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A REVISION OF THE *COLIAS ALEXANDRA* COMPLEX (PIERIDAE) AIDED BY ULTRAVIOLET REFLECTANCE PHOTOGRAPHY WITH DESIGNATION OF A NEW SUBSPECIES[1]

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This paper presents a study of the distribution and taxonomy of the *Colias alexandra* complex. The role of ultraviolet photography as an aid to taxonomic studies is discussed and is employed in assigning *C. alexandra* populations to various color groups. Visible light characters (pigmentation and facies) are combined with uv reflectance patterns to arrive at the taxonomic conclusions presented. One concludes from this study that some populations of *alexandra* can be assigned to specific subspecies, while others are best listed as clinal or intergrade forms. Based upon uv photography, *C. harfordii* and *C. barbara* are assigned to the *alexandra* complex. As a consequence of recent work by Brown (1973), a new subspecies of *alexandra* is proposed.

Butterfly color patterns are produced by both pigmentation and optical effects. The brilliant prismatic colors associated with many tropical species are produced by visible light interference with the structures of certain wing scales. As shown by Mazokhin-Porshnyakov (1954) and Nekrutenko (1964), certain Coliadinae reflect ultraviolet light from particular wing areas such that interference patterns are produced.

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Ghiradella, Eisner, Hinton, and Silberglied (pers. comm. and in review) have determined that these uv reflection patterns are structural and are analogous to the white-light-produced brilliant irridescent blues in the genus *Morpho*. Silberglied (pers. comm.) has shown that interference of uv light rays in the layered lamellae which comprise the ribs of special wing scales is responsible for the "luminous" patches shown in the accompanying figures. Close spacing of the ribs is indicative of strong uv reflection.

Kolyer & Reimschuessel (1969) reported some scanning electron microscope studies of *Colias eurytheme* Boisduval but did not interpret the structure of the scales. The lamellae are shown in Figs. 2c & d of their paper. A simple method for making uv photographs has been described by Ferris (1972b).

Ultraviolet reflectance photography can be used as a taxonomic aid as suggested by Nekrutenko (1964). Some species of *Colias* are reflective; others are not. Reflection is used here in a relative sense and is applied to fresh undamaged specimens. There is always some reflection of uv light, but only certain species reflect sufficient energy to produce bright patterns. Reflection in *Colias* generally occurs from the discal areas (dorsal) of the secondaries and varies considerably for the primaries. Males of certain species are reflective, while the females of the North American species are non-reflective. Ultraviolet photography of the non-reflective species is of no taxonomic value except to separate reflective and non-reflective species in questionable cases.

Colias alexandra males exhibit a uv reflectance pattern which appears as a luminous patch on the secondaries and is constant in all of the color forms. The term "luminous" is used here to describe the appearance of the reflection pattern in a black-and-white photograph. The amount of reflectance from the primaries varies from insignificant in the pure yellow races to considerable in the orange races. Fig. 3 illustrates the features which separate *alexandra* from other North American *Colias*. Figs. 4–5 illustrate examples of *C. alexandra* as they appear under white light photography and uv photography. A dull background has been used purposely to eliminate spurious uv fluorescence.

Ultraviolet photography is used here to assign *alexandra* populations to various color groups. It shows that several populations which appear yellow to the human eye, exhibit uv interference patterns characteristic of the yellow-orange group. These populations are therefore placed with the yellow-orange group rather than with the "pure" yellow group. Uv photography cannot be used to make assignments at the subspecies level generally, although it does show that *C. barbara* and *C. harfordii* belong in the *alexandra* complex.

