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REASSESSMENT OF THE *COLIAS ALEXANDRA* GROUP, THE LEGUME-FEEDING SPECIES, AND PRELIMINARY CLADISTIC ANALYSIS OF THE NORTH AMERICAN *COLIAS* (PIERIDAE: COLIADINAE)[1]

Clifford D. Ferris[2]

INTRODUCTION

The *Colias alexandra* complex or group (subsequently dissolved) has been a puzzle for many years. W. H. Edwards described *Colias alexandra* in 1863, and also in that year, *Colias christina.* He then described *C. edwardsii* in 1870, followed by *C. astraea* in 1872. In 1898, Skinner proposed the trinomials: *C. a. alexandra, C. a. edwardsii, C. c. christina,* and *C. c. astraea.* In 1935, Klots described *C. christina krauthii.* Six additional taxa have been associated with the *alexandra* group: *C. emilia* W. H. Edwards, 1870; *C. harfordii* Hy. Edwards, 1877; *C. barbara* Hy. Edwards, 1877; *C. alexandra columbiensis* Ferris, 1973; *C. alexandra kluanensis* Ferris, 1981; *C. alexandra apache* Ferris, 1988. In 1973, F. M. Brown placed *emilia* as a junior synonym of *edwardsii.* Also in 1973, Ferris placed *barbara* as a junior synonym of *harfordii,* and proposed the trinomial combination *C. alexandra harfordii.* Recently a new species closely related to the *alexandra* group was described by Ferris (1989a) as *pseudochristina.* Gillette (1989) described it as *C. occidentalis wasatchia,* but this butterfly is not a subspecies of *occidentalis* Scudder, and it manifests some characteristics unique among the North American *Colias* (Ferris, 1989a, and this paper).

Over the years, various authors have placed the taxa associated with the *alexandra* group as trinomial combinations with several different species of *Colias.* These actions are summarized in a prior paper (Ferris, 1988a). Until about thirty years ago, *alexandra* and *christina* were treated as separate species. Then, without explanation, Klots in 1961 (*in* Ehrlich and Ehrlich) combined these two into the single taxon, *alexandra.* dos Passos

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followed suit in his 1964 synonymic list, and, except for minor variations, this has been the arrangement followed until now (see Klots *in* Howe, 1975). I can find no published work which indicates specific reasons for combining these two taxa, but I presume that *alexandra* and *christina* were synonymized based upon similarity of wing shape, superficial morphology of the adults, and perhaps common host-plant family (although a weak reason considering that the majority of *Colias* species utilize legumes). Ferris (1973, 1988a) presented UV-reflectance analyses of this group. In the 1988 paper, he pointed out that several sibling species might exist in the *alexandra* group.

Treating *alexandra* as a single polymorphic species is unsatisfactory when one assesses habitat preferences, geographic distributions, male UV-reflectance patterns (Ferris, 1973, Fig. 3), and especially the wing patterns presented by the associated females. For the study reported here, 84 characters associated with the North American *Colias* were selected for a phylogenetic analysis. These characters apply equally well to *Colias* on a worldwide basis, but additional features would have to be added to accommodate some of the South American and central Asian species. These analyses suggest that what has been called the *Colias alexandra* group is actually polyphyletic.

MATERIALS AND METHODS

Ultraviolet Photographic Methods.

The first use of ultraviolet photography in the study of insects is credited to Lutz (1924). Nekrutenko (1964, 1965a, b) revived this method and applied it to Old World members of the Coliadinae. Eisner *et al.* (1969) applied television methods to obtain pictures without having to resort to film exposure and development. Ferris (1972a) described a simple method for photographing UV-reflectance produced by butterfly wings, and he applied that method in a revision of the *Colias alexandra* "complex" (1973).

Four different phenomena produce a reflectance pattern when butterfly wings are exposed to UV irradiation. The primary source of reflectance is from specialized ridged cover scales which act as miniature diffraction gratings. Photographs of these scales were first published by Kolyer & Reimschuessel (1969), but they did not recognize their function. Subsequently Ferris (1977, 1985) published additional photographs. This mode of UV-reflectance is purely structural and is produced by lamellar ridges associated with the specialized cover scales. The lamellae are spaced such that maximum reflection occurs in the near ultraviolet at wavelengths between 300 and 400 nm. The patterns associated with this type of reflectance are useful as taxonomic characters.

A second type of reflection is produced by an optical interference filter effect, analogous to the reflected colors produced by a thin film of oil covering a water surface. This type of reflectance is seen in species in which the wing-scale layer that covers the wing membrane is thin. It is subsequently referred to as the thin layer effect or phenomenon. This type also occurs when cover scales are highly fenestrated and their longitudinal ridge lines are thin (Downey & Allyn, 1975), or the scales themselves are unusually thin.

A third source of light emitted from wing surfaces exposed to UV irradiation is fluorescence, which occurs when a chemical on the wing surface (usually a contaminant such as exuded body grease) emits light in the visible wavelength range in response to excitation by short wavelength irradiation in the ultraviolet. UV fluorescence may also occur in some chemical compounds. In this instance, short wavelength UV irradiation evokes fluorescence at wavelengths in the near UV. Fluorescence at visible wavelengths is not photographed when a Wratten 18A filter (see below) is used. This filter blocks the visible wavelengths.

A fourth phenomenon is sometimes observed in which a diffuse reflectance is recorded from the basal regions of the dorsal wing surfaces. Heavy concentrations of basal hairs produce a UV-light scattering phenomenon in much the same manner as the scattering of sunlight when it strikes a curved reflecting surface, such as a chrome auto bumper. This effect can be seen to some extent in Figs. **31**, **36**, **68**, and **101**.

The fundamental components associated with a suitable UV photography system include a camera lens that passes wavelengths in the 300-400 nm range, a filter that blocks visible light but passes near UV (Wratten 18A), a suitable light source, and film that responds to UV radiation (Kodak Tri-X, 5063, TMAX, or Panatomic-X). Originally, quartz-glass lenses (pure SiO_2) were used for UV photography since common soda-lime glass absorbs UV light. The compound lenses used in modern high quality 35 mm single-lens-reflex cameras pass sufficient light amounts in the 300-400 nm range to be useful. The spectral characteristic of the photographic system used here is shown in Fig. 1. The optical path consists of a Wratten 18A UV-pass filter, a 3 diopter closeup lens, and an f2.8 Soligor-Miranda 55 mm lens. The wavelength of maximum transmission is approximately 371.3 nm with absorbance equal to 0.82. Photographic exposure time is increased to compensate for the optical path absorbance. The absorbance of the lens system minus the filter is 0.05 in the visible portion of the spectrum.

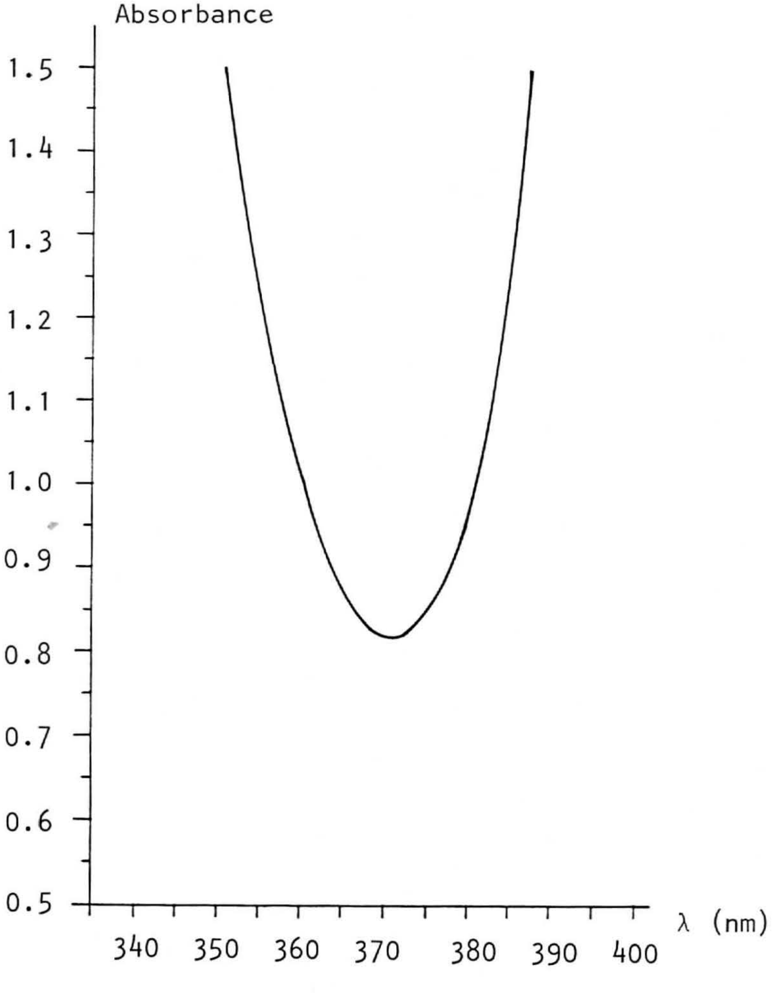

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Figure 1. Optical absorbance characteristic of camera system obtained using a Bausch & Lomb model 2000 scanning spectrophotometer.

In my experience, the most critical element of a UV photographic system is the light source. Since a diffraction grating effect is involved, the angle of incidence of the UV irradiation relative to wing surfaces and the position of the camera film-plane is critical. This point was made apparent by Nekrutenkos work. In one paper (1965a), he reported gynandromorphism disclosed by UV photography (using a single mercury vapor light source). Later it was shown that illumination angle had produced a "gynandromorphic effect" (1965b). I discussed this problem in my 1972(a) paper and suggested a two-lamp method to eliminate such difficulties. This is generally a good solution, but a better one is to use a fluorescent ring light.

Some researchers, including the author, have used two angled photoflash lamps as the light source, but I have discovered a serious problem with this approach. Apparently the emission spectrum of a xenon photoflash lamp does not give broad coverage in the 300-400 nm range. This situation may produce a photographic recording with an incomplete reflectance pattern. To illustrate this problem, the same specimen is shown in Figs. **14** and **15**. The photograph in Fig. **14** was taken using two Sunpak 120C flash lamps. Note that there is no reflectance pattern from the forewing (FW). A ring fluorescent lamp was used to produce the photograph shown in Fig. **15**. Note the well-developed FW reflectance pattern. Fluorescent lamps normally use mercury vapor as the source of UV irradiation, and this excites the fluorescence of the phosphor coating inside the lamp. In comparison with some photoflash lamps, a much broader UV spectrum is produced. I have not experimented with ring photoflash lamps.

I have used different illumination methods over the years for my UV photographic analyses, but I recently repeated all of my earlier studies using ring-fluorescent illumination. A generic "cool white" ring lamp, with an inner diameter of 6", was used. The bottom of the lamp was positioned approximately 2" above the wing surface of the specimen to be photographed, and the specimen was placed in the center of the ring. These recent studies have uncovered some patterns not previously observed. I also discovered an error in the photograph of a ♀ of *krauthii* (shown as Fig. 5d in my 1973 paper). Filtered UV light sources were used to take this photograph, but some visible light was also produced. Apparently, I neglected to place the Wratten 18A filter in front of the camera lens after focusing the camera. Consequently the published photograph is a composite of UV and visible-violet reflectance. Based on current studies, females of *krauthii* are non-reflective in the UV spectrum. Females of *Colias christina* occasionally produce slight dorsal forewing (DFW) UV-reflectance (see Fig. 5b, e of the same paper). The reflectance in the cell area shown by the ♀ in Fig. 5b results from a contaminant on the FW surface.

Several workers have asserted that butterflies must be orange to be UV-reflective. This is clearly not the case. Ultraviolet reflectivity (from specialized cover scales) is independent of wing-pigment color. It is coincidental that the ♂♂ of many orange *Colias* are UV-reflective; their associated orange ♀♀, however, are seldom UV-reflective. On a worldwide basis, many yellow *Colias* species are UV-reflective, but so too is the very strongly reflective *C. chlorocoma* Christoph, a pale greenish white butterfly. O. R. Taylor has informed me that by selective breeding of *C. eurytheme* Boisduval, he has produced yellow ♂♂ which are equally as UV-reflective as normal orange ♂♂.

The UV photographs reproduced herein represent only a very small fraction of the specimens photographed. Typically at least ten male specimens per species were photographed, while the number varied for females depending upon the reflection characteristics displayed. Exceptions include *C. johanseni* Troubridge & Philip to which the author had limited access, and atypical or aberrant specimens. In highly-variable species such as *alexandra*, *christina*, and *pseudochristina*, many tens of photographs were made. The photographs included in this paper represent typical UV-reflectance patterns in those species which manifest uniform patterns, or the range of variation in those species in which UV-reflectance is variable. In the North American UV-reflective species, it is the DFW pattern that changes when variation occurs. The VHW pattern shows little variation, except with specimen age and sloughing off of the specialized reflective cover scales.

Light Microscopy.

Genitalic and wing-scale studies mentioned in this paper were conducted using a new microscope from the recently-released line of Olympus instruments, specifically an SZ6045 high-resolution zoom stereo 'scope equipped with a 100AL-2X auxiliary conversion lens. This instrument permits high-resolution viewing to 250X.

Genitalic Studies.

My examination to date of preserved adult North American *Colias* has not identified any useful taxonomic characters associated with the legs, antennae, eyes, or genitalia. The male genitalia of all of the N.A. *Colias* are similar in gross morphology, although Berger (1986) illustrated several different forms for some of the Old World species, and he established subgenera on this basis. This matter will be addressed in a subsequent paper. Peterson (1963) did extensive morphometric analysis of the male genitalia of a number of *Colias* species and noted some differences, but his findings are now incomplete because of the taxa that have been described in the ensuing years. Several apparently useful genitalic characters have been identified for separating several Old World *Colias* species (Jarvis, 1953; Reissinger, 1989), but these identical characters are not consistent among specimens from the same colony of any given North American species. (See additional comments below.) Some of the male genitalic characters that I have examined are the number and shape of the spiny projections found at the tip of the aedeagus, everted vesicae, the shape of the valvae and distribution of their associated papillae, and the shape of the uncus and superuncus. It was necessary to fabricate a special #36 gauge syringe needle for vesica eversion, since this small size of needle is no longer commercially available [#33 is the smallest gauge currently manufactured]. A custom microscope-stage jig was also fabricated to facilitate vesica eversion. In the North American *Colias,* the vesicae lack any distinguishing characteristics. The slight variations in the shape of this membranous structure within males of a given species are equal to the variations across species. There are no cornuti. The spiny projections noted above erupt from the chitonized tip of the aedeagus. The general female genitalic characters of *Colias* have been discussed in some detail by Stern and Smith (1960). In the females, I have primarily examined the lamina dentata, and the general morphology of the compound corpus bursae. In *Colias,* there is an auxiliary sac or appendix bursae. I have examined the relative sizes of the two bursae and the length and diameter of the connecting duct. To date I have not been able to find any consistent characters; however these studies are continuing.

The very lengthy paper by Reissinger, cited above, deals only with *Colias alfacariensis* Ribbe. In the male genitalia, there is a thumb-like projection from the distal edge of the valve that immediately differentiates this species from its congeners. The genitalic section of the paper by Jarvis, cited above, presents some problems. He has attributed considerable significance to the ratio of the width of the lamina dentata to wing span. According to the text, however, only one specimen of each of four species was so measured. For females of essentially the same size of any given North American *Colias* species, I have found that the width of the lamina dentata varies considerably. Jarvis, in males, also attributed significance to the general shape of the tip of the aedeagus (his Fig. 3) for species separation. Again, only limited numbers of specimens were examined. Two males of *Colias crocea* (Fourcroy) from Alfacar, Granada, Spain, that I examined were different from British examples of this species illustrated by Jarvis (Fig. 3, #1-3). One specimen had six spines on the tip of the aedeagus, and the other seven, while the specimens illustrated by Jarvis show only five. Additionally one of my specimens matched his specimen #2 (except for the number of spines) of *crocea,* but my second specimen (except for having 7 instead of 6 spines) matched his specimen #4 of *fieldii* (Ménétriés) from Kashmir. If one examines the genitalia of only a few specimens of *Colias,* one can easily and incorrectly infer structural significances that prove to be inconsistent after many specimens are examined. The two genitalic illustrations of *fieldii* (Jarvis, Fig. 3, #4-5) are really quite different. It is interesting to note that the "lock-and-key" genitalic hypothesis for species separation has been refuted in the pierid genus *Tatochila* Butler by Shapiro & Porter (1989) and Porter & Shapiro (1990).

Cladistic Analysis.

Various approaches were investigated before arriving at a method for generating the cladograms shown herein, including a limited-character manual computation using the modified Wagner algorithm as presented by Wiley (1981). Various out-groups were examined. Tests were conducted using weighted and unweighted characters, and polarity reversals were also investigated. At the suggestion of Dr. J. Y. Miller, strict binary coding was adopted as the method of choice. For the binary coding used, 0 is the absence of a character and 1 indicates the presence of the character. This approach should remove any bias, other than the echelon of characters selected. For the final analysis using both PAUP and HENNIG 86, 84 characters were defined for the North American *Colias*. In part, this number of characters reflects the adoption of strict binary coding.

Strict binary coding does present one problem regarding color, because it implies that none of the colors coded is the plesiomorphic character. To investigate this problem, characters no. 2-6, and 84 were independently weighted as 2. The topography of the cladograms did not change. As would be expected, minor changes occurred in tree length, and the consistency, homoplasy, and retention indices. The results suggest that orange is perhaps the plesiomorphic character, but all species of *Colias* need to be examined before any such conclusions are made.

As is shown in Table 5 of Appendix 1, the characters selected to differentiate *Colias* species relate to color, UV-reflectance pattern, aspects of maculation, wing shape, voltinism, and larval host. The only useful *structural* character that I have identified so far, is the presence or absence of UV-reflecting scales. Insufficient information about the immatures of the North American species precludes use of their characters. Possibly there are some larval structural features, such as those used by Troubridge in differentiating two species of *Oeneis* (Troubridge & Parshall, 1988), but I have not investigated this subject. With regard to larval color and maculation, several species have polymorphic larvae (Gerould, 1921; Hayes, "1980"; Hoffmann & Watt, 1974). Some aspects of wing maculation which are useful in separating the males of the North American species are not useful for separating the females.

The order of the characters in Table 5 is somewhat random, reflecting the recognition of additional characters as series of each species were being studied during my coding of the character matrix, and the selection of *Zerene* Hübner as the out-group. The character descriptions apply to averages across subspecies or local populations within the geographic distribution of a species as a whole. For example, the females of *Colias meadii* are coded (1) for polymorphism (characters 14 and 16) based upon Wyoming, Idaho, and Canadian populations, although in Colorado alone the "alba" form occurs only rarely and apparently not at all in New Mexican populations. Characters that are not typical of a given species but occasionally appear (less than 10% of the time) in some specimens, such as the presence of "eurytheme" spots, have been coded as absent except for those species in which these characters normally occur.

After examining genera of the Coliadinae on a global basis, I have selected *Zerene* as the out-group for the current study. *Zerene* has many similarities to *Colias*, but there are some very distinct differences in the male genitalia, in addition to wing maculation and the falcate FW apex. These differences (at the genus level) are enumerated in Table **5** (characters 57, 58, 73 − 83), and in Figures **130-131** included in Appendix **1**. Removal of *Zerene* from the data matrix does not alter the topography of the remaining tree. The reader should note that Opler (1992) has lumped *Zerene* with *Colias*, an action with which I do not agree.

The cladograms shown herein were generated using the Macintosh™ version of PAUP (3.0h), and were verified using HENNIG 86. They were refined for publication using the software package MacClade version 2.1 developed by Wayne P. and David R. Maddison at the Museum of Comparative Zoology, Harvard University. MacClade has some very convenient graphical features with regard to tracing characters, elucidating character reversals, and checking for equivocation in character evolution.

The data matrix yielded a single stable cladogram. The HENNIG 86 analysis was first run using the options mhennig, and bb (branch and bound), with the following results: tree length = 201; CI = 0.41; RI = 0.55. The data matrix was then analyzed using successive approximations to character weighting under the options m, bb, xs, w, and cc. There was no change in the resulting cladogram. This same cladogram was obtained using the heuristic option of PAUP. Successive approximations to character weighting yielded an identical cladogram. The CI calculated by PAUP was 0.418 as opposed to 0.41 by HENNIG 86. All other data were the same. MacClade also produced the same minimum length tree as was found with PAUP and HENNIG 86.

The last section of this paper presents a preliminary cladistic analysis of the North American *Colias,* which includes the circumpolar species *hecla* Lefèbvre, *nastes* Boisduval, and *palaeno* (L.) The most parsimonious tree based upon the data matrix shown in Fig. 132 of Appendix 1 is shown in Fig. 2. What is of interest for the present discussion is that *krauthii* splits out completely from the "*alexandra* group," and the subsequent arrangement of the remaining taxa. The taxon *harfordii* has been retained in the general analysis, and this matter is discussed below.

The position of *occidentalis* does not support the actions of various authors in the past (especially McHenry, 1963) in associating this species with *alexandra.* An analysis of character evolution (using MacClade) also does not support placing various subspecies of one as subspecies of the other, as McHenry proposed and has been perpetuated by Gillette ("1987"[1989]). Field observations certainly support that *alexandra* and *occidentalis* are separate species. They are sympatric [see subsequent comment] in various areas in Oregon and Washington, aside from the fact that ♂♂ of *alexandra* are strongly UV-reflective, and those of *occidentalis* are totally non-reflective. This matter was discussed at some length in a prior paper (Ferris, 1988a), and needs no further elaboration here. The use above of the term sympatric is in the strict sense. I have collected both species flying together in the same forest clearing at the same time and on the same day. While *occidentalis* might be considered a forest species and *alexandra* a prairie or Transition Zone species, there are areas in Oregon and Washington where forest and sagebrush prairie interdigitate. It is in such localities that I have taken these two species together.

The taxa *harfordii* and *boothii* (= *thula*) were included in the analysis for completeness. Based upon the topography shown in Fig. 2, I feel that the designation "*alexandra* complex" is no longer appropriate. Before the new taxonomic assignments are addressed, it is necessary to examine briefly the taxon *harfordii.*

The Taxonomic Position of Colias harfordii.

I consider *harfordii* to be a subspecies of *alexandra,* but I included it in the general data matrix so that its taxonomic position could be evaluated. It differs from the other *alexandra* subspecies in only 3 characters: voltinsim (Table 5 characters 32, 33); rim width of the dorsal hindwing (DHW) discal spot (Table 5 characters 46, 47); DHW discal spot color (Table 5 characters 51, 52). *C. alexandra harfordii* is always multivoltine, while the other *alexandra* subspecies exhibit variable voltinism. Since *harfordii* occurs in a geographic area in which the climate permits several annual generations and the other subspecies occupy less favorable regions, voltinism is not particularly significant in this case. The fact that the DHW discal spot is always orange in *harfordii*, which it is variable from orange to yellow in other *alexandra* populations is perhaps basis for separation at the subspecific level, but hardly at the species level.

Burns (1975) reported electrophoretic studies on some North American *Colias* using isozymic characters of a single dimeric esterase (ES-D). The legume-feeding species, as opposed to the willow-feeding and heath-feeding species, exhibit high variation because their ES-D isozymes have wide mobility ranges. Three populations of *harfordii* and eleven of *alexandra* were examined. His ES-D analysis showed that *harfordii* and *alexandra* are very similar. Both exhibited from 14 to 17 different alleles in single populations. The approximate mobility range of the ES-D isozymes in R_f units was 0.33-0.58 for *alexandra,* and 0.35-0.59 for *harfordii.* The approximate number of R_f units spanned for *alexandra* was 25, and 26 for *harfordii.* Similar studies of *eurytheme* yielded ca. 25 alleles, R_f range

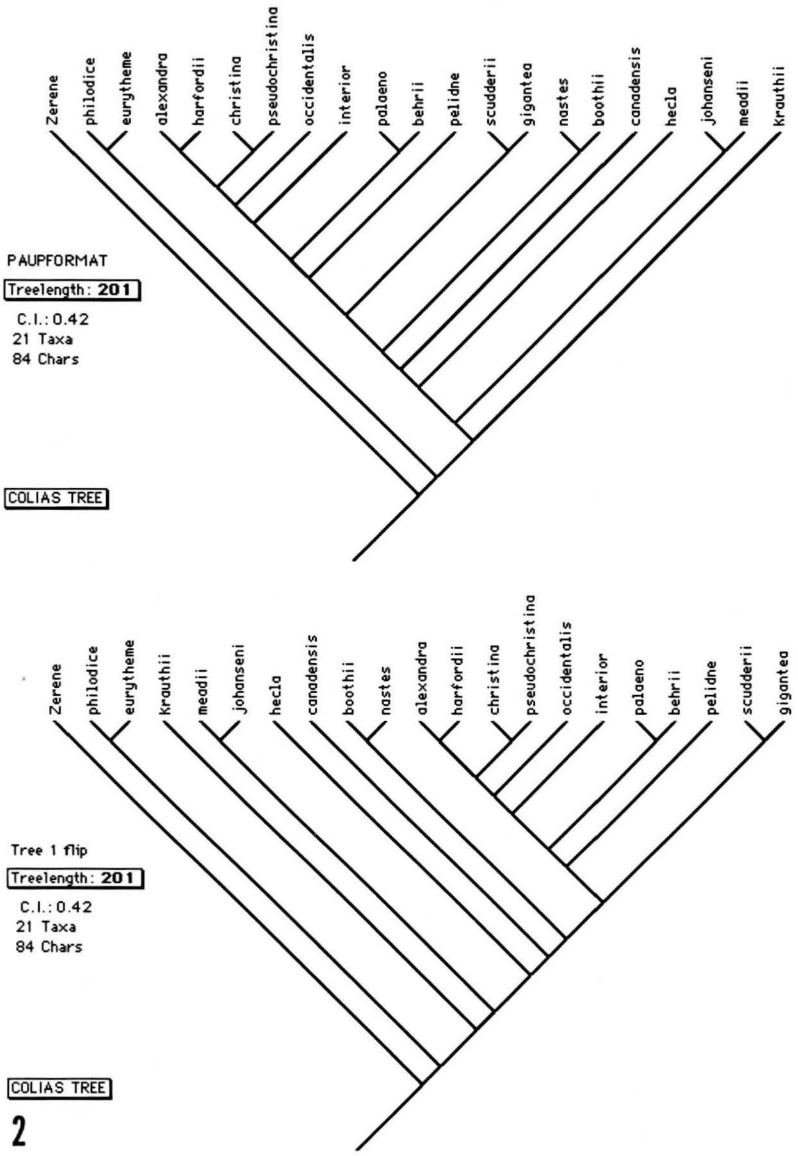

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Figure 2. Most parsimonious cladogram of the N.A. *Colias* species with *harfordii* included and *Zerene* as the out-group. Cladogram generated by PAUP and printed using MacClade. Upper tree matches PAUP format shown in Fig. 126; lower tree is the same cladogram, but with the branches flipped to elucidate relationships.

of 0.15-0.63, and approximate number of R_f units spanned = 49. The *alexandra* populations studied included examples from the La Sal Mtns., UT [nr. *edwardsii*], and Greenlee Co., AZ [*apache*].

The immature stages of many North American *Colias* are poorly known, and some are unknown. Mature larvae of *harfordii* are described by Emmel & Emmel (1973) as green with a lateral white stripe that encloses a vermilion line. The mature larvae of *a. alexandra* are apparently variable. Scott (1986) stated that they are green with a white lateral stripe that encloses orange dashes. Hayes ("1980"), on the other hand, has reported and illustrated the mature larvae and pupae from a Gunnison Co., CO population of *a. alexandra.* The larvae are green with distinct lateral stripes that mimic highlights on the host plant stems (*Lathyrus leucanthus* Rydb.), and the pupae are also green with lighter lines that mimic leaf highlights.

Since larval phenotype in many butterfly species is controlled by environment, these slight differences between *harfordii* and *alexandra* larvae provide no useful information for making a taxonomic decision. The mature larvae of *christina* are reported by Scott (1986) to be similar to those of *a. alexandra.* Consequently, gross descriptions of larvae are not particularly useful.

Color Citations.

Whenever possible, colors have been referenced to the color charts that appear in Smithe, 1975. In such instances, the color name is capitalized and referenced to a chart number when it is first used.

Designation of Lectotypes for Three Henry Edwards Taxa.

Although Henry Edwards described a number of new butterfly species, he failed to designate specific holotypes. For this reason, I have selected an appropriate lectotype for each of the three North American *Colias* species that he described. He also described a form of *eurytheme,* "amorphae", which is not treated here.

Henry Edwards published many of his descriptions of new taxa in serial form as "Pacific Coast Lepidoptera, No. —" in the Proceedings of the California Academy of Sciences. These articles appeared from 1873 (No. 1) until 1878 (No. 30). According to Beutenmüller (1891), Nos. 23-30 (1877-78) were never formally published because the Academy lacked the funds to do so. Edwards circulated typewritten copies of these articles, including a reference to the appropriate issue of the Proceedings, which has caused some citation problems when ones tries to obtain copies through libraries. Some years ago, I obtained xerographic copies of several of these typescripts. Consequently, I am reproducing transcriptions of the original descriptions for the three *Colias* taxa discussed herein. Misspellings (but not of scientific names) have been corrected, and items underlined in the original have been replaced by italics. For this reason, these descriptions are not set in quotation marks. These descriptions appear below in the appropriate locations. Because of disparities in the label and catalogue information relative to the Hy. Edwards specimens discussed below, I have not designated any specimens as paralectotypes.

TAXONOMIC DISCUSSION

The phenotypic characters that apply to the five species that have been assigned formerly by various authors to the *alexandra* group are enumerated in outline form in the paragraphs that follow. Normal and UV-reflectance patterns are examined and distribution maps are provided. The order of presentation of subspecies is geographic from south to north. Tentative evolutionary relationships will be addressed in the concluding paper of this series. The terms population or local population used herein do not imply subspecies, but rather refer to geographic populations in which individuals share certain common characters. Original spelling of taxa has been preserved. Unless otherwise noted, all specimens illustrated are in the author's collection. *Note:* Differential diagnosis of all of the North American *Colias* is provided by the character matrix and Fig. **115** shown in Appendix **1**.

Colias alexandra W. H. Edwards, 1863

General characteristics of the species.

Coloration of the ♂ ♂: Dorsally bright yellow varying from lemon-yellow to Spectrum Yellow (Smithe #55); ventrally olivaceous or pale grayish-green on HW especially, produced by melanic scales, some of which overlie the yellow ground-color scales, while others are interspersed among the yellow scales. FW apices acute. DFW cell spot black and prominent. Width of black marginal border variable within and across populations. Veins in border outlined by yellow scales; some yellow overscaling in border cell spaces in very fresh specimens. DHW discal spot usually concolorous with wing ground color, but sometimes orange. Ventral hindwing (VHW) discal spot usually small and opalescent white; essentially unrimmed in prairie populations, but finely rimmed with pinkish or dusty-rose scales in some cismontane and boreal association populations. In some populations, there is a smaller second and superior VHW discal spot. Its frequency of occurrence is normally less than 1%. Caudal and thoracic vestiture often infused with pink hairs. Wing fringes variable from yellow to pink. Legs usually pinkish. Adult size variable across populations. *UV-reflectance of the ♂ ♂*: Distal bright luminous patch between the discal spot and the dark wing margin occupying approximately 50% of the DHW surface. DHW discal spot is non-reflective. FW reflectance variable: none in some specimens; thin vertical band basad of the dark marginal border in most specimens; thin vertical band with suffusion radiating basad on either side of the veins in the cell spaces in some (usually northern and a few montane) populations. FW area occupied by reflectance pattern less than 50%.

Coloration of the ♀ ♀: The ground color may be as in the males, or variable from yellow to white depending upon population. White ♀ ♀ predominate in southern Alberta. The FW apices are generally less acute than in the ♂ ♂. Dorsal maculation varies from absent through dark dusting at the FW apices to a fully-developed fenestrated wing border. Most females have at least some dark maculation in the FW apical area. In some populations, there is a smaller second and superior VHW discal spot. Its frequency of occurrence is normally less than 10%. Other characters are as in the ♂ ♂. UV-reflectance is absent.

Habitat: Basically a prairie (sagebrush-steppe) and transition zone species, but also inhabits foothill canyons, and open areas in aspen-coniferous forest up to 10,000′ (3050 m). *C. alexandra* is a species which occurs locally in Great Plains Grassland, Sagebrush Desert, and open areas in Rocky Mountain Montane Forest (as defined in Benson & Darrow, 1981).

Voltinism: Variable depending upon geographic locality and local environmental conditions.

Distribution: From northern Baja California (*harfordii*) and Arizona northward into southern Alberta (S. of 52° N) and British Columbia (S. of 53° N). Adults from Arizona, New Mexico, and west of the Rocky Mtns. in the Great Basin northward are generally larger in size than adults from eastern prairie populations.

Colias alexandra harfordii Hy. Edwards, 1877
Figs. **3-6**

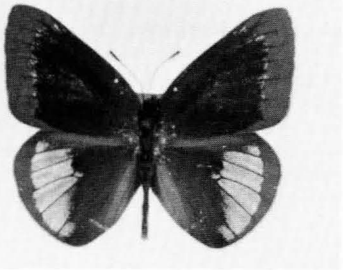
Colias harfordii Hy. Edwards, 1877. Pac. Coast Lepid., (24):9. TL — Havilah, Kern Co., California. LT and 4 ST's (5 ♂ ♂) in AMNH [the O.D. cites 7 ♂ ♂]. Male and female "types" (actually pseudotypes) illustrated by Holland (1949: pl. 68, Figs. 20-21). (See below for designation of the LT and further discussion.)

= *Colias barbara* Hy. Edwards, 1877. Pac. Coast Lepid., (24):7-8. TL — Emended herein [see below] to San Bernardino, San Bernardino Co., California. LT and 1 ST (2 ♀ ♀) in AMNH. Male and female "types" (actually pseudotypes) illustrated by Holland (1949:

pl. 68, figs. 18-19).

= *Colias barbara* Hy. Edwards; Strecker, 1878:82.
= *Colias chrysotheme* ab. f. "harfordii" Hy. Edwards; Strecker, 1878:83.
= *Colias harfordii harfordii* Hy. Edwards; Skinner, 1898:69.
= *Colias harfordii barbara* Hy. Edwards; Skinner, 1898:69.
= *Eurymus hartfordii* [*sic*] (Hy. Edwards); Dyar, 1902:10.
= *Eurymus hartfordii* [*sic*] syn. barbara (Hy. Edwards); Dyar, 1902:10.
= *Eurymus harfordii* (Hy. Edwards); Barnes and Benjamin, 1926a:8.
= *Eurymus occidentalis barbara* (Hy. Edwards); Barnes and Benjamin, 1926a:8.
= *Colias occidentalis barbara* Hy. Edwards; Comstock, 1927:52.
= *Colias harfordii* Hy. Edwards; McDunnough, 1938:8.
= *Colias occidentalis barbara* Hy. Edwards; McDunnough, 1938:8.
= *Colias barbara* Hy. Edwards; Holland,1949:294.
= *Colias harfordi* Hy. Edwards; Holland, 1949:294.
= *Colias occidentalis barbara* Hy. Edwards; McHenry, 1963:210; 215.
= *Colias occidentalis harfordii* Hy. Edwards; McHenry, 1963:210; 216.
= *Colias barbara* Hy. Edwards; dos Passos, 1964:42.
= *Colias harfordii* Hy. Edwards; dos Passos, 1964:42.
= *Colias alexandra barbara* Hy. Edwards; Ferris, 1973:68; 71.
= *Colias alexandra harfordii* Hy. Edwards; Ferris:1973:68; 71.
= *Colias alexandra harfordii* Hy. Edwards; Orsak, 1978:82.
= *Colias harfordii* Hy. Edwards; Miller and Brown, 1981:80.
= *Colias harfordii* syn. *barbara* Hy. Edwards; Miller and Brown, 1981:80.
= *Colias alexandra harfordi* Hy. Edwards; Ferris, 1988:5.
= *Colias alexandra harfordi* syn. *barbara* Hy. Edwards; Ferris, 1988:5.
= *Colias occidentalis harfordii* Hy. Edwards; Gillette, "1987"[1989]:58.

Coloration of the ♂♂: Ground color close to Spectrum Yellow. Deeper yellow color V with melanic overscaling variable and reduced. Pink color present in vestiture, fringes, and legs. DHW discal spot orange. VHW spot large and pink-rimmed.
UV-reflectance of the ♂♂: HW typical; FW normally manifests a thin vertical band basad of the dark marginal band, but may be non-reflective.
Coloration of the ♀♀: As in the ♂♂, but usually paler and rarely with an orange flush D. "Alba" ♀♀ very rare. Maculation D varies from apical dusting to a weak fenestrated border. Other characters are as in the ♂♂.
Typical FWL (measured from the base of the wing to the end of vein R_5 at the margin): ♂♂ 21-28 mm; ♀♀ 22-28 mm.
Habitat: Coastal and interior mountain ranges and canyons.
Biology: Reported larval hosts include *Astragalus antisellii* (Gray), *A. douglasii* (T. & G.) Gray, *A. douglasii* var. *parishii* (Gray) Jones, *Lotus crassifolius* (Benth.) Greene, *L.*



3

Figure 3. D UV-reflectance pattern in a ♂ *C. a. harfordii* from Tehachapi, Kern Co., CA, 23.vii.18, leg. J. A. Comstock.

scoparius (Nutt.) Ottley (oviposition). Multivoltine with generations in early spring, June-July, and a late generation in late September-early October. There is apparently a distinctive and uncommon spring form that occurs in San Diego Co., CA in ii-iii (see Garth & Tilden, 1986, p. 109). I have not seen specimens. Three other *Colias* species that I know of produce parallel late winter or early spring forms. These forms occur in *eurytheme, philodice,* and occasionally in bivoltine colonies of *alexandra.* I have in my collection, or have seen such specimens of *alexandra* from Idaho (Lemhi Co.), Montana (vic. Great Falls, Cascade Co., specimens in AMNH), and Oregon (Grant and Harney Cos.)
Distribution: Northern Baja California (Sierra San Pedro Martir) into southern California northward, formerly to Contra Costa and Sonoma Cos. (old records). Contemporary records include: Kern, Los Angeles, Santa Barbara, Ventura Cos. Map: Fig. **23**.
Discussion: The placement of *harfordii* remains tentative. Its general phenotype and UV-reflectance pattern places it in the *alexandra* group. Cladistic analysis in which *harfordii* is treated as a separate species locates *harfordii* on a bifurcated branch with *alexandra,* as shown in Fig. 2. The major differences between these two taxa are in *harfordii* the frequent presence of "eurytheme" spots on the VHW and the reduced amount of VHW melanic overscaling. The frequent appearance of the ventral maculation of *eurytheme* in museum specimens of harfordii suggests that *harfordii* occasionally hybridizes with *eurytheme* and perhaps *philodice* as well. This situation was mentioned briefly by Orsak (1977, p. 82). Priestaf (1974) described a putative hybrid between *harfordii* and *eurytheme.* Although coincidental, he also reported that both species use *Astragalus antiselli* as larval hosts in Oso Canyon, San Rafael Mtns., Santa Barbara Co., CA.

