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On the unstabilized genus name for the Nearctic greater fritillaries (Lepidoptera: Nymphalidae: Argynnini)

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Abstract

There is current disagreement among researchers on whether the Nearctic greater fritillaries, a group that includes several endangered and threatened species, should remain in the genus *Speyeria* Scudder—in use for 80 years—or be placed as a subgenus of the Palearctic *Argynnis* Fabricius. A review of the recent scientific literature covering this group revealed the extent of this controversy in that only about half of the articles consulted recognized *Speyeria* as a subgenus of *Argynnis*. A summary of molecular phylogenetic studies using a variety of genetic markers provides a possible explanation for why this taxonomic change is controversial. These studies confirmed that species assigned to *Speyeria*, although generally morphologically similar to *Argynnis*, form a monophyletic group, a widely-accepted criterion for generic status. Thus, the controversy centers mainly on (1) the issue of taxonomic stability of a long-accepted genus name, (2) the need for increased taxon sampling of Palearctic taxa in phylogenomic studies, and (3) whether genetic divergence thresholds, including those of DNA barcodes analyzed here, can confidently be used as an aid in delimiting genera in the greater fritillaries. Based on the evidence presented here it is proposed that *Speyeria* be reinstated to full genus status.

Key words: *Argynnis*, COI barcodes, genetic divergence, nomenclature, *Speyeria*

Introduction

The nomenclature of North American nymphalid butterflies commonly known as greater fritillaries (Heliconiinae, Argynnini) is currently unstabilized. This group is currently comprised of 19 species and more than 130 subspecies (Pelham 2023), several of which are listed as endangered or threatened, but confusion exists on whether they should be assigned to the genus *Argynnis* Fabricius or *Speyeria* Scudder. For example, The International Union for Conservation of Nature's Red List of Threatened Species (IUCN) recognizes the regal fritillary *Argynnis idalia* (Drury) as vulnerable (Walker *et al.* 2022). The U.S. Fish and Wildlife Service, however, currently lists *Speyeria callippe callippe* (Boisduval), *Speyeria zerene behrensii* (W. H. Edwards) and *Speyeria zerene myrtleae* dos Passos & Grey as endangered, and *Speyeria zerene hippolyta* (W. H. Edwards) and *Speyeria nokomis nokomis* (W. H. Edwards) as threatened. In comprehensive lists of species available online, Nearctic fritillaries also are assigned to either *Argynnis* (Pelham 2023) or *Speyeria* (Savela 2025).

Up until the mid-20th century, the Nearctic fritillaries were placed in the genus *Argynnis* along with a similar group of species restricted to the Old World. Overall, the Nearctic and Palearctic greater fritillaries consist of at least 40 nominal species and more than 260 described subspecies (Savela 2025). Based on morphological analysis of male genitalia in this widespread group, dos Passos and Grey (1945) first proposed separating the Nearctic fritillaries from the Palearctic *Argynnis* (including *Fabriciana* Reuss and *Mesoacidalia* Reuss) and placing them in the genus *Speyeria*. Recognition of *Speyeria* as a valid genus had been generally accepted by the scientific community, but recently Zhang *et al*. (2020) proposed placing *Speyeria* as a subgenus of *Argynnis* based on phylogenomic relationships and DNA barcode genetic divergence analysis. Although this change had been proposed previously, based mainly on morphological analysis of genitalia (Simonsen 2006) and molecular phylogenetic analysis that included only one species of *Speyeria* (Simonsen *et al*. 2006), it was not widely accepted (Dunford 2009; de Moya *et al*. 2017). The proposal of Zhang *et al*. (2020), however, is now being incorporated into species' lists (Pelham

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2023; Warren *et al*. 2024; iNaturalist 2025), but a review of the recent scientific literature (Table 1) shows no consensus on which generic name should apply to the Nearctic fritillaries, a group of considerable conservation interest (McHugh *et al*. 2013; Wells & Tonkyn 2014; Sims 2017; Hill *et al*. 2018; Riva *et al*. 2020). A review of molecular studies on phylogenetic relationships and genetic divergence in the Argynnini presented here provides insight into this taxonomic controversy and questions the placement of *Speyeria* as a subgenus of *Argynnis*.

TABLE 1. Recent references that assigned the Nearctic greater fritillaries to the genus *Speyeria* or *Argynnis*.

