

THE GENUS *SPEYERIA* AND THE *Speyeria atlantis*/*Speyeria hesperis* COMPLEX: SPECIES  
AND SUBSPECIES ACCOUNTS, SYSTEMATICS, AND BIOGEOGRAPHY  
(LEPIDOPTERA: NYMPHALIDAE)

By

JAMES CHRISTOPHER DUNFORD

A DISSERTATION PRESENTED TO THE GRADUATE SCHOOL  
OF THE UNIVERSITY OF FLORIDA IN PARTIAL FULFILLMENT  
OF THE REQUIREMENTS FOR THE DEGREE OF  
DOCTOR OF PHILOSOPHY

UNIVERSITY OF FLORIDA

2007

© 2007 James Christopher Dunford

To my family, James F. Dunford, Karen and Lee Schwind, and Kim Dunford, as well as my extended family, Robert Sr., Mary Jane, Robert Jr., Michael, Scott, Jeff and Mark Zukowski, and George and Rena Dunford, and Carole Parshall; and finally my life long friends, Mitch Adams, Scott Brady, Stuart Iselin, John Kropp, Walter Schultz, and Greg Smith, who stood by my side as I pursued my entomological studies. Without their support (and patience), this would not have been possible. Good scientists surround themselves with great ones, and without the help of the superb biologists that I have had the great pleasure to work with along the way, I would not have attained some of my goals in life.

## ACKNOWLEDGMENTS

I would like to thank my co-chairs Lee D. Miller and Jacqueline Y. Miller (Florida Museum of Natural History, McGuire Center for Lepidoptera and Biodiversity [MGCL]). Their guidance, advice, patience and most of all friendship have made this research possible. I would also like to thank my remaining committee members Thomas C. Emmel (MGCL), Paul Z. Goldstein (MGCL), John B. Heppner (Florida State Collection of Arthropods [FSCA]), James E. Maruniak (University of Florida, Entomology and Nematology Department [UF-Ent. & Nem. Dept.]), Carla M. Penz (University of New Orleans, Biology Department), and Jon Reiskind (University of Florida, Zoology Department), for providing their time, expertise, and support in the form of recommendation letters and encouragement. Most of this research would not have been possible without them. I truly admire the great amount of knowledge my collective committee has provided to the scientific community, and I hope to someday be as established and prominent as they are.

A very special thanks goes to the institutions, professional societies, and government agencies who provided financial support for this research; they are: American Museum of Natural History [AMNH] (Theodore Roosevelt Memorial Grant), Florida Entomological Society (mini-grants and scholarships), Florida Museum of Natural History and Paul Goldstein (research assistantship), United States Navy (Health Services Collegiate Scholarship Program), UF-Ent. & Nem. Dept. (teaching assistantship), and University of Florida Jack L. Fry Award (teaching scholarship).

Numerous individuals from around the country and the world provided specimens, images, specimen locality data, supervision in collections under their care, access to literature in libraries, and their expertise on topics covered in this project. I am extremely grateful for the time they spent helping this dissertation come to fruition and I sincerely hope I do not forget to

acknowledge anyone who contributed: Thomas Allen (West Virginia), George Austin (Nevada State Museum [NSM], MGCL), George Baumgartner (NSM), Barbara Beck (University of Alberta), Jim Beck (Alberta), James Boone (Field Museum of Natural History), Su Borkin (Milwaukee Public Museum [MPM]), Brett Boyd (MGCL), Bruce Boyd (Nevada), Craig Brabant (University of Wisconsin-Madison, Department of Entomology [UWM-Dept. Ent.]), Colin Brammer (Utah State University Insect Collection [EMUS]), Brian Brown (Natural History Museum of Los Angeles County [LACM]), Jon Bremmer (MGCL), Kim Goodger Buckmaster (British Museum of Natural History [BMNH; now NHM]), Shawn Clark (Monte L. Bean Museum of Life Science-Brigham Young University), Robert Ekin (Idaho), Clifford Ferris (Wyoming), Mike Fisher (Colorado), Daniel Glaeske (Saskatchewan), Traci Grzymala (MGCL volunteer), Crispin Guppy (British Columbia), Wilford Hanson (EMUS), Richard Holland (New Mexico), Martin Honey (BMNH; now NHM), William Houtz (Pennsylvania), Seungjin Jang (MGCL volunteer), Joan Jass (MPM), Ted Kirkpatrick (West Virginia), Scott Klette (NSM), Norbert Kondla (British Columbia), Hugo Kons, Jr. (American Entomological Institute), James Kruse (University of Alaska-Museum of the North), Robert Lasley (MGCL), Ross Layberry (Ontario), Deborah Matthews Lott (MGCL Research Associate), Heather Manley (MGCL), Gary Marrone (South Dakota), Daniel Marschalek (UWM-Dept. Ent.), Sterling Mattoon (California), Don Miller (Vermont), Paul Opler (C. P. Gillette Museum of Arthropod Biodiversity, Colorado State University), Kenelm Philip (Alaska), Ted Pike (Alberta), Beverly Pope (Florida Department of Agriculture and Consumer Services, Department of Plant Industry Library [FDACS, DPI Library]), Eric Quinter (AMNH), John Rawlins (Carnegie Museum of Natural History), Jim Reynolds (BMNH; now NHM), Robert Robbins (National Museum of Natural History), Don Rolfs (Washington), Richard Romeyn (Wisconsin), Gary Ross (Louisiana),

Ronald Royer (Minot State University), Alice Sanders (FDACS, DPI Library), Dennis Schlicht (Iowa), James Scott (Colorado), Scott Shaw (University of Wyoming Insect Museum), Jon Shepard (Washington), Thomas Simonsen (University of Copenhagen, University of Alberta), Steven Sims (Missouri), Charlie Slater (Colorado), Steve Spomer (University of Nebraska, Department of Entomology), Ray Stanford (Colorado), David Wagner (University of Connecticut), Andrew Warren (Oregon State University, Department of Entomology and FLMNH), Andrew Williams (UWM-Dept. Ent.), Barry Williams (University of Illinois, Department of Animal Biology, University of Wisconsin, Madison Howard Hughes Medical Institute), and Weiping Xie (LACM). I would also like to thank Alex Borisenko, Robert Hanner, Evgeny Zakharov (Canadian Barcode of Life Network, University of Guelph), and Kevin Nixon (Diversity of Life, Cornell University) for providing workspace on their web sites and assistance with molecular analyses and distributional databasing respectively; their web sites are invaluable tools for modern taxonomic and systematic research and dissemination of these kinds of data.

I am forever indebted to several people who not only provided specimens, images, and distributional information, but also took the time to entertain and guide me to collecting sites in various regions of the western U.S. Paul Opler and Evi Buckner-Opler allowed me to stay in their home while collecting in Colorado. Paul kindly invited me on the 2003 Gilpin Co. Butterfly Count and took me to several collecting sites in the *Speyeria*-rich Rocky Mountains. Don Rolfs took care of me at his home in Washington and showed me a thing or two about hiking in the Cascades, which were at much higher elevation than my home in Florida. Bob Ekin taught me how to catch fritillaries throughout the western U.S. with a net in one hand and a beverage in the other, and Bob Martin took me deep into the Scapegoat Wilderness in Montana and instructed

me on how to deal with grizzly bears. Cliff Ferris graciously allowed me to visit his home in Laramie, Wyoming to examine his extensive *Speyeria* collection.

Several faculty, students, and staff in the UF-Ent. & Nem. Dept and FLMNH, McGuire Center were invaluable informational resources and were always willing to help with my various teaching and research endeavors, projects and administrative issues over the years. First and foremost, I would like to thank George Austin at the MGCL. He was not only a source for important references, but he was also an inspiration to me professionally and personally. I also thank the following individuals for making research at UF a rewarding and fulfilling experience: Kathryn Barbara, Marc Branham, Eileen Buss, Lyle Buss, Jerry Butler, Seth Bybee, John Capinera, Paul Choate, Pete Coon, James Cuda, Jaret Daniels, Aissa Doumbouya, Christine Eliazar, Thomas Fasulo, John Foltz, Howard Frank, Judy Gillmore, Debbie Hall, Donald Hall, Sharon Hoopaugh, Nick Hostettler, Pam Howell, Philip Kaufman, Steve Lasley, John Leavengood, Norman Leppla, James Lloyd, Ale Maruniak, Raquel McTiernan, Jane Medley, Jason Meyers, Jennifer Meyers, Eugenio Nearn, J. Akers Pence, Leslie Rios, Emily Saarinen, Nancy Sanders, Mike Sanford, Kelly Sims, Grover Smart, Andrei Sourakov, Ricardo Vazquez, and Jennifer Zaspel.

Finally, I thank close family and friends: Kim Dunford, James F. Dunford, Karen and Lee Schwind, Bob, Jeff, Mark, Midge and Scott Zukowski, Mitch Adams, Scott Brady, Stuart Iselin, Brett Favre, John Kropp, and Greg Smith. A little insanity can go along way, especially when your interest in an odd topic such as entomology becomes a career. Thanks for rooting for me, and most of all, treating me like a normal human being.

# TABLE OF CONTENTS

	<u>page</u>
ACKNOWLEDGMENTS .....	4
LIST OF TABLES .....	11
LIST OF FIGURES.....	12
ABSTRACT.....	17
CHAPTER	
1 INTRODUCTION AND LITERATURE REVIEW: RESEARCH BACKGROUND, JUSTIFICATION, OBJECTIVES, AND HYPOTHESES .....	19
<i>Speyeria</i> Butterflies: Introduction and Literature Review .....	19
Overview and Taxonomic History .....	19
Life History .....	27
Research Background and Justification.....	36
Taxonomy and Systematics .....	36
Conservation.....	42
Subspecies and Species Criteria .....	44
Objectives and Hypotheses.....	49
Objectives .....	49
Central and Peripheral Hypotheses .....	50
2 <i>SPEYERIA</i> DIAGNOSIS AND KEY TO SPECIES, SPECIES ACCOUNTS, AND <i>SPEYERIA ATLANTIS</i> AND <i>SPEYERIA HESPERIS</i> SUBSPECIES ACCOUNTS.....	51
Materials and Methods .....	52
<i>Speyeria</i> Diagnosis .....	55
Key to the Species of <i>Speyeria</i> .....	59
Species Accounts .....	61
<i>Speyeria idalia</i> .....	61
<i>Speyeria diana</i> .....	63
<i>Speyeria cybele</i> .....	65
<i>Speyeria aphrodite</i> .....	66
<i>Speyeria nokomis</i> .....	67
<i>Speyeria edwardsii</i> .....	69
<i>Speyeria coronis</i> .....	70
<i>Speyeria zerene</i> .....	71
<i>Speyeria carolae</i> .....	73
<i>Speyeria callippe</i> .....	74
<i>Speyeria egleis</i> .....	75
<i>Speyeria adiaste</i> .....	76
<i>Speyeria atlantis</i> .....	77



<i>Speyeria hesperis</i> .....	79
<i>Speyeria hydaspe</i> .....	80
<i>Speyeria mormonia</i> .....	81
<i>Speyeria atlantis</i> and <i>Speyeria hesperis</i> Subspecies Accounts .....	82
<i>Speyeria atlantis atlantis</i> .....	82
<i>Speyeria atlantis hollandi</i> .....	83
<i>Speyeria atlantis sorocko</i> .....	83
<i>Speyeria atlantis pahasapa</i> .....	84
<i>Speyeria hesperis hesperis</i> .....	84
<i>Speyeria hesperis helena</i> .....	84
<i>Speyeria hesperis beani</i> .....	85
<i>Speyeria hesperis brico</i> .....	85
<i>Speyeria hesperis ratonensis</i> .....	86
<i>Speyeria hesperis greyi</i> .....	86
<i>Speyeria hesperis lurana</i> .....	87
<i>Speyeria hesperis irene</i> .....	87
<i>Speyeria hesperis cottlei</i> .....	88
<i>Speyeria hesperis hanseni</i> .....	89
<i>Speyeria hesperis dodgei</i> .....	89
<i>Speyeria hesperis viola</i> .....	90
<i>Speyeria hesperis elko</i> .....	90
<i>Speyeria hesperis tetonia</i> .....	91
<i>Speyeria hesperis wasatchia</i> .....	91
<i>Speyeria hesperis chitone</i> .....	92
<i>Speyeria hesperis electa</i> .....	92
<i>Speyeria hesperis schellbachii</i> .....	93
<i>Speyeria hesperis dorothea</i> .....	93
<i>Speyeria hesperis nausicaa</i> .....	94
<i>Speyeria hesperis capitanensis</i> .....	94
 3 PHYLOGENY OF <i>SPEYERIA</i> .....	 130
Materials and Methods .....	137
Taxon Sampling .....	139
Character Sampling .....	139
Phylogenetic Analyses .....	139
Results and Discussion .....	140
 4 BIOGEOGRAPHY AND GENITALIC SURVEY OF <i>SPEYERIA</i> WITH EMPHASIS ON OVERLAPPING <i>SPEYERIA ATLANTIS</i> AND <i>SPEYERIA HESPERIS</i> POPULATIONS .....	     164
Materials and Methods .....	170
Taxon Sampling .....	170
Preparation of Material .....	171
Databasing .....	172
Results and Discussion .....	173

5 SUMMARY AND CONCLUSIONS .....	195
APPENDIX.....	201
COI SEQUENCES FOR 16 SPECIES OF <i>SPEYERIA</i> .....	201
LIST OF REFERENCES.....	206
BIOGRAPHICAL SKETCH .....	245

## LIST OF TABLES

<u>Table</u>	<u>page</u>
2-1. Checklist of <i>Speyeria</i> species and subspecies treated herein .....	96
2-2. List of museum abbreviations.....	97
3-1. List of taxa included in the primary analyses .....	148
3-2. Synopsis of characters and states used for phylogenetic analyses. ....	149
3-3. Data matrix for characters. ....	150
4-1. <i>Speyeria atlantis</i> and <i>Speyeria hesperis</i> subspecies and associated ventral.....	
hindwing characters .....	181
4-2. Species and subspecies examined and descriptions of male genitalic armature. ....	182

## LIST OF FIGURES

<u>Figure</u>	<u>page</u>
2-1. Original description for ‘ <i>Idalia</i> ’ ..	98
2-2. Wing terminology associated with species of <i>Speyeria</i> . ..	99
2-3. Wing venation and cell scheme. ....	99
2-4. Images of adult <i>Speyeria diana</i> ..	100
2-5. Type images for <i>Speyeria diana</i> . ....	100
2-6. Type images for <i>Speyeria cybele</i> . ....	101
2-7. Type images for <i>Speyeria aphrodite</i> .....	101
2-8. Images of <i>Speyeria idalia</i> life stages .....	102
2-9. Type images for <i>Speyeria idalia</i> . ....	102
2-10. Male genitalic armature, <i>Speyeria idalia</i> . ....	103
2-11. Type images for <i>Speyeria nokomis</i> . ....	103
2-12. Type images for <i>Speyeria nokomis</i> . ....	104
2-13. Type images for <i>Speyeria edwardsii</i> .....	104
2-14. Digitus located on left valva, <i>Speyeria edwardsii</i> .....	105
2-15. Type images for <i>Speyeria coronis</i> .....	105
2-16. Habitus image of <i>Speyeria zerene</i> ( <i>gunderi</i> ) .....	106
2-17. Type images for <i>Speyeria zerene</i> . ....	106
2-18. Type images for <i>Speyeria carolae</i> . ....	107
2-19. <i>Speyeria callippe</i> ( <i>harmonia</i> ) .....	107
2-20. Type images for <i>Speyeria callippe</i> . ....	108
2-21. Type images for <i>Speyeria egleis</i> . ....	109
2-22. Type images for <i>Speyeria adiaeste</i> .....	110
2-23. Type images for <i>Speyeria adiaeste</i> .....	110

2-24. Type images for <i>Speyeria atlantis</i> .....	111
2-25. Type images for <i>Speyeria hesperis</i> .....	111
2-26. Type images for <i>Speyeria hydaspe</i> .....	112
2-27. Habitus image of <i>Speyeria mormonia (artonis)</i> .....	112
2-28. Type images for <i>Speyeria mormonia</i> .....	113
2-29. Type images for <i>Speyeria atlantis canadensis</i> .....	114
2-30. Type images for <i>Speyeria atlantis hollandi</i> .....	114
2-31. Type images for <i>Speyeria atlantis sorocko</i> .....	115
2-32. Type images for <i>Speyeria atlantis pahasapa</i> .....	115
2-33. Type images for <i>Speyeria hesperis helena</i> .....	116
2-34. Type images for <i>Speyeria atlantis dennisi</i> .....	116
2-35. Type images for <i>Speyeria hesperis beani</i> .....	117
2-36. Types images for <i>Speyeria hesperis brico</i> .....	117
2-37. Holotype of <i>Speyeria hesperis ratonensis</i> .....	118
2-38. Type images for <i>Speyeria hesperis greyi</i> .....	118
2-39. Type images for <i>Speyeria hesperis lurana</i> .....	119
2-40. Type images for <i>Speyeria hesperis irene</i> .....	119
2-41. Holotype of <i>Speyeria hesperis hanseni</i> .....	120
2-42. Type images for <i>Speyeria hesperis dodgei</i> .....	121
2-43. Type images for <i>Speyeria hesperis viola</i> .....	121
2-44. Type images for <i>Speyeria hesperis elko</i> .....	122
2-45. Type images for <i>Speyeria hesperis tetonia</i> .....	122
2-46. Type images for <i>Speyeria hesperis wasatchia</i> .....	123
2-47. Type images for <i>Speyeria hesperis chitone</i> .....	123
2-48. Type images for <i>Speyeria hesperis electa</i> .....	124

2-49. Type images for <i>Speyeria hesperis nikias</i> .....	124
2-50. Holotype of <i>Speyeria hesperis schellbachi</i> .....	125
2-51. Type images for <i>Speyeria hesperis dorothea</i> .....	125
2-52. Type images for <i>Speyeria hesperis nausicaa</i> .....	126
2-53. Type images for <i>Speyeria hesperis capitaneus</i> .....	126
2-54. Lamoille Canyon, Ruby Mountains, Nevada.. .....	127
2-55. Hospital Flats, near Mt. Graham, Pinaleño Mountains, Arizona. ....	127
2-56. View of Pinaleño Mountains in the morning.....	128
2-57. View of Pinaleño Mountains in the early afternoon.....	128
2-58. Open glade in Sandia Mountains, New Mexico. ....	129
3-1. Intuitive phylogeny of subtribe Argynnina .....	151
3-2. Intuitive phylogeny of <i>Speyeria</i> . ....	151
3-3. Dendrogram of genetic similarity between 10 <i>Speyeria</i> species.....	152
3-4. Phylogenetic interpretation of <i>Speyeria callippe</i> subspecies. ....	152
3-5. Strict consensus tree of Argynnini.....	153
3-6. Phylogeny of <i>Speyeria</i> based on 30 characters. ....	154
3-7. Phylogeny of <i>Speyeria</i> generated at Barcode of Life Data Systems .....	155
3-8. Phylogeny of <i>Speyeria</i> based on COI.....	156
3-9. Phylogram of <i>Speyeria</i> based on COI. ....	157
3-10. Phylogeny of <i>Speyeria</i> based on combined morphology and COI.....	158
3-11. Phylogram of <i>Speyeria</i> based on combined morphology and COI .....	159
3-12. Phylogeny of <i>Speyeria</i> and additional outgroup taxa based on COI.....	160
3-13. Phylogram of <i>Speyeria</i> and additional outgroup taxa based on COI. ....	161
3-14. Phylogeny of Argynnini .....	162
3-15. Phylogeny of <i>Argynnis</i> based on COI.....	163

4-1. Illustration and associated terminology of male genitalic armature of <i>Speyeria</i> .....	
<i>atlantis</i> .....	184
4-2. Male genitalic armature ( <i>Speyeria idalia</i> ) and associated terminology. ....	184
4-3. Distributional map of <i>Speyeria atlantis</i> and <i>Speyeria hesperis</i> subspecies.....	185
4-4. Distribution map for <i>Speyeria atlantis</i> in the northeastern United States .....	185
4-5. Distribution map for <i>Speyeria hesperis</i> (sample interactive aerial topo map generated..... at DiversityofLife.org). ....	186
4-6. Distribution map for <i>Speyeria atlantis-hesperis</i> subspecies.....	186
4-7. Ventral hindwing images of <i>Speyeria atlantis</i> and <i>Speyeria hesperis</i> subspecies .....	187
4-8. Examples of wing vouchers.....	187
4-9. Male genitalia of <i>Speyeria</i> .....	188
4-10. Male genitalia of <i>Speyeria</i> .....	188
4-12. Male genitalia of <i>Speyeria cybele</i> (Missouri).....	189
4-13. Male genitalia of <i>Speyeria atlantis</i> (West Virginia).....	189
4-14. Male genitalia of <i>Speyeria hesperis electa</i> (Wyoming). ....	189
4-15. Male genitalia of <i>Speyeria hesperis hesperis</i> (Wyoming).....	190
4-16. Male genitalic armature.....	190
4-17. Male genitalic armature.....	190
4-18. Male genitalic armature.....	191
4-19. Male genitalic armature.....	191
4-20. Male genitalic armature.....	191
4-21. Male genitalic armature.....	192
4-22. Male genitalic armature.....	192
4-23. Male genitalic armature.....	192
4-24. Image of bursa copulatrix.....	193

4-25. Male genitalia of <i>Speyeria</i> .....	193
4-26. Male genitalic armature.....	194
4-27. Images of adult <i>Speyeria</i> using ultraviolet light.....	194



Abstract of Dissertation Presented to the Graduate School  
of the University of Florida in Partial Fulfillment of the  
Requirements for the Degree of Doctor of Philosophy

THE GENUS *SPEYERIA* AND THE *Speyeria atlantis*/*Speyeria hesperis* COMPLEX: SPECIES  
AND SUBSPECIES ACCOUNTS, SYSTEMATICS, AND BIOGEOGRAPHY  
(LEPIDOPTERA: NYMPHALIDAE)

By

JAMES CHRISTOPHER DUNFORD

December 2007

Chair: Lee D. Miller

Cochair: Jacqueline Y. Miller

Major: Entomology and Nematology

*Speyeria* Scudder (1872) (Nymphalidae: Heliconiinae: Argynnini) are medium to large butterflies that represent conspicuous members of North American Lepidoptera. *Speyeria* is presently comprised of 16 species, and according to some authors, over 100 subspecies. Long included in the Old World genus *Argynnis*, they differ from their Eurasian relatives primarily in genitalic structure and were considered generically distinct from *Argynnis* in 1945. 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 wing pattern changes in *Speyeria*. The *Speyeria atlantis* and *Speyeria hesperis* species complexes are represented by several widely distributed, geographically variable subspecies. These subspecific taxa have distributions that range from the eastern United States and Canada, west to California, as far north as Alaska, and south to Arizona and New Mexico. Each subspecies occurs more or less sympatrically, either by latitude or elevation, with other members of the group, thus providing useful models for evolutionary studies.

Detailed species and subspecies diagnoses for 16 *Speyeria* species and 25 *Speyeria atlantis-hesperis* subspecies are compiled. Each diagnosis includes a synonymy, type specimen

data and image, taxonomic information and morphological descriptions, distributions, and life history information. Distributional data is gleaned from museum and private collection locality records and databased in order to understand the degree of sympatry of *Speyeria atlantis* and *S. hesperis* forms. Several errors in the nomenclature, type specimen data, and morphological descriptions for *Speyeria* are also identified.

Phylogenetic analyses are also conducted on the 16 currently recognized species of *Speyeria*. Investigation of useful external and internal morphological characters was made, including a survey of the genitalia of *Speyeria* with emphasis on the *Speyeria atlantis-hesperis* complex. Phylogenetic analyses are based on combined morphological, life history, and genetic data. The genus apparently represents a relatively recent radiation of species, with the only clear divergence being those members of the *Semnopsyche* ‘clade.’ Based on combined morphological and molecular analyses, *Speyeria* represent a monophyletic grouping. This work provides relevant insight into the inter- and intraspecific relationships and evolutionary history of *Speyeria*, and provides information pertinent to conservation strategies and priorities for this taxon.

## CHAPTER 1 INTRODUCTION AND LITERATURE REVIEW: RESEARCH BACKGROUND, JUSTIFICATION, OBJECTIVES, AND HYPOTHESES

### ***Speyeria* Butterflies: Introduction and Literature Review**

#### **Overview and Taxonomic History**

*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 butterflies 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 currently defined, 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 2006c). Until further data can be analyzed and convincingly corroborated with the recent findings of these phylogenetic studies, the name *Speyeria* will be retained herein.

*Speyeria* is presently comprised of 16 species (Opler and Warren 2005), 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* (W.H. 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* species 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.

Adults are more or less orange in color with darker wing veins and spots, often with silver or cream-white ventral hindwing spots. The silver spots owe their metallic appearance to refracted light rather than pigmentation (Scott 1988). Determinations are made primarily by utilizing 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 deceased individuals. 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.

*Speyeria* species have been collected and examined in great detail in the past and continue to be of major interest for 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. 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 (Holland 1898: 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). C. F. 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 have provided a foundation for subsequent studies on *Speyeria* and closely related groups (Grey 1964, 1970; Rindge 1987; Wilkinson 1988a, b). Studies conducted by Guppy (1953) and later by Grey et al. (1963) and Mattoon et al. (1971) 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 *Speyeria*.

Historically, three *Speyeria* species (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 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 definitively listed *Semnopsyche* as a junior synonym for *Speyeria*. Dos Passos and Grey (1947) prepared an extensive revision of the group in accordance with the latest concepts of speciation and systematics at that time and listed 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).

*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 Passos and Grey 1945a; Dornfeld 1980). They were considered generically distinct from *Argynnis* by dos Passos and Grey (1945a); 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 molecular evidence that suggests the remainder of *Argynnis* is paraphyletic if *Speyeria* is retained as a separate genus.

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*) utilizing 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*, but criticized the use of one set of characters, those of male genitalia. 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 heliconian 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 hostplant 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 (Brower 2000b; Wahlberg et al. 2003b; 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 utilizing modern systematic techniques. Based on adult and larval morphology utilizing phylogenetic analyses, Penz and Peggie (2003) suggested that Heliconiinae be divided into four groups, and included *Speyeria* within the Argynnini. Their study utilized *S. aphrodite* and *S. mormonia*, each representing hypothetically derived and basal *Speyeria* species, respectively. 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, however, the fairly recent morphological and molecular work of Brower (2000c) 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* Reuss [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).

Present day computer websites such as The Nymphalidae Systematics Group (date last accessed



Aug 2007) and Tree of Life Web Project (date last accessed Aug 2007) follow the taxonomic works of Simonsen et al. (2006) and utilize *Argynnis* when listing *Speyeria* species.

Much of the speciation and 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 have indisputably 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). Hammond (1990) noted that *Speyeria callippe* populations have evolved and spread by a peripheral budding process southward and eastward across much of western North America. Lowland deserts and high mountain ranges combined with Pleistocene climatic fluctuations have likely served as isolating barriers during this process. The creation of new, descendant populations *via* major ecological shifts into new environments have allowed for morphological changes in *S. callippe*.

*Speyeria* and their larval hostplants *Viola* L. (Violaceae) have proven to be vigorous colonizers of ash-pumice habitats in the Cascades where other Lepidoptera species have been completely excluded from this habitat due to restrictive limitations in their physiology and ecological adaptations (Hammond 1981). This may have been the case as climate and environmental changes occurred during glacial and interglacial episodes. Montane faunas

(including several *Speyeria* species) of the remaining coniferous forests on the Great Plains, such as those in the Black Hills, apparently represent relicts of former, more extensive populations that now occur further west and should be considered a distinct area of speciation (Johnson 1975). 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).

Many *Speyeria* also exhibit considerable ecological plasticity and adults frequently invade the habitats of related species. However, there appears to be a sharp segregation among species in the types of habitat utilized by the larvae (Hammond 1974, 1981). *Speyeria* larvae do not appear to be restricted to any particular species of violet and will feed on any native violet that happens to be growing in the appropriate habitat. The broad acceptance of many violet species in the laboratory (Scott 1986b) and in the field suggests that other habitat factors besides hostplant availability strongly affect the distribution and abundance of *Speyeria* (Swengel 1997). Ecological segregation of *Speyeria* species, which may be occurring at present, is largely the result of interspecific competition for the larval food plant in various habitats (Hammond 1974, 1981). Adult nectar source distribution and availability may also play a role in selection of hostplant individuals or even species in habitats where the two are proximal to each other (Murphy et al. 1984; Ross 2003).

Violets exhibit environmental plasticity (Valentine 1956) and species mirror the habitat diversity of *Speyeria*. In western North America, various violet species will grow in wet boggy meadows, dry or well-drained meadows, mesic forests, and xeric grasslands or mountainsides (Baird 1942; Hammond 1981). Butterfly biology has been linked to host plant strategies, and

population attributes and geographical distribution may be significantly and substantially affected by host choice and the strategies of hostplants (Dennis et al. 2004). Ehrlich and Raven (1964) noted that significant patterns exist in the hostplant relationships of Heliconiini and Argynnini, and that their diversification may have taken place from a common ancestor associated with their respective assemblages of plants.

Evolutionarily speaking, *Speyeria* are prone to local adaptations and show the effects of genetic drift. At any one point in time, species and subspecies “states” become fixed into differentiated wing patterns and colors, and workers have responded by describing species or subspecies. *Speyeria* species have been the subjects of evolutionary-related studies on geographical variation and speciation (e.g., Grey 1951; Moeck 1957; Grey et al. 1963; Hammond 1978, 1990; Scott et al. 1998). However, there has not been a comprehensive, modern cladistic analysis for *Speyeria* and several questions still need to be addressed: Which species are basal and which are derived? Which subspecies designations, if any, are valid? Is full species status warranted for any subspecific taxa and what were/are the pre- and post-isolating mechanisms of these cryptic species? Present-day phylogenetic approaches utilizing molecular, morphological and life history traits may provide an additional tool to address some of these unanswered systematic questions.

### **Life History**

The Argynnini presently comprise over 100 species and six genera as currently defined by Simonsen et al. (2006). Almost all species are found in temperate, arctic or alpine areas mainly in Palearctic or Nearctic Regions, although a few species occur in the mountains of South America and Africa (Seitz 1924; Sbordoni and Forestiero 1998; Smart 1989; Simonsen et al. 2006). Argynnini is also represented in Australia and New Guinea in swampy habitats by the widely distributed *Argynnis inconstans* (= *hyperbius*) Butler (Common and Waterhouse 1972;

Simonsen et al. 2006). Adults frequent open fields, moist meadows, or open woodlands near streams, while others seem to be restricted to coastal dunes, tallgrass prairies or high mountains (Opler and Malikul 1998; Opler and Wright 1999; Glassberg 2001a,b). During the summer months, they may be abundant in forest clearings, along roadsides, and on flower-rich slopes and in meadows in mountainous regions. *Speyeria* often prefer tall nectar sources such as thistles, wild asters, and sunflowers, as well as penstemons, mint and dogbane (Dornfeld 1980; Scott 1986b). They may not, however, be effective pollen dispersers for some plants. *Speyeria cybele* and *S. aphrodite* were observed to carry many pollinia of *Asclepias exaltata* on their legs (Broyles and Wyatt 1991). However, upon alighting on a flower, they would often grasp the petals rather than reproductive parts, reducing the chances of both pollinium insertion and removal (Broyles and Wyatt 1991). Adult *Speyeria* are strong fliers and can fly many kilometers (especially in late summer) and are rather long lived (several weeks to 2-3 months from May-September) (Scott 1986b; Tilden and Smith 1986; Pyle 1995; Opler and Malikul 1998; Opler and Wright 1999). All members of the genus are univoltine (Scott 1986b; Opler and Wright 1999). Scott and Epstein (1987) noted that in temperate climates, the longer the life span (many *Speyeria* individuals live longer than a year from egg to the end of adulthood), the longer the flight period is for adult butterflies.

Adult males typically emerge a week before females, and males patrol for potential mates (Hammond 1974; Scott 1975, 1986b). Courtship is rather elaborate, and pheromone cues from both sexes may be a reproductive barrier between species (Hammond 1974; Scott 1986b; Scott et al. 1998). *Speyeria atlantis* [as well as other Argynnnini (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. The tip of the abdomens of female Argynnini (including *Speyeria*) contain paired glands normally hidden in the abdomen that aid in courtship (Scott 1986b). 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.

Copulation and oviposition in *Speyeria* were examined in detail by Arnold and Fischer (1977). No true morphological ovipositor or external genitalia are present in female *Speyeria*, and the copulatory mechanism is based on the morphology and manipulative maneuverability of the abdominal segments. The ovipositor is frequently short in Lepidoptera, taking the form of a pair of broad, setose anal papillae (Scoble 1995). The male's genitalia are everted by the sequential contraction of pre-genital segments and by the increased pressure exerted by dorsal and longitudinal muscles located on each segment. The female prepares for the reception of the male by raising and retracting the apical portion of the abdomen, thus exposing the ostium bursae making it ready for reception of the intromittent organ of the male. With the extrusion of the male external genital apparatus, the tegumen is extended and lowered, and the uncus is placed upon the dorsum of the female's anal papillae [however, Scott (1984) noted that the male's uncus actually fits beneath the papilla analis during mating in all butterflies]. The male genital valves, bearing a structure known as the digitus, spread laterally, allowing the anal papillae of the female to rest in fusiform pouches, thus fixing the position of the female. The phallus (=penis) is then inserted through the ostium bursae and a spermatophore passes through to the corpus bursae. At the time of oviposition, a fertilized egg lies in the posterior portion of the common oviduct. An increase in intra-abdominal pressure, the peristaltic movements of the oviducts, and the

compression and extension of posterior abdominal segments help to squeeze the egg out of the common oviduct. Eggs are fertilized as they intercept the ductus seminalis.

Females of most species delay egg-laying until late summer or fall and usually oviposit rather haphazardly near their hostplants rather than carefully placing them on the plant as do most butterflies (Ritchie 1944; Howe 1975; Scott 1986b; Opler and Wright 1999). Since the larvae apparently do not discriminate between different species of violets, the female must discriminate between different habitats in order to prevent interspecific competition between species (Hammond 1974, 1981). Reproductive diapause has been exhibited in *S. coronis* and *S. zerene* in California during the warm, dry months of the summer flight period (Sims 1984). This diapausal period delays the onset of oviposition until late summer or early fall and thus decreases the exposure time of overwintering first instar larvae to desiccating conditions. Fritillaries are fecund butterflies, with some species capable of laying over 1,000 eggs (Ross 2003; Wagner 2005). They are known to deposit eggs on twigs, leaves, stones and other debris (Scott 1986b; Allen et al. 2005). Some females will oviposit on the underside of hostplants (Arnold and Fischer 1977; Kopper et al. 2000). Eggs bear camouflage coloration and are slightly rounded, tapering toward the apex. They are highly sculptured and contain a large amount of lipid, and are likely adapted to withstand considerable environmental pressures including submergence, frost, ground dwelling predators and microbes (Hammond 1974; Ross and Henk 2004).

Eclosion occurs two to three weeks after eggs are laid, and first instar larvae will drink water but will not feed on violets for seven to eight months (Wagner 2005). The eggshell, which is consumed by the larva, contains a large amount of lipid, which probably serves as an energy source during larval diapause (Hammond 1974). Few individuals weather winter conditions, but female biology compensates for this by allowing females to lay hundreds of eggs (Mattoon et al.

1971; Ross 2003; Wagner 2005). *Speyeria*, like other cold adapted insects, probably survive adverse environmental conditions through physiological adaptations such as freeze tolerance or freeze avoidance (Chapman 1998). Freeze tolerant insects can withstand the formation of internal ice by promoting extracellular ice formation at relatively high subzero temperatures by synthesizing nucleating agents in the hemolymph, whereas freeze avoiding insects prevent lethal intracellular ice formation by an extended ability to supercool and by the masking or absence of ice nucleating agents (Palmer et al. 2004). *Speyeria* larvae do have the ability to respond to various stimuli such as light, heat, and mechanical agitation while in captivity, and diapause may actually prove to be more of a quiescent state (Mattoon et al. 1971). The ability to respond to these stimuli and seek shelter in nature may also have an important role in larval survival during adverse environmental conditions. Adult *Speyeria* in montane habitats have been observed responding to cool summer evenings and morning dew by shivering their wings and basking in the sun to control body temperatures (C. Penz, pers. comm.).

Larvae pass through six instars (Scott 1986b), overwintering as first instars and breaking diapause to complete development the following season (Scott 1986b; Wagner 2005). Edwards (1880a), however, observed larvae feeding on violet and proceeding to a third molt before the onset of winter in Illinois, but they were not able to overwinter and later died. Larvae of *Speyeria* are generally secretive and feed primarily at night (Scudder 1889; Opler and Wright 1999) (but see McCorkle and Hammond 1988; Kopper et al. 2001a; Mooreside et al. 2006), typically returning to hiding places under host leaves or nearby vegetation during the day (Hammond 1974; Ferris and Brown 1981; Opler and Wright 1999; Wagner 2005). Final instars are sizable insects (e.g., *S. cybele*= approximately 55 mm in body length) and are capable of consuming two or more full-grown hostplants (Wagner 2005). Many species are black with lighter markings and

bear three rows of branching spines of various colors on either side of the body (Allen et al. 2005). As with many nymphalid larvae, there are six stemmata on either side of the head capsule and numerous secondary setae (Stehr 1987). Secondary setae are also present on the thorax and abdomen. Like other members of the Heliconiinae, they lack mid-dorsal spines, but unlike other Heliconiinae, lack spines on the head (Scott 1986b; Layberry et al. 1998). Allen et al. (2005) and Wagner (2005) have provided color images of several species.

*Speyeria* larvae feed on various violet species (*Viola*), and in laboratory conditions they are known to feed on every American violet species tested (Mattoon et al. 1971; Brittnacher et al. 1978; Hammond 1981; Scott 1986b). In many cases, the specific violet utilized by a particular speyerian species is poorly known in the wild (Hammond 1974; Allen et al. 2005). There are only a few hostplant records that are not of the genus *Viola* and some may be dubious records (Durden 1965; Robinson et al. 2002). Pupation occurs inside a simple tent made of strands of silk stretched between surrounding surfaces (Allen et al. 2005). The pupa, or chrysalis, is suspended with the head down as in most other nymphalids and on average in nature lasts approximately 14 days (Mattoon et al. 1971).

There are only a few records of species of *Speyeria* being attacked by natural or potential predators. Scudder (1889) reported *S. aphrodite* adults were found in the crops of the common nighthawk and chimney swift; larvae were also found in the stomachs of the black-throated bunting and the towhee. Avian predation of *Speyeria mormonia* was recorded by Hendricks (1986). Two individuals were captured, the wings were torn off, and the body was eaten by nesting water pipits in Wyoming. Three *Speyeria* [*S. diana* (males), *S. aphrodite*, and *S. cybele*] were eaten by deer mice in model-mimicry experiments conducted by Brower and Brower (1961).



*Speyeria* likely gain protection from potential predators in a variety of ways. *Speyeria diana* females have been implicated in a Batesian mimicry complex with a distasteful papilionid and other nymphalid species (Scudder 1889; Poulton 1909; Ehrlich and Ehrlich 1961; Adams and Finkelstein 2006). In some species, an eversible gland, capable of producing a bad odor, is located on the dorsum of the adult female abdomen (Clark 1926; Harvey 1991). Larvae also bear a gland located ventrally just behind the head and before the first pair of legs that is likely used for defense against predators (Scott 1986b; McCorkle and Hammond 1988). McCorkle and Hammond (1988) note that *Speyeria* larvae do possess a fleshy, eversible osmeterium (not homologous with that of Papilionidae), but the strength of the scent emitted varies. The odor is stronger in larger species such as *S. coronis* and *S. edwardsii*. Other avoidance measures during the larval stages include taking refuge under leaves during the day and feeding at night. First instar larvae will also often hibernate inside grass stems (Scott 1986b). Eggs in some species may also contain phytochemicals used to deter potential predators (Ross 2003; Ross and Henk 2004).

Ackery (1988) reviewed the larval hostplants of nymphalid butterflies and presented a classification that noted the affinities of related plant families Violaceae and Passifloraceae and associated host plant use of argynnine and heliconiine species. *Viola* is the largest genus within the Violaceae, comprised of 525-600 species worldwide (Ballard et al. 1999). There is an extensive north-temperate distribution that belies the otherwise tropical affinities of the family. *Viola* is distributed throughout most of the frost-free regions of the world, ranging widely across temperate habitats of the Northern Hemisphere and into higher elevations of mountain systems towards the equator. Primary centers of morphological and taxonomic diversity reside in the Alps and Mediterranean region, Himalayas and mountainous regions of eastern Asia and the

South American Andes (Ballard et al. 1999). Secondary centers are the Pacific Coastal region of the United States, the Appalachian temperate forests and Atlantic Coastal Plain of the eastern United States, and the mountains of central and northern Mexico (Ballard et al. 1999). Floral structure is remarkably uniform and species from opposite ends of the world and from highly disparate habitats exhibit similar prefertilization floral characters, especially those concerned with attraction and manipulation of pollen vectors (Beattie and Lyons 1975).

Morphological, ecological and cytological studies on *Viola* have been conducted. Seed dispersal mechanisms and predator avoidance measures in *Viola* are primarily those of explosive seed ejection away from the parent plant, ant exploitation and seed transportation or both (Beattie and Lyons 1975). Most species combine both systems while a few are purely myrmecochorous, possibly highly evolved with specific ant species, thus limiting the distribution of some of the *Viola* species concerned. Seed predation or consumption by *Argynnis* (= *Speyeria*) larvae as well as other lepidopteran and bird species has been observed, with heavy predispersal damage of unripe ovaries occurring (Beattie and Lyons 1975). Predispersal and postdispersal seed predation may have been a selective force in the evolution of dispersal mechanisms in *Viola* (Beattie and Lyons 1975).

A diverse group of insect pollinators associated with *Viola* has provided a sexual system of systematic cross-pollination simultaneously producing variation and invariance, and this may have been partially responsible for the success of the genus in temperate regions where there is a general paucity of pollen vectors (Beattie 1971, 1974). The various activities and morphologies of these pollinators allow for the deposition of pollen to the stigma in diverse ways, and there is a spectrum of cross- or self- pollination effects. New genetic recombinants with corresponding opportunities for adaptation to new or changing environments, or an appropriate strategy in

stable environments by producing offspring similar to the parents can be selected as the need arises, providing a system of great evolutionary versatility (Beattie 1971). Pollen heteromorphism is also exhibited in *Viola*, and several pollen morphs differing in aperture number can be produced by the same flower (Dajoz 1999; Nadot et al. 2000). Because pollen tube germination occurs through the aperture, it is hypothesized the aperture number could affect pollen grain fitness (Nadot et al. 2000). In violets, aperture number apparently increases with elevation due to polyploid species (which exhibit pollen heteromorphism) being more abundant at higher elevations. This is likely due to pollinator conditions, as it has been shown that pollination reliability decreases with elevation (Nadot et al. 2000).

Polyploidy has likely played a role in the evolution of *Viola* and species hybridize readily. Cytological studies involving *Viola* were conducted by Clausen (1927, 1929), Fothergill (1941, 1944) and Harvey (1966). Clausen's work focused on the cytological conditions found in hybrid European *Viola* species, namely chromosome numbers, in order to compare chromosome and morphological relationships. Species delimitations and interspecific relationships involving the behavior and number of chromosomes indicated that species of the same systematic subgroup belonged as a rule to the same series of chromosome numbers. Fothergill (1941) investigated the survivorship of various cytological types and the actions selected upon them in the wild. Chromosome lengths were later measured by Fothergill (1944) to provide additional descriptions and classifications of *Viola* chromosomes. Ballard et al. (1999) used internal transcriber spacer DNA sequences for 42 widespread *Viola* taxa in phylogenetic analyses to support an Andean origin of the genus. The relationships presented based on the nuclear ribosomal data showed generally a close congruence with relationships indicated by chromosome numbers and corroborated some previous hypotheses of species relationships and diversification within *Viola*.

An Andean origin of *Viola* may have played a role on the separation of *Speyeria* and Palearctic groups such as *Argynnis*

*Speyeria* and their larval hostplants *Viola* are amongst the best indicator organisms of native, undisturbed ecological communities in North America (Hammond 1981, 1995). They are also among the first organisms to be eliminated from such communities as a result of human–caused disturbances (Hammond and McCorkle 1984). A few *Speyeria* have been declining over the past 200 years, and several have been listed as either federally/state endangered or threatened [e.g., *S. idalia*, *S. diana*, *S. nokomis* (Edwards), *S. zerene hippolyta* (Edwards)]. The position of *Speyeria* in conservation and land management issues is well known (Hammond and McCorkle 1984; Launer et al. 1994; Kelly and Debinski 1998; Williams 1999, 2002; Swengel 1993, 2004; Swengel and Swengel 2001; Patterson 2002). Elucidating the inter- and intraspecific relationships and evolutionary history of *Speyeria* may provide information pertinent to conservation strategies and priorities.

## **Research Background and Justification**

### **Taxonomy and Systematics**

Despite the likelihood that wing facies may be rather ‘plastic’ characters [i.e., environmentally influenced (see Hovanitz 1941; Watt 1968, Kingsolver and Wiernasz 1991; Scoble 1995)] and capable of reverting back to original states depending on fluctuating contact/isolation with other populations, butterfly species, including *Speyeria*, are typically delimited utilizing wing characters (Opler and Krizek 1984; Scott 1986b; Emmel 1998; Opler and Wright 1999; Glassberg 2001a,b). The “nymphalid ground plan” was originally proposed separately in the 1920’s by B. N. Schwanwitsch (1924) and F. Söffert (1927) to provide a general scheme and nomenclature for butterfly wing patterns based on a system of bands and spots that run from the anterior to the posterior margin of each wing. Pattern elements consist of

a system of homologies that are identifiable across thousands of lepidopteran species, and are broken down into the following main components: discal spot, central symmetry system, wing root band, basal symmetry system, border ocelli system, marginal and submarginal bands, and parafoveal element (Nijhout 1991). This plan represents the maximal pattern found in the nymphalids, but it is not, however, exhibited in its entirety in any one species. The scheme deviates in each taxon, in which subordinate ground plans for particular taxa are utilized, and often special (i.e., informal) terminology is employed for these subordinate plans. The plan does not suggest primitive conditions of butterfly color patterns exhibited within the Lepidoptera, but may be the basis (by recognizing wing pattern homologies) for which primitive patterns and evolutionary significance and systematics may be elucidated by further studies on groups such as *Speyeria*.

Taxonomically, these patterns have been utilized mainly to distinguish related species. Sister generic taxa to *Speyeria* such as *Heliconius* Kluk exhibit deceptively simplistic deviations from the nymphalid ground plan, while others such as *Agraulis* Boisduval and LeConte are easily derived from the basic plan (Nijhout 1991). The nymphalid ground plan provides an overall organizing principle that can be used to identify various spots and bands that comprise these wing patterns.

Species and subspecies of *Speyeria* are commonly delimited based on banding, discal coloration, spot coloration and size differences (Dornfeld 1980; Hammond 1978; Ferris and Brown 1981). In the evolution of *Speyeria*, wing markings appear to be highly conservative and reliable diagnostic characters, while wing colors are less stable (Hammond 1990). Pierid and papilionid butterfly populations in cold climates have much darker, more heavily melanized ventral hindwings than do populations in warm climates (Watt 1968; Guppy 1986). Habitat may

be important in determining species and subspecies, and the amount of solar radiation (including factors such as latitude, temperature, elevation, humidity, degree of lack of vegetation, soil type) on larvae and pupae may play a role in color variation as it does in other lepidopterans (Hovanitz 1941; Moeck 1957; Janzen 1984; Pyle 1995; Layberry et al. 1998; Ellers and Boggs 2004).

Basal, melanic, suffusion of wings is extremely plastic in *Speyeria*, and subject to repeated convergence and reversal (Hammond 1990). “Alpine melanism” may be an adaptation to cooler environments as butterflies at higher elevations and latitudes are often darker than populations at lower elevations and latitudes (Guppy 1986), and this may play a role in the wing coloration of northern and montane *Speyeria*. Deviation from the nymphalid ground plan, and the subordinate ground plan exhibited within *Speyeria* traditionally used to recognize species/subspecies and evolutionary history (while avoiding wing “coloration” where possible), will be the basis for inference and comparison within the phylogenetic analyses presented later in this treatment.

Genitalic morphology shows peculiar patterns of variation among animal species (Eberghard 1985; Arnqvist 1997, 1998; Mutanen 2005). Traditionally, species-specificity in genitalia has been assumed to serve as a mechanical isolation system between species (the lock-and-key hypothesis) (Arnqvist 1998). Most recent studies suggest, however, that such variation may also be because of sexual selection (Lloyd 1979; Eberhard 1996; Arnqvist 1997). These two hypotheses provide different predictions on genital variation within and between species.

*Speyeria* genitalia have largely proven to be taxonomically uninformative, and detailed genitalic examination has largely been ignored in this group (Hammond 1978; Ferris and Brown 1981).

Dos Passos and Grey (1945a) conducted a survey of male genitalic structures in Argynninae (including *Speyeria*) butterflies and provided detailed illustration of several species, including the male genitalic armature (=capsule) of *S. atlantis*. Generic characters for male *Speyeria*

genitalia include a semi-rectangular plate (=digitus) located near the dorsal lobe of the valvae, but otherwise the armature is more conventional in type and comparatively unspecialized (dos Passos and Grey 1945a). It is apparent that genitalic data can conclusively separate the *Semnopsyche* group [= *S. cybele*, *S. diana*, *S. aphrodite*] and Callippe group [= *S. atlantis*, *Speyeria hesperis* (Edwards) *Speyeria callippe* (Boisduval), *Speyeria zerene* (Boisduval), *Speyeria coronis* (Behr), *Speyeria egleis* (Behr), *Speyeria hydaspe* (Boisduval), *Speyeria mormonia* (Boisduval)], but the male armature is otherwise largely homogenous (dos Passos and Grey 1945a). Their work, however, was based on examination of slide-mounted genitalia and some structures may have been distorted and difficult to examine.

Significant slide mounted genitalia collections do exist in museums ([i.e., F. H. Chermock Collection-Allyn Museum of Entomology (now McGuire Center for Lepidoptera and Biodiversity)], but preliminary examination of closely related *Speyeria* yields no apparent taxonomically informative characters (Dunford unpublished data). Recently, however, genitalic examination of insects including Lepidoptera has improved via better preparatory and illustrative techniques (Scoble and Krüger 2002; Simonsen 2006a,b; Zaspel and Weller 2006). Utilizing modern genitalic preparatory and imaging techniques could yield taxonomically informative characters that have not been identified to date within *Speyeria*. An attempt to reevaluate the significance of genitalia within *Speyeria* is critical to provide additional taxonomically and evolutionarily informative characters.

In general, mitochondrial genes are useful data for evolutionary studies such as species delimitation, population structure and gene flow, hybridization, phylogeographic histories, and phylogenetic relationships (Vogler et al. 1993; Brower 1997; Zimmermann et al. 2000; Levy et al. 2002; Wahlberg et al. 2003a; Segraves and Pellmyr 2004; Strehl and Gadau 2004;

Vandewoestijne et al. 2004; Wahlberg et al. 2005; Memon et al. 2006). Their small size and relative ease to purify (relative to nuclear genes) (i.e., buoyant density, high copy number in cells, and location within an organelle) allow researchers to isolate these genes more readily (Simon et al. 1994). Because of the properties of mtDNA (i.e., various regions evolve rapidly in base substitutions and sequence length, has a constant initial rate of evolution, is maternally inherited, and is unlikely to recombine), mtDNA represents an unbiased neutral marker for maternal ancestry, and is a good tool to help reveal the historical relationships among populations (Brower 1994a; Simon et al. 1994).

Nuclear genes have also been shown to be useful for phylogenetic studies in butterflies (Brower and DeSalle 1994, 1998; Brower and Egan 1997). Single copy genes, such as *wingless*, have been used in reconstructing species level to subfamily and family level relationships in nymphalid and riodinid butterflies, respectively (Brower and DeSalle 1998; Brower 2000b; Campbell et al. 2000). *Wingless* and other nuclear genes may be phylogenetically informative at deeper levels than the saturation point (relationship between substitutions and sequence divergence) of mitochondrial DNA (Brower and DeSalle 1998). Inclusion of other nuclear genes such as elongation factor 1 $\alpha$  in phylogenetic studies further resolved relationships among species groups within the same genus and clades at the subfamily rank and lower in Noctuoidea (Brower and DeSalle 1994; Mitchell et al. 2000; Peña et al. 2006).

The rate of evolution of mitochondrial and nuclear DNA and ribosomal RNA in animals varies among lineages, among genes, and within genes, and thus several different gene regions have been utilized in phylogenetic analyses (Martin and Pashley 1992; Simon et al. 1994; Soto-Adames et al. 1994; Templeton et al 1995; Brower and Egan 1997; McCracken and Sheldon 1998; Abraham et al. 2001; Kondo et al. 2003; Yang and Yoder 2003; Omland et al. 2006). COI



and COII protein coding genes have been the most widely used mitochondrial gene regions in Lepidoptera phylogenetic analyses for some time (Brower 1994b, 1996b; Brown et al. 1994; Sperling and Hickey 1995; Pollock et al. 1998; Caterino and Sperling 1999; Nice and Shapiro 1999; Wahlberg and Zimmermann 2000; Zimmermann et al. 2000; Caterino et al. 2001; Monteiro and Pierce 2001; Kruse and Sperling 2002; Wahlberg et al. 2003a, 2005; Vandewoestijne et al. 2004; Mallarino et al. 2005; Simonsen et al. 2006c). However, controversy has arisen regarding the utility of DNA to delimit species and species relationships on its own. Practical and theoretical problems raised by reliance on DNA-based identifications, especially DNA barcoding of the COI gene region, have been discussed by Sperling (2003), Wheeler (2003), Will and Rubinoff (2004), Ebach and Holdrege (2005), Brower (2006), and Dasmahapatra and Mallet (2006). More recent phylogenetic analyses now incorporate multiple gene regions, morphological, and other life history data (Mitchell et al. 2000; Abraham et al. 2001; Kruse and Sperling 2002; Bitsch et al. 2004; Mallarino et al. 2005; Braby et al. 2006; Gompert et al. 2006; Simonsen et al. 2006).

Studies on speyerian genetics have been conducted in the past. Chromosome work was conducted by Maeki and Remington (1960) and Miller and Miller (1966). Chromosome numbers taken from male testes by Maeki and Remington (1960) for several *Speyeria* range from 29 to 30, although some counts may have been too high. Miller and Miller (1966) counted 27 for *Speyeria aphrodite ethne* (Hemming). Brittnacher et al. (1978) used electrophoresis to study the body enzymes of California *Speyeria* and found that five Callippe-group species could not be distinguished, whereas the other species could be (the enzymes of *Speyeria hydaspe* and *Speyeria adiaspe* were also similar). Tebaldi (1982) utilized starch gel electrophoresis of six enzymes to analyze the relationships between three phenotypes of *Speyeria atlantis* and found

that the phenotypes could only be considered ‘semispecies’. Williams (2001a, 2002) examined the COI and COII gene regions for *Speyeria idalia* and suggested splitting the eastern and western United States populations into two subspecific taxa based on 18 parsimony-informative sites and spot size on the ventral hindwings. Several *Speyeria* have also been incorporated into higher-level taxonomic studies, and gene regions and sequences have been databased on the DNA database GenBank (Martin and Pashley 1992: *S. atlantis*; Brower and Egan 1997: *S. cybele*; Pollock et al. 1998: *S. mormonia*; Williams et al. 2002: *S. idalia*).

