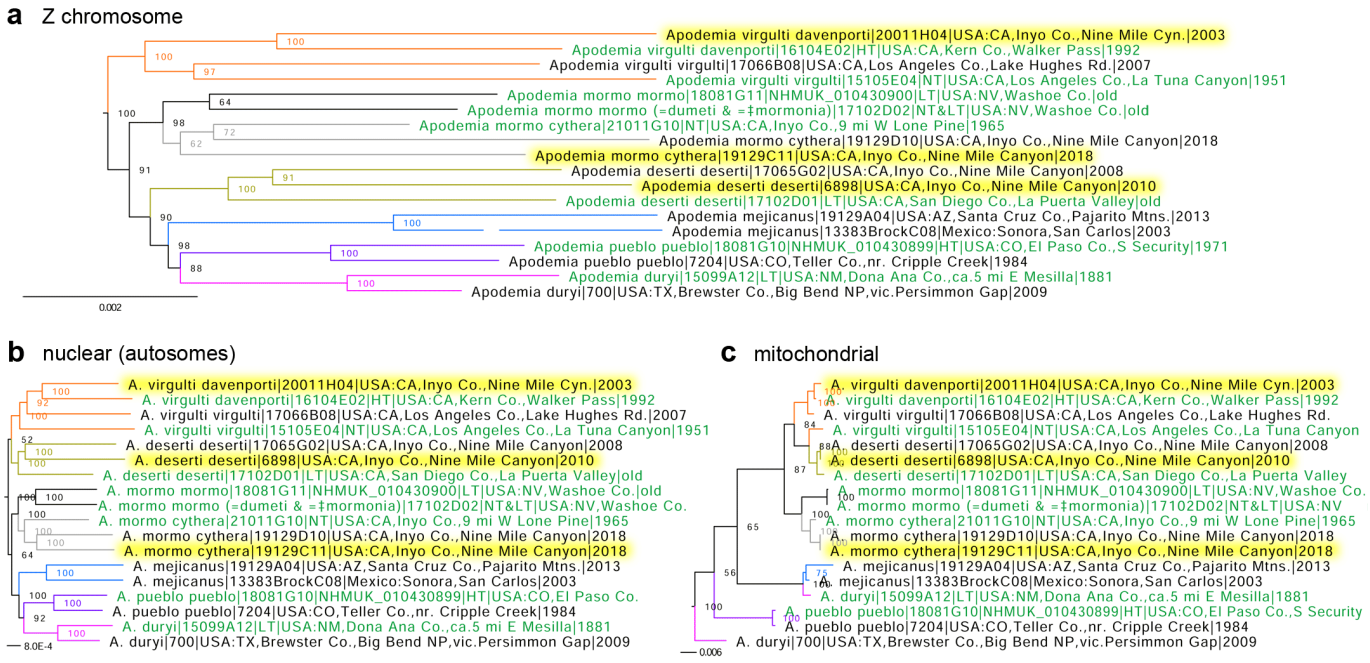

Fig. 27. Phylogenetic trees supporting the identification of three distinct *A. mormo* group species found along Ninemile Canyon, Inyo Co., California, constructed from protein-coding regions in: **a)** the Z chromosome, based on 417,840 positions, **b)** the nuclear genome (autosomes), based on 4,536,930 positions, and **c)** the mitochondrial genome. Clades of different species are colored differently: *A. virgulti* (orange), *A. mormo* (black, with *A. mormo cythera* in gray), *A. deserti* **stat. nov.** (olive), *A. mejicanus* (blue), *A. pueblo* **stat. nov.** (violet), and *A. duryi* (magenta). Primary type specimens are labeled in green font, and three specimens from Ninemile Canyon shown in Fig. 28 are highlighted in yellow. Ultrafast bootstrap (Hoang et al. 2018) values are shown at nodes. A gap in one terminal branch indicates that a segment of the branch was cut out to reduce its length (allowing an increase in font size), i.e., a branch with a gap is longer than shown.