Speyeria	***Argynnis***
Bladon *et al*. (2025)	Bried *et al*. (2025)
Bourn *et al*. (2024)	Chmielewski *et al*. (2023)
Campbell *et al*. (2022)	Deitsch *et al*. (2025)
Chappell *et al*. (2023)	Edwards *et al*. (2024)
Cole *et al*. (2025)	Geest *et al*. (2024)
Doll *et al*. (2022a)	Harman & Hoback (2025)
Doll *et al*. (2022b)	James (2025)
Gordon *et al*. (2024)	King & Schultz (2024)
Hamon *et al*. (2025)	Marschalek & Wolcott (2024)
Harman *et al*. (2024)	Nelson (2025)
Henry *et al*. (2024)	Pavulaan (2022)
Kuster & Miller Hesed (2024)	Plendl *et al*. (2024)
Livraghi *et al*. (2025)	Post van der Burg (2024)
Marschalek & Deutschman (2024)	Post van der Burg *et al*. (2023)
Reis *et al*. (2025)	Runquist *et al*. (2024)
Smithwick *et al*. (2024)	Rutins *et al*. (2022)
Tilley *et al*. (2022)	Weschler & Tronstad (2024)
Whipple & Moss (2024)	

Materials and methods

To evaluate acceptance of the proposed placement of *Speyeria* as a subgenus of *Argynnis*, a Google Scholar web search of peer-reviewed scientific journal citations published since 2023 for each of the 19 species of Nearctic greater fritillaries was conducted, first under the genus name *Argynnis* and then under *Speyeria*. The web search began for articles published in 2023 to provide a reasonable time frame for assessing acceptance of the taxonomic change in 2020, and was terminated on 21 September 2025. However, several articles from 2022 that cited Zhang *et al*. (2020) but nonetheless retained the genus *Speyeria* (Campbell *et al*. 2022; Doll *et al*. 2022a, b), two papers that used *Argynnis* and recognized that *Speyeria* was the previously accepted name (Pavulaan 2022; Rutins 2022), and one paper that dealt with the larval host plant of the threatened *Speyeria n. nokomis* (Tilley *et al*. 2022), were also included.

Mitochondrial DNA barcode sequences (cytochrome *c* oxidase subunit I; COI or *cox1*) of the Argynnini were downloaded from the Barcode of Life Data Systems (BOLD; Ratnasingham & Hebert 2007) and GenBank (see Table 2). Barcodes were available for 15 of the 19 Nearctic species recognized as *Argynnis* by Pelham (2023), treated here in the genus *Speyeria*, together with nine of the ten species of Palearctic *Argynnis* and seven of the eleven species of *Fabriciana*, recognized by Savela (2025). Barcodes were also available for Palearctic taxa from an historically unstabilized group (*Mesoacidalia*), previously considered a distinct genus, or a subgenus of *Argynnis*, and most recently placed as a synonym of *Speyeria* (de Moya *et al*. 2017; Savela 2025). The three species in this group, *S. aglaja* (Linnaeus), *S. alexandra* (Ménétriés), and *S. clara* (Blanchard), were analysed separately from Nearctic *Speyeria* in genetic distance calculations owing to their uncertain taxonomic position. Uncorrected mean genetic distances (*p*-distances) of among species, abbreviated here as '*d* ', were calculated in MEGA version 5.0.5 (Tamura *et al*. 2011).

