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## STUDIES IN THE LYCAENINAE (LYCAENIDAE)

### 2. Taxonomy and Evolution of the Nearctic *Lycaena rubidus* Complex, With Description of a New Species

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Editor's Note: This paper is the second in a series on the Lycaeninae. The first paper in this series was by C. D. Ferris on *Lycaena phlaeas* (Bull. Allyn Mus., 18, 1974). In future numbers of the *Bulletin* additional papers by various authors will be published as part of the series.

#### Introduction

*Lycaena rubidus* (Behr), the "Ruddy Copper", is one of the most familiar "copper butterflies" of western North America. Its populations extend from the plains of Nebraska westward to the Pacific Ocean and form disjunct distributions in southern Arizona and California north to prairies adjacent the Rocky Mountains of Alberta. The butterfly larvae feed on *Rumex* and *Oxyria* species (Polygonaceae), plants characterizing grassland environs widely divergent in altitudinal and general ecological affinity. Populations of the species being distributed throughout many of these habitats, environmental and historical influences on its evolution have been diverse.

Our goal in this paper is to present a dynamic view of variation, divergence, and radiation in the *L. rubidus* complex and at the same time provide a taxonomic revision of the group with traditional taxonomic categories applied in a realistic, consistent, and useful manner.

The revision of any group can result not only in changes of nomenclature, but discovery of errors in concepts about a group's taxonomy. In *L. rubidus* this research has resulted in changing the usages of some of the most familiar names to North American lepidopterists. These situations should be introduced clearly at the beginning.

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Behr named *Chrysophanus rubidus* in 1866, type series "one ♂" from the "interior of Oregon." After Behr's career as director of the California Academy of Science, his collection was deposited there (San Francisco *Chronicle*, 1926; Essig, 1931; P. H. Arnaud, Jr. and F. M. Brown, pers. com.). This collection was destroyed in the 1906 earthquake and fire (Brown, 1969; P. H. Arnaud, Jr. and F. M. Brown, pers. com.). Unfortunately, no source is available to confirm if Behr labelled his primary type. It is known that he possessed a series of specimens labelled *rubidus* from the "interior of Oregon" (Brown, 1969; and pers. com.). Brown located two of these in the Carnegie Museum of Natural History in Pittsburgh, Pennsylvania. Miller located two males in the Strecker collection at the Field Museum in Chicago, Illinois (L. D. Miller, Pers. Comm.). None of these bears the designation as primary type. Cottle (1926) mentions Behr's peculiar habits in coveting valuable specimens and not allowing other professionals to see them. The Carnegie Museum apparently received the two Behr specimens through exchanges of material Behr made with W. H. Edwards (Brown and Downey, 1970, F. M. Brown and L. D. Miller, pers. comm.). Strecker's collection is at Field Museum, W. H. Edwards' at the Carnegie (Brown, 1969). From Brown's conclusion that the two specimens in the Carnegie Museum and the two males at the Field Museum represent the only remaining Behr individuals (Brown, 1969), and the other information just reviewed, we are assuming that the type referred to in Behr's description is lost and a neotype must be designated. We use one of his remaining specimens for this designation.

Prior to the present revision, the usage of the name *rubidus* has not been based Behr's description, any record of the characters of his original type, or his remaining specimens in Pittsburgh or Chicago. Instead, it has been used from common knowledge of the wing characters of the species on the North American west coast, particularly California. Consequently, up to the present time the nominate designation *rubidus rubidus* has been used for the entire generally lowland and non-melanic distribution of *rubidus* in the Nearctic. One other subspecies, characteristically melanic (*sirius* W. Edwards), was designated and became used for montane populations in the Rocky Mountains. Research in the present study indicates that this view, notwithstanding particular difficulties with the type material mentioned above, is entirely incompatible with real relationships within the group. Study of the two Behr specimens from which a neotype for the name *rubidus* is designated in this paper, along with present-day representatives from the region, shows that the nominate subspecies designation applies to only one melanic subspecies of limited range. Secondly, this study shows that the major segregations warranting subspecific status in the complex come from two basic origins: populations not influenced by the continental glaciations of the Pleistocene, which are generally non-melanic, and presently disjunct populations which evolved melanic morphs in apparent relationship to these geologic events. Those in the latter category which evolved around the distributions of the continental glaciers are called "periglacially evolved melanics" in this paper. The nominate subspecies represents one of these.

The availability of a name for the vast array of generally lowland populations formerly viewed as the nominate subspecies is further complicated by the situation in the montane melanic strains traditionally called *r. sirius*. These Rocky Mountain populations evolved melanic strains in apparent relation to montane glaciations of the Pleistocene. In some cases they are known to feed on *Oxyria*, not *Rumex*. However, the nature of their present population structure and the post-glacial pattern of physiographic and phytogeographic change in the area makes it impossible (as explained in detail later) to apply a subspecific category to them that is consistent with the others applied in this paper and is definable in a way usable to the taxonomist. If *Oxyria*-feeding populations were able to be defined as a subspecies, there is no evidence that the types of *sirius* are from an *Oxyria*-feeding population. In fact, the elevation of the type locality is too low for the reported occurrence of the plant. Since the name *sirius* is not recognized in this revision as a subspecies limited to the Rocky Mountains (as is its common usage) but instead

part of a complicated "stair-step" cline with lowland non-melanic populations, it is the only name available for the populations extending from the Rockies westward to the Sierras of California. Its original description, therefore, actually applies to only one extreme morph at the end of this cline.

The changes in the usages of these two familiar names, along with the designation of a new species from an allopatric population until recently unknown to lepidopterists, or previously considered conspecific with *L. rubidus*, are two of the notable changes in this revision. Other subspecies of *rubidus*, and the new species, have been described according to criteria given in the following section.

### Methods and Materials

As in any group, the *Lycaena rubidus* complex displays many magnitudes of variation. There are aggregates of populations forming homogeneous and allopatric divergences in wing and genitalic characters, and there are aggregates, homogeneously divergent in wing and genitalic characters, which are not allopatric but show minor secondary intergradation. Both of these groups, we feel, represent significant levels of speciation within the complex and warrant subspecific status. Beneath these is a larger array of populations, as a whole sympatric, which by analysis of many traits, evidence widespread gene flow between their populations. These show some divergence in regional wing characters, but little in genitalia. Some workers, viewing only regional samples, might want to give these taxonomic names. However, in the larger view they can be demonstrated as populations with only moderate segregation from the whole group. In this paper, such regional groupings of moderate divergence are called "regional morphs." On another level, less tied to specific regions, are broad clines due to environmental gradations or occasional unique populations isolated in one locality. We call these "environmental morphs" and "isolates" respectively. None of these categories is given a taxonomic name since these are inconsistent with the integrity of populations we have chosen as subspecies. Groupings of local populations we have given subspecific status show allopatry or minor secondary intergradation, major divergence in infraspecific wing and genitalic characters, and are not the same population as others so designated. Those we have chosen not to name are, regardless of moderate isolation or divergence, part of another population.

In *L. rubidus* (as will be discussed later) the rate of divergence has been slower in the males than in the females. Thus, males are ideal for study of basic patterns of segregation and to check these, females can be used as a secondary resource. This is especially true since, as opposed to some other Lycaenidae, male genitalia are useful infraspecifically in the group and female genitalia are not. The degree of variation in the females also allows a finer analysis of relationships in populations which show minor but still consistent variation in the males. This is important in relationships since distinct male traits seem to disappear more quickly in secondary intergradation than those of females.

In accord with these observations, 530 male specimens in series of 17-33 specimens from 32 composite localities (formed by combining closely related localities among 89 collection sites) were submitted to an analysis of 111 wing characters. Characters of apparent taxonomic significance were selected and these analyzed on available smaller series of 5-11 specimens from 39 additional localities. The total number of males analyzed for the selected traits by these two methods was 767. Then, smaller samples from less collected areas were examined individually and their relationships to the above results ascertained. The total number of males examined by all methods was 1,402 specimens.

In a similar fashion, 33 characters of 189 male genitalia from 55 localities were analyzed.

An analysis of female wing characters by the method used for males was begun but abandoned as redundant. Examination of females was then limited to a study of melanism and the relation of females' traits to specific problems arising

with the males. These placed a check on any erroneous evaluations from the males. The total number of females studied was 749. Also, 189 female genitalia from 55 local populations were studied.

Results were tabulated in the following way. Local populations which showed occurrence of a given trait at the 70% frequency level (or occasionally the 50% level to aid fine separations) were connected on individual maps by a circumscribing line (like an "isotherm"). Maps for all traits were then superimposed to show the relation-

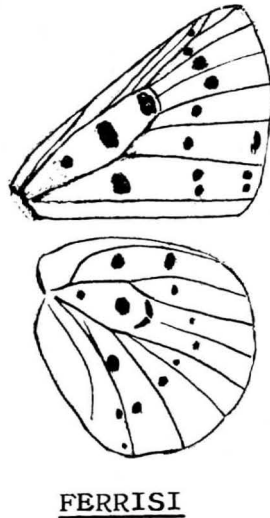
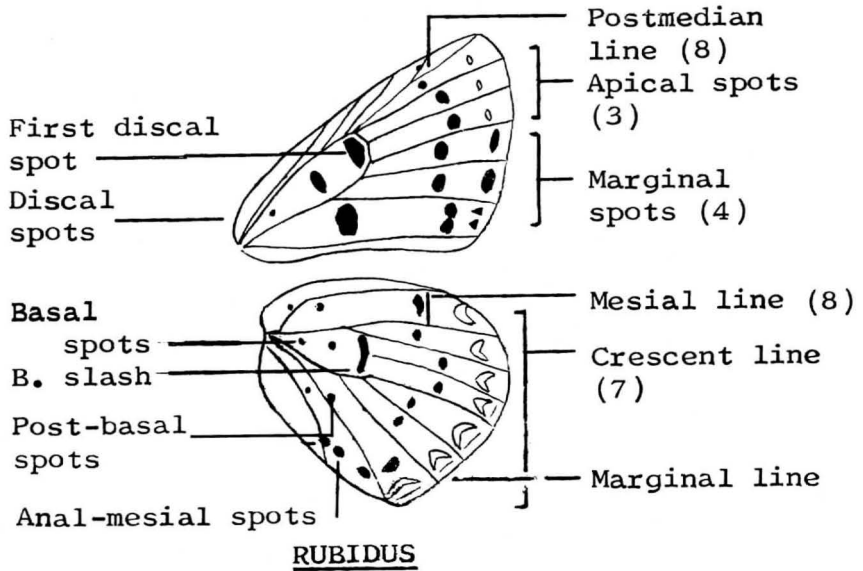


Fig. 1. Wing shape and venation of *L. rubidus* and *ferrisi* showing maximum degree of markings and standardized terms for referring to these.



ships of all the traits. For publication these were stylized to reduce "busyness". In this paper these are called "topographic maps of affinities of characters." Those figured illustrate the affinities of characters describing the major segregations we have called subspecies in the complex, and also show the extent of variation within them. They do not show the relationships between widely separated aggregations in the complex. Since some of these may have once been sympatric, these are discussed in the text. Terminology was standardized for reference to wing traits. These are summarized in Figure 1. Color terms were used from Ridgway (1912) and explained in an appendix for those without access to this source.

Research for this paper was done by both authors and the manuscript prepared by the first. Changes and editing were done by both and those credited in the acknowledgments. Decisions on interpretation and presentation of the data were made by the first author, so inquiries concerning these aspects of the paper best go to him.

Depositions of data comprise 945 pages of trait analysis, notes, tables, and drawings, which are currently deposited at the American Museum of Natural



Fig. 2. Map of the western United States showing number of specimens studied from various localities in the analysis of 111 male characters of the wing (results in Figure 5).

History. Museum or individual depositions of material examined during the study are as follows (with abbreviations used in the text cited):

#### Institutions

Allyn Museum of Entomology (AME)  
 American Museum of Natural History (AMNH)  
 California Academy of Sciences (CAS)  
 Carnegie Museum of Natural History (CMNH)  
 Chadron State College (Nebraska) (CSC)  
 Los Angeles County Museum of Natural History (LACM)  
 Montana State University (MSU)  
 Ohio State University (OSU)

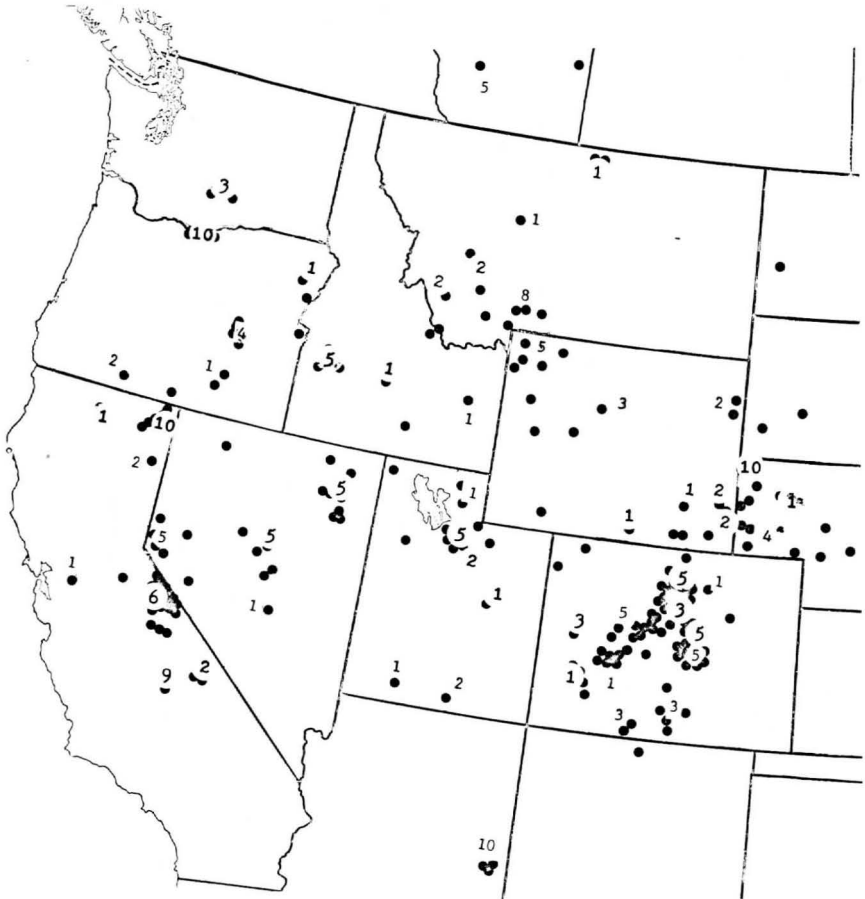


Fig. 3. Map of the western United States showing number of specimens studied from various localities in the analysis of 33 characters of the male genitalia (results in Figure 6). A duplicate sample of female genitalia from each locality was also studied. A few slight differences from Fig. 2 result from later examination of some material in the general study.

United States National Museum of Natural History (USNM)  
 University of California, Berkeley (UCB)  
 University of Montana (UM)  
 University of Nebraska (UN)  
 University of Northern Iowa (UNI)

Individuals

F. Martin Brown (FMB)  
 Clifford D. Ferris (CDF)  
 Kurt Johnson (KJ)  
 Ray E. Stanford (RES)

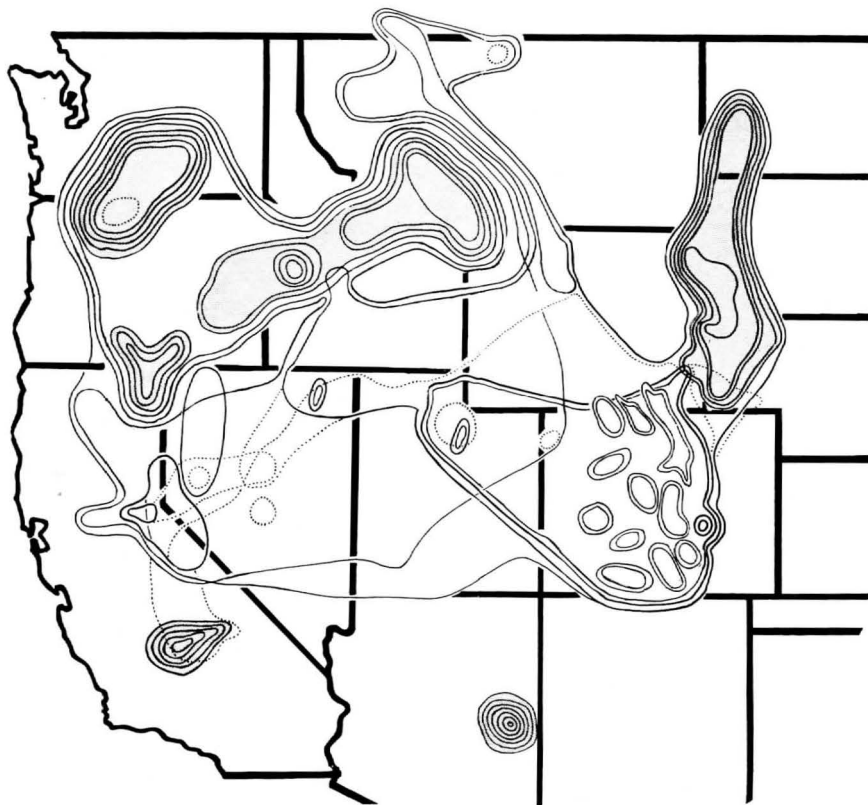


Fig. 4. "Topographic Map of Affinities" of 53 selected male characters of the wing in *rubidus* and *ferrisi* (see Appendix I for list of 53 characters chosen as taxonomically significant from 111 characters of the wing). The map is stylized. Each solid line encloses populations have 2 characters in common at the 70% frequency level. Dotted lines enclose populations with 1 character in common. Overlapping or conjunction of lines indicates intergradation in these characters. Stipled areas represent aggregations of populations sharing many characters. These correspond to taxa described in the paper. It should be noted that though distinct groupings of unique characters are shown for montane Rocky Mountain populations, these are actually clinal with lowland populations.

## Results

The taxonomic descriptions of six subspecies of *rubidus* and one new species hitherto considered conspecific with *rubidus* are presented based on the analysis of data summarized in the following figures. These descriptions are based on a standardization of terminology for characters of the wing presented in Fig. 1 and for the genitalia on the individual genitalic drawings.

The number and locations of individuals studies from specific localities in the analysis of 111 wing traits in 727 male specimens, for both *rubidus* and the new species, are shown in Figure 2. The number of genitalic dissections of males studied from specific localities is shown in Figure 3. The results of the analysis of individuals

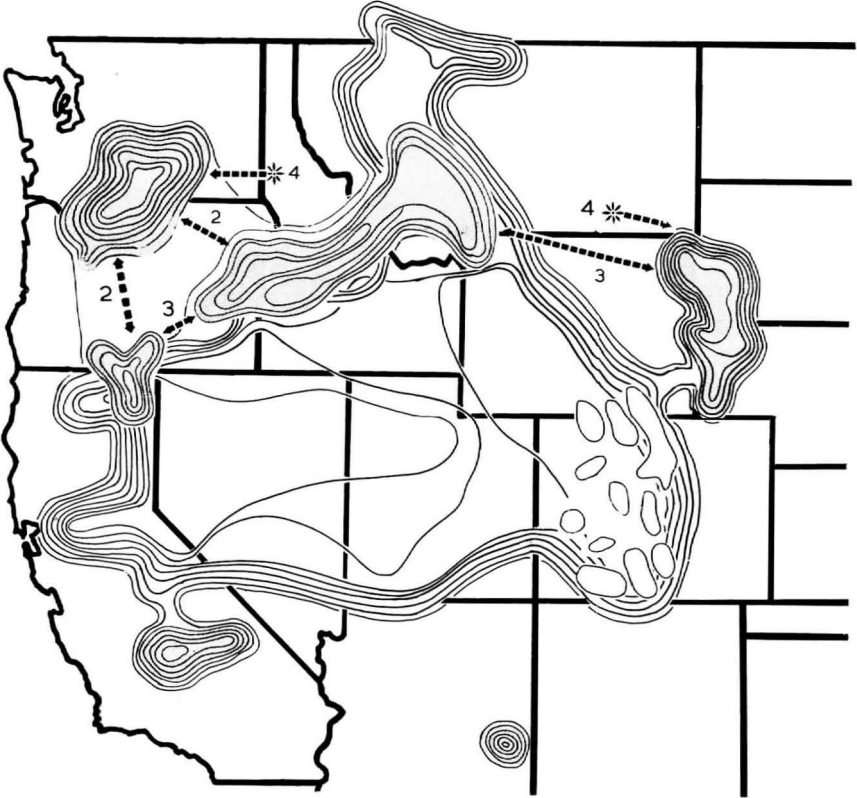


Fig. 5. "Topographic Map of affinities" of 33 selected male characters of the genitalia in *rubidus* and *ferrisi* (see Appendix I for list of 33 characters chosen as taxonomically significant from 47 genitalic characters). The map is stylized. Each solid line encloses populations having 1 character in common at the 70% frequency level. Overlapping of conjunction of lines indicates intergradation in these characters. Stippled areas represent aggregations of populations sharing many characters. These correspond to taxa described in the paper. It should be noted that though distinct groupings of unique characters are shown for montane Rocky Mountain populations, these are actually clinal with lowland populations. The dashed arrows and numbers between widely allopatric populations show the number of characters in common between them. Two of these are joined by an arrow and asterisk (\*).

in Figure 2 are illustrated by the map of affinities of characters presented in Figure 4. The results of investigations of geographic affinities of characters in the male genitalia are shown in Figure 5. The frequencies of degrees of melanism in the females are illustrated in Figure 6. The degree of melanism related to altitude for specimens with exact altitudinal data is given in Figure 7. The distributions of the subspecies of the *rubidus* complex in relation to montane and lowland areas of the Nearctic are shown in Figure 8. A diagrammatic illustration of the location of "horizontal" and "vertical" variation in the group is given in Figure 9. Locations of figures illustrating male and female genitalia for taxa described are given with the particular description. Representative female genitalia of all Nearctic congeners and lateral valval shapes of all of these and the *rubidus* subspecies are presented in Figures 10, 11, 12 and 13 respectively. Figure 14 illustrates the probable evolutionary relationships in the *rubidus* complex and the newly described species. Figure 15 shows the temporal distributions of the taxa described. A brief synopsis of *Rumex* and *Oxyria* in western North America is presented as an Appendix.

*Lycaena rubidus* has been divided into six subspecies meeting the criteria for this category described in the Materials and Methods: they are described below and discussed in a following section. A new species is also described.

### Taxonomic Descriptions

The order for taxonomic descriptions in the *rubidus* complex corresponds with probable phyletic relationships explained in the Discussion and Conclusions and is summarized below with a condensation of distinctive traits for the species and subspecies groups.

#### Diagnostic Trait Groupings for Species and Subspecies

##### Species

- Wing shape as in Fig. 1a. Sexes dimorphic in under surface characters. Forewing, under surface, discal area hardly more orange than rest of wing. hindwing, under surface, lacking very large post-basal spots. Female genitalia, breadth of parabolic lamellae more than half length. Male genitalia, valvae breadth less than one third length, process several toothed. Present subspecies becoming distinct during late Pleistocene..... *L. rubidus*.
- Wing shape as if Fig. 1b. Sexes not dimorphic in under surface characters. Forewing, under surface, discal area always bright orange while costa, apex, margin and also hindwing Drab Grey to brownish. Hindwing, under surface, very large post-basal spots. Female genitalia, breadth of parabolic lamellae less than half length. Male genitalia, valval breadth more than one third length, caudal end curved ventrad, process usually a single large tooth. Pre-Pleistocene isolation from *L. rubidus* ..... *L. ferrisi*.

##### Subspecies Groups of *L. rubidus*

###### "Peri-glacial" Melanics.

Hindwing, under surface, spots in mesial line, anterior one large and dark, rest uniformly lighter; anal-mesial spots present; crescent line usually obvious; forewing, under surface, apical spots usually present. Melanism in females of "flat" coloration. Male genitalia: saccus "toothed", cephalad end of aedeagus "hooked", valval process "bevelled".... *L. r. rubidus*; *L. r. duofacies*; *L. r. longi*;  
*L. r. perkinsorum*.

###### Non-melanics Subspecies with Clinal "Montane-glacial" Melanics.

Hindwing, under surface, spots in mesial line irregular in occurrence and

expression; anal-mesial spots absent; crescent line variously obscured; forewing, under surface, apical spots absent. Melanism, if present in females, of "sheen" coloration. Male genitalia: saccus variously "crowned", cephalad end of aedeagus "knobbed", valval process "tapered".....*L. r. sirius*.

*Other Subspecies.*

Hindwing, under surface, Avallaneous [upper case colors from Ridgway, 1912], with only markings lighter blotches along crescent line and discal slash. Female non-melanic, underside Cinnamon Buff with mesial line located more basally than other subspecies. Forewing, spots most often oblongate. Male genitalia: saccus "rounded", cephalad end of aedeagus nearly without "knob", valval process "scattered".....*L. r. monachensis*.

We follow Opler (*in* Howe, 1975) and include these species in the subgenus *Tharsalea* Scudder.