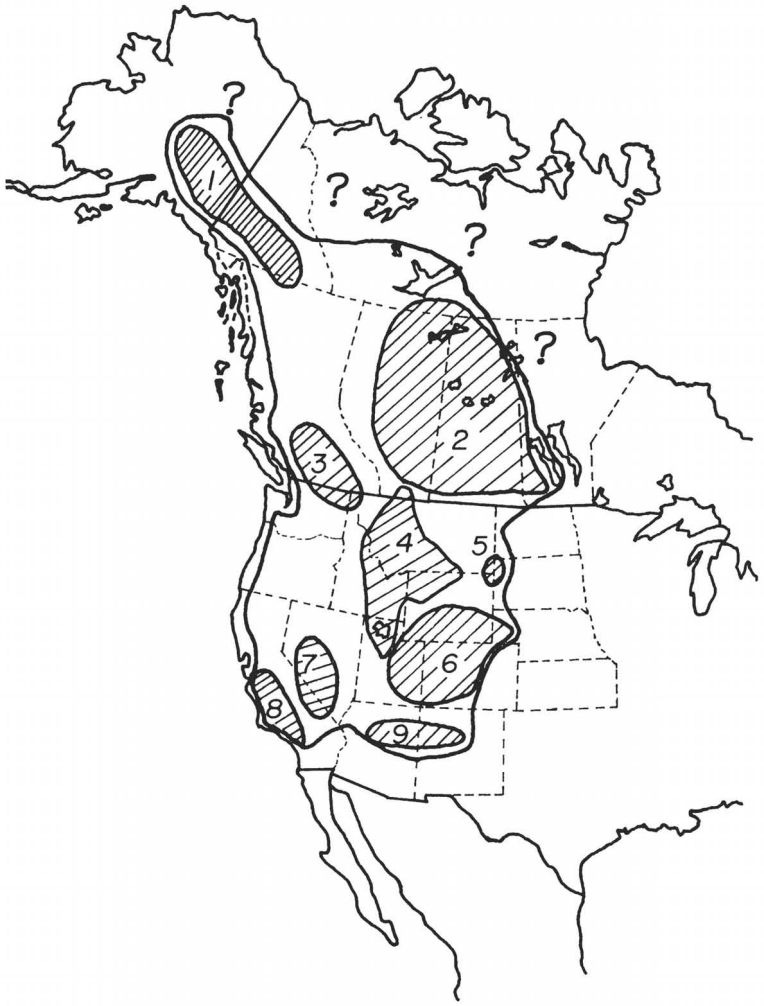


Fig. 1. Distribution of *Colias alexandra* in North America. The outer solid line encloses the known areas in which *alexandra* has been found. The northern boundary is still in doubt as indicated by (?). The shaded areas represent distinct subspecies as follows: 1, unnamed Alaska-Yukon segregate; 2, *christina*; 3, *columbiensis*; 4, *astraea*; 5, *krauthii*; 6, *alexandra*; 7, *edwardsii*; 8, *barbara* and *harfordii*; 9, Arizona-New Mexico segregate. The remaining areas within the boundary represent intergrade forms which cannot be clearly identified as any one given taxon.

Biology

The life histories of several members of the *alexandra* group have been published and are cited in Davenport & Dethier (1937). Larval food-plants are members of the Leguminosae. There is a paucity of specific

hostplant records in the literature, but these records include: *C. alexandra*: *Astragalus, Thermopsis, Trifolium repens* (Davenport & Dethier, 1937); *Astragalus serotinus* (Opler, unpublished); *A. miser* (Shields, et al., 1969). *C. christina*: *Trifolium* (Davenport & Dethier, 1937). *C. harfordii*: *Astragalus* (Davenport & Dethier, 1937); *A. antisellii* (Locoweed) (R. C. Priestaf, 1972, pers. comm.). Davenport & Dethier list additional authors who have reported hostplant preferences for *alexandra.*

Colias alexandra is found in a wide variety of habitats. Generally it frequents open areas, and in forested land is found in clearings and along roads or cuts. Males may be found at puddles along dirt roads where they sometimes congregate in large numbers. Some of the subspecies are common in open sagebrush regions (Upper Sonoran Desert), while others frequent the Transition Zone (aspen-conifer association), and still others are found in meadows or clearings in the Canadian Zone. In the Far North, *alexandra* appears to prefer open clearings in the taiga (spruce-scrub biome). Pigmentation in the adults does not appear to be correlated with habitat. To some extent, correlation with latitude exists, with more orange color appearing in the north.

Distribution and Taxa

The *C. alexandra* complex is widely distributed in western North America (Fig. 1). Three distinct color forms are recognized: yellow, yellow and orange, and orange, in addition to clinal forms in which specimens from a given geographic location vary from yellow into almost pure orange (Ferris, 1972a). Currently recognized taxa belonging to the *alexandra* complex are indicated below according to visible-light color (pigmentation).

YELLOW POPULATIONS—TAXA

Colias alexandra alexandra Edwards, 1863 [T. L. Front Range, west of Denver, Colorado].
Colias alexandra edwardsii Edwards, 1870 [T. L. Virginia City, Storey Co., Nevada].
Colias alexandra emilia Edwards, 1870 [T. L. Oregon]. See discussion below.

YELLOW-ORANGE POPULATIONS—TAXA

Colias alexandra astraea Edwards, 1872 [T. L. Yellowstone Lake, Wyoming].
Colias alexandra christina Edwards, 1863 [T. L. Slave River Crossing, N.W.T., Canada].

