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Three butterfly genera across the Central Texas Suture Zone

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ABSTRACT. Genome-scale analyses of butterfly specimens across the Central Texas Suture Zone revealed that several taxa currently treated as subspecies exhibit genomic differentiation similar to that observed between species. Further investigation and genomic sequencing of additional specimens from across the ranges of these taxa support this conclusion and result in the following changes to nomenclature and taxonomy. Two new subspecies of Nymphalidae Rafinesque, 1815 are described: *Asterocampa louisa monterra* Grishin, **ssp. n.** (type locality in Mexico: Nuevo León) and *Asterocampa clyton plana* Grishin, **ssp. n.** (type locality in USA: Texas, Denton Co.). The following taxa are recognized as species, not subspecies: *Asterocampa louisa* D. Stallings & Turner, 1947, **stat. nov.** (not *Asterocampa clyton* (Boisduval & Le Conte, [1835])), *Libytheana bachmanii* (Kirtland, 1851), **stat. rest.** and *Libytheana larvata* (Strecker, [1878]), **stat. rest.** (not *Libytheana carinenta* (Cramer, 1777)) in Nymphalidae; *Polites* (*Wallengrenia*) *clavus* (Erichson, [1849]), **stat. rest.** and *Polites* (*Wallengrenia*) *jobrea* (Dyar, 1918), **stat. rest.** (not *Polites* (*Wallengrenia*) *otho* (J. E. Smith, 1797)) in Hesperiidae Latreille, 1809. The following are valid subspecies, not junior subjective synonyms: *Asterocampa clyton subpallida* (W. Barnes & McDunnough, 1913), **stat. rest.** (not *Asterocampa clyton texana* (Skinner, 1911)), *Asterocampa leilia cocles* (Lintner, [1885]), **stat. rev.** (not *Asterocampa leilia leilia* (W. H. Edwards, 1874)), *Asterocampa celtis montis* (W. H. Edwards, 1883), **stat. rest.** and *Asterocampa celtis jeffermont* J. Scott & M. Fisher, 2008, **stat. rest.** (not *Asterocampa celtis antonia* (W. H. Edwards, [1878])), and *Asterocampa celtis alicia* (W. H. Edwards, 1868), **stat. rev.** (not *Asterocampa celtis celtis* (Boisduval & Le Conte, [1835])). *Libytheana carinenta fulvescens* (Lathy, 1904), **stat. nov**. is not a species but a subspecies-level taxon. Nomen nudum "*Pamphila lacordairii*, Boisd." published by Godman (1900) belongs in synonymy with *Polites* (*Wallengrenia*) *clavus*, **stat. rest.** and not with *P.* (*W.*) *otho*. A **lectotype** of *Libythea larvata* Strecker, [1878] (type locality in USA: Texas, Bexar Co.) is designated. *Doxocopa laure laure* (Drury, 1773) is recorded for the United States from southeastern Arizona. Taxonomic lists of *Asterocampa* Röber, 1916 and *Libytheana* Michener, 1943 are provided.

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

ZooBank registration: https://zoobank.org/82379027-DA60-4AE3-80EF-4796A2283135

INTRODUCTION

Historically, the concept of a suture zone was introduced by Remington (1968) to describe a restricted geographic region that serves as a collective boundary for many pairs of closely related parapatric or narrowly sympatric species. While most North American suture zones are situated in the western half of the continent and are typically defined by prominent mountain ranges, more nuanced zones exist to the east. These eastern zones often lack conspicuous physical barriers, complicating the identification of isolation mechanisms between species. Despite academic debate regarding the validity of some of Remington's original designations (Swenson and Howard 2004), the Central Texas Suture Zone remains a well-documented contact point for eastern and western populations. This is particularly evident in avian studies, which identify over 20 pairs that split into distinct species along this Texas boundary (Newton 2003; Swenson and Howard 2005). Remington (1968) characterized the Central Texas Suture Zone as a "mature zone," noting that many of these species pairs maintain strong reproductive isolation and exhibit

minimal hybridization upon contact (Rising 1983). A similar pattern is observed in Lepidoptera, with at least 25 butterfly species pairs reaching their contact zones in Central Texas (Scott 1986).

Not all groups of populations on different sides of a suture zone correspond to different species, and many species freely cross the zone. Thus, suture zones offer a model for studying speciation and understanding the differences between species that are constrained by the zone and those distributed on both sides of it. To investigate the genomic signatures and evolutionary scenarios of speciation across the Central Texas Suture Zone, we sampled 25 butterfly species pairs spanning the eastern and western boundaries of this transition. For each pair, we performed RNA-seq analysis to study their genetic divergence (Cong et al. 2019a and in press). The "eastern" populations typically represent taxa broadly distributed across the eastern USA, extending from Texas to Florida and northward into Canada; these regions are generally characterized by a cooler, more humid climate. Conversely, the "western" populations encompass taxa distributed from central Texas southward into Mexico and often westward toward the Pacific coast. This southwestern zone is notably warmer and more arid, particularly as one moves farther west.

The 25 selected pairs of butterfly populations represented the entire spectrum along the speciation continuum (Powell et al. 2013), from conspecific populations, through putative incipient species to well-differentiated species. As a result of that study (Cong et al. 2019a and in press), we found that divergence and gene exchange in the Z chromosome serve best to distinguish between distinct species and conspecific populations. All pairs that were considered well-differentiated species exhibited larger F_{st} (a measure of genetic divergence) and smaller G_{min} (a measure of gene flow or hybridization). Confidently conspecific pairs show $F_{st} < 0.1$ and $G_{min} > 9\%$, as expected for closely related populations. Notably, several taxa currently classified as subspecies exhibit genetic differentiation levels consistent with those of reproductively isolated species.

Here, we build upon that study and focus on the nomenclature and taxonomy of three genera: *Asterocampa* Röber, 1916 and *Libytheana* Michener, 1943 in Nymphalidae Rafinesque, 1815, and *Polites* Scudder, 1872 (subgenus *Wallengrenia* Berg, 1897) in Hesperiidae Latreille, 1809. In these genera, we previously found that taxa currently recognized as subspecies are genetically differentiated at the species level (Cong et al. 2019a and in press), and therefore taxonomic changes should be made. Our previous work was of a more general nature, presenting the method and addressing the functions of proteins associated with speciation, and thus did not include taxonomic adjustments. The present work aims to examine the taxonomic status of species and subspecies in these genera. In addition to using whole-genome shotgun data instead of RNA-seq, we also sequenced a larger number of specimens from across their ranges. Although primarily North American taxa are analyzed, we include comprehensive taxonomic coverage of the two genera (*Asterocampa* and *Libytheana*) and revise their nomenclature and taxonomy, which are summarized as synonymic lists.

MATERIALS AND METHODS

Here, we use the same methods and 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; Zhang et al. 2023b–d; Zhang et al. 2024a–c; Zhang et al. 2025a–d). Specimens used mostly come from museum and private collections (see Acknowledgments for a list), along with some collected in the field by the authors. When possible, we obtain whole-genome shotgun datasets of primary type specimens to serve as objective references for species and subspecies names (Cong et al. 2021; Zhang et al. 2022a). A single leg is usually used for DNA extraction, which is carried out non-destructively to enable subsequent morphological examination. If DNA is not already degraded due to age, it is fragmented prior to genomic library construction. An illumina platform generating 150-base-pair (bp) reads is used for sequencing. Our protocols do not rely on the amplification of specific genes; instead, we sequence all extracted DNA. Consequently, the method is applicable to century-old specimens with highly fragmented DNA, frequently ~30–50 bp in length.

For each specimen, we use all sequencing reads to assemble exons of protein-coding genes as guided by a reference genome available for a closely related species. We construct three phylogenetic trees using IQ-TREE v1.6.12 under the GTR+GAMMA model (Nguyen et al. 2015): one from genes inferred to reside on the Z chromosome, a second based on autosomal (nuclear) loci, and a third derived from the mitochondrial genome. All codon positions represented by the majority of specimens are included in an alignment that is generated dynamically and not saved, and the total number of positions used in each nuclear genome tree (from several hundred thousand to several million) is reported in the corresponding figure legends. Mitochondrial genomes are approximately 15,000 bp in length. We use ultrafast bootstrap to quantify statistical significance: support $>97\%$ is regarded as strong; values $<90\%$ are considered weak and indicate unresolved relationships or significant gene flow (Hoang et al. 2018). Additional details of the protocols we use are provided in our publications (Li et al. 2019; Zhang et al. 2022b).

Phylogenetic trees are visualized, rotated, and colored using FigTree (Rambaut 2018). Our taxonomic conclusions stem from genomic phylogenies, with phenotypic evidence used for additional support. This strategy reflects the vast amount of information present in genomes, which encompass not only characters manifested in adult wing patterns and genitalia that have traditionally been used in butterfly taxonomy, but also genetic signals associated with life history, ecological networks, reproductive biology, and diet. Although direct prediction of phenotypes from genomic sequences is not yet possible, combined datasets of protein-coding DNA function as crucial proxies, and well-supported phylogenies provide a framework that guides taxonomic research. Collectively, this analysis results in a taxonomic framework that is congruent with both evolutionary history and genomic evidence.

The present study focuses on taxa at the species and subspecies ranks. Species limits are assessed using multiple criteria, 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 and in press), COI barcode divergence of approximately $>2\%$ (Hebert et al. 2003) coupled with phenotypic differentiation (Lukhtanov et al. 2016), and the presence of prominent, strongly supported clades in phylogenetic trees (Zhang et al. 2022c). Because mitochondrial genomes frequently introgress across species (Bachtrog et al. 2006; Cong et al. 2017), some species may share identical COI barcode sequences (Burns et al. 2008; Zhang et al. 2023a). Additional discussion of these criteria is given by Zhang et al. (2022a) in the section “Species, subspecies, and genomics.”

Subspecies represent early stages in the speciation process of diverging populations that have not yet developed sufficient reproductive isolation. Subspecies are geographically isolated groups of populations characterized by consistent phenotypic traits, traditionally satisfying the '75% rule', while retaining the capacity for interbreeding (Mayr 1982; Monroe 1982). In practice, because reproductive compatibility is seldom verified, butterfly subspecies are predominantly established through wing pattern differences. Consequently, it remains a challenge to determine if such subspecies represent distinct genomic lineages or merely plastic responses to environmental variables. We use a combination of phylogenetic and phenotypic evidence to delimit subspecies. Because our subspecies delimitation stems from genomic analysis, the DNA characters for subspecies that we provide in descriptions are stronger than morphological characters and are expected to hold for nearly all specimens. While many subspecies correspond to confidently supported clades that do not yet meet the criteria of distinct species, we recognize that not all subspecies need to be monophyletic, and some subspecies may originate within others by gaining a phenotypic trait (Zhang et al. 2026).

For newly described subspecies, we give a justification for their validity and a brief comparative description of phenotypic characters, together with diagnostic DNA characters in the nuclear genome. DNA characters are deduced from protein-coding genes using our established protocol (see SI Appendix in Li et al. (2019)). The strategy for finding robust DNA characters, detailed in Cong et al. (2019b), aims at providing diagnoses that are expected to hold as additional specimens, subspecies, and species are added to the analysis.

