BULLETIN OF THE ALLYN MUSEUM

3701 Bayshore Rd.
Sarasota, Florida 33580

Published By
The Florida State Museum
University of Florida
Gainesville, Florida 32611

Number 96 12 July 1985

REVISION OF *COLIAS BOOTHII* CURTIS, *COLIAS THULA* HOVANITZ AND *COLIAS NASTES* BOISDUVAL IN NORTH AMERICA (PIERIDAE: COLIADINAE)[1]

Clifford D. Ferris[2]

INTRODUCTION

It is necessary to begin a paper of this nature with a caveat. The findings presented defining the probable "true" nature of *Colias boothii* Curtis and *C. thula* Hovanitz are based upon examination of many thousands of museum specimens and the author's interpretation thereof, coupled with his experience in the field. The theory presented could be tested ultimately by laboratory crossing of virgin females of *C. hecla* Lefèbvre and *C. nastes* Boisduval with males of the opposite species and then rearing from the ova produced. This would be a difficult task for several reasons. The life histories of both species in North America are only incompletely known. An additional problem is the maintenance under laboratory conditions of an adequate biomass of the arctic legume larval host plants. Consistent with other *Colias* species, it is assumed that the larvae exhibit hibernal diapause, which introduces the difficult problem of maintaining the larvae during this time. Perhaps diapause could be broken by regulating photoperiod and/or growth chamber temperature. While such problems are not insurmountable, they are sufficiently complex to deter direct hybridization studies.

In many butterfly genera, the structures of the male genitalia provide useful information for taxonomic decisions. In *Colias*, however, the male genitalia are very similar for all of the species. A biometric study of these structures in *Colias* was conducted by Peterson (1963), from which he was able to group various species of this genus. He demonstrated that *C. hecla* and *C. nastes* are very closely related and stated that gene introgression has occurred between these two species.

Another diagnostic tool available to the taxonomist is gel electrophoresis. Johnson has published studies on the enzyme α-glycerophosphate dehydrogenase, as elucidated by gel

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[1] Published with the approval of the Director, Wyoming Agricultural Experiment Station as Journal Article No. JA 1342.

[2] Bioengineering Program, University of Wyoming, Laramie, Wyoming 82071. Research Associate: Allyn Museum of Entomology/Florida State Museum, Sarasota, FL; Florida State Collection of Arthropods, Division of Plant Industry, Florida Department of Agriculture and Consumer Services, Gainesville. Research Associate in Entomology: Los Angeles County Museum of Natural History, Los Angeles, CA.

electrophoresis, relative to five species of *Colias*, but *hecla* and *nastes* were not included in his studies (1976, 1977a, b). It should be possible to verify hybridization, beyond reasonable doubt, between two *colias* species by this technique. As is the case with direct hybridization studies, there are practical problems. Diagnostic enzymes would have to be identified, and more important, the gel separations would have to be carried out in the field using freshly-caught specimens (not any easy task), or field-collected material would have to be held at cryogenic temperatures for subsequent laboratory analysis (an even more difficult problem).

The relative abundance of *C. boothii* is variable and its geographic boundaries appear to be somewhat fluid based upon anecdotal comments in the literature (Holland *et al.*, 1935; Hovanitz, 1963a, b; Ferris *et al.*, 1983). This situation has led many specialists to suggest informally that *C. boothii* possibly represents a hybrid *C. nastes X C. hecla.* Avinoff *in* Holland *et al.* (1935) made a fairly strong statement in this regard.

In May 1984, I visited the Biosystematics Research Institute in Ottawa to examine various arctic butterflies in order to obtain data relative to a multiple-author publication on Canadian Arctic Lepidoptera. During the course of this study and the examination of several thousand specimens in the *C. nastes-thula-boothii-hecla* group, some consistent maculation and distribution patterns emerged. During a subsequent visit in November to the Allyn Museum/Florida State Museum, I examined material originally in the Strecker, Chermock, and Hovanitz collections. Ultraviolet photographic analysis and scanning electron microscope studies of wing scales conducted during my visit further confirmed the occurrence of the patterns noted previously. The conclusions drawn herein are based upon these sources and data, and additional material in my personal collection.

The data presented in the sections which follow suggest very strongly that *C. boothii* and *C. thula* represent two expressions of a hybrid swarm from the parent species *C. nastes* and *C. hecla.* This premise leads to the recognition that two previously considered subspecies of *nastes* are actually three-fourths *nastes* - one-fourth hecla hybrid forms. Appendix B provides a genetic analysis to support the conclusions drawn. Consequently a revision of the *C. nastes* group is required. The presentation in this paper is thus ordered with an initial discussion of the hybrid swarm theory and supporting data. Final conclusions are then drawn based upon the evidence presented. The final section of the paper contains the *C. nastes* revision.

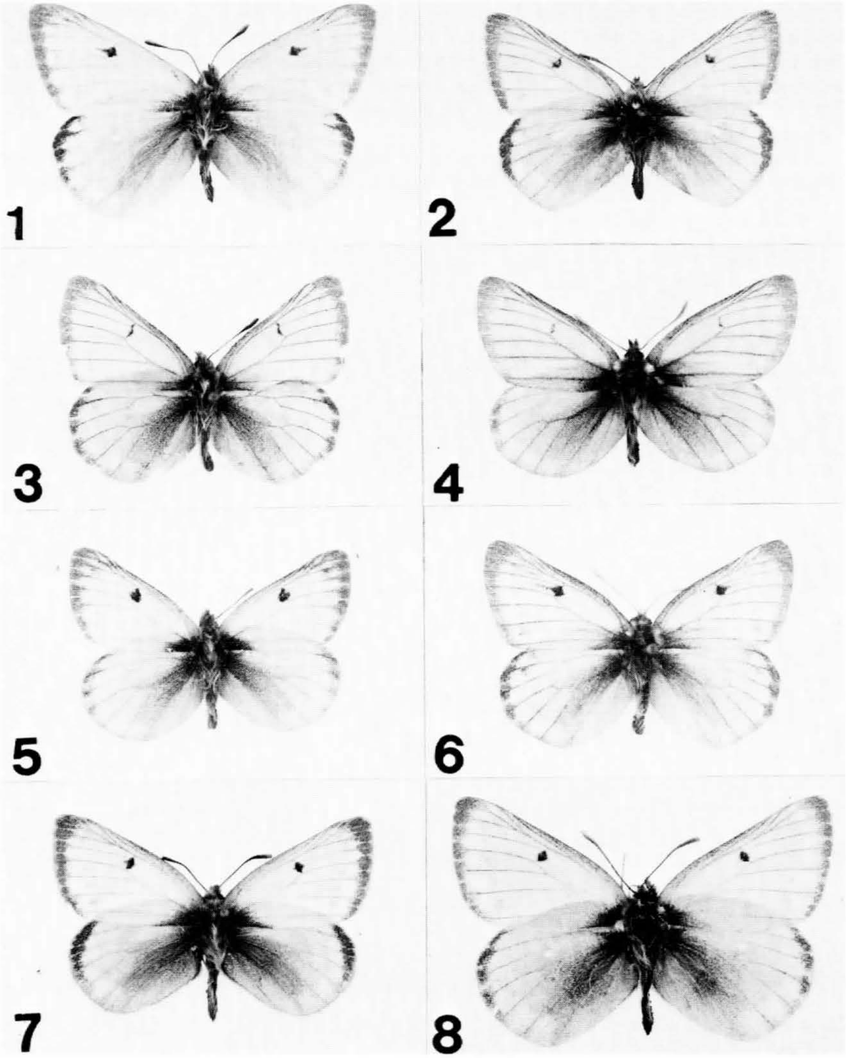
Original Descriptions of *C. boothii* and *C. nastes thula*

John Curtis supplied a detailed description of *C. boothii* and *C. chione* as well as illustrations of both (1835). In contemporary literature, the latter taxon has been treated as a form of *boothii.* The types of both taxa were collected in the Boothia Peninsula, N.W.T., Canada during the summer of 1830. The supposed types were purchased by William Barnes from the Oberthür collection and were eventually placed in the National Museum of Natural History in Washington. They were figured in Holland *et al.* (1935) in plate 26, figs. 11-11a, *chione;* figs. 12-12a, *boothii* ♂; figs. 13-13a, *boothii* ♀. The specimens illustrated do not agree very well with the illustrations in Curtis (plate A, figs 3-6), especially the pair of *boothii.* Verity (1911) also illustrated the male "type" of *boothii* (plate 43, fig. 37) and the accompanying caption (in translation) reads: "from the collection of Curtis, Doubleday and Guenée in the Oberthür collection." When the "type" illustrated by Holland *et al.* is overlaid with the "type" illustrated by Verity, the two specimens do not match. Neither specimen is a good match for the Curtis illustration. In the Hope Museum Collections at Oxford University in England, there are five specimens of *boothii* collected by Sir John Ross. One male bears the handwritten label: "Chione Curtis Ross Appen." The label associated with the other specimens reads: "Boothii Curt. Ross App." Three of these specimens (the *chione* and a pair of the *boothii*) match reasonably closely the illustrations in the Curtis Appendix to the Ross report in which these taxa were described. One key is the shape of the DFW cell spot as it appears in the Curtis plate and in photographs of the specimens. Thus the "type" that Verity illustrated and the "type" in the NMNH appear to be incorrectly labeled. Hence the Oxford specimens and the NMNH specimens must be considered as syntypes at this point. The whereabouts of the specimen illustrated by Verity is unknown. Barnes had attempted to purchase all of the North American type specimens in the Oberthür Collection, but it appears that he was sold some false material.

For completeness, the Curtis descriptions are reproduced below.

"10. *Boothii.* Yellow, posterior margins blackish, cilia rosy; a black spot on the superior wings, the disc orange, and a spot of the same colour on the inferior.

"Expansion of wings two inches.

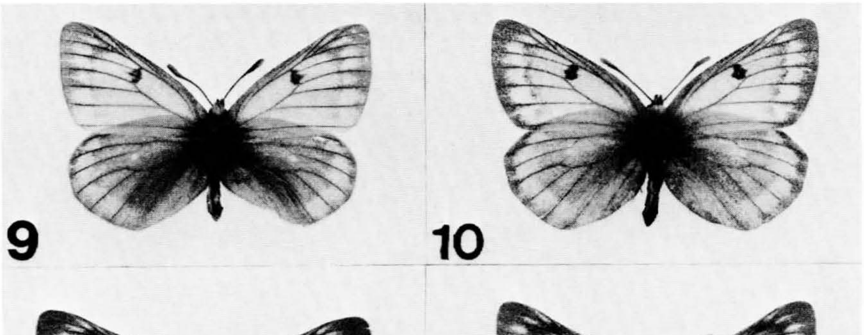


Figures 1-8: *Colias boothii* (odd numbers) and *Colias thula* (even numbers) males, D. Locality data: (1) Coral Harbour, Southampton Is., N.W.T. (3) Repulse Bay, N.W.T. (5, 7) Spence Bay, N.W.T. (2, 4, 6) Cambridge Bay, N.W.T. (8) Holman, Victoria Is., N.W.T. Specimens in Canadian National Collection.

"Pl. A, fig. 3 ♂, 4 ♀, 5 underside of ♀.

"*Male.* Antennae crimson, the club beneath ochreous, above brown: thorax and abdomen black, clothed with long whitish hairs, rosy on the collar and head; wings sulphur colour, freckled with black at the base, and the posterior margins forming a dentated fimbria, which vanishes before reaching the anal angle; costa and cilia rosy, the nervures sometimes rather dark in the superior wings, with a large space of orange not approaching the costa or posterior margin; at the apex of the discoidal cell is a black sublunulate spot; inferior wings with a large orange spot on the disc, and sometimes a small one above it; *underside* thickly freckled with black, especially the inferior wings, but less so at the posterior margins; the entire edges of the wings are rosy; superior with a whitish dot on the black spot, which is variously formed; inferior with a large and small whitish spot on the disc, surrounded with a reddish-chestnut colour, forming two tails towards the posterior margin, a spot of the same colour at the base, and frequently a lunate brown spot on the upper edge; legs rosy.

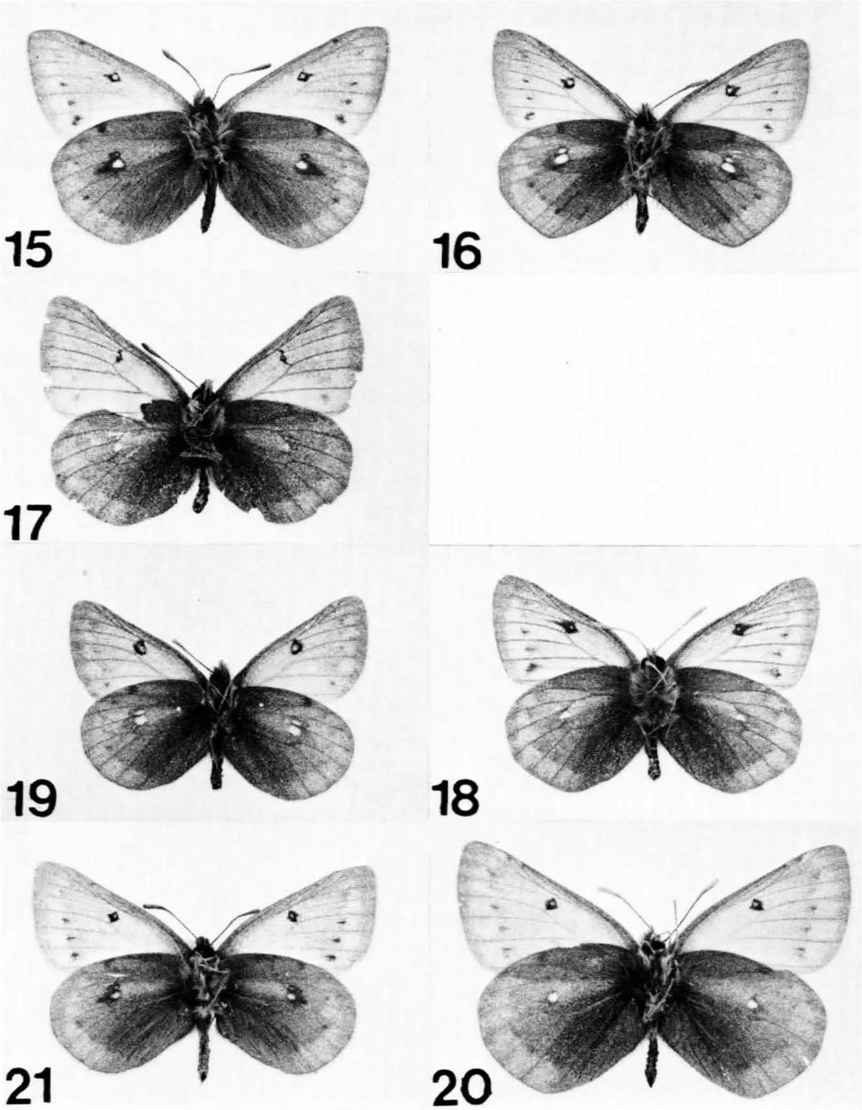
"*Female.* Similar to the male, but the black freckled fimbria to the wings is broader and ornamented with seven large yellow spots in the superior, and six in the inferior,



Figures **9-14:** *Colias boothii* (odd numbers) and *Colias thula* (even numbers) females, D. Locality data: **(9)** Coral Harbour, Southampton Is., N.W.T. **(11, 13)** Repulse Bay, N.W.T. **(10, 12)** Cambridge Bay, N.W.T. **(14)** Holman, Victoria Is., N.W.T. Specimens in Canadian National Collection.

which are, excepting these spots, entirely freckled with black, and have a greenish tinge; the *underside* is darker and brighter than in the male, the inferior wings and the freckled parts of the superior are green, parallel to the posterior margin is a line of subtrigonate spots, very distinct and black in the superior, and reddish-brown in the inferior wings.

"A small specimen of the male, I observe, has indistinct yellow spots on the fimbria of the superior wings, and the castaneous comet-shaped spots on the underside of the



Figures 15-21: Ventral views at *Colias boothii* (odd numbers) and *Colias thula* (even numbers) shown in Figs. 1-8 respectively (Fig. 4 omitted).

inferior are very small, and in one female the black spot in the upper, and the orange spots in the inferior wings are very large, and in another female the upperside very much resembles the male.

"At the request of Commander Ross, I have named this handsome insect after Felix Booth, Esq., the munificent patron of the Expedition.

"11. *Chione. Male,* yellow, superior wings orange on the disc, with an orange spot near the centre of all the wings. *Female?* with the nervures and a spot near the disc black, with a broad black fimbria spotted yellow.

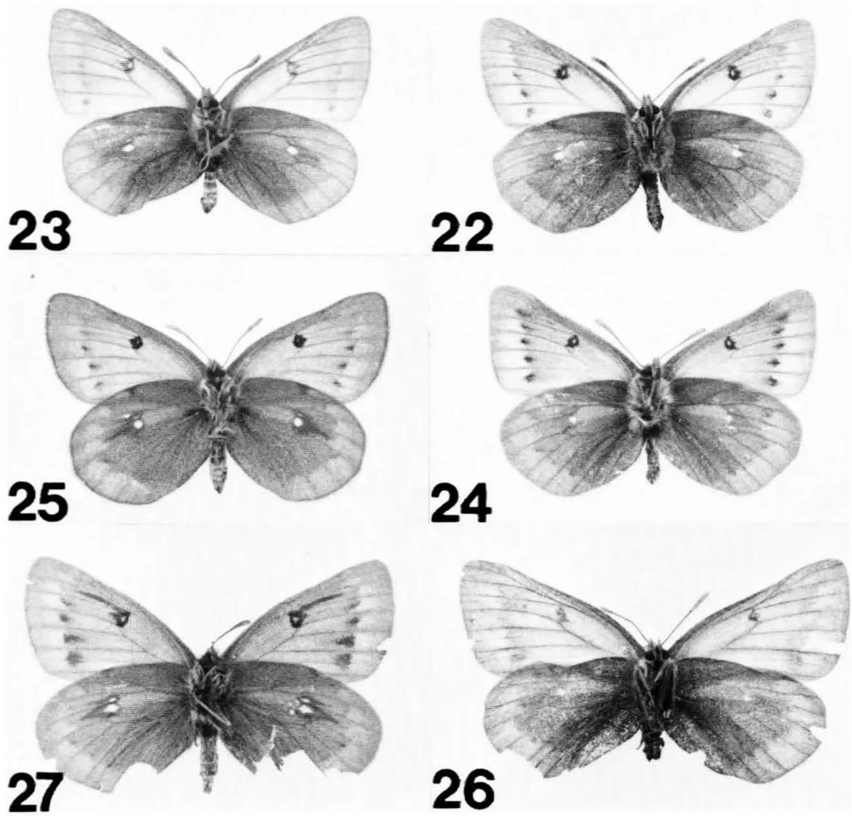
"Expansion one inch eight lines to one inch ten lines.

"Pl. A, fig. 6, ♂.

"*Male* similar to *C. boothii,* but the spot at the apex of the discoidal cell is orange, and the posterior margins of the wings are very slightly freckled with black; the underside in some examples resembles the female rather than the male of the same species.

"*Female,* greenish sulphur, superior wings slightly orange on the disc, with the nervures and a lunulate spot black, a broad black fimbria bearing six or seven small sulphureous spots; inferior with a similar fimbria, but less perfect, and an orange spot on the disc; *underside* pale greenish sulphur, similar to *C. boothii,* but having only one comet-shaped spot on the under wings."

Although it has been treated as a full species in several recent checklists (Miller & Brown,



Figures 22-27: Ventral views of *Colias boothii* (odd numbers) and *Colias thula* (even numbers) shown in Figs. 9-14 respectively.

1981; Hodges *et al.*, 1983), Hovanitz described *thula* as a subspecies of *C. nastes.* The type series was collected along the Meade River south of Pt. Barrow, Alaska (70°45'N, 156°30'W) during the summer of 1952. the holotype male and allotype female are in the collection of the National Museum of Natural History. Of this species, Hovanitz stated: "The *C. nastes* are in appearance more like specimens of this species from Scandinavia than they are like any others from North America." More will be stated about Scandinavian material later in this paper. Hovanitz's original description (1955) is now reproduced for reference. The types along with additional material are illustrated in the paper.