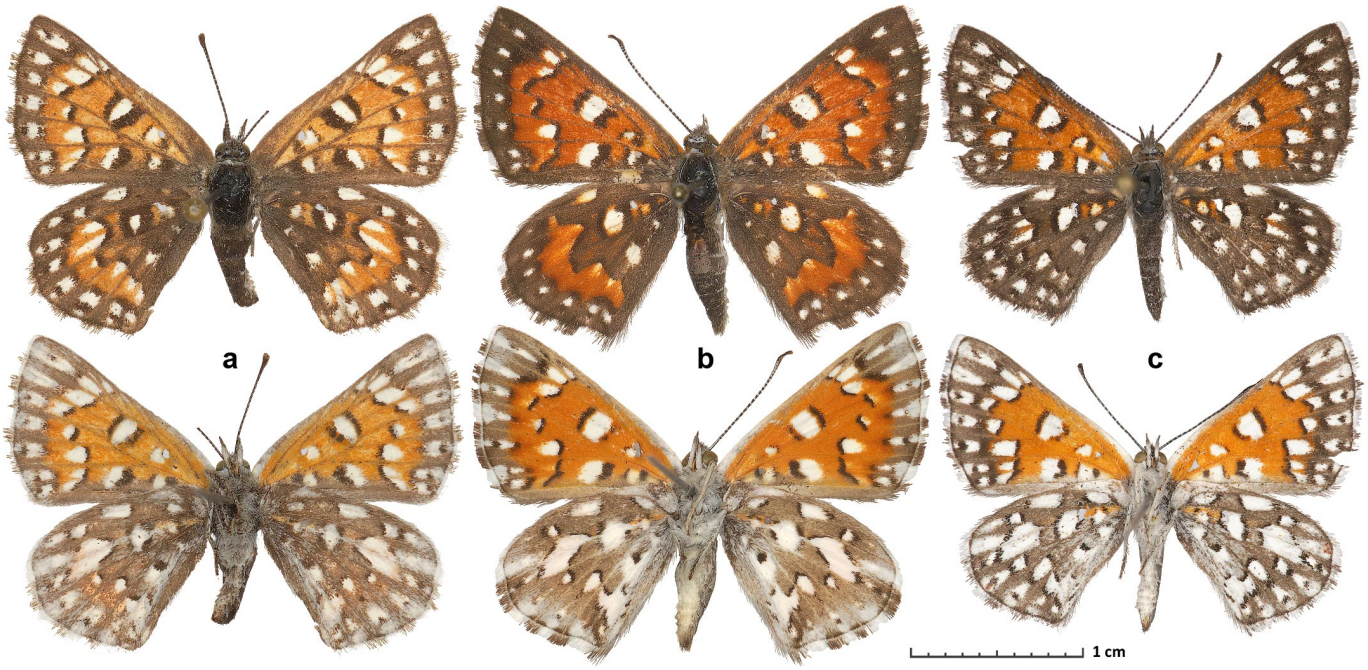

Fig. 28. Three *A. mormo* group species found along Ninemile Canyon, Inyo Co., California, males, K. Davenport leg.: **a)** *A. virgulti davenporti* NVG-20011H04, 1.5 mi E of Tulare Co. line, 18-May-2003; **b)** *A. mormo cythera* NVG-19129C11, 5-Aug-2018; and **c)** *A. deserti deserti* **stat. nov.** NVG-6898, Milepost 4 Canyon, 30-Apr-2010. See Fig. 27 for confirmation of their identification by genomic similarity to the primary type specimens of these taxa.

and their comparison with primary type specimens provide identification from first principles and confirm the presence of three species (Fig. 27). These three "biotypes" of *A. mormo* in Southern California were already discussed in detail by Pratt and Ballmer (1991), who detailed phenotypic and life history differences between them and hypothesized that they may represent three distinct species. Here, through genomic comparison, we demonstrate that these occur along Ninemile Canyon and confirm that they are genetically distinct at the species level. Three specimens of these species are shown in Fig. 28 (highlighted yellow in the trees, Fig. 27). *Apodemia* (*Apodemia*) *virgulti davenporti* J. Emmel, T. Emmel & Pratt, 1998 (type locality USA: California, Kern Co., Walker Pass) is characterized by more developed white spots even within the postdiscal orange bands and yellower orange tones (Fig. 28a). *Apodemia* (*Apodemia*) *mormo cythera* (W. H. Edwards, 1873) (type locality USA: California, Inyo Co., 9 mi W of Lone Pine) has reduced white spotting and is redder in color (Fig. 28b). *Apodemia* (*Apodemia*) *deserti deserti* W. Barnes & McDunnough, 1918, **stat. nov.** (type locality USA: California, San Diego Co., Mason Valley) has a white-spotted brown hindwing (Fig. 28c) and can be distinguished (when alive) by grayish eyes (Fig. 29d), distinct from the greenish-yellow eyes of the other two species (Fig. 29b, c).

Species delimitation in the *Apodemia mormo* group

We used sympatric or nearly sympatric taxa of *Apodemia* that can be confidently identified (either by their eye color or genomic sequencing), as discussed in the two sections above, to learn how they separate in genomic trees and thus calibrate a species-delimitation approach. Our strongest argument for sympatry concerns the pair of taxa in Sycamore Canyon, Santa Cruz Co., Arizona (Fig. 26a, b). Because of this sympatry, we consider *A. mejicanus* and *A. apache* **sp. n.** to be species distinct from each other. They form distinct clades in the Z chromosome tree (Fig. 20a dark blue vs. blue), which agrees with the general notion of how distinct species should segregate in trees.

