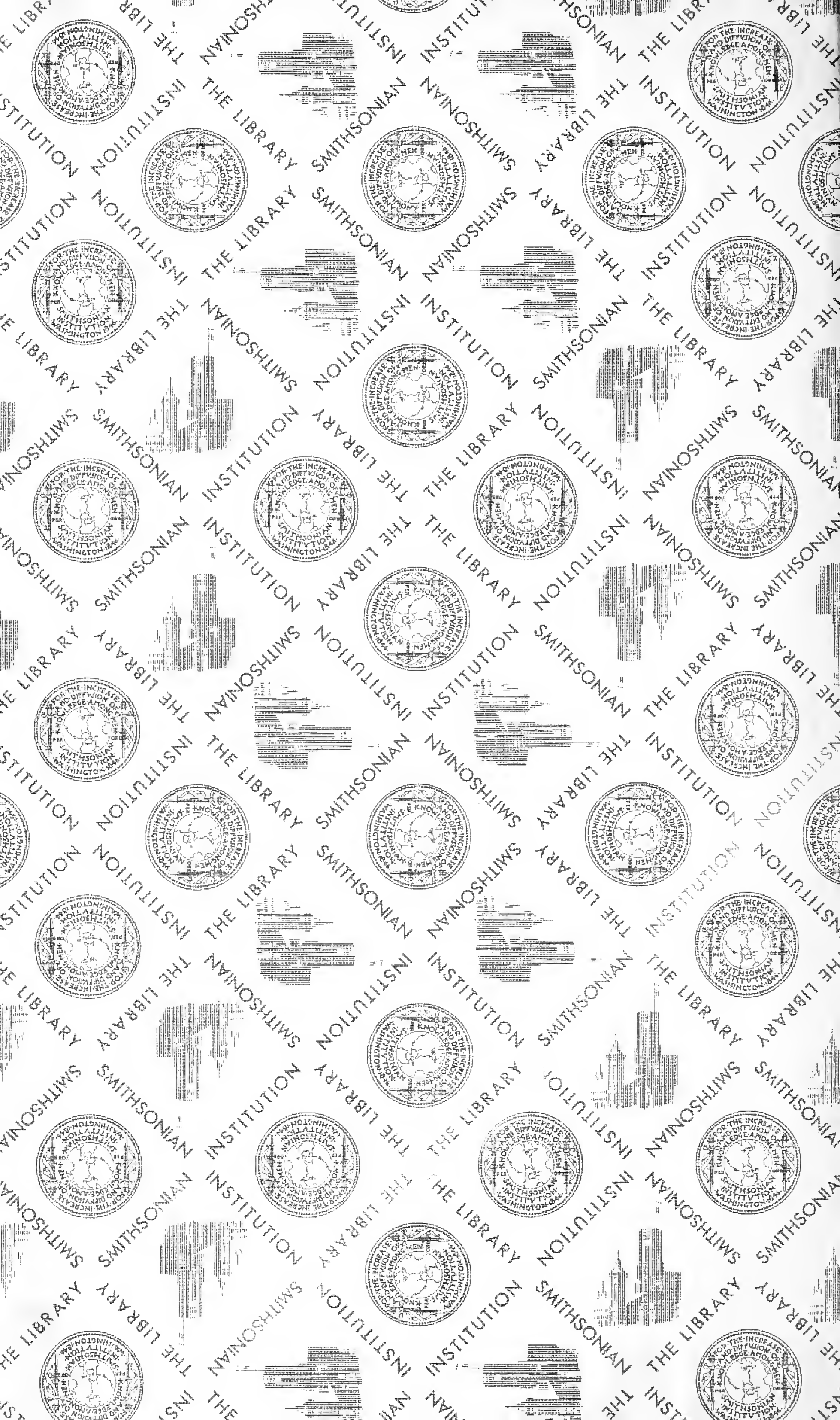

THE JOURNAL OF RESEARCH ON THE LEPIDOPTERA

Established in 1962

Edited by WILLIAM HOVANITZ

Volume 1

1962 – 1963

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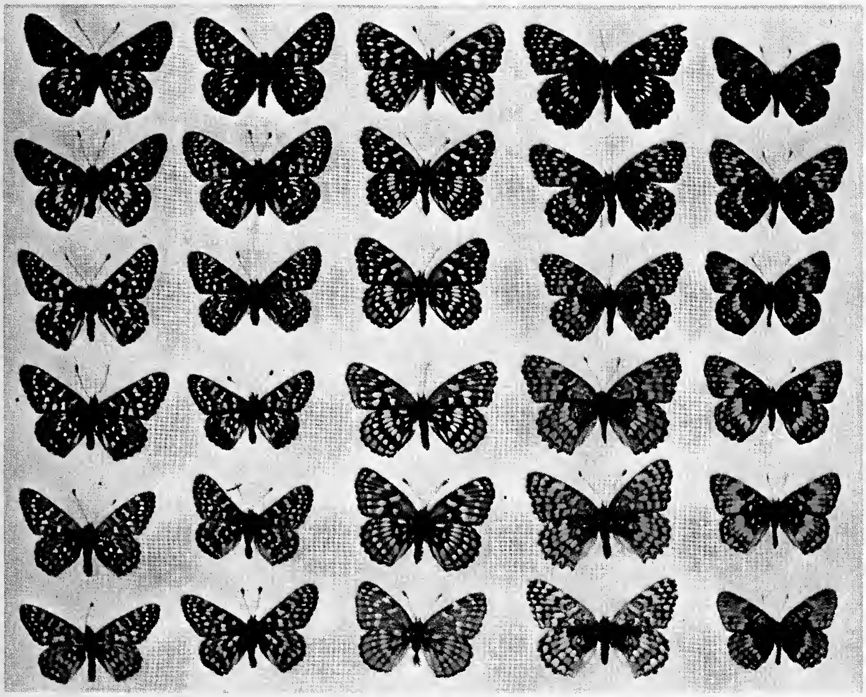

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WITH EMPHASIS ON ENVIRONMENTALLY AND GENETICALLY INDUCED VARIATION, population analysis, evolution, phylogenetic taxonomy, zoogeography, comparative morphology, ecology, geographical variation, speciation, physiology, etc. In short, *quality work on any aspect of research on the Lepidoptera.*

THE PURPOSE OF THE JOURNAL is to combine in one source the work in this field for the aid of students of this group of insects in a way not at present available. The JOURNAL will attempt to publish primarily only critical and complete papers of an analytical nature, though there will be a limited section devoted to shorter papers and notes.

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Journal of Research on the Lepidoptera 1(1):1, 1962

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EDITORIAL

Starting a new journal is not an easy matter, nor is it a matter free of controversy. This is especially the case where a new journal, as this one, is started without the support of an existing society. This journal is intended as a meeting ground for papers on all aspects of the biology of the Lepidoptera, moths and butterflies alike. Too many entomological journals don't offer publication of articles of the length necessary to present sound data and completeness of effort. The Lepidoptera are a group of insects second to none in the scope of our knowledge about them: work in this field has reached the higher levels of learning and a journal is required to keep pace with this knowledge at the same level.

A journal with a wide scope is our aim — narrow in the taxonomic sense but wide in the biological sense. The journal will attempt to publish primarily only critical and complete papers of an analytical nature, though there will be a limited section devoted to shorter papers and notes. There will be emphasis on environmentally and genetically induced variation, population analysis, evolution, phylogenetic taxonomy, zoo-geography, comparative morphology, ecology, geographical variation, speciation, physiology, etc.

It has been very gratifying to receive so many subscriptions on the basis of merely a brochure; every effort will be made to keep the journal up to the standard expected of us. The response in so short a time has served to show those who have generously provided the finances that a journal of this type has been needed and will fill a desirable niche.

We are happy to publish in this first issue a number of papers which the authors were able to get ready on "short notice". There is a preponderance on one taxonomic group, but with different points in mind. With this first issue out, *we offer the pages of this journal to all with papers to publish on the Lepidoptera that fit the intent of the journal.* A wider range of papers will come in future issues.

Journal of Research on the Lepidoptera 1(1):3-20, 1962

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VARIATION IN THE SILVERING OF *ARGYNNIS (SPEYERIA) CALLIPPE* IN THE INTERIOR MOUNTAIN AREA OF SOUTH CENTRAL CALIFORNIA

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In a comprehensive study of the geographic variation of *Argynnis (Speyeria) callippe* Boisduval, based on examination of about 2750 specimens from many localities well distributed through out the range of the species in California, Hovanitz (1943) recognized several main divisions of this species complex. Among them are the "South Coast Range Population" extending from the San Francisco Bay area southward through the Coast Ranges into Lower California and the "Western Sierra Nevada Populations" extending in a band along the western Sierra Nevada, at moderate elevations from the region west of Lassen Peak southward to about the Greenhorn Mountains at the southern end of the Sierra Nevada. He found that these two population groups are connected through a "Southern Zone of Intergradation" by a "series of steps across the Piute Mountains, the Tehachapi Mountains and the Sierra Madre Range."[1]

He characterizes the populations in the Southern Zone of Intergradation as follows:

> "From the Santa Monica Mountains on the coast, where the typical *callippe* of this (the South Coast Range) region lives, it is found that in going inland (Charlton Flat, Mint Canyon and 'Ridge Route') the lightness of all colors increases. The butterfly becomes smaller and the light colored band and spots on the upper surface of the wings tend to become obliterated, leaving a more uniformly colored wing surface such as is present in the western Sierra Nevada gradient. However, the yellow-brown color is very much lighter than in the latter and the band on the under side of the hind wings is still yellow; the spots are still always fully silvered. The tendency toward these conditions is the more marked the farther from the coast and the farther into the Tehachapi Range the populations exist. In the Tehachapi Range, the butterflies are very lightly colored and the band on the upper surface of the wings is rare; the spots are still silvered. At Havilah, Piute Mountains, the population consists of some silvered, some unsilvered and some intermediate spotted

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[1] This range is not named on many maps. It lies parallel to, and south of, the middle portion of the Cuyama River which is the long north branch of the shorter Santa Maria River shown discharging into the ocean at about lat 35° in Fig. 1.

> individuals (this is the type locality of *macaria* Edws.); the exact frequency of these types is not known, but there is a high percentage of silvered and unsilvered present . . . In the Greenhorn Mountains, the segregation into a silvered population on the eastern side of the summit and an unsilvered one on the western side is decidedly apparent, though mixing occurs toward the south, where the populations unite".

The main purpose of this paper is to describe semi-quantitatively the variation of silvering within the Southern Zone of Intergradation. The silvery decoration of animals is far less common than the pigmental coloration. While Hovanitz (1941) has found general qualitative correlations of the pigmental coloration of butterflies with environmental conditions, he finds the significance of silvering in *callippe* "quite incomprehensible" (Hovanitz, 1943, p. 420). Some peculiarities of the silvering data revealed by the semi-quantitative treatment in this paper suggests that studies of its physico-chemical nature and genetic control might be rewarding. An hypothesis is advanced as a point of departure for such studies.

THE SAMPLES

The material for this study consists of complete series of *callippe* that I collected during June 8 to 15, 1957 in company with Fred T. Thorne, and one sample from Bouquet Canyon consisting of part of a series taken in 1952 by Thorne and kindly given to me. In breaking the series Thorne exercised no conscious selection for color or pattern, though worn and damaged specimens were discarded.

Parallel or convergent evolution among the Argynnids in some regions presents problems of species identification. In the Southern Zone of Intergradation this problem arises between *callippe* and *coronis* Behr. The latter, as the subspecies *hennei* Gunder, flies with *callippe* and resembles it so closely that confident identification requires either great familiarity with both species or known series from the region for comparison. L. P. Grey is in possession of both and kindly reviewed my field identifications. These had been made in consultation with Thorne. At the time neither of us had previous acquaintance with *hennei,* though we were both familiar with several other subspecies of *coronis*. Two specimens I had labelled *callippe* proved to be undoubted *coronis.* One labelled callippe came back from Grey with the notation, "Could this be *coronis?* (Don't ask me!." Another labelled *coronis* bore Grey's notation "I think it is a *callippe*." The last two, when spread and compared with the now-available good series of *hennei,* appear to me to be undoubted *coronis,* though the under side wing surface (the only surface exposed to Grey's examination) is remarkably like the *callippe* from the same locality. These four speciments have been excluded from the samples.

In the list that follows, the collections are grouped by localities. Each group contains mainly specimens taken at one location, to which have been added a few specimens from nearby locations. Those in the main group, I believe, are members of a single interbreeding colony; the others may consist of strays from the same colony in some instances, and in others, may be strays from some other colony. All localities are in Kern County except Sandberg's and Bouquet Canyon which are in Los Angeles County. Distances from named places are given to the nearest mile (1.61 km) measured on a straight line on large-scale road maps. Directions, also determined from such maps, are referenced to true North and stated in Mariners' abbreviations appropriate to the 32-point compass. Thus southwest is given as SW, southwest by west as SWxW and west southwest as WSW. These are 11.25° steps and allowing for measuring inaccuracy are correct to about the nearest 15°. Elevations were taken by aneroid altimeter graduated in 100-foot (30.5 m) units and probably accurate to ± 200 feet. Botanical names are according to Jepson (1923 - 1925), Abrams (1940, 1944 and 1951) and Abrams and Ferris (1960). Nomenclature of the butterflies follows the list by McDunnough (1938) except for the genus (*Speyeria*), which, at the species and subspecies level follows the arrangement of Dos Passos and Grey (1947).

A. East slope, Greenhorn Mountains. June 12, 1957, 18 males and 1 female taken 6 miles WSW of Kernville, elevation 4900 ft., along the road leading steeply from Isabella Reservoir to Greenhorn Mountain Park passing between Tittle and Rattlesnake Creeks, in association of Digger Pine (*Pinus sabiniana* Dougl.), Oak (*Quercus* sp), California Fremontia (*Fremontia californica* Torr.), and chaparral broken by grassy areas, with Yerba Santa (*Eriodictyon* sp.) flowers as nectar attractant; included in addition is 1 male taken 8 miles WxS of Kernville, elevation 5500 ft., Transition Zone, in a small roadside opening in Yellow Pine (*Pinus ponderosa* Dougl.) and Incense Cedar (*Libocedrus decurrens Torr.*) forest.

B. West slope, Greenhorn Mountains. June 12, 1957, 58 males and 6 females taken 27 miles NE of Bakersfield, elevation 3300 ft., near the foot of Eugene Grade, in Digger Pine, Blue Oak (*Qurcus douglasii* Hook & Arn.) and grass association, with violets (*Viola* sp.) abundant; included in addition are 3 males and 1 female taken 26 miles NNE of Bakersfield, elevation 3000 ft., in Blue Oak and grass association, with riparian flora along a small creek.

C. Havilah. June 11, 1957, 13 males and 1 female taken 2 miles S of Havilah, elevation 3100 ft., Digger Pine, mixed oak and chaparral association with riparian flora along a small creek, mostly attracted to Yerb Santa flowers; in addition are 1 male from 1 mile north of Havilah, elevation 2800 ft., and another from 5 miles S of Havilah, elevation 3900 ft.

D. Walker Basin. June 11, 1957, 30 males and 6 females taken 10 miles SxW of Havilah, at the south end of Walker Basin, elevation 3200 ft., Blue Ok and Grass association with sagebrush and violets. Hoarhound (*Marrubium vulgare* L.) attracted a few individuals, but most were taken in the characteristic slow, fluttering flight displayed when on breeding grounds.

E. Tehachapi. June 14, 1957, 12 males and 7 females taken 8 miles W of Tehachapi (the town), elevation 4700 ft., at the eastern end of Bear Valley in Blue Oak and grass association, with patches of sagebrush (*Artemisia tridentata* Nutt.), mostly acctracted to Wallflower (*Erysimum* sp.) flowers; in addition are 3 males from 7 miles W of Tehachapi, elevation 4600 ft., and 1 female from 3 miles SW of Tehachapi, elevation 4600 ft.

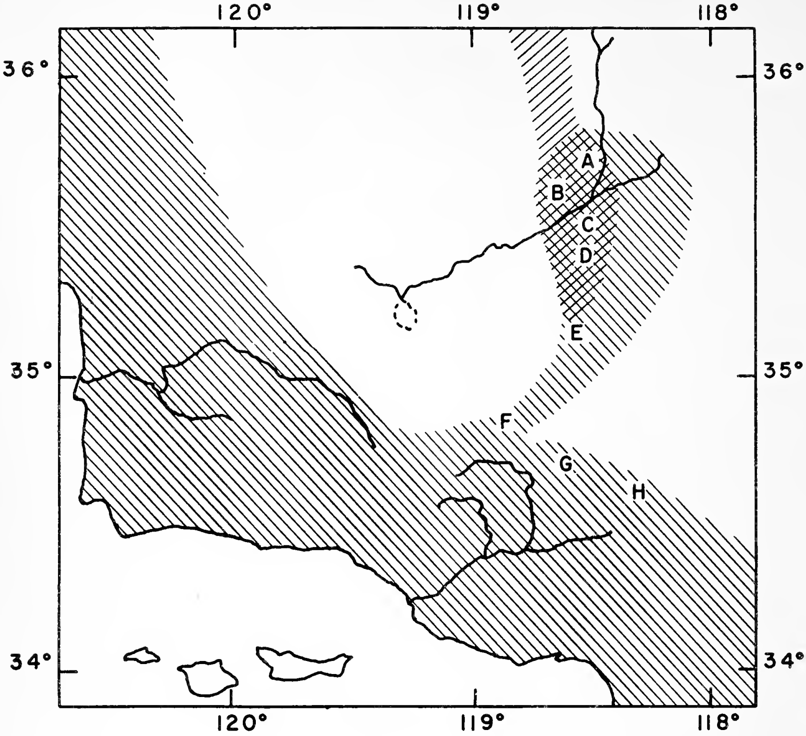

FIGURE 1. Location of populations sampled (letters "A to H") superimposed on the distribution of *Argynnis (Speyeria) callippe* (shaded area) adapted from a portion of Hovanitz' map (1943, Fig. 1) showing the distribution of the "silvered spots" character by shading lines slanted upward to the left and the "unsilvered spots" character by shading lines slanted upward to the right. The Kern River (upper right) separates the Greenhorn Mountains to the north from the Piute Mountains to the south as it flows to a sink in the lower San Joaquin Valley (blank area at upper middle). At middle left is the Santa Maria River with the Cuyama River as its long north fork. At the lower right is the Santa Clara River. The crests of the higher mountains and ridges of the transverse series of ranges lie north of the Santa Clara River Drainage and south of the Cuyama River.

F. Lebec. June 8, 1957, 24 males and 8 females; June 9, 1957, 26 males and 4 females; and June 15, 1957, 11 males and 15 males; total, 61 males and 27 females taken 1 mile S of Lebec, elevation 3600 ft., in oak and grass association with adjacent chaparral including sagebrush (*A. tridentata*), Buckwheat Brush (*Eriogonum fasciculatum* Benth.) and Yerba Santa; some were at flowers of the last, others in breeding-ground flight.

G. Sandberg's (on old Ridge Route). June 9, 1957, 12 males and 3 females; June 15, 1957, 1 male and 2 females; total, 13 males and 5 females taken 9 miles ESE of Gorman in Digger Pine and sagebrush (not *A. tridentata*) association, with violets. Breeding ground behavior was predominant.

H. Bouquet Canyon. June 11 and 12, 1951, 18 males collected by Fred T. Thorne at "upper Bouquet Canyon, 4 miles down from Pine Creek — Lake Hughes road" (estimated 16 miles W of Palmdale, estimated elevation 3400 ft.).

HABITAT AND MESOSCALE DISTRIBUTION

According to these records *callippe* in this region occupies elevations from 2800 to 5500 feet, but occurs in good concentrations only between 3100 and 4900 feet, generally, the upper portion of the Upper Sonoran Life Zone. Its habitat is marked characteristically by scattered Blue Oak, Digger Pine, and sparse chaparral with sagebrush (*A. tridentata*) often pesent. Usually there are broad areas or small patches of grass present. Practically all of the localities are in grazing land, but at the time of our trip it was being very lightly grazed.

Violets were noted at only three of the locations. Where they were seen, the plants were abundant, mature, with fully-developed seed capsules and appeared about to dry up. Where violets were not seen, either they had dried up already, or the collecting was of members of the colony that had been drawn by nectar sources somewhat away from the site of the larval food plant.

During the trip we collected at 31 locations within the geographic range and elevation limits of this butterfly. Of these, seven obviously were in, or close to, *callippe* colonies; five locations yielding only one or several specimens, evidently were not as close; and the remaining 19 locations where we took none probably were distant from colonies, though this may not have been true for a few places where we sighted an Argynnid or two which could have been either this species or *coronis.* These indications favor a population model consisting of well-separated, compact colonies from which individuals do not stray often or far. This pattern is more accentuated in this region than in most others within my collecting experience.

Butterflies of 30 other species were taken at one or another of the seven locations where *callippe* were caught in good numbers. *Plebeius acmon* West. and Hew. and *Hesperia lindseyi* Holland were the most ubiquitous, occuring at most locations from the Greenhorn Mountains to Sandberg's. The former were taken in small numbers while the latter, in some locations were very abundant. In addition to these, the most common and prevalent in the Greenhorns and the Piutes were *Euphydryas chalcedona* Doubleday and Hewitt, *Melitaea palla* Boisduval, and *Strymon saepium* Boisduval; while through the Tehachapi to Sandberg's they were *Minois silvestris* Edwards and *Argynnis coronis* Behr. If one of the specimens whose identification was questioned by

Grey is, as I believe, *coronis,* this species extended north at least to Havilah. Inasmuch as all coronis taken on this trip were fresh males, and in other regions within my collecting experience *coronis* flies somewhat later than *callippe,* it is likely that a week or two later in the season *coronis* would have been found to be even more consistently a companion of *callippe.*

RELATIVE ABUNDANCE

The relative abundance in butterfly populations may be significant in studies of variation. From records extending through many years, Ford (1945) found that a rapid increase in abundance of the colonial butterfly *Euphydryas aurina* Rott was accompanied by "an extraordinary outburst of variation". When the increase ceased, the colony settled down to a comparatively uniform type, different from the one prevailing prior to the increase. Scientists differ as to the interpretation and significance of this phenomenon as a mechanism in evolution. Whatever the interpretation, if the generality of this phenomenon is to be ascertained, records must be accumulated through the years for a number of butterfly populations.

To this end, there are placed on record in Table 1, estimates of relative abundance of *callippe* in each of the seven colonies sampled in 1957. This estimate is in terms of catching rate and assumes that the number caught in unit time is proportional to the abundance of the population in the area of collecting. It is homologous in concept to the measure "catch per unit of effort" almost universally and successfully (sometimes "calibrated" to a absolute abundance by tag-and-recapture experiments) used as a basic statistic in studying the dynamics of fish population fluctuations (Ricker 1940). For *callippe* I have computed the catching rate, R, according to the formula:

$$R = \frac{N_c}{H - k\ N_t}$$

where N_c is the number of *callippe* caught, H is the time, in hours, in the collecting period, N_t is the total number of specimens of all species caught (including *callippe*) during the collecting period, and k is a constant whose value depends on the methods and dexterity of the collector in caring for a specimen once it is in the net. By timing myself in the caring, individually, for each of 150 specimens of a number of species from all families except Megathymidae under typical field conditions, I found my k value to be 0.0155 hours (37.8 seconds).

In repeated samplings of several species I have found R to be surprisingly stable. For *callippe,* the three samplings at Lebec are an example of this. Although stable, R as computed by this formula should be regarded only as a first-order approximation, or index, of true relative abundance, because it is affected by systematic error and several sources of variability, not all of them random. A more sophisticated iterative treatment theoretically should improve R, but it involves assumptions of uncertain merit awaiting test.

TABLE 1. Relative abundance in terms of catching rate, R, in number per males and by the per cent of the males that were fresh.

Locality, date (1957) and elevation	Catching rate (R)	Per cent males	Per cent of males fresh
A. E. slope, Greenhorns, el. 4900 ft., June 12	* 39	84	86
B. W. slope, Greenhorns, el. 330 ft., June 12	**227	91	52
C. Havilah, el. 3100ft., June 11	16	93	15
D. Walker Basin, el. 3200 ft., June 11	* 44	83	87
E. Tehachapi, el. 4600 - 4700 ft., June 14	33	67	79
F. Lebec, el. 3600 ft., June 8	24	75	84
F. Lebec, el. 3600 ft., June 9	24	87	69
F. Lebec, el. 3600 ft., June 15	30	42	45
G. Sandberg's, el, 4000 ft., June 9	17	80	75

In the meantime, of most concern is that R increasingly underestimates abundance as the latter increases, presenting simultaneous catching opportunities more often and usually avail can be taken of only one of them at a time. Recognizing this, the values in Table 1 that probably were moderately underestimated owing to this factor are marked with an asterisk, and the one value that was grossly underestimated is marked with a double asterisk. At the other end of the scale, when only one or two specimens are caught during a collecting period, R has large error owing to random variability of incidences of encounters. Avoiding this, Table 1 gives catching rates computed for only the first-listed location under each locality, except for Tehachapi where the times and catches of the first two locations were pooled for computing the catching rate.

Another error source is that as kN_t approaches H, a small error in k produces a large error in R. This approach was not close enough to be critical for the values given in Table 1, though the value for the west slope of the Greenhorn Mountains may have been moderately affected.

Every collector can think of a number of other obvious sources of error or variability such as weather conditions, unusual concentrations at attractants, etc., These obvious ones can be avoided by comparing only sets of samplings taken under reasonably similar conditions, as is true for the set in Table 1 except as later noted.

Of course the catching rate reflects the relative abundance only at the stage of flight at which the collecting was done, and may yield values departing substantially from the inherent abundance. An estimate of the stage of the flight is afforded by the relative numbers of fresh and worn individuals. In Table 1, recorded as "fresh" were individuals without readily perceptible random loss of scales or fringe. Damage reasonably attributable to accidental causes, such as notches, tears, breaks and rubbed streaks or patches was not considered. The data are given for males only, there not being enough females to yield reliable percentages. The two sexes were not combined for this statistic because this would introduce extraneous variability owing to the tendency of females to emerge later than males. As evidence of this, only four of the 53 females listed in Table 2 were worn. More direct evidence is afforded by the Lebec samples. Those of June 8 and 9 were mostly males and mostly fresh. About a week later more than half of the males were worn and the females, all fresh, outnumbered the males. The sample from Havilah is anomalous in respect of percentage worn in relation to sex ratio. Although most of the males were worn, only one female was taken. Probably the greater ease of collecting males at the Yerba Santa flowers diverted us from the females which probably were widely scattered for ovipositing in the adjacent area which appeared to be the likely habitat for violets, though the plants were not observed, doubtless having dried up before our visit. At Sandberg's the catching rate was substantially depressed by a strong breeze sweeping the exposed slope and wafting many a disturbed butterfly out of stalking or pursuit range.

Appraising the catching rates in the light of these qualifying factors, the presence of some worn males at all localities indicates that the *callippe* flight was well developed throughout the region. But the high percentage of fresh males and the scarcity of females suggests that the flight had not yet reached its peak at most localities except Lebec where it probably was near peak stage on June 15 and Havilah, where the male flight had apparently passed its peak. Allowing for the differences in stage of flight and the collecting difficulties at Sandberg's, it appears that relative abundance was capable of attaining a height-of-flight index of 30 to 40, probably closer to the latter, at all localities except the location on the west slope of the Greenhorn Mountains where abundance was at least an order of magnitude higher, and at Walker Basin where it probably was substantially higher than 40 per hour, though well below that on the west slope of the Greenhorn Mountains. Although we did not trace out the geographic extent of a colony in any of the localities, the impression gained while collecting, was that these two colonies covered more extensive areas than the rest. It may be concluded, first, that the samples were drawn from near the middle of the flight period and hence probably represent nearly the modal characteristics of the population in each colony; and second, the colonies varied quite widely in population size, perhaps through more than one order of magnitude. Further results may emerge if comparisons with changed levels of abundance become possible in the future.

VARIATION IN SILVER SCALING

The silver scaling in *callippe,* as in Argynnids generally, is confiined to certain pattern elements on the ventral wing surface. For the most part these are well defined spots in the apical and subapical area of the fore wing and all well defined spots in all areas of the hind wing. In addition, on heavily silvered individuals, silver scales may form ill defined streaks along the inner margin and in some of the interspaces between spots in the basal and discal areas of the hind wing. The present study is confined to the well defined spots of the hind wing. When unsilvered these spots are a light buff color, usually sharply bordered or outlined by brown scales. Some or all of the spots may be partly silvered. Then the silver scales and buff scales stand out in sharp contrast to each other when specimens are held in the best relation to the light source and the eye to bring out the specular quality of the silver scales.

A fully quantitative measure of the degree of silvering would be the ratio of silvered scales to all scales in the area potentially subject to silvering. To avoid spending a prohibitive amount of time counting scales, I have employed a subjective system of scoring based on general appearance. It would have been desirable, too, to utilize exclusively the pristine fresh individuals, but to avoid reducing the number below levels needed for tests of significance, I have scored the slightly and moderately worn individuals along with the fresh ones, excluding only those whose loss of scales caused serious doubt as to their correct score. The penultimate column of Table 2 shows the number excluded for this reason.

Because the amount of silvering sometimes differed appreciably in the basal and discal area, which will be called "disc" for brevity, from that in the submarginal area, called "margin", the two portions of the wing were scored separately. Four grades of silvering were recognized: Grade 0 for complete lack of silver scales: Grade 1, when there were only flecks of silver well separated by buff scales; Grade 2, when some of the spots were unsilvered, others were partly silvered and still others were fully silvered, or any combination of two of these conditions; and Grade 3, when all spots were so fully silvered that there were no readily perceptible buff scales. The Disc Grade and the Margin Grade were treated as half scores and added together to arrive at the individual Score. Thus there are seven possible scores: 0 to 6, inclusive.

Of the 238 individuals scored, 50 had half scores that differed from each other by one grade point. None differed by more than one. Of the 50 with different half scores, the Disc Grade was higher than the Margin Grade for 40 individuals and lower for 10. Curiously, for the two Greenhorn Mountain samples and the Havilah sample, pooled, the ratio was 33:4, while for the Walker Basin, Tehachapi and Lebec samples, also pooled, it was 7:6. The difference between the ratios 33:4

and 7:6 is statistically significant (p=0.02) despite the small numbers in the latter. It is possible that the tendency for the marginal row of spots to be less silvered than the disc spots is linked to the general lack of silvering in the three northernmost localities.

TABLE 2. Frequency distribution of silvering scores

Sex and sample	Score							Mean	Not Scored	Total
	0	1	2	3	4	5	6			
Males:										
A. E. slope, Greenhorns	5	3	1	1	—	2	7	3.16	—	19
B. W. slope, Greenhorns	17	8	7	6	4	8	7	2.42	7	64
C. Havilah	2	1	—	2	—	2	4	3.73	4	15
D. Walker Basin	1	2	1	—	1	2	19	5.08	4	30
E. Tehachapi	1	—	—	1	—	—	13	5.40	—	15
F. Lebec	1	1	1	1	1	1	39	5.54	15	60
G. Sandberg's	—	—	—	—	—	—	10	6.00	3	13
Total	27	15	10	11	6	15	99	4.16	33	216
Females:										
A. E. slope, Greenhorns	—	—	1	—	—	—	—	2.00	—	1
B. W. slope, Greenhorns	—	—	2	3	—	—	—	2.60	—	5
C. Havilah	—	—	—	—	—	—	—	—	1	1
D. Walker Basin	—	—	—	1	1	1	3	5.00	—	6
E. Tehachapi	—	—	1	1	—	—	6	5.01	—	8
F. Lebec	1	—	—	—	—	—	25	5.77	1	27
G. Sandberg's	—	—	—	—	—	—	5	6.00	—	5
Total	1	—	4	5	1	1	39	5.12	2	53

The mean score for males is 4.16 and for females is 5.12 (Table 2), suggesting that females tend toward more silvering than males. But four-fifths of the females were taken at Walker Basin, Tehachapi and Lebec where silvering in both sexes is nearly complete. If we pool these three sampls and class together the individuals with scores 0 to 4 inclusive, and similarly those with scores 5 and 6, in order to have high enough numbers for statistical test, we find no significant difference between the sexes (P = 0.9). Accordingly, further analysis deals with both sexes combined, as shown graphically in Fig. 2.

The arrangement of samples in Fig. 2 is in ascending order of their means. This also arranges them from north to south except for the reversal of samples A and B. Where samples are near the same parallel of Latitude and have appreciable meridianal displacement, as among A, B and C as one group and F, G, and H as another, their means also ascend from west to east.

The slopes of the lines connecting the means in Fig. 2 should not be taken as representing gradients of silvering in the sense of reflecting unit increase of silvering per unit distance. The panels are not spaced in proportion to distance, but merely to accommodate the height of the bars. The means, themselves, are defective because the scores do not represent even gradations in amount of silvering. Further, because of

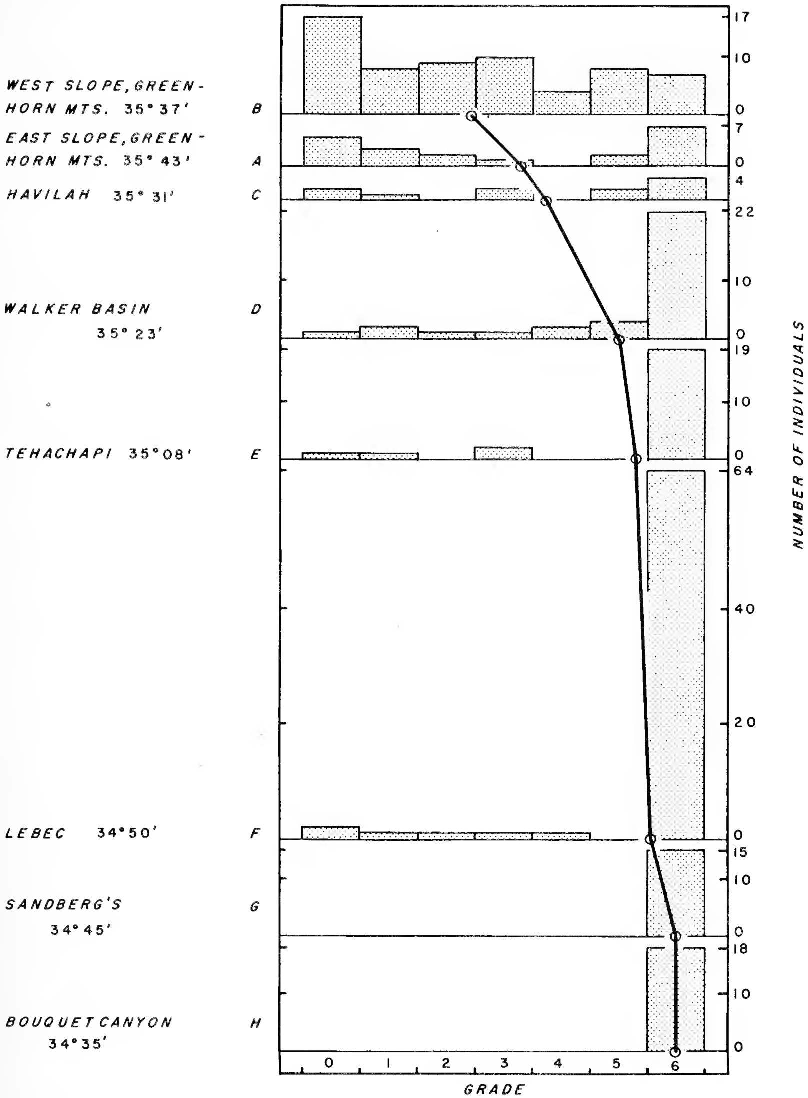

FIGURE 2. The degree of silvering of the several samples, shown as histograms of the number of individuals according to grade (see text); and the mean grades, shown as small circles connected with heavy straight lines.

the prevalence of low numbers at the middle scores, the distributions depart widely from the bell-shaped normal probability curve and the parametric test commonly applied to means would not yield reliable probabilities even if the means were not otherwise defective. The means were computed and connecting lines were supplied in the graph only to give a general perspective of the amount and direction of differences between localities.

For a more careful assessment, the significance of the differences between samples, as to the numbers of individuals falling into the several silvering classes, can be made by the chi-square test which requires neither a normal distribution nor uniform class size. It does require a pooling of the original score classes to provide a minimum of five as the expected number on a class. To meet this requirement, the data have been grouped into two classes: (1) individuals with Scores 0 - 4, which can be described as "unsilvered" and partly silvered"; and (2) those with Scores 5 and 6, which can be described as "silvered or nearly so". With this grouping the approximate probability, P, of the difference between any two samples in respect of the ratio of "unsilvered and partly silvered" to "silvered or nearly so" occurring by chance can be found by entering the table of chi-square distribution on one degree of freedom with the value of chi square computed from the 2 x 2 contingency table according to the method given by Fisher (1948, p. 85). For greater precision the Yates correction for continuity was incorporated and P was found by graphical interpolation between tabular values. The results are given in Table 3 as a matrix in which the chi-square values betyeen all combinations of pairs of samples are shown in the upper right portion and the corresponding values of P in the lower left portion.

TABLE 3. Chi-square values (upper right) and probability values (lower left) between pairs of samples.

Locality and sample		Sample						
		B	A	C	D	E	F	G
W. Greenhorns	B		2.37	2.97	>10	>10	>10	>10
E. Greenhorns	A	0.16		0.02	4.63	5.10	>10	7.14
Havilah	C	0.08	0.50		1.24	1.74	0.83	5.78
Walker Basin	D	<.001	.03	.19		.05	.84	2.32
Tehachapi	E	<.001	.02	.18	.50		.64	1.36
Lebec	F	<.001	<.001	.34	.34	.40		.37
Sandberg's	G	<.001	.008	.02	.14	.19	.50	

The three northern samples, A, B, and C form a group within which there is no statistically significant difference at the five per cent probability level (P = 0.05), and the four southern samples, D to G, inclusive, form another such group. But these groups are not discrete from each other. Sample C from Havilah differs no more significantly from D, E, and F than from A and B, indeed, somewhat less. The sum of chi squares among A, B and C is 5.36; df are 3; and P is 0.14. The comparable values among C, D, E, and F are: Chi-square, 5.34; df, 6; P, 0.48. The indeterminate position of Havilah relative to the two groups, most probably is due to the small number in the sample from there. With such a small sample it would require a very strong contrast in silvering ratio to prove statistical significance. Until more material is available it remains uncertain whether the population at Havilah resembles more closely those to the North or those to the South in respect of silvering, or whether it is truly intermediate as suggsted by Fig. 2.

Likewise, the sample from the east slope of the Greenhorn Mountains is small and does not test significantly different from that of the west slope. But for the Greenhorn Mountains there are two sources of additional data. Thorne and I scored both his catch and mine while in the Greenhorns and this record includes about twice as many individuals as given in Table 2. We used three categories: "unsilvered", "part silvered", and "silvered", corresponding somewhat inexactly to the Scores 0 - 1, 2 - 4 and 5 - 6, respectively, of Table 2. Hovanitz (1934) reported the number of individuals in a sample from the east side of the Greenhorn Mountains, elevation 5500 feet, and from the west side at Cedar Creek, elevation 5000 feet, according to three categories: "not silvered or very slightly so", "intermediate" and "well - or fairly-well silvered". Assuming these categories correspond approximately to those of Thorne-Sette, the data may be pooled as follows:

East side:

	Unsilvered	Intermediate	Silvered	Total
Thorne - Sette	6	15	17	38
Hovanitz	0	2	14	16
Total	6	17	31	54
West side:				
Thorne - Sette	72	24	32	128
Hovanitz	10	8	4	22
Total	82	32	36	150

With more data it is possible to use a 2 x 3 contingency table for a more discriminating test. This yields a probability far less than one in a thousand that the west side and east side samples could have been drawn from a population containing the same proportions of unsilvered, partly, silvered, and silvered members. This does not prove that there is no mixing between the populations of the west and east slopes; it only indicates the extreme unlikelihood of enough interchange to form a thorough mixture. But when it is considered, in addition, that the ridge of the mountain is clothed with transition forest within which no colonies of *callippe* were found, it seems clear that the interchange, if any, must be slight and probably by way of mixing with the more silvered populations to the South at different rates on the two sides of the mountain range as suggested by Hovanitz (1943, p. 411).