Lectotype Designations:

Colias barbara Hy. Edwards, 1877

Original description in "Pacific Coast Lepidoptera No. 24. Notes on the genus Colias [*sic*], with description of some apparently new forms", pp. 7-8, and circulated as typewritten "reprints" [cited by Edwards as from the Proceedings of the California Academy of Science, February 5, 1877].

C. Barbara. Hy. Edw. n.sp.?

Whole upper surface bright canary yellow, with a black cloud at base of wings, densest on the primaries, and a few scattered black scales are visible along the costa. The marginal band of the primaries is composed of black atoms, through which the yellow of the ground color is distinctly seen. It is broadest at the apex, thence narrowing slightly, and continued of equal width to the internal angle. In this respect it differs greatly from *Laurentina,* in which the band is apical only, and obsolete before reaching the internal margin. The costal edge of primaries is pinkish, most distinct at the base; the discal spot is small, ovate, deep yellow, surrounded by a black ring. The secondaries are totally destitute of any border. The discal spot is circular, pale orange, surmounted by a smaller spot of the same color. Head in front and above, dull yellow, with a pink fringe. Palpi yellow at their base, pink at the tips. Antennae brownish pink; club, chestnut brown. Thorax black, with long, pale greenish yellow hairs. Abdomen black above, with yellow atoms on the side.

Under side.- Primaries pale lemon yellow, powdered along the margin with black atoms, more broadly so at the apical and costal edges. Costa and fringes decidedly pink. Discal spot with the yellow centre very plainly marked. Secondaries more closely and thickly powdered with black atoms, giving a greenish appearance to the surface, and with a dark rose pink streak the base. Discal spot large, circular, clear white, surmounted by a smaller one, each surrounded by a brownish ring. Under side of thorax and abdomen bright lemon yellow, the former with very long hairs. Tibiae yellow; tarsi pink. Expanse wings, 2.00 inch. Male unknown.

Two females (Coll. Hy. Edw.), Santa Barbara, Baron v. Osten Sacken; Gilroy, J. Behrens.

Discussion: Edwards cited 2 female syntypes as did Beutenmüller (1892) from Santa

Barbara, California. Based upon the locality labels attached to the specimens, neither is from Santa Barbara; one is from San Bernardino Co., and the other is from Santa Clara Co. The pin labels on one specimen are as follows: (1) a round label inscribed "7005"; (2) a locality label "San Bernardino [in Hy. Edw's handwriting]/[printed] California"; (3) [printed museum label] with handwritten number "No. 3440 Collection Hy. Edwards."; (4) [handwritten by Hy. Edw.] "Colias harfordii Hy. Edw. = Barbara Type ♀"; (5) [AMNH printed label] "Type specimen"; (6) [AMNH printed label] "Type no. A.M.N.H." The pin labels on the second specimen are as follows: (1) a round label inscribed "7005"; (2) a locality label "Gilroy, Sta. Clara Co. [in Hy. Edw's handwriting]/[printed] California"; (3) [printed museum label] with handwritten number "No. 3439 Collection Hy. Edwards."; (4) [handwritten by J. McDunnough] "True type ♀ of C. barbara Hy. Edw. vide orig. desc. JMcD."; (5) [AMNH printed label] "Type specimen; (6) [AMNH printed label] "Type no. A.M.N.H."

In the original Hy. Edwards catalogue, in his handwriting, the entry for no. 7005 reads: "Colias Barbara Hy. Edw. Califor. Ost. Sacken." In the AMNH catalogue for the Hy. Edwards collection, there are the following entries: (1) for no. 3439 - "3439 7005 Colias harfordii Hy. Edw. ♀ Santa Clara Co., Calif. Osten Sacken Type specimen."; (2) for no. 3440 - "3440 7005 Colias harfordii Hy. Edw. ♀ San Bernardino, Calif." There is the additional and much later notation for both specimens: "This [for *harfordii*] should read "barbara" fide Hy. Edw's own catalog. ABK [Alexander B. Klots]."

Lectotype Designation: Over the years, many California specialists have questioned the occurrence of *C. barbara* = *harfordii* as far north as Sta. Clara Co. For this reason, I have designated the specimen [no. 3440 7005] from San Bernardino Co. as the lectotype. A red label inscribed in black ink (handwritten) has been affixed to the specimen pin and reads: "LECTOTYPE ♀/ Colias barbara/Hy. Edwards. Designated/by C. D. Ferris 7.v.1990." Based upon the specimen label information, the type locality should be emended to San Bernardino, San Bernardino Co., California. [FWL of lectotype = 2.5 cm]

Colias harfordii Hy. Edwards, 1877

Original description in "Pacific Coast Lepidoptera No. 24. Notes on the genus Colias [*sic*], with description of some apparently new forms", p. 9, and circulated as typewritten "reprints" [cited by Edwards as from the Proceedings of the California Academy of Science, February 5, 1877].

C. harfordii. Hy. Edw. n. sp.?

Bright lemon yellow. Primaries with the border moderate in width, equal throughout its entire length, and more or less serrate on its inner edge. The band is divided by the nervures, but as in *Chrysomelas,* never to its extreme edge. The discal spot is oblong, yellow, surrounded by black. Secondaries with the marginal border narrower than in the primaries, and ending somewhat abruptly before reaching the submedian nervure. Beneath, the wings are uniformly pale orange, a little palest [*sic*] on the internal margin of the primaries, and devoid of the black or grayish scales so apparent on *Occidentalis* and *Chryomelas* [*sic*]. Discal spot of primaries same as upper side. That of secondaries is clear white, surrounded by a brownish pink ring, and there is a faint indication of a row of submarginal spots of the same color on both wings. Fringes, costal edges, antennae, and feet, rose pink. Expanse wings, 1.75 in., 1.90 inch.

From seven males, (Coll. Hy. Edw.) Contra Costa Co. (Hy. Edw.). Havilab [*sic*], Kern Co. (R. H. Stretch).

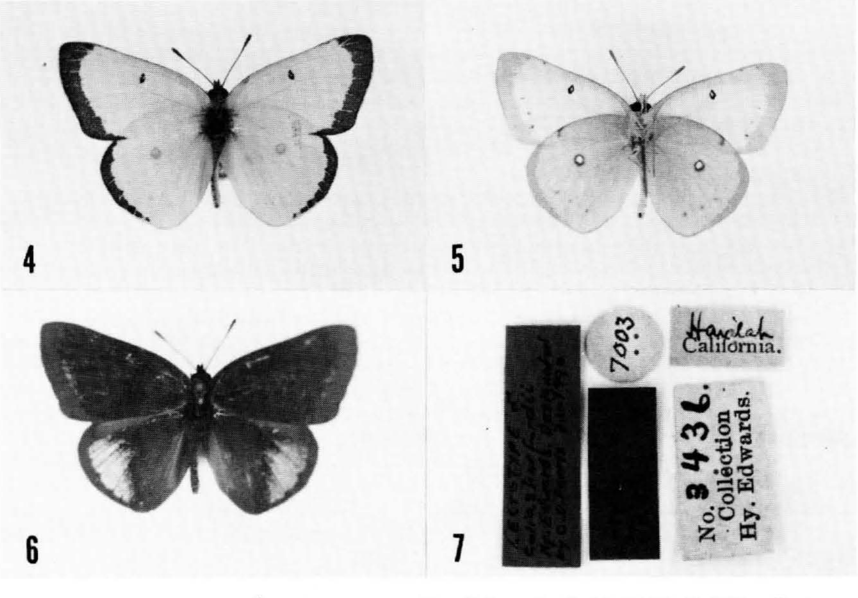
I have named this species in compliment to Mr. W. G. W. Hartford, the earnest and talented curator of the California Academy of Sciences, who has added many treasures to my collection.

This is the species formerly sent by me to Mr. W. H. Edwards, as the lemon colored variety of *Keewaydin,* and figured by him as such in the first series of "Butterflies of N. America." I am now fully convinced that it is not a variety of *Keewaydin,* though it may be and extreme and small form of either *Chrysomelas* or *Occidentalis*, a fact which cannot be proved until the female is known to us.

Discussion: Edwards cited 7 male syntypes from Contra Costa and Kern Cos., California, while Beutenmüller (1892) cited only 5 ♂♂ from "California." There are 5 ♂♂ in the AMNH type collection. The associated specimen labels read as follows: Specimen no. 1 — (1) "California" [printed]; (2) "4" [round, hand written]; (3) "No. 3437 Collection Hy. Edwards." [printed with hand written number]; (4) red, printed A.M.N.H. type label. Specimen no. 2 — (1) "7003" [round, hand written]; (2) "Havilah [in Hy. Edw's handwriting]/California"; (3) "No. 3436 Collection Hy. Edwards." [printed with hand written number]; (4) red, printed A.M.N.H. type label. Specimen no. 3 — Same as no. 2. Specimen no. 4 — Same as no. 2, plus "Colias Harfordii Hy. Edw. Type ♂" [hand written by Hy. Edw.]. Specimen no. 5 — Same as no. 2, but without the "7003" round label.

In the original Hy. Edwards catalogue, in his handwriting, the entry for specimen no. 4 reads: "Colias keewaydin var. Fields of Medicago S. Francisco, Cal. HE [collector] 3 [March 18]68 Probably a variety of No. 3 [as keewaydin, from San Francisco]. This is C. harfordii Hy. Edw.... [illegible] distinct from keewaydin H.E." The entry for "7003" reads: "7003 Colias Harfordii Hy. Edw. Califor. Stretch." In the AMNH catalogue for the Hy. Edwards collection, there are the following entries: (1) for no. 3436 — "3436 7003 Colias harfordii Hy. Edw. ♂ Havilah, California Hy. Edwards [collector - - !!] Type specimen."; (2) for no. 3437 — "3437 4 Colias harfordii Hy. Edw. ♂ San Francisco, Calif. Hy. Edwards [collector] Type specimen."

Lectotype Designation: I have designated as the lectotype of *Colias harfordii* the specimen referenced as no. 2 above, since it closely fits the original description. A red label inscribed in black ink (handwritten) has been affixed to the specimen pin and reads: "LECTOTYPE ♂/ Colias harfordii/Hy. Edwards. Designated/by C. D. Ferris 7.v.1990." This specimen and its labels are illustrated in Figs. 4-7. The UV-reflectance pattern shown in Fig. 6 is typical of *alexandra*, and the ssp. *harfordii* (compare with Fig. 3). [FWL of lectotype = 2.4 cm]



Figures 4-7. Lectotype ♂ of *C. harfordii* Hy. Edwards. D (4), V (5), D UV-reflectance (6), specimen labels (7). Specimen in AMNH type collection.

Colias alexandra apache Ferris, 1988.
Fig. **8**

Colias alexandra apache Ferris, 1988. Bull. Allyn Mus., (116):8-11. TL — 13 mi. E. of McNary, 2520 m., Apache Co., Arizona. HT in AME.

= *Colias alexandra apache* Ferris; Ferris, ed., 1989b:23.

Coloration of the ♂♂: Ground color bright lemon-yellow. Pink vestiture and fringes absent (all yellow including legs). VHW discal spot unrimmed.
UV-reflectance of the ♂♂: HW typical; FW normally manifests a thin vertical band basad of the dark marginal band.
Coloration of the ♀♀: As in the ♂♂, but usually paler V and sometimes with an orange flush D. "Alba" ♀♀ are unknown. Maculation D varies from immaculate to a weak fenestrated border. Other characters are as in the ♂♂.
Habitat: Montane (usually above 2450 m) in open areas in Ponderosa Pine forest (Rocky Mountain Montane Forest).
Typical FW length: ♂♂ 25-30 mm; ♀♀ 30-32 mm.
Biology: Oviposition on *Astragalus* sp. in the Manzano Mtns., Torrance Co., NM; *Thermopsis* sp. reported as the larval host in the White Mtns., AZ. Flight period mid-vi to late viii depending upon locality and the onset of the summer rains. This ssp. may be bivoltine.
Distribution: Mogollon Rim and White Mtns. of AZ (Apache, [southern] Coconino, Gila, Graham, Greenlee, Navajo Cos.); locally in several mountain ranges in NM (Catron, Grant, McKinley, Sierra, Torrance Cos.). Clinal forms into *a. alexandra* occur in Sandoval and Taos Cos., NM. Map: Fig. **23**.
Common name: Common names are generally included in field guides and other popular publications, and I provided none for this butterfly in its original description. I propose the name Apache Sulfur.

Colias alexandra edwardsii W. H. Edwards, 1870
Figs. **9-10**

Colias edwardsii W. H. Edwards, 1870. Trans. Amer. ent. Soc., 3:11. TL — vic. Virginia City, Nevada. LT in CMNH, designated by F. M. Brown, 1973; Trans. Amer. ent. Soc., 99:67. Male and female "types" (actually pseudotypes) illustrated by Holland (1949: pl. 68, Figs. 24-25). The male (Fig. 24) is the lectotype designated by Brown (1973:65-66).

= *Colias emilia* W. H. Edwards, 1870. Trans. Amer. ent. Soc., 3:12. TL "Oregon", restricted to Crump Lake, Lake Co., Oregon, and neotype designated by F. M. Brown, 1973; Trans. Amer. ent. Soc., 99:68-72. NT in CMNH. See also Ferris (1973:68) for additional

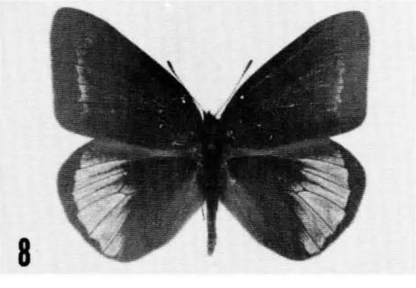


Figure 8. D UV-reflectance pattern in a ♂ *C. a. apache* from Ditch Camp, Apache Co., AZ, 9.vii.76.

discussion.
= *Colias edwardsii* W. H. Edwards; Strecker, 1878:82.
= *Colias emilia* W. H. Edwards; Strecker, 1878:82.
= *Colias alexandra edwardsii* Behr; Skinner, 1898:69.
= *Colias alexandra emilia* W. H. Edwards; Skinner, 1898:69.
= *Eurymus alexandra edwardsii* (W. H. Edwards); Dyar, 1902:10.
= *Eurymus alexandra emilia* (W. H. Edwards); Dyar, 1902:10.
= *Eurymus alexandra edwardsii* (W. H. Edwards); Barnes and Benjamin, 1926a:8.
= *Eurymus alexandra emilia* (W. H. Edwards); Barnes and Benjamin, 1926a:8.
= *Colias alexandra edwardsii* W. H. Edwards; McDunnough, 1938:8.
= *Colias alexandra emilia* W. H. Edwards; McDunnough, 1938:8.
= *Colias edwardsi* W. H. Edwards; Holland, 1949:295.
= *Colias emilia* W. H. Edwards; Holland, 1949:295.
= *Colias occidentalis edwardsii* W. H. Edwards; McHenry, 1963:210; 215.
= *Colias occidentalis emilia* W. H. Edwards; McHenry, 1963:210; 216.
= *Colias alexandra edwardsii* W. H. Edwards; dos Passos, 1964:43.
= *Colias alexandra emilia* W. H. Edwards; dos Passos, 1964:43.
= *Colias alexandra edwardsii* W. H. Edwards; Brown, 1973:57; 65.
= *Colias alexandra edwardsii* W. H. Edwards; Ferris, 1973:60; 71.
= *Colias alexandra edwardsii* W. H. Edwards; Miller and Brown, 1981:81.
= *Colias alexandra edwardsi* W. H. Edwards; Ferris, 1988:3.
= *Colias alexandra edwardsi* W. H. Edwards; Gillette, "1987"[1989]:58.

Coloration of the ♂♂: Ground color bright lemon-yellow. The dorsal dark borders tend to be narrower than in other subspecies. VHW normally gray-green in aspect owing to moderate overscaling by melanic scales. Pink color present in vestiture, fringes, and legs.

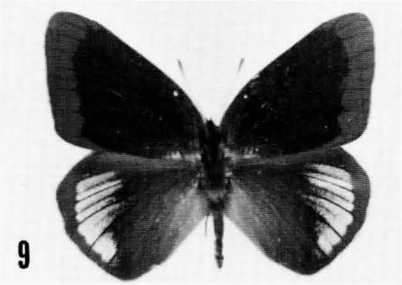


Figure **9**. D UV-reflectance pattern in a ♂ clinal form of *C. alexandra* nr. *edwardsii* from the Stansbury Mtns., Tooele Co., UT, 6.viii.64, leg. K. B. Tidwell.

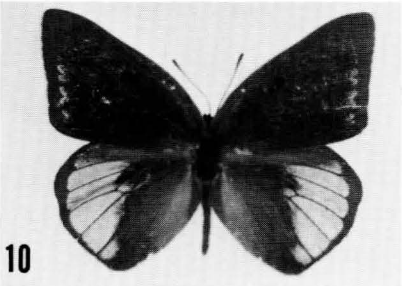
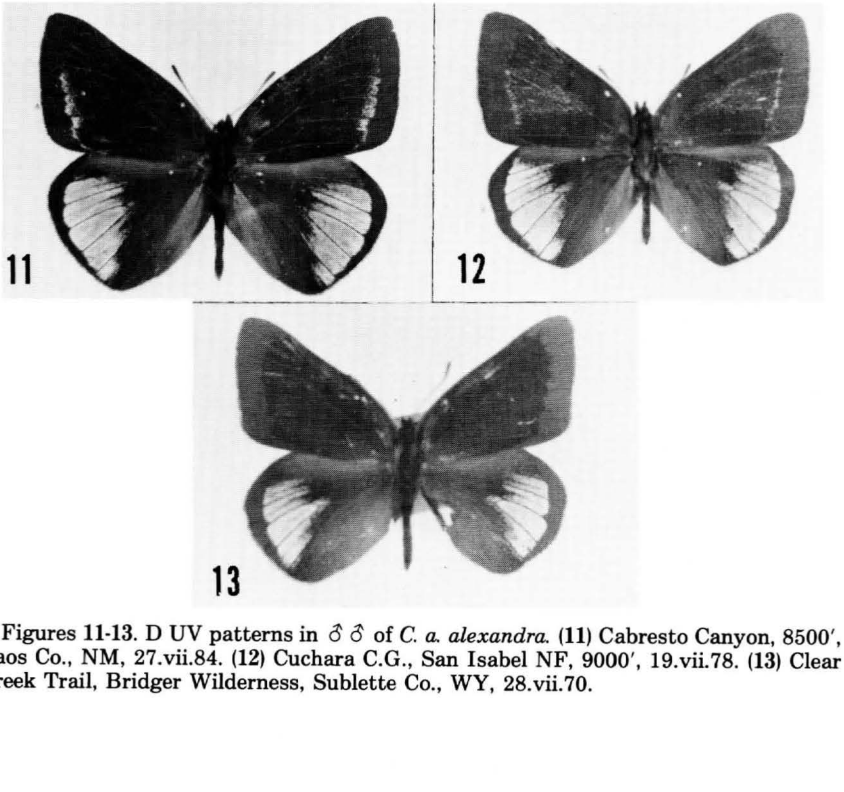


Figure **10**. D UV-reflectance in a ♂ of *C. a. edwardsii* from Jett Canyon, Nye Co., NV, 3.viii.57, leg. O. Shields.

DHW discal spot normally concolorous with ground color, occasionally orange. VHW discal spot small and usually with a narrow pink rim.
UV-reflectance of the ♂ ♂: HW typical; FW variable from none to a thin vertical band basad of the dark marginal band.
Coloration of the ♀ ♀: As in the ♂ ♂, sometimes with a pale orange flush. True "alba" ♀ ♀ are unknown; rarely are pale specimens seen. Maculation D varies from immaculate to a partially-developed fenestrated border. The DHW discal spot is often orange. Other characters are as in the ♂ ♂.
Typical FWL: ♂ ♂ 27-30 mm; ♀ ♀ 29-31 mm.
Habitat: Normally in canyons in arid areas.
Biology: Reported larval hosts include *Astragalus, Medicago, Thermopsis,* and *Trifolium.* Flight period mid-v to early ix depending upon locality. At least two generations per year in many areas; perhaps three in some areas in favorable years.
Distribution: Arizona Strip (including northern Coconino Co.) and Great Basin to at least central Utah with clinal forms in the Sierra-Cascade Divide region from northern California into Oregon and northward. Specimens collected by the author in early August, 1989 in central Moffat Co., CO (just SE of Maybell) are intermediate between *edwardsii* and typical *alexandra.* The first generation of the Moffat Co. population apparently flies in June based upon a record by R. E. Stanford from 19 mi. W of Craig on 19.vi.73. Map: Fig. **23**.

Colias alexandra alexandra W. H. Edwards, 1863
Figs. **11-13**

Colias alexandra W. H. Edwards, 1863. Proc. ent. Soc. Philadelphia, 2: 14-15. TL — "Pike's Peak", restricted to foothills W. of Denver, Colorado by F. M. Brown, 1973. Trans. American ent. Soc., 99:60. LT in CMNH, designated by F. M. Brown, 1973. Trans.



Figures 11-13. D UV patterns in ♂ ♂ of *C. a. alexandra.* **(11)** Cabresto Canyon, 8500′, Taos Co., NM, 27.vii.84. **(12)** Cuchara C.G., San Isabel NF, 9000′, 19.vii.78. **(13)** Clear Creek Trail, Bridger Wilderness, Sublette Co., WY, 28.vii.70.

American ent. Soc., 99:62.

= *Colias alexandra* W. H. Edwards; Strecker, 1878:81.
= *Colias alexandra alexandra* W. H. Edwards; Skinner, 1898:69.
= *Eurymus alexandra alexandra* (W. H. Edwards); Dyar, 1902:10.
= *Eurymus alexandra alexandra* (W. H. Edwards); Barnes and Benjamin, 1926a:8.
= *Colias alexandra alexandra* W. H. Edwards; McDunnough, 1938:8.
= *Colias alexandra* W. H. Edwards; Holland, 1949:249.
= *Colias occidentalis alexandra* W. H. Edwards; McHenry,1963:210; 215.
= *Colias alexandra alexandra* W. H. Edwards; dos Passos, 1964:43.
= *Colias alexandra alexandra* W. H. Edwards; Brown, 1973:57; 59.
= *Colias alexandra alexandra* W. H. Edwards; Ferris, 1973:71.
= *Colias alexandra alexandra* W. H. Edwards; Miller and Brown, 1981:81.
= *Colias alexandra alexandra* W. H. Edwards; Ferris, 1988:2.
= *Colias alexandra alexandra* W. H. Edwards; Gillette, "1987"[1989]:58.

Coloration of the ♂♂: Ground color bright lemon-yellow. VHW normally gray-green in aspect because of moderate overscaling by melanic scales. Pink color weakly present in vestiture, fringes (sometimes absent), and legs. DHW discal spot normally concolorous with ground color. VHW discal spot small and unrimmed. (See *Discussion* below.)
UV-reflectance of the ♂♂: HW typical; FW normally manifests a thin vertical band basad of the dark marginal band, occasionally radiating basad on either side of the veins in the cell spaces (some montane populations).
Coloration of the ♀♀: As in the ♂♂, but usually paler V. Maculation D varies from immaculate to a full fenestrated border. Other characters are as in the ♂♂. "Alba" ♀♀ are common in some populations, especially in Alberta and in the prairie populations found in Gallatin, Judith Basin, Lewis & Clark, Toole, and Wheatland Cos., MT; rare to absent in others. In a population in Albany Co., WY which the author has studied for more than 20 years, the occurrence of the "alba" form varies annually. In 1990 when the species was unusually common, the "alba" form represented 16% of the ♀♀ collected [N = 67 all ♀ morphs], the largest percentage recorded over the time period indicated. Also in 1990, the VHW discal spot was double in 11% of the ♀♀ collected, a higher than usual percentage.
Typical FWL: ♂♂ 24-30 mm; ♀♀ 21-30 mm.
Habitat: High prairies (shrub-steppe) and montane canyons up to 10,000' (3050 m).
Biology: Oviposition on *Lupinus* sp. and *Thermopsis montana* var. *divericarpa* (A. Nels.) Dorn observed by the author in Wyoming; *Astragalus, Lathyrus, Oxytropis, Thermopsis,* and *Medicago* reported by Ellis (1974). *Lathyrus leucanthus* Rydb. normally used as host in Gunnison Co., CO with limited success and increased time to maturity on *Lupinus* sp. and *Vicia americana* Muhl. (Hayes, "1980"). Members of a single population are apparently monophagous, but larval host plant varies among populations (Hayes, "1980"). Normally univoltine with adults from mid-vi into viii depending upon locality and elevation. Bivoltine in favorable years in Sioux Co., NE (early vi and again in late vii), Slope Co., ND (v-vi and again in viii), and some localities in Alberta (v, vii-viii). Also recorded as bivoltine vic. Piney Creek, 6000', Arapahoe Co., CO (late v and again in early vii; specimens leg. M. S. Fisher); apparently bivoltine in certain areas of southern-to-central Idaho. In early September, 1989, a second generation emerged at the East Fork Field Station of the Wyoming Game and Fish Dept., Fremont Co., WY. Adults were on the wing into early October (*fide* K. Bagdonas). In years when the weather is cooler than normal, *alexandra* may have a protracted single emergence which gives the false impression of bivoltinism.
Distribution: Northern New Mexico, Colorado, eastern Utah, Wyoming, southern Idaho, eastern Montana, western Nebraska, western South and North Dakota, northwards across SW Saskatchewan and into the prairie regions of Alberta to 52°N. Map: Figs. **23-24**.
Discussion: Foothill canyon populations in northern Wyoming, southern Idaho (Lemhi Co., in particular), eastern Montana, and southern Alberta frequently have orange DHW discal spots and the VHW discal spot is rimmed with pink.

Colias alexandra columbiensis Ferris, 1973
Figs. **14-18**

Colias alexandra columbiensis Ferris, 1973. J. Lepid. Soc., 27(1):68-71. TL — Anderson Lake, D'Arcy, British Columbia. HT in CNC.

= *Colias alexandra alexandra* W. H. Edwards; Jones, 1951:5.
= *Colias alexandra edwardsii* W. H. Edwards; Jones, 1951:5.
= *Colias alexandra emilia* W. H. Edwards; Jones, 1951:5.
= *Colias alexandra columbiensis* Ferris; Miller and Brown, 1981:81.
= *Colias alexandra columbiensis* Ferris; Ferris, 1988:6.

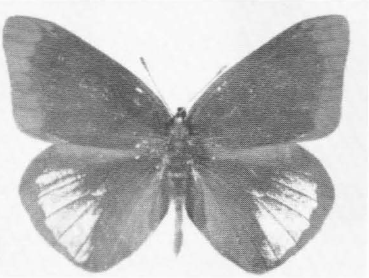

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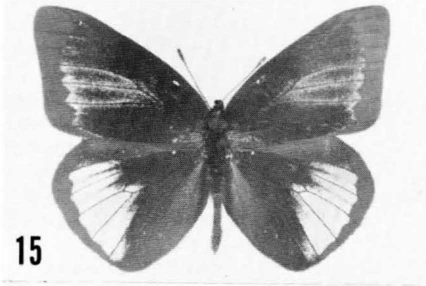
Figure **14.** D UV-reflectance pattern in a ♂ of *C. a. columbiensis* from vic. Moyie Springs, Boundary Co., ID, 18-19.vii.86 (incomplete pattern as described in main text).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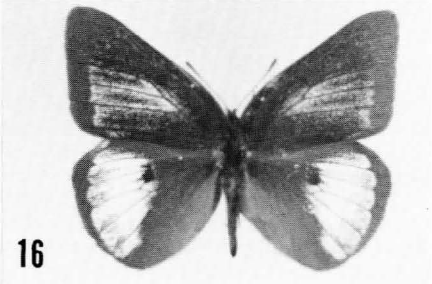
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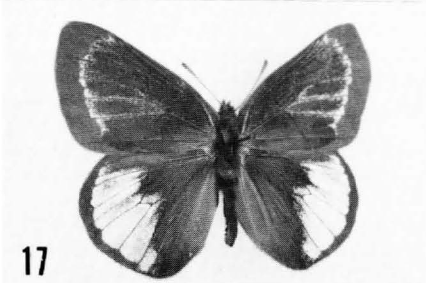
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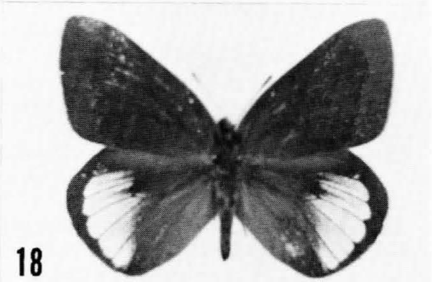
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Figures **15-18.** D UV patterns in ♂ ♂ of *C. a. columbiensis.* **(15)** Vic. Moyie Springs, Boundary Co., ID, 18-19.vii.86. This is the same specimen as shown in Fig. **14**; note difference in reflectance pattern. **(16)** nr. Liberty, Ferry Co., WA, 8.vii.75, leg. L. P. Grey. **(17)** HT from Anderson Lake at D'Arcy, B.C., 17.vi.86, leg. J. McDunnough; specimen in CNC. Specimen has been tilted to show full extent of UV-reflectance pattern shown as Fig. 6f, p.69 in Ferris, 1977. **(18)** Big Bar road nr. Jesmond, B.C., 5.vii.81.

Coloration of the ♂♂: Ground color bright yellow. VHW ground color varies from Spectrum Yellow (Smithe #55) to light yellow-orange (no Smithe equivalent) with moderate overscaling by melanic scales. The overall aspect is a warmer color than in other *alexandra* sspp. excepting *harfordii*. Pink color is present in vestiture, fringes, and legs. DHW discal spot is often orange. VHW discal spot variable in size and rimmed with pink scales.
UV-reflectance of the ♂♂: HW typical; FW normally manifests a thin vertical band basad of the dark marginal band with inwardly radiating rays in the cell spaces of the central portion of the wing. Adult size tends to diminish toward the northern extent of the species' range.
Coloration of the ♀♀: Variable from bright yellow to creamy-white; often with an orange blush. "Alba" ♀♀ are common in some local populations; rare to absent in others. Maculation D varies from immaculate to a very faintly defined fenestrated border. Other characters are as in the ♂♂.
Typical FWL: ♂♂ 25-29 mm; ♀♀ 27-30 mm.
Habitat: Open areas in coniferous forest.
Biology: Reported host plants include *Astragalus* sp. and *Lupinus* sp. This subspecies occurs also in association with *Lathyrus*, *Thermopsis*, and other legumes. Adults typically from early vii to early viii. Univoltine.
Distribution: Western Montana, across northern Idaho, and into southern British Columbia, primarily in the Columbia and Fraser River drainages (upper Okanogan Valley region, southern and central interior, Kootenay Mtns.). Map: Figs. **23-24**.
Discussion: Several correspondents have suggested to me that *columbiensis* should be treated as a separate species. At the present time, I can find no basis for doing so. This subspecies blends (in visual pattern) evenly into *C. a. alexandra* in the eastern portion of its range, and there is a very broad region of transition (with many intermediate forms) from *columbiensis* into *edwardsii* in the western portion.

Colias alexandra intermediate populations
Figs. **19-22**

As would be expected, intermediate forms occur along the tension zones between the designated subspecies. *C. a. harfordii* is geographically isolated from other populations of *alexandra* and thus intermediate forms are not seen. In geologic time, however, intermediate populations may have existed in the region between Tulare Co. and Mono Co., CA. *C. a. apache* is also isolated with the exception of the extreme NE portion of its range, where it blends into *a. alexandra*. The blending of *edwardsii* into *alexandra* appears to be gradual along the eastern edge of the Great Basin.

Populations that occur along the northern boundary of the Great Basin exhibit the greatest variability in phenotype. The geographic region involved extends from Mono, Lassen, and Modoc Cos. in California, Washoe, Humboldt, and northern Elko Cos. in Nevada into the contiguous regions of Idaho (Owyhee Co.) and Oregon (Lake, Harney, Malheur Cos. northward), with a NW extension along the Snake and Columbia River Valleys in suitable habitats. This geographic region forms a very diffuse tension zone between *edwardsii* and *columbiensis*.

Males are generally of large size and frequently resemble *edwardsii*, especially in very-dry-region populations. The UV-reflectance pattern is characteristic of both *edwardsii* and *columbiensis*.

Females are extremely variable. Dorsal color varies from bright yellow through pale yellow into creamy-white. Some specimens may exhibit an orange blush. Dorsal maculation in the females ranges from immaculate to a very dense fenestrated pattern, and is independent of wing ground color. In some colonies, there is very little variation in female phenotype, while in others it is possible to collect all of the forms noted above.

In both sexes, the DHW discal spot may be either pallid or orange. Ventrally the ground color and quantity of melanic cover scales varies widely. The VHW discal spot is rimmed with pink (sometimes heavily) and varies in size. This spot is sometimes double producing a modified vertical "figure 8" pattern.

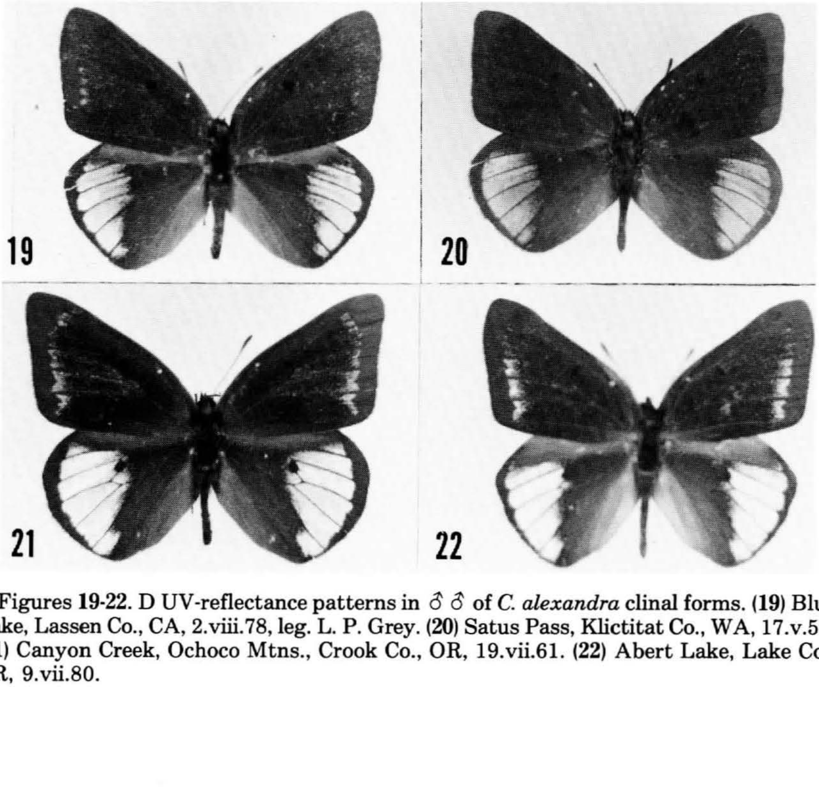
Oviposition has been observed on a tall-growing *Astragalus* [*miser* Dougl.??] in the Blue Mtns., Asotin Co., WA by Barry Sullivan [*fide* P. C. Hammond]. Oviposition on *Medicago sativa* L. was observed by J. P. Pelham at Sentinel Gap, Kittitas Co., WA on 14.viii.83. This is an unusual host record, however, Tabashnik *et al.* (1981) and Tabashnik (1983) have discussed oviposition preference and host plant shift in two other native species, *C. eurytheme* and *C. philodice eriphyle.*

These Great Basin populations are at least bivoltine in some areas. Records for Baker Co., OR include v-vi and viii. A. M . Shapiro has informed me that *alexandra* is occasionally bivoltine in Mono and Sierra Cos., CA, and that the Sierra Co. population feeds on *Astragalus* sp. Map: Fig. **23**.

Colias alexandra orange aberrations

Occasionally male specimens of *C. alexandra* are collected in which the post-median area of the DHW has a distinct orange flush. This orange color is normally of a different hue and sometimes more intense than the D orange coloration of *christina*, *krauthii*, or *pseudochristina.* Based upon my examination of museum material, this DHW color aberration appears to be more common (on a relative basis) in *columbiensis* than in other subspecies. I have not seen it in *apache, harfordii, alexandra,* pure *edwardsii,* and only rarely in the northern Great Basin clinal forms. John Hinchliff (pers. comm.) collected one such male along the Moses Meadow Road in Okanogan Co., WA on 10 June, 1992.

A unique male specimen, taken by F. A. Sperling and sent to me by L. F. Gall, superficially resembles *pseudochristina.* It was collected at Spring Creek, 8700′ in Gunnison Co., CO on 14.vii.78 near a mudpuddling site, and "in company with normal pure yellow ♂ *alexandra*" (label data). The DFW are uniformly yellow-orange with the marginal-border veins similarly colored. The DHW are mainly yellow-orange (more intense than the DFW) fading toward yellow along the costal and inner margins. The DHW discal spot is



Figures **19-22.** D UV-reflectance patterns in ♂♂ of *C. alexandra* clinal forms. **(19)** Blue Lake, Lassen Co., CA, 2.viii.78, leg. L. P. Grey. **(20)** Satus Pass, Klictitat Co., WA, 17.v.52. **(21)** Canyon Creek, Ochoco Mtns., Crook Co., OR, 19.vii.61. **(22)** Abert Lake, Lake Co., OR, 9.vii.80.

concolorous. The DFW cell spot is crescentic as in *pseudochristina.* This specimen resembles typical *alexandra* V, except that the ground color is pale yellow-orange as opposed to lemon-yellow. The UV-reflectance pattern is typical of normal *alexandra.* There is a thin reflective line along the inner edge of the DFW dark marginal border, and the DHW pattern is typical of *a. alexandra.* This specimen may represent an ancestral form, or perhaps it is a recessive expressing ancient contact between *alexandra* and *pseudochristina* when the latter was more widely distributed (see Fig. **80** and associated text). There is no evidence based upon facies that the specimen is a hybrid between *alexandra* and *eurytheme,* such as the hybrids illustrated by Ae (1959).