Next, *A. apache riftoria* **ssp. n.** is likely sympatric with *A. duryi* in southern New Mexico (Fig. 26f, e), and both taxa indeed stand out as prominent non-sister clades in the Z chromosome tree (Fig. 20a red vs. magenta). We note that *A. apache riftoria* **ssp. n.** originates within *A. apache apache* **sp.**

n. (red is a subclade of blue in Fig. 20a), and therefore we do not treat *riftoria* as a species-level taxon but propose it as a subspecies instead. Then, we see that the separation between *A. mejicanus* and *A. duryi* clades (Fig. 20a dark blue vs. magenta) is no less than that between either *A. mejicanus* and *A. apache* **sp. n.** or *A. duryi* and *A. apache riftoria* **ssp. n.** Moreover, *A. duryi* and *A. mejicanus* are not sister clades. Therefore, *A. mejicanus* and *A. duryi* are species distinct from each other. These considerations support recognizing *A. mejicanus*, *A. duryi*, and *A. apache* **sp. n.** as three species distinct from one another and strongly suggest that the *A. mormo* group consists of at least three species.

We find that *A. apache texana* **ssp. n.** is sister to all other *A. apache* **sp. n.** sequenced populations (Fig. 20a cyan vs. blue with orange and brown) and is rather prominently separated from them. Thus, it is conceivable that *A. apache texana* **ssp. n.** is a species-level taxon. However, its separation from other *A. apache* **sp. n.** populations is smaller than that between *A. duryi* and *A. mejicanus*, and we conservatively propose *texana* as a subspecies of *A. apache* **sp. n**. In the autosome tree, *A. apache texana* **ssp. n.** does not segregate from *A. duryi* (Fig. 20b cyan vs. magenta), indicating extensive gene exchange between these two likely sympatric taxa, and suggesting that this exchange may even affect the Z chromosome. Therefore, it is possible that the cyan clade of *A. apache texana* **ssp. n.** is "pulled away" from the rest of *A. apache* **sp. n.** by these regions introgressed from *A. duryi*, instead of suggesting that *texana* is a distinct species. A more detailed population-level study with an emphasis on gene exchange to extend our present phylogenetic-level analysis will help answer these questions about the status of *A. apache texana* **ssp. n.**

Next, we looked for the clades in this tree of the same prominence as those of *A. duryi*, *A. mejicanus*, and *A. apache* **sp. n.** In their immediate neighborhood, only one such clade with 100% bootstrap support remains, the one representing *A. pueblo* **stat. nov.** (Fig. 20a violet with red). It is no less prominent than others and is not confidently associated with any other clade. While it is sister to *A. duryi* (Fig. 20a magenta), the support for this relationship is not strong, only 60%. Except *A. duryi*, *A. pueblo* **stat. nov.** is not monophyletic with any species. This leaves *A. pueblo* **stat. nov.** unassociated with any other species and suggests that it is a species of its own. These arguments explain our treatment of *A. pueblo* **stat. nov.** as a species-level taxon and leave us with four mutually distinct *Apodemia* species: *A. mejicanus*, *A. duryi*, *A. apache* **sp. n.**, and *A. pueblo* **stat. nov.**

Inspection of the *A. pueblo* clade reveals that *A. pueblo mescalero* **ssp. n.** forms a subclade sister to all other *A. pueblo* **stat. nov.** specimens we sequenced (Fig. 20a red). Therefore, both taxa (the nominotypical and *mescalero*) are monophyletic and well supported. However, the separation between the two clades is markedly smaller than the separation we observe between distinct species in this neighborhood of the tree. Hence, we propose *A. pueblo mescalero* **ssp. n.** as a subspecies.

Phenotypically, *A. apache* **sp. n.** is similar to *A. deserti* **stat. nov.**: both have greenish-gray eyes, a blackish, white-spotted hindwing in most individuals, and an orange patch in the middle of the forewing. This pair is likely parapatric, recorded near each other in south-central Arizona (Fig. 31 diamonds vs. stars). Their ranges correlate with the ranges of two different *Eriogonum* species (Fig. 21). In the Z chromosome tree, *A. apache* **sp. n.** and *A. deserti* **stat. nov.** are not sister taxa and they belong to different clades (Fig. 20a blue vs. olive), although in the autosome tree, proximal populations of *A. apache* **sp. n.** experience introgression from *A. deserti* **stat. nov.** (Fig. 20b two blue specimens form a clade sister to olive with pink). Due to their Z chromosome tree non-sister position, *A. apache* **sp. n.** and *A. deserti* **stat. nov**. are not likely to be conspecific, which leads us to accept five mutually distinct *Apodemia* species: *A. mejicanus*, *A. duryi*, *A. apache* **sp. n.**, *A. pueblo* **stat. nov.**, and *A. deserti* **stat. nov**.