Turning southward, past Havilah, there is at Walker Basin a small proportion of unsilvered and partly silvered individuals in the population. The low proportion continues with only slight further diminution in going from Walker Basin in the Piute Mountains, through the Tehachapi Mountains to Lebec. This uniformity suggests a relatively brisk interchange between colonies in this stretch of mountains, probably coupled with strong environmental selection against unsilvered individuals.

Then at Sandberg's, only a short distance beyond Lebec, all individuals are silvered, This is true also for the specimens from Bouquet Canyon (not included in the scoring table because they were only a part of a series). But my sample from Sandberg's is too small to assuredly include unsilvered or partly silvered individuals if they constitute only a small percentage of the population. There is historical evidence, in Gunder's (1930) list of butterflies of Los Angeles County, of the occurance of unsilvered *callippe* at several localities in the transverse ranges south and southeast of Lebec. Under "*Araynnis macaria laurina* Wri. THE UNSILVERED MACARIA FRITILLARY, a transition form." Gunder recorded one male collected by Comstock "June 10, 1922, Ridge Route;" one male collected by Friday "June 19, 1929, Pine Canyon;" and two males and one female collected by Gunder "June 25, 1921, Bouquet Canyon." "Ridge Route" probably is identical to, or at least near, the locality I give as "Sandberg's"; "Bouquet Canyon" may be identical to, or near the locality of the Thorne collection here listed under the same place name; Pine Valley lies about halfway between the two. The last is definitely on the desert side of the transverse ranges, while the other two localities are near the crest dividing the drainage to the desert from the drainage to the Pacific. The Thorne collection is definitely from the Pacific drainage side. It is probably that this crest marks the southern limit of the unsilvered or partly silvered form.

Reviewing, there is a mixture of unsilvered, partly silvered and fully silvered *callippe* extending through the Southern Zone of Intergradation, from the Greenhorn Mountains in the North, southward through the Piute and Tehachapi ranges, to the crest of the series of ranges extending transversely across California at about latitude 34° 40' N. Most of the change from the predominantly unsilvered condition in the north to the predominantly silvered condition in the South, take place in about the northernmost one-fourth of the Zone. Through the remaining three-fourths. beginning at about the midlength of the Piute Mountains, where a high degree of silvering already has been reached. the increase in silvering is very gradual. Although it is still perceptibly incomplete at Lebec near the Southern end of the Tehachapi, unsilvered and partly silvered become so rare beyond there that one should not expect to encounter evidence of the unsilvered condition without drawing large samples from the population. It is reasonable to conclude that this is the southern limit of the tendency toward lack of silvering in the ventral hind-wing spots of *callippe.* To express this finding in Fig. 1, the area shaded with lines slanted upward to the right should be extended to include localities E, F, G and doubtfully H. When so extended, the southern limit of lack of silvering would more nearly agree with the southern limits of "uniformly colored red-brown upper surface" and "lack of brown pigment between spots on the underside of the hind wings" as mapped by Hovanitz (1943, Figs. 2 and 4).

DISCUSSION

Although this description adds some details to the distributional pattern of silvering in *callippe,* it raises more questions than it answers. Some are concerned with geographic limits. How much farther north does silvering extend? Does it taper off gradually from the western Greenhorn Mountains northward as does the opposite condition from Walker Basin southward, or does it end abruptly a short distance north of the sampled Greenhorn Mountain localities? Does the more silvered population of the eastern slope of the Greenhorn Mountains end as in a cul-de-sac co-terminal with the limits of the Kern River drainage, or does it extend northward as a tongue along the higher Sierra Nevada toward silvered populations such as those near Downieville and Gold Lake?

More perplexing questions concern the processes governing silvering. The distribution of individuals among the seven score classes reveal a paucity of intermediates in the middle of the range (histograms A and C in Fig. 2). Could such a frequency distribution arise from simple Mendelian inheritance, or is a more complex mechanism required?

The existance of intermediate degrees of silvering suggests similarity with the example of simple Mendelian inheritance described by Ford (1945, p. 173) for the Currant Moth, *Abraxas grossulariata* L., which, in its commonest form, has wings with a white background. In its less comomn form, *lutea* Cockerell, the white is replaced by a deep yellow. When these two forms are interbred the heterozygotes have a pale yellow background. Mating an individual homozygous for white with one homozygous for deep yellow, produces offspring intermediate between the two parents. There is no dominance. Taking this as a model for silvering in *callippe,* and using Ford's system for notation we may use the symbols C^uC^u, C^uC^s and C^sC^s for representing the unsilvered (Score 0), the partly silvered (Scores 1 - 5), and the completely silvered (Score 6) phenotypes, respectively. For such a model, in a population containing equal numbers of the two homozygotes (C^uC^u and C^sC^s), we should find $C^uC^u : C^uC^s : C^sC^s$: 1 : 2 : 1. None of our samples have equal numbers of homozygotes, but if we pool samples A, B and the ratio is 24 : 51 : 18. This differs from the ratio 1 : 2 : 1 by no more than one would expect from random sampling variability in about half of the samples drawn ($P = 0.44$). We may conclude that there is no evidence *against* the hypothesis that silvering is controlled by a single pair of alleles of the phenotypes scored 1 to 5 may be lumped as the heterozygous component of the population.

However, in the Currant Moth, equal doses for white and for deep yellow produced a color about half way between the two homozygotes. In *callippe* there are very few individuals about half silvered. Individuals scored 3 and 4 comprise less than one-third of the category with scores 1 to 5. Perhaps some more complex genetic system may account for this peculiar distribution within the partly silvered segment of the population. But I am attracted by the idea that some chemico - physical process, such as crystallization may be involved. These tend to be triggered by very slight differences in conditions, and once triggered, go to completion.

In this connection it is also interesting that in areas of potential silvering, the single scales, as viewed with a hand lense, appear either totally buff or totally silver, never in between.

In pursuing this idea, I have found only a little information on the silvery decorations of the Lepidoptera in the literature that bear on its chemical nature. Mayer (1897) makes direct reference to its nature in the Argynnids, saying " . . . Dimmock ('83) has shown that the silvery white and milk-white colorations are due to optical effects produced by reflected light. In the silvery white scales, however, such as the under surface of the hind wings of Argynnis, there must be a reflecting surface toward the observor, for both silvery and milk-white colors appear simple milk-white by reflected light." According to Fox (1953, p. 289) uric acid, derived from chrysalid metabolism, deposited in the wings of the adult butterfly; guanine and uric acid contribute opaque whiteness and glistening silvery aspects. Ford (1945), although discussing extensively the physical and chemical nature of butterfly coloration, is silent on the nature of silvering. Taylor, (1925) points out that guanine (also spelled guanin) deposited in crystalline form imparts the silvery appearance prevalently displayed by pelagic fishes, while bottom fishes with prevalently white undersurfaces have their "subdermal tissues heavily charged with *amorphous* guanin, which is chalky white." He describes guanine crystals, after they have been processed into pearl essence for making artificial pearls, as ". . . very thin light blades, floating in a liquid . . . [which] show their maximum luster when they are oriented parallel to each other . . . [when] pointing promiscuously in all directions, the effect will be a metallic or dull pearly luster."

While one would prefer evidence derived directly by analysis of the substance as it occurs in *callippe,* it is not far fetched to suppose that this substance is guanine, sometimes deposited as crystals disposed with appropriate orientation to give the specular effect that we call silvery, and sometimes in amorphous form adding whiteness to the pigmental brown to produce the light buff of the unsilvered spots. On this supposition it is necessary that the "silvering gene" control only the conditions within the pupal scale-sac fluid so as to precipitate guanine amorphously for buff scales, or alternatively, as crystals for the silver scales. Presumably, in homozygotes the balance of influences is well to one side of the critical point so that the deposite in all scales is always amorphous, or always crystalline. In the heterozygotes, too, it may take place on the "all or none" basis, but by single scales. Under the equal and opposite influence of the two alleles the equilibrium may be very unstable and readily tipped to one side or the other of the critical point. This could be mediated by very slight differences in environmental conditions of the particular microclimate of a pupal individual at the precise time of color deposition in the scale sacs. This would tend to affect nearly all of the scales of an individual alike, swinging most of them toward one side of the critical point more often than nearly equal numbers to each side. Small differences between members of the colony as to pupation site, date and time of day of deposition of salts in the wing sacs, or even the rate of drying after eclosion, might provide the variety of conditions necessary to produce the observed peculiar frequency distribution of the supposed heterozygous phenotypes.

This set of ideas is not advanced as an explanation, but as an hypothesis inviting test by those having interest and competence in the fields of experimental breeding or biochemistry, or both.

It is a pleasure to acknowledge the stimulus to undertake this analysis and the material help received from William Hovanitz; the generosity of Fred Thorne in giving specimens and sharing his uncommon collecting serendipity; and the kindness of Paul Grey in reviewing my identification of many hundreds of specimens of this and other Argynnids.

LITERATURE CITED

ABRAMS, LEROY. 1940-1951. Illustrated Flora of the Pacific States, vols. 1-3, 4 vols. Stanford.

ABRAMS, LEROY AND R. S. FERRIS. 1960. Illustrated Flora of the Pacific States, vol. 4. Stanford.

DOS PASSOS, C. F. AND L. P. GREY. 1947. Systematic Catalogue of Speyeria with designation of types and fixation of type localities. *Amer. Mus. Novitates*, no. 1370: 1-30.

JEPSON, W. L. 1923-25. A Manual of the Flowering Plants of California. Berkeley.

FISHER, R. A. 1948. Statistical Methods for Research Workers. Hafner, N. Y. 10th Ed.

GUNDER, J. D. 1930. Butterflies of Los Angeles County, California. *Bull. Sou. Calif. Acad. Sci.* 29 (2): 39-95.

HOVANITZ, WILLIAM. 1941. Parallel ecogenotypical color variation in butterflies. Ecology 22: 259-284.

1943. Geographical variation and racial structure of *Argynnis callippe* in California. *Amer. Nat.* 77:400-425.

MAYER, ALFRED G. 1897. On the color and color-patterns of moths and butterflies. *Bull. Mus. Comp. Uool. Cambridge* 30 (4): 169-256.

RICKER, W. E. 1940. Relation of "catch per unit effort" to abundance and rate of exploitation. *J. Fishery Res. Board Canada,* Toronto.

TAYLOR, HARDEN F. 1925. Pearl essence: its history, chemistry, and technology. Appendix to: *Rept. U.S. Commissioner Fisheries for 1925. Bur. Fish. Doc. 989.* Washington, D.C.

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THE EFFECT OF VARIOUS FOOD PLANTS ON SURVIVAL AND GROWTH RATE OF PIERIS[1]

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THE CLOSE RELATIONSHIP between most phytophagous insects and their host plants is a general phenomenon known by most entomologists. This relationship is so outstanding that field naturalists can often locate colonies of any particular insect most readily by first searching out the host plants, as they often are larger and more obvious to the eye than the insects themselves.

What is not so well known is (1) the extent to which it is possible for any particular species or race to survive on various food plants, and (2) the causes of the attraction to, and survival of, any race of insect on a particular plant.

It is the purpose of this paper to indicate something of the range of ability to survive of two insects, *Pieris rapae and Pieris protodice,* (the "cabbage or mustard "butterflies) on various cruciferous plants. In other papers, it is intended to go into the various aspects of the development of food plant preferences in insects, including its causes, evolution, and relationship to origin of phylogenetic groupings.

THE MATERIAL AND METHOD

The experimental work to be reported on here and in subsequent papers has been carried out in Arcadia, Southern California. All species of the genus *Pieris* (Lepidoptera: Pieridae) found in southern California have been utilized for the study. The geographical ranges and specific food plants of the species existing in southern California are being described elsewhere (Hovanitz, 1962) and the general distribution of the species of North America in another paper (Hovanitz, 1962). Five species of *Pieris* exist in this area, *P. rapae* (a European immigrant), *P. protodice, P. beckeri, P. sisymbrii* and *P. napi.* Each of these occupies a specific habitat and is restricted to a different food plant.[3]

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[2] The authors wish to express their great appreciation to Dr. W. S. Stewart, Director, Los Angeles State and County Arboretum for great cooperation in making this work possible.

[3] Some taxonomists consider *Pieris occidentalis* to be a distinct species separate from *Pieris protodice,* rather than a geographical race, ecological race or local phenotypic form. If this were the case, there would be six species in southern California.

Pieris rapae is the easiest species to breed under greenhouse conditions and has been used for most experiments. It aslo has a wider range of satisfactory food plants than the others. As a European immigrant, it remains restricted largely to plants of European origin and has never adapted itself under natural conditions to any American native. Contrariwise, *Pieris protodice,* a native species, has never adapted itself to any European plant grown in cultivation, but has assumed an "economic" role only in utilization of European plants (mustards) growing in semi-wild habitats. The other *Pieris* are restricted entirely to one or a few native species of plants.

The food plant tests were made in several series at different times of the year and with different species of plants. Each series was run for the purpose of comparing the influence of several plants (usually five) on growth rate and mortality. For each series, a group of twenty larvae, obtained as follows, were grown on each plant. Female *Pieris rapae* were allowed to oviposit on a kale plant in the greenhouse. For the first series, the eggs were removed from the kale leaf and placed on leaves of the plant being tested in a petri dish. On all other tests, the eggs were allowed to hatch on kale, and to eat on it for one or two days before removal to the tested plants. In order to minimize the effects of variable environmental conditions, all tests of a series were grown at the same time and place. For example, eggs laid on September 11, 1959, were used for the first test. On September 14, 1959, the larvae were measured for the first time, and then successively thereafter each day until pupation. The dates of larval (or pupal) deaths were noted.

The later tests were similar except that (1) the origin of the parents was different, (2) one or two day old larvae were used instead of eggs, (3) the time of year and (4) place of breeding was different. Data on origin of the material for each test are indicated in Table 1.

TABLE 1: Source of larvae used in these experiments.

Series	Species	Food Source	Locality collected	Date of experient	Generations from wild
1	*Pieris rapae*	Cabbage	Western Orange County	Sept. 11, 1959	1
2	"	"	"	Oct. 9, 1959	2
3	"	"	"	Nov. 25, 1959	4
4	"	"	"	Feb. 20, 1960	6
5	"	"	"	Feb. 20, 1960	6
6	"	"	"	Aug. 2, 1960	11
7	"	"	"	Sept. 19, 1960	12
8	*Pieris protodice*	Mustard	Laguna Beach	Aug. 27, 1959	1
9	"	"	San Fernando Valley	July 18, 1960	1
10	"	*Cleome*	Owens Valley	July 21, 1960	1

SERIES NO. 1

Series No. 1 was conducted for the purpose of comparing the effect of the following plants on growth rate, size and mortality: black mustard (*Brassica nigra*), garden nasturtium (*Tropaeoum majus*), bladder pod (*Isomeris arborea*) and watercress (*Nasturtium officinale*) (Table 2). The females used for the source of larvae were obtained from an open cabbage field isolated from any other cruciferous food plant source and over which the adults were swarming in huge numbers. The probability that they came from any other source is infinitesimal.

TABLE 2. Viability and growth rate of *Pieris rapae* grown on different kinds of food plants (Series 1).

Plant	Number	Number and percent of larvae died		Days from egg to pupation	Range of variation in larval growth
Nasturtium	20	16	50%	20	3
Kale	20	2	10%	12	2
Mustard	20	8	40%	13	3
Watercress	20	18	90%	17	1
Nasturtium	20	16	80%	18	5
Isomeris	20	10	50%	20	3

The mortality (Table 2, Series 1) was highest on watercress (90%), next highest on garden nasturtium (80%), then Isomeris (50%), mustard (40%) and least on kale (10%). The rate of development as determined by the first larva to pupate, was most rapid on kale (12 days), least rapid on Isomeris (20 days), and increasingly more rapid on nasturtium (18 days), watercress (17 days) and mustard (13 days). The range in variation of larval growth was greatest for nasturtium, since five days elapsed between the first larva to pupate and the last. The range as indicated in the table should be interpreted with the fact in mind that only a fraction of the original twenty larvae remained at the time of pupation. In other words, only two larvae pupated out of twenty that were fed on watercress. Had more survived, the range between the dates of pupation might have been greater.[4]

The growth rates of the larvae on the various plants were obtained by measuring ten larvae of each group each day and obtaining the average length. These were then plotted and a curve drawn for each. These curves are shown in Figure 1.

Measurements of the larvae were started on the third day after hatching as they were so small prior to that time. However, great

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[4] It should be noted that the watercress used in these experiments was obtained by purchase in a food market while all other plants were grown in the laboratory. It has occassionally been found that despite repeated washings, insecticide residues may be present upon such commercial vegetables and that these may cause death of larvae feeding upon them.

differences already were apparent between the larvae grown on the various plants. Those on kale were 4.7mm long as compared with those on Isomeris which were only 1.5mm long. Those on nasturtium were 1.8mm, those on watercress were 1.9mm and those on mustard were 3.9mm. The kale-group larvae were over three times the size of the Isomeris group larvae. Increase in size of the larvae on subsequent days was fastest when the larvae were grown on kale, second fastest on mustard, and about equally as poor on each of the other three plants. The largest sized larva was that grown on Isomeris (24mm) as compared with that on kale (22.2mm) but after eight more days of larval life. Those on watercress and nasturtium pupated at 20mm and those on mustard at 17.9mm.

It appears that the greatest proportional size difference in the larval groups occurred during the first three days, but that most of the loss in size was later recovered by a longer growth period.

SERIES NO. 2

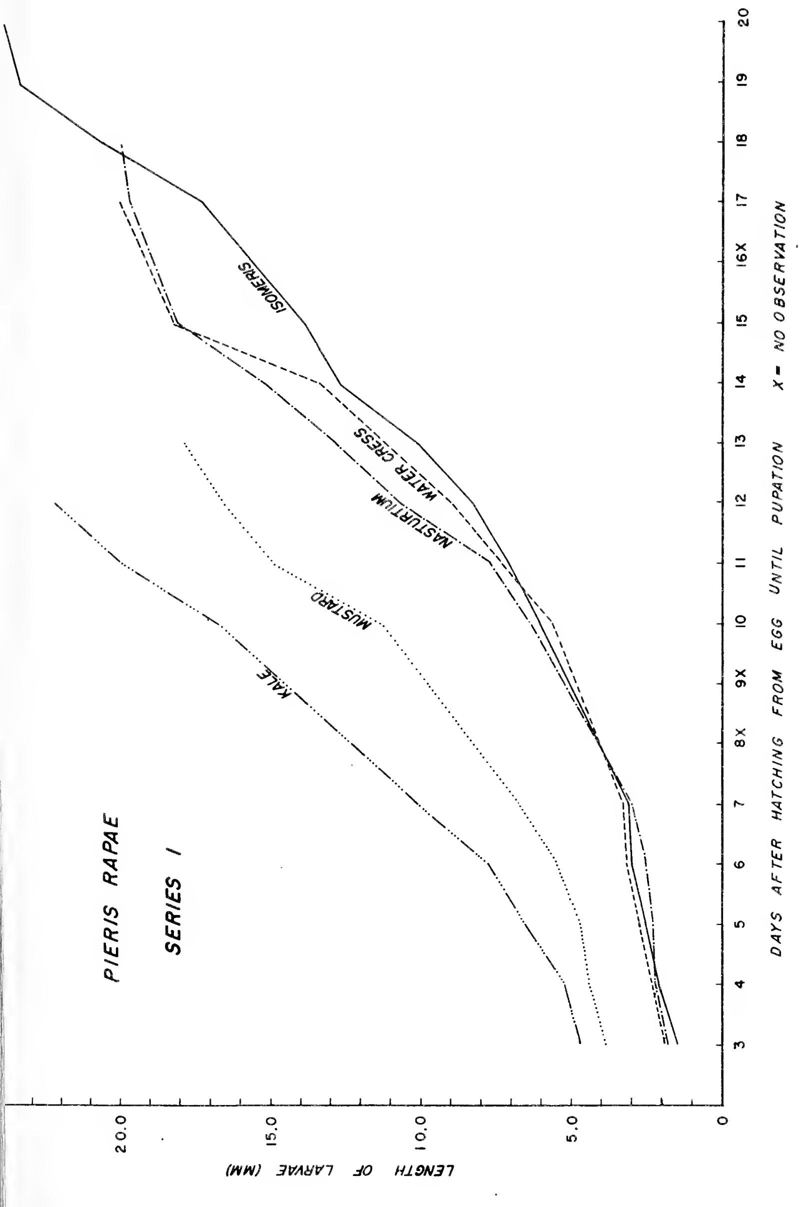
The tests of Series No. 2 were carried out in order to correct what were thought to be defects in the experiments of Series No. 1. These were two in number. The first was the high mortality in the eggs when they were removed from kale and placed on the other plants. This problem was averted by letting the larvae hatch on the kale plant before moving to the tested plants. The second presumed defect was the possibility of increased mortality of the very young larvae on the new plants, due solely to physical characteristics, toughness, etc. This was partially averted by allowing the larvae two days of feeding on kale before transference to the tested plants.

One change in food plant was made in this test: radish obtained from a food market was employed in place of watercress. Another inevitable change was the climatic condition under which the tests were conducted. They were changed slightly by the fact that the tests were carried out starting October 9, 1959, instead of September 11, 1959.

TABLE 3. Viability and growth rate of *Pieris rapae* grown on different kinds of food plants (Series 2).

Plant	No.	No. and % of larvae died		No. and % of pupae died		Total No. and % died		Days from egg to pupation	Range of variation in larval growth
Kale	20	2	10%	0	0	2	10%	11	2
Mustard	20	2	10%	3	15%	5	25%	13	4
Radish	20	8	40%	5	25%	13	65%	13	5
Nasturtium	20	8	40%	2	10%	10	50%	14	5
Isomeris	20	12	60%	3	15%	15	75%	15	3

The mortality (Table 3) in this series was generallly not so high



1. Growth rates of larvae of *Pieris rapae* grown on various plants (Series No. 1).

as in the series just preceding, though that on kale was the same at 10%, those on mustard dropped from 40% to 10%, on nasturtium dropped from 80% to 40% and on Isomeris increased from 50% to 60%. Watercress was not tested this time but instead radish[5] was used, with a resulting mortality of 40%. The better survival of these larvae is probably correlated with the fact that they were all grown during the first two days on kale.

Generally, the time (minimum days) to pupation in this series has been decreased (Fig. 2). The time on kale has been decreased one day, on mustard it remains unchanged, and on nastrutium and Isomeris it has been reduced five days. These reductions are probably correlated with the more successful survival of the young larvae on kale for the first two days, as compared with Series No. 1.

SERIES NO. 3

The tests of Series No. 3 are identical with those of Series No. 2 with the exception that they were started November 25, 1959 instead of October 9, 1959; in addition, the larvae by this time were four generations removed from the wild and inbred.

The larval mortality for all plants other than nasturtium was increased considerably in Series No. 3 compared with Series No. 2; 10% to 30% for kale, 10% to 35% for mustard, 40% to 80% for radish and 60% to 75% for Isomeris (Table 4). The data are comparable for the percentage of pupae died.

TABLE 4. Viability and growth rate of *Pieris rapae* grown on different kinds of food plants (Series 3).

Plant	No.	No. and % of larvae died		No. and % of pupae died		Total No. and % died		Days from egg to pupation	Range of variation in larval growth
Kale	20	6	30%	0	0	6	30%	15	2
Mustard	20	7	35%	0	0	7	35%	16	5
Radish	20	16	80%	1	5%	17	85%	19	4
Nasturtium	20	7	35%	1	5%	8	40%	16	6
Isomeris	20	15	75%	2	10%	17	85%	18	8

The length of larval life has also been increased considerably in Series No. 3 tests, and thus also the range of variation in larval growth.

The reasons for these differences between Series No. 2 and No. 3 are probably two fold. First, the later time in the season has meant that the conditions of growth were somewhat different, primarily in the temperature.

The larvae were grown in a greenhouse in which the temperature was not well-regulated. Therefore, the temperature of the October

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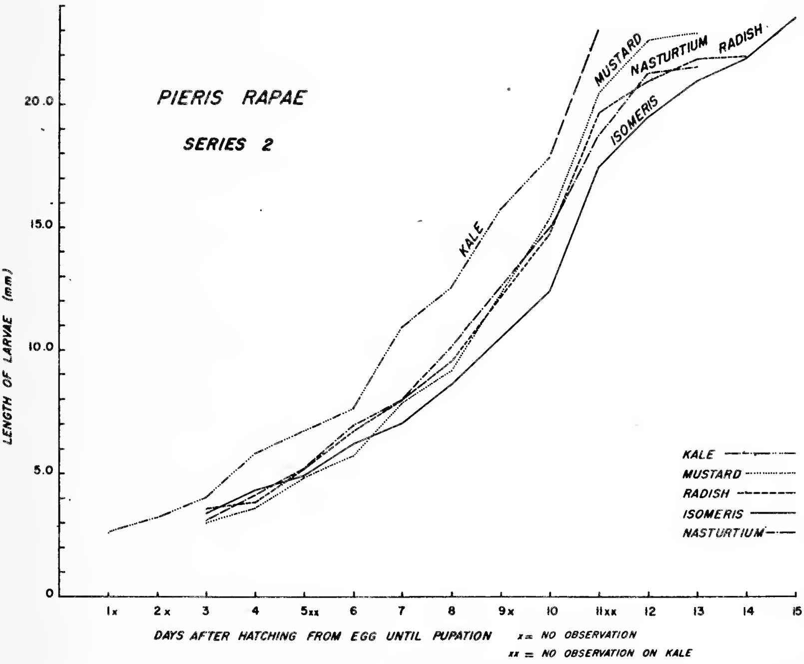
[5] The radish used in this particular experiment, but not in others reported on by us, was obtained in a food market. Refer to footnote (4) for possible latent effects.

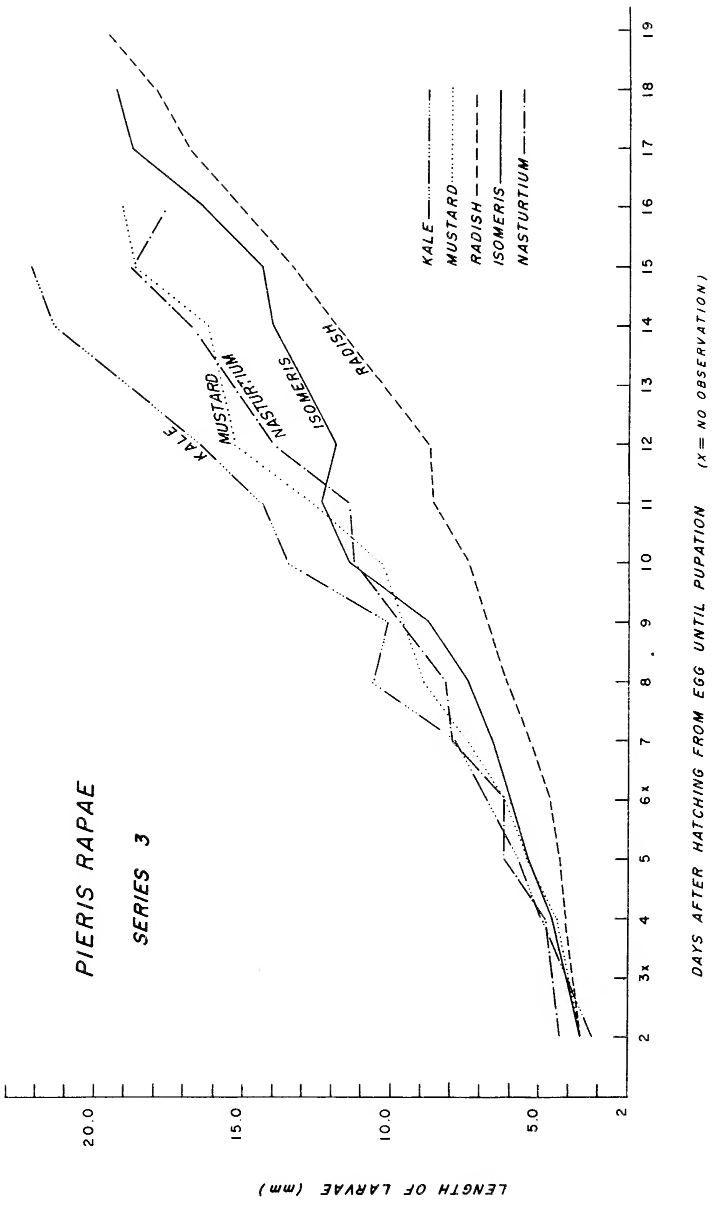
tests (Series No. 2) was higher than for the November tests (Series No. 3). This would profoundly influence the results insofar as the absolute growth rates are concerned. On the other hand, it did not affect the relative growth rates on the various food plants. These are still in the same descending order: kale, mustard, radish, nasturtium and Isomeris.



2. Growth rates of larvae of *Pieris rapae* grown on various plants (Series No. 2).

The differential increase in size of the larvae on the various food plants is better shown in Series No. 3 (Fig. 3) than in Series No. 2 (Fig. 2). This is because the slower development rate served to exaggerate the differences between each strain. The larvae grown on kale grew larger at a faster rate than the larvae on any other plant, followed by mustard, nasturtium, Isomeris and radish. In Series No. 2, the order of the latter two were reversed. It is interesting to note that the ultimate size of the larvae which grew slowest was seldom equal to the size of those larvae which grew fastest. In fact, there is almost a direct relationship between these events.

A second reason for the difference between the mortality and growth data of these two series may be of genetic significance. The extent of inbreeding in the laboratory population by the fourth generation would have been sufficient to (a) increase the mortality, (b) slow



3. Growth rates of larvae of *Pieris rapae* grown on various plants (Series No. 3).

development rate, (c) decrease size, (d) magnify the difficulties of feeding on abnormal plants by the simple means of decreasing overall vigor by the accumulation of allelic recessive lethal genes in the laboratory strain which had not yet had a chance to be eliminated by the selective effects of homozygosity.

SERIES NO. 4 AND 5

Series No. 4 was a test to compare various garden vegetables for their usefulness to *Pieris rapae*. These vegetables were mustard, kale, kohlrabi, broccoli and brussels sprouts. Series No. 5 was a similar test for various other plants. These were mustard (as before), nasturtium, radish, turnip and Isomeris. The tests were made in two series on February 20, 1962, using larvae following six generations of inbreeding, but of the same strain as used heretofore. In both of these tests, the larval mortality was higher on comparable plants used in previous tests. This again was probably due to the effects of inbreeding.

TABLE 5. Viability and growth rate of *Pieris rapae* grown on different kinds of food plants (Series 4).

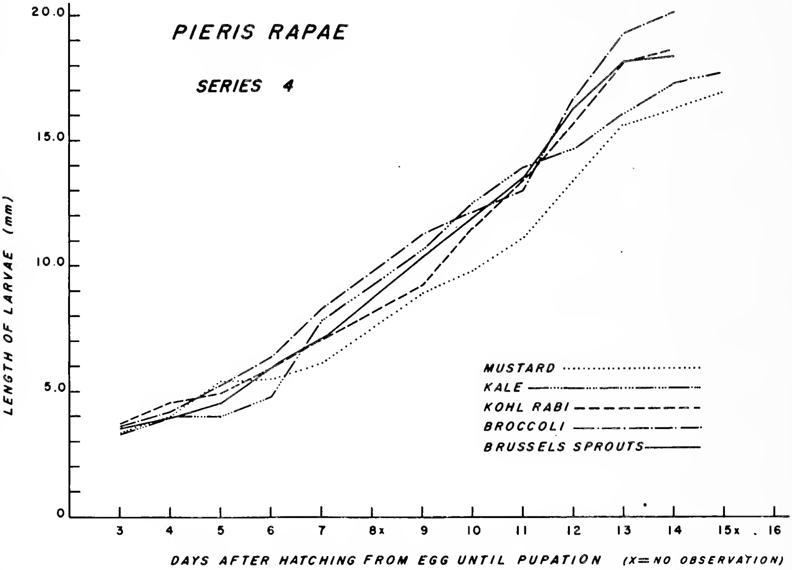
Plant	No.	No. and % of larvae died		No. and % of pupae died		Total No. and % died		Days from egg to pupation	Range of variation in larval growth
Mustard	20	9	45%	0	0	9	45%	15	9
Kale	20	5	25%	2	10%	7	35%	15	10
Kohl Rabi	20	9	45%	0	0	9	45%	14	9
Broccoli	20	9	45%	0	0	9	45%	14	9
Brussels Sprouts	20	10	50%	0	0	10	50%	14	9

In Series No. 4 (Table 5), the data show that the larvae on kale had the lowest mortality rate (25%) while all the other plant tests were about the same (45-50%). Despite this, however, larvae from kohlrabi, broccoli and brussels sprouts reached pupation ahead of those on kale or mustard.

TABLE 6. Viability and growth rate of *Pieris rapae* grown on different kinds of food plants (Series 5).

Plant	No.	No. and % of larvae died		No. and % of pupae died		Total No. and % died		Days from egg to pupation	Range of variation in larval growth
Mustard	20	9	45%	0	0	9	45%	15	9
Nasturtium	20	19	95%	0	0	19	95%	16	—
Radish	20	14	70%	2	10%	16	80%	15	13
Turnip	20	13	65%	0	0	13	65%	15	4
Isomeris	20	12	60%	0	0	12	60%	18	14

In Series No. 5 (Table 6), the data show that the lowest mortality again was on mustard but with considerably higher mortality on the other plants: for example, 95% on nasturtium, 70% on radish and 60-65% on turnip and Isomeris. The length of larval life was longest on Isomeris (18 days) and about the same (15-16 days) on other plants. The range of larval growth period varied greater with radish and Isomeris than with any of the other.

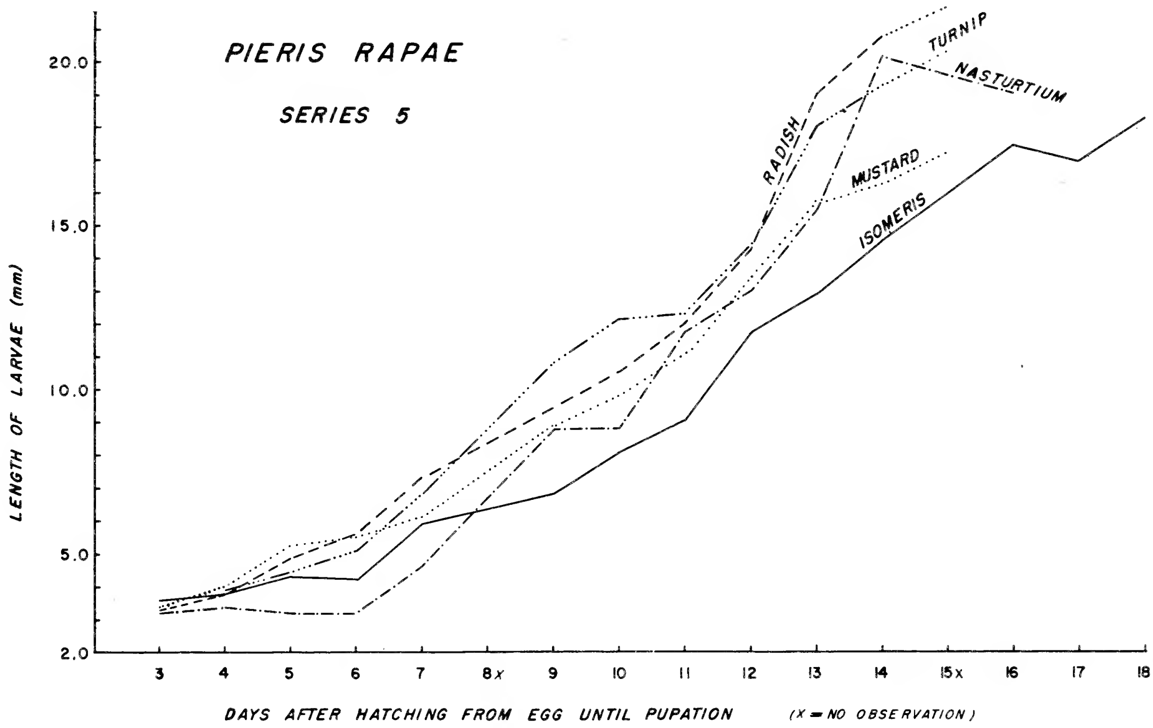


4. Growth rates of larvae of *Pieris rapae* grown on various plants (Series No. 4).

The rate of increase in size (Fig. 4) was more rapid with broccoli, kohlrabi and brussels sprouts than with kale and mustard. It is believed that this may be correlated with a more turgid or water-content condition of these plants as compared with the drier or stiffer condition of the kale and mustard. For some reason, in Series No. 5, also, the increase in size of the larvae was not up to expectations on the mustard since the larvae on radish, turnip and nasturtium all exceeded those on mustard in final size (Fig. 5).

SERIES NO. 6

Series No. 6 was tested on August 2, 1960 with the use of larvae eleven generations from the wild. One new plant, (*Cleome lutea*), was tested in this series, since this plant was found to be primary food plant for *Pieris protodice* in Owens Valley, California. Mortality data



5. Growth rates of larvae of *Pieris rapae* grown on various plants (Series No. 5).

for kale , mustard, nasturtium and Isomeris, (Table 7) compared well with previous data obtained on these plants (Series 1, 2, 3, 4 and 5). *Cleome* was only slightly less effective in maintenance of larval life, the mortality rate being 30% as compared with 20% for kale and mustard. The relative lengths of larval life and the range of variation in larval growth also compares favorably with previous data. The higher mortality as seen in Series 3, 4, 5 and 6 has here been reduced to nearly the level of Series No. 1.

TABLE 7. Viability and growth rate of *Pieris rapae* grown on different kinds of food plants (Series 6).

Plant	No.	No. and % of larvae died		Days from egg to pupation	Range of variation in larval growth
Kale	20	4	20%	12	3
Mustard	20	4	20%	13	3
Nasturtium	20	10	50%	13	3
Cleome	20	6	30%	14	5
Isomeris	20	12	60%	18	6

The differences between growth curves for each of the plants tested has been greatly increased in this test as compared with earlier tests. The factors responsible for this are unknown but may be due to a reduced adaptability caused by increased homozygosis (Fig. 6).

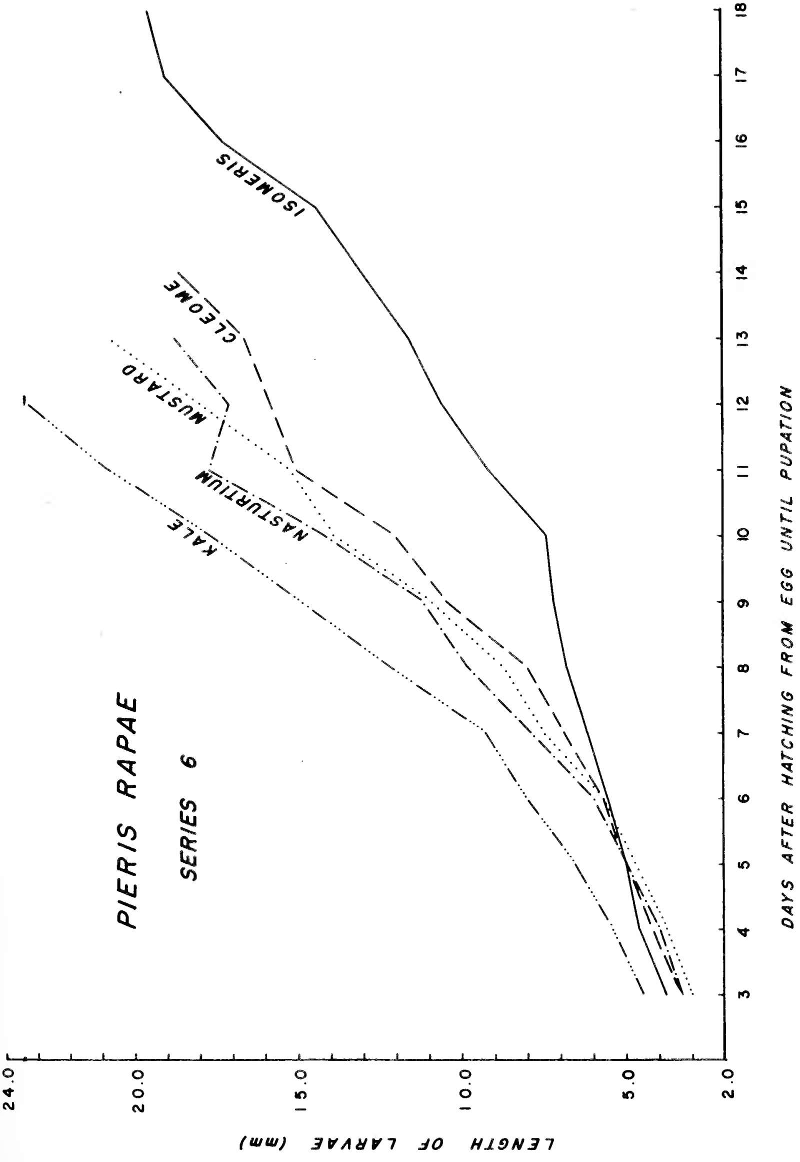
The larvae on kale were larger than those of any other plant at all times during their growth period. Pupation occurred the twelfth day. The larvae grown on nasturtium were almost the same size as those grown on mustard, whereas in Series No. 1 (Fig. 1) the larvae on mustard grew faster and larger. The larvae on *Cleome* were fourth in size on any day, while those on Isomeris were fifth.