"DESCRIPTION: *Holotype,* male; size of wing 20 mm. (measured from thorax at costal vein to apex), wing expanse 38 mm. (measured from outer margin of fore wing to same of opposite wing); ground color pale lemon yellow with a scattering of black scales toward margins, especially on hind wing and at base of wings; underside hind wings and tip of apex of fore wings yellow but heavily suffused with black scales; ground color of fore wings underside white, hind wing-cell spot white surrounded by red, spot with small satellite; pattern on upper side of wings consisting of marginal row of black with an indecisive inner edge tending toward a female-type of pattern but not like other North American males of *C. nastes.*

"*Allotype* female; size of wing and expanse same as in male; color as in males except slightly lighter ground color; pattern is that typical of a female *Colias* with fully developed border pattern from apex to inner margin of fore wings but almost entirely undeveloped on hind wings. Hind wings nearly the same in male and female."

THESIS

It is now asserted that *C. boothii* and *C. thula* are different color morphs of the same insect, and moreover that they represent the F_1 generation of *C. nastes X C. hecla.* Supporting data appear in the sections that follow.

Visible - Light Data

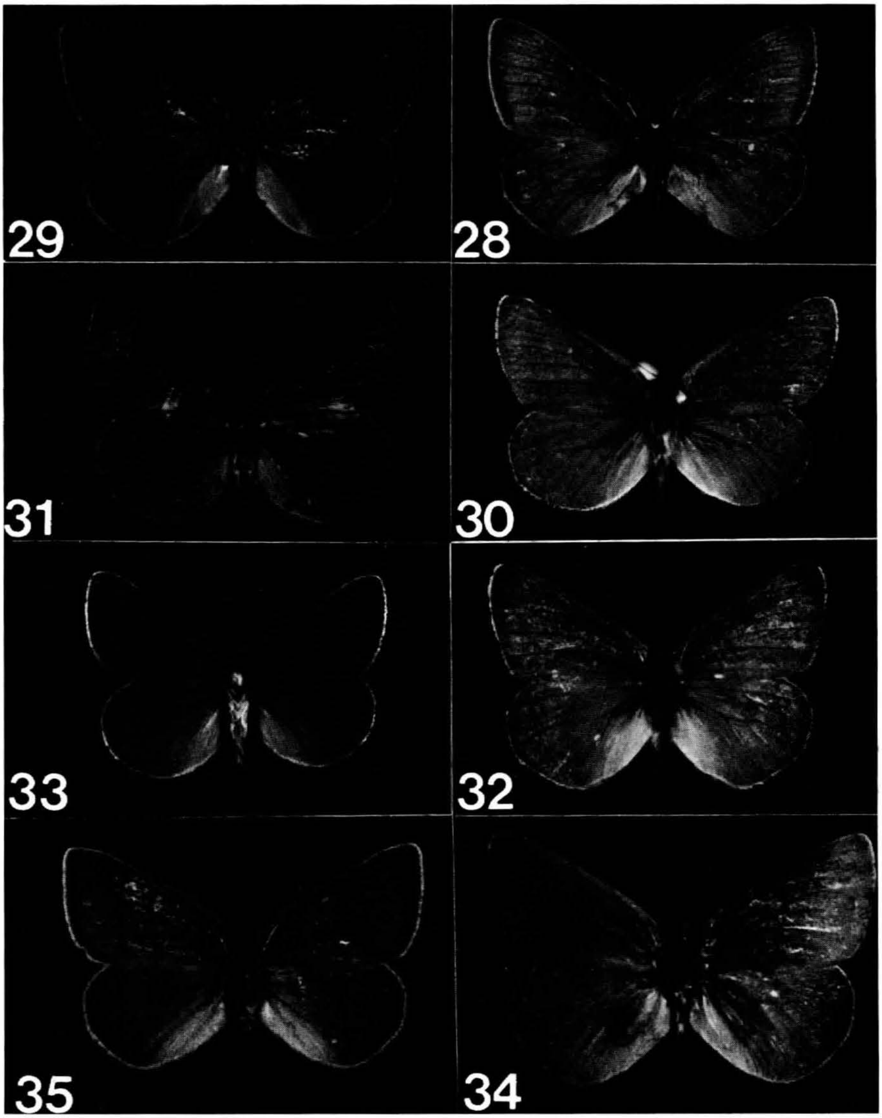
Figs. **1-8** illustrate males of *C. boothii* (odd numbers) and *C. thula* (even numbers) photographed using panchromatic film without the aid of filters. Figs. **9-14** illustrate females of *C. boothii* (odd numbers) and *C. thula* (even numbers) photographed under the same conditions as the males. Note in these side-by-side comparisons that the maculation is virtually identical between the two taxa once color is removed as a variable. Figs. **15-27** show the undersides of the same specimens. There is some degree of variability, but this is to be expected, since both *hecla* (Ferris, 1982) and *nastes* (later section of this paper) display considerable ventral variability. The underside of the specimen of Fig. **4.** is not shown since this butterfly was used for SEM studies following photography of its upperside. The specimens shown in Figs. **1-27** illustrate the typical range of variation of these two taxa.

Ultraviolet - Light Data

Figs. **28-41** illustrate the same specimens as shown in Figs. **1-14** photographed under UV illumination using a Wratten 18A filter. A non-reflective background was used to prevent any backlighting. All of the specimens are very slightly reflective, but the brilliant reflectance exhibited by *C. hecla* is not present. The reflectance patterns produced by both *boothii* and *thula* are similar. Most of the reflectance variation among the specimens can be attributed to their condition. Some were rather worn and had partially lost their reflective cover scales. See also Appendix B regarding variable reflectance.

Figs. **42-47** illustrate males of two subspecies of *C. hecla,* and *C. nastes nastes* photographed using visible light (even numbers) and UV light (odd numbers). Figs. **48-53** show respectively two subspecies of *C. hecla, C. boothii, C. thula, C. nastes* f. "rossii", and *C. nastes nastes* photographed under UV light. *C. hecla* is rather variable in its UV reflectance pattern as indicated by Figs. **43** and **48** *(C. hecla hela)* and Figs. **45** and **49** *(C. hecla hecla).* In part this is real, and in part the differences observed are related to specimen age (loss of cover scales) and the angle of which the UV light strikes the wing surfaces. *C. hecla* is strongly reflective to incident UV light, while *boothii*, *thula* and *nastes* appear to be weakly reflective. Figs. **54-55** are UV photographs of the lectotypes of two *nastes* subspecies.

Figs. **56-57** are respectively dorsal and ventral views under UV illumination of a peculiar specimen from Arctic Bay, Baffin Is., N.W.T. Under visible light dorsally, the left side



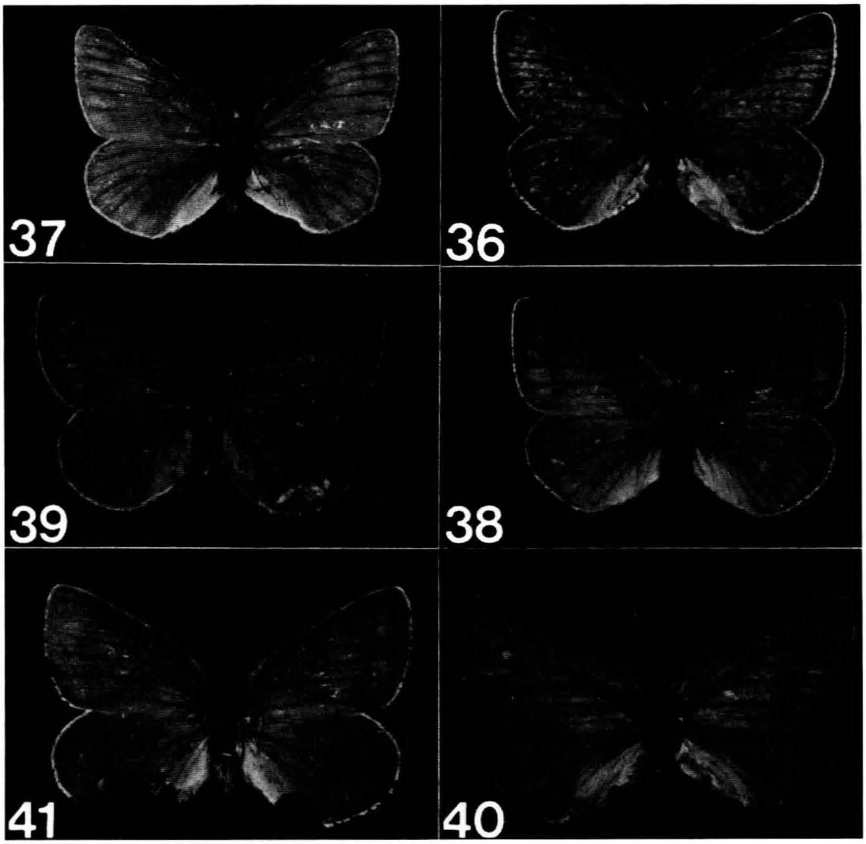
Figures **28-35**: Ultraviolet light photographs of *Colias boothii* (odd numbers) and *Colias thula* (even numbers) shown in Figs. **1-8** respectively.

resembles a typical *thula*, while the right side is colored yellow-orange as in *boothii* except for the FW apex which is white as in *thula*. Ventrally the color pattern is reversed. The V surface of the *thula*-like side resembles *boothii* (right side in Fig. **57**). It is bright olivaceous with the DHW discal spot strongly produced distally. The V surface of the *boothii*-like side (left side in Fig. **57**) resembles many *thula*. It is gray and the VHW discal spot is not strongly produced distally. In effect, both the D and V surfaces exhibit mosaic patterns which are emphasized when the specimen is photographed under UV illumination.

UV photographic studies tend to support the premise that *boothii* and *thula* are simply color morphs of the same butterfly. The next section examines wing scale structure using the scanning electron microscope.

Scanning Electron Microscope Data

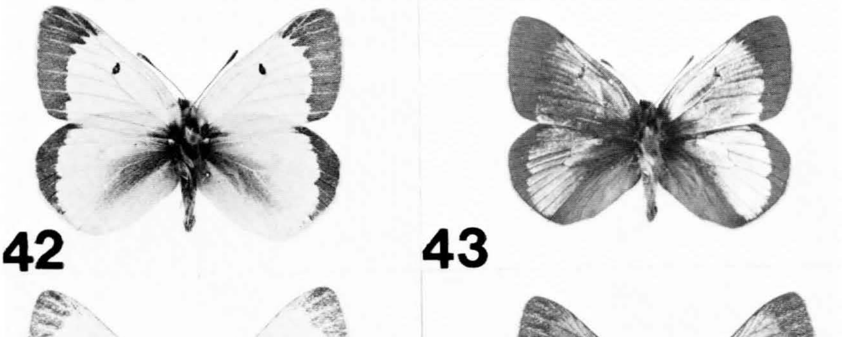
Figs. **58-63** are respectively SEM photographs of the DFW scales of the specimens shown in Figs. **48-53**. The pointers indicate cover scales which reflect UV light. The reflective cover scales possess wavy ridge lines, while the non-reflective basal scales have parallel ridge lines. The fine structure of this type of scale has been elaborated by Ghiradella *et al.* (1972). These scales are present in *hecla*, *boothii* and *thula*, but not in *nastes* f. "rossii"



Figures **36-41**: Ultraviolet light photographs of *Colias boothii* (odd numbers) and *Colias thula* (even numbers) shown in Figs. **9-14** respectively.

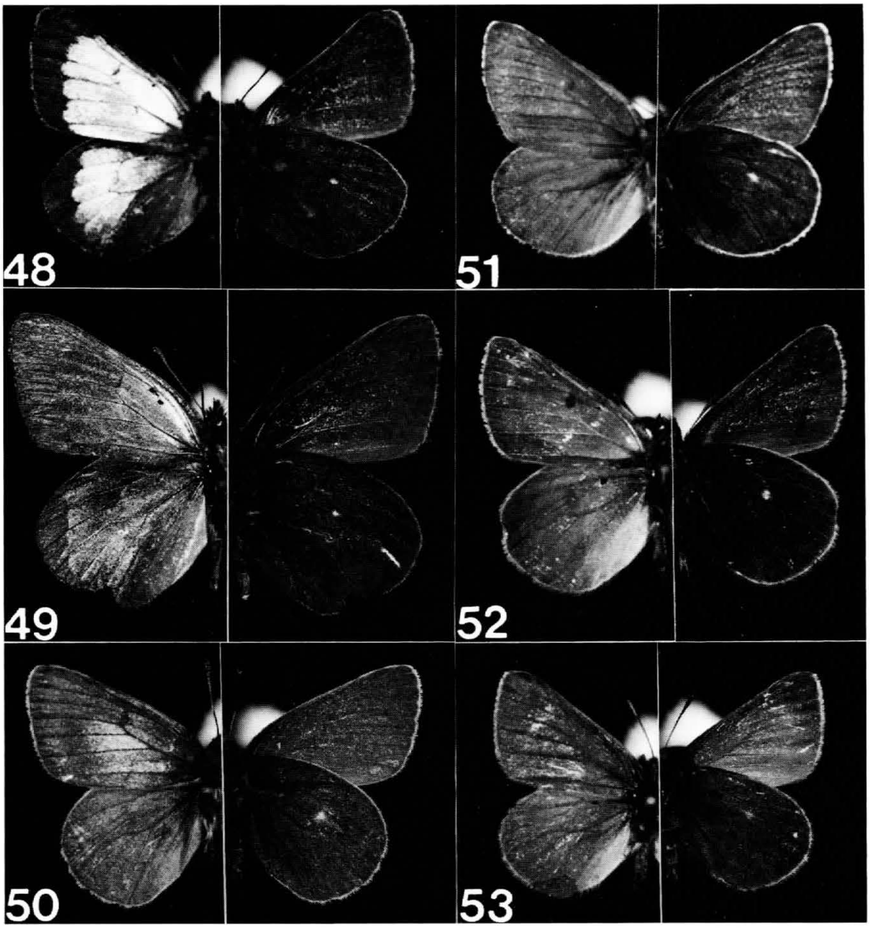
or in typical *nastes*. Many of the cover scales in *C. nastes* seem to be rather fragile (especially on the HW) and apparently curl to some extent when dehydrated in preparation for SEM examination. This deformation causes the scales to resemble slightly the scales in *hecla* and *boothii/thula* that are responsible for UV reflectance. Under high magnification, these *nastes* scales lack the structural components associated with the UV-reflective scales found in *hecla* and *boothii/thula*. There is some reflectance produced by the wings of *nastes* and the probable source is discussed in the next paragraph. The wings of both *C. boothii* and *C. thula* display far fewer UV-reflective cover scales than are found in *hecla*. This is certainly consistent with the results of UV photography and supports the theory that these two taxa represent hybrid forms.

Figs. **64-67** are magnifications respectively of the reflective scales shown in Figs. **58-61**. Figs. **68-69** are magnifications of the common scales found in *nastes*. The layered lamellar ridges (pointers) are the UV-reflecting structures. In *hecla* (Fig. **64**), there are 5-6 lamellae contained in the ridge lines. In *hela* (Fig. **65**), the ridge lines consist of only 4-5 lamellae,



Figures **42-47**: *Colias hecla hela*, Churchill, Manitoba, ♂, D, normal photograph (**42**) and UV light photograph (**43**). *Colias hecla hecla*, mile 111, Steese Hwy., Alaska, ♂, D, normal photograph (**44**) and UV light photograph (**45**). *Colias nastes nastes*, Nain. Labrador, ♂, D, normal photograph (**46**) and UV light photograph (**47**). Specimens in C. D. Ferris Collection.

which results in a reduction in UV reflectance. The reflective scales in *boothii* (Fig. **66**) also contain 4-5 lamellae in the ridge lines. The ridge lines on the cover scales in *C. thula* (Fig. **67**) are more finely structured and the scale substrate is more open than in preceding examples. In *C. nastes* f. "rossii" (Fig. **76**), all of the scales are of the basal type and there are no UV-reflective cover scales. This agrees with the absence of any significant UV reflectance (Fig. **52**). *C. nastes nastes* (Fig. **69**) also exhibits one form of scale. The structure is highly fenestrated with open windows defined by the longitudinal ribs and the crossribs (see Downey & Allyn, 1975 for definitions). The cover scales, however, have very thin ridge lines similar to those found in some species of the Nymphalidae genera *Junonia*, *Eunica* and *Myscelia*, and which produce blue reflectance. This ridge-line structure may account for some reflectance in the near UV as observed in Figs. **47** and **53**. The optical effect produced by the thin ridge lines is analogous to the reflected colors produced by a thin film of oil covering a water surface.

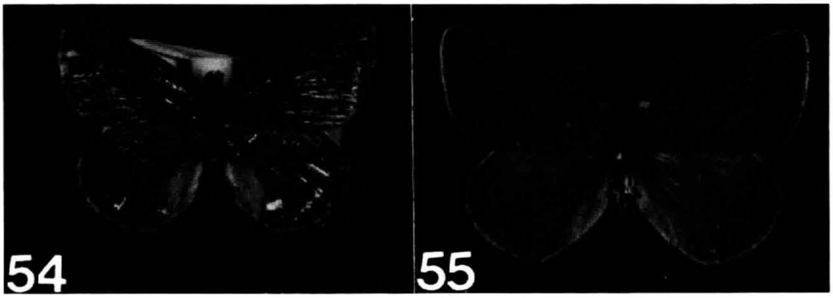


Figures **48-53**: UV light photographs of male *Colias*; D left and V right. *Colias hecla hecla* (**48**). *Colias hecla hela* (**49**). *Colias boothii* (**50**). *Colias thula* (**51**). *Colias nastes* fm. "rossii" (**52**). *Colias nastes nastes* (**53**). Specimens in Allyn Museum of Entomology / Florida State Museum Collection.

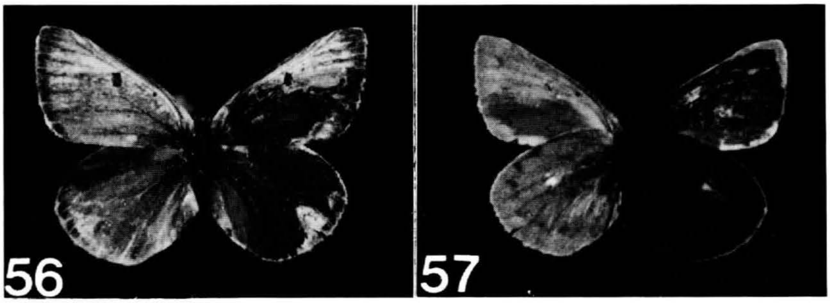
Figs. **70-73** illustrate the structure of the basal (non-reflecting) scales in *hecla* (FW), *thula* (FW & HW) and *nastes* (HW). Note the presence (pointers) of oblate spheroidal particles normally found in the wing scales of Pierids. The HW scales in *nastes* (Fig. **73**) appear to be very fragile and apparently curl when dehydrated, thus producing the contorted aspect displayed in the figure.

Figs. **74-79** are respectively DHW scans of the same specimens shown in Figs. **58-63.** Again the pointers denote the UV-reflecting cover scales. The scales are virtually identical to those on the FW in each case, with the exception of *C. nastes* (Fig. **79**) in which the curling of the HW cover scales is evident, and *C. boothii* in which no lamellar (UV-reflecting) scales are present. Note that the HW scales in *thula* (Fig. **77**) are single-layered without distinct cover and basal scales. This is also true to some extent in *boothii* (Fig. **76**).