Returning to possibly sympatric populations, we see that *A. deserti* **stat. nov**. may co-occur with *A. mormo* northeast of Phoenix, Maricopa Co., Arizona (Fig. 26h, g) and in the Spring Mts., Clark Co., Nevada (Fig. 26d, c), and with both *A. mormo* and *A. virgulti* along Ninemile Canyon, Inyo Co., California (Figs. 27, 28), establishing them as three mutually distinct species. Both *A. mormo* and *A. virgulti* form prominently distinct clades in the Z chromosome tree, not sister to any other taxa and thus being distinct from them all (Fig. 30a). For the distinction of *A. maxima* **stat. rest.**, see a dedicated section above (p. 7) leading us to propose that the *A. mormo* group consists of eight species: *A. mejicanus*, *A. duryi*, *A. apache* **sp. n.**, *A. pueblo* **stat. nov.**, *A. deserti* **stat. nov.**, *A. mormo*, *A. virgulti*, and *A. maxima* **stat. rest**.

A preliminary taxonomic list of the *Apodemia mormo* group

The results of this work are summarized in a preliminary taxonomic list of the *A. mormo* group species, subspecies, and synonyms. We arrange species into subgroups (not an ICZN-regulated category), which are not necessarily monophyletic, but one subgroup stands out by its grayish eye color, aiding its identification in the field (Fig. 29). Species are ordered to maximize phenotypic similarity and geographic proximity among the list neighbors without disrupting the confidently supported phylogenetic order in the Z chromosome tree (Fig. 30d): i.e., a strongly supported clade in the tree is a contiguous segment in the list. The range of the *A. mormo* group (Fig. 31) can be approximated by a circle with many taxa confined to its boundary, set by the ocean in the west, the west–east biota boundary in the east, and northern Mexico in the south. To arrange taxa by geographic proximity without violating the phylogeny, this circle is cut at the Gulf of California, because we noticed that *A. maxima* **stat. rest.** and *A. mejicanus* are most distinct genetically from each other, belonging to two different major clades (Fig. 30), despite their phenotypic similarity (more orange, less brown, larger white spots) that is probably convergent. The choice of *A. maxima* **stat. rest.** as the first taxon in the list sets the order dictated by the phylogeny and geographic proximity that ends with *A. mejicanus*. The category of taxonomic change is shown in red font. Comments are given following a vertical bar | after the type locality; an equal sign = precedes junior subjective synonyms given in their original genus combinations, and ‡ is added to indicate a junior objective synonym. The list covers 33 valid taxa (with 2 subjective and 1 objective synonyms) comprising 8 species (1 new and 3 elevated from subspecies) and 25 additional subspecies (12 new).