DNA character states are given relative to the reference genome of *Heliconius melpomene* (Linnaeus, 1758) (hm) (Davey et al. 2016). The notation used is as follows: hm1547.7.2:T197C meaning

position 197 in exon 2 of gene 7 from scaffold 1547 of the *H. melpomene* reference genome (hm) is C, having changed from T in the ancestor. When characters are specified for the sister clade of the diagnosed taxon, the following notation is used: hm630.5.7:C93C (not T) meaning that position 93 in exon 7 of gene 5 on scaffold 630 is occupied by the ancestral base pair C, which was changed to T in the sister clade (so it is not T in the diagnosed taxon). 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/wqmv6. Providing this link to these sequences with highlighted character positions 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 on appearance and locality, without DNA sequencing of these specimens; therefore, some identifications may be erroneous.

Whole-genome shotgun datasets obtained in this study will be deposited in the NCBI database (https://www.ncbi.nlm.nih.gov) under BioProject PRJNA1436023. Associated BioSample records contain more detailed locality information and further label data for specimens included in the phylogenetic trees. Tree figures provide abbreviated information about each specimen, with data fields separated by vertical bars "|": taxon name, DNA sample code, type status, locality, and year of collection ("old" if not stated on the labels and likely collected 100–150 years ago). Type status abbreviations are: HT holotype, LT lectotype, ST syntype, NT neotype, PT paratype, and PLT paralectotype. 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 with accessions PZ138018–PZ138020. Abbreviations or acronyms for collections are listed in the Acknowledgments, and UTSW stands for the freezers in the Grishin lab.

RESULTS AND DISCUSSION

Analysis of genetic differentiation and gene flow between pairs of closely related taxa separated by the Central Texas Suture Zone revealed several cases in which distinct species are currently treated as subspecies (Cong et al. 2019a and in press). Because it did not focus on taxonomy or nomenclature, that study did not propose any changes in the status of the taxa involved. Here, we simply formalize some findings from Cong et al. (2019a, and in press) and place them in the context of current taxonomy. Specifically, we carry out a more detailed taxonomic analysis of the genera *Asterocampa* Röber, 1916 and *Libytheana* Michener, 1943 and the subgenus *Wallengrenia* Berg, 1897 (of *Polites* Scudder, 1872), focusing on species known from the United States.

Family Nymphalidae Rafinesque, 1815

Asterocampa louisa D. Stallings & Turner, 1947 is a species distinct from *Asterocampa clyton* (Boisduval & Le Conte, [1835])

As the genomic analysis demonstrates (Cong et al. 2019a and in press) (Figs. 1a–c, 13), *Asterocampa clyton louisa* D. Stallings & Turner, 1947 (type locality in USA: Texas, Hidalgo Co.) originally described as a subspecies, is genetically differentiated from *Asterocampa clyton* (Boisduval & Le Conte, [1835]) (type locality in USA: Georgia, Burke Co.) at the species level. Therefore, we propose that *Asterocampa louisa* D. Stallings & Turner, 1947, **stat. nov.** is a species distinct from *Asterocampa clyton* (Boisduval & Le Conte, [1835]). In the United States, *A. louisa* **stat. nov.** is recorded from the Lower Rio Grande Valley region. Phenotypically (Figs. 2, 3), it is distinguished from *A. clyton* (Figs. 1d–g, 4) by a paler, less tawny appearance, more similar in ground color to *Asterocampa celtis* (Boisduval & Le Conte, [1835]) (type locality in USA: Georgia, Burke Co.) (Figs. 5d–g, 6). We suggest "Tan Emperor" as the English name for *A. louisa* due to the more washed-out, less vibrant, and grayer coloration of this species.

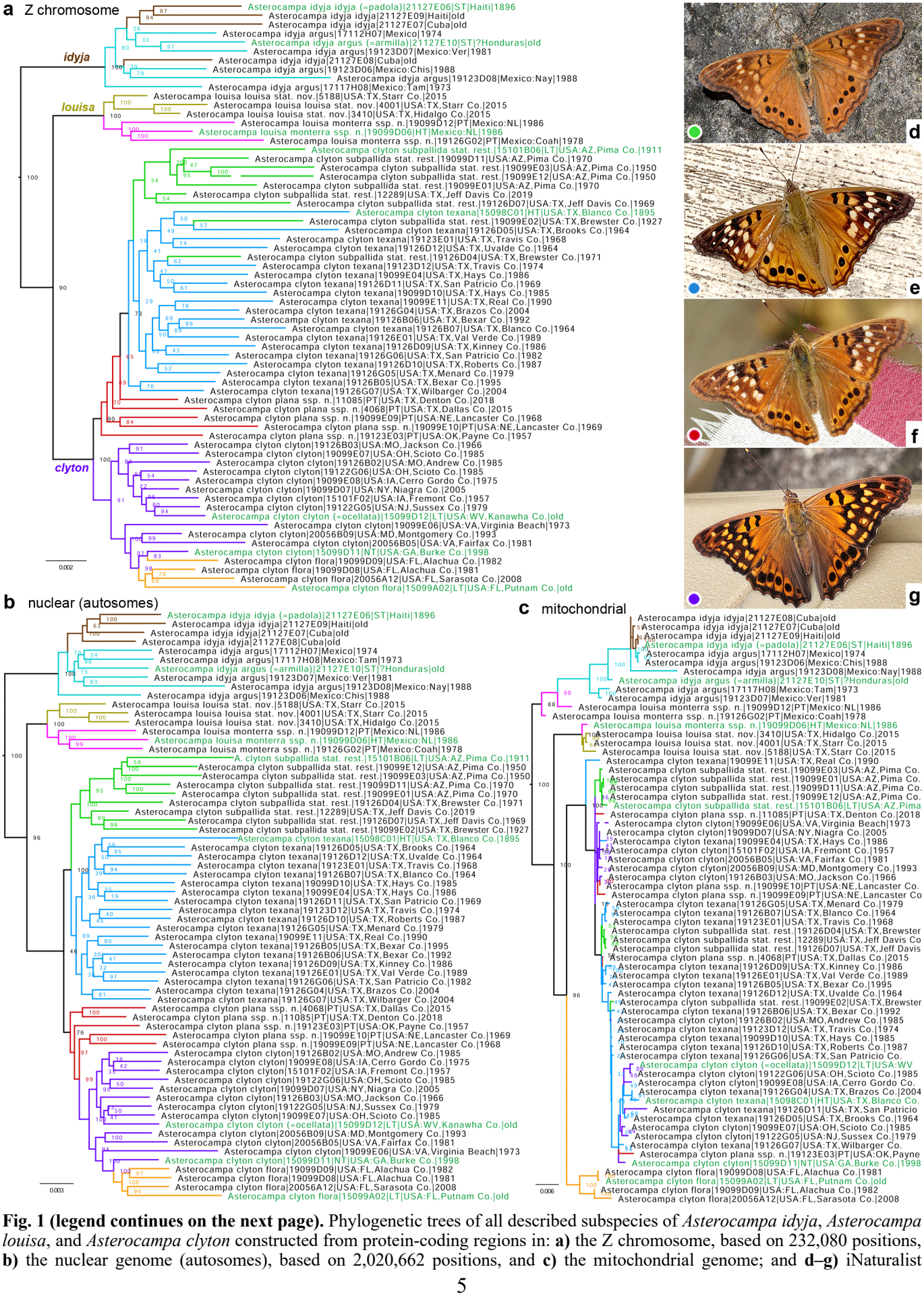

Fig. 1 (legend continues on the next page). Phylogenetic trees of all described subspecies of *Asterocampa idyja*, *Asterocampa louisa*, and *Asterocampa clyton* constructed from protein-coding regions in: **a)** the Z chromosome, based on 232,080 positions, **b)** the nuclear genome (autosomes), based on 2,020,662 positions, and **c)** the mitochondrial genome; and **d–g)** iNaturalist

observations (the color of the dot in the lower left of each image corresponds to the color of the species in the trees): **d)** *A. clyton subpallida* **stat. rest.** observation No. 245956963, USA: Arizona, Pima Co., Santa Rita Mts., Florida Canyon, GPS 31.7598, −110.8447, 5-Oct-2024 © Ken Kertell; **e)** *A. clyton texana* observation No. 275929630, USA: Texas, Comal Co., New Braunfels, Landa Park, GPS 29.7088, −98.1363, 28-Apr-2025 © dtroup; **f)** *A. clyton plana* **ssp. n.** observation No. 8286534, USA: Texas, Dallas Co., Oct-2017 (obscured) © Richard Barnes; **g)** *A. clyton clyton* observation No. 304075492 (photo 548126734) USA: Tennessee, Hamilton Co., Chattanooga, GPS 35.0898, −85.2657, 5-Aug-2025 © Curtis Burke; 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 different subspecies are colored differently: *A. idyja idyja* (brown), *A. idyja argus* (cyan), *A. louisa louisa* **stat. nov.** (olive), *A. louisa monterra* **ssp. n.** (magenta), *A. clyton subpallida* **stat. rest.** (green), *A. clyton texana* (blue), *A. clyton plana* **ssp. n.** (red), *A. clyton clyton* (violet), and *A. clyton flora* (orange). Clades corresponding to species are labeled in the Z chromosome tree. Ultrafast bootstrap (Hoang et al. 2018) values are shown at nodes. Gaps in terminal branches indicate that a segment of a branch was cut out to reduce its length; i.e., the branch with the gap is longer than shown.

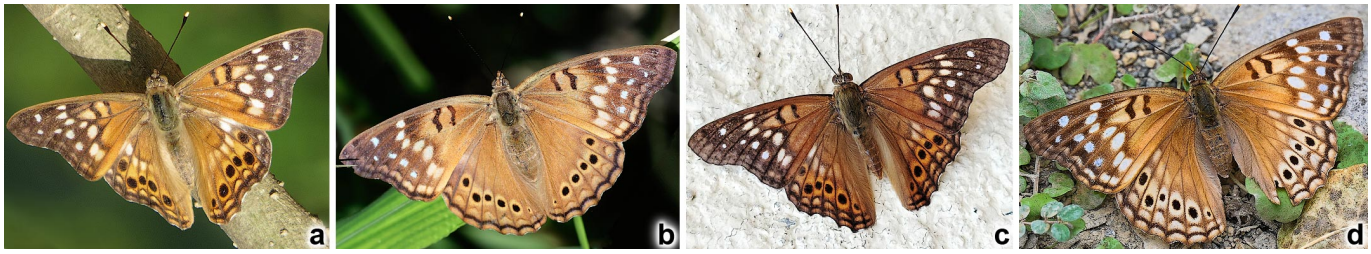

Fig. 2. Subspecies of *Asterocampa louisa* **stat. nov.**, iNaturalist observations: **a–b)** *A. louisa louisa* from USA, Texas, Hidalgo Co., Mission, National Butterfly Center, GPS 26.1798, −98.3665: **a)** ♂ observation No. 250711310, 6-Nov-2024 © marylusk and **b)** ♀ observation No. 330190036, 7-Dec-2025 © Roger Woodruff; **c–d)** *A. louisa monterra* **ssp. n.** from Mexico, Nuevo León, Monterrey: **c)** ♂ observation No. 214825406, GPS 25.6473, −100.2659, 10-May-2024 © Rodolfo Salinas Villarreal; **d)** ♀ observation No. 137573737, GPS 25.5635, −100.2588, 3-Oct-2022 © Jose S. Garza Herrera; images are brightened, rotated, cropped, and (a) flipped (left-right inverted); CC BY-NC 4.0 https://creativecommons.org/licenses/by-nc/4.0/.