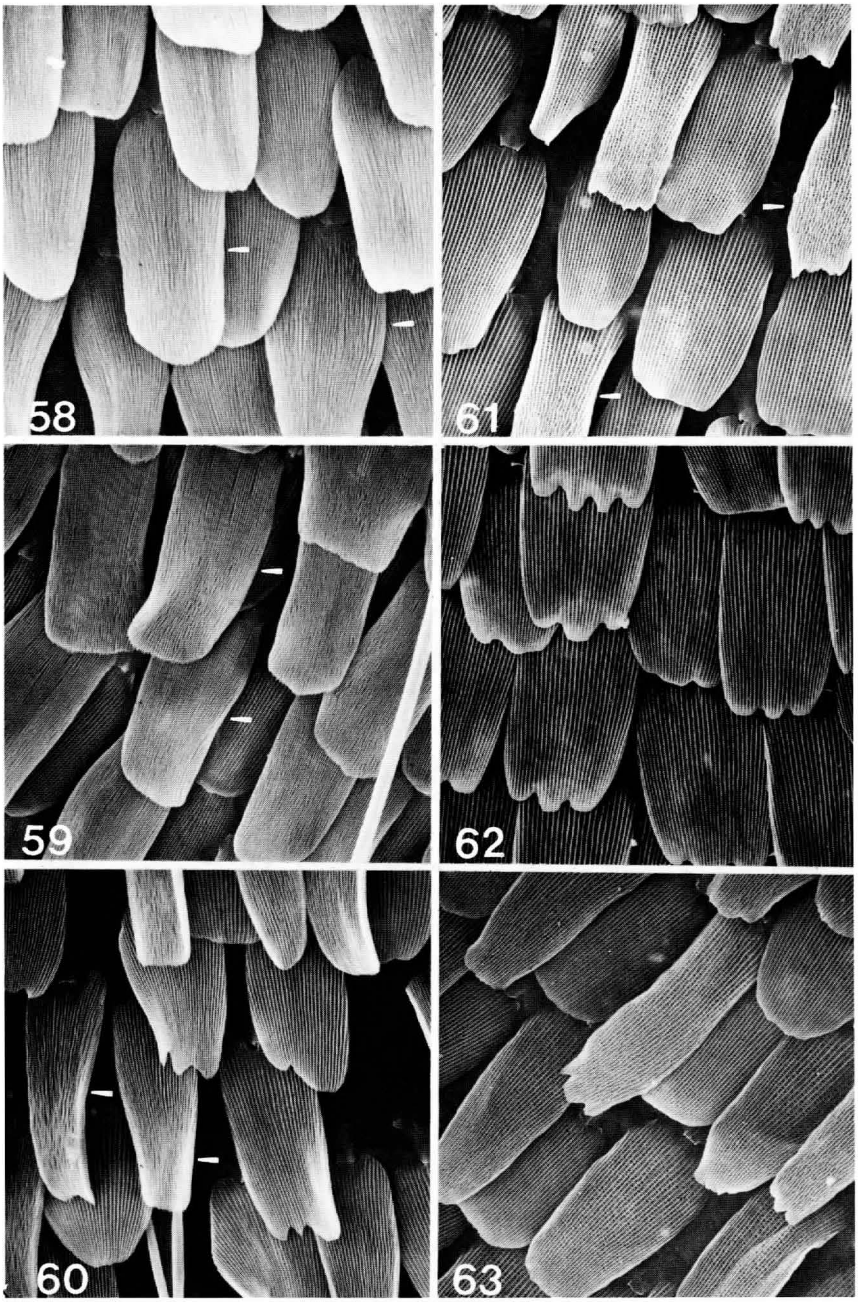
Figs. **80-85** are respectively scans at higher magnification of the same specimens shown in Figs. **74-79.** The HW UV-reflective scales in *hecla* and *hela* (Figs. **80-81**) are virtually identical to the FW scales (Figs. **64-65**). The HW scales in both *boothii* (Fig. **82**) and f. "rossii" (Fig. **84**), which are non-reflective, exhibit substantial covering of the normal fenestrations by a membranous structure. This structure acts as a highly reflective surface in some genera, but its function in this instance is unknown, since neither *boothii* nor fm. "rossii" reflect any significant amount of UV light from the HW. The thickened ridge lines (pointer) of the *thula* scale (Fig. **83**) may produce some UV reflectance, but this is equivocal. Fig. **85** is a typical *nastes* HW basal scale (non-reflective).



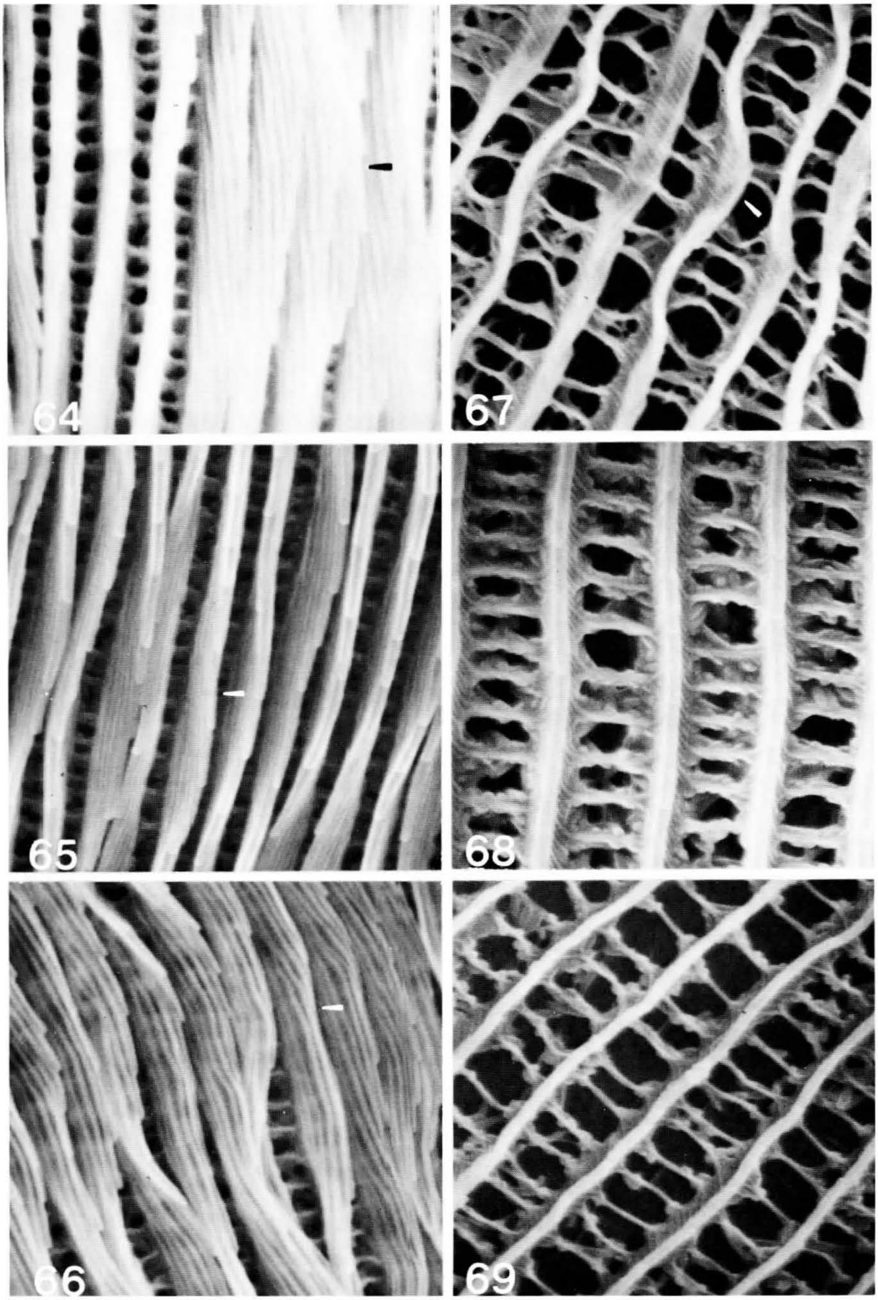
Figures **54-55**: UV photographs of lectotypes of *Colias nastes moina* ♂, D (**54**) and *Colias nastes streckeri* ♂, D (**55**). Specimens in Strecker Collection at the Allyn Museum of Entomology / Florida State Museum.



Figures **56-57**: UV photograph of male *Colias* mosaic between *Colias boothii* and *Colias thula*. D (**56**) and V (**57**). Locality: Arctic Bay, Baffin Is., N.W.T. Specimen in AME / FSM Collection.



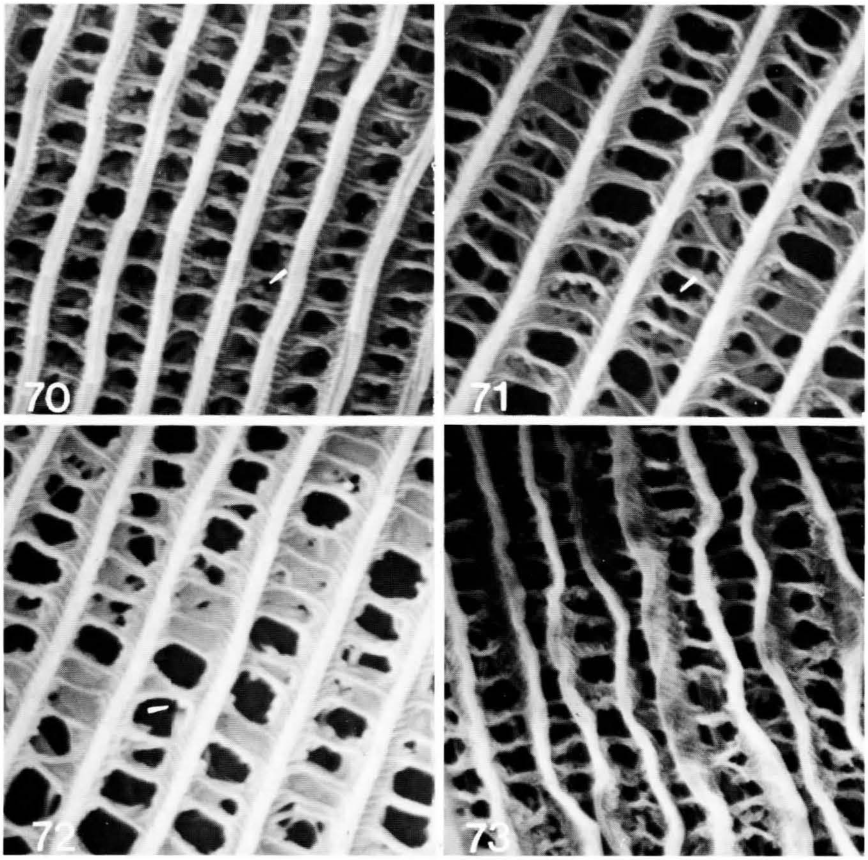
Figures 58-63: Photographs of SEM scans of the DFW of six male *Colias* specimens. Magnification = 500X. *Colias hecla hecla* (58). *Colias hecla hela* (59). *Colias boothii* (60). *Colias thula* (61). *Colias nastes* fm. "rossii" (62). *Colias nastes nastes* (64). The pointers indicate cover scales with layered-lamellar (UV-reflective) ridge-lines.



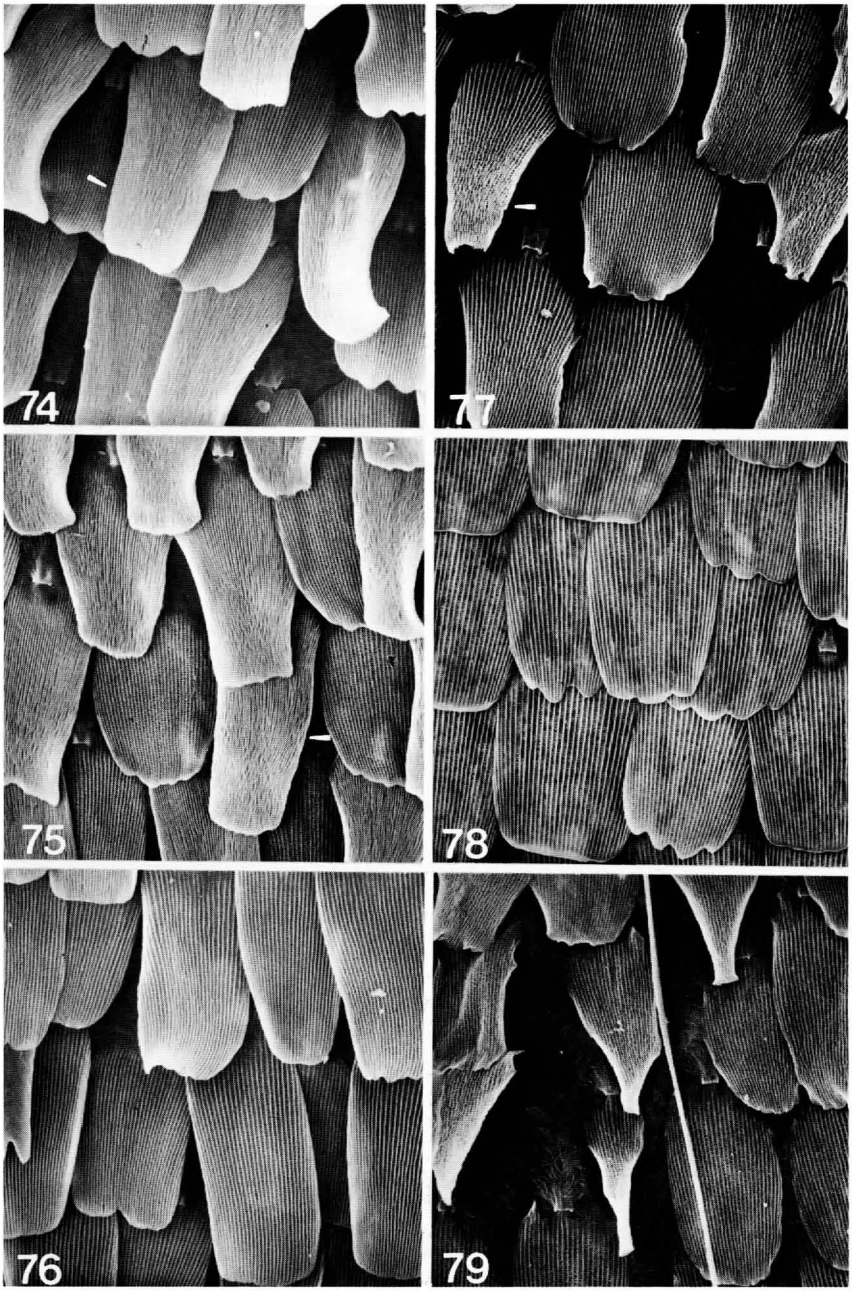
Figures **64-69**: Smae as Figs. **58-63** respectively but at 10,000X magnification. The pointers indicate the layered lamallae on the right-lines.

Optical Reflectance Scans

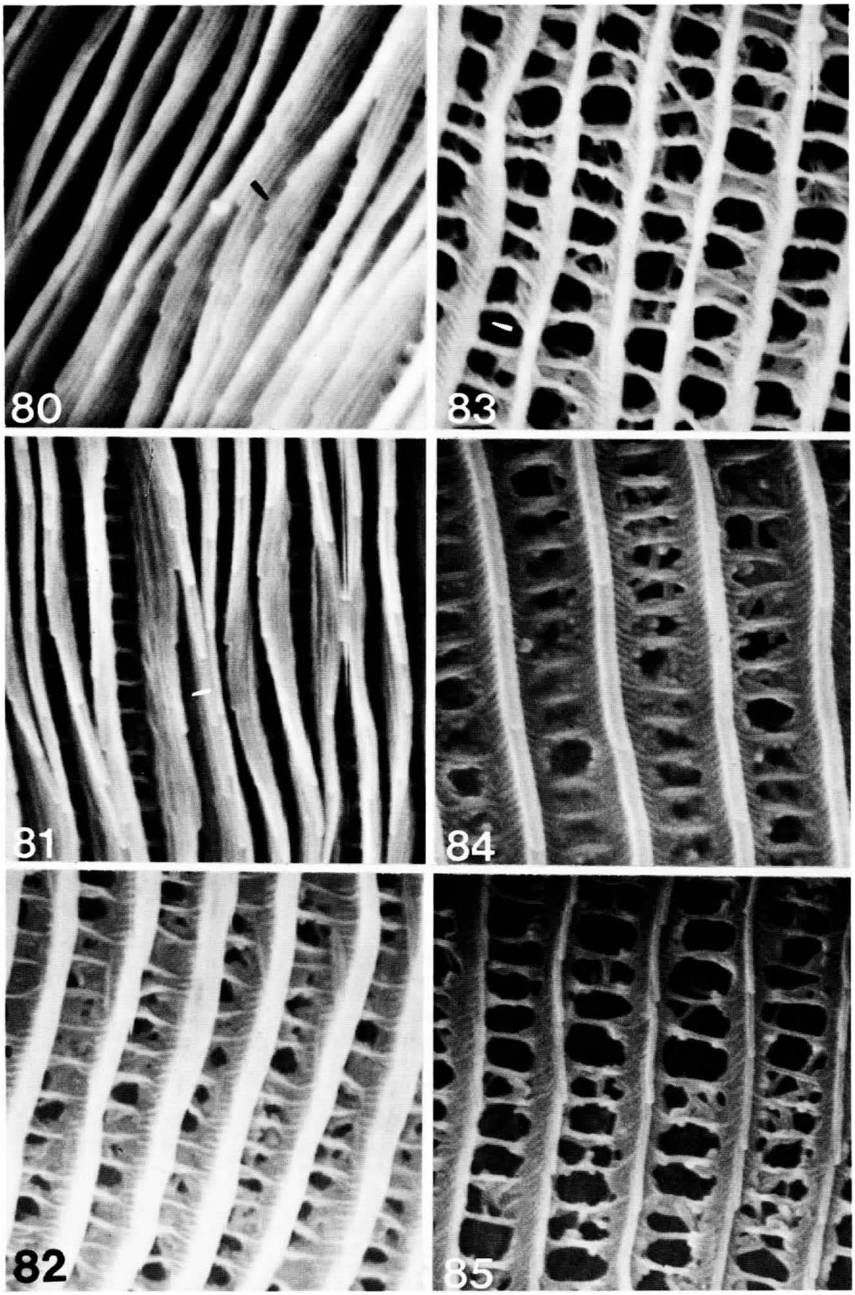
Specimens of the taxa under investigation were subjected to optical reflectance scans over the wavelength range 800 nm to 350 nm. The specimens were illuminated using a high-intensity tungsten lamp, and the light reflected from the dorsal wing surfaces was directed using front-surfaced concave mirrors through the monochromator (2 nm fixed slit width) and optical detector of a Perkin-Elmer model 2280 Atomic Absorption-Emission Spectrometer. Correction for the spectral response of the instrumentation system was achieved by taking the difference between the light energy reflected by the specimens and that reflected from a standard photographic white card. This step is necessary to correct for non-uniform spectral characteristics of the exciter lamp and optical detector. Thus the results shown in Fig. **86** are reflectance from the butterfly wings *relative to the reflectance produced by a standard photographic white card.* The raw data are presented in Appendix C and Fig. **130**. The data presented in Fig. **86** are not absolute values of reflectance. The reflectance level of the white card is the horizontal "0" line in Fig. **86**.



Figures **70-73**: Photographs of SEM scans of the D wing scales of four *Colias* males. Magnification = 10,000X. Basal scale structure (non-UV reflective) of *Colias hecla hecla* DFW (**70**). Basal scale structure of *Colias thula* DFW (**71**) and DHW (**72**). Cover scale structure of *Colias nastes nastes* DHW (**73**). The pointers indicate the spheroidal particles mentioned in the text.



Figures 74-79: Photographs of SEM scans of the DHW of six male *Colias* specimens. Magnification = 500X. *Colias hecla hecla* (**74**). *Colias hecla hela* (**75**). *Colias boothii* (**76**). *Colias thula* (**77**). *Colias nastes* fm. "rossii" (**78**). *Colias nastes nastes* (**79**). The pointers indicate cover scales with layered-lamellar (UV-reflective) ridge-lines.

