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Taxonomic overview of the greater fritillary genus *Speyeria* Scudder and the atlantis - hesperis species complexes, with species accounts, type images, and relevant literature (Lepidoptera: Nymphalidae)

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Abstract. A taxonomic overview for the fritillary genus *Speyeria* Scudder (= *Argynnis* Fabricius) and its placement within the Heliconiinae (Nymphalidae) is presented. Taxonomic accounts, type images, and relevant literature for the 25 subspecies within the *Speyeria atlantis* (Edwards) and *Speyeria hesperis* (Edwards) complexes and the 16 nominate *Speyeria* species are included. Errors in nomenclature are identified, taxonomic, life history, and distributional information are updated, and type locality information is discussed. Images of primary type specimens for all 16 *Speyeria* species and the 25 subspecies in the atlantis - hesperis complexes appear together in color here for the first time. One new combination of a species-subspecies is created: *Speyeria hesperis hanseni* Emmel, Emmel, and Matoon, 1998, **new combination**, which was previously *Speyeria atlantis hanseni* Emmel, Emmel, and Matoon.

Key words. *Argynnis*, bibliography, fritillary, Lepidoptera, North America, Nymphalidae, *Speyeria*, synonymy, taxonomy, types.

Introduction

Speyeria Scudder, 1872 (Nymphalidae: Heliconiinae: Argynnini), or greater fritillaries, are medium to large butterflies that represent conspicuous members of North American Lepidoptera. The genus was named in honor of a German lepidopterist, Adolph Karl Speyer, who specialized in butterfly studies (Opler and Krizek 1984; Zirlin 1996; Guppy and Shepard 2001). The origin of the common name “fritillaries” is obscure, and one explanation is that the adults resemble the lily genus *Fritillaria* (Guppy and Shepard 2001). The Latin term “*fritillus*” means “dice box”, and could also refer to the spotted pattern on the wings (Field 1938). *Speyeria*, as treated herein, is restricted to North America (absent in southeastern regions of the United States and most of Mexico) (Elwes 1889; Howe 1975; Hammond 1978). Morphologically similar genera exist in other temperate parts of the world and together may be considered the temperate-zone counterpart to tropical Heliconiini (Hammond 1978; Scott 1986b). Recent workers have treated *Speyeria* as a subgenus of the primarily Palearctic genus *Argynnis* Fabricius 1807 (Tuzov 2003; Simonsen 2004, 2006c). Until further data can be analyzed with the recent findings of Dunford (2007) (also see **Discussion**), the name *Speyeria* is retained here.

Speyeria is presently comprised of 16 species (Opler and Warren 2005, Pelham 2008; but see Scott 2008a,b) (see Table 1), and according to some authors, over 100 subspecies (dos Passos 1964; McHenry 1964; Hammond 1978; Ferris and Brown 1981; Miller and Brown 1981; Hodges 1983; Ferris 1989a,b). *Speyeria cybele* (Fabricius), *S. aphrodite* (Fabricius), *S. idalia* (Drury), and *S. atlantis* (Edwards) occur in the eastern half of North America (east of the Mississippi River), each with distributions or subspecies occurring in the west, while *S. diana* (Cramer) of the eastern United States is restricted to the Appalachian and Ozark Mountains (Scott 1986b; Opler and Malikul 1998; Opler and Wright 1999; Glassberg 2001a,b). The remaining species occur in the western regions of North America. All but three *Speyeria* are extremely variable [exceptions include *S. diana*, *S. idalia*, and *S. edwardsii* (Reakirt)], with the western North American species in particular fragmenting into numerous geographic races that are often clinally joined with considerable intergradation or blending occurring. To illustrate the diversity of forms in most species complexes, the *S. atlantis* and *S. hesperis* (Edwards) complexes are covered herein. *Speyeria atlantis* and *S. hesperis* are presently comprised of 25 subspecies, four and 21 respectively

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(Emmel et al. 1998c; Scott et al. 1998; (but see Scott 2008b) (see Table 1), and range from the eastern United States and Canada, west to California, as far north as Alaska, and south to Arizona and New Mexico (Grey 1951; Moeck 1957; Hammond 1978).

Adults are more or less orange in color with darker wing veins and spots, often with silver or cream-white ventral hindwing spots (Figure 1). The silver spots owe their metallic appearance to refracted light rather than pigmentation (Scott 1988). Determinations are made primarily by wing facies and geographical location, and because of this, specific and subspecific identification is difficult in many taxa due to subtle wing pattern variations. Eye coloration has been proposed to discern some of the more widespread North American species (Glassberg 2000), although this coloration is usually lost in museum specimens. Within *Speyeria*, adult morphological variation between species and subspecies is by and large the following: overall size; degree of sexual dimorphism; wings: dorsally by ground color, intensity of black markings, degree of dark basal suffusion, prominence of marginal band, thickness of veins on the wings; ventrally by the general ground color of the discal region, size, shape, color and position of spots on the hindwings, and color and width of submarginal band between the two outer rows of spots on hindwings (Figure 5).

Speyeria have been studied in great detail in the past and continue to be of major interest to professional and amateur collectors. Those who have studied the genus for years have often contradicted themselves, and competent authors living at some distance from one another have described the same species under different names. Two authors, W. H. Edwards (1863a,b; 1864a; 1869; 1870; 1874a,b; 1878; 1879a,b; 1881; 1883) and J. D. Gunder (1924; 1927; 1929; 1931; 1932; 1934), described numerous *Argynnis* (= *Speyeria*) species, subspecies, and aberrant forms before species limits and clinal patterns were more readily recognized by subsequent authors. Geographic variation in *Speyeria* was first studied in detail by Comstock (1927 = 1989 reprint), Holland (1898, 1931), and later by Grey (1951), Moeck (1957), Hovanitz (1967), Howe (1975), and Hammond (1978). The earlier works listed dozens of 'species' names (e.g. Holland 1898 with 47 species), but subsequent authors realized that most of these 'species' were no more than geographical forms or races associated with a few polytypic species (dos Passos and Grey 1947; Howe 1975; Hammond 1978; Miller and Brown 1981; Scott 1986b). Dos Passos and L. P. Grey, two amateur lepidopterists, played an important role in sorting out species relationships and geographical variation within *Speyeria*, and presented methodologies and substantial collections that provide a foundation for subsequent studies on *Speyeria* and closely related groups (Grey 1964, 1970; Rindge 1987; Wilkinson 1988a, b). Studies conducted by Guppy (1953), Grey et al. (1963), Mattoon et al. (1971), and recently by James (2008) elucidated some of the difficulties of rearing *Speyeria*. The ability to break natural larval diapause during breeding experiments was helpful in understanding ecological data and in turn species limits within the group.

Historically, three species of *Speyeria* (i.e., *S. diana*, *S. cybele*, *S. aphrodite*) have been recognized as the subgenus *Semnopsyche* Scudder (1875) based primarily on differences in the female genitalic armature (dos Passos and Grey 1945a, 1947; Klots 1951; Hammond 1978; Ferris and Brown 1981). Scudder (1875) first included only *S. diana* in the *Semnopsyche* group, separating it from *Argynnis* (= *Speyeria*) based on wing and leg morphology. Miller and Brown (1981) correctly placed *Semnopsyche* as a synonym of *Speyeria* but did not provide a reason for doing so; they likely followed the recommendation of dos Passos and Grey (1947). Upon further examination of the female genitalic armature of *Speyeria idalia* (the generotype of the genus), Grey (1989) discovered a "secondary" bursal sac similar to those found in the *Semnopsyche* group, and thus confirmed *Semnopsyche* as a junior synonym for *Speyeria*. Dos Passos and Grey (1947) prepared an extensive catalog of *Speyeria* in accordance with the latest concepts of speciation and systematics at that time listing 13 species and 96 subspecies. Since then, several additional subspecies have been described, three subspecies have been elevated to full species status, and some names have been declared synonyms (e.g., Garth 1949; Moeck 1947, 1950; Austin 1983; Hammond and Dornfeld 1983; Holland 1988; Emmel and Austin 1998; Emmel and Emmel 1998a,b; Emmel et al. 1998d; Gatrell 1998; Scott et al. 1998; Williams 2001a).

Taxonomic relationships

Speyeria, long included in the Old World genus *Argynnis* (Argynninae) (Elwes 1889; Snyder 1900; Lehmann 1913; Seitz 1924), differ from their Eurasian relatives primarily in genitalic structure (dos

Table 1. Checklist of species/subspecies treated herein organized in the order of appearance in the text.

Taxon	Page
<i>Speyeria idalia</i> (Drury)	7
<i>Speyeria diana</i> (Cramer)	11
<i>Speyeria cybele</i> (Fabricius)	13
<i>Speyeria aphrodite</i> (Fabricius)	14
<i>Speyeria nokomis</i> (Edwards)	15
<i>Speyeria edwardsii</i> (Reakirt)	17
<i>Speyeria coronis</i> (Behr)	18
<i>Speyeria zerene</i> (Boisduval)	19
<i>Speyeria carolae</i> (dos Passos and Grey)	21
<i>Speyeria callippe</i> (Boisduval)	22
<i>Speyeria egleis</i> (Behr)	23
<i>Speyeria adiate</i> (Edwards)	24
<i>Speyeria atlantis</i> (Edwards)	25
<i>S. atlantis atlantis</i> (Edwards)	27
<i>S. atlantis hollandi</i> (Chermock and Chermock)	28
<i>S. atlantis sorocko</i> Scott, Kondla, Spomer	28
<i>S. atlantis pahasapa</i> Spomer, Scott, Kondla	29
<i>Speyeria hesperis</i> (Edwards)	29
<i>S. hesperis hesperis</i> (Edwards)	30
<i>S. hesperis helena</i> dos Passos and Grey	31
<i>S. hesperis beani</i> (Barnes and Benjamin)	31
<i>S. hesperis brico</i> Kondla, Scott, Spomer	32
<i>S. hesperis ratonensis</i> Scott	33
<i>S. hesperis greyi</i> Moeck	33
<i>S. hesperis lurana</i> dos Passos and Grey	34
<i>S. hesperis irene</i> (Boisduval)	34
<i>S. hesperis cottlei</i> (Comstock)	35
<i>S. hesperis hanseni</i> Emmel, Emmel, and Mattoon	36
<i>S. hesperis dodgei</i> (Gunder)	37
<i>S. hesperis viola</i> dos Passos and Grey	37
<i>S. hesperis elko</i> Austin	38
<i>S. hesperis tetonia</i> dos Passos and Grey	39
<i>S. hesperis wasatchia</i> dos Passos and Grey	39
<i>S. hesperis chitone</i> (Edwards)	40
<i>S. hesperis electa</i> (Edwards)	40
<i>S. hesperis schellbachi</i> Garth	41
<i>S. hesperis nausicaa</i> (Edwards)	42
<i>S. hesperis dorothea</i> Moeck	43
<i>S. hesperis capitaneensis</i> R. Holland	43
<i>Speyeria hydaspae</i> (Boisduval)	44
<i>Speyeria mormonia</i> (Boisduval)	45

Passos and Grey 1945a; Dornfeld 1980). They were considered generically distinct from *Argynnis* by dos Passos and Grey (1945a; Warren et al. 1946); all North American taxa named since that time have been described within *Speyeria*. Nonetheless, *Argynnis* was retained in some popular guides and other literature (e.g., Garth 1950; Garth and Tilden 1963; Hovanitz 1962, 1963a,b; Sette 1962). McHenry (1963, 1964) attempted to resurrect the use of *Argynnis*, but this has not been followed in North America (Scott 1986b; Opler and Malikul 1998; Opler and Wright 1999; Glassberg 2001a,b). However, recent work conducted by Simonsen (2006a,b,c) and Simonsen et al. (2006) have provided some morphological and mo-

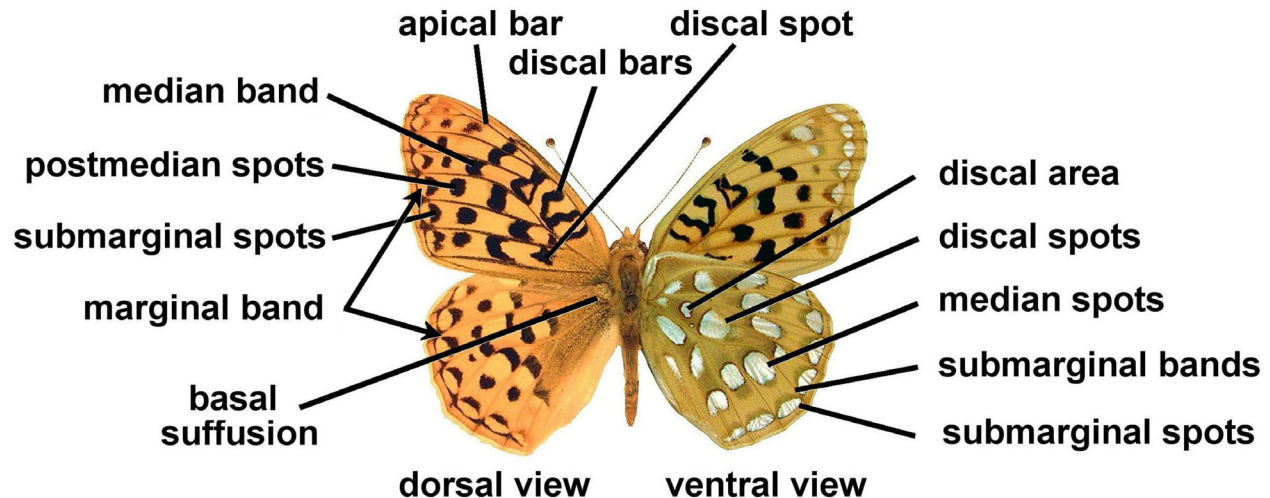


Figure 1. Wing terminology associated with species of *Speyeria*. Image by James C. Dunford and Kelly R. Sims.

lecular evidence that suggests the remainder of *Argynnis* is paraphyletic if *Speyeria* is retained as a separate genus (but see **Discussion**).

Reuss (1922, 1926a,b) erected the subfamily Argynninae based on genitalic and androconial characters and divided *Argynnis* into different subtribes and genera. Warren (1944) conducted a revision of European argynnines based primarily on male genitalia and concentrated on the genus *Boloria* Moore. At the same time, dos Passos and Grey (1945a) provided a revision of the argynnines (primarily *Speyeria*) using genitalic structures. Warren et al. (1946) divided the Argynninae and placed *Boloria* within the Boloriidi, distinguishing the tribe from others in the Argynnidi (i.e., *Speyeria* and *Argynnis*). Grey (1957, 1989) later agreed with some of Warren's assertions of affinities between *Speyeria* and genera such as *Mesoacidalia* Reuss, but criticized the use of one set of characters, those of male genitalia (Figure 4). Ackery (1988) partially adopted the classification of Warren (1944) and dos Passos and Grey (1945a) but included the New World genera *Yramea* Reuss and *Euptoieta* Doubleday. Ehrlich (1958) included *Speyeria* within the Nymphalinae but noted that the heliconi taxa were worthy of subfamilial rank and appeared to fall in closely with *Argynnis* and its allies. Scott (1984), based on numerous morphological and behavioral characters taken mostly from previous studies, noted the close relationship between the Heliconiini and Argynnini and stated that the two tribes cannot be sustained on a worldwide basis due to inconsistencies with host plant use, humeral veins, and larval head spines, and suggested that they be combined into Heliconiini by priority. The subfamily Heliconiinae has only been recently delimited as it is now by Harvey (1991), when he placed the Argynninae (i.e., *Argynnis* and *Speyeria*) within the heliconiine tribe Heliconiini based on adult and larval morphology. Subsequent higher systematic work within the Nymphalidae has also included *Argynnis* and/or *Speyeria* within Heliconiini (Penz 1999; Brower 2000; Wahlberg et al. 2003; Freitas and Brown 2004).

Since the precladistic works of Warren (1944, 1955), dos Passos and Grey (1945a), and Moeck (1957), and early systematic works of Shirôzu and Saigusa (1973) and Hammond (1978), only a few workers have treated genera within the Argynnini using modern systematic techniques. Based on adult and larval morphology using phylogenetic analyses, Penz and Peggie (2003) suggested that Heliconiinae be divided into four groups, and included *Speyeria* within the Argynnini. The argynnines in their study were the most derived monophyletic group within the Heliconiinae, implying that species diversification within the group occurred more recently than the emergence of ancestral neotropical heliconiines. By contrast, the fairly recent morphological and molecular work of Brower (2000a) placed the neotropical taxa as more derived than the argynnine fritillaries, indicating that there is difficulty in accurately recovering the evolutionary history of taxa that emerged a long time ago (Penz and Peggie 2003).

The morphological and molecular work of Simonsen et al. (2006) provided evidence of monophyletic groups for six genera within the Argynnini, reducing *Speyeria* to a subgenus of *Argynnis*. In both of these studies, the European genera *Fabriciana* Reuss and *Mesoacidalia* [both genera are included in *Argynnis*

in Simonsen et al. (2006)] are hypothetically closely related to *Speyeria*. In addition, a 'fairly well-supported clade' comprising all *Argynnis* species (including *Speyeria*) supports the unification of all larger fritillaries in one genus (Simonsen et al. 2006). Hypothetically closely related heliconiine taxa with distributions in North America include *Clossiana* Reuss (= *Boloria*) and *Euptoieta* (Harvey 1991; Penz and Peggie 2003, Simonsen 2005). Present day computer websites such as The Nymphalidae Systematics Group (2009) and Tree of Life Web Project (2009), as well as recent journal publications (James 2008 uses both *Speyeria* and *Argynnis*; Scott 2008b), follow the taxonomy of Simonsen et al. (2006) and use *Argynnis* when listing species of *Speyeria*. This usage, however, may be premature and will likely confound the treatment of *Speyeria* and/or *Argynnis* in forthcoming publications much like it had done before (see *Speyeria hesperis greyi* subspecies profile; also see **Discussion**).

Material and Methods

Speyeria have been the subjects of evolutionary-related studies on geographical variation and speciation (e.g., Grey 1951; Moeck 1957; Grey et al. 1963; Brittnacher et al. 1978; Hammond 1974, 1978, 1981, 1990; Scott et al. 1998). However, there has not been a comprehensive, modern cladistic analysis for this group. To gain a better understanding of *Speyeria* taxonomy, life histories, distributions, and to correctly associate images of type material with their accompanying names, detailed species and subspecies accounts were compiled based on current literature, fieldwork, and collection data. Diagnoses and life history information for the 16 species of *Speyeria* primarily pertain to the 'nominated taxon' for each species unless otherwise indicated. Distributional information for *Speyeria* was obtained from the literature, and distributional information for *S. atlantis* and *S. hesperis* was also taken from specimen label data available in institutions and private collections. Images of primary and a few miscellaneous type specimens are included for most of the taxa discussed herein. Many type images are presented here in color for the first time. Errors in nomenclature are identified, and taxonomic and life history information is also updated and discussed. Compilation of these accounts and availability of type images will assist present-day phylogenetic analyses that address the evolution of *Speyeria* and related taxa.

Numerous publications, directly and indirectly relevant to *Speyeria*, were reviewed to compile the species accounts. Morphological and behavioral terminology follows primarily that of Hammond (1974; 1978) and Scott (1986b). Scientific and/or vernacular names for adult and larval food sources included in each account are written as they appear in the original publication unless otherwise noted (i.e., no attempt was made to change a vernacular name to a scientific name and vice versa; and because of the number of reported host names no attempt was made to use the current taxonomy [including author] of plant species). Recognition of nomenclatural errors, synonymies and type information was greatly facilitated by dos Passos and Grey (1947), McHenry (1964), Brown (1965), Miller and Brown (1981) and Ferris (1989a,b), but several other taxonomic works were also used and are referenced in the accounts.

Synonymies presented herein include only the most important nomenclatural actions. More detailed synonymies can be found in the above-mentioned works. Type specimen information included herein is primary type data only (i.e., holotype, lectotype, or neotype); secondary type information is not included in most accounts. Author names and year of publication appearing within [brackets] in synonymies are references in which the name combination was first used. Additional text in (parentheses) appearing in synonymies is included to provide brief clarification of nomenclatural actions. Bracketed text (i.e., sex of specimen) in the **Type label data** section was included on the original label as a symbol. Specific epithets in synonymies typed in upper case are intentional and are presented as they appear in the original literature. Species accounts are largely presented in order according to Opler and Warren (2005). However, the type species for the genus, *Speyeria idalia* (Drury), is presented first in this treatment (Table 1). *Speyeria atlantis* and *S. hesperis* subspecies accounts are largely presented in order following Scott et al. (1998). Common names associated with *Speyeria* were taken from Scudder (1889), Miller (1992), The International Lepidoptera Survey (2009), and original species and subspecies descriptions when vernacular names were included.

In addition to the literature cited in the species accounts, the following literature was also used for life history and distributional information: Acorn (1993), Adams and Finkelstein (2006), Allen (1997), Allen et al. (2005), Austin (1981, 1985), Brooks (1942), Brown et al. (1957), Cary and Holland (1992), Clark and Clark (1951), Cohen and Cohen (1991), Comstock J. A. (1989-reprint of original 1925 work), Comstock W.

P. (1940), Covell and Straley (1973), Davenport (1995, 1998), DeFoliart (1956), Dornfeld (1980), Douglas and Douglas (2005), Drees and Butler (1978), Dunford (2005), Dunford and Ekin (2005), Ebner (1970), Edwards (1873), Ellis (1975), Ely et al. (1983), Emmel (1964, 1998), Emmel and Emmel (1973), Emmel et al. (1992), Eriksen (1962), Ferge (2002), Ferris (1971a,b, 1976), Ferris and Brown (1981), Field (1938), Fisher (2005), Fleishman et al. (1997), Fleishman et al. (2001a), Fleishman et al. (2005), Garth (1950), Garth and Tilden (1963), Garth and Tilden (1986), Glassberg (2001a,b), Gochfeld and Burger (1997), Gregory (1975), Grey (1972), Guppy and Shepard (2001), Hardesty and Groothuis (1993), Harris (1972), Heitzman and Heitzman (1996), Hinchliff (1994, 1996), Holland (1974, 1984), Holland and Cary (1996), Holmes et al. (1991), Hooper (1973), Hubbard (1965), Irwin and Downey (1973), Johnson (1972), Klassen (1984), Kohler (1980), Koziol (1994), Lafontaine and Wood (1997), Larsen and Bovee (2001), Lavers (2006), Layberry et al. (1998), Marrone (1994), Masters (1972), Miller and Brown (1981), Miller and Hammond (2003), Nelson (1979), Nielsen (1999), North American Butterfly Association (2001), O'Brien (1983), Opler and Krizek (1984), Opler and Malikul (1998), Opler and Wright (1999), Orsak (1978), Pavulaan (1990), Pyle (1995), Riotte (1962), Rolfs (2005), Saunders (1932), Scott (1973, 1975, 1986a,b, 1992, 2006a,b), Scott et al. (1968), Scott and Scott (1978), Scott et al. (1998), Scudder (1889), Shapiro and Shapiro (1973), Shields (1963, 1966), Shields et al. (1970), Shields and Emmel (1973), Shuey et al. 1987), Shull and Badger (1972), Shull (1987), Simmons (1963), Snyder (1896), Stewart et al. (2001), Threatful (1988), Tietz (1952), Tilden (1963), Tilden and Huntzinger (1977), Tilden and Smith (1986), Toliver et al. (2001), Tuttle (1996-2006), Wagner (2005), and Warren (2005).

