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A REVIEW OF GEOGRAPHIC VARIATION AND POSSIBLE EVOLUTIONARY RELATIONSHIPS IN THE *COLIAS SCUDDERII-GIGANTEA* COMPLEX OF NORTH AMERICA (PIERIDAE)

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ABSTRACT. The geographic variation in the *Colias scudderii-gigantea* complex of North America is reviewed. Transitional populations suggest that *C. gigantea* should be taxonomically treated within a broader polytypic concept of *C. scudderii*. Two of these transitional populations are described as new subspecies; *C. s. gracemma* in the Big Horn Mountains of Wyoming and *C.* s. *kohleri* in the mountains of western Montana. In addition, *C. s. nortepacifica*, new subspecies, is described from a remote region of southwestern British Columbia. Possible evolutionary relationships are examined with regard to the biogeography and paleohistorical climatic fluctuations and glaciations of the Pliocene-Pleistocene periods over the past seven million years. A phylogenetic hypothesis for the *chrysotheme* species group of *Colias* is presented that postulates reticulate hybrid fusion or introgression has played an important role in the evolution of this group of *Colias*.

Additional key words: Biogeography, phylogeny, glaciations, Pliocene, Pleistocene.

The genus *Colias* (Pieridae: Coliadinae) is a large and complex group of butterflies that is widely distributed throughout most of the world. Verhulst (2000) provided a monographic treatment of the genus, and recognized up to 85 species-level taxa. However, many of these taxa may be geographic subspecies or semispecies of complex polytypic species or superspecies (Hammond & McCorkle 2003). The genus is highly conservative in morphology with minimal genitalic differences among most of the species, with the exception of the subgenus *Zerene* (Verhulst 2000). Eleven major species groups may be distinguished within the genus on the basis of wing color pattern characters, including the subgenus *Zerene*. The latter group is often elevated to full generic status on the basis of morphological divergence.

Over the past twenty years, we have conducted extensive studies of species complexes closely related to *C. occidentalis* Scudder within the *chrysotheme* group of species. The present paper serves as an introduction to this group, and provides a detailed review of the *C. scudderii-gigantea* complex. Additional papers are planned that will review the *C. pelidne-palaeno* complex and the *C. occidentalis-alexandra* complex. These complexes are of considerable interest from an evolutionary perspective. Evolutionary theory predicts that intermediate or transitional linkages should exist in modern day species complexes resulting from incipient speciation processes. As a consequence, the taxonomic delineation of species boundaries is often difficult for such intermediates. Such complexes may provide considerable evidence regarding the actual mechanical processes of cladogenesis and speciation as they have taken place in the past, and may be taking place today.

As we define the *chrysotheme* species group, it consists of 11–15 species, depending upon interpretations of species boundaries. This group is confined to North America, with the exception of two species that are widespread in Eurasia. It is most similar and probably most closely related to the *crocea* species group in Eurasia and Africa, but differs in the absence of an androconial scale patch on the costal margin of the male dorsal hindwing. Other wing pattern characters that serve to distinguish most members of the *chrysotheme* group from the *crocea* group include (1) a lighter orange to yellow dorsal ground color, (2) reduced size of discal spots on fore and hindwings, and (3) a reduction or absence of heavy black melanic scaling on the dorsal hindwing of females. However, the Eurasian *C. chrysotheme* Esper tends to be intermediate in these latter characters between the North American species of the *chrysotheme* group and *C. crocea* Fourcroy.

Within the *chrysotheme* group, we recognize two subgroups based upon biology and some wing color pattern differences. The *chrysotheme* subgroup consists of the Eurasian *C. chrysotheme* and the North American species *C. eurytheme* Boisduval and *C. philodice* Godart. Together with *C. crocea*, these species are characterized on the ventral hindwing by having a double-ringed discal spot and black submarginal spots. Females always have fully developed black borders on the dorsal wings, and a simple yellow-orange or white (alba) color dimorphism. All four species are highly vagile or even migratory. Their larvae feed on weedy legumes (Fabaceae) such as *Vicia*, *Trifolium*, and *Medicago* species that colonize disturbed and temporary habitats.

In sharp contrast, the *occidentalis* subgroup is usually characterized by having a single-ringed discal spot and reduced or absent black submarginal spots on the ventral hindwing. The black border of females is often reduced or completely absent. In addition, females also show an intermediate yellow-white or cream (semi-alba) color morph. These species are often very sedentary, and live in very local colonies in association with more stable habitats that support long-lived, perennial larval foodplants. The subgroup is comprised of three closely related species complexes that show numerous intermediate linkages. *Colias occidentalis* Scudder and *C. alexandra* Edwards form one complex that feeds on legumes, with *C. occidentalis* being possibly the primitive, ancestral species of the subgroup because of its close similarities with *C. philodice* and *C. eurytheme*. A more specialized, derived complex of species feed on *Vaccinium* shrubs (Ericaceae) growing in montane, boreal, and high Arctic habitats. These include the North American species *C. pelidne* Boisduval, *C. interior* Scudder, *C. behrii* Edwards, *C. chippewa* Edwards, and the Eurasian species *C. palaeno* Linnaeus. A third group that appears to be closely related to both *C. occidentalis* and *C. pelidne* is the *C. scudderii-gigantea* complex, feeding primarily on dwarf willows (*Salix* spp. – Salicaceae) growing in montane, boreal, or Arctic regions of North America. This species complex is the subject of the present paper.

Ferris (1987) has prepared the most recent monograph of the *C. scudderii-gigantea* complex. He recognized two separate species, *C. scudderii* Reakirt isolated in the southern Rocky Mountains, and *C. gigantea* Strecker distributed through the central and northern Rocky Mountains and across Canada and Alaska. However, other authors such as Scott (1986) have treated *C. gigantea* as a geographic subspecies of *C. scudderii*. In recent years, much additional information has been acquired from important geographic localities through the central Rocky Mountains. Four different intermediate populations show transitions from the typical Colorado *C. scudderii* to more northern populations of the *gigantea* type as discussed below. These are distributed in northeastern Utah, Wyoming, and southwestern Montana. Thus, we follow the taxonomic treatment of Scott (1986) in combining taxa of the *gigantea* type within a broader polytypic concept of *C. scudderii*.

MATERIALS AND METHODS

For this study, we examined about 1000 specimens of the *C. scudderii* complex from throughout the distribution of this species, but particularly from the Rocky Mountain region. In addition, we also examined about 900 specimens of *C. occidentalis* from across central Oregon to examine the relationship of this species to the *C. scudderii* complex.

Because of strong sexual dimorphism in this complex, males and females were studied separately. We measured forewing length from the wing base to the apex. We also quantified three wing color pattern characters in the male and two characters in the female. These characters all show continuous variation, and are probably controlled by polygenic complexes of multiple loci and alleles. However, for the purpose of this work, we wanted to simplify the analysis by reducing the variation classification to only a few classes. The characters and their classification are defined as follows.

1. Male ventral hindwing ground color olive-green, yellow-green, yellow, or orange. Since these colors present a situation of continuous variation and are probably highly polygenic, orange was classified as any tint of orange, ranging from very dark orange to pale yellow-orange. Likewise, olive-green was classified as darker shades without any yellow tinge, while yellow-green was classified as a paler green shade with a distinct tinge of yellow.
2. Male discal spot on ventral hindwing large, medium, or small. Spot size also shows a continuous range of variation, and was the most difficult to classify in an objective manner. A large spot was defined as covering one half or more of the discal cell width at the distal end of the cell, while a small spot covered only one third or less of discal cell width. A medium spot was subjectively treated as intermediate between these extremes. We also considered a subcategory of large spot called a giant spot that covers nearly two thirds of the discal cell width.
3. Male discal spot on ventral hindwing with or without a satellite spot.
4. Female dorsal ground color yellow, cream (semi-alba), white (alba), or orange. Again, orange was classified as any shade of orange including an orange flush on a yellow background.
5. Female black wing border on dorsal forewing heavy (both inner and outer parts of border present), reduced (usually only a thin portion of inner border present), or absent (only slight black traces of border present or none).

Tables 1 and 2 show the frequencies of polymorphic variants within these five characters in various

TABLE 1. Frequencies of phenotypic variation in males of *Colias scudderii* for ground color, discal spot size, and satellite spots on the ventral hindwing at various geographic localities.