ORANGE POPULATIONS—TAXA

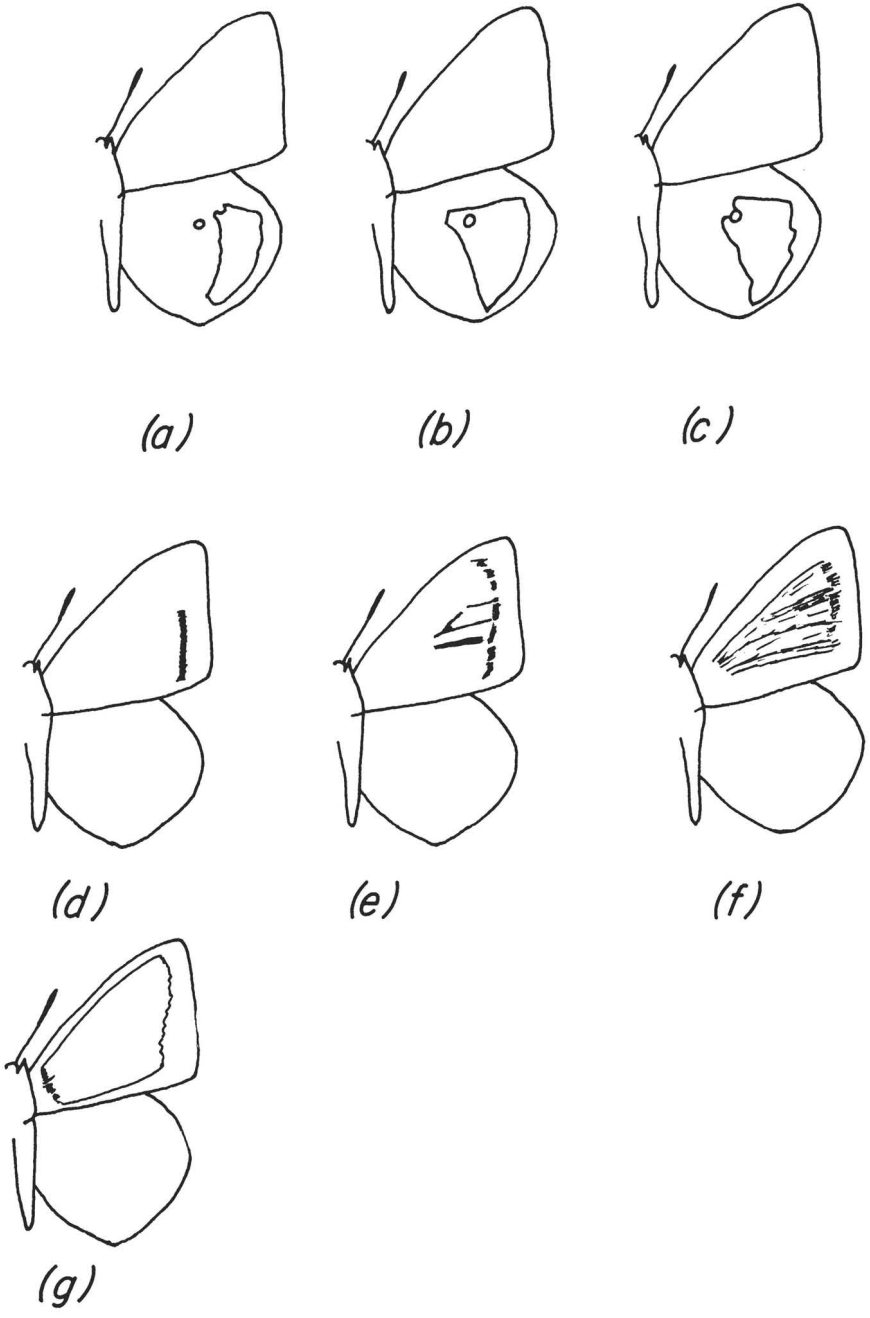
Colias alexandra krauthii Klots, 1935 [T. L. Black Hills, 12 miles west of Custer, Custer Co., South Dakota].

The taxon *alberta* Bowman has been omitted as it appears to describe a hybrid situation and suppression of this name has been recommended

Fig. 2. Distribution of *Colias alexandra* isolates. Open circles—yellow populations; half-open circles—yellow-orange populations; solid circles—orange populations.

(Ferris, 1972a). This and other possible *alexandra* crosses are discussed in the paper cited.

When long series of *alexandra* of a given subspecies or from a given locality are examined, one notices substantial variation in pigmentation and, in the females, maculation. Some individual males from yellow-orange races appear yellow under white light. When photographed under uv illumination, they exhibit luminous patches on the primaries which


(a)
(b)
(c)
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(f)
(g)

are characteristic of the yellow-orange group. In the current study, uv photography is used to assign various races or populations to one of the three designated color groups. Race or population should not be inferred as synonymous with subspecies. The uv patterns for each group are discussed below.

There is considerable variation in uv reflectance pattern as well as in pigmentation. The former is illustrated by the accompanying figures. Only *C. a. alexandra* and *C. a. krauthii*, the poles so-to-speak, exhibit minimal variation. The angle at which uv radiation strikes the wing surfaces affects the reflection pattern (Nekrutenko, 1965). If specimens are flat-mounted and illuminated as suggested by Ferris (1972b), this problem is minimized.

In the following paragraphs, reference is made to various isolated populations. These represent clinal and intergrade forms which do not merit subspecific recognition. Localities are shown in Fig. 2.

YELLOW POPULATIONS—DISTRIBUTION

Arizona, California, Colorado, Nebraska, Nevada, New Mexico, Oregon (isolate), Utah, Wyoming, Montana (?).

The yellow races are distinguished by lacking forewing luminosity (or exhibiting only a trace at most) under uv illumination and by having yellow (concolorous with the ground color) discal spots on the dorsal surface of the secondaries in the males. This definition differs from previous ones which included populations that have orange discal spots. Generally the orange-spotted specimens exhibit forewing luminosity.

YELLOW-ORANGE POPULATIONS—DISTRIBUTION

California, Idaho, Montana, Nevada (Elko, Nye, Washoe Cos.), Oregon, Utah, Washington, Wyoming, Alberta, British Columbia, Manitoba, Northwest Territories, Saskatchewan. Recently a single orange-discal-spotted male *alexandra* was collected by M. S. Fisher (Parker, Colorado) in Elbert Co., Colorado, an eastern plains region of the state. Further collecting is necessary to ascertain if this specimen is from a yellow-orange isolate with possible affinity to the Black Hills *krauthii*, or a hybrid with *philodice* or *eurytheme*. Undoubtedly other yellow-orange isolates, not shown in Fig. 2, will be found as collectors penetrate into little-collected areas.