Colias pseudochristina Ferris, 1989
Figs. **26-29**

Colias pseudochristina Ferris, 1989. Bull. Allyn Mus., (128):1-11. TL — N. Fork of the

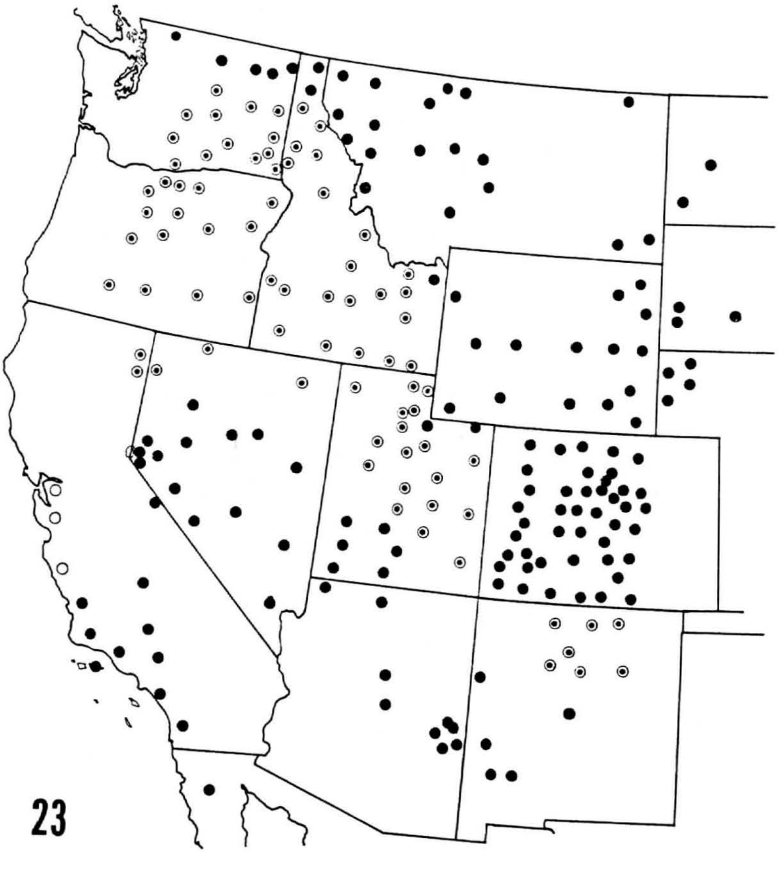


Figure 23. Distribution of *Colias alexandra* south of the Canadian border. Circles with pupils indicate clines. Open circles indicate old records for which there are no contemporary records. The dots are located in the counties from which records exist, and do not indicate specific collection sites, which are generally more numerous than the dots indicate.

Provo River, Summit Co., Utah. HT in Allyn Museum of Entomology, Sarasota, FL.
= *Colias occidentalis wasatchia* Gillette, "Autumn 1988"[1989]. Utahensis, 8(4): 38-51. TL — "A ridge 2.3 mi west of the SW end of Strawberry Reservoir, elev (2408m)/7900 ft, on the west side of the W Strawberry Rsv road, and 1.9 mi south of East Portal, Wasatch Co, Utah (Strawberry Reservoir NW 1:24,000 USGS map)." HT "...will be deposited in the Monte L. Bean Museum of the Brigham Young University campus, Provo, Ut, UT." (See note at end of this monograph concerning dates of publication.)

General characteristics of the species.

Coloration of the ♂♂: Dorsal ground color orange (approximately Smithe #18 Orange Yellow, but less saturated), blending to yellow toward the FW costal margin, at the wing bases, and towards the outer and inner margins of the HW. Melanic scales are concentrated at the wing bases. Wing borders black, but heavily dusted in the cell spaces with whitish scales, and with the veins outlined by orange scales. DFW cell spot prominent, black and crescentic or D-shaped with slight pupil (bow of D basad). DHW discal spot is concolorous with the background color. VHW ground color is pale yellow-orange, but a light dusting of the wings with melanic scales produces an overall yellow-greenish aspect, especially to the HW. The pupil of the VHW discal spot is pearly-white and heavily ringed by dusty-rose scales. Occasionally this spot is vertically double. There are some pinkish hairs caudad (palpi), but generally the body vestiture is yellow. The wing fringes are pink except at the tornus and along the inner margin of the FW where they are pale yellow. Legs with pinkish hairs blending to pale yellow.

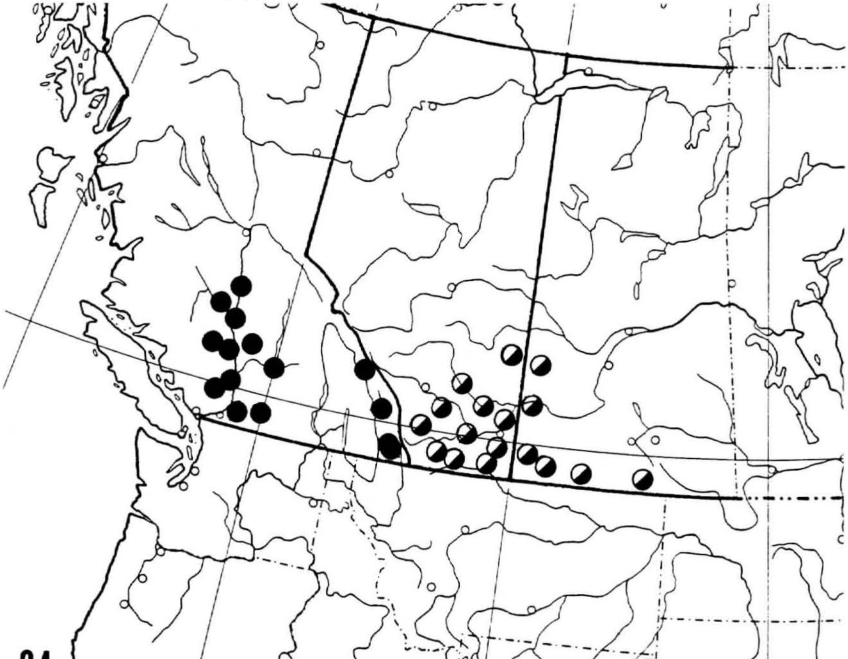


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Figure 24. Distribution of *Colias alexandra* north of the Canadian border. Solid circles represent *a. columbiensis*; half-open circles represent *a. alexandra.* The dots are located in the general areas from which records exist, and do not indicate specific collection sites, which are more numerous than the dots indicate.

UV-reflectance of the ♂♂: HW pattern reduced as compared to *alexandra* sspp.; FW pattern greater than 50% of wing area, radiates distally from the wing base, and may fill the entire central area of the wing.
Coloration of the ♀♀: Variable from strongly orange-flushed through yellow to creamy-white (sometimes with very faint orange blush). Maculation D varies from immaculate to a narrow solid border. The fenestrated border typical of other *Colias* ♀♀ occurs only very rarely. Other characters are as in the ♂♂.
Typical FWL: ♂♂ 23-29 mm; ♀♀ 26-31 mm.
Habitat: Open areas in coniferous forest (Rocky Mountain Montane Forest) in specialized habitat characterized by rocky ground, the presence of *Wyethia* sp., and early desiccation of the herbaceous vegetation. The Strawberry Reservoir, Wasatch Co., UT habitat differs from all of the other sites that I have visited. The slopes are covered primarily by sagebrush and aspen. The coniferous forest begins at much higher elevation than that at which I collected *C. pseudochristina*, although these butterflies may occur in forest clearings later in the season. The Strawberry Reservoir locality is probably the southernmost colony

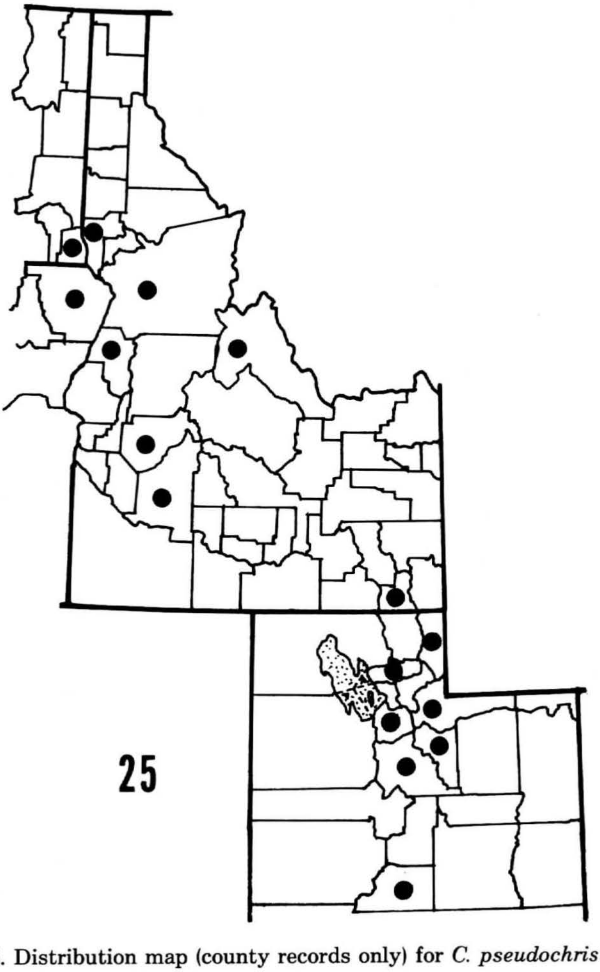


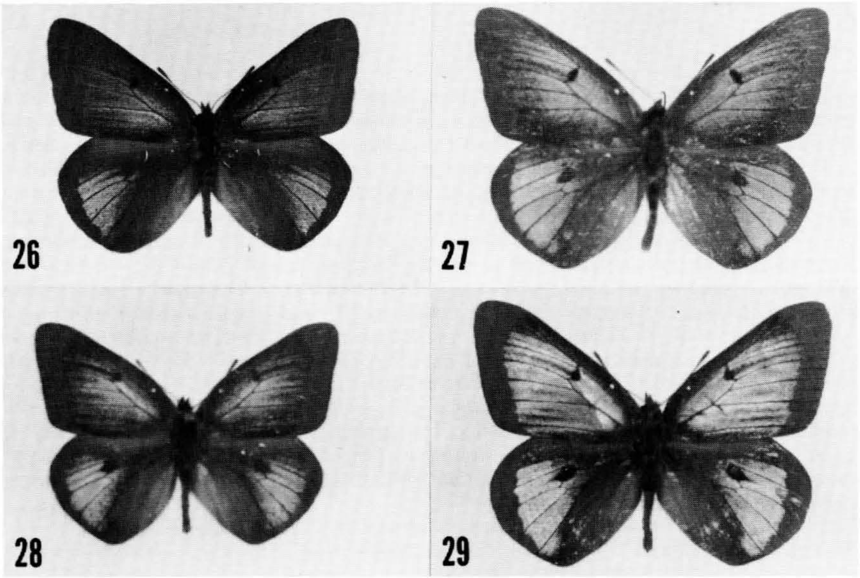
Figure 25. Distribution map (county records only) for *C. pseudochristina*.

of *pseudochristina*, and this situation may account for the somewhat atypical habitat. Although *Lathyrus* sp. may occur at this site, I found only *V. americana* when I visited the area in June of 1990, and this is the plant with which the females were in association. These two plant genera are easily separated by the form of the style in the seed pod, and should not be confused with one another.

Biology: Adults normally in association with *Vicia americana* Muhl., and various *Lathyrus* species. Oviposition observed on *Lathyrus pauciflorus* Fern. in the Blue Mtns., Asotin Co., WA by Barry Sullivan (*fide* P. C. Hammond). Gillette (1989) reported the larval hosts in Utah as *L. lanszwertii* Kell., *L. pauciflorus*, and *L. brachycalyx* Rydb. At a *pseudochristina* colony in Summit Co., UT that I have visited on several occasions, I have found only *V. americana* growing. In Franklin Co., ID, the plant association is *L. lanszwertii*. Gillette also stated that he has reared *pseudochristina*, but information about the early stages was not included in his paper. Adults typically from late v to late vii depending upon locality and elevation. Univoltine, but occasionally with protracted emergence.

Distribution: Oregon (Wallowa Co.); Utah (Rich, Salt Lake, Sevier, Summit, Utah, Wasatch, Weber Cos.); Idaho (Adams, Boise, Elmore, Franklin, Idaho, Lemhi, Nez Perce Cos.); Washington (Asotin Co., Blue Mtns.). Very local. Based upon the distribution map (Fig. 25) for this species, one would expect it to occur also in at least Cache, Morgan, and Sanpete Cos. in Utah, but I have no confirmed records. I have found suitable habitats for this species in Tooele Co., UT (Stansbury Mtns.), but apparently *pseudochristina* is absent. Other areas contiguous to the known geographical distribution for this species apparently lack suitable habitat, and I have not found either the butterfly or its habitat in Uinta Co., WY, Moffat Co., CO, or Elko Co., NV. Map: Fig. **25**.

Additional comments: In my experience with this species, the females are normally sedentary and expose themselves only to intercept passing males, or occasionally to fly to a nectar source. If the females are startled, they rapidly seek shelter in the nearest



Figures 26-29. D UV patterns in ♂♂ of *C. pseudochristina*. **(26)** HT, North Fork of the Provo River, Summit Co., UT, 13.vi.61; specimen in AME (shown as Fig. 4 in Ferris, 1989a). **(27)** N. Fk. Provo River, Summit Co., UT, 21.vi.88. **(28-29)** Williams Creek Trail, Cache NF, Franklin Co., ID, 6.vi.88.

stand of tall shrubs or trees. When weather conditions are favorable, however, the females can be extremely active. Such was the case on both 7 and 21 June, 1990 at the Williams Creek Trail site in Franklin Co., ID. These days were hot, perfectly calm, and without clouds all day. Few males were present, but tens of females were observed exhibiting oviposition behavior about *Lathyrus* plants and sipping nectar from *Wyethia* blossoms. In Elmore Co., ID on 8 June, 1992, both sexes were observed nectaring avidly and exclusively on *Chaenactis douglasii* (Hook.) H. & A. (Dusty Maiden), a composite with rather inconspicuous flowers.

The males of this species exhibit a flight pattern which is different from all other N.A. *Colias* including *occidentalis.* Given the opportunity, *Colias* males will fly along topographic disjunctions such as forest roads, powerline cuts, gullies, streams, and solifluction ridges (arctic areas). I have never observed this behavior in males of *pseudochristina.* I have taken specimens flying across such disjunctions, but never flying along them. This behavioral character increases the difficulties encountered when collecting this species. Another trait of *Colias* is "puddling", in which primarily males gather at mud, moist sand, or the edges of puddles and seeps. On hot days, even the arctic species manifest this behavior. I have only once seen *pseudochristina* at moist sand (2 ♂♂ Elmore Co., ID, 14-vi-93), but I have taken *occidentalis* at mud in Oregon and Washington.

Common name: Common names are generally included in field guides and other popular publications, and I provided none for this butterfly in its original description. I propose the name Intermountain Sulfur, in recognition of its geographic distribution.

Colias christina W. H. Edwards, 1863

General characteristics of the species.

Coloration of the ♂♂: This species is somewhat variable in phenotype. In the "classical" form, the wings are basally yellow and distally orange. This color transition is abrupt and gives the aspect that the wings have been over-painted with an orange band. More often, the color transition is diffuse, and some specimens show orange patches superimposed upon the yellow ground color. Ventral color repeats D color (although somewhat more diffused); VHW lightly covered by melanic cover scales producing a slight olivaceous aspect with some melanic dusting of the VFW along the costal margin and at the apex (occasionally). DFW cell spot variable: solid black and round or vertically elongated, with or without pupil, sometimes vestigial, sometimes crescentic. Width of black border variable within and among local populations, and border outlined along the veins by yellow-orange scales. DHW discal spot large, orange, and often with a paler pupil. VHW discal spot usually large with opalescent pale pupil; heavily rimmed by dusty-rose scales which often radiate outward from the rim. Head and caudal portion of thorax covered with pink hairs; palpi yellow V. Abdomen and remainder of thorax with yellow vestiture Wing fringes pink replaced by yellow at outer angles. Legs with pink and yellow hairs.

UV-reflectance of the ♂♂: Bright luminous patch occupying 50% or more of DHW surface. DHW discal spot is non-reflective. DFW generally highly reflective except for marginal border and basally. DFW cell spot is non-reflective.

Coloration of the ♀♀: The ground color may be as in the males, but paler, or variable to white, with or without a D orange blush. Dorsal maculation various from nearly absent (rare) through dark dusting at the FW apices to a fully-developed fenestrated wing border. Other characters are as in the ♂♂. Occasional ♀♀ may show some patchy UV-reflectance in the FW central area.

Habitat: Clearings in montane and boreal forests, and forest edges.

Distribution: Northern Wyoming northward to Manitoba, Alberta, N. British Columbia into the Yukon and Northwest Territories.

Colias christina astraea W. H. Edwards, 1872 **[Revised Combination]**

Figs. **30, 31**

Colias astraea W. H. Edwards, 1872. Trans. Amer. ent. Soc., 4:61. TL — Yellowstone Lake, Yellowstone N.P. HT in CMNH. Male and female "types" illustrated by Holland (1949: pl. 68, figs. 26-27). Holland's illustrations are not of the types. This taxon was described from a single male, and not the one shown by Holland. See Brown (1973:73-74) for a complete discussion. Additional description, including the female, appears in Edwards, 1884. Papilio, 4:30-34.

= *Colias astraea* W. H. Edwards; Strecker, 1878:83.
= *Colias christina astraea* W. H. Edwards; Skinner, 1898:69.
= *Eurymus christina* syn. *astraea* (W. H. Edwards); Dyar, 1902:10.
= *Eurymus christina* f. "astraea" (W. H. Edwards); Barnes and Benjamin, 1926a:8.
= *Colias christina* f. "astraea" W. H. Edwards; McDunnough, 1938:8.
= *Colias astraea* W. H. Edwards; Holland, 1949:297.
= *Colias occidentalis astraea* W. H. Edwards; McHenry, 1963:210; 215.
= *Colias scudderii astraea* W. H. Edwards; dos Passos, 1964:43.
= *Colias alexandra astraea* W. H. Edwards; Brown, 1973:57; 72.
= *Colias alexandra astraea* W. H. Edwards; Ferris, 1973:60; 71.
= *Colias alexandra astraea* W. H. Edwards; Miller and Brown, 1981:81.
= *Colias alexandra astraea* W. H. Edwards; Ferris, 1988:4.
= *Colias alexandra* f. "astraea" W. H. Edwards; Gillette, "1987"[1989]:58.

Coloration of the ♂♂: Generally similar to the description given above for the species as a whole. Orange color tends to be not quite so bright as in the nomenotypical ssp. DHW discal spot smaller and somewhat subdued. V more olivaceous owing to heavier dusting of melanic scales. VHW discal spot usually small with thin well-defined margin.
UV-reflectance of the ♂♂: HW as in species description. FW variable; usually as in the nomenotypical ssp., but reduced in some examples from Wyoming. Pattern always emanates from the inner edge of the dark wing border and radiates basad in the cell spaces.
Coloration of the ♀♀: I have seen only the "alba" form in this sex. The ground color is usually dead white, occasionally with an orange blush. The wing borders vary from dusted to a fully-developed and dark fenestrated pattern. The DHW discal spot is generally pallid and not bright orange. Otherwise the general coloration is as in the ♂♂. The FW apices are less acute than in the ♂♂.
Typical FWL: ♂♂ 22-26 mm; ♀♀ 26-28 mm.
Habitat: Montane in forest clearings and canyons.
Biology: Specific host plants unknown. Adults normally in late vii into viii. Museum specimens dating from the 1930s show late vi in the vicinity of Great Falls, Cascade Co., MT. This may be attributable to the climatic conditions that occurred during the "dust bowl" years. Univoltine.
Distribution: Northern Wyoming from Sheridan Co. westward to Teton Co. and Yellowstone N.P., thence northward in western Montana to the Canadian border. Not recorded from Idaho. Local and apparently generally uncommon. A cline with *christina* occurs from Glacier N.P. northwards in Alberta to the Banff area. Map: Fig. **46**.

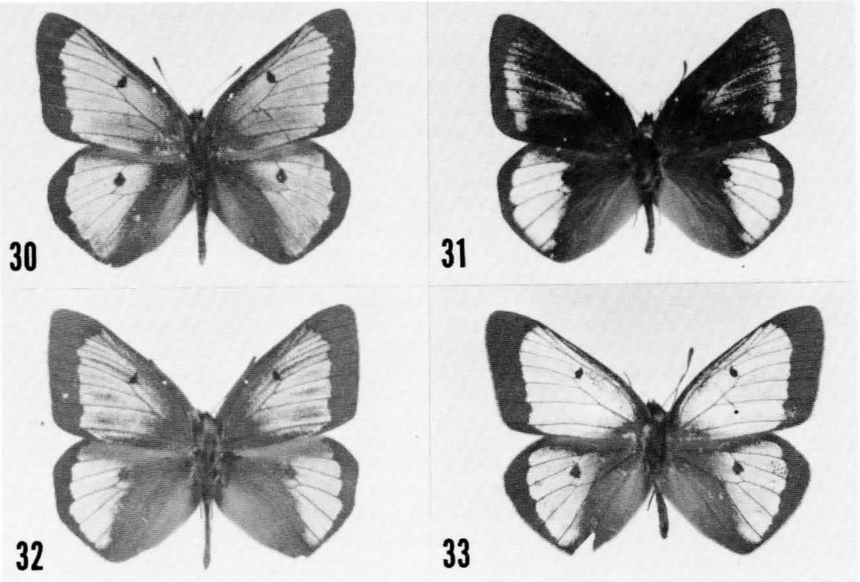
Colias christina christina W. H. Edwards, 1863 **[Revised Combination]**
Figs. **32-36**

Colias christina W. H. Edwards, 1863. Proc. ent. Soc. Philadelphia, 2:79-80. TL — "portage of the Slave River", N.W.T. Lectotype in CMNH, designated by F. M. Brown, 1973; Trans. Amer. ent. Soc., 99:63. Male and female "types" (pseudotypes) illustrated by Holland (1949: pl. 68, Figs. 14-15). See Brown (1973:73-74) for discussion of the type.

= *Colias pelidne christina* W. H. Edwards; Strecker, 1872-1900:133.
= *Colias pelidne christina* W. H. Edwards; Strecker, 1878:81.
= *Colias christina christina* W. H. Edwards; Skinner, 1898:69.
= *Eurymus christina* (W. H. Edwards); Dyar, 1902:10.

= *Eurymus christina* (W. H. Edwards); Barnes and Benjamin, 1926a:8.
= *Colias christina* W. H. Edwards; McDunnough, 1938:8.
= *Colias christina* W. H. Edwards; Holland, 1949:296.
= *Colias christina* W. H. Edwards; Jones, 1951:4.
= *Colias occidentalis christina* W. H. Edwards; McHenry, 1963:210; 215.
= *Colias alexandra christina* W. H. Edwards; dos Passos, 1964:43.
= *Colias alexandra christina* W. H. Edwards; Brown, 1973:57; 62.
= *Colias alexandra christina* W. H. Edwards; Ferris, 1973:60;71.
= *Colias alexandra christina* W. H. Edwards; Miller and Brown, 1981:81.
= *Colias alexandra christina* W. H. Edwards; Ferris, 1988:3.
= *Colias christina christina* W. H. Edwards; Gillette, "1987"[1989]:58.

Coloration of the ♂ ♂: Generally similar to the description given above for the species as a whole. Orange color is bright in the nomenotypical ssp. DHW discal spot normally



Figures **30-35**. UV patterns in ♂ ♂ of *C. christina* sspp. **(30-31)** *C. c. astraea.* Nr. Burgess Jct., Sheridan Co., WY, 26.vii.69 **(30)**. Shell Creek Canyon, Big Horn Co., WY, 30.vii.76 **(31)**, possibly a hybrid between *alexandra* and *c. astraea.* **(32-35)** *C. c. christina.* Clear Lake, Manitoba, 15.vii.76 **(32)**, leg. M. Klassen. Alaska Hwy., mi. 220 nr. Ft. Nelson, 8.vii.48 **(33)**. Ca. 5 mi. W. of Mayo, YT, 13.vii.86 **(34)**. Salt River S. of Ft. Smith, NWT, 24.vii.47 **(35)**.

pronounced. VHW discal spot usually pronounced with a well-defined margin, and sometimes double.

UV-reflectance of the ♂♂: As above in species general description.

Coloration of the ♀♀: As above in species general description. Phenotype somewhat variable as a function of geography. Specimens from the southern end of the species' range tend to be more brightly colored than examples from N. British Columbia and the Northwest Territories. Adult color is less saturated northward. Occasional ♀♀ may show some patchy UV-reflectance in the FW central area.

Typical FWL: ♂♂ 24-29 mm; ♀♀ 25-28 mm.

Habitat: Open or disturbed areas in coniferous (boreal) forest, including road cuts, river valleys, lake shores, gravelly "balds", abandoned gravel pits, and hilltops.

Biology: Reared by Walter Krivda (The Pas, Manitoba) on *Hedysarum alpinum var. americanum* Michx. Krivda (1979) reported that at The Pas, Manitoba, the host plant grows in almost pure clay soil along ditches that border sphagnum bogs. The first instar larvae occur singly per plant, and display "a characteristic rosy band running parallel to the feet." This maculation affords protective coloration to the larvae, since the new growth on the foodplant is "rose-wine coloured." Univoltine over most of its range with adults in vi and vii. Two generations in the Cypress Hills, Saskatchewan reported by Hooper (1973); first generation mid-vi to mid-vii, second generation in early viii.

Distribution: From the Riding Mtns. and The Pas region in western Manitoba westward and northward to the Peace River District of British Columbia (Stikine River, Pink Mtn.) into the NWT (to vic. Ft. Smith) and Yukon T. (Mayo and Dawson City areas). Map: Fig. **47**.

Colias christina clines
Figs. **38-43**

Originating in the Glacier N.P. area of northern Montana and extending to at least the Banff-Seebe region in S. Alberta, a cline exists between *c. astraea* and *c. christina*. Based upon several series that I have examined that were collected in different years, phenotype is plastic and apparently variable to some degree on an annual basis. It is not entirely clear where pure *christina* takes over, but about 52°N seems to be the boundary. Specimens from Prospect Mtn. appear to be *christina*. The phenotypes observed in some eastern foothill areas along the Rocky Mtns. of southern Alberta suggest the occurrence of occasional hybridization with *C. a. alexandra*. Perhaps some of the variability noted in *astraea* throughout its geographic range is produced by periodic hybridization with *alexandra*.

A short series of specimens in the AMNH collected in various years from 1921 to 1936 in Glacier N. P., Montana contains 9♂♂ of the *christina* phenotype, 1 yellow-orange ♀ of the *christina* phenotype, and 4 white ♀♀ of the *astraea* phenotype. Collection dates range from 4-16.viii.

On 15-16.vii.1970, I collected extensively along the Kananaskis Forest Road from Coleman to Seebe, Alberta. A series of *Colias* was taken consisting of 22 ♂♂ and 15 ♀♀. Of the males, five resemble *a. alexandra* dorsally and ventrally also except for the VHW discal spot, which varies from the normal prairie form found in that species to the form found in *astraea*. The 17 remaining ♂♂ resemble *christina* D, but V blend between *astraea* and *christina*. Four of the ♀♀ are of the typical white *astraea* phenotype, eight resemble typical yellow-orange *christina*, and three appear to be hybrids with *philodice*, or else very heavily maculated aberrants of *christina*. One of the yellow ♂♂, the three hybrid or aberrant ♀♀, three of the normal yellow-orange ♀♀, and eight of the normal ♂♂ were taken flying together in the same small forest clearing just south of Seebe. Figs. **39-43** illustrate the UV-reflectance patterns produced by five of these specimens. These patterns vary from those produced by typical *alexandra* to those characteristic of typical *christina*. Although I have visited this region in subsequent years, I have taken only typical *christina*. It appears that I may have encountered a hybrid swarm in 1970. Hovanitz (1965) illustrated a series of 10 ♂♂ and presented a very brief discussion of this situation. The "more complete discussion" to which he alluded was not published prior to his death. Individual males of *alexandra* sometimes wander large distances from the central colony, and may thus encounter *christina* females with which they mate. Ehrlich (1984) has discussed dispersion in *C. alexandra*.

The specimen shown in Fig. **38** resembles in all visible respects a typical example of prairie *a. alexandra*. The UV-reflectance pattern, however, is that produced by typical *christina*. It is the only prairie *alexandra*-like specimen that I have ever examined that shows this pattern. It was collected by Norbert Kondla in the Kootenai Plains Grassland east of Banff Park. Normal *christina* occurs within the confines of the park.

It is specimens such as those described in the preceding paragraphs that have apparently led some authors to combine *alexandra* and *christina* into a single species. In the past, I adopted this approach as well, but as discussed below, this combination does not fit satisfactorily with field observations, known geographic distributions, and phylogenetic analyses.

For comparison purposes with the "*alexandra* group" of species, a photograph of the UV-reflectance pattern produced by a typical ♂ specimen of *Colias eurytheme* is shown in Fig. **37**. Note the fully-developed pattern on both the FW and HW, and the full reflectance of the DHW discal spot.

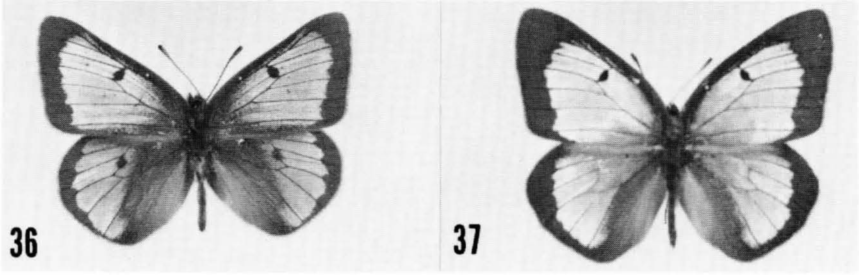
Colias krauthii Klots, 1935 **[Revised Status]**

General characteristics of the species.

Coloration of the ♂ ♂: Dorsally bright orange with extension of this color along the veins in the black borders of the wings. The inner margin of the DFW black border tends to be more irregular than in other species within the *alexandra* group. Some slight yellow coloration basally and along the DFW costa in some specimens. Ventral color repeats D color but is paler; VHW lightly covered by melanic cover scales producing a slight olivaceous aspect with postdiscal melanic dusting of the VFW. DFW cell spot prominent and with or without pupil. Width of black border variable. DHW discal spot of medium size and concolorous with wing; not particularly prominent. VHW discal spot of medium size with opalescent pale pupil; cleanly rimmed by dusty-rose scales. Head and caudal portion of thorax covered with pink hairs; palpi yellow V. Abdomen and remainder of thorax with yellow vestiture. Wing fringes pink with occasional intrusions by yellow hairs. Legs with pink and yellow hairs.

UV-reflectance of the ♂ ♂: Bright luminous patch occupying 50% or more of DHW surface. DHW discal spot is non-reflective. DFW highly reflective except for marginal border and basally. DFW cell spot is non-reflective.

Coloration of the ♀ ♀: Generally as in the ♂ ♂. Dorsal fenestrated border pattern fully developed; openings normally yellow rather than orange. DHW discal spot generally more prominent than in the ♂ ♂. The VHW color is frequently a distinctive pale mossy green,



Figures **36-37**. D UV-reflectance patterns in ♂ ♂ of *C. c. christina* and *C. eurytheme*. **(36)** *C. c. christina* from Prospect Mtn., Alta., 19.vii.84. **(37)** *C. eurytheme* from Midnight Meadows, head of Cabresto Canyon, Taos Co., NM, 27.vii.88.

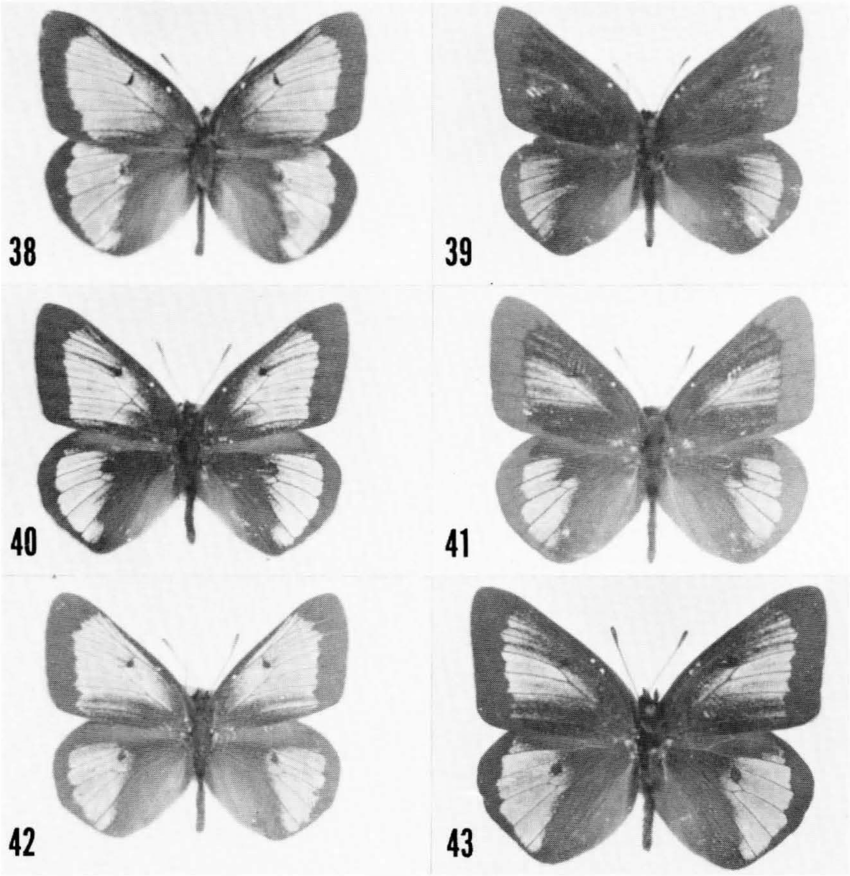
quite unlike that found in *christina*. The white or "alba" form is unknown, and apparently does not occur.

Habitat: Open and disturbed areas in montane and boreal forest.

Distribution: Disjunct; Black Hills region of South Dakota and extreme NE Wyoming, and southern Yukon Territory into E. Alaska.

Colias krauthii krauthii Klots, 1935 **[Revised Status and New Combination]**

Fig. **44**



Figures **38-43**. UV patterns in ♂ ♂ of *Colias* from southern Alberta. **(38)** typical prairie phenotype (visual) of *C. a. alexandra*, Kootenay Plains E. of Banff N.P., Alta., 22.vi.78, leg. N. Kondla. UV-reflectance pattern is that of *christina*. Specimen is perhaps aberrant or a hybrid. **(39)** possible hybrid *C. a. alexandra x c. astraea* or *C. a. alexandra* migrant from S. of Seebe, Kananaskis Forest Road, 16.vii.70; specimen is yellow. **(40)** possible hybrid *C. a. alexandra x c. astraea* from Jct. Highwood Rd. and Kananaskis Forest Road, 15.vii.70; specimen is yellow with slight orange blush on FW. **(41-43)** *C. c. astraea-christina* clinal forms. **(41)** S. of Seebe, Kananaskis Forest Road, 16.vii.70; specimen has an orange blush FW and HW. **(42)** Lombreck, Kananaskis Forest Rd., 15.vii.70; specimen has an orange blush FW and HW. **(43)** Cat Creek, Kananaskis Forest Rd., 16.vii.70; specimen resembles typical *christina*.

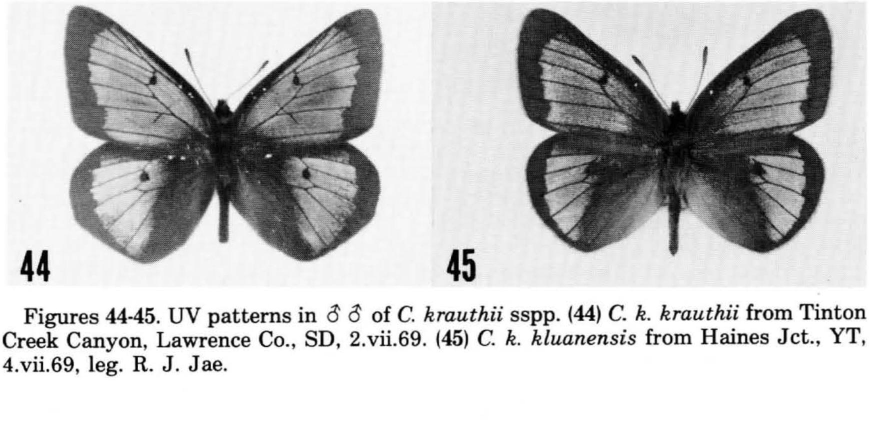
Colias christina krauthii Klots, 1935. Amer. Mus. Novitates, (767):1-2. TL — Black Hills, 12 mi. W. of Custer, Custer Co., South Dakota. HT in AMNH.

= *Colias christina krauthii* Klots; McDunnough, 1938:8.
= *Colias occidentalis krauthii* Klots; McHenry, 1963:210; 216.
= *Colias alexandra krauthii* Klots; dos Passos, 1964:43.
= *Colias alexandra krauthii* Klots; Brown, 1973:57.
= *Colias alexandra krauthii* Klots; Ferris, 1973:60; 71.
= *Colias alexandra krauthii* Klots; Miller and Brown, 1981:81.
= *Colias alexandra krauthi* Klots; Ferris, 1988:6.
= *Colias christina krauthi* Klots; Gillette, "1987"[1989]:58.