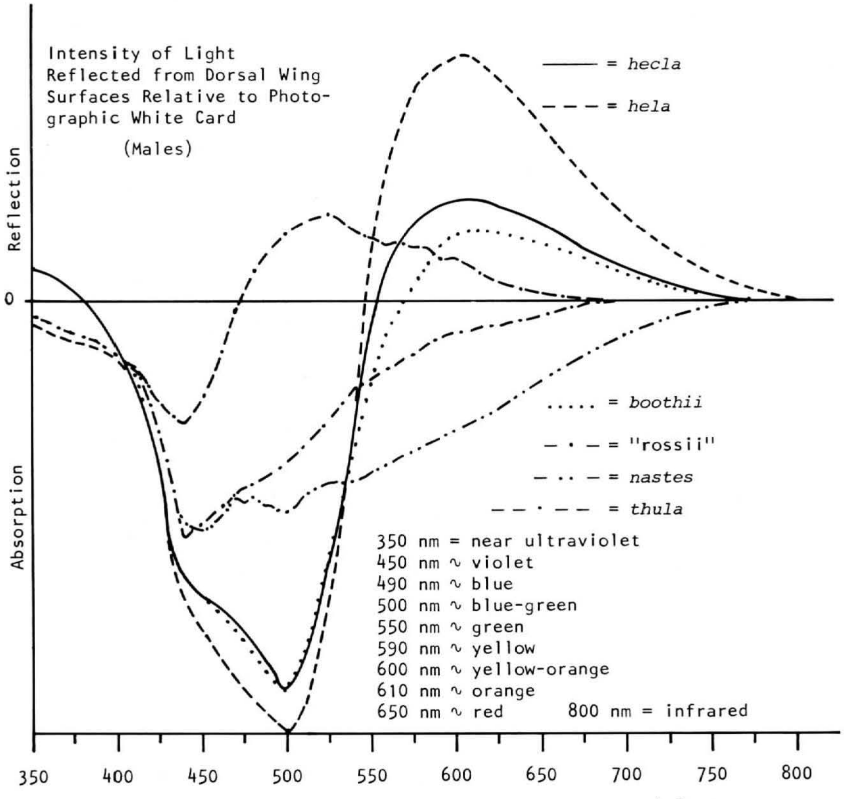


Figures **80-85**: Same as Figs. **74-79** respectively but at 10,000X magnification. The pointers indicate the layered lamellae on the ridge-lines.

The white card is strongly reflective in the UV portion of the spectrum as can be seen in Figs. **43**, **45**, **47** for which a white card was used as a background. The sensitivity of optical detector was adjusted for each specimen such that the energy reflected at 800 nm was the same as that reflected by the white card. Because of this adjustment, which was different for each specimen, the curves shown in Fig. **86** cannot be compared on an absolute basis. The "Absorption" region in Fig. **86** represents light absorption relative to the white card. The "Reflectance" region in Fig. **86** represents light reflection relative to the white card baseline. The interpretation of the data presented in Fig. **86** is as follows:

Colias hecla hecla: Reflects light in the red-to-yellow portions of the spectrum; absorbs light in the blue-green portion of the spectrum (maximum absorption at 500 nm); reflects light in the near ultraviolet.

Colias hecla hela: Reflects light strongly in the red-to-yellow portion of the spectrum: absorbs light in the blue-green portion of the spectrum (maximum abs. at 500 nm); becomes



86

Figure 86: Scan of reflected light intensity from six male *Colias* specimens as a function of optical wavelength in nanometers.

reflective again in the near ultraviolet.

Colias boothii: Pattern similar to *hecla* and *hela*, but less reflective in the orange and near ultraviolet portions of the spectrum.

All three of the above species exhibit peak reflection in the region 600-610 nm, and maximum absorption in the region 495-505 nm.

Colias nastes f. "rossii": No distinct reflectance peak in the yellow-orange portion of the spectrum, but broad absorption in the blue-violet portion of the spectrum, which is indicative of some pigmentation of yellow-orange hue (which the specimen scanned did have).

Colias nastes nastes: No distinct reflectance peak; absorption in the blue-violet region consistent with the yellow-greenish color of the specimen.

Colias thula: Broad reflection peak in the blue-green portion of the spectrum which is consistent with the white ground color of the specimen; weak absorption peak in the violet portion of the spectrum (which is consistent with the presence of any xanthopterin in addition to leucopterin in the ground color - see Appendix B); indication of reflection in the near ultraviolet.

The relatively undefined spectral response curves produced by *nastes* and *nastes* f. "rossii" can be attributed to the dark-dusted dorsal aspect of these two butterflies. The melanic cover scales damp out the reflection produced by the colored basal scales. The specimen of *thula* scanned was quite bright and produced a more clearly defined response curve.

It must be recognized that the data presented in Fig. **86** represent average reflectance of *diffused* light. The spectral response curves shown in the figure represent pigmental effects and gross structural effects. The fine-structure reflectance produced by the layered lamellae of the specialized scales is somewhat damped out. The "0" reference line, however, does indicate strong reflectance in the UV region since the white card is strongly reflective to UV illumination as noted above. Strong UV reflectance is best visualized by photographic methods.

Absorption in the blue-green portion of the spectrum is consistent with reflection in the yellow-orange portion of the spectrum. Thus we would expect *hecla*, *hela* and *boothii* to be more absorptive in the blue-green region than the paler "rossii", *nastes* and *thula*.

The data obtained from the visible light scans are entirely consistent with the data obtained by the scanning electron microscope and the photographic methods presented previously. Again it must be emphasized that the absorbance reflectance characteristics shown in Fig. **86** are relative to a standard white card and are not absolute. A standard photographic white card is approximately 90% reflective to incident illumination and should produce about equal reflectance throughout the visual spectrum, or it would not appear white. Thus the curves presented in Fig. **86** should be reasonably accurate in reproducing the true reflectance profiles of the specimens examined.

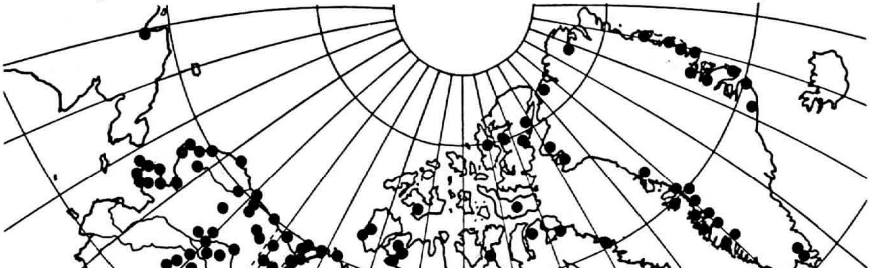
The data shown in Fig. **86** are based upon single specimens and do not represent averages of many specimens. They are consistent with the results presented by Roland (1978) relative to his studies on thermoregulation and reflected radiation in *Colias hecla*, *meadii* and *nastes.* His data (plotted in a different manner), however, indicate stronger absorption in the ultraviolet region than photographic records and my data suggest.

Geographic Distribution

Figs. **87-89** illustrate the geographic distributions of *C. hecla*, the *boothii/thula* complex and *C. nastes* in North America. Tables **1** and **2** in the Appendix delineate specific locality and regional distributions for these taxa. The map legends define the subspecific symbols for *hecla* and *nastes.* In Fig. **88**, the squares designate phenotypic *thula* and the solid circles phenotypic *boothii.* The triangles represent phenotypic intergrades between *thula* and *boothii.* The inverted triangles designate areas from which the "rossii" phenotype has been recorded, but not *boothii* or *thula.*

On a regional basis (Table 2), *boothii* and *thula* occur only where *hecla* and *nastes* also occur. This is true too of "rossii". On a specific locality basis, with a few exceptions, as shown in Table 1, *boothii*, *thula* and "rossii" only occur where *hecla* and *nastes* are present as well. One can probably safely assume that the missing species (*hecla* or *nastes*) is present in the few areas from which we do not have records. In many areas, *hecla* and *nastes* occupy different ecological niches and one of the two species may have been missed by collectors. In my experience, *C. nastes* colonies tend to be quite local and the butterflies tend not to disperse from the central colony. On the other hand, *C. hecla* generally disperses rather widely and is more visible to collectors owing to its bright color (as is also true of *boothii*). *C. nastes* is frequently difficult to see in the field because of its color which blends well with its environment. In montane regions of the arctic, *nastes* usually occurs at high elevation (ridges and mountain tops), while *hecla* frequents lower areas. The tendency of *hecla* to disperse widely brings it into contact with *nastes* colonies. In the Ogilvie Mts. in the Yukon, I have seen individuals of *hecla* carried on the wind from valleys below to the ridgetops where colonies of *nastes* reside. Singleton males of *hecla* are often encountered along roads and other barren localities where there are few nectar sources and no appropriate larval host plants.

In some regions, there is a temporal separation between adults of *hecla* and *nastes* as well as an environmental separation. In these regions, *hecla* normally flies early in the season (June) and *nastes* later (mid-July into August). In other areas, one of the two species may occur uncommonly, such as *hecla* in Labrador and in the vicinity of Churchill, Manitoba, and *nastes* at Pink Mt. in British Columbia. These localities, in which



87

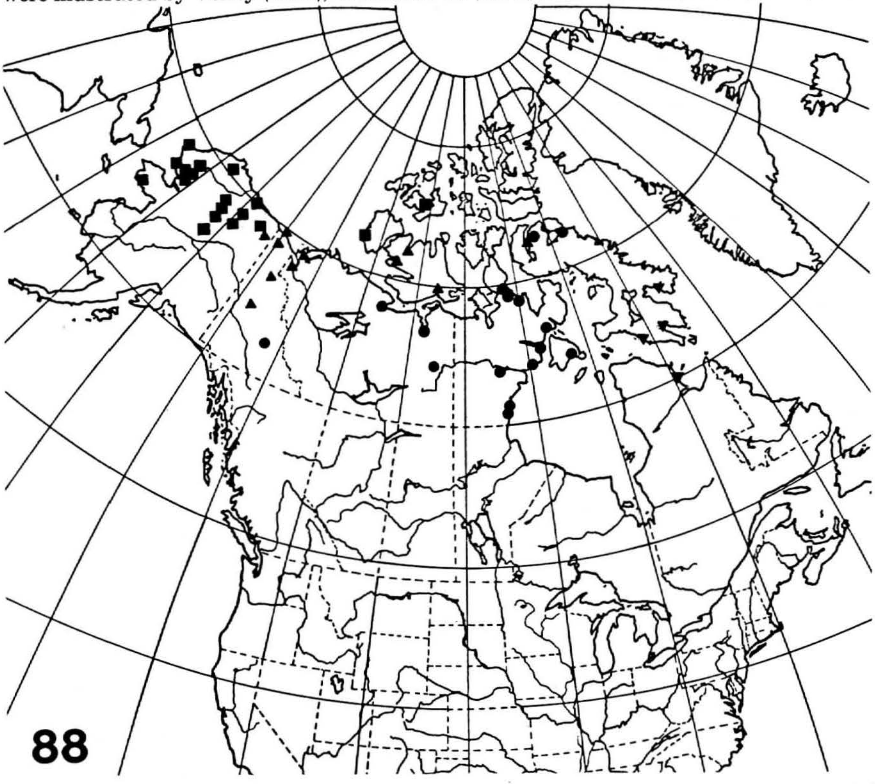
Figure 87: Distribution map for *Colias hecla* in North America. Solid circles = *C. h. hecla*. Solid triangles = *C. h. hela*. Inverted solid triangles = *C. h. canadensis*. Open triangles = cline between *C. h. hecla* and *C. h. canadensis*. Open circle = material not available for examination.

asynchrony, allopatry, or low-population density exists do not generally produce the *boothii* or *thula* phenotypes. On the other hand, in localities where the flight periods of *hecla* and *nastes* overlap and the two species are not environmentally isolated, such as at Coral Harbour on Southampton Island, we find both *boothii* and "rossii".

The factors cited in the preceding paragraph easily explain the fluid nature of the distribution of the *boothii/thula* complex. Arctic butterflies are strongly subject to annual variation as a function of weather conditions. Population densities vary significantly from year-to-year, and emergence dates vary widely depending upon seasonal conditions. If, as it has been asserted, *boothii* and *thula* represent hybrids between *hecla* and *nastes*, these factors could easily explain the variability noted in the density and distribution of these butterflies. In some years there may be few interspecific matings, while in other years they may occur frequently.

Old World Forms

Colias hecla sulitelma Aurivillius and *C. nastes werdandi* Zetterstedt occur in Lapland. Various form and aberrational names have been applied in both species and these taxa were illustrated by Verity (1911), Holland *et al.* (1935) and Hovanitz (1963b; 1973). Five



88

Figure 88: Distribution map for *Colias boothii/thula* complex in North America. Solid circles = *C. boothii*. Solid squares = *C. thula*. Solid triangles = *C. boothii-thula* phenotypic intergrades. Inverted solid triangles = areas from which only the "rossii" phenotype has been recorded. The tension zone between the *thula-boothii* phenotypes in which intermediate forms occur extends from the Kavik River region of eastern Alaska into the Yukon Territory.

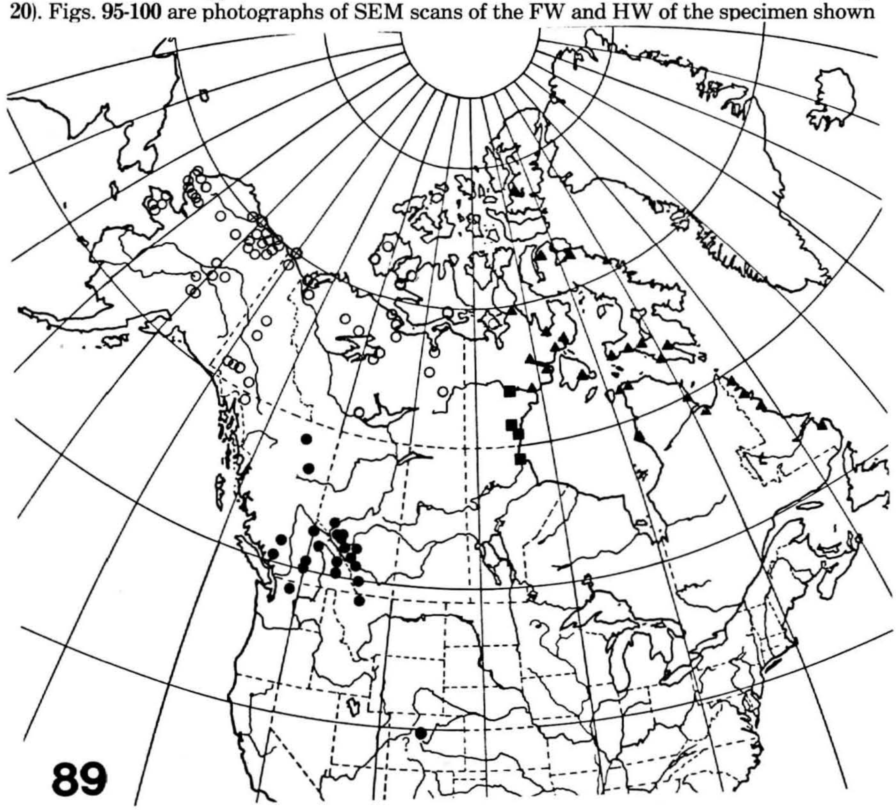
of these names are pertinent to this discussion.

Colias nastes werdandi ab. "christienssoni" Lampa, 1885

Verity illustrated this form (from Lapland) in plate 42, figs. 42-44. These photographs are an excellent match for *boothii*. The specimens illustrated in Holland *et al.* (pl. 27, figs. 41-42) from Nyland, Finland resemble "rossii" rather than "christienssoni".[3] One can infer from the colored plates in these two works that both *boothii* and "rossii" phenotypes occur in arctic Europe.

Colias nastes werdandi ab. "immaculata" Lampa, 1885

This taxon is illustrated in Verity (pl. 42, fig. 40 from Quickjok, Sweden) and in Holland *et al.* (pl. 27, figs. 37-39 from Nyland Hangö, Finland).[3] Two males from Jebrentjakko nr. Abisko, Sweden are illustrated in Figs. **90-91**. This form matches *thula* exactly. The UV reflectance patterns shown in Figs. **92-93** are also consistent with *thula*. Fig. **94** shows the underside of a typical *werdandi* ♂ from Abisko, Sweden (compare with *thula*, Fig. **20**). Figs. **95-100** are photographs of SEM scans of the FW and HW of the specimen shown



89

Figure **89**: Distribution map for *Colias nastes* in North America. Solid triangles = *C. n. nastes*. Solid squares = *C. n. moina*. Open circles = *C. n. aliaska*. Solid circles = *C. n. streckeri*.

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[3] These localities as stated in Holland *et al.* must be incorrect. They are situated at the southernmost tip of Finland where neither *nastes* nor *hecla* occur (K. Mikkola, *in litt.*).

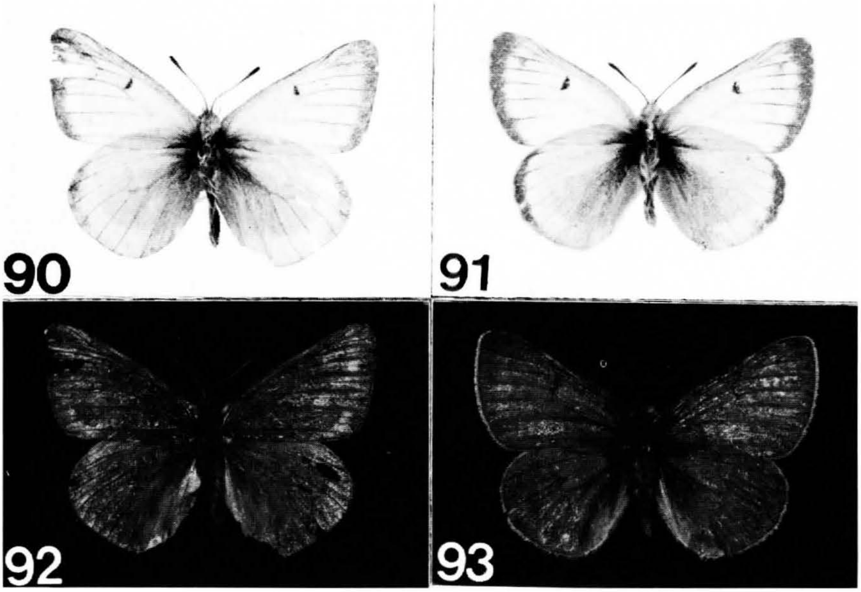
in Figs. **90** and **92**. When these SEM photographs are compared with their *thula* counterparts as follows: Figs. **95-61**; **96-67**; **97-71**; **98-77**; **99-83**; **100-72**, the similarities are striking. The main difference is slightly more curling of the scales of "immaculata" and this is probably only an artifact of the SEM preparation process. When Figs. **96-67** and **99-83** are compared, the longitudinal ridge lines in "immaculata" appear more distorted or wavy than in *thula*. These structures also appear to be somewhat deeper in "immaculata" with more pronounced marginal flutes. These features, however, may be simply artifacts associated with the angle of inclination of the specimens relative to the scanning beam. On the basis of the photographic evidence presented, we must conclude that the *thula* phenotype also occurs in the Old World, but has been treated as only an aberrational form of *nastes werdandi*.

Colias nastes werdandi fm. "zemblica" Verity, 1911

Based upon Verity's description and the associated black-and-white photograph (pl. 71, fig. 10), this taxon represents another *boothii* phenotype. The type locality for this form is the island of Novaya Zemlya which lies between the Barents and Kara Seas.

Colias hecla sulitelma ab. "sandhali" Lampa, 1885

Colias hecla sulitelma ab. "citrina" Staudinger, 1901



Figures **90-93**: *Colias nastes werdandi* ab. "immaculata" (D) from Jebrentjakko nr. Abisko, Sweden, 26.vii.52 photographed under normal illumination **(90-91)** and UV illumination **(92-93)**. Specimens in AME/FSM Collection.

The Lampa name refers to a yellow form of *sulitelma* which is similar to a *boothii* phenotype. The Staudinger name applies to a yellow female morph which could be interpreted as a *boothii* phenotype.

The geographic distribution of *nastes werdandi* in Scandinavia lies within the distribution of *hecla sulitelma* according to maps 35 and 42 in Higgins and Riley (1975). Thus the potential exists for hybridization between these two species. Based upon my examination of museum specimens and the illustrations provided by Verity and Holland *et al.*, it is clear that *boothii, thula* and "rossii" phenotypes occur in Scandinavia.