Asterocampa louisa monterra Grishin, new subspecies

https://zoobank.org/A67AC3F7-C19F-4416-9CAA-181D1FC03B07

(Figs. 1a–c part, 2c–d, 3, 13 part)

Definition and diagnosis. Genomic analysis reveals that populations of *Asterocampa louisa* D. Stallings & Turner, 1947, **stat. nov.** (type locality in USA: Texas, Hidalgo Co.) from Coahuila and Nuevo León in Mexico form a distinct clade in both nuclear genome trees (Figs. 1a, b, 13a, b) and are genetically differentiated from the nominotypical populations at the subspecies level. Therefore, these Mexican populations represent a new subspecies. It is similar to the nominotypical subspecies (Fig. 2a, b) in having less saturated, grayer brown tones of the wings with well-developed pale spots (Figs. 2c, d, 3), which are even more contrasty in appearance; and differs by males with characteristically darker brown (vs. yellower in the nominotypical subspecies) ground color of the dorsal side of wings (basal half of the forewing and the hindwing) and a more frequently present submarginal eyespot in the forewing cell CuA_1-CuA_2; and by females with larger pale spots in the discal forewing band and a more prominently two-toned dorsal hindwing with a browner basal half and a paler, grayer distal half. This two-toned hindwing pattern may also be present in males. Due to relatively unexplored and extensive individual variation, this subspecies is best identified by DNA, with diagnostic base pairs in the nuclear genome: hm2006265-RA.7:T39G, hm2008209-RA.2:A163C, hm2007759-RA.5:T135C, hm2013551-RA.3:A151G, hm2017231-RA.5:T48C; 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-19099D06, GenBank PZ138018, 658 base pairs:

TACTTTATATTTTATTTTTGGAATTTGAGCAGGAATAGTTGGAACTTCTCTTAGTTTATTAATTCGATCTGAATTAGGAAATCCAGGTTCATTAATTGGAGATGATCAAATTTATAATACT
ATTGTTACAGCTCATGCTTTTATTATAATTTTTTTTATAGTTATACCTATTATAATTGGAGGATTTGGAAATTGATTAGTACCTTTAATATTAGGAGCCCCTGATATAGCTTTTCCTCGAA
TAAATAATATAAGATTTTGATTATTACCCCCTTCATTAATACTGCTAATTTCAAGAAGAATTGTTGAAAATGGAGCAGGAACTGGATGAACAGTATACCCACCACTTTCTTCCAATATTGC
TCATGGAGGATCTTCAGTTGATTTAGCAATTTTTTCATTACATTTAGCCGGAATTTCATCAATTTTAGGGGCAATTAATTTTATTACTACAATTATTAATATACGAATTAATAATTTATCT
TTCGATCAAATACCTTTATTTGTATGAGCAGTAGGAATTACAGCTTTACTTTTATCATTACCCGTATTAGCTGGAGCTATTACTATACTTCTTACTGATCGAAATATTAATACAT
CATTTTTTGATCCTGCTGGAGGAGGAGATCCAATTCTTTACCAACATTTATTT

Fig. 3. *Asterocampa louisa monterra* **ssp. n.** type specimens from Mexico in dorsal (right or above the panel letter) and ventral (left or below) views: **a) holotype** ♂ NVG-19099D06 Nuevo León, Raíces, 7–9-Jul-1986 [USNM] and paratypes, R. O. Kendall & C. A. Kendall leg., in TAMU, unless indicated: **b)** ♂ NVG-19126G03 Nuevo León, Cola de Caballo, eclosed 27-Apr-1979, reared from larva on *Celtis laevigata* Willd.; **c)** ♂ NVG-19126G01 Coahuila, 3 mi N of Parras, 4-Nov-1978; **d)** ♀ NVG-19126F11 data as (b) but 7-May-1979; **e)** ♀ NVG-19126G02 data as (c); **f)** ♀ NVG-19099D12 Nuevo León, La Nogalera, road above Cola de Caballo, 25-Jul-1986, collector unknown [USNM]. Gray "F" indicates flipped (left-right inverted) images.

Type material. Holotype: ♂ deposited in the National Museum of Natural History, Smithsonian Institution, Washington, DC, USA (USNM), illustrated in Fig. 3a, bears the following four rectangular printed labels, three white: [Nymphalidae VII/7–9/1986 | Asterocampa louisa M | Raices, NL, Mexico], [DNA sample ID: | NVG-19099D06 | c/o Nick V. Grishin], [USNMENT | {QR Code} | 00944988], and one red [HOLOTYPE ♂ | Asterocampa louisa | monterra Grishin]. **Paratypes:** 3♂♂ and 3♀♀ from

Mexico: Nuevo León: 1♀ NVG-19099D12, USNMENT_00942765, La Nogalera, road above Cola de Caballo, 25-Jul-1986 [USNM] (Fig. 3f) and Cola de Caballo, R. O. Kendall & C. A. Kendall leg., ex larvae on *Celtis laevigata* Willd. [TAMU]: 1♂ NVG-19126G03, 27-Apr-1979 (Fig. 3b), 1♂ NVG-19126F12, 7-May-1979, and 1♀ NVG-19126F11, 7-May-1979 (Fig. 3d) and Coahuila, 3 mi N of Parras, 4-Nov-1978, R. O. Kendall & C. A. Kendall leg. [TAMU]: 1♂ NVG-19126G01 (Fig. 3c) and 1♀ NVG-19126G02 (Fig. 3e).

Type locality. Mexico: Nuevo León, Raíces.

Etymology. The name is derived from Monterrey, which is the major city in the vicinity of the type locality.

Distribution. Currently known from the mountain regions in Coahuila and Nuevo León, Mexico.

Asterocampa clyton subpallida (W. Barnes & McDunnough, 1913) is a valid subspecies distinct from *Asterocampa clyton texana* (Skinner, 1911)

Originally described as a subspecies, *Chlorippe clyton subpallida* W. Barnes & McDunnough, 1913 (type locality in USA: Arizona, Pima Co.) (Fig. 4h) has been treated as a junior subjective synonym of *Asterocampa clyton texana* (Skinner, 1911) (type locality in USA: Texas, Blanco Co.) (Fig. 4g) (Friedlander 1987; Pelham 2008, 2023). Our genomic analysis reveals that specimens from west Texas and Arizona form a distinct clade sister to, but confidently separated from, *A. clyton texana* (Figs. 1a–c, 13). Therefore, we propose that *Asterocampa clyton subpallida* (W. Barnes & McDunnough, 1913), **stat. rest.**, is a valid subspecies distinct from *Asterocampa clyton texana* (Skinner, 1911).

Asterocampa clyton plana Grishin, new subspecies

https://zoobank.org/96E133FD-0D02-46D9-8210-4A221064EE01

(Figs. 1a–c part, 1f, 4d–f, 13 part)

Definition and diagnosis. Genomic analysis reveals that *Asterocampa clyton clyton* (Boisduval & Le Conte, [1835]) (type locality in USA: Georgia, Burke Co.) (Figs. 1g, 4b, c) is more closely related to *Asterocampa clyton flora* (W. H. Edwards, 1876) (type locality in USA: Florida, Putnam Co.) (Fig. 4a) than to other eastern and northern populations traditionally associated with the nominotypical subspecies (Figs. 1a–c, 13). While this result is biogeographically sensible, it poses taxonomic challenges. It is conceivable to synonymize *A. clyton flora* with *A. clyton clyton*, thus resulting in a monophyletic broadly distributed eastern subspecies. However, due to wing pattern differences of Florida populations, we keep *A. clyton flora* as a valid subspecies and treat the rest of the clade as *A. clyton clyton*, which is paraphyletic with respect to *A. clyton flora*. Subspecies are usually defined by wing pattern differences between groups of populations and therefore do not need to be monophyletic. Some subspecies at the boundary of the range may originate within a broadly distributed subspecies, thus rendering it paraphyletic (Zhang et al. 2026). In addition to the prominent and confidently supported (100%) nuclear genome clade of *A. clyton flora* with *A. clyton clyton*, we find that specimens from the South-central Plains region occupy an intermediate position in the tree between the eastern and western populations (Figs. 1a–c, 13), being at the base of the *A. clyton flora* together with *A. clyton clyton* clade. These specimens do not form a clade, likely due to variable fractions of gene exchange with western subspecies, but the clade of *A. clyton flora* together with *A. clyton clyton* is genetically differentiated from them at the subspecies level. Therefore, these Central Plains specimens represent a new subspecies. This new subspecies (Figs. 1f, 4d–f) is similar to both *A. clyton clyton* (Figs. 1g, 4b, c) and *Asterocampa clyton texana* (Skinner, 1911) (type locality in USA: Texas, Blanco Co.) (Figs. 1e, 4g) and is somewhat intermediate in wing patterns between them, differing from them and other subspecies by the following combination of characters: yellowish discal and postdiscal forewing spots are typically more prominent and paler than in *A. clyton clyton* and *A. clyton flora* and are more similar to *A. clyton texana*, but the ground is redder than in the latter subspecies, being more similar to the two former subspecies; it

Fig. 4. Subspecies of *Asterocampa clyton* ♂♂ from USA in dorsal (right or above the panel letter) and ventral (left or below) views: **a)** *A. clyton flora* **lectotype** NVG-15099A02 FL, Putnam Co., Palatka, old [CMNH]; **b–c)** *A. clyton clyton*: **b) neotype** NVG-15099D11 GA, Burke Co., at Savannah River, 6-Aug-1998, R. R. Gatrelle leg. [CMNH] and **c)** non-type NVG-15101F02 IA, Fremont Co., Waubonsie State Park, 5-Jul-1957, O. D. Spencer leg [USNM]; **d–f)** *A. clyton plana* **ssp. n.**: **d) holotype** NVG-25043B12 TX, Denton Co., Flower Mound, eclosed 26-Sep-1997, N. V. Grishin leg. [MGCL] and paratypes: **e)** NVG-19123E03 OK, Payne Co., Stillwater, 3-Oct-1957, C. J. McCoy leg. [TMMC] and **f)** NVG-19099E09 NE, Lancaster Co., Lincoln, 5-Jun-1968, O. D. Spencer [USNM]; **g)** *A. clyton texana* **holotype** NVG-15098C01 TX, Blanco Co., Round Mountain, 31-Jul-1895 [CMNH]; **h)** *A. clyton subpallida* **lectotype** NVG-15101B06 AZ, Pima Co., Baboquivari Mts., Aug-old [USNM].