Coloration of the ♂♂: As above in species general description.
UV-reflectance of the ♂♂: As above in species general description.
Coloration of the ♀♀: As above in species general description. The "alba" form is unknown.
Typical FWL: ♂♂ 25-29 mm; ♀♀ 25-29 mm.
Habitat: Open meadows, along streams and road cuts in coniferous forest.
Biology: Larval host plant not recorded. The legumes associated with the habitats of *krauthii* are: *Astragalus adsurgens* Pall. var. *robustior* Hook.; *A. alpinus* L. var. *alpinus* L.; *A. flexuosus* (Hook.) Dougl. ex G. Don; *A. tenellus* Pursh; *Hedeysarum occidentale* Greene; *Oxytropis campestris* (L.) DC. var. *gracilis* (A. Nels.) Barneby; *Vicia americana. Hedysarum alpinum* L. (var. *philoscia* Rollins) is recorded from Custer, Lawrence, and Pennington Cos., SD, and Weston Co., WY (Barkley, 1986). This plant has erroneously been reported in early literature as *H. boreale* Nutt. The author has not found this plant, however, at the habitats that he has visited. Based upon a process of elimination, the most probable larval hosts are *A. adsurgens* and *H. occidentale.* It is very possible that *krauthii* is opportunistic and utilizes several leguminous larval host plants. Univoltine with adults from late vi into viii.
Distribution: Black Hills of South Dakota (Custer, Fall River, Lawrence, Pennington Cos.), and extreme northeastern Wyoming in the Bear Lodge Mts. and the Black Hills (Crook and Weston Cos.). Apparently a relict subspecies based upon its very limited geographic distribution (restricted to the Black Hills and Bear Lodge Mtns.). A general discussion of butterfly relict populations in the Black Hills and adjacent regions appears in Johnson, 1975. Map: Fig. **46**.

Colias krauthii kluanensis Ferris, 1981 [**New Combination**]
Fig. **45**

Colias alexandra kluanensis Ferris, 1981. Bull. Allyn Mus., (63):1-4. TL — Haines Junction,



Figures **44-45**. UV patterns in ♂♂ of *C. krauthii* sspp. (**44**) *C. k. krauthii* from Tinton Creek Canyon, Lawrence Co., SD, 2.vii.69. (**45**) *C. k. kluanensis* from Haines Jct., YT, 4.vii.69, leg. R. J. Jae.

Yukon Territory. HT in AME.

= *Colias "yukonensis"* Berger, 1986. *Nomen nudum.* This taxon is described in a key, and the information provided is inadequate to identify the species unequivocally. The TL is given only as the Yukon Territory, and there is no designation of a HT or indication of where the type has been placed.
= *Colias alexandra kluanensis* Ferris, 1981; Ferris, 1988:6.
= *Colias alexandra kluanensis* Ferris, 1981; Ferris, ed., 1989b:23.

Coloration of the ♂♂: As above in species general description. Dorsal color slightly less intense; melanic overscaling V slightly more dense.
UV-reflectance of the ♂♂: As above in species general description.
Coloration of the ♀♀: Generally as above in species general description. Increased yellow suffusion dorsally basad of the fenestrated wing borders. Veins D tend to be outlined with black overscaling; some light dusting by melanic scales in cell spaces. Slightly smaller in size than nomenotypical subspecies. High-altitude specimens (4000′) tend to be a bit smaller and more melanic than those from low-altitude. To date, the "alba" form is unknown.
Typical FWL: ♂♂ 22-24 mm; ♀♀ 22-27 mm. Slightly smaller in size than nomenotypical subspecies.
Habitat: Open and disturbed areas in forested regions including roadsides, revegetated pipeline rights of way, old burns, cleared areas, and dry meadows.
Biology: Oviposition observed by G. Anweiler upon *Hedysarum boreale* Nutt. var. *Mackensii* (Rich.) C. L. Hitchc. It should be noted that *Hedysarum* seems to be a pioneer in disturbed areas in northern Canada. Univoltine with adults from the first week of vii to the first week of viii.
Distribution: Southern Yukon Territory along the Alaska Highway from Whitehorse to Dry Creek, E. of the Alaska border, and in E. Alaska along the Nabesna Road between Slana and Nabesna. The first confirmed Alaska record is for a ♂ collected by a member of the Alaska Lepidoptera Survey on 3.viii.86, but not mounted and identified until early

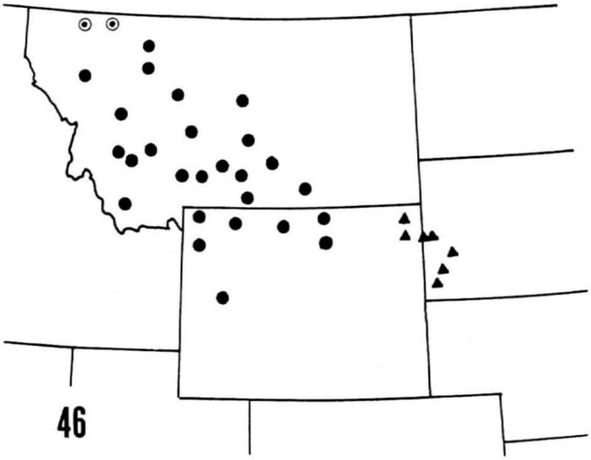


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Figure **46.** Distribution map for *C. c. astraea* (solid circles), *C. christina* cline (open circles with pupils), and *C. k. krauthii* (solid triangles). The open square represents the Grant Co., OR population of uncertain origin (discussed subsequently in the text). The dots are located in the counties from which records exist, and do not indicate specific collection sites, which are generally more numerous than the dots indicate.

1989 (*fide* K. W. Philip 22.ii.89). Additional specimens were collected by K. W. Philip on 10.vii.89 along Nabesna Road at Jack Creek, Trail Creek, and mile 28.5. This subspecies may be more widely distributed than records indicate, since access into areas away from the Alaska Hwy. is difficult. On the other hand, it may be a relict species that has expanded its range during the past 50 years as a consequence of the construction of the Alaska Hwy. and the subsequent extension by its larval host *Hedysarum boreale* into new areas. Map: Fig. 47.

Discussion: It is possible that *kluanensis* is a species distinct from *krauthii.* At the present time, however, the only major character that I can find that separates them is geography. Several minor differences, including average size of the adults, separate them at the subspecific level.

Colias occidentalis Scudder 1862

General characteristics of the species.

Coloration of the ♂♂: Dorsally bright lemon yellow; ventrally with varying hues of yellow to golden yellow, with light melanic over-scaling. FW apices rounded. DFW cell spot variable from prominent, black, and rounded to crescentic and nearly obsolete. Width of black margin variable, but of average width for the genus. Veins in border may or may

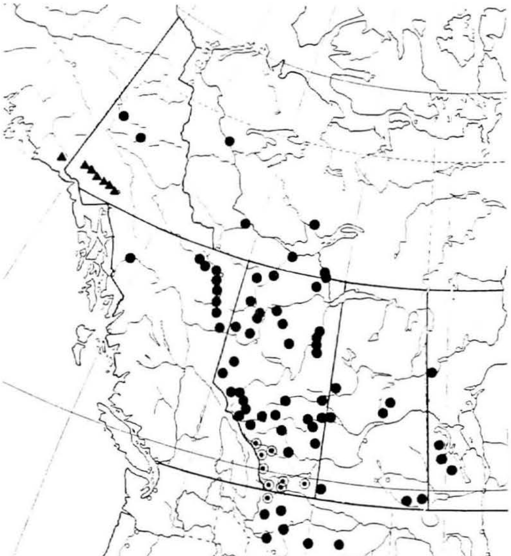


Figure 47. Distribution map for *C. c. christina* (solid circles N. of Canadian border), *C. christina* cline (open circles with pupils), *C. c. astraea* (solid circles S. of Canadian border), partial distribution for reference (see Fig. 25), and *C. k. kluanensis* (solid triangles). The *christina* dot in extreme NW B.C. may represent an erroneous record. The dots are located in the general regions from which records exist, and do not indicate specific collection sites, which are more numerous than the dots indicate.

not be outlined with yellow scales. DHW discal spot variable from orange to concolorous with wing ground color. VHW discal spot with average rim width; sometimes double. Wing fringes pink, replaced by yellow at FW outer angle. Legs pink, and body vestiture a mixture of pink and yellow hairs. Size moderately uniform across populations; ♀♀ generally larger than ♂♂.

UV-reflectance of the ♂♂: Absent. Specialized reflecting scales do not exist.

Coloration of the ♀♀: Variable, varying from bright yellow as in the ♂♂, to a very pale yellow to pale creamy white. DFW border varies from pronounced and fenestrated to nearly obsolete. DHW border normally poorly developed to vestigial. Other characters as in the ♂♂.

Habitat: Hilly open areas in moderately dry coniferous (fir) forest.

Biology: Immature stages apparently unknown. Reported larval host plants are *Vicia, Melilotis,* "legumes", and several suspected genera including *Astragalus, Lathyrus,* and *Lupinus.* I have always found this species in association with either *Lathyrus* or *Vicia.* In early July, 1988 I collected *C. o. occidentalis* in the Ochoco Mtns., Crook Co., OR. Female oviposition behavior was noted (and confirmed in 1992) about plants of *Lathyrus lanszwertii* Kell. Oviposition upon this plant has been confirmed by D. V. McCorkle (*fide* P. C. Hammond). In 1989, I found *occidentalis* in association with *L. nevadensis* Wats. in Kittitas Co., WA.

Voltinism: Univoltine with adults from early v into viii depending upon locality; typically late vi.

Distribution: Locally distributed in portions of NW California into Oregon, central and western Washington, southern mainland British Columbia, and portions of southern Vancouver Is. The distribution map shown for *occidentalis* as **Fig.** 40 in my 1988(a) paper was in error with regard to Vancouver Is. and the B.C. mainland northern range A corrected version is shown as Fig. **64**. The Field, B.C. record (black dot with ?) represents a specimen in the Canadian National Collection which I examined, and may have been mislabeled as to locality. The distribution in Oregon has been reduced, since occurrence of this species in Baker and Wallowa Cos. is questionable. This matter is addressed in a subsequent section that discusses phenotypes of uncertain origin. The Santa Cruz Co., CA record has also been deleted.

Colias occidentalis chrysomelas Hy. Edwards 1877

Figs. **48-51**

Colias chrysomelas Hy. Edwards, 1877. Pac. Coast Lepid., (24):8-9. TL — Napa Co., California. LT and 4 ST's inAMNH. See below for further discussion and designation of the LT.

= *Colias occidentalis* syn. *chrysomelas* Hy. Edwards; Strecker, 1878:82.
= *Colias occidentalis chrysomelas* Hy. Edwards; Skinner, 1898:69.
= *Eurymus occidentalis* syn. *chrysomelas* (Hy. Edwards); Dyar, 1902:10.
= *Eurymus occidentalis chrysomelas* (Hy. Edwards); Barnes and Benjamin, 1926a:8.
= *Colias occidentalis chrysomelas* Hy. Edwards; McDunnough, 1938:8.
= *Colias chrysomelas* Hy. Edwards; Holland, 1949:293.
= *Colias occidentalis chrysomelas* Hy. Edwards; Jones, 1951:4.
= *Colias occidentalis chrysomelas* Hy. Edwards; McHenry, 1963:210; 215.
= *Colias occidentalis chrysomelas* Hy. Edwards; dos Passos, 1964:42.
= *Colias occidentalis chrysomelas* Hy. Edwards; Miller and Brown, 1981:80.
= *Colias occidentalis chrysomelaena* Hy. Edwards; Miller and Brown *in* Hodges, *et al.*, 1983:52.
= *Colias occidentalis chrysomelaena* Hy. Edwards; Ferris, 1988a:19.
= *Colias occidentalis chrysomelas* Hy. Edwards; Gillette, "1987"[1989]:58.

Coloration of the ♂♂: As above in species general description, except ventrally the ground color varies to a dark golden yellow in some specimens. The DFW black border may be quite wide.

UV-reflectance of the ♂♂: Absent.

Coloration of the ♀♀: As above in species general description. The ♀♀ D tend to be more uniformly yellow, and both the DFW and DHW marginal borders more pronounced than in the nomenotypical subspecies. Ventrally the ground color is darker than in *o. occidentalis*. Pale ♀♀ have been collected, but generally not the true "alba" form. One record of the latter by J. R. Tucker from Buckhorn Ridge along the Shasta-Trinity Co. line, CA in mid-vi, 1991.

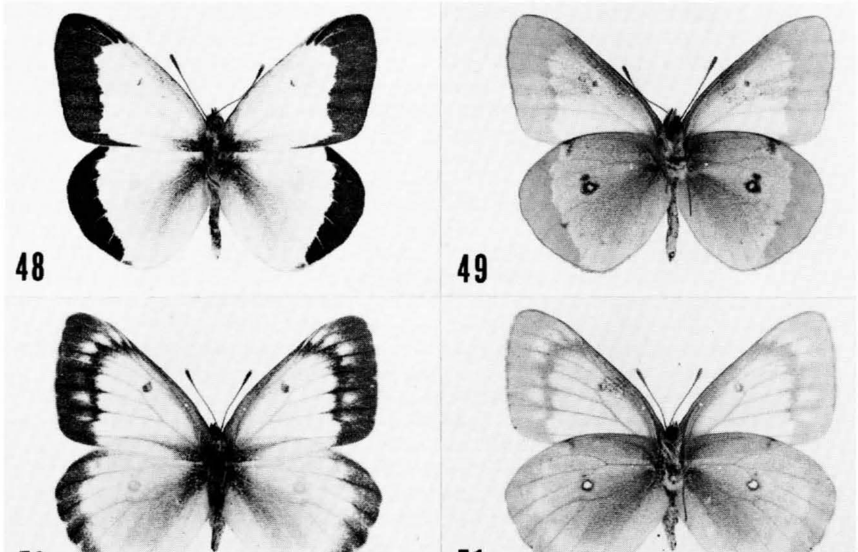
Typical FWL: ♂♂ 25-29 mm; ♀♀ 27-31 mm.

Habitat: As above in species general description. In the Trinity Alps, this butterfly frequents lower montane coniferous forest among Douglas Fir and Yellow Pine, as reported by Shapiro, *et al.*, 1979(1981). It is often found on NE-facing slopes in Douglas Fir forest at sites that are moist in spring, but which dry out in summer.

Biology: As above in species general description. According to Shapiro, *et al.*, 1979(1981), host plant associations are *Lupinus albicaulis* Dougl. ex Hook. and *Lathyrus pauciflorus* Fern ssp. *browni* (Eastw.) Piper.

Voltinism: Univoltine with adults from late v into vi; to mid-vii in the Trinity Alps. Oviposition observed by A. M. Shapiro on both *Lathyrus* sp. and *Lupinus* sp. on Goat Mt., Colusa Co., CA. Oviposition on *Lathyrus latifolus* reported by J. R. Tucker on Buckhorn Ridge, County Line Rd. between Shasta and Trinity Cos., CA, 3200' (975m) in mid-vi, 1991.

Distribution: Coastal ranges of California from Napa and Sonoma Cos. northward along the North Coast Range and spreading into the Klamath Assemblage of mountains to the latitude of Mt. Shasta. County records are shown in Appendix 2. The record for Santa Cruz Co. is probably erroneous and has not been plotted, as is also the case with the Lassen Co. record. Map: Fig. **64**. Clinal forms between typical *o. occidentalis* and *o. chrysomelas* Hy. Edwards have been found in Jackson Co., OR. I have examined such material collected by John Hinchliff of Portland, OR along Soda Mtn. Rd. on 26.vi.87.



Figures **48-51**. Photographs of typical specimens of *Colias o. chrysomelas*. **(48)** ♂ D from Camp Ellendale, Glenn Co., CA, 5.v.73, leg. J. R. Mori; **(49)** same, V. **(50)** ♀ D, same data; same, V **(51)**.

Lectotype Designation:

Colias chrysomelas Hy. Edwards, 1877

Original description in "Pacific Coast Lepidoptera No. 24. Notes on the genus Colias [*sic*], with description of some apparently new forms", pp.8-9, and circulated as typewritten "reprints" [cited by Edwards as from the Proceedings of the California Academy of Science, February 5, 1877].

C. Chrysomelas. Hy. Edw. n. sp.

Size of *C. Eurytheme.* Male. Bright citron yellow, occasionally, but very rarely, with a slight orange tint. Marginal band very broad, black, powdered with yellow scale and cut by the nervures, but never to the extreme margin. At the apex, the nervures are very broad and distinctly yellow. The discal spot is remarkably small, usually a mere dot, and not unfrequently entirely wanting. Costal margin pink, with a few black scale. At the base of the wings, a distinct black cloud, most strongly marked in the male. Secondaries with the marginal band very broad, as in primaries, *distinctly cut by the nervures,* with the discal spot only faintly shown on the upper surface.

Under side, primaries lemon yellow along the internal margin and on the disc; orange at the base, along the costa, and at the apex. The disc of the wing is closely powdered with black scales. Secondaries, orange, all except the margin densely covered with black scales. Discal spot, pink, surrounded with brown, which latter color forms a smaller patch surmounting the discal spot. Near the apex is a brown dash, and one or two very faint submarginal points are visible beyond the middle of the wing. The fringes are decidedly and broadly rose pink, and there is a dash of the same color at the base of the secondaries. Antennae bright rose pink, thorax black, with long yellow hairs. Abdomen blackish above, lemon yellow beneath. Expanse wings, 2.00 inch.

Female. Paler than the male, with the marginal broad band, but broken up into a series of yellow clouds, with no distinct form. Discal spot small and incomplete, as in the male. On the secondaries the band is almost obsolete and does not extend beyond the median nervure. The discal spot is pale orange. Fringes broad, rose pink. Lower side similar to the male, except that the discal spot of secondaries is usually pinkish white, surrounded by a purplish brown ring. Expanse wings, 2.25 inch.

Seven ♂, five ♀. Napa County, Cal. (Coll. Hy. Edw.). I have no doubt whatever of the distinctiveness of this species. It is almost nearly allied to *C. occidentalis* (Scud.), the original types of which species are now before me. It differs in the extreme width of the marginal band, equally broad on primaries and secondaries, and always distinctly cut by the nervures on both wings; by its much larger size, and by the paler ground color of the female, with more pronounced marginal border. The usual absence of the discal spot of [the] primaries is also a strongly marked character. I have seen an albino female of this species.

Discussion: Edwards cited 7 ♂♂ and 5 ♀♀ syntypes from Napa Co., California, while Beutenmüller (1892) cited only 2 ♂♂ from Napa Co. There are 2 ♂♂ and 3 ♀♀ in the AMNH type collection. The associated specimen labels for the 2 ♂♂ read as follows: Specimen no. 1 — (1) "2308 Calfn [in Hy. Edws handwriting]; (2) "Colias chrysomelas Hy. Ed. Type ♂" [hand written by Hy. Edw.]; (3) "No. 3447 Collection Hy. Edwards." [printed with hand written number]; (4) red, printed A.M.N.H. type label; (5) printed "Type Specimen" label. Specimen no. 2 — (1) "2308 Califor" [hand written by Hy. Edw.]; (2) "No. 3448 Collection Hy. Edwards." [printed with hand written number]; (3) red, printed A.M.N.H. type label; (4) printed "Type Specimen" label.

In the original Hy. Edwards catalogue, in his handwriting, the entry for specimen no. 2 reads: "Colias interior Scud. Vancouver Island Dr. Bremmer" [!]. In the AMNH catalogue for the Hy. Edwards collection, the entry for specimen no. 1 reads: "3447 2308 Colias chrysomelas Edwards ♂ California Hy. Edwards [collector] Type specimen." The entry for specimen no. 2 reads: "3448 2308 Colias chrysomelas Edw. variety ♂ California Hy.

Edwards [collector] Type specimen." The location of the remaining 5 ♂♂ and 2 ♀♀ is unknown.

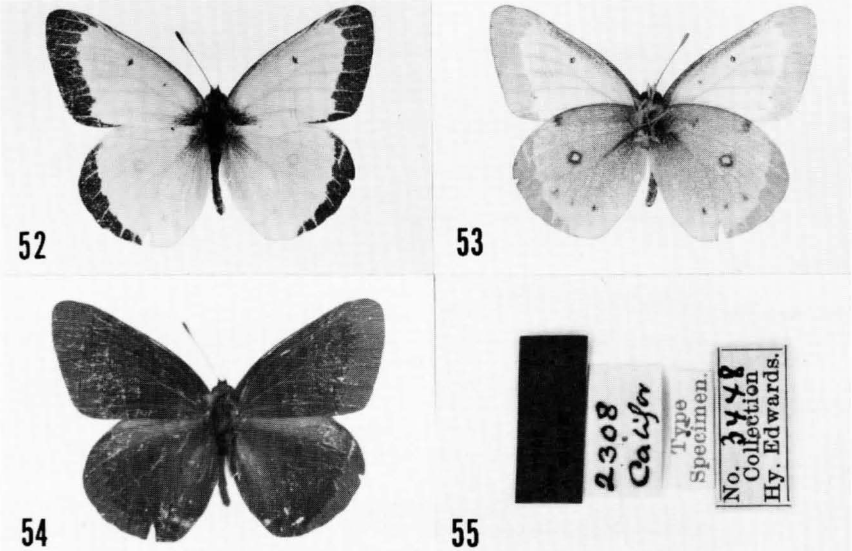
Specimen no. 2 (Figs. **52-55**) is enigmatic. It bears no resemblance whatsoever to *chrysomelas*, nor does it resemble *interior* (see above). It has a peculiar orange flush D which may be natural, or may be induced by a chemical agent such as overexposure to cyanide fumes. In visual pattern, it is closest to the Grant Co., Oregon population discussed in the main body of this paper. I seriously question that this specimen was collected in California, and I have affixed comment labels to the specimen pin so stating. I suspect that this specimen may have been collected in eastern Oregon. As Fig. **54** verifies, the specimen is not UV-reflective, and thus is not *pseudochristina*, which it also resembles superficially.

Lectotype Designation: I have designated as the lectotype of *Colias chrysomelas* the specimen referenced as no. 1 above, since it closely fits the original description. A red label inscribed in black ink (handwritten) has been affixed to the specimen pin and reads: "LECTOTYPE ♂/ Colias chrysomelas/Hy. Edwards. Designated/by C. D. Ferris 7.v.1990." This specimen and its labels are illustrated in Figs. **56-59**. There is no UV-reflectance in this species as Fig. **58** confirms. FWL of lectotype = 2.8 cm.

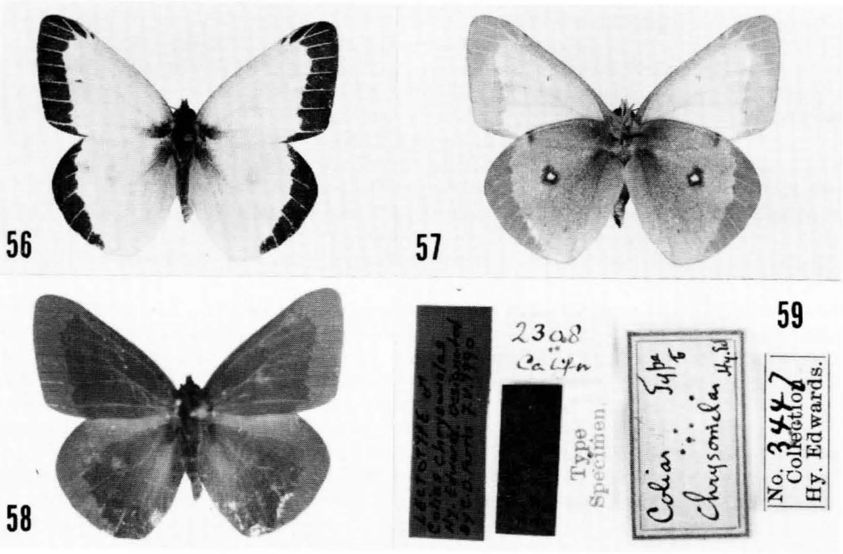
Colias occidentalis occidentalis Scudder 1862
Figs. **60-63, 133-134**

Colias occidentalis Scudder, 1862. Proc. Boston Soc. Nat. Hist., 9:109-110. TL — "Gulf of Georgia" [British Columbia]. LT, designated by Ferris (1988a), in MCZ (Type no. 16603). Two cotypes bear the same MCZ type number label. The ♀, however, is an "alba" form of *C. eurytheme* Boisduval. The male and female "types" illustrated by Holland (1949: pl. 68, figs. 16-17) are specious. See discussion in Ferris (1988a).

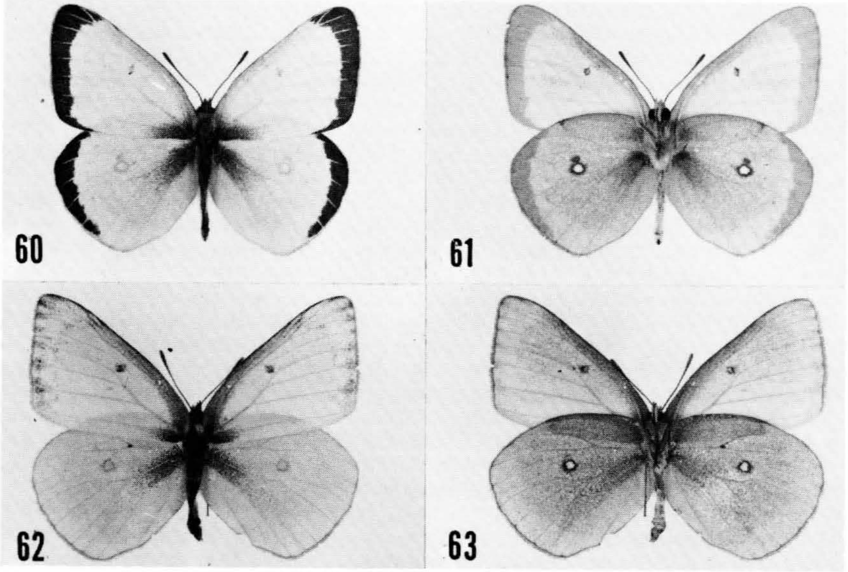
= *Colias philodice occidentalis* Scudder; Strecker, 1878:82.
= *Colias occidentalis occidentalis* Scudder; Skinner, 1898:69.



Figures **52-55**. Enigmatic ♂ specimen from Hy. Edwards type series of *C. chrysomelas*. D (**52**), V (**53**), D UV-reflectance (**54**), specimen labels (**55**). Specimen in AMNH.



Figures 56-59. Lectotype ♂ of *C. chrysomelas* Hy. Edwards. D **(56)**, V **(57)**, D UV-reflectance **(58)**, specimen labels **(59)**. Specimen in AMNH type collection.



Figures 60-63. Photographs of typical specimens of *Colias o. occidentalis*. **(52)** ♂ D, Satus Pass Ski Area, Klickitat Co., WN, 16.vi.62, leg: R. E. Woodley; same, V **(53)**. **(54)** ♀ D, Wellington, Vancouver Is., B.C., Can., 6.vii.72, leg. R. Guppy; same, V **(55)**.

= *Eurymus occidentalis* (Scudder); Dyar, 1902:10.
= *Eurymus occidentalis* (Scudder); Barnes and Benjamin, 1926a:8.
= *Colias occidentalis occidentalis* Scudder; McDunnough, 1938:8.
= *Colias occidentalis* Scudder; Holland, 1949:293.
= *Colias occidentalis occidentalis* Scudder; Jones, 1951:4.
= *Colias occidentalis occidentalis* Scudder; McHenry, 1963:210; 215.
= *Colias occidentalis occidentalis* Scudder; dos Passos, 1964:42.
= *Colias occidentalis occidentalis* Scudder; Miller and Brown, 1981:80.
= *Colias occidentalis occidentalis* Scudder; Miller and Brown in Hodges, *et al.*, 1983:52.
= *Colias occidentalis occidentalis* Scudder; Ferris, 1988a:17.
= *Colias occidentalis occidentalis* Scudder; Gillette, "1987"[1989]:58.

Coloration of the ♂♂: As above in species general description, with V ground color remaining bright yellow. The DFW borders of the ♂♂ are more narrow than in *chrysomelas.* Occasionally non-UV-reflective orange or orange-flushed males of *occidentalis* are collected, typically in the Ochoco Mtns. in Oregon. They seem to occur more frequently in years when the spring is hot and dry, such as was the case to some degree in 1990, and especially in 1992. The latter was a drought year with abnormally high June temperatures (above 34°C). *C. occidentalis* experienced a population explosion in the Ochoco Mtns. in 1992, and 25 (11%) orange or orange-flushed males were observed in a total series of 225 males. None of these specimens was UV-reflective. Additional discussion appears below in the "Grant County, Oregon Population" section.
UV-reflectance of the ♂♂: Absent (see Figs. **133-134**).
Typical FWL: ♂♂ 25-27 mm; ♀♀ 28-30 mm.
Coloration of the ♀♀: As above in species general description.
Habitat: As above in species general description.
Biology: As above in species general description. Univoltine with adults from late vi into viii depending upon locality. In June, 1992, *occidentalis* literally swarmed in the Ochoco Mtns. of Oregon, and I observed ovipositions on *L. lanszwertii* in both Crook and Wheeler Cos. from 8:52 AM to 12:04 PM (PDT). Eggs were deposited singly on the upper surface of the leaves of the host at approximately mid-leaf length. Ova were placed from the leaf edge to the mid-vein. Leaves in "branchlets" close to the tops of the plants were selected as oviposition sites.
Distribution: Spotty distribution in western and north-central Oregon, central and western Washington, southern mainland British Columbia, and portions of southern Vancouver Is. Map: Fig. **64**.
Additional comments: From my observations of this butterfly, adults fly only when air temperature and solar radiation exceed some critical level, different from that required to initiate flight behavior of other sympatric species. Although other species (including *Colias*) may be on the wing, or can be flushed from cover, this is not the case with *occidentalis,* until its particular environmental requirements are met, whatever they may be. On very hot mornings (25°C and above), *occidentalis* may be flying as early as 7:00 AM (PDT). The only quantitative studies that I know of on this subject in *Colias* are those by Leigh and Smith (1959) and Watt (1968). Kingsolver (1985) has published a survey article that presents observations upon *Colias* in particular. I have also noted that both sexes will move into open areas, such as logged-out sites, at midday. This seems to be a mate-locating strategy, since I have observed both courtship and rejection flights.

Discussion of DFW UV-reflectance Patterns in the Former "*alexandra* Group"

The manner in which the DFW UV-reflectance patterns manifest themselves in the various species of the former "*alexandra* group" is diagnostic. The pattern produced by *pseudochristina* is unique as it always originates basally and radiates distally in a *diffuse* manner. The cell spaces are completely luminous within the reflective portions of the wing (Figs. **26-28**). In some specimens, the luminous region may occupy the complete wing surface exclusive of the dark marginal border, and along the costal and inner margins

(Fig. **29**). There is always some DFW reflectance, as opposed to *alexandra* in which the DFW may be non-reflective. The non-reflective DFW cell spot appears distinctly. Relative to the DHW UV-reflectance pattern, the discal spot normally appears as a non-reflective black oval spot. It may be partially obscured in some specimens that manifest a reduced HW reflectance (Fig. **26**).

Some specimens of *alexandra* produce no detectable DFW UV-reflectance (Figs. **9, 13, 18, 20**). When reflectance is present, the pattern always originates at the inner edge of the dark marginal border and radiates basally. In some specimens, only a bright narrow line, or suggestion thereof, is seen (Figs. **3, 8, 10-11, 19, 21-22**). More typically, the luminous pattern extends inwardly in the cell spaces, but along the veins such that the central regions of the cell spaces appear dark (Figs. **12, 15-17**). Normally there is a wide dark region below the costal margin and above the inner margin. The non-reflective DFW discal cell spot is usually obscured, and appears only faintly, if at all, against the dark background. The DHW UV-reflectance pattern in *alexandra* normally terminates distad of the discal spot. A notch may appear in the margin of the UV pattern at the location of this spot, but the spot is not outlined.

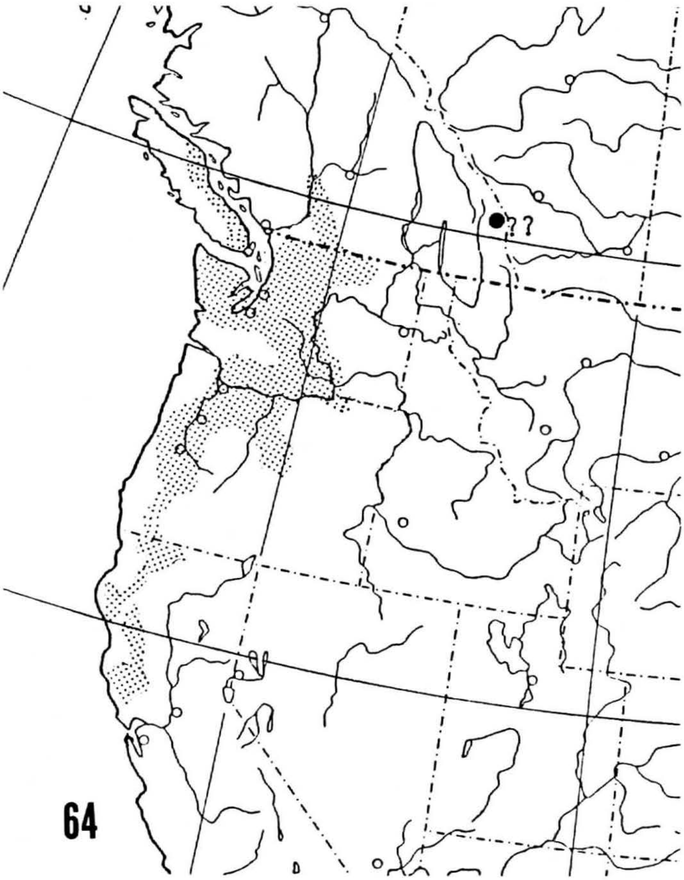


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Figure **64**. Map showing distribution of *Colias occidentalis*. The black dot represents the record from Field, B.C.; see text for further discussion. The small open circles locate principal cities and are unrelated to the species-distribution plots.

The DFW UV-reflectance pattern produced in *christina* is variable. It emanates from the marginal border and radiates basally. In its fully-developed form, essentially all of the wing surface is luminous except for the dark marginal border and the non-reflective discal spot (Fig. **33**). In other specimens, the costal margin may not reflect (Figs. **30, 35-36**). Occasionally, the pattern is not fully developed. In these specimens, the costal margin, the inner margin, the basal area, and central portions of some cell spaces may appear non-reflective (Figs. **32, 34**). Based upon the UV-reflectance pattern shown in Fig. **31**, this specimen is most probably a hybrid between *alexandra* and *c. astraea*, although the visible color pattern resembles the latter. Typically both the DFW cell spot and the DHW discal spot appear as non-reflective dark dots. The veins in both FW and HW appear as fine dark lines.

The DFW UV-reflectance pattern is always well-developed in *krauthii.* It emanates from the marginal border and radiates basally. It may or may not extend to the base of the wing (Figs. **44-45**). The degree to which the costal marginal and inner marginal areas reflect is variable. The DFW cell spot and DHW discal spot appear as prominent non-reflective dots, and the veins appear as equally prominent dark lines.

Relative to the possible hybrid specimens (as discussed above) shown in Figs. **38-43**, Figs. **38, 40, 42-43** illustrate patterns that are reasonably typical of *christina.* The patterns produced by the specimens shown in Figs. **39** and **41** are characteristic of *alexandra,* especially Fig. **39**.

A Note about the Geographical Distribution of the Former "*alexandra* Group"

When the geographic distribution south of the Canadian border of these species is examined closely, we see a spotty mosaic pattern of orange phenotypes overlying a broader distribution of yellow phenotypes. North of the Canadian border, the pattern reverses and the orange phenotypes dominate. Many regions are now known in which *alexandra* and *pseudochristina, alexandra* and *christina,* and *alexandra* and *krauthii* occur in close proximity (see maps and locality data in Appendix 2), although they may not be sympatric in the strict sense. In several areas in Oregon, Washington, and southern British Columbia, *alexandra* and *occidentalis* have been collected at the same site. Specific data from Oregon from my 1990 and 1992 field collecting for strict sympatry of *alexandra* and *occidentalis* are: Wheeler Co., 29.vi.90, open clearing in forested hillside along FR 2600/700, Ochoco NF, ca. 4200′ (1280 m), ca. 0.2 road mi. from jct. with US 26, 9-10:00 AM (PDT); Wheeler Co., 29.vi.90, large logged-out clearing in forest off FR 2600/600, Ochoco NF, ca. 4800′ (1460 m), 0.8 road mi. from jct. with US 26, 10:10-11:00 AM (PDT) [several *C. eurytheme* were also taken]; 22.vi.92, new logged-out clearing in forest along FR 2600/600, Ochoco NF, ca. 4700′ (1434 m), 0.6 road mi. from jct. with US 26, 9:00 AM to 3:00 PM (PDT) [three *C. eurytheme* were also taken]. Grant Co., 28.vi.90, edge of forest along Fields Creek just N of Billy Fields Campground, Malheur NF, 3800-3900′ (1160-1190 m), ca. 4:00 PM (PDT) [see discussion below of Grant Co. *occidentalis* population].

The northern limit of *C. alexandra* is 52° N in Alberta and about 53° N in British Columbia. I can find no records of *christina* from southern British Columbia. There is a clean break between *alexandra columbiensis* on the west side of the Rocky Mtns. in southern British Columbia, and *christina astraea/christina christina* on the east side of the mountains in Alberta. Further eastward, *C. a. alexandra* occurs on the prairie. *C. c. christina* first appears in British Columbia north of 56° N in the Peace River region.

Colias pseudochristina occupies a very restricted environmental niche, and is locally distributed in the Intermountain Region. *Colias krauthii* occurs in two isolated and geographically compact subspecies, and differs from the other species in the group in that "alba" females are unknown. The nomenotypical subspecies is surrounded by prairie *alexandra.* Subspecies *kluanensis* occurs as a compact distribution apparently isolated from *christina.* The currently-known diagnostic characters that separate *kluanensis* from *krauthii* are geography, and the melanic appearance and overall smaller size of *kluanensis* as compared to *krauthii.* The former occurs in the Yukon Territory and eastern Alaska, and the latter in western South Dakota as an apparent relict population.