***Lycaena (Tharsalea) rubidus* (Behr)**

*Chrysophanus rubidus* Behr, 1866, Proc. Ent. Soc. Phil., 6: 208.

*Chrysophanus rubidus* Behr, 1866: 208. Edwards, 1874: t. I, *Chrysophanus*; 1878: 517. Holland, 1898: 255; 1930: 252. Coolidge, 1907: 120.

*Lycaena rubidus*: Kirby, 1871: 345. Strecker, 1874: 92. Barnes and Benjamin, 1926:

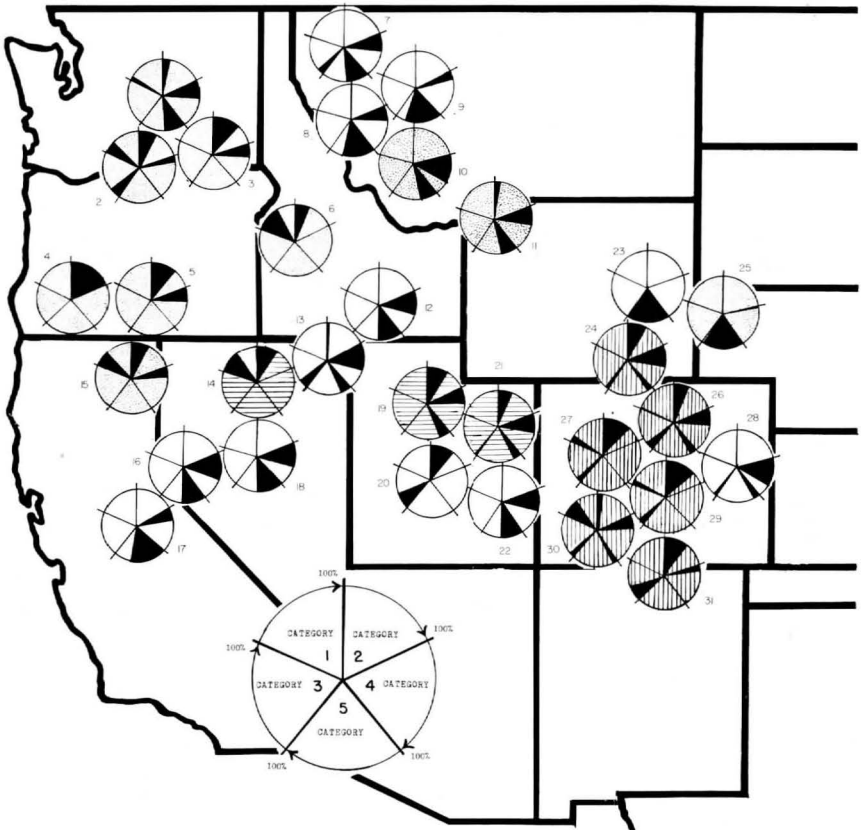
Fig. 6. Map of the western United States illustrating degree of melanism in females in various aggregations of populations (these correspond generally to specimen numbers in Figure 2). Each circle is divided into five sections representing five degrees of melanistic expression. Each section illustrates 1-100% expression of that trait, in clockwise shading (see inset). These categories are: Section 1, upper surface of both wings completely brown-black. Section 2, as in one but streaked with gold or orange. Section 3, as in 1 and 2 but entire patches of forewing gold or orange. Section 4, both wings generally orange with random slight darkening. Section 5, both wings bright immaculate orange. Stippled circles represent periglacially evolved melanics. Vertical hatching represent montane glacially evolved melanics of the Rocky Mountain region, probably of same phyletic origin. Horizontal hatching represents independently evolved montane glacial melanic populations.

The samples are from composites of localities representing similar morphs. These are: 1. Yakima Plateau, Washington. 2. Wasco County, Oregon. 3. Goodnow Hills, Washington. 4. Klamath Basin, Oregon. 5. Lakeview area, Harney County, Oregon. 6. Boise area, Boise County, Idaho. 7. Lethbridge, Alberta. 8. Butte, Montana. 9. Great Falls, Montana. 10. Beaverhead, Gallitan, Madison, Park, and Powell counties, Montana. 11. Yellowstone and Grand Teton Natl. Parks. 12. Sawtooth Natl. Forest, Blaine County, Idaho. 13. Plains around Ruby Mountains, Elko County, Nevada. 14. Montane areas, Ruby Mountains, Elko County, Nevada. 15. Warner Mountains, Modoc County, California. 16. Reno area, Nevada. 17. Mono County, California. 18. Toyable Natl. Forest, Lander County, Nevada. 19. Wasatch Mountains, Utah. 20. Mt. Timpanogos, Utah County, Utah. 21. Uinta Mountains, Utah. 22. Salt Lake City vicinity, Utah. 23. Goshen and Platte counties, Wyoming. 24. Laramie Mountains, Wyoming. 25. Pine Ridge escarpment, Nebraska. 26. northern Front Range, Clear Creek County northward, Colorado. 27. Lake County, Colorado. 28. El Paso and Douglas counties, plains, Colorado. 29. southern Front Range, Park, Teller, and Fremont counties, Colorado. 30. West Elk Mountains, Gunnison County, Colorado. 31. Culebra, Cumbres Ranges, Colorado.

Counties have been given where they help limit or locate sample sites, not where several are included in an area.

15. McDunnough, 1938: 26. Clench (*in* Ehrlich and Ehrlich), 1961: 223.  
*Chalceria rubida* (sic): Scudder, 1876: 126.  
*Chalceria rubidus*: Dyar, 1902: 41.  
*Heodes rubidus*: Barnes and McDunnough, 1917: 15.  
*Lycaena* (*Lycaena*) *rubidus*: dos Passos, 1964: 60.  
*Lycaena* (*Tharsalea*) *rubidus*: Opler (*in* Howe), 1975: 313.

*Diagnosis.* Easily separated from all other previously described congeners by





bright iridescent orange upperside of males, rivaled only by *L. cupreus* (Edwards) which is brighter and has a broad dark marginal border on the upperside of both wings, brightly contrasting and varying ground colors beneath on both wings, and

CATEGORY OF MELANISM

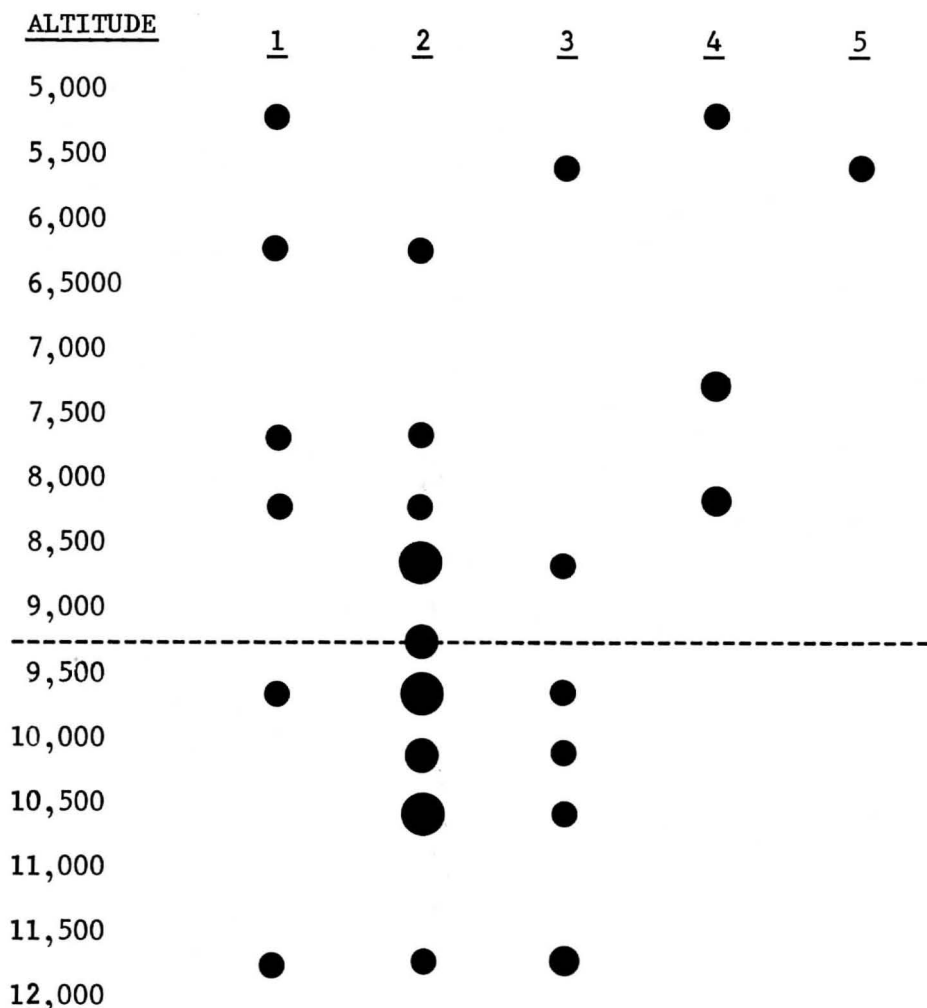


Fig. 7. Relation of melanistic expression in *rubidus* females with present-day altitudes. The categories of melanism are the same as in Figure 6, and are plotted in relation to increasing elevation. Data are from specimens with exact altitude noted on their labels. The dashed line represents the generally lowest elevation for occurrence of *Oxyria digyna*. The size of symbols represents numbers of specimens represented in samples: small circle, 1-6 specimens; medium circle, 7-12 specimens; large circle, 13-18 specimens. Horizontal reading at any altitude gives number of specimens in sample from each altitudinal range displaying particular category of melanism.

more spots basad the mesial line, under surface, hindwings. Female upperside approaches some other *Lycaena* but can be readily separated by undersurface characters cited in the description.

Distinguishable from the new species described in this paper by (1.) the new species' lacking sexual dimorphism of the wing under surfaces, (2.) not having its characteristic wing shape (Fig. 1b), and (3.) lacking its distinct wing characters — under surface, contrasting ground color between discal area, forewing, and its costa, apex, margin, and the hindwing; large spots in the post-basal area.

Easily distinguishable from all Nearctic species by male and female genitalia (Figs. 10, 11, 12, and 13).

*Male.* Upper surface of wings: Bright Xanthine Orange (Ridgway colors upper case) to darker dull copper, usually brighter along margin. Spots in cell, both

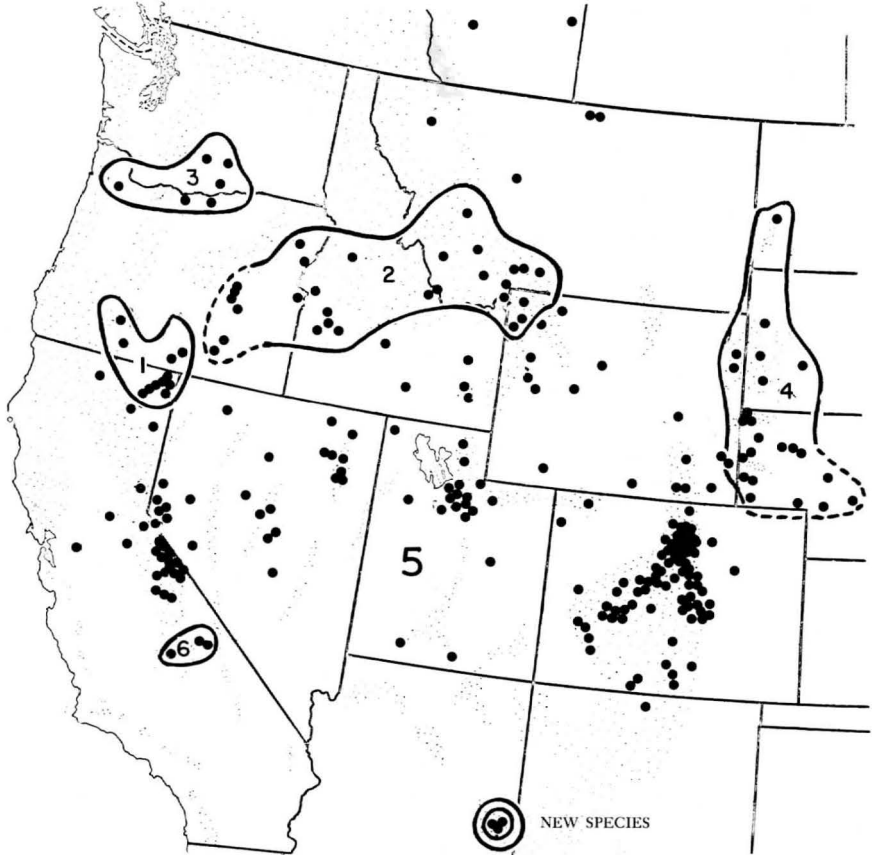


Fig. 8. Map of the western United States showing collection sites of specimens examined in this study. Localities are grouped by enclosing lines representing taxa described in this paper. These are: double lines in Arizona — *L. ferrisi*, new species. Rest — subspecies of *L. rubidus*: enclosed by lines, 1. *L. r. rubidus*; 2. *L. r. duofacies*; 3. *L. r. perkinsorum*; 4. *L. r. longi*; 6. *L. r. monachensis*. Widely distributed *L. r. sirius* is represented by the remaining dots and its cosmopolitan, clinal, distribution symbolized by the enlarged number 5. Lines enclosing local populations representing particular subspecies are dashed where samples indicate infrequent occurrence.

wings, usually black pigmented on upper surface, rest variably visible through from under surface. Under surface of wings: ground color Ochraceous Buff to Avallaneous. Varying from full complement of markings illustrated in Fig. 1a to combinations distinctive of particular subspecies, to completely immaculate.

Length of forewing: Range in all subspecies: 13.0 mm to 19.0 mm.

*Female.* Upper surface of wings: Varying from bright Ochraceous Orange in non-melanic populations to completely Mummy Brown or gold-tinged brown in melanic populations. All spots black pigmented on upper surface. Orange marginal line on both wings except in extremely melanic populations. Under surface of wings: Pale Cream or yellowish, to more olive. All forewing spots (Fig. 1a) expressed, hindwing spots variously expressed or immaculate, depending on the subspecies.

Length of forewing: Range in all subspecies: 14.0 mm to 21.0 mm.

*Male Genitalia.* Fig. 18. Genitalia of the neotype *L. rubidus* (Behr) designated in this paper.

*Female Genitalia.* Fig. 10, genitalia.

*Early Stages.* Undescribed.

*Foodplants.* Long known to feed on *Rumex* species (Brown, Eff, and Rotger, 1957; Ehrlich and Ehrlich, 1961; Ferris, 1971b); little specific information on local or regional foodplants has been published. Four species of *Rumex* are known as foodplants for subspecies described later in this paper. *Oxyria digyna* (L.) is known as a foodplant at high altitudes in one subspecies but the geographic extent of its usage is not known. *Potentilla* has been mentioned by one source as a possible foodplant (Ferris, 1971b).

*Distribution.* On the Great Plains, from southern Alberta south through western North Dakota, South Dakota, and Nebraska to southern Colorado. In the Rocky Mountains, from near Banff, Alberta, south through Montana, Wyoming and Colorado, invading New Mexico only in the Culebra Range. West from there through Idaho, Utah and Nevada, with specimens reported from northern Arizona (San Francisco Peaks). In the west coast states from the Yakima Plateau of Washington south through the Columbia River Basin, and the eastern Oregon plains south through the Klamath Basin into the Sierra Nevada Mountains of California to Mono County. An isolated population in Tulare and Inyo counties and a reported single specimen from Monolith, Kern County (Emmel and Emmel, 1973). From altitudes of 150' to 11,500'.

*Flight Period.* Fig. 15. Single-brooded, varying from mid-May through early July to late June through August.

*Remarks.* When studied in great detail, this species can be divided into six subspecies fitting the criteria for usage of that category given in the Materials and Methods. Montane Colorado populations above 9-9,500' on *Oxyria* could constitute a seventh such category but it is not known exactly how these occur in relation to present altitudes and phytogeographic admixtures (see Remarks under *L. r. sirius* and Discussion). Also, it is not known whether the usage *Oxyria* has also evolved in other high altitude melanic populations (see Remarks under *L. r. sirius*), or whether other high altitude *Rumex* species like *R. pauciflorus* Nutt., *R. occidentalis* Wat., *R. densiflorus* Osterh. or several in the "*R. triangulivalis* group" are also being utilized. Further, no consistent genitalic differences have been found in analysis of *rubidus* at high altitudes in relation to those of more lowland


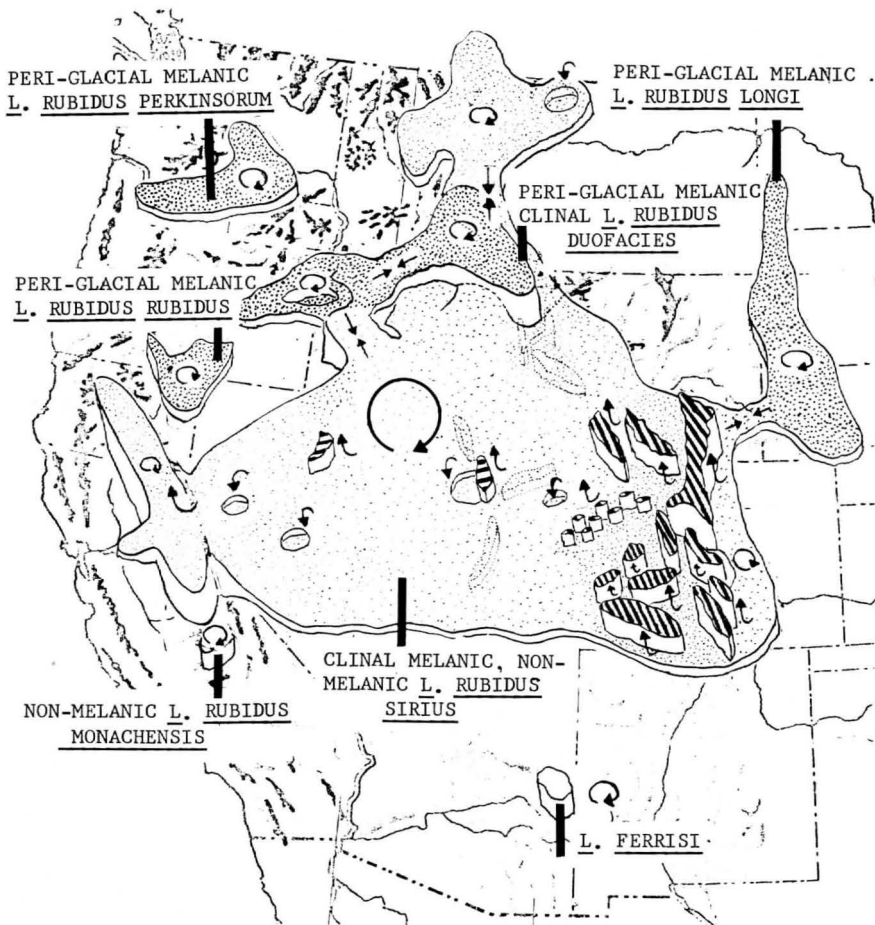






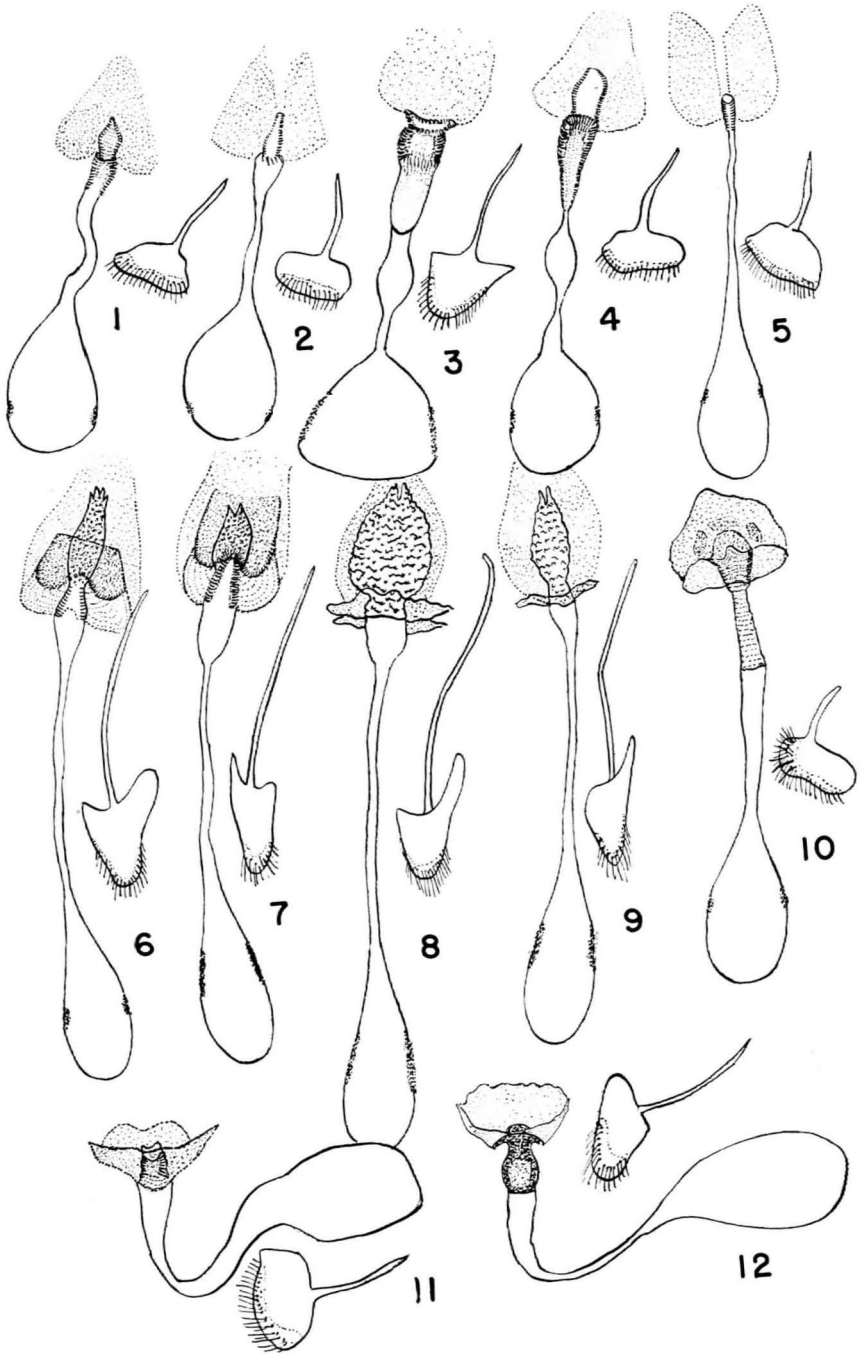
Fig. 9. Diagrammatic illustration of variation in *rubidus* and *ferrisi*. Darkly stippled areas are ranges of peri-glacially evolved subspecies of *rubidus*. Lightly stippled areas represent the range of *L. r. sirius*. Oblique hatching represents areas where montane glacial melanics have evolved in the central in the Colorado and adjoining Rocky Mountains. Horizontal hatching illustrates areas where similar montane melanic morphs have independently evolved. Three dimensional heights show general elevation relationships. Specific symbols are given in the accompanying legend.

areas. Likewise, because of physiographic variation, it is difficult to define any consistent stratification of characters, especially genitalic, which would indicate the presence of two populations regularly separated by altitude across the central Rocky Mountains. Instead, there is as much variation in kinds of divergence from low altitude to high altitude in one mountain range as another, and nothing



VARIATION IN LYCAENA RUBIDUS AND LYCAENA FERRISI

- |  |  |
|--|--|
| <br>WIDESPREAD GENE FLOW<br>WITHIN ONE SEGREGATION<br>RESULTING IN CONSISTENT<br>CHARACTERS | <br>ALTITUDINAL CLINE TO MELANIC<br>MORPH |
| <br>SECONDARY INTERGRADATION  | <br>CLINE TO MESIC MORPH                  |



approaching consistent divergence of traits of the other populations designated as subspecies in this paper. The subspecies of *rubidus* can be organized as follows:

1. Peri-glacially evolved melanic segregations: four populations, mostly allopatric, probably formerly continuous in distribution, and still sharing wing and genitalic traits setting them apart from all other populations of the species.

2. One central population varying from montane glacially evolved melanic populations to regional variations and climatically induced morphs, exhibiting clinal traits in wings and genitalia, but as a group distinct from those above.

3. Unique isolated populations showing distinct divergence of characters of wings and genitalia.

*Etymology.* The word *Lycaena* is from the Greek *Lycaea*. The history of the word is feminine but the usage is now of "common" gender allowing the ending *us* on *rubidus* to stand.

*Subspecies*  
Peri-glacial Melanic Segregations



Fig. 10. Representative female genitalia of Nearctic *Lycaena* species. 1. *L. helloides* (Boisduval); 2. *L. dorcas* Kirby; 3. *L. hyllus* (Cramer); 4. *L. mariposa* Reakirt; 5. *L. nivalis* (Boisduval); 6. *L. xanthoides* (Boisduval); 7. *L. editha* (Mead); 8. *L. rubidus* (Behr); 9. *L. ferrisi*, new species; 10. *L. heteronea* Boisduval; 11. *L. epixanthe* (Boisduval and LeConte); 12. *L. phlaeas* (Linnaeus).