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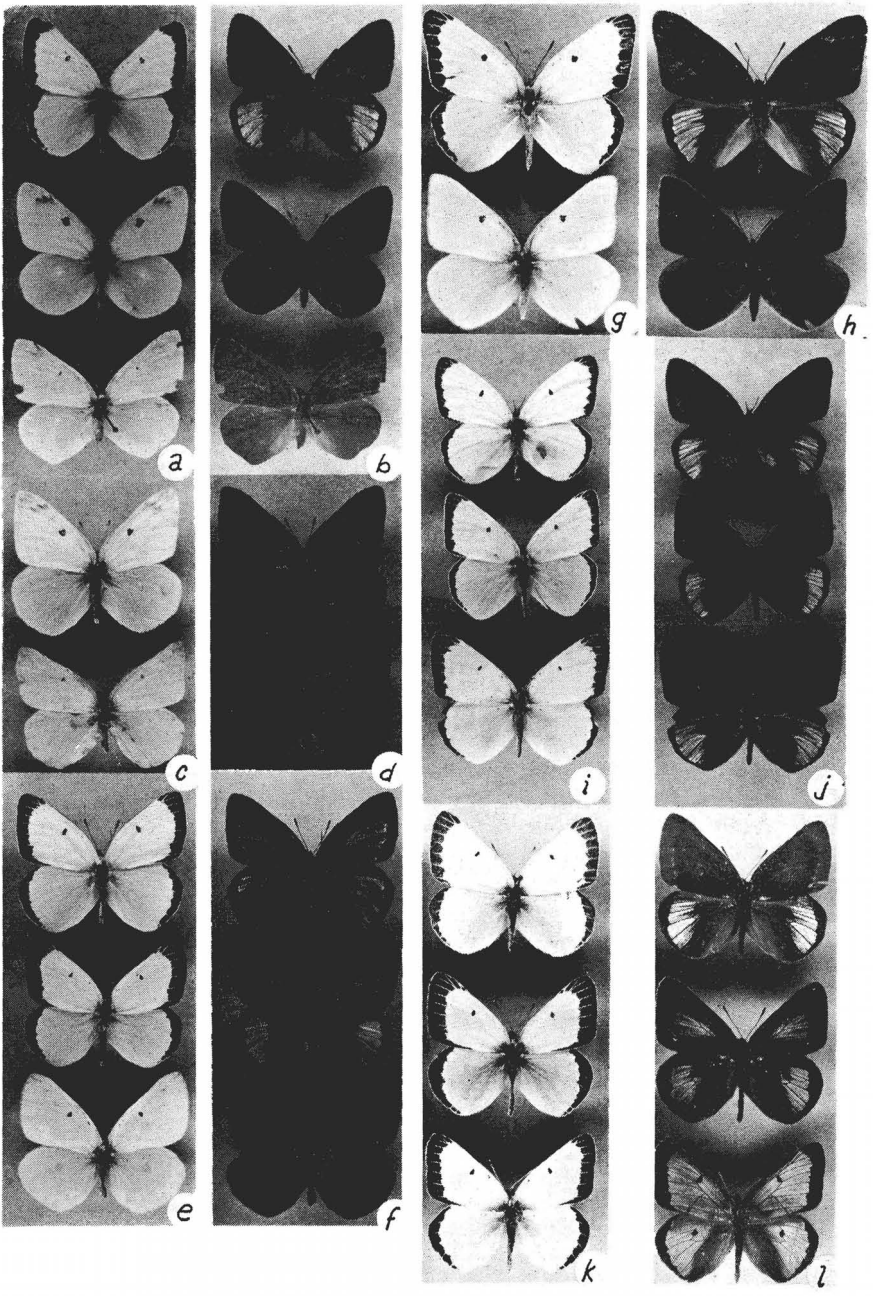
Fig. 3. General extent of luminous patches as they appear on the wings of the males in the *Colias alexandra* complex. Hindwing patches in (a) yellow group; (b) orange group; (c) yellow-orange group. The discal spots, shown as open circles, are generally black in uv photographs. Forewing patches in (d) transition yellow to yellow-orange populations (submarginal band); (e) some yellow-orange populations (submarginal band and portions of some cells near veins); (f) other yellow-orange populations (central portion of wing generally reflects with some dark areas); (g) orange populations (wing reflects almost uniformly except for marginal areas).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Some of the yellow-orange races appear yellow under visible light, except that the discal spot on the dorsal surface of the hindwings is orange. Individual male specimens may show a dark yellow or a pale yellow-orange flush discally and limbally on the upper side of the secondaries and females may exhibit considerable orange. Under uv illumination, luminous patches appear on the forewings. Individuals of *C. a. astraea* may appear to be pure yellow except for the orange discal spot, but this subspecies as a whole ranges from yellow to orange. For this reason, populations with orange discal spots in the males are classified in the yellow-orange group based upon uv patterns and not visible light (pigmentation) appearance.

Southern Alberta appears to represent a complex blend-zone region. In the area from Calgary to Banff and east of the Rocky Mountains, specimens can be taken which represent *alexandra, astraea, christina*, and *krauthii*. It is frequently possible to collect two or three good "subspecies" at the same locality. This situation is typical of the intergrading which occurs in the *alexandra* complex and is the reason for the restricted ranges shown in Fig. 1.