Phenotypes of Uncertain Origin

One nagging problem has not been resolved by UV photography, field observations, or "classical" taxonomic methods, but a solution is suggested below. I have in my collection from Oregon, twenty-seven orange-flushed male specimens from Crook and Wheeler Cos. of what otherwise appear to be *Colias o. occidentalis.* These phenotypes occur sporadically in eastern and central Oregon. There are anecdotal reports of similar butterflies from eastern Washington. I have not seen any Washington specimens other than typical *C. pseudochristina* from Asotin Co. Paul C. Hammond (*pers. comm.*) has indicated to me that Dornfeld (1980) treated such Oregon specimens as *eurytheme.* These butterflies are definitely not *eurytheme,* but what they are remains enigmatic. It is possible that some of these are simply aberrant specimens of *occidentalis* in which the orange pigment (erythropterin) is expressed instead of the normal yellow pigment (xanthopterin, or perhaps sepiapterin; see Watt, 1964). Occasional hybridization with *eurytheme* is another possibility. I can find no records of such specimens from British Columbia (*fide* C. Guppy, Royal British Columbia Museum). A possible origin of these specimens is discussed below. With regard to the Dornfeld Collection, because of lack of time, I have not been able to examine it *in situ,* and loan requests have gone unanswered.

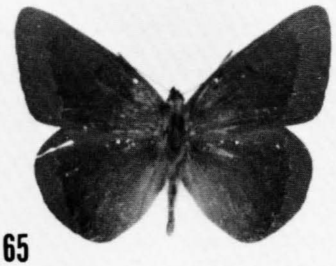
Grant County, Oregon Population

Figs. **65-72**

A perplexing local population from Grant Co., Oregon (US Hwy. 395 at jct. with FR 064 and 913 N. of Long Creek Summit and south of the community of Long Creek, ca. 5000′ [T10S R30E S21]) was sampled by N. S. Curtis and W. F. Wehling in 1987, by Curtis and the author in 1988, and again by the author in 1989 and 1990. A final visit was made in 1992. According to Curtis, colony density was considerably greater in 1987 than in 1988. Density was again low in 1989, but this was true of virtually all butterfly species in this geographic region as a consequence of extended drought conditions and intermittent low temperatures. I have a specimen series consisting of 72 ♂♂ and 21 ♀♀ from this locality. The ♂♂ of this population are variable in color and UV-reflectance, and vary from those that resemble *occidentalis* to two worn specimens that resemble *pseudochristina* in both visual and UV-reflectance pattern. One ♂ is close to *alexandra* in both visual and UV-reflectance pattern.

The only consistent factor in this population is the variability of phenotype in both sexes, but especially in the ♂♂. Size and wing shape vary widely, as does the width of the D dark wing borders in the ♂♂, and the amount of dark maculation D in the ♀♀. In some specimens (both sexes) the FW outer margin is convex, while in the majority, it is straight, and in the remainder, the margin is concave. In both sexes, the DHW discal spot varies from whitish to orange, and the DFW cell spot varies from nearly obsolete to prominent with some spots pupiled. The shape of the DFW cell spot varies from oval to crescentic in both sexes. In the ♀♀, the D ground color varies from pale yellow to off-white with a few specimens showing a slight orange blush.

Dorsally (visual pattern only) some of the yellow ♂♂ resemble *philodice,* others look like *alexandra,* and some resemble *occidentalis.* Some of the orange ♂♂ look like *c. astraea,* a few like *pseudochristina,* and others resemble orange-colored *occidentalis* (UV-reflectance patterns shown in Figs. **68-69**). Ventrally the pattern is equally variable, with some specimens having a single VHW discal spot, while in others this spot is vertically double (5♂♂, 2♀♀ in the 1988 sample). The spot shape varies from circular to oval. In some, the V color resembles *alexandra,* while in others it is like *occidentalis,* and the remainder are similar to *pseudochristina.* Figure **65** illustrates the lack of UV reflectance from a typical yellow *occidentalis* phenotype. The two worn ♂♂ that visually strongly resemble *pseudochristina* produce the UV reflectances illustrated in Figs. **70** and **72**. One of the yellow ♂♂ (Fig. **71**) manifests a weak *pseudochristina* UV-reflectance pattern. Two of the yellow ♂♂ (Figs. **66-67**) have UV-reflectance patterns similar to *alexandra,* but subdued. Several ♂♂ have "*eurytheme*" spots on the VHW, and 3♂♂ and 1♀ have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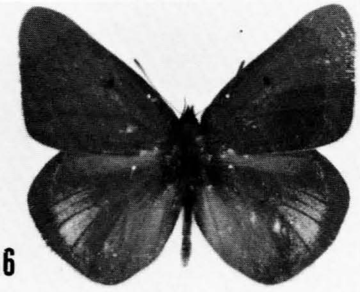
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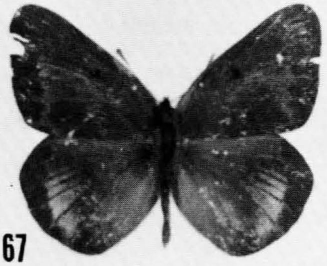
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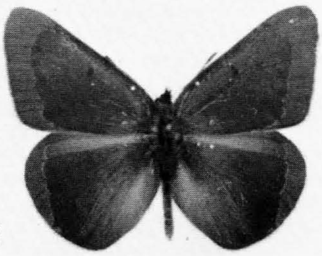
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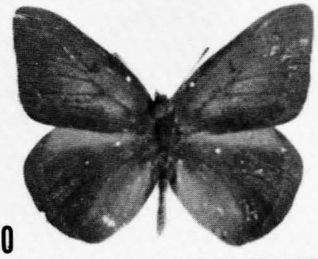
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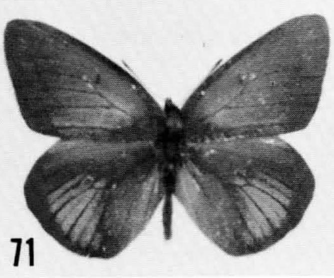
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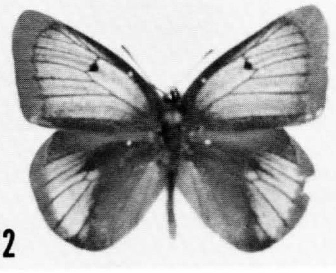
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Figures **65-72**. D UV-reflectance patterns in ♂♂ of *Colias* of uncertain origin from Grant Co., Oregon US Hwy. 395 at jct. with FR 064 and 913, ca. 4800-5000′, Grant Co., OR, 1-2.vii.88. **(65)** yellow resembling *occidentalis*, non-UV reflective [light areas are scattering from basal hairs and rubbed areas]. **(66-67)** yellow with reduced HW *alexandra*-like UV-reflectance pattern. **(68-69)** orange resembling *occidentalis* excepting color and without UV-reflectance. **(70)** orange with very weak UV pattern similar in extent to that produced by *pseudochristina*. **(71)** yellow with very weak UV pattern similar in extent to that produced by *pseudochristina*. **(72)** orange with strong UV pattern similar in extent to that produced by *pseudochristina*.

a suggestion of a double-ringed VHW discal spot as found in *eurytheme* and *philodice.* In 1989, I did collect *eurytheme* flying at the site, however this spot pattern seems to be a plesiomorphic character in *Colias* which is expressed occasionally in virtually all of the species. Also in 1989, I collected two pairs of the fairly typical Great Basin phenotype of *alexandra* at a locality on the opposite side of the ridge from the US 395 site. *Colias philodice* was common in 1989 along US 395 and US 26 in irrigated low-land areas, but I took no specimens in the ridge region.

The ♀♀, both D and V, superficially resemble the imagines of *C. alexandra* from the Blue Lake area in Lassen and Modoc Cos., California. In this regard, they are more consistent than the ♂♂.

The base of the collection site is toward the top of a long ridge through which there is a cut (not really a pass) to accommodate the highway. The top of the ridge supports relatively open Douglas Fir forest. As one moves from the ridgetop, there is an abandoned logging road with small clearings in moderately dense coniferous forest. The ridgetop habitat is typical of that in which *occidentalis* normally occurs.

A similar population from the Fields Creek area, Malheur Nat. For., Grant Co. (approx. 30 road miles southwest of the site described above) was reported in 1987 by Curtis (*pers. comm.*). When Curtis and I visited this locality in 1988, very few *Colias* were seen. I took some specimens close to typical *C. o. occidentalis* (both sexes), and a single very small ♂ with a slight orange blush on the FW; otherwise the dorsal maculation is similar to *occidentalis.* The wing shape is different from typical *occidentalis*, however, and the HW shape resembles that found in *eurytheme.* Ventrally three distinct submarginal "eurytheme" spots are present on the HW with the additional costal-margin spot characteristic of that species. There is the suggestion of a double ring about the VHW discal spot. This specimen exhibits no detectable UV-reflectance. On the basis of these characters, I consider this specimen to be a probable hybrid with *eurytheme.* In 1989, I found only a total of three ♂♂ at this spot despite several visits in favorable weather. Additional visits in 1990 to Fields Creek and along Tex and Murderer's Creeks produced only six ♂♂ and three ♀♀ of fairly typical *occidentalis* phenotype.

Two potential and available larval host plants for the Grant Co. population are *Lathyrus nevadensis* Wats. and *Vicia americana* Muhl.

Data from 1988-1989 relative to these Grant Co., Oregon colonies are shown in Table 1 below. If we total all of the specimens entered in Table 1, the results are as follows: D orange and UV-reflective, 13 (15.9%); D orange and not UV-reflective, 26 (31.7%); D yellow and UV-reflective, 10 (12.2%); D yellow and not UV-reflective, 33 (40.2%).

Table 1: Grant Co., Oregon ♂ Phenotypes

	US 395 Site				**Fields Creek Site**			
	1988		**1989**		**1988**		**1989**	
Phenotype	N	%	N	%	N	%	N	%
D Orange; UV-reflective	5	13.5	8	22.9	0	0	0	0
D Orange; No UV-reflectance	12	32.4	12	34.3	1*	14	1	33
D Yellow; UV-reflective	7	18.9	2	5.7	1	14	0	0
D Yellow; No UV-reflectance	13	35.1	13	37.1	5	72	2	67

*Possible hybrid with *eurytheme.*

Various theories can be proposed to explain this situation, including a hybrid swarm. Another theory, which I reject a *priori* (based upon the analysis that follows) is that *pseudochristina* is a subspecies of *occidentalis,* and the Grant Co. population is simply a cline between the two subspecies. This would be an easy and most likely correct explanation if the ♂♂ of both species were all UV-reflective or all not UV-reflective. The fact that *pseudochristina* is strongly reflective with a very distinctive pattern, and that *occidentalis* is totally non-reflective (as verified by SEM analysis) creates a difficulty with the subspecies concept. Especially in *Colias,* color, and to some degree wing pattern, is vagile. A shift from orange to yellow, for example, is a matter only of a small change in the chemical structure of a pterin pigment. Some years ago, Remington (1954a, b) noted that pigment color in *Colias* may depend upon a single gene. Since then, additional investigations have been conducted by Watt (1964, 1967, 1968, 1969, 1972, 1973) concerning the pteridine pigments in *Colias* and their significance. Komai & Ae (1953) have suggested that in the DHW discal spot, orange (red) seems to be dominant over yellow (or pale). The change from UV-reflectivity to non-reflectivity requires elimination of the specialized UV-reflecting scales. These are complex structures, and one can *speculate* that they should be under the control of several genes at least, if not a sequence of genes. On the other hand, it often takes only one gene to suppress a character. The inheritance of these specialized UV-reflecting scales is unclear, and may prove to vary in hybrids between two species depending upon the parent species. I proposed (Ferris, 1985) that UV-reflectance in males is a dominant trait if *C. hecla* (or *canadensis*) ♂♂ hybridize with a non-reflective species such as *nastes*, but this theory is unproved in the laboratory and may well be incorrect. A summary of studies conducted by Silberglied and Taylor (1973) indicates that UV-reflectance is controlled by the X-chromosome, and that it is a recessive trait when *C. eurytheme* ♂♂ hybridize with a non-reflecting species such as *philodice*. This result, however, does not explain the presence of UV-reflective ♀♀ as well as ♂♂ in some species, such as *chrysotheme* Esper, and variable reflectance in the ♀♀ of other species such as *christina* and *johanseni* Troubridge & Philip. This situation suggests that several UV-inheritance mechanisms may exist. Silberglied and Taylor also suggested that UV-reflectance in the ♂♂ is a species-isolating mechanism, or to use their term — "it may be the butterflies' own *carte de visite.*" Based upon these arguments at the species level, I can not accept that *pseudochristina* is a subspecies of *occidentalis.*

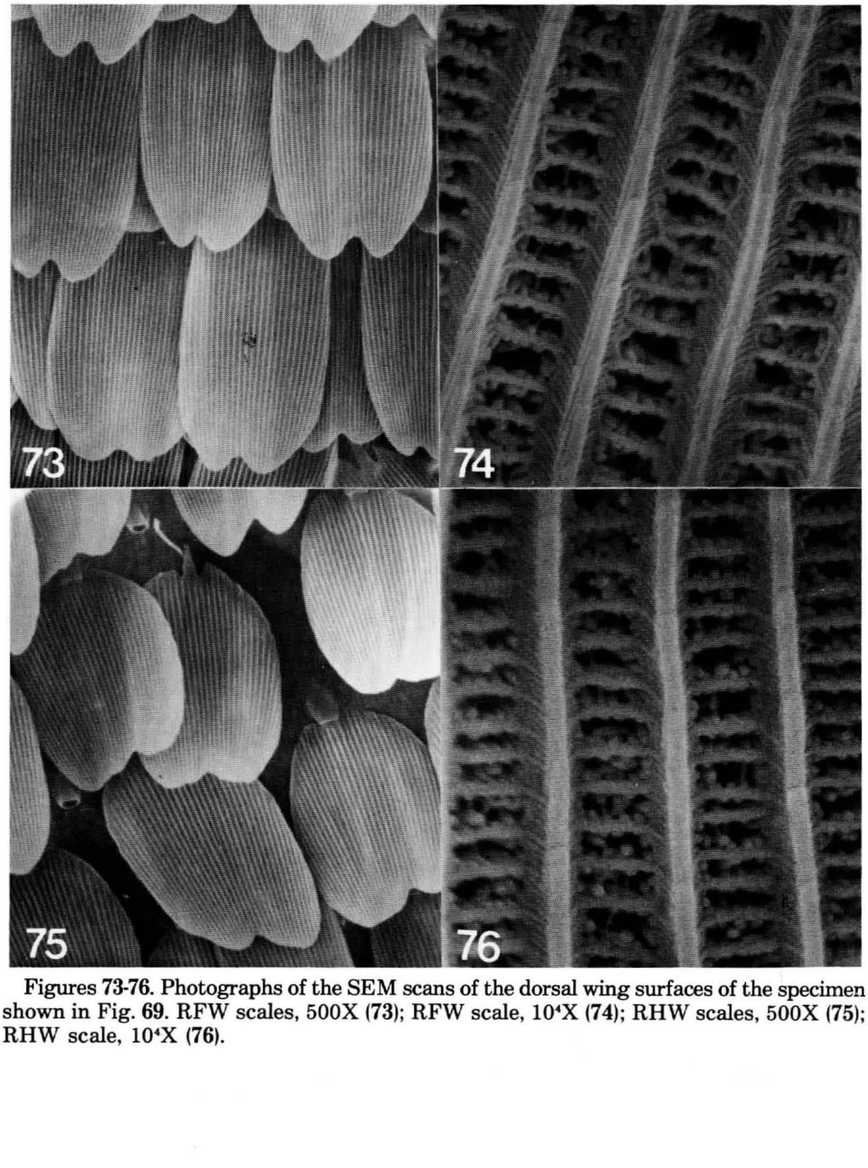
As the data in Table 1 indicate, the Grant Co. population is highly polymorphic for secondary sexual characters, which is unusual. Normally in hybrid situations, sexual selection should operate efficiently (and rapidly) on them, unless they are inversely frequency dependent (a phenomenon known as Ehrmann's "rarity effect"). Should this be the case, then the male characters appear to be secondary sexual ones that are X-linked with UV-reflectance and with pheromones. This is even more peculiar if the studies by Grula & Taylor (1978, 1979, 1980a, b) on *eurytheme-philodice* hybrids apply generally in *Colias*. Consequently, I feel that the most plausible explanation is quite different and lies in an interpretation of the cladogram shown in Fig. 2, and the various analyses which follow below.

Adults of the Grant Co. population exhibit the behavioral patterns of *occidentalis,* and not those of *pseudochristina.* Males may be taken at puddles or seeps and they regularly fly along topographic disjunctions. Females are regularly observed at flowers and flying about the presumed host plants.

Analysis of Wing Scales

SEM analysis of the D wing scales of the specimen shown in Fig. **69** yielded curious results. This specimen is typical of the orange ♂♂ that do not produce any UV-reflectance other than the thin layer effect (HW in this specimen). The left HW is abraded, which accounts for the striations shown in the photograph. No specialized UV-reflective scales were detected by the SEM analysis nor were any scales of the form that appears in some hybrids (as discussed in the next section). Figures **73-74** illustrate the nature of the DFW scales. These are typical non-UV-reflective pigmented scales with normal dentate distal margins. Under 10^4 X magnification, pigment globules are evident filling the fenestrations between the scale ribs or ridge lines. Figures **75-76** illustrate the nature of the scales in the DHW discal region. In UV-reflective species, this is the region of the wing on which the greatest concentration of specialized reflective scales normally occurs. There are two abnormalities (Fig. **75**). There is only one layer of scales, the basal layer, whereas normally there are three layers composed of the cover scales, an intermediate layer, and the basal layer. Additionally, the scales are of reduced length. Otherwise (Fig. **76**), the scales exhibit normal morphology. All that can be said at this point is that the DHW manifests an unusual wing-scale pattern, and one that has not been seen in any *Colias* species that I have examined to date.

To confirm that the specimen subjected to SEM analysis was not aberrant, its intact left half and the remaining 71 ♂♂ were examined at 250X magnification using an Olympus light microscope. All of the specimens manifested reduced scale coverage (with varying degree) as compared to typical *occidentalis* and *pseudochristina*. Two layers of scales was the rule. While the SEM photo shown depicts perhaps an extreme example (by accident) of the wing-scale pattern, I have identified similar patterns in two of the other orange ♂♂. Using fresh to worn specimens, the shingling of the dorsal wing scales in 20 *occidentalis* ♂♂ and 16 *pseudochristina* ♂♂ was also examined. These two species are highly uniform with respect to the density of their wing scales, and show a shingling pattern that is normal for other N.A. *Colias*.



Figures **73-76**. Photographs of the SEM scans of the dorsal wing surfaces of the specimen shown in Fig. **69**. RFW scales, 500X **(73)**; RFW scale, 10^4X **(74)**; RHW scales, 500X **(75)**; RHW scale, 10^4X **(76)**.

During microscopic examination, four types of cover scale profile were noted in the DHW discal region, as regards the non-UV-reflective scales. Outlines of these scales are illustrated in Fig. 77. In *pseudochristina*, specialized UV-reflecting scales dominate, but there are some type 3 scales, and one specimen had a few type 2 scales. In *occidentalis*, the scales are generally type 2 with again a single specimen showing some small tooth type 3 scales. The 72 specimens from the Grant Co. population exhibited a wide variety of scale type. The non-UV-reflective orange specimens produced the most variability, with a few specimens having primarily only one of the four scale types. Other specimens showed a mixture of 1-2, 1-2-3, 2-3, 2-3-4. The non-UV-reflective yellow specimens showed type 3 scales primarily, with some specimens a mix of 1-2 or 2-3, and 1-2-3 in one specimen. The scale types in the UV-reflective specimens follow the same general pattern in regard to specimen color as in the non-reflective specimens, with the addition of specialized UV-reflective scales.

Discriminant Analysis

Discriminant analysis (DA) is a statistical method used to classify individuals (I=individual butterfly specimens) into mutually exclusive groups based upon a set of independent variables or characters (Dillon & Goldstein, 1984; Kachigan, 1986). An early form of DA was developed by C. G. Sibley (1950, 1954; Sibley & West, 1958) in his studies of the hybridization between two birds, the Red-eyed and Collared Towhees in Mexico. More recently in the Lepidoptera, Collins (1984) applied DA to a hybrid study in the saturniid genus *Hyalophora*. When a hybrid swarm is suspected and based on the probabilities generated by the DA, a certain percentage of the individuals from the original (*a priori*) hybrid population will actually fall into one or the other of the parental populations. Similar analyses can be calculated for three or more groups of populations.

Conceptually, DA is reasonably straight-forward, but the calculations involved in finding the statistics, and then testing them with respect to the groups becomes complex and tedious when large numbers of specimens are involved. Commercial computer software

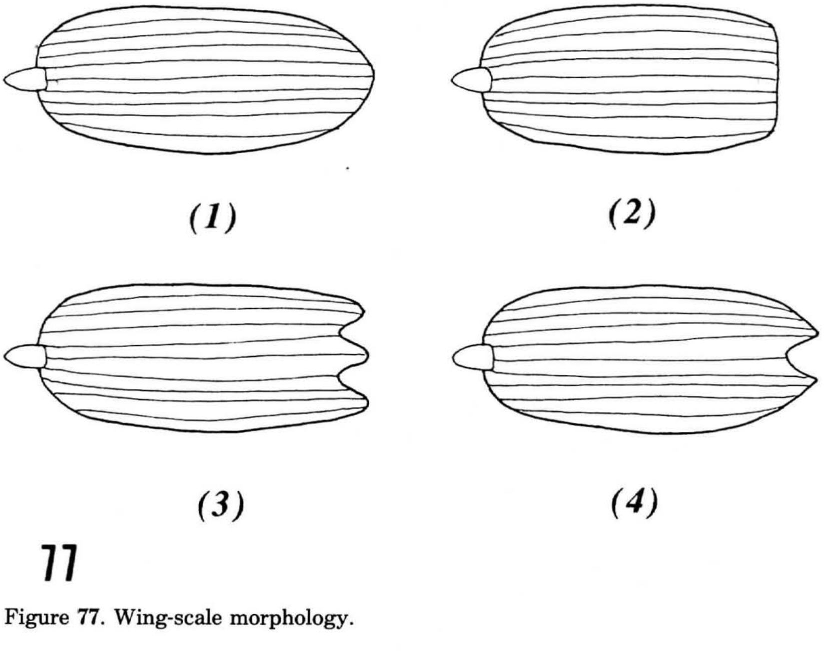


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Figure 77. Wing-scale morphology.

is available which eliminates the necessity for longhand calculations. The DA included here was executed on the University of Wyoming VAX computer cluster using the program SPSS-X [SPS;2] release 3.1 for VAX/VMS systems.

Analysis was restricted to male specimens. Ideally, the parental populations should be selected from geographic areas closest to the location of the suspected hybrid (Grant

Species	**Character Number**										**N**
	1	2	3	4	5	6	7	8	9	10	
		•						•		•	1
occidentalis	•						•			•	22
$N_{tot} = 32$		•						•	•		1
	•						•		•		3
	•							•	•		5
			•					•		•	12
			•					•	•		9
		•						•	•		1
		•						•		•	2
	•							•		•	8
	•						•			•	11
	•							•	•		4
Grant Co.	•						•		•		2
$N_{tot} = 72$		•						•		•	1
			•	•		•		•	•		3
		•		•		•		•		•	2
			•	•		•		•		•	3
		•		•		•		•	•		1
	•			•		•		•		•	4
	•			•		•	•			•	1
	•			•		•		•	•		2
			•	•	•			•		•	2
			•	•	•			•	•		2
	•			•	•		•		•		2
			•	•		•		•	•		34
pseudochristina			•	•		•		•		•	33
$N_{tot} = 68$		•		•		•		•		•	1

Characters

1. D color = yellow
2. D color = orange over yellow.
3. D color = orange.
4. HW is UV-reflective.
5. FW is partially UV-reflective, but < as in *pseudochristina.*
6. FW is UV-reflective, as in *pseudochristina.*
7. DHW discal spot = yellow.
8. DHW discal spot = orange.
9. VHW discal spot = double (8), or partially double (δ).
10. VHW discal spot = single.

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Figure 78. DA data table.

Co.) population. Visual examination of the 32 ♂♂ of *occidentalis* that I collected in 1990 in Wheeler Co., OR satisfied me that they represent a *relatively* pure population. None was UV-reflective. The colonies of *pseudochristina* that are geographically closest to the Grant Co. population are located in Wallowa Co. OR, Asotin Co., WA and Adams Co., ID, but I have seen only a very few specimens, and I have none in my personal collection. The colonies from these areas appear to generate low numbers of individuals. A series of 34 ♂♂ that I have from Elmore Co., ID were supplied by N. S. Curtis, and are not representative since they were culled from a larger series. Consequently I have used 68 ♂♂ of *pseudochristina* that I collected in Franklin Co., ID in 1988-1990. Only the 72 ♂♂ from the Long Creek Summit colony were used in the analysis. The Fields Creek-Tex Creek colony is very diffuse, is geographically removed from the Long Creek Summit colony, and I have only a limited number of specimens. Ten easily identified characters were selected for analysis. The data used in the DA are shown in Fig. **78**. Strict binary coding was used, with 0 representing the absence of a character and 1 the presence of the character. In Fig. 78, the dots represent the presence of the associated character; blanks indicate the absence of the associated character. The selection rule used in the SPS;2 program was: maximize minimum Mahalanobis distance (D^2) between groups. The results of the discriminant analysis are presented in Fig. **79** and Table 2.

The DA results indicate that 1 specimen (1.5%) from the Franklin Co., ID population of *pseudochristina* classifies into the hybrid Grant Co., OR population. Seven specimens (21.9%) from the Wheeler Co., OR population of *occidentalis* classify into the hybrid population. From the Grant Co., OR population, 13 specimens (18.1%) classify into *occidentalis,* and 7 (9.7%) into *pseudochristina.* The remaining 52 specimens (72.2%) classify

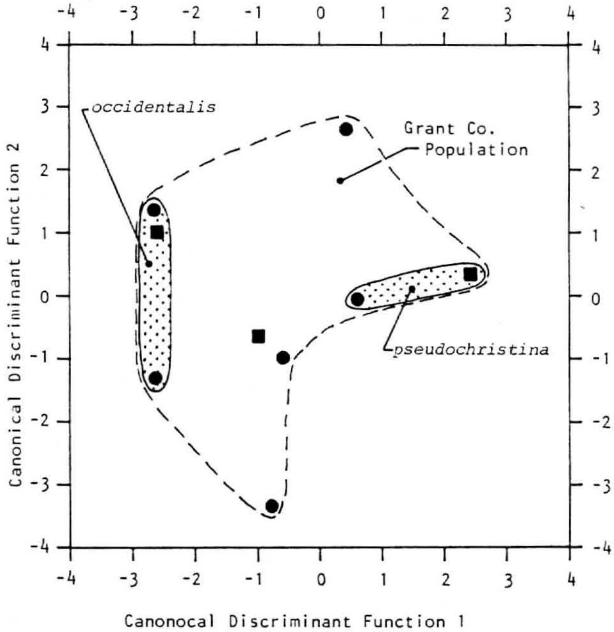

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Figure 79. DA plot.

Table 2: Classification Results

Actual Species (Actual Group)	Number of Specimens	Predicted Species (Group) Membership		
		occidentalis	hybrid	*pseudochristina*
occidentalis	32	25 78.1%	7 21.9%	0 0.0%
hybrid	72	13 18.1%	52 72.2%	7 9.7%
pseudochristina	68	0 0.0%	1 1.5%	67 98.5%

Percent of "grouped" specimens correctly classified: 83.72%.

Classification Processing Summary

172 specimens were processed.

0 specimens were excluded for missing or out-of-range species (group) codes.

0 specimens had at least one missing discrimination variable.

172 specimens were used for printed output.

as hybrids. These results are reflected in the graphical presentation shown as Fig. **79**. Based upon this discriminant analysis, one can infer that *occidentalis* and *pseudochristina* clearly separate into two species. The values of the canonical discriminant functions L_1 and L_2 that locate the group centroids are shown in Table **3**.

Table 3: Canonical Discriminant Functions Evaluated at Species-group Centroids

Species	L_1 (X-axis)	L_2 (Y-axis)
occidentalis	−2.54082	0.85696
hybrid	−1.06702	−0.54634
pseudochristina	2.32547	0.17519

Hardy-Weinberg Equilibrium Analysis.

A Hardy-Weinberg equilibrium analysis was applied to the Long Creek Summit population using the UV-reflectance character in the males, with the results as shown in Table **4**. There is very close agreement between the observed and theoretical values. The chi-squared test results strongly support the hybrid hypothesis.

Paleoecological Evidence

A moderate body of literature is available with regard to the Late-Quaternary environments of the United States (Wright & Porter, 1983; Wright, 1983). Earlier geological history is summarized in Hunt (1974) and Stanley (1989). During the most recent glacial interval, the Cordilleran ice sheet extended southward into northern portions of Washington, Idaho, and Montana (Waitt & Thorson, 1983). Mountain glaciers were widely scattered south to Arizona (Burke & Birkeland, 1983; Porter, *et al.*,1983). Principal locations of these glaciers were in the Cascade Range of Washington and Oregon, the Sierra Nevada in California, in the higher mountains north of the Snake River Plain in Idaho (Beaverhead, Lemhi, and Lost River Ranges, Payette River Highlands, Salmon River Mtns.) and western Montana (Beartooth Uplift, Gallatin Range, Northwest Montana Mtns.), in western Wyoming (Absaroka, Teton, and Wind River Ranges, Yellowstone Plateau), in Utah (Raft River and Wasatch Ranges, La Sal and Uinta Mtns.), in Colorado (Front and Park Ranges, San Juan Mtns.), and Sierra Blanca Peak and the Sangre de Cristo Mtns. in New Mexico. In eastern Oregon, the Steens (Harney Co.), Blue (Grant

Table 4: Hardy-Weinberg Equilibrium — UV-Reflectance Inheritance in ♂♂

Species	Ideal Mendelian Population	Observed Population H-W Equilibrium (N = 72)
occidentalis	$p = 0.5$; 25%	$p = 0.45$; 20%
pseudochristina	$q = 0.5$; 25%	$q = 0.55$; 31%
hybrid	$2pq = 0.5$; 50%	$2pq = 0.49$; 49%

Agreement of ♂ UV-Reflectance Frequencies with the Hardy-Weinberg Expectations

Field Observations (N = 72)

Genotype*	Expected Proportion	Expected Number	H-W Number	H-W Proportion
uu	0.25	18	22	0.31
UU, Uu	0.75	54	50	0.69
		72	72	

$\chi^2 = 1.185$; D.F. = 1; probability = 0.28

Based on Hardy-Weinberg Grouping (N = 72)

Genotype*	Expected Proportion	Expected Number	H-W Number	H-W Proportion
uu	0.25	18	22.3	0.31
Uu	0.50	36	35.3	0.49
UU	0.25	18	14.4	0.20
		72	72	

χ^2 2 = 1.761; D.F. = 1 (because of agreement in allele frequency); probability = 0.197 ≈ 0.20

*uu = *pseudochristina* (UV-refl. ♂♂); UU = *occidentalis* (no UV-refl.); Uu = hybrid (no UV-refl.)

Co.), and Strawberry Mtns. (Grant Co.) were glaciated. Other areas throughout the western U.S. supported small glaciers (less than 15 km long). As discussed by Péwé (1983), a periglacial environment existed throughout much of the Intermountain Region south of the Cordilleran ice sheet. Alpine permafrost still exists today in the North Cascades in Washington, in the Uinta Mtns. of Utah, and at high elevations in the mountains of Colorado, Wyoming, and Montana.

During the Late Wisconsin (25,000 to 10,000 years B.P.) as the glaciers retreated, large pluvial lakes formed in many basin regions of the western U.S. Some of the larger lakes include Lake Lahontan, centered in Nevada, and Lake Bonneville (of which Great Salt Lake is a remnant), centered in Utah. Many lakes of lesser extent existed throughout the region, such as the Bull and Temple Lake regions in western Wyoming. In Oregon, pluvial lakes occupied all of the closed basins, and today remnants remain in some regions as lakes or marshy areas (Smith & Street-Perrott, 1983). As these lakes evaporated over geologic time, desert regions developed with concomitant environmental changes (Spaulding *et al.*, 1983). During the Late Wisconsin, increased effective moisture was present throughout these now arid areas, and widespread woodlands covered lowlands which today nurture only scrub. A vegetational history of the western U.S. has been summarized by Baker (1983). Soil development during the Late-Quaternary has been summarized by Shroba & Birkeland (1983). Wells (1983) has summarized the paleobiogeography of montane islands in the Great Basin during the Holocene.

What emerges from the studies cited above, is a scenario of substantial and sequential environmental changes from the Late Wisconsin to the present time. The currently existing arid regions have replaced late-Pleistocene coniferous and oak woodlands. As stated by Wells (1983): ". . .these woodlands have been isolated by complementary contraction to the slopes of higher mountains that rise like islands from the modern desert sea." Johnson (1975) discussed bird species on "montane islands" in the Great Basin region. Species densities and broad patterns of evolution in fishes during the Late Cenozoic have been discussed by Smith (1981), and he has summarized western paleohydrography. Recent work related to the Great Basin (J. H. Brown, 1971, 1978; Grayson, 1987; W. A. Akersten, *pers. comm.*, 1990), has shown that currently known disjunct distributions of montane vertebrates can be explained as follows: The mountains associated with the Great Basin can be compared to islands which have become isolated by warmer and more xeric lowlands. When the climate was more benevolent than it is today, the lowlands that were not under water could be crossed or inhabited by organisms which subsequently disappeared when the climate became more severe (hotter and drier). Remaining isolated populations of these organisms survive in separate mountain ranges, and the principles of island biogeography (MacArthur & Wilson, 1963) may now be applied to describe these populations. Wilcox *et al.*, (1986) have confirmed that montane butterfly fauna in the Great Basin behave in much the same manner as birds in regard to biogeography. They found that the differences in the insular biography of butterflies and vertebrates appear to reflect basic ecological differences among the taxa. A recent paper by Austin (1992) addresses isolate biota in the Great Basin, and specifically populations of the satyrid butterfly *Cercyonis pegala* (Fabricius).

Discussion of Results

We can infer that the Franklin Co., ID *pseudochristina* population is essentially pure. Based upon the characters used in the DA, only one specimen out of 68 (1.5%) was indicated as misclassified. This result is not significant. These 68 specimens represent all of those remaining in the author's possession from his field collecting during 1988-1990. The 32 specimens from Wheeler Co., OR represent all of the ♂♂ collected in 1990 (the first year in which I collected in this area). The results indicate that this population is not pure *occidentalis,* since 21.9% ≈ 22% classify as *pseudochristina.* It would be desirable to have a sample size greater than 32, but no additional specimens were observed during the last week in June 1990 when the collections were made. The flight season was foreshortened because of extremely hot and dry weather. To my knowledge, this Wheeler Co. colony on the eastern slopes of the Ochoco Mtns. is the most eastern population of relatively pure *occidentalis.* Regarding misclassified individuals from the hybrid population, the number that are categorized as *occidentals* (13, 18.1%) are essentially double the number identified as *pseudochristina* (7, 9.7%).

In the simplest hybrid situation under controlled laboratory conditions, we would expect the parent-hybrid-parent ratio to be 1:2:1 or 25%:50%:25%. In this instance based upon the discriminant analysis, the ratios are 1:3.99:0.536 (≈ 1:4:0.54) or 18.1%:72.2%:9.7%. On the other hand, the results of the Hardy-Weinberg equilibrium analysis of UV-reflectance in the ♂♂ (Table 4) are very close to the theoretical values.

The results obtained from the Hardy-Weinberg equilibrium analysis and the discriminant analysis taken in conjunction with field observations and visual inspection of the Grant Co., OR population suggest several possible explanations for this peculiar butterfly. The obvious one is that of a simple hybrid swarm generated by the breakdown of species-isolating mechanisms when the two parental species were either sympatric or parapatric. Because of climatic changes following the last ice age, this hybrid swarm has now become geographically isolated (island biogeography) from each parent species. Based upon the paleoecological evidence cited above, I do not believe that isolation is recent and a consequence of man-made changes during the past century.

I favor another explanation, however. If we propose that a species which is the common ancestor to *pseudochristina* and *occidentalis* was once widely distributed throughout the geographic region now occupied by its two daughters, then we can arrive at another plausible explanation for the Grant Co. population. We can further theorize that the two daughter species became isolated as a consequence of climatic changes, and concomitant modification of habitats. Certainly today there is considerable environmental isolation, some of which is man-made during the past century. The Grant Co., Oregon colonies occupy relatively undisturbed (except for logging operations) ridge and hillside sites in dry coniferous forest at the southern end of the Blue Mtns. The region for miles around them is either arid sagebrush-association habitat, or has been widely modified and converted to agricultural uses. Thus these colonies are analogous to an island biogeography situation, but the isolation has been generated by the disappearance of suitable habitat rather than by water. The nearest colony of *occidentalis* thus far is in the Ochoco Mtns. in Wheeler and Ochoco Cos. some 70 air miles to the west. The intervening area is extremely arid (essentially badlands) except for some limited agricultural use. The nearest colonies of pure *pseudochristina* that I know of are several hundred miles distant to the east and northeast. Although transected by forested ridges, much of the intervening regions are arid, and have been converted to heavy agricultural uses in contemporary time. The main distribution of pure *occidentalis* lies well to the west of the southern section of the Blue Mtns., as is shown in Fig. **80**. The distribution of *pseudochristina* lies well to the northeast and east, as is also shown in Fig. **80**.

One can argue that central-to-western Grant Co. was the geographic region of disjunction between *pseudochristina* and *occidentalis*. As climatic conditions changed, *occidentalis* dispersed westward, but we still find occasional plesiomorphic phenotypes along the eastern edge of its range, especially in the Ochoco Mtns. Also as a consequence of these climatic changes, *pseudochristina* became isolated in suitable environmental niches to the northeast and east. What we see now in Grant Co. is a relict population in which species separation is incomplete.