Locality	olive-green	yellow-green	yellow	orange	large	medium	small	sat.	no sat.
1	0.79	0.21	0.00	0.00	0.25	0.30	0.45	0.27	0.73
2	1.00	0.00	0.00	0.00	0.33	0.33	0.33	0.50	0.50
3	0.26	0.74	0.00	0.00	0.55	0.25	0.20	0.84	0.16
4	0.25	0.25	0.50	0.00	0.65	0.27	0.08	0.75	0.25
5	0.00	0.00	0.69	0.31	0.54	0.23	0.23	0.81	0.19
6	0.00	0.01	0.67	0.32	0.46	0.26	0.28	0.73	0.27
7	0.04	0.24	0.63	0.09	0.50	0.28	0.22	0.82	0.18
8	0.00	0.00	0.60	0.40	0.43	0.37	0.20	0.83	0.17
9	0.00	0.00	0.28	0.72	0.38	0.28	0.34	0.66	0.34
10	0.00	0.00	0.58	0.42	0.37	0.32	0.31	0.89	0.11
11	0.00	0.00	0.50	0.50	0.25	0.33	0.42	0.92	0.08
12	0.05	0.05	0.40	0.50	0.35	0.45	0.20	0.80	0.20

1. Colorado, Rocky Mts. n = 108 (*C. s. scudderii*)
2. Utah, Uinta Mts. n = 6 (*C. scudderii* Uinta population)
3. Wyoming, Big Horn Mts. n = 73 (*C. s. gracemma*)
4. Wyoming, Wind River Mts. n = 55 (*C. s. harroweri*)
5. Wyoming, Absaroka Mts. n = 26 (*C. s. kohleri*)
6. Montana, Centennial Mts. n = 95 (*C. s. kohleri*)
7. Montana, Pioneer Mts. n = 147 (*C. s. kohleri*)
8. Montana, Flint Creek Mts. n = 35 (*C. s. kohleri*)
9. Alberta and British Columbia n = 29 (*C. s. mayi*)
10. Manitoba, Riding Mts. n = 19 (*C. s. mayi*)
11. Manitoba, Hudson Bay at Churchill n = 12 (*C. s. gigantea*)
12. Yukon and Alaska n = 20 (*C. s. gigantea*)

populations of the *C. scudderii* complex at strategic locations across the North American landscape. We attempted to assemble a minimum sample of 10 specimens for each population to show at least the major variations within these populations, although 15–20 specimens provides better insight into frequencies. The larger samples of 50 or more were useful for detecting rare variants in populations. It should be noted that these are composite samples comprised of individuals from many localities, and do not represent single or local colonies.

RESULTS AND DISCUSSION

***Colias occidentalis* and possible evolutionary relationships.** Relationships among the various *Colias* species in western North America have been very confused in the past. This is due to the existence of numerous intermediate or transitional populations, not only within species complexes, but also between complexes. Hybridization also appears to be an important evolutionary process in these butterflies. As a consequence, applying the taxonomic definition of species has been very difficult, often arbitrary, and artificial. We are using the biological species concept based upon reproductive isolation in sympatry, but even this concept is often inadequate for the taxonomic delineation of species boundaries. Nevertheless, the various intermediate or transitional populations that exist in the modern day provide much evidence regarding the past evolutionary history of the butterflies, and are the basis for the following evolutionary theories.

Ferris (1993) conducted a cladistic analysis of the group, and recognized five species feeding on legumes within the *occidentalis* subgroup. The typical form of *C. occidentalis* along the West Coast is yellow with no UV-reflectance. It is extremely similar to *C. philodice eriphyle* Edwards in most characteristics, particularly those *C. occidentalis* populations in southwest Oregon and northwest California. The primary differences between the two species are that *C. occidentalis* has a single-ringed discal spot and heavier black melanic scaling on the ventral hindwing. By contrast, populations in the central and northern Rocky Mountains and across central Canada are more

TABLE 2. Frequencies of phenotypic variation in females of *Colias* for dorsal ground color and development of the black wing border at various geographic localities.

Locality	white	cream	yellow	orange	heavy	reduced	absent
1	0.50	0.19	0.31	0.00	0.03	0.19	0.78
2	0.60	0.20	0.20	0.00	0.00	0.00	1.00
3	0.30	0.38	0.30	0.02	0.18	0.32	0.50
4	0.05	0.10	0.76	0.09	0.09	0.57	0.34
5	0.08	0.33	0.58	0.00	0.42	0.17	0.41
6	0.22	0.17	0.61	0.00	0.39	0.39	0.22
7	0.19	0.10	0.70	0.01	0.09	0.20	0.71
8	0.00	0.00	0.88	0.12	0.18	0.41	0.41
9	0.00	0.14	0.86	0.00	0.14	0.29	0.57
10	0.67	0.33	0.00	0.00	0.00	0.50	0.50
11	0.70	0.30	0.00	0.00	0.30	0.40	0.30

1. Colorado, Rocky Mts. n = 32 (*C. s. scudderii*)
2. Utah, Uinta Mts. n = 5 (*C. scudderii* Uinta population)
3. Wyoming, Big Horn Mts. n = 40 (*C. s. gracemma*)
4. Wyoming, Wind River Mts. n = 21 (*C. s. harroweri*)
5. Wyoming, Absaroka Mts. n = 12 (*C. s. kohleri*)
6. Montana, Centennial Mts. n = 23 (*C. s. kohleri*)
7. Montana, Pioneer Mts. n = 87 (*C. s. kohleri*)
8. Alberta and British Columbia n = 17 (*C. s. mayi*)
9. Manitoba, Riding Mts. n = 7 (*C. s. mayi*)
10. Manitoba, Hudson Bay at Churchill n = 6 (*C. s. gigantea*)
11. Yukon and Alaska n = 10 (*C. s. gigantea*)

divergent with orange dorsal color and UV-reflectance on both fore and hindwings of males. Ferris (1993) recognized these populations as three taxonomic species, *C. christina* Edwards, *C. pseudochristina* Ferris, and *C. krauthii* Klots. The fifth legume feeder is *C. alexandra*, which is mostly yellow with a UV-reflecting patch on the dorsal hindwing. Finally, Ferris (1987) also reported *C. gigantea* from central Oregon.

Warren (2005) has followed Ferris (1993) in treating *C. christina* as distinct from *C. occidentalis*. However, as discussed by Hammond & McCorkle (2003), a long clinal gradient between yellow *occidentalis* forms and orange *christina* forms exists across the entire Intermountain region between the Cascades and Rocky Mountains. We examined long series of specimens from many localities. The Cascade populations are nearly monomorphic yellow, but one orange specimen was found in Jefferson County, Oregon at the closest geographic point between the Cascades and the Ochoco Mountains to the east. This gives a ratio of about 99% yellow and 1% orange for the Jefferson County population. Eastward, we found the yellow:orange ratio to be about 90:10 in the Ochoco Mountains, 70:30 in the Aldrich Mountains, 50:50 in the central Blue Mountains, 30:70 in the northern Blue Mountains, 10:90 in the Wallowa Mountains, and 5:95 in central Idaho. We also found that up to 12% of specimens from the east slope of the Rocky Mountains in Alberta are mostly yellow with only a slight orange flush, and that the frequency of yellow or near yellow butterflies increases southward in Montana (see Kohler, 2006). Because of these long, gradual clines between yellow and orange morphs, we suggested that the *christina* group should be taxonomically treated as subspecies of *C. occidentalis*. Throughout the Great Basin and Intermountain regions, *C. occidentalis* feeds primarily on legumes such as peas (*Lathyrus* spp.) and false lupines (*Thermopsis* spp.). In sharp contrast, *C. alexandra* functions as a fully distinct biological species in these same regions, and specializes on highly toxic legumes such as milk-vetches (*Astragalus* spp.) and locoweeds (*Oxytropis* spp.).