SERIES NO. 7

This series was conducted in order to place the plant *Thelypodium affine* into position relative to the other standard test plants in the laboratory. *Thelypodium affine* is a native cruciferous plant from the desert regions which is not known to be a food plant of any *Pieris* species, though another *Thelypodium* species is the food plant of *Pieris sisymbrii.*

TABLE 8. Viability and growth rate of *Pieris rapae* grown on different kinds of food plants (Series 7).

Plant	No.	No. and % of larvae died		Days from egg to pupation	Range of variation in larval growth
Kale	20	5	25%	16	3
Mustard	20	6	30%	17	4
T. affine	20	14	70%	22	5
Isomeris	20	12	60%	18	6
Nasturtium	20	8	40%	17	6



6. Growth rates of larvae of *Pieris rapae* grown on various plants (Series No. 6).

The tests of Series No. 7 (Table 8) were carried out on September 19, 1960, using larvae after twelve generations of laboratory inbreeding and growing on kale. The larvae grew relatively well on mustard, kale and nasturtium. The effectiveness of Isomeris was as previously tested. *Thelypodium affine* was the poorest of all these plants as far as effectively providing the larva with stimulation to feed.

The mortality of the larvae on *T. affine* was 70% as compared with 60% on Isomeris, 40% on nasturtium, 30% on mustard and 25% on kale. The length of larva life was increased from 16 days on kale to 22 days on *Thelypodium*. The final size of the larvae was reduced from 22mm long on kale to only 18mm long on the *Thelypodium* larvae which survived. (Fig. 7).

GENERAL OBSERVATIONS ON PIERIS RAPAE TESTS

The seven series of tests on *Pieris rapae* larvae have indicated several significant points:

(1) Larvae from strains grown previously on cabbage or kale have a lower mortality rate, have a faster development rate, and a greater size when grown on kale than when grown on any other plant tested. When similar larvae are grown on mustard, these factors are decreased slightly. The order of decrease for plants other than these two is in the order approximately as follows: nasturtium, *Cleome,* radish, Isomeris, and *T. affine*. Plants of the cabbage group: kohlrabi, broccoli and brussels sprouts, are about the same as cabbage or kale. Turnip is about the same as radish.

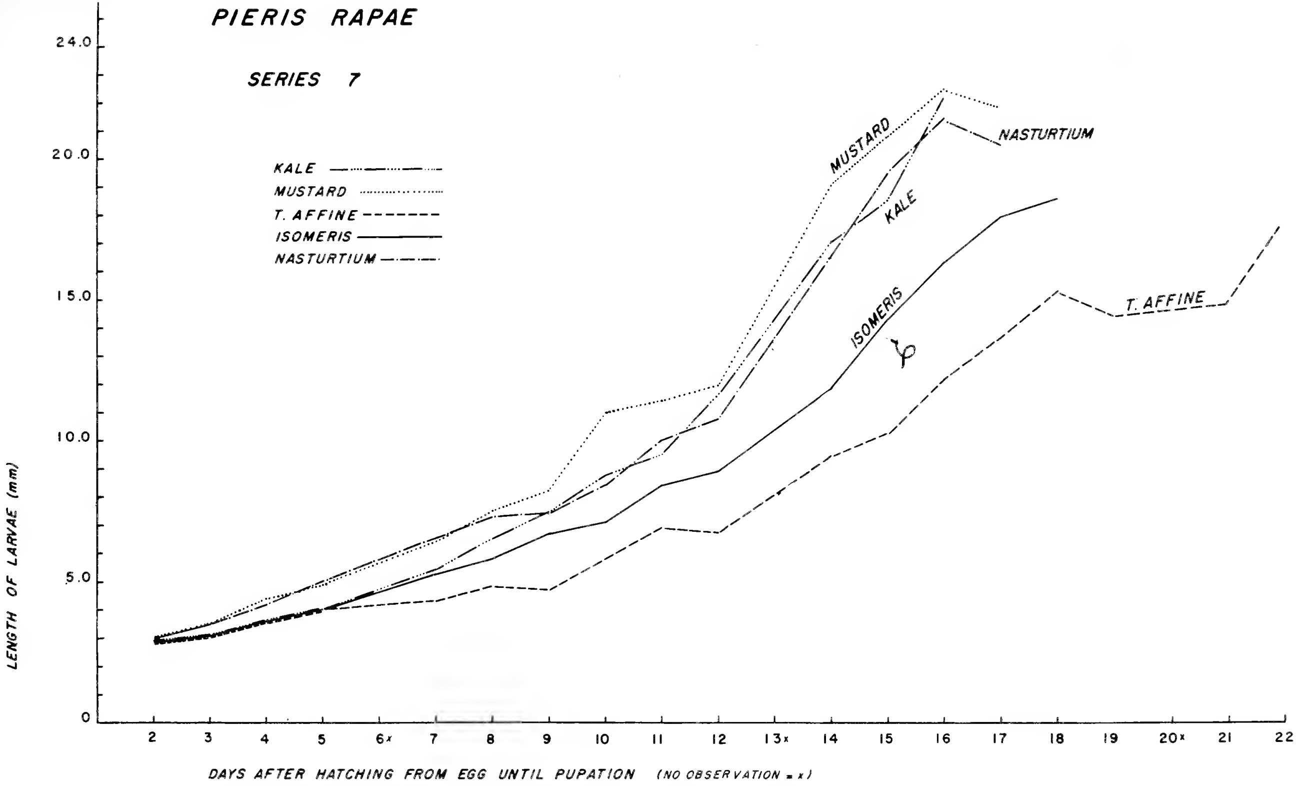
(2) Higher mortality in the tests is generally correlated with a slower development rate, a delayed time to pupation and smaller size of the larva and pupa. There are some exceptions to this rule; for example, the final size of the larva may be as great when the growth rate was slow on one plant as when it was fast on another. This has been indicated, however, only for plants of the cabbage group.

(3) Mortality rates in the various test series have been variable. These variations in mortality have been thought not only to be due to the genetic effects of inbreeding but also partly to the changed environmental conditions encountered while the tests were conducted, such as lower temperatures, etc. of the changing seasons. Lower temperatures slow the developing rate, and increase the relative humidity. Increased humidity permits the larvae to be attacked by bacterial or viral diseases to a much greater degree.

SERIES NO. 8

Tests of Series No. 8, 9 and 10 were conducted with larvae of *Pieris protodice* rather than with *Pieris rapae.*

The first series with this species (No. 8) was conducted on August 27, 1959, utilizing larvae one generation from the wild. The



7. Growth rates of larvae of *Pieris rapae* grown on various plants (Series No. 7).

females of the previous generation were obtained in a field of black mustard, not near any other source of food plant, and in which eggs and larvae were found on that plant. This is good evidence that the natural plant utilized here as larval food was mustard.

In this series, the food plants tested as larval food were mustard, kale, radish, Isomeris and nasturtium. The mortality of larvae of *Pieris protodice* on these plants increased in the order just stated, namely, 10% on mustard, 20% on kale, 55% on radish, 55% on Isomeris and 95% on nasturtium (Table 9). Deaths in the pupa stage on kale, radish and Isomeris materially increased the total mortality before adult emergence. This was not increased on mustard.

TABLE 9. Viability and growth rate of *Pieris protodice* grown on different kinds of food plants (Series 8).

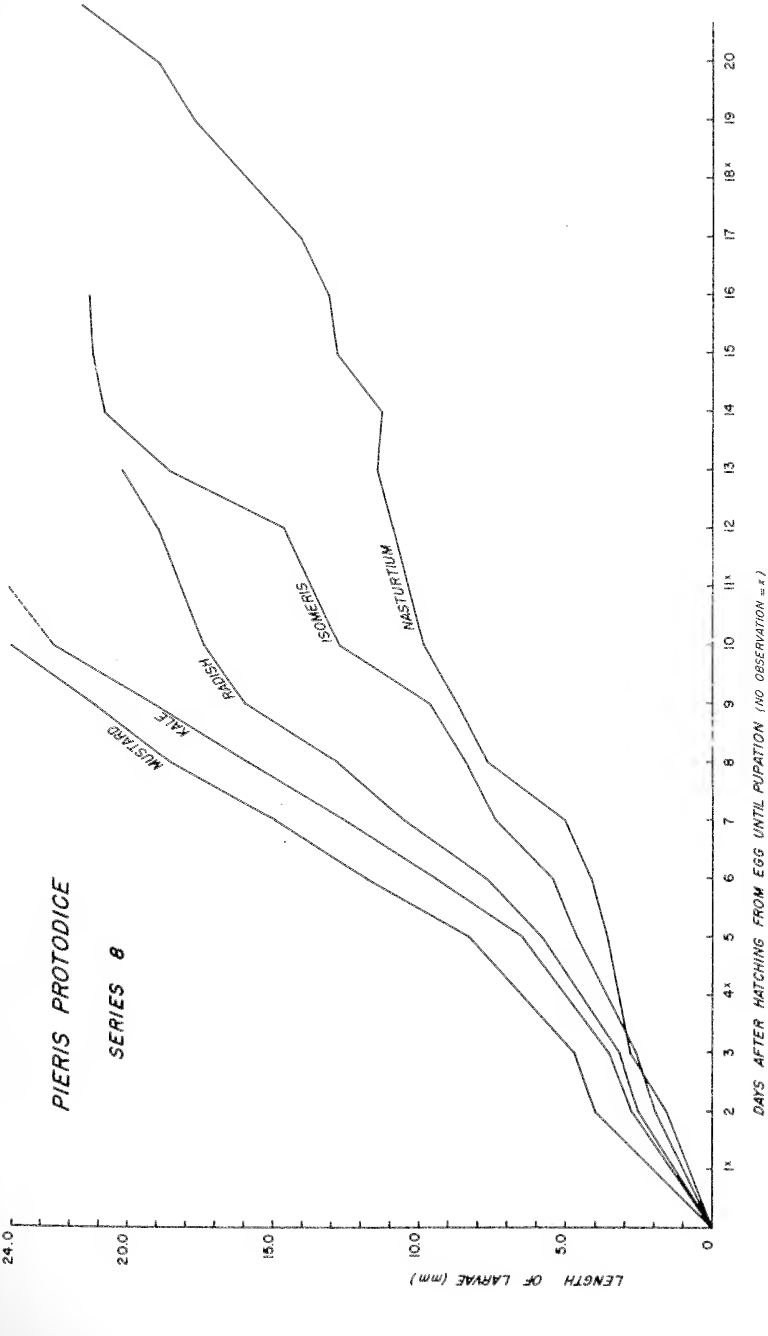
Plant	No.	No. and % of larvae died		No. and % of pupae died		Total No. and % died		Days from egg to pupation	Range of variation in larval growth
Mustard	20	2	10%	0	0	2	10%	10	2
Kale	20	4	20%	2	10%	6	30%	11	2
Radish	20	11	55%	4	20%	15	75%	13	3
Isomeris	20	11	55%	3	15%	14	70%	16	3
Nasturtium	20	19	95%	—	—	19	95%	21	—

The length of larval life was greatly different on the various food plants, ranging from ten days on mustard, eleven days on kale, thirteen days on radish, sixteen days on Isomeris to twenty-one days on nasturtium. This wide variation in length of larval life is greatly different from anything encountered with *Pieris rapae.* It would indicate a fundamental difference in food plant adaptability between these two species, *Pieris rapae* being much more versatile in its requirements than *Pieris protodice.*

The size of the larvae at various days after hatching (Fig. 8) indicates that the mortality data are in close correlation with the size increments of the larvae with respect to food plants involved. Larvae on mustard and kale increased to 24mm in length, those on radish, Isomeris and nasturtium to 20-21mm each.

SERIES NO. 9

Discovery that *Pieris protodice* utilizes *Cleome lutea* as a natural food plant in the Owens Valley prompted a series of tests involving this plant. Both Series No. 9 and Series No. 10 were carried on for the purpose of testing *Cleome* in comparison with other plants used as standards. Series No. 9 utilized *Pieris protodice* larvae bred from adults obtained from mustard fields in the San Fernando Valley while Series No. 10 utilized *Pieris protodice* larvae obtained from *Cleome*



8. Growth rates of larvae of *Pieris protodice* grown on various plants (Series No. 8).

plants in the Owens Valley (Big Pine). There is no chance that the San Fernando population had access to *Cleome* but there is a chance that the Owens Valley population did have limited access to mustard.

TABLE 10. Viability and growth rate of *Pieris protodice* grown on different kinds of food plants (Series 9).

Plant	No.	No. and % of larvae died		Days from egg to pupation	Range of variation in larval growth
Mustard	20	6	30%	14	3
Cleome	20	7	35%	14	4
Nasturtium	20	18	90%	17	2
Isomeris	20	8	40%	17	5

The Series No. 9 larvae (Table 10) showed highest mortality on nasturtium (95%), just as in Series No. 8, with the lowest mortality on mustard (30%), next highest on *Cleome* (35%) and then Isomeris (40%). This corresponds well with comparable data in Series No. 8.

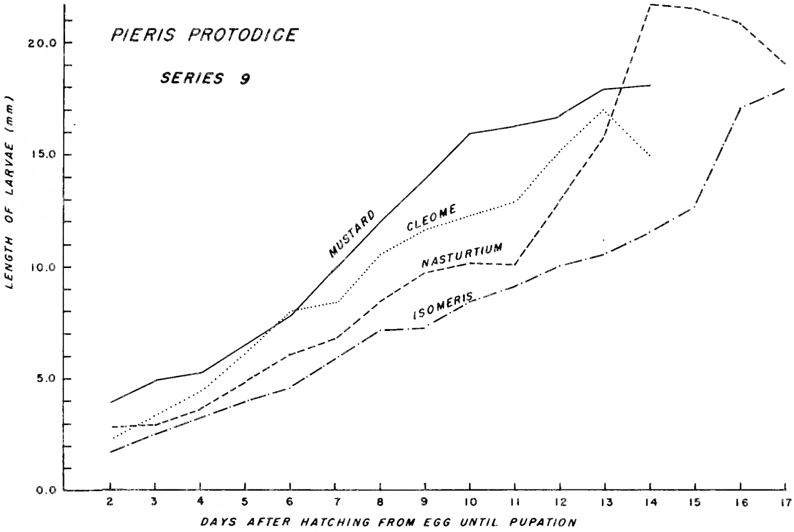
The growth increment curves for this series are somewhat comparable with the preceding series except for the one surviving larva on nasturtium which increased to a size greater than that attained by larvae on any other plant. The differences between the growth curves, however, are not as distinct and clear as in Series No. 8, perhaps because of temperature differences between the two. *Cleome* is almost as satisfactory as mustard as a food plant for these larvae. (Fig. 9).

SERIES NO. 10

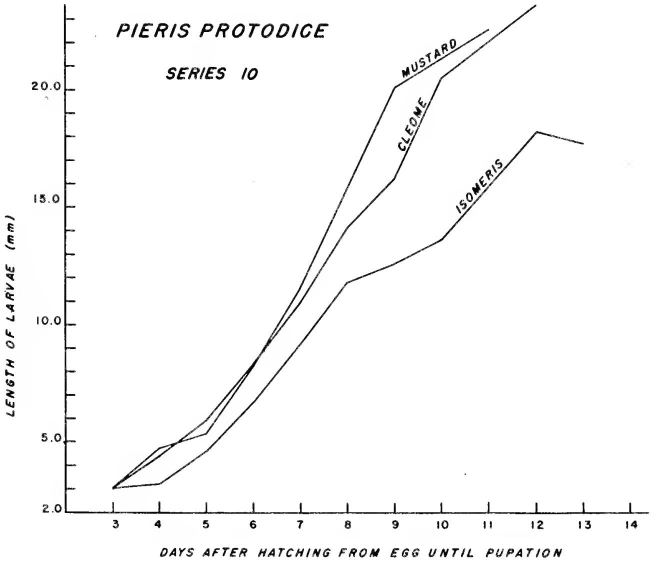
This series was run almost contemporaneously with the preceding and involved larvae from the Owens Valley strain grown on *Cleome.* The mortality (Table 11) was lowest on mustard (20%), second lowest on *Cleome* (30%) and then Isomeris (35%). There was a greater range of larval growth rates on this group of larvae on Isomeris than in any other group as well as the lowest mortality on this plant in any of the larvae tested. The growth increment curves for these larvae indicate that the larvae do not show much difference in their reaction to mustard and *Cleome* but that mustard is still slightly better, and Isomeris is always poorer. Final size of the larvae, however, was larger for the *Cleome* (23 mm) than for the mustard (22 mm) or the Isomeris (18 mm). (Fig. 10).

TABLE 11. Viability and growth rate of *Pieris protodice* grown on different kinds of food plants (Series 10).

Plant	No.	No. and % of larvae died		Days from egg to pupation	Range of variation in larval growth
Mustard	20	4	20%	11	3
Cleome	20	6	30%	12	5
Isomeris	20	7	35%	13	7



9. Growth rates of larvae of *Pieris protodice* grown on various plants (Series No. 9).



10. Growth rates of larvae of *Pieris protodice* grown on various plants (Series No. 10).

GENERAL OBSERVATIONS ON *PIERIS PROTODICE* TESTS

The three series of tests on *Pieris protodice* have indicated several significant points: (1) Larvae from strains obtained from mustard or *Cleome* populations had equally good survival value on mustard plants. The following plants gave decreasing survival value to the larvae: (Series 8) kale, radish, Isomeris and nasturtium. (Series 9) *Cleome,* nasturtium, Isomeris. (Series 10) *Cleome,* Isomeris. (2) Higher mortality in the tests is generally correlated with a slower development rate, a delayed time to pupation and smaller size of larvae and pupae.

DISCUSSION

The tests described in the preceding pages have indicated some significant information regarding the effect of various food plants on survival in two species of *Pieris.* The ability to survive on different food plants is not an all or none relationship, but rather is a relationship based upon relative ability to survive. In the most extreme case, all larvae may die rather than eat a completely unacceptable plant. On the other hand, plants may be placed in an order of desirability with regard to the ability of larvae to survive, or to grow satisfactorily, on plants which they may accept at least reluctantly.

The tests described in this report are based upon using three criteria to indicate the desirability of a plant to the larvae. The first of these is the ability to survive, or the reverse which is the mortality, expressed as a percentage of the total larvae which died during the experiment. The second criterion is the daily size increment during the life of the larva. This actually tests two factors: (1) the physiological usefulness of the food to the larvae and (2) the total amount of food eaten and uilized, which may be a direct result of the stimulatory activity of the plant toward the larvae. The third criterion is the range in variation of larval growth. The significance of this criterion is in more doubt than the other two, but the range indicated would in some degree show the genetic variability present in the larval population toward physiological adaptation to the particular plant.

The results just described show that some plants are much more suitable for larval food to certain larvae than are other plants. The reasons for this greater suitability are not made clear. In those cases where higher mortality, slower growth rate, size increments and final size are correlated, the cause of the poor growth could be lack of nutriment in the plant, or lack of larval ingestion of the plant. In other cases where larval mortality may be high, as with the broccoli, Kohlrabi and Brussels sprouts tests (Table 5) but growth rate rapid and size large (Fig. 4), there are probably two factors involved. The rapid increase in size could be due to a high attraction to a very nutritious plant, but secondary conditions surrounding the plant may be conducive to a higher mortality, namely, high water content in the plant itself, or high humidity surrounding the plant which would increase the susceptability of the larvae to virus and bacterial infections.

Toughness of leaves of a plant cannot be ruled out as a factor involved in larval speed of growth. Some leaves are too tough for the larvae to feed upon easily. Leaves of the same plant vary in this regard; succulent leaves at the shoot apex are usually much more desirable than older, mature leaves. This may be caused by toughness, or it may be caused by the greater perception of attractive substances permeating from younger leaves. At any rate, the relative uniformity of the tests in the different series is good evidence for the conclusion that this factor has not been of major significance.

The greater ability of *Pieris rapae* as compared with *Pieris protodice* to survive on a variety of common cruciferous plants is interesting in view of the fact that both succeed well on black mustard. *Pieris rapae* survives better on kale over mustard and *P. protodice* survives better on mustard over kale. However, on most other cruciferous plants tested, there was a wide disparity between their preferences. The selections made by the strains of larvae shown by these experiments complements perfectly the known differences in geographical and ecological distribution of the two species concerned, and indicates that there is little natural competition between the species for food plants. This shows also why *Pieris rapae* is always associated with European cruciferous plants, weeds or truck crops, while *Pieris protodice* is generally associated with other cruciferous plants.

Takata (1957, 1959, 1961) has published a number of papers which bear upon this problem. None of these deals precisely with the effect of various food plants on survival and growth rate of *Pieris*, but rather deals only with selection preferences by the larvae and the adult. Further considerations of the relation of this work of Takata on *Pieris rapae crucivora* to the present general program will therefore be made in a complementary paper entitled "Three Factors affecting larval choice of food plant" to be published in this journal.

A visit to our project by W. H. Dowdeswell of England during the course of these experiments was followed by a similar study of more limited extent on *Pieris napi* L. in England. Dowdeswell found that two populations of this Pierid were feeding on different cruciferous plants. By switching the food plants in laboratory experiments on testing the larvae, he found as we had, that there was a higher mortaity and decreased growth rate when the larvae were fed on plants not the normal food plant for that population (Dowdeswell and Willcox, 1961).

SUMMARY

1. Tests were made of the ability to survive of larvae of two species of Lepidoptera, *Pieris rapae* and *Pieris protodice* on various food plants.

2. Three criteria were tested: (a) mortality, (b) growth rate and size increment, (c) range in variation of larval growth.

3. Seven series of tests involving *Pieris rapae* were conducted showing the results summarized under the heading "General Observations on *Pieris rapae* Tests."

4. Three series of tests involving *Pieris protodice* were conducted showing the results summarized under the heading "General Observations on *Pieris protodice* Tests."

5. *Pieris rapae* has significantly different requirements for food plants than *Pieris protodice,* even though the tested larvae were both from mustard-bred strains.

6. The native adaptability of *Pieris rapae* to survive on various plants is better than that of *Pieris protodice.*

7. The causes of differences in survival value of the larvae on different food plants are believed to be several, but the main one is the total amount of food eaten and utilized.

LITERATURE CITED

DOWDESWELL, W. H. AND H. N. A. WILLCOX. 1961. Influence of the food plant on growth rate and pre-imaginal mortality in the green-veined white butterfly *Pieris napi* (L). *Entomologist* 94:2-8.

HOVANITZ, W. 1962. The ecological and geographical distribution of Pieris species in Southern California. *J. Res. Lepidoptera* 1: in press.

HOVANITZ, W. 1962. The distribution of the species of the genus Pieris in North America. *J. Res. Lepidoptera* 1 (1): this issue.

TAKATA, N. 1957. Studies on the host preference of cabbage butterflies (*Pieris rapae* L.) III. Mechanism of food preference of cabbage butterfly larvae. *Jap. J. Ecol.* 7(3):117-119.

TAKATA, N. 1959. Studies on the host preference of common cabbage butterfly, *Pieris rapae crucivora* Boisduval. IV. Tendencies of food preference in relation to total quantity of the host plants cultivation. *Zoological Magazine (Japan)* 68(5):187-192.

TAKATA, N. 1959. Studies on the host preference of common cabbage butterfly, *Pieris rapae crucivora* Boisduval. VI. Change in the food preference of larvae when reared successively by the definite food plant for several generation. (Preliminary report) *Jap. J. Ecol.* 9:224-227.

TAKATA, N. 1961. Studies on the host preference of common cabbage butterfly, *Pieris rapae crucivora* Boisduval. XI. Continued studies on the oviposition preference of adult butterflies. *Jap. J. Ecol.* 11(3):124-133.

TAKATA, N. 1961. Studies on the host plant preference of the common cabbage butterfly, *Pieris rapae crucivora* Boisduval. XII. Successive rearing of the cabbage butterfly larva with certain host plants and its effect on the oviposition preference of the adult. *Jap. J. Ecol.* 11(4): 147-154.

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GENERAL CHARACTERISTICS OF THE MOVEMENTS OF VANESSA CARDUI (L.)

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It is a matter of common knowledge that the populations of many species of butterflies participate in large and extensive mass movements. While several workers, notably C. B. Williams of England, have done extensive work in this field, relatively few investigators have made it their principal subject of research. Though much pertinent information has been assembled and certain tentative conclusions may be reached, it cannot be said that the movements of butterflies are as well understood as certain other phases of the study of these insects.

Most movements of butterflies, while usually referred to as migrations, would not meet the criteria set up by students of vertebrates for defining migrations. The migrations of birds, for example, involve cyclic movements. There is a going out and a return. Few butterflies other than the Monarch [Danaus plexippus (L.)], habitually possess such a rhythmic pattern of movement. Even with the Monarch, the individuals that return are usually (probably always) not the same individuals that initiated the outward movement, but are the offspring of these original individuals.

Many movements of butterflies are relatively local wanderings, and may be in one direction in one local area, but in a different direction in another area a relatively few miles away. For example, in the fall of 1960, Tilden noted *Libytheana bachmanii* (Kirt.) (the Snout Butterfly) moving southwesterly in large numbers in the vicinity of Continental, Pima Co., Ariz., on Sept. 14. The next day, Sept. 15, equally large numbers of this species were observed moving up-canyon (northward) in Sycamore Canyon, Santa Cruz Co., about thirty-five miles south of Continental by air line, though considerably further by road.

The very conspicuous movements of certain species have been regarded as depending on population pressures, leading to a mass exodus. These may be considered as emigrations from the populated area, and as immigrations into surrounding area. Such movements frequently appear to be in one direction only. Unless the insects were to find suitable conditions at the far end of the movement, establishment would not result. Such movements have been thought to account in part for the finding of strays far beyond the normal ranges of the species.

Movements of an altitudinal nature have been observed. *Nymphalis californica* (Bdv.) has been seen ascending the Sierra Nevada of California in great numbers. Such movements may result in finding sufficient larval food plants for a subsequent brood. In 1960, Tilden found this species in outbreak numbers of adults at Manzanita Lake, Lassen Volcanic National Park, Calif., on June 10-17. Numerous larvae in various stages of development were found on *Ceanothus spp.* Adults could be observed many miles below the Park, working their way up the mountain. It may be significant to note that this species passes the winter as an adult. It seems plausible that these altitudinal movements of adults are the usual way for adults to reach the higher elevations, where they act as parents of a late high elevational brood. This might be a fruitful field of investigation.

The often spectacular "migrations" of *Vanessa cardui* (L.) present an interesting condition somewhat intermediate between true migrations and other types of movements. Return movements seem not to be clearly documented in regard to this species. However, reproduction has been observed repeatedly along the route, and the offspring take up the movement when they emerge as adults. These mass movements of *Vanessa cardui* thus proceed in periodic waves, alternating with relative lulls between, and the whole process has much more continuity than is characteristic of the movements of most other butterfly species.

Much of the basic work on the movements of *Vanessa cardui* has been done by C. H. Abbott. Others, including Sudgen, Woodbury and Gillette in Utah, have made contributions. Among the various titles that form the literature on the movements of this species in western United States, some are short observational notes only. Others present a considerable amount of detailed study. Abbott has attempted to understand the nature of these movements and has produced several penetrating papers on the subject.

The last great movement was in 1958. Abbott traces three or more generations extending up to or beyond the Central Valley of California. Other generations carried the waves through the Bay Region of California on into Oregon. The generations involved in the northern portions of the movement become less clear.

The first generation seems to have originated in northern Mexico, the second in the Imperial Valley of California, western Arizona and the eastern Mohave Desert of California, the third in western Mohave Desert, and the fourth in the Central and Coastal Valleys of California, and to the Bay Region. Abbott (1959) has presented material that includes the observations of a number of workers, and has coordinated this material. In addition, the following observations are here presented for the first time.

Tilden found many dead adults in western Arizona (Mohave County) and in the vicinity of Needles, California, as well as large numbers of moving adults, March 30-31, 1958. From Barstow, San Bernardino Co., west to Mohave, Kern Co., great numbers of adults were flying northwesterly on March 31. Later that day adults were seen moving through Tehachapi Pass, Kern Co., and spilling into the San Joaquin Valley east of Bakersfield, Kern Co. On April 20 to May 9, eggs and larvae were abundant in the Salinas Valley, Monterey Co.

On May 30 - June 1, Tilden found large numbers of adults along the Redwood Highway (Route 101) between San Rafael, Marin County, and Cloverdale, Sonoma County, moving northwesterly. Dead adults were seen as far west as Booneville, Mendocino County, where but a few living adults remained. This may mark the western edge of the movement.

In the vicinity of The Geysers, Sonoma County, adults were moving northwesterly in large numbers in overcast weather (fog) on June 1, before noon. Larvae were abundant on *Amsinckia* (Fiddleneck) and on the introduced Spanish Thistle (*Carduus*), in various stages of development.

Two interesting reports were from Oregon. Ray Albright reported large numbers of *Vanessa cardui* moving in a north-north-easterly direction on May 18-19, 1958, while on May 20-21, equally large numbers were observed moving in exactly the opposite direction. He attributes this reversal of direction to the insects meeting a cold front, since a storm was in progress some distance beyond the place toward which the insects were noted to be flying. The other report was from David Huntzinger at Crater Lake National Park. He noted that *Vanessa cardui* was abundant there in 1958, though scarce or absent in 1957.

On April 1, 1958, Tilden observed what is apparently a new observation for the United States. Large numbers of *Vanessa cardui* were flying north-westerly in the rain. Between Vidal, San Bernardino County, and Desert Center, Riverside County, the rain was light to moderate, but rather cold. Between Indio and Whitewater Canyon, later the same day, the flight still continued in heavy to very heavy rainfall. This seems to indicate that adults may continue to fly, once on the wing, even in heavy precipitation. It would seem *a priori* that initiation of a flight during rain might be less likely.

From observations so far recorded it is possible to generalize on some of the characteristics of the movements of *Vanessa cardui*. Some of these generalizations have been set forth by Abbott and others, while some are suggested here for the first time.

1. The adults tend to fly into the wind. This may be a key point in attempting to explain the prevailing direction of the movements. During the time of year when *Vanessa cardui* is moving, the prevailing winds in California are north-westerly, and the movements of the

butterflies are also in a north-westerly direction, almost or quite directly into the prevailing winds. Sudgen, in 1937, noted a northerly direction of flight in Utah. Sudgen, Woodbury and Gillette, in 1947, noted a north-easterly direction of flight. Observations to be made in the future might very well take special note of the wind direction as well as the direction of the insects' flight, to find how complete this correlation between wind direction and flight direction may be.

2. The adults move at a rather equal velocity in relation to one another, resulting in a fairly constant spacing of the individuals. There have been some observations made where this did not seem to be the case, but for the most part, this generality seems to hold.

3. The insects tend to fly over obstacles rather than around them. At times this appears to the observer quite amusing, even ridiculous. If a tree, building or parked car obstructs the route, the adults fly over the top of the obstruction, when in some instances it would appear that a veering to the right or left would be more easily accomplished. The obstruction, whether it be low or tall, is barely cleared. On March 30, 1958, Tilden observed them piling directly over a small building near Barstow, San Bernardino County, the only building for miles in an open desert.

4. The adults tend to fly at rather even densities. If a line is marked off between two points, fifty or one hundred feet apart, and the insects crossing this line per minute are counted, the results from several one minute counts are surprisingly similar. If then the observer drives his car several miles, sets up another station and makes another series of counts, the results will again be similar, and frequently quite close to those of the previous station. But in widely separated areas, the count may be very different. That is, while the density on the Mohave Desert, for instance, may be quite constant, counts made in San Diego County at another time might indicate a different density. Further study may shed light on the possibility that density of flight is related to density of population.

5. *Vanessa cardui* adults will fly in overcast, at least after the movement is under way. This has been observed between Victorville and Needles, San Bernardino County, March 31, 1958, and near The Geysers, Sonoma County, May 31 and June 1, 1958.

6. They have been observed once at least in the United States *(vide supra)* to fly in large numbers during moderate to very heavy rainfall.

7. The migrating individuals are all of one species. Other species of butterflies do not seem to become involved in the mass movements of *Vanessa cardui.*

8. The individuals in the flights are of both sexes. This was noted independently by sampling in 1958, by both Tilden and O. E. Sette. The sex ratio of the insects when engaged in a flight is very nearly the same as that of *Vanessa cardui* at any other time, 0.5 or one half

of each sex. Tilden took a sample of fifty adults, and found twenty-seven males, twenty-three females. The numbers taken by Sette are not recorded. This phase of the investigation deserves further study and this is planned for the future.

9. The females from the above sample were not greatly gravid. None had eggs ready to oviposit. This suggests that the females may drop out of the flight when ready to oviposit. If this be true, it might explain the tendency to reproduce along the flight routes.

10. The total movement proceeds in waves, or phases, which so far appear to be based on broods, a conclusion which seems to be well supported by the work of Abbott.

In the light of current findings, it is possible to reconstruct, at least to some degree, the nature of the populations of *Vanessa cardui* during and prior to the flights.

1. The first (initiating) brood apparently originates to the south, in northern Mexico or southwestern Arizona.

2. Findings from those movements that have been studied indicate that large flights can occur only in years when there has been sufficient rainfall on the deserts for a large growth of vegetation, enough to support such populations of *Vanessa cardui.*

3. The food plants in the desert areas, as noted by many observers, are principally Boraginaceae, especially *Cryptantha,* but also *Amsinckia.* Malvaceae have also been reported. Thistles and other composites seem to be of little importance at this time.

4. Upon emergence of the adults, each succeeding brood begins to fly into the wind, which in the deserts of California at this season (early spring) results in a north-westerly direction of flight.

5. These adults reproduce at some point along the line of flight. Time and place of reproduction presumably depend on the condition of the insects and the presence of suitable vegetation. Information on how far the females fly before reproducing, and the precise reason for selecting a certain place for reproduction, would add much to our knowledge.

6. Four to five broods, perhaps more, succeed one another before the force of the movement is spent.

7. The northern extent of the movement is at least to the San Francisco Bay Region of California. In some years, such as 1958, the effect extends into northern California, and apparently further, to Oregon and perhaps even Washington. Information as to the relationship between the *Vanessa cardui* in California and those in Oregon and Washington during such outbreak years is badly needed.

Williams and Abbott have raised the question as to whether *Vanessa cardui* is found north of the Imperial Valley, Imperial County, Calif., in any but outbreak years. There seems to be good evidence that it is. An examination of pinned specimens from many parts of California shows specimens taken in almost every year for many years back. As a Professor at San Jose State College, Tilden has examined hundreds of student collections over a period of fourteen years, and has also examined other specimens dating back to 1920. Some specimens of *Vanessa cardui* appear in student collections every semester. It is evident that this species is a normal component of the butterfly fauna in many parts of California. It is probable, however, that this local endemic population has little or nothing to do with the mass movements which from time to time are superimposed on it.

Two other items seem worth mentioning. Firstly, moderate to large populations of *Vanessa cardui* may be found late in the fall at high elevations in the mountains of the western United States. Specifically, Tilden found hundreds of adults at Hannagan's Meadows, White Mountains, Arizona, September 12, 1960. A fair population was found at Barton Flats, San Bernardino County, Calif., in September, 1957. Similar populations have been reported from the Sierra Nevada of California and elsewhere. The nature of these populations is not known, but it would seem that they are independent of the populations concerned with the great flights that occur in certain years.

Secondly, the mass flights of *Vanessa cardui* are of a very irregular nature. They are not regularly cyclic and do not occur at predictable intervals. However, some success in predicting these flights has been possible through knowledge of rainfall on the desert. Several workers foresaw the 1958 outbreak in the gathering populations of the southwest deserts.

An interesting and provocative suggestion of how rainfall may be necessary for mass movements of this species, was observed by Tilden September 11, 1960, at Yucca, Mohave County, Arizona. Late summer rains were plentiful and vegetation was well developed. Numerous freshly emerged adults of *Vanessa cardui* were present, and reproduction was in progress, with larvae of various stages on *Cryptantha.* It seemed that the basis for a movement was all prepared. However, the winter rains did not materialize, and on March 26, 1961, the area around Yucca was dry and no *Vanessa cardui* were to be found. If this abortive season is contrasted with the abundant rainfall of 1958 over the entire area, it points to a dependence of these populations on ample winter rainfall in the areas that are far enough south to act as reservoirs for populations that can engage in a mass flight.

Several questions are raised: (1) Why do these insects move at all, rather than remaining where they are? Possibly food may become scarce, but populations exist that do not move out in such a systematic manner under lowered food conditions. (2) Why is the flight directed? Why do not these insects move randomly in any direction open to them? The tendency to fly into the wind may be a clue here. Or have such movements been repeated so many times over the history of the species, that the tendency to fly in one direction has been selected for? (3) What causes the adults to reproduce here and there along the route? Why do they not merely fly on until exhausted? Present information may suggest some tentative answers, but such answers, while plausible, are not yet supported by sufficient data.

The author would add that this attempt at a synthesis of our knowledge concerning the movements of *Vanessa cardui* in western United States is prompted more by interest on his own part than by a desire to inform others. The purpose of this paper is to bring into focus our ignorance of the real basis of this interesting phenomenon, with a hope that future work will help to clarify some of the little known facets of the problem.

LITERATURE CITED

ABBOTT, C. H. 1941. The 1941 migration of the painted lady butterfly, (*Vanessa cardui*) in southern California. *Bull. Ecol. Soc. Amer.,* 22:13.

——— 1946. Mapping the 1945 migration of *Vanessa cardui* in southern California. Bull. Ecol. Soc. Amer. 27:49.

——— 1950. Twenty-five years of migration of the painted lady butterfly, *Vanessa cardui,* in southern California. Pan-Pac. Ent., 26:616-172.

——— 1951. A quantitative study of the migrations of the painted lady butterfly, *Vanessa cardui* L. Ecol. 32:155-171.

——— 1959. The 1958 migration of the Painted Lady Butterfly, *Vanessa cardui* (Linnaeus), in California. Pan-Pac. Ent., 35:83-84.

ESSIG, O. E. 1926. A butterfly migration. *Pan-Pac. Ent.,* 2:211-212.

SMITH, RAY F., & E. GORTON LINSLEY. 1945. Migration of *Vanessa cardui* (Linn.). *Pan-Pac. Ent.,* 21:109.

SUGDEN, JOHN W. 1937. Notes on the migrational flights of *Vanessa cardui* in Utah. *Pan-Pac. Ent.,* 13:109-110.

SUGDEN, JOHN W., ANGUS M. WOODBURY & CLYDE GILLETTE. 1947. Notes on the migration of the painted lady butterfly in 1945. *Pan-Pac. Ent.,* 23:79-83.