Northern Utah specimens, especially from Tooele and Wasatch Counties, tend toward both *astraea* (in the males) and *christina* (in the females). The latter frequently show an overwashed orange coloration.

Specimens of *alexandra* from Nevada have generally been determined to be subspecies *edwardsii*. A small series in the collection of the Los Angeles County Museum of Natural History taken by A. O. Shields in Jett Canyon, Toiyabe Range, Nye Co., Nevada is clearly from a yellow-orange population. The discal spots (dorsal secondaries) are orange in both sexes and distinct luminous patches show on the forewings of the males under uv light. Some specimens from the same locality are phenotypically *edwardsii*. Peter Herlan (Carson City, Nevada) has found yellow-orange populations in Elko and Washoe Counties as well. The occurrence of these isolates is as yet unexplained.

California specimens from Lassen (Blue Lake area, Warner Moun-

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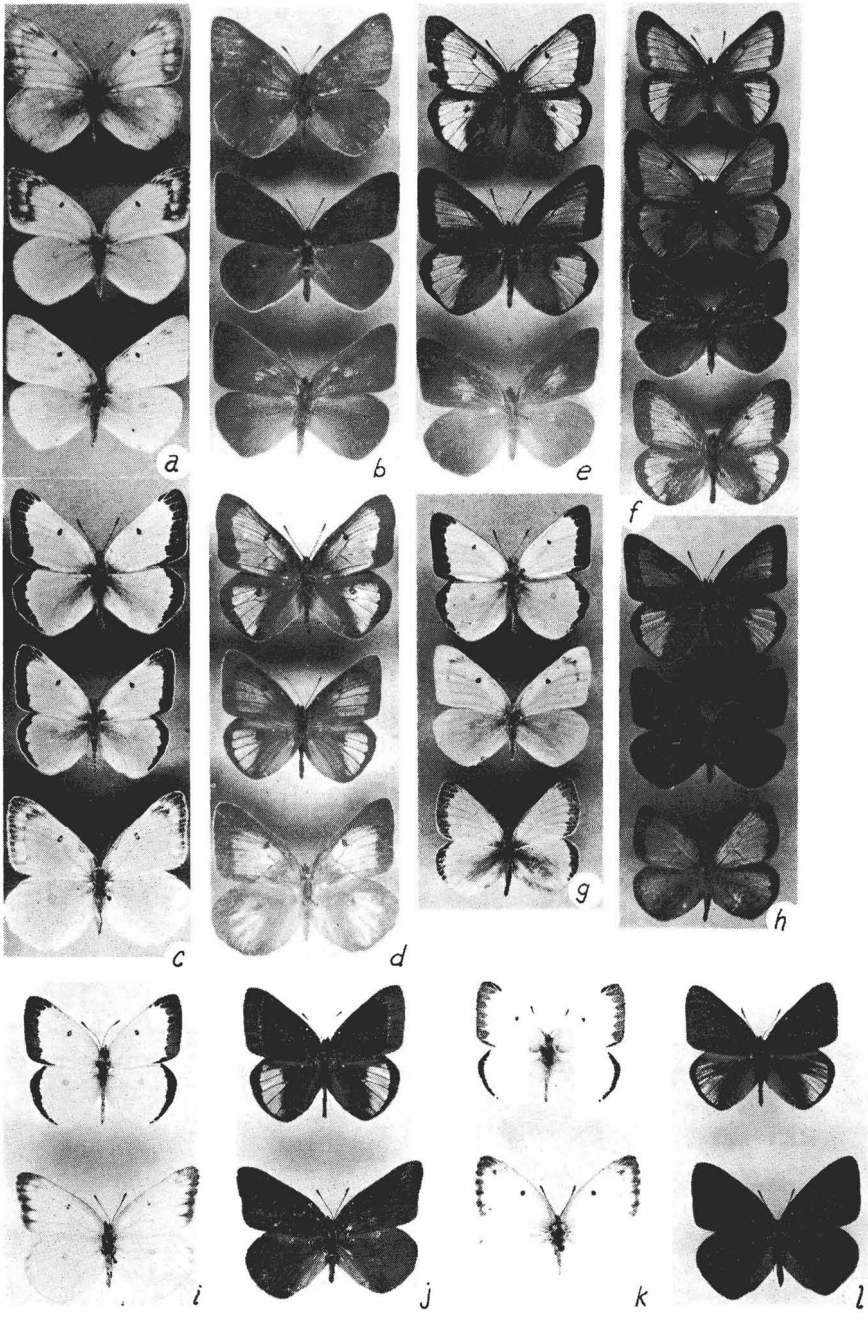
Fig. 4. Specimens of *Colias alexandra* photographed under white (left) and ultraviolet (right) light. **a** & **b**, *C. a. alexandra*, Albany Co., Wyoming; ♂, normal ♀, white ♀. **c** & **d**, ♀ ♀ of *C. alexandra*; top, Tooele Co., Utah; bottom, Catron Co., New Mexico. **e** & **f**, *C. alexandra*; top ♂, Boundary Co., Idaho; bottom pair, S of Golden, British Columbia. **g** & **h**, *C. alexandra*, pair from Utah; ♂ Tooele Co., ♀ Wasatch Co. **i** & **j**, ♂ ♂; top, *C. a. "emilia,"* Okanogan Co., Washington (see text); middle, *C. a. edwardsii*, Lander Co., Nevada; bottom, segregate, Apache Co., Arizona. **k** & **l**, ♂ ♂ of *C. a. astraea*; top, Sublette Co., Wyoming; middle, S of Seebee, Alberta in blend-zone region; bottom, Sheridan Co., Wyoming (orange form).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tains) and Modoc Counties show the orange discal spot in the males and considerable orange scaling in the females. Under uv light, luminous patches show on the forewings of the males.