Scott (2008a) published a detailed review of several works mentioned above which includes corrections to nomenclature and image determinations. Although the literature review here was intended to be fairly comprehensive, not all of the published life history and distributional information currently available for *Speyeria* is cited herein. There are numerous private unpublished distributional and life history data that could be added to these profiles.

Additional locality data (State: County or Country: Province) for *S. atlantis* and *S. hesperis* were gleaned from specimen label data in museum and private collections listed here. Museums with associate acronyms used in the text are repositories where types were photographed. Many museum acronyms follow the Bishop Museum's Abbreviations for Insect and Spider Collections of the World (Evenhuis 2007). Museum and private collections studied include: (**AMNH**) American Museum of Natural History, New York, NY; (**BMNH**) British Museum of Natural History [now Natural History Museum], London, UK; (**CMNH**) Carnegie Museum of Natural History, Pittsburgh, PA; (**CNIC**) Canadian National Collection, Ottawa, Ontario, Canada; (**CSUC**) C. P. Gillette Museum of Arthropod Biodiversity, Ft. Collins, CO; (**FMNH**) Field Museum of Natural History, Chicago, IL; Clifford Ferris, Laramie, WY; (**FSCA**) Florida State Collection of Arthropods, Gainesville, FL; (**FSMC**) Allyn Museum of Entomology [now located at the McGuire Center for Lepidoptera and Biodiversity], Gainesville, FL; (**LACM**) Natural History Museum of Los Angeles County, Los Angeles, CA; (**MGCL**) McGuire Center for Lepidoptera and Biodiversity, Gainesville, FL; Crispin Guppy, Quesnel, British Columbia, Canada; Norbert Kondla, Genelle, British Columbia, Canada; (**MCPM**) Milwaukee Public Museum, Milwaukee, WI; (**MBSM**) Monte L. Bean Life Science Museum, Brigham Young University, Provo, UT; (**NMNH**) National Museum of Natural History [United States National Museum], Smithsonian Institution, Washington, DC; (**NVMC**) Nevada State Museum, Carson City, NV; James Scott, Lakewood, CO; Steve Spomer, Lincoln, NE; (**EMUS**) Utah State University Insect Collection, Logan, UT; (**ESUW**) University of Wyoming Insect Museum, Laramie, WY; and Andrew Warren, Gainesville, FL. Abbreviated records (i.e., state and county information) are included in the subspecies accounts.

Type specimen images provided by various museum personnel are indicated in figure captions; camera and lighting specifics are not known. I took images of many type specimens in 2004 with an Olympus Stylus six-megapixel digital camera attached to a six-inch tall camera tripod under the natural lighting present at each museum. The background included with each specimen was blue-grey card stock. No flash was used to take images in order to reduce the reflection of silver wing scales present on most specimens. Image enhancement (i.e., focus sharpening and color adjustment) included in this study was completed using Adobe Photoshop CS2 (version 9.0). Color adjustment was made while comparing the computer image with the actual specimen; however, in some cases true specimen color is not precisely matched in the images included herein (natural, outdoor lighting would likely produce truer wing color

images). To fit within the space allotted in the plates or for legibility, type labels may have been reduced or enlarged and may not appear at the same scale as the corresponding type image.

***SPEYERIA* SCUDDER, 1872**

Argynnis Fabricius, 1807: ix. Genotype: *Papilio paphia* Linnaeus, 1758: 481. [Some authors considered *Speyeria* as a subgenus of *Argynnis*, see **Taxonomic Relationships**.]

Speyeria Scudder, 1872: 23. Genotype: *Papilio Nymphalis Phaleratus Idalia* Drury, 1773: 1.

Semnopsyche Scudder, 1875: 258. Genotype: *Papilio Nymphalis Phaleratus Diana* Cramer, 1777: 4, 148. [Treated as a subgenus of *Speyeria* by dos Passos and Grey 1947.]

Neocidalia Reuss, 1926a: 69. Genotype: *Papilio cybele* Cramer, 1775 [sic, attribution error].

The type species for *Speyeria* Scudder, 1872, *Papilio idalia* Drury, 1773, is described in the three volume monograph entitled: *Illustrations of natural history, wherein are exhibited upwards of two hundred and forty figures of exotic insects, according to their different genera by D. Drury*. The original description contains three hand colored illustrations and a fairly brief description of 'Idalia' (Figure 2). *Speyeria idalia* was described from individuals taken in New York on 28 June, with no further locality information. The original designation of *Speyeria* was monotypic, containing only *S. idalia*. Drury's description has been a source of potential error in that specimens used for the description are presumed lost. Because the type specimen was apparently lost since the time of Drury's description, dos Passos and Grey (1947) designated a neotype based on a male specimen labeled 'No. 1349 Coll. J. Angus, West Farms, New York City' housed at the American Museum of Natural History.

***SPEYERIA* SPECIES ACCOUNTS**

***Speyeria idalia* (Drury, 1773)**

(Figure 2-3, 4A, 6)

Papilio Nymphalis Phaleratus Idalia Drury, 1773: 1 (Figure 2)

Argynnis astarte Fisher, 1858: 179.

Argynnis Ashtaroth Fisher, 1859: 352.

Argynnis Idalia-Infumata Oberthür, 1912: 315.

Argynnis idalia Drury form *dolli* Gunder, 1927: 286.

Argynnis idalia Drury form *pallida* Eisner, 1942: 124.

Speyeria idalia (Drury) [dos Passos and Grey 1945a].

Common names. Regal fritillary, regal silverspot butterfly, regal silver-wing, ideal argynne, eastern regal fritillary, prairie regal fritillary.

Type deposited. Neotype (male) designated by dos Passos and Grey (1947) at American Museum of Natural History (Figure 6).

Type locality. See Figure 2 for original description. New York. Defined by dos Passos and Grey (1947) based on neotype as New York City, New York County, New York.

Type label data. "No. 1349, coll. J. Angus, West Farms, New York City.; NEOTYPE, Pap. Nym. Phal. Idalia Drury".

Identification, taxonomy, and variation. Adult wingspan ranges from 68-106 mm. The forewings in males and females are bright orange-brown with black markings. The veins in the forewing of the male are thick and dark but there is no basal suffusion. Dorsal hindwings are black with a postmedian row of white spots and submarginal row of orange (male) or white (female) spots. The ventral hindwing disc is a deep olive and the spots are large and silver. The black surface on the dorsal hindwings distinguishes *S. idalia* from most other *Speyeria*. The genitalia is similar to those in the *Semnopsyche* group. The male



Figure 2. Original description and colored illustrations for 'Idalia' reproduced from Drury 1773.

has a thick, hooked uncus (Figure 4A) and there is a secondary bursal sac in the female. Prior to Williams (2001a,c; 2002), there were no 'subspecific' taxa designated under *S. idalia*. Based on adult wing morphology and molecular evidence, Williams separated the western and eastern (Pennsylvania) *S. idalia* populations. The name *Speyeria idalia occidentalis* Williams (Type locality Will County, Illinois) has been given to the western populations. Eggs are pale green when newly laid, changing to tan as the larva develops inside. Larvae (Figure 3A) are velvety black with ochre-yellow or dull orange markings and transverse stripes. The dorsal spines are silver-white with black tips. The top half of the larval head capsule is bright red-orange. Scudder (1889) described the six larval instars in detail. Pupae (Figure 3B) are approximately 28 mm in length, light brown, tinged with pink, and bear black spots on the wing cases. There are also yellow transverse bands on the abdomen. Detailed egg, larval instar, and pupal descriptions are included in Edwards (1879d).

Range. Formerly known from Manitoba south through the plains states to central Colorado [likely a stray in central Colorado (Scott 2008a p. 114)] Kansas, northeastern Oklahoma, and Missouri; in the east from New Brunswick south to northwest North Carolina. Many colonies, however, have disappeared due mostly to habitat loss. Scudder (1889) reported *S. idalia* as far south as northern Georgia (but see Calhoun

FIG. I. The female.—Expanding full four inches.

FIG. II. The male.—Expanding about three inches and an half.

Upper-side. **T**HE *Antennæ*, are dark brown.—The *Head* and *Thorax*, of a deep brown orange.—The *Superior Wings*, are of a dark orange, their anterior and external edges being bordered with black. Near the latter, are eight white spots on the wings of the female, (but not on the male.) Above these, the female has five, and the male six, round black spots; those of the latter being smallest. Several black waves and streaks, are dispersed on other parts of the wings.—The *Inferior Wings*, are of a fine dark blue, almost black, and are a little dentated; the superior ones being plain. Near the external edges, is a row of cream coloured spots, consisting of seven, which, in the male, are red. Above these, is another row of the same number of cream coloured spots, situated near the middle of the wings. The upper part of these wings, next the body, is covered with brown orange coloured hairs.

Under-side. FIG. III.—The *Head*, *Breast* and *Feet*, are dark blue, nearly black.—The *Superior Wings*, dark orange, with some triangular silver spots placed along the external edges; whose upper points are edged with black, and are generally more distinct in the female than the male. The several black waves and streaks seen on the upper-side, are here more faint, some being scarce visible.—The *Inferior Wings*, are of a dark olive brown, with twenty-six different shaped silver spots on each; one of which, in the center of the wing, being divided by a short black line.

I received them from New York, where they were taken the 28th of June.

I have not seen them described in any author.



Figure 3. Images of *Speyeria idalia* life stages. **A)** Larva. **B)** Pupa. **C)** Adult on butterflyweed, Crawford County, Wisconsin. Images A-B by David L. Wagner; C by James C. Dunford.

2007), Louisiana (but see Hovanitz 1963a), and Arkansas, and also reported it to be abundant in Connecticut and Massachusetts. Dos Passos and Grey (1947) listed the following states: Maine, Vermont, New Hampshire, Massachusetts, Connecticut, Rhode Island, New York, New Jersey, Maryland, Delaware, Pennsylvania, Virginia, West Virginia, Indiana, Ohio, Michigan, Illinois, Wisconsin, Kansas, Nebraska, Montana, South Dakota. It has been extirpated from most of New England except for a few offshore islands (but see Schweitzer 1993; Wagner 1995), and also extirpated from the mainland of New York, New Jersey, and Delaware (Evers 1994; Gochfeld and Burger 1997). It has also been extirpated in many areas in the Great Lakes region (Douglas and Douglas 2005) and is now rare or absent from many areas east of the Mississippi River (Opler and Wright 1999). Adults may wander long distances, and many records represent observations of single wandering individuals (Opler and Wright 1999). Currently, *S. idalia* are found in good numbers in the Great Plains states, with fragmented populations in the Midwest, and only a few known populations in the east (Pennsylvania and Virginia) (Schweitzer 1993; Mason 2001; Williams 2001a; Mooreside et al. 2006).

Life history. Habitat includes Upper Austral to Transition Zone in wet meadows/fields, marshlands, and prairie. Open grassy areas, such as mid-grass or tall-grass prairies, are preferred habitat. Life history studies and land management issues are numerous for *S. idalia* (Swengel 1993, 2004; Swengel and Swengel 2001; Wagner 1995; Glassberg 1998a,b; Debinski et al. 2000; Mason 2001; Ferster 2005; Kelly and Debinski 1998; Kopper et al. 2000; Kopper et al. 2001a,b,c; Ross 2001; Shepherd and Debinski 2005; Keyghobadi et al. 2006). Swengel (1997) reported *S. idalia* were significantly more abundant in larger Midwestern prairies with topographic diversity and management by haying or grazing. *Speyeria idalia* are reportedly sensitive to fire, and management activities should both address the temporal and spatial aspects of the resource needs of the butterfly (Evers 1994; Swengel 1997; Swengel and Swengel 2001; Swengel 2004). Eggs are laid singly near host plants or on host plants (Scudder 1889) and unfed first instar larvae hibernate. Oviposition site selection may be influenced by the presence of grass and forb overstory for protection against solar radiation and harsh overwintering conditions (Kopper et al. 2000). Females do not lay many eggs until August or early September (Scott 1986b; Kopper et al. 2001c), and a single individual is capable of laying nearly 2,500 eggs (Wagner 1995). Larvae have been observed feeding on violets during the day (Kopper et al. 2001a; Mooreside et al. 2006). Flight period is from June through early September. *Speyeria idalia* is either listed as endangered, threatened, or are of special concern in several states (Shuey et al. 1987; Evers 1994, Schlicht 1997; Mason 2001; Vaughan and Sheperd 2005b). Williams (1999, 2001a,b,c) suggested that the subspecific status of the eastern population of *S. idalia idalia* has important conservation implications and should result in federal emergency listing for this taxon. Habitat loss, due to development and agriculture, is the likely cause of the decline of *S. idalia* in

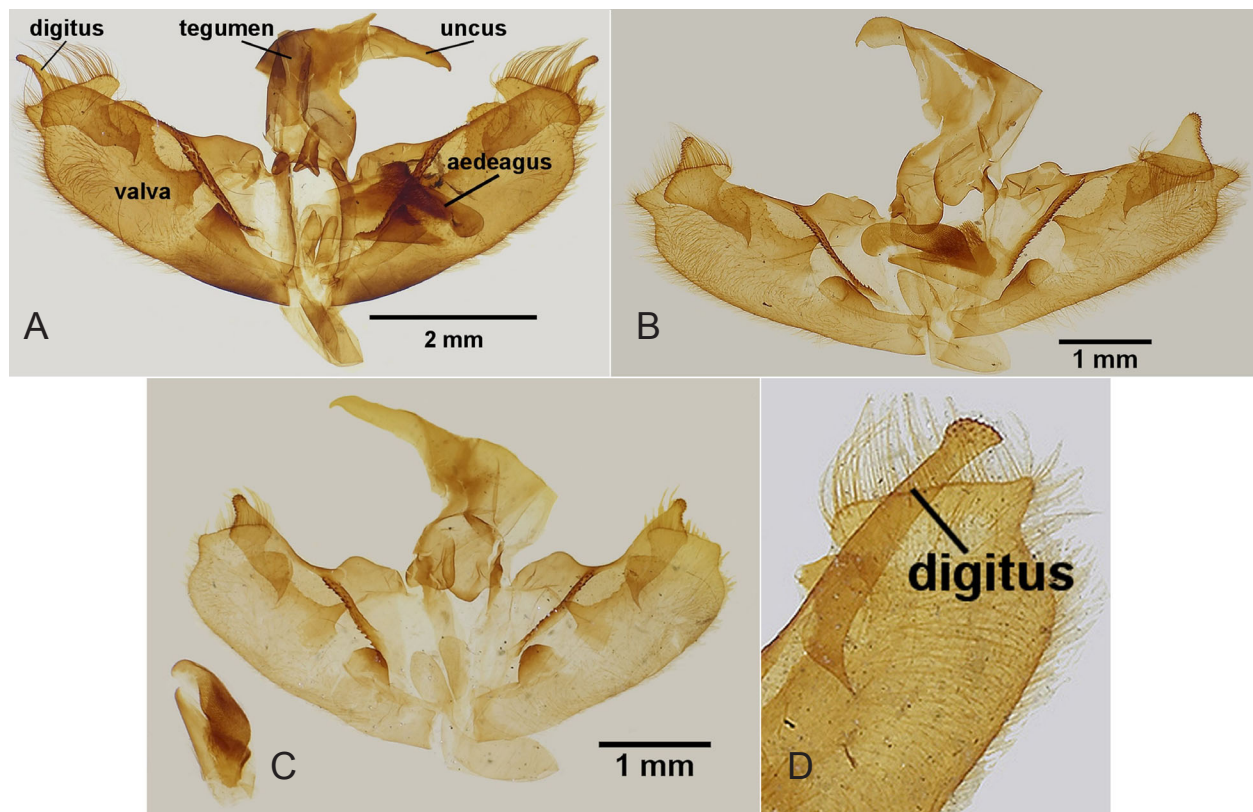


Figure 4. Male genitalic armature. **A)** *Speyeria idalia* (locality unknown). **B)** *Speyeria cybele* (Nebraska). **C)** *Speyeria hesperis* (aedeagus removed) (Idaho). **D)** Digitus located on left valva, *Speyeria edwardsii* (Nebraska). Images by James C. Dunford.

many areas (Vaughan and Sheperd 2005b), but their decline may also be due to pesticide spraying for gypsy moths control in some regions (Evers 1994). Larval host plant decline (Kelly and Debinski 1998) and lack of suitable nectar sources (Wagner 1995) may also explain the disappearance of *S. idalia*. Wagner (2005) reported a nuclear polyhedrosis virus in captive bred populations, and this may also be a factor in the decline of some wild populations. Small, isolated populations are vulnerable to extirpation and loss of genetic diversity unless ovipositing females can find other suitable habitats. Ries and Debinski (2001) suggested the movements of adults are influenced by the quality of habitat, and that they are less likely to exit from suitable habitat. It has also been reported that *S. idalia* is non-migratory and generally stay within the same local area throughout their lifetime (Scott 1986b). Keyghobadi et al. (2006) have shown that *S. idalia* populations in Pennsylvania occupying three, relatively nearby meadows exhibited restricted gene flow and unique genetic signatures. This suggests there may be fine-scale genetic subdivision in areas where *S. idalia* populations have been largely extirpated. The results presented by Williams et al. (2002) and Williams et al. (2003) indicated that microsatellite markers have shown increased differentiation and decreased genetic diversity in the isolated, eastern *S. idalia* populations. Midwestern populations, which are presently experiencing the same effects of habitat fragmentation, are also more likely to experience the associated increase in extinction risk due to both genetic and demographic factors (Williams et al. 2003).

Larval host plants. *Viola pedatifida*, *V. papilionacea*, *V. lanceolata*, *V. pedata*, *V. sagittata*, *V. sororia* (Swengel 1997; Robinson et al. 2002; Douglas and Douglas 2005).

Adult food sources. Common milkweed, butterfly milkweed, swamp milkweed, pasture and field thistles, alfalfa, butterfly weed, black-eyed Susan, wild bergamot, blackberry, dogbanes, crown vetch, Deptford pink, spotted knapweed, ox-eye daisy, dotted blazing star, prairie blazing star, purple coneflower, black Sampson (Shapiro and Shapiro 1973; Debinski et al. 2000; Ross 2002; Douglas and Douglas 2005; Ferster

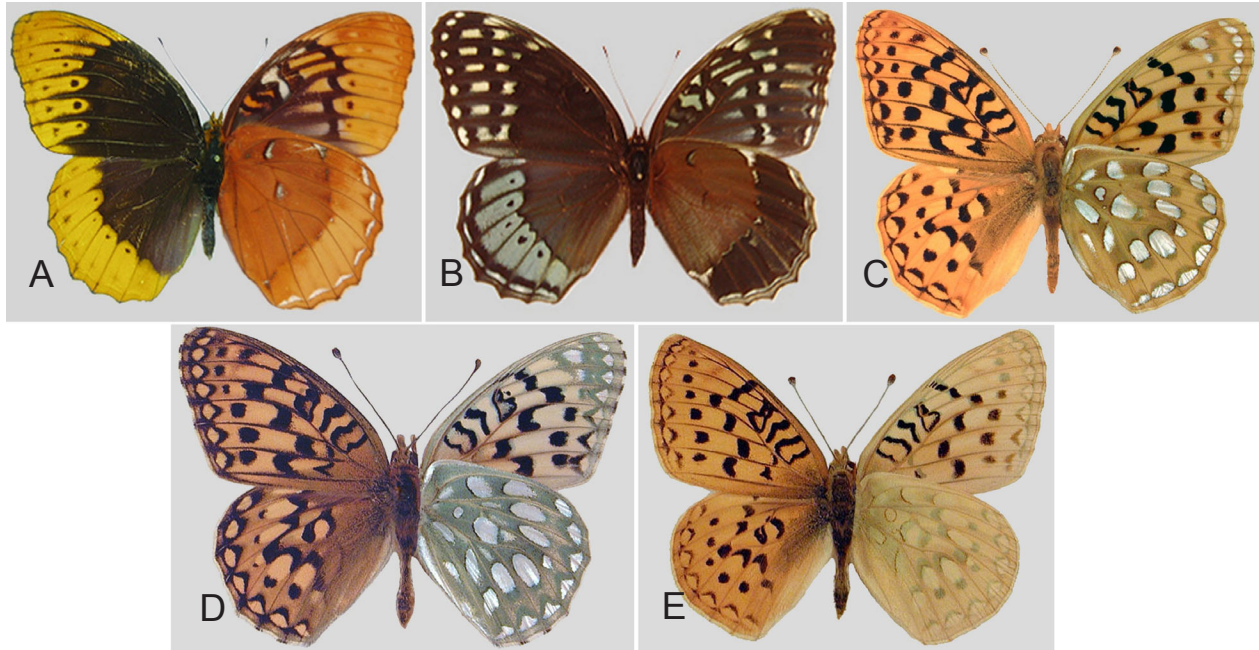


Figure 5. Habitus images of adult *Speyeria* spp., each image with dorsal (left) and ventral (right) view. **A)** *Speyeria diana*, male. **B)** *Speyeria diana*, female. **C)** *Speyeria zerene gunderi* (Comstock), male; Nevada. **D)** *Speyeria callippe harmonia* dos Passos and Grey, male; Nevada. **E)** *Speyeria mormonia artonis* (Edwards), male; Nevada. Images by James C. Dunford.

2005; Shepherd and Debinski 2005; also see Kopper et al. 2001b for *S. idalia* and nectar source phenologies).

***Speyeria diana* (Cramer, 1777)**
(Figure 5A-B, 7)

Papilio Nymphalis Phaleratus Diana Cramer, 1777: 4, 148.

Argynnis diana (Cramer) [Holland 1931].