WILLIAMS, C. B. 1958. Insect Migration. xiii +235 pp., 11 plates, 22 photos, 49 maps & diagrams. Collins, London.

WOODBURY, ANGUS M., JOHN W. SUGDEN & CLYDE GILLETTE, 1941. Notes on migrations of the painted lady butterfly in 1941. *Pan-Pac. Ent.,* 18:165-176.

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THREE FACTORS AFFECTING LARVAL CHOICE OF FOOD PLANT[1]

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PRIOR TO THE INITIATION of comprehensive tests of the attraction by larvae of *Pieris rapae* of various food plants, a number of preliminary trials were made to test the effect of external factors which might influence the correctness of these tests. Of the factors which were thought most important, the following were selected for trial:

(1) Influence of direction of air movement ("wind").
(2) Influence of age (size) of larvae.
(3) Influence of food previously eaten by larvae, or strain of larvae.

EFFECT OF WIND MOVEMENT

An experiment devised to test this factor was set up as follows: A nursery flat about 24 inches square was filled with vermiculite. Pots of plants, each about the same size, were placed in the vermiculite spaced about as shown in Figure 1. The table under the flat was marked A, B, C and D. The direction of the wind movement was at side B. In the tests, larvae were placed in the central area, shown by a small circle and allowed to go to the plants, or to leave the flat.

Ten different larvae were used for each experiment, and these were used a total of ten times each. Thus, each experiment involved 100 trials.

The wind direction relative to the position of the plants was changed by turning the flat by 90° after each 100 trials, as shown by the illustration (Fig. 1). The first position tested was with mustard toward the dirction from which the breeze came (side B). The results of the preferential selection by the larvae are shown on Table 1.

Kale was selected by 19% of the larvae, mustards by 56%, radish

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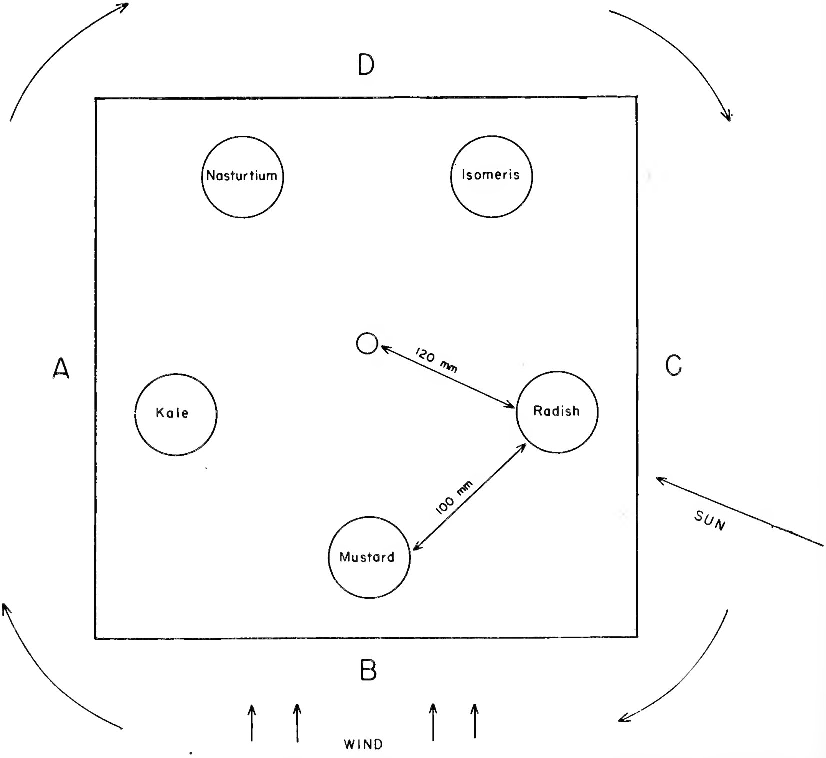
TABLE 1. The effect of wind movement on the choice of food plants by larvae of *Pieris rapae*

	Kale	Mustard	Radish	Nasturtium	Isomeris	None	Total no. of trials
	A 19	B 56	C 18	D 3	D 1	3	100
90°	D 20	A 20	B 52	C 4	C 2	2	100
90°	C 43	D 25	A 26	B 2	B 0	4	100
90°	B 53	C 15	D 13	A 8	A 5	6	100

Ten 14.1 mm to 15.7 mm kale-bred larvae of *Pieris rapae* were used per test with each test ten times at each position. The parents of the larva were collected at western Orange County in a cabbage field.

by 18%, nasturtium by 3% and Isomeris by 1%. Larvae which left the flat without selection amounted to the additional 3%.

With the flat turned 90° so that the radish was now in position B (in the direction of the wind), the selection results were very different. Kale remained relatively unchanged at 20%, mustard dropped from



1. The set-up for the selection experiments. The arrows indicate the direction of turning of the nursery "flat." The direction of wind and sun are indicated.

56% to 20%, radish rose from 18% to 52% at position B, while the remainder were unchanged.

With a further 90° turn in the direction of the arrows (Fig. 1), the radish plant was now opposite the direction of the wind, and nasurtium-Isomeris was toward the wind. Kale at position C to the right side now rose from 20% to 43%, mustard at position D (away from the wind) rose slightly and was now 25%, radish at the left side was now 26% and nasturtium-Isomeris (toward the wind) was still relatively unchanged at 2%.

The final 90° turn placed kale in the position toward the wind. Here, 53% of the larvae went to kale, 15% to mustard (right side), 13% to radish (opposite side), and 13% to nasturtium-Isomeris (left side).

CONCLUSIONS:

(1) Of the four sides of the flat which could face the direction of the wind, the plants on that side were favored in three of the four arrangements, namely, mustard, radish and kale. Only when the nasturtium-Isomeris combination was toward the wind was the frequency in position B not increased. In fact, at that time, it was *decreased.*

(2) These tests, of course, cannot indicate which of the three favored plants are relatively more favored since they each received about the same percentage of selection when toward the wind. However, when away from the wind, radish received fewer selections than either kale or mustard.

(3) The Isomeris-nasturtium combination received its highest selection when in position A (left side). In this position also, more larvae left the flat without a plant selection than in any other position.

(4) The higher selection of kale (43%) while at position C (right side), than radish (26%) while at position A (left side) seems to indicate a preference for kale rather than for radish.

(5) The lowest selection for the nasturtium-Isomeris combination was when it was in position B (toward the wind). This would seem to indicate that these plants (and Isomeris especially) repel rather than attract larvae of *Pieris rapae.*

(6) The data indicate that the direction of wind movement is of great importance in larval selection of food plant, since in all cases where the plant has a positive effect on selection, that position in the direction of the wind has by far the greatest selective influence. It is apparent that the reverse is also true, that if a plant is repellent, the effect is greatest when the wind comes from that direction.

[NOTE: The differences between the figures indicated are so great that the element of chance being involved is negligible. A chi-square test on the first trial gives a probability of less than one in a million that the differences are due to chance alone.]

EFFECT OF LARVAL SIZE ON PLANT SELECTION

Tests for the determination of influence of larval size on plant selection were made in the same manner as indicated previously, except that all tests were carried out in a room with no wind or breezes. Nevertheless, the flat was turned 90° three times for each test. This applies to all subsequent tests for the sake of safety. Two series of tests were made, using larvae of different origin.

The first series of tests (Table 2) was carried out with the use of kale-bred larvae. Larvae of different ages and sizes (size is roughly proportional to age) were separated and measured. Four larvae were isolated, these being the following sizes:: 8.4, 14.7, 19.0 and 21.0 mm in length. The tests were carried out by five trials of a given larva at each position with respect to the direction of the wind (Fig. 1), giving a total of 20 trials for each size larva.

TABLE 2. Choice of five kinds of plants by different sized larvae of *Pieris rapae* (Series 1)

Size of larvae (mm)	The number of times and percentage larva goes to						Total Number of trials
	Kale	Mustard	Radish	Nasturtium	Isomeris	None	
21.00	16—80%	4—20%	0— 0	0—0	0—0	0—0	20
19.00	13—65%	3—15%	3—15%	1—5%	0—0	0—0	20
14.70	11—55%	4—20%	4—20%	1—5%	0—0	0—0	20
8.40	10—50%	5—25%	5—25%	0—0	0—0	0—0	20

One single kale-bred larva was used for each size; tested each larva five times at each position.

The 8.4 mm larva selected kale 50% of the time, radish 25% of the time and mustard 25% of the time.

The 14.7 mm larva selected kale 55%, mustard 20%, radish 20% and nasturtium 5% of the time.

The 19.0 mm larva selected kale 65%, mustard 15%, radish 15% and nasturtium 5% of the time.

The 21.0 mm larva selected kale 80% and mustard 20% of the time and no others.

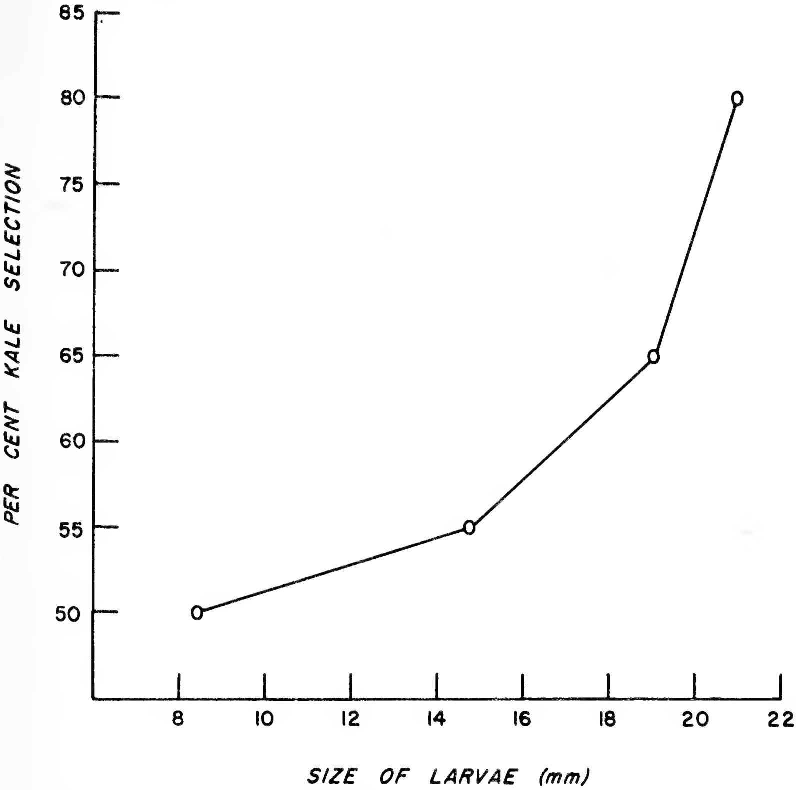
The probability, as caculated by chi-square, that the differences as indicated might be due to chance are less than 1/million, 1/100,000, 1/500, 1/500 respectively for each experiment.

CONCLUSIONS:

(1) The increase in selection of kale for each experiment is correlated with increase in size of the larvae (Fig. 2).

(2) Kale is the plant selected over all the others in this experiment. It should be noted that the larvae had been bred on kale prior to the experiment, and previous generations had been bred on cabbage.

(3) Not one larva went to Isomeris. This is interesting in view of the observation in the preceding experiments that Isomeris was



2. The relation between size (and age) of larvae and the percentage of the time kale was selected. The size of the larvae is directly correlated with an increase in selection of kale.

repellent to *Pieris rapae* larvae.

(4) The older or larger the larvae, the greater the selection of kale over all other plants (Fig. 2). The relationship is not a straight-line, but rather a geometric increase. This indicates that there is an increase in the critical powers of food perception in the older or larger larvae.

In the Series No. 2 tests (Table 3), larvae were used which had previously been grown on nasturtium. They were obtained from Ventura County on nasturtium and were continued in the laboratory on that plant.

Two larvae 22.4 mm in length, and four larvae 16.5 mm in length were used in this experiment. Otherwise, the trials were managed in the same way as in previous experiments with the exception that the total number of trials was 80 for large larvae and 160 for the smaller larvae.

The selection by these larvae bred on nasturtium (Table 3) was radically different from the selection by larvae bred on kale (Table 2). The selections of kale by the small larvae bred on nasturtium were 15% as compared with 55% for a comparable size bred on kale. The selections of kale by the large larvae bred on nasturtium were 22% compared with 80% for a comparable size bred on kale. The greatest shift in food plant selections for the nasturtium-bred small larvae was 49% to mustard as compared with 25%, 9% to nasturtium as compared with 0%, and 16% with no selection as compared with 0%. For the large larvae, comparable data were 34% to mustard as compared with 20%, 33% to nasturtium as compared with 0%, and 9% with no selection as compared with 0%.

CONCLUSIONS:

(1) The shifts in food-plant-selection by the larvae grown on different plants are highly significant and indicate a direct relationship between the feeding habits of the larvae, and their selection when given a free choice.

(2) The direct relationship between the size (and age) of the larvae and their selection of the plant previously eaten is clearly indicated.

(3) A plant previously of nearly negligible selection may be the most highly selected if the larvae have been grown on that plant. For example, larvae selected nasturtium over all others (33%) after being bred on that plant (Table 3), whereas larvae bred previously on kale had almost no selectivity for that plant.

INFLUENCE OF PREVIOUS FOOD PLANTS OF LARVAE

Additional experiments to test the influence of previous exposure to larval food plants are reported on here.

The first comparative test involves two strains of *Pieris rapae,* one from a population growing in the wild on black mustard and the other growing on cabbage. These strains were kept in the laboratory for several generations; the mustard strain was bred for over six generations on mustard in the laboratory and the kale strain was bred on kale in the laboratory for over ten generations.

Larvae were selected for these experiments which had a size of 14 to 16 mm. Using twenty-five larvae of each strain, 600 tests of selection were made (Table 4): the selected plants were mustard, kale, nasturtium, Isomeris and Cleome.

The only significant differences detected in the tests between the two strains were the relative selections made of mustard and kale. Larvae from the mustard-bred strain selected mustard 61% of the time compared with the kale-bred strains of larvae of 24% on that plant. On the other hand, kale was selected by the mustard-bred larvae 20%

TABLE 3. Choice of five kinds of plants by different sized larvae of *Pieris rapae* (Series 2)

Size of larvae	The number of times and percentage larvae go to						Total number	No. of
(mm)	Kale	Mustard	Radish	Nasturtium	Isomeris	None	of trials	larvae
22.4	18—22%	27—34%	1— 1%	26—33%	1—1%	7— 9%	80	2
16.5	24—15%	79—49%	16—10%	14— 9%	1—0.7%	26—16%	160	4

nasturtium-bred larvae were used in these tests; they were collected in Ventura County on nasturtium plants and fed in the laboratory on nasturtium. 25 different, 14 to 16 mm larvae were used for each test.

TABLE 4. Food plant choice by larvae of *Pieris rapae* previously fed on different food plants (Series I).

	The number of times and percentage larvae go to						Total
Type of larvae	Mustard	Kale	Nasturtium	Isomeris	Cleome	None	Trials
Mustard-bred	364—60.7%	119—19.8%	56—9.3%	18—3.0%	12—2.0%	31—5.2%	600
Kale-bred	144—24.0%	354—59.0%	50—8.3%	21—3.5%	15—2.5%	16—2.7%	600

Mustard-bred larvae were collected in the Arboretum and raised on black mustard in the laboratory for over six generations. Kale-bred larvae were collected in western Orange County on cabbage and raised on kale in the laboratory for over 10 generations.

TABLE 5. Food-plant choice by larvae of *Pieris rapae* previously fed on different food plants (Series II).

		The number of times and percentage larvae go to						Total number
Type of larvae		Mustard	Kale	Nasturtium	Isomeris	Radish	None	of trials
Nasturtium-bred	(2)	28—35.0%	10—12.5%	12—15.0%	1—1.3%	11—13.9%	18—22.3%	80
Kale-bred	(2)	18—22.5%	39—48.8%	3— 3.8%	0—0	18—22.5%	2— 2.5%	80

The nasturtium-bred larvae were from Ventura County, collected in a nasturtium garden. The parents of the kale-bred larvae were collected in western Orange County on cabbage; the larva are the first generation fed on kale.

of the time as compared with 59% by the kale-bred larvae. Testing these differences by chi-square using the four-fold table indicates a probability of less than 1/million that the differences could be due to chance alone. This may be calculated in another way, that is, by taking 364 + 354 = 718 for one value and 119 + 144 = 263 for the other. The expectation that these differences might be due to chance alone, that is, that the deviations $\frac{718 - 981}{2}$, and $\frac{971 - 263}{2}$ are not due to chance is well over one in a million.

CONCLUSIONS:

(1) The shift in selection of mustard or of kale according to whether or not the larvae were from a kale or mustard strain is indicated by the experiments. The data are highly significant at an incredibly high level.

(2) There is no significant change indicated in the selective level of the other plants involved as to whether or not the larvae were from the mustard or kale strain.

The second series of data on the problem of food plant selections involves nasturtium-bred larvae from a nasturtium strain and kale-bred larvae from a cabbage strain (Table 5). The experiments were carried out as before, two larvae of each strain were used, the same size for a total of forty trials each, of which ten were in each position as indicated in Figure 1.

The differences between the plant selections are again highly significant. The nasturtium-bred larvae as compared with the kale-bred larvae preferred mustard (35% as compared with 22.5%) and nasturtium (15% over 4%). The kale-bred larvae preferred kale (49% over 12.5%) and radish (22.5% over 14.0%). Neither selected Isomeris to any extent. A high proportion (22%) of the nasturtium-bred larvae rejected all plants.

CONCLUSIONS:

(1) As in previous experiments, there was a shift in selection by the larvae according to the previous larval food plants.

(2) This shift in selection was in the direction of the plant they had previously fed on. For example, nasturtium-bred larvae selected nasturtium better than did kale-bred larvae.

(3) Even though nasturtium-bred larvae selected nasturtium better than did kale-bred larvae, mustard was preferred over nasturtium and over kale.

(4) The greater selection of mustard over kale by nasturtium-bred larvae is significant not only in this experiment but also in a previously indicated test (Table 3). In both cases, kale is poorly preferred as compared with mustard when the larvae were nasturtium-bred.

(5) Radish is of lower selective influence when the larvae are

nasturtium-bred than when they are kale-bred. This was indicated also in previous tests (Tables 3 and 1).

(6) A significantly higher percentage of rejects (22%) are made by the nasturtium-bred larvae than by the kale-bred. This was also indicated in previous tests (Table 3 as compared with 1, 2 or 4).

DISCUSSION

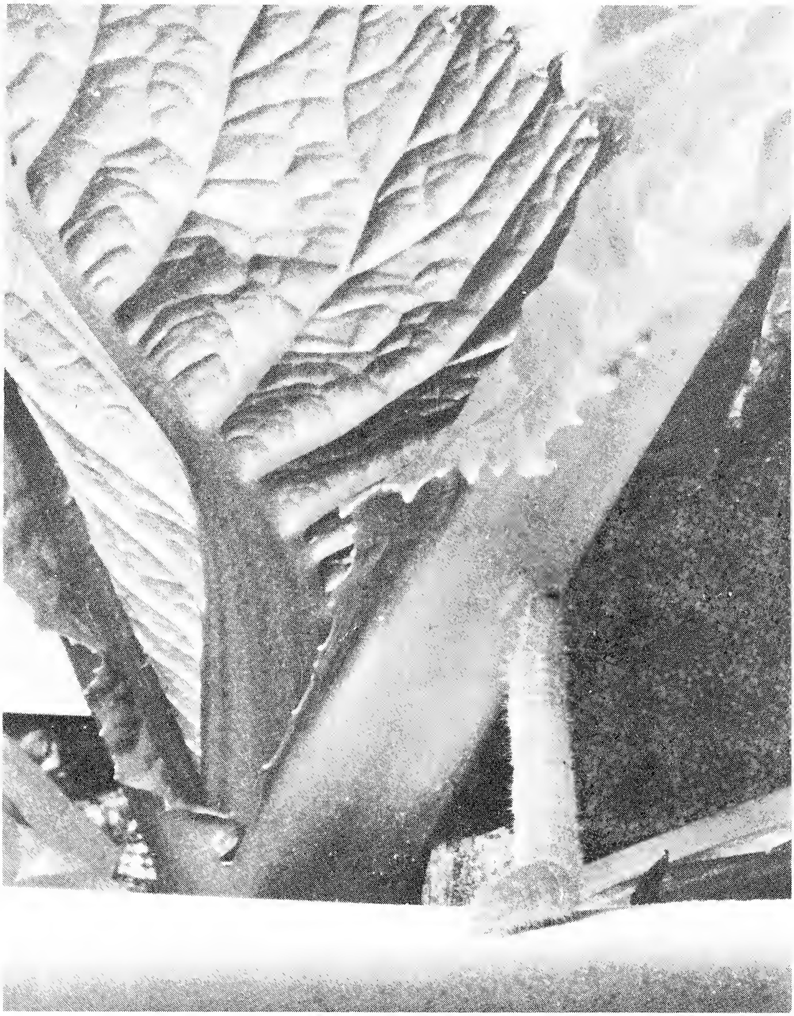
All three factors, investigated as to their relevance in influencing larval choice of food, have been shown to be important in that regard. These factors are:

(1) Influence of air movement.
(2) Influence of age (size) of larvae.
(3) Influence of food previously eaten by larvae, or strain of larvae.

In addition, by virtue of the laboratory set-up used in these experiments, some further conclusions may be drawn which are not completely in accord with some previous conclusions reached by others. One of these further conclusions is with regard to the ability of lepidopterous larvae to "recognize" food plants from a distance. In the present experiments, the larvae were attracted to the plants from a distance of over 120 mm without any difficulty and responded in most cases immediately.

Chin (1950) reports that the larvae of the Colorado potato beetle *(Leptinotarsa)* could not perceive its food plant from a distance farther than 2mm. Gupta and Thorsteinson (1960) tested the olfactory response of the larvae of the diamond backed moth [*Plutella maculipennis* (Curt.)] toward mustard oil odors and found that 5 mm was the maximum distance of response. Dethier (1959) in a study on food plant distribution and density and larval dispersal as factors affecting insect populations, states in relation to field observations that "Larvae find new food-plants by chance alone." It is presumed that he had reference to the gross search for new food plants, not the closer relationship. In the case of the experiments of Chin, and Gupta and Thorsteinson, the screen test was used. In this, the larvae were placed on a screen *above* the food plant or other attractive source. In the present experiments, the larvae were *below* the food plants. This difference could account for a fundamental difference when testing for an odiferous substance heavier than air. Under natural conditions, our observations have always indicated that larvae tend to climb upwards rather than down so that tests involving simulated natural conditions should be best performed with the attraction above rather than below the larvae (Fig. 3). This point will be covered more fully in tests to be described in later papers.

In a paper available to us after the tests here indicated were performed, (Takata, 1959), there has been indicated a change in food plant preference of larva when reared successively on different food



3. Larva of *Pieris rapae* on edge of pot during one of the selection experiments reaching out to black mustard plant three to four inches away. The larva had already traveled several inches under directed impulse to get this far.

plants for several generations. These results complement ours, even though the technique of testing used by Takata was different. He used cabbage and radish with *Pieris rapae crucivora* larvae. In testing, he used actual feeding experiments of the weight of leaves of the plants eaten by the larvae.

SUMMARY

The evidence in this paper indicates (1) that larvae of *Pieris rapae* are capable of detecting their preferred food plant from a distance of at least 120 mm under the conditions of these experiments, (2) that the direction of wind movement is very important to detection of food plant, presumably through odor, (3) that the older and larger larvae are much better at selecting the preferred food plant at least at a distance and (4) that the influence of food previously eaten by the larvae, or the strain of the larvae, directly influences their choice of food in the direction of the previously eaten food.

LITERATURE CITED

CHIN, CHUN-TEH. 1950. Studies on the physiological relations between the larvae of *Leptinotarsa decemlineata* Say and some solanaceous plants. H. Veenman and Sons, Wageningen, Holland. pp. 1-88.

DETHIER, V. G. 1959. Food plant distribution and density and larval dispersal as factors affecting insect populations. *Canad. Entom.* 91: 581-596.

GUPTA, P. D. AND A. J. THORSTEINSON. 1960. Food plant relationships of the diamond-backed moth *(Plutella maculipennis* (Curt.)). I. Gustation and olfaction in relation to botanical specificity of the larva. *Ent. exp. and appl.* 3 (1960) :241-250.

TAKATA, N. 1959. Studies on the host preference of common cabbage butterfly, *Pieris rapae crucivora* (Boisduval). VI. Change in the food preference of larvae when reared successively by the definite food plant for several generations (preliminary report). *Jap. J. Ecol.* 9:224-227.

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THE GENERIC, SPECIFIC AND LOWER CATEGORY NAMES OF THE NEARCTIC BUTTERFLIES

PART 1 — *The Genus Pieris*

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PREFACE

INTRODUCTION

The author has asked that I write a brief introduction to this, the first of a series of compilations of generic, species and lower category names of the Nearctic butterflies. The objects of the work are (1) to give a complete list of all the names proposed for the butterflies of the Nearctic region from the year 1758 until the date of publication of the list, (2) to indicate the date and place where originally published, (3) to indicate the types of the genera, species and lower category names where known, (4) to indicate the type locality in the original author's words for types, except those for the generic names, and (5) to indicate the location where types have been deposited where indicated by the author.

The biological application of these names so indicated is not to be attempted in this series. Instead, this effort is left to the individual who makes a comprehensive study of the biology of the groups concerned, such a person rarely having the time and inclination to make the detailed and laborious studies of nomenclature as such. There is urgent need for a work such as this even in a field as well civilized as the Lepidoptera; in fact, this kind of work is so long overdo that the civilized state is rapidly reverting to chaos. Each new volume which appears from the press on this group of insects plows under well established names with no reason given to justify such destruction. A most valuable start in the direction of making reason out of chaos was started by Francis Hemming in his "The Generic Names of the Holarctic Butterflies" published in 1934. This work is proceeding also in the same direction.

When the various parts of this work are completed, it is expected to reissue the whole as a separate volume. Then, perhaps we can prevail upon Mr. McHenry to go on to a similar effort with the moths.

William Hovanitz

EACH ENTRY for the generic names includes the following: the name, the author's name, the most accurate determinable publication date, the bibliographical reference (including the volume or subvolume for the date indicated), the type species, the selection of the type species and the supporting data to justify the type indicated.

Each entry for the specific names includes the following: the name as originally given, the author's name, the most accurate determinable publication date, the bibliographical reference, data on type locality, sex, season, etc., other spellings of the name and notations of any homonym.

The date of publication of a name is indicated in a manner that shows its relative accuracy; for example, "mailing" and "release" dates if known are given preference over "publication" dates if they are not the same. All dates are given in English and normally in the sequence of day, month and year. Where more than one date is indicated, the more accurate one is given after the less accurate one. Dates ascertained directly from a source whose purpose was the determination of time of publication of a work are given without brackets; others, ascertained less directly are given in brackets and explained in a footnote. Combinations of dates with and without brackets may be given when necessary.

I have seen originals or photostats of all references except as noted but have been unable to ascertain the contents and dates for the various parts of Verity's Rhopalocera Palaearctica.

The names of the genus *Pieris* are listed under the five species indicated, since in this genus the separation does not involve great difficulty. I have been aided in this regard by William Hovanitz, or by reference to the original description. Should these be in error, no harm is done since the total list, not the biological interpretation of the categories to which the names applied, is the purpose of the listing.

Should anyone find names which have been inadvertently omitted from this listing, a great service will be rendered to so notify the author or the editor of this fact so that corrections may be made.

I take this opportunity to express my gratitude for the use of facilities and to the staffs at the Allan Hancock Foundation Library of the University of Southern California, and at the Los Angeles County Museum Library & Entomological Department. A debt of gratitude is tenderd to the photographic service sections of the U. S. Department of Agriculture Library, Harvard College Library, New York Public Library, University of California Library and Cornell University Library. An extended exchange of correspondence with Mr. C. F. DosPassos has been most helpful.

LIST OF GENERIC NAMES USED OR AVAILABLE FOR PIERIS

ASCIA Scopoli.
Type: *monuste* L.

- **MANCIPIUM Hübner.**
  - Type: *hellica* Hübner = *hellica* L. = *helice* L.
- **PIERIS Schrank.**
  - Type: *brassicae* of var. authors = *brassicae* L.
    - ***ANDROPODUM* Hubner.**
      - Type: *brassicae* Hübner = *brassicae* L.
    - ***GANORIS* Dalman.**
      - Type: *brassicae* L.
    - ***TACHYPTERA* Berge**
      - Type: *brassicae* L.
- **PONTIA Fabricius.**
  - Type: *daplidice* Fab. = *daplidice* L.
- **SYNCHLOE Hübner.**
  - Type: *callidice* Butler = *callidice* Esper = *callidice* Hubner

ASCIA SCOPOLI. 1777. Introd. Hist. Natur.: 434, no. 175. Includes among others no. 80 (="*P. D.* [*C.*] *monuste*" of Linnaeus, 1767) which in turn is *Papilio D. C. monuste* Linnaeus, 1764.

Type *Papilio D*[*anaus*]. *C*[*andidus*]. *monuste* Linnaeus. 1764. Museum Ludovicae Ulricae ([I]) : 237, no. 56.

Type Selection. Scudder. 1872 [in or pre-June][1]. Syst. Rev. Some Amer. Butt., p. 40. Says of Ascia: "*Type Papilio monuste* Linn."

MANCIPIUM HÜBNER. [1 Jan. 1807] - [19 Dec. 1807][2]. Samm. Exot. Schmett. 1: pl. [141], ff. 1-4. Gives "*Mancipium vorax hellica*". As used by Hübner, *hellica* is considered to be *hellica* Linnaeus, 1767 which in turn is *helice Linnaeus,* 1764.

Type. *Papilio D*[*anaus*]. *C*[*andidus*]. *helice* Linnaeus. 1764. Museum Ludovicae Ulricae ([I]) : p. 243, no. 62.

Type Selection. Hübner. As above. Gives only *hellica,* at the time, which becomes the type.

PIERIS SCHRANK. 1801. Fauna Boica 2(1): 152, no. 198; 2(1): 160-170, nos. 1283-1296. Includes *Pieris brassicae* which he says is *Papilio brassicae* of Goeze, Borkhausen, Brahm, and Esper. Of these authors, *brassicae* is considered to be *brassicae* Linnaeus, 1758.

Type. *P*[*apilio*]. *D*[*anaus*]. [*Candidus*] *brasicae* Linnaeus. 1758. Syst. Nat. 10th Ed. 467-468, no. 58.

Type Selection. Latreille. 1810. Consid. Gén. Anim. Crust. Arach. Ins. p. 440. Says: "Pieride. *Pontia brassicae, Fab.*". As used by Latreille, *brassicae* Fabricius is considered to be *brassicae* Linnaeus, 1758.

ANDROPODUM HÜBNER. 1822. [post 22 Sept.].[3] Syst.-Alph. Verz. pp. 2-5, 7-9. Includes "*Brassicae* L. 401-403. Andropodum vorax."

Type. *P*[*apilio*]. *D*[*anaus*]. [*Candidus*] *brassicae* Linnaeus. 1758. Syst. Nat. 10th. Ed. 1:467-468, no. 58.

Type Selection. Hemming. Sept. 1933. Entomologist: 66(844): 199. Says of Andropodum: "Type = *Andropodum brassicae* Linn."

GANORIS DALMAN. 1816. Kongl. Vetenskaps Academiens Handlingar 1816(1): 61-62, no. 8; 1816(1): 86-90, nos. 1-10; tablet 1, no. 8; tablet 2, no. 8. Includes *G. brassicae* in which he cites Linnaeus Fauna Sv., pp. [269] - [270], no. [1035] (this is *brassicae* Linnaeus, 1761, which is *brassicae* Linnaeus, 1758).

Type. *P*[*apilio*]. *D*[*anaus*]. [*Candidus*] *Brassicae* Linnaeus. 1758. Syst. Nat. 10th Ed. 1:467-468, no. 58.

Type Selection. Dalman. As above. Says of Ganoris: "Generis Typus: *Pap. brassicae*".

TACHYPTERA BERGE. 1842. Schmetterlingsbuch, p. 19, pp. 92-105. Not seen, given as per Hemming, 1934.

Type. P[*apilio*], .D[*anaus*]|, [*Candidus*] *brassicae* Linnaeus. 1758. Syst. Nat. 10th. Ed. 1:467-468, no. 58.

Type Selection. Hemming. Feb. 1934. Entomologist: 67(849):38. Says of Tachyptera: "Type = *Papilio brassicae* Linn., 1758."

PONTIA FABRICIUS. 1807. In Illiger. Magazin fur Insektenkunde. 6: 283, no. 23. Includes: "*Pap . . . Daplidice*". As used by Fabricius *daplidice* is considered to be *daplidice* Linnaeus, 1758.

Type. P[*apilio*]. D[*anaus*]. [*Candidus*] *daplidice* Linnaeus. 1758. Syst. Nat. 10th Ed. 1:468, No. 2.

Type Selection. Curtis. 1824. Brit. Entom. 1: pl. 48. Not seen, given as per Hemming, 1934.

SYNCHLOE HÜBNER. 1818 [post 22 Dec.][4]. Zutr. Samm. Exot. Schmett. 1st. 100 (text in 1): p. 26, under no. 76. (Synchloe autodice). Includes "*S. callidice*". Refers to his earlier publication of this butterfly.

Type. *Papilio callidice* Hübner. [24 Dec. 1799] - [13 Apr. 1800][5]. Samm. Europ. Schmett. (Papiliones): plate 81, figs. 408-409. Page 63, no. 5 and plate 108, figs. 551-552 were published later.

Type Selection. Butler. 12 Sept. 1870. Cistula Ent. 1(3):51. Says of Synchloe: "Type *S. callidice* Esper". As used by Butler *callidice* Esper is considered to be *callidice* Hübner [24 Dec. 1799] - [13 Apr. 1800].

LIST OF SPECIES AND LOWER CATEGORY NAMES USED OR AVAILABLE FOR PIERIS

1. P. (PONTIA) BECKERII EDWARDS.
   beckerii Edwards.
   gunderi Ingham.
   pseudochloridice McDunnough.
2. P. (PONTIA) SISYMBRII BOISDUVAL.
   elivata (B. & B.).
   flava Edwards.
   flavitincta Comstock, J. A.
   sisymbrii Boisduval.
   transversa (B. & B.)
3. P. (PONTIA) PROTODICE BOISDUVAL & LECONTE
   calyce Edwards.
   nasturtii Edwards (Bdv. Ms.).
   nelsoni Edwards.
   occidentalis Reakirt.
   protodice Boisduval & LeConte.
   vernalis Edwards.
4. P. (PIERIS) NAPI (LINNAEUS).
   acadica Edwards.
   aestiva Edwards.
   arctica Verity.
   borealis Grote.
   casta Kirby.

castoria Reakirt.
cottlei Gunder.
cruciferarum Boisduval.
flava Edwards.
flava Edwards.
frigida Scudder.
hulda Edwards.
hyemalis Edwards.
iberides Boisduval.
macdunnoughii Remington.
marginalis Scudder.
microstriata Comstock, J. A.
mogollon Burdick.
napi (Linnaeus).
nasturtii Boisduval.
ochsnheimeri Staudinger.
oleracea Harris.
pallida Scudder.
pallidissima B. & McD.
pseudobryoniae Verity.
pseudoleracea Verity.
pseudonapi B. & McD.
resedae Boisduval.
venosa Scudder.
virginiensis Edwards. 1870.
virginiensis Edwards. 1881.

5. P. (PIERIS) RAPAE (LINNAEUS).
aestivus Verity.
immaculata De Selys-Longchamps.
immaculata Cockerell.
immaculata Skinner & Aaron.
metra Stephens.
novangliae Scudder.
rapae (Linnaeus).
yreka Reakirt.

1. PIERIS (PONTIA) BECKERII EDWARDS.

beckerii Pieris Edwards. [Sept. 1871][6]. Butt. N. Amer. 1(8) : [28a] - [29]; plate [81], figs. 4-7. ♂ & ♀ described. "Virginia City, Nevada, April 1870." "Four individuals". McDunnough, 1 Dec. 1928, spells *beckeri.*

gunderi, Ascia beckerii Ingham. 14 Apr. 1933. Pan-Pacific Ent. 9(2):75. Holotype ♀ : "Bouquet Canyon, Los Angeles County, Calif". "Bred from larva". "emergence date June 21, 1932". Type deposited: Calif. Acad. Sci., San Francisco, Calif.

pseudochloridice, Pieris beckeri McDunnough. 1 Dec. 1928. Can. Ent. 60(11): 266-267. Holotype ♂: "Oliver, B[ritish]. C[olumbia]., April 24 . . . No. 2861 in the Can. Nat. Coll., Ottawa". Allotype ♀ : "Oliver, B.C., April 22". Paratypes — 1 ♂: "Hedley, B. C., May 15". 1 ♀: "Osoyoos, B.C." 1+: "Osoyoos, B.C."

2. PIERIS (PONTIA) SISYMBRII BOISDUVAL.

elivata, Ascia sisymbrii Barnes & Benjamin. 8 Dec. 1926. Bull. Sou. Calif. Acad. Sci. 25(3):88, no. 33a. "Type locality: Glenwood Springs, Colo.". "Number and sexes of types: Holotype ♂ May 1895, Allotype ♀ May 1895, 7 ♂ 14 ♀ Paratypes, various dates April to June".

flava, Pieris sisymbri Edwards. Apr. 1883. Butt. N. Amer. 2(11): [67]; plate [15]. fig 5. ♀ described. No locality, series data nor dates given.

flavitincta, Pieris sisymbrii Comstock, J. A. 20 Feb. 1924. Bull. Sou. Calif. Acad. Sci. 23(1) : 19-20; plate 7, fig. 9. ♀ described. "The example before us was captured . . . April 30th, 1911 at Cranbrook, British Columbia". Intends to propose new name for *flava* Edwards.

sisymbrii, Pieris Boisduval. 1852 [25 Feb. - 22 Dec.]^{7}. Ann. Soc. Ent. France. 2nd Ser. 10 (2):284, no. 8. ♀ described. [California]. No series data nor dates given. Edwards, Apr. 1883, spells *sisymbri.*

transversa, Ascia sisymbrii Barnes & Benjamin. 8 Dec. 1926. Bull. Sou. Calif. Acad. Sci. 25(3): 88, under no. 33. "Type localities: Paradise, Cochise Co., Ariz.; Redington, Ariz.". "Number and sexes of types: Holotype ♂, Allotype ♀, 1 ♀ Paratype, all March; 1 ♂ Paratype, no date".

3. PIERIS (PONTIA) PROTODICE BOISDUVAL & LECONTE.

calyce, Pieris Edwards. Nov. 1870. Trans. Amer. Ent. Soc. 3(?) sign. 25: 189, no. 1 (Nomen nudum); 189. ♂ described. "From Nevada; in the collection of Henry Edwards". No series data nor dates given.

nasturtii, Pieris Edwards (Boisduval Ms. name). [9 May 1864]^{8}. Proc. Ent. Soc. Phila. 2(4): 501, no. 1 (Nomen nudum); 501. ♂ & ♀ described. "San Francisco; from Dr. Behr, who informs me that it is common in some localities in the vicinity of that city". No series data nor dates given.

nelsoni, Pieris Edwards. Apr. 1883 Butt. N. Amer. 2(11): [71] - [72]; plate [15], figs. 6-7. "1 ♂ . . . St. Michael's Alaska, June, 1881".

occidentalis, Pieris Reakirt. June 1866. Proc. Ent. Soc. Phila. 6 (pp. 121-152): 133-134. ♂ & ♀ described. "Hab. - Rocky Mountains, Colorado Territory, California, (Coll. Tryon Reakirt)". No series data nor dates given.

protodice, P[ieris]. Boisduval & LeConte. 1829. Hist. Gén. Icon. Lepid. Chen. l'Amer. Sept. 1(5):45-46. Plate 17, figs. 1-3 published later. ♂ & ♀ described. "Elle parait au printemps et a la fin de juin aux environs de New-York. Nous en avons vu un individu pris dans le Connecticut".

vernalis, Pieris Edwards. [9 May 1864]^{8}. Proc. Ent. Soc. Phila. 2(4): 501, no. 2 (Nomen nudum); 2 (4):501-502. ♂ & ♀ described. "In the collection of Mr. Geo. Newman and Mr. Wilt are several specimens, taken, as I am informed, at Red Bank, New Jersey, in the month of May". "There is also in the Society's collection a pair from the Rocky Mountains, that appear to be identical with it".