### **Conservation**

Understanding and appropriately defining biodiversity in order to conserve it is becoming a significant social and scientific goal (Haney and Power 1996; Lambeck 1997; Wilson 1999, 2002; Blackmore 2002; Pyle 2002; Woese 2004). However, these environmental “values” may vary depending on experiences with and appreciation for local landscapes (Noss 1990; Hunter and Brehm 2004). Monitoring, by means of transect counts and various sampling measures, has historically been utilized to assess the effects of management on local butterfly abundance and diversity (Owen 1975; Pollard 1982). Until recently, systematics has contributed relatively little to the theory and practice of conservation and land management (Soltis and Gitzendanner 1999). However, phylogenetic analyses of conspecific populations and the application of appropriate species concepts often reveal multiple lineages that can be viewed as evolutionary distinct units in need of some level of conservation (Hazevoet 1996; Soltis and Gitzendanner 1999). Multiple characters and diagnostic character states must be examined and the processes that influence those characters must be understood to accurately delineate species and units for conservation (Goldstein et al. 2005; Gompert et al. 2006).

Climate and habitat change, whether by natural cause or anthropogenic alterations, is widely accepted as the most important factor in butterfly decline (e.g., including some members

of *Speyeria*), as its multitude of important effects include a decrease of breeding sites and removal of important resources (New 1997; Hammond and McCorkle 1984; Hammond 1995; Shapiro 1996; Hill et al. 1999a,b; Parmesan et al. 1999; Warren et al. 2001; Hill et al. 2002; McLaughlin et al. 2002; Dennis et al. 2004; Scott 2006c). There is a great need for well-designed experiments to reveal the effects of climate and other environmental factors on *Speyeria* and other butterfly and invertebrate species (Dornfeld 1980; Thomas 1984; Hammond 1995; Black et al. 2001; Bossart and Carlton 2002). These kinds of data may lead to a better understanding of the variability in forms encountered in the field and the effect that these factors have on population viability. The data may also identify lineages worthy of conservation and help set appropriate and scientifically valid management priorities (Hazevoet 1996; Soltis and Gitzendanner 1999). Additionally, it may be wise to be cognizant of the values associated with species richness and biodiversity in such studies to begin to understand the human dimensions associated with biological conservation (Jacobson and McDuff 1998; Sapolsky and Ehrlich 2003; Hunter and Brehm 2004).

Are taxonomy and systematics, as they are currently employed for the evolution of *Speyeria*, appropriate mechanisms to sort out local degrees of specific ‘purities’ (see Shapiro 2002)? Varying degrees of geographic and reproductive isolation (pre and post-mating), local population characteristics (i.e., dispersal capabilities, hostplant preferences, local climatic conditions) and genetic heritage over time drive speciation mechanisms within *Speyeria* (Grey 1951; Moeck 1957; Hammond 1978; Williams 2001b). When and where do we warrant protection for a given species or subspecies? How will comprehensive phylogenetic analyses affect decisions made for or against protecting these species and their habitats? What is the overall ‘health’ of habitats where *Speyeria* occur? Utilizing phylogenetic analyses,

biogeography, and interpreting but not biasing these data with conservation in mind (Shapiro 2002) will require use of applicable species concepts for *Speyeria*.

### **Subspecies and Species Criteria**

The question of subspecies and whether or not a subspecies is an ‘absolute’ or simply a ‘prevailing trend’ may not be important. Naming a taxon attracts attention, and recognition and attention can mean the difference between continued survival and extinction of a population or geographic race. It can even affect the survival of a species, if further study proves a subspecies is actually a cryptic species. The “subspecies concept” can be important and valid systematically, and has the potential to enhance our understanding of speciation, dispersal, and geographic variation (Patten and Unitt 2002). There are examples of mismanaged “megafauna” [i.e., tuatara (*Sphenodon* sp.), dusky seaside sparrow (*Ammodramus nigrescens*)] because cryptic species were not recognized or populations/lineages were not conserved, but rather the “species” was conserved (Meffe and Carrol 1997; Winston 1999). It may be time to reevaluate species criteria (and conservation paradigms, especially those from the vertebrate perspective), to emphasize the fact that a given species or subspecies concept works for some taxa but not all (Mishler and Donoghue 1982; Lloyd 2001; Hunter 2006).

Taxonomists typically name subspecies on the basis of average character differences between populations (Gillham 1956; Patten and Unitt 2002). A common method for describing *Speyeria* subspecies has been to name populations or groups of individuals representing points along a continuum of geographic variation (or clines). Subspecific taxon names within *Speyeria* are assigned to populations occupying various geographic areas based on the author’s own discretion, typically lacking a testable criterion. Because many taxon “names” are arbitrary at the subspecies level, and given the characters analyzed (e.g., wing coloration) and the way in which many *Speyeria* subspecies were described (e.g., lacking testable, intra- or interspecific

comparisons), these subspecies have relatively little biological significance. In other words, they may not be a single lineage of ancestral-descendant populations that maintains its own identity from other such lineages but has not lost its ability to breed with another lineage unless under geographic isolation. Two workers may not agree on species/subspecies delimitations. However, subspecific trinomials do recognize degrees of variation, and provide a starting point to further analyze intra- and interspecific relationships in a phylogenetic framework. Taxonomists should objectively describe the patterns of variation discovered in nature, and then translate them into subspecies or species level descriptions based on testable hypotheses while avoiding arbitrary decision-making (Wilson and Brown 1953; Van Son 1955; Gillham 1956; Brower 2000a; Kons 2000). A subspecies of *Speyeria*, following in part Kons (2000), Patten and Unitt (2002), and Cicero and Johnson (2006), is defined herein as follows: it is a distinct monophyletic lineage, allopatric from its closest relatives by having approximately 75% of a population lying outside 99% of the range of other populations for a given, uncontaminated character set, possessing several identical sclerotized structures (e.g., genitalia) but having differences in wing facies. These subspecies *could* be considered valid species or a taxon for conservation purposes, depending on which working species concept is applied (to be described below).

Since the typological species concept promulgated by Linnaeus in the mid 18<sup>th</sup> century, several interpretations of “species” concept have been advanced (Mayr 1942; Wiley 1978; Paterson 1985; Eldredge and Cracraft 1980; Mallet 1995; Van Regenmortel 1997; Baker and Bradley 2006). The major component to the Biological Species Concept (BSC) is that a species is reproductively isolated from other species that could potentially come in contact with it (Mayr 1942). The BSC allows for the recognition of interactions within populations in time and space that create or maintain species. However, the BSC has raised several issues regarding its

application (Sokal and Crovello 1970; Mallet 1995; Hazevoet 1996; Luckow 1995; Gornall 1997). It is difficult to apply this concept to uniparental entities or fossil taxa and it is operationally difficult to determine reproductive isolation if the related “species” are not sympatric. It is also impossible to know whether or not members of a “species” are interbreeding without actually observing individuals in copula. Many species have never actually been observed mating, so much of what is considered a “species” is actually based on morphological examination and assumptions (Sokal and Crovello 1970). Incipient and polytypic species are difficult to define and the BSC applies only to populations viewed in a narrow window of time. Thus, the BSC is also not evolutionarily meaningful and does not consider a species as an evolutionary unit. Finally, the BSC allows for nonmonophyletic taxa and does not produce taxa useful for cladistic analyses (Donoghue 1985).

Recognizing some of the problems mentioned above, additional species concepts were developed, and portions of the following concepts define the working species concept utilized herein. The Evolutionary Species Concept (ESC) describes a species as a single lineage of ancestral descendent populations of organisms which maintains its own identity from other such lineages and which has its own evolutionary tendencies and historical fate (Wiley 1978). Kohn (2000) provided a more concise definition: a species is a monophyletic lineage biologically capable of reticulating with a different evolutionary lineage; the point at which an evolutionary lineage loses its ability to merge with another lineage is theoretically and biologically significant and separates a “species lineage” from an ancestral one.

The Phylogenetic Species Concept (PSC) allows for the recognition of species in well-defined monophyletic clades and recognizes the evolutionary potential of these lineages (Eldredge and Cracraft 1980; Hazevoet 1996; Claridge et al. 1997). The PSC also recognizes

synapomorphies within individuals or populations, and thus they are assumed to be more closely related than individuals or populations lacking those synapomorphies. An evolutionary hypothesis of true genealogical relationships is represented in a cladogram/phylogram and often results in a hierarchy of monophyletic groups (Baum 1992; Luckow 1995). A species, as defined by the PSC, is the smallest diagnosable cluster of individual organisms within which there is a pattern of ancestry and descent (Cracraft 1982; Nixon and Wheeler 1990). The species is thus an irreducible, or basal, unit distinct from other such units. Any character unique to a population or set of populations would diagnose them as “species,” even if they interbreed with other species (Nixon and Wheeler 1990). Because the PSC incorporates history and reflects phylogeny, it is useful for species delineation and preserving biodiversity (Goldstein et al. 2000; Goldstein et al. 2005; but see Scott 2006a). Whether morphological or molecular (or more importantly both) synapomorphies are utilized to delimit taxa, applying the PSC would allow analyses to identify small clades within “species” that comprise one or a few populations from a small geographic area (Nixon and Wheeler 1990; Goldstein et al. 2005). Geographically distinct populations containing phenotypically and genetically differentiated, phylogenetically diagnosable “races” or “forms” (=evolutionary units) could be considered full species (Kons 2000; Brower 2000a).

Phylogenetically based classifications may be required to set conservation priorities and develop informed conservation strategies. Phylogenetic analyses can help identify population lineages that may represent biological entities worthy of conservation. Conservation, or the practice of, has in the past been a reactionary process. If analyses can provide useful hypotheses for the evolutionary significance of populations, especially those specifically related to invertebrates, perhaps conservation issues and laws can be addressed long before a species’ existence becomes a “crisis” (Scott 2006c). Utilizing the PSC could alter existing conservation

paradigms and justify the preservation of the evolutionary *potential* of clades as well as help identify actively speciating groups.

Species should be natural, monophyletic taxa and bear biologically and evolutionary significant characteristics that distinguish them from related monophyletic taxa. However, because evolution is an ongoing process, species criteria must be flexible enough to accept that there are cases, such as with *Speyeria*, where lineages are in a state of transition in the speciation process, and that some taxon delimitations at present will have to be made more arbitrarily. The phylogenetic work and ultimate conservation goals of this study, in conjunction with the examined group, require that a combination of species concepts be followed. Favoring any one species concept over another may bias the interpretation of the results herein. It is difficult to put a universal “law” or definition on what a “species” is, and as scientific data continue to accrue, species concepts will also change.

No species concept should be viewed as an absolute criterion for protecting species or populations, but rather should be viewed as part of the framework from within which identification of conservation and management goals can be achieved effectively (Goldstein et al. 2000). Each geographically and hypothetical reproductively isolated *Speyeria* population, whether currently recognized as a full species or infraspecific category, may be unique and maintain its own distinct gene pool and evolutionary potential, thus worthy of conserving. Utilizing aspects of the BSC, the ESC, and the PSC in this study will appropriately elucidate the reproductive and evolutionary processes exhibited by *Speyeria*, while providing a means in which to address conservation issues. This does not, however, mean that these species concepts will be applied whenever it conveniently suits the scientific purpose herein. Rather, it is a means



to provide *flexibility* for prevalent anthropocentric issues and laws relevant to the taxonomy, systematics, and conservation of invertebrate fauna such as *Speyeria*.

### Objectives and Hypotheses

Accurate species and subspecies identification remains problematic for some *Speyeria* taxa, and determinations are often affixed by locality. It is imperative to choose useful characters and avoid individual aberrations, mutations and characters subject to environmental influences. Further investigation into use of wing facies to delimit *Speyeria* taxa is warranted, 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 diagnoses. A suite of useful and environmentally stable characters, including the external morphologies of adults and immature stages, genitalia, DNA sequences, and life history traits, is still needed for *Speyeria*. Beyond the scope of this study, further ecological (e.g., pheromone testing) studies, examination of wing patterns and coloration under ultra-violet light, DNA sequences of several gene regions, and rearing and cross breeding studies are also warranted.

### Objectives

- 1. Develop detailed species and subspecies diagnoses for 16 *Speyeria* species and 25 *Speyeria atlantis-hesperis* subspecies. Each diagnosis will include synonymies, type specimen data, taxonomic information and morphological descriptions, distributions, and life history information.
- 2. Infer a phylogeny and test the monophyly of the 16 currently recognized species of *Speyeria* species based on combined morphological, life history, and genetic/sequence data. Investigation of useful external and internal morphological characters will be made.
- 3. Survey the genitalia within *Speyeria* the *Speyeria atlantis-hesperis* complex to determine if there are evolutionary informative characters for phylogenetic analyses.
- 4. Database distributional data for *Speyeria atlantis-hesperis* gleaned from museum and private collection locality records on Diversity of Life web-site.

- 5. Develop *Speyeria* DNA barcode database for COI gene at Barcode of Life Data Systems, University of Guelph, for use in future molecular analyses.
- 6. Compile, identify, label, and properly preserve *Speyeria* specimens for frozen tissue collection to be utilized for future molecular research at the McGuire Center for Lepidoptera and Biodiversity.
- 7. Photograph type specimens for 16 *Speyeria* species and 25 *S. atlantis-hesperis* subspecies, and photograph wings on specimens utilized for morphological and genetic studies.
- 8. Illustrate and photograph internal and external morphological characters utilized in analyses.

### **Central and Peripheral Hypotheses**

The central hypothesis is the following: If comprehensive species diagnoses, taxonomic reviews, biogeographical data, and phylogenetic analyses are compiled and conducted, they may provide a better understanding of the inter- and intraspecific relationships, evolutionary history, and the accuracy of nomenclature associated with *Speyeria*. The peripheral hypothesis is the following: If appropriate species concepts are applied to the results of the phylogenetic analyses and compilation of biogeographical data, they may provide additional justification for conserving members of this taxon.

## CHAPTER 2

### *SPEYERIA* DIAGNOSIS AND KEY TO SPECIES, SPECIES ACCOUNTS, AND *SPEYERIA ATLANTIS* AND *SPEYERIA HESPERIS* SUBSPECIES ACCOUNTS

A diagnosis for *Speyeria* (Scudder 1889), based on the genotypic species *Speyeria idalia* (Drury), is included here as baseline for comparative morphology and phylogenetic studies of members of this genus (Table 1). A key to adult *Speyeria*, modified from Ehrlich and Ehrlich (1961), Ferris (1971a), Hammond (1978), and Scott et al. (1998), is also included to aid in species identifications. I attempted to use the least regionally variable characters in developing the key, but the key presented here is at best superficial and should be used in conjunction with color images of adult habitus to aid in the identification of *Speyeria*. Geographical information is also included in the key for some species.

To gain a better understanding of nomenclature, taxonomy, life histories, and distributions, the species and subspecies accounts were compiled based on the available literature, field-work, and collection data. Diagnoses and life history information primarily pertain to the nominate taxon for each species unless otherwise indicated. Larval hostplant and adult food records include those reported in the literature for nominate as well as subspecific taxa. Images of primary and a few miscellaneous type specimens are also included for many of the taxa discussed herein. Distributional information for *Speyeria* was obtained from the literature and detailed distributional information for *Speyeria atlantis* (Edwards 1863a) and *Speyeria hesperis* (Edwards, 1864a) was also taken from specimen label data available in institutions and private collections. Errors in nomenclature are identified, and taxonomic and life history information is also updated and discussed. Compilation of these accounts has also provided baseline data and characters for systematic work and analyses reported in subsequent chapters.

## Materials and Methods

Numerous publications, directly and indirectly relevant to *Speyeria* species, were reviewed to compile the following accounts. An attempt to maintain a standard terminology for morphological and behavioral traits associated with *Speyeria* in the literature was made; morphological and behavioral terminology follow 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 no attempt was made to use the current taxonomy of plant species) unless otherwise noted. Recognition of nomenclatural errors, synonymies and type information was greatly facilitated by reference to dos Passos and Grey (1947), McHenry (1964), Brown (1965), Miller and Brown (1981) and Ferris (1989a,b), but several other taxonomic works were also utilized and are referenced in the profiles. 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. Bracketed author(s) and year of publication are references for which the name was first used as it appears in these accounts. Bracketed text (i.e., sex of specimen) in the Type Label Data section was included on the original label as a symbol and is included to indicate the sex of the specimen. Species accounts are 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. *Speyeria atlantis* and *S. hesperis* accounts are presented in order following Scott et al. (1998). Common names associated with *Speyeria* were taken from Scudder (1889), Miller (1992), The International Lepidoptera Survey (2007), and original species and subspecies descriptions when vernacular names were included.

In addition to specific literature cited in the accounts, the following literature was utilized for life history and distributional information: Acorn (1993), Adams and Finkelstein (2006), Allen (1997), Allen et al. (2005), Austin (1981), Austin (1985b), Brooks (1942), Brown et al. (1957), Cary and Holland (1992), Clark and Clark (1951), Cohen and Cohen (1991), Comstock J. A. (1989-reprint from original publication date of 1925), Comstock W. P. (1940), Covell and Straley (1973), Davenport (1995), Davenport (1998), DeFoliart (1956), Dornfeld (1980), Douglas and Douglas (2005), Drees and Butler (1978), Dunford (2005), Dunford and Ekin (2005), Ebner (1970), Ellis (1975), Ely et al. (1983), Emmel (1964, 1998), Emmel and Emmel (1973), Emmel et al. (1992), Eriksen (1962), Ferge (2002), Ferris (1971b), Ferris (1976a), 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), Hinchliff (1996), Holland (1974), Holland (1984), Holland and Cary (1996), Holmes et al. (1991), Hooper (1973), Hubbard (1965), Irwin and Downey (1973), Johnson (1972), Klassen (1984), Kohler (1980), Kozial (1994), Lafontaine and Wood (1997), Larsen and Bovee (2001), Lavers (2006), Layberry et al. (1998), Marrone (1994), Masters (1972), Miller and Brown (1981), 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 (1973a), Scott (1975), Scott (1986a,b), Scott (1992), Scott (2006a,b), Scott et al. (1968), Scott and Scott (1978), Scott et al. (1998), Scudder (1889), Shapiro and Shapiro (1973), Shields (1963), Shields (1966), Shields et al. (1970), Shields and Emmel (1973), Shuey et al.

(1987), Shull and Badger (1972), Shull (1987), Simmons (1963), Snyder (1896), Stewart (2001), Threatful (1988), Tietz (1952), Tilden (1963), Tilden and Huntzinger (1977), Tilden and Smith (1986), Toliver et al. (2001), Tuttle [Ed.] (1996-2006), Wagner (2005), and Warren (2005).

Coverage of the literature was meant to be as comprehensive as possible, but not all of the published life history and distributional information currently available for *Speyeria* is cited.

Additional locality data for *S. atlantis* and *S. hesperis* was gleaned from specimen label data from the following museum and private collections (acronyms for museums primarily follow the Bishop Museum's Abbreviations for Insect and Spider Collections of the World (<http://hbs.bishopmuseum.org/codens/codens-inst.html>) (last visited September 2007): Allyn Museum of Entomology (AME) [currently McGuire Center for Lepidoptera and Biodiversity (MGCL)-Florida Museum of Natural History (FLMNH)], American Museum of Natural History (AMNH), Carnegie Museum of Natural History (CMNH), C. P. Gillette Museum of Arthropod Biodiversity (CSUC), Field Museum of Natural History (FMNH), Clifford D. Ferris, Florida State Collection of Arthropods (FSCA), McGuire Center for Lepidoptera and Biodiversity-Florida Museum of Natural History (MGCL-FLMNH), Crispin Guppy, Norbert Kondla, Milwaukee Public Museum (MPM), Monte L. Bean Life Science Museum (Brigham Young University-BYU), James A. Scott, Steve Spomer, Utah State University Insect Collection (EMUS), University of Wyoming Insect Museum (ESUW) and Andrew D. Warren. Abbreviated records (i.e., state and county information) are included in the subspecies accounts. Locality records were also exported in Microsoft Excel spreadsheet format to personnel at DiversityofLife.org (DOL) (<http://www.diversityoflife.org/>) for databasing. Distributional maps are generated by selecting a given species/subspecies and following the instructions. Maps are either in road, aerial satellite imagery, or hybrid (i.e., road map and aerial satellite) format. A

navigation and zoom function allows the user to visualize the entire distribution or to focus on single locality data points.

Type specimen images were taken by the author 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 utilized to take images in order to reduce the reflection of silver wing scales present on most species. Enhancement of images (i.e., focus sharpening and color adjustment) included in this study was completed utilizing 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 probably produce the most accurate wing color images). Type specimen images provided by various museum personnel are indicated; camera and lighting specifics are not known. Table 2 includes a list of the museum names and abbreviations where specimens were photographed. Species names included in the figure captions are written following the current taxonomy; thus, they are not always the name associated with the specimen when it was described. Names that were not given to the species when it was described are preceded by an = sign.

### ***Speyeria* Diagnosis**

*Speyeria* Scudder, 1872 p. 23

Genotype: *Papilio Nymphalis Phaleratus Idalia* Drury, 1773 p. 1; 1770 p. 25

*Argynnis* Fabricius 1807 p. ix

Genotype: *Papilio paphia* Linnaeus, 1758 p. 481

*Semnopsyche* Scudder, 1875 p. 258 [treated as a subgenus by dos Passos and Grey, 1947]

Genotype: *Papilio Nymphalis Phaleratus Diana* Cramer, 1777 pp. 4, 148

*Neoacidalia* Reuss, 1926 p. 69

Genotype: *Papilio cybele* Cramer, 1775 [sic]

The adult description for *Speyeria*, presented here from Scudder (1889, p. 528), is based on the genotypic species, *Speyeria* [*Papilio*] *idalia* (Drury, 1773). The following description is slightly modified to include more recent morphological terminology and excludes some extraneous descriptive wording, but is in large part verbatim: Head rather large, profusely covered with moderately long hairs, longest about the base of the antennae. Slightly and broadly depressed dorsally, broader than high, but not as broad as the eyes; dorsal margin broadly angular, the apex depressed between the antennae, its lateral margins nearly straight; ventral margin broadly rounded and depressed only slightly. Vertex of head large and swollen, but scarcely rising above the upper level of the eyes, twice as broad as long, the posterior margin broadly rounded and flattened medially, the anterior margin sloping extended forward and angulate with apex removed. Eyes large, full, and not covered with scales or hairs. Antennae inserted in deep pits with a transverse channel between them, separated by a space fully equal to the diameter of the apex of the pedicel; longer than the abdomen, composed of 52 segments, the last 13 of which form a slightly depressed cylindrical club; each segment flattened ventrally, suboval in shape, three times as broad as scape, two and a half to three times as long as broad. Palpi small and thin, approximately half the length of the eye, curving slightly forward, the apical joint about one-sixth the length of the penultimate segment and thickly clothed with recumbent scales, the basal two joints with long, coarse, projecting hairs on each side, the third segment with shorter, scale-like hairs which grow longer in advance of the eyes, curving upward to partially encircle them.

Prothoracic lobes moderately large, not swollen, slightly flattened anteriorly, the dorsal surface nearly straight, both ends well rounded, scarcely four times as broad as long, and slightly



higher than long. Paired articulated dorsal plates long and slender, slightly enlarged, more than three times longer than the widest point, the base moderately broad or nearly square, the posterior lobe tapering rapidly next to the base, the tip well rounded, the dorsal margin slightly curved, scarcely sinuate, the ventral margin angulate.

[Note: Wing venation in this study follows the Comstock-Needham system (see Figure 2-3) for the reasons discussed in Miller (1969); wing terminology included here is presented as it appears in Scudder (1889)]

Forewing (see Figure 2-1A) seven-eighths as long as broad, the costal margin rather strongly convex, the medially portion less so, the apical angle well-rounded; outer margin nearly straight, rounded off toward the angles; inner margin slightly convex in males, slightly concave in the females. First superior subcostal vein arising beyond the middle of the outer half of the upper margin of the cell; second vein at the end of the cell, or slightly within the extreme limit of its upper border, which is pushed outward slightly at this location; this vein at approximately two-thirds the distance from the apex of the cell to the outer border; the fourth vein is a short distance beyond it, about half way between the apex of the cell and the outer border; second inferior subcostal vein arising two-fifths the way down the cell; the latter slightly more than two-fifths the length of the wing, three times as long as broad. Last median vein connected with the vein closing the cell, nearly half as far beyond its base as it is from the base of the first vein.

Hindwing (see Figure 2-1A) very strongly and roundly shouldered next to the base, beyond which it is slightly (females) or strongly (males) convex, the outer angle broadly rounded. Outer margin regularly or fully rounded, very slightly at the upper subcostal vein (males) or very fully rounded, prominent, and roundly angulated at the upper median vein (females); inner margin broadly and abruptly expanded next to the base, beyond that straight nearly to the tip of the

internal vein, beyond that excised and slightly and roundly emarginated, the angle rounded. Precostal vein curved strongly outward; first subcostal vein midway (males) or two-thirds (female) the distance from the branching point of the costal and subcostal veins to the origin of the second subcostal vein; cell closed. Androconial scent scales (males) ribbon-shaped, equal and slender, approximately 23 times longer than broad, the basal portion black, the rest transparent, terminating in a lancet-shaped fringed tip.

Forelegs small, cylindrical, either clothed as the other legs (females) or also with a few short hairs on either side not projecting greatly (males); tibiae scarcely more than one-third as long as the hind tibia, the tarsi slightly shorter than the tibia; tarsi composed of either a single undivided segment with a bluntly conical apex (males), or five segments, visible without denudation, of which the first segment forms fully three-fifths of the whole tarsus, the second segment nearly half of the remainder, the fourth is small and the fifth segment is the smallest; each of the segments except the terminal segment bearing short, rather stout spurs ventrally, all segments also bear a row of minute spines ventrally on either side (females). Middle tibiae five-sixths the length of the hind tibiae, bearing a row of long, slender, scarcely tapering, slightly diverging spines ventrally on either side, the terminal ones developed to very long and slender, scarcely tapering spurs; the tibiae also bear numerous, short, slender, nearly recumbent spines dorsally and on the inner margin. Tarsi have four uniformly spaced rows of numerous, short, stout, slightly curving spines, the apical ones of each segment longer than the rest; similar spines are located dorsally on all of the segments, scarcely occurring in longitudinal rows. Tarsal claws long, rather stout, strongly curved at base, beyond the base nearly straight and equal, the apical third falcate and tapering to a pointed tip; pulvillus minute.

Male genitalic armature (see Figure 2-10) stout, globose, arched, hook (=uncus) large, strongly compressed, longer than the centrum (=tegumen), somewhat curved and directed slightly downward, the tip minutely hooked; clasps (=valvae) large, broad and long, more than twice as long as broad, slightly curved in either direction, the upper process of valvae arising near the middle of the dorsal margin, several times longer than broad, the basal half nearly equal, beyond that greatly tapering; main blade of valve expanding roundly at tip and beyond the middle of the dorsal margin, and especially at the dorsal posterior angle, where a small process (=digitus) is directed upward and slightly forward and inward.

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 (Figure 2-1A) and a fairly brief description of ‘Idalia’ (Figure 2-1B). *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 *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.

### Key to the Species of *Speyeria*

Abbreviations: VHW=ventral hindwing; DHW=dorsal hindwing;  
M=medial wing vein; A=anal wing vein

[see Figures 2-2 and 2-3 for wing terminology; Figure 2-3 follows primarily the Comstock Needham system, as presented by Miller, 1969 (p. 46)]

1. Female genitalia: bursa copulatrix prolonged and constricted to form a secondary sac .....2

1'. Bursa copulatrix simple (ovoid), not constricted to form a secondary sac (partial secondary sac occurs in <i>S. idalia</i> ).....	4
2. VHW with basal two-thirds uniform in color, without silver or whitish spots; males and females sexually dimorphic (males with orange DHW band; females with bluish band on DHW)(occurs east of the Rocky Mountains).....	<i>S. diana</i>
2'. VHW with basal two thirds with silver or whitish spots; males and females with slight sexual dimorphism (females without bluish band on DHW).....	3
3. Males with M <sub>1</sub> -2A dorsal wing veins appearing widened dorsally due to dark scaling along them; DHW on females without rosy-tinged patch in median area towards inner margin; both sexes tending to brownish wing coloration ventrally.....	<i>S. cybele</i>
3'. Males with scaling of dorsal wing veins thin or absent dorsally (resembling females in this respect); DHW on females usually with a rosy-tinged patch in median area towards inner margin; both sexes tending to reddish wing coloration ventrally.....	<i>S. aphrodite</i>
4. Male genitalia with uncus comparatively wide, ventrally excavate near tip.....	5
4'. Male genitalia with uncus more uniformly tapering, not ventrally excavate near tip.....	6
5. DHW with one (male) or two (female) rows of whitish spots (occurs east of the Rocky Mountains).....	<i>S. idalia</i>
5'. DHW not bearing one or two rows of whitish spots (occurs primarily in Rocky Mountain states and west of the Rocky Mountains).....	<i>S. nokomis</i>
6. Male genitalia with valva bearing a long process (=digitus), this process three to four times as long as broad; large, conspicuous silver spots on VHW.....	<i>S. edwardsii</i>
6'. Male genitalia with valva bearing relatively short process (=digitus), this process less than three times as long as broad; VHW spots smaller, may be silver or unsilvered.....	7
7. DHW spots unsilvered or obsolete (restricted to central California).....	<i>S. adiaspe</i>
7'. DHW spots silver or cream colored [some populations of <i>S. mormonia</i> (e.g., White Mountains, Arizona) bear obsolete DHW spots].....	8
8. VHW disc dark reddish to maroon in color, usually with conspicuous wash of lavender overscaling, spots cream or unsilvered (occurs in Rocky Mountains and primarily west of the Rocky Mountains).....	<i>S. hydaspe</i>
8'. VHW disc devoid of conspicuous lavender overscaling [some populations of <i>S. zerene</i> (e.g., Sierra Nevada Mountains) bear lavender overscaling], spots silvered or unsilvered.....	9
9. VHW disc green, greenish brown, or brown (green scaling also occurs in a few <i>S. coronis</i> , <i>S. zerene</i> , <i>S. egleis</i> and <i>S. mormonia</i> populations), slender elongate median spots, almost devoid of yellow submarginal band, discal spots always silver (only occurs west of the Mississippi River).....	<i>S. callippe</i>
9'. VHW disc various colors (usually not green), yellow submarginal band usually present, median spots variously shaped.....	10
10. VHW disc never with green scaling.....	11
10'. VHW disc usually without green scaling, but with some populations having green scales on disc.....	13
11. Occurring in the Spring Mountains in southern Nevada.....	<i>S. carolae</i>
11'. Not occurring in the Spring Mountains in southern Nevada.....	12
12. VHW spots always silvered, chocolate-brown to blackish brown disc.....	<i>S. atlantis</i>
12'. VHW spots cream colored, but may be silver, disc usually reddish [a few populations (e.g., Raton Mesa, New Mexico and Ruby Mountains, Nevada) bear a brownish disc].....	<i>S. hesperis</i>

13. Male with dorsal wing scaling of M<sub>1</sub>-2A veins “thin” and similar to female; size small on the average relative to remaining species in key (forewing length 22-26 mm).....*S. mormonia*
- 13'. Male with widened dorsal wing scaling of M<sub>1</sub>-2A veins compared to those of female; size on the average larger (forewing length usually greater than 26 mm).....14
14. VHW disc color not so reddish and tending to brown, may be overscaled with green; discal spots may be silver, partially silver, or opaque.....*S. egleis*
- 14'. VHW disc color brownish to greenish or dark red in some populations; discal spots usually silver.....15
15. Generally larger wingspan than *S. zerene*, usually with greenish-brown on VHW disc, varying to dark red-brown in some populations.....*S. coronis*
- 15'. Generally smaller wingspan than *S. coronis*, VHW disc with light buff, brown VHW disc to colors overlapping with *S. coronis* .....*S. zerene*

### Species Accounts

Note: Author names and year of publication appearing in brackets are references for which the name was first used as it appears in these accounts]

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

[dos Passos and Grey 1945a]

(Figure 2-8)

*Papilio Nymphalis Phaleratus Idalia* Drury, 1773 p. 1; 1770 p. 25

*Argynnis astarte* Fisher, 1858 p. 179

*Argynnis Ashtaroth* Fisher, 1859 p. 352

*Argynnis Idalia-Infumata* Oberthür, 1912 p. 315

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

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

**Common names.** Regal Fritillary, Regal Silverpot 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 2-9).

**Type locality.** See Figure 2-1B for original description. New York. Fixed 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 has a thick, hooked uncus (Figure 2-10) 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 has been given to the western populations. Eggs are pale green when newly laid, changing to tan as the larva develops inside.

Larvae (Figure 2-8C) 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 2-8B) 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, 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 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). 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 hostplants or on hostplants (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 Shepherd 2005a,b). Williams (1999, 2001a, 2001c) 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 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 captivity bred populations, and this may also be a factor in the decline of some wild populations. Small, isolated populations are vulnerable to local extinction 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 (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 hostplants.** *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 bergamont, blackberry, dogbanes, crown vetch, Deptford pink, spotted knapweed, ox-eye daisy, dotted blazing star, prairie blazingstar, purple coneflower, black Sampson (Shapiro and Shapiro 1973; Debinski et al. 2000; Ross 2002; Douglas and Douglas 2005; Ferster 2005; Shepherd and Debinski 2005; also see Kopper et al. 2001b for *S. idalia* and nectar source phenologies).

***Speyeria diana* (Cramer, 1777)**

[dos Passos and Grey 1945a]

(Figure 2-4A male; 2-4B female)

*Papilio Nymphalis Phaleratus* Diana Cramer, 1777 pp. 4, 148

**Common names.** Diana Fritillary, Great Smokies Fritillary, Ozark Diana Fritillary.

**Type deposited.** Holotype (male) (see Miller and Brown 1981) at The Natural History Museum, London (Figure 2-5).

**Type locality.** The original description (Cramer 1777) did not contain a collection date, sex of specimen, or series data; “en Virginie”. Fixed 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. 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.

**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.) and *Limenitis astyanax* (F.) in various parts of the species range (Scudder 1889; Ehrlich 1961). 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 hostplants.** *Viola papilionacea*, *V. cucullata*, *V. cornuta*, *V. sororia*; partially reared on *Vernonia noveboracensis* (Compositae) (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)**

[dos Passos and Grey 1945a]

*Papilio Nymphalis Phaleratus Cybele* Fabricius, 1775 p. 516

*Papilio Nymphalis Phaleratus Daphnis* Cramer, 1775 p. 89; 1776 p. 152

*Papilio Nymphalis Phaleratus Daphnis*? Martyn, 1797 p. 7

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

**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 British Museum of Natural History (Figure 2-6).

**Type locality.** The original description (Fabricius 1775) did not contain a collection date, sex of specimen, or series data; “Habitat in America”. Fixed 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.** Adult wingspan ranges from 65-105 mm. There are several ‘subspecies’ included within the *S. cybele* species complex. 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*, 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, similar to those in *S. aphrodite*, *S. diana*, *S. idalia*, and *S. nokomis*. 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 1880b) 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 dorsally 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 *cybele* (Edwards 1880b).

**Range.** The *S. cybele* species complex extends 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 considered common. Records for *S. cybele* exist as far south as Mississippi (Lafayette County-Mather 1966) and Florida (Kimball 1965; Heppner 2003). It was once considered common in areas such as Staten Island, but was reportedly rare in the early 1970's (Shapiro and Shapiro 1973). 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 *cybele* and noted considerable fluctuations in its numbers from one season to the next.

**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* and unfed first instar larvae hibernate; however, Scudder (1889) noted that eggs are also laid upon the leaves and stalks of the hostplant. 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 hostplants.** *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).

**Adult food sources.** Butterfly milkweed, *Asclepias exaltata*, common milkweed, 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; 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)**

[dos Passos and Grey 1945a]

*Papilio Nymphalis Phaleratus* Aphrodite Fabricius, 1787 p. 62

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

*Argynnis aphrodite* aberrant *bakeri* Clark, 1932

**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 2-7).

**Type locality.** The original description (Fabricius 1787) did not include a collecting date, sex of specimen, or series data; “Habitat in America meridionali”. Fixed 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.** Adult wingspan ranges from 50-84 mm. Males are typically orange-brown and there is 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  $M_3$  and  $CuA_1$ . 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). There are several known subspecies within *S. aphrodite* and the 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.** The range of the *S. aphrodite* complex extends from the eastern United States the Appalachians in 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. There is an isolated population in the White Mountains of eastern Arizona [*S. a. byblis* (Barnes and Benjamin)]. 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 *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* or where *Viola* 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 under mahogany bushes and other places in August and September 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. Flight period is late June through mid-September.

**Larval hostplants.** *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 foodplants, 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* (W. H. Edwards, 1863b)**

[dos Passos and Grey 1945a]

*Argynnis Nokomis* W. H. Edwards, 1863b p. 221

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

**Common names.** Nokomis Fritillary, Western Seep Fritillary.

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

**Type locality.** Rocky Mountains and mountains of California. Neotype (male) (Figures 2-11) fixed 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 *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 2-12) 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.** Adult wingspan ranges from 63-80 mm. There are several ‘subspecies’ included in *nokomis* complex. 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 *nokomis*.

**Range.** 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). *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. Known localities are widely separated due to restricted habitat.

**Life History.** Habitats include Upper Sonoran to Canadian Zone moist meadows near streams, permanent spring fed meadows, marshlands, boggy streambanks, and seeps; 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 *nokomis* is confined to mesic seep habitats with great expanses of unsuitable, xeric habitat isolating populations. Eggs are laid singly and haphazardly near hostplants. 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. This species tends to fly on the average later than most other *Speyeria* species. 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. A population [*S. nokomis coerulescens* (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* in the central Great Basin.

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

**Adult food resources.** Thistles (Scott 1986b).

*Speyeria edwardsii* (Reakirt, 1866)

[dos Passos and Grey 1945a]

*Argynnis Edwardsii* Reakirt, 1866, p. 137

*Acidalia Edwardsi montana* Reuss, 1926, p. 439

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

**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 2-13).

**Type locality.** California; Pike's Peak, Teller County, Colorado Territory. Fixed by dos Passos and Grey (1947) based on lectotype as Pike's Peak, Teller 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 upperside. 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 *callippe* bears ventral hindwing marginal spots that are more pointed rather than rounded inwardly as they appear on *edwardsii*. *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 2-14) 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 to northern New Mexico, west to the Dakotas and western Nebraska and Oklahoma. 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). 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 hostplants.** *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)**

[dos Passos and Grey 1945a]

*Argynnis Coronis* Behr, 1864 p. 435

*Argynnis californica* Skinner, 1917 p. 328

**Common names.** Coronis Fritillary, Crown Fritillary, California Fritillary.

**Type deposited.** Putative lectotype (male) (but see Emmel 1998b) designated by dos Passos and Grey (1947) at Carnegie Museum of Natural History (Figure 2-15).

**Type locality.** California. Fixed by dos Passos and Grey (1947) based on lectotype as Alma, Santa Clara County, California. However, Brown (1965) questioned this 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 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. A label indicating that it is the neotype of *Argynnis coronis* Behr, designated by W.H. Edwards, 1865, was added to the specimen. This label was also not associated with the specimen I examined. It is possible that 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 was located at the time I visited the CMNH.

**Type label data.** *Coronis* Behr's type, Juba B type.

**Identification, taxonomy, and variation.** Several forms of this species range 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 *Speyeria 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 *Speyeria 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. 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 hostplants.** *Viola beckwithii*, *V. douglasii*, *V. nuttallii*, *V. purpurea* (Robinson et al. 2002).

**Adult food resources.** Mint, thistle.

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

[dos Passos and Grey 1945a] (Figure 2-16)

*Argynnis Zerene* Boisduval, 1852 p. 303

*Argynnis monticola* Behr, 1863 p. 84

**Common names.** Zerene Fritillary.

**Type deposited.** Lectotype (male) designated by dos Passos and Grey (1947) at National Museum of Natural History (Figure 2-17).

**Type locality.** California. Fixed 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-restricted 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., Boisdual. Ann. Fr. 1852. p. 303; EX MUSAEOL Dris. BOISDUVAL; Oberthur Collection; Type A zerene Bdv. a/c Hofer; Barnes Collection.

**Identification, taxonomy, and variation.** Adult wingspan is 48-67 mm. There are several 'subspecies' included within the *zerene* species complex and wing coloration is highly variable (see Grey and Moeck 1962; Grey 1972). The upperside 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.** *Speyeria zerene* forms range 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. z. hippolyta* (Edwards), *S. z. behrensii* (Edwards), and *S. z. myrtleae* dos Passos and Grey] and some populations along the California coast have been extirpated.

**Life history.** Depending on geographic location, *zerene* forms occur in a wide array of habitats. 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. zerene 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. zerene myrtleae* and *S. zerene hippolyta* (Launer et al. 1994). *Speyeria zerene behrensii*, *S. zerene hippolyta*, and *S. zerene myrtleae* are presently listed as federally endangered. Several life history studies and land management discussions occur in the literature for these rare *zerene* forms (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. zerene hippolyta* (as well as *Speyeria* in general) in detail. Flight period 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.

**Larval hostplants.** *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)**

[Emmel and Austin 1998]

*Speyeria zerene carolae* (dos Passos and Grey) [dos Passos, 1961 p. 221]

*Speyeria coronis carolae* (dos Passos and Grey) [dos Passos and Grey, 1947 p. 11]

*Argynnis coronis carolae* dos Passos and Grey, 1942 p. 2

**Common names.** Carol's Fritillary.

**Type deposited.** Holotype (male) at American Museum of Natural History (Figure 2-18).

**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 M<sub>3</sub>, 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 form between *S. coronis* and *S. zerene* (Scott 1986b). Formerly recognized as a subspecies within the *S. coronis* complex (dos Passos and Grey 1942, 1947), and later *S. zerene* complex by dos Passos (1961) and Austin (1981), *S. carolae* was considered a distinct species by Emmel and Austin (1998) and Austin (1998b) based on differences in wing patterns and chromosome numbers (but see North American Butterfly Association 2001). 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 hostplant *Viola charlestonensis* support full species status (Emmel and Austin 1998).

**Range.** Isolated in southern Nevada's Spring Mountains in 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 hostplants.** Probably *Viola charlestonensis* (Emmel and Austin 1998).

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

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

[dos Passos and Grey 1945a]

(Figure 2-19)

*Argynnis callippe* Boisduval, 1852 p. 302

**Common names.** Callippe Fritillary, Callippe Silverspot.

**Type deposited.** Lectotype (male) designated by dos Passos and Grey (1947) at National Museum of Natural History (Figure 2-20).

**Type locality.** California. Fixed 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 MUSAEO Dris. BOISDUVAL; Oberthur Collection; Type callipe Bdv. a/c Hofer; Barnes Collection.

**Identification, taxonomy, and variation.** Adult wingspan is 47-74 mm. There are several geographic forms with variable coloration on the wings. 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* species, 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 utilizing

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.** The *S. callippe* species-complex extends 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 *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). 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 new 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 1983, Connor et al. 2002).

**Larval hostplants.** *Viola beckwithii*, *V. douglasii*, *V. nuttallii*, *V. pedunculata*, *V. purpurea*, *V. purpurea quercetorum*; *Artemisia*? (Compositae) (Durden 1965; Hammond 1995; Robinson et al. 2002).

**Adult food resources.** Thistles (Pyle 1995).

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

[dos Passos and Grey 1945a]

*Argynnis Egleis* Behr, 1862 p. 174

*Argynnis montivaga* Behr, 1863 p. 84

*Argynnis Astarte* Edwards, 1864b p. 435

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

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

**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 2-21).

**Type locality.** California. Fixed by dos Passos and Grey (1947) based on lectotype [=neotype of Emmel et al. (1998b)] as 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 *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 21).

**Type label Data.** Prob. Type egleis Bdv.; Egleis Bdv. California; EX MUSAEOL 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.** Adult wingspan is 44-59 mm. There are several subspecific forms in the *S. egleis* species complex. 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. zereene*, *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 *egleis* form, very closely resembles members of the *Speyeria 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 *egleis* is found throughout the entire Sierra Nevada above 6,000 ft. (Emmel and Emmel 1998a).

**Life history.** *Speyeria egleis* forms occur in mixed woodlands, open rocky slopes, meadows and streambanks. 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 pine cones, sticks, and stones in California (Lembert 1893). Flight period is from early June through early October.

**Larval hostplants.** *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 adiate* (W. H. Edwards, 1864)**

[Emmel and Emmel 1973]

*Speyeria egleis adiate* (W. H. Edwards), 1864b p. 436; [dos Passos and Grey 1945a]

*Argynnis Adiate* W. H. Edwards 1864b, p. 436

*Argynnis Adiante* Boisduval 1869, p. 61

*Argynnis Adraste* W. F. Kirby 1871, p. 160

*Argynnis adianthe* Barnes and McDunnough, 1917 p. 8

**Common names.** *Adiate* 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 2-22). 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 Adiate*, housed at the

Carnegie Museum of Natural History, as the lectotype for *S. adiate* (Figure 2-23) (also see Type Locality and Type Label Data sections below).

**Type locality.** California. Fixed by dos Passos and Grey (1947) as Santa Cruz, Santa Cruz County, California. F. M. 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 *adiaste* populations are (or were) known from the city of Santa Cruz.

**Type label data.** From dos Passos and Grey (1947): Adiante Bd Calif.; EX MUSAEODris. 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.** Adult wingspan 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. 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. 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 1983, Garth and Tilden 1986).

**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 hostplants 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 *adiaste* forms is due to fire suppression and resulting habitat change (Scott 1986b).

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

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

#### ***Speyeria atlantis* (W. H. Edwards, 1863)**

[dos Passos and Grey 1945a]

*Argynnis Atlantis* Edwards, 1863a p. 54

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

*Argynnis atlantis canadensis* dos Passos, 1935

*Speyeria atlantis canadensis* (dos Passos) 1935 [dos Passos and Grey 1947] [synonymized by Scott et al. 1998] (Figure 2-29)

**Common names.** Atlantis Fritillary, Mountain Silverspot, Mountain Fritillary, Mountain Silver-spotted Butterfly

**Type deposited.** Lectotype (male) designated by dos Passos and Grey (1947) at American Museum of Natural History (Figure 2-24).

**Type locality.** Mountainous districts of the northern states and parts of British America. Fixed by dos Passos (1935) based on lectotype as Hunter, Greene County, Catskill Mountains, New York. Brown (1965) noted that Holland's 1931 image of *atlantis* is a much better match of the *atlantis* that occurs 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 *atlantis*.

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

**Identification, taxonomy, and variation.** Adult wingspan ranges from 50-69 mm. *Speyeria atlantis* forms are widespread and variable. Prior to splitting of the hypothetically distinct species *Speyeria hesperis* from *S. atlantis*, there were over 25 subspecific or geographical forms associated with the *S. 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. 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, and because there are several reports of the two forms interbreeding in various parts of their range (North American Butterfly Association 2001) The nominate, eastern *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. R. Holland (1969) noted that specimens taken from Hawkes Bay, Newfoundland were even smaller and more red than *S. a. canadensis* taken at the type locality, Doyles Station. This variability notes the probable relationship of nominate *atlantis* with *S. a. canadensis* and further corroborates the decision by Scott et al. (1998) to sink the smaller Canadian *atlantis*. An *atlantis* form occurs in the mountains of West Virginia that may be an undescribed subspecies (Gatrelle 1998). Larvae 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. Disjunct populations exist in the Black Hills of South Dakota (see Grey et al. 1963) [*S. atlantis pahasapa* Spomer, Scott, Kondla], central Colorado [*S. atlantis sorocko* Scott, Kondla, Spomer], and northwestern Montana, northern Idaho, and Manitoba [*S. atlantis hollandi* (F. H. Chermock)]. *Speyeria atlantis* has been tentatively recorded in northeastern Illinois but is likely not a resident (Bouseman and Sternberg 2001).

**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 *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.

Eggs are laid near the base of hostplant. 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). Flight period is mid June to September. The mobility of western “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.

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

**Adult food resources.** Milkweeds, vetches, mints, mud, dung (Scott 1986b; Douglas and Douglas 2005).

#### ***Speyeria hesperis* (W. H. Edwards, 1864)**

[Scott et al. 1998]

*Speyeria atlantis hesperis* (W. H. Edwards), 1864a p. 502 [dos Passos and Grey 1945a]

*Argynnis Hesperis* W. H. Edwards, 1864a p. 502

**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 2-25).

**Type locality.** Fixed 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 1964.

**Identification, taxonomy, and variation.** Formerly considered a subspecies of *S. atlantis*, *S. hesperis* is variable throughout its range and a number of subspecific taxa have been recognized. *Speyeria hesperis* and *S. atlantis* occur together or in close proximity in many areas of the western North America and in South Dakota. Dos Passos and Grey (1965) noted that *hesperis* represented an unsilvered subspecies of *S. atlantis* along the Front Range in Colorado. Tebaldi (1982) (also see Ferris 1983) utilized starch gel electrophoresis of six enzymes to analyze the relationships among three phenotypes of *Speyeria 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 *atlantis* always silvered. 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 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* as it does in adults (see Scott et al. 1998) due to various local climatic conditions.

**Range.** *Speyeria hesperis* ranges 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 hostplants.** *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).

***Speyeria hydaspe* (Boisduval, 1869)**

[dos Passos and Grey 1945a]

*Argynnis Hydaspe* Boisduval, 1869 p. 60

**Common names.** Hydapse Fritillary, Lavender Fritillary.

**Type deposited.** Lectotype (male) designated by dos Passos and Grey (1947) at National Museum of Natural History (Figure 2-26).

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

**Type label data.** Monticola Behr. Hydaspe Bd. Californ.; EX MUSAEOL Dris. BOISDUVAL; Argynnis Hydaspe Bdv Californie; Argynnis Hydaspe [male], Boisduv. ex 2 typic. specim.; Type hydaspe a/c Hofer; Oberthur Collection; Barnes Collection.

**Identification, taxonomy, and variation.** Adult wingspan is 41-58 mm. There are several subspecific taxa associated with *S. hydaspe*, but they 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 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 *Speyeria atlantis* populations in the Pacific Northwest and California Sierra Nevada Mountains resemble *S. hydaspe*. Kondla (2001) clarified the taxonomic relationships and nomenclature associated with *hydaspe* 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 *Speyeria zerene*. Larval coloration is likely variable throughout the range of *S. hydaspe* due to various local climatic conditions.



**Range.** *Speyeria hydaspe* forms range 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 hostplants.** *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).

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

[dos Passos and Grey 1945a]

(Figure 2-27)

*Argynnis Mormonia* Boisduval, 1869 p. 58

**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 2-28).

**Type locality.** Oregon. Fixed 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 fixed. Miller and Brown (1981) later restricted the type locality to the vicinity of Pyramid Lake, Nevada. Emmel et al. (1998a) further restricted the type locality to Little Valley, W. of Washoe Lake, Washoe County, Nevada.

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

**Identification, taxonomy, and variation.** *Speyeria mormonia* can be identified by the smaller size compared to those of other *Speyeria* (wingspan 38-60 mm); on average it is the smallest species in the genus. The antennal clubs are relatively expanded compared to other *Speyeria* species. There are several subspecific forms included within the *mormonia* species complex. 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*. Distinct 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, *Speyeria mormonia luski* (Barnes & 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.

**Range.** *Speyeria mormonia* occurs along the mountainous regions of western North America from south-central Alaska south to central California in the Sierras and east-central Arizona, and north-central New Mexico, and 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 does occur at sea level in Alaska and to sagelands and plains in the Great Basin and Black Hills.

**Life history.** Known to occur in mostly subalpine habitat, including Canadian to lower Alpine zone meadows, or moist prairie valleys/meadows, and openings in subarctic forests. *Speyeria mormonia* forms are the most likely member of the genus to occur in high mountain habitats. Females lay eggs singly and haphazardly near hostplant. 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 far, especially females, and can stray into foothills or the Colorado plains. Boggs (1986, 1987a,b, 1988, 1997a,b), Boggs and Jackson (1991), Boggs and Ross (1993), and Boggs et al. (2004), have provided 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*, not directly encroached upon by human development, may be among the first victims of long term climate warming trends.

**Larval hostplants.** *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.*).

### ***Speyeria atlantis* and *Speyeria hesperis* Subspecies Accounts**

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

[dos Passos and Grey 1947]

[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 *Speyeria atlantis canadensis*): Newfoundland, New Brunswick, Nova Scotia, Ontario, Quebec.

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

[dos Passos and Grey 1947]

*Argynnis atlantis Holland* Chermock and Chermock, 1940 p. 82

**Common name.** Holland's Fritillary.

**Type deposited.** Holotype at Canadian National Collection (Figure 2-30).

**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.** Adult wingspan ranges from 50-60 mm. The discal and basal areas located on the ventral forewing and hindwing are deep brown compared to paler *atlantis* forms. This subspecies is considered the western terminus of the *atlantis* cline (Howe 1975).

**Range.** Riding Mountains of Manitoba, Peace River region, British Columbia.

**Life history.** Nothing could be gleaned from the literature.

**Larval hostplants.** *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, Spomer, 1998**

Forms of this subspecies may have been referred to as *Speyeria hesperis* [*atlantis*] *electa* (Edwards) [= *Argynnis Cornelia* Edwards], *S. hesperis* [*atlantis*] *nixies* (Hermann), or *Speyeria hesperis* [*atlantis*] *hesperis* (Edwards) in the past (see synonymies for these species).

**Common names.** Southern Rockies Fritillary.

**Type deposited.** Holotype at American Museum of Natural History (Figure 2-31).

**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.) states that this subspecies may be a redecoration of the form known as *S. hesperis nixies* (which has since been synonymized under *S. hesperis electa* by Scott et al. 1998). Adult wingspan is on average 60 mm.

**Range.** Southern Rockies.

**Life history.** Nothing could be gleaned from the literature.

**Larval hostplants.** *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, Kondla, 1998**

Forms of this subspecies may have been referred to as *Speyeria atlantis lurana* dos Passos and Grey in the past.