This thesis adequately explains the population observed in Grant Co., in which phenotypes range from close to *pseudochristina* to close to *occidentalis*. If we accept that the genealogy suggested by Fig. 2 is reasonably correct, the occasional *alexandra*-like specimens can be explained by recessive individuals in which an ancestral form is expressed. The females of both *pseudochristina* and *occidentalis* exhibit relatively little variation in phenotype. This situation may be used to explain the *relative* uniformity of the female phenotypes in the Grant Co. population. The problems noted above concerning inheritance of the UV-reflectance trait and UV-reflectance as a species-isolating mechanism seemingly would not enter in an incomplete speciation situation such as I have proposed. As for adult color, Remington (1954) suggested that wing color in *Colias* is controlled by one or two pair of genes, and that no dominance is involved. Grula and Taylor (1980) found this hypothesis to be consistent with their studies in *C. eurytheme* and *philodice*. Additional comments about color inheritance in *Colias* appear in Robinson (1971). If inheritance of UV-reflectance in the ♂♂ is a recessive trait in the species involved here, then the phenotypes listed in Table **1** are exactly what one would expect to find. Additionally, the SEM analysis detected no wing scales of the form that appears in at least some hybrids between UV-reflective and non-reflective species. This aspect of scale morphology is discussed in the next section.

In respect to the map shown as Fig. **80**, Grant Co., Oregon is outlined. The black hexagon marks the general area in which the two colonies described above are located. County records for *pseudochristina* are shown as solid circles, and those for *occidentalis* are shown as open circles. The three triangles represent Baker, Umatilla, and Wallowa Co. records for *occidentalis* taken from map no. 19 on page 231 of Dornfeld's book (1980). I have not been able to verify all of these records, as noted previously. They may represent *occidentalis*, or additional local populations of the Grant Co. butterfly, or possibly misidentifications of *alexandra*. In museum collections, I have found many specimens of *alexandra* misplaced as *occidentalis*. The square added to the Umatilla Co. triangle represents a confirmed record for *occidentalis* based upon a specimen collected by W. A. Neill along the McKay River on 1.vi.69 (*fide* J. Hinchliff). The solid circle added to the Wallowa Co. triangle represents a record of *pseudochristina* (*fide* P. Hammond). Dornfeld's map dot for *occidentalis* in Grant Co. is undoubtedly the population under discussion. Fig. **80** omits the distribution of *occidentalis* in Canada, and the reader should refer to Fig. 64.

Note Added in Revision: The Long Creek Summit habitat cited at the beginning of this section no longer exists. In 1989, I noted new survey stakes throughout the locality. When I visited the site on the morning of 24 June, 1990, the ridge and associated abandoned logging road area formerly occupied by the butterfly colony were gone. They had been blasted away entirely to accommodate the road cut for a realignment of US Hwy. 395. The small meadow at the base of the former habitat had been bulldozed to a large extent and was serving as a parking area for heavy equipment. No butterflies of any species were observed. Ten specimens of this endemic *Colias* were collected during the next four days at other locations in Grant Co., including Fields Creek road and along Tex Creek to Murderer's Creek southwest of Mt. Vernon. One male is orange-flushed, while the

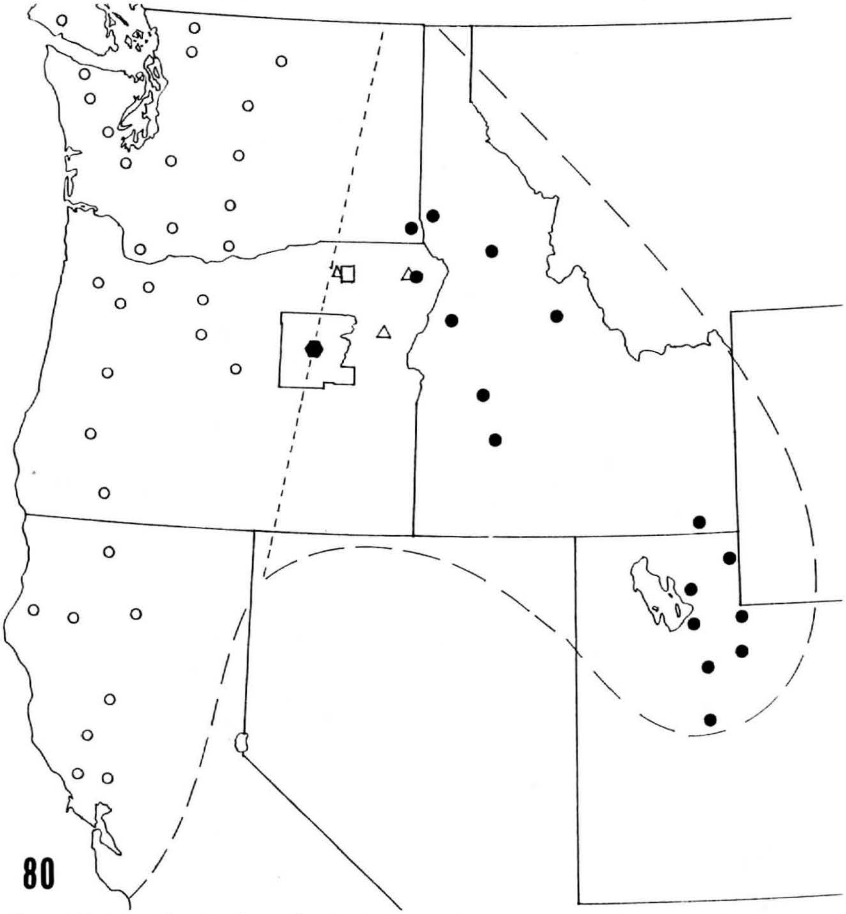

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Figure 80. Map showing hypothesized distribution in the U.S. of the immediate ancestor to *C. pseudo-christina* and *C. occidentalis* (area within long dashes). The short-dash line is the hypothesized line of disjunction. Black hexagon is location of Grant Co., OR population. County records are plotted for *C. pseudochristina* (solid circles) and *C. occidentalis* (open circles). The open triangles indicate probable misidentifications of *alexandra* as *occidentalis*. See text discussion.

remaining specimens (6♂♂, 3♀♀) resemble typical *occidentalis.* The orange-flushed male was taken flying along a forest road in the same ridge system as the destroyed colony, but several miles to the southwest. At this point, I do not know if sufficient individuals remain to re-establish the Long Creek Summit population. The habitat where the colony was concentrated is clearly gone, and in the past, as in 1990, I found only occasional singleton specimens elsewhere in the ridge system. When I drove over Long Creek Summit in May, 1991, the road work had been completed, and little of the former habitat remained.

Because of a very warm and dry spring, some species of *Colias* virtually swarmed in eastern Oregon in June, 1992. I explored the ridge complex between Mt. Vernon and Long Creek Summit in some detail. Twenty-eight specimens (13♂♂, 15♀♀) of the Grant Co. isolate were collected at four different localities. Eight of the males are yellow with one UV-reflective; five of the males are orange with two UV-reflective. A few specimens were observed at Long Creek Summit, but what little remains of the original habitat has now suffered a final indignity by the introduction of grazing cows. Only eight butterfly species were observed at this site in 1992, while I recorded 30 species at the same time of year prior to the new road construction. Because of a sudden change in the weather from hot and dry to cold, fog, and torrential rains, I was unable to survey the Fields Creek/Tex Creek area in 1992.

Observations about Putative Hybrids in *Colias*

Various specialists disagree about the frequency of hybridization between *Colias* species. Hovanitz (1944, 1949, 1963a, b) maintained that relatively widespread and frequent interspecific matings occur in the wild. On the other hand, Taylor (1972) has stated that *C. eurytheme* and *philodice* are sexually isolated under most natural conditions, and hence do not interbreed with any appreciable frequency. Work in progress by A. M. Shapiro (*pers. comm.*) suggests that the frequency of wild *eurytheme-philodice* hybrids varies widely based upon geography. The studies conducted by Ae (1959) indicate that some species of North American *Colias* have the potential to interbreed successfully. It is difficult, however, to translate laboratory studies into what occurs in the wild.

I have discussed possible hybridization between various species of *Colias* in two previous papers (Ferris, 1972b, 1985). Based upon field observation and study of the visual patterns exhibited by museum specimens, hybridization appears to be uncommon between some species that are truly sympatric (in the microhabitat sense). A specific example is *C. a. alexandra, C. philodice eriphyle,* and *C. scudderii* which fly together in mid-July in the same open areas along the North Fork of the Little Laramie River in the Medicine Bow NF, Albany Co., WY [T16N R73W S17E 9160′ (2790m)]. I have collected in this area for over twenty years, and although I have seen males of these species attempt courtship with females of the others, I have never seen an interspecific mating, nor have I collected any specimens that appear to be hybrids. I have collected coupled pairs of the same species. It would appear that regular contact between two species reinforces whatever isolating mechanisms may exist, and hybridization occurrences are very low. The highest incidence of putative hybridization seems to occur when two species are parapatric or allopatric, and males from one species enter the geographic region occupied by the second. Periodic northerly migrations by *C. eurytheme* and subsequent hybridization with resident species are responsible for the *C. alberta* Bowman phenotype (Ferris, 1972b), and most probably for the orange-flushed form of *C. philodice eriphyle* W. H. Edwards (see below).

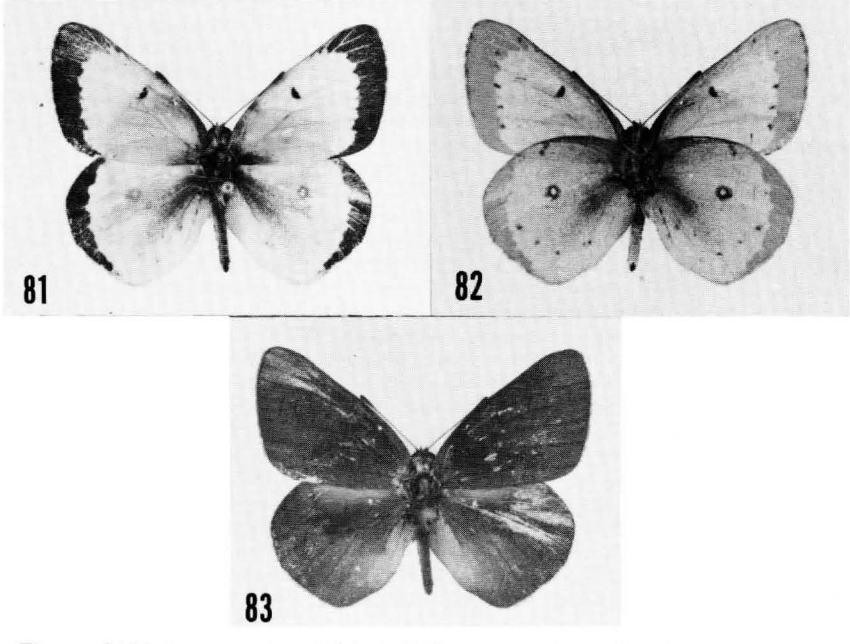
Although the occasional presence of "eurytheme" spots on the VHW of species other than *eurytheme* and *philodice* most probably is the expression of a plesiomorphic character of the genus *Colias,* I suspect that in some instances in North America, this maculation results from occasional hybridization between a normally unspotted species and either migratory *eurytheme* or perhaps resident *philodice.*

Parapatry may be either geographic or ecologic. For example, *C. hecla* Lefèbvre and *C. nastes* frequently occupy the same geographic region, but they are environmentally isolated. Colonies of *nastes* are normally situated on high ridges, while *hecla* is a valley or low-elevation denizen. Males of *hecla,* however, are regularly observed flying through *nastes* habitats. This is one of the factors that has led me to consider *boothii* Curtis to be a hybrid between *hecla* and *nastes*. Further discussion of *boothii* follows below and in the subsequent section dealing with cladistic analysis.

Orange-flushed *Colias philodice eriphyle*

Colias [philodice] eriphyle W. H. Edwards, 1876 was described from a series of "Some thirty individuals of this species and of both sexes, . . ." Brown (1973, p. 87) selected from the Edwards series, as the lectotype for this taxon, the specimen illustrated (in color) as Fig. 15 in Pl. 35 of Holland (both editions). The TL is Lac la Hache [current spelling from provincial map], British Columbia. The specimen shown in Holland is clearly yellow dorsally without any orange flush. Edwards mentioned in his OD: "the costal margin of primaries immediately at base orange tinted, sometimes decidedly; . . .", but he said nothing about any dorsal orange flush or orange patches. With some frequency, specimens are collected in the general environs of Lac la Hache which manifest distinct pale orange-flushed areas dorsally extending from the basal area of the wings into the central area. Over the years, some collectors have erroneously taken this phenotype to represent *eriphyle*. Based upon SEM photographs of the wing scales of such specimens, and a comparison with SEM photographs of the scales from a laboratory hybrid *philodice x eurytheme*, these specimens appear to be natural hybrids between these two species. Such specimens do not manifest UV-reflectance associated with specialized reflecting scales.

Figures 81-83 are of a laboratory ♂ hybrid *Colias eurytheme* ♂ *x C. philodice eriphyle* ♀. The parents are from California stock, and the specimen was generously provided by Dr. A. M. Shapiro (University of California-Davis). Dorsally, the specimen is basally orange-flushed on both the FW and HW. The darkened areas shown in Fig. 81 represent staining that occurred in the relaxer, but they approximate the orange areas. The streaky UV-reflectance shown in Fig. 83 is membrane reflectance from the thin layer phenomenon,



Figures 81-83. Photographs of ♂ hybrid *Colias eurytheme* ♂ *x C. philodice eriphyle* ♀ from California stock: D (81); V (82); D UV-reflectance (83).

and was caused by emergence difficulties which resulted in the sloughing off of some of the scales. SEM photographs of the dorsal wing scales are shown in Fig. **84-85**. Fig. **84** shows typical dentate cover scales on the FW. Fig. **85** shows normal DHW dentate cover scales overlaid by a set of atypical scales. The distal margins of these scales are relatively smooth, as is the case in UV-reflective scales, but the ridge lines are similar in form to those found in normal (non-reflective) scales. In UV-reflective scales, the ridge lines are more closely spaced and appear thickened. They are also higher than the ridge lines found in normal cover scales. Typical UV-reflective scales in C. *eurytheme* were illustrated by Kolyer and Reimschuessel (1969) in their Fig. 3a (top, left, and bottom scales; normal dentate cover scale in middle), Figs. 3b, c, although they did not realize at the time the UV-reflective property of these scales. *Fide* Shapiro, the orange color is more evenly distributed in *eurytheme x philodice* hybrids than in pure *eurytheme*, and lacks the patchy appearance found in some seasonal forms of the latter.

Figures **88-89** illustrate a specimen in the Allyn Museum of Entomology collection from Spences Bridge [current spelling], B.C., similar in color pattern to the known hybrid *eurytheme x philodice.* As is shown in Fig. **89**, except for some thin layer reflectance along the DHW costal and inner margins, this specimen is not UV-reflective. SEM photographs of the dorsal wing scales of this specimen are shown in Figs. **86-87**. Note the similarity of Fig. **84** with **86**, and of **85** with **87**. The same DHW abnormal scales appear as occur in the known hybrid. These abnormal scales are also thin in both specimens, as noted by the fact that the edges of the scales beneath reflect through them (arrows on photos). Based upon the similarity of these abnormal scales, I suggest that field-caught orange-flushed "*philodice*" are in fact hybrids between *philodice eriphyle* and *eurytheme.* That they appear to occur more commonly in British Columbia than in the U.S., supports the comment made above concerning hybridization between allopatric and parapatric species. *C. philodice* is a resident species in British Columbia, but *C. eurytheme* is an occasional migrant to the Lac la Hache region.

The abnormal scales that appear in the hybrid do not have open fenestrations as are found in typical UV-reflecting scales. Instead, what would be the open areas are partially filled by pigment globules, as is shown in Fig. **91**. A normal cover scale is shown in Fig. **90**. These SEM photographs support the statement made by Silberglied & Taylor (1973) that UV-reflectance in hybrids of *Colias eurytheme* with non-reflective *Colias* species is a recessive trait. Abnormal scales, however, are produced. This phenomenon was not recognized by Silberglied & Taylor because they did not conduct SEM studies.

Colias alexandra harfordii x C. eurytheme

In the Allyn Museum of Entomology collection, there are several specimens from Bouquet Canyon, Los Angeles Co., CA of what appear in phenotype to be hybrids between *alexandra harfordii* and *eurytheme.* In this instance, either species could be the ♂ parent. SEM photographs of the wing scales are shown in Figs. **92-95**.

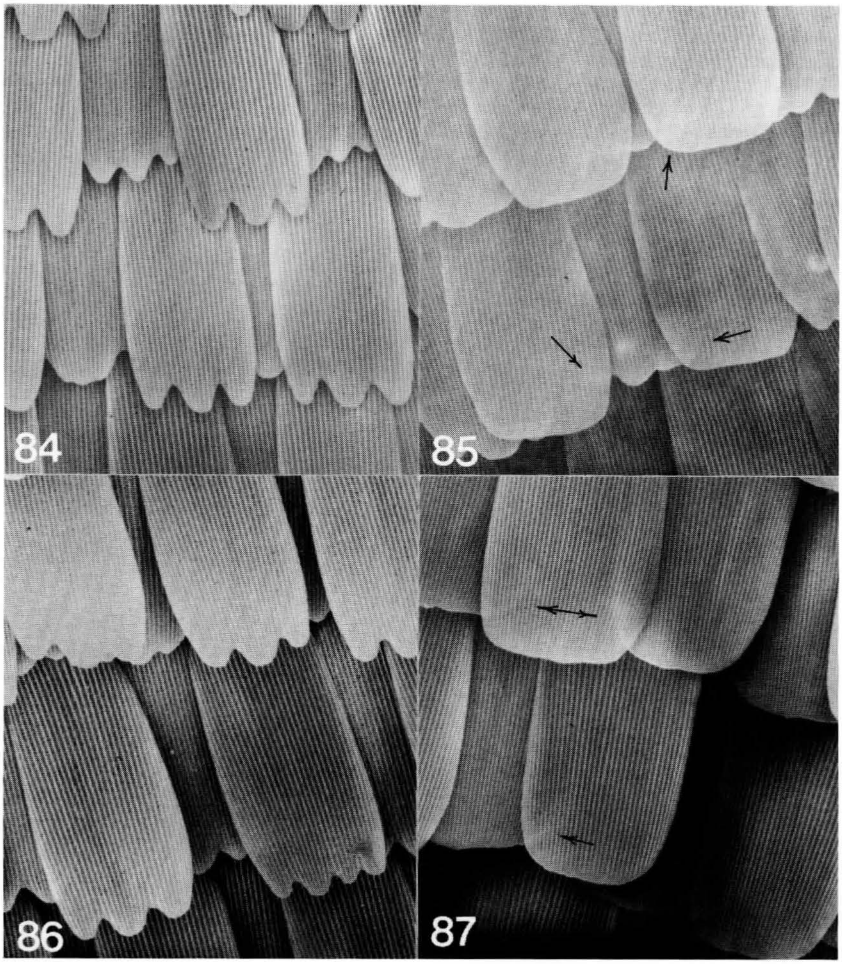
Fig. **92** shows typical dentate cover scales from the DFW, and Fig. **93** is a magnified portion of one of these scales that shows pigment globules deposited within the fenestrations. Note that the ridge lines are simple and low. Fig. **94** illustrates scales from the DHW, and the single arrow points to a UV-reflective scale. The distal margins were observed to be atypical for UV-reflective scales (as is the case for the scale indicated), but the ridge lines are closely-spaced as compared with a normal cover scale (double arrow). Fig. **95** is a photograph at higher magnification of one of these UV-reflective scales, and verifies the presence of the layered (lamellar) structure of these ridge lines that is typical of UV-reflective scales. Note the differences at the same magnification between Figs. **93** and **95**. Since both parents represent UV-reflective species, the putative hybrid is also reflective (recessive trait), but the shape of the reflective scales is slightly abnormal compared to other SEM photos that I have examined.

Colias philodice eriphyle x C. alexandra edwardsii

In his discussion of the N. A. *Colias*, Hagen ["1883"(1884), p. 155] reported the field collection of a coupled pair consisting of a ♂ *C. philodice eriphyle* and a ♀ *C. alexandra edwardsii.* Although from the article cited it appears that Dr. Hagen accurately identified these two species, there is always the possibility of a misidentification of one of the butterflies.

Colias eurytheme x C. m. meadii.

June D. Preston collected a ♀ *Colias eurytheme* coupled with a ♂ *C. m. meadii* on

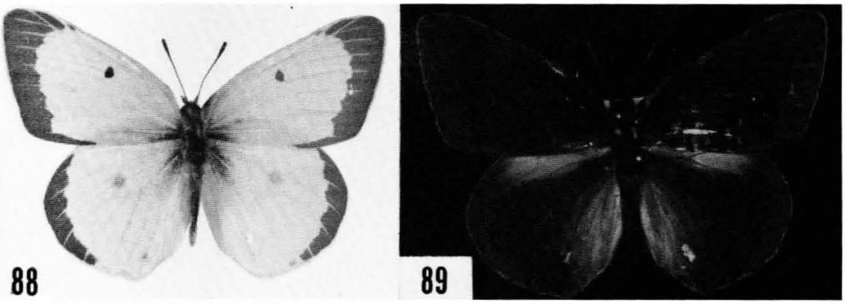


Figures **84-87**. Photographs of the SEM scans of the dorsal wing surfaces of hybrid ♂ *Colias*. Typical DFW dentate scales of specimen shown in Figs. **81-83** (**84**), and DHW scales (**85**). Typical DFW dentate scales of specimen shown in Figs. **88-89** (**86**), and DHW scales (**87**). Arrows point to "print through" of scales beneath the cover scales. Magnification = 500X.

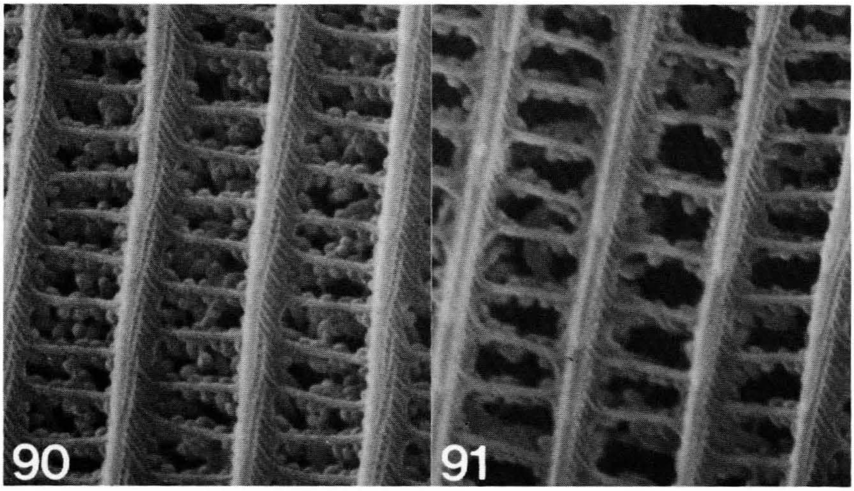
6.viii.1985. The locality was on the Beartooth Plateau in Carbon Co., MT, 2 road miles north of the Wyoming border on US Hwy. 212 at 10,000′ (3050m). The pair was flushed from the vegetation, and the female was the active flier. Based upon the photographs of the pair that I have examined, the wing expanse of the *eurytheme* ♀ is 27% larger than the expanse of the *meadii* ♂. The specimens were preserved, but no attempt was made to obtain ova.

Colias boothii and *thula*

In my 1985 paper, I suggested that *Colias boothii* Curtis and *thula* Hovanitz represent different color forms of the same butterfly, and in addition, that they are hybrids between *nastes* and *hecla*. Hovanitz (1963a, b) originally postulated the hybrid theory for *boothii*. Based upon current knowledge of the N.A. *Colias*, either *canadensis* or *hecla*, or both may represent one of the parents if the hybrid theory is valid. The cladograms shown in Figs. **2**, **126**, and **128**, suggest that *canadensis* is the orange parent; however, *boothii* occurs at various localities on the North Slope in Alaska (in conjunction with both *hecla* and

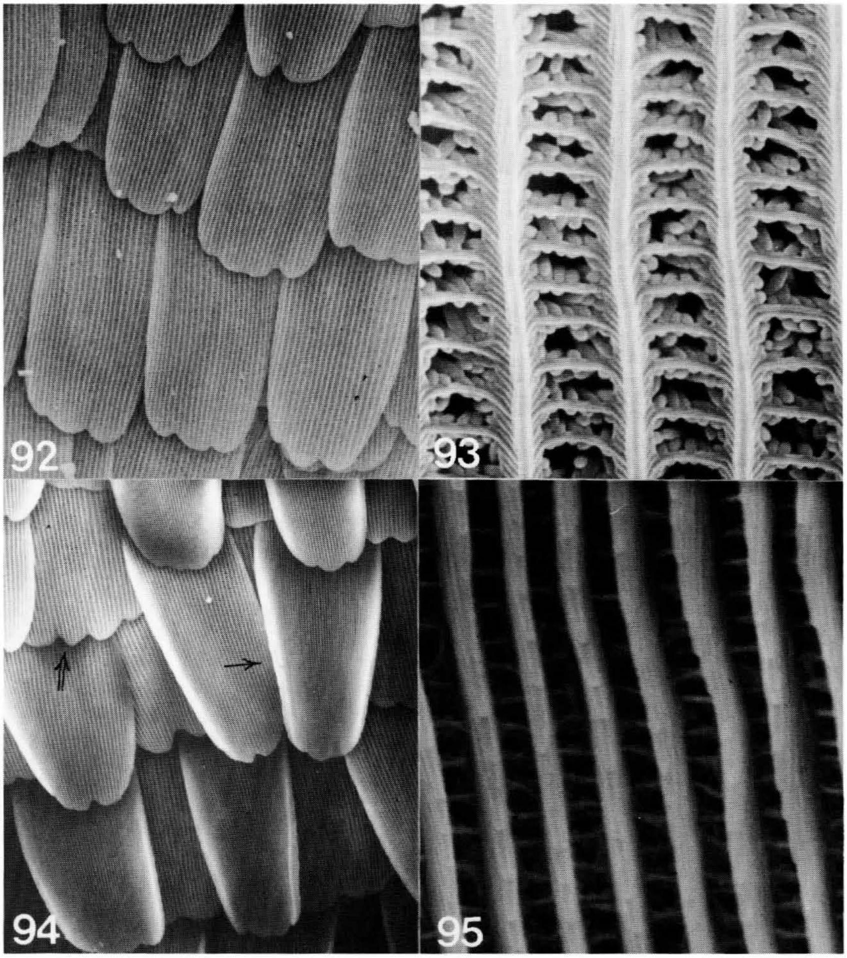


Figures **88-89**. Photographs of putative ♂ hybrid *Colias eurytheme* ♂ *x C. philodice eriphyle* ♀ from Spences Bridge, BC: D (**88**); D UV-reflectance (**89**). Specimen in AME.



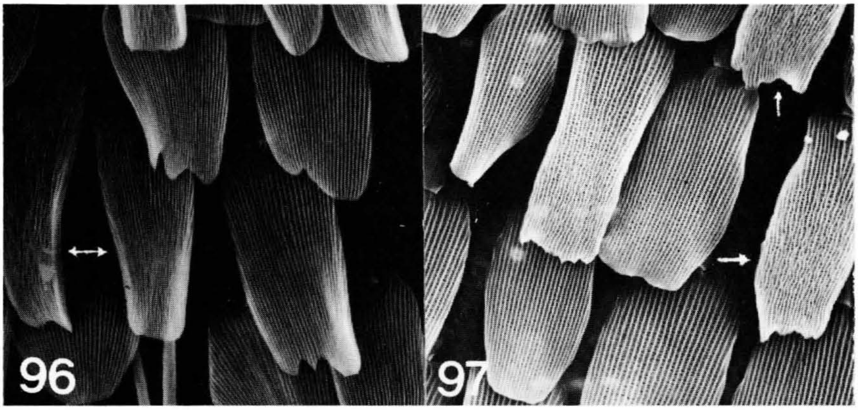
Figures **90-91**. Photographs of SEM scans of D wing scales of hybrid ♂ shown in Figs. **81-83**. Normal cover scale (**90**); abnormal scale (**91**). See text for discussion. Magnification = 10^4X.

nastes) from which *canadensis* is absent. The northernmost record that I have for *canadensis* in this region is a specimen that I collected well south of the Chandalar Shelf south of the Brooks Range. Based upon my collecting with three colleagues on the North Slope in Alaska during 1991, I now have no doubts that *boothii* and *thula* are simply color forms of the same insect. This species was taken intermittently from Galbraith Lake north of Atigun Pass to approximately 30 miles south of Prudhoe Bay. Adults of the population from Ice Cut in the valley of the Sagavanirktok River vary in color from the pale greenish-white associated with nomenotypical *thula* through various shades of yellowish-white, yellow, yellow-orange, to orange nearly as bright as in specimens from Baker Lake, N.W.T.

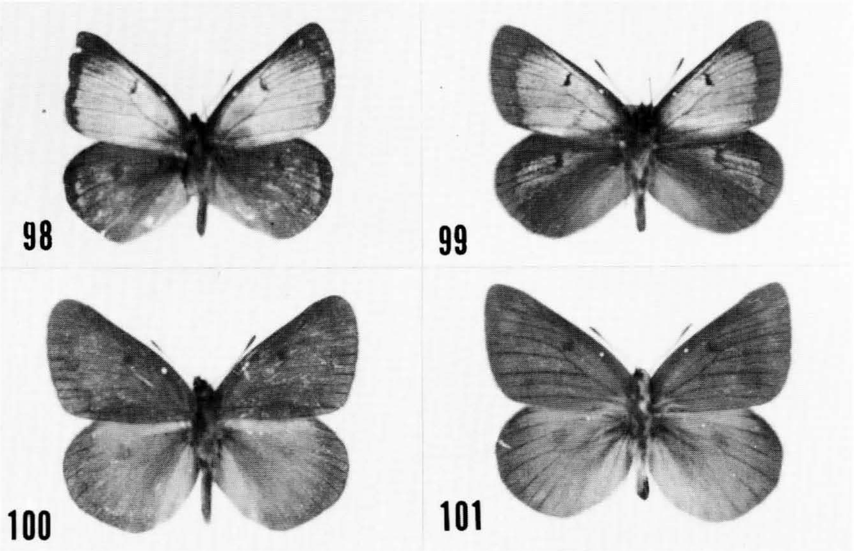


Figures **92-95**. Photographs of SEM scans of the dorsal wing surfaces of a probable ♂ hybrid *C. alexandra harfordii x eurytheme* from Los Angeles Co., CA. **92-93**: typical DFW dentate cover scales; 500X (**92**), single scale at 10^4X (**93**). DHW scales (**94**) at 500X: single arrow points to UV-reflective scale; double arrow points to normal scale. UV-reflective scale at 10^4X (**95**).

What is relevant to the current discussion is the shape of the UV-reflective scales in these butterflies. They too are abnormal (note arrows), as is shown in Figs. **96-97**, which lends additional credence to the hybrid theory. Figs. **98-101** illustrate the UV-reflectance patterns produced by *boothii* ♂ ♂. The illustrations in my 1985 paper were much too dark. Strong FW reflectance with none visible or restricted to the upper portion on the HW is characteristic of the orange phenotype. Form "thula" (Figs. **100-101**) has a more



Figures **96-97**. Photographs of SEM scans (500X) of DFW scales of ♂ ♂ of *C. boothii*. Normal orange form (96) and white "thula" form (97). White arrows point to reflective scales.



Figures **98-101**. UV patterns in ♂ ♂ of *Colias boothii/thula*. **(98-99)**: *C. boothii* from Baker Lake, NWT: 24.vii.72 (f. "chione", **98**); 6.vii.70 **(99)**, both leg. J. A. Ebner. **(100-101)**: *C. boothii: thula* phenotype vic. Omilak airstrip, W. side of Darby Mtns., Seward Pen., AK, 20.vi.86 (**100**, slight yellow-orange flush on FW); Bernard Harbour, NWT, 7.vii.88 (**101**), leg. J. Troubridge.

diffused general reflectance pattern resulting from sparsely distributed specialized cover scales. The results from SEM studies were presented in the paper cited, and two of those photos were reproduced above in the previous section as Figs. **96-97**. At present, I know of only two other *Colias* species worldwide in which the DFW UV-reflectance pattern is more developed than that of the DHW. These species are *christophi* Grum-Grschimaîlo and *wiskotti* Staudinger, both from Asia, and both with very distinctive (and atypical of *Colias* as a whole) dorsal maculation. In these two species, however, the male and female phenotypes are very consistent within local populations, and do not exhibit the high degree of polymorphism found in *boothii*. Pending new information, I continue to treat *boothii* as either a hybrid swarm, or an emerging species.

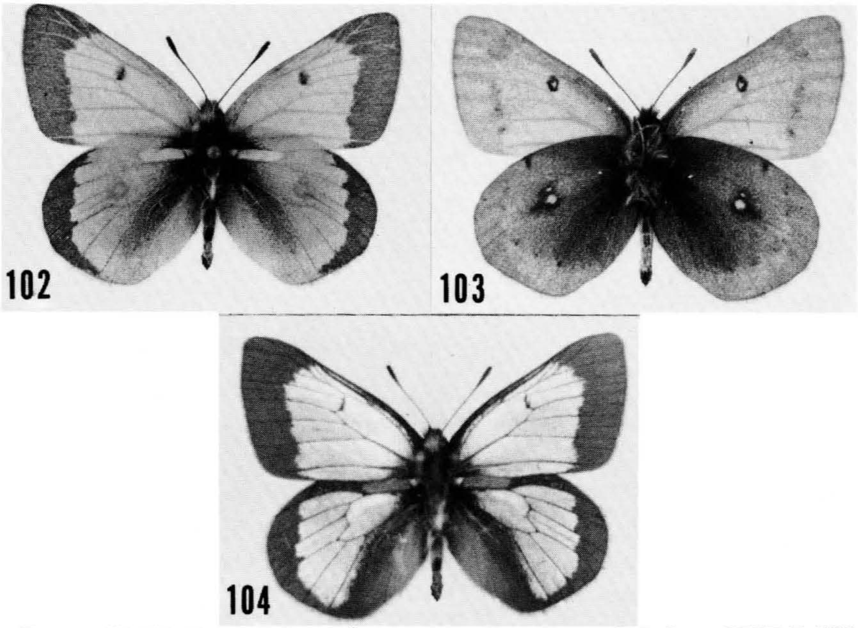
Old World Records

There are some records from Europe of *Colias* hybrids. K. Mikkola *(in litt.)* has reported specimens collected some years ago by V. V. Mikkola at Kilpisärvi in Finnish Lapland that appear to be hybrids between *palaeno* (L.) and *hecla*. Lorkovic'(*in* Kudrna, 1990) has illustrated a ♂ and ♀ of the cross *C. crocea* ♀ *x hyale* ♂. In another article ["1985(86)"], he has discussed hybridization in *Colias* and species-isolating mechanisms. There is an additional record from the Alai Mtns. in the eastern (former) USSR of the hybrid *C. eogene* Felder *x cocandica* Erschoff (Schulte, 1988).

Colias johanseni Troubridge and Philip, 1990
Figs. **102-108**

Colias johanseni Troubridge and Philip, 1990. Can. Ent., 122(1-2):15-20. TL — Bernard Harbour, Northwest Territories. HT in CNC.

This species was described recently, and the reader is referred to the original description

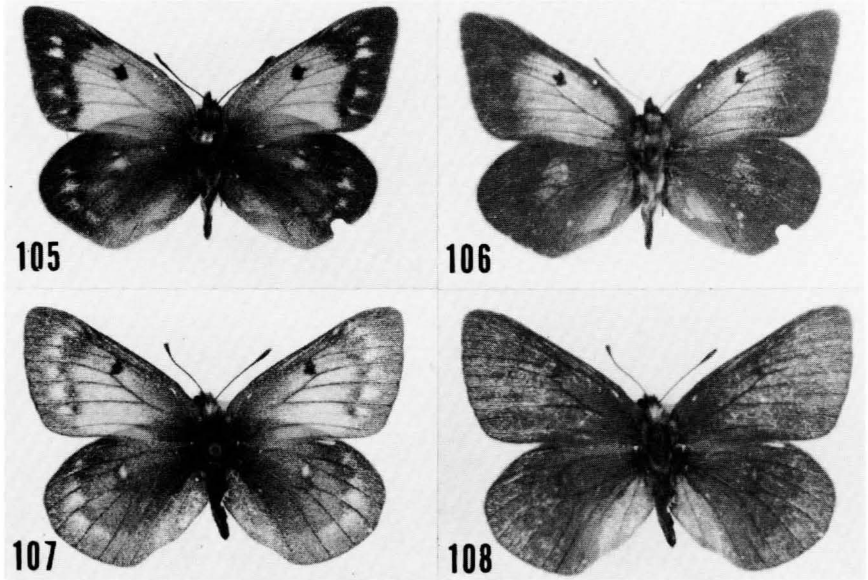


Figures **102-104**. Photographs of ♂ *C. johanseni* from Bernard Harbour, NWT: D (**102**); V (**103**); D UV-reflectance (**104**), leg. J. Troubridge.

for details. It is presumed to feed on a specific legume, *Hedysarum Mackensii* Richards. It and *meadii* are the only N.A. species in which the ♂♂ normally have an androconial ("sex") patch at the humeral angle of the DHW. The ♂♂ are highly UV-reflective (Fig. **104**), as are also some of the ♀♀ (Fig. **106**), a feature not mentioned in the original description. The major reflective pattern in the ♀♀ is limited to the FW, which is generally the case in Old World species in which the ♀♀ are reflective. The second specimen (Fig. **108**) appears to be non-reflective. There is some thin-layer effect produced by the wing membrane, and there may be some weak UV-reflectance from specialized scales just distad of the FW central region. *Colias johanseni* is apparently restricted to Bernard Harbour, NWT. This butterfly was briefly mentioned by Curtis and Ferris (1985, p. 7). This synoptic description is included here since the taxon is included in the character matrix used in the ensuing cladistic analysis.