4. PIERIS (PIERIS) NAPI (LINNAEUS).

acadica, Pieris napi Edwards. June 1881. Papilio 1(6):86-88 (in pt.), sub no. 1; p. 98, no. 1 of no. 3; p. 99; plate 3, figs. 10-11. It appears that one pair was from Southern Newfoundland and was taken in the last week in July, it also appears another set (1 ♂ 2 ♀) had emerged from pupae in August and was from the same locality.

aestiva, Pieris napi oleracea Edwards. June 1881. Papilio 1(6):86-88 (in pt., Nomen nudum), sub no. 1; 1(6):89-95 (in pt.) sub no. 3; 1(6):95-98 (in pt.), sub no. 4; 1(6):98, no. 3 of no. 3;

1(6):99; plate 3, figs. 15-16. ♂ & ♀ described. "NewYork" (see figs. explanation, p. 99). "summer brood". No series data given.

arctica, Pieris napi frigida Verity. 1905-1911. Rhopal. Palaearctica: pp. 333-334 (in pt., cites figs 32-33 on plate XXXII and figs. 16-17 on plate LXVII as *P. n. f. arctica*); plate XXXII, figs. 32-33; plate XXXII explanation page, figs. 32-33 (gives as *P. n. frigida*); plate LXVII, figs. 16-17; plate LXVII explanation page, figs. 16-17 (gives as *P. n. arctica*); p. xxviii (cites figs. 31-33 & 36-37 on plate XXXII and figs. 16-17 on plate LXVII, gives as *P. n. f. arctica*). "31 . . . ♂ (ile d'Yesso, Japon)". "32 . . . ♂ (Norvege sept.)". "33 . . . ♂ (Nulato, Alaska)". "36 . . . ♀ (Nulato, Alaska)". "37 . . . ♀ (Finmark, Scandinavie)". "16 . . . ♀ (Saltdalen, Norvege sept.)". "17 . . . ♀ (Laponie)". Figs. 31, 33, 36: [coll. de Joannis]. Fig. 32: [coll. Stefanelli]. Fig. 37: [coll. Obth.] Fig. 16: [e coll. Mourray]. Fig. 17: [e coll. Leach]. No series data nor dates given.

borealis, Ganoris oleracea Grote. Nov. 1873. Bull. Buffalo Soc. Nat. Sci. 1(4) sign. 24:185. "months of June and July, on the Island of Anticosti". No series data nor sex given.

casta, Pontia Kirby, W. 1837. In J. Richardson. Fauna Boreali-America (4):288, no. 1; plate 3, fig. 1. "Three specimens taken in Lat. 65°". No sex given.

castoria, Pieris Reakirt. [11 June 1866] - [13 Feb. 1867][9]. Proc. Acad. Nat. Sci. Phila. [18](3):238, no. 2. ♂ described. "Hab. - California. Coll. Tryon Reakirt". No series data nor dates given.

cottlei, Pieris napi castoria Gunder. 6 July 1925. Ent. News 36(7):197-198, no. 9; plate 5, fig. 9; Holotype ♂ : "(author's Coll.), Anderson Springs, Lake County, California, May 5, 1919".

cruciferarum, Pieris Boisduval. 1836 [in or post Apr.][10]. Hist. Nat. Ins. Spec. Gén Lepid. 1 (text in 1):519, no. 119. ♂ described. "dans les provinces septentrionale des Etats-Unis". No series data nor dates given.

flava, Pieris napi pallida Edwards. June 1881. Papilio 1(6):89-95 (in pt., unnamed), sub no. 3; 98, sub no. 2 of no. 3. "Washington Terr[itory].". "One of these [a ♀] is yellow on the upper side". No date given.

flava, Pieris napi venosa Edwards. June 1881. Papilio 1(6):88-89 (in pt., unnamed), sub no. 2; 98, sub no. 1 of no. 2. Fig. 7 of plate 2 (although not so named in plate explanation, p. 99) appears to be *flava*. "A large percentage of female *Venosa* are yellow on the upper side". No locality, series data nor dates given.

frigida, Pieris Scudder. Sept. 1861. Proc. Boston Soc. Nat. Hist. (8(?) sign. 12:181-182. "Two . . . males . . . two females". "on Caribou Island, Straits of Belle Isle". No dates given.

hulda, Pieris Edwards. Sept. 1869. Trans. Amer. Ent. Soc. 2(?) sign. 48:370. "From Kodiak, 1 ♂. Coll. of Henry Edwards". No date given.

hyemalis, Pieris napi oleracea Edwards. June 1881. Papilio 1(6):88-89 (in pt., Nomen nudum), sub no. 2; 89-95 (in pt.), sub no. 3; 95-98 (in pt.), sub no. 4; 99; plate 2, fig. 8. ♂ & ♀ described. Directly and indirectly cites material from New Hampshire, Massachusetts, Lake Superior area and Mt. Hood, Oregon. No series data nor dates given.

iberides, Pieris Boisduval. [1869, pre 1 Nov.][11]. Ann. Soc. Ent. Belgique 12 (in 1):39, no. 9. ♂ & ♀ described. [California]. No series data nor dates given.

macdunnoughii, Pieris napi Remington. 17 Sept. 1954. The Lepid News 8(3-4):75. A new name for *Pieris napi pseudonapi* Barnes & McDunnough, 5 Dec. 1916. See *pseudonapi* for series data.

marginalis, Pieris Scudder. Sept. 1861. Proc. Boston Soc. Nat. Hist. 8(?) sign. 12:183. "(1 ♂ ,1 ♀) which are in the Museum of Comparative Zoology". The male . . . from Gulf of Georgia, and the female from Crescent City, California". No dates given.

microstriata, Pieris napi Comstock, J. A. 12 Sept. 1924. Bull. Sou. Calif. Acad. Sci. 23(4):125. Holotype [♂]: "Eldredge, Sonoma County, California. March 13, 1911". Allotype [♀]: "same locality and on the same date". "Paratype; one male - same locality and date".

mogollon, Pieris napi Burdick. 28 Sept. 1942. Can. Ent. 74(8):154-155. Holotype ♂: "Mogollon Range, Catron Co., New Mexico, 5-7-40. No. 5222 in the Can . . . Nat . . . Coll . . . , Ottawa". Allotype ♀: "same data". "Paratypes. 2 ♂, same data; 3 ♂, Sierra Blanca, Lincoln Co., N. M., 5-25-40; all in the Can . . . Nat . . . Coll . . . , Ottawa. 1 ♂, Mogollon Range, Catron Co., N. M., 5-7-40 and 1 ♀, Sierra Blanca Range, Lincoln Co., N. M., 5-20-40; in the U . . . S . . . Nat . . . Mus . . Fifty-six paratypes from the above locations in the collection of the author, from which other museums will be supplied".

napi, P[apilio]. D[anaus]. [Candidus] Linnaeus. 1758. Syst. Nat. 10th. Ed. 1:468, no. 60. No locality, series data, sex nor dates given. Edwards, June 1881, spells *napae.*

nasturtii, Pieris Boisduval. [1869, pre 1 Nov.][11]. Ann. Soc. Ent. Belgique (12) (in 1):38-39, no. 7. ♂ described. "dans les champs decouverts au pied de la Juba". "Nous n'avons vu que des males". No series data dates given. A homonym of *Pieris nasturtii* Edwards, [9 May 1864].

ochsenheimeri, Pieris Staudinger. End Apr. 1886. Ent. Zeitung Stettin 47(4-6):199-200. ♂ & ♀ described. "wo sie die beiden Haberhauer in Anzahl Ende Juni bei Namagan, jedenfalls hoch in den Gebirgen ge fangen hatten. Auch Maurer sandte mir in demselben Jahre ein im Alai-Gebirge (sudlich von Margelan) gefangenes + ein". No series data given.

oleracea, Pontia Harris. 10 July 1829. The New England Farmer & Horticultural Jour. 7(51):402. "Habitat . . . in New Hampshire, and Massachusetts". No series data nor sex given. "two broods in a season": [May-June - August].

pallida, Pieris Scudder. Sept. 1861. Proc. Boston Soc. Nat. Hist. 8 (?) sign. 12:183. "five specimens (3 ♂, 2 ♀), which are in the Museum of Comparative Zoology". "Gulf of Georgia". No dates given.

pallidissima, Pieris napi Barnes & McDunnough. 5 Dec. 1916. Contrib. Nat. Hist. Lepid N. Amer. 3(2):59; 142; plate 6, figs. 4-5 & 10. "second generation (July, August)". "type ♂ and ♀ from Provo, Utah". No series data given.

pseudobryoniae, Pieris napi frigida Verity. 1905-1911. Rhopal. Palaearctica: p. 146 (cites figs. 46-37 on plate XXXII, gives as *P. n. f. pseudobryoniae*); plate XXXII, figs. 36-37; plate XXXII explanation page, figs. 36-37 (gives as *P. n. frigida*); p. xxviii (cites only fig. 37, gives as *P. n. f. arctica pseudobryoniae*). "36 . . . ♀ (Nulato, Alaska) [coll. de Joannis]". "37 . . . ♀ (Finmark, Scandinavie) [coll. Obth.]". No series data nor dates given.

pseudoleracea, Pieris napi frigida Verity. 1905-1911. Rhopal. Palaearctica: p. 146; plate XXII, fig. 38; plate XXXII explanation page, fig. 38; p. xxviii. "38 . . . ♂ (Labrador) [e coll. Boisduval in coll. obth.]". No series data nor dates given.

pseudonapi, Pieris napi Barnes & McDunnough. 5 Dec. 1916. Contrib. Nat. Hist. Lepid. N. Amer. 3(2):57; 142; plate 6, figs. 1-3. "type ♂ and ♀ taken at Silverton, Colo . . . in the last week of July". No series data given. A homonym of *Pieris melete pseudonapi* Verity, 1905-1911.

resedae, Pieris Boisduval. [1869, pre 1 Nov.][11] Ann. Soc. Ent. Belgique 12 (in 1):38-39, no. 8. ♀ described. "Nous ne connaissons cette espece que par un seul individu femelle pris . . . sur les bords du Sacramento". No date given.

venosa, Pieris Scudder. Sept. 1861. Proc. Boston Soc. Nat. Hist. 8(?)

sign. 12:182-183. "twenty specimens (5 ♂, 15 ♀), brought to the Museum of Comparative Zoology, from San Mateo and Mendocino city, California". No dates given.

virginiensis, Pieris Edwards. Jan. 1870. Trans. Amer. Ent. Soc. 3(?) sign. 2:10, no. 5 (Nomen nudum); 13-14. ♂ & ♀ described. "Not uncommon in the Kanawha district [West Virginia] in the month of May, and there replacing *Oleracea.* I have received from Mr. Saunders occasionally specimens taken by him at London, Canada". No series data given.

virginiensis, Pieris napi oleracea hyemalis Edwards. June 1881. Papilio 1(6):95-98 (in pt.), sub no. 4; 98, under no. 2 of no. 2. " . . . *Virginiensis* . . . has become a true species, although unquestionably, in a higher latitude, it appears as an occasional aberration only of *Oleracea*". Specimen data is obscure. A homonym of *virginiensis* Edwards, Jan. 1870.

5. PIERIS (PIERIS) RAPAE (LINNAEUS).

aestivus, Pieris rapae Verity. 16 May 1913. Jour. Linn. Soc. (London), Zool. 32(215):177-178. "summer brood". No locality nor series data given.

immaculata, Pieris rapae De Selys-Longchamps. 1857. Ann. Soc. Ent. Belgique 1 (in 1):5, under no. 5. [Belgique]. No series data, sex nor dates given.

immaculata, Pieris rapae Cockerell. Apr. 1889. Entomologist: 22(311):99. No locality, series data, sex nor dates given. Cites p. 161 in Newman's Brit. Butt. A homonym of *Pieris napi immaculata* De Selys-Longchamps, 1857.

immaculata, Pieris rapae Skinner & Aaron. 2 July 1889. Can. Ent. 21(7): 128-129. "five specimens in the collection of Am. Ent. Soc., Dr. Skinner and E. M. Aaron". No sex nor dates given. A homonym of *Pieris rapae immaculata* De Selys-Longchamps, 1857 and Cockerell, Apr. 1889.

metra, Pontia Stephens. 1 Aug. 1827. Illust. Brit. Ent. 1(?) sign. d:19-20, no. 4:146-147 published later. ♂ & ♀ described. "The insect occurs early in April and a second time towards the end of June. I obtained specimens of the first brood at Hertford; and of the second I captured some this season, at Ripley at the latter period".

novangliae, Ganoris rapae Scudder. Apr. 1872. Can. Ent. 4(4):79. "Two of my specimens were taken in June and July, 1869 — one . . . in Shelbourne, N[ew]. H[ampshire] . . . the other . . . in Waterville, M[aine]., and all are males".

rapae, P[apilio]. D[anaus]. [Candidus] Linnaeus. 1758. Syst. Nat. 10th. Ed. 1(in 1):468, no. 59. No locality, series data, sex nor dates given.

yreka, Pieris Reakirt. [11 June 1866] - [13 Feb. 1867][9]. Proc. Acad. Nat. Sci. Phila. [18](3):238, no. 1. ♂ & ♀ described. "Hab. - California. Coll. Tryon Reakirt". No series data nor dates given.

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[1] Amer. Nat. 6: 354-359. Work is reviewed in June 1872 number.

[2] Hemming, 1937. Hubner 1:327-437.

[3] The work title page signature date qualified by preface signature date on page vi.

[4] Title page signature date qualified by preface signature on page 6.

[5] Hemming. 1937. Hubner. 1:146-324.

[6] Hemming. 1931. Proc. Ent. Soc. London. Ser. A. 6: 42-45. Gives actual dates of publication for the parts of Edwards's Butt. N. Amer., (Ser. I).

[7] Tome 10 title page signature date qualified by the meeting date of 25 Feb. (p. 275) and the evidence indicating that the tome to page 489 was published before the meeting of 22 Dec. (p. lxxxii in Bulletin).

[8] Proc. Ent. Soc. Phila. 1864. 3: p. 695. Notes that No. 4 of Vol. 2 of Proc. Ent. Soc. Phila. was received at 9 May 1864 meeting.

[9] Index Scient. Cont. Jour. & Proc. Acad. Nat. Sci. Phila., 1812-1912: pp. xii-xiii. Gives dates of receipt for various parts of the early volume of the Proceedings.

[10] Tome I title page signature date qualified by preface date (p. xii).

[11] Trans. Ent. Soc. London 1869: p. xix (in Proc.). Notes receipt of Tomes 1-12 of the Ann. Soc. Ent. Belg. at 1 Nov. meeting. Tome 12 title page signature date: 1868-1869. I assume the date is fixed on the publication of Tome 12. I have no data for the separate except that its title page signature date is 1869.

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THE DISTRIBUTION OF THE SPECIES OF THE GENUS PIERIS IN NORTH AMERICA[1]

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THE NORTH AMERICAN SPECIES of the Genus *Pieris* are distributed from the Arctic Ocean to Guatemala. However, none of the species of the genus (sensu stricto) exist in habitats which would be considered as tundra or arctic-alpine on the one hand, or as wholly tropical on the other. To this extent, the genus compares somewhat with Colias; the latter, however, contains two species that do exist in the tundra habitat.

The concept of a species which has been applied here is the same as that which has been applied previously to the species of the genus Colias in drawing the distribution maps for that genus (Hovanitz, 1950). This concept is based upon the consideration that the most important factor in stability of a species is the genetical population — or the interbreeding unit. Since, however, genes and their combinations cannot be seen, nor analyzed except by means of their effects on the appearance and physiology of the individuals carrying them, they must be studied through a comparative study of their morphological, anatomical or physiological characteristics. Thus, a name applied to one population may be applied to another population, or to many populations, if their characteristics indicate that a similarity exists between the hereditary makeup of such different populations. Such a name may cover quite a diversity of differences in the same population, or even a diversity of different populations if they are genetically separated one from the other by geographical or ecological means. The extent of gene interchange as well as the evaluation of the isolation mechanism determines whether or not one population should be considered as the

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[3] The base maps used in this paper are from Goodes Series of Base Maps by the University of Chicago Press, used by permission.

"same species" as another, or a "subspecies" or "geographical race" of it, or should not be considered significantly different. These criteria will be more exhaustively dealt with in a later paper. For practicability, different criteria must be used at different times and in varying circumstances. The ultimate taxonomic designation is a product of weighing a great number of problems, some factors being known and others unknown, with the hope that the best result may be achieved. Another general rule underlies these studies; namely, that stability and uniformity are desirable in nomenclature, and that past taxonomic decisions should not be upset by hasty, poorly-thought-out changes. But the past should not remain immutable when the decision to change is demanded by sound study or experimental evidence. Implicit in all taxonomic studies is perhaps an amount of individual opinion, perhaps greater than in many more experimental sciences, but even this can be greatly reduced by conscious effort to separate fact from opinion. It is the belief of the author that all facts upon which decisions are based should be stated; these are the "data" which can be refuted. New decisions should be made then only upon presentations of new data. Taxonomy by "hunches" is to be avoided; decisions should be accompanied by evidences for and against any decisions made.

THE SPECIES OF PIERIS

There are five clearly defined species of *Pieris* in North America. Of these, only four were native prior to 1800. Besides these, there are two other groups of related populations which might be considered "species," or sibling species, and a large number of geographical variations within each of these species, many of which are distinctive enough to be called "geographical races" or subspecies. Division of the species into geographical races is not to be considered in this paper, with the exception of the two sibling species just mentioned.

Pieris rapae. This is one of two common European species of *Pieris,* the first immigrants of which appear to have been introduced into North America prior to 1860. Since that time, the species has spread over the whole of the Unitd States and much of Canada and Mexico, wherever the natural vegetation has been at least partially replaced by European weeds, such as black mustard, or by cruciferous agriculture. This species has a wide range of habitat which is suitable for its existence, since it is found from the warm parts of the Gulf of Mexico nearly to the tundra of Canada, and from the Imperial Valley below sea level to high mountain meadows in the Sierra Nevada or the Rocky Mountains. The food plants utilized are a variety of cruciferous plants, among which are all varieties of cruciferous garden vegetables (cabbage, kohlrabi, kale, etc.) as well as many weedy plants such as mustards, radish, sisymbrium, etc. Some garden flowers such as nasturtium are also utilized. In view of the "weedy" nature of this species, no map is given to illustrate its distribution.

Pieris napi (Fig. 1). This species is found throughout northern Europe and Asia where there is in effect a continuity with the forms of North America across the Bering straits and the islands of the Bering Sea. This is the most northern of all of the species of *Pieris,* its range extending to the edge of the tundra or slightly beyond along its northern limits. The northern distributional limit from the Mackenzie River and east follows closely the northern limits of the tree line. The species exists along both the Pacific and Atlantic coast lines, but extends farther southward on the Pacific Coast than on the Atlantic Coast. The southern-most population on the immediate Pacific Coast line is at Lopez Canyon, San Luis Obispo County, California at about 35° north latitude. On the east coast at sea level, the most southern locality known is along the coast of New York and Connecticut opposite Long Island at 42° north latitude. However, at increasing elevations in the Appalachian Mountains southward, *P. napi* (or *P. virginiensis*) may be found as far south as the Great Smoky Mountains of Tennessee and North Carolina at about 35° north latitude. The southernmost extension of range of *Pieris napi* in the strict sense is in the vicinity of Connecticut and the Appalachians of Vermont, New Hampshire and Massachusetts. Westward, the range passes through the lower part of Ontario, Michigan, Wiconsin, Minnesota, Manitoba, Saskatchewan and Alberta, always staying north of the prairies. A fuller discussion of the relation of *Pieris napi* to *P. virginiensis* is to be had in a separate paper to follow this one.

Where the range of *P. napi* reaches the Rocky Mountains in central Alberta, the species extends clear to the Pacific coast and southward in the Rocky Mountains at increasing elevations to southern New Mexico and Arizona. The species appears to be absent in the drier ranges of the Great Basin and northward in the sagebrush country into south-central British Columbia. Elsewhere, it is widely distributed in the habitats that it prefers, these being damp wooded areas with partial shade, and temperatures not over seventy degrees Fahrenheit..

Of interest in the search for extensions of range are the following specific locations on the southern parts of the range of *Pieris napi:*

California: *Coast* — San Luis Obispo County, Lopez Canyon, December through May.
California: Western side Sierra Nevada, Merced County, Yosemite Valley, 3-4000 feet, April-May.
California: Eastern side Sierra Nevada, Placer County, 6-7000 feet, June.
Nevada: No records at present.
Arizona: Apache County, White Mountains, August; Gila County, "Globe" July.
New Mexico: Otero County, James Canyon, Cloudcroft, August, Catron 6, Mogollon, May, August.
Georgia: No records.

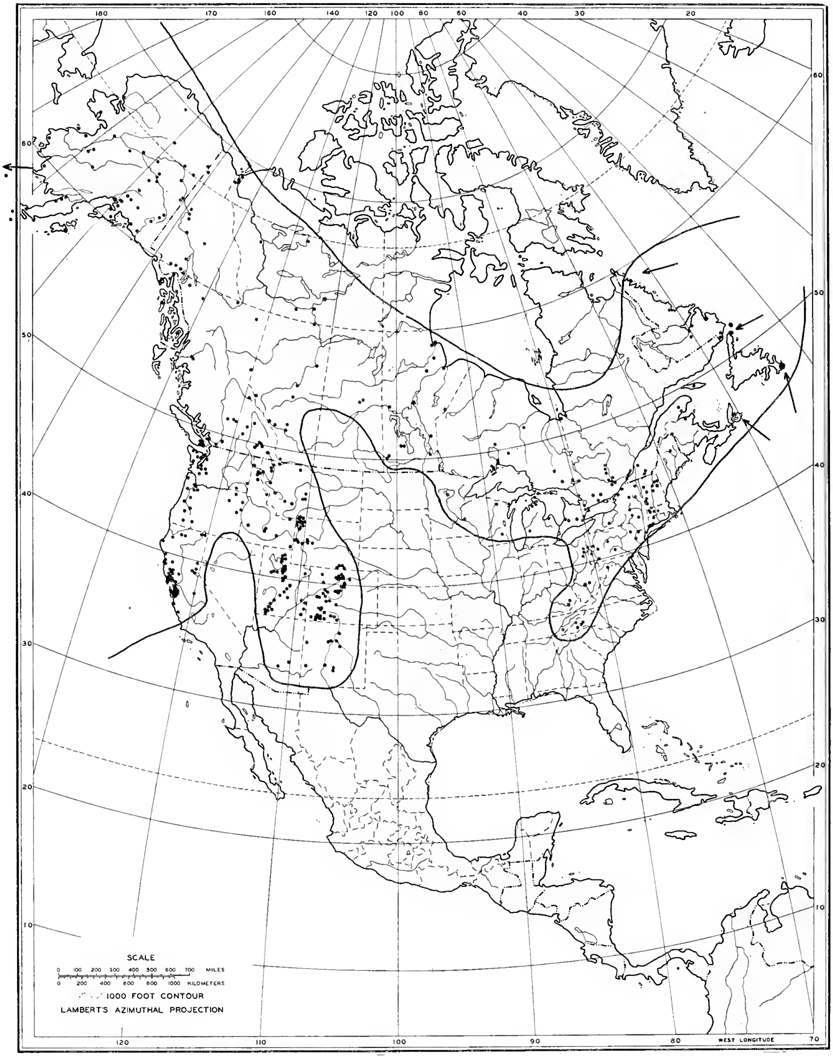

FIGURE 1. Map showing the North American distribution of *Pieris (Pieris) napi.*

South Carolina: No records.

North Carolina: Black Mountains, April.

Tennessee: Great Smoky National Park, Cherokee, April.

Some other points of interest in the distribution of this species are the following records:

Pribilof Islands, Alaska, July. Mouth of the Mackenzie River, North West Territories.

Great Bear Lake, N.W.T. Churchill, Manitoba (Hudson Bay). James Bay, Hudson Bay, Quebec. Ramak, Labrador

Pieris napi is the only known butterfly to inhabit the Aleutian Islands or the islands of the Bering Sea. This ability is probably correlated with its adaptation to existence at temperatures below 70°F, with low solar radiation and high humidity.

Pieris (Pontia) protodice (Fig. 2). This is the most widely distributed species of *Pieris* in North America. Some prefer to place this species, together with the following two species, in a separate genus *Pontia* for which there is much to recommend. To do so, however, would reduce the size of the genus *Pieris* beyond what would seem reasonable, and, therefore, to obviate this difficulty, and yet show phylogenetic relationship, *Pontia* would best be retained as a subgenus name.

Pieris protodice is best adapted to habitats with more sunshine than is required by *P. napi.* It also is enabled to survive in habitats much too warm for that species. However, cold does not seem to be a limiting factor as long as there is a short warm season and plenty of sunlight. These conditions, to some degree, pertain to the area occupied by the species. It apparently does not flourish in areas of continual hot temperatures as indicated by its absence in all fully tropical climates.

Pieris protodice differs from *P. napi* in its absence all along the immediate Pacific Coast from northern California through Alaska in keeping with its dislike for cool, cloudy areas. It is absent in the northern half of Alaska but eastward its distributional limits parallel those of the timbered area, as with *P. napi.* East of the Hudson Bay, however, *P. protodice* is absent north and east of Ottawa and New York State. The reasons for this event are baffling unless the present distribution of the species has been greatly disturbed by man in the eastern regions of North America as has been found true for *Colias eurytheme. Pieris protodice* prefers sunny, open fields as compared with *P. napi* which prefers partially shaded, damp areas. The cutting of the eastern deciduous forest to produce open fields for agriculture has aided both *Colias eurytheme* and *Pieris protodice* in extending their ranges and population density. It has probably also reduced the range and population density of *Pieris napi* since the habitats are conflicting. This probably accounts for the known diminution of *Pieris napi* in the region of Cambridge, Massachusetts where they were once exceedingy abundant, and now rare.

FIGURE 2. Map showing the North American distribution of *Pieris (Pontia) protodice.*

Pieris protodice is found throughout the southeast from Long Island to the southern part of Florida and around the Gulf of Mexico to Guatemala. It is very abundant in the highlands of Mexico but may be found nearly everywhere except in woods or forested areas. It is found from the southern tip of Lower California northwards, having a great preference for open areas. It is possible that its great abundance in southern California coastal areas is a recent event, correlated with the change of the natural perennial grasslands to annual European grasses, mixed with *Brassica nigra,* the black mustard. It reaches its greatest abundance, however, in the desert regions where conditions of cool nights, hot days, full sunlight and periodic extensive abundance of food plants (*Cleome, Brassica, Sisymbrium,* etc.) allow the species to swarm in clouds. In such areas, the population abundance is usually limited by the periodicity of available water.

In the mountain areas, the species is spread from the lowest valleys to the top of the highest mountains. The author has collected *Pieris protodice* at the top of Mt. Whitney, 14,500 feet elevation, the highest point in the United States south of Alaska, and in the bottom of Death Valley and Imperial Valley below sea level.

The relationship of *Pieris occidentalis* to *Pieris protodice* is here left in doubt, but for the purposes of the map (Fig. 2), they are considered forms of one species. This point will be considered in more detail in a future paper. There is no doubt that at higher elevations and cooler temperatures, populations exist which have a blacker, fuller pattern on their wings than populations which exist at lower elevations at higher temperatures. The preponderance of the evidence suggests that these differences are not hereditarily controled, but that they are dependent entirely upon the environmental conditions. Within the species as a whole, as with *P. napi,* the darker individuals exist in the more northern latitudes at cooler temperatures than the lighter ones. However, this relationship must be reconciled with local factors. In Colorado, Brown (1957) has shown that *P. occidentalis* appears to form definite populations at high elevations whereas *P. protodice* forms populations at low elevations. F. Rindge, however, in a personal communications has found both in considerable number in the same valley in Utah. These points cannot be reconciled at the present time. *P. protodice* when exposed to low temperatures develops a color pattern (more extensive melanin) which is similar to, or identical with, *P. occidentalis.* They could very likely be genetically the same and if they are genetically the same, they are not deserving of a scientific or Latin name of significance nomenclatorially. This point has not been proved, however. In the case of geographical variations, such deviations are considered subspecific unless proved otherwise. In the case of altitudinal or seasonal differences, such as in *Pieris protodice* or *Colias eurytheme,* it is suggestd that Latin names not be applied except to geographically isolated populations and then in a subspecies sense only.

FIGURE 3. Map showing the North American distribution of *Pieris (Pontia) sisymbrii.*

Pieris (Pontia) sisymbrii. (Fig. 3) The *Pontia* subgenus of the Pierids all prefer dry habitats with considerable sunshine exposure, unlike *Pieris napi* or even *Pieris rapae* which prefer or can survive in shade and high humidity. *Pieris sisymbrii* is one of these. Its habitats are always open, highly exposed, usually rocky places. It prefers cool temperatures but with high solar radiation. It lives in the spring time in the desert, as in the Mohave Desert where it flies at temperatures of highs not over 70° F, even though the temperatures later in the year will be over 100° F. It also lives in the mountains at elevations of over 10,000 feet in June and July. In the coastal area of California, its habitats are usually dry, rocky areas (serpentine, etc.) which are more dry and more exposed to solar radiation than its general position on the map would indicate.

Geographically (Fig. 3), the species exists throughout the mountainous areas of the west from the Yukon Territory to Mexico. It probably also exists in northern Mexico but there are no records. Outside of this area, there are a series of locations in the Northwest Territories from the Great Bear Lake southward past the Great Slave Lake to Lake Athabasca. Between these locations and the Rocky Mountains there are no locations known. This is probably due to lack of many suitable habitats. Collectors would do well to increase the known distribution of this species. It has a wide distribution but is characterized by the extreme isolated nature of them. Its habitats are narrowly restricted even on the desert and the adults have a short adult life, flying for only a few weeks during the year at any one place. The species aestivates and hibernates as a pupa which is very hard and impervious to water.

There is relatively little variation between the individuals in a population in this species, and also relatively little variation geographically between populations. Some variations have been described, however, and will be considered in a subsequent paper.

Pieris protodice is a species which is generally distributed and has many generations per year; it is therefore genetically and physiologically pliable as is necessary to meet these changed conditions. On the other hand, *Pieris sisymbrii* is greatly restricted to isolated habitats, and the adults fly only a short time; thus, the species genetically may be said to have developed a narrower range of tolerance through a narrower range of selective factors of the environment.

Pieris (Pontia) beckerii. (Fig. 4). Of all the species of North American *Pieris, P. beckerii* has the most restricted geographical range, extending from south-central British Columbia east of the Cascade Mountains southwards east of the Sierra Nevada into the deserts of southern California (Fig. 4). Its eastward limits coincide with the Rocky Mountain system in Montana, Wyoming and Colorado. The species does not extend into New Mexico so far as is known, unlike *Pieris sisymbrii.* The most southern-known limits are southwestern

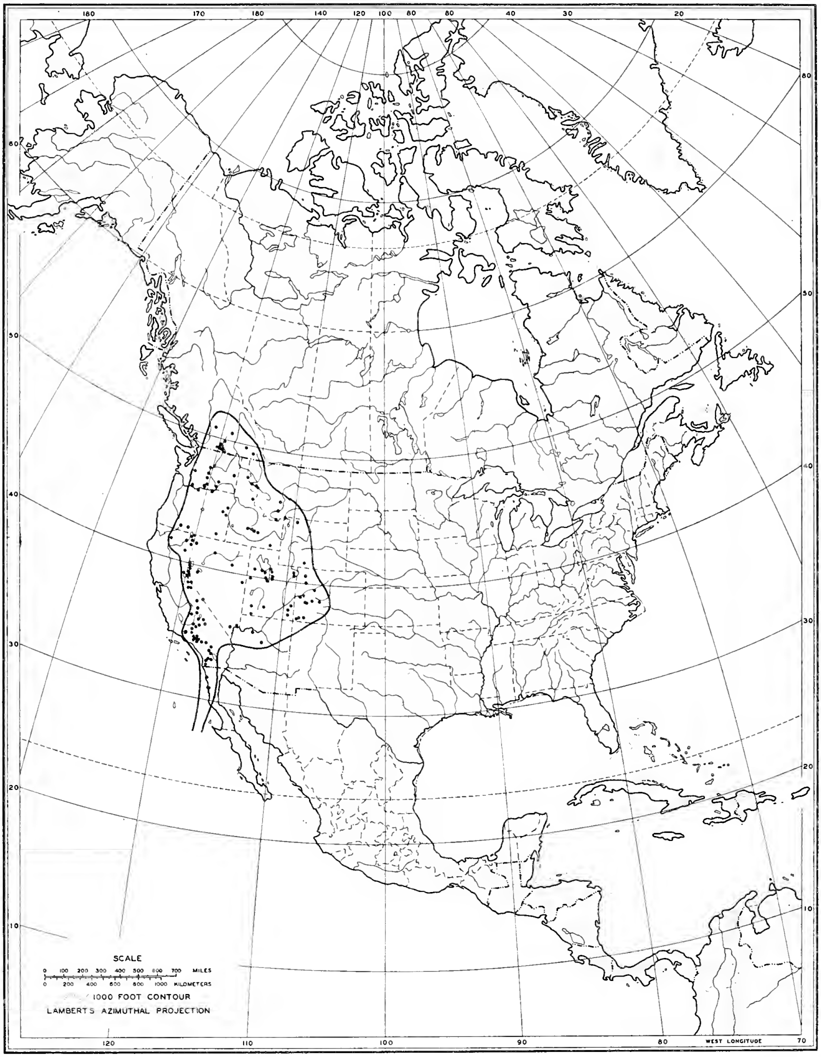

FIGURE 4. Map showing the North American distribution of *Pieris* (*Pontia*) *beckerii.*

Colorado, central Arizona, and southern Nevada, except for California where the species may be found in the foothills of the mountain ranges especially on the desert side. However, the species has been found on the coastal side in the area of the Santa Susana Valley (Moorpark), San Fernando Valley, Santa Clara River Valley and on the immediate coast from San Diego and southwards.

Pieris beckerii exists at elevations of sea level at the coast and some parts of the desert to 9000 feet in the mountain valleys. It has always been found in areas that are relatively dry or desert-like with high solar radiation. Its distributional range coincides almost perfectly with that of the semi-arid brushlands extending from the rain-shadow valleys of central British Columbia, throughout the Great Basin and inter-mountain valleys of the Rocky Mountains. The factors that limit its distribution in southern Arizona, New Mexico and northern Mexico are unknown. Perhaps there is a lack of proper food plant. The distribution of the species in southern California south of the Great Basin is correlated closely with the distribution of *Isomeris arborea,* its preferred food plant. It seems likely, however, that some other plant may also satisfy for this purpose. There is little doubt that intensive searching for additional populations of *Pieris beckerii* in the range of *Isomeris* will extend the distribution some considerable distance, especially in the south Coast Ranges of California, the foothills of the Sierra Nevada and southward in Baja California.

Unlike *Pieris sisymbrii* which has a single short generation per year, in southern California, *Pieris beckerii* has a succession of generations with the bulk of the adult flight being correlated with the time of of the winter rains. However, in the mountainous regions north of the Mohave Desert, the species has only one known generation, in the early summer.

There is little geographical, local population, or seasonal variation in *Pieris beckerii.* However, some races have been described and will be considered in a later paper.

LITERATURE CITED

BROWN, F. M., D. EFF AND B. ROTGER. 1957. Colorado butterflies. *Proc. Denver Mus. Nat. Hist.* Nos. 3-7:1-368.

HOVANITZ, WILLIAM. 1950. The Biology of Colias butterflies. I. The distribution of the North American species. *Wasmann J. Biol.* 8:49-75.

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DID THE CATERPILLAR EXTERMINATE THE GIANT REPTILE?

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THE ABRUPT DISAPPEARANCE of the giant reptile during the Cretaceous period brought to an end a very successful plant-animal system. For 120 million years the reptile population had roamed over large areas of the earth, subsisting in the lush vegetation covering such areas. From the standpoint of the reptile's subsistence, plant life was unlimited. It was an apparently inexhaustible resource.

The possibility that the great reptiles disappeared as a result of malnutrition and starvation has been considered and discarded as quite untenable. That highly evolved plant-feeding animals do not normally become limited in numbers by starvation is axiomatic. Nicholson (1954) pointed out that the major influence which prevents phytophagous animals from reducing the earth's vegetation to extreme sparseness is their attack by natural enemies.

Exhaustibility of plant life, an inherent characteristic of many plant and animal relations, is rarely realized, being usually precluded through the regulation of the animal population by its natural enemies (Flanders 1959). Thus, the Cretaceous populations of the vegetarian reptiles, by serving as prey for populations of highly efficient predatory reptiles, were kept at levels well within the limits set by the amount of plant life. At the same time these predators served also to suppress the evolution of competitive types of animals of similar size such as the mammal.

The geological record of the Cretaceous period, however, reveals a series of events which may have culminated in the temporary destruction of vast amounts of plant life, a period in which the vegetarian reptiles may have been so devitalized that they either failed to reproduce or fell easy prey to their predatory relatives.

The critical events which could have led up to the disappearance of the giant reptile were: (1) the replacement of the ancient fern-like plants by phanerogamic plants; and (2) the emergence of the Lepidoptera, an insect order which with few exceptions feeds only on such plants (Imms, 1930).

The background against which these events should be visualized is the world-wide dominance of insects both in species and in population densities, a dominance which existed throughout the Age of Reptiles and the Age of Mammals. The pre-Cretaceous insect fauna appears to have been quite similar in kind and in numbers to the post-Cretaceous insect fauna except for the lack of species which fed on flowering plants (Carpenter 1952). A number of such species were subsequently derived from the pre-Cretaceous insect orders of Coleoptera, Diptera, Hemiptera, Hymenoptera and Orthoptera, species whose immediate progenitors had presumably already acquired their natural enemies.

According to Imms (1931), it is practically certain that the Lepidoptera is pre-Tertiary in origin, highly organized individuals being represented in Eocene rocks. The paucity of insects in Cretaceous rocks is attributed to the absence in that period of suitable fresh-water deposits in which specimens could have accumulated and become fossilized.

Plant-feeding insects like other plant-feeding animals acquire natural enemies which serve to conserve the plant life upon which they subsist. The fact that the conservation of plant life is a function of the natural enemies of Lepidoptera has been demonstrated during the past sixty years by the importation and establishment in North America of the natural enemies of the caterpillar for otherwise the reduction in brown-tail moth, *Nygmia phaeorrhoea* (Donovan), the satin moth, *Stilpnotia salicis* (Linnaeus), and the larch caseberer, *Coleophora laricella* (Hubner) (Clausen 1956). During the past three years the writer, by using the grain moth *Anagasta* and its natural parasite, *Exidechthis,* has demonstrated in the laboratory the role of a natural enemy in the conservation of plant material. In a constant environment parasitization continuously conserved the plant material despite the presence of a persistent feeding population of *Anagasta.*

In nature, therefore, a community of plant-feeding animals consisting, say, of a pentatomid bug, a grasshopper, a moth caterpillar, a vole, a rabbit, and an ungulate depending on the same resource, grassland vegetation, can remain stabilized for a long period of years (Elton 1946). Such stabilization, however, consists in the total amount of plant life conserved, not in the relative abundance of the plant species involved, an abundance determined by the phytophagous animals through their effect on the competitive capacities of the plant species (Wilson 1949).

Devastations of plant life by caterpillars can occur today whenever the regulating action of their natural enemies is disrupted by environmental factors. Graham (1939) reported that during a ten-year period ending in 1920 an eruption of the spruce budworm, *Choristoneura fumiferana* (Clemens), was characterized by flights of moths so numerous that in the tree tops they had the apparance of a snow storm. During this eruption the caterpillars destroyed a volume of wood sufficient to supply all of the pulp mills then operating for a period of forty years.