**Common name.** Dakota Fritillary.

**Type deposited.** Holotype at American Museum of Natural History (Figure 2-32).

**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.

**Range.** Black Hills, South Dakota.

**Life history.** Nothing could be gleaned from the literature.

**Larval hostplants.** *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 hesperis* (Edwards, 1864)**

[Scott et al. 1998]

[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**

[Scott et al. 1998]

*Argynnis lais* Edwards, 1883 p. 209 [this name was a primary homonym for *Argynnis lais* Scudder 1875, and dos Passos and Grey proposed a replacement name (*Speyeria atlantis helena*) in 1955] (Figure 2-33)

*Speyeria atlantis lais* (Edwards, 1883 p. 209) [dos Passos and Grey 1947; synonymized by Scott et al. 1998]

*Argynnis lais* form *dennisi* Gunder, 1927 p. 287 (Figure 2-34)

*Speyeria atlantis dennisi* dos Passos and Grey, 1947 [synonymized by Scott et al. 1998] [Gunder (1927) described this subspecies as *Argynnis lais* transitional form *dennisi* and dos Passos and Grey (1947) listed it as *Speyeria atlantis dennisi*; also see Masters (1973, 1974)]

*Speyeria atlantis helena* dos Passos and Grey, 1955 pp. 95-96

**Common name.** Northwestern Fritillary.

**Type deposited.** Lectotype (male) designated by dos Passos and Grey (1947) at Carnegie Museum of Natural History (Figure 2-33).

**Type locality.** From dos Passos and Grey (1947): Red Deer River, Alberta, Canada; Fixed by dos Passos and Grey (1947) as Edmonton, Alberta, Canada.

**Type label data.** According to dos Passos and Grey 1955, the type of *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 hostplants.** *Viola* spp.

**Adult food resources.** As with most *Speyeria*, *S. a. 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)**

[Scott et al. 1998]

*Dryas atlantis* race *beani* Barnes and Benjamin, 1926 p. 92

*Argynnis atlantis beani* Barnes and Benjamin form *hutchinsi* Gunder, 1932 p. 280

*Speyeria atlantis hutchinsi* dos Passos and Grey, 1947 [synonymized by Scott et al. 1998]

*Speyeria atlantis beani* (Barnes and Benjamin, 1926 p. 92) [the race *beani* has also been placed within *Speyeria electa* by Howe 1975]

**Common name.** Bean's Fritillary

**Type deposited.** Holotype at National Museum of Natural History (Figure 2-35).

**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 *hesperis*. Adult wingspan ranges from 50-55 mm. The ventral hindwing disc is usually bright red and the spots can silvered, entirely or partially unsilvered.

**Range.** Northern Washington, northern Idaho, British Columbia and the mountains of Alberta.

**Life history.** Nothing could be gleaned from the literature.

**Larval hostplants.** *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, Spomer, 1998**

Forms of this subspecies may have been referred to as *Speyeria hesperis [atlantis] beani* (Barnes and Benjamin) or *Speyeria hesperis [atlantis] helena* dos Passos and Grey in the past.

**Common name.** Brico Fritillary.

**Type deposited.** Holotype at Canadian National Collection (Figure 2-36).

**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.

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

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

**Larval hostplants.** *Viola* spp.

**Adult food resources.** As with most *Speyeria*, *S. a. 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**

[Scott et al. 1998]

*Speyeria atlantis ratonensis* Scott, 1981 p. 4

**Common names.** None.

**Type deposited.** Holotype at Natural History Museum of Los Angeles County (Figure 2-37).

**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 *atlantis-hesperis* forms, it is similar to *S. h. greyi* in Nevada. This subspecies 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, *helena* advanced north while *ratonensis* move upward.

**Larval hostplants.** *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**

[Scott et al. 1998]

*Speyeria atlantis greyi* Moeck 1950 pp. 61-64 [some authors (e.g., Hodges 1983; Austin 1998; Scott et al. 1998) have inadvertently included parentheses around Moeck, and it has been perpetuated in the literature; however, *greyi* was originally described within *Speyeria* and the parentheses were in error (see Dunford and Austin 2007)].

**Common name.** Grey's Fritillary.

**Type deposited.** Holotype at American Museum of Natural History (Figure 2-38).

**Type locality.** Lamoille Canyon, Ruby Mountains, Elko County, Nevada (Figure 2-54).

**Type label data.** *Speyeria atlantis greyi*, n. ssp. Holotype [male]; Lamoille Canyon 8-8500'-July 24, 1949 (Moeck) Ruby Mts., Nevada. [Austin 1998b provided additional type specimen data].

**Identification, taxonomy, and variation.** Both sexes bear alight reddish buff ground color, similar to *S. h. chitone*. Their appearance overall is pale, and lacks the red hues of other *hesperis* and *atlantis* forms. Adult wingspan ranges from 45-50 mm.

**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 hostplants.** *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**

[Scott et al. 1998]

*Speyeria atlantis lurana* dos Passos and Grey, 1945 p. 8

**Common name.** Lurana Fritillary.

**Type deposited.** Holotype at American Museum of Natural History (Figure 2-39).

**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 *Speyeria atlantis pahasapa* (Scott et al. 1998). 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 hostplants.** *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)**

[Scott et al. 1998]

*Speyeria atlantis irene* (Boisduval, 1869 p. 60) [dos Passos and Grey 1947]

*Argynnis irene* Boisduval, 1869 p. 60

*Argynnis cottlei* Comstock, 1925 p. 64 [*cottlei* has been changed from sunk in synonymy to subspecies status by Emmel et al. 1998c]

**Common name.** Irene Fritillary.

**Type deposited.** Lectotype (female) designated by dos Passos and Grey (1947) at National Museum of Natural History (Figure 2-40).

**Type locality.** Interior of California. Fixed 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 *irene* is not found in the immediate vicinity of Massack. Emmel et al. (1998a) restricted the type locality to 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 MUSAEOL Dris. BOISDUVAL; Oberthur Collection; Type irene Bdv. a/c Hofer; Barnes Collection.

**Identification, taxonomy, and variation.** Adults are similar to *S. h. dodgei*, *S. h. hanseni*, *S. h. cottlei* (see Emmel 1998c) as well sympatrically occurring *S. zerene*. Ventral hindwing spots are cream colored. 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 hostplants.** *Viola purpurea* (Emmel et al. 1970).

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

**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)

[Warren 2005 is the first to use *cottlei* with *hesperis* after Emmel et al. 1998c raised it from synonymy and placed it under *atlantis*]

*Argynnis cottlei* Comstock, 1925 p. 64 [see dos Passos and Grey 1947]

*Speyeria atlantis cottlei* (Comstock, 1925 p. 64) [placed in the '*atlantis*' complex by Emmel et al. (1998c); this species should be placed with former western '*atlantis*' forms that conform to the *hesperis* subspecies complex listed by Scott et al. (1998)]. This subspecies may have been referred to as *S. hesperis [atlantis] irene* (Boisduval) in the past.

**Common name.** Cottle's Fritillary.

**Type deposited.** The specimen utilized for description was in the J. E. Cottle collection, San Francisco (Comstock 1925; dos Passos and Grey 1947). At present, the type specimen 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) however synonymized the name with *Speyeria atlantis irene* and designated a lectotype for *irene* taken from Massack, Plumas County, California. Emmel et al. (1998c) resurrected the name from synonymy based on examination of the type for *irene* and the distribution of *S. cottlei*.

**Type label data.** I have not seen this specimen. According to Emmel et al. (1998c), a single specimen was used to describe *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 *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 *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 *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 *S. zerene* complex and *S. h. irene*. There is a complete lack of silver scaling on the ventral hindwings. Adult wingspan ranges from 50-55 mm.



**Range.** According to Emmel et al. (1998c), *S. atlantis 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 hostplants.** *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 hansenii* Emmel, Emmel, and Mattoon, 1998 new combination**

[included within *hesperis* here for the first time]

*Speyeria atlantis hansenii* Emmel, Emmel, and Mattoon, 1998c p. 152 [described in the *atlantis* subspecies complex by Emmel et al. (1998c), this species should be placed with western ‘*atlantis*’ forms that conform to the *hesperis* subspecies complex listed by Scott et al. (1998).] Forms of this subspecies may have been referred to as *Speyeria hesperis [atlantis] irene* (Boisduval) in the past.

**Common name.** Hansen’s Fritillary

**Type deposited.** Holotype at Natural History Museum of Los Angeles County (Figure 2-41).

**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. hansenii* is slightly dusker appearance dorsally and more pale ventrally due to extensive cream scaling. Adult wingspan ranges from 50-55 mm.

**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 atlantis hansenii* flies from late June to early August, with a peak flight period during early July.

**Larval hostplants.** *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)**

[Scott et al. 1998]

*Speyeria atlantis dodgei* (Gunder, 1931 p. 46) [dos Passos and Grey 1947]

*Argynnis dodgei* Gunder, 1931 p. 46

**Common name.** Dodge’s Fritillary.

**Type deposited.** Holotype at American Museum of Natural History (Figure 2-42).

**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 dodgei* resembles *S. hydaspe* 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.

**Larval hostplants.** *Viola bellidfolia* (Shields et al. 1969).

**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**

[Scott et al. 1998]

*Speyeria atlantis viola* dos Passos and Grey, 1945 p. 10

**Common name.** Viola's Fritillary

**Type deposited.** Holotype at American Museum of Natural History (Figure 2-43).

**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. I have observed adults flying along roadsides nectaring on flowers along with *Speyeria hydaspe* near Crater Lake, Oregon.

**Larval hostplants.** *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**

[Scott et al. 1998]

*Speyeria atlantis elko* Austin, 1983 pp. 244-245

**Common name.** Elko Fritillary.

**Type deposited.** Holotype at Nevada State Museum (Figure 2-44).

**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.** Range includes only 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 hostplants.** *Viola* spp.

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

**Label data associated with specimens examined.** NV: Elko.

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

[Scott et al. 1998]

*Speyeria atlantis tetonia* dos Passos and Grey, 1945 p. 9

**Common name.** Teton Fritillary.

**Type deposited.** Holotype at American Museum of Natural History (Figure 2-45).

**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 *hesperis*. Adult wingspan ranges from 45-50 mm. This subspecies also closely resemble *Speyeria 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 hostplants.** *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**

[Scott et al. 1998]

*Speyeria atlantis wasatchia* dos Passos and Grey, 1945 p. 9

**Common name.** Wasatch Fritillary.

**Type deposited.** Holotype at American Museum of Natural History (Figure 2-46).

**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.** This subspecies is similar to *S. h. chitone*. Ventral hindwing spots 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 Hostplants.** *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)**

[Scott et al. 1998]

*Speyeria atlantis chitone* (Edwards, 1879b p. 82) [dos Passos and Grey 1947]

*Argynnis chitone* Edwards, 1879b p. 82

**Common name.** Chitone Fritillary.

**Type deposited.** Lectotype (male) designated by dos Passos and Grey (1947) at Carnegie Museum of Natural History (Figure 2-47). Brown (1965), however, noted that 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. Fixed 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 this subspecies are generally larger than *S. h. wasatchia* and have a heavier black patterning above. The ventral hindwing disc 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 hostplants.** *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)**

[Scott et al. 1998]

*Argynnis Electa* Edwards, 1878 p. 143

*Argynnis Cornelia* Edwards, 1892 p. 106

*Speyeria atlantis electa* (Edwards, 1878 p. 143) [dos Passos and Grey 1947]

*Argynnis nikias* Ehrmann, 1917 p. 55 (Figure 2-49)

*Speyeria atlantis nikias* (Ehrmann, 1917 p. 55) [dos Passos and Grey 1947] [synonymized by Scott et al. 1998]

Some workers have treated the form '*electa*' as a valid species including the subspecies now placed within the '*hesperis*' group (Howe 1975, Bird et al. 1995), but unless further analyses prove otherwise, it will be treated here within the species *hesperis*.

**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 2-48).

**Type locality.** Colorado. Fixed 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.

**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 *atlantis* except by locality labels. Adult wingspan ranges from 55-60 mm.

**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.

**Larval hostplants.** *Viola sororia affinis* (Scott 1992).

**Adult food resources.** Yellow composites (Bird et al. 1995).

**Locality data associated with specimens examined.** WY: Albany, Carbon. There were numerous individuals taken from Colorado examined at various museums, but in many cases they were difficult to discern from *Speyeria hesperis hesperis*.

***Speyeria hesperis schellbachii* Garth, 1949**

[Scott et al. 1998]

*Speyeria atlantis schellbachii* Garth, 1949 p. 1

**Common name.** Schellbach's Fritillary.

**Type deposited.** Holotype at Natural History Museum of Los Angeles County (Figure 2-50).

**Type locality.** Neal Spring, north rim of Grand Canyon, 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.** Adult are active in secluded draws along springs.

**Larval hostplants.** *Viola* spp.

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

**Locality data associated with specimens examined.** AZ: Coconino.

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

[Scott et al. 1998]

*Speyeria atlantis dorothea* Moeck, 1947 pp. 73-75

**Common name.** Dorothy's Fritillary.

**Type deposited.** Holotype at American Museum of Natural History (Figure 2-51).

**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*, the basal suffusion 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., *callippe*, *atlantis*, *egleis*, *adiaste*).

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

**Life history.** Adults in can be observed in open glades in the Sandia Mountains (Figure 2-58).

**Larval hostplants.** *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 nausicaa* (Edwards, 1874)**

[Scott et al. 1998]

*Argynnis Nausicaa* Edwards, 1874b p. 104

*Argynnis ?aphrodite* form *Arizonensis* Elwes, 1889 p. 546

*Speyeria atlantis nausicaa* (Edwards, 1874b p. 104) [dos Passos and Grey 1947]

**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 2-52).

**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 *hesperis*. 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 *nausicaa*. The forewings are pointed, and the ventral hindwing spots are always silver with the discal area violaceous in color. Two ‘forms’ of *S. h. nausicaa* may 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 2-55). Afternoon rains during the summer months in the Arizona mountains hinders their activity. Adults will become inactive fairly rapidly when the sun is covered by clouds (Figures 2-56 and 2-57). 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 hostplants.** *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 capitanensis* R. Holland, 1988**

[Scott et al. 1998]

*Speyeria atlantis capitanensis* R. Holland, 1988 p. 2

**Common name.** Capitan Mountain Fritillary.

**Type deposited.** Holotype at American Museum of Natural History (Figure 2-53).

**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 from *S. h. nausicaa* and *S. h. dorothea*, more closely resembling *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 2-59). Adults were active from mid to late morning hours through the early afternoon.

**Larval hostplants.** *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.

Table 2-1. Checklist of *Speyeria* species and subspecies treated herein.

---

<i>Speyeria diana</i> (Cramer)
<i>Speyeria cybele</i> (Fabricius)
<i>Speyeria aphrodite</i> (Fabricius)
<i>Speyeria idalia</i> (Drury)
<i>Speyeria nokomis</i> (Edwards)
<i>Speyeria edwardsii</i> (Reakirt)
<i>Speyeria coronis</i> (Behr)
<i>Speyeria carolae</i> (dos Passos and Grey)
<i>Speyeria zerene</i> (Boisduval)
<i>Speyeria callippe</i> (Boisduval)
<i>Speyeria egleis</i> (Behr)
<i>Speyeria adiastra</i> (Edwards)
<i>Speyeria atlantis</i> (Edwards)
<i>S. atlantis atlantis</i> (Edwards)
<i>S. atlantis hollandi</i> (Chermock and Chermock)
<i>S. atlantis pahasapa</i> Spomer, Scott, Kondla
<i>S. atlantis sorocko</i> Scott, Kondla, Spomer
<i>Speyeria hesperis</i> (Edwards)
<i>S. hesperis hesperis</i> (Edwards)
<i>S. hesperis helena</i> dos Passos and Grey
<i>S. hesperis beani</i> (Barnes and Benjamin)
<i>S. hesperis brico</i> Kondla, Scott, Spomer
<i>S. hesperis ratonensis</i> Scott
<i>S. hesperis greyi</i> Moeck
<i>S. hesperis lurana</i> dos Passos and Grey
<i>S. hesperis irene</i> (Boisduval)
<i>S. hesperis cottlei</i> (Comstock)
<i>S. hesperis hanseni</i> Emmel, Emmel, and Mattoon
<i>S. hesperis dodgei</i> (Gunder)
<i>S. hesperis viola</i> dos Passos and Grey
<i>S. hesperis elko</i> Austin
<i>S. hesperis tetonia</i> dos Passos and Grey
<i>S. hesperis wasatchia</i> dos Passos and Grey
<i>S. hesperis chitone</i> (Edwards)
<i>S. hesperis electa</i> (Edwards)
<i>S. hesperis schellbachii</i> Garth
<i>S. hesperis nausicaa</i> (Edwards)
<i>S. hesperis dorothea</i> Moeck
<i>S. hesperis capitaneus</i> R. Holland
<i>Speyeria hydaspe</i> (Boisduval)
<i>Speyeria mormonia</i> (Boisduval)

---



Table 2-2. List of museum abbreviations.

---

AME-Allyn Museum of Entomology (now housed at McGuire Center for Lepidoptera and Biodiversity)
AMNH-American Museum of Natural History
BMNH (now NHM)-British Museum of Natural History
CMNH-Carnegie Museum of Natural History
CNC-Canadian National Collection
CSUC-C.P. Gillette Museum of Arthropod Biodiversity (Colorado State University)
FMNH-Field Museum of Natural History
FLMNH-Florida Museum of Natural History
FSCA-Florida State Collection of Arthropods
LACM-Natural History Museum of Los Angeles County
MGCL-McGuire Center for Lepidoptera and Biodiversity
MPM-Milwaukee Public Museum
MBSM (BYU)-Monte L. Bean Life Science Museum (Brigham Young University)
NMNH (formerly USNM)-National Museum of Natural History (United States National Museum)
NSM-Nevada State Museum
UAM-University of Alaska Museum of the North
EMUS-Utah State University Insect Collection
IRCW-University of Wisconsin Insect Research Collection
ESUW-University of Wyoming Insect Museum

---



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

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

*Upper-side.* THE *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 2-1. Original description for '*Idalia*'. A) hand colored illustrations included with original description, B) text included with original description (taken from Drury 1773).

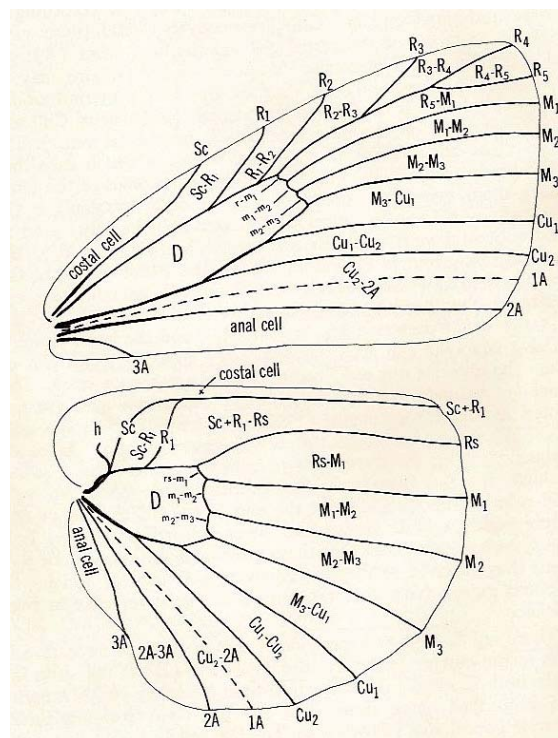
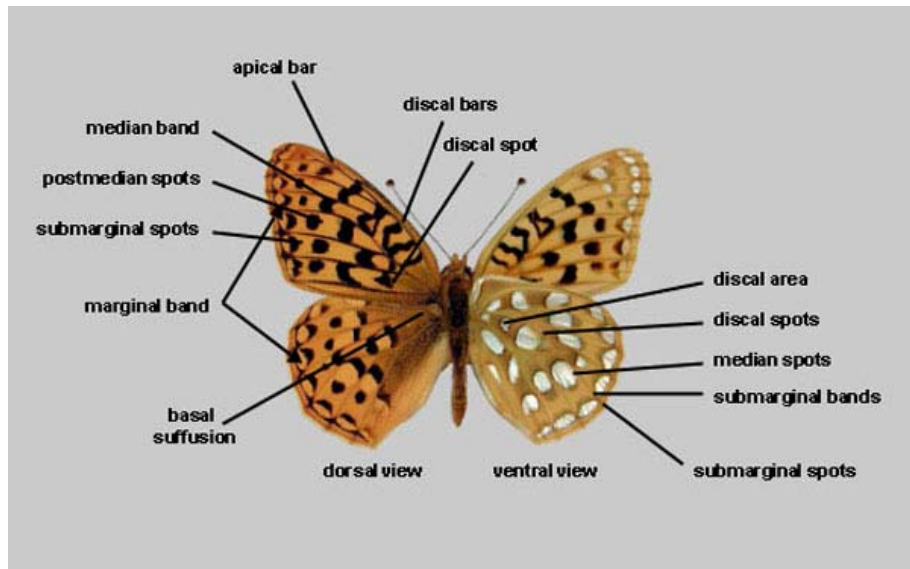




Figure 2-4. Images of adult *Speyeria diana*. A) male, B) female. Each image with dorsal (left) and ventral (right) view. Images by James C. Dunford.

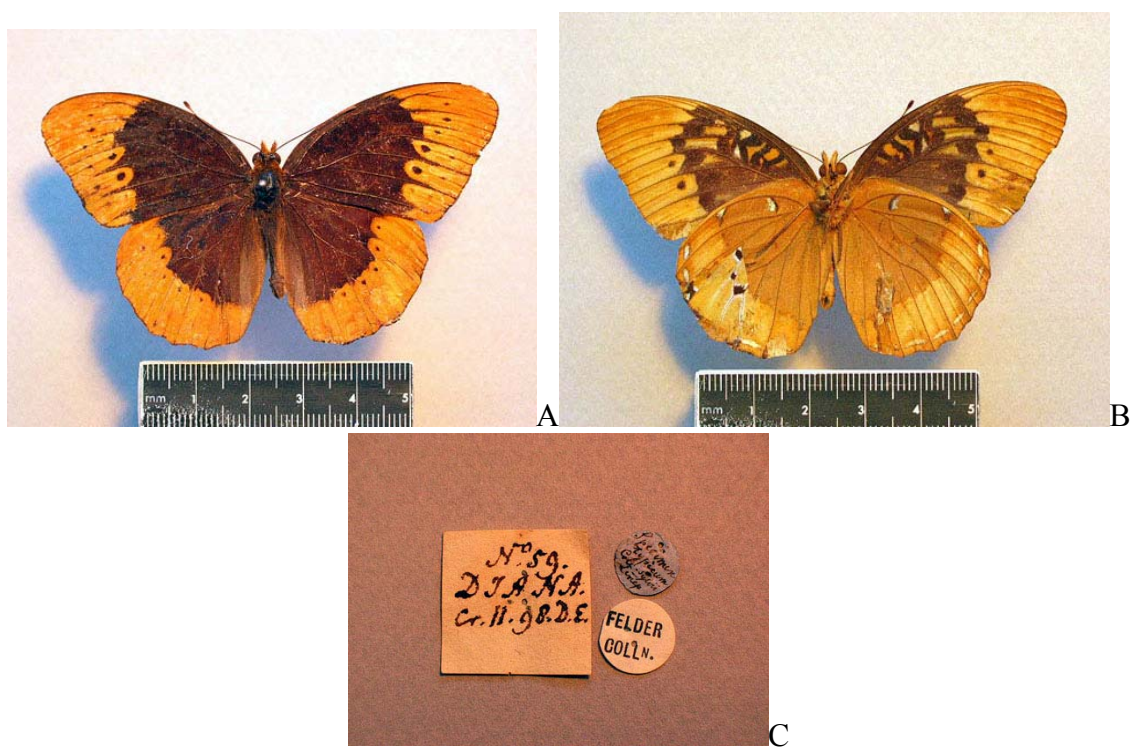


Figure 2-5. Type images for *Speyeria diana*, BMNH. A) holotype=*Speyeria diana*, male, dorsal view, B) holotype=*Speyeria diana*, male, ventral view, C) holotype. =*Speyeria diana* label data. Images by Kim Goodger Buckmaster.





Figure 2-6. Type images for *Speyeria cybele*, BMNH. A) neotype=*Speyeria cybele*, female, dorsal view, B) neotype=*Speyeria cybele*, female, ventral view, C) neotype=*Speyeria cybele* label data. Images by Kim Goodger Buckmaster.



Figure 2-7. Type images for *Speyeria aphrodite*, AMNH. A) neotype=*Speyeria aphrodite*, male, dorsal view, B) neotype=*Speyeria aphrodite*, male, ventral view. Images by James C. Dunford.

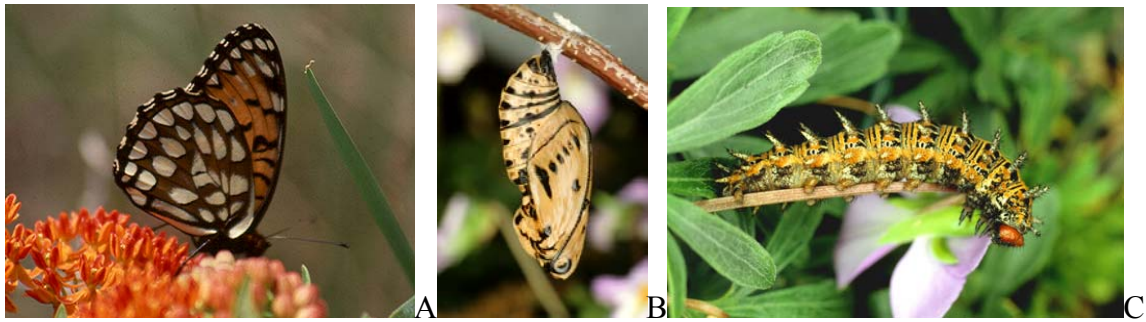


Figure 2-8. Images of *Speyeria idalia* life stages. A) adult on butterflyweed, Crawford County, Wisconsin, image by James C. Dunford, B) pupa, image by David L. Wagner, C) larva, image by David L. Wagner.



Figure 2-9. Type images for *Speyeria idalia*, AMNH. A) neotype=*Speyeria idalia*, male, dorsal view, B) neotype=*Speyeria idalia*, male, ventral view. Images by James C. Dunford.

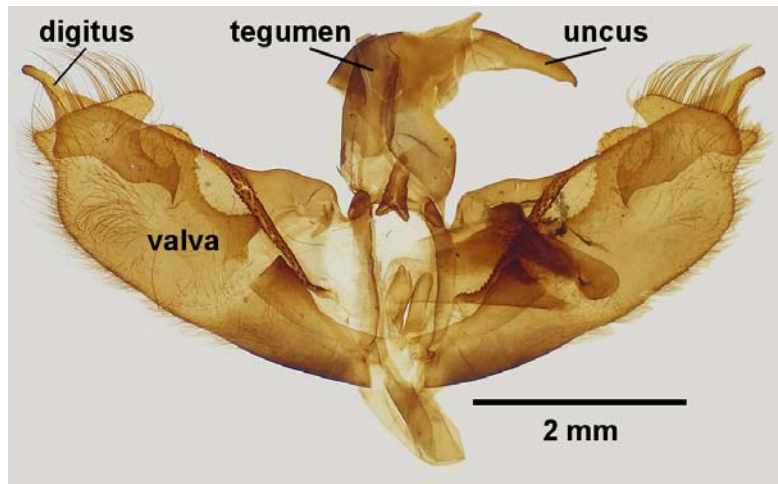


Figure 2-10. Male genitalic armature, *Speyeria idalia*. Image James C. Dunford.



Figure 2-11. Type images for *Speyeria nokomis*, AMNH. A) neotype=*Speyeria nokomis*, male, dorsal view, B) neotype=*Speyeria nokomis*, male, ventral view. Images by James C. Dunford.



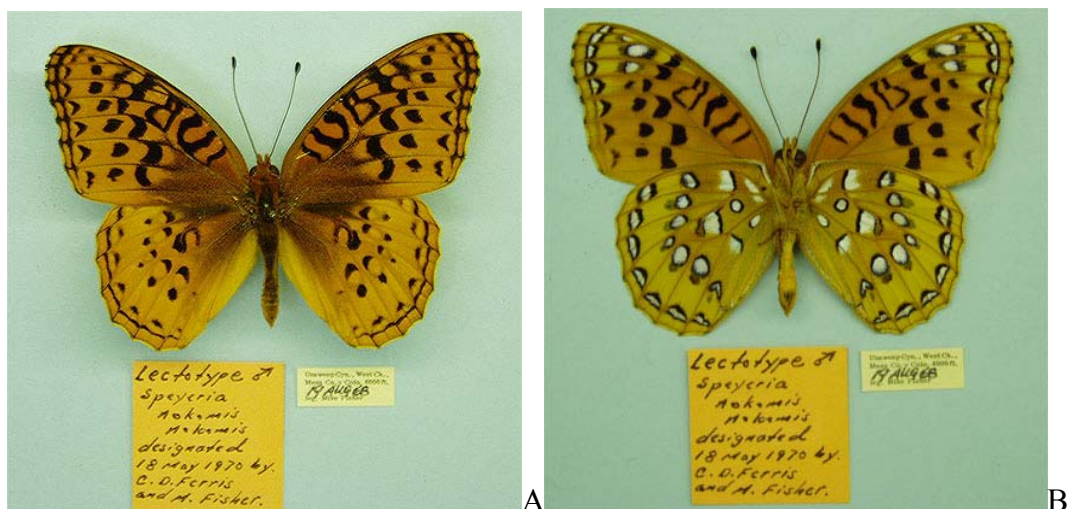


Figure 2-12 Type images for *Speyeria nokomis*, AMNH. A) lectotype=*Speyeria nokomis*, male, dorsal view, B) lectotype=*Speyeria nokomis*, male, ventral view. This specimen is no longer recognized as the name bearing type. Images by James C. Dunford.



Figure 2-13. Type images for *Speyeria edwardsii*, FMNH. A) lectotype=*Speyeria edwardsii*, male, dorsal view, B) lectotype=*Speyeria edwardsii*, male, ventral view. Images by James C. Dunford.



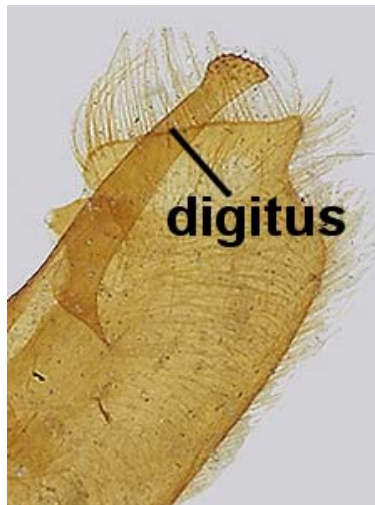


Figure 2-14. Digitus located on left valva, *Speyeria edwardsii*. Image by James C. Dunford.



Figure 2-15. Type images for *Speyeria coronis*, CMNH. A) neotype=*Speyeria coronis*, male, dorsal view, B) neotype=*Speyeria coronis*, male, ventral view. Images by James C. Dunford.



Figure 2-16. Habitus image of *Speyeria zerene* (*gunderi*), male; Nevada. Dorsal (left) and ventral (right) views. Image by James C. Dunford.



Figure 2-17. Type images for *Speyeria zerene*, NMNH. A) lectotype=*Speyeria zerene*, male, dorsal view, B) lectotype=*Speyeria zerene*, male, ventral view, C) lectotype=*Speyeria zerene* label data. Images by Robert Robbins.



Figure 2-18. Type images for *Speyeria carolae*, CMNH. A) holotype=*Speyeria carolae*, male, dorsal view, B) holotype=*Speyeria carolae*, male, ventral view. Images by James C. Dunford.



Figure 2-19. *Speyeria callippe* (*harmonia*), male; Nevada. Dorsal (left) and ventral (right) views. Image by James C. Dunford.



Figure 2-20. Type images for *Speyeria callippe*, NMNH. A) lectotype=*Speyeria callippe*, male, dorsal view, B) lectotype=*Speyeria callippe*, male, ventral view, C) lectotype=*Speyeria callippe* label data. Images by Robert Robbins.





Figure 2-21. Type images for *Speyeria egleis*, NMNH. A) neotype=*Speyeria egleis*, female, dorsal view, B) neotype=*Speyeria egleis*, female, ventral view, C) neotype=*Speyeria egleis* label data. Images by Robert Robbins.



Figure 2-22. Type images for *Speyeria adiaeste*, NMNH. A) lectotype=*Speyeria adiaeste*, female, dorsal view, B) lectotype=*Speyeria adiaeste*, female, ventral view, C) lectotype=*Speyeria adiaeste* label data. This is no longer recognized as the name bearing type. Images by Robert Robbins.



Figure 2-23. Type images for *Speyeria adiaeste*, CMNH. A) lectotype=*Speyeria adiaeste*, male, dorsal view, B) lectotype=*Speyeria adiaeste*, male, ventral view. Images by James C. Dunford.



Figure 2-24. Type images for *Speyeria atlantis*, CMNH. A) lectotype=*Speyeria atlantis*, male, dorsal view, B) lectotype=*Speyeria atlantis*, male, ventral view. Images by James C. Dunford.



Figure 2-25. Type images for *Speyeria hesperis*, CMNH. A) neotype=*Speyeria hesperis*, male, dorsal view, B) neotype=*Speyeria hesperis*, male, ventral view. Images by James C. Dunford.





Figure 2-26. Type images for *Speyeria hydaspe*, NMNH. A) lectotype=*Speyeria hydaspe*, male, dorsal view, B) lectotype=*Speyeria hydaspe*, male, ventral view, C) lectotype=*Speyeria hydaspe* label data. Images by Robert Robbins.



Figure 2-27. Habitus image of *Speyeria mormonia* (*artonis*), male; Nevada. Dorsal (left) and ventral (right) views. Image by James C. Dunford.





Figure 2-28. Type images for *Speyeria mormonia*, NMNH. A) lectotype=*Speyeria mormonia*, male, dorsal view, B) lectotype=*Speyeria mormonia*, male, ventral view, C) lectotype=*Speyeria mormonia* label data. Images by Robert Robbins.



Figure 2-29. Type images for *Speyeria atlantis canadensis*, AMNH. A) lectotype=*Speyeria atlantis canadensis*, male, dorsal view, B) lectotype=*Speyeria atlantis canadensis*, male, ventral view. Now synonymized with *Speyeria atlantis* (Scott et al. 1998). Image by James C. Dunford.

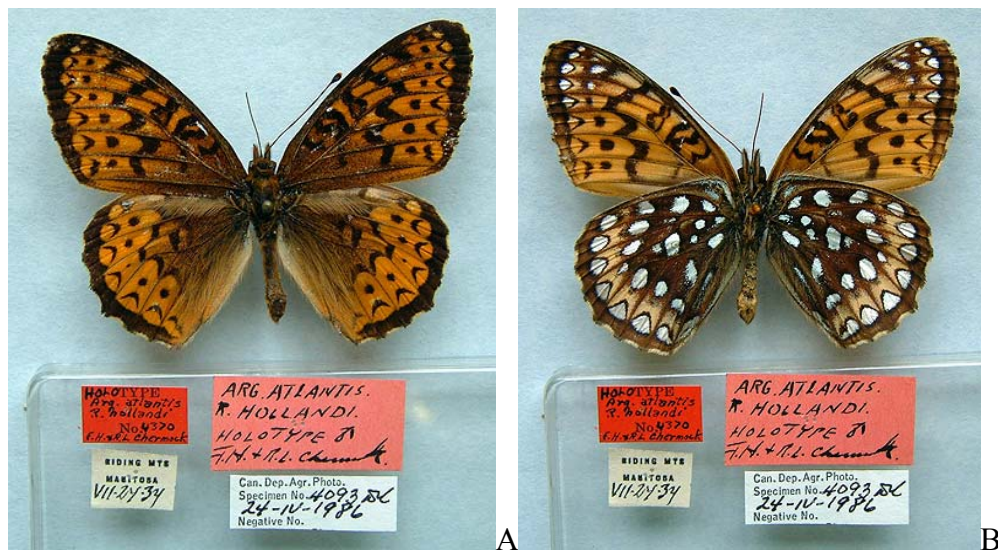


Figure 2-30. Type images for *Speyeria atlantis hollandi*, CNC. A) holotype=*Speyeria atlantis hollandi*, male, dorsal view, B) holotype=*Speyeria atlantis hollandi*, male, ventral view. Images by Norbert Kondla.



Figure 2-31. Type images for *Speyeria atlantis sorocko*, AMNH. A) holotype of *Speyeria atlantis sorocko*, male, dorsal view, B) holotype of *Speyeria atlantis sorocko*, male, ventral view. Images by James C. Dunford.

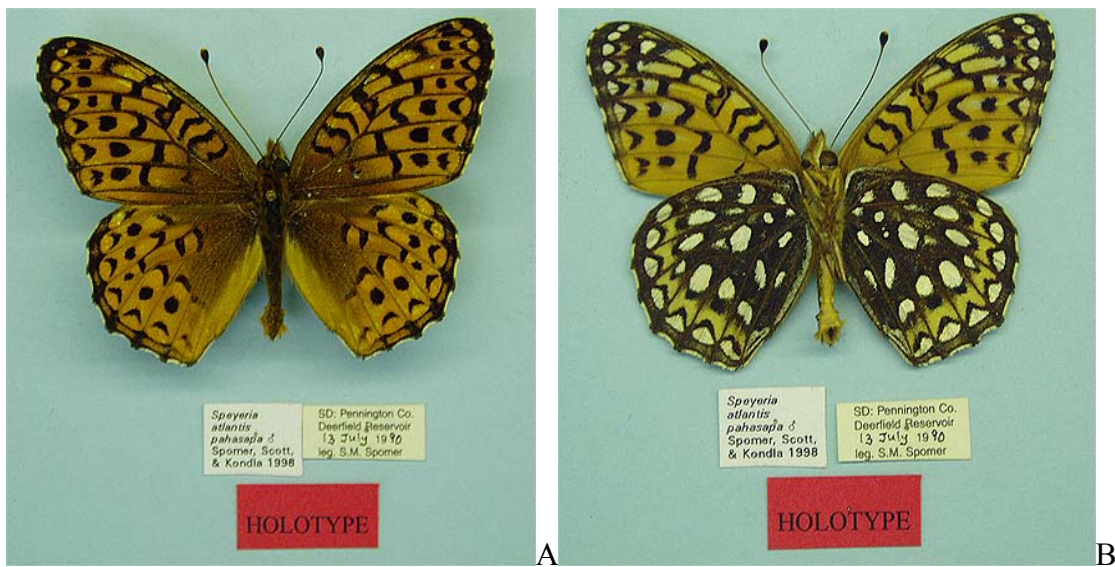


Figure 2-32. Type images for *Speyeria atlantis pahasapa*, AMNH. A) holotype of *Speyeria atlantis pahasapa*, male, dorsal view, B) holotype of *Speyeria atlantis pahasapa*, male, ventral view. Images by James C. Dunford.



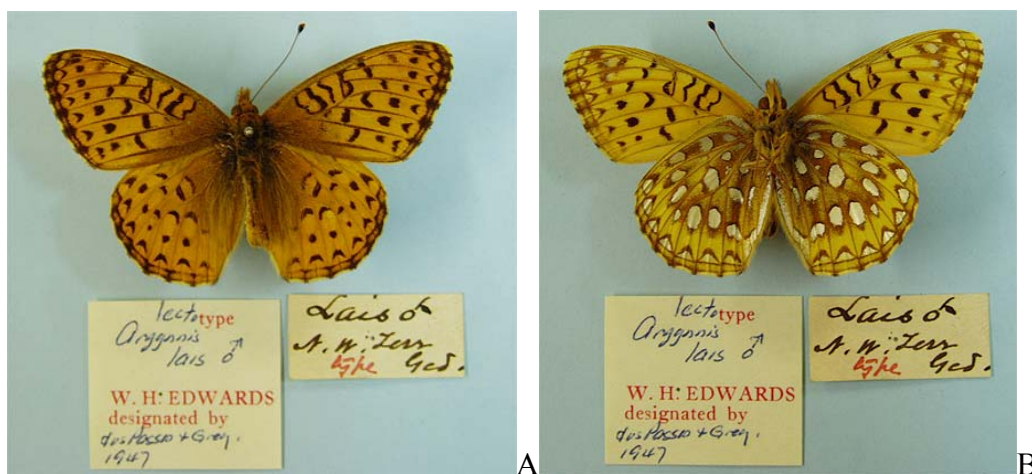


Figure 2-33. Type images for *Speyeria hesperis helena*, CMNH. A) lectotype=*Speyeria hesperis helena*, male, dorsal view, B) lectotype=*Speyeria hesperis helena*, male, ventral view. Images by James C. Dunford.



Figure 2-34. Type images for *Speyeria atlantis dennisi*, AMNH. A) holotype=*Speyeria atlantis dennisi*, male, dorsal view, B) holotype=*Speyeria atlantis dennisi*, male, ventral view. Now synonymized with *Speyeria hesperis helena* (Scott et al. 1998). Image by James C. Dunford.



Figure 2-35. Type images for *Speyeria hesperis beani*, NMNH. A) holotype=*Speyeria hesperis beani*, male, dorsal view, B) holotype=*Speyeria hesperis beani*, male, ventral view, C) holotype=*Speyeria hesperis beani* label data. Images by Robert Robbins.



Figure 2-36. Types images for *Speyeria hesperis brico*, CNC. A) holotype of *Speyeria hesperis brico*, male, dorsal view, B) holotype of *Speyeria hesperis brico*, male, ventral view. Images by Norbert Kondla.

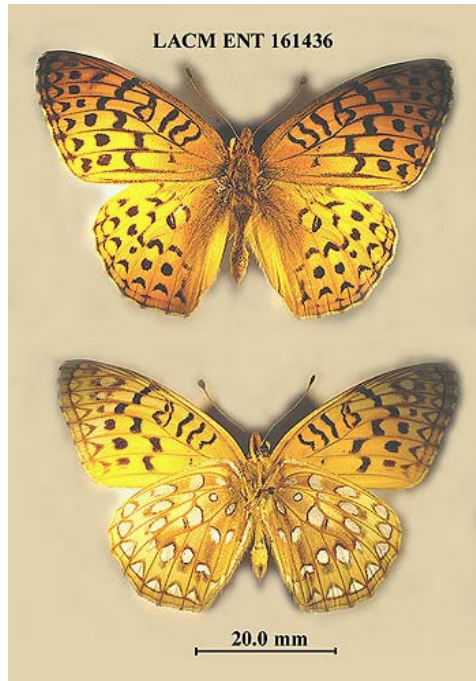


Figure 2-37. Holotype=*Speyeria hesperis ratonensis*, male, dorsal and ventral view, LACM.  
Image by Weiping Xie.



Figure 2-38. Type images for *Speyeria hesperis greyi*, AMNH. A) holotype=*Speyeria hesperis greyi*, male, dorsal view, B) holotype=*Speyeria hesperis greyi*, male, ventral view.  
Images by James C. Dunford.



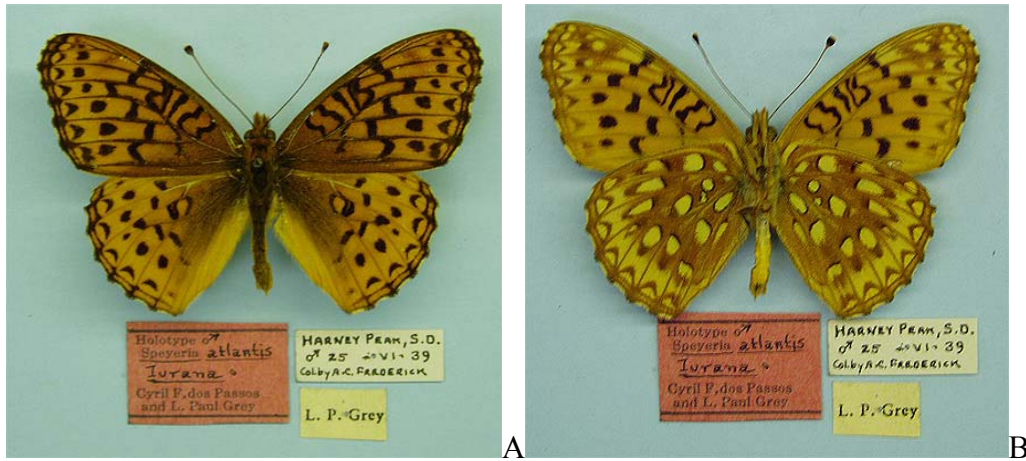


Figure 2-39. Type images for *Speyeria hesperis lurana*, AMNH. A) holotype=*Speyeria hesperis lurana*, male, dorsal view, B) holotype=*Speyeria hesperis lurana*, male, ventral view. Images by James C. Dunford.



Figure 2-40. Type images for *Speyeria hesperis irene*, NMNH. A) lectotype=*Speyeria hesperis irene*, female, dorsal view, B) lectotype=*Speyeria hesperis irene*, female, ventral view, C) lectotype=*Speyeria hesperis irene* label data. Images by Robert Robbins.



Figure 2-41. Holotype=*Speyeria hesperis hanseni*, male, dorsal and ventral view, LACM.  
Image by Weiping Xie.



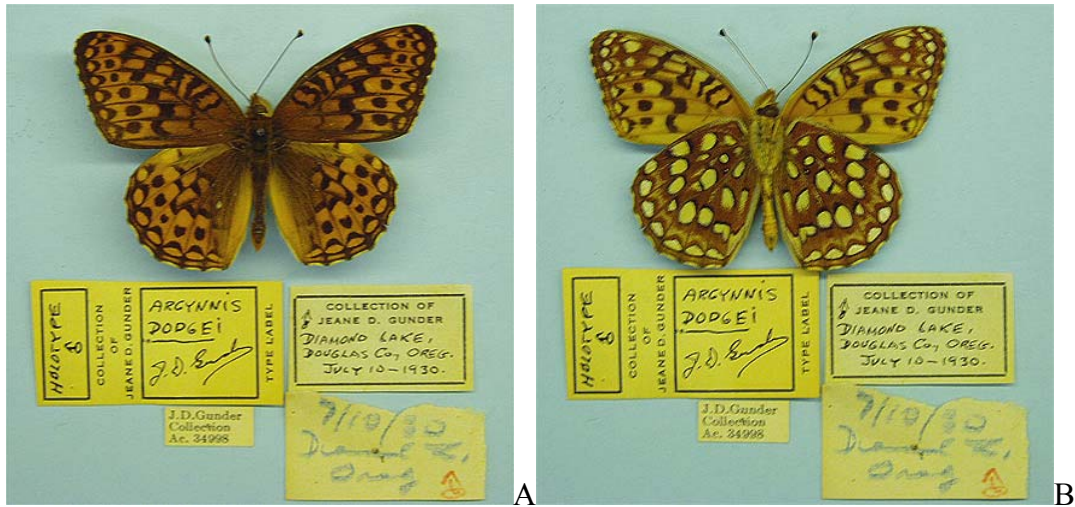


Figure 2-42. Type images for *Speyeria hesperis dodgei*, AMNH. A) holotype=*Speyeria hesperis dodgei*, male, dorsal view, B) holotype=*Speyeria hesperis dodgei*, male, ventral view. Images by James C. Dunford.

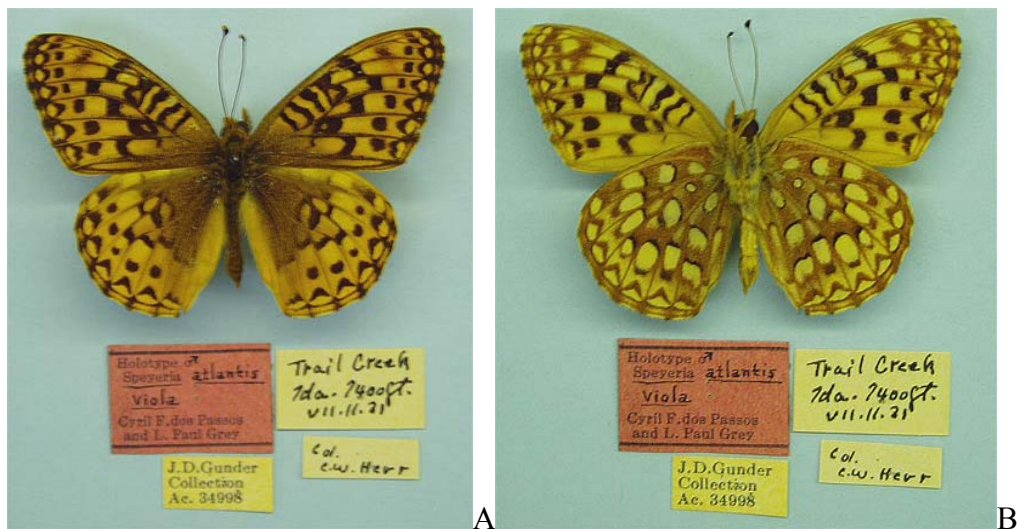


Figure 2-43. Type images for *Speyeria hesperis viola*, AMNH. A) holotype=*Speyeria hesperis viola*, male, dorsal view, B) holotype=*Speyeria hesperis viola*, male, ventral view. Images by James C. Dunford.



Figure 2-44. Type images for *Speyeria hesperis elko*, NSM. A) holotype=*Speyeria hesperis elko*, male, dorsal view, B) holotype=*Speyeria hesperis elko*, male, ventral view. Images by George Baumgartner and Scott Klette.



Figure 2-45. Type images for *Speyeria hesperis tetonia*, AMNH. A) holotype=*Speyeria hesperis tetonia*, male, dorsal view, B) holotype=*Speyeria hesperis tetonia*, male, ventral view. Image by James C. Dunford.



Figure 2-46. Type images for *Speyeria hesperis wasatchia*, AMNH. A) holotype=*Speyeria hesperis wasatchia*, male, dorsal view, B) holotype=*Speyeria hesperis wasatchia*, male, ventral view. Images by James C. Dunford.

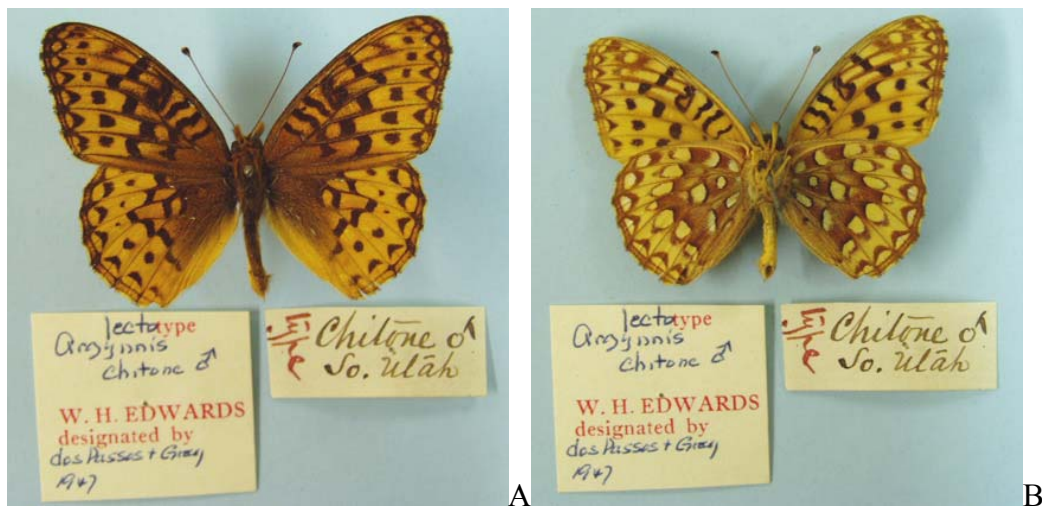


Figure 2-47. Type images for *Speyeria hesperis chitone*, CMNH. A) lectotype=*Speyeria hesperis chitone*, male, dorsal view, B) lectotype=*Speyeria hesperis chitone*, male, ventral view. Images by James C. Dunford.





Figure 2-48. Type images for *Speyeria hesperis electa*, CMNH. A) lectotype=*Speyeria hesperis electa*, male, dorsal view, B) lectotype=*Speyeria hesperis electa*, male, ventral view. Images by James C. Dunford.



Figure 2-49. Type images for *Speyeria hesperis nikias*, CMNH. A) lectotype=*Speyeria hesperis nikias*, male, dorsal view, B) lectotype=*Speyeria hesperis nikias*, male, ventral view. Now synonymized with *Speyeria hesperis electa* (Scott et al. 1998). Image by James C. Dunford.



Figure 2-50. Holotype=*Speyeria hesperis schellbachi*, male, dorsal and ventral view, LACM.  
Image by Weiping Xie.



Figure 2-51. Type images for *Speyeria hesperis dorothea*, AMNH. A) holotype=*Speyeria hesperis dorothea*, male, dorsal view, B) holotype=*Speyeria hesperis dorothea*, male, ventral view. Images by James C. Dunford.



Figure 2-52. Type images for *Speyeria hesperis nausicaa*, CMNH. A) lectotype=*Speyeria hesperis nausicaa*, male, dorsal view, B) lectotype=*Speyeria hesperis nausicaa*, male, ventral view. Images by James C. Dunford.



Figure 2-53. Type images for *Speyeria hesperis capitanensis*, AMNH. A) holotype=*Speyeria hesperis capitanensis*, male, dorsal view, B) holotype=*Speyeria hesperis capitanensis*, male, ventral view. Images by James C. Dunford.





Figure 2-54. Lamoille Canyon, Ruby Mountains, Nevada. Image by James C. Dunford.



Figure 2-55. Hospital Flats, near Mt. Graham, Pinaleno Mountains, Arizona. Image by James C. Dunford.



Figure 2-56. View of Pinaleno Mountains in the morning. Image by James C. Dunford.



Figure 2-57. View of Pinaleno Mountains in the early afternoon. Image by James C. Dunford.





Figure 2-58. Open glade in Sandia Mountains, New Mexico. Image by James C. Dunford.



Figure 2-59. Roadside flowers, Capitan Mountains, New Mexico. Image by James C. Dunford.

### CHAPTER 3 PHYLOGENY OF *SPEYERIA*

*Speyeria*, (Nymphalidae: Heliconiinae: Argynnini) as currently defined, is restricted to North America (absent in southeastern regions of the United States) (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). Long included in the Old World genus *Argynnis* (Argynninae) (Elwes 1889; Snyder 1900; Seitz 1924), *Speyeria* differ from their Eurasian relatives primarily in genitalic structure (dos Passos and Grey 1945a; Dornfeld 1980). They were considered generically distinct from *Argynnis* by dos Passos and Grey (1945a); all North American taxa named since that time have been described within *Speyeria*. Recent workers have, however, treated *Speyeria* as a subgenus of the primarily Palearctic genus *Argynnis* Fabricius 1807 (Tuzov 2003; Simonsen 2006c). Simonsen (2006a,b,c) and Simonsen et al. (2006) have provided some morphological and molecular evidence that suggests *Argynnis* is paraphyletic if *Speyeria* is retained as a separate genus.

*Speyeria* is presently comprised of 16 species (Opler and Warren 2005), 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* (W.H. 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. Historically, three *Speyeria* species (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).

Simonsen (2004) hypothesized that the tribe Argynnini likely originated approximately 35 million years ago (=Oligocene Epoch) in the Eastern Palearctic /Nearctic Region based on historical zoogeography. Argynnina (including *Speyeria* and *Argynnis*) probably originated in the Eastern Palearctic/Afrotropics Regions and spread into the Western Palearctic Region on several occasions and the Nearctic Region once. Pleistocene glaciations likely promoted speciation in *Speyeria* because divergence among allopatric glacial refugia or founder events during recolonization of previously glaciated areas would have promoted differentiation (Hammond 1990). Climatological events and geological history, 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).