Speyeria diana (Cramer) [dos Passos and Grey 1945a].

Common names. Diana fritillary, Great Smokies fritillary, Ozark Diana fritillary.

Type deposited. Holotype (male) (see Miller and Brown 1981) at Natural History Museum, London (Figure 7).

Type locality. The original description (Cramer 1777) did not contain a collection date, sex of specimen, or series data; “en Virginie”. Defined by dos Passos and Grey (1947) based on putative holotype (see Miller and Brown 1981) as Jamestown, James City County, Virginia.

Type label data. “ex collection Tring Museum, ex collection Felder, ex collection M. J. C. Sylvius van Lennep”.

Identification, taxonomy, and variation. Adult wingspan ranges from 88-112 mm. Both sexes are distinctive and superficially unlike other greater fritillaries. Adults are sexually dimorphic with the male’s general appearance orange and black and the female’s blue and black (Figure 5A-B). A similar sexual dimorphism occurs in western North America with *S. nokomis* and with Eurasian *Argynnis* that range through regions of higher rainfall and higher summer temperatures (Hovanitz 1963b). Males bear black wing bases and are orange distally while females are black basally and bluish distally. The veins in

the forewing of the male are thick and dark. *Speyeria diana* also lacks silver spots on the ventral hindwings, the discal bars are completely obliterated, and the postmedian and submarginal spots are greatly reduced, distinguishing them from most other *Speyeria*. A rare form of the female occurs that has green instead of blue on the hindwings (Opler and Krizek 1984). No subspecies has been designated for *S. diana*; however, there is some variability in individuals, but this is not abundantly apparent at the population level. Clark and Clark (1951) reported differences in wing facies due to elevational changes in Virginia populations. Female genitalia in *S. diana* differ from most other *Speyeria* by having a secondary bursal sac, closely allying *S. diana* with *S. cybele* and *S. aphrodite*. In the male the digitus is distinct, widening distally bearing an abrupt ventral angle with an outline unique to *S. diana*. Females are especially fecund with well over a thousand ova recorded (Ross and Henk 2004). Eggs are light yellow when they are deposited, and turn gray by day four or five, reflecting the color of the developing larva (Allen 1997; Ross and Henk 2004). Mature larvae are approximately 65 mm in length, velvety black to purple with rows of black spines that are red to orange basally. Dorsal spines are proportionately longer than those located laterally. There occasionally is a double row of white spots located dorsally. The larval head capsule is orange above and black below, but is more angulate than those of closely related *S. cybele* and *S. aphrodite*. Pupae are approximately 30 mm in length, mottled light brown and red, and bear tubercles on the abdomen. Duration of the pupal stage is approximately 20 days.

Range. It is currently restricted to the interior highlands of Arkansas, Oklahoma and Missouri (Carlton and Nobles 1996; Rudolph et al. 2006). It is also known in the southern Appalachians from western Virginia, West Virginia to northeast Georgia and Alabama (Scott 1986b; Moran and Baldrige 2002). Moran and Baldrige (2002) recorded it from 14 different Arkansas counties, 11 of these representing county records, indicating that it is more widespread than previously thought. It was extirpated in southeastern Virginia in about 1951 (Opler and Krizek 1984; Scott 1986b), and is considered uncommon or extirpated in many other parts of its range. Historical populations in the Midwest and the Virginia Piedmont were extirpated in the 1800s (Opler and Krizek 1984; Rudolph et al. 2006). Dos Passos and Grey (1947) listed records from the following states: Pennsylvania, Virginia, West Virginia, North Carolina, South Carolina, Georgia, Alabama, Kentucky, Indiana, Tennessee, Illinois, Arkansas. The Illinois records are reported from Clay, Union, and Vermilion counties, where it may have had a regular occurrence in the southern third of the state (Irwin and Downey 1973).

Life history. Habitat is mostly Upper Austral to Transition Zone in deciduous and pine woodland near streams, rich forested valleys and mountainsides. Clark and Clark (1951) noted that thick undergrowth, usually with alders and rhododendrons, is usually present. Females will walk on the forest floor, laying single eggs on dead leaves and twigs near *Viola* spp., mostly in late summer. Larvae emerge in the late fall and hibernate until the following spring when they commence feeding on violet leaves and flowers. Adult males begin flying one week earlier than females and patrol woodland habitats. Females likely mimic *Battus philenor* (L.), *Limenitis astyanax* (F.), and some papilionids in various parts of the species range (Scudder 1889; Poulton 1909; Ehrlich and Ehrlich 1961; Adams and Finkelstein 2006). However, Hovanitz (1963b) hypothesized that there may be an environmental relationship affecting wing coloration and patterns by noting that they may be correlated to the high humidity and temperatures where *S. diana* occurs. Flight period is mid-June through early August, rarely into September. In Arkansas's Ouachita Mountains, male *S. diana* emerge as early as late May and females emerge approximately 7-10 days later (Rudolph et al. 2006). Females have been observed as late as mid October in northern Georgia (Adams and Finkelstein 2006). *Speyeria diana* is of conservation concern and the cause of extirpations and range contractions are likely due to habitat alteration (Allen 1997), harvest of old growth forests (Hammond and McCorkle 1983), strip mining (Vaughan and Shepard 2005a), and loss of nectar plants (Moran and Baldrige 2002; Rudolph et al. 2006). The Xerces Society currently lists *S. diana* as vulnerable (Vaughan and Shepard 2005a).

Larval host plants. *Viola papilionacea*, *V. cucullata*, *V. cornuta*, *V. sororia*; also partially reared on *Vernonia noveboracensis* (Compositae) (Scudder 1975; Tietz 1972; Scott 1986b; Robinson et al. 2002).

Adult food resources. Reported to visit milkweeds including swamp milkweed and butterfly weed, ironweed, red clover, dung, carrion, damp soil, wads of grass, vomitus of coyotes, and human sweat (Opler and Krizek 1984; Krizek 1991; Opler and Malikul 1998; Rudolph et al. 2006). Rudolph et al. (2006) listed several plant species as primary nectar sources in Arkansas including *Asclepias tuberosa*, *Monarda fistulosa*, *Cirisium carolinianum*, and *Echinacea purpurea*; *Asclepias syriaca* was recorded as a nectar source in western Virginia (Krizek 1991).

***Speyeria cybele* (Fabricius, 1775)**

(Figure 4B, 8)

Papilio Nymphalis Phaleratus Cybele Fabricius, 1775: 516.

Papilio Nymphalis Phaleratus Daphnis Cramer, 1775: 89; 1777: 152.

Argynnis Cybele aberration *Baal* Strecker, 1878: 111.

Speyeria cybele (Fabricius) [dos Passos and Grey 1945a].

Common names. Great spangled fritillary, cybele fritillary, yellow-banded silver wing.

Type deposited. Holotype (female) (= neotype of dos Passos and Grey 1947; see Miller and Brown 1981) at Natural History Museum, London (Figure 8).

Type locality. The original description (Fabricius 1775) did not contain a collection date, sex of specimen, or series data; "Habitat in America". Defined by dos Passos and Grey (1947) based on alleged holotype as New York City, New York County, New York.

Type label data. "cybele, Fab., Syst. Ent. P. 516 n. 311 (1775), United States; Papilio Cybele Fabr. Sp. Ins. No. 477; NEOTYPE, Papilio Nymph. Phalerat. Daphnis? Martyn, designated by dos Passos and Grey 1947, p. 6".

Identification, taxonomy, and variation. There are approximately 10 described subspecies in the cybele complex. Adult wingspan ranges from 65-105 mm. The western races show a sexual dimorphism in which the ground color of the male is bright orange and the female is yellow with darker scales located near the base. Some, such as *Speyeria cybele leto* (Behr), exhibit sexual dimorphism with males being bright orange and females being nearly white. Older literature, as well as contemporary works, treat 'leto' as a distinct species (Holland 1931; Edwards 1864b; Scudder 1875; Howe 1975; Kondla 2004). Eastern and western populations reportedly intergrade or show mixed wing characteristics where they meet in Alberta and Montana (Glassberg 2001a). *Speyeria cybele* bear silver spots on the ventral hindwings, but these spots are reduced compared to other *Speyeria* species. The ventral discal area is typically brown and the submarginal band is wide and yellowish in color. Males have prominent sex scaling on along forewing veins. The eyes on living adults are yellow-green (Glassberg 2001a). Female genitalia in *S. cybele* differ from most other *Speyeria* by having a secondary bursal sac, closely allying *S. cybele* with *S. diana* and *S. aphrodite*. The male genitalic armature bears a hooked uncus (Figure 4B), similar to those in *S. aphrodite*, *S. diana*, *S. idalia*, and *S. nokomis*, which differs from the relatively unhooked, less excavate uncus of the remaining species of *Speyeria* (Figure 4C). Eggs are light yellow when first deposited and turn pale brown after 3-4 days. Duration from oviposition to larval eclosion is reportedly 12-17 days (Edwards 1880) or 22-23 days indoors (Ross and Henk 2004). Mature larvae are approximately 51 mm in length, are typically chocolate-brown on the ventral surface, and bear dorsal black spines that are red-yellow to orange at the base. There is also a row of gray spots located dorsally. The larval head capsule is orange above and black below. Pupae are mottled dark brown, occasionally with reddish-orange over the wing cases. The anterior abdominal tubercles are usually black or black and yellow in color. Duration of the pupal stage is 16 to 20 days in eastern *S. cybele* (Edwards 1880).

Range. Forms of *S. cybele* occur from the east coast to the west coast in the United States and Canada, south to northeastern California, New Mexico, and eastward to central Arkansas (reportedly common in Clay, Greene, and Craighead Counties in northern Arkansas (Lavers 2006) and the northern portions of

Georgia, Louisiana, and Mississippi. The range of nominate *S. cybele* includes much of the eastern United States, where it is still considered common. It was once considered common in areas such as Staten Island, but was reportedly rare in the early 1970's (Shapiro and Shapiro 1973). Records for *S. cybele* exist as far south as Mississippi (Lafayette County-Mather 1966) and Florida (Kimball 1965; Heppner 2003). Some *S. cybele* forms may be declining in western North America because of habitat changes such as the loss of habitat (Opler and Wright 1999). Howe (1975) reported a decline in eastern Kansas *S. cybele* and noted considerable fluctuations in its numbers from one season to the next. It has recently been reported in Cowley County, Kansas and McCurtain County, Oklahoma (Tuttle 2007) and populations should continue to be monitored in these regions.

Life history. Habitat includes Transition to Canadian Zone in moist deciduous woods and moist meadows, conifer forest openings, aspen-lined streams or glades, valleys, prairies, and along roadsides. Females mate immediately after emerging in May and June but do not commence oviposition until August or September, strongly suggesting reproductive diapause (Sims 1984). Eggs are typically laid singly near dead or dying *Viola* spp. and unfed first instar larvae hibernate; however, Scudder (1889) noted that eggs are also laid upon the leaves and stalks of the host plant. First instars commence feeding the following spring. Adults are swift fliers and males patrol all day while seeking females; females carry males while mating. Males typically frequent flower heads more often than females; the females remain hidden and rarely venture out into the open. Ross (2002, 2004) noted that dead or decoy adult *S. cybele* placed on nectar sources attracted additional *S. cybele* individuals as well as other butterfly species. Flight period is mid-June through mid-September.

Larval host plants. *Viola rotundifolia*, *V. papilionacea*, *V. palustris*, *V. adunca*, *V. adunca* variation *bellidifolia*, *V. sororia*, *V. canadensis* (Scott 1986b; Swengel 1997; Robinson et al. 2002; Heppner 2003). Western *S. c. leto* also reportedly feeds on *V. glabella*, *V. nuttalli*, and *V. sempervirens* (Warren 2005); also *V. adunca* (Jonathan Pelham, pers. comm.).

Adult food sources. Butterfly milkweed, *Asclepias exaltata*, common milkweed, *Buddleia*, ironweed, thistles, dogbane, knapweed, vetches, red clover, purple coneflower, Joe-Pye weed, and black-eyed Susan, also occasionally feed on dung (Howe 1975; Scott 1986b; Broyles and Wyatt 1991; Gochfeld and Burger 1997; Opler and Malikul 1998; Ross 1998; Foote 2002; Ross 2002; Douglas and Douglas 2005). Rudolph et al. (2006) listed several plant species as primary nectar sources in Arkansas, including *Asclepias tuberosa*, *Monarda fistulosa*, *Cirisium carolinianum*, *Echinacea purpurea*, *Carduus nutans*, and *Liatris squarrosa*.

***Speyeria aphrodite* (Fabricius, 1787)**
(Figure 9)

Papilio Nymphalis Phaleratus Aphrodite Fabricius, 1787: 62.

Argynnis cybele Fabricius form *Bartschi* Reiff, 1910: 255.

Argynnis aphrodite aberration *bakeri* Clark, 1932: 19.

Speyeria aphrodite (Fabricius) [dos Passos and Grey 1945a].

Common names. Aphrodite Fritillary, silverspot fritillary, silver-winged butterfly, Venus fritillary, Venus's argynne.

Type deposited. Neotype (male) at American Museum of Natural History (Figure 9).

Type locality. The original description (Fabricius 1787) did not include a collecting date, sex of specimen, or series data; "Habitat in America meridionali". Defined by dos Passos and Grey (1947) based on neotype as New York City, New York County, New York.

Type label data. "No. 22, New York City and vicinity. Coll. S. L. Elliot".

Identification, taxonomy, and variation. There are approximately 10 described subspecies in the aphrodite complex. Adult wingspan ranges from 50-84 mm. Males are typically orange-brown and there are specialized sex scales along forewing veins. These veins are as thin as they are on females and this is unique to *S. aphrodite* (as well as *S. mormonia*). Another unique wing characteristic, reported by Guppy and Shepard (2001), is the presence of a faint black circle or “halo” surrounding the black spot located between wing veins M3 and CuA1. There is frequently little basal suffusion in the male, but the females usually exhibit some basal suffusion. Females are typically larger and have darker wing bases than do the males. Most *S. aphrodite* individuals have silver spots on the underside of the hindwings and the discal area is cinnamon brown to red-brown. The ventral hindwing submarginal band is narrow and invaded by disc coloration. Eye coloration in living adults is dull yellow-green (Glassberg 2001a). The aphrodite complex is geographically variable, both in immature and adult stages. Eggs are usually reddish brown at maturity. Larvae are typically brown-black with the spines ochre or brown. The larval head capsule is light orange above and black below. Pupae are brownish-black with yellow wing cases and gray abdomen. There are spines or tubercles located on the abdomen.

Range. Forms of *S. aphrodite* occur range from the eastern United States, south along the Appalachians into northern Georgia south to North Carolina, north to Nova Scotia and New Brunswick in Canada, west to southern and central parts of British Columbia, Nebraska, south to New Mexico and Arizona. There are also isolated ‘*aphrodite*’ populations in the White Mountains of eastern Arizona [*S. a. byblis* (Barnes and Benjamin)] and Big Horn Mountains of Wyoming [*S. a. ethne* (Hemming)]. The range of nominate *S. aphrodite* includes central New York and southern Vermont southward to Pennsylvania, Maryland and Virginia.

Life history. Habitats include dry Transition Zone to Canadian Zone brushland or open woods, moist prairies, streamsides, foothills, mountain meadows/slopes, and old fields. Dry habitat species such as *S. aphrodite* delay laying most of their eggs until late August or September and they usually oviposit in places where the violets have dried up for the year. Eggs are laid singly near *Viola* spp. or where violets will appear next spring (often under shrubs) (Scott 1986b). Females may be able to detect olfactory cues of the violets’ dormant roots (Pyle 1995). In the Colorado foothills, females lay eggs in August and September under mahogany bushes and other places where violets have long since senesced (Pyle 1995). Unfed first instar larvae hibernate. Larvae commence feeding the following spring and eat leaves of violets. Males patrol most of the day while seeking females, especially in open areas in western North America (Scott 1975). Flight period is late June through mid-September.

Larval host plants. *Viola lanceolata*, *V. fimbriatula*, *V. nuttallii*, *V. papilionacea*, *V. nephrophylla*, *V. primulifolia* variation *acuta*, *V. sagittata*, *V. sororia*, *V. tricolor*, and *V. adunca* (Scott 1986b; Scott 1992; Robinson et al. 2002). Tietz (1972) also reported *Passiflora incarnata*, *Podophyllum peltatum*, and *Portulaca oleracea* as food plants, all of which are likely erroneous.

Adult food sources. Milkweed, *Asclepias exaltata*, dogbane, black-eyed Susan, Queen Anne’s lace, hawkweeds, thistles, mints, rabbitbrush, *Echium* spp. (Broyles and Wyatt 1991; Opler and Malikul 1998; Opler and Wright 1999; Foote 2002; Douglas and Douglas 2005).

***Speyeria nokomis* (Edwards, 1863b)**

(Figure 10-11)

Argynnis Nokomis Edwards, 1863b: 221.

Acidalia Semnopsyche nokomis form *valesinoides-alba* Reuss, 1926: 69.

Speyeria nokomis (Edwards) [dos Passos and Grey 1945a].

Common names. Nokomis fritillary, western seep fritillary.

Type deposited. Neotype (male) designated by dos Passos and Grey (1947) at American Museum of Natural History (Figure 10).

Type locality. Rocky Mountains and mountains of California. Neotype (male) (Figure 10) defined by dos Passos and Grey (1947) as Mount Sneffels, Ouray County, Colorado; however, dos Passos and Grey (1965) reconsidered this designation and Brown (1965) noted that this locality was an unlikely habitat for *S. nokomis* and that the specimen does not fit the original description. Ferris and Fisher (1971) revised the type locality and designated a lectotype (male) (Figure 11) taken from Colorado for *S. nokomis*. Ferris and Fisher (1971) discuss the likelihood that the type locality for *S. nokomis nokomis* was probably somewhere in eastern Utah; however, the specimen they designated as lectotype is taken from Mesa County, Colorado (see below). Grey (1989) later noted that *S. nokomis* does occur at Mt. Sneffels, based on collection records located at the AMNH. Although the true type locality and type specimen will likely remain obscure or missing, the neotype designation provided by dos Passos and Grey (1947) is reaffirmed by Grey (1989).

Type label data. Taken from dos Passos and Grey (1947): "Oslar Sneffels Mts Ouray Co Col Aug 9000 Ft.; *A. nokomis*; Ex Coll. Wm. C. Wood Acc 36915; NEOTYPE, Argynnis Nokomis [male], Edwards".

Identification, taxonomy, and variation. There are approximately 7 described subspecies in the *nokomis* complex. Adult wingspan ranges from 63-80 mm. Male dorsal wing coloration is orange with sparse black dots while females are black basally and whitish outwardly with many black spots. The dorsal submarginal dark chevrons do not touch the black marginal line. Forewings are pinkish-orange ventrally with white spots. Discal coloration is variable in both sexes depending on the geographic location. The ventral hindwing disc on males and females is light to dark brown with submarginal band tan in many regions; females bear a gray-green disc with the submarginal band yellow-green in California and Nevada populations. Eastward populations tend to have darker hindwing discs. The hindwings on both sexes have relatively small silver spots and they typically bear black edges. Most forms of *S. nokomis* exhibit sexual dimorphism.

The uncus on the male genitalia is hooked and similar to those of *S. idalia* and the *Semnopsyche* group; however, the female has only a single bursal sac. The eye coloration in living specimens is yellow-green (Glassberg 2001b). The egg is cream colored when laid and becomes tan after a few days. Detailed egg morphology is included in Scott and Mattoon (1981). Larvae typically bear a yellow to orange dorsal stripe and yellow to orange transverse stripes with rows of yellow- orange or black spines. Black patches surround spines dorsally and laterally. Female larvae typically feed ten days longer than do males (Allen et al. 2005). Detailed larval descriptions, including setal maps, are included in Scott and Mattoon (1981). Pupae are black with center of wing cases orange, and bear orange stripes on the abdomen. Pupae vary in coloration throughout the range of *S. nokomis*.

Range. *Speyeria nokomis* is presently known from eastern California to western Colorado, south through eastern Arizona and western New Mexico, with populations as far south as Mexico. Tuttle (2007) noted that R. Holland reported specimens located in the CMNH were taken in the 1930's from the Mescalero Apache Reservation in the Sacramento Mountains and represent the southern-most occurrence of nominate '*nokomis*'. Known localities are widely separated due to restricted habitat. Many populations are declining because of capping of springs and other habitat modifications caused by human disturbances such as livestock grazing (Hammond and McCorkle 1984).

Life History. Habitats include Upper Sonoran to Canadian Zone moist meadows near streams, permanent spring fed meadows, marshlands, boggy streamsides, and seeps; *S. nokomis* can be found in canyons with pinyon pines and junipers. Britten et al. (1994) studied the isozyme variability of *S. nokomis* populations in the Great Basin and noted that there was little gene flow between populations, further confirming that *S. nokomis* is confined to mesic seep habitats with great expanses of unsuitable, xeric habitat isolating populations. Eggs are laid singly and haphazardly near host plants. Unfed first instar larvae hibernate, and some later instars may also aestivate during drought conditions from April through June (Scott 1986b). Larvae overwinter in grass stems after emerging (Pyle 1995). Males patrol all day in meadows or along streams seeking females, especially in valley bottoms if the spring is on a slope. Scott (1975) noted that males would fly about 1/2 meter off the ground and dip into to hollows to search. This

species tends to fly on the average later than most other *Speyeria*. Flight period is usually from late July to mid September or mid August to mid September in the southern part of its range. The range of *S. nokomis* was likely more continuous during moister climatological times. Populations are now separated by vast desert landscapes. Scott (2008a) estimates that 50% of *S. nokomis* sites were lost by 1900 due to water diversion. A population [*S. nokomis coeruleascens* (W. J. Holland)] that once flew high in the Santa Catalina Mountains north of Tucson, Arizona has not been seen since 1938 and presumably has been extirpated (Glassberg 2001b). Fleishman et al. (2001b) note that extinction and colonization events for *S. nokomis* populations in the Great Basin are related to multiple aspects of habitat quality, such as extreme climatic events and grazing-mediated availability of nectar. The results from Britten et al. (1994) indicate there is little gene flow among *S. nokomis* populations in the Great Basin, and that these populations have lost genetic variability as the result of small effective populations sizes and genetic drift; thus, conservation of individual colonies may be important for the evolutionary potential of this species. Results from mark and recapture studies conducted by Britten et al. (2003) indicate that suitable but vacant habitat patches should be maintained for potential recolonization by *S. nokomis apacheana* (Skinner) in the central Great Basin.