The capacity of a lepidopteran in the absence of its natural enemies to reduce great areas of lush vegetation to extreme sparseness and to maintain it so thereafter was demonstrated in Australia when the caterpillars of *Cactoblastis cactorum* (Berg) imported from Argentina in 1925 destroyed within six years approximately 50 million acres of the prickly pear, *Opuntia* spp. Dodd (1929) in reporting on this devastation stated that great care had been taken not to set free any of the natural enemies of the catrpillar for otherwise the reduction in prickly pear would have been of minor proportions.

It is evident that the plant-consuming capacity of a caterpillar population could equal that of a giant reptile population and that this capacity because of the caterpillar's very short life cycle could be attained at a much greater rate. Supplementing this capacity was a power of survival much greater than that of the giant reptile, the minimum food requirements of the individual caterpillar being infinitesimal relative to that of the individual reptile.

Nevertheless, there is no reason to believe that the caterpillar and the giant reptile could not have subsisted together on the same vegetation if the caterpillar, immediately upon its Cretaceous emergence, had been subject to a regulation by natural enemies as effective as was that of the vegetarian reptile by its predatory relatives.

The theory that the caterpillar exterminated the giant reptile rests on the assumption that between the emergence of the new insect order and its accessions of regulative natural enemies there occurred a brief period in which the caterpillar population regulated the world's supply of plant food, a condition conducive to great variations in abundance of plant life and of caterpillar life, a condition characterized by "feast and famine" in which the caterpillar was able to survive but not the great reptile.

The inherent weakness of the reptile was an extraordinary need for an abundance of plant material. Only a few years of plant scarcity could have exterminated it. Hordes of caterpillars, in rapid consumption of fig and breadfruit, laurel and willow, oak and magnolia, could have so restricted the spatial distribution of the giant reptile that either its diet was inadequate or it was unable to avoid its natural enemies.

The small size of today's descendent reptiles, the vegetarian turtle, the predatory crocodile, the snake, and the lizard, is evidence of the giant reptile's elimination by starvation and predation.

The abrupt end of the Age of Reptiles during the Cretaceous period is ascribed to a newly emerged order of insects, the Lepidoptera, on the supposition that for a brief period it regulated the world's supply of plant life at starvation levels for the dependent reptiles. Thus, the giant reptiles which had survived during eons characterized by great changes in climate, continental uplifts, and different diets may have been exterminated by the lowly caterpillar.

LITERATURE CITED

CARPENTER, F. M. 1952. Fossil insects. *1952 U.S.D.A. Year Book.* pp. 14-19.

CLAUSEN, C. P. 1956. Biological control of insect pests in the continental United States. *U.S.D.A. Tech. Bull. No. 113,* 151 pp.

DODD, ALAN P. 1929. The progress of biological centrol of prickly pear in Australia. *Commonwealth Prickly-Pear Board, Brisbane Qld.* 44 pp.

ELTON, CHARLES. 1946. Competition and the structure of ecological communities. *Jour. Animal Ecol.* 15: 54-68.

FLANDERS, S. E. 1959. Biological control. *Jour. Econ. Ent.* 52: 784-5.

GRAHAM, S. A. 1939. Principles of forest entomology. McGraw-Hill, N.Y. 410 pp.

IMMS, A. D. 1930. A general textbook of entomology. E. P. Dutton & Co., Inc., N.Y. 703 pp.

IMMS, A. D. 1931. Recent advances in entomology. P. Blakiston's Son & Co., Inc., Philadelphia. 374 pp.

NICHOLSON, A. J. 1954. An outline of the dynamics of animal populations. *Australian Jour. Zool.* 2:9-65.

WILSON, F. 1949. The entomological control of weeds. *Int. U. Biol. Sci. Ser. B.* 5: 53-64.

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1140 W. Orange Grove Ave., Arcadia, California, U.S.A.

FURTHER EVIDENCE OF THE DISTRIBUTION OF SOME BOREAL LEPIDOPTERA IN THE SIERRA NEVADA[1]

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EXCEPT WHERE ROADS penetrate the high country, little or only scanty information is abailable concerning the animal life of the high Sierra of California. This condition is extant because these mountains are high, rugged and largely accessible only by trail. The fact also that collecting gear must be packed in and out encourages few people to undertake such studies.

Our knowledge of the Lepidoptera fauna of the Sierra stems largely from the work of Garth (1935) and Tilden (1959). Garth's study of the *Butterflies of Yosemite National Park* is notable since he not only provides a list of species taken within the confines of the park, but relates them to the life-zones in which they are normally found to fly. Tilden has refined the latter concept in his Tioga Pass studies by listing associations of smaller scope than life-zones.

While backpacking the John Muir Trail[2] during the summers of 1953, 1954 and 1955, the author made spot collections of Lepidoptera at various locations along the route (Figure 1). Such was a brief attempt to add information similar to that of Garth and Tilden to our knowledge of the day-flying Lepidoptera in high areas from Yosemite on the north to Mount Whitney on the south. All forms collected and altitudes at which they were taken are listed in Table 1. To alleviate any confusion, all nomenclature is after McDunnough (1938). Altitudes were determined from Starr (1953).

Since Garth (1935) and Tilden (1959) have shown that various species fly only within certain altitudinal ranges while others are unrestricted in their flight, there is little need to repeat similar fiindings here. However, the data collected does extend the known altitudinal range of several species. The following were taken at elevations higher than previously recorded and are associated with the life-zone of this extension.

---

[1] My thanks to Nelson Baker, Santa Barbara Museum of Natural History, for help with identification of the material and W. Hovanitz for aid in preparation of this paper.

[2] The John Muir Trail follows a 225 mile route along the Sierra crest from Yosemite Valley on the north to Mount Whitney on the south. Except for a short distance out of Yosemite Valley (elevation 4,000′), altitudes range from approximately 7,000′ to 14,500′.

Argynnis mormonia (Arctic-Alpine)
Euphydryas chalcedona (Transition, Canadian)
Lycaena helloides (Canadian, Hudsonian)
Plebeius aquilo podarce (Arctic-Alpine)
Plebeius saepiolus (Arctic-Alpine)
Plebeius icarioides (Hudsonian, Arctic-Alpine)
Plebeius acmon (Hudsonian)

Garth does not list *Lycaena helloides* above the Transition zone nor *Plebeius saepiolus* above the Hudsonian. Even though Tilden does not actually say, he intimates that both species transcend all zones. In the event that any confusion may arise, both species are included in the above list.

It is of interest that those forms listed in this paper, which also are found in Colorado, have already been collected in that state from life-zones here described as extensions (Brown *et al,* 1957).

LITERATURE CITED

BROWN, F. M., D. Eff and B. Rotger. 1957. Colorado Butterflies. *Proc. Denver Mus. Nat. Hist.,* Nos. 3-7:1-368.

GARTH, JOHN S. 1935. Butterflies of Yosemite National Park. *Bull. So. Cal. Acad. Sci.,* 34(1):1-39.

McDUNNOUGH, J. 1938. Check List of the Lepidoptera of Canada and the United States of America: Part I, Macrolepidoptera. *Mem. So. Cal. Acad. Sci.,* 1:1-275.

STARR, JR., WALTER A. 1953. Guide to the John Muir Trail and the High Sierra Region. *Sierra Club, San Francisco,* 130 pp.

TILDEN, J. W. 1959. The Butterfly Associations of Tioga Pass. *Wasmann J. Biol.,* 17(2):249-271.

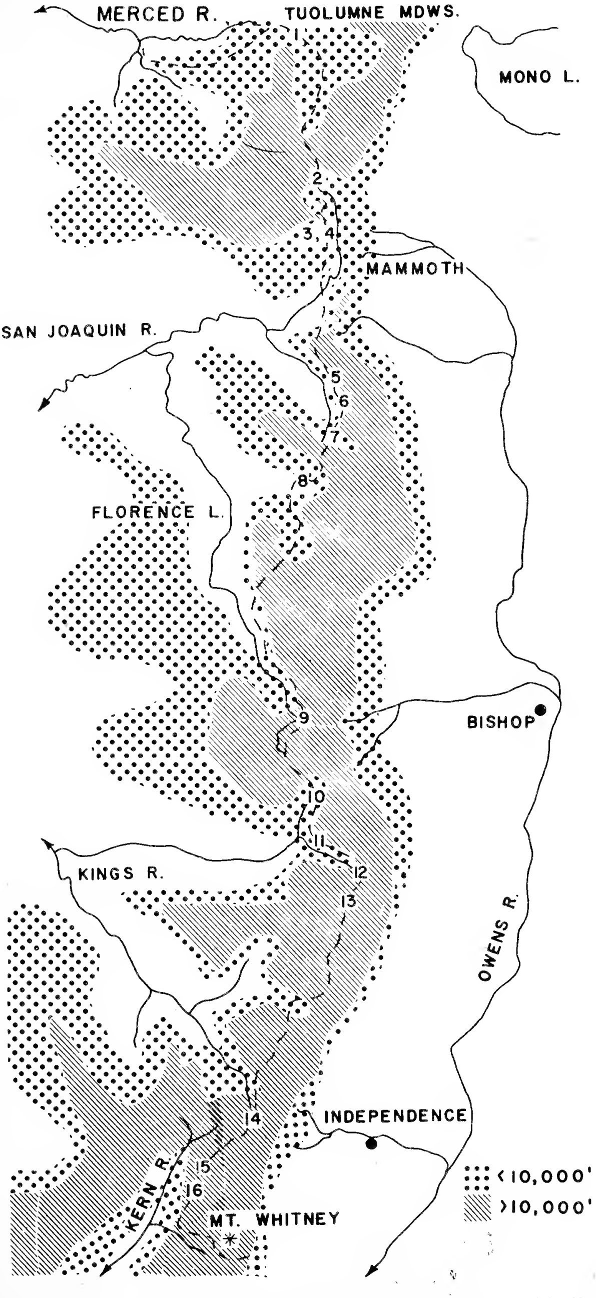

Figure 1. Collection Sites Along the John Muir Trail (Site number refers to Table 1)

Table 1.
John Muir Trail Collection Sites, Listed by Elevation, and the Species and Number Taken

	Canadian		Hudsonian									Arctic Alpine				
	Quail Meadows 7,700' : 7-8-54	Palisade Creek 8,125' : 7-31-55	Tuolumne Mdws. 8,700' : 6-29-54	Shadow Creek 8,750' : 7-2-54	Shadow Creek 9,000' : 7-1-54	Little Pete Mdw. 9,100' : 7-12-55	1000-Island L. 9,850' : 6-30-54	Purple Lake 10,000' : 7-6-54	Duck Lake Trail 10,100' : 7-5-54	Cascade Valley 10,400' : 7-5-54	Mdl. Palisade Low. L. 10,650' : 7-28-53	Evolution Lake 10,990' : 7-26-53	Upper Bubbs Cr. 11,000' : 7-29-54	Tyndall Creek 11,000' : 7-29-54	Bighorn Plateau 11,500' : 7-31-54	Mather Plateau 11,500' : 7-30-53
Map Location Number	8	11	1	4	3	10	2	6	5	7	12	9	14	15	16	13
Papilio zelicaon Luc.							1									
Papilio rutulus Luc.	1															
Parnassius clodius Men.	1				1				1							2
Colias eurytheme Bdv.	1		2												1	
Colias behrii Edw.													1	6		3
Pieris sisymbrii Bdv.					1		1									
Pieris occidentalis Reak.														1	4	
Argynnis montivaga Behr					1											
Argynnis mormonia Bdv.														1		
Brenthis epithore Edw.	1		1													
Euphydryas chalcedona Dbldy. & Hew.		1														
Euphydryas sierra Wgt.		1														
Euphydryas nubigena Behr								1	1							
Melitaea palla Bdv.	1	1														
Phyciodes montana Behr	8	3			2				1							
Polygonia zephyrus Edw.								2								

Nymphalis antiopa L.		1	1													
Junonia coenia Hbn.	1															
Basilarchia lorquini Bdv.	1	1														
Callophrys dumetorum perplexa B. & B.								2								
Lycaena editha Mead														3		
Lycaena helloides Bdv.				1		1										
Lycaena cupreus Edw.			1						1			1			4	
Leptotes marina Reak.			1													
Plebeius aquilo podarce F. & F.	2		1			3								3	3	
Plebeius saepiolus Bdv.	2		2			1	1		1					4		
Plebeius icarioides Bdv.	3	6	1					1						1		
Plebeius acmon West & Hew.			1	1	1			1								
Plebeius shasta comstocki Fox													3	3	2	
Philotes battoides Behr								5						1	1	
Lycaenopsis pseudargiolus echo Edw.					1											
Thoybes nevada Scud.			1				1	1								
Polites sabuleti tecumseh Grin.		1												1	2	
Celerio lineata Fabr.										1						
Pseudohazis hera Harr.											1					
Anarta cordigera Thun.														3		

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ARGYNNIS AND SPEYERIA

BY WILLIAM HOVANITZ
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The use of names for nomenclatorial purposes involves judgment on two levels. The first level involves nomenclatorial laws, and the second is the judgement on the part of the taxonomist as to the most reasonable and useful application of a name for a biological category.

When a name is being considered for use on the generic level, the first point is its nomenclatorial availability. Here, it is important that the name not be a homonym, and that it have priority according to the established laws of nomenclature. A species is designated as the *type species* of that genus. For example, the species *paphia* L. has been designated as the type species of the genus *Argynnis.*

Once the type species has been established for a genus, and there are no doubts of the nomenclatorial status of either, the specific name or the generic name, no one who wishes to remain within established criteria for nomenclatorial uniformity and fairness has any right to change this name. The generic name is strictly applied, however, only to the one species. It is the prerogative of any individual to use the same generic name for other species if he deems that the species concerned ought to be considered congeneric. Strictly speaking, it is possible for each species in existence to be the type species for a different generic name. If each of these names were used, each species would be in a different genus and the beneficial effects of binomial nomenclature would be rendered worthless.

The purpose of a binomial nomenclature is to indicate relationships by grouping related species into the same genus. How this should be done is the prerogative of the individual taxonomist. It is assumed that such a person will use the method that is best suited to his purposes in showing relationships.

The genus *Argynnis* in the broad sense is composed of many species, some of which can be grouped into categories having biological similarities, but which are smaller in content than the genus when considered with a broad view. Generic names have been used for some of these smaller categories with various species designated as types. It is perfectly satisfactory from a nomenclatorial as well as a biological standpoint to do this. This is the situation with regard to the use of *Speyeria.* The type species of the name as a genus is *idalia.*

For those persons who wish to consider *idalia* as not congeneric with *paphia,* or with any other older name, *Speyeria* is a valid generic name. Or, it can be used in a subgeneric sense, in which case *Argynnis* would again be used as the generic name.

This author believes that the broad use of the genus *Argynnis* is preferable to the practice of restricting the name to the *paphia* group of species, and further believes that the genus can be divided into some more or less satisfactory subgenera of which *Speyeria* is one. Our American species then would be designated *Argynnis* (*Speyeria*) *idalia* to show its relationship. The other American Argynnids then would also continue to use the name *Argynnis* rather than *Speyeria.*

It is not the purpose of the editor of this journal to insist on any particular terminology for to do so would impinge on the freedom of the scientific worker, who alone has the right to make his choice. This editor can only insist on sound data to back the decisions of authors in their use of terminology, as in drawing conclusions from their work.

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THE JOURNAL OF RESEARCH ON THE LEPIDOPTERA

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Details in Ecology 22: 259-284, 1941.

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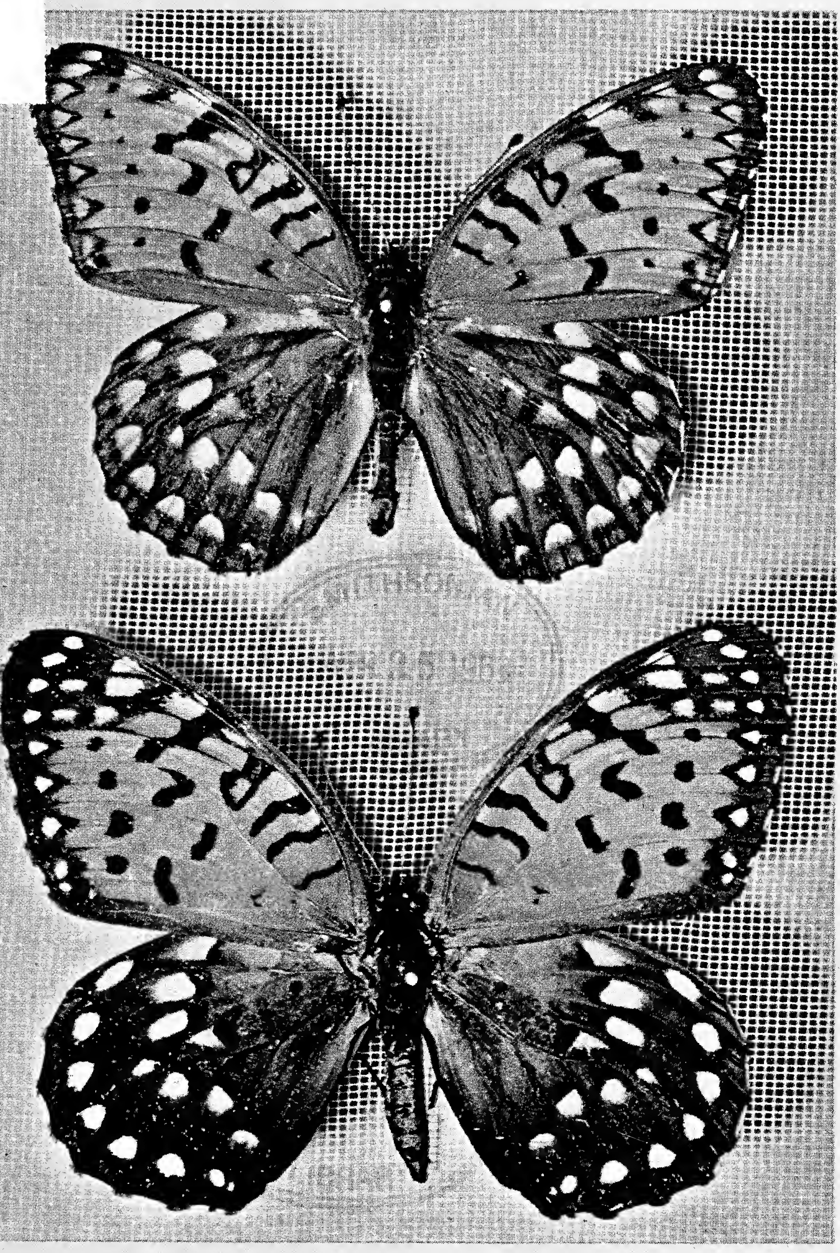
See special notice on page 162 and on bottom of inside front cover.



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COMPOSITION AND RELATIVE ABUNDANCE IN A TEMPERATE ZONE BUTTERFLY FAUNA

THOMAS C. EMMEL AND JOHN F. EMMEL

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THE DONNER PASS AREA, lying on the crest of the Sierra Nevada range in Placer County, California, provides a rich variety of habitats lying between 6900 and 8300 feet elevation. During the summers of 1956 and 1960, the authors made an intensive study of this region and we have reported elsewhere (Emmel & Emmel, 1962a, 1962b) on the ecology and factors affecting distribution of the 74 species composing the butterfly fauna. We wish to report here the interesting data obtained on the faunal composition and relative abundance of species within the seven major Rhopalocera groups recorded in the Donner Pass area, and to evaluate the possible factors influencing this distribution of species.

INTRODUCTION

Hovanitz (1958) has recorded the occurrence of Rhopalocera families and genera at each five degrees of latitude and 1000 meters of elevation above sea level for the entire New World. However, this study did not include the *numbers* of species or genera in each family that occurred in each of these areas. Tilden (1959) divided the butterflies of the Tioga Pass area under five plant associations; Emmel & Emmel (table 1, 1962a) partitioned the Donner Pass fauna under four plant associations. But these authors did not compare the faunas of each association or attempt to ascribe reasons for the greater number of species of a particular family in one association than another. The purpose of this paper is to report an examination of the composition and habitat associations of the Donner Pass fauna and from this examination to derive some understanding of the factors affecting the distribution and success of species in a butterfly family within a given set of environments.

DESCRIPTION OF STUDY AREA & METHODS

In a previous paper (Emmel & Emmel, 1962a), four general vegetational associations representing the union of floras from three life zones (Transition, Canadian, and Hudsonian) were delineated, and may be briefly reviewed.

1. The *Wet-Meadow* habitats (elevation 7000-7260 feet) support verdant expanses of grasses (*Poa* species) and sedges (*Carex*), *Lilium, Mimulus, Delphinium, Castilleia,* and other wildflowers, with scattered thickets of willows (*Salix*) along the stream banks. *Trifolium, Viola, Aster, Potentilla,* and other lepidopterous food plants (see table IV) are common.

2. *Dry-Meadow* areas (elevation 6800-7600 feet) are moist in the spring but are dry throughout July and August. Fireweed (*Epilobium angustifolium*), *Achillia, Calyptridium,* and *Penstemon,* as well as grasses, are typical plants. Food plants include *Ribes, Polygonum, Lupinus, Gnaphalium,* and others as listed in table IV.

3. Dense *Forest* (elevation 6800-7600 feet), mainly of Canadian-Zone trees, covers about one-half of the total Pass area. Red Fir (*Abies magnifica*), *Pinus contorta, P. monticola,* and Mountain Hemlock (*Tsuga mertensiana*) represent the majority of the forest trees. Only three known butterfly food-plant genera are found here: *Pinus, Arceuthobium,* and *Ceanothus.*

4. The *Montane* areas (elevation 7160-8383 feet) are generally open talus slopes, where the dry, almost soilless environment discourages the growth of most trees. Included in the flora of these mountain peaks are Rabbit Brush (*Chrysothamnus*), Sage Brush (*Artemisia*), Mule-Ears (*Wyethia mollis*), *Lupinus,* and *Sedum* species. *Eriogonum, Astragalus, Potentilla, Ceanothus,* and other food plants in Table IV, are widely distributed here.

Thus the diversity of vegetational associations in this temperate-zone locality provides habitats and food plants for a considerable number of butterfly species, and it is of interest to compare the relative success of species in different families in colonizing this favorable yet rather small area (six square miles) in the Sierra. In 1956 and 1960, the *number of species* (see Emmel & Emmel, 1962a, for a detailed listing) in each of the four vegetational zones was determined by intensive collecting throughout Donner Pass.

In the course of studying the influence of meteorological conditions on the flight activity of these species in 1960, daily counts of the numbers of flying butterflies were made within the 500 x 800 feet "Lodge Meadow" study area (see Emmel & Emmel, 1962b), which contained 46 species recorded for the Pass (see Table III). This area is composed of both wet and dry meadows. These counts were made by direct observation and represented numbers seen for each species between 10 and 12 a.m. daily. The total number of butterflies recorded in this latter study was 7,720. To determine "success" in *numbers of flying adults,* the daily counts for numbers of individuals for each of the species in a family were added together, and this figure was calculated as a percentage of the total for all families. Thus the contribution of each family toward the composition of the Donner

Pass butterfly fauna can be compared on a percentage basis, both as regards numbers of species and numbers of individuals.

OBSERVATIONS

Some 74 butterfly species were found in the Donner Pass area, and these species belonged to seven of the major families of Rhopalocera found in the western United States. The number of species in each of these groups varied from 1 for the Danaidae to 28 for the Lycaenidae, or in terms of percentage of the total Pass fauna, 1.4% to 37.8% of all the species. Table I shows the composition of the Rhopalocera groups recorded in the *total* Pass area.

Table II and Figure 1 show the composition of the butterfly fauna recorded in *each* of the four general habitats of the Donner Pass area; the figures in Table II represent the per cent of total species in each habitat that belong to each family, while the graphs in Figure 1 show actual number of species for each family in each habitat. It is immediately obvious that the *montane* and *dry-meadow* habitats have the largest faunas of the four areas, and that the Lycaenidae family is usually dominant as regards number of species.

As stated earlier, it was possible to obtain some data on the number of individuals of each species (46 in all) occurring in the Lodge Meadow study area. The composition and relative abundance of the six major Rhopalocera groups recorded there are given in Table III. For the most part, there is a good correlation between number of species and number of individuals for each family.

DISCUSSION AND CONCLUSIONS

The number of butterfly species found in this six-square-mile area of the Sierra Nevada is unusually high. Tilden (1959) records only 43 species as occurring in the Tioga Pass region, representing a study area of approximately the same size although of somewhat higher elevations (over 9941 feet above sea level). Garth (1935) records about 100 species for all of Yosemite National Park (area 1,179 square miles, elevations from 2000 to 13,090 feet), and the present authors and Lloyd M. Martin (personal communication) can note from their experience that the average restricted Sierran locality seems to support around 35 to 65 species. Thus the Donner Pass area is particularly interesting from the standpoint of invesigating the reasons for the occurrence and abundance of a species in a specific habitat, for as noted earlier (Emmel & Emmel, 1962a) this region is a meeting place for a variety of habitats and a high number of plant species, and these factors may be viewed as possible reasons for this variety of Rhopalocera.

The relative proportions in number of species among the Rhopalocera groups involved seems to follow the relative number as found throughout North America north of Mexico (determined from Ehrlich, 1961). The descending order of these groups in terms of number of

TABLE I. Composition of the seven major Rhopalocera groups recorded in the Donner Pass area.

Family	No. of Species	% of Total Species
Papilionidae	5	6.8
Pieridae	8	10.8
Danaidae	1	1.4
Satyridae	2	2.7
Nymphalidae	20	27.0
Lycaenidae	28	37.8
Hesperiidae	10	13.5
TOTALS	74*	100.0%

*In our earlier paper (Emmel & Emmel, 1962a), 74 species and 2 "forms", Anthocaris sara reakirti and Colias eurytheme amphidusa, were listed, making a total of 76 phenotypically-distinct entities.

species is (both in the continent and local Pass faunas): Lycaenidae, Nymphalidae, Hesperiidae, Pieridae, Papilionidae (follows Satyridae in the continent fauna), Satyridae, Danaidae.

However, when the total Pass fauna is divided in terms of occurrence in each of four habitats, patterns of apparent preference for certain habitats emerge — both for all families combined and for individual groups (Table II and Figure 1). The highest total number of species (60) occur in the *montane* habitats, the next highest (55) in the *dry meadow* areas, the third highest (44) in the *wet meadows,* and the lowest number (26) in the forest areas. The descending sequence of environmental support of number of butterfly species is thus:

Montane > Dry Meadows > Wet Meadows > Forest.

This pattern, obtained by comparing numbers of Rhopalocera species, is probably explained by the observed fact that the *montane* areas contained a greater variety of "mico-habitats" than any other area. These micro-habitats included small stream areas, exposed mountain tops, open and brushly talus slopes, etc., ranging from 7100 to 8383 feet in elevation, the greatest range in altitudes for any of the four "macro-habitat" areas considered. Such variation in ecological conditions (especially from edaphic and climatic standpoints) permits a wide variety of potential food plants to flourish. Axelrod (1960) has commented on the marked diversity of habitats in montane areas and the possible influence of this condition on early angiosperm evolution through permitting rapid development and adaptive radiation. Such diversity also influences butterfly distribution, variation, and speciation (see Emmel & Emmel, 1962a; Le Gare & Hovanitz, 1951; Moeck, 1957), and provides potential areas for successful invasion by butterflies already occurring elsewhere.

The large number of total species in the *dry meadow* areas is believed to be due to the great variety of known food plants occurring there; the *wet meadows* supported correspondingly fewer food-plant species. The *forest* areas contained the least variety of micro-habitats and food plants; also, solar radiation, an important influence on butterfly flight habits (see Emmel & Emmel, 1962b), was obviously at a considerably lower level in this habitat than in the other three. Table IV shows the number of known food-plant genera in each habitat for each Rhopalocera group. These and the preceding data agree with the theory that a greater variety in each of these Sierran butterfly groups is more likely to occur where micro-habitats and food plants are most varied, as these conditions, together with a high level of solar radiation, provide support for a wider selection of species than in such areas as pine forests.

This theory can be applied equally to the question of why one group has more species than another group in a certain habitat. The Papilionidae are more successful in forest than in montane areas in terms of per cent of total species there, but they actually have the most species in the latter areas. So we must consider:

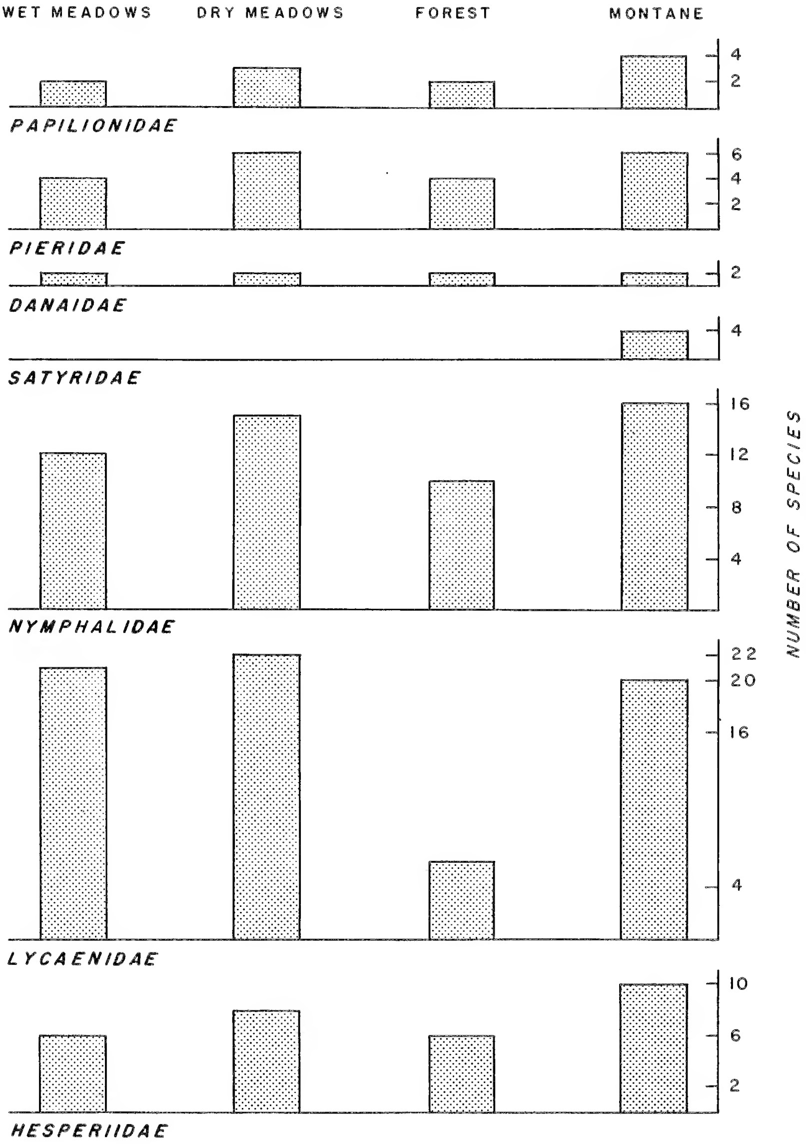

Fig. 1. Numerical composition of the butterfly fauna recorded in each of the four general habitats of the Donner Pass area.

1) That habitat in which the group has its highest *percentage* of the total species population:

Papilionidae	Forest (7.7%)
Pieridae	Forest (15.4%)
Danaidae	Forest (3.8%)
Satyridae	Montane (3.3%)
Nymphalidae	Forest (38.4%)
Lycaenidae	Wet Meadows (45.5%)
Hesperiidae	Forest (19.2%)

2) That habitat in which the group has the most species (direct number):

Papilionidae	Montane (4)
Pieridae	Dry Meadows, Montane (6)
Danaidae	(1 in each habitat)
Satyridae	Montane (2)
Nymphalidae	Montane (16)
Lycaenidae	Dry Meadows (22)
Hesperiidae	Montane (10)

The really significant consideration in evaluating a group's contribution to the fauna in a series of habitats would seem to be the *number* of species it has existing in each habitat. Of course, a further and perhaps more important consideration would be the number of individuals of the group in that habitat, but these data were not obtained. However, speaking from the standpoint of number of species the butterfly groups are uniformly most successful in the montane and dry meadow habitats.

As opposed to evaluating the most suitable habitat for most groups, one can also consider the success of individual groups in colonizing or existing in the various habitats. In the wet meadow, dry meadow, and montane habitats, the Lycaenidae are the most abundant group—with 20 to 22 species in such areas. The Nymphalidae take second place (10 to 16 species) except in the forest zone where they lead the other groups in number of species. The Hesperiidae are third—with 5 to 10 species in each zone—except for being second in the forest areas (leading the Lycaenidae). The Pieridae are uniformly fourth (4 to 6 species) while the Papilionidae have only 2 to 4 species in each zone. There is only one species in the Danaidae (all habitats, however) and two in the Satyridae (montane habitat only).

This apparent relative success of each group, in our opinion, is not due to a "better" adaptation (the result of natural selection) of a group's species in one or another habitat, as Ehrlich (1962) has emphasized. Instead, from our observations, success is likely due to the fact that food plants of species in the seven Rhopalocera families were more varied (as to number of kinds; Table IV), generally more numerous (as to number of individuals of each plant species), and

TABLE II. Composition of the butterfly fauna recorded in each of the four general habitats of the Donner Pass area.*

Family	Habitat Area**			
	Wet Meadows	Dry Meadows	Forest	Montane
Papilionidae	4.5	5.5	7.7	6.7
Pieridae	9.1	10.9	15.4	10.0
Danaidae	2.3	1.8	3.8	1.7
Satyridae	0.0	0.0	0.0	3.3
Nymphalidae	27.3	27.3	38.4	26.7
Lycaenidae	45.5	41.0	15.4	35.0
Hesperiidae	11.4	14.5	19.2	16.7
(1) TOTAL SPECIES	44	55	26	60
(2) PERCENTAGE OF TOTAL PASS FAUNA (74 species) REPRESENTED:	59.5%	74.3%	35.2%	81.1%

*The numbers in each vertical column (file) represent percent of total species in that one habitat (the total number of species is found at the bottom of each column). The actual numbers of species of that family in each habitat, from which the preceding percentages were calculated, are shown in graphic form in Figure 1.

**See Emmel & Emmel (1962a) for map and complete description of all habitats in the Pass area.

more generally distributed for the Lycaenids than for the Nymphalids, for Nymphalids than for Hesperids, etc. It is concluded in this paper that the composition of a butterfly fauna is affected by the requirements (or adaptation) of each butterfly species in that fauna for a certain food plant, in addition to a certain level of solar radiation and other factors as noted in Emmel & Emmel, 1962a. In turn, food plants obviously have grater chances of finding proper environmental conditions in a macro-habitat that contains a number of varied micro-habitats, each with particular edaphic and climatic conditions. The greater the number of host food plants, the greater the number of potentially successful butterfly species, and this theory is believed to account for the observed distribution of the 74 butterfly species (of seven major groups) among the four macro-habitats of the Donner Pass area.

TABLE III. Composition and relative abundance of the six major Rhopalocera groups recorded in the Lodge Meadow habitat.

Family	No. of Species	% of Total Species	% of Total Individuals Recorded
Papilionidae	2	4.4	4.7
Pieridae	4	8.7	9.8
Danaidae	1	2.2	0.3
Nymphalidae	15	32.6	44.9
Lycaenidae	16	34.8	23.2
Hesperiidae	8	17.4	16.7
TOTALS	46	100.1%	99.6%

SUMMARY

1. The Donner Pass area in Placer County, California, supports an extraordinary number (74) of Sierran Rhopalocera species, and its varied habitats and vegetational associations make the area particularly interesting for investigating the basis for the occurrence and abundance of a species and a family in a specific habitat.

2. The number of species in the seven major families of the Pass area are proportionately equivalent to the numbers of species in these

TABLE IV. Number of known food plant genera in each habitat for each Rhopalocera family*

Rhopalocera Family	Habitat Area			
	Wet Meadows	Dry Meadows	Forest	Montane
PAPILIONIDAE	*Salix*	--	*Ceanothus*	*Cymopterus* *Salix* (stream) *Ceanothus* *Prunus* *Sedum*
PIERIDAE	Cruciferae genera *Trifolium*	Cruciferae genera *Trifolium*	*Pinus*	Cruciferae genera
DANAIDAE	--	--	--	--
SATYRIDAE	(Grasses)	(Grasses)	(Grasses)	Grasses
NYMPHALIDAE	*Viola* *Castilleia* *Salix* *Plantago*	*Castilleia* *Aster* *Cirsium* *Ribes* *Gnaphalium* *Lupinus*	*Ceanothus*	*Castilleia* *Aster* *Chrysopsis* *Ceanothus* *Salix* (stream) *Lupinus*
LYCAENIDAE	*Salix* *Lupinus* *Trifolium* *Potentilla*	*Ceanothus* *Lupinus* *Polygonum* *Ribes* *Eriogonum* *Potentilla* *Calyptridium* *Trifolium*	*Arceuthobium* *Pinus*	*Ceanothus* *Lupinus* *Polygonum* *Sedum* *Eriogonum* *Astragalus*
HESPERIIDAE	*Potentilla* Grasses *Sidalcea*?	*Potentilla* Grasses *Sidalcea*	--	*Potentilla* Grasses

*Data summarized from text of Emmel & Emmel, 1962a.

groups as found for the whole of North America (north of Mexico). From most to least number of species: Lycaenidae, Nymphalidae, Hesperiidae, Pieridae, Papilionidae (follows Satyridae for North American fauna), Satyridae, Danaidae.

3. The highest total number of butterfly species in Donner Pass occurs in the *montane* habitats (60 species). The *dry meadow* habitats support 55 species, the *wet meadow* habitats have 44 species, and the *forest* areas have 26 species occurring in them.

4. The basis of this distribution is explained by the theory that a greater food-plant diversity occurs in the areas (such as the montane macro-habitats) that have a number of micro-habitats, each with particular edaphic and micro-climatic conditions, and that this host-plant diversity promotes the immigration and continued successful existence of more Rhopalocera species than in less diversified macro-habitats (such as these Sierran forest habitats). The possible influence of such factors as solar radiation and climate acting directly on butterflies rather than plants is also considered.

5. Data obtained on the number of flying individuals of all species found in the Lodge Meadow area showed there was usually a good correlation between number of species and number of individuals for each family in this restricted Sierran locality.