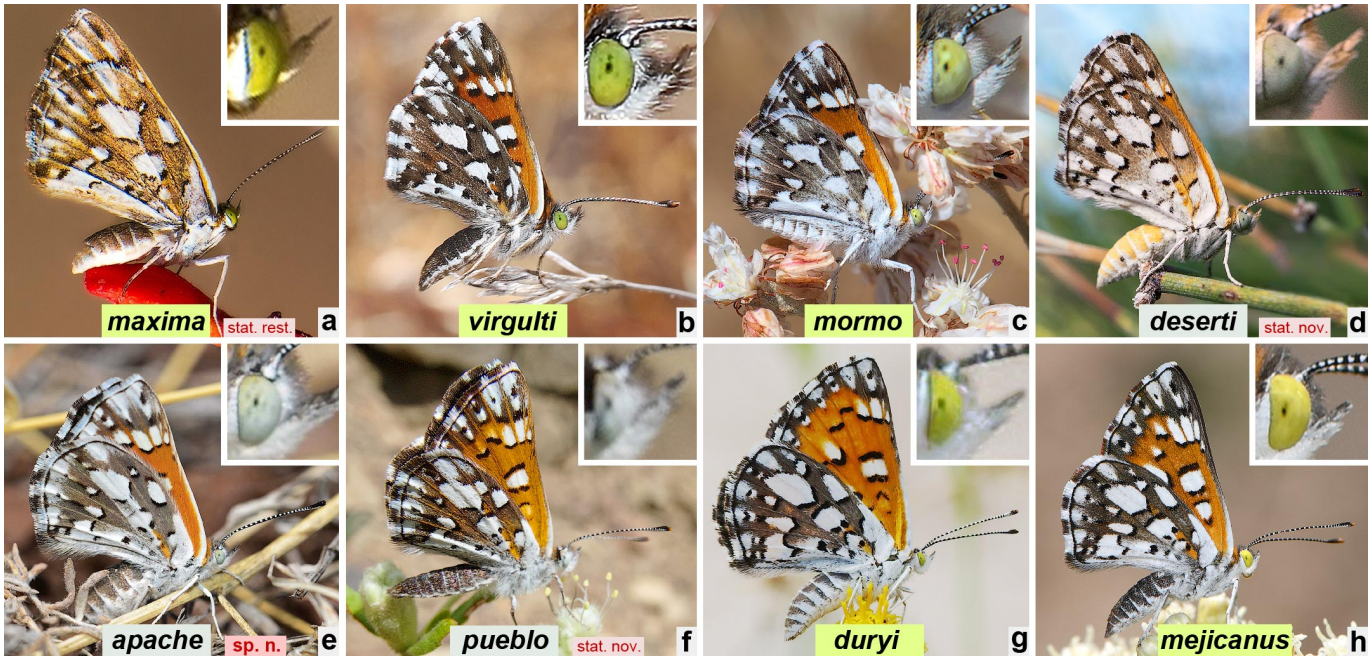

Fig. 29. Eye color of all valid *A. mormo* group species, iNaturalist observations: **a)** *A. maxima maxima* **stat. rest.**, observation No. 320589989 Mexico: B.C.S., La Paz, 24.2450, −110.1505, 12-Oct-2025 © Diana Laura G López; **b)** *A. virgulti peninsularis*, observation No. 290779073 USA: California, San Diego Co., Roberts Ranch Trailhead, 32.8236, −116.6270, 9-Jun-2025 © datrinite; **c)** *A. mormo mormo*, observation No. 179159474 USA: Oregon, Wasco Co., White River Falls SP, 45.2413, −121.0935, 18-Aug-2023 © Zach Kemp; **d)** *A. deserti deserti* **stat. nov.**, observation No. 139085470 USA: California, San Diego Co., Anza-Borrego Desert State Park, Ranchita, 33.1044, −116.4755, 16-Oct-2022 © Jess Mullins; **e)** *A. apache apache* **sp. n.**, observation No. 103907181 USA: Arizona, Apache Co., Greens Peak Rd. W of Springerville, 3-May-2011 © Ken Kertell; **f)** *A. pueblo pueblo* **stat. nov.**, observation No. 30457313 USA: Colorado, Las Animas Co., TNC's Fisher's Peak Ranch, 37.0144, −104.4785, 24-Jun-2019 © Christian Nunes; **g)** *A. duryi*, observation No. 160241468 USA: Texas, Brewster Co., Big Bend National Park, May-2023 (data obscured) © Dennis Vollmar; **h)** *A. mejicanus*, observation No. 243828867 USA: Arizona, Santa Cruz Co., Atascosa Mts., Rd. to California Gulch off Ruby Rd. 23-Sep-2024 © Ken Kertell; images are color-corrected, brightened, rotated, cropped, and some flipped, CC BY-NC 4.0 https://creativecommons.org/licenses/by-nc/4.0/. Insets show a magnified view of the head of the same specimen. Species names are given below images on a background representing the typical eye color of these species. Photographs were taken by different cameras in different lighting conditions and white balance settings; therefore, colors may not be fully comparable between images. Nevertheless, the greenish-yellow tint of the eyes in **a–c)** and **g–h)** vs. more grayish eyes in **d–f)** is conveyed.