Larval host plants. *Viola sororia* (Emmel et al. 1970; Scott and Mattoon 1981; Scott 1986a; Robinson et al. 2002).

Adult food resources. Thistles (Scott 1986b), especially Arizona red thistle (Cliff Ferris, pers. comm.).

***Speyeria edwardsii* (Reakirt, 1866)**

(Figure 4D, 12)

Argynnis Edwardsii Reakirt, 1866: 137.

Acidalia Edwardsi montana Reuss, 1926: 439.

Argynnis edwardsii Reakirt form *edonis* Gunder, 1934: 125.

Speyeria edwardsii (Reakirt) [dos Passos and Grey 1945a].

Common names. Edward's fritillary, green fritillary.

Type deposited. Lectotype (male) designated by dos Passos and Grey (1947) at Field Museum of Natural History (Figure 12).

Type locality. California; Pike's Peak, Teller County, Colorado Territory. Defined by dos Passos and Grey (1947) based on lectotype as Pike's Peak, Teller County, Colorado. Subsequently defined by F. Brown (1965) as "Empire, Clear Creek County, Colorado".

Type label data. "A. Edwardsii, Orig. Type, Reak Coll; Lectotype, *Argynnis edwardsii* Reakirt, Det. By dos Passos and Grey 1947; *Argynnis edwardsii* Reak., Col., Empire city. Reak., Orig. Types Originals of Edwd's figs. In Butt. N.A. Strecker Colln. 13311, Field Museum Nat. Hist.; Lepidoptera Type Photograph No. 86, Field Museum".

Identification, taxonomy, and variation. This is one of the larger *Speyeria* with pointed forewings. Adult wingspan ranges from 51-85 mm. The dorsal wing surface in both sexes is bright tawny and dark markings are moderate except along the margin where they are well marked with chevrons that point toward the wing base. The ventral forewings are bright pinkish orange at base and shading to yellow toward the distal margin with the same black pattern as upper side. The ventral hindwings bear oval or elongate silver spots and the disc is mottled with a dull greenish olive coloration. There are no subspecific names associated with *S. edwardsii* and there is little wing variation throughout its range. *Speyeria callippe* may be superficially similar in appearance where their ranges overlap, but *S. callippe* bears ventral hindwing marginal spots that are more pointed rather than rounded inwardly as they appear on *S. edwardsii*. Hammond (1990) hypothesized that *S. edwardsii* may have evolved directly from *Speyeria callippe semivirida* (McDunnough) (but see Scott 2008a: 80). *Speyeria coronis* is also similar but bears

large, round median spots on the hindwing disc. The uncus on the male genitalia is clawed and slender, unlike the previous 5 species discussed above. The digitus (Figure 4D) on each valva is long and slender and unlike any other member in the genus (others have more or less a short, club-like digitus). Eggs are greenish yellow and generally shaped like the rest of *Speyeria*. Larvae are dark yellow dorsally, with gray laterally and a black dorsal stripe. The upper four rows of spines are gray at the base; the lower two rows of spines are orange at the base. The pupa is approximately 22 mm in length and brown with anterior portions reddish in color. The wing cases are yellow-brown with dark streaks along the veins. Detailed egg, larval instar, and pupal descriptions are included in Edwards (1888b).

Range. *Speyeria edwardsii* is known from southern Alberta east to Manitoba, south through the Dakotas, western Nebraska and Oklahoma, and west to northern New Mexico. They are seldom found above 10,000 ft in Colorado. Stray records also exist in Kansas (Ely et al. 1983).

Life history. Habitat includes short grass prairie, foothills, meadows, glades, open pine forests, valleys and roadsides. Individuals are known to migrate into the mountains during the midsummer months with females moving back into the prairies during the late summer to lay eggs (Opler and Wright 1999). Males will patrol for females all day in open areas regardless of topography (Scott 1975). Flight period extends from mid-May through late October. Edwards (1888b) noted the egg stage is approximately 10 to 11 days. Larvae, which pass through five molts after overwintering as a first instar, feed for approximately 45 days before pupating. The duration of the pupal stage is approximately 15 days. Scott (1986a, 2006b) reports various oviposition substrates for *S. edwardsii*.

Larval host plants. *Viola adunca*, *V. nuttallii* (Scott 1986a; Robinson et al. 2002).

Adult food resources. Thistles, coneflowers, *Penstemon angustifolius*, *Penstemon albidus* (Hammond 1995; Pyle 1995).

***Speyeria coronis* (Behr, 1864)**

(Figure 13)

Argynnis Coronis Behr, 1864: 435.

Argynnis californica Skinner, 1917: 328.

Speyeria coronis (Behr) [dos Passos and Grey 1945a].

Common names. Coronis fritillary, crown fritillary, California fritillary.

Type deposited. Putative lectotype (male) (but see Emmel et al. 1998b) designated by dos Passos and Grey (1947) at Carnegie Museum of Natural History (Figure 13).

Type locality. California. Defined by dos Passos and Grey (1947) based on lectotype as Alma, Santa Clara County, California; subsequently determined not to be a syntype and was redesignated as neotype by dos Passos and Grey (1965). Brown (1965) also questioned the original designation and use of the term lectotype with the specimen dos Passos and Grey examined because type specimens were likely lost in an earthquake. He stated that the specimen was not of the type series and was not available for selection as lectotype. The specimen that I examined in March 2004 did not bear these two labels listed by Brown (1965): a label written by L. P. Grey that he considers this specimen typical and an identifying label added by Brown. Emmel et al. (1998b) discuss further this situation and conclude that it was possible that Behr likely described *coronis* from material collected by P. Lorquin, including one extant specimen. Therefore, it could be valid for a neotype specimen. Miller and Brown (1981) consider Edwards to have designated this specimen as a neotype by labeling it "Coronis [male]/Behr's type". Emmel et al. (1998b) added a label to the specimen indicating that it is the neotype of *Argynnis coronis* Behr, designated by W.H. Edwards. This label was also not associated with the specimen I examined. It is possible the image included herein is not the lectotype designated by dos Passos and Grey (1947), or it is unclear where the associated label data mentioned above were located at the time I visited the CMNH (March 2004).

Type label data. “*Coronis* Behr’s type, Juba B type”.

Identification, taxonomy, and variation. There are approximately 7 described subspecies in the *coronis* complex ranging from the Rockies to the Pacific states. Adult wingspan ranges from 49-86 mm. Both sexes are generally orange to pale orange, and the forewing margins are nearly straight, with wing bases slightly darkened. The ventral hindwing discs are generally mottled brown and bear rounded inward or flattened silver spots capped pale green or greenish-brown. Populations in western Colorado and eastern Utah bear pale and slightly green tinged discs while populations in the Great Basin are greenish-gray. The submarginal band located on the ventral surface of the hindwings is yellow to pale buff. Eggs are ribbed and tan in color. Larvae bear black and brown spots with orange or black lateral spines. The upper four rows of spines are typically black and somewhat lighter at the base; the lower two rows of spines are typically orange-yellow at the base. Larval coloration is variable throughout the range of *S. coronis*. Pupae are whitish, with black markings and resemble those of *S. callippe*. *Speyeria coronis* is hypothetically closely related to *S. zerene* and in some locations they are difficult to separate in the field. Their large size, thin, light veins in the male, and large, round, silver median spots on the ventral hindwing should distinguish *S. coronis* from most other *Speyeria*. Along the central coast of California, *S. coronis* and *S. callippe* are indistinguishable except that on average, *S. coronis* is larger and brighter orange dorsally, paler ventrally, and the hindwing postmedian spots (termed ‘spangles’) show through to a lesser extent when viewed dorsally. *Speyeria carolae*, formerly considered an intermediate form between *S. coronis* and *S. zerene*, is known only from mountains in southern Nevada and is presently considered a distinct species (Emmel and Austin 1998).

Range. *Speyeria coronis* is known from northern Washington south to northwest Baja California, northeast throughout the Great Basin and central Rockies to Montana, Wyoming, and into western South Dakota and Nebraska.

Life history. *Speyeria coronis* is known from several habitat types, including oak woodlands, mountain slopes, foothills, mixed conifer forests, meadows, prairie valleys, chaparral, and sagebrush flats/scrub. This species often congregates on hillsides and meadows overgrown with rabbitbrush and sage (Dornfeld 1980). In forest openings, they often frequent flowers along mountain streams. Males of *S. coronis* may emerge two weeks in advance of females, and may be on the wing in late May or early June before the arrival of other *Speyeria* species. Males will patrol for females all day in open areas regardless of topography (Scott 1975). *Speyeria coronis* and closely related *S. zerene* have an adult diapause in the summer (Brittnacher et al. 1978, Scott 1979). Females diapause (delay oviposition) in California and reappear in late August through September. Flight period is from late May to October, depending on locality and elevation. This species is usually found at low to middle elevations. *Speyeria coronis* forms occur at sea level in parts of California and up to 9,000 ft. in Colorado.

Larval host plants. *Viola beckwithii*, *V. douglasii*, *V. nuttallii*, *V. purpurea* (Robinson et al. 2002). In Washington, *S. coronis* also feed on *V. trinervata* (Warren 2005).

Adult food resources. Mint, thistle.

***Speyeria zerene* (Boisduval, 1852)**

(Figure 5C, 14)

Argynnis Zerene Boisduval, 1852: 303.

Argynnis monticola Behr, 1863: 84 (synonymized by Dos Passos and Grey 1947).

Speyeria zerene (Boisduval) [dos Passos and Grey 1945a].

Common names. Zerene fritillary.

Type deposited. Lectotype (male) designated by dos Passos and Grey (1947) at National Museum of Natural History (Figure 14).

Type locality. California. Defined by dos Passos and Grey (1947) based on lectotype as Yosemite Valley, Mariposa County, California. However, Masters (1979) (and also see Grey 1989) disputed this locality because it was unlikely that P. Lorquin collected specimens from Yosemite Valley before 1856. Masters listed Agua Fria, Mariposa County, as the likely type locality because Lorquin collected there in 1850-1851. Agua Fria is closest to Yosemite Valley and is in the same biotic province. However, Agua Fria is no longer in existence but was a gold camp and the county seat of Mariposa County in 1850. It was located on Aqua Fria Creek just west of the present town of Mariposa and approximately 35 miles southwest of Yosemite Valley. Emmel et al. (1998a) dismissed the likelihood of Lorquin traveling to Mariposa County before 1852 based on his travels to the Feather River region during those times, thus re-defined the type locality to Hwy 70 at Chambers Creek, North Fork Feather River, Plumas County, California.

Type label data. “Zerene. Bois. Calif. Californie.; Argynnis Zerene l’un des 2 types., Boisduval. Ann. Fr. 1852. p. 303; EX MUSAEO Dris. BOISDUVAL; Oberthur Collection; Type A zerene Bdv. a/c Hofer; Barnes Collection”.

Identification, taxonomy, and variation. There are approximately 16 described subspecies in the zerene complex. Adult wingspan is 48-67 mm. Wing coloration in this complex is highly variable (see Grey and Moeck 1962; Grey 1972; Warren 2005). The upper side ground color of the wings varies from deep orange to pale yellow or brown to tan and the underside of the hindwings shows great variability depending on geographic location. The ground color of the inner discal area ranges from maroon through various shades of reddish-brown through tan (discal coloration is generally violet-brown in Sierra Nevada Mountains, yellow in Great Basin, and slightly greenish brown in southern Wyoming and Colorado); the band located outside of the disc runs from lavender to tan or yellow; hindwing spots are usually silvered but not always (they are yellowish in California and southern Nevada). The three anterior spots in the median band area are all separate, the second spot is round and larger, and the third spot is narrower and slanted away from the second. *Speyeria zerene*, *S. coronis*, *S. callippe*, *S. egleis*, and *S. atlantis* are very similar to each other in some regions. The thin, light veins in the male, and the large round, silver median spots on the ventral hindwing should distinguish *S. zerene* from most other *Speyeria* with the exception of *S. coronis*. Variation at the subspecific level is also parallel within these species. Eggs are cream to pinkish-tan. Larvae are typically black with yellowish to gray-tan dorsal stripes. The top two rows of spines are generally black, the middle row may be black or yellow, and the bottom row yellow. Larvae are somewhat variable in coloration throughout the range of *S. zerene*. Pupae are similar to those of *S. nokomis* and hang vertically within leaves tied with silk as in most *Speyeria*.

Range. Forms of *S. zerene* occur from southeastern Alaska, southwestern Canada, south to central California, Arizona, New Mexico, Utah, Montana, and southwestern Colorado. The U.S. Fish and Wildlife Service has listed a few subspecific forms as either threatened or endangered [i.e., *S. zerene hippolyta* (Edwards), *S. zerene behrensii* (Edwards), and *S. zerene myrtleae* dos Passos and Grey] and some populations along the California coast have been extirpated (Hammond and McCorkle 1984). Some Oregon populations of *Speyeria zerene* nr. *bremnerii* (Edwards) are now extinct (Warren 2005).

Life history. Depending on geographic location, zerene complex occurs in a wide array of habitats. Warren (2005) noted that populations in Oregon exist from near sea level to approximately 9,000'. Several subspecies occur along forest roads and in moist ravines and montane conifer forests, while some [i.e., *S. zerene gunderi* (Comstock)] occur in the open expanses of sage and rabbitbrush. The Behren's Fritillary (*S. z. behrensii*) and Hippolyta Fritillary (*S. z. hippolyta*) occur in unlikely habitat along the weather-beaten, salt-spray meadow coastline of the Pacific Ocean. Habitat destruction is the likely cause of the decline of the *S. z. myrtleae* and *S. z. hippolyta* (Launer et al. 1994). *Speyeria z. behrensii*, *S. z. hippolyta*, and *S. z. myrtleae* are presently listed as federally endangered. Several life history studies and land management discussions occur in the literature for these declining zerene complex (McCorkle 1975; McCorkle and Hammond 1988; Launer et al. 1994; Patterson 2002; Connor et al. 2002). McCorkle and Hammond (1988) discuss the life history of *S. z. hippolyta* (as well as *Speyeria* in general) in detail. Flight period of *S. zerene* is as early as late June to July, while some (i.e., *S. z. behrensii* and *S. z. hippolyta*)

appear on the wing in August and September. Scott (1975) reported that males in Colorado and Idaho populations would patrol all day in open areas.

Larval host plants. *Viola adunca*, *V. cuneata*, *V. lobata*, *V. nuttallii*, *V. psychodes*, *V. purpurea*, *V. beckwithii* (Scott 1986b; Hammond 1995; Robinson et al. 2002).

Adult food resources. As with other *Speyeria*, there are numerous plant species from which *S. zerene* likely nectar on.

***Speyeria carolae* (dos Passos and Grey, 1942)**

(Figure 15)

Argynnis coronis carolae dos Passos and Grey, 1942: 2.

Speyeria coronis carolae (dos Passos and Grey) [dos Passos and Grey 1947].

Speyeria zerene carolae (dos Passos and Grey) [dos Passos 1961].

Speyeria carolae (dos Passos and Grey) [Emmel and Austin 1998].

Common names. Carol's fritillary.

Type deposited. Holotype (male) at American Museum of Natural History (Figure 15).

Type locality. Charleston Park, Clark County, Nevada.

Type label data. "Charleston Park, Clark Co., Nev., 8-9, VII, 1928, 8,000 ft.; ARGYNNIS C. CAROLAE, C. F. dos Passos and L. P. Grey; J. D. Gunder Collection Ac. 34998; Holotype".

Identification, taxonomy, and variation. Average wingspan is approximately 56 mm. *Speyeria carolae* is generally darker and bears slightly different wing shape and coloration than those of *S. coronis* and *S. zerene*. The dorsal color of both sexes is bright reddish-orange; the ventral forewing is heavily flushed with reddish-orange anteriorly to or beyond vein M3, and this is usually more extensive than on *S. zerene* and *S. coronis*. The ventral hindwing disc varies from reddish-brown to brown and the spots are moderately large. The spots range from silvered to mostly unsilvered. *Speyeria carolae* has been hypothesized to be an intermediate between *S. coronis* and *S. zerene* (Scott 1986b) and may represent an extant, remnant form of the ancestral lineage between both of these species. Formerly recognized as a subspecies within the coronis complex (dos Passos and Grey 1942, 1947), and later the zerene complex by dos Passos (1961) and Austin (1981), *S. carolae* was considered a distinct species by Emmel and Austin (1998) and Austin (1998) based on differences in wing patterns and chromosome numbers (but see North American Butterfly Association 2001; Scott 2008a, p.54). The nearest *Speyeria* population to those of *S. carolae* is in southwestern Utah, approximately 225 km to the northeast. The geographic isolation and the low probability of present-day gene flow and probable, precinctive larval host plant *Viola charlestonensis* support full species status (Emmel and Austin 1998).

Range. Isolated in southern Nevada's Spring Mountains (Clark County). Type material was taken in the Charleston Range between elevations of approximately 6,000-11,000 ft. It is regarded as the most restricted *Speyeria* species in geographical range (Howe 1975; Emmel and Austin 1998).

Life history. Adults occur in dry forests, hillsides, meadows, and riparian habitats above 6,000 ft. in the Spring Range (Austin 1981; Fleishman et al. 2005).

Larval host plants. Probably *Viola charlestonensis* (Emmel and Austin 1998).

Adult food resources. (George Austin, pers. comm.): *Erysimum asperum* (Brassicaceae), *Apocynum androsaemifolium* (Apocynaceae), *Rosa woodsii* (Rosaceae), *Lupinus* sp. (Fabaceae), *Angelica scabrida* (Apiaceae), *Chaenactis* sp., *Cirsium* sp. (Asteraceae) [latter is principal source].

***Speyeria callippe* (Boisduval, 1852)**

(Figure 5D, 16)

Argynnis callippe Boisduval, 1852: 302.*Speyeria callippe* (Boisduval) [dos Passos and Grey 1945a].**Common names.** Callippe fritillary, callippe silverspot.**Type deposited.** Lectotype (male) designated by dos Passos and Grey (1947) at National Museum of Natural History (Figure 16).**Type locality.** California. Defined by dos Passos and Grey (1947) as San Francisco, San Francisco County, California. Although it is now extinct in San Francisco, it likely once flew on the slopes on Mt. Davidson where *Viola pedunculata* has been recorded (Emmel et al. 1998a).**Type label data.** “Calippe. Boisd. Calif. Californie., *Argynnis Callippe* Boisduval type; EX MUSAEODris. BOISDUVAL; Oberthur Collection; Type callippe Bdv. a/c Hofer; Barnes Collection”.**Identification, taxonomy, and variation.** There are several geographic forms (approximately 19 described subspecies) with variable coloration on the wings (Moeck 1957; Howe 1975; Warren 2005) in the callippe complex. Adult wingspan is 47-74 mm. The dorsal wing surface is generally red-brown to light tawny, depending on geographic location. Dark markings are evenly spaced, providing a distinctive checkered or lattice appearance. The ground coloring on the ventral surface varies from reddish to yellowish brown, sometimes with heavy black scaling. The discal area on the underside is commonly powdered by with green scales (especially in the Plains, Rockies, and Great Basin) but may be brown (California and southwest Oregon) in some forms, with spots on the ventral hindwings large and usually silver but may be unsilvered (California and southwest Oregon) in some forms. A general trend in wing patterning and coloration is apparent west and east of the Cascade-Sierra Nevada Mountains. Populations east of the mountains have tan, brown, or red-brown ventral ground coloration with either silvered or unsilvered spots and a tan submarginal band in the ventral hindwing. Populations in western North America vary from pale green to deep blue-green ventrally either without a submarginal band or only a narrow yellow-green band. *Speyeria coronis* may be confused with *S. callippe* (especially along the central California coast) but hindwing marginal spots on *S. callippe* are usually triangular shaped and bordered inwardly only by a thin dark border; other *Speyeria*, including *S. coronis*, usually bear differently shaped spots and darker, wider borders. The pale median and submarginal spots show through the wings above (termed ‘spangles’) on *S. callippe*, especially in females along the Pacific Coast. These spangles provide a two-toned appearance when viewed from above. Geographical variation for *S. callippe* has been studied (Hovanitz 1943; Sette 1962; Arnold 1983, 1985). Hovanitz (1943) studied California populations and hypothesized that racial or genealogical relationships are more or less the same, and that subspecific taxa there do not provide clear evidence of divergence. He did recognize several main divisions of the callippe complex, namely those in the South Coastal Range, western Sierra Nevadas, and a southern zone of intergradation along the Piute Mountains and Sierra Madre range. Sette (1962) examined the variation of silvering in the southern zone of intergradation and hypothesized that there may be a “silvering-gene” present during the pupal stage under optimal environmental conditions, and speculated guanine was the substance responsible for silvering in *S. callippe*. Arnold (1985, 1983) examined the wing characters of 16 subspecies using 75 principle component analyses and graph clustering techniques to describe variation and suggested reducing the number of subspecies to three (but see Hammond 1986). Larvae are mottled brown and black with black (or paler) dorsal stripes and many orange to yellow or black branching spines. Eggs are pale yellow, becoming pinkish brown. Pupae are whitish, with black markings similar to *S. nokomis*. **Range.** Forms of *S. callippe* occur from the Pacific Coast from southeastern British Columbia south to northwestern Baja California, northeast through the Great Basin and Rockies to southern Manitoba, and to western parts of South Dakota, Nebraska, and central Colorado.

Life history. *Speyeria callippe* occurs in a variety of habitat types, including grasslands, oak and pine woodlands, sagebrush, chaparral, valleys, brushy hillsides, and prairie ridges. Dry-habitat *Speyeria* species such as *S. callippe* delay laying most of their eggs until late August or September and they usually oviposit in places where the violets have dried up for the year. Eggs are laid mainly under shrubs where violets will appear the following season (Scott 1986b). In most areas males patrol hilltops to wait for females, but in California males tend to patrol grasslands and avoid hillsides (Opler and Wright 1999). Scott (1975) noted that in the Front Range of Colorado, males patrol close to the ground all day and occasionally perch on shrubs. Populations with green and brown ventral hindwings interbreed along the eastern edge of the Sierra Nevada and Cascade Mountains. Flight period is from April through September, and in many areas, these are the first greater fritillaries flying each season. *Speyeria callippe callippe* is listed as endangered and nearly extinct in coastal northern California (i.e., San Francisco Bay Area) by the U. S. Fish and Wildlife Service (Hammond and McCorkle 1984, Connor et al. 2002).