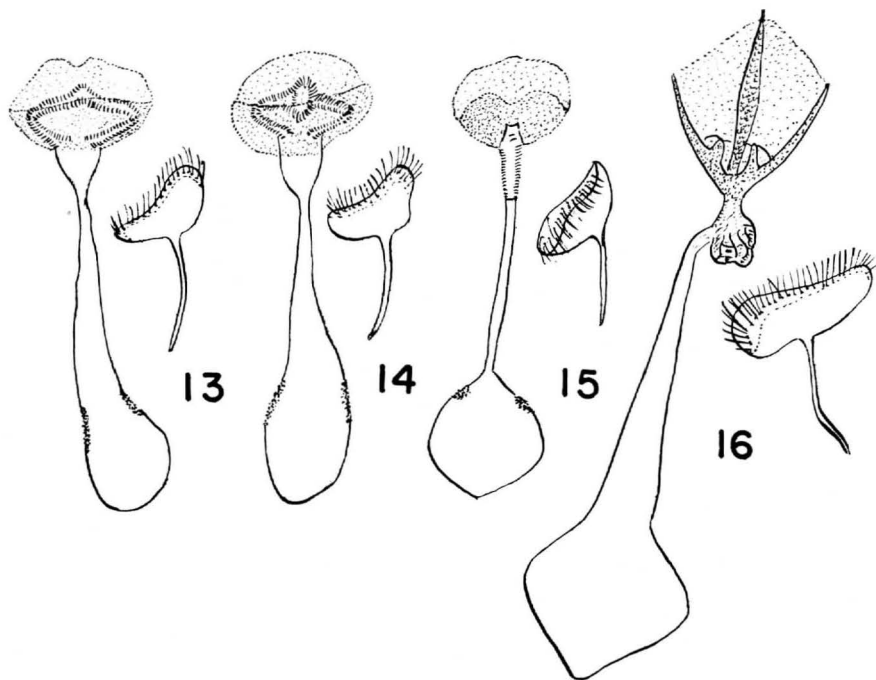


Fig. 11. Representative female genitalia of Nearctic *Lycaena* species, (continued). 13. *L. cupreus snowi* (W. Edwards); 14. *L. cupreus cupreus* (W. Edwards); 15. *L. hermes* (W. Edwards); 16. *L. arota* (Boisduval). *L. gorgon* (Boisduval) was not available for study.

**Lycaena (Tharsalea) rubidus rubidus** (Behr)

Fig. 16, 17, 18; 13f.

*Chrysophanus rubidus* Behr, 1866: 208. Edwards, 1874: t. I, *Chrysophanus*; 1878: 517. Holland, 1898: 255; 1930: 252. Coolidge, 1907: 120.

*Chrysophanus* (sic) *Rubidus* (sic): Wright, 1906: 217.

*Lycaena rubidus*: Kirby, 1871: 345. Strecker, 1874: 92. Leussler, 1938: 277. Clench (in Ehrlich and Ehrlich), 1961: 223. Brown, 1969: 169. Johnson, 1972 (1973): 25, 60.

*Lycaena (Tharsalea) rubidus*: Opler (in Howe), 1975: 313.

*Chalceria rubida* (sic): Scudder, 1896: 126.

*Chalceria rubidus*: Dyar, 1902 (1903): 41.

*Heodes rubidus*: Comstock, 1925: 175, 239.

*Heodes rubidus rubidus*: Barnes and McDunnough, 1917: 15.

*Lycaena rubidus rubidus*: Barnes and Benjamin, 1926: 15. McDunnough, 1938: 26. Brown, Eff and Rotger, 1957: 152.

*Lycaena (Lycaena) rubidus rubidus*: dos Passos, 1964: 60.

*Diagnosis.* Distinguishable from non-melanic populations by high frequency of melanism in the females, and by general traits of peri-glacially evolved morphs, listed below.

Males, hindwing, under surface, mesial line, first spot dark, rest uniformly lighter; white crescent line either present or somewhat evident beneath strong ground coloring (crescents more obvious on females). Characteristic peri-glacial markings more obscured by ground color than on other such subspecies. Females, shade of melanism buff-brown (*i.e.*, Verona Brown), orange extensively invading; bright marginal orange line on hindwing and forewing to vein  $M_1$ . Under surface, ground color bright to whitish, spots obscured. Pale orange marginal line often developed.

Male genitalia distinguishable from non-melanic morphs by "toothed" condition of the saccus; from other peri-glacial subspecies, save one (*L. r. duofacies*), by "elbowed" shape of falces.

*Male.* Upper surface of wings: Bright iridescent Xanthine Orange, with Cadmium Orange margin. Spots visible through from under surface often pigmented black above, especially spot at apex, discal cell. Under surface of wings: Pale Ochraceous to Olive Buff, both wings. Forewing, all spots discal, postmedian, and marginal present; apical spot often present. Hindwing, mesial line complete, first spot darker, rest uniformly lighter, sometimes obscured by ground color but still evident. Discal slash usually vague or gray; crescent line present but not outstanding, usually faintly lighter above ground color. Anal mesial spots usually not present.

Length of forewing: neotype 16.4 mm; range of 20 male specimens, 15.0 mm to 18.0 mm, mean 17.4 mm.

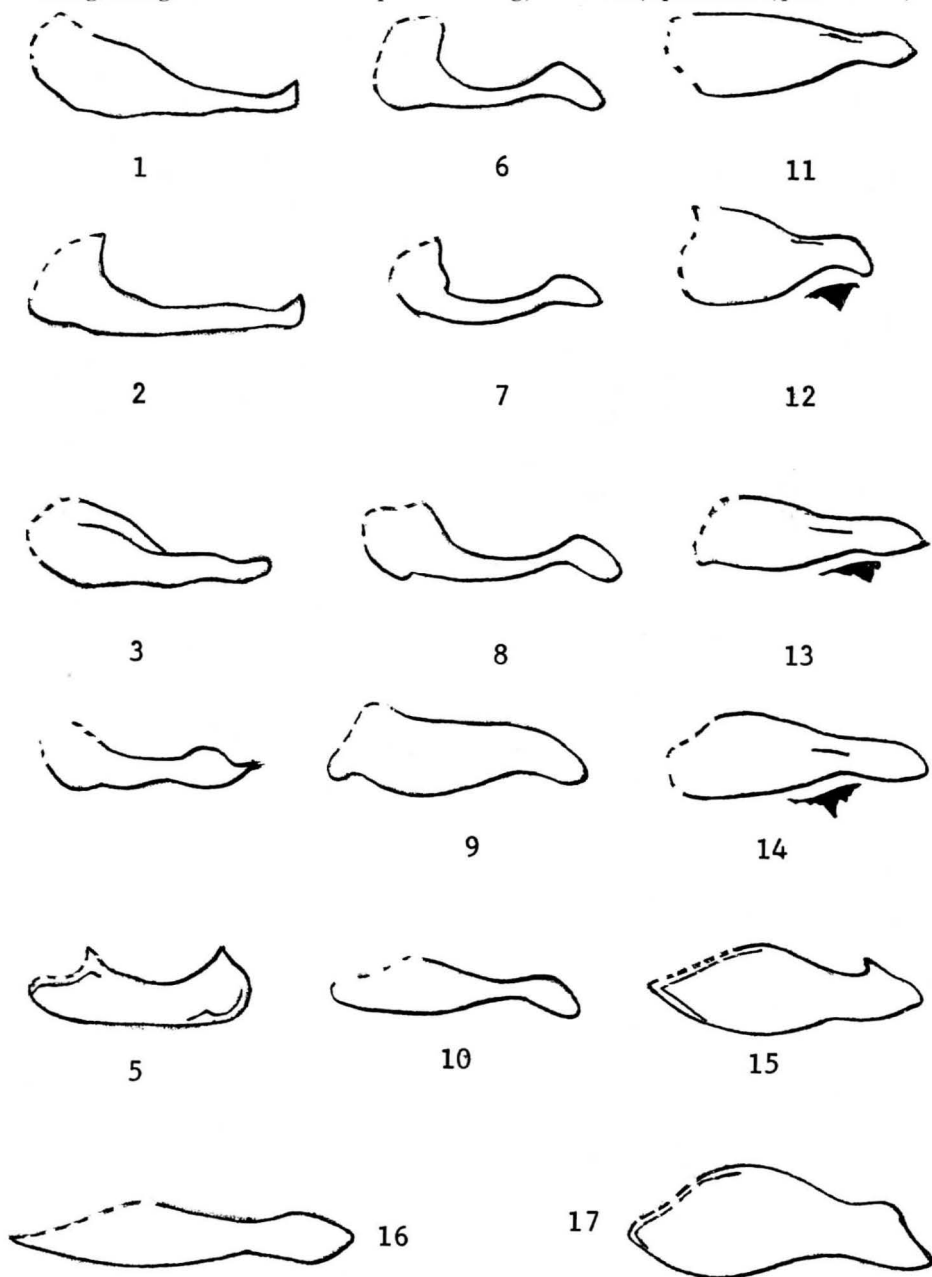
*Female.* Upper surface of wings: Verona Brown, extensive areas of buff especially in discal area of forewing. Orange marginal line pronounced, entire hindwing and forewing to vein  $M_1$ . Under surface of wings: hindwing, ground color,



Fig. 12. Representative male genitalia of Nearctic *Lycaena* species, lateral view of the valvae. Drawn from lateral aspect with ventral surface of valvae perpendicular to viewer. 1. *L. heteronea*; 2. *L. nivalis*; 3. *L. gorgon*; 4. *L. epixanthe*; 5. *L. phlaeas*; 6. *L. helloides*; 7. *L. dorcas*; 8. *L. mariposa*; 9. *L. hyllus*; 10. *L. hermes*; 11. *L. rubidus*; 12. *L. ferrisi*, new species; 13. *L. editha*; 14. *L. xanthoides*; 15. *L. cupreus cupreus*; 16. *L. arota*; 17. *L. cupreus snowi*. Dotted line represents beginning of cephalad structure of valvae curving behind vinculum. These may or may not have specific structures which are not drawn here. Dark line on *L. xanthoides*, *L. editha*, *L. rubidus* and *L. ferrisi* represent location of valval process, drawn immediately below each representation.



Cartridge Buff, "porcelain" (a condition where heavy smooth scaling makes the ground color appear to shine, as contrasted to appearing "flat" in coloration) in appearance. Hindwing, mesial line, first spot black, rest uniformly lighter gray, discal slash light gray; crescent line white, visible brightly over ground color; orange marginal line well developed. Forewing, Olive Buff, spots discal, postmedian,



marginal, distinct.

Length of forewing: Remaining Behr female 17.2 mm; range of 20 female specimens, 16.0 mm to 19.0 mm, mean 18.1 mm.

*Male Genitalia.* Fig. 18, 14f. Saccus "toothed", lateral shape, valvae, as in species; valval process initial caudal cluster of teeth, then tapering cephalad; cephalad tip, aedeagus, "hooked", uncus, wide; falces, gradually tapered from broad "elbow", ventral "shoulder" often at "elbow."

*Female Genitalia.* Fig. 10. As in the species.

*Early Stages.* Unknown

*Foodplant.* Not specifically known for subspecies.

*Type.* Described from "one ♂" from the "interior of Oregon" by Behr, probably a specimen from the Klamath Basin, from which Behr is known to have had a small series (F. M. Brown, pers. com.). All evidence indicates the primary type<sup>2</sup> was destroyed in the 1906 San Francisco fire. Two of Behr's original series of *rubidus*, a male and a female, survive in the Carnegie Museum of Natural History (Brown, 1969; P. H. Arnaud, Jr., pers. comm.; F. M. Brown, pers. com. and specimens in the Strecker collection, Field Museum of L. D. Miller, pers. comm.) are extant. Our decision is that a neotype designation is warranted as follows. Neotype: The remaining male specimen of *rubidus* originally owned by Behr, now in the collection of the Carnegie Museum of Natural History, bearing the labels "Rubidus ♂/Oreg.", "Collection/W. H. Edwards", "May be a/Syntype of/rubidus Behr/H. K. C[lench] 1972" and "Allyn Museum photo/No. 032776-9/10" and a label in Dr. Lee D. Miller's hand: "neotype of *Chrysophanus rubidus* Behr. Designated by K. Johnson and G. Balogh, 4 July 1976." The neotype and its genitalia (KJ #705) are deposited in the Carnegie Museum. It is illustrated in Fig. 16.

*Distribution.* Warner Mountains of Modoc County, California, east at least to Cedarville, west at least to Alturas, northwest into Klamath Basin to Upper Klamath Lake, east into Lake County, Oregon, at least to Lakeview.

<sup>2</sup>A short note found in the *Entomological News* subsequent to the writing of this paper (Ent. News 7: 261) confirms that Behr kept his primary types but distributed other specimens of his series to Strecker and W. H. Edwards. Strecker listed his material from Behr's original series in Supplement 3 of *Lepidoptera, Rhopaloceres and Heteroceres* on page 22. He does not list specimens of *rubidus*, though his collection contained two males so labeled.

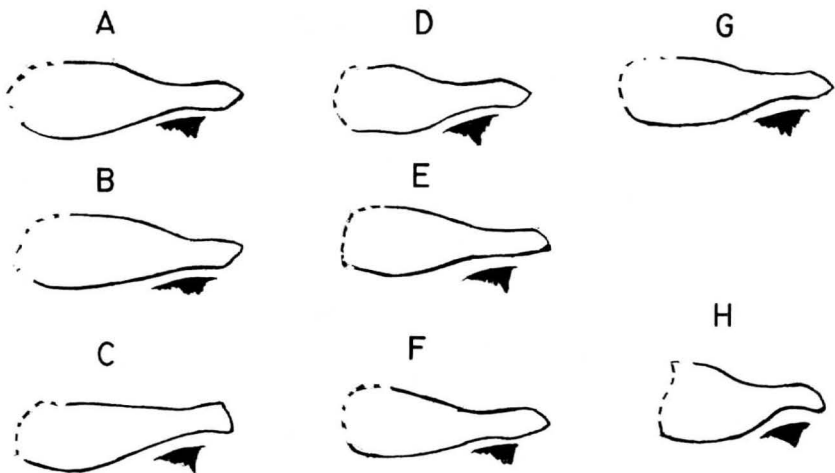


Fig. 13. Lateral view of the valvae in *rubidus* subspecies and *ferrisi*. Drawn and with dotted lines as explained in Fig. 12. The typical shape of the valval process is drawn immediately below each representation.

*Flight Period.* Single-brooded, dates on specimens range from to 28 June to 30 July.

*Remarks.* The original Behr series, probably collected in the Klamath Basin, are from this peri-glacially evolved subspecies. Its present range is probably a relict of formerly continuous distribution with the three other peri-glacial subspecies. Non-melanic females, one represented by Behr's remaining female comprise 23.0% of the population. A representative melanic female characteristic of 77.0% of the population is figured in Fig. 17. The genitalia of *L. r. rubidus* are closest to the next subspecies and both are convergently distributed northeastward and southwestward respectively in scattered localities on the eastern Oregon plains. Other known specimens of *L. r. rubidus* are from Horse Prairie, 5 mi. E. Lakeview, Lake County, Oregon; Klamath Falls, Ft. Klamath, Klamath County, Oregon; Alturas, Buck Creek, 4 mi. E. Canby, Cedarville, Davis Creek, Surprise Valley near Ft. Bidwell, Willow Ranch, Modoc County, California.

We examined 40 males and 30 females of *rubidus*.

***Lycaena (Tharsalea) rubidus duofacies*, new subspecies**

Figs. 19, 20; 13a

*Chrysophanus sirius*: Holland, 1898: 255; 1930: 252.

*Heodes rubidus*: Comstock, 1925: 175.

*Lycaena rubidus*: Clench (in Ehrlich and Ehrlich), 1961: 223.

*Lycaena (Tharsalea) rubidus*: Opler (in Howe), 1975: 313.

*Lycaena rubidus sirius*: Brown, Eff and Rotger, 1957: 152.

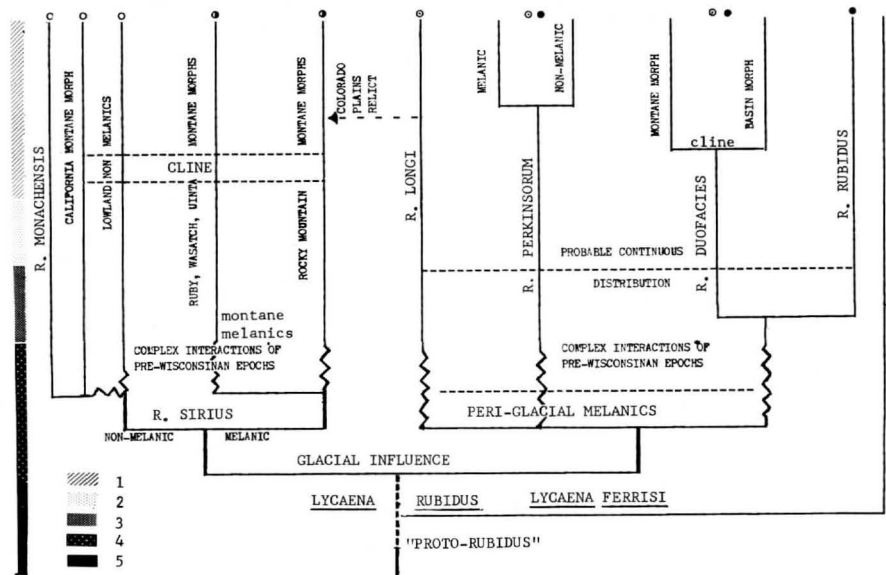


Fig. 14. Probable phyletic relations in the *rubidus* complex, illustrating Pleistocene evolution of *rubidus* subspecies and pre-Pleistocene isolation of *ferrisi*. Small dots at top represent present morphs of *rubidus* subspecies; black dots, melanic morphs of peri-glacial origin; half-black dots, melanic morphs of montane origin; white dots with black center, former peri-glacial melanic morphs returned to non-melanism since the Wisconsinan; white dots, non-melanic morphs. Approximate time scale is given, as condensed on the left into five sections.

*Diagnosis.* Two morphs — higher altitude peri-glacial morph with normal peri-glacial males, moderately dark melanic females, and an arid lowland or “basin” morph in western Idaho with very dark melanic females and males darker above with more pronounced peri-glacial traits on the under surface. Genitalia the of the two morphs alike, the subspecies infrasubspecifically clinal.

Basin morph: males recognized by dark purplish-orange upper side and pronounced markings characteristic of peri-glacial morphs on a bright “porcelain” yellow cream under surface. Females melanic. Montane morph: both sexes recognized by pale ochraceous under surface, with first spot in mesial line dark, rest uniformly lighter and usual occurrence of anal-mesial spots. Females generally orange.

*Male.* Basin Morph: Upper surface of wings: dark iridescent Vinnaceous Rufous tinged violet, spots usually not obviously visible through from under surface. Under surface of wings: hindwing ground color bright Cream Buff with “porcelain” appearance, darker yellow to rusted on the forewing. Forewing, apical spots sometimes present. Hindwing, spots highly visible but often same color as ground color surrounded by lighter shading, thus they appear “imprinted” into heavily scaled ground color. Mesial line, first spot dark, obviously black pigmented, rest “imprinted” as described above. Crescent line and discal slash similarly “imprinted”.

Montane morph: Upper surface of wings bright iridescent Xanthine Orange with Cadmium Orange margin. Most spots visible through from under surface. Under surface of wings: ground color dull pale Ochraceous Buff to somewhat grayer; forewing more orangish. Forewing, all spots, discal, postmedian, and marginal pronounced; apical spots sometimes present; discal slash present as white or light gray over ground color; crescent line usually obvious; anal-mesial spots present on distinctly marked individuals.

Length of forewing: Holotype, 19.0 mm. 18 paratypes, range 16.0 mm to 19.5 mm, mean 18.6 mm.

*Female.* Basin morph. Upper surface of wings: Mummy Brown, darker distally, sometimes with ochraceous orange streaked on forewing or covering entire discal cell. Marginal orange line often present, both wings from entire hindwing to vein  $M_1$  of forewing. Under surface of wings: ground color bright Cream Buff, forewing more yellow. Forewing, spots often enlarged; apical spots often present; Hindwing, ground color obscuring whole surface; mesial line, first spot usually black pigmented, rest either uniformly lighter, obscured by ground color, or “imprinted”; anal mesial spots present if mesial line visible; crescent line often obscured or “imprinted”; discal slash absent or vague over ground color.

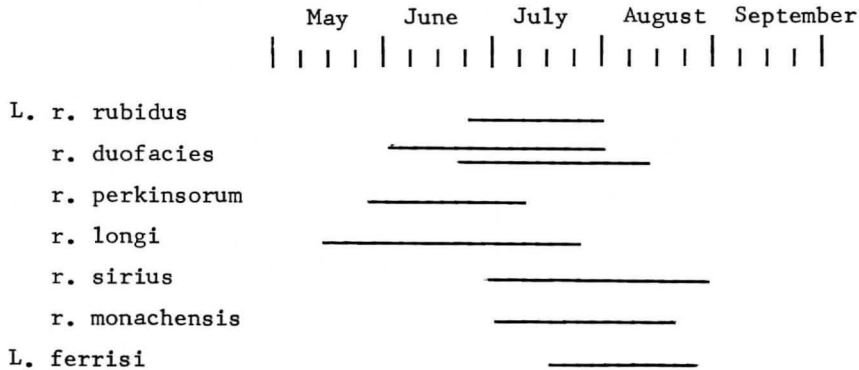


Fig. 15. Relationship of the flight periods of *rubidus* subspecies and *ferrisi*. The flight period of *L. r. duofacies* is figured for the basin morph, above, and the montane morph, below.

Montane morph. Upper surface of wings: as above but much less melanic; forewing, except marginal and submarginal area, very orange; hindwing more melanic. Under surface of wings: ground color Ochraceous Buff, pale Cream Buff, or paler; hindwing, most markings, except mesial line, obscured. Mesial line, first spot usually black pigmented, enlarged; rest uniformly lighter and smaller. Forewing more orange, all markings present.

Length of forewing: Allotype, 19.6 mm. Range of 4 paratypes, 16.0 mm to 21.0 mm, mean 19.7mm.

*Male Genitalia.* Fig. 20, 13a. Saccus "toothed" (montane) to "semicrowned" (basin); lateral shape valvae as in species; valval process with initial caudal cluster of teeth, then tapering cephalad; cephalad tip, aedeagus "hooked"; uncus, wide; falces, gradually tapered from broad "elbow", with ventral "shoulder" often at "elbow" (basin), to thinner (montane).

*Female Genitalia.* Fig. 10. As in species.

*Types.* Holotype ♂, Bogus Basin nr. Boise, Boise County, Idaho, 6000', July 1944, collector unknown. Allotype ♀, same. Both deposited AME. Paratypes: *Males.* AME, data of primary type (2) [number of specimens]; Boise, Idaho, July, "JHM", (4); Boise, Idaho, June, 1960, C. Callaghan, (3); Kuna, Idaho, July, "JHM", (1). LACM, data of primary type (1); Boise, Idaho, July "JHM", (1). AMNH, data of primary type (1); Boise, Idaho, July, "JHM", (1). USNM, data of primary type (1); Boise, Idaho, July "JHM", (1). CMNH, data of primary type (1); Boise, Idaho, June, 1960, C. Callaghan, (1). *Females.* LACM, data of primary type (1). AMNH, Boise Basin, no other data, (1). USNM, data of primary type (1). CMNH, data of primary type (1).

*Distribution.* The montane areas of western Montana, from Powell County, southeast to Gallatin County (Bozeman) into Yellowstone National Park (Sheep-eater Cliffs) in Wyoming. West through Bitterroot and Salmon River Mountains [not same as Salmon Mountains] of Idaho as montane morph, west from there as basin morph from Boise Basin and Bogus Basin, Boise County, Idaho, to Boise. Then northwest in scattered localities to Baker County, Oregon, and south to

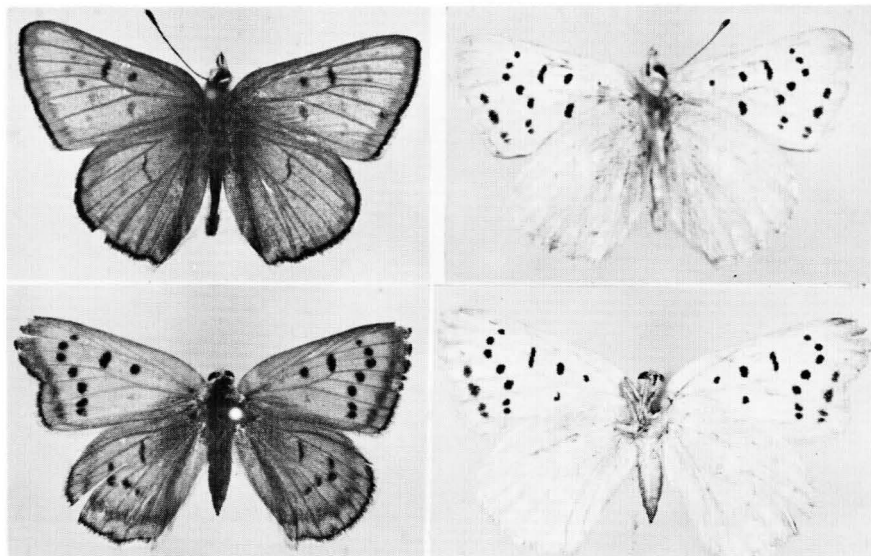


Fig. 16. Neotype (male) and female of Behr's original series of *rubidus*. Top left, upper surface, neotype (CMNH); right, under surface, same. Bottom left, upper surface, female (CMNH); right, under surface, same.