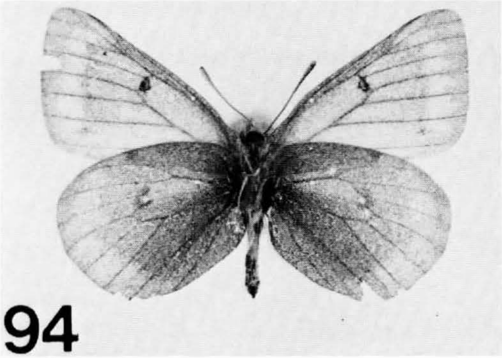
Many Old World specialists have treated these phenotypes as either aberrations or forms of either *nastes* or *hecla*. Kaisila (1950), however, discussed and illustrated presumed hybrids between these two species collected from the region of Kilpisärvi in Finland. The phenotype was that of f. "christienssoni". Kaisila included somewhat primitive sketches of wing scales and indicated the intermediate nature of "christienssoni" relative to *hecla* and *nastes*. Although quite rare, this form occurs intermittently at Kilpisärvi, which lies at the northernmost tip of Finnish Lapland (K. Mikkola, *in litt.*). This is the only locality in Finland where *C. nastes* occurs. *C. palaeno* (L.) is very rare at this locality, but at Utsjoki, Finland *C. palaeno* and *C. hecla* occur together. A few specimens were collected by A. V. V. Mikkola about twenty years ago in this region that appear to be hybrids between these two species. They are larger and brighter than f. "christienssoni" (K. Mikkola, *in litt.*).

A Field Observation

Freshly caught males of both *C. hecla* and *C. nastes* emit sweet-smelling odors that appear similar, if not identical, to the human observer. In fact, this is a quick method for separating the similar-appearing sexes of *nastes* in the field. The females of both species do not produce this scent. The aroma disappears quickly upon death of the butterfly. If the origin of this scent is a pheromone, then it is possible that males of *nastes* and *hecla* produce biochemically similar pheromones. Such a situation would enhance interspecific matings.

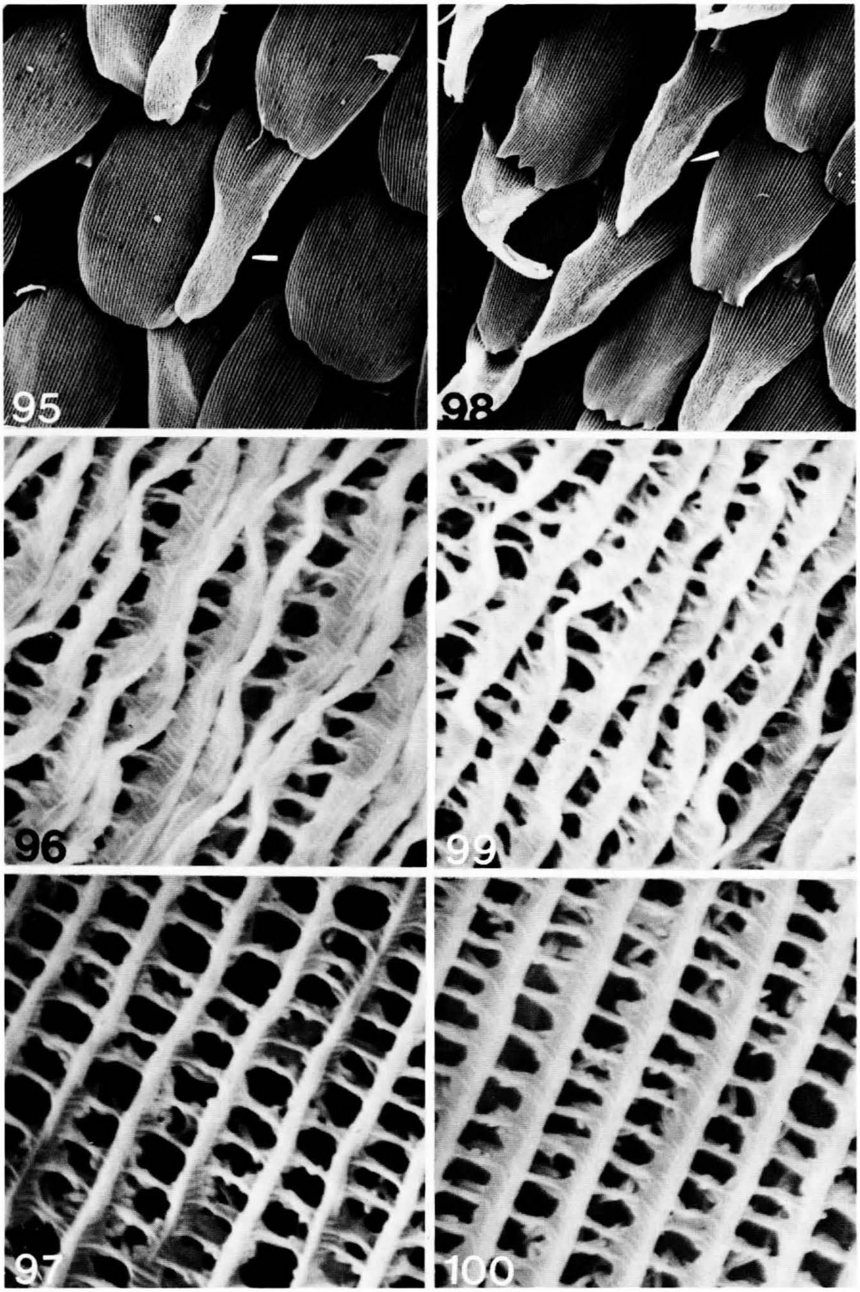
CONCLUSION

Based upon the evidence presented above, it is concluded that *Colias boothii* and *C. thula* represent two color morphs of a hybrid swarm between *Colias hecla* and *C. nastes.* In the extreme western arctic regions, the nastes greenish-white color gene is expressed in the hybrid, while elsewhere the *hecla* yellow-orange color gene is expressed in the hybrid, with a few individual exceptions (Figs. 56-57). An explanation for this phenomenon is presented in the narrative accompanying Appendix B. C.L. Remington has described the



94

Figure 94: *Colias nastes werdandi* ♂ (V) from Norrbotten nr. Abisko, Sweden, 11.vii.75. Specimen in C. D. Ferris Collection.



Figures **95-100**: Photographs of SEM scans of wing-scale structure of the specimen of *Colias nastes werdandi* ab. "immaculata" shown in Figs. **90, 92**. DFW scales at 500X showing UV-reflective cover scales (pointer) **(95)**. Layered-lamellar ridge-lines of DFW UV-reflective scale at 10,000X **(96)**. DFW basal scale at 10,000X **(97)**. DHW scales at 500X showing reflective scales (pointer) **(98)**. Layered-lamellar ridge-lines of DHW UV-reflective scale at 10,000X **(99)**. DHW basal scale at 10,000X **(100)**.

genetics of some species of *Colias* as related to adult color in a series of papers to which the reader is referred (1954a, b, c; 1956).

The variability of *boothii* over its range can be explained by two factors:

1. Subspecific differences in the parent populations of *nastes* and *hecla.*
2. Different genotypes that produce similar, but not identical, phenotypes as enumerated in the tables presented in Appendix B.

C. thula is somewhat more stable since the parent species are *C. hecla hecla* and *C. nastes aliaska* Bang-Haas. Additional variation can be attributed to back-crosses (Appendix B) and the normal variation observed in arctic species as a consequence of environmental conditions.

The forms "rossii" and "gueneei" (see discussion of *nastes* which follows) are presumed to represent the three-quarters *nastes* X one-quarter *hecla* phenotype, while *boothii* and *thula* represent one-half *nastes* X one-half *hecla.* In the one-quarter *nastes* X three-quarters *hecla* combination, apparently the *hecla* orange color dominates and imagines are not readily distinguishable, although there are several characters which may be diagnostic as follows: 1. Smearing of the VHW discal-spot pink border toward the outer margin; a character more commonly found in *nastes* than *hecla.* 2. Paler yellow-orange (or yellow in ♀♀) color in both sexes than occurs in normal *hecla.* 3. Males with narrower-than-normal dark borders, although this variation does occur in "pure" *hecla* colonies in Greeland as well as in other *Colias* species. 4. Temporal shift in flight period. In most areas in which the flight season has not been compressed by unfavorable climatic conditions, *C. hecla* flies early in the season and *nastes* late in the season, on a relative basis. *C. boothii* and *C. thula* generally fly from mid-to-late season. It has been suggested that in some areas there are two sibling species in the *Colias hecla* complex which are sympatric but allochronic (J. Troubridge, J.D. Lafontaine, *in litt.*). On the basis of my studies, I would suggest that the later-flying *hecla*-like insect represents the one-quarter *nastes* X three-quarters *hecla* imago. In some instances, I suspect that *hecla* has a protracted emergence (*C. hecla canadensis* Ferris at Pink Mt., British, Columbia) and that there may be some shifts in adult maculation as a result of varying climatic conditions during the maturation and prepupal stages of the larvae.

In areas in which *boothii* occurs, frequently specimens of otherwise normal *nastes* manifest a brightly colored DHW discal spot. I suggest that these imagines represent various crosses such as seven-eights *nastes* X one-eighth *hecla.* We do not see the parallel situation in examples of *hecla* because of the apparent dominance of the *hecla* color gene.

The conclusions presented above are supported by the analysis contained in Appendix B.

Based upon museum series, it appears that *boothii* and *thula* occur only where the following conditions are met: 1. *C. nastes* and *C. hecla* are sympatric. 2. The flight seasons of *C. nastes* and *C. hecla* overlap. 3. The colony sizes of the two parent species are on the same order of magnitude.

There are regions in which *C. nastes* and *C. hecla* are sympatric in the broad sense, but neither *C. boothii* nor *C. thula* has been reported. In such areas, one or more of the following conditions may exist: 1. Flight periods of the two parent species are asynchronous. 2. Extreme habitat separation, such as *nastes* on mountain tops and *hecla* in valleys. 3. Low population density of one or both parent species. For example, *C. boothii* has not been reported from southern Alberta where *C. nastes streckeri* Grum-Grschimailo and *C. hecla canadensis* occur. In this region, there is both extreme temporal and altitudinal separation of these two species.

There are phenotypes recorded from arctic Scandinavia which resemble North American *boothii* and *thula.* Except as noted above, European specialists have generally treated these butterflies as forms or aberrations of either *nastes* or *hecla.* Based upon the evidence presented above, these phenotypes appear to represent *C. nastes werdandi X C. hecla sulitelma.*

Population densities and geographic distribution of *boothii/thula* appear to fluctuate widely. This situation does not suggest a stable species, but rather a hybrid situation. Based upon the data presented herein, it is suggested that in future checklists and catalogues that *Colias boothii* be listed under *Colias hecla* as a hybrid form with *Colias nastes,* and that *Colias thula* be listed under *Colias nastes* as a hybrid form with *Colias* *hecla.* The name *boothii* takes publication priority over *thula* by 120 years.

Hovanitz (1963a, b) proposed that sympatric species in *Colias* could evolve through natural hybridization, and he discussed *C. boothii* in some detail in this regard. This theory has yet to be proved conclusively, and based upon the data presented in this paper, I do not feel that *boothii* can be considered as yet as a separate species, although it may be developing in that direction.

The possibility has also been considered that *nastes* and *hecla* may not be full biological species, but rather represent ecologically isolated phenotypes of a single polymorphic species without true genetic isolation. Based upon currently available evidence, I feel that *C. nastes* and *C. hecla* are indeed separate, albeit closely related, species. The phenotypic variability observed in *hecla* (dark border width in the males, varying UV reflectance, hue) and *nastes* (colored DHW discal spot, dorsal color flush) is easily explained on a simple genetic basis as demonstrated in Appendix B.

North American *Colias nastes* Boisduval

North American *Colias nastes* Boisduval

The previous assertion that the taxa *rossii* and its synonym *gueneii* apply to hybrid forms requires a revision of the species *Colias nastes.* There are four apparently closely related species: *nastes* Boisduval; *ladakensis* C. & R. Felder; *cocandica* Erschoff; *tyche* Böber = *melinos* Eversmann. The three latter insects occur in Asia and one or more of them may prove to be conspecific with *nastes. C. nastes jucuttica* Kurentsov was described from the Siberian region. Lack of study material and the author's unfamiliarity with Asian habitats precludes any further discussion of these species. A few comments have been made about *C. nastes werdandi* from Lapland in a prior section of this paper. Consequently the discussion that follows is restricted to North American *C. nastes.*

Colias nastes nastes Boisduval, 1832

Original Description: Icon. Hist. Lepid. Europe: 245-46, pl. 8, figs. 4 (D) & 5 (V).

Type Locality and Location of Type: The Boisduval description does not give an exact type locality, only "Labrador". Boisduval also cited North Cape and Iceland as localities for *nastes.* Subsequent authors have agreed that the Labrador specimen in Boisduval's series best fits the illustration provided, and on this basis it has been treated as the type. In the strict sense, it is a lectotype rather than a holotype. Various later authors have restricted the type locality to northeastern Labrador. The lectotype passed from Boisduval to Oberthür, then to Barnes, and finally to the National Museum of Natural History, Washington, D.C.

The original description is in Latin, followed by an extended description of the female (not figured by Boisduval) in French, in which it is compared with the European *phicomone* Esper. Translated from the Latin, the original description reads: "Wings of the male above greenish-sulphureous, of the female, whitish-yellowish, border in common blackish separated by spots; beneath forward [FW] a little eye-spot, behind [HW] red [spot] pupilled in white; antennal club yellow beneath." As is the case with many of the early butterfly descriptions, this one is not very enlightening. A typical pair from Nain, Labrador is shown in Figs. **101-104.** Dorsally the males are pale lemon-yellow to nearly white in some examples, overscaled with dark scales which gives the visual impression of greenish-yellow. The dark scales which overlay the pale portions of the wings and also comprise the dark markings are charcoal-gray rather than pure black. In fresh specimens, the dorsal surface of the antennae and all of the wing margins (FW costa included) are rose-pink excepting the FW tornus and FW inner margin along which the cilia are the same color as the pale ground color of the wings. The palpi are basically the same color as the wings with interspersed dark hairs. The upper portion of the frons is pink as in the wing borders. The thoracic and abdominal vestiture dorsally is silvery-white. Ventrally the ground color is the same as dorsally, but the dark aspect (especially of the HW) results from increased density of the dark overscaling. The FW cell spot is small. The HW discal spot is silvery-white heavily ringed with pink scales; usually produced distally. The females are very similar in maculation to the males. The major difference is in the dorsal ground color, which appears pale gray (normally) owing to nearly white basal scales overlaid by darker cover scales. The colors in *nastes* cannot be compared satisfactorily with the color chips in the Smithe color chart (1975). When nominate *nastes* is compared on a geographic basis with other *nastes* subspecies, it is easily distinguishable by its lack of color and gray aspect.

Colias pelidne standfussi Röber, 1909

Original Description: In Seitz, Grossschmett. Erde, 5:91.

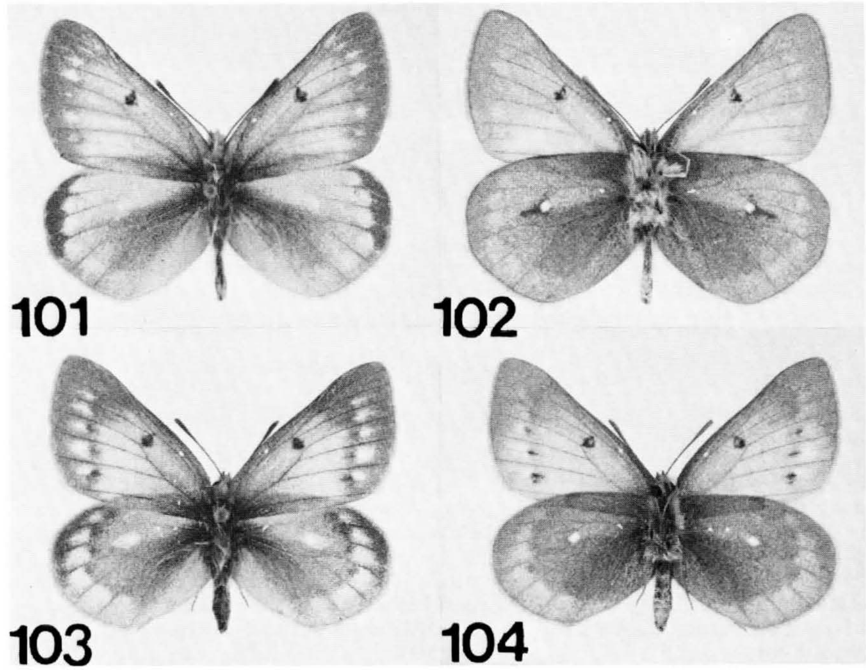
Type Locality and Location of Type: TL not stated. Type probably in Zoologische Museum der Humboldt Universität, Berlin, DDR.

Miller and Brown (1981) associated the name *standfussi* with *C. n. nastes.* Röber's description suggests that this taxon may represent a hybrid *peldine X nastes,* or is perhaps an aberration of *pelidne* Boisduval and Le Conte.

Colias nastes nastes f. "rossii" Guenée, 1864, **NEW DESIGNATION**

Original Description: Ann. Soc. Ent. France, 4:199-200.

Type Locality and Location of Type: Boothia Felix = Boothia Peninsula, Northwest



Figures **101-104**: Typical specimens of *Colias nastes nastes* from Nain, Labrador, 14-16.vii.75. ♂, D (**101**) and V (**102**); ♀, D (**103**) and V (**104**). Specimens in C. D. Ferris Collection.

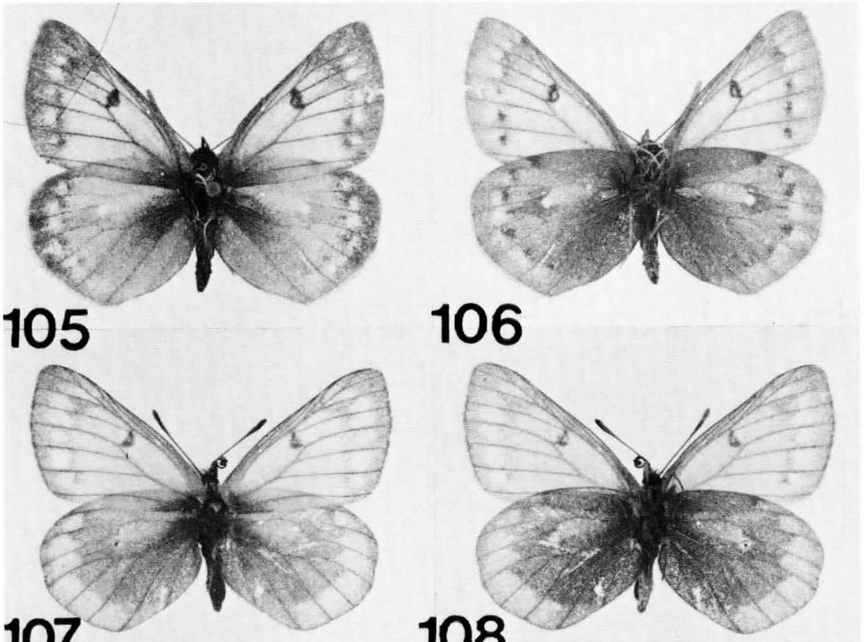
Territories, Canada. The male holotype passed from Guenée to Oberthür, to Barnes, and thence to the National Museum of Natural History, Washington, D.C. It was figured by Holland *et al.* (1935; pl. 26, figs. 8-8a).

Based upon prior discussion, the taxon *rossii* is hereby demoted from subspecific status to that of a form of *nastes nastes* with the recognition that the name properly applies to a hybrid form. In his original description, Guenée indicated some uncertainty about the placement of *rossii*, questioning whether it was a form of *nastes* ["An Var. *Nastes*?"] although he went on to describe it as a full species. Translated from the French, Guenée's description reads: "I receive from Monsieur Doubleday, with the rare *Colias* that I have just described, three individuals of another species of the same genus provided likewise from the expedition of Captain J. Ross, and which is perhaps only a local variety of *nastes*, but which, however, offers notable differences.