SYSTEMATIC LIST OF RHOPALOCERA OCCURRING AT DONNER PASS, PLACER COUNTY, CALIFORNIA

PAPILIONIDAE

1. *Papilio zelicaon* Lucas
2. *Popilio indra indra* Reakirt
3. *Papilio rutulus* Lucas
4. *Papilio eurymedon* Lucas
5. *Parnassius clodius baldur* Edwards

PIERIDAE

6. *Neophasia menapia* Felder & Felder
7. *Pieris sisymbrii* Boisduval
8. *Pieris protodice* Linnaeus
9. *Pieris rapae* Linnaeus
10. *Euchloe creusa hyantis* Edwards
11. *Anthocaris sara* form *julia* Edwards
12. *Colias eurytheme* Boisduval
13. *Colias philodice eriphyle* Edwards

DANAIDAE

14. *Danaus plexippus* Linnaeus

SATYRIDAE

15. *Ceononympha tullia californica* Westwood
16. *Cercyonis sthenele oetus* Boisduval

NYMPHALIDAE

17. *Speyeria cybele leto* Behr
18. *Speyeria zerene zerene* Boisduval
19. *Speyeria coronis snyderi* Skinner
20. *Speyeria atlantis irene* Boisduval
21. *Speyeria mormonia arge* Strecker
22. *Boloria epithore* Edwards
23. *Chlosyne palla* Boisduval
24. *Chlosyne hoffmanni hoffmanni* Behr
25. *Phyciodes campestris montana* Behr
26. *Phyciodes mylitta* Edwards
27. *Polygonia zephyrus* Edwards
28. *Nymphalis californica* Boisduval
29. *Nymphalis milberti* Latreille
30. *Nymphalis antiopa* Linnaeus
31. *Vanessa cardui* Linnaeus
32. *Vanessa atalanta* Linnaeus
33. *Vanessa virginiensis* Drury
34. *Vanessa carye* Hubner
35. *Precis lavinia* Cramer
36. *Limenitis lorquini* Boisduval & Leconte

LYCAENIDAE

37. *Satyrium californica* Edwards
38. *Satyrium sylvinus* Boisduval
39. *Satyrium saepium* Boisduval
40. *Satyrium behrii* Edwards
41. *Satyrium fuliginosa* Edwards
42. *Strymon melinus* Hubner
43. *Callophrys johnsoni* Skinner
44. *Callophrys nelsoni* Boisduval

45. *Callophrys augustinus iroides* Boisduval
46. *Callophrys eryphon* Boisduval
47. *Callophrys dumetorum perplexa* Barnes & Benjamin
48. *Lycaena arota virginiensis* Edwards
49. *Lycaena editha* Mead
50. *Lycaena nivalis* Boisduval
51. *Lycaena cupreus* Edwards
52. *Lycaena heteronea* Boisduval
53. *Everes comyntas amyntula* Boisduval
54. *Plebejus anna* Edwards
55. *Plebejus saepiolus* Boisduval
56. *Plebejus icarioides* Boisduval
57. *Plebejus shasta* Edwards
58. *Plebejus acmon* Westwood & Hewitson
59. *Plebejus (acmon?) lupini* Boisduval
60. *Agriades glandon podarce* Felder & Felder
61. *Glaucopsyche lygdamus behrii* Edwards
62. *Philotes enoptes* Boisduval
63. *Philotes battoides intermedia* Barnes & McDunnough
64. *Celastrina argiolus echo* Edwards

HESPERIIDAE

65. *Thorybes nevada* Scudder
66. *Pyrgus ruralis* Boisduval
67. *Pyrgus communis* Grt.
68. *Erynnis juvenalis* Fabricus
69. *Erynnis afranius* Lint.
70. *Hesperia juba* Scudder
71. *Hesperia nevada* Scudder
72. *Hesperia harpalus* Edwards
73. *Polites sonora* Scudder
74. *Polites sabuleti tecumseh* Grin.

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LITERATURE CITED

AXELROD, DANIEL I. 1960. The evolution of flowering plants. In *The Evolution of Life,* Sol Tax, ed. Pp. 227-305. Univ. of Chicago Press.

EHRLICH, PAUL R., & A. H. 1961. *How to Know the Butterflies.* Brown, Dubuque, Iowa. 262 pp.

————————, & RICHARD W. HELM. 1962. Patterns and populations. *Science* 137: 652-657.

EMMEL, THOMAS C., & JOHN F. EMMELL. 1962a. Ecological studies of Rhopalocera in a High Sierran community — Donner Pass, California. I. Butterfly associations and distributional factors. *Journ. Lepid. Soc.* 16: 23-44.

————————, 1962b. Ecological studies of Rhopalocera in a High Sierran community — Donner Pass, California. II. Meteorologic influence on flight activity. *Journ. Lepid. Soc.,* in press.

GARTH, JOHN S. 1935. Butterflies of Yosemite National Park. *Bull. So. Cal. Acad. Sci.* 34: 37-75.

HOVANITZ, WILLIAM. 1958. Distribution of butterflies in the New World. In *Zoogeography.* American Association for the Advancement of Science, Publication No. 51, Washington, D. C. Pp. 321-368.

LE GARE, MARY JUDE, & WILLIAM HOVANITZ. 1951. Genetic and ecologic analyses of wild populations in Lepidoptera. II. Color pattern variation in Melitaea chalcedona. *Wasmann J. Biol.* 9: 257-310.

MOECK, ARTHUR H. 1957. Geographic variability in Speyeria. Milwaukee Entomological Society. 48 pp.

TILDEN, J. W. 1959. The butterfly associations of Tioga Pass. *Wasmann J. Biol.* 17: 249-271.

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THE ARGYNNIS POPULATIONS OF THE SAND CREEK AREA, KLAMATH CO., OREGON

PART I: THE EFFECT OF THE FORMATION OF MT. MAZAMA ON THE AREA AND ITS POSSSIBLE INFLUENCE ON THE BUTTERFLY FAUNAS OF THE SAND CREEK BASIN.

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INTRODUCTION

THE POPULATIONS OF ARGYNNIS (SPEYERIA) found in eastern Oregon share with similar populations in many parts of western United States, a tendency to great variation and to a breakdown of the distinctive appearance of many of the named geographical phenotypes (subspecies). The region drained by Sand Creek, lying east of Crater Lake in Klamath County, Oregon, is occupied by populations of *Argynnis* exhibiting this variation to a marked degree.

The Sand Creek area was chosen for study not only because of the variability of its *Argynnis* fauna, but in particular because it is a region the recent geological history which is fairly well understood, and inferences may be drawn of the possible effect of this geological history on the several species of *Argynnis* now inhabiting this region.

Part I of this paper will deal with the recent geological history of Mt. Mazama and the nearby lands to the east of Crater Lake, and the possible influence of these events on the faunas now living in this region. Part II will attempt an analysis of the variation of these *Argynnis* populations, and is postponed until much more field work can be done so that a proper appreciation of the extent of variation is possible.

BACKGROUND

The stability of certain isolated populations has been interpreted as due to long occupation of the present habitat. This time element has been construed as allowing stabilization, without undue influence from surrounding populations. Such conditions infer stability in the habitat, without the disturbing influence of earth changes in the area. Such stable habitats have been referred to as refugia.

Opposed to such a condition of stability, many portions of the earth's surface have been subjected to changes more frequently, and some of these changes have occurred in very recent times. Eastern Oregon is a region of many lava flows, and scoria and cinder falls, and the effects of these actions are still clearly visible in numerous places. It is suggested that such phenomena must have had a major effect upon any butterfly populations existing in the regions where such events took place.

THE SAND CREEK BASIN AND ITS RECENT GEOLOGICAL HISTORY

Sand Creek rises at Anderson Spring, elevation 7088 ft, slightly northeast of Kerr Notch in Crater Lake National Park, and runs easterly, leaving the park in the near vicinity of the now unused East Entrance. It continues out of the park, the elevation gradually decreasing. The area chosen for study is that from Lost Creek Campground, Crater Lake National Park, 5972 ft., located between Sand Creek and its branch, Wheeler Creek, and the point at which Highway 232 ("Old 97") crosses Sand Creek. This area is readily accessible. Work in the Crater Lake National Park was possible under a permit from the National Park Service.

The *Argynnis* samples indicate that the following species are represented: *Argynnis* (*Speyeria*) *coronis* Behr, *zerene* Bdv., *callippe* Bdv., *egleis* Behr, *atlantis* Edw., and *hydaspe* Bdv. Possibly others may be present in lesser numbers but have not yet been collected. It is interesting to note that *Argynnis cybele* (*leto*) appears to be absent from the region, and also from all of Crater Lake National Park, though common west of the Cascade divide, and also in the Blue Mountains of eastern Oregon. The scarcity in the Sand Creek Basin of suitable wet habitats, or the recency of earth surface changes, may be clues to its absence.

Fair samples of these various species, collected by the author and also by others, have been examined, and it is evident that the degree of variation is surprising. As stated above, analysis of these and future samples is postponed until later, but enough information is now available to make it apparent that the populations of each species involved are far from stable. Many individuals resemble no named geographic segregate. Some species are represented by individuals resembling two or more named segregates and it is evident that no equilibrium in phenotype has been reached by any of the several species inhabiting the area.

Crater Lake is not a true crater, but a caldera, brought into its present form by the collapse inwardly of the summit of Mt. Mazama. In its most developed state, Mt. Mazama was more than 12,000 ft. in height. During the Pleistocene, it developed its greatest elevation, produced a great lava flow, and was subsequently glaciated extensively. The effects of this glaciation are visible around the present rim of the lake. Later, the present Crater Lake was formed by the collapse inwardly of the upper mile or so of Mt. Mazama, with attendant glowing avalanches of scoria and pumice and great clouds of pumice dust. The area east of the lake was covered with pumice and scoria from the glowing avalanches. The land still further east was covered by pumice falls that reached a depth of ten feet or more close to the mountain, and gradually thinned out easterly, extending in at least a very thin layer, approximately fifty miles to the east.

It is believed that the glaciers, or some of them, must still have been present when the collapse took place, since the residue of scoria and pumice is light in certain areas around the rim. This would be the situation if the scoria and pumice fell onto glaciers and was carried away in part. If it had fallen in every case on bare ground, it would be left there. This may explain why the present pumice soils are more extensive in the non-glacial areas. It is believed also that the collapse took place in winter, because there is relatively little evidence of severe forest fires in the wake of the collapse. If the collapse had taken place in the summer, it has been reasoned that the forest fires surely would have been more extensive.

There seems to be agreement that most or all of the vegetation was destroyed within the effective range of the scoria and pumice avalanches and of the heavier pumice fall. If this is correct, the present vegetation of the entire region must have regrown since the collapse took place. The rate of recovery of the vegetation seems to have been inversely proportional to the depth of the pumice and scoria that covered a given area. The prevailing winds are believed to have been much the same then as now, basically western, since the pumice was carried much further east than west.

The Sand Creek Basin is situated so that it received very heavy pumice fall, and very probably, extensive to complete vegetational destruction.

Carbon dating of wood that is imbedded in the pumice, and which is therefore assumed to have been charred by the glowing avalanches of pumice and scoria, sets the time of the collapse at 6640 ± 250 years. In round numbers, popular accounts state this as 6550 years. From this it is inferred that the Sand Creek Basin became a sterile habitat at that time.

It is of interest to observe that such streams as Upper Sand Creek and Wheeler Creek, below Kerr Notch, have deep V-shaped canyons, geologically very young and without sign of glaciation such as that found on the rocks of the Rim above. From this it seems clear that Sand Creek acquired its present bed recently. Indeed, its present course may very well be consequent to the recent geological events of the area. The depth of the pumice is also clearly visible.

Knowledge of the date when the vegetation was destroyed allows some speculation concerning present vegetational cover of the region. Recovery of the vegetation must have lagged for many years. The types of vegetation found in the total Crater Lake region permit some understanding of the relative times of recovery. In Crater Lake National Park, the forest along the southern boundary is a mature Sierran Coniferous Forest of Ponderosa Pine, Sugar Pine, White Fir, Douglas Fir and Incense Cedar, with an understory of Snow Brush (*Ceanothus velutinus*) and Greenleaf Manzanita (*Arctostaphylos patula*). The forest of the flanks of the mountain on the southern and western slopes is a mature Mountain Hemlock-Shasta Fir Forest, with increasing amounts of Subalpine Fir at higher elevations. Such forests have relatively less understory. The highest elevations support Whitebark Pine.

Northerly and easterly, in the areas of greater pumice fall, (as for instance the Pumice desert) the forest has not even yet succeeded in taking over the denuded and pumice-covered land. In the intermediate areas where the forest is slowly invading and colonizing the pumice soils, the successful pioneer is Lodgepole Pine, which on such soils forms a singularly uniform and barren type of forest with very few underplants.

The soils of the study area are formed of pumice and scoria and from the foregoing evidence, are derived from the pumice fall from the collapse of Mt. Mazama. The forest here is essentially Lodgepole Pine Forest, of the type found also on the pumice at higher elevations in the park. The soils and the forest are evidently contemporary in the Sand Creek Basin, with those occurring on pumice within the park itself. We should regard the forest cover of the Sand Creek Basin as equally recent.

Dating of the pumice fall and the destruction of the vegetation give a reference point. Vegetational recovery must involve a very considerable period of time. This reasonably will be longer in areas where the pumice fall is deeper. While no exact figure can at present be suggested for the age of the current forest cover of the Sand Creek Basin, it must be very much less than 6640 ± 250 years. Very likely portions of it may be a fraction of this age.

From this it seems evident that the *Argynnis* populations of the Sand Creek Basin (and similar areas) are occupying habitats that are the opposite of refugia. The time in occupation of contemporary populations on such disturbed areas is brief.

DISCUSSION

Assuming an area from which vegetation has been destroyed, with attendant soil changes, and with sufficient time elapsed to allow new vegetation to occupy the area, we may well expect certain things to take place, among which the folowing may be suggested.

1. The vegetation that recolonizes the land will in all possibility be different than that which previously grew in the area. Most likely many previous floral components would now find the area inhospitable.

2. Recolonization of the habitat by organisms would theoretically

be possible from any portion of the surrounding regions. It may be expressed by saying that recolonization could be expected to be *multi-directional* unless some factor prevented recolonization from one or more directions.

3. Such recently recolonized areas would contain mixed populations the components of which may have moved in from any of the surrounding regions.

4. If such heterogeneous populations are studied before adequate time for stabilization has passed, it is predicted that great variation in individual phenotype will be present.

Expressing this in terms more directly related to the *Argynnis* populations of the Sand Creek Basin, it is tentatively concluded that the variability of these several populations is in part a result of the recency with which they have established themselves in this area following a major change in habitat, and in part a result of recolonization by an unknown number of varying populations from the surrounding regions.

Less tangible are two other possibilities. One is that the time during which the Sand Creek Basin was unsuitable for habitation by *Argynnis* was of sufficient duration to allow the surrounding populations which it separated, to diverge to some extent. The other is that the recent forest cover of the pumice soils may differ sufficiently in its selective factors so that the eventual stable population may when developed differ from those around it.

Thanks are due to the National Park Service, and in particular to Park Naturalist Bruce Black, for extensive courtesies and helpful information.

REFERENCES

BRIGGS, LYMAN J. 1962. When Mt. Mazama lost its top. *National Geographic,* 122 (1): 128-133.

MOECK, ARTHUR H. 1957. Geographic variability in *Speyeria. The Milwaukee Entomological Society,* 48 pp.

WILLIAMS, HOWELL. 1961. Crater Lake — The story of its origin. University of California Press, Berkeley & Los Angeles. XII + 98 pp., 10 plts., 8 figs.

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CATERPILLAR VERSUS DINOSAUR?

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A PAPER BY S. E. FLANDERS in the first issue of *The Journal of Research on the Lepidoptera* (Flanders, 1962) bears the intriguing title, "Did the caterpillar exterminate the giant reptile?" In his discussion, the "abrupt end of the Age of Reptiles during the Cretaceous period is ascribed to a newly emerged order of insects, the Lepidoptera, on the supposition that for a brief period it regulated the world's supply of plant life at starvation levels for the dependent reptiles." The argument for this hypothesis rests in part on modern examples of large-scale devastation of certain species of plants by the larvae of Lepidoptera, and in part on assumptions concerning the time of origin and expansion of this order, the nature of plant life during the Cretaceous period, and the habits and relationships of the "giant reptile."

Many explanations have been proposed for the extinction of dinosaurs and several other groups of reptiles at the end of the Cretaceous, but there is not yet any general agreement as to the most important causes. The proposals are conjectures, having little or no direct evidence to support them. The theory under discussion adds another to the list. The consensus among paleontologists now is that one or two "causes" are not sufficient, and that the extinction of these animals is a more complicated phenomenon than it has seemed. While it is possible that destruction of food-plants by caterpillars has at times contributed to extinction of some herbivorous reptiles, and thus indirectly to that of their predators, the present writer thinks that a close look at what happened in the Mesozoic might be helpful in judging this hypothesis.

Our knowledge of fossil Lepidoptera is scanty, but the earliest known moth appears to be *Eoses triassica,* described from Upper Triassic beds in Queensland (Tindale, 1945). It is known only from a fore and hind wing, of which the venation agrees broadly with that of Jugatae (Homoneura); Tindale placed it in a new, more primitive suborder, Eoneura. Thus the order must have originated more than a hundred million years before the extinction of dinosaurs, although leaf-eating caterpillars might not have characterized the earliest genera and families of moths. Reports of moths and butterflies from the Jurassic lithographic limestone in Bavaria are based on specimens now attributed to other orders, especially Homoptera. Unless more information appears in Frank M. Carpenter's forthcoming volume on fossil insects in the "Treatise on Invertebrate Paleontology," we can say nothing specific about Lepidoptera of the Jurassic and Cretaceous; none are mentioned in the "Traité de Paleontologie," vol. III (1953). In the Cenozoic, however, moths and butterflies of modern families are known, apparently from the Eocene on.

It is reasonable to suppose that the rise of Lepidoptera coincided with that of flowering plants. These plants are known first from the Jurassic, but at least sixteen modern families are represented in Lower Cretaceous rocks; by the late Cretaceous many existing species of trees had appeared. The length of the Cretaceous was about 70 million years. From its close to the present time was a little less, say 63 million years, according to recent determinations (Kulp, 1961). But we cannot, in the nature of the case, show evidence that caterpillars appeared in great numbers in the late Cretaceous, or that they were then so free of parasites or predators that they could, by worldwide devastation of all sorts of plants, bring starvation upon the reptiles.

Some of the statements of Flanders concerning reptiles bear comment from the viewpoint of a paleontologist. For instance, "The inherent weakness of the reptile was an extraordinary need for an abundance of plant material . . . The small size of today's descendent reptiles, the vegetarian turtle, the predatory crocodile, the snake, and the lizard, is evidence of the giant reptile's elimination by starvation and predation." A sauropod, hadrosaur, ankylosaur or ceratopsian dinosaur may have eaten a large quantity of vegetation, the amount depending on size and activity. These animals were present in the late Cretaceous and occupied a position comparable in some ways to that of the browsing mammals of the Cenozoic. But their extinction does not seem to have been abrupt; it was a slow, uneven decline probably extending through millions of years, and does not differ so far as we know from the decline and disappearance of various other groups of animals at earlier and later times. The flying pterosaurs, whose food was probably fish, declined and died out at about the same time as the dinosaurs. So also did mosasaurs, a specialized line of giant marine fish-eating lizards; so too the very different aquatic plesiosaurs, as well as a few late Cretaceous ichthyosaurs and carnivorous dinosaurs.

No living reptiles are directly descended from any of the above-mentioned Mesozoic reptiles. Turtles and crocodiles originated in the Triassic and have continued with no fundamental changes to the present time. Lizards are known first from the Jurassic, snakes from the Cretaceous, and their size cannot be taken as evidence of any changes among the giant reptiles. These giant reptiles were clearly not a single natural group, nor, on the other hand, were all members of the orders to which they belonged of great size. In the two orders of dinosaurs, for example, there were some species, both early and late, that failed to reach the size of an average alligator.

Efforts to explain the extinction of dinosaurs and various other reptiles in the Cretaceous period ought to take into account a number of possible causes. The one proposed by Flanders does not give the answer to several problems, such as the disappearance of various unrelated and ecologically different groups, not necessarily of large animals, and the survival beyond the Cretaceous of certain other reptiles, not necessarily small. There is no evidence of either a biological or a geological catastrophe of large proportions at the close of the Mesozoic, unless the slow retreat of epicontinental seas in some areas can be so described. Probably the answer will eventually be found in a combination of many factors.

LITERATURE CITED

FLANDERS, S. E. 1962. Did the caterpillar exterminate the giant reptile? *J. Res. Lepid.*, 1(1): 85-88.

KULP, J. LAURENCE. 1961. Geologic time scale. *Science,* 133 (3459): 1105-1114.

TINDALE, N. B. 1945. Triassic insects of Queensland. *Proc. Roy. Soc. Queensland,* 56 (5): 37-46.

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GEOGRAPHICAL DISTRIBUTION AND VARIATION OF THE GENUS ARGYNNIS

I. INTRODUCTION

II. ARGYNNIS IDALIA

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I. INTRODUCTION

THE GENUS ARGYNNIS in the comprehensive sense covers a wide variety of form and size in Nymphalid butterflies. The geographical distribution of the genus as a whole is somewhat comparable to that of Colias but is actually wider in some areas due to a tropical group in the eastern hemisphere. A natural desire to have a greater similarity of type within a "genus" and a desire of some workers to "split" to the ultimate has left the genus in a diverse state of fragmentation. This has been aided by regional preferences and the difficulty for most Lepidopterists to observe and study members of the group from continents other than their own. The members of the genus from the smaller isolated continents such as North America and South America have apparently either diverged slightly from the type on the largest land mass (Eurasia) or they have retained more primitive features. In North America only two of the several subdivisions of type within the Argynnis appear ever to have arrived for colonization. These two have diverged to such an extent on that continent that residents of that continent of natural inclination should consider them as of different genera (*Boloria* and *Speyeria*). One of these (*Speyeria*) is only slightly different from one of the species groups of Eurasian *Argynnis,* namely, *aglaja, adippe, niobe,* etc. and placed by some in a genus *Brenthis* which is not the usage of *Brenthis* used in North America by others.

The variety of the genus in Eurasia is much greater than in North America. It is natural to expect that the types present in Eurasia which would be most like those now present in North America would be those whose climatic adaptations would be the most similar to the conditions present in the area where a land bridge exists now or did exist in the immediate past. This is the area of Alaska and adjacent Siberia. The *Boloria* group is the best adapted to the climates of this area and may even now be considered for all practical purposes to have "continuity" across the barrier at the Bering straits. With the possibility of gene flow not very remote, it is not difficult to see why *Boloria* of North America and Asia (Europe) should be much alike. In fact, several species of *Boloria* can and do go under the same species name on both continents, just as do three species of Colias which have the same geographical relationships to the land bridge.

The species which are the most remote in their climatic preferences from the climates of the Bering area are those species which are the most divergent on the two continental areas; these are the most southern types. *Argynnis paphia* is the member of a southern subgenus of *Argynnis* in Eurasia and this subgenus apparently never colonized America. Instead, a type similar to *aglaja* apparently did colonize America and from this presumably all the American Argynnids of the larger (*Speyeria*) type subsequently were derived. It is an hypothesis that the most extreme types in North America, such as *idalia, diana* and *nokomis,* which bear considerable pattern and color relationship to Eurasian species such as *paphia, sagana, childreni,* etc. were derived independently from them from *aglaja* — like ancestors under the selective influence of the comparable conditions of climate to which they were subjected (hot-humid summers). Comparative correlations of the *facies* of the butterflies with climates at different parts of the world will be made later in this series.

The *Argynnis* of South America bear no close relationship apparently to the *Argynnis* of any other part of the world. There is no easy way at the present time for them to have arrived there by migration from other continents. Only two alternate proposals seem possible. The first of these is that these *Argynnis* were isolated many years ago (the early Tertiary) from the other *Argynnis* of the world and that they arrived there by migration from North America at a time when North America was inhabited by a more primitive type. They might also have arrived from Africa early in the evolution of the genus should there be reason to believe seriously in the past movement of South America away from a more close proximity to Africa. The second proposal on the origin of the South American *Argynnis* is one of independent origin in South America from some tropical or subtropical relative of the North American *Argynnis.* This proposal seems very weak in view of the lack of any close relative that would seem to be a likely ancestor. *Dryas* (*Colaenis*), *Dione* and *Euptoieta* seem to be out of the question, though this may be only based upon superficial appearances. They feed upon similar plants, a factor greatly favoring the argument, especially with regard to *Euptoieta* which inhabits cold country in the Andes, feeds on violets and has much the same habits as *Argynnis* itself.

The question comes up as to what is a genus. Should the entire group which has been pictured here be considered one genus, or should it be raised up to a sub-family or even a family. If the latter, then should the major groups be raised from subgeneric level to the generic? If so, then how many groups at this level should be recognized? The question is then condensed to one problem. There really is no biological entity which can be known as a genus. All hopes to the contrary, the genus is solely a matter of convenience in nomenclature, which should show as much as possible, phylogenetic relationships. The system should start at the bottom of the classification heirarchy. If it is known what should be considered species, sufficient related species ought to be put into a genus to make a reasonable group on the basis of numbers and morphological (genetical) similarity. Should too few species be put into a genus the advantages of the binomial nomenclature are destroyed, in much the same way as would occur if every person had the family name *Smith.* A further criterion, in addition to size and uniformity, is geographical coverage. It is a natural phenomenon that isolation leads to differentiation. Related members of a species group may diverge slightly due to continental isolation and yet in all other ways be closely knit as a single group. The decision here must rest on the needs of the taxonomist in showing relationships and the usefulness to biologists. Nomenclature bears one major value: that of usefulness. If different generic names were to be used on each continent, a degree of provincialism would develop which would be hard to penetrate; local butterfly books in North America and in Europe have now diverged to such an extent in terminology that the only way a novice can determine relationships between the butterflies of Europe and North America is to look at the specimens—an ironic turn of events since that should be the purpose of nomenclature. As a result therefore, it is the hope that there may be a return to the larger genera of the past; this is the thesis upon which the use of *Argynnis* here is based, without necessarily accepting the assumption that the generic limits and the characters used for their delimitation should remain as in the past if more specific future work should show the need for change.

II. *ARGYNNIS* (*SPEYERIA*) *IDALIA*

This representative of the North American *Argynnis* differs in appearance from the usual *Speyeria* probably more than any other except possibly for *A. diana.* The details of its pattern which are distinctive and different from the standard *Argynnis* pattern are the greatly increased black pigment around the borders of the wings, even extending to the basal section and nearly covering the hind wings, but at the same time leaving free of black pigmentation, the marginal and submarginal rows of spots (fig. 1 and 2). The general *facies* therefore is distinctive and different from any other *Argynnis.* At the same time, the black pattern elements of the center of the fore wing are reduced rather than expanded as in all other related *Argynnis.* It therefore shows a development of a pattern not only unlike that of the *Argynnis,* including the subgenus *Speyeria* as indicated by Dos Passos and Grey, but a trend in a diametrically opposed direction. The distinctiveness of this species is such as to need no real description or detailed analysis. Likewise, from the study of specimens throughout the geographic range of the species, there are no geographical variations apparent, though there are in-

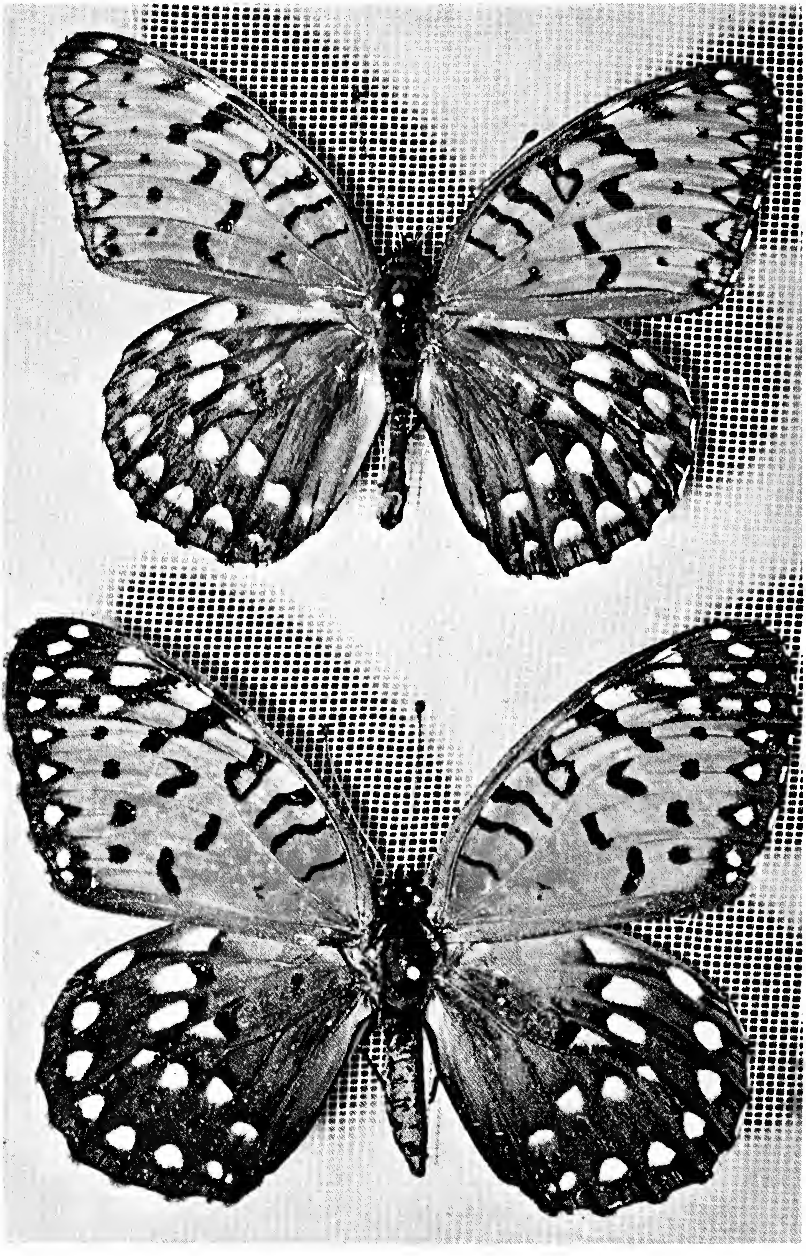

Fig. 1. *Argynnis idalia,* upper side; top: male; bottom: female. from Oak Park, Illinois. July 8, 1906. F. S. Daggett.

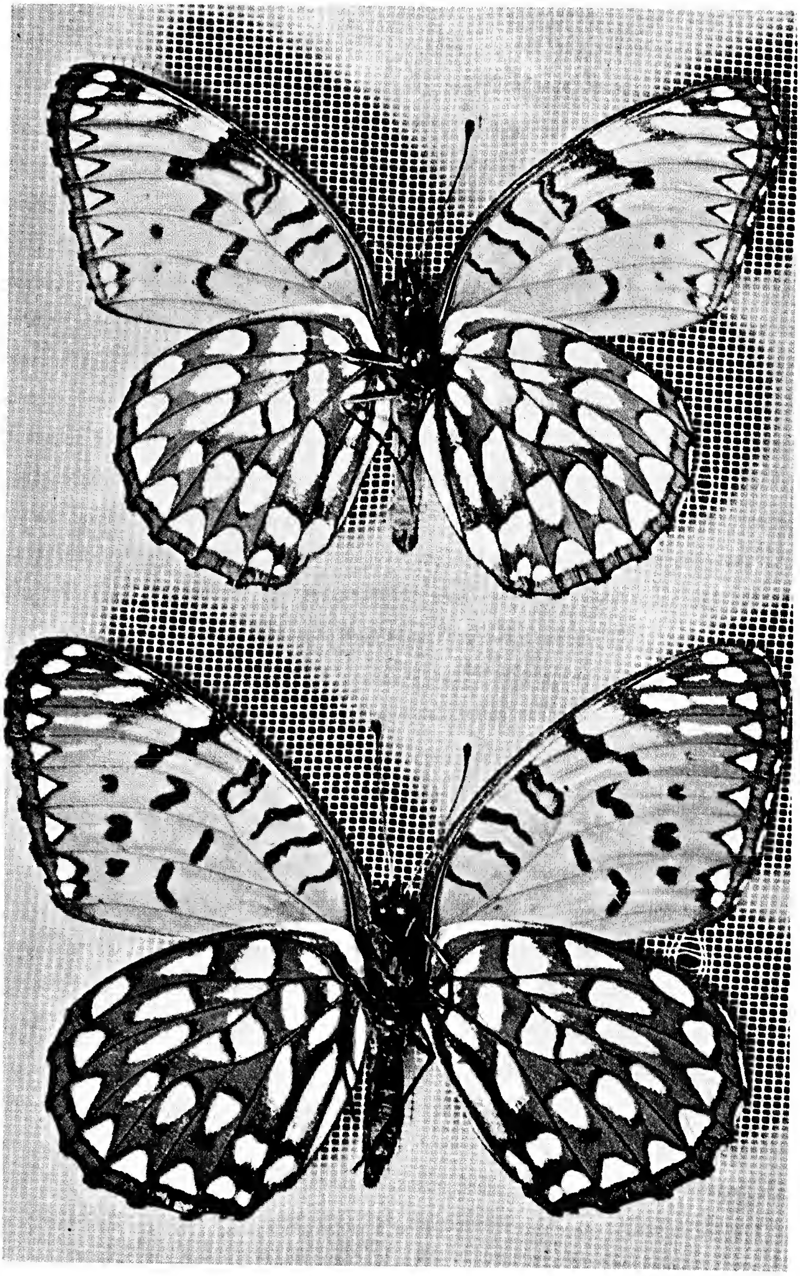

Fig. 2. *Argynnis idalia,* same as fig. 1 only lower side.

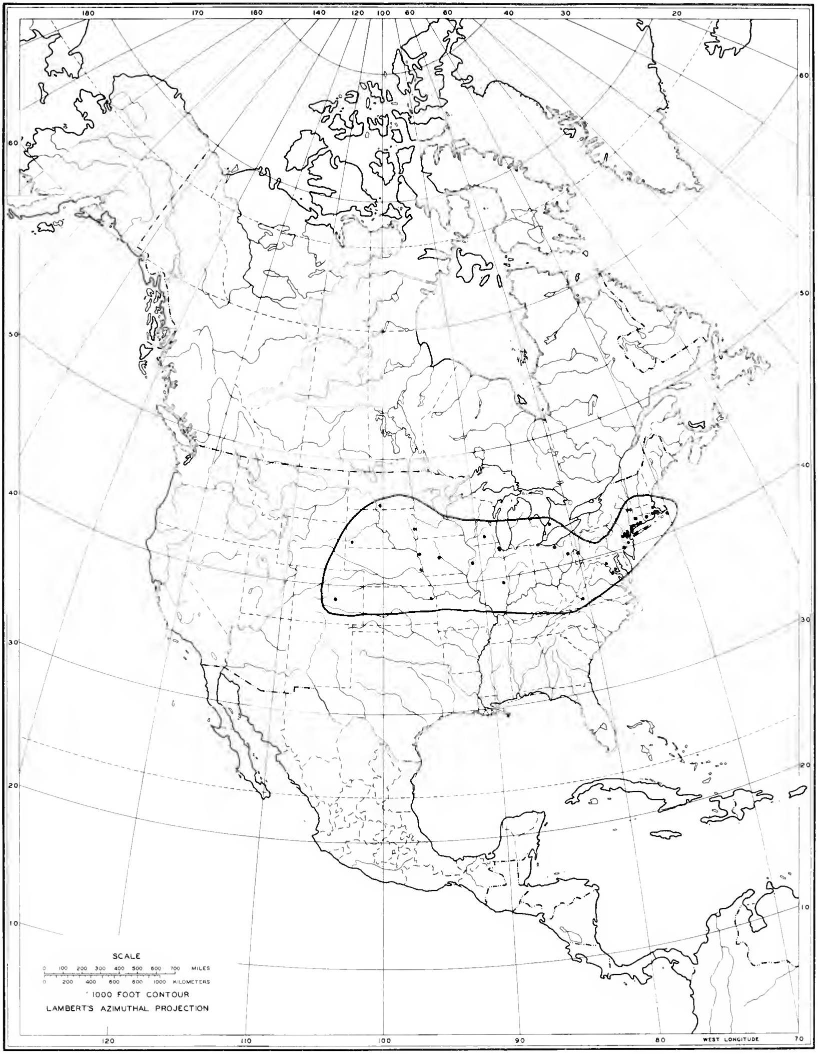

Fig. 3. Map of North America showing the distribution of *Argynnis idalia.*

dividual differences in size and slight differences in the pattern observed on an individual basis. Perhaps statistical differences could, and will, be detected in the future.

The distribution of this species is limited to a central and eastern location across the United States and a small part of Canada. The biological reasons for this restricted distributional range are not known. It can be seen from the map (fig. 3) that the species ranges from New England (specimens which I have seen come from as far as Massachusetts though records indicate Portland, Maine as the furthest point reached north and east), southward to North Carolina (probably erroneous records indicate Georgia), and west to Colorado and North Dakota (probably erroneous records indicate Montana). There are records or indications in old literature for Arkansas but I have seen no specimens from there. The species seem to prefer the area south of the Canadian life zone, that is, the Transition life zone of sorts, though it is pretty hard to outline any definite climatic zonation. Records indicate that it is to be found in most of the southern counties of Michigan and the southern counties of Minnesota. Scudder (1889) writes: "This butterfly belongs to the Alleghanian fauna, though its distribution appears to be somewhat irregular. It inhabits lowlands and is much more abundant in the extreme eastern portion of its range than elsewhere, unless it be the western prairies." Mention of it in Louisiana by Strecker is most probably in error.

A further discussion of the range of this species will be deferred until the maps of other species have been published, which will be used for comparison.

REFERENCES

DOS PASSOS, C. F. AND L. P. GREY. 1947. Systematic catalogue of Speyeria (Lepidoptera, Nymphalidae) with designations of types and fixations of type localities. *Amer. Mus. Novitiates* No. 1370.

————. 1945. A genitalic survey of Argynninae (Lepidoptera, Nymphalidae). *Amer. Mus. Novitates* No. 1296.

MACY, R. W. AND H. H. SHEPARD. 1941. Butterflies (of Minnesota). *Univ. Minn., Minneapolis.*

MOORE, SHERMAN. 1960. A revised annotated list of the butterflies of Michigan. *Occasional Papers of the Museum of Zoology, University of Michigan.* No. 617.

SCUDDER, S. 1889. The Butterflies of the Eastern United States. *Cambridge, Mass.*

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THE RELATION OF PIERIS VIRGINIENSIS EDW. TO PIERIS NAPI L.

SPECIES FORMATION IN PIERIS?

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In a previous paper (Hovanitz, 1962), it was indicated that a fuller discussion of the relationship of *Pieris napi* L. to *Pieris virginiensis* Edw. would be forthcoming. In that paper, the map showing the distribution of *P. napi* included the distribution of *P. virginiensis* but a closer distinction between the two was not indicated because of the reduced size of the map included. A more detailed map showing the relationships between the two biological entities under discussion is included with this paper, together with a description of the known facts of the lines of separation of the two "species" or races, and a summary of the events that have most probably occurred in relation to the two groups up to the present time.

On the map in the previous paper (Hovanitz 1962), the range of *Pieris napi* L. for the eastern United States included *virginiensis* as well as *napi* itself. The race of *napi* with which we are concerned here is known as *oleracea*. This race blends northwards and westwards into other races by imperceptible gradations. *Pieris napi oleracea* (known also by the summer brood names, *aestiva* Edw., *hyemalis* Edw. and *acadica* Edw.) may be considered the name for the race of *napi* east of 90° Longtitude and south of 50° N. latitude, more or less, with the exception of the area south of New York state (38° N). Other names can be found in McHenry (1962). The area south of New York state and east of 90° Longitude is occupied by the race or species *virginiensis*. In New York state and other points in the vicinity, or close to the southern limits of *oleracea*, there are populations which in some cases appear to be more closely related to *virginiensis* than to *oleracea*, and in other cases, are more closely related to *oleracea* with occasional individuals similar to *virginiensis*. The status of the line of contact between *oleracea* and *virginiensis* is not one of free and even blending such as might be expected of freely interbreeding individuals in a case of solely geographical isolation. Populations are rather clearly either *oleracea* or *virginiensis* as the case may be, with only occasional examples of intermediates giving some hint of the nature of introgression at the line of contact.

The contact of these two species or races bears a close relationship to the similar situation between the species or races *Basilarchia astyanax* and *B. arthemis* in the same general area (Hovanitz 1949).

Specimens of *P. napi* studied in various collections have permitted a map to be drawn showing the detailed distribution of *oleracea* and *virginiensis* (fig. 1). On this map, locations where *oleracea* (or *napi* in the species sense) are known are shown by the letter *N* and *virginiensis* locations are shown by the letter *V*. In addition to the indications on the map, there are reasons for assuming that each of these races overlaps the other even greater than seems indicated on the map. Due to lack of specific data (e.g. "New York"), some of these indications could not be shown on the map. These details will be mentioned below.