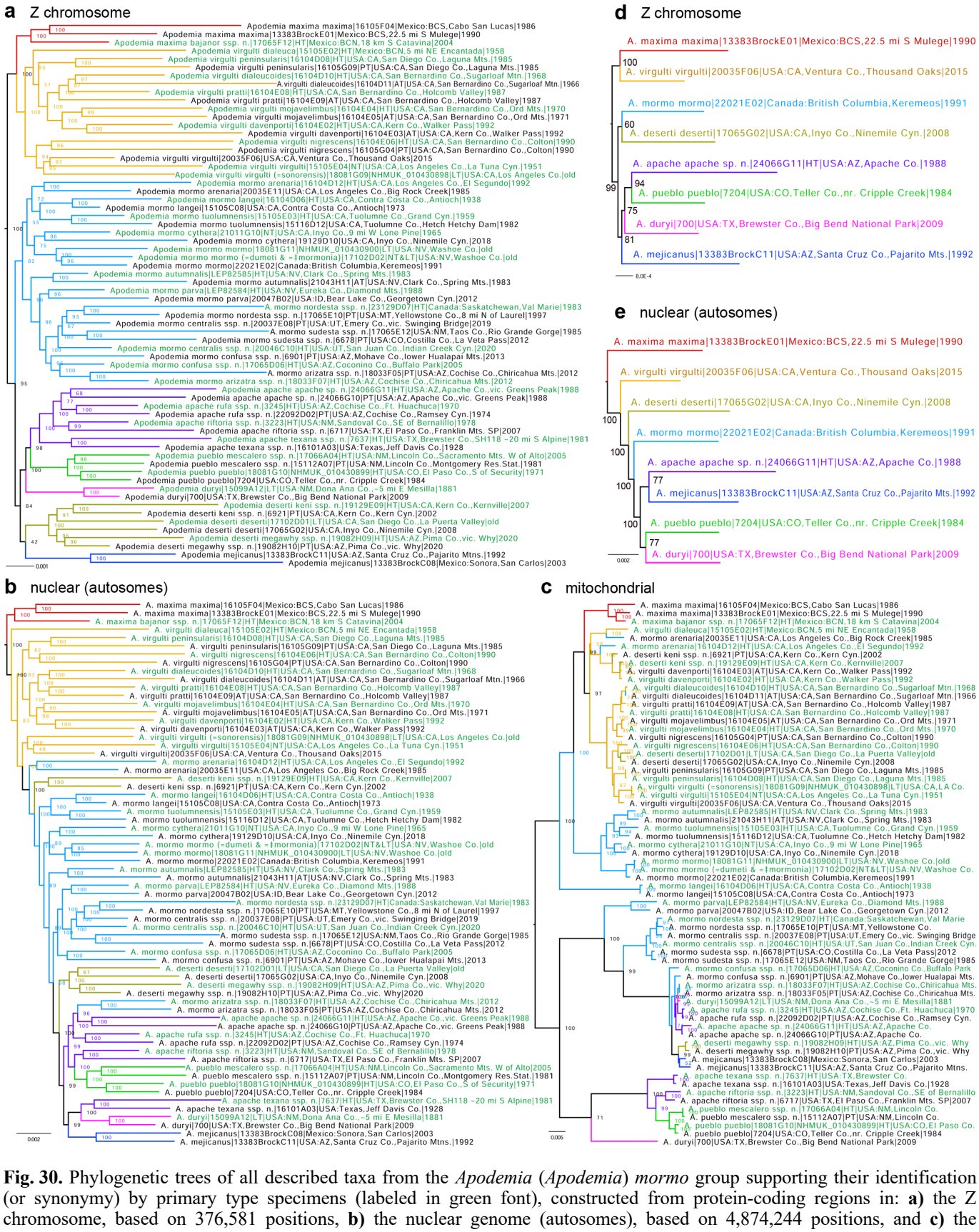

Fig. 30. Phylogenetic trees of all described taxa from the *Apodemia* (*Apodemia*) *mormo* group supporting their identification (or synonymy) by primary type specimens (labeled in green font), constructed from protein-coding regions in: **a)** the Z chromosome, based on 376,581 positions, **b)** the nuclear genome (autosomes), based on 4,874,244 positions, and **c)** the mitochondrial genome. Trees including one specimen per species (with a higher-quality genomic dataset) were constructed similarly from: **d)** the Z chromosome, based on 498,714 positions; and **e)** the nuclear genome (autosomes), based on 12,294,045 positions. Different species are colored differently: *A. maxima* **stat. rest.** (red), *A. virgulti* (orange), *A. mormo* (blue), *A. deserti* **stat. nov.** (olive), *A. apache* **sp. n.** (violet), *A. pueblo* **stat. nov.** (green), *A. duryi* (magenta), and *A. mejicanus* (dark blue). Ultrafast bootstrap (Hoang et al. 2018) values are shown at nodes.