"It is of the form of *nastes*; but the wings are perhaps a little more rounded. The male is characterized above by a very light orange tinge in the area corresponding to that of *boothii*. The veins are less separated in black on a background much less dusted than in *nastes*. Moreover, *the inner margin is clearly more convex than in nastes* ♂, which makes the wing appear larger; the border is larger than that of *nastes* and intersected with a series of seven sulphur or greenish spots, cleanly separated interiorly as exteriorly and extending almost to the rib.

"The female is greenish-white but always a little more washed with yellow than in *nastes*.

"The undersides of the wings of both sexes are greenish-white, more tinted with yellow in the ♂. On the forewings, the series of subterminal blackish spots is complete and strongly defined. On the secondaries, this series is continued and thusly bounds the very dark portion of the disc, separating a clearly cut-off border, which appears dentate or



Figures **105-108**: *Colias nastes* fm. "rossii". ♂ from Spence Bay, N.W.T., D (**105**) and V (**106**); ♀ from Coral Harbour, Southampton Is., N.W.T., D (**107**) and V (**108**). Specimens in C. D. Ferris Collection.

sinuate interiorly, because the spots are not all in the same line. The brick-colored cell spot has a large white pupil also strongly circumscribed.

"I repeat that this *Colias* has an aspect distinct from *nastes*, especially from those from Labrador, and if the differences that I have enumerated are found in additional examples, I have no doubt in their validity.

"I give to this *Colias* the name of the celebrated explorer who brought it back from the pole with *boothii*."

Of *rossii*, it is interesting to note that Avinoff (*in* Holland *et al.*, 1935) made the following comment: "In regard to the nomenclatorial designation of the race of Southampton Island I am not in favor of accepting the name *rossi* [*sic*], since it was definitely used for an aberrant, possibly hybrid, form characterized by the presence of an orange tinge on the upper side. We cannot amplify the description as worded by the original author and disregard his indication of the unusual tinge in the color of the upper side, consequently the normal type of the race of *nastes* as found in Boothia Felix and apparently identical with the one from Southampton Island should receive a new name."

Colias nastes nastes f. "gueneei" Avinoff, 1935, **NEW DESIGNATION**

Original Description: A. Avinoff *in* Holland *et al.*, Mem. Carnegie Mus., 12(part 2, section 5):13-14, pl. 27, figs. 1, 11, 21-22, 25-27, 31-32.

Type Locality and Location of Type: Southampton Island, Northwest Territories, Canada. The holotype is in the collection of the Carnegie Museum of Natural History, Pittsburgh, PA.

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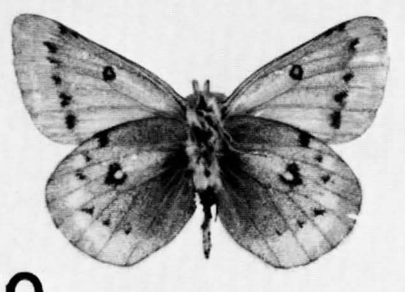

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Figures 109-111: Lectotypes of *Colias nastes moina*. ♂, D (**109**), V (**110**) and specimen labels (**111**). Specimen in Strecker Collection at AME/FSM.

Based upon prior discussion, the taxon *gueneei* is hereby demoted from subspecific status to that of a form of *nastes nastes* with the recognition that the name properly applies to a hybrid form. The original description is only two sentences: "The description would then be as follows: similar to *rossi* [*sic*], but lacking the orange tint on the upper wings. This character is typical for the normal representatives of *nastes* in both arctic localities mentioned heretofore [Boothia Felix; Southampton Island]."

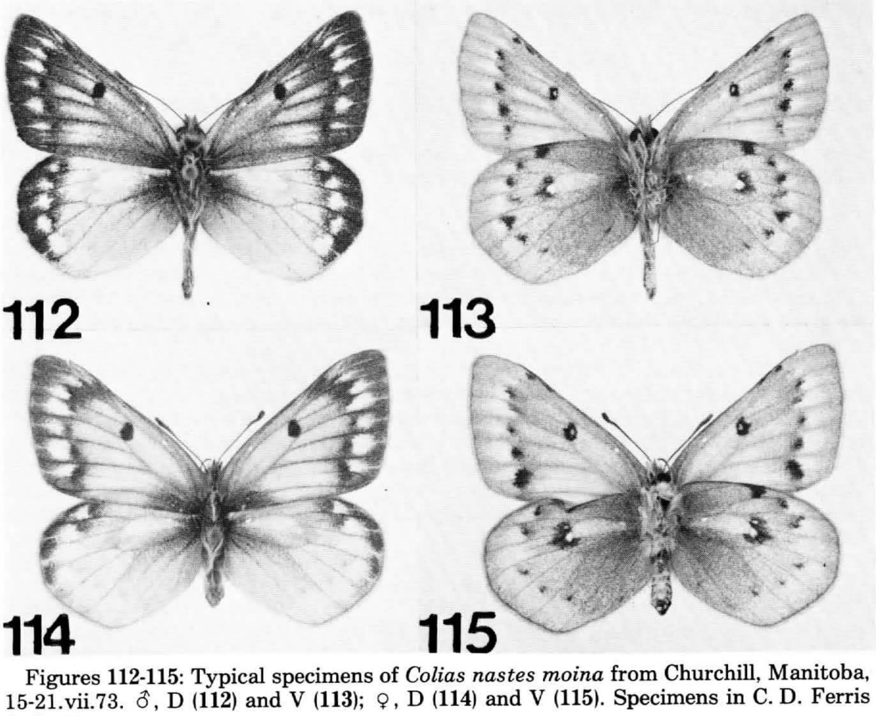
Plate 27 in Holland *et al.* (1935) illustrates in color the range of *nastes-boothii-*"rossii"-*hecla* phenotypes found on Southampton Is. All of these and some additional forms can be found in the extensive Southampton Is. holdings in the Canadian National Collection and the collection of the Allyn Museum of Entomology/Florida State Museum. The specimen shown in fig. 26 is a typical *nastes nastes,* although the figure caption refers to it as "*Colias nastes gueneei* ♀, dark form." Typical specimens are shown in Figs. **105-108.**

Geographic Distribution: C. n. nastes occurs in the eastern arctic regions along and east of the 90th meridian as shown by the solid triangle in Fig. **89.** It occurs along the west coast of Hudson Bay south to the vicinity of Chesterfield Inlet. Just west of the 90th meridian along the 70th parallel there is a tension zone between the nominate species and *nastes aliaska* Bang-Haas.

Colias nastes moina Strecker, 1880

Original Description: Bull. Brooklyn Ent. Soc., 3:34.

Type Locality and Location of Type: "A considerable distance above Fort Churchill on west coast of Hudson's Bay." The type locality may be in Manitoba north of the present community of Churchill-Ft. Churchill as usually stated in references, or more likely the



Figures 112-115: Typical specimens of *Colias nastes moina* from Churchill, Manitoba, 15-21.vii.73. ♂, D (**112**) and V (**113**); ♀, D (**114**) and V (**115**). Specimens in C. D. Ferris Collection.

type series came from the vicinity of Eskimo Point, Northwest Territories, Canada. A lectotype is in the Strecker Collection currently located at the Allyn Museum of Entomology / Florida State Museum, Sarasota, FL, and is illustrated in Figs. **54, 109-111.**

Strecker wrote a reasonable description of *moina* and indicated differences from the nominate species as follows: "This, which I presume is but a variety of *Nastes,* still differs decidedly from the Labrador examples in the brightness of the yellow colour and the depth and sharpness of the black markings of upper surface; and beneath in the beautiful light lively colour, which in the typical *Nastes* is dull olivaceous and heavy, and in the prominent row of dark sub-marginal spots which are entirely wanting in the secondaries and only indicated on primaries by a few indistinct dots.

"Further the ♀ of *Nastes* is white or greenish white, whilst in the present form it scarcely differs in its yellow colour from the ♂."

Figs. **112-115** illustrate typical *moina* from Churchill, Manitoba.

Colias nastes moina ab. "harperi" (Gunder), 1932

Original Description: Can. Ent., 64:278. Described in the genus *Eurymus.*

Type Locality and Location of Type: Ft. Churchill, Manitoba. ♀ holotype in collection of American Museum of Natural History, New York.

This is a strongly melanic aberration of normal female *moina.*

Geographic Distribution: As indicated by the solid black squares in Fig. **89**, *moina* has a restricted distribution ranging along the west coast of Hudson Bay from Churchill, Manitoba northward to Baker Lake, N.W.T. Specimens from Chesterfield Inlet, N.W.T. are closer to *nastes nastes* than to *nastes moina.*

Colias nastes aliaska Bang-Haas, 1927

Original Description: Horae Macrolepid., 1:41, pl. 5, figs. 24 (♂) & 25 (♀)

Type Locality and Location of Type: "Ramport" [*sic*] = Rampart, Alaska. Holotype in Zoologische Museum der Humboldt Universität, Berlin, DDR.

The original description is very brief, and translated from the German it reads: "Wingspan: ca. 40 mm. Considerably larger than the preceding race [referring to *C. n. streckeri* - see below]. FW of ♂ is colored very dark gray, excepting the green submarginal spot row and the white discoidal area. HW green, darker margin, which is interrupted by green streaks at the vein ends. Discal spot light yellow, in the ♀ the FW is green colored."

Basically, *aliaska* is characterized by a very dusky aspect dorsally in the males. The yellowish basal scales are very heavily overlain with melanic scales giving an overall aspect of dark olivaceous coloring. The dark FW marginal border is interrupted by narrow bright streaks or flecks in the cells between the veins. The HW are somewhat paler than the FW and the pale cell spots in the marginal border are larger and more diffuse. Dorsally the females are paler than the males and have a more yellowish-greenish cast than the dark olivaceous coloring of the males. A typical pair from the Yukon Territory is shown in Figs. **116-119.**

Colias nastes aliaska ab. "cocandicides" Verity, 1911

Original Description: Rhop. Palaearctica xxxvii, pl. 71, figs. 7, 9 (♂ holotype), 8 (♀ "cotype").

Type Locality and Location of Type: "Territoire de Barren", 67°40'N, 114°30' W [vic. Coppermine River, N.W.T., Canada]. The type may be in the British Museum (N.H.).

The figure captions for plate 71 list figs. 7-9 as *C. nastes rossi* [*sic*]. The prefatory page xxxvii and page 355 show the aberrational name "cocandicides" for the specimens figured. Based upon the poor black-and-white photographs and the accompanying text, this name appears to apply to a pale form of *C. nastes aliaska.*

Geographic Distribution: All of the western arctic region from the 100th meridian westward, and shown as the open circles in Fig. **89**.

Colias nastes subarctica (McDunnough), 1928 (= *C. nastes aliaska* Bang-Haas, 1927]

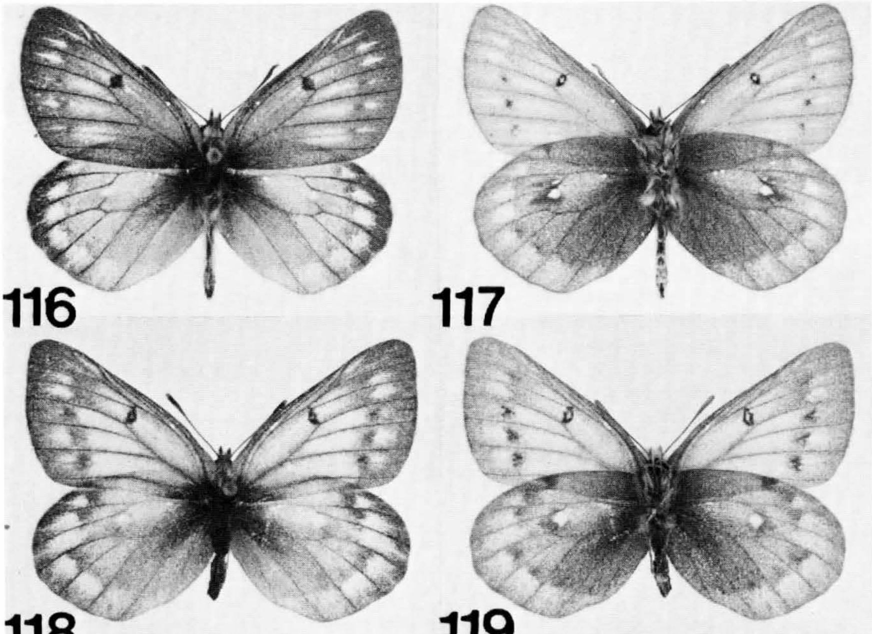
Original Description: Can. Ent., 60:270-271. Described in the genus *Eurymus.*

Type Locality and Location of Type: Bernard Harbour, Northwest Territories, Canada. Type No. 2863 in the Canadian National Collection, Ottawa, Ontario and illustrated in Figs. **120-122**.

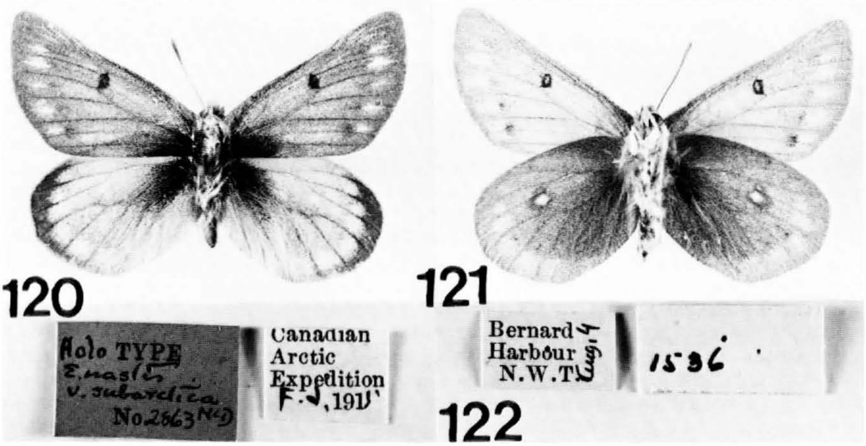
McDunnough provided a reasonably comprehensive description of *subarctica,* but apparently he was unaware of the Bang-Haas publication in which *aliaska* was described a year earlier. I have examined material from the western Northwest Territories, the Yukon Territory and Alaska, and I can see no reason to retain *subarctica* as a valid subspecies. Thus this taxon is placed as a junior synonym of *aliaska* which predates it in publication by a year.

Colias nastes streckeri Grum-Grschimailo, 1895

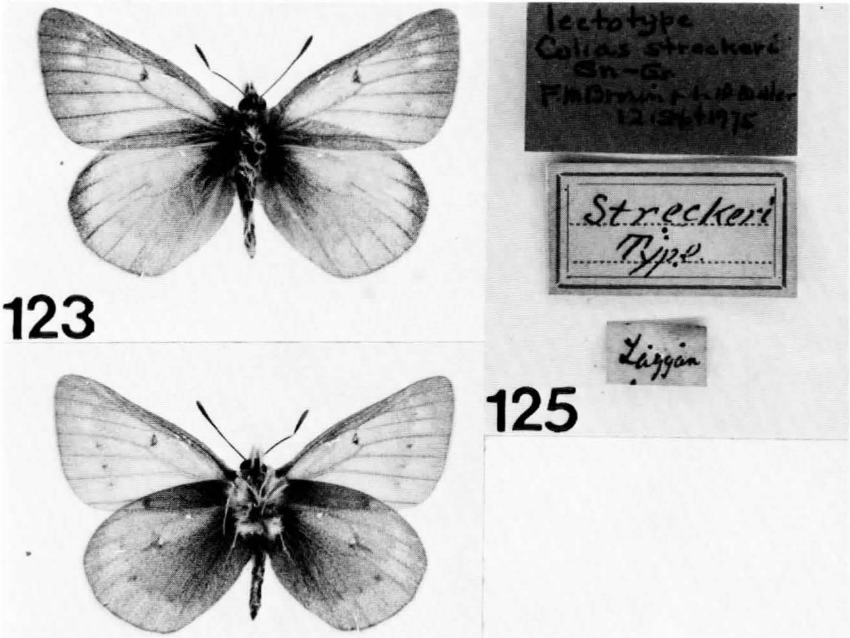
Original Description: Horae Soc. Ent. Rossiae, 29:290-291.



Figures **116-119**: Typical specimens of *Colias nastes aliaska* from Windy Pass, Ogilvie Mts., Yukon Territory, 13.vii.84. ♂, D (**116**) and V (**117**); ♀, D (**118**) and V (**119**). Specimens in C. D. Ferris Collection.



Figures 120-122: Holotype male of *Colias nastes subarctica*. D (120), V (121) and specimen labels (122). Specimen in Canadian National Collection.



Figures 123-125: Lectotype of *Colias nastes streckeri*. ♂, D (123), V (124) and specimen labels (125). Specimen in Strecker Collection at AME/FSM.

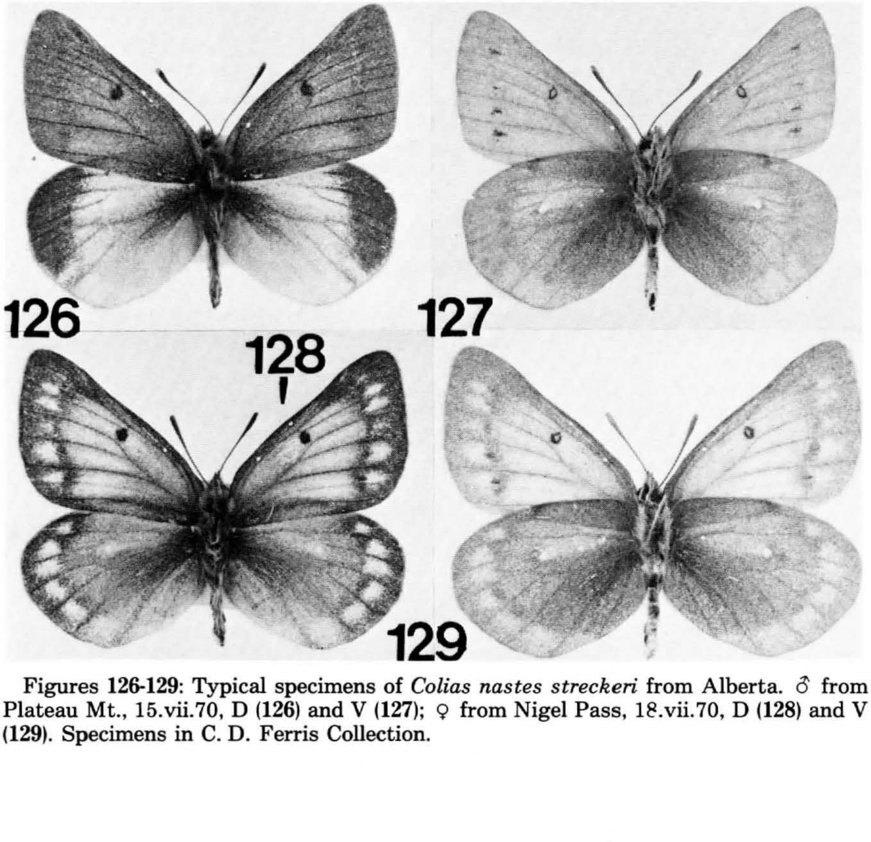
Type Locality and Location of Type: Laggan [Lake Louise], Alberta, Canada. Lectotype in the Strecker Collection, currently housed in the Allyn Museum of Entomology / Florida State Museum, Sarasota, FL; illustrated in Figs. **55, 123-125.**

The description freely translated from the original and very poor Latin reads: "Form effectively transitional to *Colias cocandica.* Wings ♂ ♀ greenish sulphureous; marginal border of the forewing wider, in discal region veins rarely dusted with blackish; discocellular spot of the hindwing pale yellow, beneath enlarged toward the external margin [and] bidentate [and] red as in *C. eogene* and *cocandica.*

"One specimen of this variety received from the German lepidopterist Dr. O. Staudinger in 1891 under the name 'Colias behrii?', four specimens collected in the province of Alberta at Laggan, from the American lepidopterist H. Strecker, in whose honor this form is named."