frequently has at least a partly developed postdiscal eyespot in forewing cell CuA_1-CuA_2; the discal paler band on the ventral hindwing is usually more conspicuous than in other subspecies; and the outer margin of the forewing is less prominently concave in the middle, particularly compared to eastern subspecies. Due to extensive individual variation and intergradation with other subspecies, this subspecies is best identified by DNA, with diagnostic base pairs in the nuclear genome: hm2002778-RA.1:G454C, hm2013583-RA.57:C12T, hm2013583-RA.57:C33G, hm2016761-RA.2:C64T, hm2007115-RA.1:G60A, hm2015971-RA.5:C131C (not T), hm2011417-RA.1:G1056G (not A), hm2011417-RA.1:C1086C (not A), hm2016912-RA.8:T150T (not A), hm2016912-RA.8:C153C (not G); 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-11085, GenBank PZ138019, 658 base pairs:

TACTTTATATTTTATTTTTGGAATTTGAGCAGGAATAGTTGGAACTTCCCTTAGTTTATTAATTCGATCTGAATTAGGAAATCCAGGTTCATTAATTGGAGATGATCAAATTTACAATACT
ATTGTTACAGCTCATGCTTTTATTATAATTTTTTTTTATAGTTATACCTATTATAATTGGAGGATTTGGAAATTGATTAGTACCTTTAATATTAGGAGCCCCTGATATAGCTTTTCCTCGAA
TAAATAATATAAGATTTTGATTATTACCCCCTTCATTAATACTACTAATCTCAAGAAGAATTGTTGAAAATGGAGCAGGAACTGGATGAACAGTATACCCACCACTTTCTTCCAATATTGC
TCATGGAGGATCTTCAGTTGATTTAGCAATTTTTTCATTACATTTAGCCGGAATTTCATCAATTTTAGGAGCAATTAATTTTATTACTACAATTATTAATATACGAATTAATAATTTATCT
TTTGATCAAATACCTTTATTTGTATGAGCAGTAGGAATTACAGCTTTACTTTTACTTTTATCATTACCTGTATTAGCTGGAGCTATTACTATACTTCTTACTGATCGAAATATTAATACAT
CATTTTTTGATCCTGCTGGAGGAGGAGATCCAATTCTTTACCAACATTTATTT

Type material. Holotype: ♂ deposited in the McGuire Center for Lepidoptera and Biodiversity collection, Gainesville, FL, USA (MGCL), illustrated in Fig. 4d, bears the following three rectangular printed labels, two white: [USA: TEXAS: Denton Co. | Flower Mound, Murrell Park | nr. Grapevine Lake, ex larva | GPS 32.998, -97.088 adult ecl. | 26-Sep-1997, Grishin N.V. leg.], [DNA sample ID: | NVG-25043B12 | c/o Nick V. Grishin], and one red [HOLOTYPE ♂ | Asterocampa clyton | plana Grishin]. Pupal exuvium is pinned with the specimen. **Paratypes:** 25♂♂ and 31♀♀: USA, Texas [UTSW]: Denton Co., Flower Mound, Murrell Park, the vicinity of the type locality, N. V. Grishin leg.: 4♀♀: 22-Sep-, 1-, 5-, 12-Oct-1996; others, except the last three, reared from larvae, eclosion dates given: 1997: 1♀ 6-May, 3♂♂: 8-, 11-, 14-May, 1♀ 17-May, 1♂ 23-Sep, 1♀ 28-Sep, 3♀♀: 4-, 8-, 10-Oct and 1998: 2♀♀: 22-, 28-Apr, 1♂&1♀ 1-May, 1♂ 2-May; 1♂ NVG-11085, 12-May-2018; 1♀ NVG-13255, 28-Jul-2021; and 1♂ NVG-14619, 25-Jun-2023; Dallas Co., N. V. Grishin leg.: 1♂ NVG-13128 Carrolton, nr. Elm Fork Trinity River, 32.9538, −96.9370, 8-Jul-2021; 2♀♀ Farmers Branch: NVG-13189, 32.9183, −96.9373, 18-Jul-2021 and NVG-13219, 32.9198, −96.9381, 23-Jul-2021; Dallas: 1♂ 10-Oct-1996; Harry S. Moss Park, 32.8892, −96.7486: 1♀ NVG-4068, 14-Jul-2015 and in a bait trap, 15-Jul-2015: 6♂♂: NVG-4081, -4085, -4086, -4089, -4091, -4092 and 1♀ NVG-4090; Robert Oren Park, 32.7239, −96.7752, 6-Jun-2021: 4♂♂: NVG-12842 to -12845 and 5♀♀: NVG-12846 to -12850; 1♀ NVG-4188 Norbuck Park, 32.8577, −96.7127, 20-Jul-2015; Trinity Forest trail: 1♀ NVG-14270 nr. Little Lemmon Lake, 32.7059, −96.7379, 6-Oct-2022 and S of Lemmon Lake, approx. 32.6923, −96.7228: 2♀♀: NVG-14592, -14593, 1-May-2023; 1♂ NVG-14594, 1-May-2023; 1♂ NVG-14823, 13-Oct-2023; 1♂ NVG-15014, 7-May-2024; 1♀ NVG-14565 Hutchins, E. Langdon Rd., 32.6733, −96.6985, 29-Apr-2023; and Lamar Co., FM1499 at Craddock Creek, 33.7942, −95.6743, N. V. Grishin leg.: 1♀ NVG-4423, 8-Aug-2015 and 1♀ NVG-6736, 7-Aug-2016; 1♂ NVG-19123E03 Oklahoma, Payne Co., Stillwater, 3-Oct-1957, C. J. McCoy leg. [TMMC] (Fig. 4e); and Nebraska, Lancaster Co., Lincoln, O. D. Spencer leg. [USNM]: 1♂ NVG-19099E09, USNMENT_01589970, ex pupa 5-Jun-1968 (Fig. 4f) and 1♀ NVG-19099E10, USNMENT_01589971, 21-Oct-1969.

Type locality. USA: Texas, Denton Co., Flower Mound, Murrell Park nr. Grapevine Lake, GPS 32.998, −97.088.

Etymology. The name is derived from the word ‘plain’ and reflects the distribution of this subspecies in the Central Plains region.

Distribution. South-Central Plains of the United States.

Asterocampa leilia cocles (Lintner, [1885]) is a valid subspecies distinct from *Asterocampa leilia leilia* (W. H. Edwards, 1874)

Originally described as a species, *Apatura cocles* Lintner, [1885] (type locality in USA: Texas, Hidalgo Co.) is currently regarded as a junior subjective synonym of *Asterocampa leilia* (W. H. Edwards, 1874)

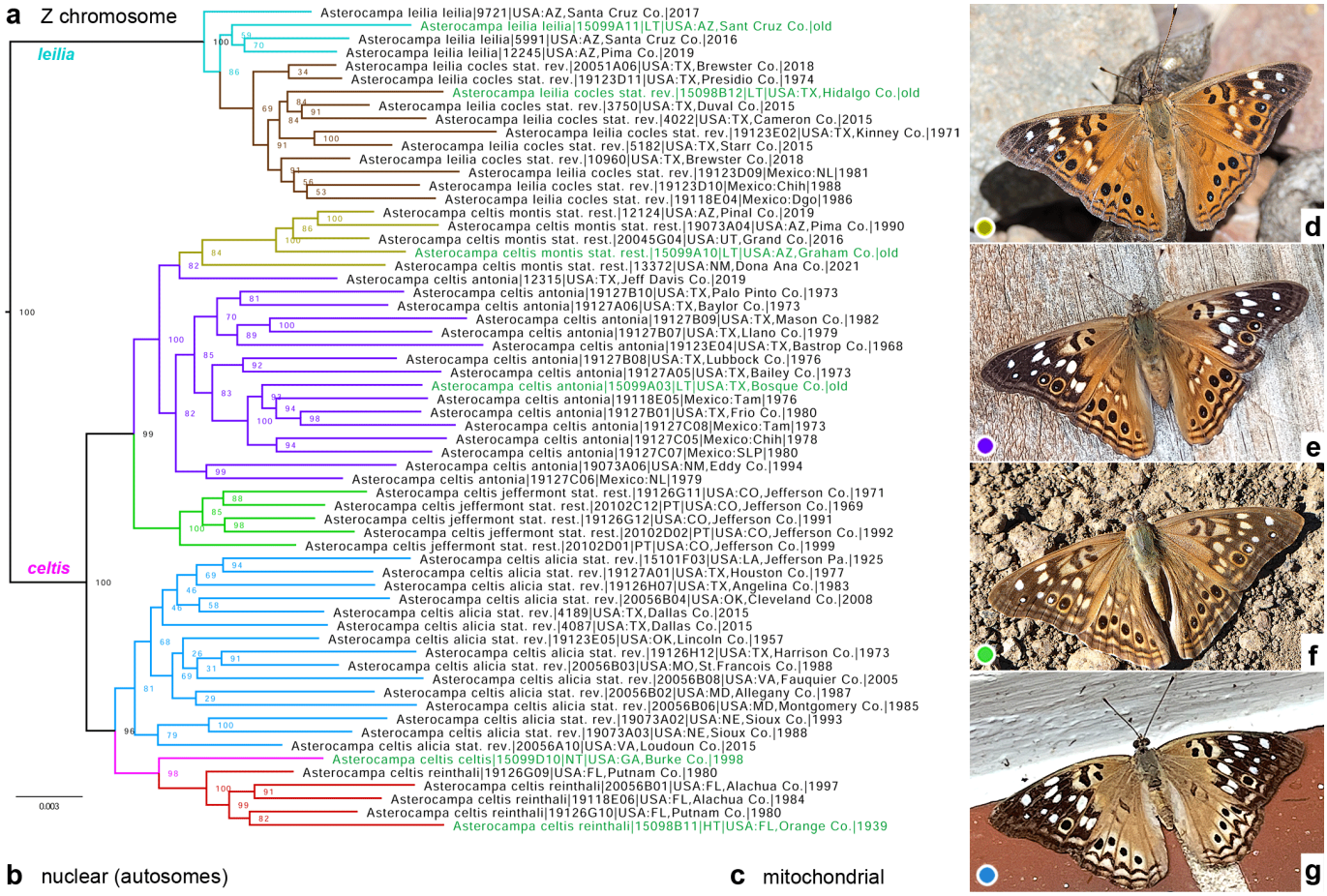

Fig. 5 (legend continues on the next page). Phylogenetic trees of all described subspecies of *Asterocampa leilia* and *Asterocampa celtis* constructed from protein-coding regions in: **a)** the Z chromosome, based on 231,429 positions, **b)** the nuclear genome (autosomes), based on 782,214 positions, and **c)** the mitochondrial genome; and **d–g)** iNaturalist observations

(the color of the dot in the lower left of each image corresponds to the color of the species in the trees): **d)** *A. celtis montis* **stat. rest.** observation No. 188218634 (photo 329357037) USA: Arizona, Pinal Co., Santa Catalina Mts., GPS 32.53933, −110.72730, 10-Jun-2023 © Mike Andersen; **e)** *A. celtis antonia* observation No. 122277341 (photo 207014608) USA: Texas, Comanche Co., Hasse, GPS 31.9616, −98.6770, 13-Jun-2022 © Austin R. Kelly; **f)** *A. celtis jeffermont* **stat. rest.** observation No. 124343705 (photo 210748939) USA: Colorado, Jefferson Co., Golden, GPS 39.7788, −105.2019, 1-Jul-2022 © David Martin; **g)** *A. celtis alicia* **stat. rev.** observation No. 310291481 (photo 560000656) USA: Louisiana, East Baton Rouge Pa., Baton Rouge, GPS 30.3630, −91.0941, 30-Aug-2025 © alice2019; 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 different subspecies are colored differently: *A. leilia leilia* (cyan), *A. leilia cocles* **stat. rev.** (brown), *A. celtis montis* **stat. rest.** (olive), *A. celtis antonia* (violet), *A. celtis jeffermont* **stat. rest.** (green), *A. celtis alicia* **stat. rev.** (blue), *A. celtis celtis* (magenta), and *A. celtis reinthali* (red). Clades corresponding to species are labeled in the Z chromosome tree. The sequence of SAMN18587694 is taken from the alignment provided in Kawahara et al. (2023). Ultrafast bootstrap (Hoang et al. 2018) values are shown at nodes. Gaps in terminal branches indicate that a segment of a branch was cut out to reduce its length; i.e., the branch with the gap is longer than shown.