Although Ferris (1987) reported *C. gigantea* from central Oregon, no actual populations have ever been found and verified. However, while we were examining some 900 specimens of *C. occidentalis* across central Oregon to study the yellow-orange cline discussed above, we observed large numbers of specimens that

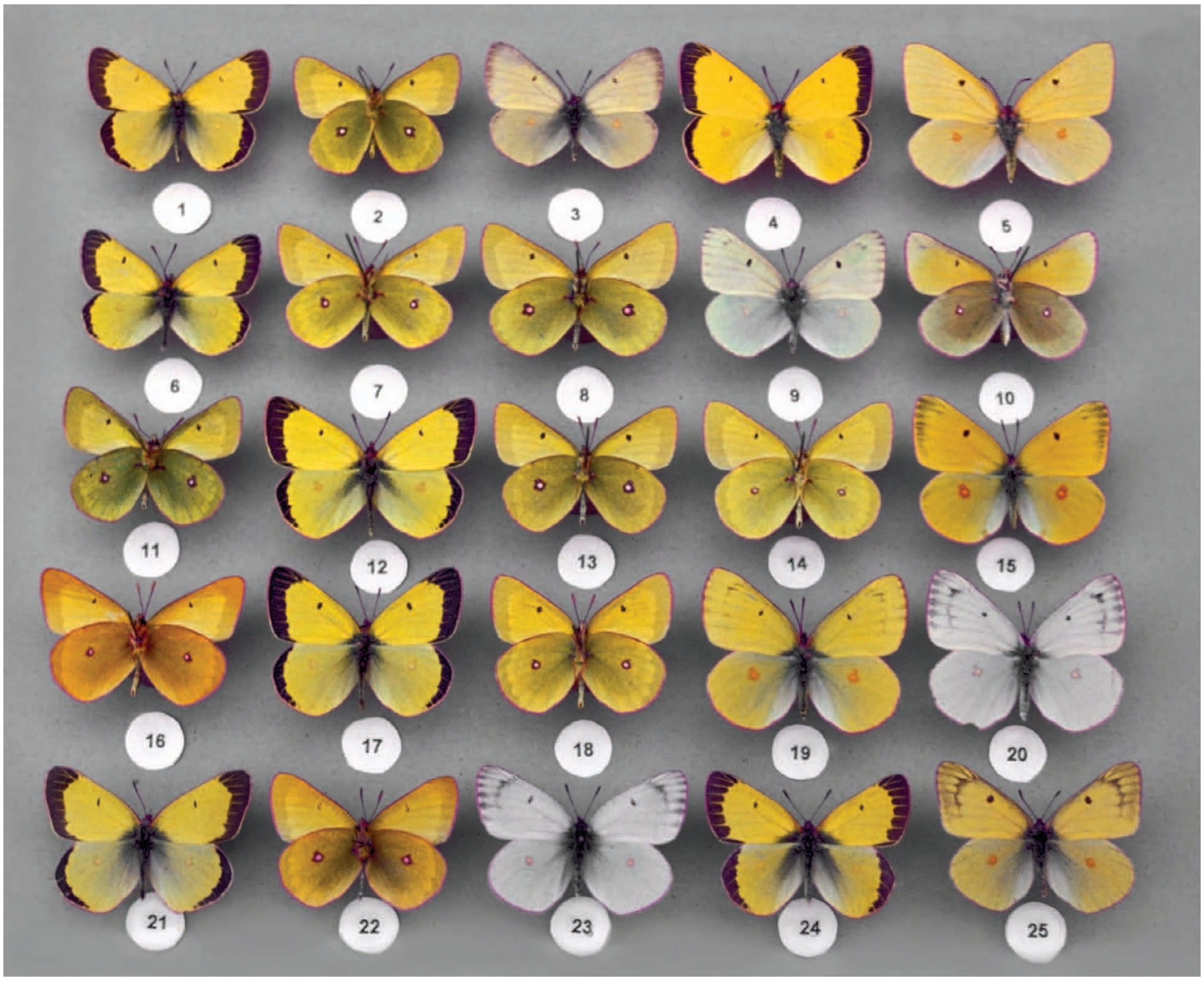

Fig. l. **(1)** *Colias scudderii scudderii*, male dorsal, Colorado; **(2)** *C. s. scudderii*, male ventral with giant discal spots, Colorado; **(3)** *C. s. scudderii*, female dorsal cream form, Colorado; **(4)** *C. s. mayi*, male dorsal , Manitoba; **(5)** *C. s. mayi*, female dorsal yellow form, Manitoba; **(6)** *C. s. gracemma*, Holotype male dorsal, Wyoming; **(7)** *C. s. gracemma*, male ventral yellow-green form with medium discal spots, Wyoming; **(8)** *C. s. gracemma*, male ventral with giant discal spots, Wyoming; **(9)** *C. s. gracemma*, Allotype female dorsal cream form, Wyoming; **(10)** *C. s. gracemma*, female ventral with bicolored hindwing, Wyoming; **(11)** *C. s. gracemma*, male ventral olive-green *scudderii*-like form, Wyoming; **(12)** *C. s. harroweri*, male dorsal, Wyoming; **(13)** *C. s. harroweri*, male ventral olive-green form with giant discal spots, Wyoming; **(14)** *C. s. harroweri*, male ventral yellow form with small discal spots, Wyoming; **(15)** *C. s. harroweri*, female dorsal orange form, Wyoming; **(16)** *C. s. mayi*, male ventral dark orange form with small discal spots, Alberta; **(17)** *C. s. kohleri*, Holotype male dorsal, Montana; **(18)** *C. s. kohleri,* male ventral yellow-orange form with medium discal spots, Montana; **(19)** *C. s. kohleri*, Allotype female dorsal yellow form, Montana; **(20)** *C. s. kohleri*, female dorsal white form, Montana; **(21)** *C. s. gigantea*, male dorsal, Alaska; (22) *C. s. gigantea*, male ventral orange form with large discal spots, Alaska; **(23)** *C. s. gigantea*, female dorsal white form, Alaska; **(24)** *C. s. nortepacifica*, Holotype male dorsal, British Columbia; **(25)** *C. s. nortepacifica*, Allotype female dorsal, British Columbia.

had a phenotype virtually identical to that of *C. gigantea*, and this phenotype appears to be the basis for Ferris` report. Moreover, we also observed extreme phenotypes within these samples that were virtually identical to those of *C. scudderii* in the southern Rocky Mountains and *C. pelidne skinneri* Barnes in the central and northern Rocky Mountains. All of the *Vaccinium-Salix* feeding species of *Colias* are yellow in the males with no UV-reflectance like the West Coast forms of *C. occidentalis*. The existence of these intermediate populations in central Oregon and the intermediate populations discussed below provide much evidence for evolutionary linkages among all three species complexes.

The above observations have suggested to us a possible theory of genealogy and evolutionary history for the *chrysotheme* species group. Based upon the cladistic analysis, a simple linear genealogy for the *chrysotheme* subgroup appears to exist across Eurasia and North America beginning with *C. crocea* in southern Eurasia. Evolutionary steps in this genealogical sequence are (1) loss of the male androconical patch in *C. chrysotheme* in northern Eurasia, (2) reduction in discal spot size and black melanic scaling in *C. eurytheme* in North America, (3) loss of orange coloration and UV-reflectance in *C. philodice*, and (4) loss of the double-ringed discal spot and black submarginal spots in West Coast forms of *C. occidentalis*.

At this point, evolutionary patterns in the *occidentalis* subgroup become very complicated. While the linear genealogy of the *chrysotheme* subgroup could be viewed in a traditional dichotomous hierarchy of a standard cladistic analysis, the *occidentalis* subgroup genealogy appears to be a multibranching or polychotomous pattern quite unlike the cladogram presented by Ferris (1993). Also, reticulate hybrid fusion or introgression appears to have played an important role in the evolution of this group of *Colias*.

An important theoretical concept is that of punctuated equilibrium (Gould & Eldredge 1977), the idea that taxa or populations are distributed through time as well as space, and share ancestor-descendant relationships as a consequence (see discussion in Hammond 1991). Such relationships are never evident in a cladistic analysis with a nested dichotomous hierarchy. Instead, ancestral taxa are thought to produce large numbers of descendant taxa during an adaptive radiation in a multibranching or polychotomous pattern, while surviving largely intact and largely unchanged through long periods of time, often as relicts in more restricted and isolated refugia. Thus, *C. occidentalis* is postulated to be the immediate ancestral parent species for three distinct daughter species; *C. pelidne*, *C. scudderii*, and *C. alexandra*.

Based upon our analysis of phenotypic variation in central Oregon populations of *C. occidentalis*, and the other intermediate populations discussed below, we suggest that both *C. scudderii* in the southern Rocky Mountains and *C. pelidne* in the central and northern Rocky Mountains represent geographic isolates of ancestral *C. occidentalis* populations from the Intermountain region. Such isolation events may have taken place in the late Miocene or Pliocene about 4–7 million years ago as conditions in the Rocky Mountains became cooler leading up to the glacial and interglacial periods of the Pleistocene. Such climatic shifts may have promoted a foodplant shift in Rocky Mountain populations away from legumes such as *Lathyrus* in favor of *Salix* and *Vaccinium* shrubs in subalpine environments.

Later during the Pleistocene, as *C. scudderii* spread northward through the central Rocky Mountains of Wyoming and Montana and into Canada and Alaska, *C. occidentalis* also spread into this region, initially hybridizing with *C. scudderii* to produce the modern *gigantea* phenotype. Eventually, Rocky Mountain populations of *C. o. christina* acquired full reproductive isolation from *C. scudderii*. The orange color and UV-reflectance of *C. o. christina* may represent characters that were acquired in the Intermountain and northern Rocky Mountain regions from hybridization with *C. eurytheme* and *C. meadii* Edwards, and these characters were strongly selective in the northern Rocky Mountains and across Canada as a way to reproductively isolate *C. o. christina* from *C. scudderii* (Ferris 1993).