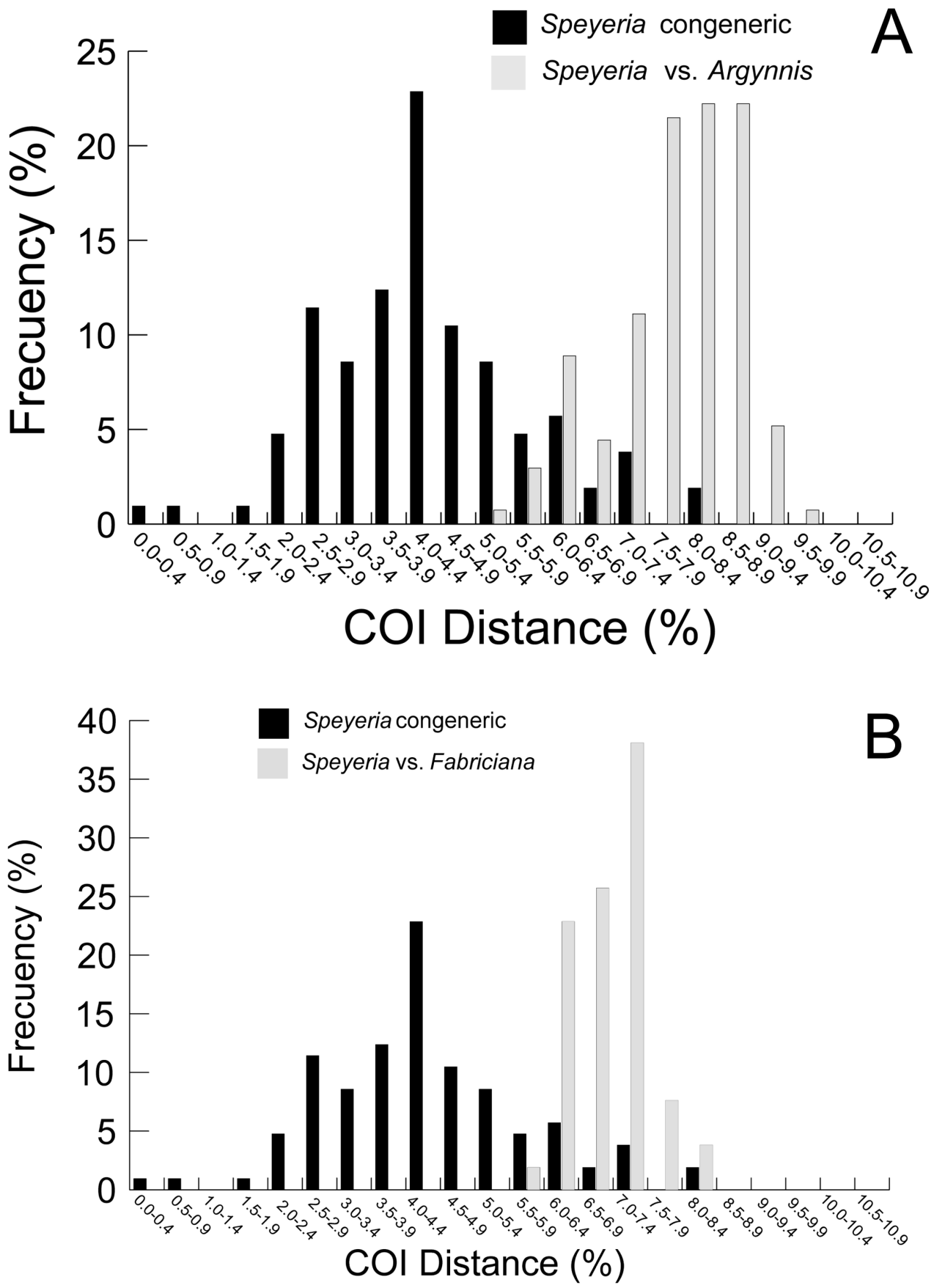

FIGURE 1. Frequencies of pairwise barcode sequence comparisons shown for intervals of 0.5% divergence in congeneric *Speyeria* species (n = 15) and (**A**) between *Speyeria* and nine species of *Argynnis* and (**B**) between congeneric *Speyeria* and seven species of *Fabriciana*.

TABLE 2. Species of Argynnini analysed for COI barcodes downloaded from BOLD and GenBank.