(type locality in USA: Arizona, Santa Cruz Co.). Genomic analysis reveals that these two taxa form separate clades in the nuclear genome trees (Figs. 5a–c, 13), and therefore their genetic differentiation argues for their distinction, at least at the subspecies level. Therefore, we propose that *Asterocampa leilia cocles* (Lintner, [1885]), **stat. rev.**, is a valid subspecies distinct from *Asterocampa leilia leilia* (W. H. Edwards, 1874).

Asterocampa celtis montis (W. H. Edwards, 1883) and *Asterocampa celtis jeffermont* J. Scott & M. Fisher, 2008 are valid subspecies distinct from *Asterocampa celtis antonia* (W. H. Edwards, [1878])

Described as subspecies, *Apatura antonia* var. *montis* W. H. Edwards, 1883 (type locality in USA: Arizona, Graham Co.) (Figs. 5d, 6f) and *Asterocampa celtis jeffermont* J. Scott & M. Fisher, 2008 (type locality in USA: Colorado, Jefferson Co.) (Figs. 5f, 6d), have been treated as junior subjective synonyms of *Asterocampa celtis antonia* (W. H. Edwards, [1878]) (type locality in USA: Texas, Bosque Co.) (Figs. 5e, 6e) (Friedlander 1987; Pelham 2008, 2023). Genomic analysis reveals that both taxa form distinct clades separate from *A. celtis antonia* and are genetically differentiated from it at the subspecies level (Figs. 5a–c, 13). Therefore, we propose to treat *Asterocampa celtis montis* (W. H. Edwards, 1883), **stat. rest.** and *Asterocampa celtis jeffermont* J. Scott & M. Fisher, 2008, **stat. rest.** as valid subspecies distinct from *Asterocampa celtis antonia* (W. H. Edwards, [1878]). Curiously, *A. celtis jeffermont* **stat. rest.** is more closely related to western subspecies in the Z chromosome tree (Fig. 5a green with violet and olive), while being in the same clade with eastern subspecies in the tree constructed from protein-coding genes in autosomes (Fig. 5b green with blue, magenta, and red).

Asterocampa celtis alicia (W. H. Edwards, 1868) is a valid subspecies distinct from *Asterocampa celtis celtis* (Boisduval & Le Conte, [1835])

Originally described as a species, *Apatura alicia* W. H. Edwards, 1868 (type locality in USA: Louisiana, vic. New Orleans) (Figs. 5g, 6c) has been treated as a junior subjective synonym of *Asterocampa celtis celtis* (Boisduval & Le Conte, [1835]) (type locality in USA: Georgia, Burke Co.) (Fig. 6b) (Friedlander 1987). However, the nuclear genomic analysis of the *A. celtis* neotype (Figs. 5a, b magenta, 6b; sequenced as NVG-15099D10) reveals that it is more closely related to *Asterocampa celtis reinthali* Friedlander, 1987 (USA: Florida, Orange Co.) (Figs. 5a, b red, 6a), which is expected from their more southeastern localities, than to more western populations, including a specimen from the vicinity of New Orleans, Louisiana (Figs. 5a, b blue, 6c; NVG-15101F03). These latter populations are not in the same clade with more eastern and northern populations we regard as nominotypical. Therefore, we propose that *Asterocampa celtis alicia* (W. H. Edwards, 1868), **stat. rev.** is a valid subspecies distinct from *Asterocampa celtis celtis* (Boisduval & Le Conte, [1835]).

Fig. 6. Subspecies of *Asterocampa celtis* ♂♂ from USA in dorsal (right or above the panel letter) and ventral (left or below) views (CMNH unless indicated): **a)** *A. celtis reinthali* **holotype** NVG-15098B11 FL, Orange Co., Ocoee, 5-Apr-1939, C. N. Grimshawe leg.; **b)** *A. celtis celtis* **neotype** NVG-15099D10 GA, Burke Co., at Savannah River, 6-Aug-1998, R. R. Gatrelle leg.; **c)** *A. celtis alicia* **stat. rest.** topotype NVG-15101F03 LA, Jefferson Pa., Harahan, 25-Aug-1925, W. D. Field leg. [USNM]; **d)** *A. celtis jeffermont* **stat. rest.** non-type NVG-19126G11 CO, Jefferson Co., Red Rocks Pk., 6-Jul-1971, J. A. Scott [TAMU]; **e)** *A. celtis antonia* **lectotype** NVG-15099A03 TX, Bosque Co., vic. Norse, old; **f)** *A. celtis montis* **stat. rest. lectotype** NVG-15099A10 AZ, Graham Co., vic. Fort Grant, old. Gray "F" indicates flipped (left-right inverted) image.

Doxocopa laure laure (Drury, 1773) is recorded for the United States

Doxocopa druryi acca (C. Felder & R. Felder, 1867) (type locality in Mexico) is a resident, or at least a temporary colonist, in the Lower Rio Grande Valley, Texas, USA, e.g., sequenced specimen NVG-3838

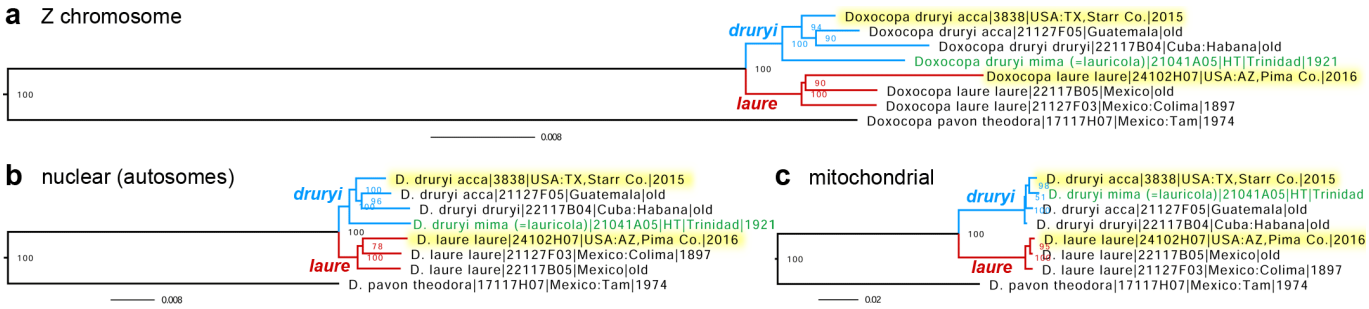

Fig. 7. Phylogenetic trees of selected *Doxocopa* species constructed from protein-coding regions in: **a)** the Z chromosome, based on 277,119 positions, **b)** the nuclear genome (autosomes), based on 5,423,079 positions, and **c)** the mitochondrial genome. The primary type specimen is labeled in green font and different species are colored differently: *D. druryi* (blue), *D. laure* (red), and *D. pavon* (black). Clades corresponding to the two species under investigation are labeled, and labels of specimens from the U.S. are highlighted in yellow. Ultrafast bootstrap (Hoang et al. 2018) values are shown at nodes.

Fig. 8. *Doxocopa laure laure* ♀ NVG-24102H07 from USA: Arizona in dorsal (left) and ventral (right) views, data in text.

from Roma, Starr Co. (Fig. 7). Genomic sequencing of a female *Doxocopa* Hübner, [1819] from USA: Arizona reveals that it is not *D. druryi acca*, but *Doxocopa laure laure* (Drury, 1773) (type locality in Honduras) (Fig. 7), consistently with its phenotype (Fig. 8). This specimen, NVG-24102H07, WRD 9203, in the research collection of Bill Dempwolf, was reared on *Celtis pallida* by Doug Mullins from an ovum obtained from a female collected in Pima County, Florida Wash near Madera Canyon on 4-Nov-2015, and the adult eclosed on 6-Jan-2016. It is the first confirmed record of *Doxocopa laure laure* for the United States. Therefore, the genus *Doxocopa* Hübner, [1819] (type species *Papilio agathina* Cramer, 1777) is represented by three species in the United States, with the third one being *Doxocopa pavon* (Latreille, [1809]) (type locality in Ecuador: Loja) as *Doxocopa pavon theodora* (Lucas, 1857) (type locality possibly in Mexico). We propose to retain the English name "Silver Emperor" for *D. druryi*, and use "Golden Emperor" for *D. laure* because the latter species has more extensive golden coloration, in particular wider and more continuous golden band on the forewing in males, while the former species has wider and more prominent silvery bands (Maza-Elvira and Maza-Elvira 2022).

Lectotype designation for *Libythea larvata* Strecker, [1878]

Two syntypes of *Libythea larvata* Strecker, [1878], both males labeled from USA: Texas, San Antonio, collected by J. Boll, were found in the FMNH collection. To define the taxonomic identity of the name *L.*

Fig. 9. Selected *Libytheana* taxa in dorsal (right) and ventral (left) views: **a)** *L. bachmanii* **stat. rest.** non-type ♂ NVG-19123G02 USA: Texas, Travis Co., 2.1 km up E Johnson Creek, 4-Oct-1977, C. J. Durden leg. [TMMC]; **b)** *L. larvata* **stat. rest. lectotype** ♂ NVG-15039A07, FMNH-INS 0000 095 255, USA: Texas, Bexar Co., San Antonio, old, J. Boll leg. [FMNH]; **c)** *L. carinenta mexicana* non-type, U.S. record (Heitzman and Heitzman 1972 [1973]), one of a series, ♀ NVG-5529 USA: Texas, Cameron Co., Boca Chica, 28-Jun-1969, J. R. Heitzman leg., genitalia NVG160110-65 [TAMU]; **d)** *L. carinenta carinenta* non-type ♂ NVG-5050 Suriname, old, B. Neumögen collection, genitalia NVG151102-05 [USNM]. Green arrows point at characters useful for identification: pale spots by the forewing costa are aligned with the patch of pale spots distad of the discal cell in *L. bachmanii* **stat. rest.**, and are offset basad in the other two species, more strongly (and typically whiter) in *L. carinenta* than in *L. larvata* **stat. rest.**; the forewing apex is more prominently lobed in *L. carinenta* than in *L. larvata* **stat. rest.** and *L. bachmanii* **stat. rest**.