Still later, *C. o. christina* spread southward through the central Rocky Mountains of Montana and Wyoming, and into the southern Rocky Mountains of Colorado to speciate into the modern *C. alexandra*, where it ecologically replaces *C. occidentalis*. The further adaptive radiation of *C. alexandra* populations throughout the western Great Plains, Great Basin, and Intermountain regions appears to be of relatively recent origin, a response to the climatic drying and desertification of these regions during the Pleistocene that resulted in a large adaptive radiation of the legume genus *Astragalus* (Isely 1983).

We realize that the above evolutionary scenarios are highly speculative, but the existence of modern intermediate populations provides important supportive evidence. Such hypotheses are potentially testable as additional evidence becomes available in the future, perhaps using molecular markers. Also, this theory serves as a background context for discussing the patterns of geographic variation and ecology within the *C. scudderii* complex below.

Subspecies Descriptions

Colias scudderii ruckesi Klots

The taxonomic status of this subspecies is somewhat confused. Klots (1937) described this taxon from the south end of the Sangre de Cristo Range in the Pecos River drainage near Santa Fe, New Mexico. The type series was collected in 1935 and 1936. According to Klots' description, this subspecies is distinctly different from the typical *C. s. scudderii* in Colorado and Wyoming. Diagnostic characters cited by Klots for *C. s. ruckesi* include (1) larger size, (2) reduction or absence of the black discal spot on the dorsal forewing, (3) a broader black marginal border in the male, (4) a deeper yellow dorsal ground color, (5) heavier and more extensive black basal suffusion, and (6) a higher frequency of the yellow morph in females.

However, Ferris (1987) collected specimens of *C. s. ruckesi* from the type locality later in the 1970's, and was not able to distinguish these from typical *C. s. scudderii* in Colorado. It is possible that warmer climatic conditions during the 1930's may have influenced the phenotype, producing larger and darker colored butterflies compared to the 1970's. We have only examined two specimens of *C. s. ruckesi*, and have no new information to contribute regarding this question. In general, peripheral isolates such as *C. s. ruckesi* often exhibit some divergence, at least in gene and phenotype frequencies, compared to more centrally located populations.

Colias scudderii scudderii Reakirt

Figure 1, Tables 1 & 2

Description. Male (n=108). Forewing length 22–25 mm, mean = 24 mm. Dorsal ground color pale yellow. Black border of forewing usually broad, sometimes narrow, with yellow veins. Small black discal spot of forewing usually prominent or reduced, rarely absent. Moderate to heavy black basal suffusion present on fore and hindwings. Discal spot on dorsal hindwing usually yellow and faint. Black scaling in medial area of ventral forewing light to absent. Ventral ground color of hindwing usually olive-green (79%), sometimes yellow-green (21%) with heavy black melanic scaling. Discal spot on ventral hindwing ringed with red, variably large (22%), medium (33%), or small (45%). A satellite spot is usually absent (73%), sometimes present (27%).

Female (n=32). Forewing length 23–26 mm, mean = 25 mm. Dorsal ground color variable, white (52%), cream (19%), or yellow (29%). Black border of dorsal forewing is usually completely absent (78%), sometimes partially present (19%), and rarely fully developed (3%). Discal spot of dorsal hindwing usually yellow and faint, rarely orange. Ground color of ventral hindwing variable, usually olive-green to yellow-green, sometimes orange. Other characters as in male.

Distribution and ecology. This subspecies is common and widely distributed throughout the southern Rocky Mountains of Colorado, extending northward through the Medicine Bow and Laramie Mountains of southeastern Wyoming in Carbon, Albany, and Converse Counties. However, populations in the Sangre de Cristo Range of south-central Colorado extending southward through northern New Mexico are tentatively assigned to *C. s. ruckesi* as discussed above.

The habitat used by *C. s. scudderii* is more variable and extends over a much broader elevational gradient than suggested by Ferris (1987). The butterfly occupies open forests of quaking aspen and conifers or open meadows within the forest at middle elevations, and subalpine or alpine meadows at high elevations at or above timberline. The high elevation populations appear to be feeding mostly on dwarf willows (*Salix* spp.) as larval foodplants, but there are also numerous records of oviposition on *Vaccinium caespitosum* Michx. in Colorado (Scott 1986; Ferris 1987).

We have also observed oviposition on *Lathyrus lanszwertii* var. *leucanthus* Rydb. in Colorado. One of us (PCH) found *C. scudderii* to be common at middle elevations on the west side of Gore Pass in Routt County during 1996. A large clear-cut was made in a dry, upland mixed forest of quaking aspen and lodgepole pine. *Lathyrus lanszwertii* had densely colonized this open clear-cut, and was a major part of the ground cover. A large colony of about 30–40 adults of *C. scudderii* was flying in this clear-cut, and at least three different females were observed ovipositing on the *Lathyrus* together with females of *C. alexandra*.

Discussion. *Colias s. scudderii* appears to be a highly specialized subspecies at least in morphology. The very small wing length combined with the monomorphic olive-green to yellow-green ground color on the ventral hindwing of males are strong diagnostic characters for this subspecies. In addition, it shows a high frequency of a small discal spot combined with no satellite spot on the ventral hindwing. In females, about 70% are white or cream in dorsal ground color and only about 30% are yellow. The black wing border in females is usually absent or greatly reduced.

In spite of these specializations, the subspecies appears to be quite generalized in ecology with polyphagous larvae, feeding on *Salix*, *Vaccinium*, and *Lathyrus*. In sharp contrast, three distinct species co-exist together in sympatry within the central and northern Rocky Mountains, with other *C. scudderii* subspecies using *Salix* exclusively as a larval foodplant, *C. pelidne* using *Vaccinium*, and *C. occidentalis* or *C. alexandra* using legumes such as *Lathyrus*. Thus, in Colorado, *C. s. scudderii* appears to be fully or partially using the foodplant niches of three different species in the central and northern Rocky Mountains, although the *Lathyrus* niche is mostly occupied by *C. alexandra* in much of Colorado (Hayes 1980).

As previously discussed, *C. s. scudderii* appears to be a sister species of *C. pelidne*, and both appear to have been isolated in the southern and north-central Rocky Mountains respectively from Intermountain ancestral populations of *C. occidentalis*. Both switched away from the ancestral *Lathyrus* foodplants in favor of *Salix* and *Vaccinium* foodplants as climatic conditions became cooler in the Rocky Mountains prior to the Pleistocene glaciations. While isolated in the southern Rocky Mountains, *C. s. scudderii* has retained this evolutionary transition into modern times using diverse and multiple larval foodplants, while sympatric northern populations have evolved very narrow foodplant specializations as part of their speciation processes.

***Colias scudderii* Uinta Range population**

An isolated population of *C. scudderii* occurs at high elevations in the Uinta Range of northeast Utah, including Summit, Daggett, Duchesne, and Uintah Counties. We have only examined a short series of 6 males and 5 females from this population (Tables 1 & 2). Most of these specimens are very similar to the Colorado *C. s. scudderii* in phenotype, but one male and one female are larger and similar in phenotype to the Wyoming *C. s. harroweri* Klots. We believe this population is transitional between the two subspecies.

Jacque Wolfe and Jack Harry (per. comm.) have made extensive ecological observations of the Uinta Range population. Most females oviposit on low *Vaccinium* species such as *V. caespitosum* growing in open conifer forests at high elevations. However, Jack Harry (per. comm.) also observed a local colony in a riparian zone along a creek where females were ovipositing on a tall *Salix* species. Thus, the Uinta Range population appears to retain polyphagous feeding habits like the Colorado populations.

In ecology, this population is intermediate between Colorado *C. scudderii* and Wyoming *C. pelidne skinneri*, and is mostly occupying the ecological niche of *C. pelidne* in the Uinta Range. However in morphology, the population appears to be intermediate between Colorado *C. s. scudderii* and Wyoming *C. s. harroweri*.

Colias scudderii gracemma Hammond & McCorkle, **new subspecies**

Figure 1, Tables 1 & 2

Description. Male (n=73). Wings often elongate. Forewing length 22–27 mm, mean = 25 mm. Dorsal ground color pale yellow. Black border of forewing variably broad to narrow with yellow veins. Small black discal spot of forewing oblong, prominent, rarely faint or absent. Moderate to heavy black basal suffusion present on fore and hindwings. Discal spot on dorsal hindwing usually yellow and faint, rarely pale orange. Black scaling in medial area of ventral forewing light to absent. Ventral ground color of hindwing usually bright yellow-green (74%), sometimes darker olive-green (26%), with heavy black melanic scaling. Discal spot on ventral hindwing ringed with red, variably large (55%), medium (25%), or small (20%). A satellite spot is usually present (84%), rarely absent (16%).