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 (Holland 1898: 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). Species and subspecies of *Speyeria* are commonly delimited based on banding, discal coloration, spot coloration and size differences (Dornfeld 1980; Hammond 1978; Ferris and Brown 1981). In the evolution of *Speyeria*, wing markings appear to be highly conservative and reliable diagnostic characters, while wing colors are less stable (Hammond 1990). Habitat may be important in

“determining” species and subspecies, and the amount of solar radiation (including factors such as latitude, temperature, elevation, humidity, lack of vegetation, dark or light soil) on larvae and pupae may play a role in color variation as it does in other lepidopterans (Hovanitz 1941; Moeck 1957; Janzen 1984; Pyle 1995; Layberry et al. 1998; Ellers and Boggs 2004). For example, pierid and papilionid butterfly populations in cold climates have much darker, more heavily melanized ventral hindwings than do populations in warm climates (Watt 1968; Guppy 1986).

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 utilizing modern systematic techniques. Based on adult and larval morphology utilizing phylogenetic analyses, Penz and Peggie (2003) suggested that Heliconiinae be divided into four groups, and included *Speyeria* within the Argynnini. Other closely related heliconiine taxa with distributions in North America included *Clossiana* Reuss (= *Boloria*) and *Euptoieta*. 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, however, the fairly recent morphological and molecular work of Brower (2000c) 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 several thousand years ago (Penz and Peggie 2003). The morphological and molecular work Simonsen et al. (2006) provided 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* Reuss [both genera are included in *Argynnis* in Simonsen et al. (2006)] are hypothetically most closely related to *Speyeria* (Figure 3-14). 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). Work conducted by Simonsen (2006c) based primarily on genitalia also indicated a close relationship between that of *Speyeria* and *Mesoacidalia* (Figure 3-5); however, the generic placement of several larger fritillary species differed from Simonsen et al. 2006.

To date, there has not been an inclusive, cladistic analysis for *Speyeria*. A few older studies have utilized multiple *Speyeria* taxa in evolutionary-related analyses (Brittnacher et al. 1978; Hammond 1978; Tebaldi 1982), but more recently *Speyeria* have been used as an outgroup for phylogenetic inferences of more or less related taxa (Martin and Pashley 1992; Brower and Egan 1997; Pollock et al. 1998; Penz and Peggie 2003; Simonsen 2004, 2006; Simonsen et al. 2006). Previous evolutionary relationships within *Speyeria* have been arbitrarily delimited, based primarily on the genitalic differences exhibited between the Semnopsyche group and the remainder of *Speyeria* [=Callippe group (Hammond 1978)], a few immature characters, and by and large adult morphological variation of the following: overall size, degree of sexual dimorphism, and the following wing characteristics: dorsally, ground color, intensity of black markings, degree of dark basal suffusion, prominence of marginal band, thickness of veins on the wings, and ventrally, 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 the hindwings.

In dos Passos and Grey's 1947 revision, *Speyeria mormonia* is presented as 'derived', while the Semnopsyche group is presented 'basally' within the *Speyeria* (Figure 3-1); however, they realized the arbitrary nature of this arrangement and could only clearly distinguish the Semnopsyche group from those in the callippe group. Hammond (1978) discussed primitive and

derived characteristics within *Speyeria* and its close relatives and realized the affinities between Eurasian *Fabriciana aglaja* (= *Mesoacidalia*) and *Argynnis*. Within *Speyeria*, he noted that *S. mormonia* taxa most closely resemble the wing coloration and ground plan patterns of old *Mesoacidalia aglaja* of the Old World. Amongst the 15 *Fabriciana* and *Argynnis* taxa he examined, *Argynnis* was considered distinct from both *Fabriciana* and *Speyeria* in wing patterning. *Argynnis* has round submarginal spots on the dorsal wing surface, and the markings on the ventral hindwings are greatly reduced and obscure. In contrast, both *Fabriciana* and *Speyeria* have crescent shaped submarginal spots and the markings on the ventral hindwing are distinct. Hammond also considered a *Semnopsyche* group or ‘*cybele* clade’, recognizing the close affinities of the male genitalia of *S. diana*, *S. idalia*, *S. aphrodite*, *S. cybele*, and *S. nokomis* (Figure 3-2). His analyses provided a more accurate representation of the evolutionary relationships within *Speyeria*, although it was based largely on untestable hypotheses.

There have also been regional systematic studies on *Speyeria*. Brittnacher et al. (1978) used electrophoresis to study the body enzymes of California *Speyeria* and found that five Callippe group species could not be readily distinguished, whereas the other five species could be (the enzymes of *Speyeria hydaspe* and *Speyeria adiaspe* were also similar). The Callippe group species could, however, be distinguished by combining chromosomal, physiological, and morphological data (see Figure 3-3). For the 10 taxa examined, species that occurred in xeric habitats clustered into two groups, while mesic inhabiting species (i.e., *S. nokomis* and *S. mormonia*) were most different from each other and from the xeric species (Figure 3-3).

Hammond (1990) provided a cladistic analysis (based primarily on wing patterns) of *Speyeria callippe* subspecies (Figure 3-4) and hypothesized that *S. callippe* was a West Coast isolate of the Appalachian-type *Speyeria atlantis* and that *Speyeria edwardsii* probably evolved from one

of the *S. callippe* subspecies that became isolated in the Great Plains east of the Continental Divide. Tebaldi (1982) utilized starch gel electrophoresis of six enzymes to analyze the relationships between three phenotypes of what was considered *Speyeria atlantis* at the time (i.e., *electa*, *nikias*, and *hesperis*) and found that the phenotypes could only be considered ‘semispecies’, and that *electa* and *nikias* were more closely related than either one was to *hesperis*. Williams (2001a, 2002) examined the cytochrome oxidase I and II gene regions for *Speyeria idalia* and suggested splitting the eastern and western United States populations into two subspecific taxa based on 18 parsimony-informative sites and spot size on the ventral hindwings.

While there has been some dispute as to the true evolutionary relationship of *Speyeria* to the primarily Palearctic *Argynnis* for some time (Hovantiz 1962, McHenry 1963; Hammond 1978; Simonsen et al. 2006), recent cladistic analyses (Simonsen 2006a,c; Simonsen et al. 2006) have only utilized members of the Semnopsyche or Cybele group in those analyses; thus they may not accurately represent *Speyeria* as a whole. In another taxonomically-related heliconiine study, Penz and Pegg (2003) utilized *Speyeria mormonia* and *Speyeria aphrodite* (=Semnopsyche group). Their tree topology exhibited some differences when compared to those presented in Simonsen et al. (2006); namely, the relationship of *Speyeria* to that of *Argynnis*. Although character usage and the taxa included in their study differed somewhat, it may be an indication that additional *Speyeria* taxa should be included in future heliconiine-related studies to provide clearer resolution of the evolutionary relationships in the group.

In general, mitochondrial genes are useful data for evolutionary studies such as species delimitation, population structure and gene flow, hybridization, phylogeographic histories, and phylogenetic relationships (Vogler et al. 1993; Brower 1997; Zimmermann et al. 2000; Levy et

al. 2002; Wahlberg et al. 2003a; Segraves and Pellmyr 2004; Strehl and Gadau 2004; Vandewoestijne et al. 2004; Wahlberg et al. 2005; Memon et al. 2006). Their small size and relative ease to purify (relative to nuclear genes) (i.e., buoyant density, high copy number in cells, and location within an organelle) allow researchers to isolate these genes more readily (Simon et al. 1994). Because its properties (i.e., various regions evolve rapidly in base substitutions and sequence length, have a constant initial rate of evolution, are maternally inherited, and are unlikely to recombine), mtDNA represents an unbiased neutral marker for maternal ancestry, and is a good tool to help reveal historical relationships among populations (Brower 1994a; Simon et al. 1994). COI coding genes have been the most widely utilized mitochondrial gene regions in Lepidoptera phylogenetic analyses for some time (Brower 1994b, 1996b; Brown et al. 1994; Sperling and Hickey 1995; Pollock et al. 1998; Caterino and Sperling 1999; Nice and Shapiro 1999; Wahlberg and Zimmermann 2000; Zimmermann et al. 2000; Caterino et al. 2001; Monteiro and Pierce 2001; Kruse and Sperling 2002; Wahlberg et al. 2003a, 2005; Vandewoestijne et al. 2004; Mallarino et al. 2005; Simonsen et al. 2006c). Recent work has also suggested that COI can aid in the resolution of diversity and in discrimination of closely allied species (Hebert et al. 2003; Hajibabaei et al. 2006; Burns et al. 2007).

Morphological, behavioral, and genetic/sequence data are equally important in understanding inter- and intraspecific relationships, and there has been a significant amount of potentially evolutionary informative data reported in the literature for *Speyeria* (dos Passos and Grey 1945a; Maeki and Remington 1960; Scott 1973a, 1975, 1979; Hammond 1974, 1978; Arnold 1975, Ferris 1983, Emmel 1998; Scott et al. 1998). The combined analysis of data from various sources commonly leads to more robust, or stable phylogenetic hypotheses (Simonsen et al. 2006), and data from past studies can be integrated with newer findings to provide



comprehensive data sets. In order to examine the specific relationships within *Speyeria*, a thorough investigation of the literature is necessary to gain insight into potentially informative characters and leads to unique and novel characters. In addition to characters previously reported in the literature, characters recovered from the genitalic analyses, and molecular sequences of the mitochondrial gene cytochrome c oxidase subunit I (COI) were utilized to examine the intra- and interspecific relationships of *Speyeria*, and to test the monophyly of this genus.

### **Materials and Methods**

Fieldwork and collaboration with nearly 30 lepidopterists in proximity to *Speyeria* populations (from Alaska to southern California, east to Maine and south to Georgia) and outgroup taxa were performed to obtain adult specimens. Information pertaining to morphology and biology of *Speyeria* was also obtained from these lepidopterists. Accurate identification was imperative to this study, and identifications were also sought from regional experts. Specimens were collected in the field and stored in ethanol for genital and molecular studies. At least five specimens of each sex for each species/subspecies were obtained, and if possible, a subset of individuals occurring in different parts of any single species/subspecies range was also obtained. An effort was made to attain samples in proximity to the type localities for each species of *Speyeria*. In addition, Old World taxa and other members of the Heliconiinae (i.e., *Boloria*, *Euptoieta*) were procured for phylogenetic analysis.

The wings of specimens taken in the field or provided by collaborating lepidopterists were clipped off most specimens and the bodies were placed in 95% ethanol. Several specimens were also kept intact and placed in glassine envelopes. The removed wings were mounted to card stock (each pair of wings with ventral and dorsal surfaces in view) and photographed to represent vouchers of specimens utilized for genital and molecular work. A five-digit number was given to each specimen to be able to track and coordinate each specimen with its respective structures.

Genital dissections were completed using at least five individuals for each species/subspecies, with selected dissections photographed. Adult male abdomens were removed and prepared using a 10% solution of KOH and subsequently placed in 70% EtOH. Genital armature (i.e., valves, uncus, aedeagus) was dissected from the abdominal pelt and the aedeagus was removed for future genital examination (i.e., vesica eversion and imaging).

Specimens housed in the American Museum of Natural History, Carnegie Museum of Natural History, McGuire Center for Lepidoptera and Biodiversity, and a few private collections were utilized for morphological examination. Results from morphological work were scored and analyzed in PAUP 4.0b10b (Swofford 2002) and MacClade version 4.0 (Maddison and Maddison 2000). Additionally, the following literature was reviewed to recover potentially informative morphological, behavioral, and genetic characters: Warren (1944), Warren et al. (1946), Maeki and Remington (1960), Miller and Miller (1966), Mosher (1969), Scott (1972, 1975, 1979, 1984), Shields and Emmel (1973), Shirôzu and Saigusa (1973), Penz (1999), Tolman (1997), Penz and Peggie (2003), Simonsen 2005,2006a,c, and Simonsen et al. (2006).

Specimens prepared for molecular analyses were subjected to the following protocols, these following those implemented by the University of Guelph, Barcode of Life Data Systems (BOLD) (<http://www.barcodinglife.org/views/login.php>). A leg or thorax was removed from an adult and DNA was extracted utilizing glass fiber plate DNA isolation. PCR amplification of COI DNA was carried out using the forward and reverse primers LepF1 (5'-ATTCAACCAATCATAAAGATATTGG-3') and LepR1 (5'-TAAACTTCTGGATGTCCAAAAAATCA-3'). The thermal cycler profile consisted of 94°C for 1 minute, five cycles of 94°C for 40 seconds, 45°C for 40 seconds, and 72°C for 1 minute; followed by 35 cycles of 94°C for 40 seconds, 51°C for 40 seconds, and 72°C for 1 minute, with

a final extension at 72°C for 5 minutes. Sequencing was completed with a Beckman Coulter Biomek® capillary sequencer located at the University of Guelph. Sequences were aligned automatically by BOLD software and/or by eye using MacClade version 4.0.

### **Taxon Sampling**

In total, 22 taxa were included in the primary analyses (Table 3-1). Sixteen species of *Speyeria* and six outgroups were chosen. Six outgroup taxa represent related heliconiine species, three of which occur in the Old World. Several widely distributed subspecific taxa of *Speyeria* were used for the molecular portion of these analyses. Several additional species (i.e., *Argynnis* spp., *Boloria* spp., *Euptoieta* spp., and *Heliconius* spp.) were incorporated into a separate COI phylogenetic analysis (see Figures 3-12 and 3-13).

### **Character Sampling**

In all, 30 morphological/behavioral/genetic characters (summarized in Table 3-2; also see Table 3-3) and over 600 molecular characters have been established to date. Many of them were taken from male genital features, followed by wing pattern and behavioral related characters. All characters chosen were binary, with the exception of five, which contained 3 or 4 states. Additional characters include immature, behavioral and genetic states. Several additional characters were accumulated but were deemed clinal, non-discrete characters that could not be easily defined for a given taxon.

### **Phylogenetic Analyses**

Phylogenetic analyses were executed utilizing PAUP 4.0b10b (Swofford 2002) and molecular sequence alignments were made in MacClade version 4.0 (Maddison and Maddison 2000). Morphological, behavioral, and molecular data sets were inferred separately and in combined analyses. Molecular data were equally weighted and unordered, and other data were coded by the author. In most cases, unless otherwise noted, analyses were carried out using

maximum parsimony and a heuristic algorithm, along with additional default settings in PAUP. Heuristic searches were run utilizing several nucleotide substitution or evolutionary models and are indicated with each tree. A maximum of 1000 trees were searched for each data set followed by a 50% majority rule, strict consensus of the best fit trees. The tree length, consistency and retention indices, and the number of parsimonious informative characters are reported in each tree. Branch support values (e.g., bootstrap and/or Bremer support) were not calculated at the time of this writing but will be in the future. Molecular sequences are currently stored on the workspace of the author at the BOLD workbench (<http://www.barcodinglife.org/views/login.php>) and will be publicly available there as well as on GenBank following publication of these results.

### Results and Discussion

Based on the morphological and behavioral data set (see Tables 3-2 and 3-3), *Speyeria* can be divided into two “groupings,” the Semnopsyche/Cybele group (including *Speyeria idalia*), and more or less the Callippe group of Hammond (1978) (Figure 3-6), which appear as unresolved polytomies in Figure 3-6. *Speyeria nokomis* is placed between these two groupings. However, *Speyeria* does not appear monophyletic, with *Fabriciana niobe* falling within *Speyeria*. Other hypothesized outgroups (i.e., *Boloria*, *Euptoieta*, and *Heliconius*) have diverged where they would expect to relative to *Speyeria*. It should also be noted that *S. hydaspe* is sister to *S. adiaspe*, which concurs with that relationship indicated by Brittnacher et al. (1978). In the past, *S. adiaspe* was hypothesized to be closely allied to *S. egleis* (dos Passos and Grey 1947, Hodges 1983) and *S. atlantis* (Hammond 1978). While genitalic characters (including the shape of the uncus, tegumen, and fenestrula, and location of the digitus) between *Speyeria* and the European genera *Fabriciana*, *Argynnis*, and *Mesoacidalia* are quite distinct, discrete genitalic characters for species of *Speyeria* are few. However, the size and shape of the uncus on the male

genitalic armature should serve to separate members of the Semnopsyche group from others in *Speyeria*. In addition, an accessory bursal sac in the females of the Semnopsyche group provides further evidence of this separation. Intermediate genitalic forms, such as those observed in *S. idalia* and *S. nokomis*, may represent a transition between those *Speyeria* taxa that bear a flattened, excavate uncus and accessory bursal sac to those that have a simple uncus and single bursal sac. Additional informative characters identified in this study include the size and shape of the digitus, especially for *S. idalia* and *S. edwardsii*. The location of this structure on the male genitalic armature is unique to *Speyeria*, but it may have been overlooked as an evolutionarily informative character within the genus and other related taxa. Other characters chosen for this analysis, namely wing and behavioral characters, may not be evolutionarily informative and should be reexamined. Homoplasy may obscure synapomorphies, especially in groups with relatively recent speciation and where retained ancestral polymorphism is still extant. Additional discrete morphological characters are currently being analyzed and input into data matrices, and will be included in future publications.

An approximately 650 base pair portion of the COI gene was sequenced for all species listed in Table 3-1 and for several additional species included in the analyses associated with Figures 3-12 and 3-13 (Note: editing and alignment in different analyses may have slightly changed the total number of available COI characters in each tree). A representative (=nominate subspecies or nearest to the species type locality) COI sequence for each of the 16 species of *Speyeria* is included in Appendix A. Because of the fairly rapid evolution of the COI region and the apparent recent divergence of many Argynnnini, COI provided a good marker to infer the evolutionary relationships of the members of this tribe.

A phylogeny generated with Barcode of Life Data Systems software indicate that *Speyeria* is a monophyletic grouping and sister to *M. aglaja* based on COI (Figure 3-7). Closely related species, such as *S. atlantis* and *S. hesperis*, largely group according to geographical locality. Trees inferred in PAUP following manual alignment of sequences also indicate *Speyeria* is monophyletic (Figures 3-8 and 3-9). In both analyses, members of the Semnopsyche/Cybele group+*Speyeria idalia* and *Speyeria nokomis* appear basal within *Speyeria*, and most closely allied to *S. adiaspe* and *S. hydaspae*. The relationship between the latter two species confirms the relationship observed in the morphological/behavioral data set. The strict consensus tree (Figure 3-8) suggests *Speyeria* is most closely related to *Argynnis paphia* and *Mesoacidalia aglaja* (*M. aglaja* appears more closely related in the phylogram presented in Figure 3-9), with *Speyeria edwardsii* appearing derived within the genus. Much of the Callippe group remains unresolved, but the species tend to group together, especially by locality (Figure 3-7). It should be noted that eastern *Speyeria atlantis* forms do not appear sister to western *S. atlantis* and *Speyeria hesperis* forms (Figure 3-7). There also appears to be a close relationship between *S. atlantis* from Ontario and *Speyeria aphrodite* (Figure 3-7). In addition, *S. aphrodite* does not appear closely related to members of the Semnopsyche group, for which it has been considered part of in the past based on genitalic similarities (dos Passos and Grey 1945a). A few anomalies observed in the tree, namely the placement of one *Speyeria diana* relative to *S. aphrodite* and *S. atlantis* from Ontario (Figure 3-7) could be due to DNA contamination or misidentification of specimens. The combined data sets including morphology, behavioral, and molecular characters (Figures 3-10 and 3-11) show similar results to that of the trees inferred from COI alone (i.e., a close relationship to *M. aglaja* and *A. paphia*) with the exception of the placement of the basal *Speyeria* taxon (*Speyeria nokomis*, not *S. idalia* or *S. diana*, as indicated by the COI data).

There are observable differences, namely in the male genitalia, between the North American and Old World Argynnini. Assuming Eurasian argynnine taxa represent a more ancient lineage due to greater differences in wing and genital morphologies than those within *Speyeria*, *Mesoacidalia aglaja* may most closely represent ancestral *Speyeria*. The next step in understanding the true evolutionary relationships within the Argynnini and their relatives is to combine *Speyeria* inclusive data sets with those covering other argynnine taxa. A preliminary analysis of publicly available COI sequence data was conducted here, which included several additional heliconiine species (Figures 3-12 and 3-13). *Speyeria* maintains a natural grouping, with *Argynnis* (= *Fabriciana*) *niobe* appearing most closely related to *Speyeria*. All *Argynnis* included in this analysis appear more closely related to *Speyeria* than does *M. aglaja*. Simonsen (2006c) (Figure 3-5) reported *M. aglaja* sister to *Speyeria* based on wing and genitalic morphology but included a different generic treatment of most of the species presented here as *Argynnis*.

Recent morphological (wing and genitalic characters) and molecular (COI and two nuclear genes) studies conducted by Simonsen et al. 2006 suggest *Argynnis* is paraphyletic if *Speyeria* is maintained as a separate genus (Figure 3-14). *Speyeria* [= *Argynnis* (Simonsen et al. 2006)] *cybele* is sister to *Mesoacidalia* [= *Argynnis* (Simonsen 2006c)] *aglaja* and closely related to *Argynnis kamala* in this study. Although there are obvious affinities between the Semnopsyche/Cybele and Callippe groups as indicated by the inclusive analyses conducted on *Speyeria* herein, members of the Callippe group and the remainder of *Speyeria* should not be excluded in phylogenetic analyses relative to the evolution of Argynnini. In addition, it is apparent from the recent literature that the use of *Argynnis* and other closely related genera continue to be used interchangeably when discussing a given species. Taxon inclusion (and

omission) and statistical analyses change tree topologies (and perceived relationships) considerably. For example, when *S. cybele* is used as the representative speyerian taxon utilizing COI without strict consensus criterion, it appears to fall within *Argynnis* (Figure 3-15) [*Argynnis* following Simonsen et al. (2006) (Figure 3-14)]. Thus, the designation of *Speyeria* as a subgenus within *Argynnis* is tentative until more robust data sets can be analyzed; *Speyeria* should be retained as a distinct genus until that time.

Percent divergence of COI, calculated at the Barcode of Life Data Systems workbench, was compared within (from different populations) and between species of *Speyeria*. Individuals selected from overlapping and more or less disjunct populations indicate that average percent divergence follows a trend in increasing percent divergence, as would be hypothesized based on the evolution of the gene. Percent COI divergence increases within *Speyeria* populations when they are more disjunct, and increase on average when they are compared to hypothetical outgroups. It is evident that species known from a single population will exhibit very low COI divergence (e.g., 0% for *Speyeria carolae* in Nevada's Spring Mountains and *S. adiate* on the California coast), while the same species known from disjunct, more or less geographically isolated populations will show a divergence as high as 4 or 5.33% (e.g., *Speyeria zerene* from California and *S. zerene* from Nevada was 5.01%; *Speyeria atlantis* from Vermont and *S. atlantis* from Wyoming was 4.5%). The divergence within the genus and between species averaged 4.3%, showing the greatest percentage of 8.4%. *Speyeria callippe* and *Speyeria idalia* indicated approximately 8.0% divergence, while *S. callippe* and *S. edwardsii* showed only a 0.16% divergence. Related genera, namely those utilized as outgroups in phylogenetic analyses, showed on average a 9.2% divergence from *Speyeria*. The highest divergence for *Argynnis paphia* was 9.2% when compared to *S. idalia*, whereas the highest divergence between *Mesoacidalia aglaja*



and a *Speyeria* taxon (i.e., *Speyeria coronis*) was 7.88%. *Boloria selene* (from North America) and *Clossiana selene* (from Europe) both showed divergences as high as 12%. All of these COI divergence data will be made publicly available at a later time.

Missing data, resulting from limited sample of taxa or only partial information on characters, can have adverse effects on cladistic results (Miller and Wenzel 1995). Thus, additional morphological and molecular characters are presently being added to this data set. Amplification of COI for additional *Speyeria* taken from various parts of a species range is ongoing. A *Speyeria* DNA barcode database for the COI gene has also been implemented at Barcode of Life Data Systems, University of Guelph, for use in future molecular analyses. This will allow for researcher augment and/or access to the DNA sequences for COI when *Speyeria* are critical taxa in phylogenetic analyses. In addition, a large tissue collection of *Speyeria* now resides at the McGuire Center for Lepidoptera and Biodiversity for future molecular research.

Species and subspecies delimitation remains problematic for many taxa within *Speyeria*, and determinations are often affixed by locality. 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 (e.g., Scott et al. 1998). It is imperative that informative characters are chosen while avoiding wing aberrations, mutations and characters subject to environmental influences. 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 diagnoses. A suite of useful and environmentally stable characters, including the external morphologies of adults and immature stages, genitalia, DNA sequences, and life history traits, will continually be needed for *Speyeria*.

Beyond the scope of this study, further ecological (e.g., pheromone testing) studies, examination of wing patterns and coloration under ultra-violet light, DNA sequences of several additional gene regions, and rearing and cross breeding studies are also warranted to better understand the evolutionary relationships of *Speyeria*. Primers for amplification of additional gene regions for *Speyeria* are available in the literature (Martin and Pashley 1992; Brower and Egan 1997; Pollock et al. 1998; Williams 2001a; Williams et al. 2002; Simonsen et al. 2006).

At issue is a growing discontent with an arbitrary taxonomic category, the subspecies, which often fails to accurately describe infraspecific variation (Arnold 1985). Most subspecies are named on the basis of one or a few wing characters, often intuitively perceived by the worker. Within *Speyeria*, there is often a greater morphological difference between subspecies than between sympatric species, and workers often call attention to rather fine (wing pattern) differences within each species. These differences are then named subspecies in order to properly define and identify the species themselves (Grey 1989). The riddle of species and subspecies, and an even more intriguing question of evolutionary meaning in local variation in relation to local environment, may come down to a better understanding of sympatry. There is still a richness of data afforded by numerous closely related and co-inhabiting ‘species’, as seen in the molecular data presented herein. Rather than arbitrarily designating subspecies or following an attempt at justifying them statistically by percent population overlap, as suggested for birds (Patten and Unitt 2002; Cicero and Johnson 2006), perhaps a mean COI (or some other gene region) percent divergence can be utilized. Depending on the working species concept, and there are many, it may be impossible to ‘define’ some *Speyeria* forms in their present state. One might be better off to let evolution ‘run its course’ with these potentially ‘incipient’ entities, and reexamine these inter- and intra-specific relationships in the [perhaps distant] future. In the

meantime, it may be wise to consider each population as evolutionary significant units, worthy of further systematic and conservation attention.

Table 3-1. List of taxa included in the primary analyses.

---

Ingroup taxa

*Speyeria diana* (Cramer)  
*Speyeria cybele* (Fabricius)  
*Speyeria aphrodite* (Fabricius)  
*Speyeria idalia* (Drury)  
*Speyeria nokomis* (Edwards)  
*Speyeria edwardsii* (Reakirt)  
*Speyeria coronis* (Behr)  
*Speyeria carolae* (dos Passos and Grey)  
*Speyeria zerene* (Boisduval)  
*Speyeria callippe* (Boisduval)  
*Speyeria egleis* (Behr)  
*Speyeria adiaspe* (Edwards)  
*Speyeria atlantis* (Edwards)  
*Speyeria hesperis* (Edwards)  
*Speyeria hydaspe* (Boisduval)  
*Speyeria mormonia* (Boisduval)

Outgroup taxa

*Boloria selene* (Denis and Schifferrmüller) (= *Clossiana selene*)  
*Euptoieta claudia* (Cramer)  
*Argynnis paphia* (Linnaeus)  
*Fabriciana niobe* (Linnaeus)  
*Mesoacidalia aglaja* (Linnaeus)  
*Heliconius* spp.

---

Table 3-2. Synopsis of characters\* and states used for phylogenetic analyses.

---

Male genitalia

- (4) uncus with dorsal spines/teeth (0) absent/weak (1) present/strong
- (16) bifid uncus (0) absent (1) present
- (18) tip of uncus (0) simple (1) excavate
- (5) juxta with apical spine(s) (0) absent (1) present
- (22) crista (0) absent (1) present
- (6) clavate ampulla (0) absent (1) present
- (7) ampulla straight (0) or bent downward (1)
- (17) digitus (located on distal end of valve) (0) absent (1) present
- (19) length of digitus (0) less than 3 to 4 times the width (1) 5 to 6 times longer than the width
- (20) dorsal, distal end of digitus (0) rounded and not extended into point (1) extended into narrow point (1)
- (13) proximal end of aedeagus (0) open (1) closed
- (21) cornuti on aedeagus (0) absent (1) present
- (27) position of harp (=digitus) on valves (0) dorsal/free (1) lateral (2) dorsal/attached (3) none
- (29) tegumen/uncus with fenestrula (0) absent (1) present
- (30) fenestrula (0) elongate, narrow (1) widest at base (2) triangular anteriorly

Female genitalia

- (14) bursa copulatrix with appendix bursa (0) absent (1) present

Wings

- (24) male forewing veins (0) “thin” (1) “thick”
- (25) “halo” surrounding ventral black median spot between veins M<sub>3</sub> and CuA<sub>1</sub> (0) absent (1) present
- (26) dorsal submarginal spots (0) round (1) crescent shaped (2) none
- (28) silver spots on ventral hindwing disc in at least one form or sex (0) absent (1) present

Behavioral

- (2) Male carries female while mating (0) male (1) female (2) either
- (3) Mate locating behavior by male (0) perching (1) patrolling (2) pheromones (3) more than 1 behavior
- (10) females oviposit on hostplant (0) or not on hostplant (1)
- (11) diapausing (overwintering) stage (0) egg/larva (1) pupa/adult
- (12) diapausing larval instar (0) 1<sup>st</sup> (1) 2<sup>nd</sup> or later
- (23) univoltine (0) multivoltine (1)

Pupal Characters

- (8) tubercles on dorsal mesal portion of abdomen (0) absent (1) present
- (9) carinate mesothorax (0) absent (1) present

Larval Characters

- (1) *Viola* used larval host plant (0) no (1) yes

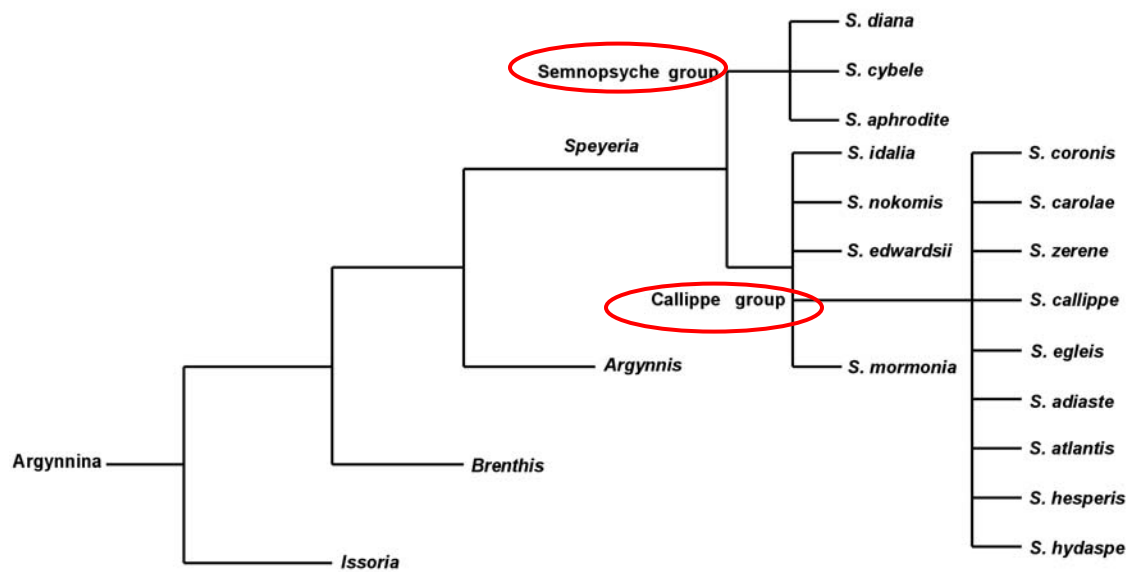
Genetic

- (15) total chromosomes in testes (0) >30 (1) 30 or more
- 

\*Numbers in parentheses to the left represent the character number input on data matrix in Table 3-3.

Table 3-3. Data matrix for characters listed in Table 3-2.

Character #	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
<i>S. diana</i>	1	?	?	0	0	0	0	1	1	1	0	0	0	1	?	0	1	1	0	0	1	1	0	1	0	1	1	0	1	1
<i>S. cybele</i>	1	2	0	0	0	0	0	1	1	1	0	0	0	1	0	0	1	1	0	0	1	1	0	1	0	1	1	1	1	1
<i>S. aphrodite</i>	1	1	1	0	0	0	0	1	1	1	0	0	0	1	0	0	1	1	0	0	1	1	0	0	1	1	1	1	1	1
<i>S. idalia</i>	1	1	?	0	0	0	0	1	1	1	0	0	0	1	?	0	1	1	0	1	1	1	0	1	0	1	1	1	1	1
<i>S. nokomis</i>	1	2	1	0	0	0	0	1	1	1	0	0	0	0	?	0	1	1	0	0	1	1	0	1	0	1	1	1	1	1
<i>S. edwardsii</i>	1	1	1	0	0	0	0	1	1	1	0	0	0	0	?	0	1	0	1	0	1	1	0	1	0	1	1	1	1	1
<i>S. coronis</i>	1	?	1	0	0	0	0	1	1	1	0	0	0	0	1	0	1	0	0	0	1	1	0	1	0	1	1	1	1	1
<i>S. carolae</i>	1	?	?	0	0	0	0	1	1	1	?	?	0	0	?	0	1	0	0	0	1	1	0	1	0	1	1	1	1	1
<i>S. zerene</i>	1	?	1	0	0	0	0	1	1	1	0	0	0	0	0	0	1	0	0	0	1	1	0	1	0	1	1	1	1	1
<i>S. callippe</i>	1	1	3	0	0	0	0	1	1	1	0	0	0	0	1	0	1	0	0	0	1	1	0	1	0	1	1	1	1	1
<i>S. egleis</i>	1	1	1	0	0	0	0	1	1	1	0	0	0	0	?	0	1	0	0	0	1	1	0	1	0	1	1	1	1	1
<i>S. adiaeste</i>	1	?	?	0	0	0	0	1	1	1	0	0	0	0	?	0	1	0	0	0	1	1	0	1	0	1	1	0	1	1
<i>S. atlantis</i>	1	0	1	0	0	0	0	1	1	1	0	0	0	0	0	0	1	0	0	0	1	1	0	1	0	1	1	1	1	1
<i>S. hesperis</i>	1	?	?	0	0	0	0	1	1	1	0	0	0	0	?	0	1	0	0	0	1	1	0	1	0	1	1	1	1	1
<i>S. hydaspae</i>	1	1	?	0	0		0	1	1	1	0	0	0	0	0	0	1	0	0	0	1		0	1	0	1	1	0	1	1
<i>S. mormonia</i>	1	2	1	0	0	0	0	1	1	1	0	0	0	0	0	0	1	0	0	0	1	1	0	0	0	1	1	1	1	1
<i>B. selene</i>	1	0	1	0	0	0	0	0	1	1	0	1	1	0	1	1	0	0	?	?	0	1	1	?	?	?	3	1	1	2
<i>E. claudia</i>	1	2	1	0	0	0	0	0	0	0	?	?	?	0	?	0	0	0	?	?	0	0	1	?	?	?	3	0	1	?
<i>A. paphia</i>	1	2	?	1	0	0	0	1	1	1	?	?	0	0	0	0	0	1	?	?	1	1	0	?	?	0	0	1	1	0
<i>F. niobe</i>	1	2	?	0	1	0	0	?	?	1	?	?	0	0	0	0	0	0	?	?	1	1	0	?	?	1	0	1	1	0
<i>M. aglaja</i>	1	2	?	1	1	0	1	?	?	1	?	?	0	0	0	0	0	1	?	?	?	1	0	0	?	1	2	1	1	0
<i>Heliconius</i> sp.	0	0	?	0	0	?	?	1	1	0	1	?	?	0	?	0	?	?	?	?	0	0	1	?	?	2	3	0	0	?



Intuitive phylogeny of subtribe Argynnina based on the literature

Figure 3-1. Intuitive phylogeny of subtribe Argynnina (*Speyeria* based on dos Passos and Grey 1947).

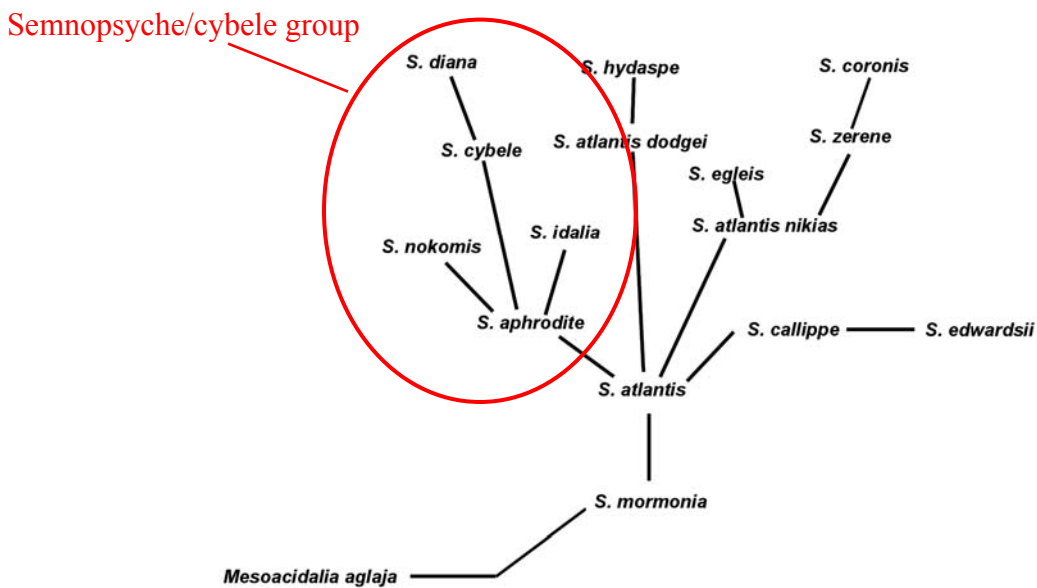


Figure 3-2. Intuitive phylogeny of *Speyeria* (taken and modified from Hammond 1978).

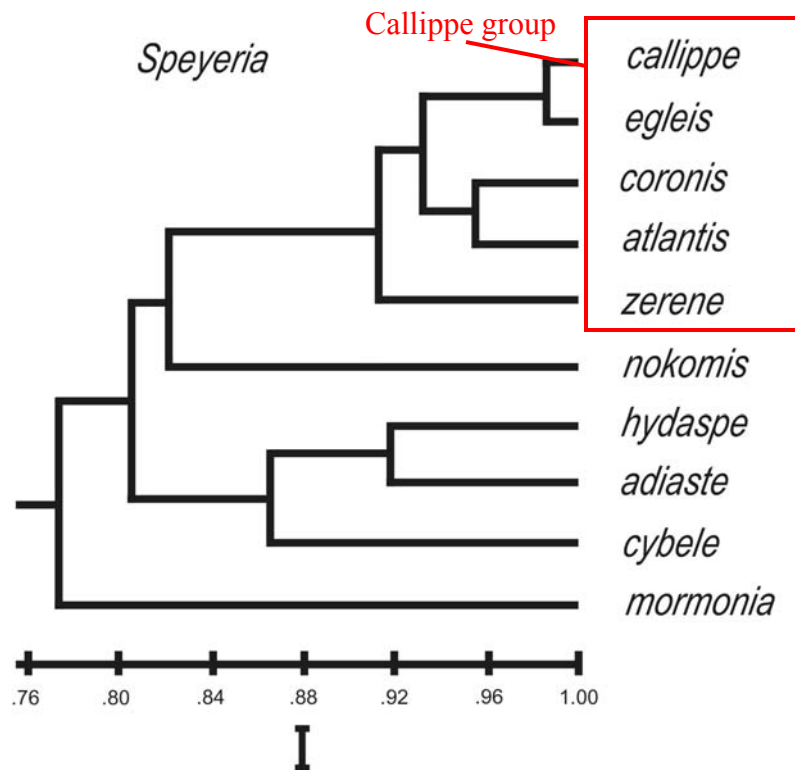


Figure 3-3. Dendrogram of genetic similarity between 10 *Speyeria* species (taken from Brittnacher et al. 1978).

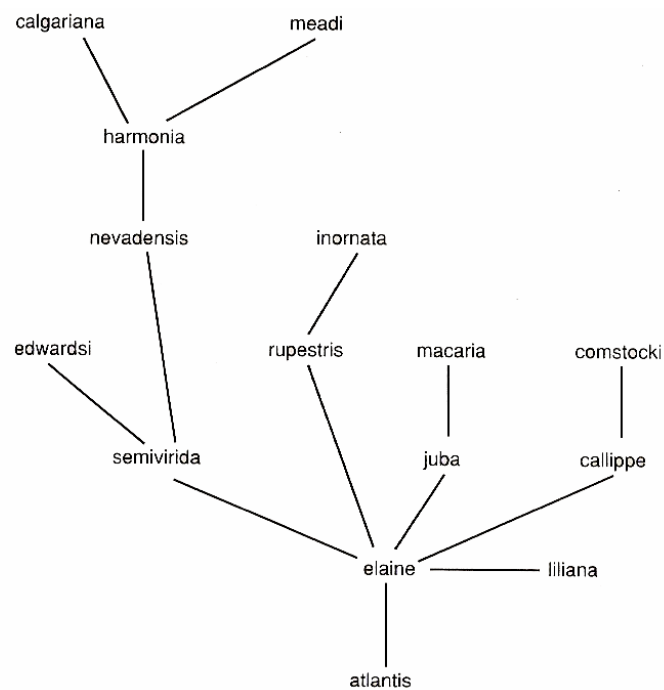
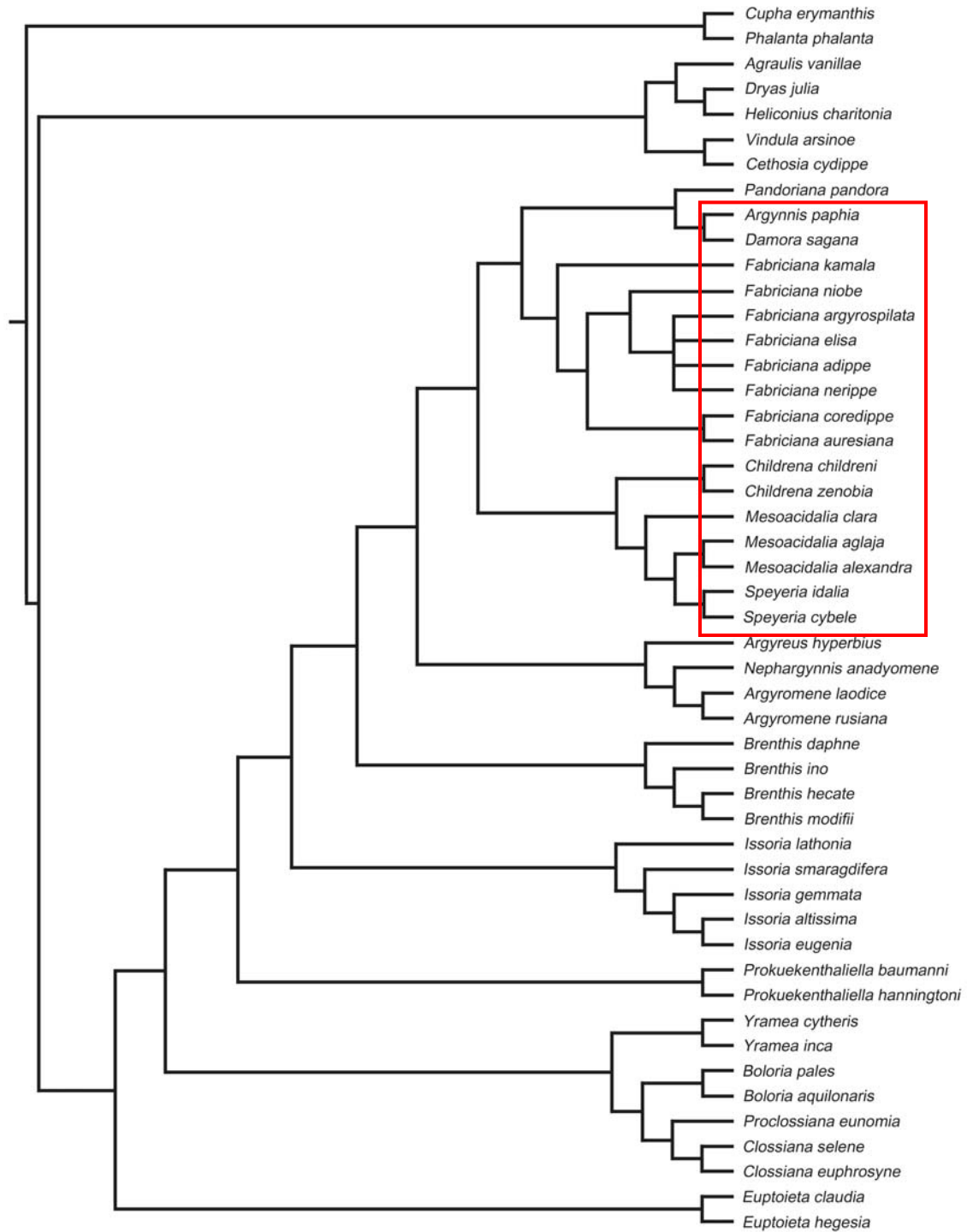


Figure 3-4. Phylogenetic interpretation of *Speyeria callippe* subspecies (taken from Hammond 1990).





**Figure 4.** The strict consensus tree of the three most parsimonious trees with length 417 (CI = 0.3765, RI = 0.7498).

Figure 3-5. Strict consensus tree of Argynnini (taken from Simonsen 2006c; Figure 4. The strict consensus tree of the three most parsimonious trees with length 417 (CI=0.3765, RI=0.7498).

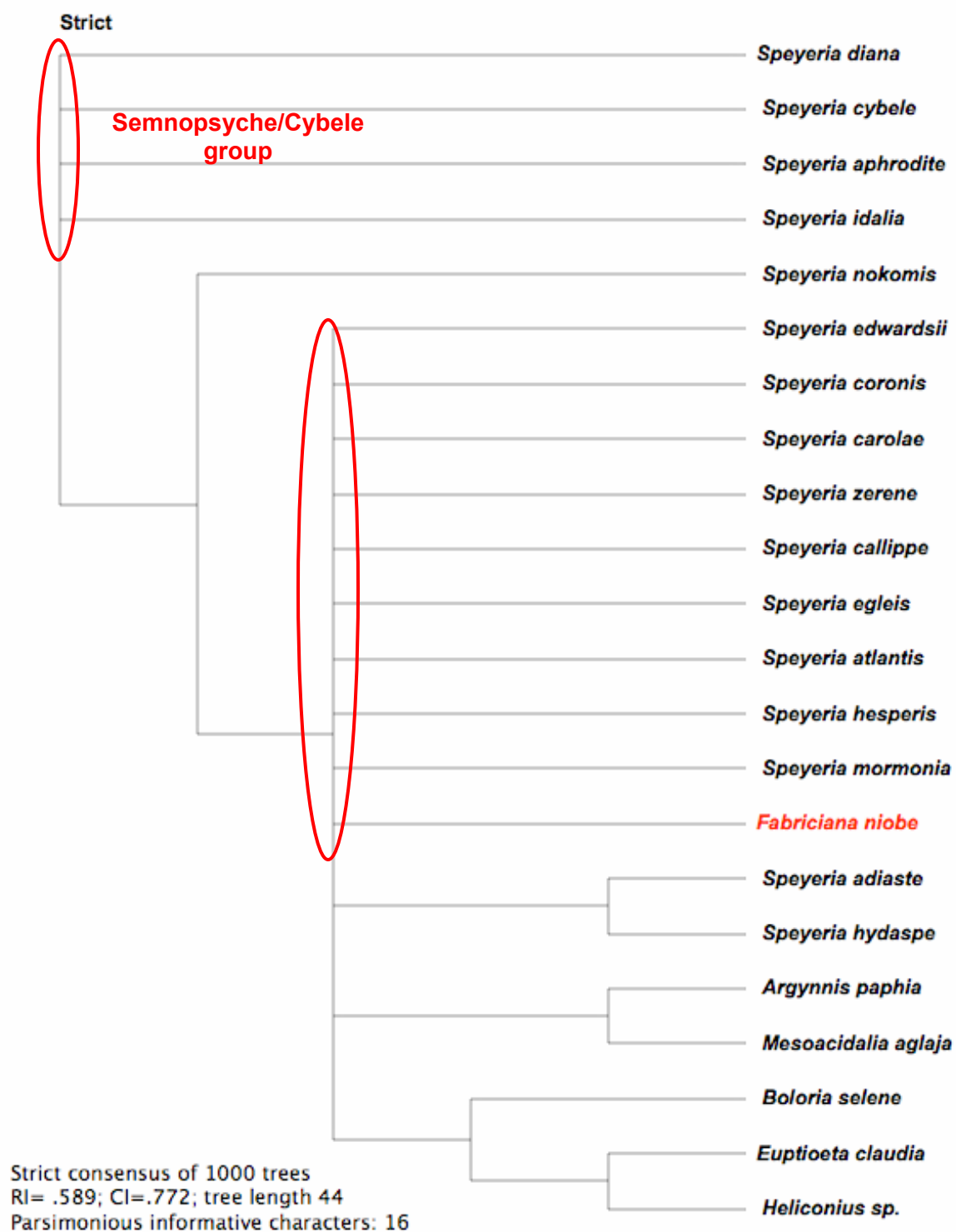


Figure 3-6. Phylogeny of *Speyeria* based on 30 characters (ovals = polytomies).



Figure 3-7. Phylogeny of *Speyeria* based on 653 characters of the mitochondrial gene COI (BOLD-Kimura 2 Parameter). Five-digit identifier, number of COI base pairs, and locality record for each specimen to the right of species name.

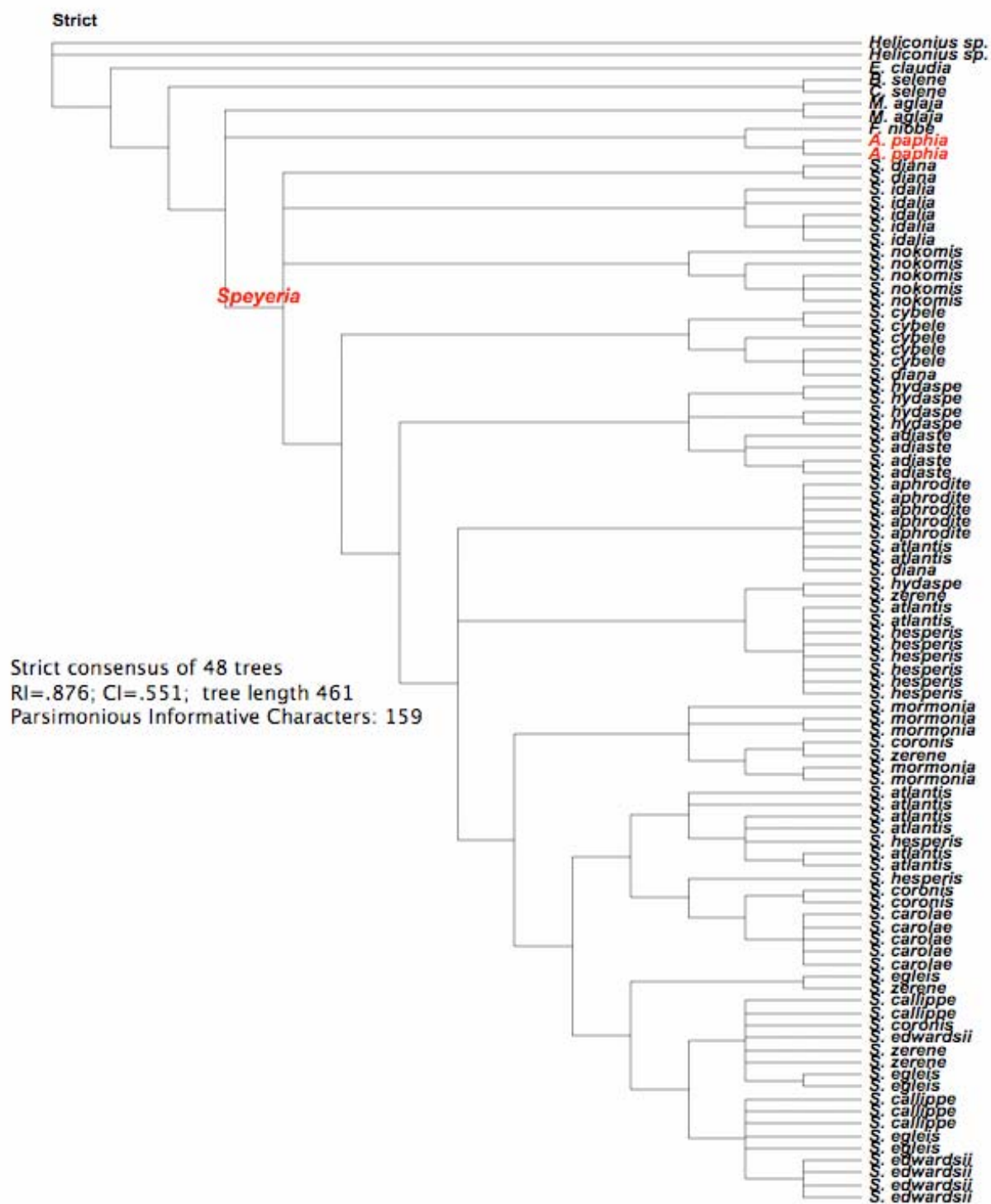


Figure 3-8. Phylogeny of *Speyeria* based on 625 characters of the mitochondrial gene COI.