Species	Locality	BOLD ID	GenBank No.
Speyeria idalia	South Dakota	CNCBF1017-14	-
Speyeria atlantis	Manitoba, Can	LCH481-04	GU097102
Speyeria aphrodite	N. Carolina	LGSM818-04	GU090190
Speyeria mormonia	Alaska	ABKWR160-07	-
Speyeria zerene	BC, Canada	BBLPA045-10	JF841090
Speyeria cybele	Missouri	BBLWU287-09	HM428662
Speyeria diana	Tennessee	GMGSB640-12	-
Speyeria callippe	California	DMML148-10	JN272492
Speyeria egleis	Montana	CNCBF684-14	-
Speyeria edwardsii	Colorado	SNA026-07	-
Speyeria coronis	California	DMML163-10	JN272494
Speyeria hesperis	-	GBMNF23150-22	OM737841
Speyeria adiaste	California	SNA056-07	-
Speyeria nokomis	Arizona	RDHP523-06	-
Speyeria hydaspe	California	DMML011-10	HQ561185
S. (Mesoacidalia) aglaja	Spain	BDE301-19	-
S. (Mesoacidalia) alexandra	-	GBMIN85316-17	KY773301
S. (Mesoacidalia) clara	-	GBMIN85317-17	KY773319
Fabriciana elisa	France	EULEP3469-16	MW502093
Fabriciana jainadeva	India	GBAAM2098-25	OR600800
Fabriciana niobe	Greece	EULEP1954-15	MW503486
Fabriciana adippe	Austria	ABOLD014-16	MN138910
Fabriciana auresiana	Morocco	EULEP2648-15	-
Fabriciana nerippe	China	BJUP172-17	-
Fabriciana kamala	Pakistan	MABUT280-12	KC158318
Argynnis laodice	China	BJUP336-17	-
Argynnis ruslana	-	GBLN4650-14	JX185828
Argynnis pandora	Italy	BCLEP113-17	MN143150
Argynnis paphia	Austria	ABOLB036-15	MN138995
Argynnis sagana	Russia	EZHBA344-07	-
Argynnis anadyomene	Japan	GBAAX67312-24	-
Argynnis childreni	China	GBAAW71470-24	PP726732
Argynnis zenobia	China	INSSD3583-21	-
Argynnis hyperbius	China	BJUP333-17	-
Euptoieta hegesia	Costa Rica	MHMXY364-09	JQ538436
Yramea cytheris	Chile	LTOLB195-09	KF492178

Results

The web search yielded 17 references that recognized Nearctic greater fritillaries as belonging to the genus *Argynnis* and 18 that placed them in *Speyeria* (Table 1). Two references not shown in Table 1 used both genus names in the same article—D'Ercole *et al*. (2024) used *Argynnis cybele* (Fabricius) and *A*. *zerene* Boisduval in the text but they were listed under *Speyeria* in the supplementary material section; Tronstad *et al*. (2025) used *Argynnis* for *A*. *idalia* but *Speyeria* for 11 other species. Also not shown in Table 1 is the study of Vernygora *et al*. (2024) who presented a web-tool to aid in resolving taxonomic issues using the *Speyeria*/*Argynnis* controversy as an example but did

not express a preference. Several references specifically stated reasons for retaining *Speyeria*, including providing consistency with previous usage in conservation-related studies (Doll *et al*. 2022a, b) and a need for more complete taxon sampling in phylogenomic studies (Livraghi *et al*. 2025).

Analysis of pairwise distances (*d*) among 15 species of *Speyeria*, and between *Speyeria* spp. and nine species of *Argynnis*, is shown in Figure 1A. Distance values are shown in 5% intervals following the format of Ward (2009), except that values are shown as frequencies rather than weighted probabilities. For *Speyeria* (congeneric) there were 105 pairwise comparisons among the 15 species, with divergence values ranging from *d* = 0.3–8.0% (mean *d* = 4.3%). The two lowest values, 0.3% for *S. callippe* vs. *S. egleis* (Behr) and 0.8% for *S. adiaste* (W.H. Edwards) vs. *S. hydaspe* (Boisduval), are less than typically found between species and probably result from the inability of COI barcodes to reliably distinguish between each pair of relatively recently diverged species (Thompson *et al*. 2019; Campbell *et al*. 2020). The pairwise distance comparisons of *Speyeria* spp. among the nine species of *Argynnis* (135 comparisons) yielded a distribution displaced to the right of *Speyeria* congeneric and showed values that ranged from *d* = 5.3–9.6% (mean *d* = 7.8%). For *Argynnis* (congeneric; not shown) the distribution of 36 pairwise comparisons was also shifted to the right of *Speyeria* congeneric distances and showed a range of *d* values of 3.7–10.0% (mean *d* = 7.6%). Based on phylogenetic evidence reviewed in the Discussion, the Palearctic *Fabriciana* and *Mesoacidalia*, which are also included in the revised *Argynnis* of Zhang *et al*. (2020), were excluded from the dataset used for Figure 1A. The distributions of barcode distances between *Speyeria* congeneric and *Fabriciana* (Fig. 1B), however, showed a similar pattern as seen in Figure 1A, although pairwise comparisons were shifted to slightly lower values (*d* = 5.7–8.1%; mean *d* = 6.9%). The distribution of distances between *Speyeria* congeneric and *Mesoacidalia* (not shown) was similar to that seen in Figure 1B (*d* = 5.7–8.0%; mean *d* = 7.1%)