Female (n=40). Forewing length 24–28 mm, mean = 26 mm. Dorsal ground color variable, white (30%), cream (38%), yellow (30%), or rarely with an orange flush (2%). Black border of dorsal forewing is usually completely absent (50%) or partially present (32%), and sometimes fully developed (18%). Discal spot of dorsal hindwing variably pale yellow to orange. Ground color of ventral hindwing blue-green to yellow-green, or bicolored darker orange in the medial portion of the wing with a paler blue-green submarginal band. Other characters as in the male.

Holotype. male, Wyoming, Johnson County, summit of Big Horn Mountains near Cloud Peak Wilderness Area, 13 July 2004, Terry Stoddard leg. The holotype is deposited in the Oregon State Arthropod Collection, Oregon State University, Corvallis, Oregon, USA. **Allotype.** female, same data and deposition as holotype, but collected 19 July 2005. **Paratypes.** 65 males and 33 females, same locality as holotype. Disposition of paratypes as follows: 41 males and 20 females to the collection of Terry Stoddard, 18 males and 8 females to the collection of Steve Van Campen, and 6 males and 5 females to the collection of Paul C. Hammond.

Etymology. The name honors Grace Stoddard and Emma Van Campen who helped collect and study this butterfly.

Distribution and ecology. This subspecies is narrowly endemic to the Big Horn Mountains in Wyoming, and is presently known only from the south end of the mountains in Johnson County near the Cloud Peak Wilderness Area. It occurs in broad, extensive willow bogs or meadows at high elevations near the summit of the mountains. Females have been observed ovipositing on a low-growing dwarf willow (*Salix* sp.) in these bogs. At somewhat lower elevations in the Big Horn Mountains, there are extensive willow bogs dominated by a different species of willow that grows much taller into a large bush or small tree. *Colias s. gracemma* was never found in association with this tall willow, and is very habitat limited as a consequence. Within the meadow and adjacent forest habitats, this species is sympatric with three other species of *Colias* including *C. pelidne skinneri*, *C. occidentalis sacajawea* Kohler, and *C. philodice*.

Diagnosis and discussion. This population is a distinctive isolate that is exactly intermediate between the Colorado *C. s. scudderii* and the more *gigantea*-like populations to the north. Although Ferris (1987) knew of this population, he may not have seen sufficient material to recognize the following unique characteristics. Characters shared with *C. s. scudderii* include (1) males that are monomorphic green on the ventral hindwing, (2) females that are commonly white or cream (68%) in dorsal ground color, and (3) females in which the black wing border is mostly reduced or completely absent (82%). Characters shared with *gigantea*-like forms include (1) a high frequency of a large discal spot on the ventral hindwing (55%), and (2) a high frequency of a satellite spot (84%). In size, *C. s. gracemma* is also intermediate between the southern and central Rocky Mountain subspecies of *C. scudderii*. Moreover, it should also be noted that extreme specimens of *C. s. gracemma* are virtually identical in phenotype to either the Colorado *C. s. scudderii* or the western Wyoming *C. s. harroweri* Klots.

This subspecies does exhibit several unique features not found commonly in the other subspecies. The wings are quite elongate compared to most other subspecies. Males usually have a bright or vivid yellow-green ground color on the ventral hindwing, in contrast to the darker olive-green ground color common in Colorado *C. s. scudderii*. Females frequently are bicolored on the ventral hindwing, with an orange medial area contrasting with a paler blue-green submarginal area. Females in other subspecies of *C. scudderii* also frequently show a darker, more brownish medial area on the ventral hindwing, as do rare females of *C. pelidne* and *C. occidentalis*, but these are rarely as contrasting as are the colors in some females of *C. s. gracemma*.

We suggest that *C. s. gracemma* represents a peripheral isolate of *C. scudderii* populations that spread northward out of Colorado during early Pleistocene glaciations, initially hybridizing with ancestral populations of *C. occidentalis* to the north that produced the modern *gigantea*-like phenotypes in northern populations.

Colias scudderii harroweri Klots

Figure 1, Tables 1 & 2

Description. Male (n=55). Forewing length 23–28 mm, mean = 26 mm. Dorsal ground color pale yellow. Black border of forewing variable, narrow to broad, with yellow veins. Black discal spot of forewing variable, small and faint to large and round. Moderate to heavy black basal suffusion present on fore and hindwings. Discal spot on dorsal hindwing faint yellow to orange. Black scaling in medial area of ventral forewing usually absent. Ventral ground color of hindwing variable olive-green (25%), yellow-green (25%), or yellow (50%) with light to heavy black melanic scaling. Discal spot on ventral hindwing ringed with red, usually large to giant (65%), sometimes medium (27%), or rarely small (8%). A satellite spot is usually present (75%), sometimes absent (25%).

Female (n=21). Forewing length 26–29 mm, mean = 27 mm. Dorsal ground color usually yellow (76%), rarely white (5%), cream (10%), or orange (9%). Black border of dorsal forewing is usually absent (34%) or partially present (57%), rarely fully developed (9%). Discal spot of dorsal hindwing usually faint orange to dark orange. Ground color of ventral hindwing yellow to blue-green. Other characters as in male.

Distribution and ecology. This subspecies is narrowly endemic to the mountains of western Wyoming in the Teton and Wind River Ranges of Teton, Sublette, and Fremont Counties. As we narrowly define this taxon, it does not occur in the Yellowstone region of Wyoming and Montana, but is replaced northward by subspecies discussed below.

The butterfly is found in a variety of willow bog habitats at middle to high elevations in the mountains. These include riparian bogs along forest streams, extensive seepage areas in semi-open lodgepole pine forests, and extensive hanging bog meadows. Females oviposit on a dwarf willow species (*Salix* sp.) in these bogs. This species is sympatric in the Wind River Range with *C. pelidne*, *C. alexandra astraea* Edwards, and *C. philodice*.

Discussion. This is the third subspecies or population that appears to be intermediate between the Colorado *C. s. scudderii* and the more *gigantea*-like populations to the north. However, unlike the *C. s. gracemma* populations to the east in the Big Horn Mountains, these western populations appear to be more directly intergrading between *C. s. scudderii* and *C. s. kohleri* (described below) in Montana. Transitional characters include larger size, a mixture of green and yellow ground colors on the ventral hindwing of males, and a high frequency of the yellow morph in females. However, extreme specimens are still identical in phenotype to the Colorado *C. s. scudderii*, particularly at the south end of the Wind River Range in Fremont County.

One character that uniquely distinguishes *C. s. harroweri* is a high frequency of a giant discal spot on the ventral hindwing. This extreme character occurs in many populations of *C. occidentalis* and *C. pelidne*, but is usually quite rare (1–5%).

In *C. s. scudderii*, the frequency of giant spots is 12%, and is 23–31% in most other populations of *C. scudderii* throughout North America. However, this character reaches the highest frequency in *C. s. harroweri* at 50%, compared to a frequency of 27% in *C. s. gracemma*.

Colias scudderii kohleri Hammond & McCorkle, new subspecies

Figure 1, Tables 1 & 2

Description. Male (n=360). Forewing length 25–29 mm, mean = 27 mm. Dorsal ground color variable, pale to dark yellow, usually medium yellow. Black border of forewing usually broad, rarely narrow, with yellow veins. Black discal spot of forewing often large and prominent, round to oblong, rarely faint or absent. Black basal suffusion on fore and hindwings usually moderate to reduced, sometimes heavy. Discal spot on dorsal hindwing pale yellow to orange. Black scaling in medial area of ventral forewing usually absent to light, rarely moderate. Ventral ground color of hindwing variable, usually yellow or orange, sometimes green. Black melanic scaling on ventral hindwing usually moderate to heavy, sometimes reduced. Discal spot on ventral hindwing ringed with red, variably large (43–54%), medium (23–37%), or small (20–28%). A satellite spot is usually present (73–83%), sometimes absent (17–27%).

Female (n=180). Forewing length 26–30 mm, mean = 28 mm. Dorsal ground color variable, usually yellow (58–70%), sometimes white (8–22%), or cream (10–33%), rarely orange (1%). Black border of dorsal forewing variable, poorly developed in some populations, well developed in other populations. Discal spot of dorsal hindwing variably pale to dark orange. Ground color of ventral hindwing variably yellow, orange, or blue-green. Other characters as in the male.

Holotype. male, Montana, Beaverhead County, summit of the Pioneer Mountains, 21 July 2002, Paul C. Hammond leg. The holotype is deposited in the Oregon State Arthropod Collection, Oregon State University, Corvallis, Oregon, USA. **Allotype.** female, same data and deposition as holotype. **Paratypes.** 93 males and 50 females, same locality as holotype. Disposition of paratypes as follows: 13 males and 16 females to the collection of Terry Stoddard, 45 males and 8 females to the collection of Steve Van Campen, 8 males and 7 females to the collection of Steve Kohler, 5 males and 4 females to the collection of David V. McCorkle, and 22 males and 15 females to the collection of Paul C. Hammond.