Burns, Harney County, Oregon. Intergrading with the third subspecies described below in the southern Sawtooth Mountains, south Custer County, Idaho, south through the Twin Falls, Twin Falls County, area.

*Flight Period.* Single-brooded. Dates on specimens range from 3 June to 30 July (Basin); 25 June to 15 August (Montane).

*Remarks.* The geographic area inhabited by *L. r. duofacies* reflects history combining Pleistocene proximity to the continental glaciers and also montane glaciers of the period. This allowed evolution of melanic strains during periods of continental glaciation with part of these losing their glacial influence during the interglacial period as others continued under the influence of remaining montane glaciers. This probably explains the presence of the lowland, definitely peri-glacial, array of local populations and clinal variation with a montane morph now partially melanic. This latter population may have begun its shift to non-melanism comparatively recently. Localities known for the occurrences of these respective morphs are: Basin morph — Kuna, Boise, Ada County; Boise Basin, Bogus Basin, Boise County; Payette, Payette County; all Idaho. Then west into Oregon [with males hindwing under surface lighter; mesial and crescent lines more visible; upper surface less deep metallic orange; females, less melanic] including Baker County (general); Grant County (Silvies); northern Harney County (general) and Malheur County (Nyssa). Montane morph — Big Hole Battlefield National Monument, 2-8 mi. E. Bannack Pass, Polaris, all Beaverhead County; Bozeman, Gallatin Gateway, Gallatin, Gallatin River, all Gallatin County; Livingston, Park County; Garrison, Powell County; Sheridan, Madison County; all Montana. East from western Montana mountains into Wyoming: Yellowstone National Park (Sheep-

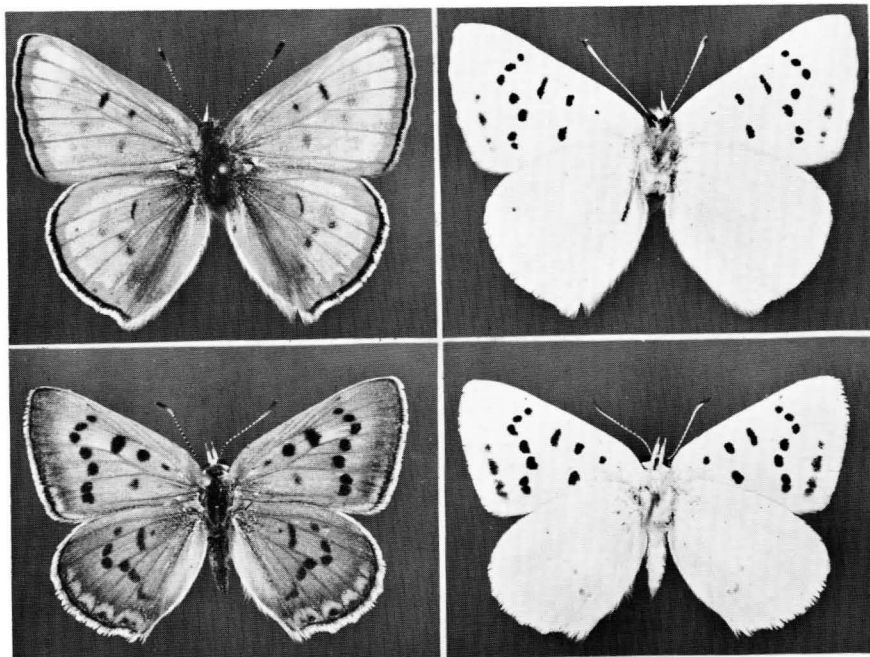


Fig. 17. Representative pair, present-day *L. r. rubidus* from Buck Creek, Warner Mountains, Modoc County, California. Female represents dominant frequency of melanism in females of the population. Top left, upper surface, male (AMNH); right, under surface, same. Bottom left, upper surface, female (AMNH); right, under surface, same.

eater Cliffs and West Yellowstone). West into Idaho: Lemhi County (Lemhi); to Salmon River Mountains (Yellow Pine), Valley County. Intergrading with northwardly dispersed *L. r. sirius* in Sawtooth National Forest (not same as Sawtooth Mountains), at Wood River, Blaine County, and similarly south to Twin Falls, Twin Falls County, to Rupert, Minidoka County, Idaho.

We examined 60 males and 19 females of *duofacies*.

*Etymology.* Taken from the Latin words *duo* (two) and *facies* (kind, types, or appearances), *ies* being the feminine ending, referring to the two morphs exhibited in this clinal subspecies.

***Lycaena (Tharsalea) rubidus perkinsorum*, new subspecies**

Fig. s 21, 22; 13c.

*Chrysophanus rubidus*: Holland, 1898: 255; 1930: 252.

*Lycaena (Tharsalea) rubidus*: Opler (in Howe), 1975: 313.

*Diagnosis.* Both sexes recognized by under surface characters, sexually dimorphic in expression: ground color Pale Olive Buff to Olive Buff; hindwings, under surface, mesial spots, first dark, rest all present but uniformly lighter; basal spots absent; anal-mesial spots almost always present; crescent line obvious, rounded around margin. Forewings, apical spots often present. Females generally deeply melanic, usually completely dark, obscuring even marginal orange; some populations varying to lighter.

*Male.* Upper surface of wings: Ground color brilliant iridescent Mars Orange, flushed purple, bright Orange Chrome along margins. Spots from under surface lightly visible. Under surface of wings: Ground color Olive Buff to Avallaneous; mesial spots, first dark, rest all present, uniformly lighter; white crescent line outstanding and rounded around wing. Anal mesial spots almost always present; basal spots absent; basal slash usually light, always entire; marginal line obscured. Forewing, light Ochraceous Buff; spots sometimes enlarged; apical spots sometimes present; first discal spot almost always entire.

Length of forewing: Holotype 15.8 mm. Range of 47 paratypes, 15.0 mm to 19.0 mm, mean 17.8 mm.

*Female.* Upper surface of wings: Mummy Brown, darker distally; occasionally streaked with yellow or with yellowish patch in discal area. Marginal orange line, both wings, usually obscured. Under surface of wings: Hindwing ground color Pale Olive Buff to Olive Buff, forewing, Warm Buff. Both often very bright. Spots, both wings, often enlarged. Forewing, apical spots almost always present; first discal spot always entire. Hindwing, first mesial spot dark, others uniformly lighter; anal mesial spots nearly always present; basal spots absent; crescents bright.

Length of forewing: Allotype, 18.8 mm. Range of 29 paratypes, 17.0 mm to 20.0 mm, mean 19.0 mm.

*Male Genitalia.* Fig. 22, 13c. Saccus "toothed"; lateral shape valvae, as in species; valval process with initial caudal tooth then tapering cephalad; cephalad end, aedeagus, "hooked"; uncus, wide; falces, "shoulder-ended".

*Female Genitalia.* As in species, Fig. 10.

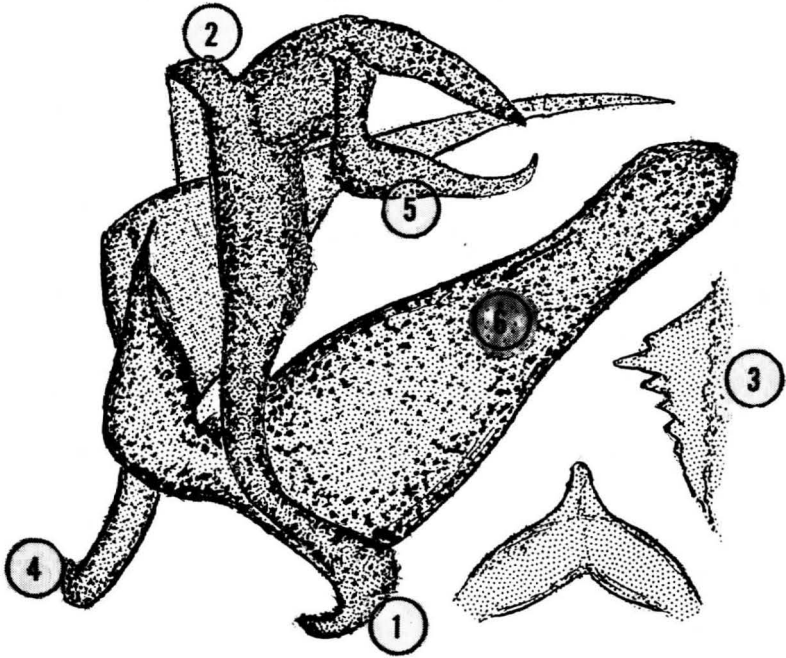
*Early Stages.* Unknown

*Foodplants.* Not specifically known for subspecies.

*Types.* Holotype ♂, 1 mi. E. the Dalles, Wasco County, Oregon, 150' altitude, 11 June 1963, S. F. and E. M. Perkins. Allotype ♀, same data. Both deposited AME. Paratypes. *Males.* all data as on primary type but date — AME, 31 May 1964 (4); 11 June 1963 (19); 6 June 1964 (15); 11 June 1962 (8); 13 June 1964 (2); 22 May 1966. LACM, 31 May 1964; 11 June 1963 (6). AMNH, 6 June 1964 (2); 11 June 1962; 13 June 1964; 11 June 1963. USNM, 13 July 1964 (2). CMNH, 11 June 1963 (2). *Females.* AME, 6 June 1964 (4); 11 June 1962 (9); 11 June 1963 (7); 13 June 1964 (2); 12 June 1962. LACM, 6 June 1964; 11 June 1962; 11 June 1963 (2). AMNH, 11 June 1963, 13 June 1964 (3), 6 June 1964. USNM, 6 June 1964, 11 June 1963. CMNH, 12 June 1962, 13 June 1964, 11 June 1962.

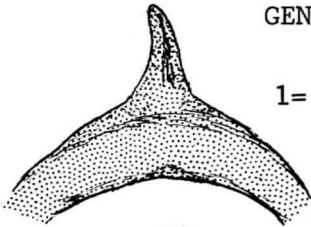


*Distribution.* Columbia River Gorge west to Washington County, Oregon, east to Goodnoe Hills, Klickitat County, Washington, then north of Yakima County,

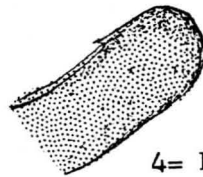
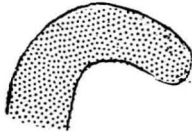


GENITALIC ASPECTS

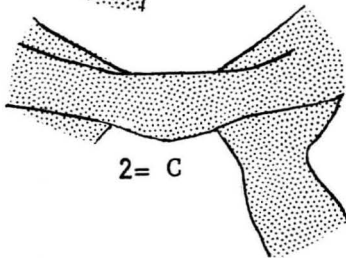
1= A and B



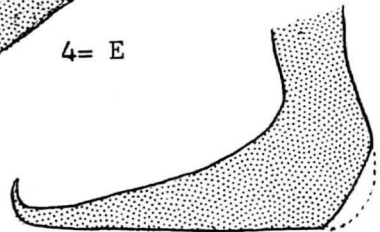
3= D



4= E



2= C



5= F

Washington.

*Flight Period.* Dates on specimens, single brooded, range from 22 May to 13 July.

*Remarks.* Columbia River Gorge populations are predominantly completely dark, Yakima Plateau and Goodnoe Hills specimens much orange. Unfortunately, large series of specimens from these localities are not supplemented by samples from intervening areas. The subspecies was probably continuous in distribution with the previous and the following subspecies. All apparently evolved in relation to the Pleistocene continental ice sheets. Male genitalia of *L. r. perkinsorum* are remarkably like those of the peri-glacial subspecies inhabiting areas of relict pine forest and post-climax prairie from northwest Nebraska north into northwestern North Dakota.

←

Fig. 18. Male genitalia of the neotype, *L. rubidus* (Behr), above. Drawn with aedeagus in place and only one bilateral aspect shown. Numbers indicate traits found taxonomically useful infraspecifically (1-5) and intraspecifically (1-6). Below, aspects of genitalia typical of drawings presented for taxa described in the paper, from present-day specimen, Buck Creek, Warner Mountains, Modoc County, California. Parts drawn represent those used in analysis for Fig. 5, and described in Appendix 1. A and B are combined to analyze shape of the saccus. The aspects are: A. Saccus, caudal view. B. Ventral of saccus, lateral view. C. Uncus, dorsal view. D. Valval process, dorsal view. E. Cephalad tip, aedeagus, lateral view. F. Falces, lateral view. These will remain the same for Figures of all male genitalia. Number 6, lateral view of the valvae, is figured separately with the other congeners.

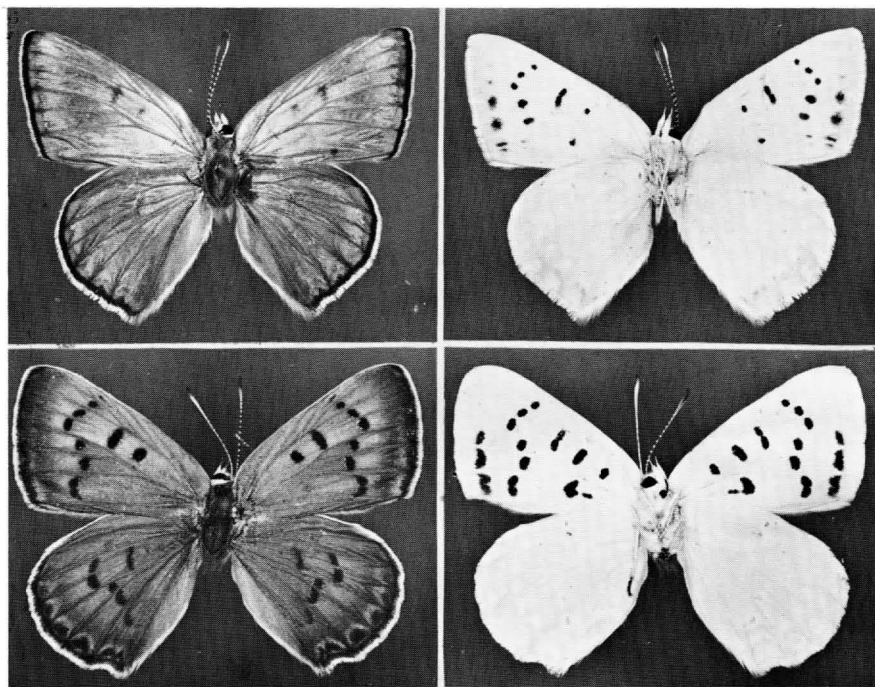


Fig. 19. Holotype and allotype of *Lycaena rubidus duofacies*, new subspecies. Top left, upper surface, holotype (AME); right, under surface, same. Bottom left, upper surface, allotype (AME); right, under surface, same.

We examined 100 males and 47 females *perkinsorum*.

*Etymology.* This subspecies is named for Mr. Stephen F. Perkins (Oregon Regional Primate Research Center, Beaverton) and Dr. Edwin M. Perkins (University of Southern California, Los Angeles) who collected the type series and are responsible for most of our knowledge of this species in the northwestern United States. It is also in recognition of their substantial contributions of specimens to the Allyn Museum of Entomology.

***Lycaena (Tharsalea) rubidus longi*, new subspecies**

Figs. 23, 24; 13e

*Chrysophanus sirius*: Barber, 1894: 20.

*Lycaena rubidus*: Clench (in Ehrlich and Ehrlich), 1961: 223.

*Lycaena (Tharsalea) rubidus*: Opler (in Howe), 1975: 313.

*Lycaena rubidus sirius*: Leussler, 1938: 277. Johnson and Nixon, 1967: 518.

*Lycaena rubidus* [ssp.]: Johnson 1972 (1973): 25.

*Diagnosis.* Peri-glacial morph, distinguished from *L. r. sirius* by peri-glacial traits: hindwing mesial band always regular; first spot pigmented black or dark brown, sometimes enlarged, rest uniformly lighter gray; crescent line obvious; anal mesial spots often present; basal spots not evident as on *sirius*. Female, peri-glacial melanic in wing shape but orange, especially on the forewing. Under surface, mesial line as on males but usually blacker; basal spot at vein 2A usually outstanding, but no other basal markings. Male genitalia, saccus "toothed"; cephalad tip, aedeagus, "hooked", these not "crowned" or "knob-ended" respectively, as on *sirius*.

*Male.* Upper surface of wings: bright iridescent Xanthine Orange,

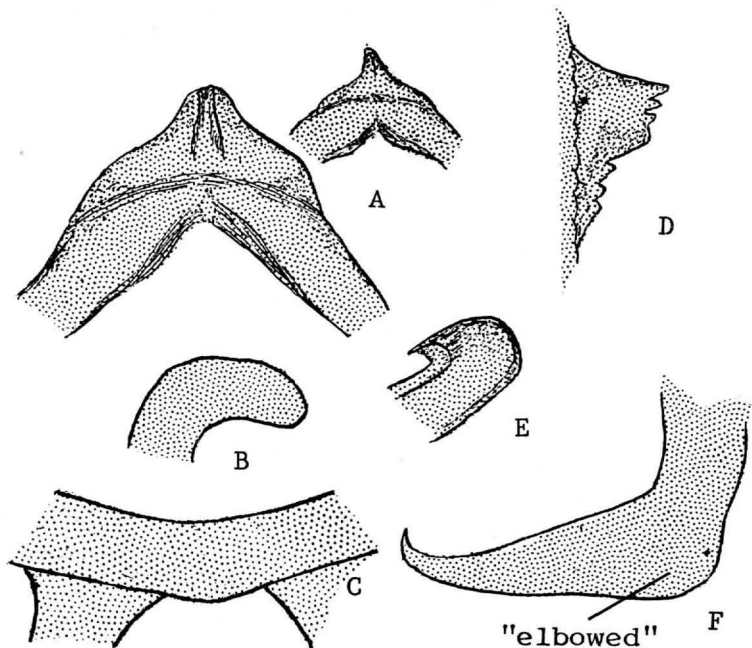


Fig. 20. Male genitalia (aspects — See Fig. 19, explanation), holotype, *Lycaena rubidus duofacies*, new subspecies. Second drawing of saccus, right of A, is a montane morph, Lemhi, Lemhi County, Idaho.

purple sheen pronounced distally, Cadmium Orange along the margin. Spots visible through from under surface. Forewing, first and second discal spot, and hindwing, discal slash, often pigmented black above. Under surface of wings: Hindwing, ground color pale Ochraceous Salmon; forewing, light Ochraceous Buff. Forewing, all spots discal, postmedian, marginal, concise but often reduced; apical spots sometimes present. Hindwing, mesial line regular, first spot black or dark brown, often enlarged, rest uniformly lighter; discal slash gray; basal spot between veins 3A and 2A often very dark; crescent line distinct, angled obliquely across wing rather than rounded around shape of margin.

Length of forewing: Holotype, 16.8 mm. Range of 57 paratypes 16.0 mm to 19.5 mm, mean 18.4 mm.

*Female.* Upper surface of wings: Peri-glacial melanic in wing shape, but forewings generally bright Ochraceous Orange base to postmedian area. Hindwing darker. Hindwing, marginal orange line pronounced forewing to vein M<sub>1</sub>. All spots boldly black above. Under surface of wings: Hindwing, ground color pale Ochraceous Salmon; forewing light Ochraceous Buff. Forewing, all spots, discal, postmedian, marginal, pronounced; apical spots sometimes present. Hindwing, mesial line regular, first spot darkest, often enlarged, rest uniformly lighter, not obscured by ground color; discal slash very light to obscured; crescent line distinct and located more obliquely across wing, not rounded as shape of margin; anal mesial spots nearly always present; orange marginal line sometimes obvious over ground color.

Length of forewing: Allotype, 18.6 mm. Range of 39 paratypes, 16.5 mm to 20.0 mm, mean 19.0 mm.

*Male Genitalia.* Fig. 24, 13e. Saccus "tcothed"; lateral shape valvae, as in species; valval process with initial caudal tooth then tapering cephalad; cephalad tip, aedeagus, "hooked"; uncus, wide; falces, with "shoulder" midway between "elbow" and caudal end.

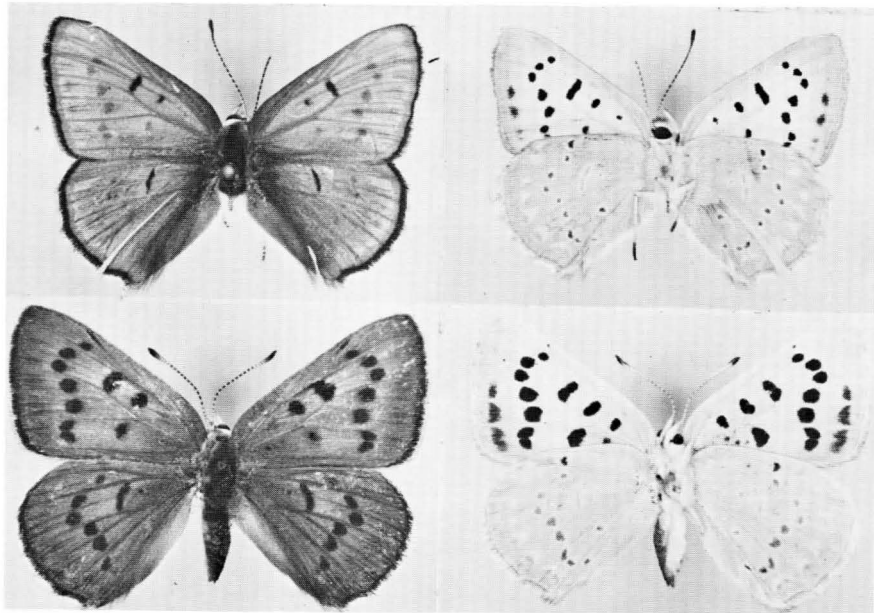


Fig. 21. Holotype and allotype of *Lycaena rubidus perkinsorum*, new subspecies. Top left, upper surface, holotype (AME); right, under surface, same. Bottom left, upper surface, allotype (AME); right, under surface, same.

*Female Genitalia.* Fig. 10. As in the species.

*Early Stages.* Unknown.

*Foodplants.* Not specifically known for subspecies, but *Rumex venosus* Pursh is a characteristic plant of the relict post-climax prairie in the Sandhills Region of Nebraska where prairie populations of *L. r. longi* survive. This same area was conifer forest as late as 300 years ago (Johnson, 1976a, 1976b; Pool, 1914; Tolstead, 1941; Weaver and Albertson, 1956; Wells, 1970b) and the prairie relicts are typical of the former pine-juniper savannah of the area. *L. r. longi* survives here and in the wooded escarpments to the north as well.