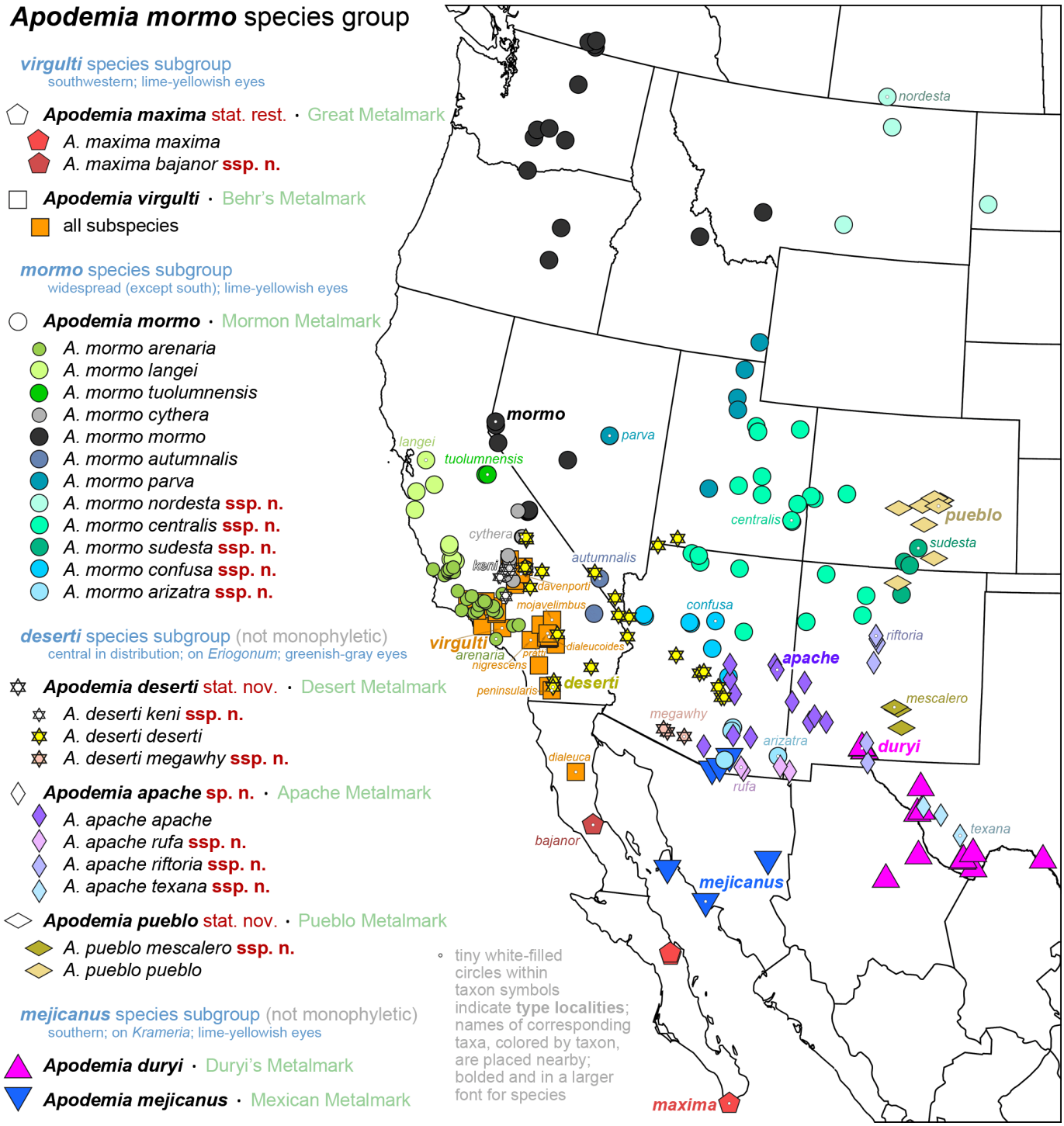

Fig. 31. Map of sequenced specimens of the *Apodemia* (*Apodemia*) *mormo* group. Species are indicated by symbol shape and subspecies by color, as detailed in the legend within the figure. *Apodemia maxima* **stat. rest.** (circles): *A. maxima maxima* (red) and *A. maxima bajanor* **ssp. n.** (dark red); *A. virgulti* (squares, orange for all subspecies, labeled with their names on the map; arrows point to their type localities in the USA: California); *A. mormo* (circles): *A. mormo arenaria* **comb. rest.** (yellow-green, smaller), *A. mormo langei* (pale yellow-green), *A. mormo tuolumnensis* (green), *A. mormo cythera* (gray, smaller), *A. mormo mormo* (black), *A. mormo autumnalis* (slate blue), *A. mormo parva* (teal), *A. mormo nordesta* **ssp. n.** (pale cyan), *A. mormo centralis* **ssp. n.** (turquoise), *A. mormo sudesta* **ssp. n.** (dark green), *A. mormo confusa* **ssp. n.** (sky blue), and *A. mormo arizatra* **ssp. n.** (pale blue); *A. deserti* **stat. nov.** (stars): *A. deserti keni* **ssp. n.** (white, smaller), *A. deserti deserti* (yellow), and *A. deserti megawhy* **ssp. n.** (pink); *A. apache* **sp. n.** (vertical diamonds): *A. apache apache* (violet), *A. apache rufa* **ssp. n.** (pale lavender), *A. apache riftoria* **ssp. n.** (periwinkle), and *A. apache texana* **ssp. n.** (pale blue); *A. pueblo* **stat. nov.** (horizontal diamonds): *A. pueblo mescalero* **ssp. n.** (olive) and *A. pueblo pueblo* (tan); *A. duryi* (upright triangle, magenta); and *A. mejicanus* (inverted triangle, dark blue). Type localities are marked with tiny white circles inside the symbols, and the names of corresponding taxa are placed nearby; species names are shown in a bold, larger font.

Genus ***Apodemia*** C. Felder & R. Felder, 1865; type species *Lemonias mormo* C. Felder & R. Felder, 1859
Subgenus ***Apodemia*** C. Felder & R. Felder, 1865; type species *L. mormo*
= *Chrysobia* Boisduval, 1869; type species =‡*Chrysobia mormonia* Boisduval, 1869 (valid name is *L. mormo*)
mormo species group

virgulti species subgroup | southwestern; lime-yellowish eyes

Apodemia maxima (Weeks, 1891), **stat. rest.**; Mexico: BCS, Los Cabos Mpio. | not *mejicanus*
Apodemia maxima maxima (Weeks, 1891); Mexico: BCS, Los Cabos Mpio. | not *mejicanus*
Apodemia maxima bajanor Grishin, **ssp. n.**; Mexico: BC (Norte), San Quintín Mpio.