Etymology. The name honors Steve Kohler, who has made an immense contribution to the study of Montana butterflies.

Distribution and ecology. This subspecies as we define it here is widely distributed in the central Rocky Mountain region, from the greater Yellowstone ecoregion in northwest Wyoming north throughout most of western Montana to Flathead County, and west to the west slope of the Bitterroot Range in Lemhi County, Idaho. Ferris (1987) has reported a record from Blaine County in south-central Idaho, but we have not been able to verify this record. Earlier reports

(Ferris 1987) from central Oregon are probably misidentified *C. occidentalis*.

This subspecies occupies extensive, open boggy meadows with dwarf willows, either at middle elevations in hanging bogs on mountain slopes and in riparian zones along creeks, or in subalpine meadows at the higher elevations in the mountains. At the type locality in the Pioneer Mountains, there are actually two distinct species of dwarf willows growing together in sympatry; one with green leaf petioles and hairy leaves, and one with red petioles and smooth leaves. The females of *C. s. kohleri* at this locality were highly selective in their choice for oviposition, and were observed to oviposit only on the red petiole-smooth leaf type of willow. This *Salix* might be either *S. boothii* Dorn or *S. planifolia* Pursh.

Diagnosis and discussion. This subspecies is extremely similar in phenotype to common forms of *C. occidentalis* across central Oregon. In fact, we know of no diagnostic character that consistently separates the two species. On average, males of *C. s. kohleri* show reduced black basal suffusion on the dorsal wings compared to males of *C. occidentalis*, but there is much overlap between them. Also, *C. s. kohleri* shows a much higher frequency of giant discal spots on the ventral hindwing (23–36%) compared to *C. occidentalis* (1–5%).

There is a slight average difference between the two species in the wing pattern of females on the dorsal forewing. In females with partial or full development of the black wing border, *C. scudderii* usually exhibits a stronger development of the inner portion of the border that appears as a thin, black line, while the outer portion is often obscure or completely absent. This development is most often exactly reversed in females of *C. occidentalis*. Again, however, this character is not consistently different between the two species, and immaculate females are essentially identical.

We suggest that *C. s. scudderii* spread northward out of Colorado during early glacial periods of the Pleistocene, eventually hybridizing with ancestral populations of *C. occidentalis* in the central Rocky Mountains of Montana. This reticulate hybrid fusion resulted in the modern *gigantea*-like phenotype of *C. s. kohleri* that closely resembles the ancestral phenotype of *C. occidentalis*, but retains the specialized larval feeding niche on dwarf willows of the *C. s. scudderii* parent. Eventually, reproductive isolation between the two species was attained, perhaps with help from the orange-UV coloration acquired later by *C. occidentalis* males in the central-northern Rocky Mountain region. Foodplant incompatibility between the legume-feeding and willow-feeding niches was probably the driving selective force that promoted eventual reproductive isolation and full speciation.

There is some geographic variation in populations of *C. s. kohleri* that is probably of evolutionary significance. The most variable populations are found at the type locality in the Pioneer Mountains of Beaverhead and Deer Lodge Counties, Montana (Tables 1 & 2). Consequently, this region is thought to be the historical center of origin for the original hybridization between *C. scudderii* and *C. occidentalis*, and the original point of origin for *C. s. kohleri*. These populations still exhibit a relatively high frequency of *scudderii*-like green colors on the ventral hindwing of males, 24% yellow-green and even 4% olive-green. Also, females are mostly immaculate (71%), and only about 29% show partial or full development of the black wing border.

In sharp contrast, the populations of *C. s. kohleri* in the greater Yellowstone ecoregion are highly divergent from the original *scudderii*-like phenotype (Tables 1 & 2), even though they are geographically closest to the *scudderii*-like *C. s. gracemma* and *C. s. harroweri* populations in Wyoming. Both the Absaroka Range population in Park County, Wyoming and the Centennial Range population in southern Beaverhead County, Montana and adjacent Fremont County, Idaho are almost monomorphic for yellow or orange colors on the ventral hindwing of males (99–100%), and very rarely show green colors (1%) of the *scudderii* type. Also, females show a much higher frequency of partial or full development of the black wing border (59–78%). For these reasons, we believe the Yellowstone region populations are of relatively recent origin, possibly spreading into this region since the last Pleistocene glaciation. They appear to have had little genetic contact with the older *C. s. harroweri* populations to the south in the Teton region.

Northward from the Pioneer Mountains, populations of *C. s. kohleri* also show reduced variation, and are mostly monomorphic yellow or orange on the ventral hindwing in Granite, Missoula, Lake, and Flathead Counties. We have seen only a few specimens from the east slope of the Rocky Mountains in northern Montana, but these closely resemble the Canadian *C. s. mayi* Chermock. A population in Lewis and Clark County appears to be intermediate between *C. s. kohleri* and *C. s. mayi*, but the population in Glacier County belongs to this Canadian subspecies.

During later periods of the Pleistocene, *C. s. kohleri* appears to have produced four distinct evolutionary lineages of the *gigantea*-type in Canada and Alaska. These include the following *C. s. mayi* to the northeast in central Canada, *C. s. gigantea* Strecker in the subarctic north, *C. s. inupiat* Harry in the far arctic north of Alaska, and an unnamed segregate in the northwest.

The evolutionary history of these four northern segregates appears to be intimately connected with the history of Pleistocene glacial and interglacial periods in Canada and Alaska.

Colias scudderii mayi Chermock & Chermock

Figure 1, Tables 1 & 2

Description. Male (n=50). Wings usually elongate. Forewing length 25–30 mm, mean = 28 mm. Dorsal ground color usually medium yellow, sometimes pale or dark yellow. Black border of forewing usually broad, rarely narrow, with yellow veins. Black discal spot of forewing usually large and prominent, round to oblong, sometimes reduced and faint. Black basal suffusion on fore and hindwings greatly reduced or completely absent. Discal spot on dorsal hindwing usually pale to medium orange, sometimes faint yellow. Black scaling in medial area of ventral forewing usually absent. Ventral ground color of hindwing yellow or orange. Black melanic scaling on ventral hindwing usually reduced or absent, but often heavier in Rocky Mountain populations. Discal spot on ventral hindwing ringed with red, variably large (37–38%), medium (28–32%), or small (31–34%). A satellite spot is usually present (66–89%), sometimes absent (11–34%).

Female (n=24). Forewing length 26–32 mm, mean = 29 mm. Dorsal ground color usually yellow, sometimes orange in western populations, white or cream in eastern populations. Black border of dorsal forewing variable, usually absent (41–57%) or partially present (29–41%), rarely fully developed (14–18%). Discal spot of dorsal hindwing pale to dark orange. Ground color of ventral hindwing yellow to orange. Other characters as in male.

Distribution and ecology. This subspecies is widely distributed across central Canada. It extends from southeast Manitoba west across central and northern portions of Manitoba, Saskatchewan, and Alberta to the Rocky Mountains, and southward along the eastern slope of the mountains to Glacier County, Montana. There is an isolated population in the Cypress Hills of Saskatchewan (Layberry *et al*. 1998). Northward, the distribution extends into the southern portions of the Northwest Territory around the Great Slave Lake. Westward, it extends throughout northeast British Columbia, and southward through the drainage of the Fraser River valley to about Jesmond, British Columbia (Guppy & Shepard 2001). In ecology, *C. s. mayi* occupies willow bogs in the taiga forest zone across central Canada, and in more isolated bogs further south in the mixed conifer-aspen parkland zone (Bird *et al*. 1995; Layberry *et al*. 1998).

Discussion. *Colias s. mayi* is the most divergent subspecies of *C. scudderii*, both from the Colorado *C. s. scudderii* and from West Coast forms of *C. occidentalis*, and is recognized by many distinctive characters. These include (1) very large size, (2) elongate wings, (3) deeper yellow dorsal ground color, (4) little or no black basal suffusion on dorsal wings, (5) often reduced or absent black melanic scaling on the ventral hindwing, (6) monomorphic yellow or orange ground color on the ventral hindwing, and (7) nearly monomorphic yellow females.

Ferris (1987) failed to recognize the distinctive differences between this subspecies and the northern sub-arctic *C. s. gigantea*, apparently because of the clinal intergradation between the two subspecies in northern Manitoba. However, Masters (1970) correctly identified the above distinctions, and recognized *C. s. mayi* as an important evolutionary segregate. There is some minor geographic variation across Canada. Populations in the Rocky Mountains tend to show more black melanic scaling on the ventral hindwing compared to more eastern populations, and are nearly monomorphic for yellow females. Orange females are somewhat frequent in Rocky Mountain populations (12%), and may represent a residue from past hybridization with orange forms of *C. occidentalis*. These are usually mis-identified as females of *C. o. christina*.