Comment on the Taxonomic Position of *C. johanseni*

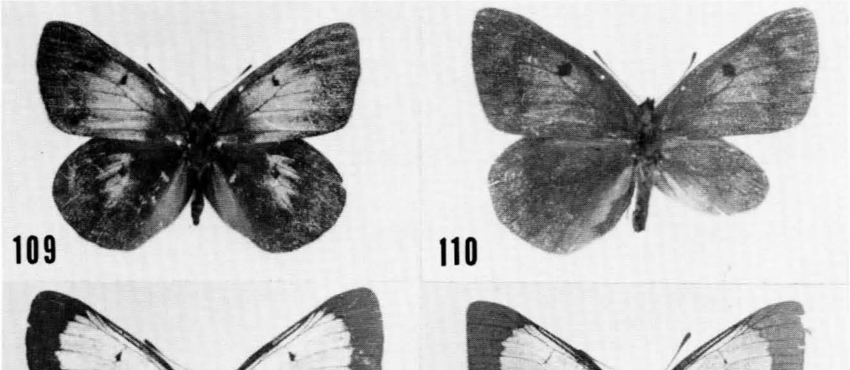
During the past six years, there have been comments in the literature concerning the placement of this taxon. Curtis & Ferris (1985) suggested that *hyperborea* Grum-Grschimaîlo might represent a subspecies of *meadii*. Scott (1986, p. 194) without comment placed *hyperborea* as a subspecies of *meadii*. Studies on the UV-reflectance patterns of *meadii*, *johanseni*, and *hyperborea* that I have conducted during the preparation of this monograph suggest that *hyperborea* is not a subspecies of *meadii*. I have been able to examine only two ♀♀ of *hyperborea*. Both are UV-reflective. One specimen (Fig. **109**) has distinct centrally reflective areas on the DFW and DHW. The other specimen (Fig. **110**) exhibits reflectance only from the DFW, but the specimen is both deformed and somewhat worn. Consequently the reflectance pattern may be atypical. As is illustrated in Fig. **106**, the reflectance from this female of *johanseni* emanates from the central regions of both wings. The dorsal UV-reflectance patterns from four ♂♂ of *hyperborea* are shown



Figures **105-108**. Photographs of dorsal surfaces of 2 ♀♀ of *C. johanseni* from Bernard Harbour, NWT, leg. J. Troubridge. UV-reflective ♀ (**105-106**): visual pattern (**105**); UV-reflectance (**106**). Essentially non-UV-reflective ♀ (**107-108**): visual pattern (**107**); UV-reflectance (**108**).

in Figs. **111-114**. The specimens illustrated represent the range of variation present in the series of this species in my collection. These reflectance patterns are very similar to that produced by the specimen of *johanseni* shown in Fig. **104**. The reader should compare, in particular, Fig. **104** with Fig. **112**.

In phenotype, *C. hyperborea* is closest to *C. meadii lemhiensis*. In general, the ♀♀ of *meadii* are not UV-reflective, while the ♂♂ reflect strongly. Of the *meadii* material that I have examined, I have found only a single ♀ of *lemhiensis* in which there is some weak and diffuse reflectance (Fig. **123**), and two ♀♀ of *m. meadii* which manifest slight DFW reflectance (Figs. **120**, **124**). The range of reflectance patterns produced by typical ♂♂ of *meadii* is illustrated in Figs. **115-119**, **121-122**. These patterns differ in one consistent character from those produced by *hyperborea* and *johanseni*. In *meadii*, there is a distinct projection of the reflectance pattern toward the anal angle of the DHW. The region of reflectance essentially extends to the outer margin in space Cu_2. This projection does not appear in the patterns produced by either *hyperborea* or *johanseni*. This feature is detailed in Fig. **125**. Fig. **115** illustrates a ♂ of *m. meadii* in which the DHW reflectance pattern

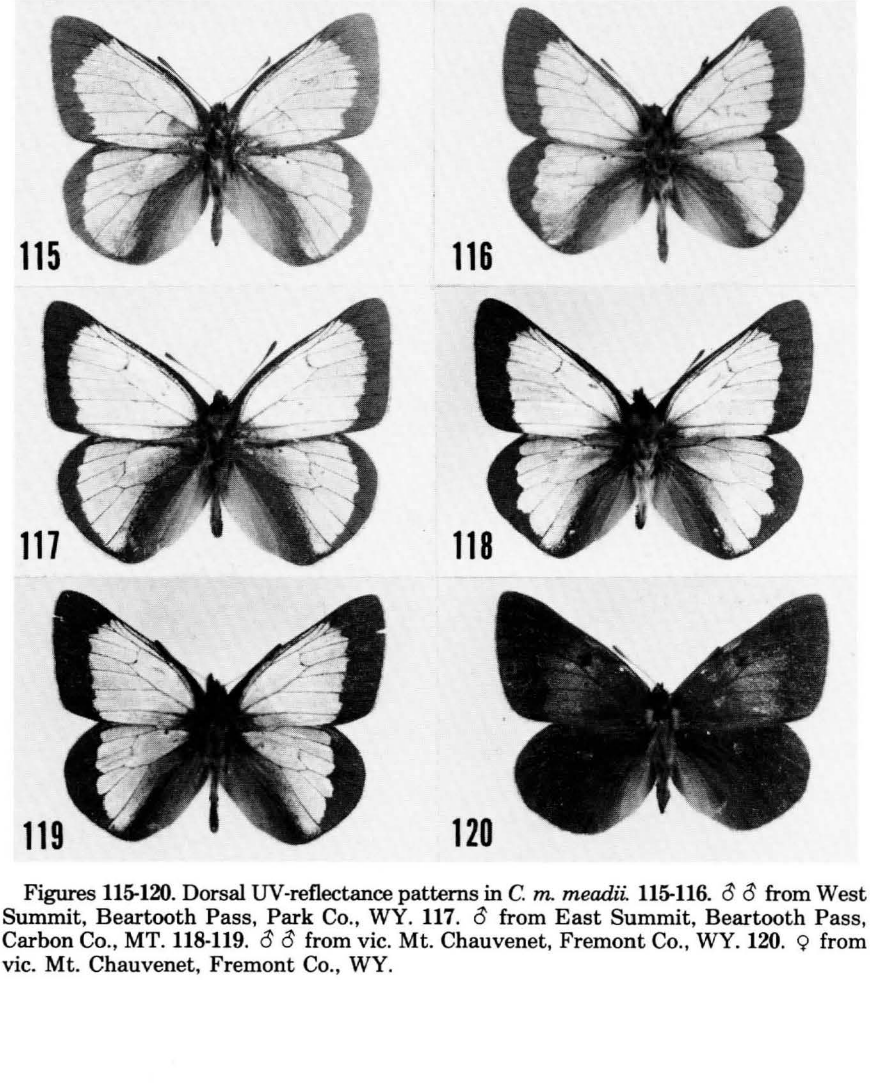


Figures **109-114**. UV-reflectance from the dorsal surfaces of 2 ♀♀ of *C. hyperborea*. Yakutia, USSR, 10.vii.87 (**109**). Tomtor, Yakutia, USSR, 27.vi.89 (**110**). UV-reflectance from the dorsal surfaces of 4 ♂♂ of *C. hyperborea* from Tomtor, Yakutia, USSR, 27.vi.89 (**111-114**).

approaches that found in *hyperborea*. This pattern is atypical in *meadii*, but has been included to show the extreme of variation. If one overlays HW photographs of these three species, it will be found that the HW of *meadii* is more produced at the anal angle than occurs in either *johanseni* or *hyperborea*. On the other hand, *johanseni* and *hyperborea* are similar. On the basis of HW shape, the UV-reflectance pattern in the ♂♂, and the usual absence of UV-reflectance in the ♀♀ of *meadii*, I suggest that neither *hyperborea* nor *johanseni* are subspecies of *meadii*. It does appear, however, that *hyperborea* and *johanseni* are closely related, and it remains to be determined if *johanseni* is a subspecies of *hyperborea*.

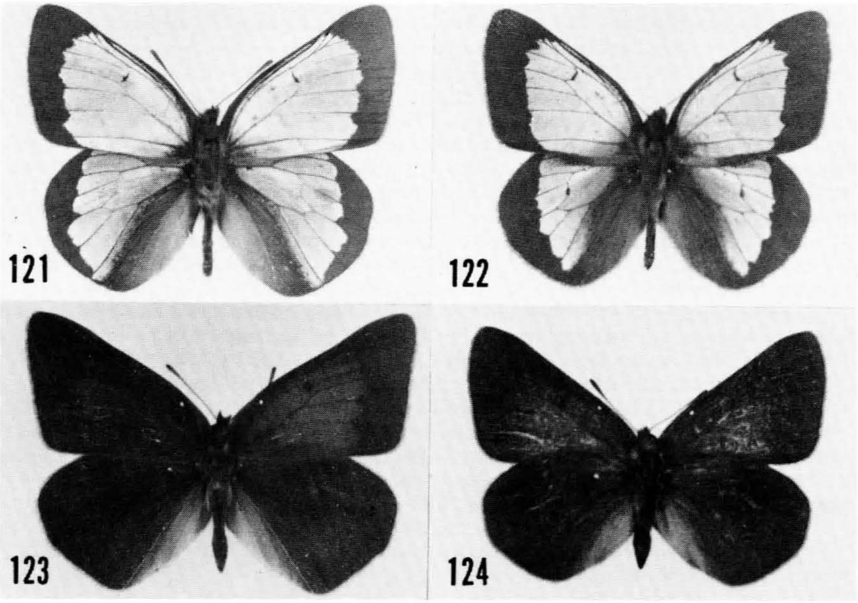
Cladistic Analysis of the N.A. *Colias*

The method used to effect the cladistic analysis was discussed in the section on "Methods and Materials." It can be argued that performing a cladistic analysis upon an incomplete group can lead to erroneous inferences, and I don't disagree. There is a more general

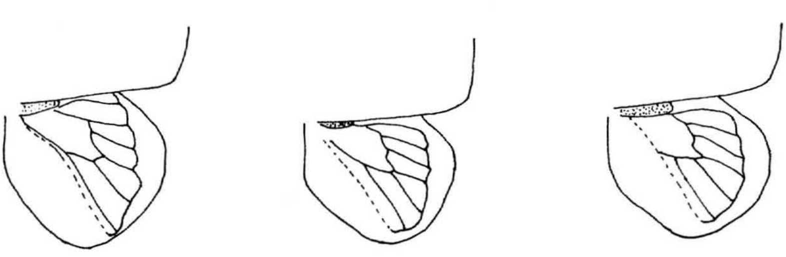


Figures **115-120**. Dorsal UV-reflectance patterns in *C. m. meadii*. **115-116**. ♂♂ from West Summit, Beartooth Pass, Park Co., WY. **117**. ♂ from East Summit, Beartooth Pass, Carbon Co., MT. **118-119**. ♂♂ from vic. Mt. Chauvenet, Fremont Co., WY. **120**. ♀ from vic. Mt. Chauvenet, Fremont Co., WY.

problem with the genus *Colias,* however, in that we do not clearly know how many species are actually involved. Many species are not well represented in museum collections, either in the U.S. or abroad. Species-subspecies relationships need to be elucidated. Additionally, a few specialists have suggested that several of the South American species should be placed in a separate genus, a subject that requires final resolution.



Figures 121-124. Dorsal UV-reflectance patters in *C. meadii.* **121-123.** *C. m. lemhiensis* from Jake's Canyon, Lemhi Co., ID. **121-122.** ♂♂. **123.** ♀. **124.** *C. m. meadii* ♀ from vic. Mt. Chauvenet, Fremont Co., WY.



meadii *hyperborea* *johanseni*

125

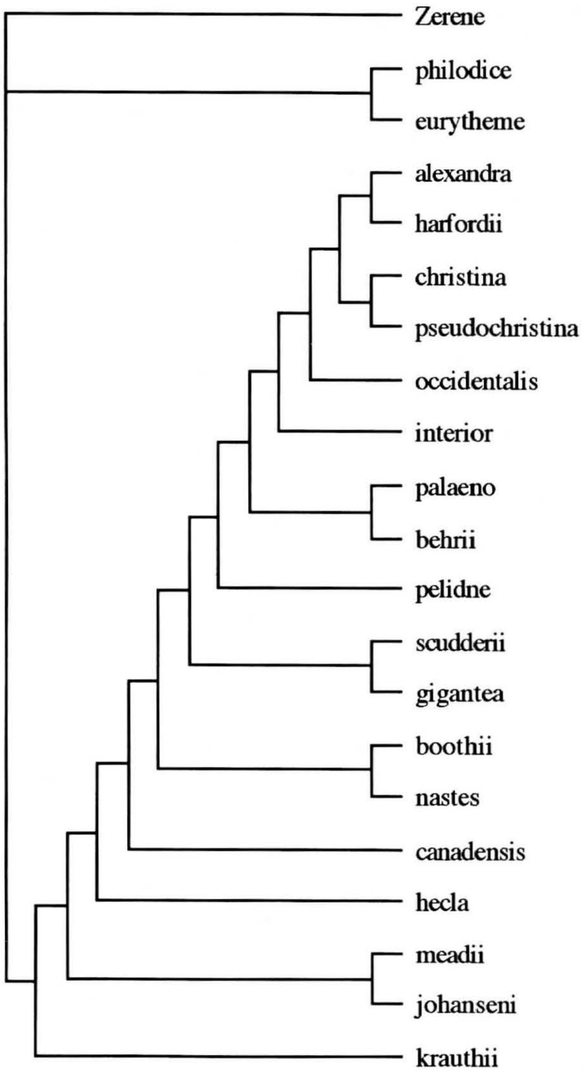
Figure 125. UV-reflectance pattern detail at DHW margin in the ♂♂ of three *Colias* species.

There is a recent precedent for limited cladistic analysis (Liebherr, 1988), and in defense of using a reduced analysis restricted to a single continent, I offer the following comments: We have more complete knowledge of the North American *Colias* fauna than of any other geographic group, although much still needs to be studied with regard to immatures. There are three plant families that are known as larval hosts of *Colias:* Leguminosae (Fabaceae); Ericaceae; Salicaceae. Based upon current knowledge, with the exception of *palaeno,* all of the species which occur outside of North America are legume-feeding species. Apparently the willow-feeding and three of the heath-feeding species have evolved in North America. The fourth heath-feeding species, *palaeno,* is widely distributed in North America. All of the N. A. *Colias* belong to the same male genitalic group, which I have confirmed independently of Berger's study (1986), although some Old World species also belong to this group. Two other widely-distributed circumpolar species, *hecla* and *nastes* are members of our fauna. The characters that I have selected apply in general to all *Colias.* Some, such as host plant, are unique to N.A. fauna. To expand the analysis to all *Colias,* additional characters unique to the South American and some of the Old World species would be required. Any cladogram derived from an incomplete species group will certainly lack branches, but I feel that it can provide some useful information and may suggest areas for further investigation.

When the character matrix shown in Fig. **132** was analyzed using PAUP, a single most-parsimonious tree resulted, as shown in Fig. **126.** Fig. **2** is the same tree, but as presented by the MacClade graphics with a branch flip. Tree length is 201 and the consistency index (CI) is 0.418 = 0.42. Other data are: homoplasy index (HI) = 0.582; retention index (RI) = 0.550. Figure **127** is a general character trace showing total changes using MacClade.

While as noted above, one must be careful about making inferences from an incomplete analysis, there are some intriguing aspects of the tree shown in Fig. **126** (and Fig. **2**). The arrangement of the *alexandra-harfordii-christina-pseudochristina-occidentalis* group of species is interesting. Its relation to the willow and heath-feeding species is curious, and may be an artifact of the incomplete species representation, but probably not. The cladogram suggests that a reversal in host plant preference occurred. On the basis of larval host, *scudderii* and *gigantea* form a monophyletic clade, as do *behrii* and *palaeno.* While each is located on separate branches, *pelidne* and *interior* lie within the portion of the tree where the other non-legume feeders reside. Figure **128** is the most parsimonious cladogram with the species grouped by host-plant preference. Tree length is 210 and the CI = 0.40. According to available fossil pollen records, this is not the order in which the associated plant families evolved (Muller, 1981). The Ericaceae are the oldest dating to the Maastrichtian in the Upper Cretaceous. Willows and legumes are Tertiary. The Salicaceae date to the Oligocene, and the legumes are newcomers dating only to the Pliocene (2.5 - 5 million years B.P.).

I feel that it is safe to make several inferences from the cladograms shown in Figs. **2, 126,** and **128.** The following species are close relatives: 1. *C. palaeno* and *behrii;* 2. *C. scudderii* Reakirt and *gigantea* Strecker; 3. *C. eurytheme* and *philodice* (a fact already established by many hybridization studies). It is reasonable to place *harfordii* as a subspecies of *alexandra.* It certainly does not belong as a subspecies of *occidentalis* where several authors have placed it. When *harfordii* is deleted from the data matrix, tree length drops only to 199 and the CI remains unchanged, which is an insignificant change. If *boothii* does represent a hybrid swarm, then the cladograms suggest that *canadensis* and *nastes* are the parent species, rather than *hecla* and *nastes,* but see additional comments below. The position of *krauthii* far removed from the former "*alexandra* group" is curious, and may be an artifact of the limited species analysis. *C. hecla* and *C. nastes* are fairly closely related, as was suggested by Peterson (1963) based upon his biometric analysis of male genitalia. This work was done before *canadensis* was recognized as a species. *C. johanseni* is somewhat of an enigma. As Troubridge & Philip (1990) pointed out, this species is known only from Bernard Harbour, N.W.T., a region that did not rise from the sea until approximately 6000 years B.P., which suggests the unusual event of very recent evolution. Its foodplant, *Hedysarum Mackensii* Richards is a widely-distributed arctic/alpine legume, but the butterfly has not been found outside of the type locality. Troubridge & Philip have proposed two possible explanations for the limited geographic



126

Figure 126. Most parsimonious cladogram of the N.A. *Colias* species with *harfordii* included and *Zerene* as the out-group. Cladogram generated by PAUP and printed using PAUP graphics.

127

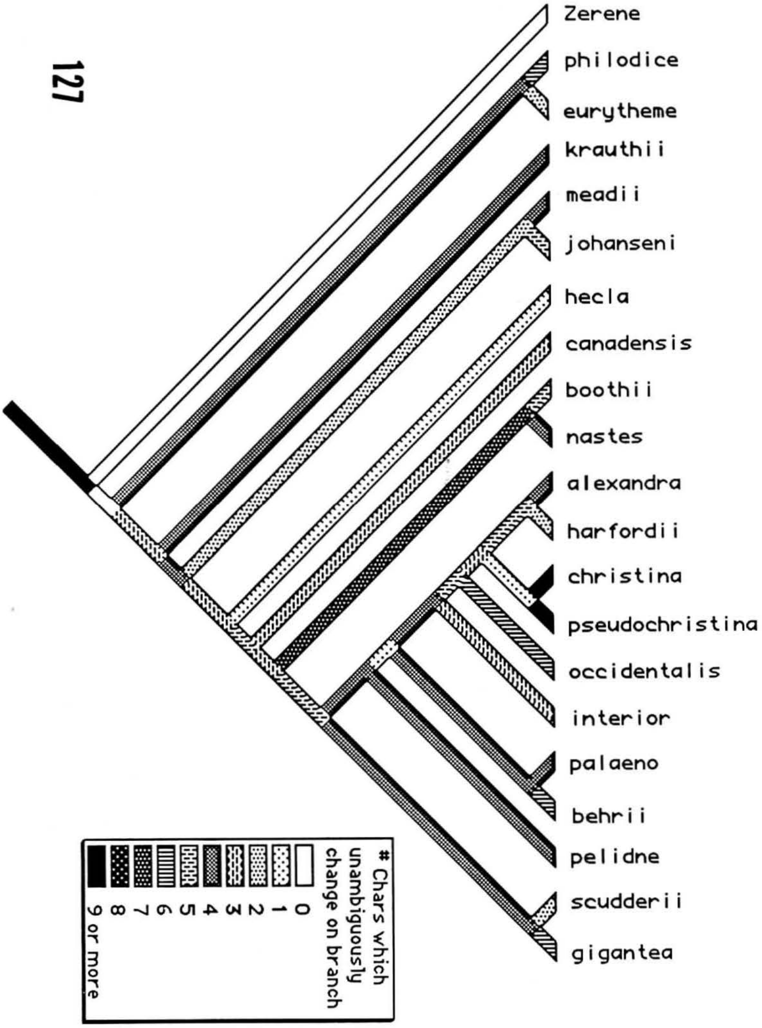
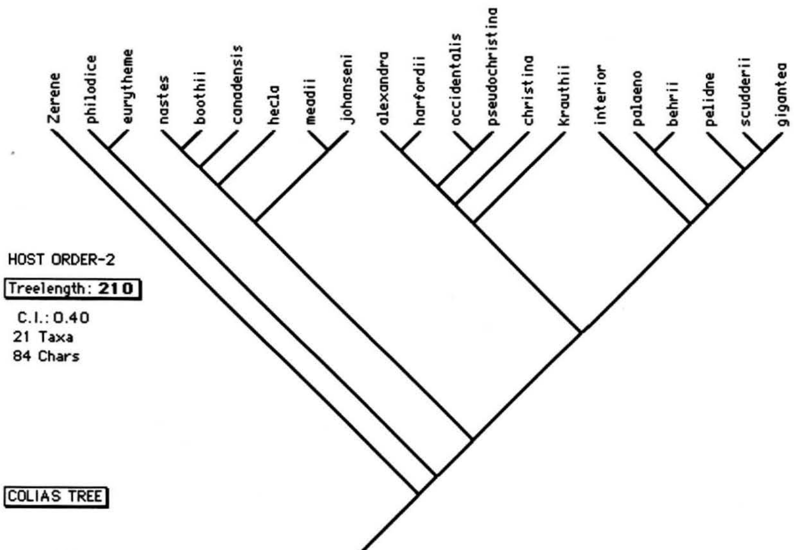


Figure 127. MacClade plot of character state changes for cladogram shown in Figs. 2 and 126.

range of *johanseni.* One is a sympatric speciation event in which *johanseni* evolved instantaneously from *hecla* following a genetic reversal. The second scenario seems more plausible regarding the position of *johanseni* in the cladograms included herein, and this is that *johanseni* colonized Bernard Harbour from unglaciated regions to the west or north. Wisconsinan refugia did exist near to Bernard Harbour, and additional colonies of *johanseni* may exist in areas that have not yet been visited by collectors. As noted above, the relationship of *johanseni* to the Siberian *C. hyperborea* needs to be elucidated. Any further inferences from the cladogram shown in Figs. **2** and **126** would be unbridled speculation.

Using the character-trace feature of MacClade, I traced all of the 84 characters used in the cladistic analysis. Very few equivocations were found other than ones related to the choice of the out-group. Numerous instances of what can be interpreted as parallelism or convergence were found, as well as reversals. This situation is not uncommon in the pierids, as noted by Shapiro (1979).

There is evidence that *boothii* is evolving into a distinct species with regard to its white form "thula" in certain areas of northern and western Alaska (*fide* K. W. Philip). At this point, I know of very few localities where *boothii* occurs in either color form and where both *nastes* and/or *canadensis* and *hecla* do not occur. In my 1985 paper, I cited several such areas in Alaska as well as Keno Hill, YT. Since then, I have been able to examine many additional specimens for which previously I had only label data. The species at Keno Hill is *canadensis* and not *boothii.* This is true for most, if not all, of the orange *boothii* records from the Yukon Territory (except for the extreme north), and for all orange "*boothii*" from interior Alaska. In many of these areas, both *nastes* and *hecla* do occur, but what has been misidentified as orange *boothii* in the past, is in fact *canadensis.* A

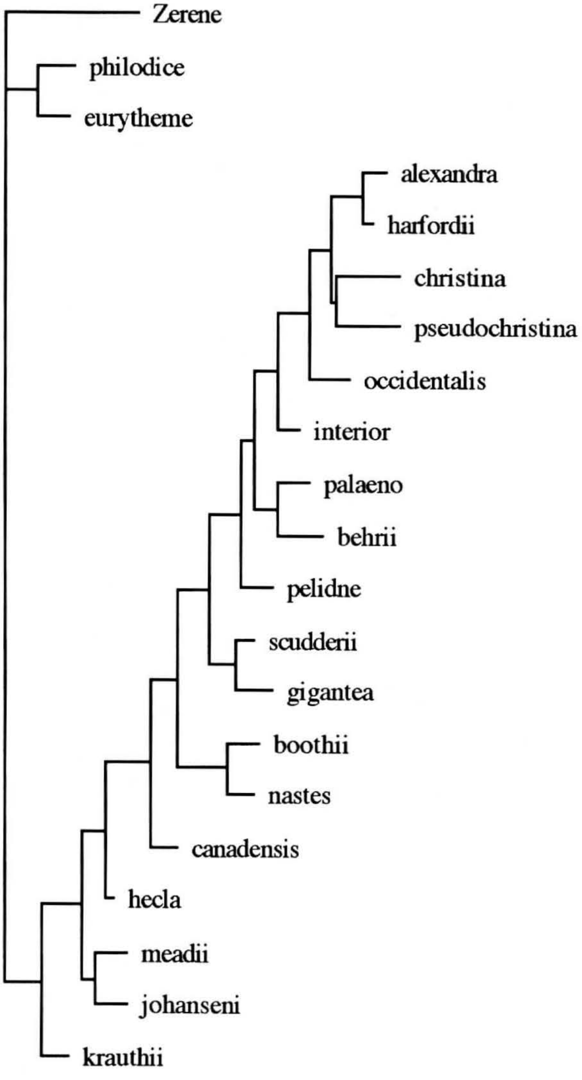


128

Figure 128. Most parsimonious cladogram of the N.A. *Colias* species with *harfordii* included and *Zerene* as the out-group when the species are segregated according to larval host plant preference. Cladogram generated by PAUP and refined and printed using MacClade.

tentative distribution map for *canadensis* was included in Ferris (1988, Fig. 26). It now appears that the orange form of *boothii* has a geographic distribution even more restricted than previously believed.

The taxonomic assignments suggested in this paper for the N.A. legume-feeding *Colias* species are summarized below (using the citation method of Hodges *et al.,* 1983). If *Colias*



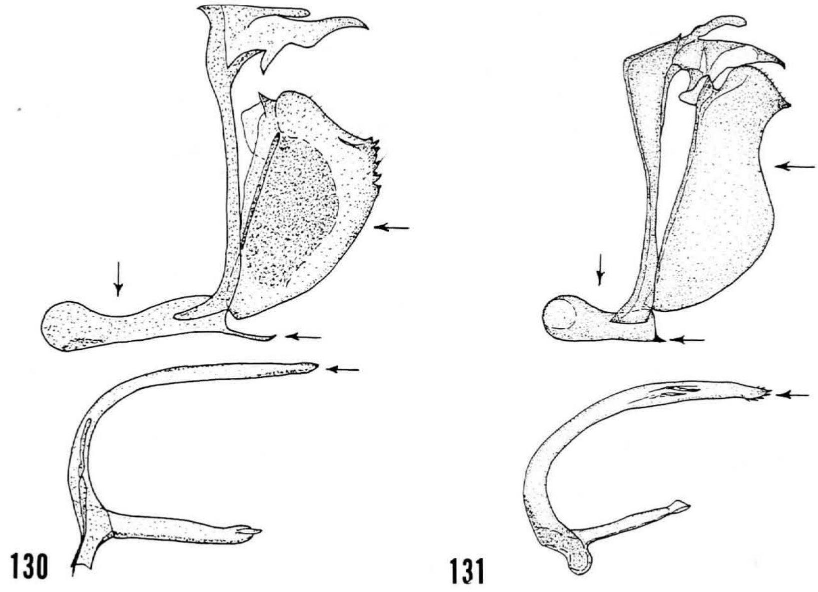
129

Figure 129. Phylogram of N.A. *Colias* generated using PAUP.

boothii is treated as a species, then *thula* is a subspecies. The order is purely alphabetical, and no phylogeny is implied.

Alphabetic Arrangement of the N.A. Legume-feeding *Colias* As Revised

Colias alexandra W. H. Edwards 1863
  a. *apache* Ferris 1988
  b. *columbiensis* Ferris 1973
  c. *edwardsii* W. H. Edwards 1870
  d. *harfordii* Hy. Edwards 1877
(?)*Colias boothii* Curtis 1835
  a. *thula* Hovanitz 1955
Colias canadensis Ferris 1982
Colias christina W. H. Edwards 1863
  a. *astraea* W. H. Edwards 1872
Colias eurytheme Boisduval 1852
Colias hecla Lefèbvre 1836
  a. *hela* Strecker 1880
Colias johanseni Troubridge & Philip 1990
Colias krauthii Klots 1935
  a. *kluanensis* Ferris 1981
Colias meadii W. H. Edwards 1871
  a. *elis* Strecker 1885
  b. *lemhiensis* Curtis & Ferris 1982
Colias nastes Boisduval "1832"[1834]
  a. *aliaska* Bang-Haas 1927



Figures **130-131**. Sketches of the ♂ genitalia of two genera of Coliadinae. *Zerene cesonia* (**130**), and *Colias eurytheme* (**131**). Arrows point to features that differ between the two species.

PAUP DATA MATRIX

Zerene	1000000000000000100010000000000100100001010001000010001011000010100000101111101110110
philodice	0000000000000011100110011000100010100000110001001010000100001001000000100000010001001
alexandra	0000000001000101100000010101000010100010000100100101000100001000100000100000010001001
palaeno	0000000000000111010001010100101000000100100100110000000000100000010001100000010001001
interior	0000000000000111010000010100101000000010001001010010001000001000101000100000010001001
pelidne	0000000000000111010000010100101000001010000110010000010100010000010000100000010001001
scudderii	0000000000000111001000010010111001001010000110010000000000001000100001010000010001001
gigantea	0000000000000111001000010010111001000010000110001001001000010000100100010000010001001
occidentalis	0000000000000101100000010100111000010000101001001001000100001000100000100000010001001
eurytheme	0100000100000011100110011000100100100000110001000110001000100001000000100000010001000
christina	0010001010001101100000010101001000010010001010000110001000001000100000100000010001000
pseudochristina	0001000000100111100000010011011000001010001001000100100100010000100000100000010001000
meadii	1100000100000101100000011001001000001000100101010010000100100001000000100000010001000
johanseni	1100000100001000100000011001011001001000100101010010001000100011000000010000010001000
krauthii	0100000100000000100000011001001000100010001001001010001000001001000000100000010001000
hecla	0100000100000000100000011000101001001000100110010010001000001001000000100000010001000
canadensis	0100000100000101100000011000111000001010000110010000101000010001000000010000010001000
behrii	0000100000000111010001010100101000000100100010010100000000000100100000110000010001000
boothii	0000011000010101100000010100010100100000010011000101000010000010100010001000010001000
nastes	0000101000000101100000010100010100101000000011000100100010000010100001001000010001000
harfordii	0000000001000101100000010101000100100010000101000110000100001000100000100000010001001

Figure 132. Character matrix used in cladistic analysis.

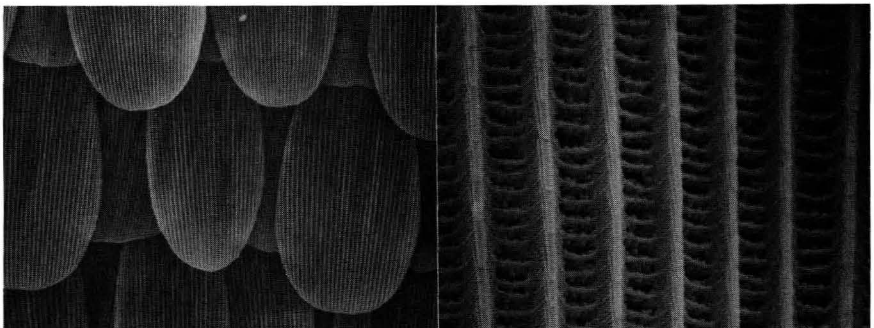
b. *moina* Strecker 1880
c. *streckeri* Grum-Grschmaîlo 1895
Colias occidentalis Scudder 1862
a. *chrysomelas* Hy. Edwards 1877
Colias philodice Godart [1819]
a. *eriphyle* W. H. Edwards 1876
b. *vitabunda* Hovanitz 1943
Colias pseudochristina Ferris, 1989

CONCLUSIONS

Based upon cladistic analysis, intensive study of UV-reflectance patterns, mapping of geographic distributions, and sympatry and synchrony of phenotypes, I have dissolved the concept of the *C. alexandra* complex of species. This action also agrees with field observations of the species involved in terms of habitat preferences. *Colias krauthii* occupies semi-xeric open areas in boreal forest. *Colias christina* occurs widely in open areas in boreal forest, generally in moderately mesic environments, such as stream or river valleys. *Colias alexandra* is basically a xeric-association species (Transition zone and sagebrush-steppe association). *Colias pseudochristina* occupies a restricted niche in Rocky Mountain Montane Forest. *Colias occidentalis* occurs in open areas in relatively dry coniferous (primarily fir) forest.

This partitioning of the original "*alexandra* group" into four species resolves the long-standing problem related to the occurrence in many geographic areas of various phenotypes of a supposed single species. It also explains the annual fluctuations in population densities observed in given localities regarding the several color forms, since multiple species are involved with independent biological cycles.

I do not feel that it is appropriate at this time to suggest a genealogy of the N.A. *Colias* species as a whole based upon the tree shown in Figs. **2** and **126**, since the data matrix is incomplete. The PAUP analysis suggested the phylogeny shown in Fig. **129**. This



Figures **133-134**. Photographs of the SEM scans of the DHW of a ♂ *C. o. occidentalis* from Tumwater Recreation Area, Thurston Co., WA (Coll. AME). There are no UV-reflecting scales. Scales typical of the non-reflective cover scales (500X) found in the genus *Colias* (**133**). Single scale at 7000X (**134**) illustrating the typical lamellar ridges characteristic of a non-reflecting cover scale in *Colias*. Pigment balls are visible filling the fenestrated areas between the longitudinal ridges and the transverse cross-linkages.

arrangement, of course, is tentative and subject to change when a phylogenetic analysis can be carried out for all known *Colias* species.

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Equipment brand names have been mentioned for reference only and such mention does not constitute product endorsement.

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Appendix 1
Cladistic Analysis

The male and female genitalia are remarkably uniform among the North American species of the genus *Colias*, so much so, that I have been unable to date to discover any useful characters that may be utilized for species identification. While the male genitalia of *Zerene cesonia* and *Z. eurydice* (Boisduval) are virtually identical, they differ substantially from the form of the male genitalia found in *Colias.* These differences are illustrated in Figs. **130** (*Zerene*) and **131** (*Colias*). In *Zerene,* the outer margin of the valve is convex and toothed, while in *Colias,* it is concave and smooth. In *Colias,* the tip of the aedeagus is adorned with spiny projections, while in *Zerene* it is smooth. The vesica in both genera is without cornuti, but after staining, the folds of the vesica within the aedeagus may be visualized as is illustrated in Fig. **131**. The bore of the aedeagus in *Zerene* is approximately double that found in *Colias.* Other differences found in the male genitalia include the length of the saccus and the distal extension of the saccus, as are denoted by the arrows in Figs. **130** and **131**. I have selected *Zerene* as the out-group based upon its similarities to *Colias* and its dissimilarities in the male genitalia.

The characters selected for cladistic analysis are defined in Table **5** below. The character matrix as used by the MacClade software is shown in Fig. **132** following the list of characters. Since the characters have been coded in a strict binary manner (either present or absent), there is no character weighting or ordering.

Table 5: Characters Used for Cladistic Analysis

Number	Character
1.	DHW ♂ "sex patch" present.
2.	♂ dorsal color orange.

3. ♂ dorsal color orange basad grading to yellow distad.
4. ♂ dorsal color suffused orange over yellow.
5. ♂ ground color whitish overscaled with yellow and melanic scales to produce the aspect of yellowish-green orgreenish-gray pale areas.
6. ♂ color variable orange to white.
7. ♂ dorsal wing pattern polymorphic.
8. ♂ UV-reflective (UVR) on hindwing (HW) and forewing (FW).
9. ♂ UVR on HW and FW with pattern radiating inward from inner edge of marginal border.
10. ♂ UVR on HW and FW with reduced (or absent) pattern radiating inward from inner edge of marginal border.
11. ♂ UVR on HW reduced and FW pattern radiates outward from wing base.
12. ♂ UVR on FW and HW pattern reduced and variable.
13. ♀ UVR on FW sometimes and variable in area.
14. ♀ polymorphic regarding dorsal color; may be white, yellow, or orange.
15. ♀ shows only "alba" color polymorphism.
16. ♀ variable polymorphism regarding dark areas of D wing pattern; absent, faint, fully-developed; extent of wing borders and fenestration variable.
17. Larval host legume.
18. Larval host Ericaceae.
19. Larval host *Salix*.
20. VHW displays "eurytheme" spots.
21. VHW discal spot has a double ring.
22. VHW discal spot is normally prominent and "dead" white.
23. ♂ DFW border variable in width, may be solid or fenestrated.
24. ♂ DFW border is solid, except perhaps for color overscaling along veins.
25. ♀ DFW border fenestrated.
26. ♀ DFW border variable in pattern; may be absent, nearly obsolete, or fully developed and fenestrated.
27. ♀ DFW border vestigial; slight dusting of dark sacles near apex or diffuse submarginal bar.
28. FW apex acute.
29. FW apex rounded.
30. VHW discal spot often distinctly double (one large spot superior as opposed to small or vestigial satellite spot).
31. Always univoltine.
32. Always multivoltine.
33. Sometimes multivoltine; some local populations produce two or more annual generations.
34. VHW discal spot sometimes produced (smeared) distally.
35. ♂ DFW cell spot round or oval.
36. ♂ DFW cell spot varies from round/oval to crescentic.
37. ♂ DFW cell spot crescentic to obsolete.
38. ♂ DFW cell spot obsolete.
39. ♂ DFW veins always colored (highlighted) in border.
40. ♂ DFW veins never colored (highlighted) in border.
41. ♂ DFW veins in border may be colored or black.
42. VHW with any melanic overscaling virtually absent (except for early-spring generations).
43. VHW with light melanic overscaling.
44. VHW with moderate-to-mossy green melanic overscaling.
45. VHW discal spot with heavy rim.
46. VHW discal spot with average rim.
47. VHW discal spot rim vestigial or absent.
48. FW outer margin normally convex.
49. FW outer margin variable.