*Types.* Holotype ♂, Cañon [hereafter using "Canyon"] Region north of Harrison, Sioux County, Nebraska, 14 July 1917, R. A. Leussler [Iowa State University Collection, given to Kurt Johnson Collection, 1969]; allotype ♀, same. Both deposited AME. Paratypes: *Males.* AME, Harrison, Sioux County, Nebraska, 19 July 1917, R. A. Leussler (1); LACM, Harrison, Sioux County, Nebraska, 14 July 1917 (14), 19 July 1917 (12); 25 July 1917 (1), 7 July 1917 (1), all R. A. Leussler; 28 June 1911, F. H. Shoemaker. AMNH, Squaw Canyon, Sioux County, Nebraska, 27 June 1896, 1 July 1896, 2 July 1896, H. G. Barber; Canyon Region north of Harrison, Sioux County, Nebraska, 19 July 1917 (2), 14 July 1917, R. A. Leussler (2); Harrison, Sioux County Nebraska, 16 May, E. I. Huntington. CMNH, Harrison, Sioux County, Nebraska, 14 July 1917, R. A. Leussler; OSU, Canyon Region north or Harrison, Sioux County, Nebraska, 5 June 1914, 5 June 1919 (3), 19 July 1917 (3), 14 July 1917 (6), 29 June 1911 (5), 25 July 1917 (3), all R. A. Leussler. CAS, Harrison, 25 July 1923, 25 July 1917; 23 July, 26 July, 14 July 1917; northwest Nebraska, 3 July, all R. A. Leussler. northwest Nebraska, 3 July, all R. A. Leussler. *Females.* AME, Canyon Region north of Harrison, Sioux County, Nebraska, 19 July 1917 (1). LACM, Harrison, Sioux County, Nebraska, 19 July 1917, 25 July 1917 (4), 14 July 1917, all R. A. Leussler; AMNH, Canyon Region north of Harrison, Sioux County, Nebraska, 25 July 1917 (6), all R. A. Leussler; Harrison, Sioux County, Nebraska, 16 May 1921, E. I. Huntington. CMNH, Canyon Region north of

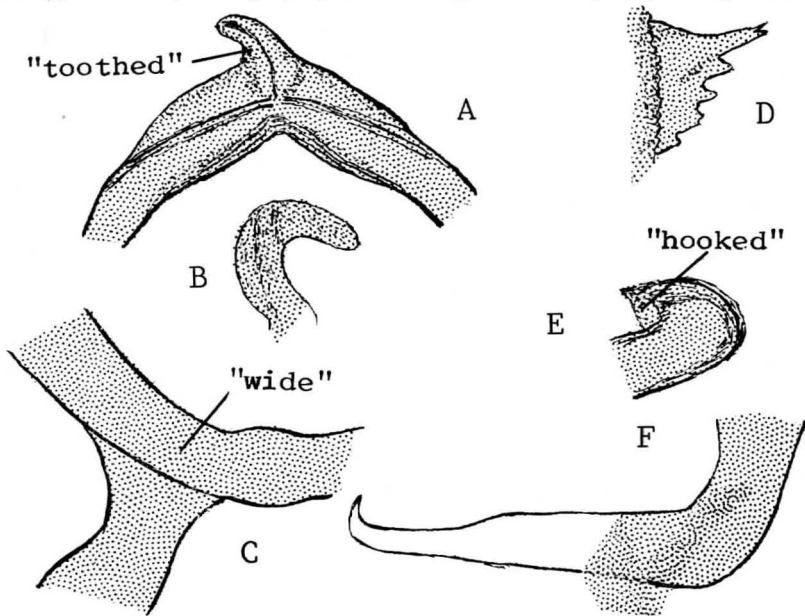


Fig. 22. Male genitalia (aspects — see Fig. 19, explanation), holotype, *Lycaena rubidus perkinsorum*, new subspecies.

Harrison, Sioux County, Nebraska, 14 July 1917, R. A. Leussler. OSU, Canhon Region north of Harrison, Sioux County, Nebraska, 25 June 1917, 5 June 1914, 5 June 1919, 29 July 1911 (2), 24 July 1911 (2), 22 July 1917 (2), 19 July 1917 (7), 25 July 1917 (3), 14 July 1917 (3), 17 July 1917 (2), all R. A. Leussler. CAS, Harrison, 19 July 1921, R. A. Leussler.

*Distribution.* Plains of western Nebraska in post-climax prairie around lakes in Sandhills Region from Cherry County (northern Nebraska) to Red Willow County (southwest Nebraska), east to Custer County (old specimens). West in canyon region of Pine Ridge escarpment (Dawes and Sioux Counties) and Wildcat Hills (Scotts Bluff, Banner Counties). North from these escarpments to Black Hills region of South Dakota and adjacent eastern Wyoming; again north along escarpments of the Little Missouri River in North Dakota. West from panhandle of Nebraska to Wyoming in relicts of former Cheyenne Ridge escarpment (now canyons of Goshen County, Wyoming). Here beginning to intergrade with plains *L. r. sirius* dispersing eastward from the Laramie Mountains of Wyoming.

*Flight Period.* Single-brooded, dates on specimens range from 16 May to 29 July.

*Remarks.* This periglacially evolved subspecies inhabits areas of relict and former pine forest on the western Great Plains. From 8,000 to about 1,700 years ago these forests covered the area from northwest and central Nebraska north to western South and North Dakota and were surrounded by pine-juniper savannah connecting them to the present-day Bighorn Mountains and Laramie Range of Wyoming. *Rumex venosus* survives on the plains where post-climax prairie relicts occur due to the high water table (Johnson, 1976a, 1976b, Pool, 1914; Tolstead, 1941). Probably, its distribution was formerly continuous with the other periglacial subspecies. It is still clearly related in genitalia to *L. r. perkinsorum*. Small numbers of specimens have been taken in recent years in all the areas mentioned under Distribution.

We examined 61 males and 50 females of *longi*.

*Etymology.* We are pleased to name this subspecies after Dr. Charles A. Long,

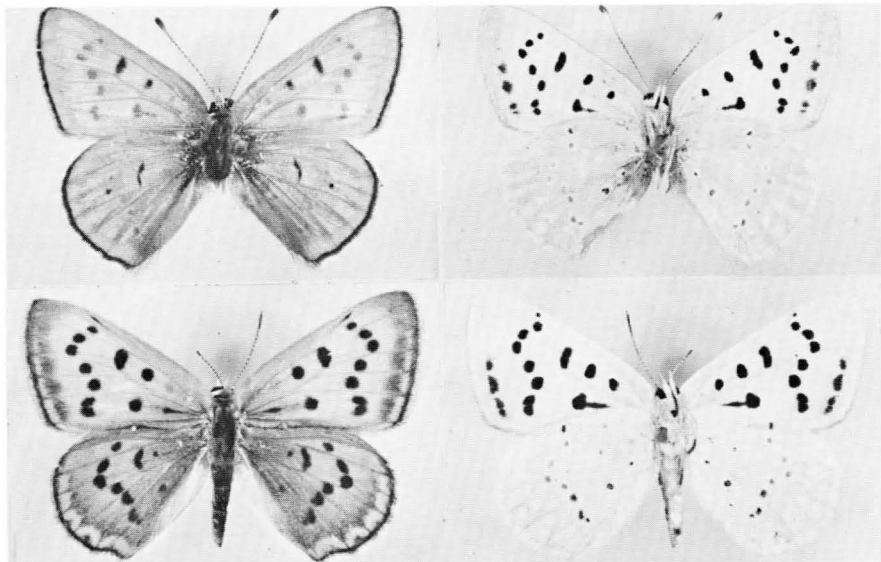


Fig. 23. Holotype and allotype of *Lycaena rubidus longi*, new subspecies. Top left, upper surface, holotype (AME); right, under surface, same. Bottom left, upper surface, allotype (AME); right, under surface, same.

Director of the Museum of Natural History, University of Wisconsin at Stevens Point; he is the former major professor of the first author, and director of the institution supporting part of this work.

Non-melanic Segregations with Montane-glacially Evolved Melanic Populations.

***Lycaena (Tharsalea) rubidus sirius* (W. Edwards)**

Figures 25, 26, 27, 28; 13d, g.

*Chrysophanus sirius* Edwards, 1871, Trans. Amer. Ent. Soc., 3:266-277.

*Chrysophanus sirius* Edwards, 1871: 270. Edwards, 1874: II, T. I, *Chrysophanus*.  
Mead, 1875: 781. Holland, 1898: 255; 1930: 252.

*Chrysophanus rubidus*: Holland, 1898: 255; 1930: 252. Coolidge, 1907: 120.

*Chrysophanus sirius* (sic): Wright, 1906: 217

*Chrysophanus* (sic) *Rubidus* (sic): Wright, 1906: 217.

*Lycaena sirius*: Strecker, 1874: 92; 1876: 100. Kirby, 1877: 765.

*Chalceria sirius*: Scudder, 1876: 126.

*Chalceria rubidus sirius*: Dyar, 1902: 41.

*Chrysophanus rubidus* var. *sirius*: Coolidge, 1907: 120.

*Heodes rubidus sirius*: Barnes and McDunnough, 1917: 120.

*Heodes rubidus*: Comstock, 1925: 175, 239.

*Lycaena rubidus sirius*: Barnes and Benjamin, 1926: 19, 163. McDunnough, 1938:  
26. DeFoliart, 1956: 98. Brown, Eff and Rotger, 1957: 152. Brown, 1969: 166.  
Ferris, 1971a: 39; 1971b: 17, 54.

*Lycaena (Lycaena) rubidus sirius*: dos Passos, 1964: 60.

*Diagnosis.* Several morphs (see Remarks) basically divided for diagnosis into two

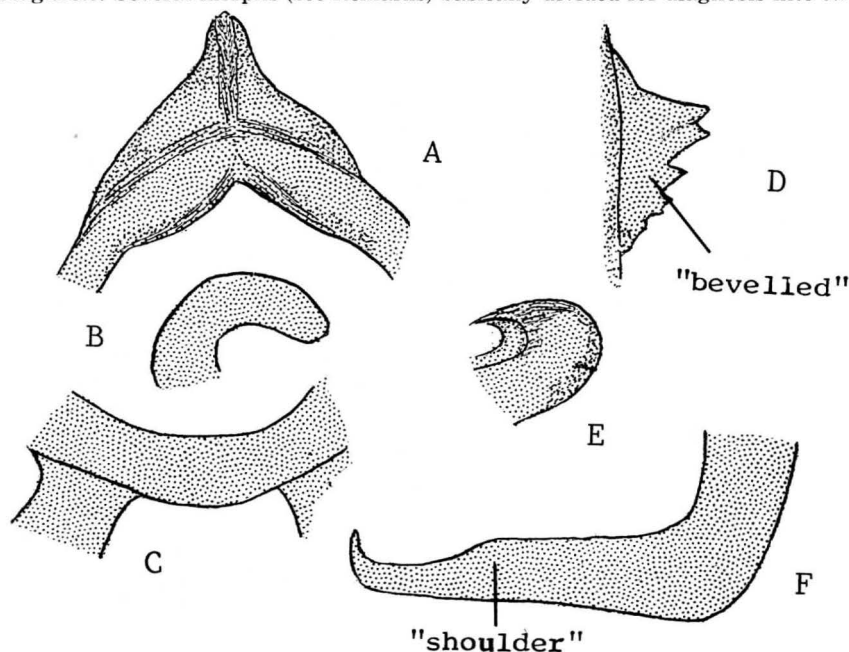


Fig. 24. Male genitalia (aspects — see Fig. 19, explanation), holotype, *Lycaena rubidus longi*, new subspecies.



extremes — “Rocky Mountain montane extreme” and “Rocky Mountain lowland and western states extreme.”

*All morphs*, both sexes, characterized by — Hindwing, under surface, irregular frequency of occurrence and degree of expression of spots in mesial line, absence of anal-mesial spots. Forewing, under surface, general lack of apical spots. Male genitalia — all morphs share characters of variously “crowned” saccus, valval process tapered from both ends, cephalad tip of aedeagus, “knob-ended”, uncus narrow, falces narrow with hump between “elbow” and caudal end.

*Rocky Mountain montane extreme*: distinguishable from other subspecies by above characters and darker upper surface with pronounced marginal black spots; limbal area, hindwing. Beneath, hindwings, high frequency of basal spots; heavy back scaling (“grizzling”) over gray ground color; crescent line obscured; discal slash usually divided into two. Forewings, first discal spot often 8-shaped; postmedian spots very often oblongate. Females increasingly melanic with altitude.

*Rocky Mountain lowland and western states extreme*: distinguishable from other subspecies by above general traits and these specifically — hindwings, under surface, sometimes immaculate, populations with spots having them limited to random occurrences in the mesial line. Forewing, under surface, spots reduced, not oblongate. Females bright orange to slightly dulled orange.

*Male.*

*Rocky Mountain montane extreme*: Upper surface of wings — dull brown iridescent Xanthine Orange, duller with increasing altitude. Hindwing, spots appearing through from under surface sometimes irregularly pigmented above; limbal area,

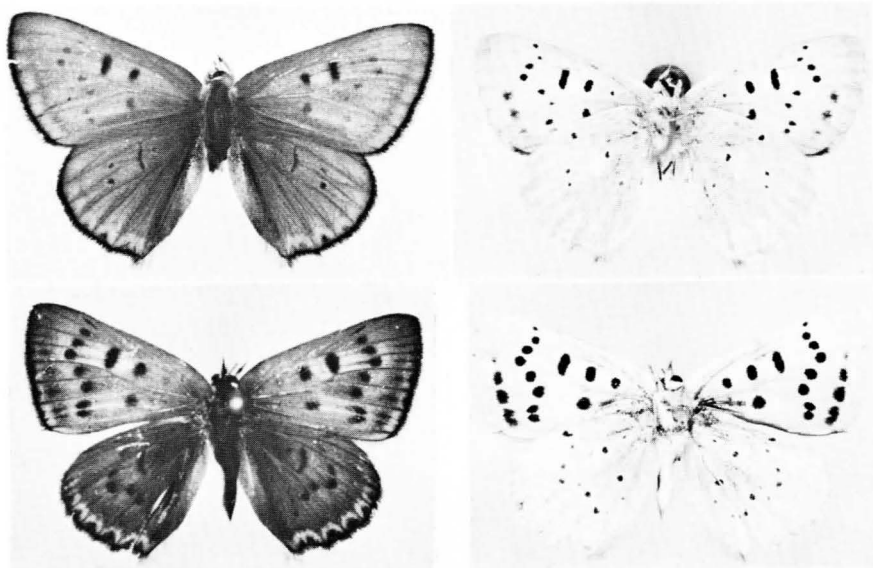


Fig. 25. Male and female paratypes of *Lycaena rubidus sirius* (W. Edwards). Top left, upper surface, paratype male (AMNH); right, under surface, same. Bottom left, upper surface, paratype female (AMNH); right, under surface, same.

black spots nearly always pronounced, making marginal orange band wavy in appearance. Under surface of wings — Hindwing, ground color whitish gray to dull gray, much “grizzling”; mesial spots irregular in occurrence and degree of expression, grizzling obscuring these and crescent line, or limiting latter to blotches; fourth, fifth, and sixth crescents dominate, if present; basal spots nearly always present; discal slash nearly always divided into two; marginal line often pronounced as orange line. Forewing, ground color Ochraceous Buff; first discal spot tending to 8-shaped, all discal spots usually surrounded by white ring over ground color; postmedian spots often oblongate.

*Rocky Mountain lowland and western states extreme.* Upper surface of wings — bright iridescent Xanthine Orange, often hardly darker than brighter margin. Hindwing, spots appearing through from under surface sometimes irregularly pigmented above; forewing, discal slash or second discal spot, or discal slash, hindwing, all reduced, sometimes pigmented above. Limbal area, black spots above reduced. Montane populations, California, Nevada, and generally distributed but local xeric populations with more spots darkened above on hindwings. Under surface of wings — ground color variable, light ochraceous to gray-white (California, Utah, lowland Wyoming), rustier (lowland Nevada), with “grizzling” (montane Nevada, Utah) see “morphs” under Remarks. Forewing, discal, postmedian, marginal spots present, often reduced, seldom oblongate; apical spots never present. Hindwing, mesial spots irregularly occurring; basal spots absent or reduced; discal slash absent or if present light and reduced; anal-mesial spots absent; crescent line absent or vaguely lighter than ground color; marginal orange line usually absent.

Length of forewing: Range of ten topotypical specimens, 14.0 mm to 17.0 mm, mean 16.0 mm. California (Mono County) 14.0 mm to 19.0 mm.

*Female.*

*Rocky Mountain montane extreme:* Upper surface of wings: Usually melanic, but with gold sheen or patches of gold or orange, more totally brown with increasing altitude. Orange marginal line usually pronounced from anal angle of hindwing to subapical area of forewing. Full complement of black spots (Fig. 1a) usually visible over ground color. Under surface of wings as on males but ground color more ochraceous.

*Rocky Mountain lowland and western states extreme.* Upper surface of wings: very bright ochraceous orange, sometimes obscured by slight sheen of melanism on hindwing (see “morphs” under Remarks). Forewing, spots above well expressed, seldom oblongate; hindwing, mesial spots irregular in occurrence; orange marginal line outstanding, hindwing to vein  $M_2$  forewing. Under surface of wings: as on males, but higher frequency of general spot expression and intensity of orange marginal line.

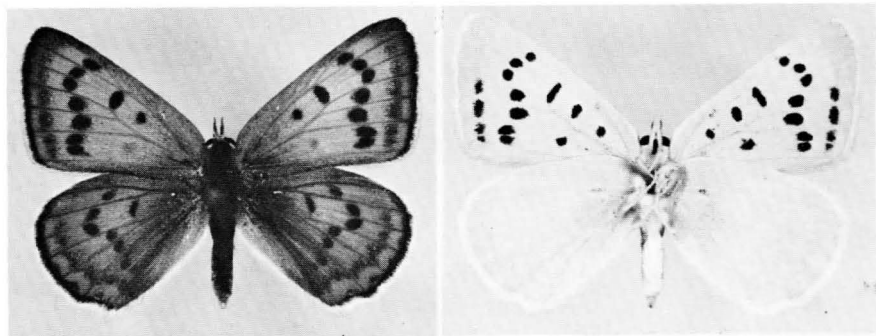


Fig. 26. Representative non-melanic female, *Lycaena rubidus sirius*, Mono County, California. Right, upper surface; Left, under surface.

Length of forewing: Range of seven topotypical specimens, 15.0 mm to 16.5 mm, mean 16.0 mm. California (Mono County) 15.0 mm to 19.5 mm.

**Male Genitalia.** Fig. 27, 28, 13 d, g. Saccus variously "crowned", decreasing in amount of crown westward; lateral shape, valvae, as in species; valval process with teeth tapering in configuration from both ends, usually with major bifurcation of teeth in montane Rocky Mountains ranging to more distinctly separated teeth westward to California; cephalad tip, aedeagus, "knob-ended", uncus, thin; falces, narrow with hump between "elbow" and caudal end.

**Female Genitalia.** As in species, Fig. 10.

**Early Stages.** Undescribed.

**Foodplants.** *Rumex* species have been recognized as the foodplant of *rubidus* for sometime (Brown, Eff and Rotger, 1957; Ehrlich and Ehrlich, 1961; Ferris 1971b; Opler, in Howe, 1975) and all of the records come from the range of *sirius*. *Rumex transitorius* Rech. (see synopsis in Appendix) has been proven the foodplant in Mono County, California (adults raised from pupae found in litter at base of plants at Warren Fork, Lee Vining Creek, 8990', Tioga Pass, Lee Vining Road "S. 16, T. 1 N., R. 25 E.", where mature larvae were also taken on *R. transitorius* 18 June 1970 and five specimens emerged 11-15 July 1970, J.F. Emmel and O. Shields, LACM). *Rumex triangulivalvis* (Dauser) Rech. is a larval foodplant in Colorado according to Opler (in Howe, 1975). *Oxyria digyna* (L.) Hill has been stated as the larval foodplant of some high altitude Colorado montane populations according to F. Martin Brown (pers. comm., and pers. comm. to Brown from other Colorado sources).

**Types.** Lectotype (Brown, 1969), "a male from the T. L. Mead Collection in the Carnegie Museum, Pittsburgh, PA. . . used as the model for Fig. 3, Plate 29, in Holland's *Butterfly Book*. "Paratypes". "Two males and a female labeled "*sirius* male (or female)/Color." in Edwards' manuscript, and "collection of/W. H.

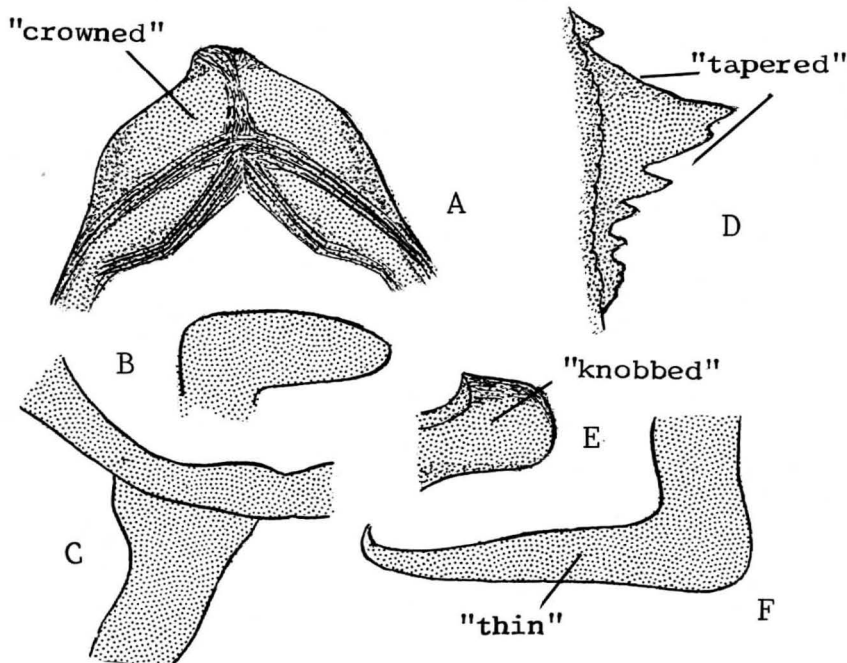


Fig. 27. Genitalia of the Rocky Mountain montane extreme of *Lycaena rubidus sirius* (aspects — see Fig. 19, explanation). Male specimen from Twin Lakes, Lake County, Colorado, type locality of *L. r. sirius*.

Edwards." in the W. H. Edwards collection at the Carnegie Museum; "Specimens with these dates: "7-12" a male; "7-13" 8 males and 2 females; "7-14" a male; "7-17" 3 males and a female; "7-20" a male. These were collected at Twin Lakes, Colorado." in the T. L. Mead Collection at the Carnegie Museum; "three T. L. Mead specimens, two males and female, in the Henry Edwards Collection (no. 4365) at the American Museum of Natural History, New York, and the Mead specimens in the Herman Strecker collection in the Field Museum, Chicago."

*Type Locality.* "taken in Colorado" (Edwards, 1871), restricted by Brown (1969) to vicinity of Twin Lakes, Lake County, Colorado.

*Distribution.* (see also "morphs" under Remarks) *Rocky Mountain montane extreme*: montane areas of Colorado and immediately adjacent mountains of New Mexico (Culebra Range) and Wyoming (Laramie and Sierra Madre Mountains), melanism occurring from about 7,500' to 11,500'. Similar morph at high elevations in Ruby Mountains of Nevada and Wasatch Mountains of Utah. *Rocky Mountain lowland and western states extreme*: blending in cline with above and occurring over entire lowland area of western United States. Varying from slightly melanic morph in Siskiyou and Cascade ranges, California, to less melanic southeast in Sierra Nevada Range through Placer County to Mono and Tuolumne counties. West from there to San Joaquin County. East in lowlands and mountains through central and northern Nevada, intergrading with *r. duofacies* in southern Sawtooth Mountains of central southern Idaho. Melanic montane strains in Ruby Mountains, Elko County, Nevada. Throughout lowland Utah with melanic strain in Wasatch Mountains, Wasatch County, Utah, through lowland western Wyoming in Green River Basin and throughout lowland Colorado. There stratified with montane melanic populations, some using *Oxyria* instead of *Rumex* as the food-plant. East onto Colorado plains, north to Wyoming adjacent the mountains and

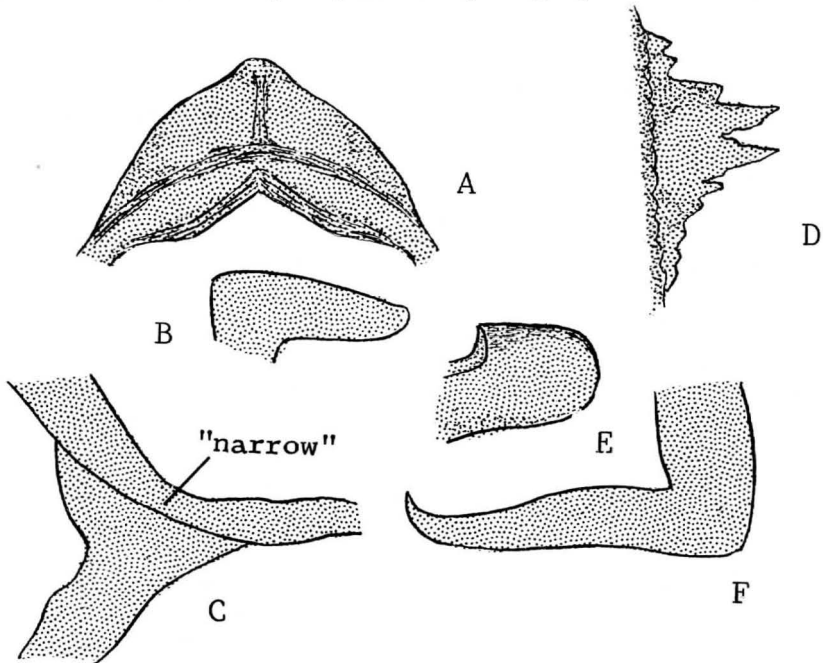


Fig. 28. Genitalia of the Rocky Mountain lowland and western states extreme of *Lycaena rubidus sirius* (aspects — see Fig. 19, explanation). Male specimen from Mono Lake, Mono County, California.

onto plains of Montana to Great Falls, Cascade County, east to Havre, Hill County, west to Flathead Basin, Lake County, and north into lowland Alberta, Canada.

*Flight Period.* One brood, late June through August.

*Remarks.* The male genitalia of this subspecies remain generally homogeneous over its entire range. The distinct regional and local morphs can be listed as follows:

1. Lowland Morph (excluding other names subspecies, lowland areas from Alberta south to southern Colorado, and west to California). Typical of the morph described as Rocky Mountain lowland and western states extreme.

2. California Montane Morph (Cascades, Siskiyou Range, south in Sierra Nevada Mountains of California). Typical of the western states extreme but slightly melanic in females, with darkening and obscuring of features on the hindwing under surface in both sexes.