As discussed by Masters (1970) and Ferris (1987), there is an apparent zone of clinal intergradation with *C. s. gigantea* in Manitoba, resulting in a higher frequency of white or cream females in eastern populations. Nevertheless, the hybrid suture zone between the two subspecies appears to be rather abrupt across much of Canada, similar to the abrupt suture zones of *Limenitis arthemis/astyanax* (Nymphalidae) and *Papilio glaucus/canadensis* (Papilionidae).

We suggest that *C. s. mayi* evolved as a northeastern segregate from *C. s. kohleri* in the taiga zone of central Canada centered in Manitoba during the Pleistocene. Its distribution has probably expanded and contracted periodically with the climatic fluctuations of the Pleistocene, following the north and south movements of the taiga zone on the northern Great Plains. During periods of glacial maxima, the distribution probably spread southward on the plains of eastern Montana and North Dakota, and moved north again back into Canada during warm interglacial periods. We suspect that *C. s. mayi* spread westward to the northern Rocky Mountains of Alberta and into British Columbia more recently since the retreat of the last glacial maxima about 12,000 years ago.

Colias scudderii gigantea Strecker

Figure 1, Tables 1 & 2

Description. Male (n=32). Forewing length 24–28 mm, mean = 26 mm. Dorsal ground color pale yellow. Black border of forewing usually broad, rarely narrow, with yellow veins. Black discal spot of forewing variable, round to oblong, sometimes large and prominent, often reduced and faint. Black basal suffusion on fore and hindwings usually moderate, sometimes light to heavy. Discal spot on dorsal hindwing pale yellow to orange. Black scaling in medial area of ventral forewing light to heavy, sometimes absent. Ventral ground color of hindwing usually yellow or orange, rarely green. Black melanic scaling on ventral hindwing moderate to heavy. Discal spot on ventral hindwing ringed with red, variably large (25–35%), medium (33–45%), or small (20–42%). A satellite spot is usually present (80–92%), sometimes absent (8–20%).

Female (n=16). Forewing length 25–29 mm, mean = 27 mm. Dorsal ground color usually white (67–70%) or cream (30–33%). Black border of dorsal forewing variable, often absent or partially present, sometimes fully developed. Discal spot of dorsal hindwing pale cream to orange. Ground color of ventral hindwing yellow, orange, or blue-green, often with very heavy black melanic scaling. Other characters as in male.

Distribution and ecology. As we narrowly define this subspecies, it is limited to true arctic or sub-arctic regions of Canada and Alaska. It is widely distributed throughout much of Yukon and Alaska extending to the south slopes of the Brooks Range, the Richardson Mountains, and west to the Seward Peninsula. Eastward, it extends to the Arctic Ocean in the Mackenzie River valley, the Great Bear Lake, and probably in the tundra-taiga ecotone regions of Northwest Territory to Hudson Bay. It then occurs to the southeast along the shores of Hudson Bay in Manitoba to the west shore of James Bay in Ontario.

C. s. gigantea occupies willow bogs in low arctic tundra and semi-forest taiga. Females have been observed ovipositing on *Salix reticulata* L. at Churchill, Manitoba (Ferris 1987). This subspecies appears to be particularly adapted to open tundra habitats, compared to the more taiga zone willow bogs of *C. s. mayi*. However, in central Alaska near Fairbanks and across central Yukon, it does occupy a more taiga semi-forest habitat.

Discussion. In sharp contrast to *C. s. mayi*, *C. s. gigantea* has experienced very little morphological divergence from *C. s. kohleri* and central Oregon forms of *C. occidentalis*. In fact, the only real difference among these taxa is the monomorphic white or cream forms of the female in *C. s. gigantea*. There is some range of variation in this subspecies. We have not seen what we would regard as a true yellow female form, but the cream form is frequently dark enough to approach yellow. Also, some females show a tinge or flush of orange on a white or cream background. Butterflies from low elevations in central Alaska near Fairbanks are often much larger in size like *C. s. mayi*, with a male forewing length of 27–29 mm. However, these still show the characters of typical *C. s. gigantea*.

A major problem with this subspecies is that there has long been confusion with arctic populations of sympatric *C. pelidne*. The latter is more narrowly limited to higher elevation montane habitats in the Mackenzie, Ogilvie, Richardson, and Brooks ranges of northwest Canada and Alaska. There appears to be considerable overlap in characters between the two species, possibly because of past hybrid introgression. We believe that Ferris (1987) actually illustrated the male and female of *C. pelidne* from the Ogilvie Mountains (his Figures 39–42), while his Figures 43–44 illustrate a typical male of *C. s. gigantea* from the Seward Peninsula. In general, males of the latter species closely resemble central Oregon forms of *C. occidentalis*, often with a strongly developed black discal spot on the dorsal forewing and a broad wing shape. By contrast, males of *C. pelidne* always have a very small, faint black discal spot with rather short, stubby wings. However, the most consistent difference between the two species may be size. Males of *C. pelidne* are consistently smaller with a forewing length of 22–24 mm (mean = 23 mm), while sympatric males of *C. s. gigantea* usually have a forewing length of 24–26 mm (mean = 25 mm).

We suggest that *C. s. gigantea* evolved as a far northern segregate from *C. s. kohleri* in the tundra-taiga zone of Alaska and Yukon during the Pleistocene. As with *C. s. mayi*, its distribution probably expanded and contracted periodically with the climatic fluctuations of the Pleistocene. During the last glacial maxima about 18,000 years ago, its distribution was probably confined to non-glaciated refugia in Yukon and Alaska (see discussion in Layberry *et al*. 1998). As the glacial ice sheets began to retreat across northern Canada about 10,000 years ago, *C. s. gigantea* spread eastward across Northwest Territory following the tundra habitat. It probably reached Hudson Bay during the warm hypsithermal period about 6000 to 9000 years ago (Layberry *et al*. 1998). At the same time, *C. s. mayi* was probably spreading northward into Manitoba from its glacial refugium on the northern Great Plains. Thus, the modern clinal intergrade zone in Manitoba between the two subspecies appears to be of very recent origin, taking place during this hypsithermal period.

An interesting biogeographic issue concerns biotic dispersal across Beringia between North America and Eurasia as discussed by Lafontaine & Wood (1988) and Layberry *et al*. (1998). Wolfe & Leopold (1967) have discussed the history of biotic interchange between Eurasia and North America during the Tertiary. Land bridges between the continents existed over Beringia and a North Atlantic connection over Greenland and Iceland up to the middle Miocene period, and then over Beringia through the Pliocene period. Tropical and subtropical biotas were exchanged between the continents through the Oligocene and Eocene periods about 25–40 million years ago, and warm temperate biotas were continuous across the continents during the early to middle Miocene about 15–25 million years ago.

However, all land connections may have been broken by seaways during the late Miocene about 7–15 million years ago as climatic conditions became cooler at high latitudes. This allowed boreal or taiga type conifer forests to evolve independently in Eurasia and North

America (Wolfe & Leopold 1967). The Beringia connection between Alaska and Siberia was re-established in the Pliocene about 3–7 million years ago, allowing a new interchange of a cold-adapted tundra biota to spread across the northern portions of the continents. However, some authors such as Petrov (1967) believe this Beringian connection was mostly broken during the Pleistocene. During periods of glacial maxima, much of Beringia was covered with either glacial ice sheets or cold, xeric grasslands rather than shrub tundra, while the Bering Strait seaway separated Alaska and Siberia during warm interglacial periods of the Pleistocene (Hopkins 1967).

These considerations are directly relevant to the inter-change of Lepidoptera populations between Eurasia and North America such as species of *Colias*. The *Vaccinium*-feeding group of *Colias* has clearly dispersed back and forth between North America and Eurasia on at least three separate occasions. The ancestral *C. pelidne* is thought to have originally dispersed from Alaska into Siberia in the early Pliocene, producing the *C. palaeno* radiation across the entire boreal region of Eurasia. This species then dispersed back across Beringia into North America to produce the modern *C. chippewa*, and this latter species dispersed a third time from Alaska into Siberia to produce *C. c. gomojunovae* Korshunov. All of these dispersal events must have taken place in the Pliocene or early Pleistocene about 1–7 million years ago if Hopkins (1967 p. 472), Petrov (1967), and others are correct that the Beringian connection between the continents was mostly broken during the late Pleistocene with respect to shrub tundra.