Discussion

Nomenclatural stability needs to be considered when changes in widely accepted generic names are proposed (ICZN 1999). The genus *Speyeria* had been widely accepted in numerous scientific publications for 80 years, and thus evidence to support changes in its taxonomic rank must be compelling. Because specific guidelines for assigning and delimiting the taxonomic rank of genus are lacking, the naming of genera has historically relied on subjective criteria (Laurin 2010; Strand & Panova 2015). The demonstration of monophyly, however, is now widely accepted by taxonomists as an objective criterion to aid in delimiting genera (Vences *et al*. 2013; Vernygora *et al*. 2024). Owing to the abundance of molecular data now available, the most reliable test of monophyly is obtained by constructing phylogenetic trees based on DNA sequences (Zhang *et al*. 2020; Vorontsova *et al*. 2023). Phylogenetic studies on the Argynnini based on a variety of molecular markers—from barcodes to genomes (de Moya *et al*. 2017; Thompson *et al*. 2019; Zhang *et al*. 2020)—confirm that the taxon *Speyeria* satisfies the criterion of monophyly.

Given the evidence of monophyly, the proposal for placing *Speyeria* as a subgenus of *Argynnis* relies mainly on morphological similarity in Palearctic and Nearctic species—although notable differences occur in ventral hindwing maculation in the *Argynnis* clade of Figure 2 in de Moya *et al*. (2017)—and in what was considered low barcode genetic differentiation and an arbitrary criterion of less prominent branch lengths (see Zhang *et al*. 2021; p. 4) on the phylogenomic tree separating the two groups (Zhang *et al*. 2020). A barcode genetic distance of 8.2% between the type species of *Speyeria* (*S. idalia*) and *Argynnis* [*A. paphia* (Linnaeus)], which corresponds to a rough guide range of 6–8% assumed for the level of subgenus (see Zhang *et al*. 2019, 2021), was included as evidence for placing *Speyeria* as a subgenus of *Argynnis* (Zhang *et al*. 2020). Generic-level barcode differences of 6–8%, however, are also found in pairwise comparisons in other butterfly taxa (Pfeiler 2024), as well as in birds and fishes (Ward 2009). In addition, when barcode divergences between additional species of *Argynnis* and *Speyeria* are calculated, *d* values can exceed 9% (Fig. 1). The overlap in barcode distances in the range of 6–8% in congeneric and confamilial comparisons (Fig. 1) suggests that this rough guide metric is not useful when used alone to conclude that different taxa showing these values belong in the same genus. Phylogenetic relationships and demonstration of monophyly also need to be considered.

In the phylogenomic study of Zhang *et al*. (2020), most of the Nearctic *Speyeria* taxa were sampled and were found to form a monophyletic group, but only three of the ten species of *Argynnis*, one of the nine described species of *Fabriciana*, and none of the *Mesoacidalia* were included. Similarities in wing maculation and male genitalia previously suggested that the three Palearctic *Mesoacidalia* species be placed in *Speyeria* (Simonsen 2006), a view

supported by phylogenetic studies (de Moya *et al*. 2017) and accepted by other workers (Polic *et al*. 2022, 2023; Savela 2025). In addition, previous studies showed *Fabriciana* and *Speyeria* resolving as sister groups (de Moya *et al*. 2017; Thompson *et al*. 2019). But even with more complete sampling of Palearctic taxa (Livraghi *et al*. 2025), it seems unlikely that additional phylogenomic evidence will support changing the generic status of *Speyeria*, given the clear resolution of *Speyeria* and *Argynnis* clades in the study of de Moya *et al*. (2017) and Zhang *et al*. (2020), albeit with lower sample sizes of *Argynnis* in the latter.

Taxonomic remarks

The demonstration that species of the Nearctic fritillaries form a monophyletic group distinct from the Palearctic *Argynnis*, and the questionable use of genetic divergence thresholds to define subgenera, argue against placing *Speyeria* as a subgenus of *Argynnis*. Accordingly, it is proposed here to reinstate the genus name of Nearctic fritillaries.

Speyeria Scudder, 1872, reinst. stat.

Retaining *Speyeria* as a valid genus will both provide taxonomic stability and facilitate communication among researchers, federal agencies, and citizen scientists involved in conservation and biodiversity monitoring programs of the greater fritillaries.

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