3. Colorado Montane Morph on *Rumex* (Montane Colorado, 7,500-9,000'). Lowland and western states extreme but smaller in size than plains individuals, showing slight melanism above and below, the larger basal spots, under surface, hindwings, and oblongation of spots on the forewing.

4. Colorado Montane Morph on *Oxyria* (Montane Colorado from 9,000 to 11,500'). Representing the extreme traits described under the Rocky Mountain montane extreme. These populations relate to evolution of melanic strains around montane glaciers during the Pleistocene when timberline was lower. They are now isolated throughout the Colorado mountains at varied altitudes depending on past geology and present latitude. Though some may be locally allopatric due to altitudinal stratification, they cannot be adequately defined as a separate population over the entire region. Any definition of this group as a subspecies having phyletic significance would be welcome, if the taxon could avoid misuse based on simple morph-characters alone.

5. Colorado Plains Morph (plains adjacent the Front Range, El Paso and Douglas Counties, Colorado). This population has distinct wing traits somewhat reflecting those of *L. r. longi*. The extent of these plains populations eastward in relation to high water table and frequency of prairie relicts (Livingston, 1954) allows some moderate isolation from the Front Range montane populations. However, the genitalia are not distinctly like those of *L. r. longi* but more like the montane Colorado populations, probably reflecting sporadic intergradation. These areas also support similarly related populations of forb-feeding *Callophrys (Incisalia)* (Lycaenidae) and *Cotias alexandra* W. Edwards (Pieridae) which have like affinities east and northward in their paleobotanical histories (see Discussion section of this paper). As discussed later, though this population may bear an old relationship with *L. r. longi* it is no longer a part of that population and not sufficiently distinct of itself to warrant a subspecific designation.

6. Ruby Mountains, Wasatch Mountains Montane Melanic Morph. Possibly independently evolved melanic populations with dark flecked under surfaces and heavily melanic females.

7. Xeric Morph (known presently from xeric areas in western Colorado, north-central Montana, eastern Idaho, southern and western Nevada) Heavily "rusted" ground color on the under surface, obscuring all markings on hindwing and with reduction of spots, under surface, forewing.

Some specimens of *rubidus*, reportedly not different than montane Colorado *rubidus*, are known from the region of San Francisco Peaks, Coconino County, Arizona (K. Roever, pers. comm.). We have been unable to secure these for study. However, if such specimens are indeed *rubidus*, this is compatible with the physiographic and paleobotanical distinctions contrasting this area and the White Mountains. These are presented in the Discussion section of this paper.

We examined 1,004 males and 502 females of *sirius*.

## OTHER SUBSPECIES

***Lycaena (Tharsalea) rubidus monachensis*, new subspecies**

Figures 29, 30; 13b.

*Chrysophanus rubidus*: Holland, 1898: 255; 1930: 252.*Heodes rubidus*: Comstock, 1925: 175.*Lycaena rubidus*: Clench (in Ehrlich and Ehrlich), 1961: 223.

Emmel and Emmel, 1973: 94.

*Lycaena (Tharsalea) rubidus*: Opler (in Howe), 1975: 313.*Lycaena rubidus rubidus*: Brown, Eff and Rotger, 1957: 152.

*Diagnosis.* Males recognized by completely Avallaneous hindwing under surface, showing only vague white discal slash and crescent line, or the latter as blotch-shaped markings heavily obscured by the ground color. Females recognized by Cinnamon Buff under surface with vague mesial line of spots, more basally located than in other subspecies.

*Male.* Upper surface of wings: dull iridescent Orange Rufous with Orange Chrome along margin, spots not visible through from under surface. Under surface of wings: Avallaneous ground color with only white blotch-like discal slash and crescents or blotch-shaped markings along the crescent line. Forewing dull Vinaeous Cinnamon, with normal complement of spots.

Length of forewing: Holotype, 15.7 mm. Range of 53 paratypes, 14.0 mm to 16.0 mm, mean 15.3 mm.

*Female.* Upper surface of wings: Ochraceous Buff with spots bold and often oblongate in shape. Under surface of wings: Hindwing, ground color Cinnamon

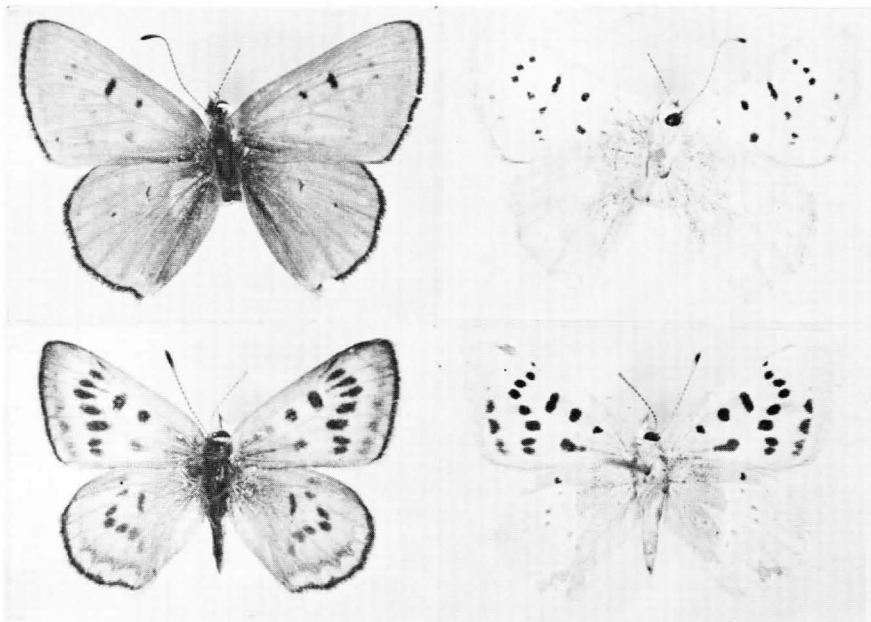


Fig. 29. Holotype and allotype of *Lycaena rubidus monachensis*, new subspecies. Top left, upper surface, holotype (AMNH); right, under surface, same. Bottom left, upper surface, allotype (AMNH); right, under surface, same.

Buff with full mesial line of spots variously darkened, these appearing more basally than distally located.

Length of forewing: Allotype, 14.7 mm. Range of 25 paratypes, 14.0 mm to 17.0 mm, mean 16.4 mm.

**Male Genitalia.** Fig. 30, 13b. Saccus "humped"; lateral shape, valvae, as in species; valval process with teeth widely separated, "incised"; cephalad tip, aedeagus, nearly without "knob"; uncus medium; falces extremely narrow, with ventral surface often folded inward.

**Female Genitalia.** As in species, Fig. 10.

**Early Stages.** Unknown.

**Foodplants.** Not specifically known for subspecies.

**Types.** Holotype ♂, Monache Meadows, Tulare County, California, 7 August 1917, E. I. Huntington. Allotype ♀, same locality, 24 July 1928, J. S. Garth. Both deposited AMNH. Paratypes: All type locality. **Males.** AME, 7 August 1917, J. A. Comstock; LACM, 13 August 1917, 3 August 1917, J. A. Comstock. AMNH, 25 July 1928, J. S. Garth, 7 August 1917, E. I. Huntington; USNM, 8-15 August (no other data) (22), 8-14 July (no other data) (18), 16-23 July (no other data) (6). CMNH, 12 August (no other data) O. Buchholz. **Females.** AME, 7 August 1917, J. A. Comstock; LACM, 13 August 1971, 7 August 1917 (5), 3 August 1917, 17 August 1912, all J. A. Comstock. AMNH, 24 July 1928, 25 July 1928, J. S. Garth; July 1920, O. Buchholz. USNM, 8-15 August (no other data) (8), 16-23 July (no other data) (4), 2-7 July (no other data), 8-14 July (no other data). CMNH, 7 August 1917, J. A. Comstock.

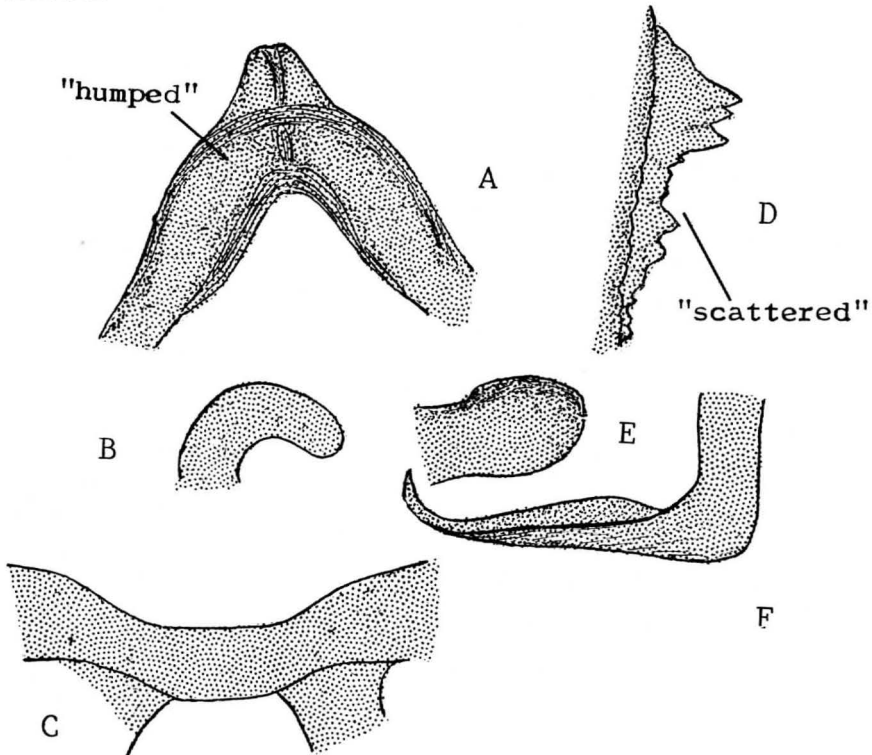


Fig. 30. Male genitalia (aspects — see Fig. 19, explanation), holotype, *Lycaena rubidus monachensis*, new subspecies.



*Distribution.* Limited to the vicinity of Monache Meadows, Tulare County, California, and some adjacent areas of Inyo County in California. May occur in other adjacent areas as well since Inyo County specimens reflect the *monachensis* genitalia.

*Flight Period.* Single brooded, dates on specimens range from 2 July to 17 August.

*Remarks.* The range of *L. r. monachensis* is allopatric from the populations of *L. r. sirius* in California. The area has been noted as producing distinct morphs in several other taxa and is mentioned as being very inaccessible to human traffic (Comstock, 1925). The population is not considered as an isolate in this paper because its genitalia are distinct like the other subspecies and also show influence on the traits of specimens from adjoining areas. Thus, the population is stable and has potential major influence on the gene pool of the species as a whole.

*Etymology.* This local subspecies is named for the type locality.

***Lycaena (Tharsalea) ferrisi*, new species**

Figs. 31, 32; 13h.

*Lycaena (Tharsalea) rubidus*: Opler (in Howe), 1975: 313.

*Lycaena rubidus*: Howe (in Howe), 1975: pl. 55, no. 26.

*Diagnosis.* Characters of the wing: distinctive wing shape, extension of veins from cell very short, with outer margin of forewing arc-shaped making wing appear short and broad, hindwing ovate. Little or no sexual dimorphism in distinctive characters of the under surface. Distinctive ground color combination — hindwing and costa, apex, and margin of forewing drab grey (sometimes rusted) framing bright

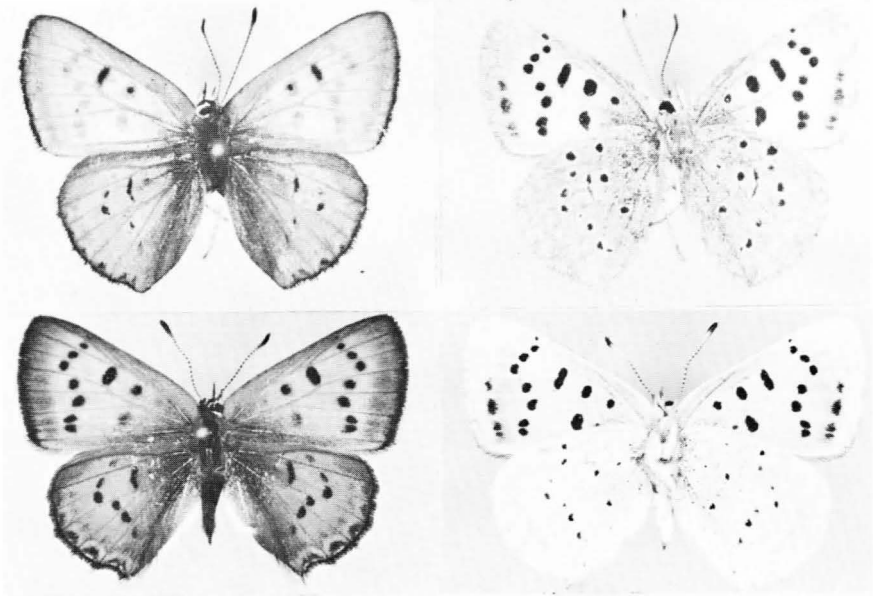


Fig. 31. Holotype and allotype of *Lycaena ferrisi*, new species. Top left, upper surface, holotype (AME); right, under surface, same. Bottom left, upper surface, allotype (AME); right, under surface, same.



ochraceous orange in discal area of forewing. Hindwing, basal markings black and enlarged, often exceeding mesial spots. Forewing, postmedian line, spot between veins  $R_3$  and  $R_{4+5}$  often pronounced. Genitalia: Length/breadth ratio of male valvae about one third smaller than any *L. rubidus* subspecies, valval process nearly always entire as one large tooth, not several teeth as in *L. rubidus*. Parabolic lamellae shape in female genitalia with length/breadth ration about two thirds that of *L. rubidus* and ductus bursae consistently shorter.

*Male*. Wing shape characterized by short extension of veins from cell, with forewing margin arc-shaped, wing appearing short and broad, hindwing ovate. Upper surface of wings: dull iridescent orange, strongly darkened between veins. Cadmium Orange along the margin. Spots visible through from under surface; forewing, first and second discal spots, and hindwing, discal slash often very dark pigmented above. Under surface of wings: hindwing ground color Drab Gray, sometimes even brown. Mesial spots uniformly enlarged and black; basal spots black, as large or larger than mesial spots; one dark anal-mesial spot often apparent; discal slash black; crescent line most often obscured by ground color. Forewing, costa apex and margin Drab Gray to brownish, framing bright ochraceous orange in discal to postmedian area; all spots discal, postmedian, marginal, prominent; most basal and discal spots enlarged; postmedian spot between veins  $R_3$  and  $R_{4+5}$  often enlarged.

Length of Forewing: Holotype, 14.6 mm. Range of 63 paratypes, 13.0 mm to 16.0 mm, mean 14.7 mm.

*Female*. Wing shape same as male. Upper surface of wings: Montane melanic morph, wing bases, marginal areas strongly melanic, discal areas brightly golden

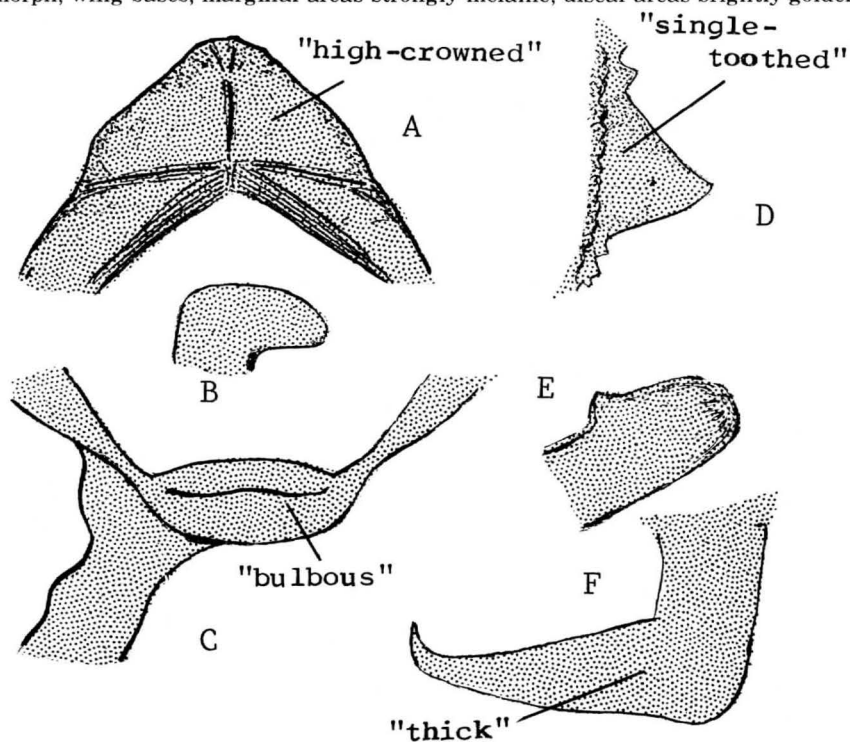


Fig. 32. Male genitalia of the holotype *Lycaena ferrisi*, new species. Aspects — see Fig. 19, explanation.

orange, occasional specimens completely melanic. Forewing, spots above in postmedian area often reduced with first and second discal spots prominent. Hindwing, mesial spots concise, often reduced; discal slash pronounced. Under surface of wings: same as males.

Length of Forewing: Allotype, 15.8 mm. Range of 22 paratypes, 14.0 mm to 17.0 mm, mean 15.3 mm.

**Male Genitalia.** Fig. 32, 13h. Saccus "high-crowned", lateral shape valvae much shorter than *rubidus*, curving slightly ventrad at caudal end; valval process usually one large single unincised tooth; cephalad tip, aedeagus, "long-ended"; uncus "bulbous"; falces "thick."

**Female Genitalia.** Fig. 10. Most like *rubidus* in genus but with parabolic shape of lamellae much smaller in breadth and ductus bursae about one third shorter.

**Early Stages.** Unknown except Funk (1975) has described ants (*Formica altipetens* Wheeler) carrying off ova from ovipositing females at Maverick, Apache County, Arizona.

**Foodplants.** *Rumex hymenosepalus* Torr. was the foodplant at Maverick, elevation 2377', where Funk (1975) observed oviposition. This is the foodplant of *Lycaena xanthiodes* (Boisduval) whose genitalia along with its close relative *L. editha* (Mead) are the closest to *L. rubidus* and *L. ferrisi*.

**Types.** Holotype ♂, Apache Ditch Camp (13 miles east of McNary), Apache County, White Mountains, Arizona, 13 August 1968, C. D. Ferris. Allotype, ♀, same data. Both deposited AME. Paratypes: *Males.* AME, type locality, 25 August 1969, 13 August 1968 (7), 14 August 1968 (2), all C. D. Ferris; 13 mi. E. McNary [Apache Ditch Camp], Apache National Forest, Apache County, Arizona, 2520 m. altitude, 19-20 July 1966 (10), Lee D. Miller. LACM, type locality, 13 August 1968 (2), C. D. Ferris. Bog Tank, nr. McNary White Mountains, 23 July 1964, J. H. Hessel. AMNH, type locality, 14 August 1968, 13 August 1968 (4), 15 August 1968 (2), all C. D. Ferris; 22 July 1964 (6), J. H. Hessel. Bog Tank nr. McNary [White Mountains], 23 July 1964 (8), J. H. Hessel. USNM, Bog Tank, 23 July 1964, J. H. Hessel; 19-20 July 1966, Lee D. Miller. CMNH, type locality, 14 August 1968, C. D. Ferris; 19-20 July 1966, Lee D. Miller; 22 July 1964, J. H. Hessel; Bog Tank, 23 July 1964, J. H. Hessel. CDF, type locality, 14 August 1968 (6), 13 August 1968 (6), all C. D. Ferris. *Females.* AME, type locality, 4 July 1969, 13 August 1968 (2), 25 August 1969 (2), all C. D. Ferris. LACM, type locality, 13 August 1968 (2), 14 August 1962 (2), all C. D. Ferris. AMNH, type locality, 15 August 1968 (2), 13 August 1968 (5), all C. D. Ferris; Bog Tank, 23 July 1964 (3), J. H. Hessel. USNM, Bog Tank, 23 July 1964, J. H. Hessel. CMNH, type locality, 15 August 1968 (2), C. D. Ferris. CDF; type locality, 13 August 1968 (4), 15 August 1968 (2), C. D. Ferris.

**Distribution.** White Mountains of Arizona, presently known from a few localities near McNary (Apache County) and recorded from Maverick and Greer, same county.

**Flight Period.** Dates on specimens range from 19 July to 25 August, one brood.

**Remarks.** This population is given species status for several reasons. First, it is obviously reproductively isolated in nature. Secondly the genitalia of both sexes are not only strikingly more divergent than any of the subspecies of *rubidus*, but have about the same hiatus in degree and kinds of differences from *rubidus* as the related species *xanthiodes* and *editha* have from each other. Further, the lateral shape of the valvae of *rubidus* is more like *xanthiodes* and *editha* than *ferrisi*'s distinctive shape. The wing shape is also unique with noticeable differences in the veins of the forewing which are much more separated affording a wider costa. There are numerous wing characters that are also distinctive, not found in any extreme of *rubidus*. The lack in *rubidus* of distinctive orange on the forewing under surface, for instance, is often used as the first step in keying it from other *Lycaena* species (Clench, in Ehrlich and Ehrlich, 1961; Ferris, 1971a). Such a method would separate *ferrisi* quickly from *rubidus*, using these keys.

Since *editha*, *xanthiodes*, *rubidus*, and *ferrisi* are closely related, there is

about the same hiatus between the first two as the latter two. Also, *editha* reportedly feeds on *Horkelia* and *Potentilla* (Rosaceae) (Holland, 1930; Klots, 1951; Brown, Eff and Rotger, 1957; Ferris, 1971b; Howe, 1975) *xanthiodes xanthiodes* on *Rumex hymenosepalis* (Klots, 1951; Ehrlich and Ehrlich, 1961) and *xanthiodes dione* Scudder on *R. obtusifolius* L. (Ehrlich and Ehrlich, 1961; Howe, 1975), while *rubidus* feeds on divergent *Rumex* and *Oxyria*. These relationships add some interesting possible evidence about phyletic relationships in the genus, as will be discussed in the concluding sections of this paper.

We examined 72 males and 48 females of *ferrisi*.

*Etymology.* It is a privilege to name this new species after Dr. Clifford D. Ferris of the University of Wyoming in recognition of his work on western Nearctic Lepidoptera. He also collected the original specimens of *L. ferrisi* from the type locality.

## DISCUSSION

### Pre-Pleistocene and Pleistocene Environments and the Evolution of *L. rubidus* and *L. ferrisi*

#### Introduction:

Students of geology and paleobotany in the western Nearctic characterize the effect of the Pleistocene glaciations on its biota in similar ways, but one point of contention concerns the origin of the fauna and flora undergoing these changes. The larger background to Pleistocene changes has importance in considering the evolution of *ferrisi* in relation to the subspecies of *rubidus*.

The classic theory concerning pre-Pleistocene origins (Darwin, 1883; Hooker and Gray, 1880; Rydberg, 1914) holds that the major circumpolar flora of the Pleistocene underwent its main circumpolar movements during the oscillations of flora corresponding to the four Pleistocene glaciations. According to this theory, southward penetration of the glaciers caused successive vegetational zones to replace each other resulting in a vast displacement and telescoping of the flora. When ice retreated and warmer climate ensued, arctic species found refugia throughout the high mountain areas of North America. More recent workers like Tolmochev (1959a, 1959b) and Hultén (1962a), however, have considered this idea oversimplified and naive of other factors and evidence. They suggest that an ancient Tertiary alpine flora was already in place by the Pleistocene, not only in North America but in other austral regions of the Northern Hemisphere and that it invaded northward in rapid radiation due to depression of the timberline (which will be discussed further later) and the availability of unstable virgin soils as the glaciers retreated and advanced. Axelrod (1970) postulates the same situation for an archaic desert flora being already in place in North America by the Tertiary. In relation to evolution in *rubidus* and *ferrisi* this debate has two consequences.

1. Evidence reviewed below suggests firstly, that the segregation of the population becoming the divergent *ferrisi* predates the Pleistocene. Secondly, evidence indicates that from an already existing montane gene pool of "proto-*rubidus*", *ferrisi* had been evolving as a southward mesic relict before its closest northern counterparts (parent stock of *rubidus* in montane Colorado closest in traits to *ferrisi* today) were caught up in the changes of the Pleistocene. These changes themselves did not reach south to "proto-*rubidus*"'s only southern segregation until the last glaciation and even then in such a fashion to isolate it further from the north.

2. Regardless of the origin of the flora affected by the Pleistocene, the general patterns influencing the present flora and its associated insects can be fairly consistently understood, especially northward where more paleobotanical studies have been done. These are the factors influencing the evolution of *rubidus* subspecies.