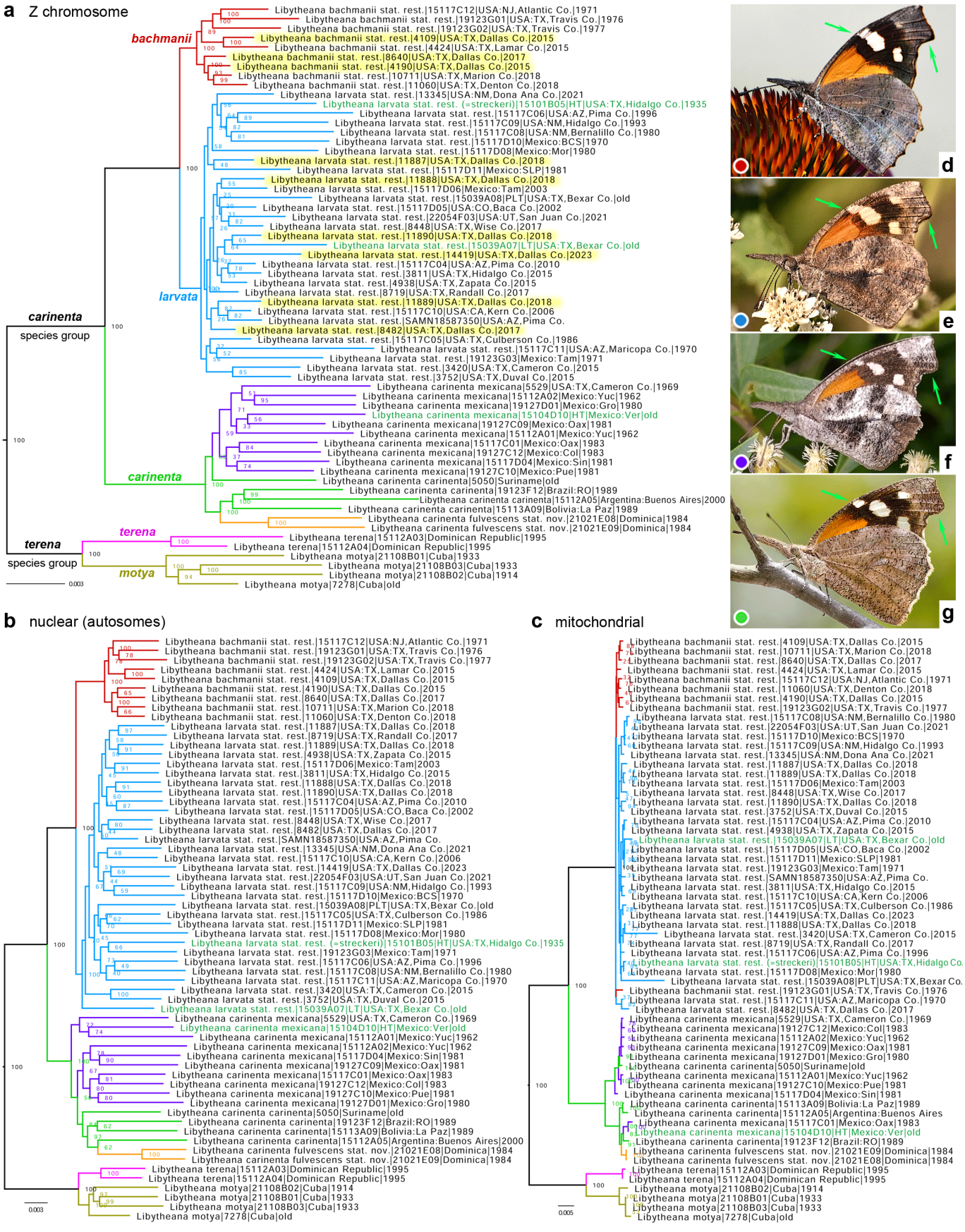

Fig. 10 (legend continues on the next page). Phylogenetic trees of all described *Libytheana* species constructed from protein-coding regions in: **a)** the *Z* chromosome, based on 310,569 positions, **b)** the nuclear genome (autosomes), based on 749,091 positions, and **c)** the mitochondrial genome; and **d–g)** iNaturalist observations (the color of the dot in the lower left of each image corresponds to the color of the species in the trees): **d)** *L. bachmanii* **stat. rest.** observation No. 296408903, USA: Ohio,

Morrow Co., Jul-2025 (obscured) © bkgs66; **e)** *L. larvata* **stat. rest.** observation No. 333078596, USA: Texas, Mission, National Butterfly Center, GPS 26.1798, −98.3665, 1-Jan-2026 © Dennis Vollmar; **f)** *L. carinenta mexicana* observation No. 242190689 (photo 431746424), Mexico: Distrito Federal, Ciudad de México, Parque Nacional Cerro de la Estrella, GPS 19.3483, −99.0929, 16-Sep-2024 © David Ortiz; **g)** *L. carinenta carinenta* observation No. 200105693, Brazil: Distrito Federal, Lago Norte, St. de Habitações Individuais Norte, GPS −15.7362, −47.8614, 22-Feb-2024 © abelardomendesjr; images are color-corrected, brightened, rotated, cropped, and (e) is flipped; CC BY-NC 4.0 https://creativecommons.org/licenses/by-nc/4.0/. Green arrows point at field marks, see Fig. 9 legend for details. In the trees, primary type specimens are labeled in green font and different species are colored differently: *L. bachmanii* **stat. rest.** (red), *L. larvata* **stat. rest.** (blue), *L. carinenta* (green, with *L. carinenta mexicana* in violet and *L. carinenta fulvescens* **stat. nov.** in orange), *L. terena* (magenta), and *L. motya* (olive). In the Z chromosome tree, clades corresponding to species and species groups are labeled, and labels of specimens from Dallas Co., Texas, are highlighted in yellow. The sequence of SAMN18674226 is taken from the alignment provided in Kawahara et al. (2023). Ultrafast bootstrap (Hoang et al. 2018) values are shown at nodes.

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larvata objectively, N.V.G. hereby designates a syntype in the FMNH collection, a male with both palpi present (the second syntype is missing the left palpus), illustrated in Fig. 9b, and bearing the following five rectangular labels (2nd with red framing, 4th blue, others white; 1st and 2nd handprinted, others printed): [5.], [L. Larvata | Streck | S. Antonio, Tex. | orig. | Type J. Boll.], [FMNH-INS | 0000 095 255], [PHOTOGRAPHED | Allie Stone 2012 | KE EMu catalog], and [DNA sample ID: | NVG-15039A07 | c/o Nick V. Grishin], as the **lectotype** of *Libythea larvata* Strecker, [1878]. The lectotype is a specimen in good condition, its head is slightly tilted to the left, and each wing has at least two pinholes. According to the label of the lectotype, the type locality of *L. larvata* becomes USA: Texas, [Bexar Co.,] San Antonio, although it is possible that this locality is approximate, and the lectotype may have been collected outside the city limits. The COI barcode sequence of the lectotype, sample NVG-15039A07, GenBank PZ138020, 658 base pairs, is:

AACTCTATATTTTATTTTTGGAATTTGAGCAGGAATAGTAGGTACATCTTTAAGTTTATTAATTCGAACTGAATTAGGAAACCCAGGATCATTAATTGGTGATGATCAAATTTATAATACT
ATTGTTACAGCCCATGCTTTTATTATAATTTTTTTTATAGTTATACCAATTATAATTGGAGGATTTGGAAATTGATTAGTACCATTAATATTAGGAGCTCCTGATATAGCATTCCCTCGGA
TAAATAATATAAGTTTTTGACTTCTACCCCCTTCATTAGTTCTATTAATTTCAAGTAGAATTGTTGAAAATGGAGCAGGAACAGGTTGAACAGTCTACCCCCCACTGTCTTCTAATATTGC
TCACGGAGGATCGTCCGTAGATTTAGCAATTTTTTCATTACATTTAGCCGGAATTTCATCAATTTTAGGAGCAATTAATTTTATTACAACTATTATTAATATACGAATTAATAATTTATCT
TTTGATCAAATACCTTTATTTGTTTGATCCGTAGGTATTACAGCTTTATTATTATTATCATTACCAGTATTAGCAGGAGCTATCACCATACTTTTAACAGATCGAAATCTTAATACTT
CATTTTTTGATCCTGCAGGAGGAGGAGACCCAATTTTATATCAACATTTATTT

Libytheana bachmanii (Kirtland, 1851) and *Libytheana larvata* (Strecker, [1878]) are species distinct from *Libytheana carinenta* (Cramer, 1777)

Originally described as species, *Libythea bachmanii* Kirtland, 1851 (type locality in USA: Ohio, Mahoning Co.) (Figs. 9a, 10d) and *Libythea larvata* Strecker, [1878] (type locality USA: Texas, [Bexar Co.,] San Antonio) (Figs. 9b, 10e) are currently treated as subspecies of *Libytheana carinenta* (Cramer, 1777) (type locality in Suriname) (Figs. 9d, 10g) (Kawahara 2009, 2013). Genomic analysis reveals species-level genetic differentiation among these 3 taxa that form three confidently supported (100%) clades in the nuclear genome trees (Fig. 10a, b). Therefore, we propose that *Libytheana bachmanii* (Kirtland, 1851), **stat. rest.** and *Libytheana larvata* (Strecker, [1878]), **stat. rest.** are species distinct from *Libytheana carinenta* (Cramer, 1777).

In *L. bachmanii* **stat. rest.**, the pale spot near the costal margin of the forewing is closely aligned with the pale patch distad of the discal cell (Figs. 9a, 10d). In *L. larvata* **stat. rest.**, the mid-costal spot is slightly offset basad, and the color of pale spots is yellower (Figs. 9b, 10e). Both species are found sympatrically in northern Texas (e.g., Dallas Co., highlighted yellow in Fig. 10a, *L. larvata* **stat. rest.** recorded during several years in March, April, and November), and *L. bachmanii* **stat. rest.** is confirmed from more southern locations such as Travis Co. in Texas (Fig. 10a). In *L. carinenta,* the mid-costal spot is even more strongly offset basad, and the forewing apical lobe is more prominent (Figs. 9c, d, 10f, g).

We note that *Libytheana carinenta mexicana* Michener, 1943 (type locality Mexico: Veracruz, Xalapa) (Figs. 9c, 10f) falls within the clade with *L. carinenta*, and is not prominently differentiated from it genetically (Fig. 10a–c violet within green). Therefore, we retain *L. carinenta mexicana* as a subspecies. Finally, we propose to keep the English name “American Snout” for *L. bachmanii*, and use “Western Snout” and “Tropical Snout” for *L. larvata* and *L. carinenta*, respectively.