Larval host plants. *Viola beckwithii*, *V. douglasii*, *V. nuttallii*, *V. pedunculata*, *V. purpurea*, *V. purpurea quercetorum* (Hammond 1995; Robinson et al. 2002); *Artemisia* (Compositae) (see Durden 1965)-this was very likely an oviposition site (Jonathan Pelham, pers. comm.).

Adult food resources. Thistles (Pyle 1995). Warren (2005) reported that *S. callippe* visit a variety of flowers, and some subspecies can be observed congregating by the hundreds on *Apocynum* flowers.

***Speyeria egleis* (Behr, 1862)**

(Figure 17)

Argynnis Egleis Behr, 1862: 174.

Argynnis montivaga Behr, 1863: 84.

Argynnis Astarte Edwards, 1864b: 435.

Argynnis montivaga Behr aberrant *mammothi* Gunder, 1924: 157.

Argynnis montivaga Behr form *boharti* Gunder, 1929: 326.

Speyeria egleis (Behr) [dos Passos and Grey 1945a].

Common names. Egleis fritillary, Great Basin fritillary, mountain rambler, montivaga.

Type deposited. Neotype (female) designated by Emmel et al. (1998a) at National Museum of Natural History (Figure 17).

Type locality. California. Defined by dos Passos and Grey (1947) based on lectotype [= neotype of Emmel et al. (1998b)] as vicinity of Gold Lake, Sierra Country, California. However, Emmel et al. (1998b) have determined the type designated as a lectotype is invalid because it could not have been one of the original syntypes in front of Behr when he described *A. egleis*. Therefore, the lectotype was redesignated as a neotype for *S. egleis*. Emmel et al. (1998b) listed the type specimen as being female, which differs from dos Passos and Grey's purported "male" lectotype. The image included herein is that of a female (see Figure 17).

Type label data. "Prob. Type egleis Bdv.; Egleis Bdv. California; EX MUSAEO Dris. BOISDUVAL; Argynnis Egleis, Bdv. [male-sic] Ex typic. specim.; Oberthur Collection; Barnes Collection". [No date, sex, or series data was provided with the original description (McHenry 1964).]

Identification, taxonomy, and variation. There are approximately 13 described subspecies in the egleis complex (Moeck 1957; Howe 1975; Warren 2005). Adult wingspan is 44-59 mm. The dorsal surface is generally orange to brown with paler postmedian and marginal spots and most individuals have dark scaling on the basal half of the wings. Males bear sex scaling on forewing veins. The ventral hindwing disc is variable depending on subspecies and can be red-brown, brown, tan, or greenish. The postmedian spots are smaller than most *Speyeria* species and may be silvered or unsilvered. The marginal spots are

generally slightly triangular to rounded with brown or greenish caps. The ventral hindwing is yellow and spots are strongly silvered in central Nevada populations but bear a dull greenish tint in parts of Montana and Alberta. *Speyeria egleis* can resemble *S. atlantis*, *S. coronis*, *S. zerene*, *S. callippe*, and *S. mormonia*, depending on geographical location. Larval coloration is variable throughout the range of *S. egleis*. *Speyeria egleis secreta* dos Passos and Grey, a less commonly encountered form, very closely resembles members of the hesperis species complex in parts of its range (Remington 1947, 1948; Eff 1956). Larvae are gray-brown or black with a dark strip inside of yellow band located dorsomedially. The top four rows of spines are generally black or yellow; the lower two rows of spines are yellow. Pupae are dark brown with yellow-brown patches, dark wing cases and dark cross stripes on abdomen. Detailed life history notes and descriptions for the egg, larval instars and pupa of *S. egleis* is provided by Edwards (1879c).

Range. *Speyeria egleis* occurs throughout the Great Basin, from southeastern British Columbia, western Oregon, Idaho, and western Montana, south to southern California, central Utah, and northwest Colorado. Nominotypical *S. egleis* is found throughout the Sierra Nevada mountains above 6,000 ft. (Emmel and Emmel 1998a).

Life history. *Speyeria egleis* forms occur in mixed woodlands, open rocky slopes, meadows and stream banks. They occur at middle to high elevations and are most common in cooler parts of the Great Basin, California Sierra Nevada and Trinity Mountains. Females have been observed ovipositing on pinecones, sticks, and stones in California (Lembert 1893). Flight period is from early June through early October. Males patrol mostly in shaded forest lanes such as abandoned roads in Colorado, whereas males patrol along hilltops in some California populations (Scott 1975). Davenport (1998) noted that forest fires and subsequent rains in the Greenhorn Mountains of California have provided suitable habitat that has enabled *S. egleis* to expand its range southward.

Larval host plants. *Viola adunca*, *V. nuttallii*, *V. ocellata*, *V. purpurea*, *V. purpurea integrifolia*, *V. purpurea venosa*, *V. walteri*; *Festuca ovina* (Gramineae); *Potentilla* (Rosaceae) (Robinson et al. 2002).

Adult food resources. As with other *Speyeria*, there are numerous plant species from which *S. egleis* likely nectar on.

***Speyeria adiaste* (Edwards, 1864)**

(Figure 18-19)

Argynnis Adiaste Edwards 1864b: 436.

Argynnis Adiante Boisduval 1869: 61.

Argynnis Adraste Kirby 1871: 160.

Argynnis adianthe Barnes and McDunnough, 1917: 8.

Speyeria egleis adiaste (Edwards) [dos Passos and Grey 1945a].

Speyeria adiaste (Edwards) [Emmel and Emmel 1973; see also Grey 1989].

Common names. *Adiaste* fritillary, unsilvered fritillary, lesser unsilvered fritillary.

Type deposited. There has been some confusion about the name and authorship of this insect. Dos Passos and Grey (1947) designated a specimen described by Boisduval as *Argynnis Adiante*, housed at the National Museum of Natural History, as a lectotype (Figure 18). However, Brown (1965; see also Emmel et al. 1998a) rejected this designation because “*Adiante*” is not recorded from the area where dos Passos and Grey chose as the type locality, and chose a male specimen described by W. H. Edwards as *Argynnis Adiaste*, housed at the Carnegie Museum of Natural History, as the lectotype for *S. adiaste* (Figure 19) (also see **Type locality** and **Type label data** sections below).

Type locality. California. Defined by dos Passos and Grey (1947) as Santa Cruz, Santa Cruz County, California. Brown (1965) did not fix locality information for the lectotype designated by him. However, he

stated that *S. adiate* is not found in the immediate vicinity of the city of Santa Cruz, but rather approximately 9 miles north of the city near Boulder Creek. Emmel et al. (1998a) further refined the dos Passos and Grey type locality to 2 miles southeast of Summit Road along Highland Way, Santa Cruz Mountains, Santa Cruz County, California because no *S. adiate* populations are (or were) known from the city of Santa Cruz.

Type label data. From dos Passos and Grey (1947): “Adiante Bd Calif.; EX MUSAEOL Dris. BOISDUVAL; Type adiante a/c Hofer; Oberthur Collection; Barnes Collection”. From Brown (1965): “Adianthe type; Adiante [female] type sent W. H. E. by Dr Boisduval & figd in But. N. A.; lectotype *Argynnis adiate* [female], W. H. Edwards designated by F.M. Brown '64 also lectotype of adiante Bdv. desig. by dos Passos and Grey '47”.

Identification, taxonomy, and variation. Sims et al. (1979) noted allozyme characters separated *S. adiate* forms from related *S. atlantis* and *S. egleis* taxa and suggested *S. adiate* is distinct genetically. There are currently 3 described subspecies in the *adiaste* complex. Adult wingspan is 45-57 mm. The dorsal ground coloring is red brown to pale brown and the ventral surface is reddish orange to pale tan. Males are bright brick red in Santa Cruz County, California or pale, washed-out tawny in south central California. Females are larger and paler than males. The ventral hindwing spot patterns are unsilvered or obsolete and bear delicate lavender-pink reflections. Larvae are reportedly similar to *S. callippe* [mottled brown and black with black (or paler) dorsal stripes and many orange to yellow or black branching spines] but with lighter gray sides (Allen et al. 2005). Pupae are similar to *S. callippe*, but the wing cases are somewhat lighter in color.

Range. *Speyeria adiate* is fairly restricted (see Grey 1989) along coastal and transverse mountain ranges in central California, from San Mateo County south to San Luis Obispo County, east to Kern County and northern Los Angeles County. Populations are very local and numbers may fluctuate from year to year. Some populations in Kern County [*Speyeria adiate atossa* (W. H. Edwards)] have been extinct since 1959 (Orsak 1974; Sims et al. 1979; Hammond and McCorkle 1984, Garth and Tilden 1986). Tuttle (2007) provided observational notes that *S. adiate* has not been extirpated from Santa Clara County, California.

Life history. *Speyeria adiate* occurs along grassy slopes and openings in redwood forests (San Mateo and Santa Cruz Counties) and in high mountain meadows in Monterey and San Luis Obispo Counties. In southern California localities, habitat is mixed chaparral and oak woodland (Hovanitz 1970). The subspecific taxa within *adiaste* appear to be distributed with their specific violet host plants and by the desiccation tolerance of first instar larvae (Sims et al. 1979). Flight period is from June to early September. It has been hypothesized that the disappearance of *S. adiate* populations is due to fire suppression and resulting habitat change (Scott 1986b).

Larval host plants. *Viola purpurea quercetorum*, *V. ocellata*? (Robinson et al. 2002).

Adult food resources. California buckeye, thistles (Opler and Wright 1999).

***Speyeria atlantis* (Edwards, 1863)**

(Figure 20-24)

Argynnis Atlantis Edwards, 1863a: 54.

Argynnis atlantis aberrant *chemo* Scudder, 1889: 573.

Argynnis atlantis canadensis dos Passos, 1935: 85.

Speyeria atlantis canadensis (dos Passos) [dos Passos and Grey 1947] (synonymized by Scott et al. 1998) (Figure 21).

Speyeria atlantis (Edwards) [dos Passos and Grey 1945a].

Common names. Atlantis fritillary, mountain silverspot, mountain fritillary, mountain silver-spotted butterfly, Newfoundland fritillary.

Type deposited. Lectotype (male) designated by dos Passos and Grey (1947) at American Museum of Natural History (Figure 20).

Type locality. Mountainous districts of the northern states and parts of British America. Defined by dos Passos (1935) based on lectotype as Hunter, Greene County, Catskill Mountains, New York. Brown (1965) noted that Holland's 1931 image of *S. atlantis* is a much better match of populations that occur in the Catskill Mountains than the very dark form dos Passos and Grey designated as lectotype, but at present the specimen designated by dos Passos and Grey represents the name bearing type for *S. atlantis*.

Type label data. "type Atlantis [male] Catskills; lectotype Argynnis atlantis [male], W. H. Edwards designated by dos Passos 1935".

Identification, taxonomy, and variation. *Speyeria atlantis* forms are widespread and variable. Adult wingspan ranges from 50-69 mm. Prior to splitting the hypothetically distinct species *S. hesperis* from *S. atlantis*, there were over 25 subspecific or geographical forms associated with the atlantis complex (Grey 1951; Moeck 1957). Scott et al. (1998) (also see Scott 1988) proposed splitting *S. atlantis* and *S. hesperis* based on wing coloration and a few larval characters. Because they behave as separate species across large parts of western North America, several works now treat *S. atlantis* and *S. hesperis* as distinct species (Scott et al. 1998; Guppy and Shepard 2001; Opler and Warren 2002; Dunford 2005; Warren 2005); thus, there are four subspecific 'atlantis' forms recognized at present. However, some authors believe that it may still be difficult to provide a species assignment for many populations based on ventral hindwing coloration and silvering of ventral hindwing spots (Pyle 2002), and because there are several reports of the two forms interbreeding in various parts of their range (North American Butterfly Association 2001) (also see discussion under *S. hesperis* profile). The nominate, eastern *S. atlantis* bears black margins along the forewings and black scaling along the veins dorsally. The ventral hindwing disc is usually purplish-brown in coloration. The remaining *S. atlantis* forms generally bear a black outer margin dorsally and chocolate or purplish-brown hindwing discs. Ventral hindwing spots are silvered in most individuals (many *S. hesperis* forms are cream colored) and the submarginal band is pale and narrow. Adults may be confused with *S. aphrodite* in many regions (including eastern North America), but *aphrodite* does not have black scaling along the wing veins and usually lacks black marginal bands dorsally. *Speyeria atlantis canadensis* (dos Passos), now synonymized under *S. atlantis* (Scott et al. 1998), is generally smaller in size. Holland (1969) noted that specimens taken from Hawkes Bay, Newfoundland were even smaller and redder than *S. a. canadensis* taken at the type locality, Doyles Station. This variability notes the probable relationship of nominate *S. atlantis* with *S. a. canadensis* and further corroborates the decision by Scott et al. (1998) to fully synonymize the smaller Canadian 'atlantis'. An *S. atlantis* population occurring in the mountains of West Virginia may represent an undescribed subspecies (Gatrelle 1998). Larvae of nominate *S. atlantis* are generally mottled black and brown with black-tipped, orange to tan spines with two cream-colored lines located dorsomedially. Larvae are somewhat variable in coloration throughout the range of *S. atlantis* (see Scott et al. 1998). Pupae are mottled brown and black, and the wing cases are grayish brown. Scudder (1889) and Edwards (1888a) provided a detailed description of the life stages.

Range. Widespread in Canada from the Yukon, Maritime Provinces and west to east central British Columbia; in the northeastern United States south to West Virginia, across the northern parts of the Great Lake region. *Speyeria atlantis* has been tentatively recorded in northeastern Illinois (Cook County) but is likely not a resident (Irwin and Downey 1973; Bouseman and Sternberg 2001). Reportedly "accidental" in Morris County, New Jersey (Gochfeld and Burger 1997). Disjunct populations exist in the Black Hills of South Dakota [*S. atlantis pahasapa* Spomer, Scott, Kondla] (see Grey et al. 1963; Scott et al. 1998), central Colorado [*S. atlantis sorocko* Scott, Kondla, Spomer], and northwestern Montana, northern Idaho, and Manitoba [*S. atlantis hollandi* (F. H. Chermock)]. Populations that are tentatively identi-

fied as *S. a. hollandi* also occur in northeastern Washington, sympatric with *S. hesperis brico* Kondla, Scott, Spomer.

Life history. Adapted for cooler climates, it frequents cool open woodlands near water, (i.e., bogs, river valleys), open coniferous forests, and old fields with forested borders. Scott (1988) indicated that the current distribution of wing characters suggests that the dark silvered forms of *S. atlantis* occupied coniferous forests in the northern U.S. and the Rocky Mountain foothills during the last ice age; they then moved higher in elevation and latitude. The unsilvered form with a reddish-brown ventral hindwing (i.e., 'hesperis' forms) occupied open forest in the southern Great Basin lowlands during the last ice age; they then spread north into the mountains, east to Wyoming and the Black Hills, and south along the Colorado mountain foothills. The mobility of western *S. atlantis* adults was studied by Moeck (1968) in Wyoming. He noted that tagged individuals were recaptured at least 50% of the time, indicating individuals moved very little from the study area. Eggs are laid near the base of host plant. First instar larvae typically do not feed until the following spring. Males patrol much of the day for available females. Mating behavior is described by Scott (1986b, 1988). *Speyeria atlantis* [as well as other Argynnini (Sellier 1973; Magnus 1958)] adults bear scent scales that lie along the veins on the dorsal side of the forewings (Grey et al. 1963; Scott 1986b). Males pursue females, draw their forewings forward, and flick the closed wings slightly open in quick bursts. Each burst of two to five flicks lasts less than a second, wafting pheromones up to the female's antennae. Courting males keep their forewings in a forward position and open and close them near the resting female to waft pheromones. Unreceptive females will flutter their wings to reject males. Flight period is mid June to September.

Larval host plants. *Viola septentrionalis*, *V. sororia affinis*, *V. adunca*, *V. canadensis* (Scott 1986b, Scott et al. 1998). Many host plant records in the literature listed for *S. atlantis* now pertain to members of the hesperis complex.

Adult food resources. Milkweeds, vetches, mints, mud, dung (Scott 1986b; Douglas and Douglas 2005); especially *Monarda* spp. in the West (Cliff Ferris, pers. comm.).

***Speyeria atlantis atlantis* (Edwards, 1863)**

(Figure 20-21)

[see species account for *S. atlantis*]

Locality data associated with specimens examined. CT: Litchfield; IA: Winneshiek; IL: Cook; IN: Lake, Vanderburgh; MA: Berkshire, Middlesex, Worcester; MD: Garrett; ME: Aroostook, Franklin, Hancock, Kennebec, Oxford, Penobscot, Piscataquis, Somerset, Washington, York; MI: Antrim, Cheboygan, Chippewa, Delta, Dickinson, Emmet, Gogebic, Houghton, Iron, Jackson, Keweenaw, Luce, Mackinac, Marquette, Ontonagon, Oscoda, Otsego, Presque Isle, Schoolcraft; MN: Aitkin, Beltrami, Cass, Cook, Hubbard, Itasca, Koochiching, Lake, Pine, Sherburne, St. Louis; NH: Carroll, Coos, Grafton, Hillsborough, Rockingham; NJ: Morris; NY: Chenango, Clinton, Columbia, Delaware, Erie, Essex, Franklin, Fulton, Greene, Hamilton, Herkimer, Jefferson, Oneida, Oswego, Tompkins, Ulster, Washington; OH: Delaware; PA: Allegheny, Berks, Cambria, Cameron, Centre, Clearfield, Clinton, Columbia, Elk, Erie, Forest, Lackawanna, Luzerne, Potter, Somerset, Sullivan, Tioga, Warren; RI: Providence; VT: Addison, Bennington, Caledonia, Chittenden, Essex, Lamoille, Orleans, Windham, Windsor; WI: Marquette, Bayfield, Burnett, Door, Douglas, Florence, Forest, Kewaunee, Langlade, Manitowoc, Marathon, Marinette, Oneida, Price, Rusk, Sawyer, Shawano, Vilas; WV: Grant, Monongalia, Pendleton, Pocahontas, Randolph, Tucker, Webster. Canadian provincial records include (some of these records were taken from specimens formerly applied to *S. atlantis canadensis*): Newfoundland, New Brunswick, Nova Scotia, Ontario, Quebec.

***Speyeria atlantis hollandi* (Chermock and Chermock, 1940)**

(Figure 22)

Argynnis atlantis Hollandi Chermock and Chermock, 1940: 82.*Speyeria atlantis hollandi* (Chermock and Chermock) [dos Passos and Grey 1947].**Common name.** Holland's fritillary.**Type deposited.** Holotype at Canadian National Collection (Figure 22).**Type locality.** Riding Mountains, Manitoba, Canada.**Type label data.** "ARG. ATLANTIS. R. HOLLANDI [male] HOLOTYPE F. H. & R. L. Chermock; HOLOTYPE Arg. atlantis R. Holland No. 4370 F. H. & R. L. Chermock; RIDING MTS MANITOBA VII-24-34; Can. Dep. Agr. Photo. Specimen No. 4093 24-IV-1986 Negative No".**Identification, taxonomy, and variation.** The discal and basal areas located on the ventral forewing and hindwing are deep brown compared to paler *S. atlantis* forms. This subspecies is considered the western terminus of the *S. atlantis* cline (Howe 1975). Adult wingspan ranges from 50-60 mm.**Range.** This subspecies occurs in the Riding Mountains of Manitoba and Peace River region of British Columbia.**Life history.** Nothing could be gleaned from the literature.**Larval host plants.** *Viola* spp.**Adult food resources.** As with most *Speyeria*, *S. a. hollandi* likely nectar on a wide variety of plants.**Locality data associated with specimens examined.** Canadian provincial records include: Manitoba.***Speyeria atlantis sorocko* Scott, Kondla, and Spomer, 1998**

(Figure 23)

Speyeria atlantis sorocko Scott, Kondla, and Spomer, 1998: 13-14.**Common names.** Southern Rockies fritillary.**Type deposited.** Holotype at American Museum of Natural History (Figure 23).**Type locality.** Near Mt. Judge, Clear Creek County, Colorado.**Type label data.** "HOLOTYPE [male] *Speyeria atlantis sorocko* Scott, Spomer, + Kondla 1997; 1 mi. NE Mt. Judge, Clear Creek Co. Colo. Aug. 5, 1987; collected by James A. Scott".**Identification, taxonomy, and variation.** Cliff Ferris (pers. comm.) stated this subspecies may be a redecoration of the form known as *S. hesperis nikias* (which has since been synonymized under *S. hesperis electa* by Scott et al. 1998). Adult wingspan is on average 60 mm.Forms of this subspecies may have been referred to as *Speyeria hesperis [atlantis] electa* (Edwards) [= *Argynnis Cornelia* Edwards], *S. hesperis [atlantis] nikias* (Hermann), or *Speyeria hesperis [atlantis] hesperis* (Edwards) in the past. See the synonymies for these taxa.

Range. Southern Rockies.

Life history. Nothing could be gleaned from the literature.

Larval host plants. *Viola sororia affinis*, *V. scopulorum*, *V. canadensis* (Scott et al. 1998).

Adult food resources. As with most *Speyeria*, *S. a. sorocko* likely nectar on a wide variety of plants.

Locality data associated with specimens examined. CO: Archuleta, Clear Creek, Conejos, Custer, Douglas, Fremont, Grand, Hinsdale, Jefferson, Larimer, Las Animas, Ouray, Rio Arriba, Routt, Saguache, San Miguel, Summit, Teller. NM: Rio Arriba.

***Speyeria atlantis pahasapa* Spomer, Scott, and Kondla, 1998**

(Figure 24)

Speyeria atlantis pahasapa Spomer, Scott, and Kondla, 1998: 13.

Common name. Dakota fritillary.

Type deposited. Holotype at American Museum of Natural History (Figure 24).

Type locality. Deerfield Reservoir, Black Hills, Pennington County, South Dakota.

Type label data. "HOLOTYPE; *Speyeria atlantis pahasapa* [male] Spomer, Scott, & Kondla 1998; SD: Pennington Co. Deerfield Reservoir 13 July 1990 leg. S. M. Spomer".

Identification, taxonomy, and variation. This subspecies is similar to *S. h. hollandi*, but the hindwing disc is much darker (blackish-brown). Adult wingspan is on average 60 mm. Forms of this subspecies may have been referred to as *Speyeria atlantis lurana* dos Passos and Grey in the past.

Range. Black Hills, South Dakota.

Life history. Nothing could be gleaned from the literature.

Larval host plants. *Viola* spp.

Adult food resources. As with most *Speyeria*, *S. a. pahasapa* likely nectar on a wide variety of plants.