This description tells very little about the actual aspect of *streckeri.* What separates *streckeri* from the other *nastes* subspecies is the nature of the dark marginal border of the FW. It is decidedly broad, as noted in the original description, but it is also frequently solid (in both sexes) and when it does contain pale spots in the spaces between the veins, they are very small. The central region of the HW dorsally is generally very pale relative to the remainder of the dorsal wing surfaces. This gives the butterflies (males especially) a distinct bicolorous aspect. The paler areas dorsally are greenish-white and specimens are occasionally laved with lemon-yellow. Material from the western slope of the Canadian Rockies in British Columbia tends to be paler than specimens from the Lake Louise region of Alberta. A typical pair of *streckeri* from Alberta is shown in Figs. **126-129.**

Colias nastes streckeri ab. "obscurata" Verity, 1911



Figures **126-129**: Typical specimens of *Colias nastes streckeri* from Alberta. ♂ from Plateau Mt., 15.vii.70, D (**126**) and V (**127**); ♀ from Nigel Pass, 18.vii.70, D (**128**) and V (**129**). Specimens in C. D. Ferris Collection.

Original Description: Rhop. Palaearctica: pl. 61, fig. 6.

Type Locality and Location of Type: Lake Louise, Alberta, Canada. The male holotype may be in the British Museum (N.H.).

This aberrational form is an extreme expression of the bicolorous nature of *streckeri* in which the FW are uniformly dark colored and the HW are very pale with little maculation in the discal region.

Colias nastes streckeri ab. "palliflava" (McDunnough), 1927

Original Description: Can. Ent., 59:154. Described in the genus *Eurymus.*

Type Locality and Location of Type: Mt. McLean, near Lillooet, British Columbia, Canada. The male holotype is Type No. 2425 in the Canadian National Collection, Ottawa, Ontario.

This aberrational form is the opposite of fm. "obscurata" and has all of the dark dorsal scaling nearly obsolete except at the wing bases and the FW apices. The DFW discal spot is also absent.

Geographic Distribution: As shown by the solid circles in Fig. 89, *streckeri* is found in the Canadian Rockies in the southern portions of Alberta and British Columbia. Colonies occur in Glacier National Park, Montana and in Okanogan Co., Washington. Specimens examined from northeastern British Columbia appear to lie within the normal variation of *streckeri* and are so placed. There are colonies on Pink Mt. and Stone Mt.

Colias nastes - Questionable Population

There are two specimens of *streckeri* in the collection of the American Museum of Natural History which bear specimen labels; "Berthoud Pass, Colorado, 7-15 August, 1919." Although the environment at the top of Berthoud Pass might be suitable to support a colony of this species, there are no other known specimens from this area, and these two specimens are presumed to have been mislabeled either by a collector or a museum preparator.

CONCLUSION - *Colias nastes*

Based upon the foregoing revision, four subspecies of *Colias nastes* are recognized in North America in accord with the diagnostic characters cited. A synonomy is shown below:

- *Colias nastes* Boisduval, 1832
  - *n. nastes* Boisduval, 1832
    - *standfussi* Röber, 1909 (possible *nastes X pelidne* hybrid)
      - f. "rossii" Guenée, 1864 (*nastes X hecla* hybrid form)
      - = f. "gueneei" Avinoff, 1935
  - *n. moina* Strecker, 1880
    - ab. "harperi" (Gunder), 1932
  - *n. aliaska* Bang-Haas, 1927
    - *subarctica* (McDunnough), 1928
      - ab. "cocandicides" Verity, 1911
  - *n. streckeri* Grum-Grschimailo, 1895
    - ab. "obscurata" Verity, 1911
    - ab. "palliflava" (McDunnough), 1927

ACKNOWLEDGMENTS

This study was initiated during a visit to the Biosystematics Research Institute, Ottawa, Ontario, Canada sponsored by the CanaColl Foundation. I am grateful to the Foundation and the efforts of J. D. and H. Lafontaine (in whose home I was a guest) and E. Becker for making this trip possible. J. D. Lafontaine and D. Kritsch of the Biosystematics Research Institute were most helpful in supplying photographs and bibliographic material used in the preparation of this paper.

Special thanks are due Lee and Jackie Miller for making publication of this paper possible, and for their many kindnesses during my visit to the Allyn Museum of Entomology/Florida State Museum and while a guest in their home.

The late Arthur C. Allyn gave most graciously of his time (as he did for many researchers) to supply the SEM photographs used throughout the text, as well as providing additional photographic support.

D. C. Ferguson, Systematic Entomology Laboratory, USDA was most helpful in providing an original copy of the difficult-to-obtain paper by Holland *et al.*

Kauri Mikkola, Dept. of Zoology, University of Helsinki, supplied information concerning Finnish Lapland fauna, and kindly brought to my attention the paper by Kaisila.

Specimens, distribution data, and bibliographic information were kindly provided by F. M. Brown, J. A. Ebner, C. S. Guppy, Y. P. Nekrutenko, K. W. Philip, E. M. Pike, J. Shepard, R. E. Stanford, and J. Troubridge.

D. W. Logan, G. A. Waikel, and J. M. Ryan, College of Engineering, University of Wyoming assisted with the reflectance-scanning modification to the spectrometer used to produce Fig. **86**.

The manuscript was reviewed by J. D. Lafontaine, K. Mikkola, and the Wednesday luncheon seminar group at the Biosystematics Research Institute. R. E. Pfadt and R. J. Lavigne, Department of Entomology, University of Wyoming critically read the manuscript and provided useful comments. I am indebted to Joan Smith-Sonneborn, Department of Zoology/Physiology, University of Wyoming for her assistance and stimulating discussions concerning the genetic aspects of this study (Appendix B).

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APPENDIX A

This Appendix contains distribution data for *Colias nastes, Colias hecla,* and the *Colias boothii/thula* complex in North America. Table 1 presents specific locality data, while Table 2 presents distribution data on a regional basis. Data for the 3220 specimens of *C. nastes* and *C. boothii/thula* examined during the course of this revision are presented following the tables. Information relative to the distribution of *Colias hecla* in North America and material examined may be found in Ferris, 1982.

In Table 1, the notation **R** refers to the "rossii" phenotype, while **X** denotes the presence of the species designated at the top of the associated column.

TABLE 1

DISTRIBUTION OF: *Colias nastes, Colias boothii/thula, Colias hecla.*

ALASKA	*nastes aliaska*	*boothii/thula*	*hecla hecla*
Anaktuvuk Pass	X	X	X
Barter Island	X		X
Beaufort Lagoon			X
Black Rapids	X		
Cape Espenberg	X		X
Collinson Point	X		X
Eagle Summit	X		X
Galbraith Lake	X	X	X
Head of Canning River	X	X	X
Hulahula River	X	X	X
Kigluaik Mts.	X		X
Kivalina River	X		X
Mt. Distin	X	X	X
Mt. Fairplay	X		
Denali National Park	X		X
Kantishna	X		
Noatak River Valley	X	X	X
Noluck Lake	X	X	X
vic. Nome	X	X	X
Nome-Teller Road	X	X	X
Ogotoruk Creek	X	X	X
Okpilak River	X		X
Rustic Village	X		
Sagwon	X	X	X
Sheenjek River	X	X	X
Toolik Lake	X	X	
12 Mile Summit	X		
Utukok River	X	X	X
Aichilik River	X	X	X

Cape Sabine		X	
vic. Healy		X	
Itigaknit Mt.	X	X	
Kavik Lake-River		X	X
Kivalina River	X	X	X
Kougarok Rd. - mi. 50	X	X	X
Schrader Lake	X	X	X
Marsh Fork	X	X	X
Sadlerochit Springs-River	X	X	X
Meade River		X	X
Umiat	X	X	X
Cape Thompson	X	X	X
Cape Lisburne	X	X	X
Prudhoe Bay	X	X	X
Rampart	X		X
Itkillik River 46 mi. Ese Umiat	X	X	X
Itkillik River W. of VABM Aruk	X		
Katakturuk River 11 mi. From Mouth	X		X
Kuparuk River 8 mi. from Mouth	X		X
Nanushuk Lake/River-Cobblestone Creek	X		X
Point Hope	X		X
Lazy Mt.	X		X
Mile 18-46 Teller Road	X	X	X

ALASKA	*nastes aliaska*	*boothii/thula*	*hecla hecla*
Mile 44-50 Kougarok Road	X	X	X
Mile 42-44 Council Road	X	X	
Harris Dome	X	X	X
Ridge N. of Wheel Creek	X		
Mile 88, 100 Steese Hwy.	X		
Lake Peters	X		X
Barter Island	X		X
Driftwood (Airstrip - Utukok River)	X		X
Wiseman		X	X
43 mi. From Mouth Aichilik River		X	X
Anachlik Island - Colville River Delta		X	X
Pipeline Camp 3 mi. S. Franklin Bluffs		X	
Kavik River Camp		X	X
Cape Sabine		X	
Kantishna Hills	X		X
Post Lake	X		
Arrietch Creek - Canning River	X		X
3-4 mi. SE Atigun Pass	X		X
Echooka Springs	X	X	X
Galbraith Lake	X	X	X
Iyichoruk Mt.	X		
Nigu River Headwaters	X		
Kuskokwim Mts.	X		
Ophir-Takotna Road ca. 5 mi. W. Takotna	X		
12 mi. N. Galbraith Lake	X		X
13 mi. S. Itkillik Lake	X		
YUKON TERRITORY			
Herschel Island	X	X	X

Keno Hill		X	X
Sam Lake	X	X	X
British Mts.	X	X	X
Ogilvie Mts.	X	X	X
Canyon Mt. nr. Whitehorse	X		
Kluane Lake/Mts. Region	X		X
North Fork Pass - Dempster Hwy.	X		X
Mile 254 Dempster Hwy.	X		X
Vic. Haines Junction	X		X
Canol Road nr. Johnson's Crossing	X		
NORTHWEST TERRITORIES - VICTORIA ISLAND			
Kuujjua River Valley	X	X	X
Holman	X	X	X
Cambridge Bay	X	X	X
Armstrong Point	X		X
71°17'N, 114° W	X	X	X
NORTHWEST TERRITORIES - BANKS ISLAND			
Masik River	X	R	X
Bernard River	X	R	X
Shoran Lake		X	X
Sachs Harbour	X	X	X
NORTHWEST TERRITORIES			
Cache Creek 20 mi. NE Aklavik		X	X
Coppermine and Coronation Bay	X	X	X
Reindeer Depot vic.	X		X
NORTHWEST TERRITORIES	*nastes aliaska*	*boothii/thula*	*hecla hecla*
Bernard Harbour	X		X
Bathurst Inlet	X	X	X
Cockburn Point	X		
Cameron Bay - Great Bear Lake	X		
Caribou Crossing - Great Slave Lake	X		
Kidlut Bay	X		
N. Shore Great Bear Lake	X		
Beechey Lake	X		X
Muskox Lake	X		X
Tuktoyaktuk		X	X
NORTHWEST TERRITORIES	*nastes moina*	*boothii*	*hecla hela*
Eskimo Point	X	X,R	X
Baker Lake	X	X,R	X
Maguse Lake	X		
MANITOBA			
vic. Churchill/Ft. Churchill	X		X

NORTHWEST TERRITORIES	*nastes nastes*	*boothii*	*hecla hela*
Chesterfield Inlet	**X**	**X**	**X**
Wager Bay - Mouth of Wager River	**X**	**X**	**X**

NORTHWEST TERRITORIES	*nastes nastes*	*boothii*	*hecla hecla*
Spence Bay	**X**	**X,R**	**X**
Ross Bay	**X**		
Repulse Bay	**X**	**X**	**X**

NORTHWEST TERRITORIES - BAFFIN ISLAND			
Pond Inlet	**X**	**X**	**X**
Arctic Bay	**X**	**R,X**	
Amadjuak Bay	**X**		
Frobischer Bay	**X**	**R,X**	**X**
Lake Harbour	**X**	**R,X**	**X**
Aitken Lake - Dorset	**X**		**X**

NORTHWEST TERRITORIES — SOUTHAMPTON ISLAND			
Coral Harbour/Coral Inlet	**X**	**R,X**	**X**

NORTHWEST TERRITORIES - ELLESMERE ISLAND			
Eureka	**X**		**X**

LABRADOR			
Nain	**X**		**X**
Ramah	**X**		
Cartwright	**X**		
Nutak	**X**		
Hebron	**X**		

QUEBEC			
Wolstenholme	**X**		
Payne Bay	**X**	**R**	**X**
Sore-Head River - E. Coast Hudson Bay	**X**		**X**
Port Harrison	**X**		**X**
Fort Chimo	**X**		**X**
Sugluk/Saglouc	**X**		**X**
Wakeham Bay	**X**		

TABLE 2

Distribution of *Colias nastes, Colias boothii/thula, Colias hecla* BY

GEOGRAPHIC REGION[4]

REGION → **SPECIES ↓**	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O
Colias nastes	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
[5]*Colias boothii*			x	x				x	x		x	x	x	x	x
[5]*Colias thula*	x	x		x	x	x	x		x	x					
Colias hecla	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x

REGIONS

A. Utukok River, Alaska
B. Kivalina River, Alaska
C. Schrader Lake, Alaska
D. North Slope, Alaska
E. Arctic Costal Plain, Alaska
F. Banks Island, N.W.T., Canada
G. Victoria Island, N.W.T., Canada
H. Baffin Island, N.W.T., Canada
I. British Mts., Yukon Terr., Canada
J. Ogilvie Mts., Yukon Terr., Canada
K. S. Coast, Coronation Gulf, N.W.T., Canada
L. NW Costal Region, Hudson Bay, N.W.T., Canada
M. Boothia Peninsula, N.W.T., Canada
N. Melville Peninsula, N.W.T., Canada
O. Southampton Island, N.W.T., Canada

[4] Alaska data from Philip (1983).

[5] In the sense of phenotype rather than as a species *per se*.

MATERIAL STUDIED

Colias nastes nastes (913 specimens): **HUDSON BAY.** Belcher Is. **JAMES BAY.** Charlton Is. **LABRADOR.** Cartwright, Hebron, Nain, Nutak, Ramah. **NORTHWEST TERRITORIES.** Spence Bay, Ross Bay, Wager Bay, Chesterfield Inlet, Repulse Bay, Wager River. **N.W.T. - BAFFIN ISLAND.** Arctic Bay, Pond Inlet, Frobischer Bay, Amadjuak Bay, Lake Harbour, Aitken Lake - Dorset. **N.W.T. - SOUTHAMPTON ISLAND.** Coral Harbour/Coral Inlet. **QUEBEC.** Fort Chimo, Payne Bay, Port Harrison, Sugluk (Saglouc), Wakeham Bay, Wolstenholme. *Colias nastes moina* (892 specimens): **MANITOBA.** Churchill - Ft. Churchill area. **NORTHWEST TERRITORIES.** Baker Lake, Eskimo Point, Maguse Lake. *Colias nastes aliaska* (312 specimens): **ALASKA.** Anaktuvuk Pass, Cape Thompson, Chandler Lake, Collinson Point, Driftwood, Eagle Summit, Lake Peters, Steese Hwy. - mile 88; 100, Umiat, Barter Island. **NORTHWEST TERRITORIES.** Beechey Lake, Bernard Harbour, Cameron Bay - Great Bear Lake, Caribou Crossing - Great Slave Lake, Cockburn Point, Coppermine, Kidlut Bay, Muskox Lake, N. Shore Great Bear Lake, Reindeer Depot, Bathurst Inlet. **N.W.T. - BANKS ISLAND.** Bernard River, Masik River. **N.W.T. - VICTORIA ISLAND.** Armstrong Point, Holman. **YUKON TERRITORY.** Canol Road nr. Johnson's Crossing, Canyon Mt. nr. Whitehorse, Firth River area - British Mts., Herschel Island, Haines Jct. vic., Kluane Lake/Mts. region, Sam Lake, Windy Pass - Ogilvie Mts. *Colias nastes streckeri* (211 specimens): **ALBERTA.** Banff, Banff-Jasper Hwy., Highwood Pass Summit, Jasper, Lake Louise (Laggan), Morraine Lake, Nigel Pass, Nordegg, Plateau Mt., Seebe, Sunwupta Pass, Wilcox Pass.

BRITISH COLUMBIA. Alaska Hwy. mi. 392 - mt. S. of Summit Pass [Stone Mt.?], Dunn Peak, Hedley, Lillooet, Mt. McLean, Whitewater Region nr. Lillooet. *Colias boothii* phenotype (535 specimens): **NORTHWEST TERRITORIES.** Baker Lake, Bathurst Inlet, Chesterfield Inlet, Coppermine, Eskimo Point, Mouth of Wager River, Repulse Bay, Spence Bay, Tuktoyaktuk. **N.W.T. - BAFFIN ISLAND.** Arctic Bay, Pond Inlet. **N.W.T. - SOUTHAMPTON ISLAND.** Coral Harbour/Coral Inlet. **YUKON TERRITORY.** British Mts. - Firth River, Dempster Hwy. - mi. 87; km. 465; 491. Sam Lake. *Colias thula* phenotype (28 specimens): **ALASKA.** Anaktuvuk Pass, Cape Thompson, Meade River, Noluck Lake, N. Fk. Kougarok River - Seward Pen., Umiat. **ALASKA - MELVILLE ISLAND.** Bailey Point, Ibbet Bay. Paratype female examined from: 70°45'N., 156°30'W. **NORTHWEST TERRITORIES - VICTORIA ISLAND.** Cambridge Bay, Holman, Kuujjua River Valley, 71°17'N., 114°W. *Colias boothii - thula* cline (2 specimens): **YUKON TERRITORY.** Dempster Hwy. - mile 87. *Colias nastes* "rossii" phenotype (327 specimens): **QUEBEC.** Payne Bay. **NORTHWEST TERRITORIES.** Baker Lake, Eskimo Point, Spence Bay. **N.W.T. - BAFFIN ISLAND.** Arctic Bay, Frobischer Bay, Lake Harbour, Pangnirtung. **N.W.T. - BANKS ISLAND.** Bernard River, Masik River. **N.W.T. - SOUTHAMPTON ISLAND.** Coral Harbour/Coral Inlet. **N.W.T. - VICTORIA ISLAND.** Head of Minto Inlet, Mt. Pelly - Cambridge Bay, Upkilik Lake. **YUKON TERRITORY.** Dempster Hwy. - km. 491.

ADDITIONAL RECORDS - SPECIMENS NOT EXAMINED

Colias nastes streckeri: **ALBERTA.** Bald Hills, Burnt Timber Lookout, Cascade Mt., Columbia Ice Fields, Divide Pass, Fossil Mt., Hailstone Butte, Kanacamp, Moose Mt., Mt. Edith Cavell, Mt. McBride, Mt. St. Piran, Peyto Lake, Pocahontas, Pope-Thoreau Pass, Prospect Mt., Red Cap Mt., Signal Mt., Storm Mt., Fortress Mt., Whistlers Mt., Toronado Pass, Whitehorn Mt., Willow Creek Pass. **BRITISH COLUMBIA.** Atlin, Crater Mt., Garibaldi Park, Mt. Ball, Panorama Ridge, Pearson Mt., Pink Mt., Vavenby, 15 mi. W. McBride., W. of Invermere. **MONTANA.** Glacier National Park. **WASHINGTON.** Okanogan Co. - Okanogan Highlands, Windy Peak. Additional records for *C. nastes aliaska* will be found in Table **1**. All of the records found in this paragraph were supplied by K. W. Philip (*pers. comm.*), J. H. Shepard (*pers. comm.*) and E. M. Pike (1978). Additional Yukon Territory records are from Ferris et al., 1983, and are to be found in Tables **1** and **2**.

APPENDIX B

Genetic Considerations

Since the beginning of this century, studies have been conducted on the genetics of the genus *Colias*. Much of this work has been summarized by Remington (1954c) and Robinson (1971). Despite over half a century of research in this area, very little is really known. In North America, only *C. philodice* Godart and *C. eurytheme* Boisduval have been studied in any detail, with *C. alexandra* W. H. Edwards and *C. scudderi* Reakirt to a lesser extent. Old World or circumpolar species investigated in various respects include *C. crocea* Geoffroy, *C. erate* Esper, *C. hecla*, *C. hyale* (L.), *C. myrmidone* Esper, *C. nastes*, and *C. palaeno* (L.). In some instances, only haploid chromosome number has been determined.