Libythea fulvescens Lathy, 1904 is not a distinct species, but is a subspecies of *Libytheana carinenta* (Cramer, 1777)

Originally described and currently regarded as a species, *Libythea fulvescens* Lathy, 1904 (type locality in Dominica) originates within *Libytheana carinenta* (Cramer, 1777) (type locality in Suriname) (Fig. 10a–c orange within green) and appears to represent an isolated, highly inbred, and genetically drifted (in terms of wing patterns) population of the latter species rather than being a species-level taxon. Due to its phenotypic distinction, we therefore propose that it be treated as a subspecies, *Libytheana carinenta fulvescens* (Lathy, 1904), **stat. nov**.

Family Hesperiidae Latreille, 1809

Polites (*Wallengrenia*) *clavus* (Erichson, [1849]) and *Polites* (*Wallengrenia*) *jobrea* (Dyar, 1918) are valid species distinct from *Polites* (*Wallengrenia*) *otho* (J. E. Smith, 1797)

Originally described as species, *Hesperia clavus* Erichson, [1849] (type locality in Guyana; lectotype sequenced as NVG-15036G07) (Figs. 11g, 12d) and *Catia jobrea* Dyar, 1918 (type locality in Mexico: Guerrero, Sierra de Guerrero) (Figs. 11f, 12c) are currently treated as a subspecies of *Polites* (*Wallengrenia*) *otho* (J. E. Smith, 1797) (type locality in USA: Georgia) (Figs. 11e, 12b) and a junior subjective synonym of *H. clavus*, respectively. Our genomic analysis reveals that all three taxa are genetically differentiated at the species level (Cong et al. 2019a and in press), with *C. jobrea* being sister to *P. otho*, while *H. clavus* is more distant from them (Fig. 11a–c). Therefore, we propose that *Polites* (*Wallengrenia*) *clavus* (Erichson, [1849]), **stat. rest.** and *Polites* (*Wallengrenia*) *jobrea* (Dyar, 1918), **stat. rest.** are valid species distinct from *Polites* (*Wallengrenia*) *otho* (J. E. Smith, 1797). *Polites clavus* does not enter the United States and is mostly a South American species. The species in the Lower Rio Grande Valley of Texas, USA is *P. jobrea*, and it is not known from elsewhere in the United States. We propose "Mexican Broken-Dash" as the English name for this species. Furthermore, we leave *Hesperia curassavica* Snellen, 1887 (type locality in Netherlands Antilles: Curaçao; holotype sequenced as NVG-22011F05), *Pamphila helva* Möschler, 1876 (type locality in Suriname; lectotype sequenced as NVG-15034F11), and *Polites winslowi* Weeks, 1906 (type locality in Venezuela: Suapure) in synonymy with *Polites* (*Wallengrenia*) *clavus* (Erichson, [1849]), **stat. rest**. Finally, we find that *Polites* (*Wallengrenia*) *egeremet* (Scudder, 1864) (Figs. 11d, 12a) is a species more distant from *P. otho* than the less similar *Polites* (*Wallengrenia*) *premnas* (Wallengren, 1860) (type locality Argentina, Buenos Aires) (Fig. 11a–c), despite superficial similarities between the former two species. This further supports their distinction at the species level in agreement with Burns (1985).

"*Pamphila lacordairii*, Boisd.," a nomen nudum published by Godman (1900) is a specimen of *Polites* (*Wallengrenia*) *clavus* (Erichson, [1849]) and not of *Polites* (*Wallengrenia*) *otho* (J. E. Smith, 1797)

"*Pamphila lacordairii*, Boisd.," a nomen nudum published by Godman (1900) without description or indication, belongs in synonymy with *Polites* (*Wallengrenia*) *clavus* (Erichson, [1849]), **stat. rest**. (type locality in Guyana; lectotype sequenced as NVG-15036G07) and not with *Polites* (*Wallengrenia*) *otho* (J. E. Smith, 1797) (type locality in USA: Georgia), as demonstrated by the genomic analysis of the "holotype" (NVG-18052D12 from the Staudinger collection, MFNB), which is placed among specimens of *P. clavus* (Fig. 11a–c violet) and away from *P. otho* (Fig. 11a–c blue). This result is consistent with the published locality of the "holotype" stated on its label ("Teffé", i.e., Tefé, in Amazonas, Brazil). This South American locality is closer to the type locality of *P. clavus*; and *P. otho*, as we presently delimit this species, is distributed only in the eastern United States, not even entering Mexico.

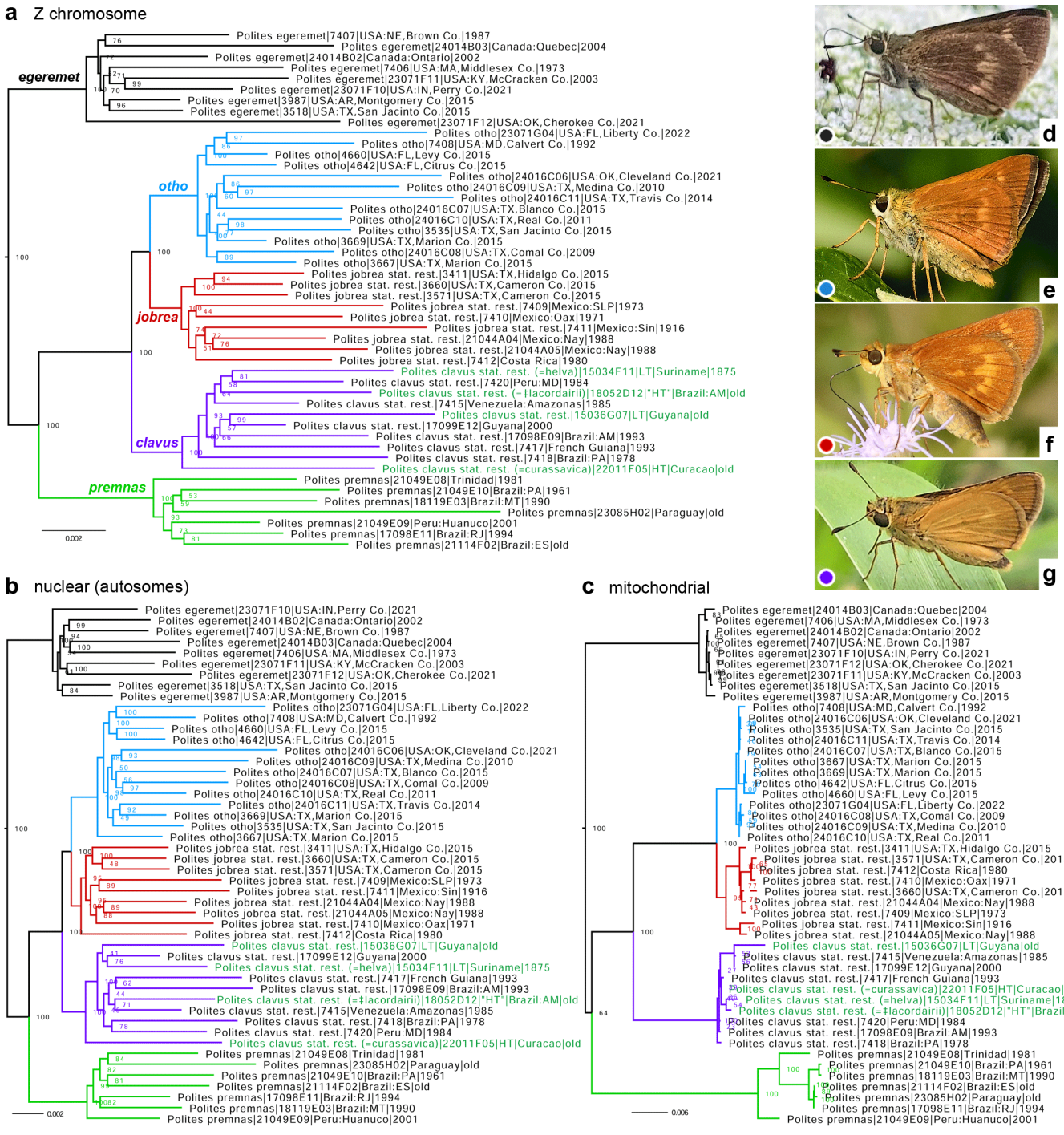

Fig. 11. Phylogenetic trees of selected *Polites* (*Wallengrenia*) species forming a clade, constructed from protein-coding regions in: **a)** the Z chromosome, based on 239,403 positions, **b)** the nuclear genome (autosomes), based on 7,987,653 positions, and **c)** the mitochondrial genome; and **d–g)** iNaturalist observations, females (the color of the dot in the lower left of each image corresponds to the color of the species in the trees): **d)** *P. egeremet* observation No. 301020223 USA: Massachusetts, Middlesex Co., Tyngsboro, GPS 42.6448, −71.4836, 25-Jul-2025 © Gus; **e)** *P. otho* observation No. 160325246, USA: Georgia, McIntosh Co., GPS 31.4748, −81.3839, 4-May-2023 © mikelchap; **f)** *P. jobrea* **stat. rest.** observation No. 334374839, USA: Texas, Hidalgo Co., Mission, National Butterfly Center, GPS 26.1786, −98.3665, 9-Jan-2026 © Dan Jones; **g)** *P. clavus* **stat. rest.** observation No. 278908281, Trinidad and Tobago: Trinidad, Mount Pleasant, Samaan Park, GPS 10.7214, −61.6103, 20-Apr-2025 © Ashleigh Chee Hing; images are color-corrected, brightened, rotated, cropped, and (e) 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 different species are colored differently: *P. egeremet* (black), *P. otho* (blue), *P. jobrea* **stat. rest.** (red), and *P. clavus* **stat. rest.** (violet). Clades corresponding to species are labeled in the Z chromosome tree. 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; i.e., the branch with the gap is longer than shown.

Fig. 12. Four *Polites* (*Wallengrenia*) species ♂♂ in dorsal (right) and ventral (left) views (USNM unless indicated): **a)** *P. egeremet* non-type NVG-7406, USA: MA, Middlesex Co., Lexington, 12-Jul-1973, J. M. Burns leg.; **b)** *P. otho* non-type NVG-7407 USA: MD, Calvert Co., Plum Point, 30-Aug-1992, J. H. Fales leg.; **c)** *P. jobrea* **stat. rest.** non-type NVG-7409 Mexico: SLP, El Salto Falls, 24-Oct-1973, W. W. McGuire leg.; **d)** *P. clavus* **stat. rest. lectotype** NVG-15036G07, No. 5527, Guyana, old [MFNB].

Taxonomic lists of *Asterocampa* Röber, 1916 and *Libytheana* Michener, 1943

To summarize the results of this work, we provide taxonomic lists of *Asterocampa* and *Libytheana* species, subspecies, and synonyms, based on Pelham (2008, 2023) with modifications and additions. The genomic phylogeny of all described *Asterocampa* species is shown in Fig. 13. The genus is partitioned into two species groups. The two nuclear genome trees show the same topology of five species (Fig. 13a, b). However, topologies within *A. clyton* and *A. celtis* confidently differ between the Z chromosome tree and the tree from the rest of the nuclear genome (autosomes): subspecies from the middle of the range (*A. clyton plana* **ssp. n.** and *A. celtis jeffermont* **stat. rest.**) group with western subspecies in the Z chromosome tree, while being in the clade with eastern subspecies in the tree based on autosomes.