Locality data associated with specimens examined. SD: Custer, Lawrence, Meade, and Pennington.

***Speyeria hesperis* (Edwards, 1864)**

(Figure 4C, 25-46)

Argynnis Hesperis Edwards, 1864a: 502.

Speyeria atlantis hesperis (Edwards) [dos Passos and Grey 1945a].

Speyeria hesperis (Edwards) [Scott et al. 1998].

Common names. Hesperis fritillary, western fritillary.

Type deposited. Neotype (male) designated by Brown (1965; see also dos Passos and Grey 1965) at Carnegie Museum of Natural History (Figure 25).

Type locality. Defined by dos Passos and Grey (1947) based on lectotype (= neotype from Brown 1965; see also dos Passos and Grey 1965) as Turkey Creek Junction, Jefferson County, Colorado.

Type label data. “Hesperis [male] type Colo; Neotype, *Argynnis hesperis* [male], W. H. Edwards designated by dos Passos and Grey 1965”.

Identification, taxonomy, and variation. Formerly considered a subspecies of *S. atlantis*, *S. hesperis* is variable throughout its range and 21 subspecific taxa are currently recognized. *Speyeria hesperis* and *S. atlantis* occur together or in close proximity, especially in cool, forested habitats, in many areas of western North America. Dos Passos and Grey (1965) noted that *S. hesperis* represented an unsilvered subspecies of *S. atlantis* along the Front Range in Colorado. Tebaldi (1982) (also see Ferris 1983) used starch gel electrophoresis of six enzymes to analyze the relationships among three phenotypes of *S. atlantis* and found that the phenotypes could be considered “semispecies.” Scott et al. (1998) divided *S. atlantis* into a distinct species based on wing coloration and wing pattern, *hesperis* having mostly unsilvered or cream colored ventral hindwing spots and *S. atlantis* always silvered. However, this situation still needs to be addressed in greater detail. The original description for *S. hesperis* identifies it as having opaque/cream colored spots (also see Figure 25). Several ‘*hesperis*’ subspecies (i.e., *S. h. electa*, *S. h. ratonensis*, *S. h. schellbachi*, *S. h. dorothea*, *S. h. nausicaa*, *S. h. capitansensis*) are apparently always silvered. It may be that *S. electa* is a valid species and represents the silver-spotted western ‘species’ in the atlantis species complex (Cliff Ferris, pers. comm.). Adult wingspan ranges from 50-68 mm. The ventral hindwing disc is red-brown to orange-brown and can be silvered or unsilvered. Scott et. al. (1998) split *S. atlantis* and *S. hesperis* forms based on wing pattern and coloration and a few larval characters. Adult eye coloration in living individuals is blue-gray in some populations, and this may help separate some populations from similar *S. aphrodite* populations, which bear dull, yellow-green eyes (Glassberg 2000). Larvae are generally solid black and bear orange spines with black tips. There are two brown lines located dorsomedially. The pupa is similar to *S. atlantis* in shape, but stouter; the color is brown on the head and wing cases. The abdomen is brown with some areas yellow-brown. Larval and pupal coloration varies throughout the range of *S. hesperis* (see Scott et al. 1998) due to various local climatic conditions.

Range. *Speyeria hesperis* occurs from Alaska, central Yukon and southwestern Northwest Territory, south through Canada east to western Manitoba, and in the western United States along the Rocky Mountains, to central California, northeastern and central Arizona, and central New Mexico.

Life history. *Speyeria hesperis* forms occur in moist meadows, gulches, and along cool slopes (Scott 1986b). Scott (2006b) observed females laying eggs on pine needles, *Quercus* leaves, grasses, and various other plants near *Viola* spp. Edwards (1888c) described the morphology of the egg, larval instars, and pupal stage and provided the phenology of each stage. Flight period is from early June to late October.

Larval host plants. *Viola canadensis* var. *scopulorum*, *V. adunca*, *V. sororia affinis*, *V. rydbergii*, *V. adunca bellidifolia*, *V. nuttallii*, *V. purpurea* (Scott 1992, 2006b; Scott et al. 1998).

Adult food resources. Yellow composites, mints (Opler and Wright 1999); especially *Monarda* (Cliff Ferris, pers. comm.).

***Speyeria hesperis hesperis* (Edwards, 1864)**

(Figure 25)

[see species account for *S. hesperis*]

Locality data associated with specimens examined. CO: Alpine, Boulder, Clear Creek, Douglas, El Paso, Gilpin, Jefferson, Larimer, Teller.

***Speyeria hesperis helena* dos Passos and Grey, 1955**

(Figure 26-27)

Argynnis lais Edwards, 1883: 209 (Figure 26).*Speyeria atlantis lais* (Edwards) [dos Passos and Grey 1947] (synonymized by Scott et al. 1998).*Argynnis lais* form *dennisi* Gunder, 1927: 287 (Figure 27).*Speyeria atlantis dennisi* Gunder [dos Passos and Grey 1947] (synonymized by Scott et al. 1998, also see Masters 1973, 1974)*Speyeria atlantis helena* dos Passos and Grey, 1955: 95-96. [replacement name for *Argynnis lais* Edwards, not *Argynnis lais* Scudder 1875].*Speyeria hesperis helena* dos Passos and Grey [Scott et al. 1998] (but see Scott 2008a: 81).**Common name.** Northwestern fritillary.**Type deposited.** Lectotype (male) designated by dos Passos and Grey (1947) at Carnegie Museum of Natural History (Figure 26).**Type locality.** From dos Passos and Grey (1947): Red Deer River, Alberta, Canada; Defined by dos Passos and Grey (1947) as Edmonton, Alberta, Canada.**Type label data.** According to dos Passos and Grey 1955, the type of *S. helena* bears the following label data: "Lais [male] N. W. Terr type Ged.; lectotype *Argynnis lais* [male] W. H. Edwards designated by dos Passos and Grey 1947".**Identification, taxonomy, and variation.** *Speyeria hesperis helena* is pale in color and bears a red-brown ventral hindwing disc. Adult wingspan ranges from 40-45 mm.**Range.** Prairie belts of Alberta and Saskatchewan.**Life history.** Nothing could be gleaned from the literature.**Larval host plants.** *Viola* spp.**Adult food resources.** As with most *Speyeria*, *S. h. helena* likely nectar on a wide variety of plants.**Label data associated with specimens examined.** Canadian provincial records include: Alberta, Manitoba.***Speyeria hesperis beani* (Barnes and Benjamin, 1926)**

(Figure 28)

Dryas atlantis race *beani* Barnes and Benjamin, 1926: 92.*Argynnis atlantis beani* form *hutchinsi* Gunder, 1932: 280.*Speyeria atlantis hutchinsi* Gunder [dos Passos and Grey, 1947] (synonymized by Scott et al. 1998).*Speyeria atlantis beani* (Barnes and Benjamin) [dos Passos and Grey 1947].*Speyeria electa* race *beani* (Barnes and Benjamin) [Howe 1975].*Speyeria hesperis beani* (Barnes and Benjamin) [Scott et al. 1998].**Common name.** Bean's fritillary**Type deposited.** Holotype at National Museum of Natural History (Figure 28).**Type locality.** Banff, Alberta, Canada.

Type label data. “*Dryas atlantis beani* Holotype [male] B & Benj; Banff Alberta, Aug. 8-15”.

Identification, taxonomy, and variation. Adults are variable in size, and usually smaller than most specimens of *S. hesperis*. The ventral hindwing disc is usually bright red and the spots can be silvered, entirely or partially unsilvered. Adult wingspan ranges from 50-55 mm.

Range. British Columbia (Columbia Trench) and the mountains of Alberta, Montana, and northern Idaho.

Life history. Nothing could be gleaned from the literature.

Larval host plants. *Viola* spp.

Adult food resources. As with most *Speyeria*, *S. h. beani* likely nectar on a wide variety of plants.

Label data associated with specimens examined. Canadian provincial records include: Alberta, British Columbia.

***Speyeria hesperis brico* Kondla, Scott, and Spomer, 1998**
(Figure 29)

Speyeria hesperis brico Kondla, Scott, and Spomer, 1998: 14.

Common name. Brico fritillary.

Type deposited. Holotype at Canadian National Collection (Figure 29).

Type locality. Castle Creek Forest Service Road, Cariboo Mountains, near McBride, British Columbia, Canada.

Type label data. “HOLOTYPE [male] *Speyeria hesperis brico* Kondla, Scott, + Spomer 1997; KM 23.5, Castle Creek Forest Service Road, S of McBride, B.C. June 18, 1995, Norbert G. Kondla; 95-6-18 B.B. K 23.5 Castle Cr. FSR N. Kondla; HOLOTYPE in Type coll. CNC No”.

Identification, taxonomy, and variation. This subspecies resembles *S. h. beani* but the disc is darker red, and the disc extends farther into the pale submarginal band ventrally. It often occurs sympatrically with *S. a. hollandi*. Adult wingspan is on average 56 mm. Forms of this subspecies may have been referred to as *S. hesperis [atlantis] beani* or *S. hesperis [atlantis] helena* in the past.

Range. Northern part of southeastern British Columbia, specifically the interior plateau.

Life history. *Speyeria hesperis brico* occurs in the Interior Cedar/Hammock bioclimatic zone and the Englemann Spruce/Subalpine fir zone.

Larval host plants. *Viola* spp.

Adult food resources. As with most *Speyeria*, *S. h. brico* likely nectar on a wide variety of plants.

Label data associated with specimens examined. Canadian provincial records include: British Columbia.

***Speyeria hesperis ratonensis* Scott, 1981**

(Figure 30)

Speyeria atlantis ratonensis Scott, 1981: 4.*Speyeria hesperis ratonensis* Scott [Scott et al. 1998].**Common names.** None.**Type deposited.** Holotype at Natural History Museum of Los Angeles County (Figure 30).**Type locality.** Raton Mesa, Colfax County, New Mexico.**Type label data.** I have not examined the label data associated with this specimen. Scott (1981) includes the following data: "Holotype, male, Raton Mesa, Colfax Co. New Mex. 21 July 1972, J. Scott".**Identification, taxonomy, and variation.** Considered one of the palest *S. atlantis-hesperis* forms, it is similar to *Speyeria hesperis greyi* in Nevada. *Speyeria hesperis ratonensis* always has silver spots on the ventral hindwings. Adult wingspan ranges from 50-55 mm.**Range.** Limited to Raton Mesa in northeastern New Mexico.**Life history.** *Speyeria hesperis ratonensis* may be a Pleistocene relict related to prairie dwelling *S. hesperis helena* in Canada (Scott 1981). The two populations likely inhabited mixed grassland and aspen forests on the southern plains. When the climate warmed, *S. h. helena* advanced north while *S. h. ratonensis* move up in elevation.**Larval host plants.** *Viola canadensis* var. *scopulorum* (= *V. rydbergii*) (Scott 1992; Scott et al. 1998).**Adult food resources.** As with most *Speyeria*, *S. h. ratonensis* likely nectar on a wide variety of plants.**Locality data associated with specimens examined.** CO: Las Animas; NM: Colfax, Union.***Speyeria hesperis greyi* Moeck, 1950**

(Figure 31)

Speyeria atlantis greyi Moeck, 1950: 61.*Speyeria electa greyi* Moeck [Howe 1975].*Speyeria hesperis greyi* Moeck [Scott et al. 1998].**Common name.** Grey's fritillary.**Type deposited.** Holotype at American Museum of Natural History (Figure 31).**Type locality.** Lamoille Canyon, Ruby Mountains, Elko County, Nevada (Figure 49).**Type label data.** "Speyeria atlantis greyi, n. ssp. Holotype [male]; Lamoille Canyon 8- 8500'-July 24, 1949 (Moeck) Ruby Mts., Nevada". [Austin 1998 provided additional type specimen data].**Identification, taxonomy, and variation.** Both sexes bear a light reddish buff ground color, similar to *Speyeria hesperis chitone*. Their appearance overall is pale, and lacks the red hues of other *S. hesperis* and *S. atlantis* forms. Adult wingspan ranges from 45-50 mm. Authors (e.g., Hodges 1983; Austin 1998; Scott et al. 1998) inadvertently included parentheses around the describer Moeck, suggesting this species was originally described in another genus. This has been perpetuated in the literature; however, 'greyi' was originally described as *Speyeria* and the parentheses were in error (Dunford and Austin 2007).

Range. Restricted to the Ruby Mountains and East Humboldt Range, Elko County, Nevada.

Life history. I observed adults flying low to the ground in aspen stands located in Lamoille Canyon, Nevada.

Larval host plants. *Viola* spp.

Adult food resources. Like most *Speyeria*, *S. h. greyi* likely nectar on a wide variety of plants.

Locality data associated with specimens examined. NV: Elko.

***Speyeria hesperis lurana* dos Passos and Grey, 1945**

(Figure 32)

Speyeria atlantis lurana dos Passos and Grey, 1945b: 8.

Speyeria hesperis lurana dos Passos and Grey [Scott et al. 1998].

Common name. Lurana fritillary.

Type deposited. Holotype at American Museum of Natural History (Figure 32).

Type locality. Harney Peak, Black Hills, South Dakota.

Type label data. “Holotype *Speyeria atlantis lurana* Cyril F. dos Passos and L. Paul Grey; HARNEY PEAK, S. D. [male] 25 VI-39 Col. By A. C. FREDERICK; L. P. Grey”.

Identification, taxonomy, and variation. Both sexes are typically unsilvered, sympatrically occurring with silvered forms being those of *S. atlantis pahasapa* (Scott et al. 1998). Cliff Ferris (pers. comm.) notes that both ‘*S. h. lurana*’ and ‘*S. a. pahasapa*’ fly together and interbreed (or at least copulate) in the Big Horn Mountains, Washakie Co., Wyoming. The status or distinctness of these two subspecies should be further evaluated. Scott (2008a) suggests that these Big Horn populations best be called ‘*lurana x dennisi*’. Adult wingspan is on average 55 mm.

Range. Black Hills, South Dakota. Also recorded in Wyoming (Grey et al. 1963).

Life history. I observed numerous individuals using creeks as flyways and feeding on various flowers in Spearfish Canyon, South Dakota.

Larval host plants. *Viola* spp.

Adult food resources. As with most *Speyeria*, *S. h. lurana* likely nectar on a variety of plants.

Locality data associated with specimens examined. SD: Custer, Harding, Lawrence, Pennington, Crook.

***Speyeria hesperis irene* (Boisduval, 1869)**

(Figure 33)

Argynnis irene Boisduval, 1869: 60.

Speyeria atlantis irene (Boisduval) [dos Passos and Grey 1947].

Speyeria hesperis irene (Boisduval) [Scott et al. 1998].

Common name. Irene fritillary.

Type deposited. Lectotype (female) designated by dos Passos and Grey (1947) at National Museum of Natural History (Figure 33).

Type locality. Interior of California. Defined by dos Passos and Grey (1947) as Massack, Plumas County, California. However, Emmel et al. (1998a) stated that the restriction of the type locality to Massack, Plumas County is unsatisfactory and note that *S. h. irene* is not found in the immediate vicinity of Massack. Emmel et al. (1998a) defined the type locality to be Gold Lake, Sierra County, California, where the 'irene' phenotype is known to occur.

Type label data. "Montivaga Behr irene Bd. Calif.; Argynnis Egleis [female] (Irene, Bdv. Lepid. Californie, p. 60) specim-typic.; EX MUSAEO Dris. BOISDUVAL; Oberthur Collection; Type irene Bdv. a/c Hofer; Barnes Collection".

Identification, taxonomy, and variation. Adults are similar to *Speyeria hesperis dodgei*, *S. hesperis hanseni*, *S. hesperis cottlei* (see Emmel 1998c) as well as the sympatrically occurring *S. zerene*. Ventral hindwing spots are cream colored on *S. h. irene*. Adult wingspan ranges from 50-55 mm.

Range. Occurs in the northern Sierra Nevadas of California, south to Yosemite in isolated colonies.

Life history. Occurs in open, dry meadows.

Larval host plants. *Viola purpurea* (Emmel et al. 1970).

Adult food resources. Western Pennyroyal (Emmel and Emmel 1962).

Locality data associated with specimens examined. CA: Alpine, Amador, Calaveras, El Dorado, Glenn, Modoc, Mono, Placer, Plumas, Sierra, Siskiyou, Stanislaus, Tuolumne; NV: Douglas, Washoe.

***Speyeria hesperis cottlei* (Comstock, 1925)**

Argynnis cottlei Comstock, 1925: 64 (see dos Passos and Grey 1947).

Speyeria atlantis cottlei (Comstock) [Emmel et al. 1998c].

Speyeria hesperis cottlei (Comstock) [Warren 2005].

Common name. Cottle's fritillary.

Type deposited. The specimen used for description was in the J. E. Cottle collection, San Francisco (Comstock 1925; dos Passos and Grey 1947). Holotype reportedly located at Natural History Museum of Los Angeles County (Pelham 2008); cannot be located (see discussion below) and a neotype designation may be needed.

Type locality. Vicinity of Alturas, Modoc County, California. Dos Passos and Grey (1947) synonymized *A. cottlei* with *Speyeria atlantis [=hesperis] irene* and designated a lectotype for *S. h. irene* taken from Massack, Plumas County, California. Emmel et al. (1998c) resurrected the name from synonymy based on examination of the type for *S. h. irene* and the distribution of *S. h. cottlei*.

Type label data. I have not seen the type specimen. According to Emmel et al. (1998c), a single specimen was used to describe *A. cottlei*, but it is not clear where the specimen is currently located. John Emmel (pers. comm.) stated the following: "Riker mounts that Comstock used for his plates in *The Butterflies of California* are still stored at L.A. County Museum--however, specimens that Comstock borrowed, such as Cottle's specimen of *Argynnis cottlei*, were returned to the persons who lent them to

Comstock. So presumably the type was returned to J. E. Cottle-- where his collection went, I'm not sure. There are some specimens of Cottle's in the American Museum of Natural History, New York. However, about 15 years ago when I was at the American Museum I did not see the type of *cottlei*. Cottle lived in San Francisco, but the type of *A. cottlei* has not turned up at the California Academy of Sciences there. Comstock's illustration (1927 [1989], *The Butterflies of California*) of the type of *A. cottlei* may be your only source for an image." A type specimen may need to be redesignated for *S. hesperis cottlei*. At the time, Comstock treated *A. cottlei* as a distinct species but speculated it may have been an unsilvered form of what is now *S. zerene hippolyta*.

Identification, taxonomy, and variation. Closely resembles members of the *zerene* complex and *S. h. irene*. However, there is a complete lack of silver scaling on the ventral hindwings of *S. h. irene*. Adult wingspan ranges from 50-55 mm. This subspecies has been referred to as *S. atlantis [=hesperis] irene* (Boisduval) in the past. *Argynnis cottlei* was raised from full synonymy with *S. h. irene* to subspecies status by Emmel et al. (1998c), who retained it in the *atlantis* species complex. This species should be placed with former western '*atlantis*' forms that conform to the *hesperis* subspecies complex listed by Scott et al. (1998). Warren (2005) was the first to use '*cottlei*' with *S. hesperis*.

Range. According to Emmel et al. (1998c), *S. h. cottlei* is known from the Warner Mountains, but blend zones with *S. hesperis dodgei* occur in the Klamath Mountains and Mt. Shasta region.

Life history. Nothing could be gleaned from the literature.

Larval host plants. *Viola* spp.

Adult food resources. As with most *Speyeria*, *S. h. cottlei* likely nectar on a wide variety of plants.

Locality data associated with specimens examined. CA: Lassen.

***Speyeria hesperis hanseni* Emmel, Emmel, and Mattoon, 1998, new species combination**
(Figure 34)

Speyeria atlantis hanseni Emmel, Emmel, and Mattoon, 1998c: 152.

Common name. Hansen's fritillary

Type deposited. Holotype at Natural History Museum of Los Angeles County (Figure 34).

Type locality. Covelo Road, Anthony Peak, Tehama County, California.

Type label data. I have not examined the label data associated with this specimen. Emmel et al. (1998c) provide the following data: "Holotype male: California, Tehama County; Anthony Peak on Covelo Road, 4 July 1968, leg. S. O. Mattoon".

Identification, taxonomy, and variation. Similar to *S. h. dodgei* and *S. h. irene*, *S. h. hanseni* is slightly dusker in appearance dorsally and more pale ventrally due to extensive cream scaling. Adult wingspan ranges from 50-55 mm. This taxon should be placed with western '*atlantis*' forms that conform to the *hesperis* subspecies complex described by Scott et al. (1998). Forms of this subspecies were likely referred to as *Speyeria hesperis [atlantis] irene* (Boisduval) in the past. See also Dunford (2007).

Range. This subspecies is known in the North Coast Ranges from Glenn County northwestward to central Humboldt County (Emmel et al. 1998c).

Life history. *Speyeria hesperis hansenii* flies from late June to early August, with a peak flight period during early July.

Larval host plants. *Viola* spp.

Adult food resources. As with most *Speyeria*, *S. h. hansenii* likely nectar on a wide variety of plants.

Locality data associated with specimens examined. CA: Glenn, Mendocino, Tehama, Trinity.

***Speyeria hesperis dodgei* (Gunder, 1931)**

(Figure 35)

Argynnis dodgei Gunder, 1931: 46.

Speyeria atlantis dodgei (Gunder) [dos Passos and Grey 1947].

Speyeria hesperis dodgei (Gunder) [Scott et al. 1998].

Common name. Dodge's fritillary.

Type deposited. Holotype at American Museum of Natural History (Figure 35).

Type locality. Diamond Lake, Douglas County, Oregon.

Type label data. "HOLOTYPE [male] COLLECTION OF JEANE D. GUNDER ARGYNNIS DODGEI [signed by] J. D. Gunder TYPE LABEL; COLLECTION OF JEANE D. GUNDER DIAMOND LAKE, DOUGLAS Co., OREG. JULY 10-1930; J. D. Gunder collection Ac. 34998; 7/10/30 Diamond Lk, Oreg [male]".

Identification, taxonomy, and variation. This subspecies bears cream to whitish colored ventral hindwing spots and a brick red disc. The marginal band along the disc is pinkish rather than buff. Adult wingspan ranges from 45-55 mm. *Speyeria hesperis dodgei* resembles *S. hydaspae* forms where these species overlap.

Range. Cascade ranges of Oregon and southern Washington, eastward into Idaho.

Life history. This subspecies is largely confined fir and pine forests and may be seen in canyons, along creeks, and in small clearings and meadows. Dornfeld (1980) briefly described the larva.

Larval host plants. *Viola bellidifolia* (Shields et al. 1970).