Apodemia virgulti (Behr, 1865); USA: CA, Los Angeles Co.
Apodemia virgulti dialeuca Opler & Powell, 1962; Mexico: BC (Norte), Ensenada Mpio.
Apodemia virgulti peninsularis J. Emmel, T. Emmel & Pratt, 1998; USA: CA, San Diego Co.
Apodemia virgulti dialeucoides J. Emmel, T. Emmel & Pratt, 1998; USA: CA, San Bernardino Co.
Apodemia virgulti pratti J. Emmel & T. Emmel, 1998; USA: CA, San Bernardino Co.
Apodemia virgulti mojavelimbus J. Emmel, T. Emmel & Pratt, 1998; USA: CA, San Bernardino Co.
Apodemia virgulti davenporti J. Emmel, T. Emmel & Pratt, 1998; USA: CA, Kern Co.
Apodemia virgulti nigrescens J. Emmel & T. Emmel, 1998; USA: CA, San Bernardino Co.
Apodemia virgulti virgulti (Behr, 1865); USA: CA, Los Angeles Co.
= *Apodemia sonorensis* C. Felder & R. Felder, 1865; USA: CA, Los Angeles Co. | junior subjective synonym

mormo species subgroup | widest range except south; lime-yellowish eyes

Apodemia mormo (C. Felder & R. Felder, 1859); USA: NV, Washoe Co.
Apodemia mormo arenaria J. Emmel, T. Emmel & Pratt, 1998; USA: CA, Los Angeles Co. | not *virgulti*
Apodemia mormo langei J. A. Comstock, 1939; USA: CA, Contra Costa Co.
Apodemia mormo tuolumnensis Opler & Powell, 1962; USA: CA, Tuolumne Co.
Apodemia mormo cythera (W. H. Edwards, 1873); USA: CA, Inyo Co.
Apodemia mormo mormo (C. Felder & R. Felder, 1859); USA: NV, Washoe Co.
= *Nemeobius dumeti* Behr, 1865; USA: NV, Washoe Co. | junior subjective synonym
=‡*Chrysobia mormonia* Boisduval, 1869; USA: NV, Washoe Co. | junior objective synonym of *N. dumeti*
Apodemia mormo autumnalis Austin, 1998; USA: NV, Clark Co., Spring Mts.
Apodemia mormo parva Austin, 1998; USA: NV, Eureka Co., Diamond Mts.
Apodemia mormo nordesta Grishin, **ssp. n.**; Canada: Saskatchewan, vic. Val Marie
Apodemia mormo centralis Grishin, **ssp. n.**; USA: UT, San Juan Co.
Apodemia mormo sudesta Grishin, **ssp. n.**; USA: CO, Costilla Co.
Apodemia mormo confusa Grishin, **ssp. n.**; USA: AZ, Coconino Co.
Apodemia mormo arizatra Grishin, **ssp. n.**; USA: AZ, Cochise Co.

deserti species subgroup | not monophyletic; central in distribution; on *Eriogonum*; greenish-gray eyes

Apodemia deserti W. Barnes & McDunnough, 1918, **stat. nov.**; USA: CA, San Diego Co. | not *mejicanus*
Apodemia deserti keni Grishin, **ssp. n.**; USA: CA, Kern Co.
Apodemia deserti deserti W. Barnes & McDunnough, 1918; USA: CA, San Diego Co.
Apodemia deserti megawhy Grishin, **ssp. n.**; USA: AZ, Pima Co.

Apodemia apache Grishin, **sp. n.**; USA: AZ, Apache Co., White Mts.
Apodemia apache apache Grishin; USA: AZ, Apache Co., White Mts.
Apodemia apache rufa Grishin, **ssp. n.**; USA: AZ, Cochise Co., Huachuca Mts.
Apodemia apache riftoria Grishin, **ssp. n.**; USA: NM, Sandoval Co., Sandia Mts.
Apodemia apache texana Grishin, **ssp. n.**; USA: TX, Brewster Co., Del Norte Mts.

Apodemia pueblo J. Scott, 1998, **stat. nov.**; USA: CO, El Paso Co. | not *mejicanus*
Apodemia pueblo mescalero Grishin, **ssp. n.**; USA: NM, Lincoln Co., Sacramento Mts.
Apodemia pueblo pueblo J. Scott, 1998; USA: CO, El Paso Co. | not *mejicanus*

mejicanus species subgroup | not monophyletic; southern; on *Krameria*; lime-yellowish eyes

Apodemia duryi (W. H. Edwards, 1882); USA: NM, Doña Ana Co.
Apodemia mejicanus (Behr, 1865); Mexico: Sonora, Guaymas Mpio. | monotypic

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