In sharp contrast, *C. scudderii* is widely distributed throughout most of Alaska today, extending west to the Seward Peninsula. Yet it has never been able to disperse across Beringia into Siberia. Certainly the boreal willow bog-tundra habitat is widespread across the northern regions of Eurasia. This evidence suggests that Petrov (1967) may be correct. *Colias scudderii* probably evolved in North America during the middle Pleistocene, and reached Alaska too late to successfully disperse across Beringia into Eurasia. The *C. pelidne* adaptive radiation is much older, and had no problem in dispersing repeatedly between the continents during the Pliocene or early Pleistocene.

Colias scudderii inupiat Harry

Description (from Harry 2007). Male (n=43). Forewing length 20–25 mm, mean ~ 23 mm. Dorsal ground color pale yellow. Black border of forewing usually medium broad with yellow veins. Black discal spot of forewing usually reduced to absent. Black basal suffusion on fore and hindwings moderate to heavy. Discal spot on dorsal hindwing pale yellow to orange. Black scaling on ventral forewing light to moderate. Ventral hindwing ground color yellow-orange, usually with strong green over-scaling. Black melanic scaling on ventral hindwing moderate to heavy. Discal spot on ventral hindwing ringed with red, sometimes with a satellite spot.

Female (n=17). Forewing length 23–27 mm, mean ~ 25 mm. Dorsal ground color usually yellow or cream. Black border of dorsal forewing variable, often absent or partially present, sometimes fully developed. Discal spot of dorsal hindwing orange. Other characters as in male.

Distribution and ecology. This subspecies was recently described from extreme northern Alaska north of the Brooks Range (Harry 2007). It occupies the foothills and coastal plain between the mountains and the Arctic Ocean. Although collection records are confined to the vicinity of the Dalton Highway, the subspecies is probably widely distributed across northern Alaska between the Brooks Range and Arctic Ocean.

Harry (2007) describes the habitat as low boggy tundra, and in bogs along small streams in the Sagwon Hills. Females were observed ovipositing on *Salix lanata* L.

Discussion. *Colias s. inupiat* differs from *C. s. gigantea* in very small size, more greenish over-scaling on the ventral hindwing, and monomorphic yellow or cream females. Both subspecies appear to be northern segregates derived from *C. s. kohleri*, which is polymorphic with yellow, cream, and white females.

Hopkins *et al*. (1982) illustrate the known extent of glaciation in Beringia during the last glacial maxima about 20,000–14,000 years ago. The combined Laurentide and Cordilleran ice sheets covered most of Canada extending through southern and eastern Yukon, and the St. Elias and Alaska Ranges were heavily glaciated across southern Alaska. The Brooks Range was also heavily glaciated across northern Alaska. However, most of western and central Alaska was non-glaciated, extending east through the Yukon River drainage of western Yukon. The arctic coastal plain north of the Brooks Range was also non-glaciated, as was the Beringian land bridge connection with Siberia. As discussed by Hopkins *et al*. (1982), most of this land is thought to have been covered with a very xeric arctic steppe or mammoth steppe composed of bunchgrasses and xeric herbs such as *Artemisia* spp. (Asteraceae). Such steppes supported herds of large mammals such as the woolly mammoth. The mesic birch-heath shrub tundra with dwarf willows is thought to have been very narrowly restricted at this time to the edge of montane glaciers where moisture from melting ice was available. This is why *C. scudderii* was probably unable to spread westward across the mammoth steppes of Beringia into Siberia during the Pleistocene.

Thus, we suggest that ancestral populations of *C. s. kohleri* with polymorphic females spread northward into Alaska from the Rocky Mountains during a warm interglacial period, possibly during the Sangamon Interglaciation about 120,000 years ago (Hopkins *et al*. 1982). During later periods of glaciation, separate populations became isolated north and south of the Brooks Range. Populations in the Yukon River drainage of central Alaska and eastern Yukon evolved into the modern *C. s. gigantea* with monomorphic white or cream females, while populations on the arctic coastal plain north of the Brooks Range evolved into the modern *C. s. inupiat* with monomorphic yellow or cream females. Of course, we have no way to know the exact timing of these events, since at least four major glacial-interglacial cycles are known to have impacted Beringia over the past 400,000 years (Hopkins *et al*. 1982). It is quite possible that *C. s. inupiat* has been isolated on the arctic coastal plain for a very long time, surviving through a number of Pleistocene climatic cycles.

Colias scudderii nortepacifica Hammond & McCorkle, **new subspecies**

Figure 1

Description. Male (n=2). Forewing length 25–26 mm. Dorsal ground color pale yellow. Black border of forewing broad with yellow veins. Black discal spot of forewing large and prominent, round to oblong. Back basal suffusion on fore and hindwings very heavy. Discal spot on dorsal hindwing pale yellow to orange. Black scaling in medial area of ventral forewing light to absent. Ventral ground color of hindwing yellow to pale yellow-orange. Black melanic scaling on ventral hindwing very heavy. Discal spot on ventral hindwing ringed with red, variably small to large. A satellite spot is variably present or absent.

Female (n=1). Forewing length 27 mm. Dorsal ground color yellow. Black border of dorsal forewing fully developed, with the inner border forming a thin black line and the outer border faint and dusky. Discal spot of dorsal hindwing orange. Ground color of ventral hindwing yellow-orange with very heavy black melanic scaling. Other characters as in male.

Holotype. male, British Columbia, Nimpo Lake, 28 July 1962, A.L. Alderman leg. The holotype is deposited in the Oregon State Arthropod Collection, Oregon State University, Corvallis, Oregon, USA. **Allotype.** female, same data and deposition as holotype. **Paratype.** male, British Columbia, Tatla Lake near Hwy. 20, 23 July 1981, Jon and Sigrid Shepard legs., deposition as holotype.

Etymology. The name refers to the Pacific Northwest.

Distribution, diagnosis and discussion. We have identified a very unusual isolate of *C. scudderii* that appears to be narrowly endemic to a remote region of southwest British Columbia. At present, it is only known from the three type specimens. These were originally identified as *C. occidentalis* based upon the very heavy black basal suffusion on the dorsal wings, and the heavy black melanic scaling on the ventral hindwing. However, these specimens differ from the typical form of *C. occidentalis* that is nearly parapatric in the drainage of the lower Fraser River valley by having a pale yellow or yellow-orange ground color on the ventral hindwing. The female has the black wing border of the *C. scudderii* type in which the inner border is present as a thin, black line, while the outer border is dusky and obscure. In sharp contrast, *C. occidentalis* has a dark orange ground color on the ventral hindwing, and the female wing border is usually more solid black at the outer border and more dusky and obscure at the inner border.

The parapatric *C. s. mayi* in the drainage around the middle Fraser River valley is also distinctly different from this new subspecies. It often has a dark orange ground color on the ventral hindwing, often with greatly reduced black melanic scaling. In addition, it differs sharply from both parapatric *C. occidentalis* and *C. s. nortepacifica* in having little or no black basal suffusion on the dorsal wings.

At present, this new subspecies is only known along Highway 20 from Tatla Lake northwest to Nimpo Lake just east of Tweedsmuir Provincial Park. As discussed by Guppy & Shepard (2001), most of British Columbia was covered with glaciers during the last glacial maxima about 18,000 years ago. However, there must have been a non-glaciated refugium in southwest British Columbia at this time, probably in the rain shadow of the Coast Mountains east of Tweedsmuir Provincial Park within the larger Chilcotin River region. A number of distinctive butterfly taxa are endemic to this region and to south-central British Columbia in general, including *C. alexandra columbiensis* Ferris (Pieridae), *Speyeria aphrodite columbia* Hy. Edwards, *S. callippe chilcotinensis* Guppy & Shepard, *S. mormonia jesmondensis* dos Passos & Grey, a form of *S. atlantis beani* Barnes & Benjamin (=*S. hesperis* of some authors), and a very dark melanic form of *S. zerene picta* McDunnough (all Nymphalidae).

We suggest that *C. s. nortepacifica* evolved as a fourth segregate from the Rocky Mountain *C. s. kohleri* in the upper Pacific Northwest during the Pleistocene. However, while both *C. s. mayi* and *C. s. gigantea* were able to achieve wide and successful distributions during the Pleistocene, *C. s. nortepacifica* was nearly exterminated by the widespread glaciations in British Columbia. Only a few populations appear to have survived into the modern day as relicts within a non-glaciated refugium. The subspecies may be quite sedentary with limited dispersal abilities. By contrast, *C. s. mayi* is thought to have entered British Columbia quite recently from Alberta, first moving west through the Peace River drainage, extending northwest-ward towards Yukon, and southward through the Fraser River drainage to about Jesmond around 10,000 years ago as the glaciers retreated from central British Columbia. There is no evidence at this time of any genetic contact or intergradation between *C. s. mayi* and *C. s. nortepacifica*.

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