Based upon the studies to date, as summarized by Remington, Robinson, and Ford (1953), indications are that the following generalizations can be made concerning the genetics of this genus: 1. Males are homogametic with *ZZ* type chromosomes. 2. Females are heterogametic with *ZW* or unpaired *ZO* type chromosomes. 3. Secondary sex characteristics in the Lepidoptera appear to be independent of gonadal control, since experiments involving gonadectomy and gonadal exchange have little or no effect upon adult morphology or behavior. On this basis, and the study of certain *Colias* gynandromorphs, it has been inferred by several researchers that secondary sex characteristics are autosomal with sex-limited expression to one or the other sex. 4. The haploid number in *Colias* is generally 31, although in a few instances 31 has been observed, such as in the oöcytes of *hyale* and the spermatocytes of *palaeno*. Federley (1938, 1942) has reported 31 for both *hecla* and *nastes* in Finland. 5. The "alba" (white) allele in the females affects oxygen binding and is a sex-limited dominant gene. 6. The "alba" gene is suppressed in the males, although "alba" male phenotypes occur upon rare occasions. Such male "alba" forms are thought to stem from a rare recessive allele (probably normally lethal) at another locus. 7. It is presumed that the "alba" genes are homologous across species. 8. Adult coloration in *Colias* is produced by the pterin pigments leucopterin (white), xanthopterin (yellow), and erythropterin (red). If an oxygen is added to xanthopterin, leucopterin results. 9. Regarding the DHW discal spot color, orange (red) appears to be dominant over yellow or pale (Komai & Aé, 1953). 10. In many geographic regions, several presumed separate species of *Colias* are sympatric and synchronic, and there is field evidence that gene introgression occurs. In fact, it may prove difficult to find a genetically segregated race of *Colias* unless it is as a single species occurring in an isolated habitat. 11. In laboratory crosses of the orange *C. eurytheme* with the yellow *C. philodice*, it has been demonstrated that adult wing color may be controlled by one or two pairs of genes with no dominance. Both parental color phenotypes are recovered in the F_2 generation and in backcrosses. Phenocopies of the hybrid forms are produced in genetically pure *C. eurytheme* by spring and autumn environments (assumed to result from short photoperiod and/or low temperature).

Experimental evidence seems to be conclusive that, for the sex-limited traits investigated, autosomal inheritance is involved. On the other hand, in view of current genetic knowledge, one could also make a case for autonomous gene expression, in which a specialized structure develops according to its own genotype and is not influenced by cells elsewhere in the organism. This phenomenon has been used to explain sexual mosaics (gynandromorphs). In *Colias*, for example, one could argue that UV-reflecting scales must have a *ZZ* component since they occur only in the males, while common scales may be either *ZZ*, *ZW*, or *ZO*. The same argument could be extended to the "alba" scales which appear only in the females, although conclusions drawn in the literature do not lead in this direction.

During the course of the studies reported in this paper, the following phenotypic characters have been examined:

A. Adult coloration.
B. Ultraviolet reflectance in the males.
C. DHW discal spot color.
D. Width of D marginal border in the males.
E. Shape of VHW discal spot: distally produced or not.

Since breeding studies have not been conducted on *C. hecla*, *nastes*, and *boothii/thula*, one can only conjucture about Mendelian inheritance in this group. The phenotypic patterns observed in the thousands of specimens examined during the course of this study suggest several inferences.

It is assumed *a priori* that the individual traits (A - E) listed above are not linked, and that they conform to Mendel's Second Law (Law of Independence), although two of the traits are sex-limited. On this basis, it is inferred from the material studied that the observed phenotypes are described by the genotypes listed below for the characters A - D.

A. Adult Coloration (Incomplete Dominance). [Color refers to the adult ground color neglecting melanic cover scales].

TAXON	GENOTYPE	PHENOTYPE
hecla	RR	orange (as in normal ♂♂ of *C. hecla*).
nastes	rr	white (actually pale yellow-green as in *C. nastes*).

CROSSES	GENOTYPE OF PROGENY	PHENOTYPE OF PROGENY
hecla X nastes = F_1	Rr	yellow-orange (*boothii*).
F_1 *X hecla*	RR, Rr	orange (*hecla*), yellow-orange (*boothii*).
F_1 *X nastes*	Rr, rr	yellow-orange (*boothii*), white (*nastes*).
F_1 *X* F_1	RR, Rr, rr	orange (*hecla*), yellow-orange (*boothii*), white (*nastes*).

Some explanation is required for the white color of *thula* since it has been assumed to represent the western arctic expression of *hecla X nastes.* During the Wisconsin period, large portions of the western arctic were unglaciated in the regions where *thula* occurs (see Ferris 1977, Fig. **46** relative to glaciation). The regions in which *boothii* now occurs were heavily glaciated. It is possible that *thula* represents a primitive form of *hecla X nastes* in which the "alba" allele dominates in both sexes. The phenotypic intermediates between *thula* and *boothii* (partially white and partially orange-flushed imagines) occur in the geographic region that was along the boundary between the glaciated and unglaciated areas in the Yukon and eastern Alaska during the Wisconsin period. The "alba" female phenotype will be discussed subsequently. One can conjecture that western arctic populations of *nastes* and *hecla* carry an allele at another locus which causes leucopterin to be synthesized rather than xanthopterin or erythropterin when the cross *hecla X nastes* occurs. The presumed cause of such a genotype is the isolation between western arctic *hecla* and *nastes* and central-to-eastern arctic *hecla* and *nastes* which occurred during the Wisconsin period. The central and eastern arctic populations of these two species were forced to the boreal regions lying to the south of the Wisconsin ice, while the western arctic populations were probably relatively sedentary. We now see evidence of relict southern populations of *hecla* and *nastes* in the southern Canadian Rocky Mtns., with isolated populations of *nastes* in northern Washington and northern Montana. During the Wisconsin separation of the western and central-eastern populations of the parent species, two different genotypes evolved. This accounts for the geographic difference in the color expression in *hecla X nastes* in North America.

Based upon examination of material from arctic Scandinavia, it appears that both *boothii* and *thula* phenotypes are produced from the cross *hecla X nastes.* This suggests heterozygous populations for the leucopterin-determining allele.

B. UV Reflectance in the Males (Sex-Limited. Incomplete Dominance).
[Structural reflectance produced by specialized cover scales on the wings].

TAXON	GENOTYPE	PHENOTYPE
hecla	UU	♂♂ UV reflective.
nastes	uu	♂♂ not UV reflective.

CROSSES	GENOTYPE OF PROGENY	PHENOTYPE OF PROGENY
hecla X nastes = F_1	Uu	partial UV reflectance, FW mainly (*boothii/thula*).
F_1 *X hecla*	UU, Uu	reflective (*hecla*), partial reflectance (*boothii/thula*).
F_1 *X nastes*	Uu, uu	partial reflectance (*boothii/thula*), not reflective (*nastes*).
F_1 *X* F_1	UU, Uu, uu	reflective (*hecla*), partial reflectance (*boothii/thula*), not reflective (*nastes*).

C. DHW Discal Spot Color (Dominant).

TAXON	GENOTYPE	PHENOTYPE
hecla	SS	strongly colored (red/orange).
nastes	ss	pale colored (yellow/whitish).

CROSSES	GENOTYPE OF PROGENY	PHENOTYPE OF PROGENY
hecla X nastes = F_1	Ss	strongly colored.
F_1 *X hecla*	SS, Ss	strongly colored.
F_1 *X nastes*	Ss, ss	strongly colored, pale colored.
F_1 *X* F_1	SS, Ss, ss	strongly colored (2), pale colored.

D. Width of D Marginal Border in the Males (Sex-Limited. Dominant).

TAXON	GENOTYPE	PHENOTYPE
hecla	nn	wide border (solid).
nastes	NN	narrow border (may have open areas).

CROSSES	GENOTYPE OF PROGENY	PHENOTYPE OF PROGENY
hecla X nastes = F_1	Nn	narrow border (*boothii/thula*).
F_1 *X hecla*	Nn, nn	narrow border (resembles narrow-border *hecla*), wide border (normal *hecla*).
F_1 *X nastes*	NN, Nn	narrow border.
F_1 *X* F_1	NN, Nn, nn	narrow border (2), wide border.

E. Shape of VHW Discal Spot.

While this character was examined, it is too variable to make any reasonable inferences at this time concerning its genetic status. The shape of the spot appears to vary to some degree based upon geography, but this is not entirely clear.

If the four traits (A - D) are now taken in concert, the traditional Punnett Square method of analysis can be used to determine genotypes.

TAXON	GENOTYPE	PHENOTYPE
hecla	RRUUSSnn	orange, ♂ strongly UV-reflective, strongly-colored DHW discal spot, ♂ wide marginal border.
nastes	rruussNN	white, not UV reflective, pale-colored DHW discal spot, ♂ narrow marginal border.

CROSS	GENOTYPE OF PROGENY	PHENOTYPE OF PROGENY
hecla X nastes = F_1	RrUuSsNn	orange (white†), partial UV reflectance, strongly-colored (variably-colored†) DHW discal spot, narrow marginal border (*boothii/thula*).

† The overall color of *thula* can be explained by the theory presented in part A (above). The color of the DHW discal spot is variable, and this can also be explained by this same theory regarding the production of leucopterin rather than xanthopterin or erythropterin.

CROSS	GENOTYPE OF PROGENY	PHENOTYPE OF PROGENY
F_1 *X hecla*	RRUUSSnn	*hecla*
	RRUUSsnn	*hecla*
	RRUUSSNn	narrow-bordered *hecla*.
	RRUUSsNn	narrow-bordered *hecla*.
	RRUuSSnn	*hecla* but reduced UV reflectance.
	RRUuSsnn	ditto
	RRUuSSNn	*hecla* but reduced UV reflectance and narrow border.
	RRUuSsNn	ditto
	RrUuSsNn	*boothii/thula*. (See note above).
	RrUuSSNn	*boothii/thula*. (See note above).

RrUUSSNn	strongly UV-reflective *boothii/thula.*
RrUUSsNn	ditto
RrUUSSnn	yellow-orange *hecla.*
RrUUSsnn	ditto
RrUuSSnn	yellow-orange *hecla* with reduced UV reflectance.
RrUuSsnn	ditto

All of the above phenotypes are seen in field-collected material, and the RrUuSSnn, RrUuSsnn, RRUuSSnn, and RRUuSsnn genotypes could easily account for the variable UV-reflectance noted in what has been considered as pure *hecla* (see Ferris, 1982).

CROSS	GENOTYPE OF PROGENY	PHENOTYPE OF PROGENY
F_1 X *nastes*	RrUuSsNN	*boothii* (or *thula,* see note above).
	RrUuSsNn	ditto
	rrUussNN	*thula.*
	rrUussNn	*thula.*
	rrUuSsNN	*thula* with variably-colored DHW discal spot.
	rrUuSsNn	ditto
	RrUussNN	*boothii* (or *thula*) with pale DHW discal spot.
	RrUussNn	ditto
	RruuSsNN	"rossii" phenotype: yellow-orange flushed, *nastes*-like phenotype with colored DHW discal spot; not UV reflective.
	RruuSsNn	ditto
	RruussNN	"rossii" phenotype with pale DHW discal spot.
	RruussNn	ditto
	rruuSsNN	*nastes* with colored DHW discal spot.
	rruuSsNn	ditto
	rruussNN	*nastes.*
	rruussNn	*nastes.*

All of the above phenotypes are observed in field-collected specimens.

In the F_1-F_1 cross shown below, only the genotypes in addition to those produced by F_1 X *hecla* and F_1 X *nastes* are tabulated. The percentage frequency-of-occurrence is also shown.

CROSS	GENOTYPE OF PROGENY	% FREQ.	PHENOTYPE OF PROGENY
F_1 X F_1	RRUUSSNN	0.39	narrow-border *hecla.*
	RRUUSsNN	0.78	ditto
	RRUuSSNN	1.56	narrow-border, partially UV-reflective *hecla.*
	RRUuSsNN	3.13	ditto
	RRUUssnn	0.39	pale DHW spot *hecla.*
	RRUUssNN	0.39	pale DHW spot, narrow-border *hecla.*
	RRUUssNn	0.78	ditto
	RRUussNN	0.78	*partially UV-reflective, pale DHW discal spot, narrow border *hecla.*
	RRUussNn	1.56	* ditto
	RRUussnn	0.78	*partially UV-reflective, pale DHW spot *hecla.*
	RRuuSsNN	0.78	§orange, not UV-reflective, narrow border.
	RRuuSsNn	1.56	§ditto
	RRuuSsnn	0.78	§orange, not UV-reflective, wide border.
	RRuussNN	0.39	§orange, not UV-reflective, pale DHW discal spot, narrow border.
	RRuussNn	0.78	§ditto

RRuussnn	0.39	§orange, not UV-reflective, pale DHW discal spot, wide border.
rrUUSSNN	0.39	§strongly UV-reflective, colored DHW discal spot *thula.*
rrUUSSNn	0.78	§ditto
rrUUSsNN	0.78	§ditto
rrUUSsNn	1.56	§ditto
rrUUSSnn	0.39	§strongly UV-reflective, colored DHW discal spot, wide-bordered *thula.*
rrUUSsnn	0.78	§ditto
rrUuSSNN	0.78	*thula* with colored DHW discal spot.
rrUuSSNn	1.56	ditto
rrUuSSnn	0.78	§*thula* with colored DHW discal spot and wide border.
rrUuSsnn	0.78	§ditto
rrUussnn	0.78	§*thula* with wide border.
rruuSSNN	0.39	*nastes* with colored DHW discal spot.
rruuSSNn	0.78	ditto
rruuSSnn	0.39	**nastes* with colored DHW discal spot and wide border.
rruuSsnn	0.78	* ditto
rruussnn	0.39	**nastes* with wide border.

The F_1-F_1 cross may be completely lethal, and it is apparently lethal for certain genotypes. Those indicated by (*) are very rare, but occasional specimens with these phenotypes are seen in museum collections. These specimens, however, may represent variations of F_1 *X hecla,* or F_1 *X nastes.* The phenotypes indicated by (§) are unknown based upon field-collected material. In all cases, the percentage frequency-of-occurrence is very small based upon standard Punnett Square analysis. Basically the F_1-F_1 cross adds no new known phenotypes that cannot be obtained from F_1 backcrosses with the two parent species.

The genotypes and associated phenotypes presented in the tables above adequately describe all of the material examined during the course of this study. Insufficient data are available to introduce the trait of emergence date of the adult butterfly. Were this information available, one could probably match phenotype and field data exactly with the genotypes proposed in the tables above.

The "Alba" Female Form.

The nature of the "alba" inheritance in *Colias* was defined by Gerould (1911, 1923) based upon his studies of *Colias philodice,* and further elaborated by Remington (1954a) and summarized in Robinson (1971). The "alba" (white) allele is dominant, sex-limited and always expressed in heterozygous females. Analysis of gynandromorphs, and the fact that the "alba" trait is suppressed in male *Colias* has led Lepidoptera geneticists to conclude that it is an autosomal trait.

The "alba" trait is summarized in the table shown below:

GENOTYPE	**♀ WING COLOR**	**♂ WING COLOR**
AA	white	yellow or orange
Aa (A+)	white	yellow or orange
aa (++)	yellow	yellow or orange

It has been proposed by Remington, among others, that the "alba" alleles are homologous across *Colias* species.

In some species of *Colias*, the frequency of the "alba" phenotype increases with latitude. The "alba" form of *Colias meadii meadii* W. H. Edwards is very rare in Colorado and New Mexico, but relatively common in northern Wyoming and southern Montana. At The Pas, Manitoba, females of *Colias gigantea* Strecker are typically yellow, while at

Churchill some 500 miles to the north, they are almost invariable white. Environmental factors seem to affect the expression of the "alba" allele, but the mechanisms are not clear. In some species, such as *C. interior* Scudder, the "alba" form appears to occur randomly. Perhaps microhabitat is a key factor, but this has yet to be established.

"Alba" females of *C. hecla* occur with some frequency is western arctic populations, but are definitely uncommon in central and eastern arctic populations. The explanation for this is perhaps the same as that proposed in section A (above) for the color of male *thula*, and is related to isolation during the Wisconsin glaciation. One can conjecture that the "alba" form has a selective advantage in the western arctic, or that perhaps mutations occurred during the Wisconsin isolation which produced the *thula* phenotype and relatively high incidence of "alba" females in the western arctic, and orange phenotypes elsewhere.

APPENDIX C

Fig. **130** presents the raw data used to formulate Fig. **86**. Trace 0 is the reflectance profile obtained from a photographic white card. It has been assumed that the white card reflects uniformly over the wavelength range scanned (800-350 nm), and it has therefore been used as a baseline correction for the incandescent light source and optical detector associated with the 2280 AA/AE spectrometer. Data for the specimens scanned are as follows:

C. hecla hecla: Greenland.
C. hecla hela: Churchill, Manitoba.
C. boothii: Baker Lake, N.W.T.
C. nastes f. "rossii": Southampton Is., N.W.T.
C. nastes nastes: Nain, Labrador.
C. thula: Seward Peninsula, Alaska.

All scans are of male specimens.

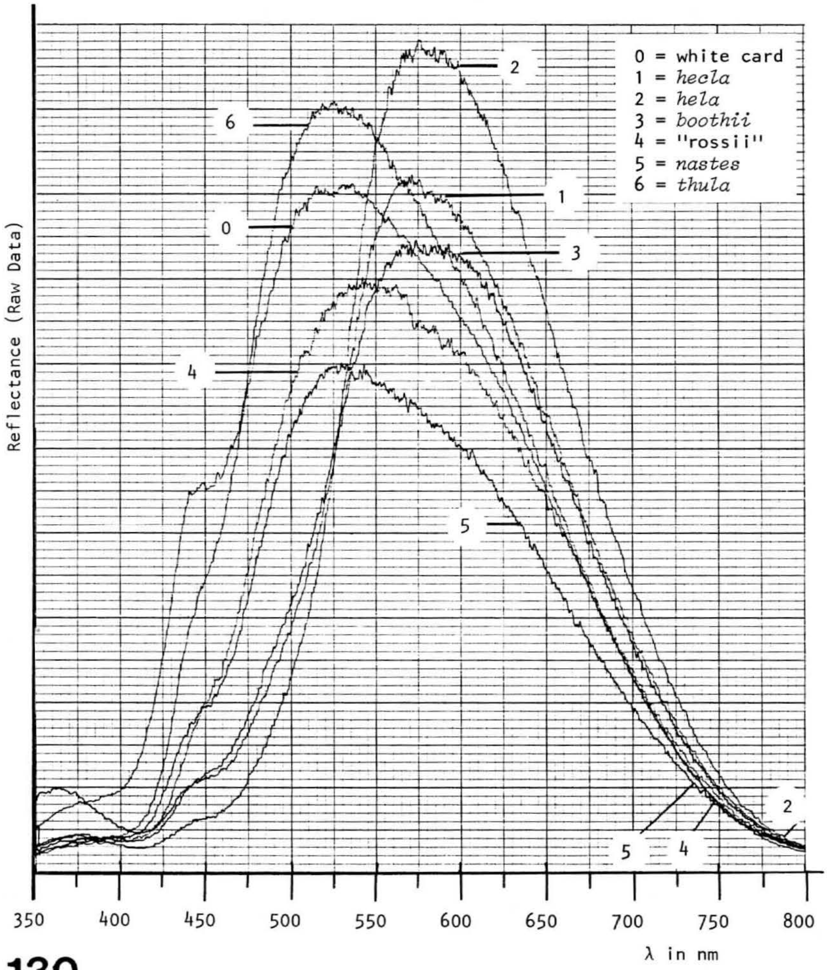

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Figure 130: Optically-uncorrected reflectance scans of six male *Colias* specimens. Corrected scans are shown in Fig. 86.

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