Oregon specimens are similar, with the exception of a population from the Canyon Creek area, Ochocho Mountains, in Crook Co. The males from this region are similar to material from British Columbia, but the females show considerable dark bordering as in *occidentalis* Scudder. Some are quite similar in pattern and color to this species. Perhaps some hybridizing has occurred, but this is speculation. *C. occidentalis* is a non-reflective species.

The northern Idaho—southern British Columbia segregate is a large insect, generally larger than nomenotypical *alexandra*. This is described as a new taxon below. At first, it can be mistaken for *gigantea* Strecker because of the forewing apical rounding, but its habitat is forest clearings and roads, not bogs. McDunnough (1928) called this butterfly *Eurymus emilia*. Initially, one would place the population with the yellow races, but the discal spot is orange and the forewings exhibit luminous patches under uv illumination (Fig. 4f; Fig. 6e, f). This butterfly does not fit Edwards's description of *emilia*, and F. M. Brown (1973) has shown that *emilia* is synonymous with *edwardsii* which has page priority.

ORANGE POPULATIONS—DISTRIBUTION

South Dakota, Wyoming, Montana (?), North Dakota (? reported by Opler, unpublished), Alberta, Manitoba, Yukon Territory, Alaska.

A butterfly has been collected in the Yukon Territory (along the Alaska Highway) and in Alaska which appears to be a member of the *alexandra* complex (Fig. 5f–h). In many respects, it is similar to *Colias hecla* Lefèbre, but the underside and the uv reflectance pattern from the upperside place it tentatively as *alexandra*. Private correspondence with other collectors indicates that F. H. Chermock may have intended to name this population.

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Fig. 5. Specimens of *Colias alexandra* photographed under white (a, c, g, i & k) and ultraviolet (b, d, e, f, h, j & l) light. **a** & **b**, ♀♀ of *C. a. astraea*; top, Johnson Co., Wyoming; middle and bottom, S of Seebee, Alberta in blend-zone region. **c** & **d**, *C. a. krauthii*, Lawrence Co., South Dakota; top, orange ♂; middle, ♂ showing some yellow; bottom, ♀ (note the luminous patches on the female). **e**, *C. a. christina*; top, ♂, Riding Mtns., Manitoba; middle and bottom, pair, S of Seebee, Alberta in blend-zone region (note slight luminous patches on forewings of ♀). **f**, *C. alexandra* (?); 3 ♂♂ and 1 ♀, Yukon Territory. **g** & **h**, *C. a. christina*; top, ♂; middle, ♀; both S of Seebee, Alberta in blend-zone region; *C. alexandra* (?); bottom, ♂, Steese Highway mile 111, Alaska. **i** & **j**, *C. a. harfordii*; pair, Kern Co., California. **k** & **l**, *C. a. barbara*; Santa Barbara Co., California.

Pure orange races of *alexandra* have been reported from the area near Beulah, Manitoba, and Pocohontas, Alberta. These may be referable to the taxon *krauthii*. The Alberta specimens superficially resemble *krauthii*, but are considerably smaller.

Taxonomic Studies

Colias alexandra barbara H. Edwards, new combination
Colias alexandra harfordii H. Edwards, new combination

In 1877, Henry Edwards published a paper in which he proposed names for two *Colias* from California. These are the taxa *barbara* [T. L. Santa Barbara, California] and *harfordii* [T. L. Havilah, Kern Co., and Contra Costa Co., California]. They have stood as distinct species until P. A. Opler (unpublished) placed *barbara* as a subspecies of *harfordii*, although Talbot (1935) listed *barbara* as a form of *harfordii*. Edwards did indicate that both insects were related to *alexandra*.

Based upon uv photographs (Fig. 5i–l), it appears that the affinity of both butterflies is with *alexandra*. These subspecies appear to represent an intermediate situation. The uv reflectance from the forewings is reduced to a trace, as in the yellow populations, but the secondary discal spot is orange, as in the yellow-orange populations.

Additional justification for this assignment lies in range and foodplant. *C. a. edwardsii* is considered rare in California, although it is locally common in nearby Nevada (Lander Co.). Another population (previously discussed) is found locally in Lassen and Modoc Counties. Since *alexandra* is known to the north of central California, it seems odd, based upon geology, ecology and geography, that it should not occur centrally and along the coast of southern California. The southern and middle coastal areas and part of the central portion of the state are the areas in which *barbara* and *harfordii* occur. As noted earlier, *harfordii* uses *Astragalus* as a larval hostplant, which is also true of *alexandra*. Thus from the uv reflectance pattern, range, and hostplant affinity, it appears reasonable to assign *barbara* and *harfordii* to *alexandra*.