Adult food resources. Mint (Dornfeld 1980).

Locality data associated with specimens examined. CA: Siskiyou; ID: Nez Perce; OR: Baker, Crook, Deschutes, Douglas, Grant, Jackson, Jefferson, Klamath, Lake, Lane, Linn, Thurston, Umatilla, Wallowa, Wheeler; WA: Yakima.

***Speyeria hesperis viola* dos Passos and Grey, 1945**

(Figure 36)

Speyeria atlantis viola dos Passos and Grey, 1945: 10.

Speyeria hesperis viola dos Passos and Grey [Scott et al. 1998].

Common name. Viola's fritillary

Type deposited. Holotype at American Museum of Natural History (Figure 36).

Type locality. Trail Creek, Sawtooth Mountains, Idaho.

Type label data. “Holotype [male] *Speyeria atlantis viola* Cyril f. dos Passos and L. Paul Grey; J. D. Gunder collection Ac. 34998; Trail Creek Ida. 7400ft. VII.11.31; Col. C. W. Herr”.

Identification, taxonomy, and variation. Both sexes are similar to *S. h. irene* but are somewhat paler in the disc. Adults are rather small and spots are entirely unsilvered on the ventral hindwings. Adult wingspan ranges from 45-50 mm.

Range. Sawtooth Mountains, Idaho and eastern Oregon.

Life history. Nothing could be gleaned from the literature.

Larval host plants. *Viola* spp.

Adult food resources. As with most *Speyeria*, *S. h. viola* likely nectar on a variety of plants.

Locality data associated with specimens examined. ID: Blaine, Boise, Camas, Custer.

***Speyeria hesperis elko* Austin, 1983**

(Figure 37)

Speyeria atlantis elko Austin, 1983: 244-245.

Speyeria hesperis elko Austin [Scott et al. 1998].

Common name. Elko fritillary.

Type deposited. Holotype at Nevada State Museum (Figure 37) [not at McGuire Center for Lepidoptera and Biodiversity as reported by Pelham (2008)].

Type locality. ca. 10 miles south of Mountain City, Wild Horse Creek Campground, Owyhee River Valley, Elko County, Nevada.

Type label data. “HOLOTYPE *Speyeria atlantis elko* Austin”.

Identification, taxonomy, and variation. The cline involved with *S. h. elko* is largely unsilvered and includes *S. h. tetonia* (Wyoming), *S. h. viola* (Idaho), *S. h. irene*, *S. h. cottlei*, and *S. h. hanseni* (California). *Speyeria hesperis elko* is pale, similar to other *Speyeria* in the Great Basin (Austin 1983). Adult wingspan ranges from 50-55 mm.

Range. Known only from the type locality: Jarbidge Mountains, Owyhee River Valley, and Independence Range, Nevada.

Life history. Males patrol the creek bottom along the Owyhee River. Adult flight period includes late June through mid-August.

Larval host plants. *Viola* spp.

Adult food resources. As with most *Speyeria*, *S. h. elko* likely nectar on a wide variety of plants (especially mints-George Austin, pers. comm.).

Label data associated with specimens examined. NV: Elko.

***Speyeria hesperis tetonia* dos Passos and Grey, 1945**
(Figure 38)

Speyeria atlantis tetonia dos Passos and Grey, 1945: 9.

Speyeria hesperis tetonia dos Passos and Grey [Scott et al. 1998].

Common name. Teton fritillary.

Type deposited. Holotype at American Museum of Natural History (Figure 38).

Type locality. Teton Mountains, Wyoming.

Type label data. "Holotype [male] *Speyeria atlantis tetonia* Cyril F. dos Passos and L. Paul Grey; Teton Mts. Wyo. VII.11.31; J. D. Gunder Collection Ac. 34998".

Identification, taxonomy, and variation. Both sexes usually lack silvering on the ventral hindwing. The discal area is lighter red ventrally than other *S. hesperis*. Adult wingspan ranges from 45-50 mm. This subspecies also closely resembles *S. egleis*.

Range. Teton Mountain region.

Life history. Adults appear in early July and fly along with similar looking *S. egleis* in parts of Teton National Park.

Larval host plants. *Viola* spp.

Adult food resources. As with most *Speyeria*, *S. h. tetonia* likely nectar on a wide variety of plants.

Locality data associated with specimens examined. ID: Bear Lake, Bonneville, Clark, Fremont, Madison, Teton; WY: Fremont, Lincoln, Sublette, Teton.

***Speyeria hesperis wasatchia* dos Passos and Grey, 1945**
(Figure 39)

Speyeria atlantis wasatchia dos Passos and Grey, 1945: 9.

Speyeria hesperis wasatchia dos Passos and Grey [Scott et al. 1998].

Common name. Wasatch fritillary.

Type deposited. Holotype at American Museum of Natural History (Figure 39).

Type locality. Payson Canyon, Payson, Utah County, Utah.

Type label data. "Holotype [male] *Speyeria atlantis wasatchia* Cyril F. dos Passos and L. Paul Grey; A. chitone Edw. Det. Gunder; Payson Canyon, Payson, Utah VII.16.32; Col. Pfouts; J. D. Gunder Collection Ac. 34998".

Identification, taxonomy, and variation. *Speyeria hesperis wasatchia* is similar to *S. h. chitone* and was considered a synonym (as *Speyeria atlantis chitone*) by Hammond (1991). Scott et al. (1998) and Pelham (2008) list *S. h. wasatchia* as a synonym of *S. h. tetonia*. Ventral hindwing spots of *S. h. wasatchia* are typically unsilvered but there are silvered forms. Adult wingspan ranges from 50-60 mm.

Range. Known from a few localities in Utah.

Life history. This subspecies can be encountered at elevations above 7,500 ft. in northern Utah.

Larval host plants. *Viola* spp.

Adult food resources. As with most *Speyeria*, *S. h. wasatchia* likely nectar on a wide variety of plants.

Locality data associated with specimens examined. UT: Davis, Box Elder, Cache, Daggett, Duchesne, Salt Lake, Sevier, Summit, Tooele, Utah, Wasatch.

***Speyeria hesperis chitone* (Edwards, 1879)**

(Figure 40)

Argynnis chitone Edwards, 1879b: 82.

Speyeria atlantis chitone (Edwards) [dos Passos and Grey 1947].

Speyeria hesperis chitone (Edwards) [Scott et al. 1998].

Common name. Chitone fritillary.

Type deposited. Lectotype (male) designated by dos Passos and Grey (1947) at Carnegie Museum of Natural History (Figure 40). Brown (1965), however, noted the specimen selected by dos Passos and Grey (1947) was not the specimen of Edward's original description. That specimen is housed in the National Museum of Natural History. Dos Passos and Grey were, however, at liberty to select any syntype and they chose the only male in the Edwards' Collection housed at Carnegie.

Type locality. Southern Utah and Arizona. Defined by dos Passos and Grey (1947) as Cedar Breaks National Monument, Iron County, Utah.

Type label data. "type Chitone [male] So. Utah; lectotype *Argynnis chitone* [male] W. H. Edwards designated by dos Passos and Grey 1947".

Identification, taxonomy, and variation. Adults of *S. h. chitone* are generally larger than *S. h. wasatchia* and have a heavier black patterning above. The ventral hindwing disc of *S. h. chitone* is either silver or unsilvered. Adult wingspan ranges from 50-55 mm.

Range. La Sal and Abajo Mountains in Utah. It is also found near Cedar Breaks National Monument.

Life history. Nothing could be gleaned from the literature.

Larval host plants. *Viola* spp.

Adult food resources. As with most *Speyeria*, *S. h. chitone* likely nectar on a wide variety of plants.

Locality data associated with specimens examined. UT: Beaver, Duchesne, Emery, Garfield, Grand, Iron, Kane, Millard, Piute, Sanpete, Sevier.

***Speyeria hesperis electa* (Edwards, 1878)**

(Figure 41-42)

Argynnis Electa Edwards, 1878: 143.

Argynnis Cornelia Edwards, 1892: 106 (synonymized by dos Passos and Grey 1947).

Speyeria atlantis electa (Edwards) [dos Passos and Grey 1947].

Argynnis nikias Ehrmann, 1917: 55 (Figure 42).

Speyeria atlantis nikias (Ehrmann) [dos Passos and Grey 1947] (synonymized by Scott et al. 1998).

Speyeria hesperis electa (Edwards) [Scott et al. 1998].

Common names. Electa fritillary, electa silverspot, cinnamon silverspot.

Type deposited. Lectotype (male) designated by dos Passos and Grey (1947) at Carnegie Museum of Natural History (Figure 41).

Type locality. Colorado. Defined by dos Passos and Grey (1947) as Rocky Mountain National Park, Colorado. Brown (1965) considered this locality untenable, and corrected it to Turkey Creek Junction, Jefferson County, Colorado. Subsequently defined as “Twin Lakes, Lake County” Colorado by Scott et al. 1998 (also see Scott 2008a: 22).

Type label data. “type electa [male] Colo. Mead ’71; *Argynnis cornelia* [male] Fide W. J. Holland; Collection W. H. Edwards; lectotype *Argynnis electa* [male] W. H. Edwards designated by dos Passos and Grey 1947”.

Identification, taxonomy, and variation. This subspecies has been recognized as a distinct species by some authors (Howe 1975; Bird et al. 1995) and is difficult to distinguish from nominate (eastern) *S. atlantis* except by locality labels. It may be that ‘*electa*’ is a valid species and represents the silver-spotted western ‘species’ in the atlantis complex (Cliff Ferris, pers. comm.). Additional taxonomic studies, those including molecular analyses, need to be conducted to address this situation. Adult wingspan ranges from 55-60 mm. Maeki and Remington (1960) dissected the testes of individuals taken from Colorado to find $n = 29$ chromosomes and illustrated the relative sizes of each.

Range. Throughout the Rocky Mountains of Colorado and in the Laramie Range of southern Wyoming.

Life history. Adults of *S. h. electa* are on the wing as early as May in Alberta (Bird et al. 1995) and fly well into September. Emmel (1964) noted that adults prefer open, dry meadow areas near Florissant, Colorado.

Larval host plants. *Viola sororia affinis* (Scott 1992).

Adult food resources. Yellow composites, white thistles (Emmel 1964; Bird et al. 1995).

Locality data associated with specimens examined. WY: Albany, Carbon. I also examined numerous individuals taken from Colorado at various museums; however, in some cases the locality data associated with *S. h. electa* individuals may have represented ‘*hesperis*’ forms.

***Speyeria hesperis schellbachi* Garth, 1949**
(Figure 43)

Speyeria atlantis schellbachi Garth, 1949: 1.

Speyeria hesperis schellbachi Garth [Scott et al. 1998].

Common name. Schellbach’s fritillary.

Type deposited. Holotype at Natural History Museum of Los Angeles County (Figure 43).

Type locality. Neal Spring, north rim of Grand Canyon, Coconino County, Arizona.

Type label data. I have not examined the label data associated with this specimen.

Identification, taxonomy, and variation. Adults are bright orange-yellow dorsally and dark basally. Adult wingspan ranges from 50-60 mm. This subspecies somewhat resembles *S. h. chitone* but is always silver on the ventral hindwing spots.

Range. Kaibab Plateau, near the Grand Canyon, Arizona.

Life history. Adults are active in secluded draws along springs.

Larval host plants. *Viola* spp.

Adult food resources. *Cirisium* spp. (Garth 1950).

Locality data associated with specimens examined. AZ: Coconino.

***Speyeria hesperis nausicaa* (Edwards, 1874)**

(Figure 44)

Argynnis Nausicaa Edwards, 1874b: 104.

Argynnis ? *aphrodite* form *Arizonensis* Elwes, 1889: 546 (synonymized by dos Passos and Grey 1947).

Speyeria atlantis nausicaa (Edwards) [dos Passos and Grey 1947].

Speyeria hesperis nausicaa (Edwards) [Scott et al. 1998].

Common names. *Nausicaa* fritillary, Arizona fritillary, Arizona silverspot.

Type deposited. Lectotype (male) designated by dos Passos and Grey (1947) at Carnegie Museum of Natural History (Figure 44).

Type locality. Rocky Canyon, Cochise County, Arizona (dos Passos and Grey 1947). However, Brown (1965) believed that the collection date may have been misread by Edwards, and states the collector (H. W. Henshaw) was likely at Rock Canyon, Graham County, Arizona.

Type label data. "Nausicaa [male] Ariza. Wheeler Ex type; lectotype *Argynnis nausicaa* [male] W. H. Edwards designated by dos Passos and Grey 1947".

Identification, taxonomy, and variation. This subspecies is one of the larger ones within the *hesperis* complex. Adult wingspan ranges from 60-75 mm. Adults are similar in appearance to *S. h. dorothea*, but there is usually some white or grey overscaling discally on the underside of *S. h. nausicaa*. The forewings are pointed, and the ventral hindwing spots are always silver with the discal area violaceous in color. There may be two 'forms' of *S. h. nausicaa* that occur in Arizona, one form, darker basally on the dorsal surface of the wings, flies at or above 10,000ft.

Range. Central and western Arizona above the Mogollon Rim. It also occurs in western New Mexico.

Life history. Adults are active in the mid morning hours in open sunny areas (Figure 50). Afternoon rains during the summer months in the Arizona mountains may hinder their daily activities (personal observations at Hospital Flat, Mt. Graham). Adults will become inactive fairly rapidly when the sun is covered by clouds. Howe (1975) noted that adults settle with their wings horizontal against the ground in the late afternoon sunshine along dirt roads in the White Mountains of Arizona.

Larval host plants. *Viola* spp.

Adult food resources. As with most *Speyeria*, *S. h. nausicaa* likely nectar on a wide variety of plants.

Locality data associated specimens examined. AZ: Apache, Cochise, Coconino, Gila, Graham, Grant, Greenlee, Navajo, Yavapai; NM: Catron, Cibola, Dona Ana, Grant, Sierra, Socorro.

***Speyeria hesperis dorothea* Moeck, 1947**

(Figure 45)

Speyeria atlantis dorothea Moeck, 1947: 73-75.

Speyeria hesperis dorothea Moeck [Scott et al. 1998].

Common name. Dorothy's fritillary.

Type deposited. Holotype at American Museum of Natural History (Figure 45).

Type locality. Sandia Peak, Sandia Mountains, Sandoval County, New Mexico.

Type label data. "HOLOTYPE [male] *Speyeria atlantis dorothea* A. H. Moeck; Sandia Peak, Sandia Mts., N. M., July 15, 1946 7,000 ft. (A. H. Moeck)".

Identification, taxonomy, and variation. Similar in size to *S. h. nausicaa* but basal suffusion of *S. h. dorothea* is somewhat heavier and black patterning is bolder. The ventral hindwing disc bear brilliant silver spots. Adult wingspan ranges from 55-70 mm. The genitalia are similar to those of the Callippe group (e.g., *S. callippe*, *S. atlantis*, *S. egleis*, *S. adiate*).

Range. Sandia, Chuska, Manzano Mountains, New Mexico.

Life history. Adults in can be observed in open glades in the Sandia Mountains (Figure 51).

Larval host plants. *Viola sororia affinis* (Scott et al. 1998).

Adult food resources. As with most *Speyeria*, *S. h. dorothea* likely nectar on a wide variety of plants.

Locality data associated with specimens examined. AZ: Apache; NM: Bernalillo, Cibola, McKinley, Otero, San Juan, Sandoval, Torrance, Valencia.

***Speyeria hesperis capitanensis* R. Holland, 1988**

(Figure 46)

Speyeria atlantis capitanensis R. Holland, 1988: 2.

Speyeria hesperis capitanensis R. Holland [Scott et al. 1998].

Common name. Capitan Mountain fritillary.

Type deposited. Holotype at American Museum of Natural History (Figure 46).

Type locality. Padilla Point, crest of Capitan Ridge, Capitan Mountains, Lincoln County, New Mexico.

Type label data. "HOLOTYPE *Speyeria atlantis capitanensis* R. Holland; 10.VII.82 leg. RWH Padilla Pt. 9200' crest of Capitan Mts. Lincoln Co., NM; Figured in Bulletin of the Allyn Museum Number 113 Fig. 2B+4 Specimen 13664; 13664. RWH *S. atlantis* ssp".

Identification, taxonomy, and variation. This subspecies is intermediate phenotypically between *S. h. nausicaa* and *S. h. dorothea*, more closely resembling *S. h. dorothea*. Adult wingspan ranges from 60-79 mm.

Range. Capitan and Sacramento Mountains, New Mexico.

Life history. I observed adults using roadside flowers for nectar and would use streams as flyways in the Capitan Mountains (Figure 52). Adults were active from mid to late morning hours through the early afternoon.

Larval host plants. *Viola* spp.

Adult food resources. As with most *Speyeria*, *S. h. capitanensis* likely nectar on a wide variety of plants.

Locality data associated with specimens examined. NM: Lincoln, Otero.

***Speyeria hydaspae* (Boisduval, 1869)**

(Figure 47)

Argynnis Hydaspae Boisduval, 1869: 60.

Speyeria hydaspae (Boisduval) [dos Passos and Grey 1945a].

Common names. Hydaspae fritillary, lavender fritillary.

Type deposited. Lectotype (male) designated by dos Passos and Grey (1947) at National Museum of Natural History (Figure 47).

Type locality. Southern California. Defined by dos Passos and Grey (1947) as Yosemite Valley, Mariposa County, California. Redefined by Emmel et al. (1998a) to Gold Lake, Sierra County, California.

Type label data. "Monticola Behr. Hydaspae Bd. Californ.; EX MUSAEO Dris. BOISDUVAL; Argynnis Hydaspae Bdv Californie; Argynnis Hydaspae [male], Boisduv. ex 2 typic. specim.; Type hydaspae a/c Hofer; Oberthur Collection; Barnes Collection".

Identification, taxonomy, and variation. There are approximately 7 described subspecies in the hydaspae complex. Adult wingspan is 41-58 mm. The subspecific taxa are fairly uniform in wing patterning and color. The dorsal wing surface is red-orange with a heavy black pattern, especially at the base. The ventral surface is purplish brown with hindwing spots relatively round and unsilvered in most populations (some individuals in the Northwest have silver spots-i.e., Vancouver Island), cream colored and edged with black. Spots located in the median band are large, first three approximately equal in size, touching or nearly so. The submarginal spots are larger in southern populations, smaller in the north and occasionally partly silvered. Some *S. hesperis* populations in the Pacific Northwest and California Sierra Nevada Mountains resemble *S. hydaspae*. Kondla (2001) clarified the taxonomic relationships and nomenclature associated with *S. hydaspae* forms in British Columbia. Eggs are cream colored and somewhat purple in color before hatching (Pyle 2002). Larvae are mostly black with yellow-orange spines laterally; in some forms, these spines are black. The upper two rows of spines are typically black; lower four rows of spines orange-brown to yellow. There are also pale yellow mid-dorsal stripes; these are much paler than those in similar looking *S. zerene*. Larval coloration is likely variable throughout the range of *S. hydaspae* due to various local climatic conditions.

Range. Forms of *S. hydaspae* occur from central British Columbia and southwestern Alberta, south in mountainous areas to southern Sierra Nevada in California, northern Utah, and northern Colorado.

Life history. This species occurs in openings in moist montane coniferous forests, often near aspens, and in mountain meadows and along roadsides. It also occurs in drier areas in British Columbia (Layberry et al. 1998). Flight period is from June to September.

Larval host plants. *Viola adunca*, *V. glabella*, *V. nuttallii*, *V. orbiculata*, *V. purpurea*, *V. sheltonii* (Scott 1986b, Robinson et al. 2002).

Adult food resources. Pussypaws, asters, thistles, mints (Pyle 1995, Opler and Wright 1999); also often scat/feces (Cliff Ferris, pers. comm.).

***Speyeria mormonia* (Boisduval, 1869)**

(Figure 5E, 48)

Argynnis Mormonia Boisduval, 1869: 58.

Speyeria mormonia (Boisduval) [dos Passos and Grey 1945a].

Common names. Mormon fritillary, mormonia fritillary, mountain fritillary.

Type deposited. Lectotype (male) designated by dos Passos and Grey (1947) at National Museum of Natural History (Figure 48).

Type locality. Oregon. Defined by dos Passos and Grey (1947) as Salt Lake City, Salt Lake County, Utah. However, Grey (1974, 1989) discussed the possibility that fixation of the type locality as “Salt Lake” was a mistake and speculated the type specimen may have been taken from somewhere in California. However, he felt it would be hard to prove given the subtle nuances in wing pattern and coloration of *Speyeria* and also felt no present concepts are disturbed if the locality remains as defined. Miller and Brown (1981) later defined the type locality to the vicinity of Pyramid Lake, Nevada. Emmel et al. (1998a) further defined the type locality to Little Valley, W. of Washoe Lake, Washoe County, Nevada.

Type label data. “Mormonia Bd. Lac Sal; EX MUSAEO Dris. BOISDUVAL; Argynnis Mormonia [male] Bdv. ex typ. sp.; Oberthur Collection; Barnes Collection”.

Identification, taxonomy, and variation. There are approximately 10 described subspecies in the mormonia complex. *Speyeria mormonia* can be identified by the smaller size (wingspan 38-60 mm) compared to other *Speyeria*; on average it is the smallest species in the genus. The antennal clubs are relatively expanded compared to other *Speyeria* species. Penz and Peggie (2003) reported that female *S. mormonia* had an accessory bursal sac, but this has not been reported previously nor observed in recent dissections I have made. The forewings are short and rounded and there is usually some basal darkening. The dorsal wing surface does not have black scaling on veins but does have a complex pattern of black spots, bars, and chevrons with a black border. The ventral surface of the hindwing disc is pale yellow to pale brown, occasionally greenish in hue (in the Cascades of Washington), but otherwise similar in color to ventral forewing. Black Hills, South Dakota populations have a dark brown disc. The silvering of the ventral hindwing spots is variable within and among populations (spots are partially silvered in the California Sierra Nevada Mountains or primarily yellow in the Great Basin), and spots tend to be smaller than on most *Speyeria*. Populations occur in northern Nevada and southeastern Oregon where individuals are unsilvered ventrally with a yellow ground color and little pattern. A subspecies isolated in the White Mountains of Arizona, *S. mormonia luski* (Barnes and McDunnough), is unlike other *S. mormonia* in appearance and bears white, ‘unsilvered’ hindwing spots rather than the usual ‘unsilvered’ condition of *S. mormonia* forms that have spots filled with brown. Eggs are small and tan-colored (may be yellowish when oviposited and become purplish-tan later). Larvae are brown to gray, or yellowish to orange with black spots and lines. Spines are short and paler at the base. Larval coloration is likely variable throughout the range of *S. mormonia* due to local climatic conditions. See Grey (1974) for discussion on *S. mormonia* subspecies concepts.