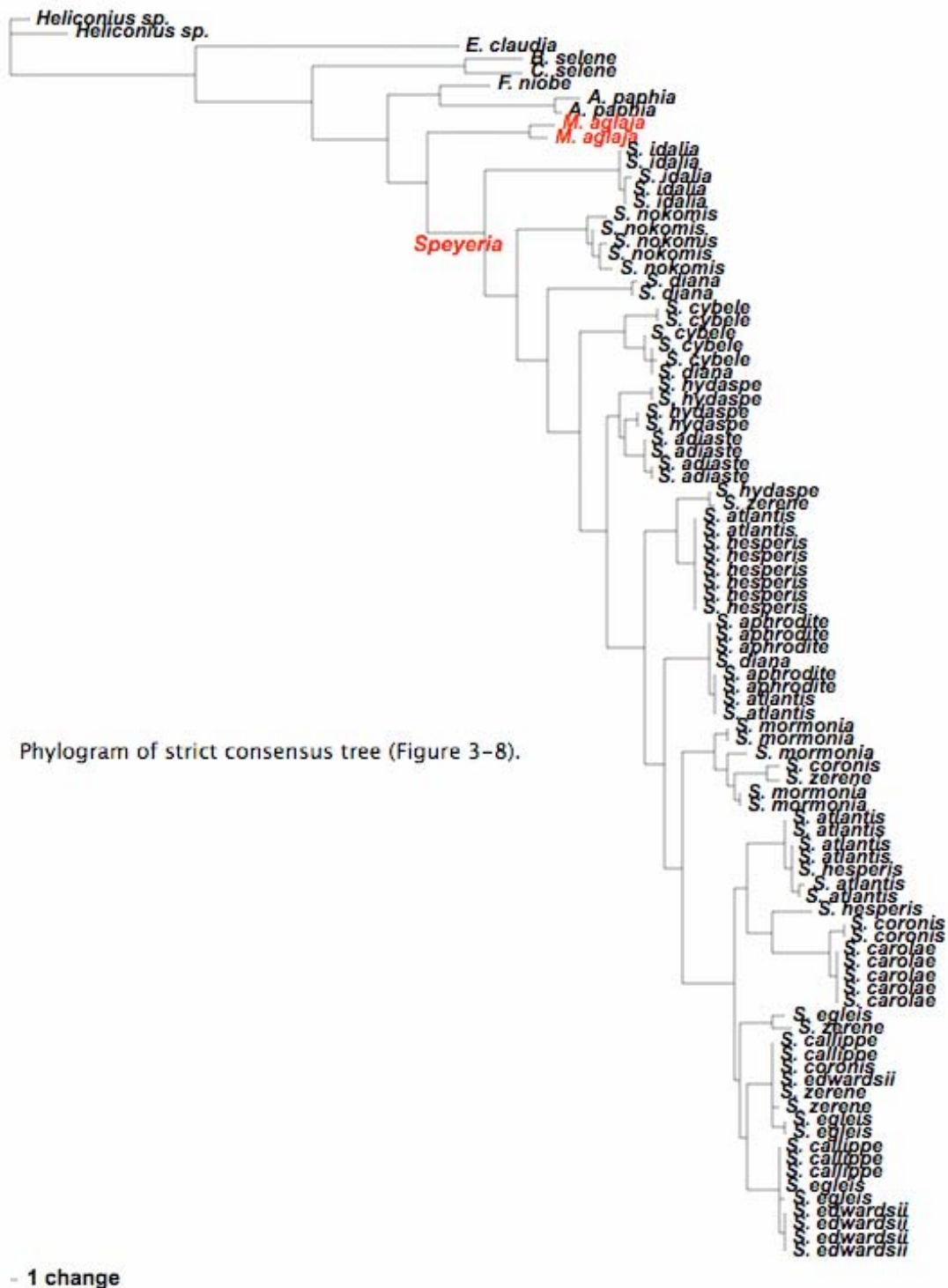


Figure 3-9. Phylogram of *Speyeria* based on the mitochondrial gene COI.











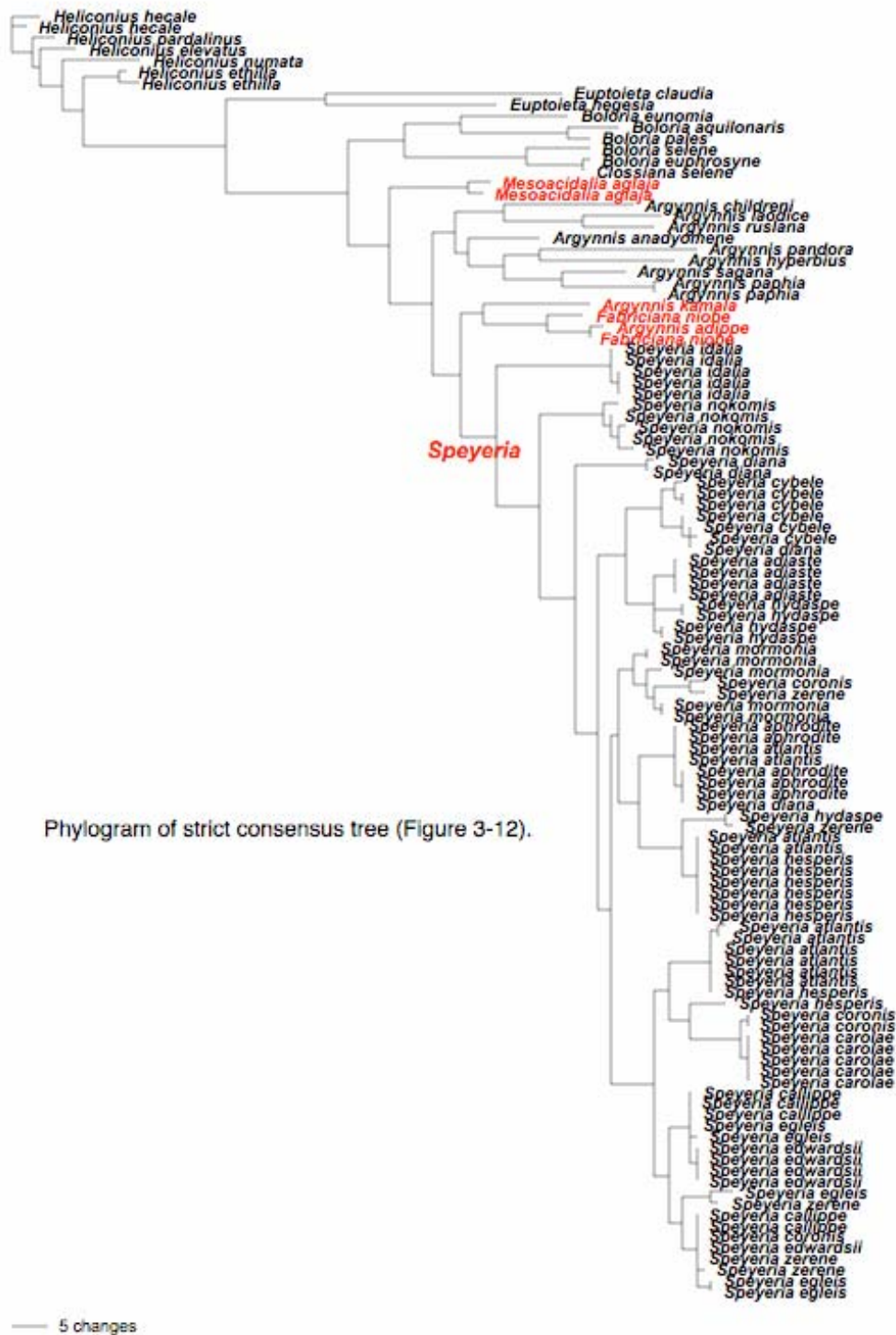


Figure 3-13. Phylogram of *Speyeria* and additional outgroup taxa based on the mitochondrial gene COI.

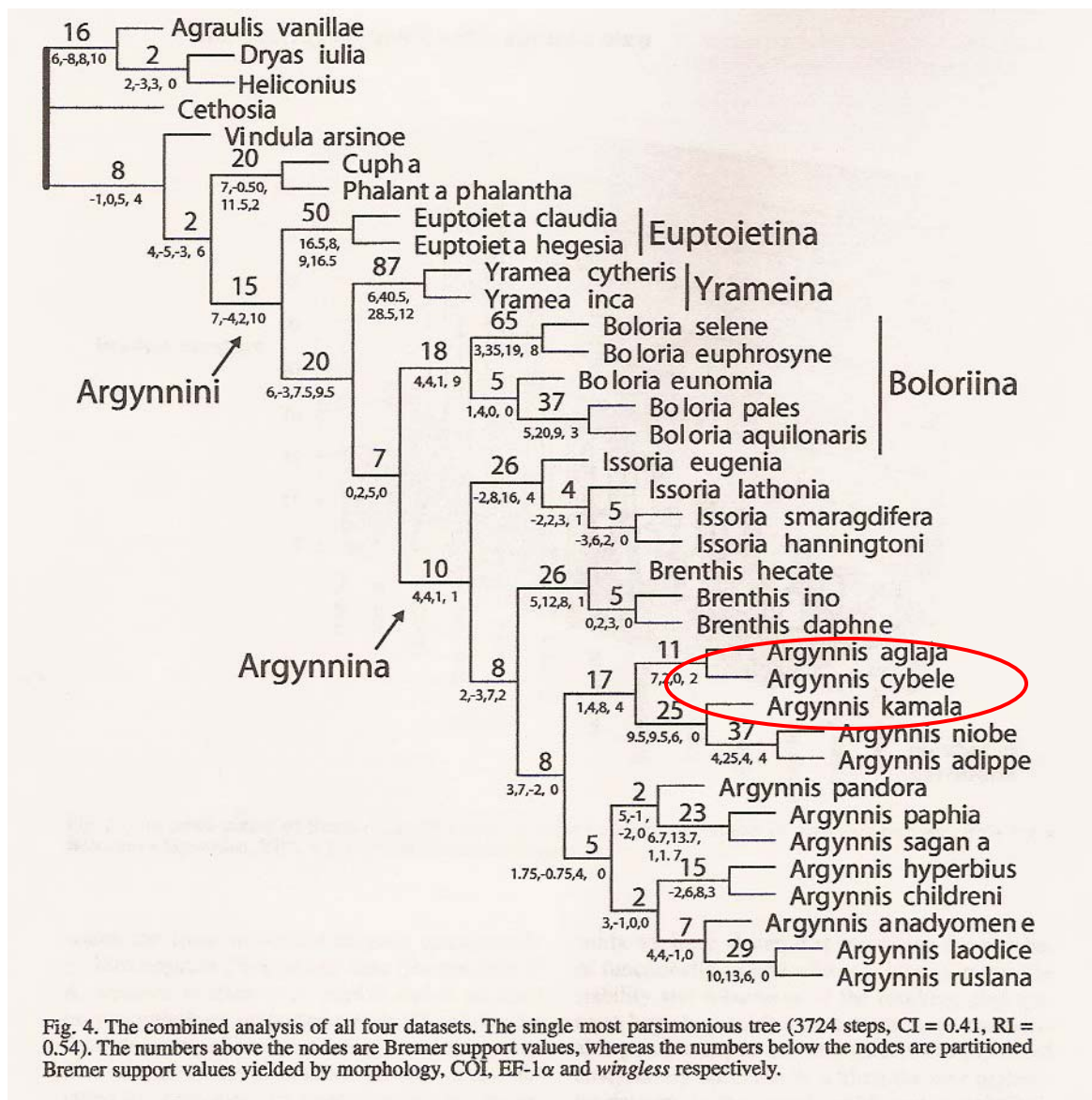


Figure 3-14. Phylogeny of Argynnini based on combined morphological and molecular sequence data [taken from Simonsen et al. 2006c; Figure 4. The combined analysis of all four datasets. The single most parsimonious tree (3724 steps, CI=0.41, RI=0.54). The numbers above the nodes are Bremer support values, whereas the numbers below the nodes are partitioned Bremer support values yielded by morphology, COI, EF-1 $\alpha$  and *wingless* respectively].

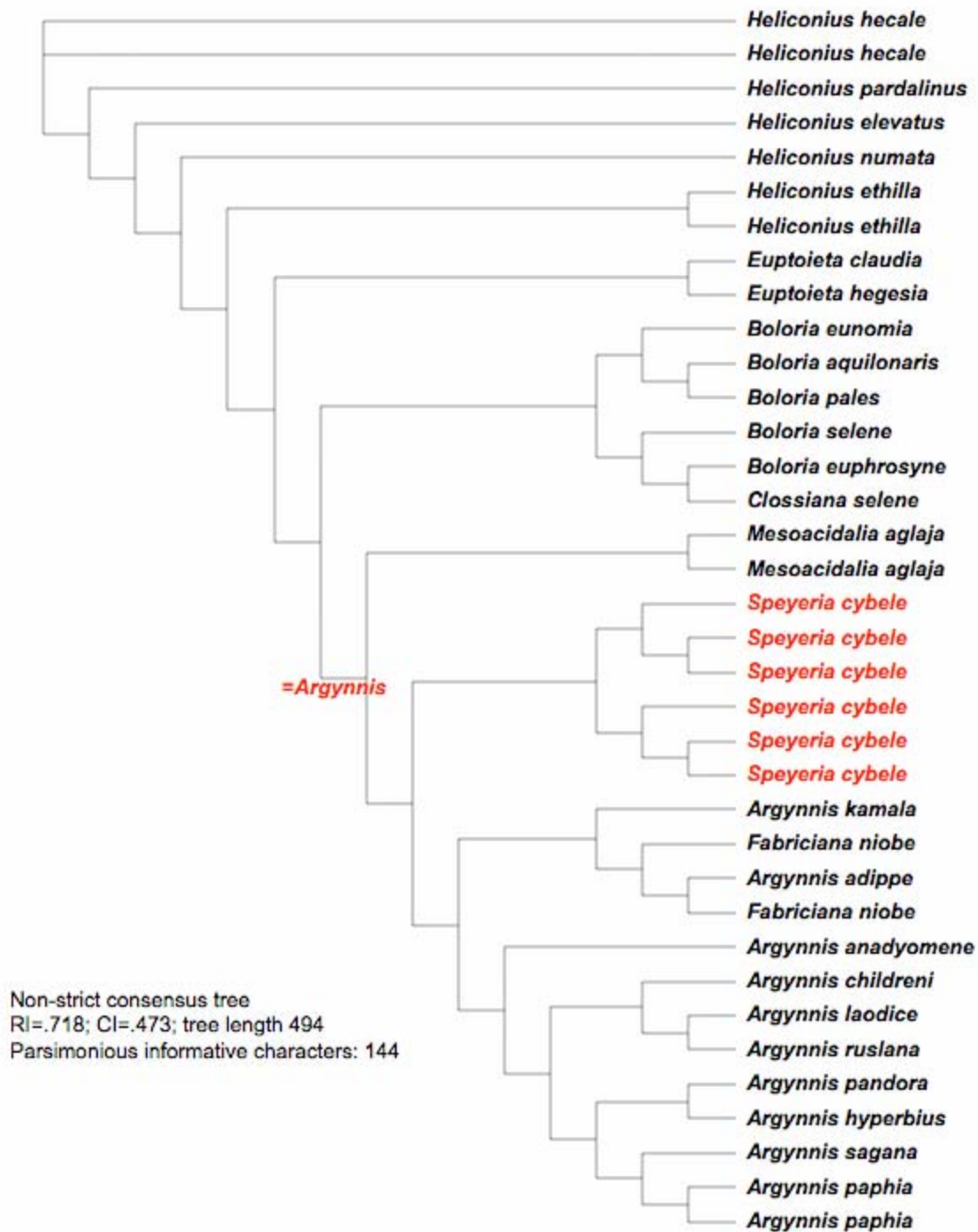


Figure 3-15. Phylogeny of *Argynnis* (following Simonsen et al. 2006) based on the mitochondrial gene COI with only *Speyeria cybele* included in analysis.

CHAPTER 4  
BIOGEOGRAPHY AND GENITALIC SURVEY OF *SPEYERIA* WITH EMPHASIS ON  
OVERLAPPING *SPEYERIA ATLANTIS* AND *SPEYERIA HESPERIS* POPULATIONS

The *Speyeria atlantis* (Edwards) and *Speyeria hesperis* (Edwards) species complexes are represented by several widely distributed subspecies (Grey 1951; Moeck 1957; Hammond 1978; Dunford 2005). These subspecific taxa have distributions that 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) (see Figure 4-3). W. H. Edwards originally described *S. atlantis* from the northeastern United States in 1863 [type locality now fixed in the Catskills Mountains, in Hunter, Greene Co., New York (dos Passos and Grey 1947)] and *S. hesperis* from Colorado in 1864. Since that time, several additional *S. atlantis* and *S. hesperis* ‘forms’ have been described (e.g., dos Passos and Grey 1945b; Moeck 1947, 1950; Austin 1983; Holland 1988; Emmel et al. 1998c; Scott et al. 1998), and there are a few regions where the two ‘species’ occur sympatrically and synchronously (Grey et al. 1963; Ferris 1983; Scott et al. 1998).

*Speyeria atlantis* and *S. hesperis* are presently comprised of 25 subspecies (Emmel et al. 1998c; Scott et al. 1998). Subspecies designation is based primarily on differences in wing facies [i.e., basal suffusion dorsally, discal coloration and silvering of spots on hindwings (see Figure 4-7)] and geographical location of populations (Howe 1975; Hammond 1978; Ferris and Brown 1981). Hammond (1990) noted that wing markings appear to be highly conservative and reliable diagnostic characters within *Speyeria*, while wing colors are less stable. Melanic, basal suffusion of wings is exceedingly plastic in *Speyeria*, and subject to repeated convergence and reversal (Hammond 1990). The ‘form’ *hesperis* was formerly recognized as a subspecies of *Speyeria atlantis* (dos Passos and Grey 1947; Grey 1951; Moeck 1957; Hammond 1978) until Scott et al. (1998) examined adult wing patterns and sympatric occurrence without interbreeding exhibited

by *atlantis* and *hesperis* forms in several regions, resurrecting the status of these entities to that of Edwards' original descriptions (Edwards 1863a; 1864a). Scott et al. (1998) designated *hesperis* and *atlantis* as distinct species based primarily on the silvering of ventral hindwing spots (and a few larval characters), and placed four silver-spotted forms into the *atlantis* species group and 19 primarily unsilvered forms into *hesperis* species group. However, earlier work by Scott (1988) indicated that a clear distinction between the two species was obscure, and that the silvered and unsilvered phenotypes are likely polymorphic forms of one species. Tebaldi (1982) and Ferris (1983) also attempted to discern the status of *atlantis* and *hesperis* in Colorado based primarily on wing facies and preliminary enzyme electrophoresis studies. Ferris (1983) suggested '*hesperis*' phenotypes might represent a sibling species of '*atlantis*' forms. Two additional subspecies, *Speyeria atlantis hansenii* Emmel, Emmel and Mattoon and *Speyeria atlantis cottlei* (Comstock) (presently listed under *S. hesperis* by the author), were described and discussed in Emmel et al. (1998c).

Much of the speciation and subspeciation within *Speyeria* probably came about in the past 10,000 years as a consequence of the last glacial retreat and the climatic readjustments in its wake (Grey 1951; Hammond 1990). 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). *Speyeria atlantis* and *S. hesperis* primarily inhabit cool, Canadian life zone habitats; their life history requirements include either the climatological elements of northern parts of North America or montane environments in the West (Scott 1986b; Opler and

Malikul 1998; Opler and Wright 1999; Glassberg 2001a,b). These subspecies are more or less isolated, and adaptations to local environmental conditions have allowed for distinct forms, especially the coloration on the ventral hindwings (see Table 4-1; Note: discal and spot coloration on hindwings is variable within some populations). In addition, the coloration in images may be artifacts of the age of the specimens, photograph lighting, and printer and paper quality (also see Introduction in Chapter 2 for discussion on photography and wing coloration).

Genitalic morphology demonstrates peculiar patterns of variation among animal species (Eberghard 1985; Arnqvist 1997; 1998, Mutanen 2005), and this variation may represent a more stable, discrete suite of characters than do the wing patterns mentioned above. Genital characteristics tend to vary greatly between Lepidoptera species, providing useful features for species delimitation (Porter and Shapiro 1990; Scoble 1995; Mutanen 2005; Simonsen 2006b). Traditionally, species specificity based on genitalia has been assumed to serve as a mechanical isolation system between species (i.e., the lock-and-key hypothesis) (Dufour 1844; Porter and Shapiro 1990; Arnqvist 1998). Most recent studies suggest, however, that such variation may also be due to sexual selection (Lloyd 1979; Eberhard 1996; Arnqvist 1997). These two working hypotheses provide different predictions on genital variation within and between species.

Genitalia of *Speyeria* have proven to be taxonomically uninformative, and detailed genitalic examination has largely been ignored in this group (Hammond 1978; Ferris and Brown 1981). Dos Passos and Grey (1945a) conducted a survey of male genitalic structures primarily in Argynninae (including *Speyeria*) butterflies and provided illustrations of several species, including the male genitalic armature (=capsule) of *S. atlantis* (Edwards) (Figure 4-1). Generic characters for male *Speyeria* genitalia include a semi-rectangular plate (=digitus) located near the dorsal lobe of the valvae (Figure 4-1), but otherwise the armature is more conventional in type

and comparatively unspecialized (dos Passos and Grey 1945a). It is apparent that genitalic data can conclusively separate the *Semnopsyche* group [= *Speyeria cybele* (Fabricius), *Speyeria diana* (Cramer), *Speyeria aphrodite* (Fabricius)] and Callippe group [= *S. atlantis*, *S. hesperis* (Edwards), *Speyeria callippe* (Boisduval), *Speyeria zerene* (Boisduval), *Speyeria coronis* (Behr), *Speyeria egleis* (Behr), *Speyeria hydaspe* (Boisduval), *Speyeria mormonia* (Boisduval)], but otherwise the male armature is largely homogenous (dos Passos and Grey 1945a).

Arnold and Fischer (1977) describe the morphology of genitalia and summarize the mechanisms of copulation in *Speyeria*, including those of *S. atlantis*, in greater detail. The ninth genital segment in male *Speyeria* is the main genitalic segment and is highly modified, bearing the aedeagus and clasping organs. A transverse, sclerotic ring termed the tegumen forms a supportive structure for the entire genitalic armature (Figures 4-1 and 4-2). The tegumen is heavily thickened for muscle attachment around its anterior edge. The tegumen also gives rise to the uncus (Figures 4-1 and 4-2), and the uncus is often specifically varied in shape and important in diagnostic value in grouping related species (dos Passos and Grey 1945a). The ventral portion of the tegumen gives rise to a large sclerite termed the vinculum (Figures 4-1 and 4-2). The vinculum is greatly expanded midventrally and extended anteriorly to form a trough-shaped inflection known as the saccus (Figures 4-1 and 4-2). Large, flattened, double walled lobes (=valvae) represent the clasping structures and are articulated with the vinculum. In *Speyeria*, a heavily sclerotized dorsal extension located on the valvae is known as the digitus (Figure 4-1 and 4-2) and may also be diagnostically important (dos Passos and Grey 1945a). The valvae are articulated dorsally at the base with the tegumen and ventrally at the base with the juxta. The juxta, a sclerite lying on the ventral surface of the anellus, supports the aedeagus. Internally, the anellus encompasses the aedeagus by acting as an eversible cone and allows for the extrusion of

the genital bulb at the time of copulation. The distal portion of the aedeagus forms an inner tube known as the vesica. During copulation, the greater part of the vesica is uncoiled and bears small chitinous teeth (=cornuti).

Female *Speyeria* possess two separate genital openings, as do all ditrysian Lepidoptera, and do not bear a true morphological ovipositor (Arnold and Fischer 1977). Fusion of the ninth and tenth abdominal segments apparently gives rise to the papillae anales, and these form a pair of setiferous lobes, one on either side of the anus and ovipositional opening. The copulatory opening, the ostium bursae, opens internally into a large sac termed the bursa copulatrix (Figure 4-24B). A secondary bursa, known in the *Semnopsyche* group (dos Passos and Grey 1945a) and *Speyeria idalia* (Drury) (Grey 1989), is considered a taxonomically important structural character in female *Speyeria* genitalia (dos Passos and Grey 1945a) (Figure 4-24A). Dilation of the bursa copulatrix readies the female for reception of the male intromittent organ. When copulation takes place, the male lowers the uncus and tegumen upon the papillae anales of the female. The male valvae embrace the anterior portion of the papillae anales and the movement of the valvae enables the sharply acuminate tip of the uncus to hook into the intersegmental membrane of the female's eight tergite. There are three points of attachment involving the uncus and the valvae, and when these are secured, the aedeagus is inserted into the female's bursa copulatrix, where the vesica are everted as the sperm is introduced.

In order to further examine the relationship of *S. atlantis* and *S. hesperis* forms (*sensu* Scott et al. 1998) and species delimitations, 13 *S. atlantis-hesperis* taxa and two members of the *Semnopsyche* group [*S. diana* (Cramer) and *Speyeria cybele krautwurmi* (Holland)] were utilized for genitalic comparisons. Several additional species, including Spring Mountain, Nevada isolate *Speyeria carolae* (dos Passos and Grey), were also examined. Genitalic dissections were made



on eastern North American *S. atlantis atlantis* (Edwards), western U.S. *atlantis* given the name *S. atlantis sorocko* by Scott et al. (1998), and *S. hesperis* [= *S. hesperis hesperis* and *S. hesperis electa* (Edwards)] populations in Colorado and Wyoming. In addition, species from sympatric populations in South Dakota, *Speyeria atlantis pahasapa* Spomer, Scott, Kondla and *Speyeria hesperis lurana* dos Passos and Grey, were also examined. Although there are several other regions where *S. atlantis* and *S. hesperis* populations overlap, this preliminary study of male genitalia may provide a stepping-stone in which to justify further genitalic examination (both male and female) of other sympatrically and synchronously occurring populations.

Male genitalia were examined in this study because the taxonomic value of these structures in species and generic level taxonomy and systematic studies is well established in Lepidoptera (dos Passos and Grey 1945a; Scoble 1995; Scoble and Krüger 2002; Simonsen 2006a,b). It is also hypothesized that rapid divergent evolution of male genitalia, which could provide some insight into the relationships of relatively young taxa such as those still considered ‘subspecies’, is one of the most general evolutionary trends in animals with internal fertilization, and in many cases the shapes of genital traits often provides the only reliable characters for species identification (Eberghard 1985; Arnqvist 1998). An attempt to reevaluate the significance of genitalia within *Speyeria* is critical to provide additional taxonomically and evolutionarily informative characters. In recent years, genitalic examination of insects has improved via better preparatory (i.e., dissection methods) and illustrative techniques (i.e., drawing and imaging technology) (Scoble and Krüger 2002; Simonsen 2006a,b; Zaspel and Weller 2006) and these modern techniques may yield taxonomically informative characters that have not been identified to date. The present study tested whether the characters of the current classification, based primarily on wing morphology, provide further evidence to support or reject the distinction of *S.*

*atlantis* and *S. hesperis*, and whether mechanical isolation or some form of sexual selection are active forces in the evolution of these species.

Examination of genitalia within the *S. atlantis* and *S. hesperis* complexes is undertaken herein. The genitalia of individuals occurring in overlapping populations of each species complex, particularly with respect to the Colorado/Wyoming and South Dakota forms, are imaged utilizing the Microoptics Digital Imaging System. Several additional genitalic morphs, representing other *S. atlantis* and *S. hesperis* subspecies, are also illustrated and discussed. Label data gleaned from over 5,000 specimens in these two species groups have also been and are presently being databased at DiversityofLife.org in order to begin to determine the degree of sympatry of *S. atlantis* and *S. hesperis* populations. Museums, private collections, and field-collected specimens were utilized to generate locality records, and distributional maps are electronically produced for the 25 *S. atlantis* and *S. hesperis* subspecies discussed herein.

## **Materials and Methods**

### **Taxon Sampling**

Specimens utilized for genitalic preparations were obtained from Lepidoptera specialists, amateur collectors, and fieldwork conducted by the author throughout much of the western United States. Subspecies identification was confirmed by at least three different Lepidoptera specialists upon examination of wing morphology and collection locality information. Slide mounted material was obtained from the F.H. Chermock Collection located at the Allyn Museum of Entomology (now The McGuire Center for Lepidoptera and Biodiversity). Species/subspecies chosen for this study include individuals that would embrace nominate *S. atlantis* and *S. hesperis* and two pairs of overlapping subspecies known from these species complexes. *Speyeria atlantis sorocko* represents a western *atlantis* form while *S. hesperis electa* occurs sympatrically in Colorado (Figure 4-3). *Speyeria a. pahasapa* and *S. h. lurana* are overlapping, isolated

populations located in the Black Hills of South Dakota. Two members of the *Semnopsyche* group (*S. diana* and *S. cybele krautwurmi*) were also chosen for ‘outgroup’ comparison. Slide mounted genitalic material borrowed from the Allyn Museum of Entomology included individuals that best represented similar (based on adult wing morphology and collection locality information) species/subspecies to those chosen for the genitalic preparations. For example, because *S. atlantis sorocko* was lacking in the slide collection, *S. atlantis hollandi* was chosen to represent a western *atlantis* form.

### **Preparation of Material**

Wings from individuals utilized for genitalic dissections were removed and glued to card stock providing a dorsal and ventral view. Wing vouchers were then placed into unit trays and photographed (Figure 4-8). Genitalic dissections were made of at least five individuals for each species/subspecies, with select dissections photographed. Adult male abdomens were removed and prepared using a 10% solution of KOH and subsequently placed in 70% EtOH. Genitalic armature (i.e., valves, uncus, aedeagus) was dissected from abdominal pelt and the aedeagus was removed and will be utilized later for future genitalic examination (i.e., vesica eversion and imaging). Dissection numbers were given to each individual utilized for imaging to track specimens and associated structures. Ventral, dorsal, and lateral view images of the male and female genitalic armature were taken utilizing the Microoptics Digital Imaging System housed at the Florida Museum of Natural History, McGuire Center for Lepidoptera and Biodiversity, and the Auto-Montage Syncroscopy System housed at the Department of Entomology and Nematology, University of Florida. Genitalic armature was positioned on top of K-Y Jelly and submerged in 70% EtOH. Bubbles were removed using insect pins and genitalic preps were positioned accordingly for desired image. Genitalic structures were then placed in glycerol filled genitalia vials and maintained together with associated abdominal pelt. The remaining structures

for each individual used for dissections were placed in 95% EtOH and are presently stored in a freezer for molecular studies.

Slide mounted genitalia borrowed from the Allyn Museum of Entomology were photographed utilizing the Auto-Montage Syncroscopy System housed at the Florida State Collection of Arthropods-Department of Plant Industry, Gainesville, Florida. Touch ups, blemish removal, and enhancement of images included in this study was completed utilizing Adobe Photoshop CS. Terminology utilized for genitalic descriptions follows that of dos Passos and Grey (1945a) (Figures 4-1 and 4-2). Select images were chosen to include herein, thus all of the genitalic images taken have not been provided. The author took all genitalic images unless otherwise noted.

### **Databasing**

Locality records were taken from specimens housed at the American Museum of Natural History (AMNH), Carnegie Museum of Natural History (CMNH), C. P. Gillette Museum of Arthropod Diversity (CSUC-C.P.) (Colorado State University), Milwaukee Public Museum (MPM), Field Museum of Natural History (FMNH), McGuire Center for Lepidoptera and Biodiversity (MGCL) [includes material from the Allyn Museum of Entomology (AME) and Florida State Collection of Arthropods (FSCA)], the Monte L. Bean Life Science Museum (MBSM) (Brigham Young University), Utah State University Insect Collection (EMUS), and University of Wyoming Insect Museum (ESUW) as well as six private collections, and specimens collected in the field. State and county information, as well as GPS coordinates, were primarily utilized for mapping species/subspecies distributions.

Locality records were exported in Microsoft Excel spreadsheet format to personnel at DiversityofLife.org (DOL) (<http://www.diversityoflife.org/>) for databasing. DOL provides software for a “plug and play” management system for biodiversity data, with tools for mapping

species distributions, image database management and retrieval, morphological data management, diagnostic key generation, cladogram display and navigation, descriptions, classifications and nomenclature. This allows for storing, retrieving, and analyzing biodiversity, systematic, taxonomic, and phylogenetic data. Distributional maps are generated by selecting a given species/subspecies and following the instructions. Maps are either in road, aerial satellite imagery, or hybrid (i.e., road map and aerial topo) format. A navigation and zoom function allows the user to visualize the entire distribution or to focus on single locality data points.

## **Results and Discussion**

Examination of closely related species of *Speyeria* yields a few apparent taxonomically informative genitalic characters. The species and subspecies that were examined from the Chermock collection and newly dissected specimens are listed and select structures are described in Table 4-2. Both sympatrically occurring Wyoming/Colorado and Black Hills *S. atlantis-S. hesperis* populations were compared and key male genitalic features are discussed below. Several additional species of *Speyeria* and *S. atlantis-S. hesperis* subspecies are also briefly described and/or illustrated.

The digitus, a distinct genitalic character for *Speyeria*, appears to be variously shaped, with the apical portion bearing a ‘finger-like’ extension or projection of different lengths and orientation. Amongst the taxa included in the dissections, it appears to project dorsally (=upward) when viewed laterally on *S. atlantis sorocko* (Figure 4-9A) and projecting posteriad (=straight back) on *S. hesperis electa* (Figure 4-9B). The saccus of *S. atlantis sorocko* also appears to be distinct from others included in the dissections. The length appears to be shorter with the apex rounded when viewed laterally (Figure 4-10A). The tegumen of *S. atlantis sorocko* appears slightly different than other *atlantis/hesperis* forms when viewed laterally (Figure 4-11). The basal margin appears to be convex, whereas on others the margin appears to be vertical with

respect to point of attachment with valvae. This may, however, be an artifact of positioning of the genitalic prep on the surface of the K-Y Jelly. The digitus is distinctly shaped in many *Speyeria*, and phylogenetically informative in *Speyeria edwardsii* (Figure 4-20B) and *S. idalia* (Figure 4-19B). Its function and placement during copulation should be explored.

The uncus appears to taper gently to a ventrad-curved claw without pronounced ventral excavation in the lateral outline. This was apparent in all of the *S. atlantis/hesperis* taxa dissected here. Grey (1951) noted that the uncus fails to separate *atlantis* from its closest relatives (=Callippe group); however, it is distinctly different in *S. idalia*, *S. nokomis*, and in members of the Semnopsyche group. The uncus of *S. cybele* is distinct in both size and shape (Figure 4-12), and this distinction is expected in members of the Semnopsyche group. It appears flattened and deeply notched at its apex. The tegumen is similar to other *Speyeria* in shape, with the exception of the outline of the basal portion, and a clear membranous portion located medially termed the fenestrula (Figure 4-26A) differs in size and shape from other non Semnopsyche *Speyeria* (Figure 4-26B), especially towards the uncus. It should be noted that the tegumen in European *Argynnis* is clearly distinct in shape and the fenestrula is diamond shaped (Figure 4-26C). The dorsal lobes, located on the basal portion of the valvae, are relatively similar in the *S. atlantis/hesperis* taxa (Figures 4-13A, 4-14A, 4-15A) and only vary slightly (=less pronounced) in *S. cybele*. The aedeagus is somewhat similar in the species examined here, with the shape of its apex the only readily discernable difference (Figures 4-13B, 4-14B, 4-15B). The uncus, distinct in the Semnopsyche forms and *S. idalia*, likely fits specifically in the attachment of females of those species. It may be that females of *S. idalia* and those of the Semnopsyche group are not only distinct in bearing an accessory bursa (Figure 4-24A), but also in points of attachment for a flattened, excavate uncus. A detailed examination of female genitalia, with

respect to the known points of attachment during copulation as listed by Arnold and Fisher (1977), would be necessary to truly test the lock and key species hypothesis.

The genitalia of Black Hills *atlantis* and *hesperis* is quite similar, and this would be expected as members of the Callippe group bear morphologically similar genitalia (dos Passos and Grey 1945a; Hammond 1978). However, in the three male specimens examined, the digitus is somewhat distinct, and this was consistent in all three. The digitus of *lurana* (Figure 4-25A) is short and the distal, ventral portion is extended into a short finger-like projection, whereas in *pahasapa* (Figure 4-25B), the digitus is about twice the length of the digitus observed on *lurana* and the distal, ventral portion does not extend into a point or finger-like projection. Within each subspecies, however, there were slight variations in overall digitus length. Other structures such as the size and shape of the uncus and valvae are similar (see Table 4-2 for additional descriptions).

Upon initial examination using the methodologies presented here, the genitalic structures of some *S. atlantis* and *S. hesperis* forms are distinct; however, additional dissections (including females) are required to truly test clinal trends and utility of genitalia for species delimitation. Additional preparatory techniques, such as vesica eversion, should also be attempted. Differences in the male genitalia of *S. atlantis* and *S. hesperis* forms examined here are not obvious. However, the images included in this study do provide some detail not described to date. The distal portion of the digitus, size and shape of the saccus, and tegumen are variable and should be further examined, especially with regard to the *atlantis* forms *S. a. sorocko* and *S. a. pahasapa*. Additionally, dissections of *S. atlantis* occurring in West Virginia should also be investigated further.

The number of individuals and taxa utilized in this study are inappropriate to provide

confirmation that *S. atlantis* and *S. hesperis* are distinct species, and additional individuals representing different subspecies (=populations) will need to be examined to develop a thorough data set and subsequent assessment in a phylogenetic framework. Although a few preparations may exhibit distinctions, they are often nullified when more specimens of a given population or various subspecies of a wide distribution are examined (dos Passos and Grey 1945a). Additional species/subspecies taken from different populations would be required to examine the potential clinal variation in genitalic morphology. Morphometric analyses may also be warranted to further explore the variation and allometry in *S. atlantis* and *S. hesperis* genitalia, to provide more detailed genitalic descriptions, and to test the lock and key hypothesis.

*Speyeria* in the Black Hills continue to be forced into close spatial contact by further drying and warming of this region, and they have been in contact temporally for some hundreds if not thousands of years (Grey et al. 1963). The question becomes were *S. atlantis* and *S. hesperis* originally separate species, or are they subspecies of one or another that have been remarkably exempt from the leveling results of intermingling and the directive mechanisms of ecology, and apparently clinging to their earlier ways of life and “Colorado” facies. Ecological separation *S. atlantis* and *S. hesperis* is apparent in some areas, with *hesperis* forms occurring in more cooler, mesic habitats (Grey et al. 1963; Hammond 1974). However, Scott et al. (1998) noted that the habitat for *S. a. pahasapa* in the Black Hills is moist meadows, whereas *S. h. lurana* occurs in drier, aspen woodland. It may be that each species in the Black Hills was adapted to wetter or drier conditions and forced into contact as one species either intruded or retreated following changing climatic conditions. In either event, genital morphology may provide little to no indication that these two entities are species, especially with regard to a lock and key hypothesis. It is likely that some other force may be acting to separate these two



“species”. Perhaps pheromone profiles (see Scott 1988) or some other form of sexual selection such as recognition of silvering and or spangles (the appearance of the ventral silvering of hindwing spots when viewed from above), especially under ultraviolet wave lengths as visualized by many Lepidoptera (Ferris 1972, 1973; Remington 1973, Scott 1973b; Knüttel and Fielder 2000, 2001; Acorn 2002; Briscoe et al. 2003), is acting to diverge these closely related entities. Initial examination of *S. atlantis pahasapa* (Figure 4-27A) and *S. hesperis lurana* (Figure 4-27B) males utilizing ultra violet lighting indicated that silver spots are more noticeable, and perhaps the presence or absence of silver spots along with flight patterns during courtship (see Scott 1986b, 1988) are used for species recognition.

It is evident in *S. atlantis-S. hesperis* forms that wing facies vary (see Table 4-1 and Figure 4-7) (see also Scott et al. 1998), and that the apparent trend is that *hesperis* forms bear unsilvered, cream-colored ventral hindwing spots while *atlantis* forms are silvered. For those populations that occur sympatrically, perhaps silver spots or lack thereof initially acted as a selective force within species, and eventually as a visual cue along with olfactory cues between species. Additional studies of *Speyeria* mating behavior and the appearance of wings under ultraviolet light may elucidate some clues as to the distinctness of spangles and/or silvering as an evolutionary force within *Speyeria*.

Tebaldi (1982) (also see Ferris 1983) utilized starch gel electrophoresis of six enzymes to analyze the relationships between three Rocky Mountain phenotypes of *S. atlantis-S. hesperis* and found that the phenotypes could be considered only “semispecies.” Perhaps, in some areas, especially those within or near the Rocky Mountains where overlapping *atlantis-hesperis* forms are prevalent (see Figure 4-3), “species” of *Speyeria* still have a great ability to come into contact with one another and gene flow is evident in a menagerie of *Speyeria* forms. Further unraveling

the true clinal trends between *S. atlantis* and *S. hesperis* will fill in the gaps between named subspecies that are partly or wholly bridged by intermediates, and provide clearer recognition of those taxa isolated to degree in which evolutionary forces have acted upon to provide distinct species.

Distributional and clinal trends for *Speyeria* have been described in detail in the past and new locality data continues to be compiled (Grey 1951; Moeck 1957; Grey et al. 1963; Hammond 1978; Scott et al. 1998). However, the workspace provided on the Diversity of Life website allows for on-going input of locality data and the ability to map *Speyeria* distributions as new locality data are compiled (sample maps generated from the Diversity of Life website are included Figures 4-4, 4-5, 4-6). In addition, one practical aspect of knowing the distributions of hostplants such as *Viola*, is that locality data from herbarium records may also help predict the distributions of *Speyeria* (and vice-versa). Herbarium data should also be incorporated with known *Speyeria* locality data in the future.

Imaging technology has recently improved via systems such as Microoptics Digital Imaging and Auto-Montage Syncroscopy. Both systems allow for high magnification, high depth of field images needed for detailed examination of morphological structures such as genitalia. Use of these imaging techniques allows for continued manipulation of genitalic preps, whereas slide mounted material is permanently set. In addition, slide mounted material provides virtually no three-dimensional vantage points, and structures potentially taxonomically informative are ‘flattened’ during slide preparation. Slide mounted material can, however, now be photographed in detail comparable to viewing slides with a compound microscope, providing a supplement or perhaps replacement for traditional examination and/or illustrative techniques. Illustration is always subject to the artists’ interpretation and ability, and detailed images

produced by a lens are likely more anatomically/proportionally accurate. This study provides a stepping-stone on which to justify further examination of other sympatrically and synchronously occurring *S. atlantis-hesperis* populations using modern imaging technology.

Choosing appropriate and accurately identified individuals for future genitalic research may prove problematic, and will require careful examination of species descriptions and detailed locality information. C. Ferris (pers. comm.) states that *S. hesperis electa* is likely the name applied to silver populations in the Rockies and Intermountain Region; however, this does not account for the silvered *S. atlantis sorocko* described by Scott et. al. (1998). In addition, Ferris (1983) stated that within central Colorado, there is an unknown isolating mechanism that causes *electa* and *hesperis* to behave as sibling species, and that the *electa* phenotype belongs with nominate *atlantis*, while *hesperis* perhaps represents a sibling species. This contradicts the current designation of *electa* within the *hesperis* subspecies complex by Scott et al. (1998). In the absence of carefully controlled rearing experiments or perhaps pheromone profiles, thorough examination of male and female genitalia may be one way to determine the status of *S. atlantis*, *S. hesperis*, and associated subspecies.

*Speyeria atlantis* and *S. hesperis* may also be of conservation interest, not necessarily from human encroachment or habitat mismanagement, but from climatic change and long term warming trends. Could cold adapted species such as *S. atlantis* and *S. hesperis* be affected by warming temperatures? Will their distributions change? Climate and habitat change, whether by natural cause or anthropogenic alterations, is widely accepted as the most important factor in butterfly decline, as its multitude of important effects include a decrease of breeding sites and removal of important resources, altering historical population distributions (New 1997; Hammond and McCorkle 1984; Hammond 1995; Shapiro 1996; Hill et al. 1999a,b; Parmesan et

al. 1999). The *S. atlantis-hesperis* complex provides an opportunity to examine these evolutionary mechanisms in a widely distributed group restricted to climatically colder latitudes and isolated boreal ‘islands’ in mountainous regions. Additional genitalic examination (including the function of the digitus in mating) in conjunction with other adult and larval characters, molecular sequences, and life history data analyzed in a phylogenetic framework, will contribute greatly to our current understanding of the intra-and interspecies relationships within *Speyeria*.

Table 4-1. List of *Speyeria atlantis* and *Speyeria hesperis* subspecies and associated ventral hindwing characters.

Species	HW ventral disc color	HW spots
A) <i>S. atlantis atlantis</i>	reddish to dark-brown (chocolate brown)	silvered
B) <i>S. a. hollandi</i>	dark-brown to blackish-brown (some gray)	silvered
C) <i>S. a. pahasapa</i>	blackish-brown (darker than <i>hollandi</i> )	silvered
D) <i>S. a. sorocko</i>	dark reddish-brown (chocolate brown)	silvered
E) <i>S. hesperis helena</i>	red-brown with large tan areas	silvered
F) <i>S. h. beani</i>	reddish-brown	silvered/unsilvered
G) <i>S. h. brico</i>	reddish-brown (darker red than <i>beani</i> )	silvered
H) <i>S. h. ratonensis</i>	brown with gray-tan areas	silvered
I) <i>S. h. greyi</i>	pale brown (some with green tinge)	silvered
J) <i>S. h. lurana</i>	red-brown with large tan areas	mostly unsilvered (cream)
K) <i>S. h. hesperis</i>	red-brown usually with pale areas	mostly unsilvered (cream)
L) <i>S. h. irene</i>	red-brown with pale tan streaks	unsilvered (cream)
* <i>S. h. cottlei</i>	reddish-brown	unsilvered (cream)
M) <i>S. h. hanseni</i>	reddish-brown with cream overscaling	unsilvered (cream)
N) <i>S. h. dodgei</i>	red-brown with pale tan streaks	unsilvered (cream)
O) <i>S. h. viola</i>	red-brown with pale tan streaks	unsilvered (cream)
P) <i>S. h. elko</i>	red-brown with pale tan streaks	unsilvered (cream)
Q) <i>S. h. tetonia</i>	reddish-brown	mostly unsilvered (cream)
R) <i>S. h. wasatchia</i>	reddish-brown	mostly unsilvered (cream)
S) <i>S. h. chitone</i>	reddish-brown	mostly silvered
T) <i>S. h. electa</i>	red-brown usually with pale areas	mostly silvered
U) <i>S. h. schellbachii</i>	reddish-brown with tan areas	mostly silvered
V) <i>S. h. nausicaa</i>	red-brown with pale tan or gray areas	mostly silvered
W) <i>S. h. dorothea</i>	reddish-brown with tan areas	mostly silvered
X) <i>S. h. capitanensis</i>	reddish-brown with tan areas	mostly silvered

(\*not pictured-Type Locality: Alturas, Modoc Co., CA)

[See Figure 4-7 for wing images corresponding to letters in table]

[Note: Discal coloration and silver or unsilvered data are averages across populations of a given subspecies. (List primarily follows the arrangement of Scott et al. 1998)]

Table 4-2. Species and subspecies examined and select descriptions of male genitalic armature.  
Dissections examined and photographed:

- *Speyeria atlantis atlantis* Vermont: Addison Co.: digitus-projection distinct, posterad to dorsad; uncus-tip curved, not expanded vertically; tegumen with fenestrula; dorsal lobes-pronounced; saccus-laterally long, rounded at apex.
- *Speyeria atlantis sorocko* Colorado: Hinsdale Co. (Figures 4-10A and 4-11): digitus (N)-projection distinct, dorsad; uncus-tip curved, not expanded vertically; tegumen with fenestrula; dorsal lobes-slightly pronounced; saccus-laterally short, rounded at apex.
- *Speyeria atlantis pahasapa* South Dakota: No county data: digitus (N)-twice the length of *S. h. lurana*, projection distinct, posterad to dorsad; uncus-tip curved, not expanded vertically; tegumen with fenestrula; dorsal lobes-pronounced; saccus-laterally long, rounded at apex.
- *Speyeria atlantis hollandi* British Columbia: digitus-projection distinct, posterad to dorsad; uncus-tip curved, not expanded vertically; tegumen with fenestrula; dorsal lobes-pronounced; saccus-laterally long, rounded at apex.
- *S. hesperis hesperis*: Wyoming: Albany Co. (Figure 4-15): digitus-projection distinct, posterad; uncus-tip curved, not expanded vertically; tegumen with fenestrula; dorsal lobes-pronounced; saccus-laterally long, slightly tapered at apex.
- *Speyeria atlantis greyi* Nevada: Elko Co.: digitus-projection distinct, posterad to dorsad; uncus-tip curved, not expanded vertically; tegumen with fenestrula; dorsal lobes-pronounced; saccus-laterally long, rounded at apex.
- *Speyeria hesperis lurana* South Dakota: Lawrence Co.: digitus (N)-half the length of *S. a. pahasapa*, projection not distinct, posterad to dorsad; uncus-tip curved, not expanded vertically; tegumen with fenestrula; dorsal lobes-pronounced; saccus-laterally long, rounded at apex.
- *Speyeria hesperis electa* Wyoming: Albany Co. (Figure 4-14): digitus-projection not distinct; uncus-tip curved, not expanded vertically; tegumen with fenestrula; dorsal lobes-pronounced; saccus-laterally long, tapered slightly at apex.
- *Speyeria hesperis schellbachi* Arizona: Coconino Co.: digitus-projection distinct, posterad to dorsad; uncus-tip curved, not expanded vertically; tegumen with fenestrula; dorsal lobes-pronounced; saccus-laterally long, rounded at apex.
- *Speyeria hesperis nausicaa* Arizona: Graham Co.: digitus-projection distinct, posterad to dorsad; uncus-tip curved, somewhat expanded vertically; tegumen with fenestrula; dorsal lobes-pronounced; saccus-laterally long, rounded at apex.
- *Speyeria hesperis capitanensis* New Mexico: Lincoln Co.: digitus-projection distinct, posterad to dorsad; uncus-tip curved, somewhat expanded vertically; with fenestrula; dorsal lobes-pronounced; saccus-laterally long, rounded at apex.
- *Speyeria diana* West Virginia: No county data.: digitus-projection moderate to extended, ventrad; uncus-tip curved, expanded vertically, excavate at tip; tegumen with fenestrula; dorsal lobes-slightly pronounced; saccus-laterally long, tapered at apex.
- *Speyeria cybele krautwurmi* Missouri: Cape Girardeau Co. (Figure 4-12): digitus-projection moderate, dorsad; uncus-tip curved, expanded vertically, excavate at tip; tegumen with fenestrula; dorsal lobes-slightly pronounced; saccus-laterally long, tapered at apex.

Table 4-2 cont.

- *Speyeria carolae* Nevada: Clark Co.: digitus (N)-projection distinct and “thumblike”, projecting distinctly dorsad; uncus-tip curved, not expanded vertically, long, extending to the tip of the digitus; tegumen-basal margin vertical; dorsal lobes-pronounced; saccus-laterally long, rounded at apex.

Additional slide mounted material examined and photographed:

- *Speyeria atlantis atlantis* (Enfield, Maine) (Figure 4-16A)
- *Speyeria hesperis irene/dodgei* (Diamond Lake, Oregon) (Figure 4-16B)
- *Speyeria hesperis chitone* (Southern Utah) (Figure 4-17A)
- *Speyeria hesperis nausicaa* (Sierra Ancha Mountains, Arizona) (Figure 4-17B)
- *Speyeria diana* (no locality data available) (Figure 4-18A)
- *Speyeria cybele* (Omaha, Nebraska) (Figure 4-18B)
- *Speyeria aphrodite* (Pennsylvania) (Figure 4-19A)
- *Speyeria idalia* (no locality data available) (Figure 4-19B)
- *Speyeria nokomis* (White Mountains, Arizona) (Figure 2-20A)
- *Speyeria edwardsii* (Sioux County, Nebraska) (Figure 2-20B)
- *Speyeria zerene* (California) (Figure 4-21A)
- *Speyeria callippe* (San Francisco, California) (Figure 4-21B)
- *Speyeria adiaspe* (Santa Cruz, California) (Figure 4-22A)
- *Speyeria hydaspe* (Big Meadows, California) (Figure 4-22B)
- *Speyeria mormonia* (948) (Menache Meadows, California) (Figure 4-23)

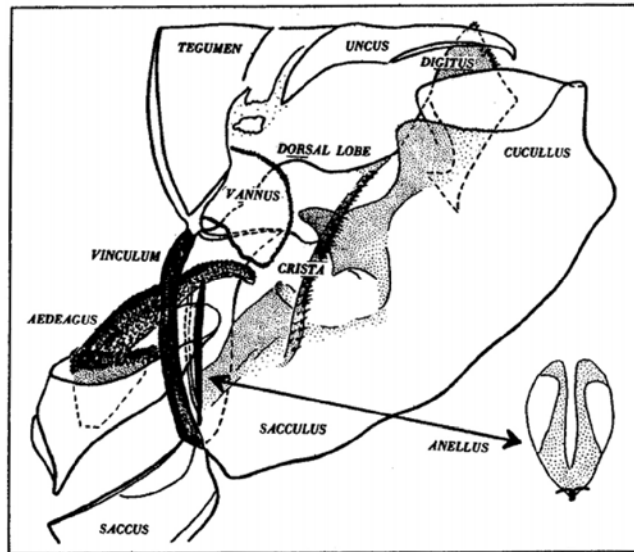


Figure 4-1. Illustration and associated terminology of male genitalic armature of *Speyeria atlantis* (after dos Passos and Grey 1945a).

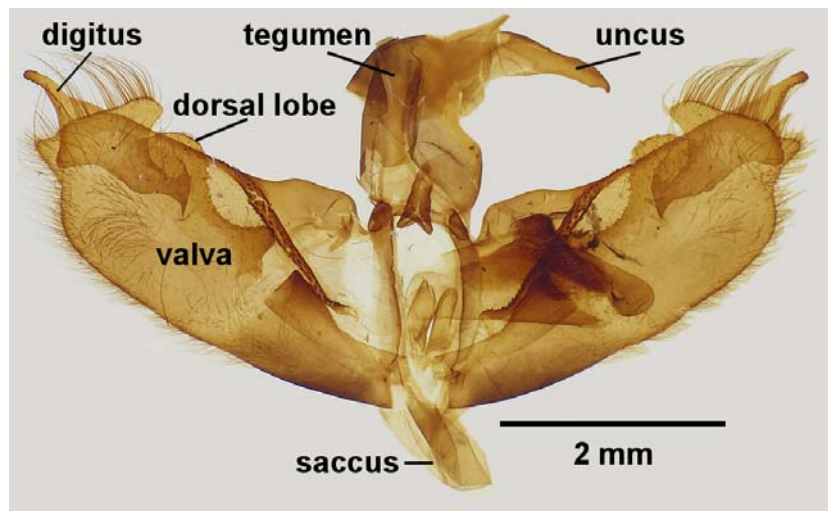


Figure 4-2. Male genitalic armature (*Speyeria idalia*) and associated terminology.



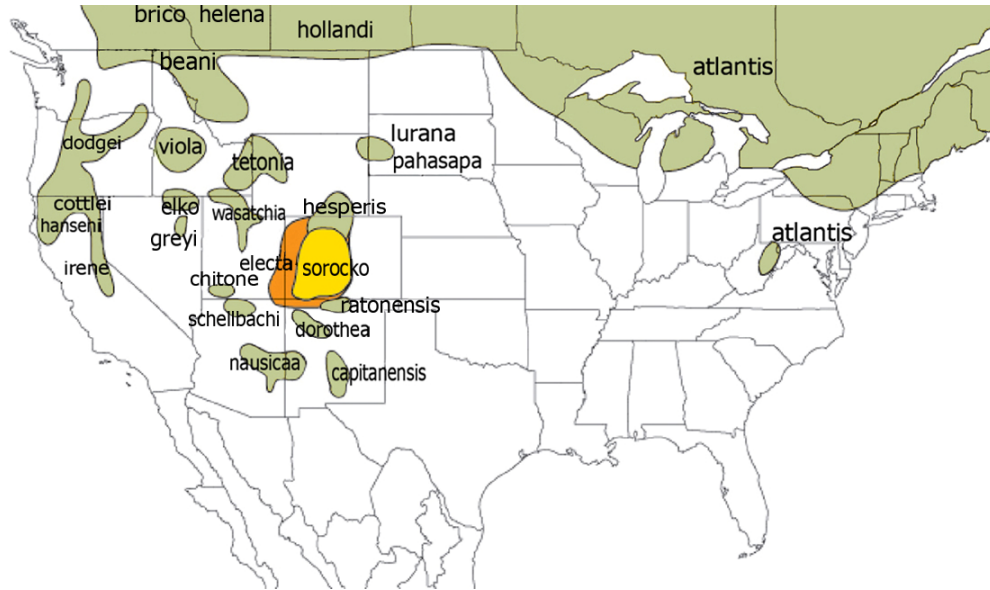


Figure 4-3. Distributional map of *Speyeria atlantis* and *Speyeria hesperis* subspecies (taken and modified from Dunford 2005; original map produced by J. Glassberg).