Colias alexandra columbiensis Ferris, **new subspecies**

Brown's treatment of *emilia* (1973) leaves the British Columbia race of *alexandra* without a name. The name *columbiensis*, derived from the type province, is proposed for this butterfly. This subspecies differs from other *alexandra* subspecies in that the apices of the forewings are definitely rounded suggesting *gigantea*. The uv reflection pattern in the males places this insect in the yellow-orange group. Comparison with other

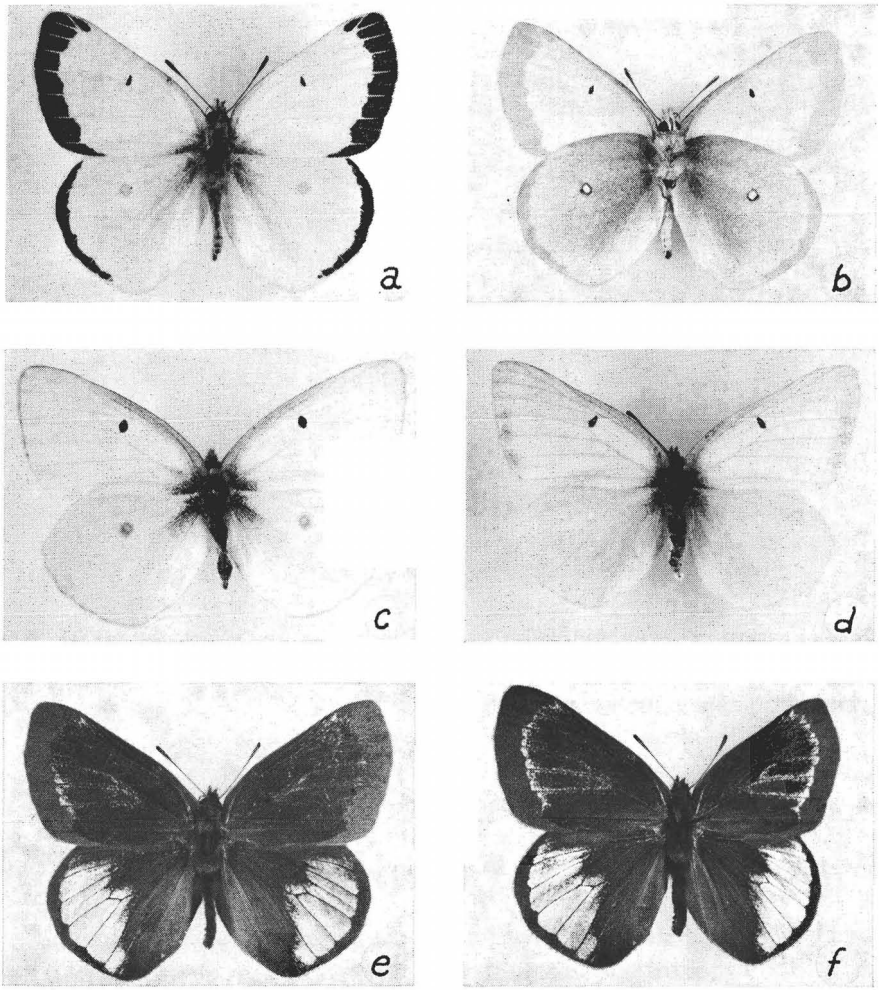

Fig. 6. *Colias alexandra columbiensis* Ferris: a, male holotype (upperside); b, same (underside); c, yellow female paratype (upperside); d, white female paratype (upperside); e, uv photograph of male holotype; f, same, but with specimen tilted to show full extent of forewing pattern on upperside.

members of this group shows that *columbiensis* differs from *christina* in that the forewings of the males show no orange color. It differs from *astraea* by being much larger, paler yellow in overall color, and is totally different in the females. *Columbiensis* females are pale yellow or white with nearly immaculate borders and generally show a large orange discal spot on the upperside of the hindwings.

In the males, the dorsal ground color is bright lemon yellow. Some specimens exhibit a dark yellow to orange flush in the discal and limbal areas of the hindwings, but do not show the pronounced orange markings which frequently occur in *astraea* and always in *christina*. The secondary discal spot is orange. The black borders are generally narrower than in nomenotypical *alexandra*. The primary cell-end spot is quite narrow. Ventrally the ground color is yellow with a slight orange flush. There is a dusting of black scales (sometimes heavy) on the secondaries. The secondary discal spot is bordered with dark pink scales and has a pearly center. Occasionally there is a satellite spot. The wing fringes are pink with some yellow as in *astraea*.

The females are dimorphic as is the case with other races of *alexandra*. Both yellow and white forms occur, as well as intermediates. The yellow females have a lemon yellow ground color frequently overwashed with pale orange, less pronounced dorsally than ventrally. In the white forms, there may be pronounced yellow-orange overwashing. Dorsally in both forms, the dark bordering varies from absent to slight. The primary cell-end spot is distinct (more so than in the males). The secondary discal spot is bright orange in the yellow forms and varies from orange to white in the white forms. Ventrally, the females are generally similar to the males, although there is a heavier overscaling of dark scales and the ground color is lighter in the white forms.