50. FW outer margin usually straight.
51. ♂ DHW discal spot orange.
52. ♂ DHW discal spot color variable from ground color through yellow-orange to bright orange.
53. ♂ DHW discal spot nearly concolorous with wing ground color.
54. ♂ DHW discal spot concolorous with ground color.
55. ♀ DHW discal spot orange.
56. ♀ DHW discal spot color from ground color through yellow-orange to bright orange.
57. FW outer margin concave.
58. ♀ D unpatterned or with dog-face pattern.
59. ♀ DFW border solid and broad, excepting possible highlighting along veins.
60. ♂ DFW border solid and narrow, excepting possible highlighting along veins.
61. ♂ DFW border solid and of average width, excepting possible highlighting along veins.
62. ♂ DFW border not as in 59-61, 76.
63. VHW post-median row of spots in cells [not "eurytheme" spot configuration].
64. ♀ DHW with well developed marginal border.
65. ♀ DHW marginal border vestigial or absent.
66. ♀ DHW marginal border present, but variable in extent.
67. ♂ DFW cell spot ellipsoidal to obsolete.
68. ♂ DFW cell spot variable in shape to obsolete.
69. ♂ DFW border with streaks in cell spaces, but veins not highlighted.
70. ♂ and ♀ DHW discal spot "prints though" as white with pastel shading of D ground color.
71. HW outer margin always visibly produced at anal angle; not smoothly curved.
72. HW margin variable at anal angle; may be slightly produced or rounded (smoothly curved).
73. ♂ D color orange or yellow.
74. ♀ D color either yellow or yellow with orange blush.
75. ♂ UVR with strong central FW pattern and reduced HW pattern.
76. ♂ DFW with "dog-face" pattern.
77. ♂ genitalia with saccus foreshortened.
78. ♂ genitalia with saccus elongated.
79. ♂ genitalia with tip of aedeagus smooth and devoid of spines.
80. ♂ genitalia valvae with convex outer margin and dentate projections (See Fig. **130**).
81. DHW discal spot double and separated, with upper spot angled distad.
82. ♂ genitalia valvae with smooth and concave outer margin (see Fig. **131**).
83. FW apex falcate.
84. ♂ dorsal color yellow.

APPENDIX 2
Collection Records and Material Studied

The records cited below are in addition to those listed in my previous papers (1973, 1976, 1981, 1982, 1985, 1988, 1989a). To conserve space, names of collectors and dates of collection (generally) are omitted. Specimen locations are noted, however, when known. The number of specimens examined of each species is shown in ( ).

Colias alexandra alexandra (201). AME: **UTAH**. Daggett Co.: Hwy. 44 just N. of Manila. Uintah Co.: Colton Ranger Sta.; E. Fk. of Dry Fk; Dry Fork Canyon. **WYOMING**: Teton Co.: Red Creek Camp, Teton NF. AMNH: **UTAH**. Uintah Co.: Dodds and Kater Hollows, 21-22 mi. NNW of Vernal. **WYOMING**. Carbon Co.: S. of Rawlins. CDF Coll.: **COLORADO**. Park Co.: Red Hill Pass. **WYOMING**. Albany Co.: Sherman Range; Sand Lake rd., Snowy Range. B. Mather Coll.: **COLORADO**. Park-Teller Co.: Top of the World, Little Blue Mtn. Park. R. C. Rosche Coll.: **SOUTH DAKOTA**. Pennington Co.: nr. Hill City, 3.ix.84. Univ. of Wyoming Coll.: **WYOMING**. Yellowstone N.P.: Blacktail Plateau, 12.vii.90.

Records only. **ALBERTA**. Altario; Brooks; Carseland; Chin Coulee at Hwy. 36; Comrey;

Cypress Hills; Dinosaur Provincial Park; Eagle Butte; ca. 11 km S. of East Coulee; Elk Water; Finnegan; Fox; Grand Forks; Grassy Lake; Hilda; Jenner; Lethbridge; McIntyre Ranch; Lodge Creek; Magrath; Manyberries; Milk River; various areas on the Milk River Ridge; Milk River-Lost River area; Oldman River at Hwy. 36; Onefour; Police Coulee area; Pulteney; Raymond; St. Mary River at SR 509; 5.6 km SE of Standard; Summerview; Taber Prov. Park; Van Cleve Coulee; Warner; Wintering Hills; Wrentham; Writing on Stone Prov. Park. **MONTANA**. Carter Co.: 2 mi. N. Ridge, 19.viii.84. Daniels Co.: 5 km N. Scoby, 1.viii.80. Prairie local populations with "alba" ♀♀ are known from the following counties: Gallatin, Judith Basin (5 mi. SE Geyser, 29.v.81; 15.v.87), Lewis & Clark, Toole, Wheatland (Roberts Ck., W. Judith Gap, 17.viii.87). Additional records are: Liberty Co.: East Butte, Sweetgrass Hills. Toole Co.: West Butte, Sweetgrass Hills, 21.vi.80; 6 mi. N. Shelby on I-15, 9.viii.75; 3 mi. W. Sunburst, 9.v.87. **SASKATCHEWAN**. Big Muddy Lake; Claydon; Cypress Hills; Estuary; Kerrobert; Killdeer Badlands; Pike Lake. **SOUTH DAKOTA**. Custer Co.: Bob Marshall Camp. Fall River Co.: 1 mi. into Red Canyon; Red Canyon vic. Hot Springs, 29.vii1.viii.91. Jackson Co.: Kadoka, 26.vii.58. **UTAH**. Nr. Snyderville, 28.vi.65.

Colias alexandra apache. (5). CDF Coll.: **NEW MEXICO**. Grant Co.: Gila NF, FR 309, 8600′ (2620m), 10.vii.91; Gila NF, Black Peak Trail from Signal Peak, 9000′ (2745m), 28.vi.91.

Colias alexandra edwardsii (4). AME. **UTAH**. Garfield Co.: Bryce Canyon. Washington Co.: road btwn. Leeds and Oak Grove CGs. AMNH: **UTAH**. Juab Co.: Trout Creek, Ibapah Mtns.

Records only. **ARIZONA**. Coconino Co.: Kaibab Plateau. **UTAH**. Kane Co.: Stout Canyon, 9.vii.87.

Colias alexandra harfordii (23). CDF Coll.: **CALIFORNIA**. Ventura Co.: Mt. Pinos. Riverside Co.: Hamilton Creek. San Diego Co.: Alpine; nr. Camp Ole Laguna; Mt. Palomar. LACM: **CALIFORNIA**. Ventura Co.: Frazier Mtn. San Diego Co.: Nellie Palomar Mtn. [sic, label data].

Records only. **CALIFORNIA**. Kern Co., Cameron Rd. adjacent to Hwy. 58 & Cache Ck., 22.ix.88. San Diego Co.: Box Canyon, Anza-Borrego State Park, 13.ii.77. San Luis Obispo Co.: Hi Mtn., 2.vi.84, 1.iv.88. Tulare Co.: (larva taken by J. F. Emmel *fide* K. Davenport) nr. Johnsondale, 19.vii.85. Ventura Co.: Frazier Mtn., vic. Chuchupate C.G; Mt. Pinos.

Colias alexandra columbiensis (92). AME: **MONTANA**. Flathead Co.: Hwy. 2, 2. mi. E. of McGregor Lake; 2 mi. NW of Little Bitterroot Lake; 1 mi. S. of Lakeside. Mineral Co.: Cabin City; SE of DeBorgia. Missoula Co.: Martina; 15.9 mi. N. of Seeley. Powell Co.: 22 mi. W. of Lincoln. AMNH. **IDAHO**. Clearwater Co.: Kelly Creek Ranger District. Shoshone Co.: Mullan; Wallace. **MONTANA**. Mineral Co.: Cabin City. Missoula Co.: Miller Ck.; Martina nr. Stark. **WASHINGTON**. Ferry Co. (locality illegible). B.C. Prov. Mus.: **BRITISH COLUMBIA**. Lac la Hache; Williams Lake. CDF Coll.: **BRITISH COLUMBIA**. 70 Mile House; Big Bar Lake Prov. Park; Kettle River, Rock Creek Prov. Park. **IDAHO**. Boundary Co.: vic. Moyie Springs. **WASHINGTON**. Pend Oreille Co.: MP 6-7 FR 4300, Colville NF.

Records only. **BRITISH COLUMBIA**. Elko. **MONTANA**. Flathead Co.: Doris Ck.; Mi. 2-3 Red Meadow Ck. Rd. from jct. North Fork Rd., 25.vi.88. Lake Co.: Rollins, 6.vii.76, 23.vii.85; Simmons Meadow, Swan River State Forest, 6.vii.83; W. side of Flathead Lake. Lewis & Clark Co.: nr. Lincoln, 16.vii.76; nr. Marysville, 13.viii.75. Lincoln Co.: Meadow Peak L.O. rd. E. Happys Inn, 6.viii.86; West Fisher River Rd. S. Libby, 22.vi.79. Mineral Co.: Nr. St. Regis, 6.vii.73, 7.vii.77; St. Regis, 5.vii.72, 24.vii.73, 22.vii.80, 11.viii.81. Missoula Co.: 9-Mile Ck., several years 3.vii-18.viii; Albert Ck. nr. Frenchtown, 1.vii.82; Blue Mtn. Rd. nr. Missoula, 11.viii.75; Bulter Ck. off 9-Mile Rd., 8-9.vii.77; Cottonwood Lakes 10 mi. E. Seeley Lake, several years 9.vii-10.viii; Hwy. 209, 16 mi. N. Seeley Lake, 29.vii.72; vic. Lolo, 5.vii.75; Lolo Ck.-Elk Meadows Rd., 17.vii.81; Miller Ck., several years 4.vii.-23.viii; Missoula, 14.vii.66; nr. Frenchtown, several years 30.vi-6.vii; Pattee Canyon, several years 9.vii-7.viii; Seeley Lake, 13.vii.81; Worden Ck. N. Lolo, several year 6-12.viii. Park Co.: Aldrich. Pondera Co.: Pike Ck. Rd. Powder River Co.: 4 mi. W. Ridge, 19.viii.84.

Ravalli Co.: 3-Mile Ck. nr. Florence, 24.vii.82; 8-Mile Ck., Florence, several years 26.vi-27.viii; Bass Ck., several years 26.vi-27.viii; nr. Skalkaho Pass, 12.viii.81; Railroad Ck. off Skalkaho-Rye Rd., 24.vii.80; Skalkaho Hwy., 25.vii.74; Sweeney Ck., 7.vii.72; Woodchuck Ck., Florence, several years, 11.vii-22.viii. Sanders Co.: 4.1 mi. NE Plains, 9.vii.65; Baldy Mtn. nr. Plains, 3.viii.69; Mud Ck., 16.vii.67, 15.vii.70. **WASHINGTON.** Okanogan Co.: Moses Meadows, 27.vii.91.

Colias alexandra clines. (170). AME: **OREGON.** Baker Co.: Cave Creek, Durkee; Pine Ck. Crook Co.: Lost Forest Camp; Ochoco Lake St. Pk. Lake Co.: Ana Reservoir. **UTAH.** Carbon Co.: Grassy Tr. Ck., Tavapulis Plateau. Grand Co.: 3 mi. W. of state line on Gateway-Castleton Rd. Piute Co.: Hwy. 93 1 mi. W. of Junction; 8 mi. W. of Marysvale. San Juan Co.: Brumley Ridge; N. side Abajo Mtns.; Buckboard Flat, Abajo Mtns.; S. side Abajo Mtns. Sevier Co.: Monroe; Paradise Valley. Tooele Co.: Bennion Ck.; Settlement Canyon; Sheeprock Mtns.; S. Willow Ck., Stansbury Mtns. Wasatch Co.: nr. Keatly. **WASHINGTON.** Spokane Co.: Mt. Spokane. AMNH: **MONTANA.** Cascade Co.: Great Falls ("alba" ♀♀ of the prairie type). **OREGON.** Baker Co.: (no locality). Gilliam Co.: Condon. Harney Co.: Frenchglen; Steens Mtns. Jefferson Co.: Warm Springs. Wallowa Co.: vic. Joseph. ? Co.: Anthony Lake, Blue Mtns. **UTAH.** Sanpete Co.: 33 mi. NW of Huntington. Tooele Co.: Stockton. CDF Coll.: **CALIFORNIA.** Lassen Co.: vic. Blue Lake. Modoc Co.: vic. Emmerson Peak on Crestline Trail. **COLORADO.** Moffat Co.: Co. rd. 17 at MP 5.5. **IDAHO.** Lemhi Co.: Gilmore town site; Jakes' Canyon, Bitterroot Range; Spring Ck. Canyon, Lemhi Range. Twin Falls Co.: Magic Hot Springs rd. 0.3 mi. S. Shoshone Basin rd. **OREGON.** Grant Co.: Vic. Blue Mtn. Summit, Malheur NF; Vic. jct. FR 3940 and FR 016; Fields Creek Rd., Malheur NF; Murderer's Creek Work Center, Malheur NF. Harney Co.: FR 2820, Malheur NF. SR 205, MP 47 N of Frenchglen. Wheeler Co.: FR 2600/600, Ochoco NF. NSM: **NEVADA.** Elko Co.: Jarbidge Mtns.; Pequop Mtns.; Ruby Valley; Washoe Co.: Fox Mtn., Granite Range, various localities.

Records only. **UTAH.** Box Elder Co.: Clear Ck., Raft River Mtns., 25.vi.76. Utah Co.: Hobble Ck. **WASHINGTON.** Asotin Co.: Blue Mtns.; Field Spring State Park, 4.vi.66. Grande Ronde R., 10 mi. SW Anatone, 28.viii.75; Grande Ronde R. and Snake R., 31.vii.75. Kittitas Co.: Boyleston, 16 mi. ESE Ellensburg, 17.vi.66; Coleman Ck., 8.2 mi. SW Colockum Pass, 20.v.66; Ellensburg, Johnson Canyon, 8.8 mi. ESE Kittitas, 30.iv.58, 12.vii.69; McPherson Canyon, 23.vi.84; Schnebly Coulee, 5 mi. WNW Vantage, 17.v.58, 10.vi.81; Sentinel Gap, W. side bench, 14.viii.83; Tamarack Spgs., 8.2 mi. SE Cle Elum, 7.vii.65; Umtanum Ck. mouth, Yakima Canyon, 24.viii.83, 23.vi.84; Vantage, 24.v.66; Yakima R. Canyon, 10.vi.84. Klickitat Co.: Brooks Memorial State Park, 2 mi. SSW Satus Pass, 6.vii.59; 2 mi. S. Goldendale, 20.v.70; Goodnoe Hills, 6.vii.28; Kusshi Ck. Hwy. 97 at Yakima Co. line, 18,24.v.63; 8.v.66, 23.v.71; Satus Pass, 17.vi.66, 12.vii.66.

Colias pseudochristina(251). CDF Coll: **IDAHO.** Elmore Co.: Rattlesnake Creek area, Boise NF; Vic. N. Fork of Long Gulch, Boise NF [both of these areas were subsequently completely destroyed by a severe forest fire in August, 1992]. Franklin Co.: Birch Creek E of Mink Creek, Cache NF; Williams Creek Trail, Cache NF. **UTAH.** Summit Co.: N. Fork Provo River, Wasatch NF. Wasatch Co.: FR 029 W of Strawberry Reservoir, Uinta NF. J. S. Nordin Coll: **UTAH.** Summit Co.: Hwy. 150, 1 mi. N. of Stillwater Camp, 8600′.

Records only. **OREGON.** Wallowa Co.: Imnaha Valley, 14.vi.88 (P. C. Hammond & D. V. McCorkle). **UTAH.** Weber Co.: Wolf Ck., N. of Eden., 20.vi.82.

Colias christina astraea (44). AME: **MONTANA.** Cascade Co.: Great Falls; Monarch. **WYOMING.** Yellowstone N.P.: various localities. AMNH: **MONTANA.** Cascade Co.: Great Falls. Gallatin Co.: Elkhorn Ranch. Meagher Co.: Kings Hill; 12 mi. S. Neihart. Powell Co.: Rock Creek Lake. **WYOMING.** Big Horn Co.: Big Horn Mtns.; 5-spring Ck. Park Co.: Beartooth Mtns.; 13 mi. SE Cooke City, MT; 25 mi. W. of Wapiti. Sheridan Co.: 13-15 mi. SW of Big Horn. Sublette Co.: Clear Ck. Valley, Wind River Mtns.; Little Sheep Mtn.; Lower Green River Lake. Yellowstone N.P. LACM: **MONTANA.** Cascade Co.: Dearborn Canyon, Great Falls. Stillwater Co.: Alpine. "Continental divide West of Yellowstone Park".

Records only. MONTANA. Beaverhead Co.: nr. Lemhi Pass, 20.vii.82. Big Horn Co.: Pryor Mtns., 14.viii.86. Carbon Co.: Mt. Inabnit nr. Red Lodge, 30.vii.74; Rosebud Valley, Beartooth Range, 16.vii.66. Cascade Co.: Little Belt Mtns., 10.viii.75; 2 mi. N. of Monarch. Deer Lodge Co.: Georgetown Lake and Hills N. of, 11-12.vii.85. Fergus Co.: Crystal Lake Rd., Big Snowy Mtns., 23.ix.75; Judith Mtns.; Little Snowy Mtns., 21.vii.75, 13.vii.76. Gallatin Co.: Owl Canyon, 20, 30.vi.28. Meagher Co.: Butterfly Springs, Little Belt Mtns.; Porphyry Peak, Little Belt Mtns., 8.viii.87; 12 mi. N. of White Sulphur Springs. Pondera Co.: Pike Ck. Rd., 10.vii.86. Powell Co.: MacDonald Pass, 29.vi.86; Rock Ck. Lake, several years 1.vii-1.ix. Silver Bow Co.: E. of Feeley below Highland L.O., 24.vii.86; bog E. of Feeley, 10.vii.85; Divide Ck. SW Butte Humbug Mtn. and mtns. E. of Feeley, 10.vii.85. Stillwater Co.: Nr. Benbow Mine, 31.viii.871; Rosebud Valley Beartooth Range, 16.vii.66. Sweet Grass Co.: Fish Ck.; Swamp Ck. Rd., several years 29.vi-13.viii. Teton Co.: 22.viii.79. Yellowstone Co. **WYOMING**. Park Co.: Dead Indian Hill.

Colias christina christina. (1). CDF Coll.: **BRITISH COLUMBIA**. Boya Lake Prov. Park, 12.vii.91.

Records only. **ALBERTA**. Altario; Blackfalds; Blackfoot Coulee; Brownvale; Beaverlodge; Bistcho Lake; Boss Hill; 35 km N. of Bear Canyon; Crimson Lake Provincial Park; Dry Island Buffalo Jump Prov. Park; Edmonton; Elkwater; Elkwater Lk.; Ft. MacKay; Ft. McMurray; Ft. Smith 13 km SE of Ft. Smith; 11 km N. of Fairview; 10 km W. of Ft. McKay; Fabyan; Indian Cabins; Kinsella; Lloydminster; 25 km S. of Manning; Mildred Lake; Mirror; Mildred Lake; Neutral Hills nr. Gooseberry Lake; 19 km E. of Northstar; Olds; Pine Lake; Pine Lake Rd. 7 km N. of Wood Buffalo Nat. Park; Red Deer; Shell Pit; Smith Portage; Stoney Mtn.; nr. Scollard; nr. Stettler; Sandhill Lake; Twin Lakes Cpgd.; Tulliby Lake; 35 km SW of Turner Valley; Wallaby Lake; Winfield; Wabasca River & Hwy. 67; 20 km W. of Zama ÇIty; 22 km SW of Zama City. **BRITISH COLUMBIA**. Dunlevy Rec. Area nr. Hudson's Hope; Prophet River Cpgd., Alaska Hwy. **NORTHWEST TERRITORIES**. Hwy. 3, km 158.

Colias christina cline (15). AME: **MONTANA**. Glacier N.P. AMNH: **MONTANA**. Glacier N.P.

Records only. **ALBERTA**. Indian Grave campground area; Kananaskis Provincial Park. **MONTANA**. Glacier Co.: 6 mi. NW Babb, 14.vii.87; St. Mary, 28.vi.66.

Records only. ALBERTA. Hwy. 11 at Abraham Lake; Adam's Ck. & Berland Riv.; Adam's L.O.; Adanac Summit; Mt. Allan; Allison Lake; Athabasca L.O.; Bald Hills; Banff; 18 & 32 km W. of Banff; Baril Ck.; Barkhead, Banff Nat. Park; Cascade Rd., Banff Nat. Park; Barrier Res.; Beauvais Lake; Beaver Ck.; Beaver Mines Lk.; Hwy. 5 at Belly River; Berland Riv.; Hwy. 11 at Bighorn Riv.; Blackstone Riv. & Hwy. 940; Blairmore; nr. Bottrel; Boulton Ck.; Bow Valley Prov. Park; Bragg Ck.; Brown Ck.; Burke Ck.; Burnt Timber Ck.; Burnt Timber L.O.; Cabin Ck. & Hwy. 940; Cadomin; Cadomin Cave; Cadomin Mtn.; Calgary; 8 km NW of Calgary; 32 km SE of Calgary; Caneron Lk.; Canmore; Cardinal Divide; Canyon Ck.; Carbondale River; Cardinal Riv. Rec. Area; Cat. Ck.; Cataract Ck.; Chain Lk. Res.; Chief Mtn. Rd. & Belly Riv.; Chinook Ridge; Clearwater Ranger Sta.; Cline River at Hwy. 11; Coalspur; Coalspur Rd. & Hwy. 940; Coalspur Rd., 6 km W. Cardinal Riv. Rec. Area; Cochrane; Coleman; Crimson Lk.; Elbow Ranger Sta.; Elbow Riv. in Bow/Crow Forest; Jct. Elbow Riv. & Little Elbow Riv.; End Mtn.; Entrance; Etherington Ck.; Exshaw; Flat Ck.; Ft. Macleod; Frank; Fred Ck.; The Gap, Oldman Riv.; Ghost Riv.; Graves Flat L.O.; Grizzly Valley; Hailstone Butte; 2 km E. of Hailstone Butte; Hand Hills; Jct. Highwood Rd. & Kananaskis Rd.; Highwood Ranger Sta.; Hillcrest; Hillspring; Hinton; 12 km W. of Hinton; Horn Ridge; Igloo, W. of Palliser Range; Indian Grave Cpgd.; Indian Reserve 148A; Jasper; Johnsons Canyon; Jumping Pound Ck. nr. forest reserve boundary; Kananaskis Forest Exp. Sta.; Jct. Kananaskis Rd. & Highwood Rd.; Kananaskis Rd. at Oldman Riv.; Lower Kananaskis Lk.; Upper Kananaskis Lk.; King Ck.; Kootenay Plains; Lake Louise [Laggan]; Lethbridge; Little Elbow Riv. Rd.; Longview; Lundbreck; Luscar L.O.; Lust Ck.; Lynx Ck.; Maclean Ck.; Magrath; Marmot Basin; Meadow Ck.; Millarville; Moose Mtn.; Mt. Hamell; Mt. Head; Morley; Mountain Park; Muskiki Lk.; Nigel Ck.; Nordegg; North Milk Riv. & Hwy. 501; North Saskatchewan Riv. & Hwy. 940; Oldman Riv. AFS Cpgd.; Upper Oldman Riv.; Onion Ck.; Onefour; Panther Riv.; Picklejar Ck.; Pigeon Mtn.; Plateau Mtn.; Pine Ck.; Pocahontas; Police Outpost Prov. Park; 6 km NE of Police Outpost Prov. Park; Pope Thoreau Pass Trail; 3 km N. of Porcupine Hills Ranger Sta.; 16 km W. of Pulteney; Prospect Ck. & Coalspur Rd.;

Racehorse Ck. at Oldman Riv.; Ram Mtn.; Raymond; Redcap Mtn.; Red Deer Riv. W. of Hwy. 940; Ribbon Ck.; 10 km NE of Robb; SW of Robb; 29 km E. of Rock Lk.; Rock Lk.; Rock Lk. Rd. & Moberly Rd.; Saracen Head; Saskatchewan Riv. Crossing; Savannah Ck.; Seebe; S. of Seebe; 6 km SE of Seebe; Sharpless Ck. Rd.; Shaw; Sheep Riv.; Shunda Mtn.; Signal Mtn.; Skyline Rd.; Seven Mile Flats; Snow Ck.; South Willow Ck.; St. Mary Rd., 13 km SW of Lethbridge; nr. Standard; Sulphur Mtn.; Sundance Canyon Rd., Banff Nat. Park; nr. Sundre; Thelma; Trap Ck.; Tripoli Mtn.; 25 km SW of Turner Valley; 8 km SW of Twin Butte; 19 km W. of Twin Butte; Vermilion Pass; Waterton Lk. Nat. Park; Watson Ck. Cpgd.; West Castle Riv.; Whiskey Gap; 8 km NE of Whiskey Gap; Whitehorse Ck. Cpgd.; Wileman Ck.; Wilkinson Ck.; William A. Switzer Prov. Park; Wilcox Pass; Windsor Mtn.; Windy Point & Hwy. 11; **MONTANA**. Glacier Co.: Looking Glass Hill vic. Two Medicine Lakes, 14, 21.vii.85 (♂♂ mixed yellow to orange, 1 "alba" ♀); 1.55 mi. on Pike Ck. Rd., S. of Morias Pass, 10.vii.86, "alba" ♀♀; Mission Lake, 26.vii.87, "alba' ♀♀.

Colias krauthii krauthii (99). AME: **SOUTH DAKOTA**. Jackson Co.: Kadoka, 2450', 26.vii.58. CDF Coll.: **SOUTH DAKOTA**: Lawrence Co.: FR 108, Black Hills NF; T3N R1E S29, 32-34. Pennington Co.: FR 111, Black Hills NF. **WYOMING**: Crook Co.: Bear Lodge Mtns., FR 838-1A, Black Hills NF; FR 807 & 808, Black Hills NF. Weston Co.: Mallo Camp road.

Records only. **SOUTH DAKOTA**. Custer Co.: 1 mi. S. Limestone Hill, 24.vi.88; Boles Canyon, 24.vi.88; Hell Canyon nr. Jewel Cave, 8.vii.89. Fall River Co.: 2.5 mi. W. of Hot Springs. Lawrence Co.: Side canyons W. of Spearfish; Little Spearfish Canyon, 9.vii.86; ONeil Pass, 21.vii.82, 26.vi.87; nr. Black Fox C.G., 12.vii.86; 2 mi. SW Dumont, 14.vii.84. Pennington Co.: Jct. Hwy. 284 and Ice Cave Rd., 25.vi.78; Horseshoe Ck., 4.vii.85; Deerfield Lake, 5.vii.85; 7 mi. S. Deerfield Lake, 23.vi.88. **WYOMING**. Weston Co.: Hwy. 85 at South Dakota state line.

Colias krauthii kluanensis (8 + slides). ALS/K. W. Philip Coll.: **ALASKA**. Nabesna Rd., 7 mi. NNW Nabesna at Jack Ck., 2900', 62°28'N, 143°06'W, 3.viii.86; (color slides examined) Nabesna Rd. at mi. 28.5, Jack Creek, and Trail Creek, 10.vii.89. **YUKON TERRITORY**. (Color slides examined) Lake Laberge, 8.vii.89; Alaska Hwy. at Burwash Creek, and mi. 1167 on 9.vii.89. NSM: **YUKON TERRITORY**. Alaska Hwy., mi. 995.2; mi. 1167. Misc. Sources: **YUKON TERRITORY**. Kluane, Donjek River and Glaciers, Alsek River; Lake Laberge.

Records only. **YUKON TERRITORY**. Bates River ca. 10 mi. below Bates Lake; toe of the Donjek Glacier; Duke River at mouth of Grizzly Creek; Braeburn Lake.

Colias occidentalis occidentalis. (538) AME Coll.: **WASHINGTON**. Thurston Co.: Tumwater Recreation Area. CDF Coll.: **OREGON**. Crook Co.: FR 3350/200, Ochoco NF; FR 2160, Ochoco NF; FR 42[00]/206. Wheeler Co.: FR2600/600 & FR 2600/700, Ochoco NF. **WASHINGTON**. Kittitas Co.: Porky Basin Rd. off Hwy. 97.

Records only. **BRITISH COLUMBIA**. Mainland: Aspen Grove; Field; N. of Lytton; S. of Lytton; Princeton; Dry Lake 10 mi. W. of Princeton; Strathcona Park. Vancouver Island: Bevan; Bowser; Comox: Courtenay; Duncan; Goldstream; Malahat; Mt. Benson; Mt. Prevost; Mt. Tzuhalem; Nanaimo Lake; Oyster River; Pt. Holmes; Quamichan Lake; Royal Oak; Saratoga Beach; Shawnigan Lake; Spectacle Lake; Tod Inlet; Victoria; Wellington. **OREGON**. Crook Co.: Crystal Creek, Ochoco NF. Umatilla Co.: McKay River along Meacham-Pilot Rock Rd.

Colias occidentalis chrysomelas. (6) CDF Coll.: **CALIFORNIA**. Colusa Co.: Deafy Glade Trail, Potato Hill.

Records only. **CALIFORNIA**. Colusa Co.: Forest rd. 0.5 mi. W. of Deafy and Lade Trail; Mill Valley; vic. Letts Lake; Goat Mtn. Summit to to ridge 13 air mi. WSW of Ladoga. Glenn Co.: S. Fk. Elk Ck, Mendocino NF. Humboldt Co.: Bald Hills Rd. on French Camp Ridge; Cedar Flat Rd. Lake Co.: Vic. Bear Ck. Guard Sta. 15 air mi. N. of Clear Lake. Mendocino Co.: Hull Mtn. Rd, 3 mi. S. of Bald Mtn. Tehama Co.: Covelo Rd. vic. N. rim of Grindstone Canyon. Shasta Co.: Anderson Springs Ridge, Shasta-Trinity Divide, 8 air mi. N. of Hwy. 36 at Harrison Gulch Guard Sta. Siskiyou Co.: Salmon forest rd. vic. Eddy Gulch L.O., Klamath NF; I-5 at headwaters of Sacramento River, Shasta Meadows, Mt. Shasta; N. Fk. Salmon R., vic. Little N. Fk. C.G. Trinity Co.: S. Fk. Mtn. Rd. vic Windy Nip. 10 mi. N. Hwy. 10.

Colias occidentalis cline. Records only. **OREGON**. Jackson Co.: Soda Mtn., T40S, R3E, S16, 21, 28, 28.vi.86; Baldy Ck. Rd., T40S, R3E, S7, 17, 18, 30.vi.91; Burnt Ck. Rd., T38S, R3E, S31, 32 and T39S R3E, S6, 7, 1.vii.91.

Colias hybrid or plesiomorphic form ? (1). Non-UV-reflective orange imago with *occidentalis* pattern and wing shape. **OREGON**. Crook Co.: W. divide, Canyon Ck. Rd., 27.vii.78, 1♂.

Records only. **OREGON**. Crook Co.: Crystal Ck., Ochoco NF, 18.vii.67, 1♂.

Colias johanseni (5). **NORTHWEST TERRITORIES**. Bernard Harbour.

Additional material as noted in main text.

Colias canadensis (24). CDF Coll.: **ALASKA**. Murphy Dome N. of Fairbanks, 11-13.vi.91; Wickersham Dome, mile 28 Hwy. 2, 16.vi.91; mile 113 Dalton Hwy., 17.vi.91.

Colias hecla hecla (146). CDF Coll.: **ALASKA**. North Slope localities along the Dalton Hwy. including Ice Cut, Oil Spill Hill, Toolik Lake, and 30 mi. S. of Prudhoe Bay opposite N. end of the Franklin Bluffs, 22.iv-8.vii.91.

Colias nastes aliaska (159). CDF Coll.: **ALASKA**. North Slope localities along the Dalton Hwy. including Ice Cut, Oil Spill Hill, Toolik Lake, and 30 mi. S. of Prudhoe Bay opposite N. end of the Franklin Bluffs, 22.iv-8.vii.91.

Colias philodice vitabunda (85). CDF Coll.: **ALASKA**. North Slope localities along the Dalton Hwy. including Ice Cut, and Oil Spill Hill, 22.iv-5.vii.91.

Colias philodice clinal form. (3) CDF Coll.: **BRITISH COLUMBIA**. Boya Lake Prov. Park, 5.vi.91, 12.vii.91.

Colias boothii (27). CDF Coll.: **ALASKA**. North Slope localities along the Dalton Hwy. including Happy Valley, Ice Cut, Oil Spill Hill, and Toolik Lake, 22.vi-8.vii.91.

Summary of State/County Records by Species

Colias alexandra. **ARIZONA**. Apache, Coconino, Gila, Graham, Greenlee, Mohave, Navajo. **CALIFORNIA**. Kern, Lassen, Los Angeles, Modoc, Mono, Nevada, Orange, Plumas, San Diego, San Luis Obispo, Santa Barbara (includes Santa Cruz Is.), Sierra, Tulare, Ventura. **COLORADO**: Arapahoe, Archuleta, Boulder, Chaffee, Clear Creek, Conejos, Costilla, Custer, Delta, Denver, Dolores, Douglas, Eagle, Elbert, El Paso, Fremont, Garfield, Gilpin, Grand, Gunnison, Hinsdale, Huerfano, Jackson, Jefferson, Lake, La Plata, Larimer, Las Animas, Mesa, Moffat, Montezuma, Montrose, Ouray, Park, Pitkin, Pueblo, Rio Blanco, Routt, Saguache, San Juan, San Miguel, Summit, Teller, Weld. **IDAHO**. Ada, Bingham, Blaine, Bonner, Boundary, Butte, Camas, Canyon, Cassia, Clark, Clearwater, Custer, Franklin, Fremont, Idaho, Jefferson, Kootenai, Latah, Lemhi, Nez Perce, Oneida, Owyhee, Shoshone, Twin Falls. **MONTANA**. Carter, Cascade, Daniels, Flathead, Gallatin, Judith Basin, Lake, Lewis and Clark, Liberty, Lincoln, Mineral, Missoula, Pondera, Powder River, Ravalli, Sanders, Toole, Wheatland. **NEBRASKA**. Banner, Box Butte, Dawes, Scotts Bluff, Sioux. **NEVADA**. Carson City, Churchill, Clark, Douglas, Elko, Esmeralda, Eureka, Humboldt, Lander, Lincoln, Lyon, Mineral, Nye, Pershing, Storey, Washoe, White Pine. **NEW MEXICO**. Catron, Colfax, Grant, Los Alamos, McKinley, Rio Arriba, Sandoval, San Miguel, Santa Fe, Sierra, Taos, Torrance. **NORTH DAKOTA**. Dunn, Slope. **OREGON**. Baker, Crook, Deschutes, Gilliam, Grant, Harney, Jefferson, Klamath, Lake, Malheur, Morrow, Sherman, Wallowa, Wheeler, Wasco. **SOUTH DAKOTA**. Custer, Fall River, Jackson, Pennington. **UTAH**. Beaver, Box Elder, Cache, Carbon, Daggett, Davis, Emery, Garfield, Grand, Iron, Juab, Kane, Morgan, Piute, Rich, Salt Lake, San Juan, San Pete, Sevier, Summit, Tooele, Uintah, Utah, Wasatch, Washington, Wayne. **WASHINGTON**. Asotin, Benton, Columbia, Douglas, Ferry, Franklin, Garfield, Grant, Kittitas, Klickitat, Lincoln, Okanogan, Pend Oreille, Spokane, Stevens, Whatcom, Whitman, Yakima. **WYOMING**. Albany, Campbell, Carbon, Converse, Crook, Fremont, Laramie, Natrona, Niobrara, Platte, Sublette, Sweetwater, Teton, Uinta, Weston, Yellowstone N.P.

Colias christina. **MONTANA**. Beaverhead, Big Horn, Carbon, Cascade, Deer Lodge, Fergus, Flathead, Gallatin, Glacier, Golden Valley, Jefferson, Lake, Meagher, Park, Pondera, Powell, Silver Bow, Stillwater, Sweetgrass, Teton, Yellowstone. **WYOMING.** Big Horn, Johnson, Park, Sheridan, Sublette, Teton, Yellowstone N.P.

Colias krauthii. **SOUTH DAKOTA.** Custer, Fall River, Lawrence, Meade (needs verification), Pennington. **WYOMING.** Crook, Weston.

Colias pseudochristina. **IDAHO.** Adams, Boise, Elmore, Franklin, Idaho, Lemhi, Nez Perce. **OREGON.** Wallowa. **UTAH.** Rich, Salt Lake, Sevier, Summit, Utah, Wasatch, Weber. **WASHINGTON.** Asotin.

Colias occidentalis. **CALIFORNIA.** Colusa, Glenn, Humboldt, Lake, Lassen (dubious *fide* S. O. Mattoon), Mendocino, Napa, Santa Cruz (probably erroneous, *fide* J. F. Emmel), Shasta, Siskiyou, Sonoma, Tehama, Trinity. **OREGON.** (?)Baker, Clackamas, Crook, Douglas, Grant, Jefferson, Lane, Marion, Umatilla, (?)Wallowa, Wasco, Wheeler, Yamhill. **WASHINGTON.** Chelan, Clallam, Clark, Jefferson, Kittitas, Klickitat, Mason, Okanogan, Pierce, Skagit, Skamania, Thurston, Whatcom, Yakima.

Note on Dates of Publication

Article 23 (a) of the ICZN Code establishes the valid name of a taxon as the oldest (first published) name applied to the taxon. When two different names are given by different authors to the same taxon, then it becomes necessary to establish which name was published first, and thus has priority. The matter of priority was discussed succinctly by E. M. Aaron (1884) [see Literature Cited] regarding the priority of several W. H. Edwards names versus those published by Herman Strecker. In summary, the date of publication of a name is not the printed date on a paper, but the mailing date that the publication is sent to subscribers. The actual mailing date of Bulletin no. 128 (which carries the description of *C. psuedochristina* Ferris) of the Allyn Museum of Entomology is the imprinted date of 22 May, 1989. The Bulletin was printed prior to the mailing date. The imprinted date of Utahensis 8(4) (which carries the description of *C. occidentalis wasatchia* Gillette) is 17 May, 1989, and is apparently the only issue of Utahensis to carry an imprint date.

To determine the date of distribution of Utahensis 8(4), numerous university and museum libraries were contacted in an attempt to locate one that date-stamps the date of reception on individual journal issues. Through the assistance of these librarians and entomological staff, it was established that copies of this issue of *Utahensis* were received or hand delivered in mid-June (June 18th forward) or early July 1989, but none of these was date-stamped. Cornell University was the only library which could be located which subscribes to Utahensis and also date-stamps journals. The date of receipt, however, was well over a year after the imprinted date of issue.

Based upon the above information and the fact that it has not been possible to verify the actual mailing date of publication for the name *wasatchia* Gillette, it is presumed here to be a junior synonym of *pseudochristina* Ferris.

This public document was promulgated at a cost of $3846.61 or $5.50 per copy. It makes available to libraries, scholars and all interested persons the results of researches in Entomology.