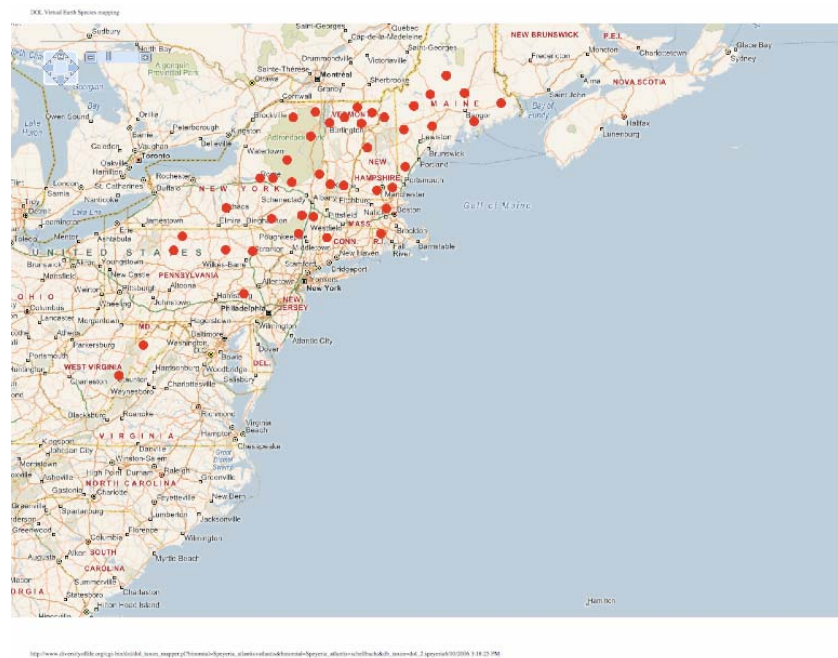


Figure 4-4. Distribution map for *Speyeria atlantis* in the northeastern United States (sample interactive road map generated at DiversityofLife.org).

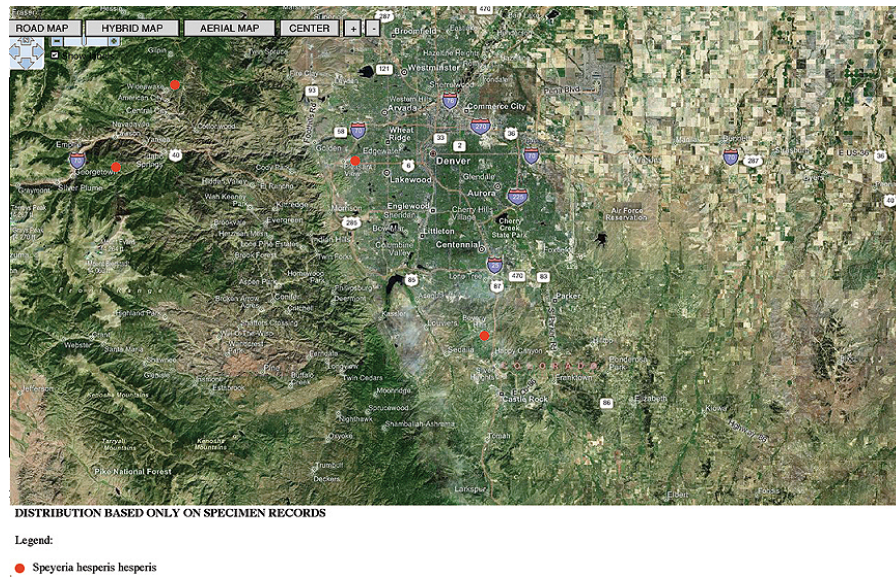


Figure 4-5. Distribution map for *Speyeria hesperis* (sample interactive aerial topo map generated at DiversityofLife.org).

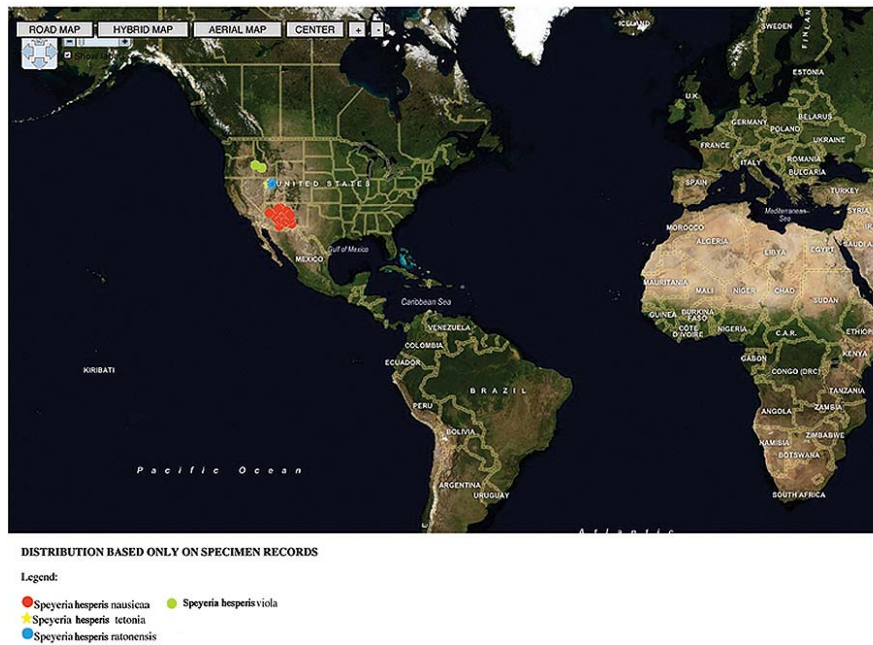


Figure 4-6. Distribution map for *Speyeria atlantis-hesperis* subspecies (sample interactive topo map generated at DiversityofLife.org).

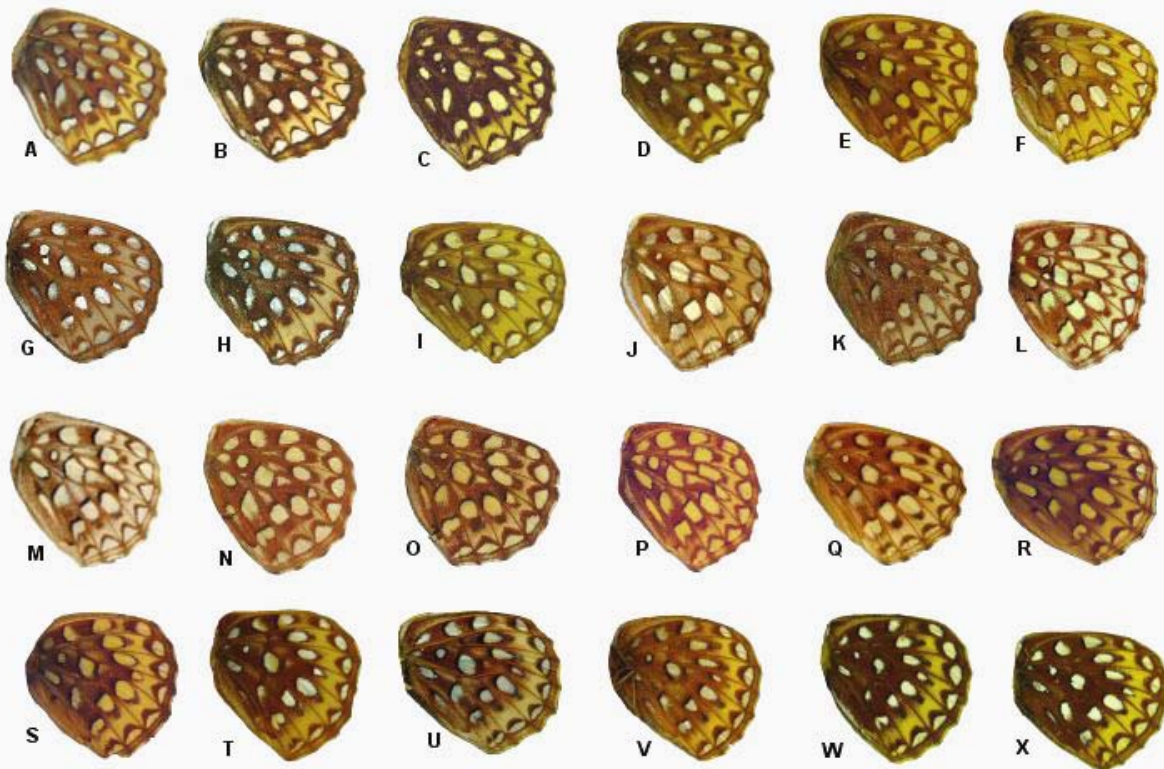


Figure 4-7. Ventral hindwing images of *Speyeria atlantis* and *Speyeria hesperis* subspecies (see Table 4-1 for letters and corresponding taxon names). Image by James C. Dunford and Kelly R. Sims.



Figure 4-8. Examples of wing vouchers. A) *Speyeria atlantis sorocko*, B) *Speyeria cybele*.



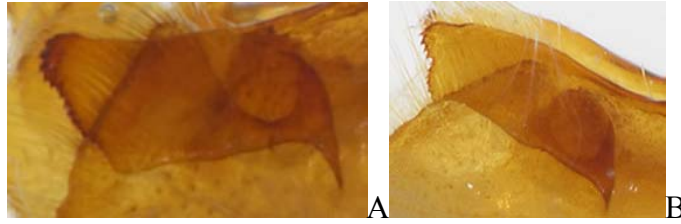


Figure 4-9. Male genitalia of *Speyeria*. A) digitus, *Speyeria atlantis sorocko* (Colorado), B) digitus, *Speyeria hesperis electa* (Wyoming).

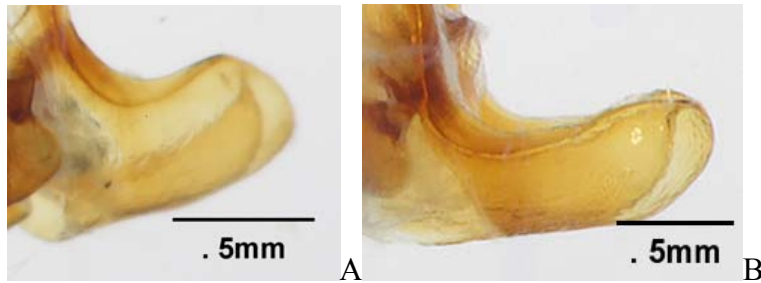


Figure 4-10. Male genitalia of *Speyeria*. A) saccus, *Speyeria atlantis sorocko* (Colorado), B) saccus, *Speyeria hesperis electa* (Wyoming).

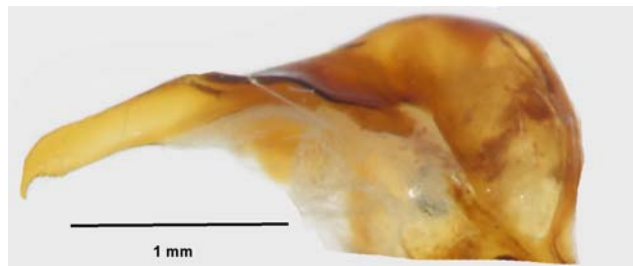


Figure 4-11. Uncus and tegumen, *Speyeria atlantis sorocko* (Colorado).

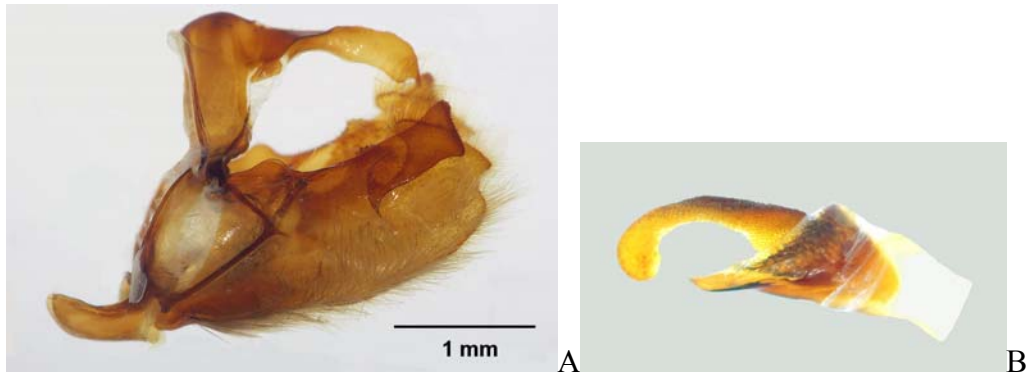


Figure 4-12. Male genitalia of *Speyeria cybele* (Missouri). A) male genitalic armature, lateral view, right side, B) aedeagus, lateral view, left side.

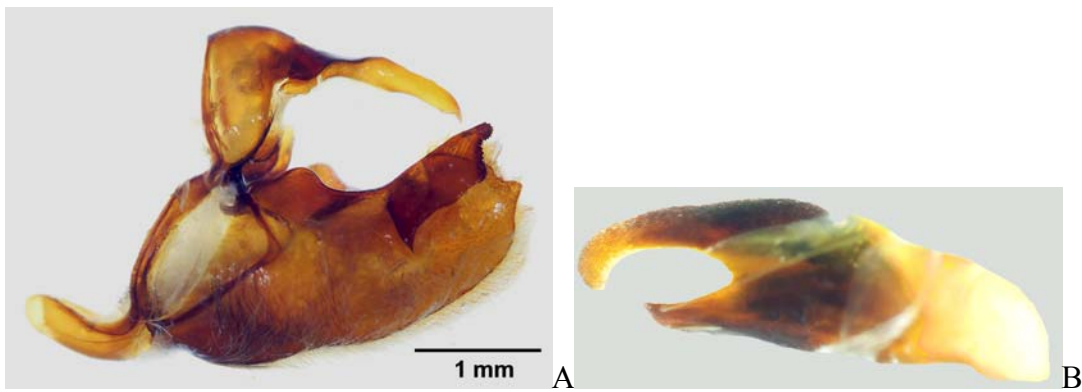


Figure 4-13. Male genitalia of *Speyeria atlantis* (West Virginia). A) male genitalic armature, lateral view, right side, B) aedeagus, lateral view, left side.

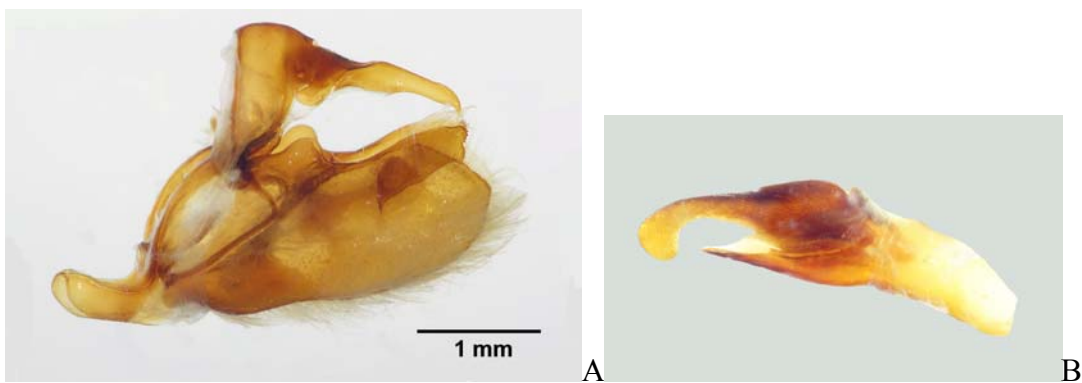


Figure 4-14. Male genitalia of *Speyeria hesperis electa* (Wyoming). A) male genitalic armature, lateral view, right side, B) aedeagus, lateral view, left side.

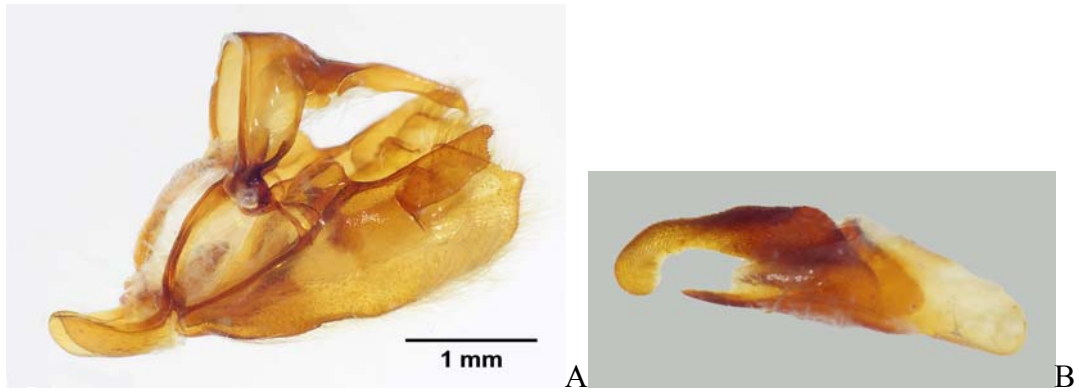


Figure 4-15. Male genitalia of *Speyeria hesperis hesperis* (Wyoming). A) male genitalic armature, lateral view, right side, B) aedeagus, lateral view, left side.

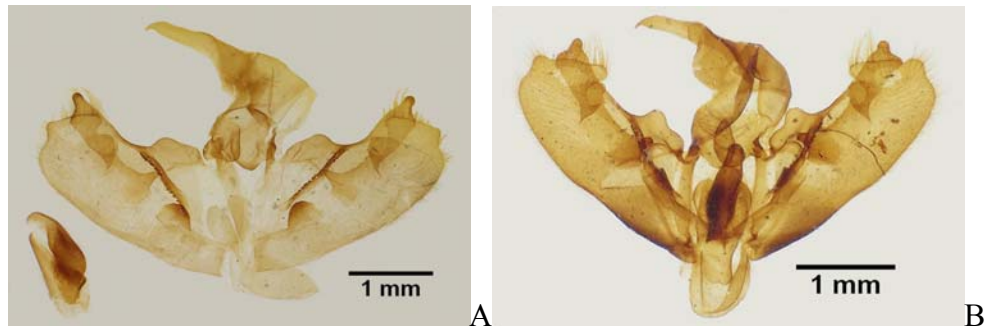


Figure 4-16. Male genitalic armature. A) *Speyeria atlantis atlantis* (Maine), B) *Speyeria hesperis irene/dodgei* (Oregon).

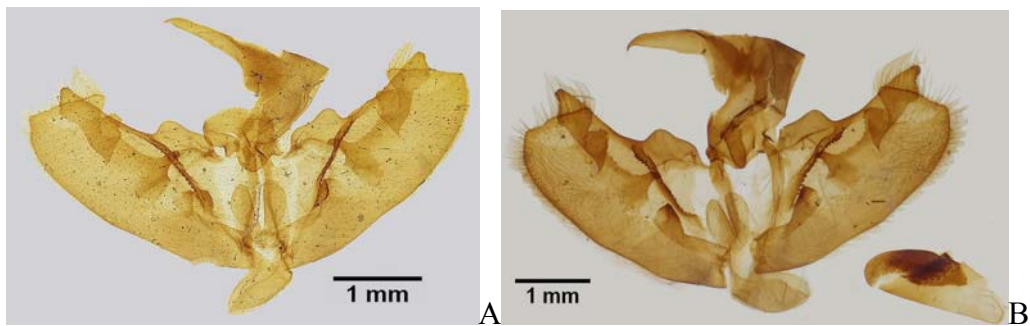


Figure 4-17. Male genitalic armature. A) *Speyeria hesperis chitone* (Utah), B) *Speyeria hesperis nausicaa* (Arizona).

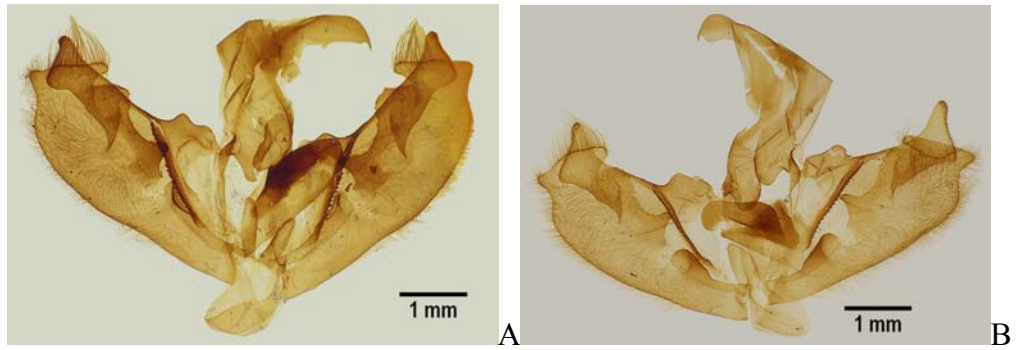


Figure 4-18. Male genitalic armature. A) *Speyeria diana* (no locality), B) *Speyeria cybele* (Nebraska).

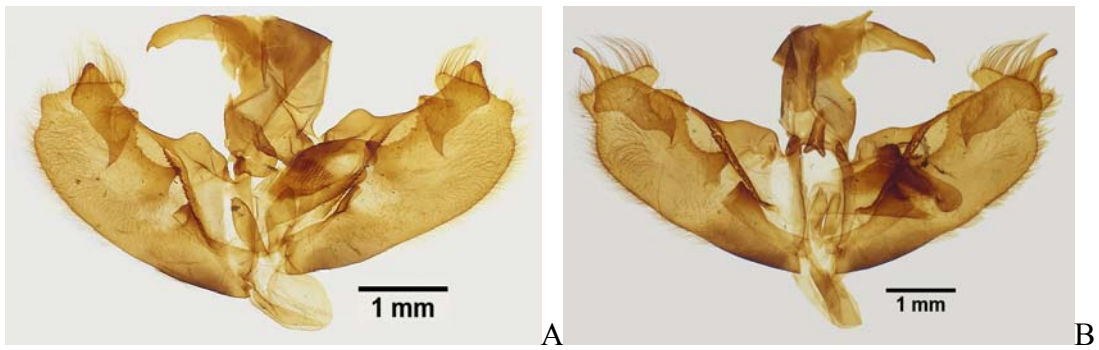


Figure 4-19. Male genitalic armature. A) *Speyeria aphrodite* (Pennsylvania), B) *Speyeria idalia* (no locality).



Figure 4-20. Male genitalic armature. A) *Speyeria nokomis* (Arizona), B) *Speyeria edwardsii* (Nebraska).

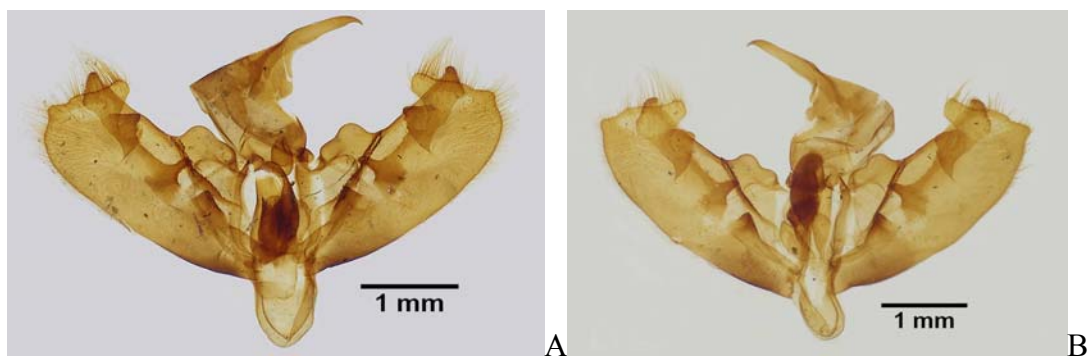


Figure 4-21. Male genitalic armature. A) *Speyeria zerene* (California), B) *Speyeria callippe* (California).

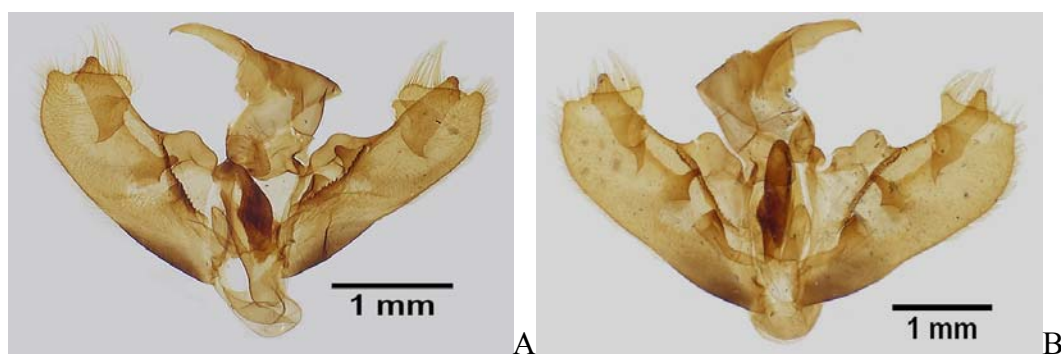


Figure 4-22. Male genitalic armature. A) *Speyeria adiaeste* (California), B) *Speyeria hydaspe* (California).

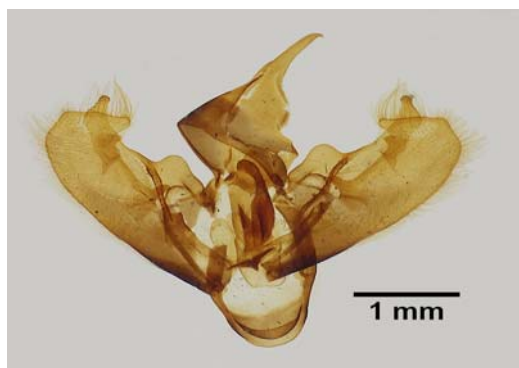


Figure 4-23. Male genitalic armature, *Speyeria mormonia* (California).



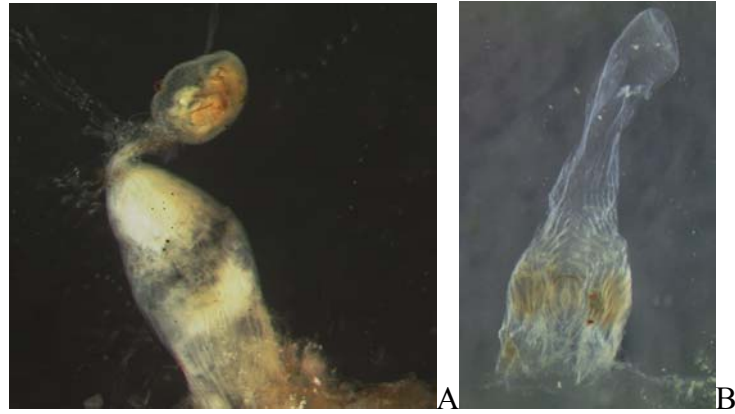


Figure 4-24. Image of bursa copulatrix A) *Speyeria diana*, B) *Speyeria carolae*.

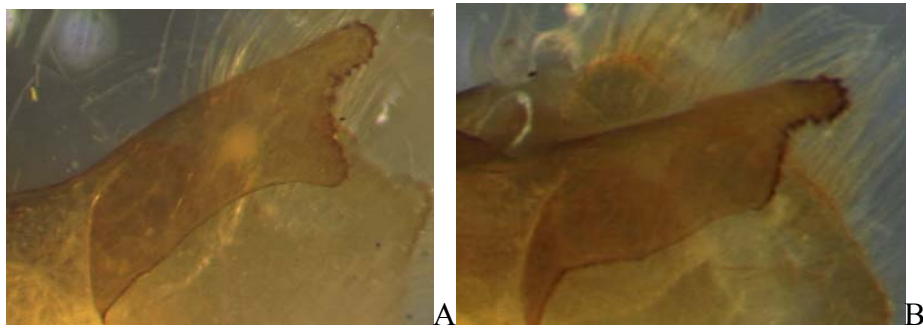


Figure 4-25. Male genitalia of *Speyeria*. A) digitus, *Speyeria hesperis lurana*, B) digitus, *Speyeria atlantis pahasapa*.

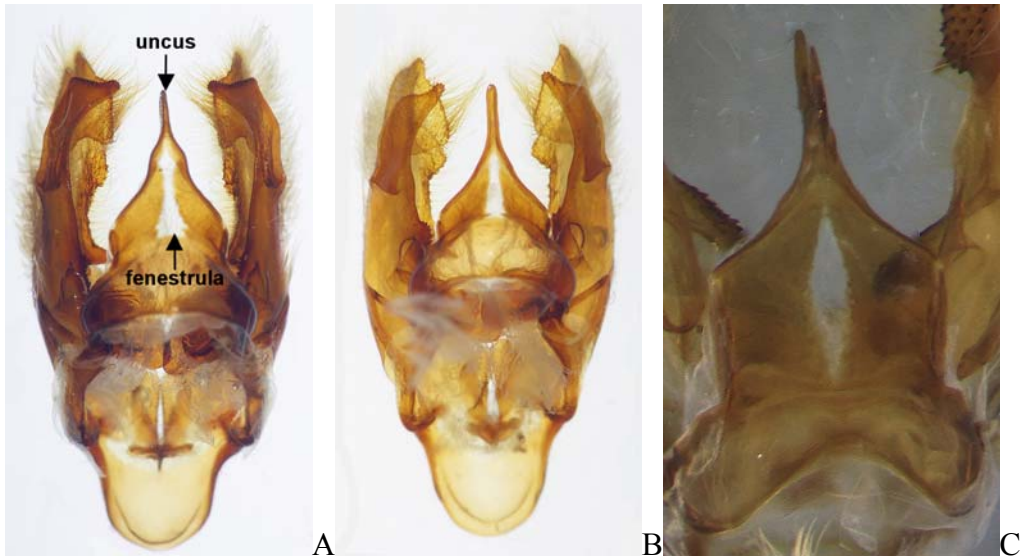


Figure 4-26. Male genitalic armature. A) dorsal view of tegumen, *Speyeria cybele*, B) dorsal view of tegumen, *Speyeria hesperis*, C) dorsal view of tegumen, *Argynnis paphia*.

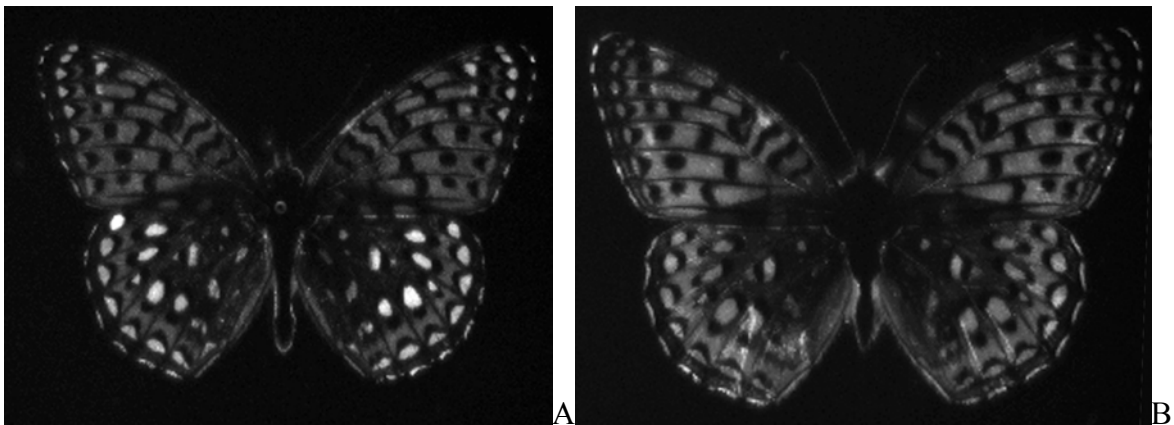


Figure 4-27. Images of adult *Speyeria* using ultraviolet light. A) dorsal surface of *Speyeria atlantis pahasapa*, B) dorsal surface of *Speyeria hesperis lurana*. Images by James C. Dunford.

## CHAPTER 5

### SUMMARY AND CONCLUSIONS

The preliminary cladistic analyses and generic review conducted herein and the previous studies conducted on *Speyeria* by dos Passos and Grey (1945a, 1947) and Hammond (1978), suggest that there is a division between the Semnopsyche/Cybele and Callippe groups. Genitalic differences provide discrete evidence that these groups diverged from one another at some point in time. A few other morphological differences, namely the overall size, degree of sexual dimorphism, and general reduction of wing patterning in the Semnopsyche/cybele group provide further evidence of their distinction from the Callippe group. However, potentially informative characters for *Speyeria* may be obscured by factors related to climatological conditions. Hot, humid summers or dry, cooler conditions likely affect local populations, and these conditions likely influence color and pattern variation of the wings. Thus, it is difficult to systematically interpret characters related to wings due to the clinal variation that is now obvious for *Speyeria* as more population locality gaps are filled.

Members of the Callippe group are nearly identical in many ways, and only under close inspection can some morphological differences be detected. However, these are not consistent across or even amongst populations; thus, they are difficult to subject to phylogenetic analyses. The Callippe group has retained many geographic forms that may represent close evolutionary links between the species. Each species within this ‘clade’ is morphologically similar across various parts of their range; thus, discrete morphological characters for subspecies cannot be readily discerned. Members of the Semnopsyche/cybele group are more restricted in their ranges and exhibit relatively fewer geographical linkages; thus, it is not surprising from an evolutionary standpoint that they have become more distinct morphologically.

It is apparent from these analyses that members of the Semnopsyche group+*Speyeria idalia* and *Speyeria nokomis* represent basal taxa within *Speyeria*. Assuming Eurasian argynnine taxa represent a more ancient lineage due to greater differences in wing and genitalic morphologies than those within *Speyeria*, *Mesoacidalia aglaja* most closely represents ancestral *Speyeria*; this was confirmed in the phylogenetic analyses conducted herein. However, the inclusion of additional taxa in the COI data set indicated that *Fabriciana niobe* may be the sister taxon to *Speyeria*, while *M. aglaja* is sister to the *Argynnis* species utilized in this analysis. The next step in understanding the true evolutionary relationships within the Argynnini and their relatives is to combine *Speyeria*-inclusive data sets with those covering other Heliconiinae. Recent morphological and molecular studies conducted by Simonsen et al. (2006) suggest *Argynnis* is paraphyletic if *Speyeria* is maintained as a separate genus. However, within those analyses members of the morphologically and molecularly distinct Cybele group are utilized as representative speyerian taxa; thus they may not accurately represent *Speyeria* as a whole. Although there are obvious affinities between the Semnopsyche/Cybele and Callippe groups, members of the Callippe group (+*S. mormonia*) should not be excluded in phylogenetic analyses relative to the evolution of Argynnini. The designation of *Speyeria* as a subgenus within *Argynnis* is tentative until more robust data sets can be analyzed; *Speyeria* should be retained as a distinct genus until that time.

There are few unique, discrete characters for species of *Speyeria*. However, the size and shape of the uncus on the male genitalic armature should serve to separate members of the Semnopsyche group from others in the genus. An accessory bursal sac in the females of the Semnopsyche group provides further evidence of this separation. Intermediate genitalic forms, such as those observed in *Speyeria idalia* and *Speyeria nokomis*, may represent a transition

between those *Speyeria* taxa that bear a flattened, excavate uncus and accessory bursal sac to those that have a simple uncus and single bursal sac. Additional informative characters identified in this study include the size and shape of the digitus. The location of this structure on the male genitalic armature is unique to *Speyeria* (and differs greatly with respect to related European taxa), but it may have been overlooked as an evolutionarily informative character within the genus. In addition, the shape of the tegumen and fenestrula in comparison with those in *Argynnis* differ. It is distinctly shaped in many taxa, and quite distinct in *Speyeria edwardsii* and *S. idalia*. Its function and placement during copulation should be explored.

Percent COI divergence increases within *Speyeria* populations when they are more disjunct, and increase on average when they are compared to hypothetical outgroups. It is evident that species known from a single population will exhibit very low COI divergence (e.g., 0% for *Speyeria carolae* in Nevada's Spring Mountains and *S. adiate* on the California coast), while the same species known from disjunct, more or less geographically isolated populations will show a divergence as high as 4 or 5.33% (e.g., *Speyeria zerene* from California and *S. zerene* from Nevada was 5.01%; *Speyeria atlantis* from Vermont and *S. atlantis* from Wyoming was 4.5%). The divergence within the genus and between species averaged 4.3%, showing the greatest percentage of 8.4%. *Speyeria callippe* and *Speyeria idalia* indicated approximately 8.0% divergence, while *S. callippe* and *S. edwardsii* showed only a .16% divergence. Related genera, namely those utilized as outgroups in phylogenetic analyses, showed on average a 9.2% divergence from *Speyeria*. The highest divergence for *Argynnis paphia* was 9.2% when compared to *S. idalia*, whereas the highest divergence between *Mesoacidalia aglaja* and a *Speyeria* taxon (i.e., *Speyeria coronis*) was 7.88%. *Boloria selene* (from North America) and *Clossiana selene* (from Europe) both showed divergences as high as 12%.

Over 8,000 individual *Speyeria atlantis*-*Speyeria hesperis* locality records taken from specimens housed at museums, private collections, and collected in the field were compiled and are currently being entered into an interactive database. The web-site located at DiversityofLife.org is still a work in progress, but many records are already available there from the present project. Distributional maps are generated by selecting a given species/subspecies and following the instructions. Maps are either in road, aerial satellite imagery, or hybrid (i.e., road map and aerial topo) format. A navigation and zoom function allows the user to visualize the entire distribution or to focus on single locality data points. Additional records, as they become known, can be continually incorporated to further realize the sympatric nature of these two closely related ‘species’.

As a result from the present work, a large frozen tissue collection of *Speyeria* now resides at the McGuire Center for Lepidoptera and Biodiversity for future molecular research. In addition, a *Speyeria* DNA barcode database for the COI gene has been implemented at Barcode of Life Data Systems, University of Guelph, for use in future molecular analyses. This will allow for researcher access to DNA sequences of this gene region whenever *Speyeria* are critical taxa in phylogenetic analyses.

Nomenclatural errors were identified after a through review of the literature associated with *Speyeria*. The description of *Speyeria hesperis greyi* Moeck (1950) had been listed as described within *Argynnis*. This was perpetuated in the literature for some time and is clarified 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 originally misled compilers of later checklists (i.e., Miller and Brown 1981; Hodges 1983) by implicating that *S. atlantis greyi* was named within *Argynnis*. This treatment was then followed by several subsequent authors.

Additional discrepancies in the literature, necessary corrections, and current taxonomies were also identified and discussed herein. The sex of the lectotype specimen for *Speyeria egleis*, as indicated in dos Passos and Grey (1947), is that of a male. A specimen bearing the same label was reported as female in 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 *Speyeria mormonia* had an accessory bursal sac, but this has not been reported previously nor observed here; this may have been erroneously recorded in the appendix of character states. This character is key in separating members of the Semnopsyche group from other *Speyeria*. One recently described taxon, *Speyeria atlantis hanseni* (Emmel et al. 1998c), should now be considered *Speyeria hesperis hanseni* 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 *Speyeria hesperis cottlei* is apparently unknown. This species was recently raised from synonymy (Emmel et al. 1998c) and a neotypic specimen may need to be designated.

Primary type specimens for all the currently recognized *Speyeria* species and *S. atlantis*-*S. hesperis* appear together in color here for the first time. This may be of importance for future taxonomic studies. Museums are now limited in curatorial personnel and access to major Lepidoptera collections is now restricted. In addition, presenting quality images of type

specimens reduces the possibility of accidental damage to these taxonomically important artifacts.

Finally, the position of *Speyeria* in conservation and land management issues is well known (Hammond and McCorkle 1984; Launer et al. 1994; Kelly and Debinski 1998; Williams 1999, 2002; Swengel 1993, 2004; Swengel and Swengel 2001; Patterson 2002). Elucidating the inter- and intra-specific relationships and evolutionary history of *Speyeria* in this study may provide information pertinent to conservation strategies and priorities. Additionally, the effects of climate change (i.e., global warming) on northern and montane species that have not been considered of conservation interest to date (e.g., *S. atlantis* and *S. hesperis*) should be investigated. Each population of *Speyeria*, whether classified as a species, subspecies, or otherwise, should be recognized as a significant evolutionary unit. The habitats in which each population occurs should be considered invaluable if the genetic diversity of this fascinating genus and its remarkable evolutionary divergence is to be preserved.



APPENDIX  
COI SEQUENCES FOR 16 SPECIES OF *SPEYERIA*

(Species here=nominate subspecies or nearest to the species type locality)

*Speyeria diana* (West Virginia: Wyoming Co.; male)

GACttTATATTTTATTTTGGGATTTGAGCAGGAATAGTAGGAACATCATTAAAGTTTAT  
TAATTCGAACTGAATTAGGTAACCCAGGGTCACTAATTGGAGATGATCAAATTTACA  
ATACTATTGTAACAGCTCATGCTTTTATTATAATTTTTTTTATAGTTATACCAATTATA  
ATTGGAGGATTTGGTAACTGATTAGTCCCCCTAATATTAGGAGCTCCAGATATAGCT  
TTCCCCCGTATAAACAATATAAGATTTTGACTTTTACCCCCATCCTTAATTTTACTTA  
TTTCTAGAAGAATTGTAGAAAATGGAGCAGGAACAGGATGAACAGTATACCCCCCT  
CTTTCTTCTAATATTGCCCATAGAGGTTCTTCAGTAGATTTAGCAATTTTCTCTTTAC  
ATTTAGCAGGAATTTCTTCTATTTTAGGAGCAATTAACCTTTATTACAACAATTATTAA  
TATACGAATTAATAGAATATCTTTTGATCAAATACCATTATTTGTGTGAGCAGTAGG  
AATCACAGCCTTACTTCTTTTACTATCTTTACCAGTTTATAGCAGGAGCTATTACAATA  
CTTTTAACTGATCGTAATTTAAATACTTCTTTTTTTGACCCTGCAGGAGGAGGAGACC  
CTATTTTATA

*Speyeria cybele* (Vermont: Caledonia Co.; male)

GACTTTATATTTTATTTTGGGATTTGAGCAGGAATAGTAGGAACATCATTAAAGTTTA  
TTAATTCGAACTGAATTAGGTAACCCAGGGTCACTAATTGGAGATGATCAAATTTAC  
AATACTATTGTAACAGCTCATGCTTTTATTATAATTTTTTTTATAGTTATACCAATTAT  
AATTGGAGGATTTGGTAACTGATTAGTCCCCCTAATATTAGGAGCTCCAGATATAGC  
TTCCCCCGTATAAACAATATAAGATTTTGACTTTTACCCCCATCCTTAATTTTACTT  
ATTTCTAGAAGAATTGTAGAAAATGGAGCAGGAACAGGATGAACAGTATACCCCCC  
TCTTTCTTCTAATATTGCCCATGGAGGTTCTTCAGTAGATTTAGCAATTTTCTCTTTAC  
ATTTAGCAGGAATTTCTTCTATTTTAGGAGCAATTAACCTTTATTACAACAATTATTAA  
TATACGAATTAATAGAATATCTTTTGATCAAATACCATTATTTGTGTGAGCAGTAGG  
AATCACAGCCTTACTTCTTTTACTATCTTTACCAGTTTATAGCAGGAGCTATTACAATA  
CTTTTAACTGATCGTAATTTAAATACTTCTTTTTTTGACCCTGCAGGAGGAGGAGACC  
CTATTTTATA

*Speyeria aphrodite* (Vermont: Caledonia Co.; male)

AAcTTTATATTTTATTTTGGGAATTTGAGCAGGAATAGTAGGAACATCATTAAAGTTTA  
TTAATTCGAACTGAACTGGGTAACCCAGGATCATTAAATTGGAGATGACCAAATTTAC  
AATACCATTGTAACAGCCCATGCTTTTATTATAATTTTTTTTATAGTTATACCAATTA  
TAATTGGAGGATTTGGTAACTGATTAGTCCCCCTAATATTAGGAGCTCCAGATATAG  
CTTTCCCTCGTATAAATAATATAAGATTTTGACTTTTACCCCCATCCTTAATTTTACTT  
ATTTCTAGAAGAATTGTAGAAAATGGAGCAGGAACAGGATGAACAGTATACCCCCC  
TCTTTCTTCTAATATCGCACATGGAGGTTCTTCAGTGGATTTAGCAATTTTCTCTTTA  
CATTTAGCAGGTATTTCTTCTATTTTAGGAGCAATTAACCTTTATCACAACAATTATTA  
ATATACGAATTAATAAAATATCTTTTGATCAAATACCATTATTCGTGTGAGCAGTAG  
GAATTACAGCCTTACTTCTTTTACTATCTTTACCAGTTTATAGCAGGAGCTATTACAAT  
ACTTTTAACTGATCGTAATTTAAATACTTCTTTTTTTGATCCTGCAGGAGGAGGTGAT  
CCTATTTTATACCAACATTTATT

*Speyeria idalia* (Missouri: St. Claire Co.; male)

AACTTTATATTTTATTTTGGGAATTTGAGCAGGTATAATAGGAACATCATTAAGTTTA  
TTAATCCGAACCTGAATTAGGAAACCCAGGATCATTAATTGGAGATGATCAAATTTAT  
ATACTATTGTGACAGCTCATGCTTTTATTATAATTTTTTTTATAGTTATAACCAATTAT  
AATTGGAGGATTTGGTAACTGATTAATCCCCTTAATATTAGGAGCCCCAGATATAGC  
TTTCCCACGTATAAATAATATAAGATTTTGACTTTTACCTCCATCTTTAACTTTAATT  
ATTTCTAGAAGAATTGTAGAAAATGGAACAGGAACAGGATGAACAGTATACCCCCC  
TCTTTCCTCCAATATTGCTCATAGAGGTTCTTCAGTAGATTTATCAATTTTTTCATTAC  
ATTTAGCGGGTATTTCTCTATTTTAGGAGCAATTAACCTTTATTACTACAATTATTAA  
TATACGAATTAATAAAATATCTTTGATCAAATGCCATTATTTATTTGAGCAGTAGG  
AATTACAGCATTACTTCTCTTATTATCTTTACCAGTTTTAGCGGGAGCTATTACAATA  
CTTTTAACTGACCGTAATTTAAATACTTCTTTTTTTTGACCCTGCAGGAGGAGGAGATC  
CCATTTTATACCAACATTTATT

*Speyeria nokomis* (Colorado: Ouray Co.; male)

AACTTTATATTTTATTTTGGGAATTTGAGCAGGAATAGTAGGAACATCATTAAGTTTA  
TTAATTCGAACCTGAATTAGGAAACCCAGGATCATTAATTGGAGATGATCAAATTTAT  
ATACTATTGTAACAGCTCATGCTTTTATTATAATTTTTTTTATAGTTATAACCAATTAT  
AATTGGAGGATTTGGTAAATTGATTAGTCCCCCTAATATTAGGAGCTCCAGATATAGC  
TTTTCTCGTATAAATAACATAAGATTTTGACTTTTACCCCCATCCTTAATTTTACTTA  
TTTCTAGAAGAATTGTAGAAAATGGAGCAGGGACAGGATGAACAGTATACCTCCT  
CTTTCCTCTAATATTGCTCATGGAGGTTCTTCAGTAGATTTAGCAATTTTCTCATTAC  
ATTTAGCAGGTATTTCTCTATTTTAGGAGCAATTAACCTTTATTACTACAATTATTAA  
TATACGGATTAATAAAATATCTTTTGATCAAATACCCTTATTCGTATGAGCAGTAGG  
AATTACAGCCTTACTTCTTTTACTATCTTTACCAGTTTTAGCAGGAGCCATTACAATA  
CTTTTAACTGATCGTAATTTAAATACTTCTTTTTTTTGACCCCGCAGGAgGAGGAGACC  
CTATTTTATACCAACATTT

*Speyeria edwardsii* (Colorado: Douglas Co.; male)

AACTTTATATTTTATTTTGGGAATTTGAGCAGGAATAGTAGGAACATCATTAAGTTTA  
TTAATTCGAACCGAAGTAACTAGGTAATCCAGGATCATTAATTGGAGACGATCAAATTTAT  
AATACCATTGTAACAGCTCATGCTTTTATTATAATTTTTTTTATAGTTATAACCAATTA  
TAATTGGTGGTTTTGGTAACTGATTAGTCCCCCTAATATTAGGAGCTCCAGATATAG  
CTTTTCCTCGTATAAATAATATAAGTTTTTTGACTTTTACCCCCATCCCTAATTTTACTC  
ATTTCTAGAAGAATTGTAGAAAATGGAGCAGGAACAGGATGAACAGTATACCCCCC  
TCTTTCCTCTAATATTGCACATAGAGGCTCTTCAGTAGATTTAGCAATCTTCTCTTTA  
CATTTAGCAGGTATTTCTCTATTTTAGGAGCAATTAACCTTTATCACAACAATTATTA  
ATATACGAATTAATAAAATATCTTTTGATCAAATACCATTATTTGTATGAGCAGTGG  
GAATTACAGCTTTACTTCTTTTATTATCTTTACCAGTTTTAGCAGGAGCTATTACAAT  
ACTTTTAACTGATCGTAATTTAAATACTTCTTTTTTTTGACCCTGCAGGAGGAGGAGAc  
CCTATTTTATACCAACATTTATT

*Speyeria coronis* (California: Monterey Co.; male)

AACTTTATATTTTATTTTGGGAATTTGAGCAGGAATAGTAGGAACATCATTAAGTTTA  
TTAATTCGAACCGAATTAGGTAACCCAGGGTCATTAATTGGAGATGACCAAATTTAT  
AACACTATTGTAACAGCTCATGCTTTTATTATAATTTTTTTTATAGTTATACCAATTA  
TAATTGGTGGATTTCGGTAACTGATTAGTCCCCTTAATATTAGGAGCCCCAGATATAG  
CTTTCCCTCGTATAAATAATATAAGTTTTTGGACTTTTACCCCCATCCCTAATTTTACTT  
ATTTCTAGAAGAATTGTAGAAAATGGAGCAGGAACAGGATGAACAGTATACCCCTCC  
TCTTTCTTCTAATATTGCACATGGAGGCTCTTCAGTAGATTTAGCAATCTTTTCTTTA  
CATTTGGCAGGTATTTCTCTATTTTAGGAGCAATTAACCTTTATCACAACAATTATTA  
ATATACGAATTAATAAAATATCTTTTGATCAAATACCATTATTTGTATGAGCAGTAG  
GAATTACAGCCTTACTTCTTTTATTATCTCTACCAGTTTTAGCAGGAGCTATTACAAT  
ACTTTTAACTGATCGTAATTTAAATACTTCTTTTTTTTGACCCTGCGGGAGGTGGAGAT  
CCTATTTTATACcaACATTTATT

*Speyeria carolae* (Nevada: Clark Co.; male)

AACTTTATATTTTATTTTGGGAATTTGAGCAGGAATAGTAGGAACATCATTAAGTTTA  
TTAATTCGAACCGAATTAGGTAACCCAGGATCATTAATTGGAGATGATCAAATTTAT  
AACACTATTGTAACAGCTCATGCTTTTATTATAATTTTTTTTATAGTTATACCAATTA  
TAATTGGTGGATTTCGGTAACTGATTAGTCCCCTTAATATTAGGAGCCCCAGATATAG  
CTTTCCCTCGTATAAATAATATAAGTTTTTGGACTTTTACCCCCATCCCTAATTTTACTT  
ATTTCTAGAAGAATTGTAGAAAATGGAGCAGGAACAGGATGAACAGTATACCCCTCC  
TCTTTCTTCTAATATTGCACATGGAGGCTCTTCAGTAGATTTAGCAATCTTTTCTTTA  
CATTTGGCAGGTATTTCTCTATTTTAGGAGCAATTAACCTTTATCACAACAATTATTA  
ATATACGAATTAATAAAATATCTTTTGATCAAATACCATTATTTGTATGAGCAGTAG  
GAATTACAGCCTTACTTCTTTTATTGTCTCTACCAGTTTTAGCAGGAGCTATTACAAT  
ACTTTTAACTGATCGTAATTTAAATACTTCTTTTTTTTGACCCTGCGGGAGGTGGAGAT  
CCTATTTTATACCAACATTTATT

*Speyeria zerene* (California: Sierra Co.; male)

AACTTTATATTTTATTTTGGGAATTTGAGCAGGAATAGTAGGAACATCATTAAGTTTA  
TTAATTCGTACTGAAGTAGGTAACCCAGGGTCATTAATTGGAGATGACCAAATTTAT  
AATACCATTGTAACAGCTCATGCTTTTATTATAATTTTTTTTATAGTTATGCCAATTA  
TAATTGGCGGATTTGGTAACTGATTAGTCCCCCTAATATTAGGAGCCCCAGATATAG  
CTTTCCCCCGTATAAATAATATAAGATTTTGGACTTTTACCCCCATCCCTAATTTTACTT  
ATTTCTAGAAGAATTGTAGAAAATGGAGCAGGAACAGGATGAACAGTCTATCCCCC  
TCTTTCTTCTAATATTGCACATGGAGGTTCTTCAGTAGATTTAGCAATTTTCTCCTTA  
CATTTAGCAGGTATTTCTTCTATTTTAGGAGCAATTAACCTTTATCACAACAATTATTA  
ATATACGAATTAATAAAATATCTTTTGATCAAATACCATTATTCGTTTGAGCAGTAG  
GAATTACCGCCTTACTTCTTTTATTATCTTTACCAGTTTTAGCAGGGGCTATTACAAT  
ACTTTTAACTGATCGTAATTTAAATACTTCTTTTTTTTGACCCTGCAGGAGGAGGTGAT  
CCTATTTTATACCAaCaTTTATT

*Speyeria callippe* (California: Tulare Co.; male)

AACTTTATATTTTATTTTGGGAATTTGAGCAGGAATAATAGGAACATCATTAAGTTTA  
TTAATTCGAACCGAAGTAGGTAATCCAGGATCATTAATTGGAGATGATCAAATTTAT  
AACACCATTGTAACAGCTCATGCTTTTATTATAATTTTTTTTATAGTTATACCAATTA  
TAATTGGTGGATTTGGTAACTGATTAGTCCCCCTAATATTAGGAGCTCCAGATATAG

CTTTTCCTCGTATAAATAATATAAGTTTTTGACTTTTACCCCCATCCCTAATTTTACTC  
ATTTCTAGAAGAATTGTAGAAAATGGAGTAGGAACGGGATGAACAGTATACCCCC  
TCTTTCTTCTAATATTGCACATGGAGGCTCTTCAGTAGATTTAGCAATCTTCTCTTTA  
CATTTAGCAGGTATTTCTCTATTTTAGGAGCAATTAACCTTTATCACAACAATTATTA  
ATATACGAATTAATAAAATATCTTTTGATCAAATACCATTATTTGTATGAGCAGTAG  
GAATTACAGCTTTACTTCTTTTATTATCTTTACCAGTTTTAGCAGGAGCTATTACAAT  
ACTTTTAACTGATCGTAATTTAAATACTTCTTTTTTTGATCCTGCAGGAGGAGGAGAT  
CCTATTTTATACCAACATTTATT

*Speyeria egleis* (California: Tulare Co.; male)

AACTTTATATTTTATTTTGGAAATTTGAGCAGGAATAGTAGGAACATCATTAAGTTTA  
TTAATCCGAACAGAAGTAACTAGGTAATCCAGGATCATTAATTGGAGATGATCAAATTTAT  
AATACCATTGTAACAGCTCATGCTTTTATTATAATTTTTTTTATAGTTATACCAATTA  
TAATTGGTGGATTTGGTAACTGATTAGTCCCCCTAATATTAGGAGCTCCAGATATAG  
CTTTTCCTCGTATAAATAATATAAGTTTTTGACTTTTACCCCCATCCCTAATTTTACTT  
ATTTCTAGAAGAATTGTGGAAAATGGAGCAGGAACAGGATGAACAGTATACCCCC  
TCTTTCTTCCAATATTGCACATGGAGGCTCTTCAGTAGATTTAGCAATCTTCTCTTTA  
CATTTAGCAGGTATTTCTCTATTTTAGGAGCAATTAACCTTTATCACAACAATTATTA  
ATATGCGAATTAATAAAATATCTTTTGATCAAATACCATTATTTGTATGAGCAGTAG  
GAATTACAGCTTTACTTCTTTTATTATCTTTACCAGTTTTAGCAGGGGCTATTACAAT  
ACTTTTAACTGATCGTAATTTAAATACTTCTTTTTTTGATCCTGCAGGAGGGGGAGAT  
CCTATTTTATATCAACATTTATT

*Speyeria adiaspe* (California: Monterey Co.; male)

AACTTTATATTTTATTTTGGAAATTTGGGCAGGAATAGTAGGAACATCATTAAGTTTA  
TTAATTCGAAGTGAAGTAACTAGGTAACCCAGGATCATTAATTGGAGATGACCAAATTTAT  
AATACCATTGTAACAGCTCATGCTTTTATTATAATTTTTTTTATAGTTATACCAATTA  
TAATTGGAGGATTTGGTAACTGATTAGTCCCCCTAATATTAGGAGCTCCAGATATAG  
CTTTTCCCCGTATAAATAATATAAGATTTTGACTTTTACCCCCATCCCTAATTTTACTT  
ATTTCTAGAAGAATTGTAGAAAATGGAGCAGGAACAGGATGAACAGTATATCCCC  
TCTTTCTTCTAATATTGCCCATAGAGGTTCTTCAGTAGATTTAGCAATTTTCTCTTTAC  
ATTTAGCAGGAATTTCTCTATTTTAGGAGCAATTAATTTTATTACAACAATTATTA  
TATACGAATTAATAAAATATCTTTTGATCAAATACCATTATTCGTATGAGCAGTAGG  
AATTACAGCCTTACTTCTTTTATTATCTTTACCAGTTTTAGCAGGAGCTATTACAATA  
CTTTTAACTGATCGTAATTTAAATACTTCTTTTTTTGACCCTGCGGGAGGAGGAGATC  
CTATTTTATACCAACATTTATT

*Speyeria atlantis* (Vermont: Caledonia Co.; male)

AAcTTTATATTTTATTTTGGAAATTTGAGCAGGAATAGTAGGGACATCATTAAGTTTA  
TTAATTCGAACCGAAGTAACTAGGTAATCCAGGATCATTAATTGGAGATGATCAAATTTAT  
AATACCATTGTAACAGCTCATGCTTTTATTATAATTTTTTTTATAGTTATACCAATTA  
TAATTGGTGGATTTGGTAACTGATTAGTCCCCCTAATATTAGGAGCCCCAGATATAG  
CTTTTCCTCGTATAAATAATATAAGTTTTTGACTTTTACCCCCATCCCTAATTTTACTT  
ATTTCTAGAAGAATTGTAGAAAATGGAGCAGGAACAGGATGAACAGTATATCCCC  
CCTTTCTTCTAATATTGCACACGGAGGCTCTTCAGTAGATTTAGCAATCTTTTCTTTG  
CATTTAGCAGGTATTTCTCTATTTTAGGAGCAATTAACCTTTATCACAACAATTATTA



## LIST OF REFERENCES

- Abraham, D., N. Ryrholm, H. Wittzell, J. D. Holloway, M. J. Scoble, and C. Löfstedt. 2001.** Molecular phylogeny of the subfamilies in Geometridae (Geometridae: Lepidoptera). *Molecular Phylogenetics and Evolution* 20: 65-77.
- Acorn, J. H. 1993.** Butterflies of Alberta. Lone Pine Publishing, Edmonton, Alberta.
- Acorn, J. 2002.** Assessing ultraviolet reflections of lepidopterans with video and digital cameras. *News of the Lepidopterists' Society* 44: 60.
- Adams, J. K. and I. L. Finkelstein. 2006.** Late season observations on female Diana fritillary (*Speyeria diana*) aggregating behavior. *News of the Lepidopterists' Society* 48: 106-107.
- Allen, T. J. 1997.** The Butterflies of West Virginia and Their Caterpillars. University of Pittsburgh Press, Pittsburgh, Pennsylvania.
- Allen, T. J., J. P. Brock, and J. Glassberg. 2005.** Caterpillars in the Field and Garden. Oxford University Press, Inc., New York, New York.
- Arnqvist G. 1997.** The evolution of animal genitalia: Distinguishing between hypotheses by single species studies. *Biological Journal of the Linnean Society* 60: 365-379.
- Arnqvist, G. 1998.** Comparative evidence for the evolution of genitalia by sexual selection. *Nature* 393: 784-786.
- Arnold, R.A. 1983.** *Speyeria callippe* (Lepidoptera: Nymphalidae): Application of Information-Theoretical and Graph-Clustering techniques to analyses of geographic variation and evaluation of classifications. *Annals of the Entomological Society of America* 76: 929-941.
- Arnold, R.A. 1985.** Geographic variation in natural populations of *Speyeria callippe* (Boisduval) (Lepidoptera: Nymphalidae). *Pan Pacific Entomologist* 61: 1-23.
- Arnold, R. A. and R. L. Fischer. 1977.** Operational mechanisms of copulation and oviposition in *Speyeria* (Lepidoptera: Nymphalidae). *Annals of the Entomological Society of America* 70: 455-468.
- Austin, G. T. 1981.** The montane butterfly fauna of the Spring Range, Nevada. *Journal of the Lepidopterists' Society* 35: 66-74.
- Austin, G. T. 1983.** A new subspecies of *Speyeria atlantis* (Edwards) (Nymphalidae) from the Great Basin of Nevada. *Journal of the Lepidopterists' Society* 37: 244-248.
- Austin, G. T. 1985a.** Nevada butterflies: Preliminary checklist and distribution. *Journal of the Lepidopterists' Society* 39: 95-118.
- Austin, G. T. 1985b.** Lowland riparian butterflies of the Great Basin and associated areas. *Journal of Research on the Lepidoptera* 24: 117-131.