This subspecies is generally larger in size than the nominate species. The forewing costal margin length of the holotype male is 26 mm, 29 mm for the yellow female, and 28 mm for the white female shown in Fig. 6. In some males from northern Idaho, the costal margin length is 32 mm. Male specimens of *C. a. alexandra* examined from the Front Range (Rocky Mtns.) area measured 23 to 25 mm.

The holotype and two female paratypes are shown in Fig. 6. In addition, the uv reflection pattern of the holotype is presented. It is typical of the yellow-orange group.

Type Series. The type series consists of 6 males and 13 females. Because of the female dimorphism, no allotype is designated.

Holotype ♂. The specimen bears two labels. The locality label is machine printed black on white, with the exception of part of the date which is handlettered in black ink, and carries the following data: Anderson Lake/D'Arcy, B.C./17 June 1926/J. McDunnough. A second red label, machine printed in black is inscribed: Colias alexandra/columbiensis Ferris/Holotype Male.

Paratypes. 5 ♂♂, same data as holotype. 1 ♀ (white), same data as holotype. 9 ♀♀, 100 Mile House, B.C.: 28 June 1938, 4 ♀♀ (white); 29 June 1938, 1 ♀ (yellow); 30 June 1938, 3 ♀♀ (1 yellow); 4 July 1938, 1 ♀ (white), leg. J. K. Jacob and G. S. Walley. 2 ♀♀ (white) Lac la Hache, B.C., 5 July 1938, leg. G. S. Walley. 1 ♀ (white) Canin Lake, B.C., 24 June 1938, leg. G. S. Walley.

Distribution. This subspecies is found in British Columbia south to Washington

(Okanogan Co.) and northern Idaho (Boundary Co.). To the southeast of this region, it intergrades with *astraea* and to the south (southern Washington, Oregon, and northern California), it intergrades with *edwardsii* and possibly *harfordii*. The Canadian Rocky Mountains appear to form an effective barrier against any significant intergrading between *columbiensis* and *christina*. Specimens collected in the Bitterroot Mtns., Ravalli Co., Montana exhibit characters associated with both *astraea* and *columbiensis*.

Colias alexandra columbiensis is figured in Holland (1931), Plate LXVIII, figs. 22, 23, as *C. emilia*. The orange discal spot in the male is poorly reproduced. The specimens shown were collected by Greene in 1894 at Osyoos, British Columbia and are in the Carnegie Museum collection. They came to Holland from W. H. Edwards who labeled them as *emilia*, even though they do not fit his description of the taxon. Wright (1907) also figures *emilia*, Plate XI, fig. 92, but at least two of the examples shown are probably *philodice eriphyle* Edwards.

The type series for *columbiensis* is placed in the Canadian National Collection, Ottawa, Ontario.

CONCLUSIONS

It is suggested that the taxa associated with the *Colias alexandra* complex be arranged as follows:

Colias alexandra alexandra Edwards
Colias alexandra edwardsii Edwards
Colias alexandra harfordii H. Edwards
Colias alexandra barbara H. Edwards
Colias alexandra columbiensis Ferris
Colias alexandra astraea Edwards
Colias alexandra christina Edwards
Colias alexandra krauthii Klots

Unnamed races which possibly merit nomenclatural recognition:

Colias alexandra Arizona-New Mexico Segregate (yellow population).
Colias alexandra Yukon Territory-Alaska Segregate (orange population).

The arrangement is roughly according to pigmentation. The taxa *alberta* and *emilia* are omitted for the reasons set forth above. Other aspects of the *alexandra* complex have been treated by Ferris (1972a).

Ultraviolet reflectance photography has been used in this study to assign the various *alexandra* populations to specific color groups. It has also been used to identify *barbara* and *harfordii* as members of the *alexandra* complex.

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THE GENETICS OF FORE AND HINDWING COLOUR IN CROSSES BETWEEN *DANAUS CHRYSIPPUS* FROM AUSTRALIA AND FROM SIERRA LEONE (DANAIDAE)

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Unlike most warningly colored species, the butterfly *Danaus chrysippus* (L.) is known to be polymorphic in large parts of its range. Before one can understand the reason for this it is necessary to determine the genetic control of the forms. Recently we obtained a stock of *D. chrysippus* from Sydney, NSW and another from Sierra Leone. This paper gives preliminary results obtained by crossing the two races.

MATERIALS AND METHODS

The material from Australia, which was sent to us as living butterflies by post, was monomorphic and typical f. *chrysippus* of the race *D. c. petilea* (Fig. 1a). The ground colour of these butterflies is tawny orange tending to nutbrown towards the costal margin of the forewing. The hindwing upperside is bordered by black, sometimes with a vestige of white spotting close to the hindwing border. The apical third of the forewing upperside is black, with a variable subapical bar of white spots.

The specimens from Sierra Leone, f. *alcippus*, differed from the Australian ones in that the ground colour was more orange and most of the hindwing was covered by a patch of white scaling (Fig. 1b, c). The pale areas of the forewings were of two types—those with a narrow costal border of nutbrown pigmentation similar to the Australian butterflies (Fig. 1b) and others in which the nutbrown extended over most of the forewing (Fig. 1c). There was not enough orange on the hindwing to determine whether its hue differed in the two Sierra Leone forms.

Hybrids between the two races were obtained by allowing the males