In the lists below, species are ordered to maximize phenotypic similarity and geographic proximity among neighboring taxa in the list without disrupting the confidently supported phylogenetic order in nuclear genome trees (Figs. 1a, b, 5a, b, 10a, b, 13a, b): i.e., a strongly supported clade in the tree corresponds to a contiguous segment in the list. New subspecies and the category of taxonomic change are shown in red font. Comments are given after a vertical bar | following the type locality; invalid and unavailable names are shown in smaller font in their original combinations: unavailable names are placed in quotes and, together with permanently invalid synonyms, are preceded by ‡ and = (nomina nuda lack the symbol =); junior subjective synonyms are preceded only by =.

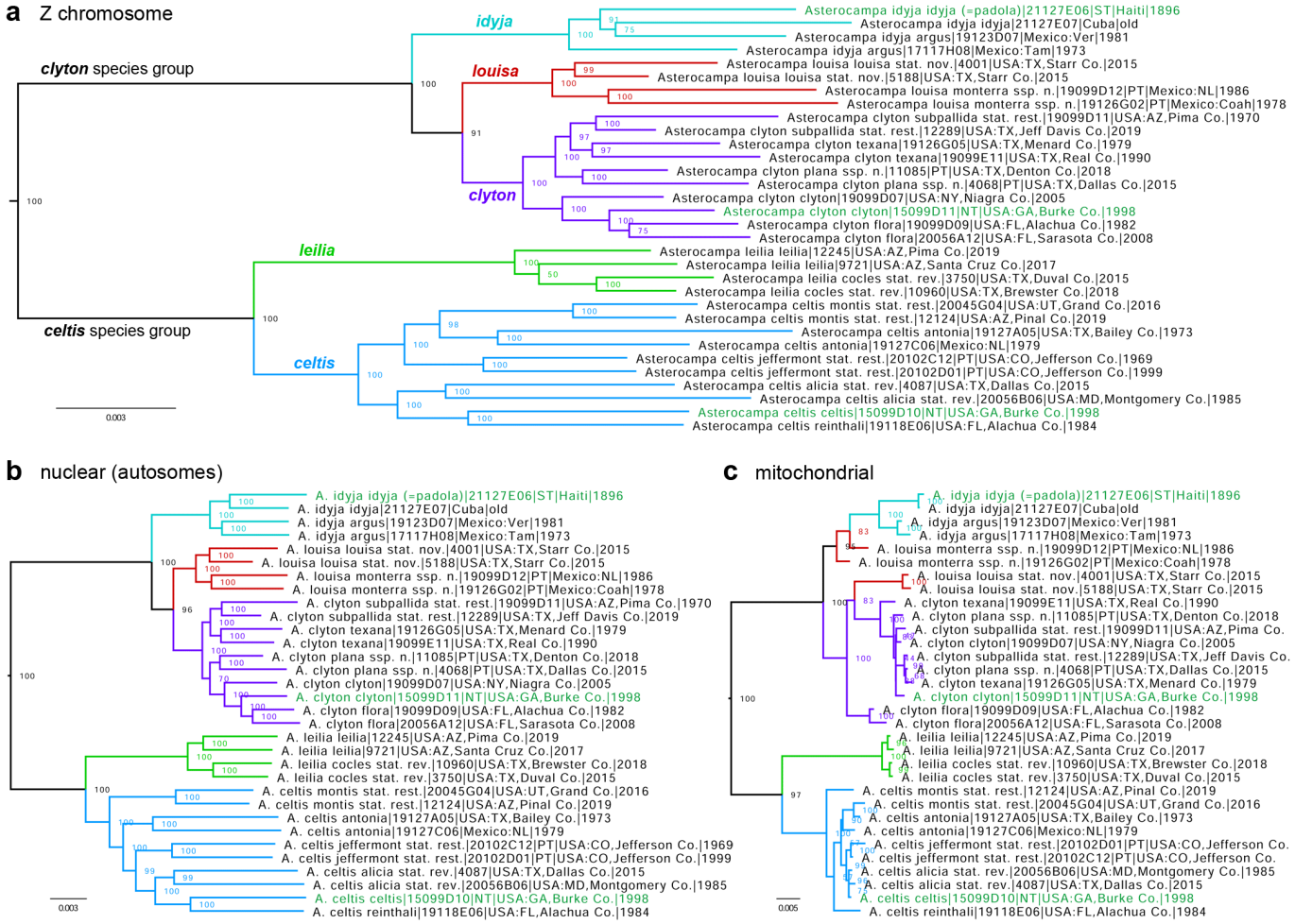

Fig. 13. Phylogenetic trees of all valid *Asterocampa* species and subspecies constructed from protein-coding regions in: **a)** the Z chromosome, based on 277,119 positions, **b)** the nuclear genome (autosomes), based on 5,423,079 positions, and **c)** the mitochondrial genome. Primary type specimens are labeled in green font and different species are colored differently: *A. idyja* (cyan), *A. louisa* (red), *A. clyton* (violet), *A. leilia* (green), and *A. celtis* (blue). Clades corresponding to different species and species groups are labeled in the Z chromosome tree. For the construction of these trees, the same positions are used as in the *Doxocopa* trees (Fig. 7); and ultrafast bootstrap (Hoang et al. 2018) values are shown at nodes.

Genus ***Asterocampa*** Röber, 1916; type species *Apatura celtis* Boisduval & Le Conte, [1837]

clyton species group

Asterocampa idyja (Geyer, [1828]); Cuba
Asterocampa idyja idyja (Geyer, [1828]); Cuba
=‡*P*[*apilio*]. *S*[*atyrus*]. *Herse* Fabricius, 1793; not stated, unknown | preoccupied by *Papilio herse* Hufnagel, 1766
= *Doxocopa idyja padola* Fruhstorfer, 1912; Haiti | junior subjective synonym
Asterocampa idyja argus (H. Bates, 1864); Guatemala: Motagua Valley
= [*Doxocopa argus*] forma *armilla* Fruhstorfer, 1912; Honduras | junior subjective synonym

Asterocampa louisa D. Stallings & Turner, 1947, **stat. nov.**; USA: TX, Hidalgo Co., Pharr
Asterocampa louisa louisa D. Stallings & Turner, 1947; USA: TX, Hidalgo Co., Pharr
Asterocampa louisa monterra Grishin, **ssp. n.**; Mexico: Nuevo León, Raíces

Asterocampa clyton (Boisduval & Le Conte, [1835]); USA: GA, Burke Co., at Savannah River
Asterocampa clyton subpallida (W. Barnes & McDunnough, 1913), **stat. rest.**; USA: AZ, Pima Co.
Asterocampa clyton texana (Skinner, 1911); USA: TX, Blanco Co., Round Mountain
Asterocampa clyton plana Grishin, **ssp. n.**; USA: TX, Denton Co., Flower Mound
Asterocampa clyton clyton (Boisduval & Le Conte, [1835]); USA: GA, Burke Co., Savannah River
= [*Apatura*] *Proserpina* Scudder, 1868; USA: IA, from Crawford to Greene Cos. | junior subjective synonym
= [*Apatura Clyton*] var. *Ocellata* W. H. Edwards, 1876; USA: WV, Kanawha Co., Coalburgh | junior subjective synonym
=‡"[*Apatura Clyton*] ab. b. ♂ *Nig*" Strecker, 1878; USA: PA, Berks Co. | infrasubspecific
=‡"*Asterocampa clyton* form *apunctus*" J. Scott, 1981; not stated, unknown | infrasubspecific
=‡"[*Asterocampa clyton*] form *geneumbrosa*" J. Scott, 1986; not stated, unknown | infrasubspecific
Asterocampa clyton flora (W. H. Edwards, 1876); USA: FL, Putnam Co., Palatka

celtis species group

Asterocampa leilia (W. H. Edwards, 1874); USA: AZ, Santa Cruz Co., Sonoita Valley, Camp Lowell
Asterocampa leilia leilia (W. H. Edwards, 1874); USA: AZ, Santa Cruz Co., Sonoita Valley
Asterocampa leilia cocles (Lintner, [1885]), **stat. rev.**; USA: TX, Hidalgo Co., Hidalgo

Asterocampa celtis (Boisduval & Le Conte, [1835]); USA: GA, Burke Co., at Savannah River
Asterocampa celtis montis (W. H. Edwards, 1883), **stat. rest.**; USA: AZ, Graham Co.
Asterocampa celtis antonia (W. H. Edwards, [1878]); USA: TX, Bosque Co., Norse
‡"[*A. celtis antonia*] form *mexicana*" Friedlander, 1987; USA: TX, Lower Rio Grande Valley and southward | nomen nudum
Asterocampa celtis jeffermont J. Scott & M. Fisher, 2008, **stat. rest.**; USA: CO, Jefferson Co.
Asterocampa celtis alicia (W. H. Edwards, 1868), **stat. rest.**; USA: LA, vic. New Orleans
=‡"[*Apatura Celtis*] ab. a. ♂♀ *Alb*" Strecker, 1878; USA: West Virginia, Kanawha Co., Coalburgh | infrasubspecific
=‡"*Chlorippe celtis* n. aberr. *inornata*" Wolcott, 1916; USA: Nebraska, Saunders Co., Ashland | infrasubspecific
Asterocampa celtis celtis (Boisduval & Le Conte, [1835]); USA: GA, Burke Co., Savannah River
=‡ *P*[*apilio*]. *S*[*atyrus*]. *Lycaon* Fabricius, 1793; not stated, unknown | preoccupied by *Papilio lycaon* Kühn, 1774
Asterocampa celtis reinthali Friedlander, 1987; USA: FL, Orange Co., Ocoee

Genus ***Libytheana*** Michener, 1943; type species *Libythea bachmanii* Kirtland, 1851

carinenta species group

Libytheana bachmanii (Kirtland, 1851), **stat. rest.**; USA: OH, Mahoning Co.
=‡"[*Libythea bachmanii bachmanii*] [f.] *kirtlandi*" W. D. Field, 1938; USA: KS, Douglas Co., Lawrence | infrasubspecific

Libytheana larvata (Strecker, [1878]), **stat. rest.**; USA: TX, [Bexar Co.,] San Antonio
= *Libytheana carinenta streckeri* Austin & J. Emmel, 1998; USA: TX, Hidalgo Co., Donna | junior subjective synonym
=‡"[*Libythea bachmanii larvata*] [f.] *streckeri*" W. D. Field, 1938; USA: TX, Hidalgo Co., Donna | infrasubspecific

Libytheana carinenta (Cramer, 1777); Suriname
Libytheana carinenta mexicana Michener, 1943; Mexico: Veracruz, Xalapa
Libytheana carinenta carinenta (Cramer, 1777); Suriname
Libytheana carinenta fulvescens (Lathy, 1904), **stat. nov.**; Dominica

terena species group

Libytheana terena (Godart, 1819); [Hispaniola]
Libytheana motya (Hübner, [1823]); [Cuba]

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