- Austin, G. T. 1998b.** Type data for butterflies described from Nevada. pp. 629-640. *In* T. C. Emmel [Ed.], *Systematics of Western North American Butterflies*. Mariposa Press, Gainesville, Florida.
- Austin, G. T. and D. D. Murphy. 1987.** Zoogeography of Great Basin butterflies: Patterns of distribution and differentiation. *Great Basin Naturalist* 47: 186-201.
- Austin, G. T., D. D. Murphy, J. F. Baughman, A. E. Launer, and E. Fleishman. 2003.** Hybridization of checkerspot butterflies in the Great Basin. *Journal of the Lepidopterists' Society* 57: 176-192.
- Baird, V. 1942.** *Wild Violets of North America*. University of California Press, Berkeley, California.
- Baker, R. J. and R. D. Bradley. 2006.** Speciation in mammals and the genetic species concept. *Journal of Mammalogy* 87: 643-662.
- Baker, A. C., C. J. Starger, T. R. McClanahan, and P. W. Glynn. 2004.** Coral reefs: corals' adaptive response to climate change. *Nature* 430: 741.
- Ballard Jr., H. E., K. J. Sytsma, and R. R. Kowal. 1999.** Shrinking the violets: phylogenetic relationships of infrageneric groups in *Viola* (Violaceae) based on internal transcribed spacer DNA sequences. *Systematic Botany* 23: 439-458.
- Barnes, W. and F. H. Benjamin. 1926.** Notes on diurnal Lepidoptera, with additions and corrections to the recent "List of diurnal Lepidoptera." *Bulletin of the Southern California Academy of Sciences* 25: 88-98.
- Baum, D. 1992.** Phylogenetic species concepts. *Trends in Ecology and Evolution* 7:1-2.
- Baum, D. A. and M. J. Donoghue. 1995.** Choosing among alternative "phylogenetic" species concepts. *Systematic Botany* 20: 560-573.
- Beattie, A. J. 1971.** Pollination mechanisms in *Viola*. *New Phytologist* 70: 343-360.
- Beattie, A. J. 1974.** Floral evolution in *Viola*. *Annals of the Missouri Botanical Garden* 61: 781-793.
- Beattie, A. J. and N. Lyons. 1975.** Seed dispersal in *Viola* (Violaceae): Adaptations and Strategies. *American Journal of Botany* 62: 714-722.
- Behr, H. H. 1862.** Our Californian argynnnides. *Proceedings of the California Academy of Natural Sciences* 2: 171-177.
- Behr, H. H. 1863.** On Californian Lepidoptera-No. III. *Proceedings of the California Academy of Natural Sciences* 3: 84-93.

- Behr, H. H. 1864.** *In* Edwards, W. H. Notes on the argynnnides of California. Proceedings of the Entomological Society Philadelphia 3: 434-436.
- Bitsch, J., C. Bitsch, T. Bourgoïn, and C. D. Haese. 2004.** The phylogenetic position of early hexapod lineages: morphological data contradict molecular data. Systematic Entomology 29: 433-440.
- Bird, C. D., G. J. Hilchie, N. G. Kondla, E. M. Pike, and F. A. H. Sperling. 1995.** Alberta butterflies. The Provincial Museum of Alberta, Edmonton, Alberta.
- Black, S. H., M. Shepard, and M. M. Allen. 2001.** Endangered invertebrates: the case for greater attention to invertebrate conservation. Endangered Species UPDATE 18: 42-50.
- Blackmore, S. 2002.** Biodiversity update-progress in taxonomy. Science 298: 365.
- Boggs, C. L. 1986.** Reproductive strategies of female butterflies: Variation in and constraints on fecundity. Ecological Entomology 11: 7-15.
- Boggs, C. L. 1987a.** Demography of the unsilvered morph of *Speyeria mormonia* in Colorado. Journal of the Lepidopterists' Society 41: 94-97.
- Boggs, C. L. 1987b.** Within population variation in the demography of *Speyeria mormonia* (Lepidoptera: Nymphalidae). Holarctic Ecology 10: 175-184.
- Boggs, C. L. 1988.** Rates of nectar feeding in butterflies: Effects of sex, size, age and nectar concentration. Functional Ecology 2: 289-295.
- Boggs, C. L. 1997a.** Reproductive allocation from reserves and income in butterfly species with differing adult diets. Ecology 78: 181-191.
- Boggs, C. L. 1997b.** Dynamics of reproductive allocation from juvenile and adult feeding: Radiotracer studies. Ecology 78: 192-202.
- Boggs, C. L. and L. A. Jackson. 1991.** Mud puddling by butterflies is not a simple matter. Ecological Entomology 16: 123-127.
- Boggs, C. L. and D. D. Murphy. 1997.** Community composition in mountain ecosystems: climatic determinants of montane butterfly distributions. Global Ecology and Biogeography Letters 6: 39-48.
- Boggs, C. L. and C. L. Ross. 1993.** The effect of adult food limitations on life history traits in *Speyeria mormonia* (Lepidoptera: Nymphalidae). Ecology 74: 433-441.
- Boisduval, J. B. A. D. 1852.** Lépidoptères de la Californie. Annales de la Société Entomologique de France 10: 275-324.
- Boisduval, J. B. A. D. 1869.** Lépidoptères de la Californie. Annales de la Société Entomologique de Belgique 12: 1-28., 37-94.



- Bouseman, J. K. and J. G. Sternburg. 2001.** Field Guide to Butterflies of Illinois. Illinois Natural History Survey, Champaign, Illinois.
- Bossart, J. L. and C. E. Carlton. 2002.** Insect conservation in America: biased information and absence of a clear agenda hinders the integration of entomological data into mainstream conservation biology research and policy, and limits participation by professional entomologists. *American Entomologist* 48: 82-92.
- Braby, M. F., R. Vila, and N. E. Pierce. 2006.** Molecular phylogeny and systematics of the Pieridae (Lepidoptera: Papilionoidea): higher classification and biogeography. *Zoological Journal of the Linnean Society* 147: 239-275.
- Briscoe, A. D., G. D. Bernard, A. S. Szeto, L. M. Nagy, and R. H. White. 2003.** Not all butterfly eyes are created equal: Rhodopsin absorption spectra, molecular identification, and localization of ultraviolet-, blue-, and green-sensitive rhodopsin-encoding mRNA's in the retina of *Vanessa cardui*. *The Journal of Comparative Neurology* 458: 334-349.
- Britten, H. B., P. F. Brussard, D. D. Murphy, and G. T. Austin. 1994.** Colony isolation and isozyme variability of the western seep fritillary, *Speyeria nokomis apacheana* (Nymphalidae), in the western Great Basin. *The Great Basin Naturalist* 54: 97-105.
- Britten, H.B., E. Fleishman, G. T. Austin, and D.D. Murphy. 2003.** Genetically effective and adult population sizes in the apache silverspot butterfly, *Speyeria nokomis apacheana* (Lepidoptera: Nymphalidae). *Western North American Naturalist* 63(2): 229-235.
- Brittnacher, J. G., S. R. Sims, and F. J. Ayala. 1978.** Genetic differentiation between species of the genus *Speyeria* (Lepidoptera: Nymphalidae). *Evolution* 32: 199-210.
- Brooks, G. S. 1942.** A checklist of the butterflies of Manitoba. *The Canadian Entomologist* 74: 31-36.
- Brower, A. V. Z. 1994a.** Rapid morphological radiation and convergence among races of the butterfly *Heliconius erato* inferred from patterns of mitochondrial DNA evolution. *Proceedings of the National Academy of Sciences USA*. 91: 6491-6495.
- Brower, A. V. Z. 1994b.** Phylogeny of *Heliconius* butterflies inferred from mitochondrial DNA sequences (Lepidoptera: Nymphalidae). *Molecular Phylogenetics and Evolution* 3: 159-174.
- Brower, A. V. Z. 1996a.** A new mimetic species of *Heliconius* (Lepidoptera: Nymphalidae), from southeastern Colombia, revealed by cladistic analysis of mitochondrial DNA sequences. *Zoological Journal of the Linnean Society* 116: 317-332.
- Brower, A. V. Z. 1996b.** Parallel race formation and the evolution of mimicry in *Heliconius* butterflies: a phylogenetic hypothesis from mitochondrial DNA sequences. *Evolution* 50: 195-221.

- Brower, A. V. Z. 1997.** The evolution of ecologically important characters in *Heliconius* butterflies (Lepidoptera: Nymphalidae): a cladistic review. *Zoological Journal of the Linnean Society* 119: 457-472.
- Brower, A. V. Z. 2000a.** Evolution is not a necessary assumption of cladistics. *Cladistics* 16: 143-154.
- Brower, A. V. Z. 2000b.** On the validity of *Heliconius tristero* Brower and *Heliconius melpomene mocoa* Brower, with notes on species concepts in *Heliconius* Kluk (Lepidoptera: Nymphalidae). *Proceedings of the Entomological Society of Washington* 102: 678-687.
- Brower, A. V. Z. 2000c.** Phylogenetic relationships among the Nymphalidae (Lepidoptera) inferred from partial sequences of the *wingless* gene. *Proceedings of the Royal Society of London B* 267: 1201-1211.
- Brower, A.V.Z. 2006.** Problems with DNA barcodes for species delimitation: ‘ten species’ of *Astrartes fulgurator* reassessed (Lepidoptera: Hesperiiidae). *Systematics and Biodiversity* 4: 127-132.
- Brower, A. V. Z. and R. DeSalle. 1994.** Practical and theoretical considerations for choice of a DNA sequence region in insect molecular systematics, with a short review of published studies using nuclear gene regions. *Annals of the Entomological Society of America*. 87: 702-716.
- Brower, A. V. Z. and R. DeSalle. 1998.** Patterns of mitochondrial versus nuclear DNA sequence divergence among nymphalid butterflies: the utility of *wingless* as source of characters for phylogenetic inference. *Insect Molecular Biology* 7: 73-82.
- Brower, A. V. Z. and M. G. Egan. 1997.** Cladistic analysis of *Heliconius* butterflies and relatives (Nymphalidae: Heliconiiti): a revised phylogenetic position for *Eueides* based on sequences from mtDNA and a nuclear gene. *Proceedings of the Royal Society: Biological Sciences* 264: 969-977.
- Brower, J. V. Z. and L. P. Brower. 1961.** Palatability of North American model and mimic butterflies to caged mice. *Journal of the Lepidopterists’ Society* 15: 23-24.
- Brown, F. M. 1965.** The types of the nymphalid butterflies described by William Henry Edwards Part I. Argynninae. *Transactions of the American Entomological Society* 91: 233-350.
- Brown, F. M., J. D. Eff, and B. Rotger. 1957.** *Colorado Butterflies*. Denver Museum of Natural History, Denver, Colorado. 368 pp.
- Brown, J. M., O. Pellmyr, J. N. Thompson, and R. G. Harrison. 1994.** Phylogeny of *Greya* (Lepidoptera: Prodoxidae), based on nucleotide sequence variation in mitochondrial cytochrome oxidase I and II: congruence with morphological data. *Molecular Biology and Evolution* 11: 128-141.

- Brown, K. S. 1965.** Some comments on Arizona butterflies (Papilionoidea). *Journal of the Lepidopterists' Society* 19: 107-115.
- Broyles, S. B. and R. Wyatt. 1991.** Effective pollen dispersal in a natural population of *Asclepias exaltata*: The influence of pollinator behavior, genetic similarity, and mating success. *The American Naturalist* 138: 1239-12249.
- Burns, J. M., D. H. Janzen, M. Hajibabaei, W. Hallwachs, and P. D. N. Hebert. 2007.** DNA barcodes of closely related (but morphologically and ecologically distinct) species of skipper butterflies (Hesperiidae) can differ by only one to three nucleotides. *Journal of the Lepidopterists' Society* 61: 138-153.
- Calhoun, J. V. 2007.** *Speyeria idalia* in Georgia: An erroneous historical record. *News of the Lepidopterists' Society* 49: 82-84, 93.
- Campbell, D. L., A. V. Z. Brower, and N. E. Pierce. 2000.** Molecular evolution of the *wingless* gene and its implications for the phylogenetic placement of the butterfly family Riodinidae (Lepidoptera: Papilionoidea). *Molecular Biology and Evolution* 17: 684-696.
- Cary, S. J. and R. Holland. 1992.** New Mexico butterflies: Checklist, distribution and conservation. *Journal of Research on the Lepidoptera* 31: 57-82.
- Carlton, C. E. and L. S. Nobles. 1996.** Distribution of *Speyeria diana* (Lepidoptera: Nymphalidae) in the highlands of Arkansas, Missouri and Oklahoma, with comments on conservation. *Entomological News* 107: 213-219.
- Caterino, M. S. and F. A. H. Sperling. 1999.** *Papilio* phylogeny based on mitochondrial cytochrome oxidase I and II genes. *Molecular Phylogenetics and Evolution* 11: 122-137.
- Caterino, M. S., R. D. Reed, M. M. Kuo, and F. A. H. Sperling. 2001.** A partitioned likelihood analysis of swallowtail butterfly phylogeny (Lepidoptera: Papilionidae). *Systematic Biology* 50: 106-127.
- Chapman, R. F. 1998.** *The Insects: Structure and Function*. 4<sup>th</sup> ed. Cambridge University Press, Cambridge, United Kingdom. 792 pp.
- Chermock, F. H. and R. L. Chermock. 1940.** Some new diurnal Lepidoptera from the Riding Mountains and the Sand Ridge, Manitoba. *The Canadian Entomologist* 72: 81-83.
- Cicero, C. and N. K. Johnson. 2006.** Diagnosability of subspecies: Lessons from sage sparrows (*Amphispiza belli*) for analysis of geographic variation in birds. *The Auk* 123: 266-274.
- Claridge, H. A. Dawah, and M. R. Wilson. 1997.** Practical approaches to species concepts for living organisms. pp. 1-15. *In* M. F. Claridge, H. A. Dawah, and M. R. Wilson. *Species: the units of biodiversity*, Chapman and Hall.
- Clark, A. H. 1926.** Notes on the odors of some New England butterflies. *Psyche* 33: 1-5.

- Clark, A. H. 1932.** The butterflies of the District of Columbia and vicinity. Smithsonian Institution Bulletin 157. x + 338 pp., 64 pls.
- Clark, A. H. and L. F. Clark. 1951.** The Butterflies of Virginia. Smithsonian Miscellaneous Collections Volume 116, Smithsonian Institution, Washington D.C.
- Clausen, J. 1927.** Chromosome number and the relationship of species in the genus *Viola*. Annals of Botany 41: 677-714.
- Clausen, J. 1929.** Chromosome number and relationship of some North American species of *Viola*. Annals of Botany 43: 741-764.
- Cohen, E. and J. Cohen. 1991.** A collecting adventure in the George Washington National Forest. News of the Lepidopterists' Society 1: 3-4.
- Common, I. F. B. and D. F. Waterhouse. 1972.** Butterflies of Australia. Angus and Robertson PTY LTD, Sydney, Australia.
- Comstock, J. A. 1925.** Studies in Pacific Coast Lepidoptera. Eight new races, forms or aberrations of California butterflies. Bulletin of the Southern California Academy of Sciences 24: 62-68.
- Comstock, J. A. 1989.** Butterflies of California. Scientific Publishers, Gainesville, FL. ix-lviii, 334 pp., 63 plates.
- Comstock, W. P. 1940.** Butterflies of New Jersey: A list of the Lepidoptera suborder Rhopalocera occurring in the State of New Jersey; giving time of flight, food plants, records of capture with locality and date. Journal of the New York Entomological Society 48: 47-84.
- Connor, E. F., J. Hafern timer, J. Levy, V. L. Moore, and J. K. Rickman. 2002.** Insect conservation in an urban biodiversity hotspot: the San Francisco Bay area. Journal of Insect Conservation 6: 247-259.
- Covell, C. V. and G. B. Straley. 1973.** Notes on Virginia butterflies, with two new state records. Journal of the Lepidopterists' Society 27: 144-154.
- Cracraft, J. 1982.** Geographic differentiation, cladistics, and vicariance biogeography: reconstructing the tempo and mode of evolution. American Zoologist 22: 411-424.
- Cramer, P. 1775.** Papillons exotiques des trois parties du monde l'Asie, l'Afrique et l'Amerique. Amsterdam, S. J. Baalde. Vol. 1. i-xxx + 1-16, 1-155, 1-96 pls.
- Cramer, P. 1777.** Papillons exotiques des trois parties du monde l'Asie, l'Afrique et l'Amerique. Amsterdam, S. J. Baalde. Vol. 2. 152 pp., 97-192 pls.
- Dajoz, I. 1999.** The distribution of pollen heteromorphism in *Viola*: ecological and morphological correlates. Evolutionary Ecology Research 1: 97-109.

- Dasmahapatra, K. K. and J. Mallet. 2006.** DNA barcodes: recent successes and future prospects. *Heredity* 97: 254-255.
- Davenport, K. 1995.** Are there Parnassians in the Greenhorn Mountains? *News of the Lepidopterists' Society* 4: 91-92.
- Davenport, K. 1998.** New observations of three fritillaries (*Speyeria* sp.; Argynninae) in the southern Sierra. *News of the Lepidopterists' Society*. 40: 26-27.
- Debinski, D., P. Drobney, and N. Smith. 2000.** Regal fritillary and its host plant studied at Neal Smith National Wildlife Refuge, (Iowa). *Ecological Restoration North America* 18: 254-255.
- DeFoliart, G. R. 1956.** An annotated list of southeastern Wyoming Rhopalocera. *The Lepidopterists' News* 10: 91-101.
- Dennis, R. L. H. and T. G. Shreeve. 1997.** Diversity of butterflies on British islands: ecological influences underlying the roles of area, isolation and the size of the faunal source. *Biological Journal of the Linnean Society* 60: 257-275.
- Dennis, R. L. H., J. G. Hodgson, R. Grenyer, T. G. Shreeve, and D. B. Roy. 2004.** Host plants and butterfly biology: Do host-plant strategies drive butterfly status? *Ecological Entomology* 29: 12-26.
- Donoghue, M. J. 1985.** Critique of the biological species concept and recommendations for a phylogenetic alternative. *The Bryologist* 88: 172-181.
- Dornfeld, E. J. 1980.** *The Butterflies of Oregon*. Timber Press, Forest Grove, Oregon. 276 pp.
- dos Passos, C. F. 1935.** Some butterflies of southern Newfoundland with descriptions of new subspecies (Lepid. Rhopal.) *The Canadian Entomologist* 67: 82-88.
- dos Passos, C. F. 1961.** Taxonomic notes on some Nearctic Rhopalocera. 2. Papilionoidea. *Journal of the Lepidopterists' Society* 15: 209-225.
- dos Passos, C. F. 1964.** A synomic list of the Nearctic Rhopalocera. *Memoirs of the Lepidopterists' Society* No. 1.
- dos Passos, C. F. and L. P. Grey. 1942.** Two new North American subspecies of *Argynnis*, with some revisional notes (Lepidoptera: Nymphalidae). *American Museum Novitates* 1214: 1-6.
- dos Passos C. F. and L. P. Grey. 1945a.** A genitalic survey of Argynninae (Lepidoptera, Nymphalidae). *American Museum Novitates* 1296: 1-29.
- dos Passos C. F. and L. P. Grey. 1945b.** A new species and some new subspecies of *Speyeria* (Lepidoptera, Nymphalidae). *American Museum Novitates* 1297: 1-17.

- dos Passos C. F. and L. P. Grey. 1947.** Systematic catalogue of *Speyeria* (Lepidoptera, Nymphalidae) with designations of types and fixations of the type localities. American Museum Novitates 1370: 1-30.
- dos Passos C. F. and L. P. Grey. 1955.** A new name for *Argynnis lais* Edwards (Lepidoptera, Rhopalocera). Journal of the New York Entomological Society 63: 95-96.
- dos Passos C. F. and L. P. Grey. 1965.** Notes on certain lectotypes and neotypes designated by the authors in their systematic catalogue of *Speyeria* (Lepidoptera: Nymphalidae). Transactions of the American Entomological Society 91: 351-360.
- Douglas, M. M. and J. M. Douglas. 2005.** Butterflies of the Great Lakes Region. The University of Michigan Press, Ann Arbor, Michigan. 345 pp.
- Drees, B. and L. Butler. 1978.** Rhopalocera of West Virginia. Journal of the Lepidopterists' Society 32: 198-206.
- Drury D. 1773.** 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. London, B. White. Vol. 1 xxvii + 132 pp, 50 pls.
- Dufour, L. 1844.** Anatomie générale des diptères. Annales des Sciences Naturelles 1: 244-264.
- Dunford, J. C. 2005.** Chasing greater fritillaries: The rise of Atlantis. American Butterflies 13: 14-25.
- Dunford, J. C. and R. J. Ekin. 2005.** Greater fritillaries at three localities in Humboldt National Forest, Nevada. American Butterflies 13: 26-32.
- Dunford, J. C. and G. T. Austin. 2007.** Nomenclatural *faux pas* for *Speyeria atlantis greyi* Moeck, 1950 (Lepidoptera: Nymphalidae). Insecta Mundi 17:1-4.
- Durden, C. J. 1965.** *Speyeria callippe* and *Artemisia*, a possible foodplant. Journal of the Lepidopterists' Society 19: 186-187.
- Ebach, M. C. and C. Holdrege. 2005.** DNA barcoding is no substitute for taxonomy. Nature 434: 697.
- Eberhard, W. G. 1985.** Sexual Selection and the Evolution of Animal Genitalia. Harvard University Press, Cambridge, Massachusetts. 244 pp.
- Eberhard, W. G. 1996.** Female Control: Sexual Selection by Cryptic Female Choice. Princeton University Press, Princeton, New Jersey. 501 pp.
- Ebner, J. A. 1970.** Butterflies of Wisconsin. Milwaukee Public Museum, Milwaukee, WI.

- Edwards, W. H. 1863a.** Descriptions of certain species of diurnal Lepidoptera found within the limits of the United States and British America-No. 2. Proceedings of the Academy of National Sciences Philadelphia 14: 54-58.
- Edwards, W. H. 1863b.** Descriptions of certain species of diurnal Lepidoptera found within the limits of the United States and British America-No. 3. Proceedings of the Academy of National Sciences Philadelphia 14: 221-226.
- Edwards, W. H. 1864a.** Descriptions of certain species of diurnal Lepidoptera found within the limits of the United States and British North America-No. 3. Proceedings of the Entomological Society Philadelphia 2: 501-507.
- Edwards, W. H. 1864b.** Notes on the argynnides of California. Proceedings of the Entomological Society of Philadelphia 3: 434-436.
- Edwards, W. H. 1869.** Descriptions of new species of diurnal Lepidoptera found within the United States. Transactions of the American Entomological Society 2: 369-376.
- Edwards, W. H. 1870.** Descriptions of new species of diurnal Lepidoptera found in the United States. Transactions of the American Entomological Society 3: 10-22.
- Edwards, W. H. 1873.** Notes on the early stages of some of our butterflies. The Canadian Entomologist 5: 223-225.
- Edwards, W. H. 1874a.** Descriptions of new species of diurnal Lepidoptera found in North America. Transactions of the American Entomological Society 5: 13-19.
- Edwards, W. H. 1874b.** Descriptions of new species of diurnal Lepidoptera found in North America. Transactions of the American Entomological Society 5: 103-111.
- Edwards, W. H. 1878.** Descriptions of new species of North American Lepidoptera. Field and Forest 3: 142-144.
- Edwards, W. H. 1879a.** Descriptions of new species of butterflies collected by Mr. H.K. Morrison, in Nevada, 1878; also remarks on some errors of synonymy and arrangement. The Canadian Entomologist 11: 49-56.
- Edwards, W. H. 1879b.** Descriptions of new species of North American butterflies; also notes upon certain species. The Canadian Entomologist 11: 81-89.
- Edwards, W. H. 1879c.** Description of the preparatory stages of *Argynnis egleis*, Bois. The Canadian Entomologist 11: 177-179.
- Edwards, W. H. 1879d.** Description of preparatory stages of *Argynnis idalia*, Drury. The Canadian Entomologist 11: 217-219.
- Edwards, W. H. 1880a.** Description of the preparatory stages of *Argynnis alcestis*, Edw. The Canadian Entomologist 12: 69-74.

- Edwards, W. H. 1880b.** Description of the preparatory stages of *Argynnis cybele*, Fabr. The Canadian Entomologist 141-145.
- Edwards, W. H. 1881.** Descriptions of new species of diurnal Lepidoptera found in the United States. Transactions of the American Entomological Society 9: 1-8.
- Edwards, W. H. 1883.** Descriptions of new species of North American butterflies. The Canadian Entomologist 15: 209-211.
- Edwards, W. H. 1888a.** Description of the preparatory stages of *Argynnis atlantis*, Edwards. The Canadian Entomologist 20: 1-3.
- Edwards, W. H. 1888b.** Description of the preparatory stages of *Argynnis edwardsii*, Reakirt. The Canadian Entomologist 20: 3-5.
- Edwards, W. H. 1888c.** Description of the preparatory stages of *Argynnis hesperis*, Edwards. The Canadian Entomologist 20: 67-69.
- Edwards, W. H. 1892.** Miscellaneous notes on butterflies, larvae, etc. Canadian Entomologist 24: 105-111.
- Eff, D. 1956.** Notes on *Speyeria egleis secreta* (Nymphalidae). The Lepidopterists' News 10: 102-106.
- Ehrmann, G. A. 1917.** Some new North American butterflies. Lepidopterist 1: 54-56.
- Ehrlich, P. R. 1958.** The comparative morphology, phylogeny and higher classification of the butterflies (Lepidoptera: Papilionoidea). The University of Kansas Science Bulletin 34: 305-370.
- Ehrlich, P. R. 1983.** Summer butterflies in Dinosaur National Monument. Journal of the Lepidopterists' Society 37: 91-92.
- Ehrlich, P. R. and A. H. Ehrlich. 1961.** How to Know the Butterflies. Wm. C. Brown Company, Dubuque, Iowa.
- Ehrlich, P. R. and P. H. Raven. 1964.** Butterflies and plants: a study in coevolution. Evolution 18: 586-608.
- Ehrlich, P. R. and R. R. White. 1980.** Colorado checkerspot butterflies: isolation, neutrality, and the biospecies. The America Naturalist 115: 328-341.
- Eisner, C. 1942.** Einige Ergebnisse der Sichtung der Gattungen *Melitaea* und *Argynnis* im Rijksmuseum van Natuurlijke Historie, Leiden. Zoologische Mededelingen 24: 116-124.



- Eldredge, N. and J. Cracraft. 1980.** Phylogenetic Patterns and the Evolutionary Process. Method and Theory in Comparative Biology. Columbia University Press, New York, New York. 349 pp..
- Ellers, J. and C. L. Boggs. 2004.** Functional ecological implications of intraspecific differences in wing melanization in *Colias* butterflies. Biological Journal of the Linnean Society 82: 79-87.
- Ellis, S. L. 1975.** *Speyeria nokomis nokomis* in Colorado. Atala 3: 11-12.
- Elwes, H. J. 1889.** A revision of the genus *Argynnis*. Transactions of the Entomological Society London. 535-575.
- Ely, C. A., M. E. Rolfs, and T. E. Labedz. 1983.** New and unusual butterfly records from Kansas. Journal of the Lepidopterists' Society 37: 256-257.
- Emmel, J. F. and T. C. Emmel. 1998a.** A review of the *Speyeria egleis* complex in California, with the description of two new subspecies (Lepidoptera: Nymphalidae). pp. 437-442. In T. C. Emmel [Ed.], Systematics of Western North American Butterflies. Mariposa Press, Gainesville, Florida.
- Emmel, J. F. and T. C. Emmel. 1998b.** A previously unrecognized subspecies of *Speyeria zerene* (Lepidoptera: Nymphalidae) from coastal northern California. pp. 451-454. In T. C. Emmel [Ed.], Systematics of Western North American Butterflies. Mariposa Press, Gainesville, Florida.
- Emmel, J. F., T. C. Emmel, and S.O. Mattoon. 1998a.** The types of California butterflies named by Jean Alphonse Boisduval: Designation of lectotypes and a neotype, and fixation of type localities. pp. 3-76. In T. C. Emmel [Ed.], Systematics of Western North American Butterflies. Mariposa Press, Gainesville, Florida.
- Emmel, J. F., T. C. Emmel, and S. O. Mattoon. 1998b.** The types of California butterflies named by Herman Behr: Designation of neotypes and fixation of type localities. pp. 95-114. In T. C. Emmel [Ed.], Systematics of Western North American Butterflies. Mariposa Press, Gainesville, Florida.
- Emmel, J. F., T. C. Emmel, and S. O. Mattoon. 1998c.** New subspecies of Nymphalidae from California and a neotype designation for *Argynnis rupestris* Behr (Lepidoptera: Nymphalidae). pp. 139-158. In T. C. Emmel [Ed.], Systematics of Western North American Butterflies. Mariposa Press, Gainesville, Florida.
- Emmel, J. F., T. C. Emmel, and S. O. Mattoon. 1998d.** A new subspecies of *Speyeria zerene* (Lepidoptera: Nymphalidae) from the San Francisco Bay Area of California. pp. 455-459. In T. C. Emmel [Ed.], Systematics of Western North American Butterflies. Mariposa Press, Gainesville, Florida.
- Emmel, J. F., O. Shields, and D. E. Breedlove. 1970 (1971).** Larval foodplant records for North American Rhopalocera, Part 2. Journal of Research on the Lepidoptera 9: 233-242.

- Emmel, T. C. 1964.** The ecology and distribution of butterflies in a montane community near Florissant, Colorado. *The American Midland Naturalist* 72: 358-373..
- Emmel, T. C. [Ed.] 1998.** Systematics of Western North American Butterflies. Mariposa Press, Gainesville, Florida. 878 pp.
- Emmel, T. C. and G. T. Austin. 1998.** What is *Argynnis carolae*? The cytotaxonomy and systematic position of a *Speyeria* relic from Nevada (Lepidoptera: Nymphalidae). pp. 443-450. *In* T. C. Emmel [Ed.], Systematics of Western North American Butterflies. Mariposa Press, Gainesville, Florida.
- Emmel, T. C. and J. F. Emmel. 1973.** The butterflies of southern California. Natural History Museum of Los Angeles County, Science Series 26: 1-148.
- Emmel, T. C., M. C. Minno, and B. A. Drummond. 1992.** Florissant Butterflies: A Guide to the Fossil and Present-Day Species of Central Colorado. Stanford University Press, Stanford, California.
- Eriksen, C. H. 1962.** Further evidence of the distribution of some boreal Lepidoptera in the Sierra Nevada. *Journal of Research on the Lepidoptera* 1: 89-93.
- Evers, D. C. [Ed.] 1994.** Endangered and threatened wildlife of Michigan. The University of Michigan Press, Ann Arbor, Michigan.
- Fabricius, J. C. 1775.** Systema entomologiae, sistens insectorum classes, ordines, genera, species, adiectis synonymis, locis, descriptionibus, observationibus. Flensburg and Leipzig, Kortii. 832 pp.
- Fabricius, J. C. 1787.** Mantissa insectorum, sistens eorum species nuper detectas adiectis characteribus genericis, differentiis specificis, emendationibus observationibus. Copenhagen, Christ. Gottl. Proft. Vol. 1, xx + 348 pp.
- Fabricius, J. C. 1807.** Systema glossatorum secundum ordines, genera, species adiectis synonymis locis, observationibus, descriptionibus, descriptionibus. Brunswick, Carolum Reichard. xii + 13 + 112 pp.
- Ferge, L. A. 2002.** Checklist of Wisconsin butterflies. Wisconsin Entomological Society Miscellaneous Publication No. 5.
- Ferris, C. D. 1971a.** A Key to the Rhopalocera [Butterflies] of Wyoming. Agricultural Experimental Station Science Monograph 21. University of Wyoming, Laramie, Wyoming.
- Ferris, C. D. 1971b.** An Annotated Checklist of the Rhopalocera [Butterflies] of Wyoming. Agricultural Experimental Station Science Monograph 23. University of Wyoming, Laramie, Wyoming.

- Ferris, C. D. 1972.** Ultraviolet photography as an adjunct to taxonomy. *Journal of the Lepidopterists' Society* 26: 210-215.
- Ferris, C. D. 1973.** A revision of the *Colias alexandra* complex (Pieridae) aided by ultraviolet reflectance photography with designation of a new subspecies. *Journal of the Lepidopterists' Society* 27: 57-73.
- Ferris, C. D. 1976a.** A checklist of the butterflies of Grant County, New Mexico and vicinity. *Journal of the Lepidopterists' Society* 30: 38-49.
- Ferris, C. D. 1983.** *Speyeria atlantis* phenotypes in the southern Rocky Mountains (Lepidoptera: Nymphalidae: Argynninae). *Journal of Research on the Lepidoptera* 22: 101-114.
- Ferris, C. D. 1989a.** A Catalogue/Checklist of the Butterflies of America North of Mexico. *Memoirs of the Lepidopterists' Society* No. 2. 280 pp.
- Ferris, C. D. 1989b.** Supplement to: A Catalogue/Checklist of the Butterflies of America North of Mexico. *Memoirs of the Lepidopterists' Society* No. 3. 103 pp.
- Ferris, C. D. and M. Fisher. 1971.** A revision of *Speyeria nokomis* (Nymphalidae). *Journal of the Lepidopterists' Society* 25: 44-52.
- Ferris, C. D. and F. M. Brown. 1981.** Butterflies of the Rocky Mountain states. University of Oklahoma Press, Norman.
- Ferster, B. 2005.** Regal fritillaries: News from the eastern front. *American Butterflies* 13: 5-12.
- Field, W. D. 1938.** A manual of the butterflies and skippers of Kansas. *Bulletin of the University of Kansas* 39: 1-328.
- Fisher, J. C. 1858.** Description of a new species of *Argynnis*. *Proceedings of the Academy of Natural Sciences Philadelphia* 10: 179-180.
- Fisher, J. C. 1859.** [Statement]. *Proceedings of the Academy of Natural Sciences Philadelphia* 11: 352.
- Fisher, M. S. 2005.** The Butterflies of Colorado. Nymphalidae-Part 2. The Subfamily Heliconiinae-The Greater and Lesser Fritillaries (Argynnini), The Longwings (Heliconiini) and the Subfamily Danainae-The Milkweed Butterflies. *Lepidoptera of North America* 7.2. Contributions of the C. P. Gillette Museum of Arthropod Diversity, Colorado State University, Fort Collins, Colorado.
- Fleishman, E., G. T. Austin, and D. D. Murphy. 1997.** Natural history and biogeography of the butterflies of the Toiyabe Range, Nevada (Lepidoptera: Papilionoidea). *Holarctic Lepidoptera* 4: 1-18.

- Fleishman, E., G. T. Austin, and D. D. Murphy. 2001a.** Biogeography of Great Basin butterflies: revisiting patterns, paradigms, and climate change scenarios. *Biological Journal of the Linnean Society* 74: 501-515.
- Fleishman, E., R. MacNally, J. P. Fay, and D. D. Murphy. 2001b.** Modeling and predicting species occurrence using broad-scale environmental variables: An example with butterflies of the Great Basin. *Conservation Biology* 15: 1674-1685.
- Fleishman, E., D. D. Murphy, and G. T. Austin. 2005.** Biodiversity patterns of spring-associated butterflies in a Mojave desert mountain range. *Journal of the Lepidopterists' Society* 59:89-95.
- Foote, K. 2002.** Black-eyed Susan (*Rudbeckia hirta* L.). *New York Flora Association Newsletter* 13: 1-6.
- Fothergill, P. G. 1941.** Studies in *Viola*. III. An account of the inheritance of certain characters in the progeny of plants of a wild population of *Viola* hybrids. *New Phytologist* 40: 139-151.
- Fothergill, P. G. 1944.** Studies in *Viola*. IV. The somatic cytology and taxonomy of our British species of the genus *Viola*. *New Phytologist* 43: 23-35.
- Freitas, A. V. L. and K. S. Brown, Jr. 2004.** Phylogeny of the Nymphalidae (Lepidoptera). *Systematic Biology* 53: 363-383.
- Garth, J. S. 1949.** Studies in Arizona Lepidoptera. I. A new subspecies of *Speyeria atlantis* (Edwards) from the Kaibab Plateau, Grand Canyon National Park. *Bulletin of the Southern California Academy of Sciences* 48: 1.
- Garth, J. S. 1950.** Butterflies of Grand Canyon National Park. *The University of Southern California Bulletin No. 11*: 1-52.
- Garth, J. S. and J. W. Tilden. 1963.** Yosemite butterflies: An ecological survey of the butterflies of the Yosemite sector of the Sierra Nevada, California. *Journal of Research on the Lepidoptera* 2: 1-96.
- Garth, J. S. and J. W. Tilden. 1986.** *California Butterflies*. University of California Press, Berkley, California.
- Gatrelle, R. R. 1998.** Two new Nymphalidae from western North Carolina: new subspecies of *Speyeria aphrodite* and *Phyciodes batesii*. *Taxonomic Report of the International Lepidoptera Survey* 1: 1-7.
- Gillham, N. W. 1956.** Geographic variation and the subspecies concept in butterflies. *Systematic Zoology* 5: 110-120.
- Glassberg, J. 1998a.** Army tries to crush butterflies NABA fights back! *American Butterflies* 6: inside cover, 23.

- Glassberg, J. 1998b.** Regal fritillary update. *American Butterflies* 6: inside cover.
- Glassberg, J. 2000.** Eyeing the greater fritillaries. *American Butterflies* 8:14-17.
- Glassberg, J. 2001a.** Butterflies through binoculars: the East, a guide to the butterflies of eastern North America. Oxford University Press, New York, NY.
- Glassberg, J. 2001b.** Butterflies through binoculars: the West, a guide to the butterflies of western North America. Oxford University Press, New York, NY.
- Gochfeld, M. and J. Burger. 1997.** Butterflies of New Jersey: A Guide to their Status, Distribution, Conservation, and Appreciation. Rutgers University Press, New Brunswick, New Jersey.
- Goldstein, P. Z., R. DeSalle, G. Amato, and A. P. Vogler. 2000.** Conservation genetics at the species boundary. *Conservation Biology* 14: 120-131.
- Goldstein, P. Z., Y. Wyner, P. Doukakis, M. G. Egan, G. Amato, H. Rosenbaum, and R. DeSalle. 2005.** Theory and methods for diagnosing species and populations in conservation. *Annals of the Missouri Botanical Garden* 92: 12-27.
- Gompert, Z., C. C. Nice, J. A. Fordyce, M. L. Forister, and A. M. Shapiro. 2006.** Identifying units for conservation using molecular systematics: The cautionary tale of the Karner blue butterfly. *Molecular Ecology* 15: 1759-1768.
- Gornall, R. J. 1997.** Practical aspects of the species concept in plants. pp. 171-187. *In* M. F. Claridge, H. A. Dawah, and M. R. Wilson (eds.), *Species: the units of biodiversity*, Chapman and Hall.
- Gregory, W. W. 1975.** Checklist of the butterflies and skippers of Canada. Lyman Entomological Museum and Research Laboratory Memoir No. 3 (Special Publication No. 10), Quebec.
- Grey, L. P. 1951.** The subspeciation of *Speyeria atlantis*. *The Lepidopterists' News* 5: 31-35.
- Grey, L. P. 1957.** Warren's argynnid classification (Nymphalidae). *The Lepidopterists' News* 11: 171-176.
- Grey, L. P. 1964.** Keeping records. *Journal of the Lepidopterists' Society* 18: 58-63.
- Grey, L. P. 1970.** On the Gunder collection of argynnids (Lepidoptera: Nymphalidae). *Journal of Research on the Lepidoptera* 8: 55-64.
- Grey, [L.] P. 1972.** Notes on *Speyeria zerene* populations in Modoc Co., California. *News of the Lepidopterists' Society* 6: 2.
- Grey, L. P. 1974a.** Variation in *Speyeria mormonia*, or, do subspecies exist? *News of the Lepidopterists' Society* 5: 1-2.

- Grey, L. P. 1989.** Sundry Argynninae concepts revisited (Nymphalidae). Journal of the Lepidopterists' Society 43: 1-10.
- Grey, L. P. and A. H. Moeck. 1962.** Notes on overlapping subspecies. I. An example in *Speyeria zerene* (Nymphalidae). Journal of the Lepidopterists' Society 16: 81-97.
- Grey, L. P., A. H. Moeck, and W. H. Evans. 1963.** Notes on overlapping subspecies. II. Segregation in the *Speyeria atlantis* of the Black Hills (Nymphalidae). Journal of the Lepidopterists' Society 17: 129-147.
- Gunder, J. D. 1924.** Several new aberrant Lepidoptera (Rhopalocera) from California. Entomological News 35: 153-158.
- Gunder, J. D. 1927.** New transition forms (Lepid. Rhopalocera). The Canadian Entomologist 59: 281-287.
- Gunder, J. D. 1929.** New butterflies and sundry notes (Lepidoptera, Rhopalocera). Bulletin of the Brooklyn Entomological Society 24: 325-332.
- Gunder, J. D. 1931.** Some new butterflies (Lepid., Rhopalocera). Bulletin of the Southern California Academy of Sciences 30: 45-48.
- Gunder, J. D. 1932.** New Rhopalocera (Lepidoptera). The Canadian Entomologist 64: 276-284.
- Gunder, J. D. 1934.** Various new butterflies (Lepid., Rhopalocera). The Canadian Entomologist 66: 125-131.
- Guppy, C. S. 1986.** Geographic variation in wing melanism of the butterfly *Parnassius phoebus* F. (Lepidoptera: Papilionidae). Canadian Journal of Zoology 64: 956-962.
- Guppy, C. S. and J. H. Shepard. 2001.** Butterflies of British Columbia. UBC Press, Vancouver, British Columbia.
- Guppy, R. 1953.** Rearing *Speyeria* in captivity. The Lepidopterists' News 7: 56.
- Hajibabaei, M., D. H. Janzen, J. M. Burns, W. Hallwachs, and P. D. N. Hebert. 2006.** DNA barcodes distinguish species of tropical Lepidoptera. Proceedings of the National Academy of Sciences 103: 968-971.
- Hammond, P. C. 1974.** An Ecological Survey of the Nymphalid Butterfly Genus *Speyeria*. Master's Thesis, University of Nebraska, Lincoln. 101 pp.
- Hammond, P. C. 1978.** Geographic variation and speciation in the Nymphalid butterfly genus *Speyeria*. Ph.D. Dissertation, Virginia Polytechnic Institute and State University, Blacksburg.

- Hammond, P. C. 1981.** The colonization of violets and *Speyeria* butterflies on the ash-pumice fields deposited by Cascadian volcanoes. *Journal of Research on the Lepidoptera* 20: 179-191.
- Hammond, P. C. 1986.** A rebuttal to the Arnold classification of *Speyeria callippe* (Nymphalidae) and defense of the subspecies concept. *Journal of Research on the Lepidoptera* 24: 197-208.
- Hammond, P. C. 1990.** Patterns of geographic variation and evolution in polytypic butterflies. *Journal of Research on the Lepidoptera* 29: 54-76.
- Hammond, P. C. 1995.** Conservation of biodiversity in native prairie communities in the United States. *Journal of the Kansas Entomological Society* 68: 1-6.
- Hammond, P. C. and E. J. Dornfeld. 1983.** A new subspecies of *Speyeria egleis* (Nymphalidae) from the Pumice Region of central Oregon. *Journal of the Lepidopterists' Society* 37: 115-120.
- Hammond, P. C. and D. V. McCorkle. 1984.** The decline and extinction of *Speyeria* populations resulting from human environmental disturbances (Nymphalidae: Argynninae). *The Journal of Research on the Lepidoptera* 22: 217-224.
- Haney, A. and R. L. Power. 1996.** Adaptive management for sound ecosystem management. *Environmental Management* 20: 879-886.
- Hardesty, R. L. and D. R. Groothuis. 1993.** Butterflies of the Laramie Mountains, Wyoming (Lepidoptera: Rhopalocera). *Journal of Research on the Lepidoptera*. 32: 107-123.
- Harris Jr., L. 1972.** Butterflies of Georgia. University of Oklahoma Press, Norman, Oklahoma. 326 pp.
- Harvey, D. J. 1991.** Higher Classification of the Nymphalidae, pp. 255-273. *In* H. F. Nijhout, *The Development and Evolution of Butterfly Wing Patterns*, Smithsonian Institution Press, Washington D. C.
- Harvey, M. J. 1966.** Cytotaxonomic relationships between the European and North American rostrate violets. *New Phytologist* 65: 469-476.
- Haslett, J. R. 1997a.** Insect communities and the spatial complexity of mountain habitats. *Global Ecology and Biogeography Letters* 6: 49-56.
- Haslett, J. R. 1997b.** Mountain ecology: organism responses to environmental change, an introduction. *Global Ecology and Biogeography* 6: 3-6.
- Hazevoet, C. J. 1996.** Conservation and species lists: taxonomic neglect promotes the extinction of endemic birds, as exemplified by taxa from eastern Atlantic islands. *Bird Conservation International* 6: 181-196.

- Hebert, P. D. N., S. Ratnasingham, and J. R. deWaard. 2003.** Barcoding animal life: Cytochrome *c* oxidase subunit 1 divergences among closely related species. *Proceedings of the Royal Society: Biological Sciences* 270: 96-99.
- Heitzman, J. R. and J. E. Heitzman. 1996.** Butterflies and Moths of Missouri. Missouri Department of Conservation, Jefferson City, Missouri.
- Hendricks, P. 1986.** Avian predation of alpine butterflies. *Journal of the Lepidopterists' Society* 40: 129.
- Heppner, J. B. 2003.** Lepidoptera of Florida. Part 1. Introduction and Catalog. *Arthropods of Florida and Neighboring Land Areas Volume 17.* Florida Department of Agriculture and Consumer Services, Gainesville, Florida.
- Hill, J. K., C. D. Thomas, and D. S. Blakeley. 1999a.** Evolution of flight morphology in a butterfly that has recently expanded its geographic range. *Oecologia* 121: 165-170.
- Hill, J. K., C. D. Thomas, R. Fox, M. G. Telfer, S. G. Willis, J. Asher, and B. Huntley. 2002.** Responses of butterflies to twentieth century climate warming: implications for future ranges. *Proceedings of the Royal Society of London B* 269: 2163-2171.
- Hill, J. K., C. D. Thomas, and B. Huntley. 1999b.** Climate and habitat availability determine 20<sup>th</sup> century changes in a butterfly's range margin. *Proceedings of the Royal Society of London B* 266: 1197-1206.
- Hinchliff, J. 1994.** The Distribution of the Butterflies of Oregon. The Oregon State University Bookstore, Corvallis, Oregon.
- Hinchliff, J. 1996.** The Distribution of the Butterflies of Washington. The Oregon State University Bookstore, Corvallis, Oregon.
- Hodges, R. W. 1983.** Check List of the Lepidoptera of American North of Mexico. E. W. Classey Limited, Oxfordshire, England.
- Holland, R. 1974.** Butterflies of six central New Mexico mountains, with notes on *Callophrys* (*Sandia*) *macfarlandi* (Lycaenidae). *Journal of the Lepidopterists' Society* 28: 38-52.
- Holland, R. 1984.** Butterflies of two northwest New Mexico mountains. *Journal of the Lepidopterists' Society* 38: 220-234.
- Holland, R. 1988.** A new subspecies of *Speyeria atlantis* (Nymphalidae) from south-central New Mexico. *Bulletin of the Allyn Museum* 115: 1-9.
- Holland, R. and S. J. Cary. 1996.** Butterflies of the Jemez Mountains of Northern New Mexico. *Journal of the Lepidopterists' Society* 50: 61-79.
- Holland, W. J. 1898.** The Butterfly Book. New York, Doubleday and McClure Co. xx + 382 pp., 48 pls.