Glacial Oscillations and the Evolution of *L. rubidus* subspecies:

1. On the continent: Following the Pliocene, there was fairly free expansion of distributions of North American flora and fauna from the Aftonian through Sangamon periods, except for some divergence along the 100th meridian where open woodland or grassland separated two broad belts of climax forest on the east and on the west (Mengel, 1970; Ross, 1970). Beginning with the Nebraskan glaciation of the Pleistocene, the continent was affected by four alternations of glacial advance and interglacial retreat coinciding with distributional isolation and distributional expansion in the flora and fauna, respectively (Rand, 1948; Ross, 1970). During glacial advance, northern species moved southward with boreal forest and tundra, where in interglacial periods they could either adapt to the coniferous forests which subsequently followed the glacial retreat northward, or retreat, in turn, before them. For biota south of the full glacial advance, the interglacial was a period of broad transcontinental banding of the flora allowing continent-wide ranges in associated fauna (Ross, 1965; Mengel, 1970). Subsequent disjunction took place with the next glacial advance, usually causing a separation east and west (Ross, 1965). In the west, where regional oscillations were taking place due to independent montane glaciations of the Pleistocene, montane forests replaced the glaciers' upland retreat in a similar fashion, forming islands in which differentiation of biota could occur. These general processes repeated four times (Ross, 1965) and were then followed by the current extended warm and dry period. During this period, arid grassland has developed in many areas as the principle source of present day disjunction between local montane or coniferous forest environments (Clements, 1945; Weaver and Albertson, 1956; Deevy and Flint, 1957; Wells, 1970a, 1970b; Wright, 1970; Johnson, 1976a).

2. In the mountains. In the montane areas, glaciation also depressed the timberline depending both on the particular amount of spatial advance in a region, along with overall effects exerted by the continental glaciers depressing the general timberline as much as 600 meters over much of the continent (Maher, 1963). Axelrod (1948) posits that the effects of this glaciation as evidenced by the relationship of presently disjunct montane populations was a continuous montane flora and fauna extending from North America to Asia and allowing north-south traffic from Asia to Mexico. Oscillation involving changes in this situation and local ones occurred, similarly, in four cycles. The patterns of the flora during such changes resulted in the wide variety of environments present locally throughout these regions and characterized by the telescoping of divergent biomes within comparatively small linear distances (Weber, 1965). As the interglacial ensued, elements of the alpine flora were effectively isolated, resulting in the various montane regions and general floral associations (Weber, 1965; Mengel, 1970).

The northern subspecies of *L. rubidus* apparently represent relicts of populations which by thermodynamic selection (Clench, 1966) evolved melanic strains during the glacial periods. They then experienced continuous transcontinental distributions during the warmer and dryer (but compared to today, cooler and wetter) periods when coniferous forests followed the retreating glaciers northward. Subsequent glaciation caused compression and isolation followed by a repetition of this entire cycle (Ross, 1965). Present populations represent the situation of *rubidus* following the Wisconsinan glaciation and isolation during the last disjunction caused by the current arid and fire-influenced plains period (Stewart, 1953; Weaver and Albertson, 1956; Wells, 1970b; Johnson, 1970a).

These populations, which are all similar in genitalic and wing characters, could have been continuous in distribution as late as 9,000 to 6,000 years ago (McIntosh, 1931; Pennak, 1963; Wells, 1970a; Johnson, 1976a) according to the timetable of conifer forest advances behind the glaciers. The present dry arid cycle, aided by range fires, began to cause fundamental disjunction (between north, central and southern Rocky Mountains, Great Basin, Black Hills) around 5000-6000 years ago (Sears, 1961; Pennak, 1963; Wells, 1970b; Johnson, 1976a) and con-

tinued to isolate forest ranges as late as 1700 to 300 years ago (Wells, 1970b; Johnson, 1976a). Those populations of butterflies representing these "periglacial" radiations have two present-day morphs, those remaining strongly melanic and those retaining the characteristic periglacial genitalia and wing shape but presently lacking strong melanism in the wings. Interestingly, the former are those in areas where data from paleoclimatological reconstructions, studies in apparent relative dispersals following the Pleistocene (from Alaska southward and United States areas northward) and present-day local relationships indicate distributions remained stable due to few temperature variations during and after the Wisconsinan Period (Ross, 1965). If such a history of climatological stability is true, there would be no reason for melanism in these areas to change. Meanwhile, such populations eastward (*L. r. longi* and the eastern edge of the cline in *r. duofacies*) were influenced by warm, arid conditions (Weaver and Albertson, 1956; Wells, 1970a, 1970b; Johnson, 1976a) which led even to the extinction of such xeric trees as *Pinus ponderosa* L. and *Juniperus scopulorum* Sarg. in most areas (Wells, 1970b). These butterfly populations, nearly genitically identical to *L. r. perkinsorum* have, in result, evidently undergone a shift back to non-melanism. Were it not for the constant montane environment during the Pleistocene (Pennak, 1963; Weber, 1965), relict scarp woodlands along present-day cool streams on the western Great Plains, and the frequency of post-climax prairie relicts eastward in areas of high water table (Pool, 1914; Weaver, 1965) these segregations might have completely disappeared.

A more complex relationship exists southward, along the interface of the plains with the Front Range of Colorado and southward. This region harbors unique relicts in a necklace-like fashion from northern Colorado south to New Mexico and then west to southeastern Arizona. These are what remains of a former spatial convergence of the Eastern Deciduous flora with the Cordilleran flora which moved southward during the Pleistocene, most especially in this case, the Wisconsinan (Ross, 1965). These will be discussed in more detail concerning the isolation of *L. ferrisi*, but it is important to mention them here because of prairie segregations (*i.e.*, on the Colorado plains) which show not only moderate divergence from montane morphs but some evidence of relationship to the large northern segregation *r. longi*. It is probable from a similar distribution and affinity in another prairie-adapted montane species (*Colias alexandra* Edwards) that these were once part of the conifer forest and pine-juniper savannah which formerly extended eastward on the plains and thence northward after the beginning of the Wisconsinan glacial retreat. North of Colorado this woodland was isolated east and west by the breakdown of cool stream connections between the Bighorn Mountains and the Black Hills at the beginning of the current arid cycle (5,000-6,000 years ago) (Sears, 1961; Weber, 1965; Wells, 1970b; Johnson, 1976a) and subsequently north and south by more recent (2,000 years) influence of drought and prairie fires (Stewart, 1953; Weaver and Albertson, 1956; Wells, 1970b; Johnson, 1976a). However, in contrast to east-west disjunction occurring between plains on the Missouri Plateau and the Bighorn and Laramie Mountains mentioned above, there was never an extreme east-west disjunction between these Colorado plains populations and their montane counterparts. They became separated effectively only from the western Nebraska populations by the breakdown of the scarp woodlands in the Cheyenne Ridge. These were formerly in the south panhandle of Nebraska, the southern limit of *r. longi*.

There is also an important distinction between the histories of these plains areas of typical *r. longi* and those of Colorado plains populations. The area of western Nebraska northward never changed from its boreal influence until after the full glacial Wisconsinan, while Colorado plains were influenced by conifer environment throughout the glaciations (Weber, 1965; Wright, 1970). It is our conclusion that the Colorado plains populations cannot be included with *r. longi* and that despite their moderate divergence and moderate isolation, represent a history of significant intergradation with the montane elements of *rubidus* not warranting

subspecific status.

Pre-Pleistocene Isolation and Subsequent Evolution of *L. ferrisi*:

Weber (1965) defines as a single floristic unit the area traditionally called the Southern Rocky Mountains. To him it includes mountains lying south of the Wyoming deserts, west of the Great Plains, north of Santa Fe, New Mexico, westward including the Wasatch, Uinta, La Sal, and Abajo Mountains, Utah, and south to the San Francisco Peaks of Arizona. He states that these areas are effectively isolated on all sides by lowland plains, deserts, and lesser mountain ranges. Likewise, physiographically, the Colorado Plateau, one nearly square singly uplifted crustal block encompassing nearly five hundred miles on a side, defines much of this same area (King, 1969; Shields, 1975). It has been degraded to form the various contemporary mountain ranges and other upland, plateaus, and canyonlands of the region.

The White Mountains represents part of another element, separated from the Southern Rocky Mountains physiographically by about 120 miles of arid lowland. It comprises the southernmost edge of parts of the Colorado Plateau that have been segregated by peripheral degradation of the formation. Here, floristically, it comprises the northern edge of a group of small mountain ranges in southern Arizona, and southwestern New Mexico, whose history is one of influence from Mexico rather than the north. The classic idea of this affinity was developed by Watson (1890) and also by Hooker and Grey (1880). More recently (Wells, 1966) it has been referred to as the "Chihuahuan sub-element" (Clichy and Sears, 1956). As will be mentioned below, one characteristic in the history of this element is its tendency to have become forced into an eastern affinity rather than a northern or western one by effects of the Pleistocene, especially the Wisconsinan.

As has been mentioned above, the present-day environment, flora, and fauna characterizing the Southern Rocky Mountains are the result of the disjunct remnants of a formerly more continuous montane biota. These were pushed to lower altitudes during the glacial periods and then divided into isolated populations during the upland retreats of the interglacial periods. Johnson (1976a) has described how this process first isolates complexes of regional upland areas and then the individual uplands within these regions themselves. On the larger level, then, in physiographic or floristic zones, retreat and isolation of the faunas has tended to pull toward the center of these zones, leaving each of them even more effectively isolated from each other. Thus, one must imagine the Southern Rocky Mountain biota and the Chihuahuan Element biota being increasingly individualized since the Pleistocene, especially since Weber (1965) and Clichy and Sears (1956) have shown that the effect of aridity not only increased southward, but began to isolate the southern areas as early as 16,000 years ago. Meanwhile, much of the northern area (Nebraska and Wyoming) was under the influence of the full glacial until at least 10,000 years ago (Weber, 1965; Wells, 1970b; Wright, 1970; Johnson, 1976a).

Studies of the paleobotany of the western United States have increased in recent years and along with these, studies in the southwest. However, Martin and Mehringer (1965) and Wright (1971) have noted that studies south of the Southern Rockies as defined by Weber (south of the San Francisco Peaks, Arizona, in particular) have been more difficult, and thus less frequent, due to the effect of long-term aridity on the study methods. Along with Clichy and Sears (1956), their scenario of Pleistocene history in the southwest would attest that prior to the Wisconsinan glaciation, there was no boreal invasion of any part of present-day Arizona or New Mexico. Thus, one can assume that prior to the Wisconsinan period, throughout the three earlier glaciations of the Pleistocene, the southwest's long-term physiographic and floristic patterns were following their perennial course in relation to continuing degradation of the physiographic landscape



and isolation of local floras and faunas by the effects of increasing southern-influenced aridity. It can be imagined that the stock of *ferrisi* was already a relict by that time, isolated southward by the physiographic isolation of the White Mountains and the division of the montane flora into the northern, moister, admixture of the Southern Rockies and the more arid one being influenced by the southern connection. This is important because it will be shown that the major disturbance to this pattern, the boreal invasion of the area during the Wisconsinan glaciation, tended to reinforce this already developed division. Its effect was to push the non-boreal elements of the San Francisco Peaks-Southern Rockies area northward and westward and those of the White Mountains southeastward, respectively.

Arizona and New Mexico experienced effects of the full glacial Wisconsinan from about 17,000 to 23,000 years ago (Martin and Mehringer, 1965). The full glacial effected by the continental glaciers was at its height from 20,000 to 14,000 years ago (Weber, 1965; Wright, 1970; Johnson, 1976a). Thus, the effects of the continental glaciers on the high altitude montane glacial advance was being felt in the south as early as before the maximum extent of glaciation in the north. It was to subside at least 6,000 years sooner. Northward coniferous advance behind the retreating glaciers began in the north about 11,000 to 12,600 years ago (Wells, 1970b; Wright, 1970; Johnson, 1976a). In the southwest, Martin and Mehringer's reconstruction indicates this montane glacial influence effected a boreal environment of spruce, fir, and pine connecting the area from the San Francisco Peaks southeastward to the White Mountains, but with a thin midsection. The biota characterizing these areas prior to that time where pushed northwestward into southeastern Utah and southeastward toward southwest New Mexico respectively, probably with no connection. Consistant with this evaluation, Shields (1975) notes his investigations also indicate that southeastern Utah retained its arid conditions throughout the Pleistocene (and much before). This boreal period lasted until about 17,000 years ago, with return to aridity beginning almost immediately. The cumulative effect was an even more total demise of pre-Wisconsinan vegetation which had already been experiencing continued disjunction into isolated populations. Moister conifer forest spread down again from the northwest and upwards from the southeast, followed almost immediately by its retreat to the respective upland refugia as the arid trend hastened. In the case of Arizona, this upwards isolation probably was even more rapid since Clichy and Sears (1956) cite the return of the full desert condition to the lowlands as early as 12,000 years ago. In the north (Wyoming and Nebraska) this did not occur until about 2000 years ago (Wells, 1970b; Johnson, 1976a). Thus any isolation in the White Mountains remained intact through the Wisconsinan.

Further evidence about the integrity of such a pre-Pleistocene isolation concerns whether the area was connected to possible dispersal routes opened up by the varying conditions of the glaciations, especially the Wisconsinan. If so, any distinct populations could then have found easy dispersal elsewhere and have been absorbed into other populations. Such openings for dispersal occurred throughout the western United States during the Pleistocene and it is important to examine whether or not the White Mountains was effected. One of these dispersal routes, to areas of the Southern Rockies, included runways opened by the convergence of the westward moving Eastern Deciduous flora and the south and eastward moving Cordilleran flora (Ross, 1965). Eastern Deciduous flora reached the eastern flanks of the Rocky Mountains probably following the full glacial of each glacial episode, but in the Wisconsinan probably from about 15,000 to 12,600 years ago. This was in response to increased moisture in the present-day plains states (Wright, 1970) and the affinity of deciduous forest to the concentric bands outlying the advancing boreal forests (Wells, 1970b). Access to northern areas of the Southern Rockies (*i.e.* the Black Hills) was cut off during the full glacial by cyclonic winds (Smith, 1965; Wright, 1970) but more southern areas probably received this invasion prior to the beginning of the glacial retreat. At any rate, this westward march of

the Eastern Deciduous Forest spread north and south along the flanks of the Rocky Mountains and converged with the Cordilleran flora which had been forced southward by boreal forest and southern movement of northern coniferous forest elements. Prevented from moving westward across the highly glaciated divide (Ross, 1965), these elements mixed for a few thousand years and then began to retreat into relicts about 10,000 - 5,000 years ago (Wells, 1970b; Wright, 1970; Johnson, 1976a) more hurriedly to the south in response to the rate of the arid cycle there (Clichy and Sears, 1956; Weber, 1965; Wells, 1966). These relicts still form a long "necklace" along the eastern front of the Rocky Mountains and are inhabited by fauna evidencing the former presence of broad north-south runways during this period (Ross, 1965). Had the White Mountains not been isolated from this occurrence, any more mesic fauna in its region would have been easily absorbed northward. This did not happen.

A northward and westward Wisconsin corridor developed when other mesic dispersal routes opened up from the Great Basin southward (Ross, 1965). In evaluating the effects of these, Ross stated they were probably the first effective Pleistocene connection between the Rocky Mountains and the Sierra (Ross, 1956; 1965). The success of this late Pleistocene corridor was undoubtedly due to the more southerly effect of the extreme glaciation characteristic of the Wisconsin. Ross mentions the location of the San Francisco Peaks as the southernmost latitude affected by this pluvial runway. Thus, in a least two cases — northwestward isolation of the more arid conifer environment due to boreal invasion of the montane area of Arizona, and effect of Pleistocene dispersal routes — the biota of the San Francisco Peaks area of Arizona had ample opportunity for absorption into other Southern Rocky Mountain elements. Meanwhile, eastward elements had the opportunity for widespread northward and eastward dispersion due to the floral convergences along the eastern flanks of the mountains. Though the White Mountains would be nearly a converging point where these two runways extended, there is no evidence either of historical participation in these events (evidence is rather to the contrary) or that any mixing of the population *ferrisi* and *rubidus* (northern Arizona and northern New Mexico northward) has occurred. It is our conclusion that this population has been isolated in more mesic environments in the White Mountains since before the four glaciations of the Pleistocene.

#### Melanism and Subspeciation

Melanism occurs in the females of *rubidus* and *ferrisi* and seems to have evolved through two parallel processes — populations affected by high elevation montane glaciations of the Pleistocene and populations evolving while circumscribed in distribution around the northern continental glaciers.

Relationships of melanism in the wings is reflected by consistent characters of the genitalia in the four peri-glacially evolved melanic subspecies *r. rubidus*, *duofacies*, *perkinsorum*, and *longi*. Consequently, these peri-glacial melanics are assumed as formerly continuous in distribution and of sufficiently early origin to allow some populations to shift back to a more orange ground color. In these melanics the wings appear heavily scaled and "flat" in color, without a sheen. Meanwhile, montane melanic populations reflect a smaller expanse of the wing, a more arch-shaped outer margin on the forewing, and their scales seem much more thinly layered. Their darkening has a shiny, often goldlike, sheen. The genitalia of the montane glacially evolved populations all indicate a probable former continuous distribution as well as their history of intergradation with associated lowland morphs. Subsequent geological and paleobotanical changes in the regions inhabited by these populations have caused local range disjunctions and in some cases complete regional allopatry of some populations from the central range of the species. These include three that are either completely allopatric or show only minor secondary intergradation — the peri-glacial melanics *r. rubidus*, *perkinsorum*, and *longi*. Another melanic population, peri-glacially evolved *duofacies*, survives with distinct



traits within at least part of the *rubidus sirius* range itself. It inhabits lowlands allopatric from *rubidus sirius* but also becomes clinally the basic montane morph of *rubidus* in the Northern Rocky Mountains. Genitalia throughout the cline evidence a common peri-glacial origin, which occurred at a juncture of montane glacial activity and the southern extreme of the continental glaciers themselves. The other melanic populations are those scattered disjunctly throughout the montane areas included in the subspecies *sirius*. These all show histories of intergradation with the transwestern Nearctic populations of the species.

Montane melanism evolved in the high altitude in relation to extensive montane glaciations during the Pleistocene. Because of the nature of these glaciers' effects on the physiography and flora, it is not possible to explain the present-day ranges of these populations by simple altitudinal or even ecological correlations. Some strongly melanic populations occur at lower altitudes where there were extensive glaciations extending outward from the mountains or where unique combinations of latitude and proximity to the continental glaciers was depressing the timberline. These populations, as evidenced by the genitalia, all bear phyletic relationships to each other and may even represent former continuous, but meandering, distribution about the full glacial Rocky Mountain glaciations. However, it is also likely that even their former relationship with lowland forms was at that time clinal. Today, these melanic populations occur along a "stair-step" pattern of montane grasslands not in precise relations to contemporary altitudinal ranges. Here, intergradation in varying degree is occurring with the lowland non-melanic populations. This pattern is so complex as to leave 1000 to 1500 feet of distinct range separation between these populations at one place (F. M. Brown, pers. com.) while at others to afford nearly total blending (M. Toliver, R. E. Stanford, pers. com.). It is easy to see why lepidopterists have puzzled at whether montane melanism was or was not a clinal phenomenon.

A unique trait of some high altitude melanic populations in Colorado is their feeding on *Oxyria* as the larval foodplant. It can be supposed from this that if this usage is fairly strict, according to Hopkins Host Plant Principles it has phyletic significance. Someone may be able to define these particular montane populations as a distinct subspecies. However, such a name would have to be applied strictly to known *Oxyria*-feeding populations suspected to have evolved from one common origin. If such a name became applied simply to wing character morphs it would certainly not have much value in relation to the other subspecies named in this paper. Even if such an *Oxyria*-feeding subspecies could be defined, the extent of its former range could not be known. *Oxyria* usage could have evolved at several parallel points in space or time, as well as usages of divergent high altitude *Rumex* species.

Montane melanism has evolved independently in at least the Ruby Mountains of Nevada and the Wasatch Mountains of Utah. These morphs are similar to montane Colorado *r. sirius* but doubtfully from the same parent stock. No names are given to these populations. They do not show genitalic divergence nor comprise major segregations exerting influence on the general characters of *rubidus* in their region.

Melanism occurs at a low frequency in montane *ferrisi*, though some individuals which are melanic may be strongly so. As mentioned before, selection for melanism in glacially influenced regions was probably from thermodynamic pressures. However, it is of interest that melanism in the males, which appears as darkening of the upper surface orange, occurs presently only on montane glacially derived subspecies, with the possible exception of the basin morph of *duofacies*. We have mentioned previously that rate of divergence in females seems to exceed that in the males. It may be that noticeable melanism in the males of *sirius* has remained stable due to the much longer history of glacial environments in their mountain regions in comparison to the limited history of those influenced only by continental glaciations of the Pleistocene. It is debatable whether there could have been a post-glacial shift back toward non-melanism in the males of peri-glacial subspecies.

It is hard to imagine, given their present-day range disjunction, how the rest of their traits could have remained so alike during such a shift. There is evidence of such a shift in the females, but likewise, their divergent under surface wing characters are the major source of sexual dimorphism in *rubidus*.

Since peri-glacially evolved melanic populations on the plains of western Nebraska north to western North Dakota have apparently had sufficient time to return to an orange condition (while maintaining wing shape and genitalia relating them directly to their melanic counterparts in the northwest United States) we must conclude that the 8,000 to 10,000 years of gradually warmer and more arid interglacial have been adequate for such a change. Using this as a measure, the resulting complexity in widely intergrading morphs (like the populations of *sirius*) can have some meaning. The integrities of any formerly allopatric montane melanics within its range have undoubtedly been disrupted. Meanwhile, even small regional populations, able to remain allopatric from the *sirius* gene pool, have undergone shifts from melanism to orange morphs. Two examples are the *perkinsorum* population on the Yakima Plateau of Washington, and the arid basin populations of *duofacies*.

#### Foodplants:

Though *Lycaena rubidus* has long been known to feed on *Rumex* sp. and more recently *Oxyria* sp., surprisingly little information concerning diversity or local utilizations has been published. This seems typical of all the species of *Lycaena* and may be a result of the assumption that the biologies of these insects are not of particular interest or usefulness for study. The unfortunately small number of foodplant records available for *L. rubidus* have been reviewed earlier in this paper. A synopsis of the two genera known as foodplants is given as an appendix to stimulate interest in this aspect of *Lycaena* study. Some remarks concerning foodplant relationships known in the genus may also be helpful in referring to the relationship of *rubidus* and *ferrisi*. Their foodplants, along with those of *xanthiodes* and *editha*, have been reviewed already.

There is a possibility, given the frequency of *Rumex* usage in *Lycaena* (6 of 13 Nearctic species which have foodplant data exclusively use *Rumex* or use it along with other plants [Ehrlich and Ehrlich, 1961; Opler, in Howe, 1975]) that it may be a primitive foodplant of the group. It is striking that if *ferrisi* was viewed as an extremely divergent subspecies of *rubidus* with a later origin (one of the Pleistocene glaciations perhaps) it might be expected to feed on some similarly regional *Rumex* species. However, the foodplant is *R. hymenosepalus* which is also the apparently exclusive foodplant of one of the two major east-west segregations of *L. xanthiodes*. The relationship of *xanthiodes xanthiodes* and *x. dione* seems by all evidence to be one of a species of long standing. In fact, they were not considered conspecific for some time. *Lycaena editha* was also formerly linked to *xanthiodes*, but discovery of its early stages separated it as a distinct species.

The separation of the two allopatric segregations *x. xanthiodes* and *x. dione* probably relates to the pre-Pleistocene east-west separation spoken of previously. Undoubtedly, the plants on which they were feeding were also undergoing speciation due to this Tertiary separation. This barrier broke down in repeating cycles during the four Pleistocene glaciations, probably the reason these two segregations are still considered to be conspecific. Their hiatus of genitalic traits is less than that of *rubidus* and *ferrisi*, which we propose were diverging off the same general foodplant stock as the *xanthiodes* parent stock of that time. However, as noted throughout the Discussion section of this paper, *ferrisi* became completely segregated. It may have preserved the usage of widely cosmopolitan *R. hymenosepalus* as part of its traits as a relict species. Meanwhile, *rubidus* went on through much divergence, along with its foodplant. The naming of *ferrisi* as a species, if considered simple "splitting" (without the phyletic rationale) might make some workers

wonder about superficially "similar" cases. One of those suggested might be *L. cupreus cupreus* (W. Edwards) and *c. snowi* (W. Edwards). We have thought about this relationship throughout the study of *rubidus*. Our opinion is that the distributional, wing character, and genitalic relationship of these two subspecies, along with the paleobotanical history would suggest their separation is middle Pleistocene. A thorough study of *cupreus* would probably describe a number of presently isolated subspecies whose disjunctions are the result of the typical montane glacial pattern, but which were probably able to intergrade as recently as the Wisconsinan.

## CONCLUSIONS

In this paper, six subspecies of *L. rubidus* have been recognized on a phyletic basis. It may be possible to describe a seventh such entity if detailed study could delineate its distributional and morphological limits. One population, formerly either unknown to lepidopterists or considered conspecific with *rubidus* has been described as a new species based on its apparent phyletic relationship with this complex and its nearest relatives *L. xanthiodes* and *L. editha*.