Range. *Speyeria mormonia* occurs along the mountainous regions of western North America, from south-central Alaska south to central California in the Sierras, east-central Arizona, north-central New Mexico, extending east to southwestern Manitoba and the Dakotas. It occurs at higher elevations and further

north than most other *Speyeria* (Opler and Wright 1999; also see Eriksen 1962, Koziol 1994). It occurs at sea level in Alaska, the sagelands of the Great Basin, and the plains of the Black Hills.

Life history. Known to occur in mostly subalpine habitat, including Canadian to lower Alpine Zone meadows, moist prairie valleys/meadows, and openings in subarctic forests. *Speyeria mormonia* is the most likely member of *Speyeria* to occur in high mountain habitats. Males patrol all day just above the ground in open vegetated areas and in meadows at lower elevations (Scott 1975). Females lay eggs singly and haphazardly near host plants. Unfed first instar larvae hibernate. Flight period is mid July through October in the southern part of its range, July through August in the northern part. Adults can fly great distances, especially females, and can stray into foothills or the Colorado plains. Boggs (1986, 1987a,b, 1988, 1997a,b), Boggs and Jackson (1991), and Boggs and Ross (1993) provide numerous studies on the ecology of *S. mormonia*. Boggs and Murphy (1997) discussed how climate change might affect *S. mormonia* individuals by reducing available nectar sources, with consequent effects on individual reproduction and survival. Montane species such as *S. mormonia* may be negatively affected by long-term climate warming trends.

Larval host plants. *Viola nuttallii*, *V. palustris*, *V. adunca*, *V. adunca* variation *bellidifolia*, *V. sororia* (Scott 1986b; Robinson et al. 2002).

Adult food resources. Sagebrush, rabbitbrush, mud (Scott 1986b; Pyle 1995), alpine fleabanes and other composites (T. C. Emmel in litt.).

Discussion

Primary type specimens for *Speyeria* and the atlantis and hesperis species complexes appear together in color here for the first time. This is of importance for future taxonomic/systematic studies because many museums are limited in curatorial personnel and access to major Lepidoptera collections is becoming more restricted. In addition, the availability of type images reduces the possibility of accidental damage to these taxonomically important specimens. Nomenclatural errors were also identified after a review of the extensive literature associated with *Speyeria*. The description of *S. hesperis greyi* Moeck (1950) had been listed as described within *Argynnis*. This was perpetuated in the literature for some time and is clarified in Dunford and Austin (2007) and here. North American greater fritillaries were considered generically distinct from *Argynnis* Fabricius, 1807 as *Speyeria* Scudder, 1872 by dos Passos and Grey (1945a); all taxa named since that time have been described within the latter genus. Nonetheless, *Argynnis* was retained in some popular guides and other literature (e.g., Garth 1950; Garth and Tilden 1963; Hovanitz 1962, 1963; Sette 1962). McHenry (1964, see also McHenry 1963) attempted to resurrect the use of *Argynnis*, but this has not been followed in North America. McHenry (1964) may well have misled compilers of later checklists (i.e., Miller and Brown 1981; Hodges 1983) by implicating that *S. atlantis greyi* was named within *Argynnis*. Several subsequent authors then followed this treatment.

Additional discrepancies in the literature, necessary corrections, and current taxonomies were also identified and discussed herein. The sex of the lectotype specimen for *S. egleis*, as indicated in dos Passos and Grey (1947), is that of a male. A specimen bearing the same label was reported as female by Emmel et al. (1998a), and was verified as such following personal examination of the purported type specimen herein. Penz and Peggie (2003) reported that female *S. mormonia* had an accessory bursal sac, and this may have simply been erroneously recorded in the appendix of character states. A secondary or accessory bursal sac is a key character in separating members of the Semnopsyche-Idalia group from other *Speyeria*. One fairly recently described taxon, *S. atlantis hansenii* (Emmel et al. 1998c), should now be considered *S. hesperis hansenii* based on Scott et al. (1998); all California taxa formerly considered 'atlantis' should receive this treatment based on the wing characteristics described by Scott et al. (1998). The location of the type specimen for *S. hesperis cottlei* is apparently unknown. This species was recently raised from synonymy (Emmel et al. 1998c) and a neotype specimen may need to be designated.

Much of the speciation/subspeciation within *Speyeria*, as we know it today, probably came about in the past ten thousand years as a consequence of the last glacial retreat and the climatic readjustments in its wake (Grey 1951; Hammond 1990). Glacial movements had a major effect on many taxa as species'

distributions shifted in response to climatic fluctuations (Wells 1983; Haslett 1997a,b; Parmesan et al. 1999; Knowles 2001). Pleistocene glaciations likely promoted speciation in groups such as *Speyeria* because divergence among allopatric glacial refugia or founder events during recolonization of previously glaciated areas would have promoted differentiation (Hammond 1990). Climatological events, especially in western North America, have resulted in numerous montane “island” butterfly populations (Howe 1975; Johnson 1975; Boggs and Murphy 1997; Fleishman et al. 2001a). Varying degrees of isolation via geographical and glacial histories, dispersal and occasional contact of disjunct populations likely provide developmental processes that produce gradients, thresholds, and pattern changes in *Speyeria* (Grey 1951; Moeck 1957; Howe 1975; Hammond 1990), and ultimately the many ‘forms’ or ‘subspecies’ in complexes such as *S. atlantis* and *S. hesperis*. The evolutionary history and status of *S. atlantis*, ‘*S. electa*’, and *S. hesperis* is in need of detailed examination in order to further stabilize the nomenclature associated with these complexes.

Species and subspecies delimitation remains problematic for many taxa within *Speyeria*, and determinations are often affixed by locality. It may be easier for most to identify *Speyeria* spp. in a given area rather than find characters that work in all regions, and a few works have provided such comparisons (Emmel et al. 1992; Warren 1998; Pyle 2002; Rolfs 2005; Glassberg 2008). To that end, Lepidoptera taxa, in particular butterflies, are often elevated to species rank on the basis of few or slight morphological differences, often without additional, significant character support. It is imperative that informative characters are chosen while attempting to avoid characters subject to environmental influences such as wing coloration and other aberrations.

Further investigation into use of wing facies to delimit *Speyeria* taxa is needed, especially with regard to the subspecies level. There may be useful morphological and behavioral characters that have been overlooked in favor of the traditional use of wing patterns and colors in species and subspecies descriptions. It is hoped that this review will provide a foundation to investigate those possibilities. While there has been some dispute as to the true evolutionary relationship of *Speyeria* to the primarily Palearctic *Argynnis* for some time (Hovanitz 1962, McHenry 1963; Hammond 1978; Simonsen et al. 2006), recent cladistic works (Simonsen 2006a,c; Simonsen et al. 2006) have only used members of the genitally distinct *Semnopsyche/Idalia* group in those analyses; thus, they may not accurately represent ‘*Speyeria*’ as a whole. Pilot studies indicate that the omission and/or addition of pertinent argynnine taxa in phylogenetic analyses change tree topologies, favoring the inclusion or exclusion of *Speyeria* within *Argynnis* (Dunford 2007). Moreover, preliminary molecular data for *S. idalia* has shown the percent divergence of COI from the remainder of ‘*Speyeria*’ is nearly as high as it is when compared to other related genera (i.e., *Argynnis*, *Boloria*), suggesting that reexamination of the status of *S. idalia* (the generotype) and *Semnopsyche* with the remainder of ‘*Speyeria*’ is warranted (Dunford in prep). A suite of informative and environmentally stable characters, including the external morphologies of adults and immature stages, genitalia, DNA sequences from multiple gene regions, and life history traits for all members of the Argynnini (from multiple ‘subspecies’ populations) is and will continually be needed for understanding the evolutionary history of *Speyeria* and related taxa. Additional morphological and molecular analyses for *Speyeria* and related taxa, based in part on Dunford (2007), are forthcoming.

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Figure 6-10. Type images for *Speyeria* spp.; dorsal, ventral, and label images. **6)** *Speyeria idalia* neotype, described as *Papilio Nymphalis Phaleratus Idalia*, male, AMNH. **7)** *Speyeria diana* holotype, described as *Papilio Nymphalis Phaleratus Diana*, male, BMNH. **8)** *Speyeria cybele* neotype, described as *Papilio Nymphalis Phaleratus Cybele*, female, BMNH. **9)** *Speyeria aphrodite* neotype, described as *Papilio Nymphalis Phaleratus Aphrodite*, male, AMNH. **10)** *Speyeria nokomis* neotype, described as *Argynnis Nokomis*, male, AMNH. Images 6 and 9-10 by James C. Dunford; 7-8 by Kim Goodger Buckmaster.



Figure 11-15. Type images for *Speyeria* spp.; dorsal, ventral, and label images. 11) *Speyeria nokomis* lectotype, described as *Argynnis Nokomis*, male, AMNH. This specimen is not recognized as the name bearing type. 12) *Speyeria edwardsii* lectotype, described as *Argynnis edwardsii*, male, FMNH. 13) *Speyeria coronis* neotype, described as *Argynnis Coronis*, male, CMNH. 14) *Speyeria zerene* lectotype, described as *Argynnis Zerene*, male, NMNH. 15) *Speyeria carolae* holotype, described as *Argynnis coronis carolae*, male, CMNH. Images 11-13 and 15 by James C. Dunford; 14 by Robert Robbins.



Figure 16-20. Type images for *Speyeria* spp.; dorsal, ventral, and label images. **16)** *Speyeria callippe* lectotype, described as *Argynnis callippe*, male, NMNH. **17)** *Speyeria egleis* neotype, described as *Argynnis egleis*, female, NMNH. **18)** *Speyeria adiante* lectotype, described as *Argynnis Adiante*, female, NMNH. This specimen is not recognized as the name bearing type. **19)** *Speyeria adiante* lectotype, described as *Argynnis Adiante*, male, CMNH. **20)** *Speyeria atlantis atlantis* lectotype, described as *Argynnis Atlantis*, male, CMNH. Images 16-18 by Robert Robbins; 19-20 by James C. Dunford.



Figure 21-25. Type images for *Speyeria* spp.; dorsal, ventral, and label images. **21)** *Speyeria atlantis canadensis* lectotype, described as *Argynnis atlantis canadensis*, male, AMNH. Now synonymized under *Speyeria atlantis* (Scott et al. 1998). **22)** *Speyeria atlantis hollandi* holotype, described as *Argynnis atlantis Hollandi*, male, CNIC. **23)** *Speyeria atlantis sorocko* holotype, described as *Speyeria atlantis sorocko*, male, AMNH. **24)** *Speyeria atlantis pahasapa* holotype, described as *Speyeria atlantis pahasapa*, male, AMNH. **25)** *Speyeria hesperis* neotype, described as *Argynnis Hesperis*, male, CMNH. Images 21 and 23-25 by James C. Dunford; 22 by Norbert Kondla.

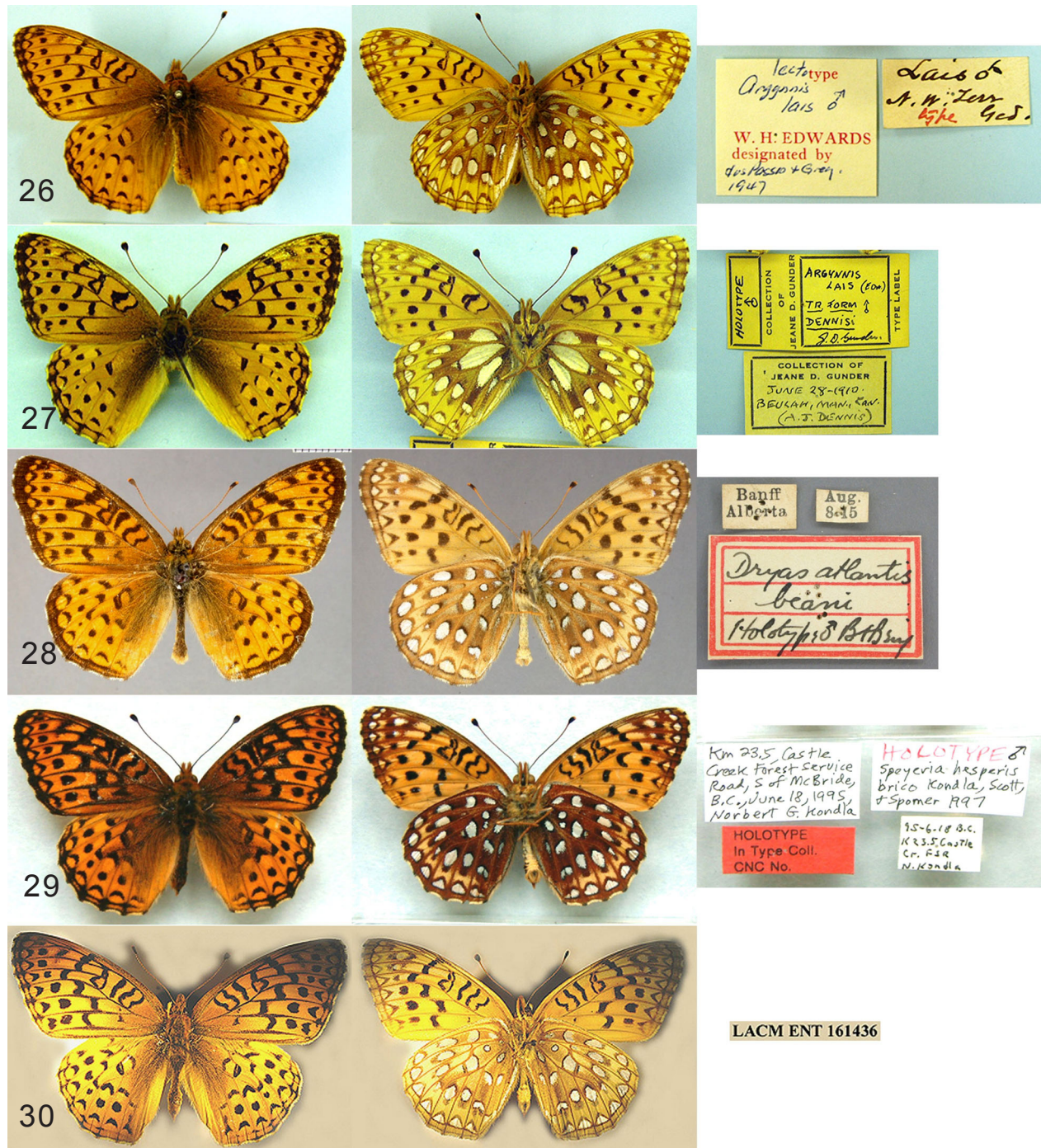


Figure 26-30. Type images for *Speyeria* spp.; dorsal, ventral, and label images. **26)** *Speyeria hesperis helena* lectotype, described as *Argynnis lais*, male, CMNH. **27)** *Speyeria atlantis dennisi* holotype, described as *Argynnis lais* form *dennisi*, male, AMNH. Now synonymized under *Speyeria hesperis helena* (Scott et al. 1998). **28)** *Speyeria hesperis beani* holotype, described as *Dryas atlantis beani*, male, NMNH. **29)** *Speyeria hesperis brico* holotype, described as *Speyeria hesperis brico*, male, CNIC. **30)** *Speyeria hesperis ratonensis* holotype, described as *Speyeria atlantis ratonensis*, male, LACM. Images 26-27 by James C. Dunford; 28 by Robert Robbins; 29 by Norbert Kondla; 30 by Weiping Xie.

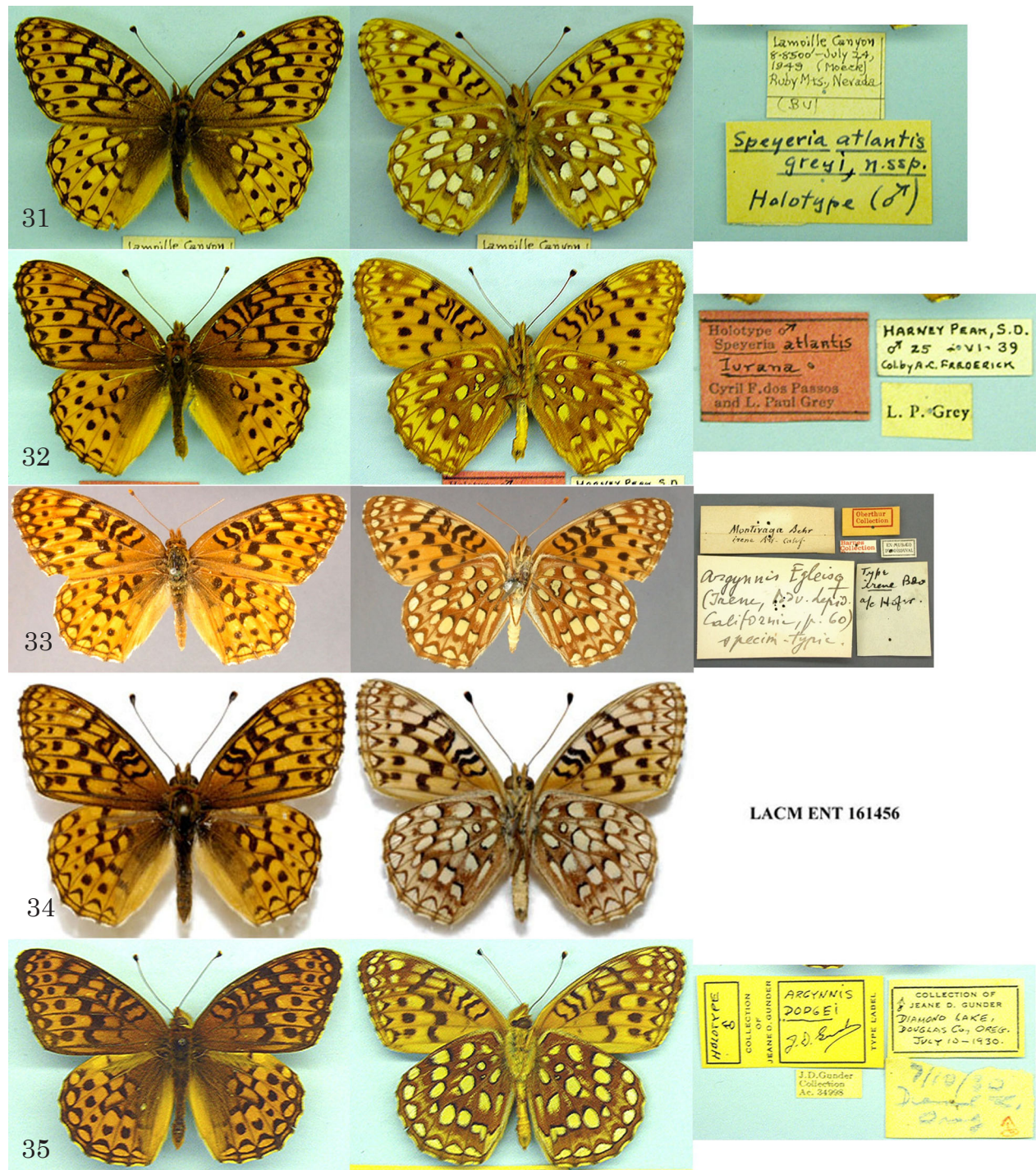


Figure 31-35. Type images for *Speyeria* spp.; dorsal, ventral, and label images. **31)** *Speyeria hesperis greyi* holotype, described as *Speyeria atlantis greyi*, male, AMNH. **32)** *Speyeria hesperis lurana* holotype, described as *Speyeria atlantis lurana*, male, AMNH. **33)** *Speyeria hesperis irene* lectotype, described as *Argynnis irene*, female, NMNH. **34)** *Speyeria hesperis hanseni* holotype, described as *Speyeria atlantis hanseni*, male, LACM. **35)** *Speyeria hesperis dodgei* holotype, described as *Argynnis dodgei*, male, AMNH. Images 31-32 and 35 by James C. Dunford; 33 by Robert Robbins; 34 by Weiping Xie.



Figure 36-40. Type images for *Speyeria* spp.; dorsal, ventral, and label images. **36)** *Speyeria hesperis viola* holotype, described as *Speyeria atlantis viola*, male, AMNH. **37)** *Speyeria hesperis elko* holotype, described as *Speyeria atlantis elko*, male, NVMC. **38)** *Speyeria hesperis tetonia* holotype, described as *Speyeria atlantis tetonia*, male, AMNH. **39)** *Speyeria hesperis wasatchia* holotype, described as *Speyeria atlantis wasatchia*, male, AMNH. **40)** *Speyeria hesperis chitone* lectotype, described as *Argynnis chitone*, male, CMNH. Images 36 and 38-40 by James C. Dunford; 37 by George Baumgartner and Scott Klette.



Figure 41-45. Type images for *Speyeria* spp.; dorsal, ventral, and label images. 41) *Speyeria hesperis electa* lectotype, described as *Argynnis Electa*, male, CMNH. 42) *Speyeria hesperis nikias* lectotype, described as *Argynnis nikias*, male, CMNH. Now synonymized under *Speyeria hesperis electa* (Scott et al. 1998). 43) *Speyeria hesperis schellbachi* holotype, described as *Speyeria atlantis schellbachi*, male, LACM. 44) *Speyeria hesperis nausicaa* lectotype, described as *Argynnis Nausicaa*, male, CMNH. 45) *Speyeria hesperis dorothea* holotype, described as *Speyeria atlantis dorothea*, male, AMNH. Images 41-42 and 44-45 by James C. Dunford; 43 by Weiping Xie.



Figure 46-48. Type images for *Speyeria* spp.; dorsal, ventral, and label images. **46)** *Speyeria hesperis capitanensis* holotype, described as *Speyeria atlantis capitanensis*, male, AMNH. **47)** *Speyeria hydaspae* lectotype, described as *Argynnis Hydaspae*, male, NMNH. **48)** *Speyeria mormonia* lectotype, described as *Argynnis Mormonia*, male, NMNH. Image 46 by James C. Dunford; 47-48 by Robert Robbins.



Figure 49-52. Habitat pictures by James C. Dunford. **49)** Lamoille Canyon, Ruby Mountains, Nevada. **50)** Hospital Flat, near Mt. Graham, Pinaleno Mountains, Arizona. **51)** Open glade in Sandia Mountains, New Mexico. **52)** Roadside flowers, Capitan Mountains, New Mexico.