- Holland, W. J. 1931.** The Butterfly Book. New and Thoroughly Revised Edition. Garden City, New York, Doubleday, Doran and Co. xii + 424 pp., 77 pls.
- Holmes, A. M., Q. F. Hess, R. R. Tasker, and A. J. Hanks. 1991.** The Ontario Butterfly Atlas. Toronto Entomologists' Association. Toronto, Canada.
- Hooper, R. R. 1973.** The butterflies of Saskatchewan. Saskatchewan Department of Natural Resources. 216 pp.
- Hovanitz, W. 1941.** Parallel ecogenotypical color variation in butterflies. *Ecology* 22: 259-284.
- Hovanitz, W. 1943.** Geographical variation and racial structure of *Argynnis callippe* in California. *The American Naturalist* 77: 400-425.
- Hovanitz, W. 1962.** *Argynnis* and *Speyeria*. *Journal of Research on the Lepidoptera* 1: 95-96.
- Hovanitz, W. 1963a.** Geographical distribution and variation of the genus *Argynnis*. I. Introduction. II. *Argynnis idalia*. *Journal of Research on the Lepidoptera* 1: 117-123.
- Hovanitz, W. 1963b.** Geographical distribution and variation of the genus *Argynnis*. III. *Argynnis diana*. *Journal of Research on the Lepidoptera* 1: 201-208.
- Hovanitz, W. 1967.** Ecological color variation in some *Argynnis* of the western United States. *Journal of Research on the Lepidoptera* 6: 197-198.
- Hovanitz, W. 1970.** Habitat-*Argynnis adiaspe*. *Journal of Research on the Lepidoptera* 9: 168, 192.
- Howe, W. H. 1975.** The Butterflies of North America. Doubleday and Company, Inc., Garden City, New York.
- Hribar, L. J. 2004.** Mosquito control of butterfly control? *Wing Beats* 15: 25.
- Hubbard, J. P. 1965.** Some butterflies of the Pinos Altos Mountains, New Mexico. *Journal of the Lepidopterists' Society* 19: 231-232.
- Hunter, L. M. and J. M. Brehm. 2004.** A qualitative examination of value orientations toward wildlife and biodiversity by rural residents of the intermountain region. *Human Ecology Review* 11: 13-26.
- Hunter, P. 2006.** Defining species: the indirect impact of humans on biodiversity. *European Molecular Biology Organization Reports* 7: 763-766.
- Irwin, R. R. and J. C. Downey. 1973.** Annotated Checklist of the Butterflies of Illinois. Illinois Natural History Survey No. 81. Urbana, Illinois.
- Jacobson, S. K. and M. D. McDuff. 1998.** Training idiot savants: the lack of human dimensions in conservation biology. *Conservation Biology* 12: 263-267.

- Janzen, D. H. 1984.** Weather-related color polymorphism of *Rothchildia lebeau* (Saturniidae). Bulletin of the Entomological Society of America 30: 16-20.
- Johnson, K. 1972 (1973).** The butterflies of Nebraska. Journal of Research on the Lepidoptera 11: 1-64.
- Johnson, K. 1975.** Post-Pleistocene environments and montane butterfly relicts. Journal of Research on the Lepidoptera 14: 216-232.
- Kelly, L. and D. M. Debinski. 1998.** Relationship of host plant density to size and abundance of the regal fritillary *Speyeria idalia* Drury (Nymphalidae). Journal of the Lepidopterists' Society 52: 262-276.
- Keyghobadi, N., K. P. Unger, J. D. Weintraub, and D. M. Fonseca. 2006.** Remnant populations of the regal fritillary (*Speyeria idalia*) in Pennsylvania: Local genetic structure in a high gene flow species. Conservation Genetics 7: 309-313.
- Kimball, C. P. 1965.** The Lepidoptera of Florida: An annotated checklist. Arthropods of Florida and Neighboring Land Areas Vol. 1. Florida Department of Agriculture, Division of Plant Industry, Gainesville, Florida. 363 pp.
- Kingsolver, J. G. and D. C. Wiernasz. 1991.** Development, function, and the quantitative genetics of wing melanin pattern in *Pieris* butterflies. Evolution 45: 1480-1492.
- Klassen, P. 1984.** Checklist of Manitoba butterflies (Rhopalocera). Journal of the Lepidopterists' Society 38: 32-39.
- Klots, A. B. 1951.** A Field Guide to the Butterflies of North America, East of the Great Plains. Houghton Mifflin Company, Boston, Massachusetts.
- Knowles, L. L. 2001.** Did the Pleistocene glaciations promote divergence? Tests of explicit refugial models in montane grasshoppers. Molecular Ecology 10: 691-701.
- Knüttel, H. and K. Fielder. 2000.** On the use of ultraviolet photography and ultraviolet wing patterns in butterfly morphology and taxonomy. Journal of the Lepidopterists' Society 54: 137-144.
- Knüttel, H. and K. Fielder. 2001.** Host-plant derived variation in ultraviolet wing patterns influences mate selection by male butterflies. The Journal of Experimental Biology 204: 2447-2459.
- Kohler, S. 1980.** Checklist of Montana butterflies (Rhopalocera). Journal of the Lepidopterists' Society 34: 1-19.
- Kolaczkowski, B. and J. W. Thornton. 2004.** Performance of maximum parsimony and likelihood phylogenetics when evolution is heterogeneous. Nature 431: 980-984.

- Kondla N. G. 2001.** Clarification of and comments on Northern *Speyeria hydaspe* subspecies (Lepidoptera: Nymphalidae). The Taxonomic Report of the International Lepidoptera Survey 3: 1-5.
- Kondla, N. G. 2004.** Conservation Overview of Butterflies in the Southern Headwaters at Risk Project (SHARP) Area. Alberta Sustainable Resources Department, Fish and Wildlife Division, Alberta Species at Risk Report No. 80. Edmonton, Alberta. ii + 35 pp.
- Kondo, K., T. Shinkawa, and H. Matsuka. 2003.** Molecular systematics of birdwing butterflies (Papilionidae) inferred from mitochondrial ND5 gene. Journal of the Lepidopterists' Society 57: 17-24.
- Kons Jr., H. L. 2000.** Phylogenetic studies of the Melitaeini (Lepidoptera: Nymphalidae: Nymphalinae) and a revision of the genus *Chlosyne* Butler. Ph.D. Dissertation. University of Florida, Gainesville.
- Kopper, B. J., R. E. Charlton, and D. C. Margolies. 2000.** Oviposition site selection by the regal fritillary, *Speyeria idalia*, as affected by proximity of violet hosts. Journal of Insect Behavior 13: 651-665.
- Kopper, B. J., D. C. Margolies, and R. E. Charlton. 2001a.** Notes on the behavior of *Speyeria idalia* (Drury) (Nymphalidae) larvae with implications that they are diurnal foragers. Journal of the Lepidopterists' Society 54: 96-97.
- Kopper, B. J., D. C. Margolies, and R. E. Charlton. 2001b.** Life history notes on the regal fritillary, *Speyeria idalia* (Drury) (Lepidoptera: Nymphalidae), in Kansas tallgrass prairie. Journal of the Kansas Entomological Society 74: 172-177.
- Kopper, B.J., S. Shu, R. E. Charlton, and S. B. Ramaswamy. 2001c.** Evidence for reproductive diapause in the fritillary *Speyeria idalia* (Lepidoptera: Nymphalidae). Annals of the Entomological Society of America 94: 427-432.
- Kozial, J. 1994.** Some unusual fritillaries from Saskatchewan. News of the Lepidopterists' Society 1: 3.
- Krizek, G. O. 1991.** Is *Speyeria diana* attracted to manure? News of the Lepidopterists' Society 6: 83.
- Kruse, J. J. and F. A. H. Sperling. 2002.** Phylogeny of Nearctic species of the *Xylosteana* ground of *Archips* Hübner (Lepidoptera: Tortricidae) based on combined analysis of morphological and mitochondrial DNA data sets. Annals of the Entomological Society of America 95: 288-301.
- Lafontaine, J. D. and D. M. Wood. 1997.** Butterflies and moths (Lepidoptera) of the Yukon. pp. 723-785, In H. N. Danks and J. A. Downes (eds.) Insects of the Yukon, Biological Survey of Canada (Terrestrial Arthropods), Ottawa.

- Lambeck, R. J. 1997.** Focal species: a multi-species umbrella for nature conservation. *Conservation Biology* 11: 849-856.
- Larsen, K. J. and J. A. Bovee. 2001.** Changes in the butterflies (Lepidoptera) of Winneshiek County, Iowa after 90 years. *Great Lakes Entomologist* 34: 43-54.
- Launer, A. E., D. D. Murphy, J. M. Hoekstra, and H. R. Sparrow. 1994.** The endangered Myrtle's silverspot butterfly: present status and initial conservation planning. *Journal of Research on the Lepidoptera* 31: 132-146.
- Lavers, N. 2006.** Northeast Arkansas butterflies: Forty years ago and today. *News of the Lepidopterists' Society* 48: 108-110.
- Layberry, R. A., P. W. Hall, and J. D. LaFontaine. 1998.** The butterflies of Canada. University of Toronto Press, Toronto, Canada. 280 pp.
- Lehmann, T. 1913.** 2. Genus: *Argynnis* F. (= *Brenthis* Hbn., *Acidalia* Hbn., *Boloria* Moore, *Speyeria* Scudd.). pp. 404-421, 429, pls. 85-88. In Seitz, A. The Macrolepidoptera of the World. A Systematic Description of the hitherto known Macrolepidoptera. The Macrolepidoptera of the American Faunistic Region. The American Rhopalocera. Stuttgart, Alfred Kernen, Vol. 5.
- Lembert, J. B. 1893.** *Argynnis egleis*. *The Canadian Entomologist* 25: 259.
- Levy, H. C., A. Garcia-Maruniak, and J. E. Maruniak. 2002.** Strain identification of *Spodoptera frugiperda* (Lepidoptera: Noctuidae) insects and cell line: PCR-RFLP of cytochrome oxidase C subunit I gene. *Florida Entomologist* 85: 186-190.
- Linnaeus, C. L. 1758.** *Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis*. Editio decima, reformata. Stockholm, Laurentii Salvii. Vol. 1. 823 pp.
- Lloyd, J. E. 1979.** Mating behavior and natural selection. *Florida Entomologist* 62: 17-34.
- Lloyd, J. E. 2001.** On research and entomological education V: a species (c)oncept for fireflyers, at the bench and in old fields, and back to the Wisconsinian glacier. *Florida Entomologist* 84: 587-601.
- Luckow, M. 1995.** Species concepts: assumptions, methods, and applications. *Systematic Botany* 20: 589-605.
- Maddison, D. R., and W. P. Maddison. 2000.** MaClade 4. Sunderland, Massachusetts. Sinauer.
- Maeki, K. and C. L. Remington. 1960.** Studies of the chromosomes of North American Rhopalocera. 4. Nymphalinae, Charaxidinae, Libytheinae. *Journal of the Lepidopterists' Society* 14: 179-201.

- Magnus, D. 1958.** Experimental analysis of some “overoptimal” sign-stimuli in the mating behaviour of the fritillary butterfly *Argynnis paphia* L. (Lepidoptera: Nymphalidae). Proceedings of the 10th International Congress of Entomology. Montreal 1956 2: 405-418.
- Mallarino, R., E. Bermingham, K. R. Willmott, A. Whinnett, and C. D. Jiggins. 2005.** Molecular systematics of the butterfly genus *Ithomia* (Lepidoptera: Ithomiinae): a composite phylogenetic hypothesis based on seven genes. Molecular Phylogenetics and Evolution 34: 625-644.
- Mallet, J. 1995.** A species definition for the Modern Synthesis. Trends in Ecology and Evolution 10: 294-299.
- Marrone, G. M. 1994.** Checklist of South Dakota butterflies (Hesperioidea and Papilionoidea). Journal of the Lepidopterists’ Society 48: 228-247.
- Martin, J. A. and D. P. Pashley. 1992.** Molecular systematic analysis of butterfly family and some subfamily relationships (Lepidoptera: Papilionidae). Annals of the Entomological Society of America 85: 127-139.
- Martyn, T. 1797.** Psyche Figures of Non Descript Lepidopterous Insects or Rare Moths and Butterflies from Different Parts of the World. London. 8 pp. + 32 pls.
- Mason, K. R. 2001.** Comparison of Prairie Sites and Classification of Their Habitat Attributes in Relation to Abundance of the Regal Fritillary Butterfly (*Speyeria idalia*)-Final Report. Minnesota Department of Natural Resources.
- Masters, J. H. 1972 (1973).** Butterfly records for three northwest Wisconsin counties. Journal of Research on the Lepidoptera 11: 175-182.
- Masters, J. H. 1973.** The collection of butterflies made by Jack Dennis at Beulah, Manitoba. Journal of the Lepidopterists’ Society 27: 33-39.
- Masters, J. H. 1974.** The proper subspecific name for *Speyeria aphrodite* (Nymphalidae) in southwest Manitoba. Journal of the Lepidopterists’ Society 28: 100-102.
- Masters, J. H. 1979.** The type locality of *Argynnis zerene* Boisduval (Nymphalidae): A correction. Journal of the Lepidopterists’ Society 33: 137-138.
- Mather, B. 1966.** *Speyeria cybele* in Mississippi. Journal of Research on the Lepidoptera 5: 253-254.
- Mattoon, S.O., R. D. Davis, and O.D. Spencer. 1971.** Rearing techniques for species of *Speyeria* (Nymphalidae). Journal of the Lepidopterists’ Society 25: 247-256.
- Mayr, E. 1942.** Systematics and the Origin of Species. Columbia University Press, New York, New York.
- McCorkle, D. V. 1975.** *Speyeria zerene hippolyta* in Oregon. Atala 3: 9-10, 17.

- McCorkle, D. V. and P. C. Hammond. 1988.** Biology of *Speyeria zerene hippolyta* (Nymphalidae) in a marine-modified environment. *Journal of the Lepidopterists' Society* 42: 184-195.
- McCracken, K. G. and F. H. Sheldon. 1998.** Molecular and osteological heron phylogenies: Sources of incongruence. *The Auk* 115: 127-141.
- McHenry, P. B. 1963.** Generic or subgeneric names closely related to *Argynnis*. *Journal of Research on the Lepidoptera* 2: 229-239.
- McHenry, P. 1964.** The generic, specific and lower category names of the Nearctic butterflies: Part 3-Argynnids. *Journal of Research on the Lepidoptera* 3: 231-268.
- McKibben, B. 1999.** *The End of Nature*. Anchor Books, New York New York.
- McKinnon, J. S., S. Mori, B. K. Blackman, L. David, D. M. Kingsley, L. Jamieson, J. Chou, and D. Schluter. 2004.** Evidence for ecology's role in speciation. *Nature* 429: 294-298.
- McLaughlin, J. F., J. J. Hellmann, C. L. Boggs, and P. R. Ehrlich. 2002.** Climate change hastens population extinctions. *Proceedings of the National Academy of Sciences* 99: 6070-6074.
- Meffe, G. K. and C. R. Carroll. 1997.** *Principles of Conservation Biology*, 2<sup>nd</sup> Ed. Sinauer Associate, Sunderland, Massachusetts. 729 pp.
- Memon, N., R. Meier, A. Manan, and K. Feng-Yi Su. 2006.** On the use of DNA sequences for determining the species limits of a polymorphic new species in the stink bug genus *Halys* (Heteroptera: Pentatomidae). *Systematic Entomology* 31: 703-710.
- Miller, J. C. and P. C. Hammond. 2003.** *Lepidoptera of the Pacific Northwest: Caterpillars and Adults*. Forest Health Technology Enterprise Team, United States Department of Agriculture.
- Miller, J. S. and J. W. Wenzel. 1995.** Ecological characters and phylogeny. *Annual Review of Entomology* 40: 389-415.
- Miller, J. Y. [Ed.]. 1992.** *The Common Names of North American Butterflies*. Smithsonian Institution Press, Washington D. C.
- Miller, L. D. 1969.** Nomenclature of wing veins and cells. *Journal of Research on the Lepidoptera* 8: 37-48.
- Miller, L. D. and F. M. Brown. 1981.** A Catalogue/Checklist of the Butterflies of America North of Mexico. *Memoirs of the Lepidopterists' Society* No. 2. 280 pp.
- Miller, L. D. and S. M. Miller. 1966.** Chromosomes from testicular preparations of Lepidoptera. *Science* 152: 529-530.

- Mishler, B. D. and M. J. Donoghue. 1982.** Species concepts: A case for pluralism. *Systematic Zoology* 31: 491-503..
- Mitchell, A., C. Mitter, and J. C. Regier. 2000.** More taxa or more characters revisited: Combining data from nuclear protein-coding genes for phylogenetic analyses of Noctuoidea (Insecta: Lepidoptera). *Systematic Biology* 49: 202-224.
- Moeck, A. H. 1947.** A new subspecies of *Speyeria atlantis* (Edwards) from New Mexico (Lepidoptera: Nymphalidae). *Entomological News* 58: 73-75.
- Moeck, A. H. 1950.** A new subspecies of *Speyeria atlantis* (Edwards) from Nevada (Lepidoptera: Nymphalidae). *Entomological News* 61: 61-64.
- Moeck, A. H. 1957.** Geographic variability in *Speyeria*: Comments, records and description of a new subspecies (Nymphalidae). Milwaukee Entomological Society Special Publication. 48 pp.
- Moeck, A. H. 1968.** Mobility in a Wyoming population of *Speyeria atlantis* as determined by tagging (Lepidoptera: Nymphalidae). *The Michigan Entomologist* 1: 279-282.
- Monteiro, A. and N. E. Pierce. 2001.** Phylogeny of *Bicyclus* (Lepidoptera: Nymphalidae) inferred from COI, COII, and EF-1 $\alpha$  gene sequences. *Molecular Phylogenetics and Evolution* 18: 264-281.
- Moore, P., D. Zercher, and P. McElhenny. 2006.** Diurnal herbivory documented for *Speyeria idalia* (Nymphalidae) larvae on *Viola sagittata* (Violaceae) in Pennsylvania. *Journal of the Lepidopterists' Society* 60: 176-178.
- Moran, M. D. and C. D. Baldrige. 2002.** Distribution of the Diana fritillary, *Speyeria diana* (Nymphalidae) in Arkansas, with notes on nectar plant and habitat preference. *Journal of the Lepidopterists' Society* 56: 162-165.
- Mosher, E. 1969.** Lepidoptera Pupae: Five Collected Works on the Pupae of North American Lepidoptera. Entomological Reprint Specialists, East Lansing, Michigan.
- Murphy, D. D., M. S. Menninger, and P. R. Ehrlich. 1984.** Nectar source distribution as a determinant of oviposition host species in *Euphydryas chalcedona*. *Oecologia* 62: 269-271.
- Mutanen, M. 2005.** Delimitation difficulties in species splits: A morphometric case study on the *Euxoa tritici* complex (Lepidoptera, Noctuidae). *Systematic Entomology* 30: 632-643.
- Nadot, S., H. E. Ballard Jr., J. B. Creach, and I. Dajoz. 2000.** The evolution of pollen heteromorphism in *Viola*: a new phylogenetic approach. *Plant Systematics and Evolution* 223: 155-171.
- Nelson, J. M. 1979.** A preliminary checklist of the skippers and butterflies of Oklahoma. *Proceedings of the Oklahoma Academy of Sciences* 59: 41-46.

- New, T. R. 1997.** Butterfly Conservation. Oxford; New York: Oxford University Press.
- Nice, C. C. and A. M. Shapiro. 1999.** Molecular and morphological divergence in the butterfly genus *Lycaeides* (Lepidoptera: Lycaenidae) in North America: evidence of recent speciation. *Journal of Evolutionary Biology* 12: 936-950.
- Nielsen, M. C. 1999.** Michigan Butterflies and Skippers. 1<sup>st</sup> ed. Michigan State University Extension, Michigan State University, East Lansing, Michigan.
- Nijhout H. F. 1991.** The development and evolution of butterfly wing patterns. In Funk VA, Cannell PF (Eds.) *Smithsonian Series in Comparative Evolutionary Biology*. Smithsonian Institution Press, Washington, DC.
- Nixon, K. C. and Q. D. Wheeler. 1990.** An amplification of the phylogenetic species concept. *Cladistics* 6: 211-223.
- North American Butterfly Association. 2001.** North American Butterfly Association (NABA) Checklist and English Names of North American Butterflies, 2nd Edition. North American Butterfly Association, Morristown, New Jersey.
- Noss, R. F. 1990.** Indicators for monitoring biodiversity: A hierarchical approach. *Conservation Biology* 4: 355-364.
- Oberthür, C. 1912.** Études de lépidoptérologie comparée. Rennes, Oberthür. Vol. 6. 356 pp., 97-160 pls.
- O'Brien, M. F. 1983.** New butterfly distribution records for northern New York State. *Journal of the Lepidopterists' Society* 37: 92-94.
- Opler, P. A. and G. O. Krizek. 1984.** Butterflies East of the Great Plains. Johns Hopkins University Press, Baltimore, MD. xvii + 294 pp.
- Opler, P. A. and V. Malikul. 1998.** A Field Guide to Eastern Butterflies. Houghton Mifflin Company, New York New York.
- Opler, P. A. and A. D. Warren. 2005.** Lepidoptera of North America. 4. Scientific Names List for Butterfly Species of North America, North of Mexico. Contributions of the C. P. Gillette Museum of Arthropod Diversity, Colorado State University, Fort Collins, Colorado.
- Opler, P. A. and A. B. Wright. 1999.** A Field Guide to Western Butterflies. Second edition. Houghton Mifflin Company, Boston, MA. xiv + 540 pp.
- Omland, K. E., J. M. Baker, and J. L. Peters. 2006.** Genetic signatures of intermediate divergence: population history of Old and New World Holarctic ravens (*Corvus corax*). *Molecular Ecology* 15: 795-808.
- Orsak, L. J. 1974.** Project Atossa-Preliminary Report. *Atala* 2: 5-8.



- Orsak, L. J. 1978.** The butterflies of Orange County, California. The regents of the University of California, Irvine, CA.
- Owen, D. F. 1975.** Estimating the abundance and diversity of butterflies. *Biological Conservation* 8: 173-183.
- Palmer, C. M., K. Siebke, and D. K. Yeates. 2004.** Infrared video thermography: a technique for assessing cold adaptation in insects. *BioTechniques* 37: 212-217.
- Parmesan, C., N. Ryrholm, C. Stefanescu, J. K. Hill, C. D. Thomas, H. Descimon, B. Huntley, L. Kaila, J. Kullberg, T. Tammaru, W. J. Tennent, J. A. Thomas, and M. Warren. 1999.** Poleward shifts in geographical ranges of butterfly species associated with regional warming. *Nature* 399: 579-583.
- Patten, M. A. and P. Unitt. 2002.** Diagnosability versus mean differences of sage sparrow subspecies. *The Auk* 119: 26-35.
- Paterson, H. E. H. 1985.** The recognition concept of species. pp. 21-29. *In* Vrba, E. S. (ed), *Species and speciation*, Transvaal Museum Monograph No. 4, Transvaal Museum, Pretoria.
- Patterson, J. M. 2002.** The 2002 survey for the presence of the Oregon silverspot butterfly, *Speyeria zerene hippolyta* (Lepidoptera, Nymphalidae), on the Clatsop Plains, Clatsop County, Oregon. Report to U.S. Fish and Wildlife Service.
- Pavulaan, H. 1990.** The skippers (Hesperioidae) of Rhode Island with recent records of the true butterflies (Papilionoidea). *Atala* 16: 6-12.
- Peña, C., N. Wahlberg, E. Weingartner, U. Kodandaramaiah, S. Nylin, A. V. L. Freitas, and A. V. Z. Brower. 2006:** Higher level phylogeny of Satyrinae butterflies (Lepidoptera: Nymphalidae) based on DNA sequence data. *Molecular Phylogenetics and Evolution* 40:29-49.
- Penz, C. M. 1999.** Higher level phylogeny for the passion-vine butterflies (Nymphalidae, Heliconiinae) based on early stage and adult morphology. *Zoological Journal of the Linnean Society* 127: 277-344.
- Penz, C. M. and D. Peggie. 2003.** Phylogenetic relationships among Heliconiinae genera based on morphology (Lepidoptera: Nymphalidae). *Systematic Entomology* 28: 451-479.
- Pollock, D. D., W. B. Watt, V. K. Rashbrook, and E. V. Iyengar. 1998.** Molecular phylogeny for *Colias* butterflies and their relatives (Lepidoptera: Pieridae). *Annals of the Entomological Society of America* 91: 524-531.
- Pollard, E. 1982.** Monitoring butterfly abundance in relation to the management of a nature reserve. *Biological Conservation* 24: 317-328..

- Porter, A. H. and A. M. Shapiro. 1990.** Lock-and-key hypothesis: lack of mechanical isolation in a butterfly (Lepidoptera: Pieridae) hybrid zone. *Annals of the Entomological Society of America* 83: 107-114.
- Poulton, E. B. 1909.** Mimicry in the butterflies of North America. *Annals of the Entomological Society of America* 2: 203-242.
- Pyle, R. M. 1995.** Field Guide to North American Butterflies. Alfred A. Knopf, Inc., New York, New York.
- Pyle, R. M. 2002.** The butterflies of Cascadia: a field guide to all the species of Washington, Oregon, and surrounding territories. Seattle Audubon Society, Seattle, WA.
- Reakirt, T. 1866.** Coloradian butterflies. *Proceedings of the Entomological Society of Philadelphia* 6: 122-151.
- Reiff, W. 1910.** *Argynnis cybele* Fabr. forma *bartschi*, f. nov. *Psyche* 17: 252-255.
- Remington, P. S. 1947.** Notes on the type locality of *Speyeria egleis secreta* dos Passos and Grey. *Entomological News* 58: 99-100.
- Remington, P. S. 1948.** A collecting trip in search of *Speyeria egleis secreta*. *The Lepidopterists' News* 2: 91-92.
- Remington, C. L. 1973.** Ultraviolet reflectance in mimicry and sexual signals in the Lepidoptera. *Journal of the New York Entomological Society* 81: 124.
- Reuss, F. A. T. 1922.** Eine Androconialform von "*Argynnis*" *niobe* L., f. n., und durchentsprechende [males] gekennzeichnete ostasiatische Formen oder Arten, die bisher zu "*adippe*" L. (rect. *cydippe* L.) gerechnet wurden, sich aber nunmehr durch Art und Verteilung der Androconien abtrennen lassen. Mit einer Revision des "Genus *Argynnis* F." *Archiv für Naturgeschichte* 87: 180-230.
- Reuss, F. A. T. 1926a.** Systematischer Überblick der Dryadinae T. Rss. mit einigen Neubeschreibungen (Lep. Rhopal.). *Deutsche Entomologische Zeitschrift*. 65-70.
- Reuss, F. A. T. 1926b.** Über Funktion der Sexualarmaturen bei Lepidopteren (Rhop.) und die resultierende Weiterentwicklung meines versuchten natürlichen Systems der Dryadinae T. R. *Deutsche Entomologische Zeitschrift* 431-330.
- Rindge, F.H. 1987.** *Speyeria* collection of Paul Grey to the American Museum of Natural History. *Journal of the Lepidopterist's Society* 41: 123.
- Riotte, J. C. E. 1962.** First additions to the northern Ontario list of butterflies. *Journal of the Lepidopterists' Society* 16: 243-245.
- Ritchie, J. D. 1944.** A method for determining food plants of Lepidoptera. *Bulletin of the Brooklyn Entomological Society* 39: 171-172.

- Robinson, G. S., P. R. Ackery, I. J. Kitching, G. W. Beccaloni, and L. M. Hernández. 2002.** Hostplants of the moth and butterfly caterpillars of America north of Mexico. Memoirs of the American Entomological Institute vol. 69. Gainesville, FL. 824 pp.
- Rolfs, D. 2005.** Butterflies of Chumstick Mountain. Published privately by the author, .
- Ross, G. N. 1998.** Butterfly feeding frenzies. Holarctic Lepidoptera 5: 43-44.
- Ross, G. N. 2001 (2005).** Survey of the butterflies of the Wah'Kon-Tah Prairie, Missouri. Holarctic Lepidoptera 8: 1-30.
- Ross, G. N. 2002.** Social butterflies. American Butterflies 10: 34-37.
- Ross, G. N. 2003.** What's for dinner? A new look at the role of phytochemicals in butterfly diets. News of the Lepidopterists' Society 45: 83-89.
- Ross, G.N. 2004.** Social Butterflies. Wildlife Conservation. May/June: 24-25.
- Ross, G. N. and M. C. Henk. 2004.** Notes on eggs and first instar larvae of three species of *Speyeria* (Nymphalidae). News of the Lepidopterists' Society 46: 53-63.
- Rudolph, D. C., C. A. Ely, R. R. Schaefer, J. H. Williamson, and R. E. Thill. 2006.** The Diana Fritillary (*Speyeria diana*) and Great Spangled Fritillary (*S. cybele*): Dependence on fire in the Ouachita Mountains of Arkansas. Journal of the Lepidopterists' Society 60: 218-226.
- Sapolsky, R. and P. Ehrlich. 2003.** Appeal of the rare. Discover 24: 61-63.
- Saunders, A. A. 1932.** Butterflies of Allegany State Park. New York State Handbook 13, Albany, New York.
- Sbordoni, V. and S. Forestiero. 1998.** Butterflies of the World. Firefly Books, Buffalo, New York.
- Schlicht, D. 1997.** Population monitoring for prairie butterflies in Minnesota-Final Report. Minnesota Department of Natural Resources Natural Heritage and Nongame Research Program. 27 pp.
- Schwanwitsch, B. N. 1924.** On the groundplan of wing-pattern in nymphalids and certain other families of rhopalocerous Lepidoptera. Proceedings of the Zoological Society of London, series B, 34: 509-528.
- Schweitzer, D. 1993.** Regal fritillaries in the East. American Butterflies 1: 9.
- Scoble, M. J. 1995.** The Lepidoptera: Form, Function and Diversity. Oxford University Press, New York, New York.

- Scoble, M. J. and M. Krüger. 2002.** A review of the genera of Macariini with a revised classification of the tribe (Geometridae: Ennominae). *Zoological Journal of the Linnean Society* 134: 257-315.
- Scott, J. A. 1973a.** Mating of butterflies. *Journal of Research on the Lepidoptera* 11: 99-127.
- Scott, J. A. 1973b.** Survey of ultraviolet reflectance of Nearctic butterflies. *Journal of Research on the Lepidoptera* 12: 151-160.
- Scott, J. A. 1975.** Mate-locating behavior of western North American butterflies. *Journal of Research on the Lepidoptera* 14: 1-40.
- Scott, J. A. 1979.** Hibernial diapause of North American Papilionoidea and Hesperioidea. *Journal of Research on the Lepidoptera* 18: 171-200.
- Scott, J. A. 1981.** New Papilionoidea and Hesperioidea from North America. *Papilio* 1: 1-12.
- Scott, J. A. 1984.** The phylogeny of butterflies (Papilionoidea and Hesperioidea). *Journal of Research on the Lepidoptera* 23: 241-281.
- Scott, J. A. 1986a.** Larval hostplant records for butterflies and skippers (mainly from western U.S.), with notes on their natural history. *Papilio* 4: 1-37.
- Scott, J. A. 1986b.** *The Butterflies of North America: A Natural History and Field Guide.* Stanford University Press, Stanford, California.
- Scott, J. A. 1988.** *Speyeria atlantis* in Colorado: Rearing studies concerning the relation between silvered and unsilvered forms. *Journal of the Lepidopterists' Society* 42: 1-13.
- Scott, J. A. 1992.** Hostplant records for butterflies and skippers (mostly from Colorado) 1959-1992, with new life histories and notes on oviposition, immatures, and ecology. *Papilio* 6: 1-185.
- Scott, J. A. [Ed.] 2006a.** Taxonomic studies and new taxa of North American butterflies. *Papilio* 12: 1-74.
- Scott, J. A. 2006b.** Butterfly hostplant records, 1992-2005, with a treatise on the evolution of *Erynnis*, and a note on new terminology for mate-collecting behavior. *Papilio* 14: 1-74.
- Scott, J.A. 2006c.** Proposals for a new insect study, commerce, and conservation law that deregulates dead insects, and proposals for fixing the endangered species act as applied to insects. *Papilio* 17: 1-17.
- Scott, J. A., S. L. Ellis, and D. Eff. 1968.** New records, range extensions, and field data for Colorado butterflies and skippers. *Journal of the Lepidopterists' Society* 22: 159-171.
- Scott, J. A. and M. E. Epstein. 1987.** Factors affecting phenology in a temperate insect community. *The American Midland Naturalist* 117: 103-118.

- Scott, J. A. and S. O. Mattoon. 1981.** Early stages of *Speyeria nokomis* (Nymphalidae). Journal of Research on the Lepidoptera 20:12-15.
- Scott, J. A., N. G. Kondla, and S. M. Spomer. 1998.** *Speyeria hesperis* and *Speyeria atlantis* are distinct species. Papilio 8: 1-31.
- Scott, J. A. and G. R. Scott. 1978 (1980).** Ecology and distribution of the butterflies of southern central Colorado. Journal of Research on the Lepidoptera 17: 73-128.
- Scudder, S. H. 1872.** A systematic revision of some of the American butterflies, with brief notes on those known to occur in Essex County, Mass. Salem, Massachusetts, The Salem Press. 62 + [2] pp.
- Scudder, S. H. 1875.** Synonymic list of the butterflies of North America, north of Mexico. Bulletin of the Buffalo Society of Natural Sciences 2: 233-269.
- Scudder, S. H. 1889.** The Butterflies of the Eastern United States and Canada with Special Reference to New England. Cambridge, published by the author. 3 Volumes. i-xxiv, i-xii, i-viii + 1958 pp. 89 pls.
- Segraves, K. A. and O. Pellmyr. 2004.** Testing the out-of-Florida hypothesis on the origin of the cheating in the yucca-yucca moth mutualism. Evolution 58(10): 2266-2279.
- Seitz, A. 1924.** The Macrolepidoptera of the World: A Systematic Description of the Hitherto Known Macrolepidoptera. Alfred Kernen Verlag Stuttgart. Vol. 5. viii + 1140 pp., 203 pls.
- Sellier, R. 1973.** Recherches en microscopie électronique par balayage sur l'ultrastructure de l'appareil androconial alaire dans le genre *Argynnis* et dans les genres voisins (Lep. Rhopalocères Nymphalidae). Annales de la Société Entomologique de France 9:703-728.
- Sette, O. E. 1962.** Variation in the silvering of *Argynnis* (*Speyeria*) *callippe* in the interior mountain area of south central California. Journal of Research on the Lepidoptera 1: 3-20.
- Shapiro, A. M. 1996.** Status of butterflies. Sierra Nevada Ecosystem Project: Final report to congress, Vol. 2, assessments and scientific basis for management options. Davis: University of California, Centers for Water and Wildland Resources. pp. 743-757.
- Shapiro, A. M. 2002.** Species concepts and conservation law: why we have a problem. News of the Lepidopterists' Society 44: 124-131.
- Shapiro, A. M. and A. R. Shapiro. 1973.** The ecological associations of the butterflies of Staten Island. Journal of Research on the Lepidoptera 12: 65-128.
- Shepherd, S. and D. M. Debinski. 2005.** Reintroduction of regal fritillary (*Speyeria idalia*) to a restored prairie. Ecological Restoration 23: 244-250.
- Shields, O. 1963.** A trip to California and Oregon for *Speyeria*. Journal of the Lepidopterists' Society 17: 111- 116.

- Shields, O. 1966.** The butterfly fauna of a yellow pine forest community. *Journal of Research on the Lepidoptera* 5: 127-128.
- Shields, O., J. F. Emmel, and D. E. Breedlove. 1970.** Butterfly larval foodplant records and a procedure for reporting foodplants. *Journal of Research on the Lepidoptera* 8: 21-36.
- Shields, O. and J. F. Emmel. 1973.** A review of carrying behavior and mating times in butterflies. *Journal of Research on the Lepidoptera* 12: 25-64.
- Shirôzu, T. and T. Saigusa. 1973.** A generic classification of the genus *Argynnis* and its allied genera (Lepidoptera: Nymphalidae). *Sieboldia* 4: 99-114.
- Shuey, J. A., E. H. Metzler, D. C. Iftner, J. V. Calhoun, J. W. Peacock, R. A. Watkins, J. D. Hooper, and W. F. Babcock. 1987.** Status and habitats of potentially endangered Lepidoptera in Ohio. *Journal of the Lepidopterists' Society* 41: 1-12.
- Shull, E. M. and F. S. Badger. 1972.** Annotated list of the butterflies of Indiana. *Journal of the Lepidopterists' Society* 26: 13-24.
- Shull, E. M. 1987.** Butterflies of Indiana. Indiana Academy of Sciences, Indianapolis, Indiana.
- Simmons, R. S. 1963.** Nine new butterfly records for the State of Maryland. *Journal of the Lepidopterists' Society* 17: 107-109.
- Simon, C., F. Frati, A. Beckenbach, B. Crespi, H. Liu, and P. Flook. 1994.** Evolution, weighting, and phylogenetic utility of mitochondrial gene sequences and a compilation of conserved polymerase chain reaction primers. *Annals of the Entomological Society of America* 87: 651-701.
- Simonsen, T. J. 2004.** Fritillary Butterflies: Phylogeny, Historical Zoogeography and Morphological Aspects of the Tribus Argynnini (Lepidoptera: Nymphalidae). Ph.D. Dissertation, Zoological Museum, University of Copenhagen. 196 pp.
- Simonsen, T. J. 2005.** *Boloria* phylogeny (Lepidoptera: Nymphalidae): tentatively reconstructed on the basis of male and female genitalic morphology. *Systematic Entomology* 30: 653-665.
- Simonsen, T. J. 2006a.** Glands, muscles and genitalia. Morphological and phylogenetic implications of histological characters in the male genitalia of fritillary butterflies (Lepidoptera: Nymphalidae: Argynnini). *Zoologica Scripta* 35: 231-241.
- Simonsen, T. J. 2006b.** The male genitalia segments in fritillary butterflies: Comparative morphology with special reference to the "rectal plate" in *Issoria* (Lepidoptera: Nymphalidae). *European Journal of Entomology* 103: 425-432.
- Simonsen, T. J. 2006c.** Fritillary phylogeny, classification, and larval hostplants: reconstructed mainly on the basis of male and female genitalic morphology (Lepidoptera: Nymphalidae: Argynnini). *Biological Journal of the Linnean Society* 89: 627-673.

- Simonsen, T. J., N. Wahlberg, A. Z. Brower, and R. de Jong 2006.** Morphology, molecules and fritillaries: Approaching a stable phylogeny for Argynnini (Lepidoptera: Nymphalidae). *Insect Systematics and Evolution* 37: 405-418.
- Simonson, S. E., P. A. Opler, T. J. Stohlgren, and G. W. Chong. 2001.** Rapid assessment of butterfly diversity in a montane landscape. *Biodiversity and Conservation* 10: 1369-1386.
- Sims, S.R. 1984.** Reproductive diapause in *Speyeria* (Lepidoptera: Nymphalidae). *Journal of Research on the Lepidoptera* 23: 211-216.
- Sims, S. R., Brittnacher, J. G., and F. J. Ayala. 1979.** Genetic confirmation of the specific status of the *Speyeria adiastra* group in California (Lepidoptera: Nymphalidae). *Pan-Pacific Entomologist* 55: 111-116.
- Skinner, H. 1917.** New species of Lepidoptera. *Entomological News* 28: 328-329.
- Smart, P. 1989.** *The Illustrated Encyclopedia of the Butterflies of the World*. Salamander Books Limited, Bedford Row, London.
- Snyder, A. J. 1896.** Some argynnids of Park City, Utah. *The Canadian Entomologist* 28: 105-107.
- Snyder, A. J. 1900.** The Argynnids of North America. pp. 27-38. *In* J. L. Hancock and O. S. Westcott [Eds.], *Occasional Memoirs of the Chicago Entomological Society Volume 1*, Chicago Entomological Society, Chicago, Illinois.
- Soltis, P. S. and M. A. Gitzendanner. 1999.** Molecular systematics and the conservation of rare species. *Conservation Biology* 13: 471-483.
- Sokal, R. R. and T. J. Crovello. 1970.** The biological species concept: a critical evaluation. *The American Naturalist* 104: 127-153.
- Sperling, F. 2003.** DNA barcoding: dues ex machina. *Newsletter of the Biological Survey of Canada (Terrestrial Arthropods)* 22. 4 pp.
- Sperling, F. A. H. and D. A. Hickey. 1995.** Amplified mitochondrial DNA as a diagnostic marker for species of conifer-feeding *Choristoneura* (Lepidoptera: Tortricidae). *The Canadian Entomologist* 127: 277-288.
- Stehr, F. W. [Ed.] 1987.** *Immature Insects, Vol. 1*. Kendall/Hunt Publishing Company, Dubuque, Iowa. 754 pp.
- Stewart, B, P. Brodtkin, and H. Brodtkin. 2001.** *Butterflies of Arizona: A Photographic Guide*. West Coast Lady Press, Arcata, California.

- Strecker, 1878.** Butterflies and Moths of North America, with Full Instructions for Collecting, Breeding, Preparing, Classifying, Packing for Shipment, etc., A Complete Synonymical Catalogue of Macrolepidoptera, with a Full Bibliography, which is added a Glossary of Terms and an Alphabetical and Descriptive List of Localities. Reading, Pennsylvania. I-ii + 282 pp., 2 pls.
- Strehl, C. P. and J. Gadau. 2004.** Cladistic analysis of paleo-island populations of the Florida harvester ant (Hymenoptera: Formicidae) based upon divergence of mitochondrial DNA sequences. *Florida Entomologist* 87: 576-581.
- Süffert, F. 1927.** Zur vergleichende analyse der Schmetterlingszeichnung. *Biologisches Zentralblatt* 47: 385-413.
- Swengel, A. B. 1993.** Regal fritillary: Prairie royalty. *American Butterflies* 1: 4-9.
- Swengel, A. B. 1997.** Habitat associations of sympatric violet-feeding fritillaries (*Euptoieta*, *Speyeria*, *Boloria*) (Lepidoptera: Nymphalidae) in tallgrass prairie. *The Great Lakes Entomologist* 30: 1-18.
- Swengel, A. B. 2004.** Good news for regal fritillaries. *Wisconsin Entomological Newsletter* June: 3-4.
- Swengel, A. B. and S. R. Swengel. 2001.** A ten-year study to monitor populations of the regal fritillary, *Speyeria idalia*, (Lepidoptera: Nymphalidae) in Wisconsin, U.S.A. *The Great Lakes Entomologist* 34: 97-115.
- Swofford, D. L. 2002.** PAUP, Version 4.0b10. Sunderland, Massachusetts. Sinauer.
- Tebaldi, A. F. 1982.** Genetic and Morphological Variation in Three Phenotypes of the Rocky Mountain Butterfly *Speyeria atlantis*. Master's Thesis, University of Wyoming, Laramie. 51 pp.
- Templeton, A. R., E. Routman, and C. A. Phillips. 1995.** Separating population structure from population history: a cladistic analysis of the geographical distribution of mitochondrial DNA haplotypes in the tiger salamander, *Ambystoma tigrinum*. 140: 767-782.
- The International Lepidoptera Survey. 2007.** Standardized Common North American Butterfly Names. (<http://tils-ttr.org/sc-nabn/index.html>) (Last accessed September 2007).
- The Nymphalidae Systematics Group. 2007.** (<http://nymphalidae.utu.fi/index.htm>) (Last accessed September 2007).
- Thomas, J. A. 1984.** The conservation of butterflies in temperate countries: past efforts and lessons for the future. pp. 333-353. *In* R. I. Vane-Wright and P. R. Ackery (eds.), *The biology of butterflies: symposium of the royal entomological society of London*, number 11. Academic Press, London.



- Threatful, D. L. 1988 (1989).** A list of the butterflies and skippers of Mount Revelstoke and Glacier National Parks, British Columbia, Canada (Lepidoptera). *Journal of Research on the Lepidoptera* 27: 213-221.
- Tietz, H. M. 1952.** The Lepidoptera of Pennsylvania: a manual. The Pennsylvania State College School of Agriculture Agricultural Experiment Station, State College, PA.
- Tietz, H. M. 1972.** An index to the described life histories, early stages and hosts of the macrolepidoptera of the continental United States and Canada. The Allyn Museum of Entomology, Sarasota, FL. 2 vols. 1-536; 537-1041 pp.
- Tilden, J. W. 1963.** The *Argynnis* populations of the Sand Creek Area, Klamath Co., Oregon. *Journal of Research on the Lepidoptera* 1: 109-113.
- Tilden, J. W. and D. H. Huntzinger. 1977.** The butterflies of Crater Lake National Park, Oregon. *Journal of Research on the Lepidoptera* 16: 176-192.
- Tilden, J. W. and A. C. Smith. 1986.** A Field Guide to Western Butterflies. Houghton Mifflin Company, Boston, MA.
- Toliver, M. E., R. Holland, and S. J. Cary. 2001.** Distribution of Butterflies in New Mexico (Lepidoptera: Hesperioidea and Papilionoidea). Published by R. Holland, Albuquerque, New Mexico.
- Tolman, T. 1997.** Butterflies of Europe. Princeton University Press, Princeton, NJ.
- Tree of Life Web Project. 2007.** *Argynnis*. Simonsen, T., N. Wahlberg, and A. V. Z. Brower. (<http://www.tolweb.org/Argynnini/70206>) (Last accessed September 2007).
- Tuttle, J. P. [Ed.]. 1996-2006.** The Lepidopterists' Society Season Summary. News of the Lepidopterists' Society. Volumes 39-49.
- Tuzov, V. K. 2003.** Nymphalidae part 1: Tribe Argynnnini: *Argynnis*, *Issoria*, *Brenthis*, *Argyreus*. In G. C. Bozano [Ed.], Guide to the Butterflies of the Palearctic Region. Omnes Artes, Milano, Italy.
- Valentine, D. H. 1956.** Variation and polymorphism in *Viola*. *Proceedings of the Royal Society of London . Series B, Biological Sciences* 145: 315-319.
- Vandewoestijne, S., M. Baguette, P. M. Brakefield, and I. J. Saccheri. 2004.** Phylogeography of *Aglais urticae* (Lepidoptera) based on DNA sequences of the mitochondrial COI gene and control region. *Molecular Phylogenetics and Evolution* 31: 630-646.
- Van Son, G. 1955.** A proposal for the restriction of the use of the term subspecies. *The Lepidopterists' News* 9: 1-3.
- Van Regenmortel, M. H. 1997.** Viral species. pp. 17-23. In M. F. Claridge, H. A. Dawah, and M. R. Wilson. *Species: the units of biodiversity*, Chapman and Hall.

- Vaughan, D. M. and M. D. Shepherd. 2005a.** Species profile: *Speyeria diana*. In Shepherd, M. D., D. M. Vaughn and S. H. Black (eds.). Red List of Pollinator Insects of North America. CD-ROM Version 1 (May 2005). Portland, Oregon: The Xerces Society for Invertebrate Conservation.
- Vaughan, D. M. and M. D. Shepherd. 2005b.** Species profile: *Speyeria idalia*. In Shepherd, M. D., D. M. Vaughn and S. H. Black (eds.). Red List of Pollinator Insects of North America. CD-ROM Version 1 (May 2005). Portland, Oregon: The Xerces Society for Invertebrate Conservation.
- Vogler, A. P., R. Desalle, T. Assmann, C. B. Knisley, and T. D. Schultz. 1993.** Molecular population genetics of the endangered tiger beetle *Cicindela dorsalis* (Coleoptera: Cicindelidae). *Annals of the Entomological Society of America* 86: 142-152. .
- Wagner, D. 1995.** Rearing regals for reintroduction: playing the odds but still losing ground. *American Butterflies* 3: 19-23.
- Wagner, D. L. 2005.** Caterpillars of Eastern North America. Princeton University Press, Princeton, New Jersey.
- Wahlberg, N., M. F. Braby, A. V. Z. Brower, R. deJong, M. Lee, S. Nylin, N. E. Pierce, F. A. H. Sperling, R. Vila, A. D. Warren, and E. Zakharov. 2005.** Synergistic effects of combining morphological and molecular data in resolving the phylogeny of butterflies and skippers. *Proceedings of the Royal Society B* 272: 1577-1586.
- Wahlberg, N., R. Oliveira, and J. A. Scott. 2003a.** Phylogenetic relationships of *Phyciodes* butterfly species (Lepidoptera: Nymphalidae): complex mtDNA variation and species delimitations. *Systematic Entomology* 28: 257-273.
- Wahlberg, N., E. Weingartner, and S. Nylin. 2003b.** Towards a better understanding of the higher systematics of Nymphalidae (Lepidoptera: Papilionoidea). *Molecular Phylogenetics and Evolution* 28: 473-484.
- Wahlberg, N. and M. Zimmerman. 2000.** Pattern of phylogenetic relationships among members of the tribe Melitaeini (Lepidoptera: Nymphalidae) inferred from mitochondrial DNA sequences. *Cladistics* 16: 347-363.
- Warren, A. D. 2005.** Lepidoptera of North America Vol. 6: Butterflies of Oregon their taxonomy, distribution, and biology. Contributions of the C. P. Gillette Museum of Arthropod Diversity, Colorado State University, Fort Collins, CO.
- Warren, B. C. S. 1944.** Review of the classification of the Argynnidi: With a systematic revision of the genus *Boloria* (Lepidoptera; Nymphalidae). *Transactions of the Royal Entomological Society of London* 94: 1-101.
- Warren, B. C. S., C. F. dos Passos, and L. P. Grey. 1946.** Supplementary notes on the classification of Argynninae (Lepidoptera, Nymphalidae). *Proceedings of the Royal Entomological Society London B* 15: 71-73.

- Warren, B. C. S. 1955.** A review of the classification of the subfamily Argynninae. Part 2. Definitions of the Asiatic genera. Transactions of the Royal Entomological Society of London 107: 381-392.
- Warren, M. S., J. K. Hill, J. A. Thomas, J. Asher, R. Fox, B. Huntley, D. B. Roy, M. G. Telfer, S. Jeffcoate, P. Harding, G. Jeffcoate, S. G. Willis, J. N. Greatorex-Davies, D. Moss, and C. D. Thomas. 2001.** Rapid responses of British butterflies to opposing forces of climate and habitat change. Nature 414: 65-69.
- Weiss, S. B., D. D. Murphy, and R.R. White. 1988.** Sun, slope, and butterflies: topographic determinants of habitat quality for *Euphydryas editha*. Ecology 69: 1486-1496.
- Wells, P. V. 1983.** Paleobiogeography of montane islands in the Great Basin since the last glaciopluvial. Ecological Monographs 53: 341-382.
- Wheeler, Q. D. 2003.** Transforming taxonomy. The Systematist 22: 3-5.
- Wiley, E. O. 1978.** The evolutionary species concept reconsidered. Systematic Zoology 27:17-26.
- Will, K. W. and D. Rubinoff. 2004.** Myth of the molecule: DNA barcodes for species cannot replace morphology for identification and classification. Cladistics 20: 47-55.
- Williams, B. L. 1999.** Regal fritillaries in a tailspin: A story of East and West, DNA, and the urgent need for the conservation of a flagship species. American Butterflies 7: 16-25.
- Williams, B. E. [L.] 2001a.** Recognition of western populations of *Speyeria idalia* (Nymphalidae) as a new subspecies. Journal of the Lepidopterists' Society 55: 144-149.
- Williams, B. L. 2001b.** The evolutionary history and conservation of *Speyeria idalia* (Lepidoptera: Nymphalidae). Ph.D. Dissertation, University of Illinois at Urbana-Champaign.
- Williams, B. L. 2001c.** Patterns of morphological variation in *Speyeria idalia* (Lepidoptera: Nymphalidae) with implications for taxonomy and conservation. Annals of the Entomological Society of America 94: 239-243.
- Williams, B. L. 2002.** Conservation genetics, extinction, and taxonomic status: A case history of the regal fritillary. Extinction and Taxonomy 16: 148-157.
- Williams, B. L., J. D. Brawn, and K. N. Paige. 2002.** Highly polymorphic microsatellite loci for *Speyeria idalia* (Lepidoptera: Nymphalidae). Molecular Ecology Notes 2: 87-88.
- Williams, B. L., J. D. Brawn, and K. N. Paige. 2003.** Landscape and genetic effects of habitat fragmentation on a high gene flow species: *Speyeria idalia* (Nymphalidae). Molecular Ecology 12: 11-20.

- Wilkinson, R. S. 1988a.** Cyril Franklin Dos Passos (1887-1986). *Journal of the Lepidopterists' Society* 42: 155-163.
- Wilkinson, R. S. 1988b.** Annotated bibliography of the entomological publications of Cyril F. dos Passos (1887-1986). *Journal of the Lepidopterists' Society* 42: 168-183.
- Wilson, E. O. 1999.** *The Diversity of Life*. W. W. Norton and Company, New York, New York.
- Wilson, E. O. and W. L. Brown, Jr. 1953.** The subspecies concept and its taxonomic application. *Systematic Zoology* 2: 97-111.
- Winston, J. E. 1999.** *Describing species: practical taxonomic procedure for biologists*. Columbia University Press, New York, New York.
- Woese, C. R. 2004.** A new biology for a new century. *Microbiology and Molecular Biology Reviews* 68: 173-186..
- Yang, Z. and A. D. Yoder. 2003.** Comparison of Likelihood and Bayesian methods for estimating divergence times using multiple gene loci and calibration points, with application to a radiation of cute-looking mouse lemur species. *Systematic Biology* 52: 705-716.
- Zaspel, J. M. and S. J. Weller. 2006.** Review of generic limits of the tiger moth genera *Virbia* Walker and *Holomelina* Herrich-Schäffer (Lepidoptera: Arctiidae: Arctiinae) and their biogeography. *Zootaxa* 1159: 1-68.
- Zimmerman, M., N. Wahlberg, and H. Descimon. 2000.** Phylogeny of *Euphydryas* checkerspot butterflies (Lepidoptera: Nymphalidae) based on mitochondrial DNA sequence data. *Annals of the Entomological Society of America* 93: 347-355.
- Zirlin, H. 1996.** Taxonomists just wanna have fun! Silver spangled goddesses. Part 1.

## BIOGRAPHICAL SKETCH

James Christopher Dunford was born in 1969 in Libertyville, Illinois. He is a graduate of Wilmot Union High School in Wilmot, Wisconsin. James earned a Bachelor of Arts degree in biology from the University of Wisconsin-Milwaukee in 1996 and a Master of Science degree in 2000 at the University of Wisconsin-Madison in entomology under the guidance of Dr. Daniel Young. During his master's research, he worked for The Nature Conservancy in Madison, Wisconsin. Upon completion of his master's degree, he worked as a curator at the Milwaukee Public Museum before accepting a teaching assistantship and eventually a research assistantship to pursue a Doctor of Philosophy at the University of Florida. In 2001, he began a research project on *Speyeria* butterflies under the guidance of Drs. Lee and Jacqueline Miller, Thomas Emmel, James Maruniak, Carla Penz, Jon Reiskind, John Heppner and Paul Goldstein. He has received national and University of Florida teaching awards, and was a recipient of the Health Services Collegiate Scholarship from the United States Navy in 2004. Upon graduation in December 2007, James will be commissioned as a Lieutenant in the U.S. Navy and serve in the medical service corps as an entomologist.