The four species *rubidus*, *ferrisi*, *xanthiodes*, and *editha* are seen as a species cluster within *Lycaena* sharing very closely related characters of the male and female genitalia and general foodplant affinities. Within this cluster *rubidus* and *ferrisi* are two closely related species as are *xanthiodes* and *editha*. There is about as much variance in wing and genitalic traits between the former two as the latter pair, which have been recognized as non-conspecific from many years. This is probably because *xanthiodes* and *editha* have arisen from major disjunctions of aggregations of populations, while *ferrisi*'s divergence is the apparent result of pre-Pleistocene segregation as a mesic relict in one isolated area.

Physiographic and paleobotanical factors affecting all the species of *Lycaena* have left a pattern of Tertiary, pre-Pleistocene, mid-Pleistocene and late Pleistocene segregations, depending on the particular patterns of niche requirements in the various parent stocks. Thus, the use of "splitting" or "lumping" by taxonomists must be tailored to the particular situation indicated by each species apparent phyletic history. For this reason it is important that more be considered than character differences in the insects themselves, (especially those simply of the wings). Reliance on differences in characters at one point in time can be deceptive as to former time spans of separation of interbreeding or potentially interbreeding populations, histories of intermittent continuous distribution or interbreeding, or affinities of populations which may be relicts of former sympatries. The taxonomist should take care that interpretation of relationships within and between groups conform to as clear a phyletic view as can be constructed. The description of such dynamic relationships within and between various species of *Lycaena* is of more interest and importance than the simple delineation of names.

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## APPENDIX I

A List of 53 Taxonomically Significant Characters of the Male Wings Used  
In Constructing Figure 5

1. Forewing, under surface, postmedian spots oblongate.
2. Forewing, under surface, first discal spot tends to split in two.
3. Hindwing, under surface, only characters visible are marginal markings and crescent line.
4. Hindwing, under surface, crescent line visible only as blotches through heavy dark scaling.
5. Hindwing, under surface, crescent line "imprinted".
6. Hindwing, under surface, crescent line light blotches in avallaneous ground color; only other mark, similar discal slash.
7. Hindwing, under surface, completely immaculate.
8. Hindwing, under surface, basal slash divided as two.
9. Hindwing, under surface, with marginal orange line.
10. Forewing, under surface, last discal spot lined with white over ground color.
11. Forewing, under surface, all discal spots lined with white over ground color.
12. Hindwing, under surface, mesial line absent, any other markings present.
13. Forewing, under surface, apical spots present.
14. Hindwing, under surface, basal spots absent, but not by obscuring.
15. Hindwing, under surface, ground color "porcelain."
16. Forewing, under surface, peri-glacial morph with no apical spots.
17. Hindwing, under surface, mesial line, first spot dark, rest uniformly lighter.
18. Both wings, upper surface, ground color dark in hue but not due to melanism.
19. Both wings, upper surface, ground color so dark as to make under surface spots invisible above.
20. Hindwing, under surface, anal-mesial spots present.
21. Hindwing, under surface, spot basad basal slash white or absent.
22. Hindwing, under surface, first mesial spot outstanding compared to all others.
23. Forewing, upper surface, first discal spot divided as two, or nearly so.
24. Forewing, under surface, discal spots and that between  $CU_2$  and 2A beneath cell, much larger than any other markings.
25. Hindwing, under surface, any six of eight mesial spots missing.
26. Both wings, upper surface, ground color along margin no brighter than rest of wing.
27. Both wings, upper surface, ground color along margin brighter and wavy in appearance, basally.
28. Both wings, upper surface, ground color along margin brighter and wavy in appearance, basally and marginally.
29. Hindwing, under surface, ground color deep rusty ochre, obscuring all markings.
30. Forewing, under surface, extra marginal spots extending toward apex.
31. Hindwing, under surface, of basal spots, only one between veins  $Sc-R_1$  is present.
32. Hindwing, under surface, crescent line rounded around curvature of wing.
33. Hindwing, under surface, crescent line more oblique across the wing.
34. Hindwing, under surface, configuration of anal-mesial spots as typical of *perkinsorum*.
35. Hindwing, under surface, configuration of anal-mesial spots as typical of *longi*.
36. Hindwing, under surface, darkly overcast with gray-black scales (grizzling), entire wing.
37. Hindwing, under surface, grizzling in basal area and along anal margin.
38. Hindwing, under surface, grizzling along anal margin only.
39. Hindwing, under surface, three basal spots present.
40. Hindwing, under surface, well-developed spot basad basal slash.
41. Hindwing, under surface, all crescents obscured except four before anal margin.



42. Forewing, under surface, first spot in postmedian line missing.
43. Hindwing, under surface, three basal spots and first spot of basal (2) present.
44. Both wings, upper and under, wing shape characteristic of Fig. 1a.
45. Both wings, upper and under, wing shape characteristic of Fig. 1b.
46. Hindwing, under surface, all three post-basal spots greatly enlarged.
47. Hindwing, under surface, first of three post-basal spots largest.
48. Forewing, both surfaces, costa on on Fig. 1b.
49. Hindwing, under surface, mesial line irregular in occurrence and expression.
50. Hindwing, under surface, mesial line irregular in occurrence and all spots reduced.
51. Forewing, under surface, first postmedian spot present.
52. Hindwing, under surface, lacking anal-mesial spots, non-melanic or montane melanic morph.
53. Hindwing, under surface, lacking anal-mesial spots, peri-glacial morph.

A List of 33 Taxonomically Significant characters of the Male Genitalia  
Used in Constructing Figure 6

1. Valval process with large initial caudal tooth, then tapered gradually cephalad (Fig. 23d).
2. As above, but not as pronounced.
3. Valval process with teeth broadly spaced (Fig. 31d).
4. Valval process tapered from both ends (Fig. 28, 29d).
5. Valval process one single unincised tooth (Fig. 33d).
6. Valval process with large initial cluster of teeth, then tapering gradually cephalad (Fig. 19, 21d).
7. Valval process tapered from both ends, but teeth more widely spaced (Fig. 29d).
8. Valval process tapered from both ends, teeth close together (Fig. 28d).
9. Lateral shape of valvae as typical of all subspecies of *rubidus* (Fig. 14).
10. Lateral shape of valvae as typical of *ferrisi* (Fig. 14h).
11. Saccus "crowned" (Fig. 28, 29a).
12. Saccus "crowned", but with small "crown" (Fig. 29a).
13. Saccus "crowned", but with large "crown" (Fig. 28a).
14. Saccus "high-crowned" (Fig. 33a).
15. Saccus "toothed" (Fig. 19, 23, 25a).
16. Saccus "toothed" to "semi-crowned" (Fig. 21a).
17. Saccus "humped" (Fig. 31a).
18. Uncus "thin" (Fig. 28, 29c).
19. Uncus "wide" (Fig. 19, 23, 25c).
20. Uncus "bulbous" (Fig. 33c).
21. Falces gradually tapered caudad from wide "elbow" (Fig. 19, 21f).
22. Falces with noticable shouldering, ventral curvature of "elbow" (Fig. 19, 21f).
23. Falces extremely broad from "elbow" to caudal end (Fig. 33f).
24. Falces narrow (Fig. 28, 29f).
25. Falces narrow, with shouldered taper midway between "elbow" and caudal end (Fig. 23, 25f).
26. Falces narrow, with curved hump between "elbow" and caudal end (Fig. 29f).
27. Falces narrow, ventral surface bent proximal (Fig. 31f).
28. Cephalad tip of aedeagus with large "knob-end" and slight dorsal tooth (Fig. 33e).
29. Cephalad tip of aedeagus with "hook"-shaped end (Fig. 21, 23, 25e).
30. Cephalad tip of aedeagus with "knob" end, no "hook" or "tooth" (Fig. 28, 29e).
31. Cephalad tip of aedeagus more "hook"-ended than "knob"-ended, but not exactly either.
32. Cephalad tip of aedeagus nearly without any "knob" or other enlargement

(Fig. 31e).

33. Cephalad tip of aedeagus nearly without any knob, but with slight hooklike tooth (Fig. 19e).

## APPENDIX II

### Index of Ridgway Colors to More Colloquial Terms (alphabetical)

- Avallaneous: Green, tinted toward olive and gray; a dull color.  
 Cadmium Orange: shiney orange, distinctly golden.  
 Cartridge Buff: A buff that is very yellow, but dull.  
 Cream Buff: A buff that is whitish-yellow in tint.  
 Cinnamon Buff: A buff with a distinctive pink cast.  
 Drab Gray: A gray tinted toward dull rusty brown.  
 Mars Orange: An orange distinctly reddish and deep hued.  
 Mummy Brown: A very flat black-brown.  
 Ochraceous Orange: Ochraceous, but distinctly orange; a very flat orange.  
 Ochraceous Salmon: Ochraceous, but distinctly yellow-pink.  
 Olive Buff: A buff with an olive cast, lighter than Avallaneous.  
 Orange Chrome: Shiny orange, distinctly reddish.  
 Orange Rufous: An orange that is reddish, but not as reddish as Mars Orange.  
 Pale Cream: Yellowish-white, more whitish than cream.  
 Pale Ochraceous: Ochraceous, but less intense, more whitish to cream.  
 Pale Olive Buff: Like Olive Buff, but lighter, with just a cast of olive.  
 Verona Brown: A brown that is distinctly yellow-buff, but very dull.  
 Vinnaceous Cinnamon: Like Cinnamon Buff but much more reddish-pink in cast.  
 Vinnaceous Rufous: An orange that is distinctly dark purplish-red in hue.  
 Warm Buff: A buff that is between Cream Buff and Cartridge buff in amount of yellowing.  
 Xanthine Orange: A bright orange, more to the yellow side than the red side.

## APPENDIX III

### A Brief Synopsis of the Genera *Rumex* and *Oxyria* in Western North America (Polygonaceae)

[authors of botanical names are cited by the official abbreviations as listed in Britton and Brown, 1970.]

The genera *Rumex* and *Oxyria* belong to the buckwheat family which contains 32 genera and about 800 species in North America. Of these, about 100 species belong to the genus *Rumex* (docks, sorrels) and a single species to the genus *Oxyria* (mountain sorrel).

I. *Rumex*. (Species marked with an asterisk (\*) have ranges or habitat features such that they are probably not utilized by *rubidus* or *ferrisi*.)

*Nine species occurring in the west have relatively limited ranges:*

*R. violascens* Rech.\* and *R. berlandieri* Meisn.\* are Sonoran species, the former ranging from southern Oregon through California to Arizona, Texas, and Mexico, the later from southern California east to Texas and south into Mexico. *R. crassus* Rech. is coastal and ranges from Los Angeles north to Washington. *R. orthoneurus* Rech.\* occurs only in extreme southeastern Arizona and into Mexico. *R. lacustris* Greene is a species of marshes, ephemeral ponds and alkali sinks from 4,500' to 8,000' in southern Oregon and California from Modoc to Mono County. *R. praecox* Rydb. is a Rocky Mountain species ranging from central Colorado north into Montana and growing on open ground along streams. *R. hesperius* Greene occurs in submontane lowlands from Alberta to Wyoming and Washington. *R. salinus* Nels. is found in submontane alkaline soils in western Wyoming and

Colorado. Finally, *R. pycnanthus* Red. (= *R. subalpinus* Jones) is a submontane and montane plant growing in moist and swampy ground in western Colorado and Utah.

*The seven remaining native species or species groups are wide-ranging:*

*R. altissimus* Wood (= *R. britannica* L.) ranges from the eastern United States to North Dakota, eastern Colorado and into New Mexico and eastern Arizona. It is found on open ground and plains along streams, below 6,000'.

*R. hymenosepalis* Torr. ranges from the southern one quarter of California to Wyoming, western Colorado, Texas, and Oklahoma and south into Mexico. The plant grows in dry, sandy washes and prairies mostly below 6,000'.

*R. venosus* Pursh is a species of the Great Plains occurring from Missouri westward. It is found in eastern and northern Colorado, north to Saskatchewan and Alberta and west to the western half of Washington and Oregon. Then to the northeast corner of California. It grows in dry, sandy soils, along roadsides, in prairies and sage scrub at and below submontane elevations. It is the characteristic *Rumex* of high water table prairie relicts in the Sandhills region of the Great Plains.

*R. paucifolius* Nutt. (= *R. geyeri* Meisn.) occurs in northwestern Colorado and the Sierra Nevadas from Tulare County north into Alberta and British Columbia. It grows in alpine areas, mountain meadows and parks from 3,500' to 12,250' and is common to alpine-boreal floras of the Rocky Mountains, Sierra Nevadas and Cascades.

*R. fueginus* Phil (= *R. persicarioides* L., *R. aritimus* L.) occurs generally across all of the western United States and Canada. It is a plant of wet places, marshes, lakes, sandy shores, often brackish locales up to 8,500 ft. probably occurring most frequently at the submontane level or below.

*R. occidentalis* Wats. and *R. densiflorus* Osterh. The latter species is considered a form of the former by some authors. *R. occidentalis* ranges from Labrador to Alaska and south on the Pacific Coast to Central California (San Francisco Bay, Klamath Lake, northeast California) and in the Great Plains to Texas as well as New Mexico and Arizona. Both forms grow in wet meadows, bogs, marshes and brackish places up to the subalpine level (10,000'). Both occur in the White Mountains. *R. fenestratus* Greene and *R. confinis* Greene appear to be synonyms of *R. occidentalis*. *R. nematopodus* Rech.\* seems to be a form of *R. occidentalis* which occurs in extreme southern New Mexico and Arizona south into Mexico.

*R. triangulivalvis* (Danser) Rech. group. Very confused synonymically. Three species most widely recognized — *R. mexicanus* Meisn., *R. utahensis* Rech., *R. transitorius* Rech. and *R. salicifolius* Weinm. The "species" *R. utahensis* Rech., *R. transitorius* Rech. and *R. californicus* Rech. are often mentioned either in relation to these species or as forms. The group as a whole ranges across the Great Plains to the Pacific Coast in Canada and in the United States as far south as San Diego County, California, southern Arizona and Texas. All are described as common and widespread in wet soils in diverse ecological communities from 300' to 11,500', Sonoran to high montane.

*Ten species of Rumex have been introduced:*

These are naturalized species or escapees from Europe and Asia. Five are limited to the Pacific States and Arizona, many in waste places of low altitude: *R. conglomeratus* Murr.\*, *R. dentatus* L.\*, *R. pulcher* L.\*, *R. stenophyllus* Ledeb.\*, and *L. kernerii* Borb.\*. Another *R. acetosa* L. occurs in wasted places in the eastern United States west to Montana and Alberta. Another, *R. patienta* L.\* grows in several restricted localities as an escapee on the west coast. Three others are widespread: *R. acetosella* L., *R. crispus* L. and *R. obtusifolius* L. These are known to be utilized by Nearctic butterflies as larval foodplants. *R. obtusifolius* is widespread in low, moist areas; *R. acetosella* and *crispus* occur in fields and waste places at many elevations but mostly below timberline.

## II. *Oxyria*.

There is a single species in the Nearctic — *O. digyna* (L.) Hill. It is circumpolar from the arctic circle south, in western North America to the Sierra Nevadas and

Warner Mountains of California to the San Francisco Peaks in Arizona, and to New Mexico in the Rocky Mountains. It is alpine and boreal, growing among cold, wet rocks, and characteristic of the elevations 9,500' to 12,500' (Colorado), 10,000' - 12,000' (Arizona).

The above synopsis is condensed from material in Abrams (1940), Booth and Wright (1950), Core (1955), Davis (1952), Harrington (1954), Harshberger (1911), Jepson (1951), Kearney and Peebles (1960), Munz and Keck (1959), Rydberg (1932; 1954) and Weber (1953), in the Literature Cited.

#### APPENDIX IV

*Material Examined* — A list of localities from which specimens were studied. Listed alphabetically by state and county.

State names: CAPITALIZED.

County names: *Italicized*.

Localities separated by semi-colons (;).

National Parks are treated as *counties*.

Ambiguous or unplaced localities are placed at the end of each state entry under the name of the state. ENE = east-north-east, etc.; Hwy = Highway; Natl. = National.

#### CANADA.

ALBERTA. Lethbridge; Medicine Hat.

#### UNITED STATES.

ARIZONA. *Apache County*: Bog Tank nr. McNary; Ditch Camp, White Mountains; Greer; 13 miles east of McNary; White Mountains.

CALIFORNIA. *Alpine County*: Ebbetts Pass; Markleeville; 39 miles NExE of Tuolumne. *Amador County*: Silver Lake. *Inyo County*: Inyo county; Onion Valley; Mono Pass. *Lassen County*: Bieber; Hallelujah Junction. *Madera County*: Agnew Meadows; Agnew pass, Devils Postpile Natl. Monument. *Modoc County*: Alturas; Buck Creek; 4 miles west of Canby; Cedarville; Davis Creek; 10 miles south of Davis Creek along Hwy 395; Modoc County; Surprise Valley near Ft. Bidwell; Valley Park; Warner Mountains, 13 miles ENE of Alturas; Willow Park; Willow Ranch. *Mono County*: below Agnew Pass; Bodie; Bridgeport; 17 miles NW of Bridgeport; Cottonwood Canyon, south of Bodie; Deep Creek, Sweetwater Mountains; Mammoth; Mammoth Lakes; Mono County; Mono Lake; Pickle Meadow; Rock Creek; Rush Creek; Swanger Creek; 4.9 miles east of Tioga Pass; Walker Canyon, north of Bridgeport; Walker River; Warren Creek; Warren Fork of Lee Vining Creek at Tioga Pass, TIN R25E section 16. *San Joaquin County*: Farmington River. *Siskiyou County*: Mt. Shasta. *Tulare County*: Monache Meadows. *Tuolumne County*: Sonora Pass; Tuolumne.

COLORADO. *Alamosa County*: South of Sand Dunes Natl. Monument. *Arapahoe County*: Deertail. *Boulder County*: Boulder Canyon; Eldora; Left Hand Canyon, near Boulder; Nederland; north of Parker Dam, Nederland; Spring Gulch; Tossler Lake; Ward. *Chaffee County*: Cottonwood Pass. *Clear Creek County*: Clear Creek; Empire; Georgetown; road east of Loveland Pass. *Conejos County*: Conejos; 3 miles north of Cumbres; Trujillo Meadows Camp, 8 miles north of Cumbres. *Costilla County*: Fort Garland; Mountain Home Lake; Ute Creek. *Custer County*: near Westcliffe. *Denver County*: Denver; Cherry Creek. *Douglas County*: 12 and 15 miles west of Deckers; Manitou Park; Palmer Lake area. *El Paso County*: Cascade; Colorado Springs; Foster Ranch; Fourtain Valley North Cheyenne Canon; Manitou; Manitou Springs north slope of Pikes Peak; Pikes Peak; Rock Creek. *Garfield County*: 25 miles east of Buford; Skinny Fish Camp. *Gilpin County*: Corona Pass Road north of Tolland; Virginia Canyon. *Grand County*:

Granby; Idlewild; St. Louis Creek Camp 3 miles SW of Fraser. *Gunnison County*: bottom of Black Canyon; Blue Mesa Reservoir; Cement Creek, 10-20 miles SE of Crested Butte; Gothic; 9 miles WSW of Gunnison, Hwys 50 and 149; Gunnison Natl. Forest; Kebler Pass; Marble; Ohio; Taylor Lake. *Huerfano County*: La Veta. *Jefferson County*: Clear Creek; Conifer; Cub Creek; Evergreen; Indian Hills; Philipsburg. *Lake County*: Independence Pass Hwy; Leadville; Malta; Tennessee Pass; Twin Lakes. *Larimer County*: Beaver Park; Estes Park; Virginia Dale. *Mesa County*: near Island Lake; Mossland Lake. *Moffat County*: Dinosaur. *Montrose County*: 16 miles SW of Montrose; Uncompahgre Plateau. *Ouray County*: near Camp Bird Mill; Hayden Mountain. *Park County*: vicinity of Alma; Beaver Creek near Fairplay; Jefferson Creek, 3-8 miles north of Jefferson; Mosquito Pass; Penna Mountain. *Park County*: vicinity Ashcroft. *Rocky Mountain Natl. Park*: Allens Park; Beaver Break; Upper Beaver Brook; Utility Camp. *Saguache County*: Blueriver; 4 miles north of Breckenridge; Dillon. *Taylor County*: Almont. *Teller County*: Catamount Creek; Crystal Creek; 4 miles west of Divide; Middle Beaver; Pikes Peak Highway; Rosemont; Woodland Park. *Weld County*: NW of Ft. Lupton. Colorado: Hall Valley; Jamesta; Plainview; South Park; Stapps Lake.

IDAHO. *Ada County*: Boise, Kuna. *Bannock County*: Pacatello. *Blaine County*: Hailey Hot Springs. *Boise County*: Bogus Basin; Boise Basin. *Bonneville County*: Idaho Falls. *Minidoka County*: Rupert. *Idaho County*: Wood River, Sawtooth Natl. Forest. *Lemhi County*: Lemhi. *Payette County*: Payette. *Valley County*: Yellow Pine. Idaho: Great Falls.

MONTANA. *Beaverhead County*: 2-8 miles east of Bannock Pass; Big Hole Battlefield Natl. Monument; Polaris. *Blaine County*: Chinook. *Cascade County*: Great Falls. *Gallatin County*: Bozeman; Gallatin; Gallatin Gateway; Gallatin River; West Yellowstone. *Hill County*: Havre. *Lake County*: Flathead. *Madison County*: Sheridan. *Park County*: Livingston. *Powell County*: Garrison. *Silver Bow County*: Butte.

NEBRASKA. *Box Butte County*: Berea. *Deuel County*: Chappell. *Keith County*: Ogallala. *Kimball County*: Kimball. *Sheridan County*: Ellsworth; Orr Ranch. *Scotts Bluff County*: Mitchell. *Sioux County*: Canyons north of Harrison; Harrison; Squaw Canyon.

NEVADA. *Churchill County*: Fallon. *Douglas County*: Long Valley; Minden. *Elko County*: Angel Lake; vicinity of Arthur; Clover Valley; Elko; Lamoille Canyon; Midas; Ruby Mountains; Ruby Valley; Wells; Wildhorse Reservoir. *Humboldt County*: Jackson Mountains. *Lander County*: Battle Mountain; 4 miles east of Austin; Mt. Challaghan; Italian Creek; Kingston Camp, 30 miles south of Austin. *Mineral County*: Powell Canyon, Wasuk Mountains. *Nye County*: Summit Canyon, Toiyabe Natl. Forest. *Storey County*: Carson City; Virginia City. *Washoe County*: Reno; Sparks; Verdi. Nevada: Toiyabe Natl. Forest.

NORTH DAKOTA. *Slope County*: near Amidon.

OREGON. *Baker County*: Baker; Durkee; Soaring Creek. *Grant County*: Silvies. *Harney County*: Blitzen Valley; Burns; Devine Canyon, 12 miles north of Burns; Frenchglen. *Klamath County*: Klamath Falls; Ft. Klamath. *Lake County*: Horse Prairie, 5 air miles east of Lakewview; Warner Creek Ski Area. *Malheur County*: Nyssa. *Sherman County*: Spanish Hollow Canyon at Hwys 80 and 97; Fulton Canyon. *Wasco County*: 1 mile east of the Dalles; Wasco. *Washington County*: Oregon Regional Primate Center.

SOUTH DAKOTA. *Butte County*: Newell. *Custer County*: south of Wind Cave Natl. Park; Teepae Canyon. *Meade County*: Bear Butte. *Pennington County*:

Wasta. *Wind Cave National Park*: same.

UTAH. *Box Elder County*: Clear Creek. Raft River Mountains. *Cache County*: Battle Creek Vineyard; 5 miles north of Mantua. *Emery County*: Huntington Canyon Camp, 22 miles NW of Huntington. *Salt Lake County*: Alta; Brighton; Little Cottonwood Canyon; Salt Lake City. *Sanpete County*: Flat Canyon Camp 33 miles NW of Huntington. *Summit County*: Park City. *Tooele County*: Settlement Canyon, Ochimon Mountains; South Willow Creek. *Utah County*: Mt. Tipanogos; North Fork Provo River. *Wasatch County*: Snake Creek Canyon; Wolf Creek Camp 14 miles west of Hanna. *Weber County*: Huntsville. Utah: American Fork; Southern Utah; Wasatch Mountains.

WASHINGTON. *Klickitat County*: Goodnoe Hills; Sand Springs Canyon. *Yakima County*: Cottonwood Creek; Sunnyside.

WYOMING. *Albany County*: east of Laramie; Pole Mountain; T115N R73W; Happy Jack Road; *Carbon County*: Smith Creek, Sierra Madre Mountains; Bottle Creek. *Converse County*: Glenrock. *Fremont County*: Wind River. *Grand Teton Natl. Park*: Jackson Hale; Teton. *Hot Springs County*: Thermopolis. *Park County*: Powell. *Platte County*: Diamond Ranch. *Sublette County*: Elkhart Park, Bridger Natl. Forest; Pinedale. *Sweetwater County*: Green River. *Yellowstone Natl. Park*: Sheepeater Cliffs; Wyoming; Black Hills; Circle F. Ranch.