On the map, it can be seen that *oleracea* extends southwards in the mountains of New England to Connecticut where it comes in contact with *virginiensis* or something like *virginiensis*. It is doubtful that these specimens are truly *virginiensis*, though they do bear some resemblance to them. Instead they are more likely abberant *oleracea*, which are genetically tending in the direction of *virginiensis* through introgression. In addition, the habitat change out of the Canadian forest typical of *oleracea* to the "Transition" lowlands might lead to a phenotypic alteration in facies. Populations of considerable size are definitely known at the present time in Vermont and New Hampshire. They are not now known in the vicinity of Boston, Mass. though they were common there before 1850. The following bears witness to a reduction in distribution of *napi* in the 1800's:

From Scudder (1889):

> "This butterfly is a member of the Canadian fauna . . ."
>
> "It is found throughout New England although seldom abundant south of the annual isotherm of 48°. Northward and eastward it is everywhere abundant and it continues to be so as far south as Williamstown, Mass. (Scudder), Dublin, N. H. (Leonard) and Portland, Me. (Scudder, Verrill). South of 42° N. L. or the northern boundary of Connecticut, it rarely occurs, although it has been taken at Farmington, Conn. (Norton), Newport, R. I. (Miss Coggeshall teste Higginson) and Fire Island Beach, Long Island (Smith). Even in the north, however, there seems to be some local causes for its abundance."
>
> "Mr. Lintner, writing in 1864, says that in Schoharie, N.Y., 'it was extremely rare until recently,' and previous to 1857, 'he had taken it but once in three years . . ." "Mr. Bacon of Natick, Mass. says that the insect by no means disturbs cabbages and turnips as it did fifteen or twenty years ago."
>
> "I recollect once seeing the college yard in Cambridge, I think it was about 1857, fairly swarming with *P. oleracea.* It is now never found, to my knowledge, anywhere in the region about Boston, and I think it is wholly confined to the less cultivated and especially the hilly districts of New England."

From Klots (1951):

> "*Napi* has . . . suffered a great restriction in habitat, and probably in habits, for it is now almost entirely limited to shaded Canadian Zone forest . . .". "Not recorded south of the Catskill Mountains in New York".

From Klots (1935) of Edwards,

> "He mentions a female taken by Mead in the last week of June at Stony Clove in the Catskill Mountains . . . many eggs were obtained . . . from the chrysalis an *oleracea* emerged." "Stony Clove is in excellent territory for *napi* (*oleracea*) but I know of no records of *virginiensis* from there." "I have . . . seen specimens of *virginiensis* from Big Indian Valley in the Catskills, where the environment is more suited to *virginiensis*."
>
> "In 1931, near McLean, Tompkins County, New York, I was able to obtain undoubtedly authentic eggs, larvae and chrysalis of *virginiensis,* through watching females ovipositing on *Dentaria diphylla* Michx."

From Fiske (1901):

> "*Pieris napi.* once common enough to be injurious to cabbages and other cruciferous plants throughout New England, has since the introduction of *rapae* become one of our rarest butterflies. Its range is now restricted to the northern and mountainous portions, and even in the fortresses of the White Mountains it is a scarce insect."

The eighteenth century idea of a "species" contributed a lot to a general confusion of the nature of the relationship between *oleracea* and *virginiensis.* It was then, and too often now, the general idea that a species was represented by a specific morphological type, without regard to the variation which a population may have within itself. Some of the best collectors and breeders of Lepidoptera have therefore become confused, having the all pervading desire to designate some biological unit as either a "species", subspecies or variety when the true relationship may not be possible with only these tools of nomenclature. For example, Edwards (1881) says:

> "*Virginiensis* . . . has become a true species, although unquestionably, in a higher latitude, it appears as an occasional aberration only of *Oleracea.*"

Also, Klots (1951) says:

> "Until very recently, *virginiensis* has been confused with *napi,* but it is now known to be a distinct species of more southern (Transition Zone) distribution."

Edwards (1868-1872) says:

> "In the Kanawha district, it replaces *Oleracea* which is yet unknown there. It is not uncommon in the month of May, frequenting open woods rather than gardens, and in this respect differing in habit from the allied species. I have never met with it later than June, though *Oleracea,* in the Northern States is most abundant after that month and continues breeding till the early autumn frosts." "I have received specimens of *Virginiensis* from Mr. Wm. Saunders of London, Canada and am informed by him that it is there a rare insect."

DIFFERENCES BETWEEN *P. NAPI OLERACEA* AND *P. NAPI VIRGINIENSIS*

The primary visible differences between *P. napi oleracea* and *P. napi virginiensis* can be observed in figs. 2 and 3. In figure 2 is shown the male and female of the upper side of *virginiensis* to the left; at the same location in figure 3 is shown the under side. These specimens are

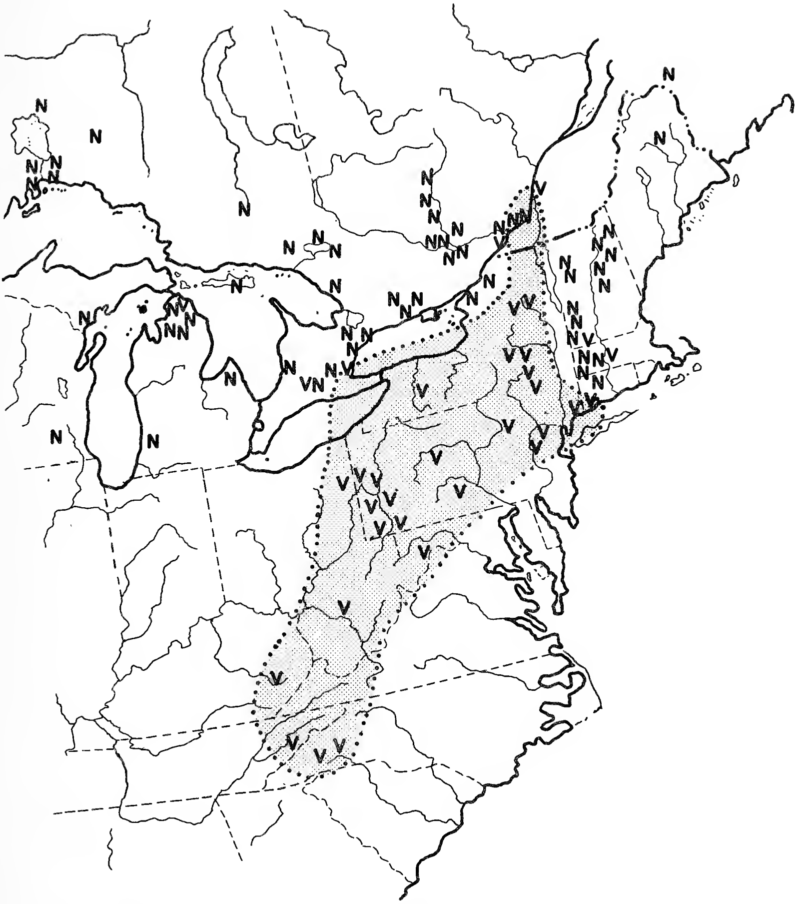

Fig. 1. Map showing the distribution in the eastern part of North America of the introgression area of *Pieris napi* races *virginiensis* and *oleracea.*

from near Pittsburgh, which although toward the north end of the range of *virginiensis* are quite typical of the populations south through the Appalachian mountains. The pattern of the upper side female should be noted as quite typical of this race, and which is only rarely present in *oleracea.* Of critical distinction, the pattern of the under side of the wings should be noted. The veins are outlined in a tan pigmentation, not heavy but rather broad in expanse, in appearance unlike any other race of *napi.*

P. napi oleracea is shown in figures 2 and 3 by the central two specimens; these are from southern New Hampshire which is near the

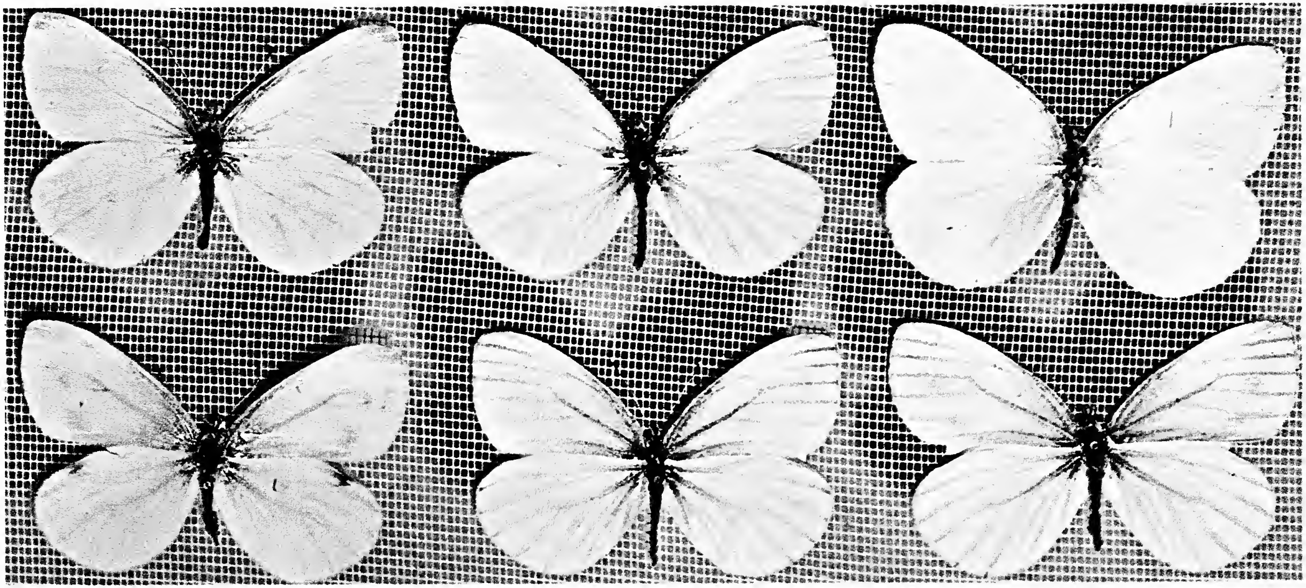

Fig. 2. LEFT: *P. napi virginiensis,* TOP: male, BOTTOM: female. Both Powerdermill Nat. Res. nr. Rector, Westmoreland C. Pennsylvania April 26, 1958. Clench.

CENTER: *P. napi oleracea,* TOP: male, BOTTOM: female. Both Jefferson, N. H. May 13, 1932. P. J. Lennox.

RIGHT: *P. napi oleracea,* TOP: male, Lincoln, Maine, July 14, 1935. BOTTOM: female, Jefferson, N. H. May 13, 1932. P. J. Lennox.

all upper side facies

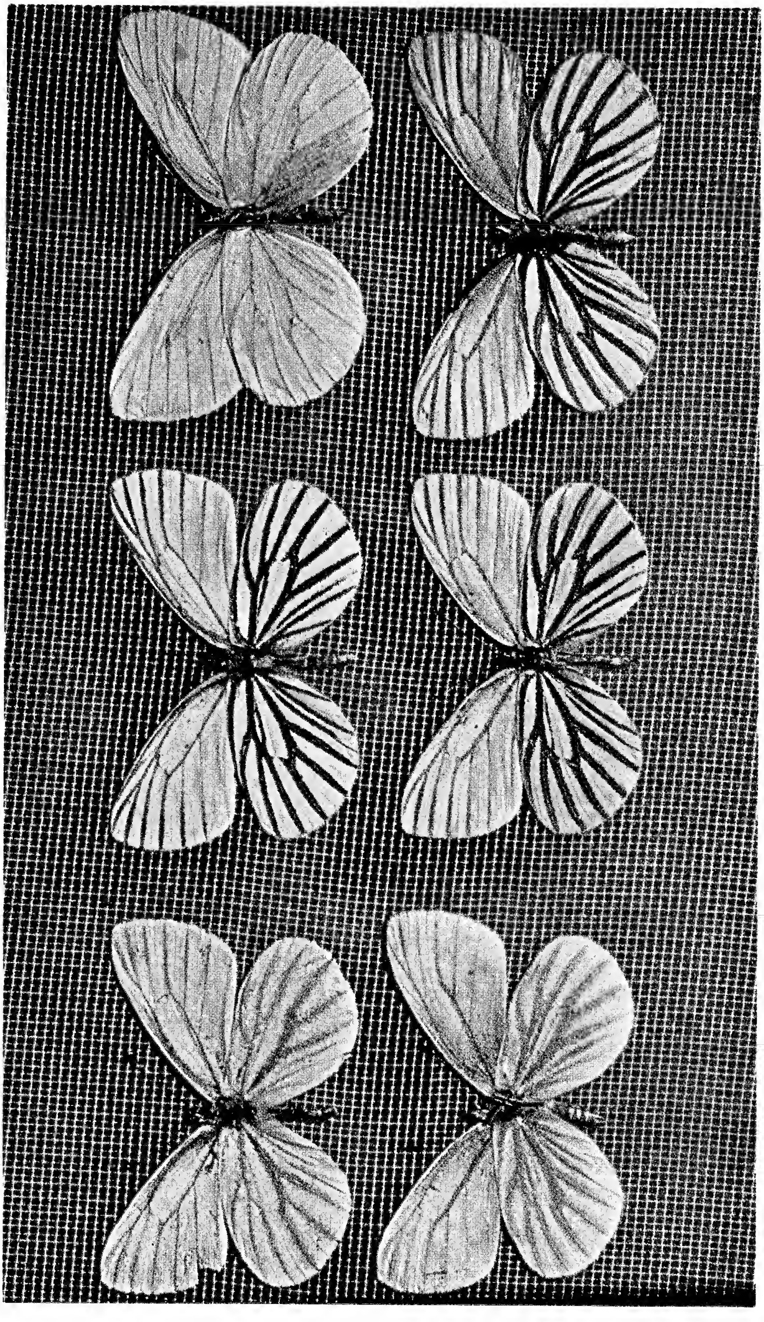

Fig. 3. Same as fig. 1, but all lower side facies

southern part of the distributional range of this species. They are however typical in appearance. Note the difference between the two races on both the upper and lower surfaces: *virginiensis* is more of chalky white on the upper side as compared with *oleracea;* the wings on the upper side tend to be veined with black near the borders and cell in *oleracea* which is replaced with a brownish "*rapae*-type" pattern in *virginiensis;* on the under side the veins are heavily lined with black in *oleracea* in a way distinctive from that of *virginiensis;* and there is a yellowish suffusion on the under side of the wings in *oleracea* not present in *virginiensis.* On the other hand, the appearance of *oleracea* changes during the seasons while that of *virginiensis* does not. There is no indication that *virginiensis* has more than the one generation per year, this occurring in early May whereas *oleracea* has a succession of generations starting in April and extending throughout the year until the cold weather of the autumn. During this extended period the weather conditions are quite different, and the effects of this on the appearance of *oleracea* are profound. The appearance of the adults emerged during the warmer part of the season are quite different. A specimen of the summer brood is shown in figures 2 and 3 at the upper right. Note the slightly increased size but more important the almost complete absence of any pigment other than white on the wing surfaces. These summer forms have been given the names *hyemalis, acadica* and *aestiva* by Edwards for the general area under consideration. As a racial name, the only one of any significance however is *oleracea.* Throughout the ranges of these races, there is fairly good uniformity in pattern and characteristics; however, it should be pointed out that within each of these races and especially *oleracea* there is a great amount of variation which tends to blend the two together. For example, a specimen at the bottom right in figures 2 and 3 is from a population of *oleracea* but shows the "*rapae*-type" pattern of *virginiensis.* The underside of the wings however makes clear that the specimen is *oleracea.*

Areas of typical *oleracea* may be described as follows: The Canadian forest areas ranging from northern Michigan across northern Ontario and Quebec into eastern Quebec, New Brunswick, Nova Scotia, Maine and the mountainous parts of the New England states as far as Massachusetts. South of these points and until the typical populations of *virginiensis* are reached in New York state, Ohio and Pennsylvania, the populations apparently are in a state of uncertainty regarding a complete divergence from the *virginiensis* or the *oleracea* genome and all the things pertaining thereto, including in addition to pattern differences, the physiological alterations required for the more southern existence, the univoltine life cycle and the changed food plant preferences. These intermediate populations lie in a line ranging from Michigan, across southern Ontario to Montreal in Quebec and southward to the Catskill Mountains of New York. Some of these can be distinguished as *oleracea* with *virginiensis* tendencies and others as *virginiensis* with *oleracea* tendencies, though the former outrank the latter. Populations which would be considered *oleracea* with *virginiensis* tendencies would be the following, with an indication of the extent of the tendency:

Michigan: Emmett Co., north part of southern peninsula (slight)
Ontario: region around London, Huntsville, Sydney Field station, Marmora, Trenton (considerable)
————: Aylmer, Bells Corners, Brittania, South March, Merivale, Constance Bay, Ottawa West (slight)
Quebec: Harrington Lake, Gatineau Park (slight)
Massachusetts: Cummington, Whately, Franklin Co., Mt. Greylock

Populations which would be considered *virginiensis* with *oleracea* tendencies would be:

Quebec: Ile Perrot (Montreal)
New York: the Adirondacks, the Catskills, Ilion, McLean
Ontario: Hamilton

Populations with little sign of intergradation on the northern end of the range of *virginiensis*:

Pennsylvania: Scranton, New Brighton, Pittsburgh, Forbes Forest, Charlevoi, Showville, Washington Co., Fayette Co., Lawrence Co.
Ohio: Canton
West Virginia: Forks of the Kanawha, Coalburgh

HABITS OF THE RACES

The rather distinct break between the geographical ranges of *oleracea* and *virginiensis* would seem to need some isolation barrier for the maintenance of its integrity. This barrier is clearly not one of water or mountain but rather one of habitat selection and the accompanying biological changes in the physiology of the races concerned. For some idea of the field habits of these races, we may refer to other authors:

Klots (1951) says of *virginiensis*:

> "Until very recently, *virginiensis* has been confused with *napi,* but it is now known to be a distinct species of more southern (Transition Zone) distribution. Its dark markings are a more smoky, diffuse brown and it lacks the yellowish tint beneath, on the HW and apex of the FW, which *napi* usually has. It is single brooded. More even than *napi,* it is limited to woods and very local."
>
> "Food: — Toothwort (*Dentaria diphylla*), probably other *Dentaria.* One brood. Adults in early May (central New York."
>
> "Range:—Transition Zone, Ontario, central New England and New York, s. to Virginia (TL. Kanawha, West Virginia)."

He says of napi *oleracea*:

> "*Napi* has . . . suffered a great restriction in habitat, and probably in habits, for it is now almost entirely limited to shaded Canadian Zone forest . . . *P. virginiensis* lacks yellowish beneath on the HW and apex of the FW and has the scaling along the veins of the HW and costa and apex of FW beneath much more diffuse and powdery looking. A rare dark form of *P. rapae* lacks dark spots above, but never has the dark-lined veins of *napi,* and has heavier scaled, less fragile looking wings."
>
> Food. Formerly, at least, nearly any cultivated or wild cruciferae; now probably chiefly limited to native, woodland species, such as toothworts (Dentaria), Rock cresses (Arabis), Winter and Water cresses (Barbarea), etc.

Three broods. Adults in late April (Massachusetts)." "Not recorded s. of the Catskill Mountains in New York."

Clark (1951) says of *virginiensis*:

"Range:—One record, Frederick County northwest of Cross Junction on the Bloomery Road (Rank 698) about 200 feet east of the West Virginia line, April 24, 1938."

"Variation — This species varies considerably in the intensity of the bordering of the veins on the under side of the hind wings. This bordering is pale in all the individuals from Virginia and adjacent West Virginia that we have seen, some having the under side of the hind wings almost immaculate white."

"Occurrence:—Confined to rich deciduous woods and extremely local, occurring in limited numbers at usually widely separated localities. The reduction in the numbers of *Pieris virginiensis* and its present occurrence only in widely separated localities are undoubtedly the result of deforestation, which has greatly reduced the areas in which it is possible for it to maintain itself." "*Pieris virginiensis* keeps strictly to the woods."

"Season:—One brood. This species appears shortly after the middle of April and flies until about the middle of May."

Clench (1958) writes of the same:

"*Pieris virginiensis* . . . common in woods . . . one brood: Late April to mid-May. One . . . capture . . . on 4 June, 1958 is surely a freak occurrence . ."

Scudder (1889) writes of the habits of *oleracea*:

"Food plants. This caterpillar feeds on various cultivated cruciferous plants, such as turnip (*Brassica rapa*), cabbage (*B. oleracea*), radish (*Raphanus sativa*), horseradish (*Nasturtium armoracia*) and mustard (*Sinapis*). Mr. Lintner considers that it prefers turnip to cabbage, for he once obtained fifty eggs fom a turnip bed and could find none on adjacent cabbage plants of the same age, and this has been my experience." Hoy, on the other hand, thinks it is found mostly on mustard. But it also occurs on some of our native plants, such as *Arabis drummondi* (Couper) and *A. perfoliata* (Fletcher), and Fitch says it occurs abundantly on the water cress (*Barbarea vulgaris*)."

"Life History. This butterfly, which appears to be generally triple brooded, passes the winter in the chrysalis, the first brood has been seen as early as April 18, but usually appears between April 27 and May 9, a week or thereabouts after *P. rapae.* For several years Fitch observed it at East Greenwich, N. Y. for the first time on May 8 and 9 and only once as early as May 6; in northern localities it is sometimes as late as the third week in May. It usually becomes abundant between the 10th and 15th of the month and continues unti the end of the first week in June. The eggs are laid during the last half of May and early in June, and hatch in from 5 to 10 days . . . the second brood . . . makes its advent during the last days of June or early July . . ., this brood in *oleracea* seems never to be very abundant . . . and to maintain itself for a comparatively short time; it becomes common by the end of the first week in July and sometimes disappears . . . before the end of the month . . . "The third brood appears as early as the last days of July but usually not before August; it . . . lasts until early September . . . Occasional specimens, . . . disclose butterflies late in September or early in October." "The species must be triple brooded in the north."

Edwards (1868-1872) writes of *virginiensis*:

"In the Kanawha district it replaces *Oleracea* which is yet unknown there. It is not uncommon in the month of May, frequenting open woods rather than gardens, and in this respect differing in habit from the allied species. I have never met with it later than June, though *Oleracea* in the

Northern states is most abundant after that month and continues breeding til the early autumn frosts." "I have received specimens of *Virginiensis* from Mr. Wm. Saunders of London, Canada and am informed by him that it is there a rare insect."

These data would tend to confirm the evidence derived from the data of museum specimens that *oleracea* is indeed a multivoltine race which breeds from April all through the year until the Autumn frosts. Our own personal experience on *napi* in California does not conflict with this opinion. Here *napi* (*venosa* and *castoria*) are continuously brooded when possible in relation to temperature and moisture conditions. They go into diapause when conditions of the food plant are unfavorable; this is usually in the summer when the food plant (*Dentaria*) dries up. In fact much of the first winter generation does likewise as Dentaria does not stay green long. This accounts for the summer or late spring generations being less abundant than the winter or early spring generations. A similar observation has been made of the generations of *napi* in New England.

The food plant difference between the races *oleracea* and *virginiensis* is important in only one way, namely in the restriction of habitat of *napi* to a different ecological niche. *Dentaria* is a plant of the open woods and partial shade. The flight period of *virginiensis* must be adjusted to meet the proper conditions of moisture requirement for the plant as well as for the degree of light availability in the deciduous forest where early spring may allow more light in the forest than in summer. The restriction of *virginiensis* to the "Transition" life zone forest may be correlated with this light and temperature relationship. The northern forest is cooler all summer long and the temperature needs of *oleracea* can be met usually in the open areas as well as in the partial shade of the forest. This would account for the different flight habits of the two races. In California, *napi* (*venosa* and *castoria*) fly only in the cool canyons where there is partial shade even though there is abundant food available for them outside in the form of wild mustards. Instead they are restricted to *Dentaria* of the shaded woods, while *Pieris rapae* and *P. protodice* fly only a few yards away in the direct sunlight and feed upon mustards.

The food plant of *oleracea* so often indicated in the literature is winter or water cress (*Barbarea*) which is apparently restricted to the vicinity of streams. There is indication that in the Catskill Mountains (New York) there may be a population of *virginiensis* on *Dentaria* while sympatrically there are populations of *oleracea* on *Barbarea.* If this is so, an excellent study could be developed to show the nature of the racial or specific isolation of these two at a region where both maintain reasonably distinct populations in close contact. The fact that *oleracea* flies in April, *virginiensis* in May and *oleracea* again in June and July indicates another additive isolation factor which would help to maintain the species or racial distinctness.

By way of conclusion, the data presented show rather conclusively that *Pieris napi oleracea* and *Pieris napi virginiensis* are not as completely separated as one might wish "species" to be but that they are not either fully racial or subspecific in the sense that their populations blend into one another as by a continual gene flow. It is therefore a matter of personal opinion whether they should be considered species or races for nomenclatorial purposes. For these purposes it is impossible to stand on the middle ground as a choice must be made. I choose to use the racial designation for the reason that the groups are almost completely allopatric, that is, the populations are geographically separated and do not occur in the same place with certainty without interbreeding and complete fusion. Also, intermediates do occur with high frequency in intermediate geographical areas. There is work to be done in this regard on the ground in important areas, such as, the Catskill Mountains, Ile Perrot (Montreal) or any other areas where a potential close unity of the two appears.

The past changes in the distribution of the species have been greatly exaggerated, especially with regard to any competition between *P. rapae* and *P. napi.* The habits of the two species are so distinct that no competition can reasonably exist. Past records of *P. napi* feeding on garden or cultivated cruciferous plants are undoubtedly correct but these larvae came from adults flying out of adjacent woods to lay their eggs on any cruciferous plants available. With the destruction of the woods in the New England states, the habitat for *napi* disappeared and then of necessity *napi* disappeared. This was the situation for the low lands. In the mountains, *napi* still exists as it did in the past.

REFERENCES

CLARK, A. H. 1951. The butterflies of Virginia. *Smithsonian Misc. Collections,* 116(7):1-195.

CLENCH, HARRY K. 1958. The butterflies of Powdermill Nature Reserve. *Research Report #1. Powdermill Nature Reserve, Carnegie Museum, Pittsburgh, Pa.*

EDWARDS, W. H. 1868-1872. Butterflies of North America. Philadelphia. *The American Entomological Society.*

FISKE, Wm. F. 1901. An annotated catalogue of the butterflies of New Hampshire. *New Hampshire College, Durham, N. H.*

HOVANITZ, WILLIAM. 1949. Increased variability in populations following natural hybridization. In *Genetics, Paleontology and Evolution, Princeton.*

————. 1962. The distribution of the species of the genus Pieris in North America. *J. Res. Lepid.* 1(1): 73-83.

KLOTS, A. B. 1935. On the life history of *Pieris virginiensis* Edws. *J. N.Y. Entom. Soc.,* 43: 139-142.

————. 1951. A field guide to the butterflies of North America, East of the Great Plains. *Houghton Mifflin Co., Boston.*

McHENRY, PADDY. 1962. The generic, specific and lower category names of the Nearctic butterflies. Part I. The Genus Pieris. *J. Res. Lepid.* 1(1): 63-71.

SCUDDER, S. H. 1889. The butterflies of the eastern United States and Canada. Vols. I-III, *Cambridge, Mass., author.*

Journal of Research on the Lepidoptera 1(2):135-156, 1963

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THE MALE GENITALIA OF SOME COLIAS SPECIES

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In most families of Lepidoptera the genitalia show such distinctive characteristics that it becomes easy to separate even closely related species. In the family *Pieridae* conditions are different. *Pieris napi* L., *P. bryoniae* Ochs., and *P. ergane* Hbn. are not separable on the basis of their male genitalia, nor are *P. rapae* L. and *P. manni* Mayer (Lorkovic 1928, Drosihn 1933). Similar conditions are present in the genus *Colias.*

Before going into details a general description of the male genitalia of *Colias* will be given (cf. fig. 1). The distal part of the VIIIth tergum is more or less slender, Kusnezov (1915) has called this part the superuncus, Warren (1950) named it the false uncus. At the base of the superuncus the tergum is incompletely sclerotized laterally. The saccus is rounded, sometimes pointed on its sides. The vinculum is long and slender. The tegumen shows a narrow process dorsally, the pseudouncus (Kusnezov 1915). The aedeagus has a long ventral arm.

According to Warren (l.c.) the claspers at their proximal end are restricted to a blunt point, attached to the vinculum. The dorsal edge is said to be drawn upwards, parallel to the vinculum, and the dorsal terminal extremity attached to the tegumen. These statements do not correspond to conditions found in *Protocolias imperialis* (Pl. I, fig. 1). In this species the proximal part of the claspers is rather similar to that of other *Colias* species. The distal part is protracted so that the clasper obtains a shape more or less similar to that of many other Pierids. It may therefore be concluded that the clasper-head with the terminal tooth is the dorsal part of the clasper.

The short pseudouncus and the marked distal lobe of the clasper give to *P. imperialis* a rather isolated position. In some characteristics it comes closer to the genera *Catopsilia* and *Anteos.* In other respects, however, such as the structure of the clasper head, *P. imperialis* is similar to *Colias,* thereby showing the relationship between these genera (cf. Klots 1929 a and b).

In the genus *Colias* the genitalia are rather variable within a species or subspecies, as will be shown below. At the same time the differences between some species are only slight. Therefore a biometrical approach seemed necessary as a complement to the general descriptions of the genitalia. The modes of measuring and the results are given first as important for the full understanding of the descriptions.

The breadth of the superuncus. The edges of the superuncus in dorsal view may a) converge distally b) run parallely or c) diverge slightly from a narrow part near the base (cf. fig. 2). The breadth was on diverging superunci measured at the narrowest basal point, on others at the corresponding place.

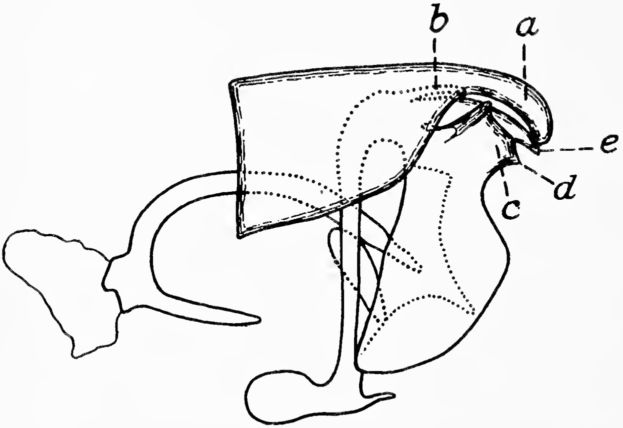


Fig. 1. The male genitalia of a *Colias*. *a* superuncus *b* pseudouncus *c* clasperhead *d* tooth of clasperhead *e* uncus

The size of a certain part of an individual may be influenced by its general size. The breadth of the superuncus has therefore been correlated with a measure of size: the wing length.

All species with genitalia similar to those of the three species previously investigated: *C. hecla, nastes* and *palaeno* are included in fig. 3. Here the breadth of the superuncus is plotted against the wing length in a logarithmic scale. The populations investigated are parted in two groups, the first with a slender superuncus, the second with a broad one. The regression line of the populations with a slender superuncus is:

$$\log \underline{y} = 0.75 \ \log \underline{x} + 0.68; \ (\underline{r} = 0.72; \ 0.02 > \underline{P} > 0.01).$$

The species along this regression line are both orange with a *hecla*-pattern, yellow with a *hecla*-pattern, and yellow with a *nastes*-pattern. The species in fig. 3 with a broad superuncus are either orange with a *hecla*-pattern or yellow with a *nastes*-pattern. These two types of species can be grouped along two regression lines. Within both groups the correlation is statistically significant.

Orange species:
$\log \underline{y} = 0.80 \log \underline{x} + 0.77;\ (\underline{r} = 0.71;\ 0.05 > \underline{P} > 0.02).$

Yellow species:
$\log \underline{y} = 1.17 \log \underline{x} + 0.30;\ (\underline{r} = 0.81;\ 0.05 > \underline{P} > 0.02).$

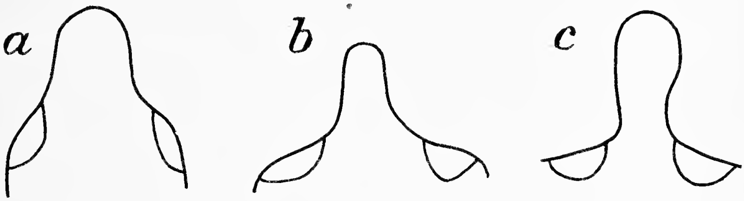


Fig. 2. Differently shaped superunci with semicircular, less sclerotized areas near the base. *a* convergent *b* parallel *c* divergent

The means of the two groups are, however, not significantly separated. An analysis of covariance gives $0.1 > \underline{P} > 0.05$.

The data on which fig. 3 have been based are tabulated in Tables 1 and 2. Among the species shown in these tables *C. nastes* is of special interest. In Scandinavia and in North America but also in Altai and the Sayan Mountains the superuncus is slender. *C. nastes* of Siberia and the Amur Province is intermediate between *nastes* of the Altai and the Sayan Mountains and the closely related, allopatric *C. montium* from S. Kansu. This species forms a transition to *C. cocandica* from Ferghana, the Issykkul, and from the Tianshan. The superuncus-breadth of all Asiatic individuals of *nastes* is plotted against wing length in fig. 4. The populations are grouped along two regression lines, though the correlation in none of the groups is statistically significant (cf. Table 1). An analysis of covariance, however, shows that the means of the two samples (shown in the figure by squares) are significantly different ($0.01 > P > 0.001$).

In the yellow series of forms there is thus no sharp limit between species with slender and broad superunci. Even within a single population, that from the Amur Province — the variation is so great that it includes superunci typical for *nastes nastes* and others typical for *cocandica* (cf. fig. 4). In the orange series of forms conditions are different as will be treated later. In fig. 5 the superuncus breadth of arctic *C. nastes* and of its sibling in the Alps, *C. phicomone,* is plotted against wing length. The differentiation has proceeded so far that hardly any overlap is present.

The wing length and breadth of the superuncus in some other *Colias* species, less similar to those treated above, are shown in Table 3. In the three pairs at the top of the table the genitalia are so similar that

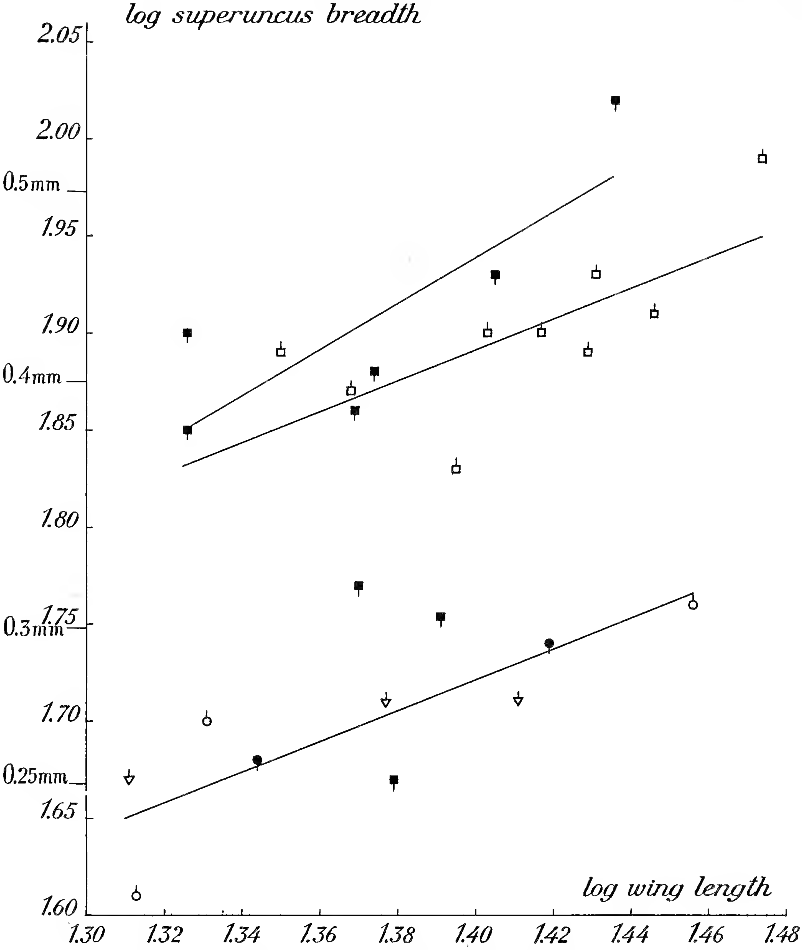


Fig. 3. Superuncus breadth of some *Colias* populations plotted against wing length. Data from Tables 1 and 2.

O Population from N. America or northern Eurasia

☐ Population from Central Asia or Central Europe

△ *C. palaeno* and *interior*

rod above=*hecla* patterns	open mark=orange color
rod below=*nastes* patterns	filled mark=yellow color

no constant differences could be found. Warren (1950) states some differences between *C. australis* and *hyale*, a statement which was not confirmed by the specimens investigated.

Two of the species of Table 3, *C. cunninghami* and *P. imperialis*, have an extremely broad superuncus. *C. vautieri*, which otherwise is

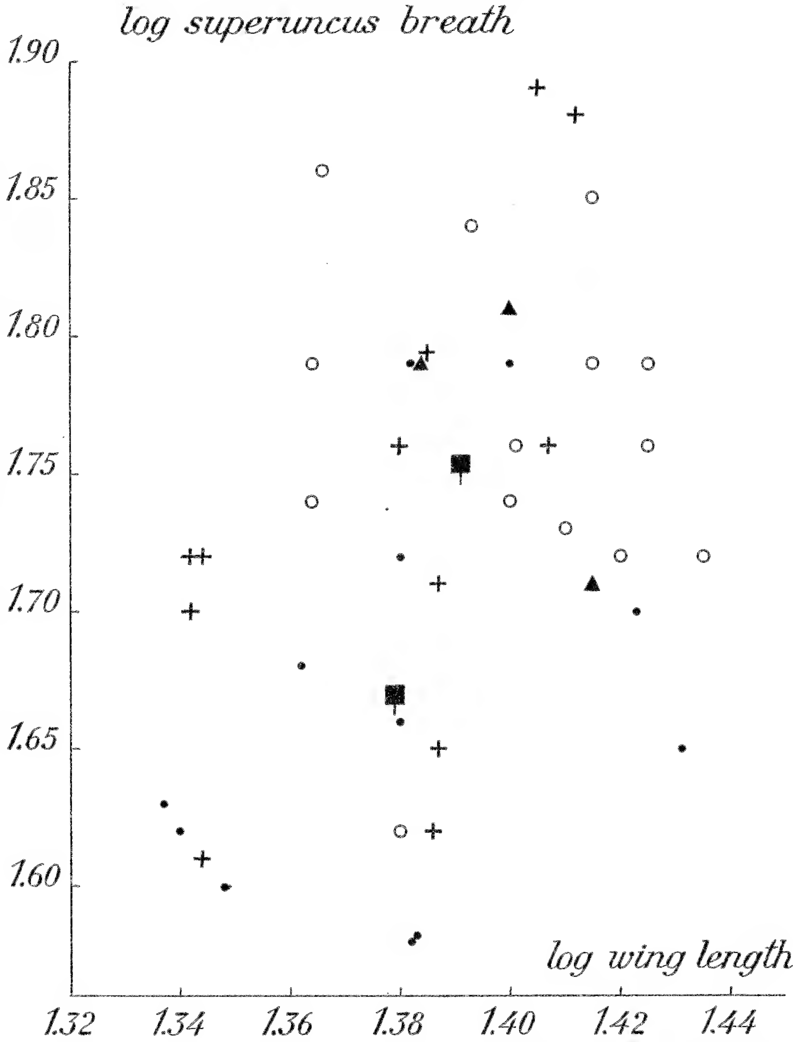


Fig. 4. Superuncus breadth of some Asiatic populations of *C. nastes* plotted against wing length. The lower square represents the mean of the dots, the upper square the mean of the remaining marks.

● Altai and Sayan Mts.
O Siberia, Taiga zone
▲ Transbaikal
+ Amur Province

rather aberrant, *C. erate,* and *myrmidone* fit well into the group of species with a broad superuncus, listed in Table 2. The remaining four species have a more slender superuncus though *C. hyale* and *australis,* like *C. montium* occupy a somewhat intermediate position.

The form of the superuncus in lateral view. During copulation

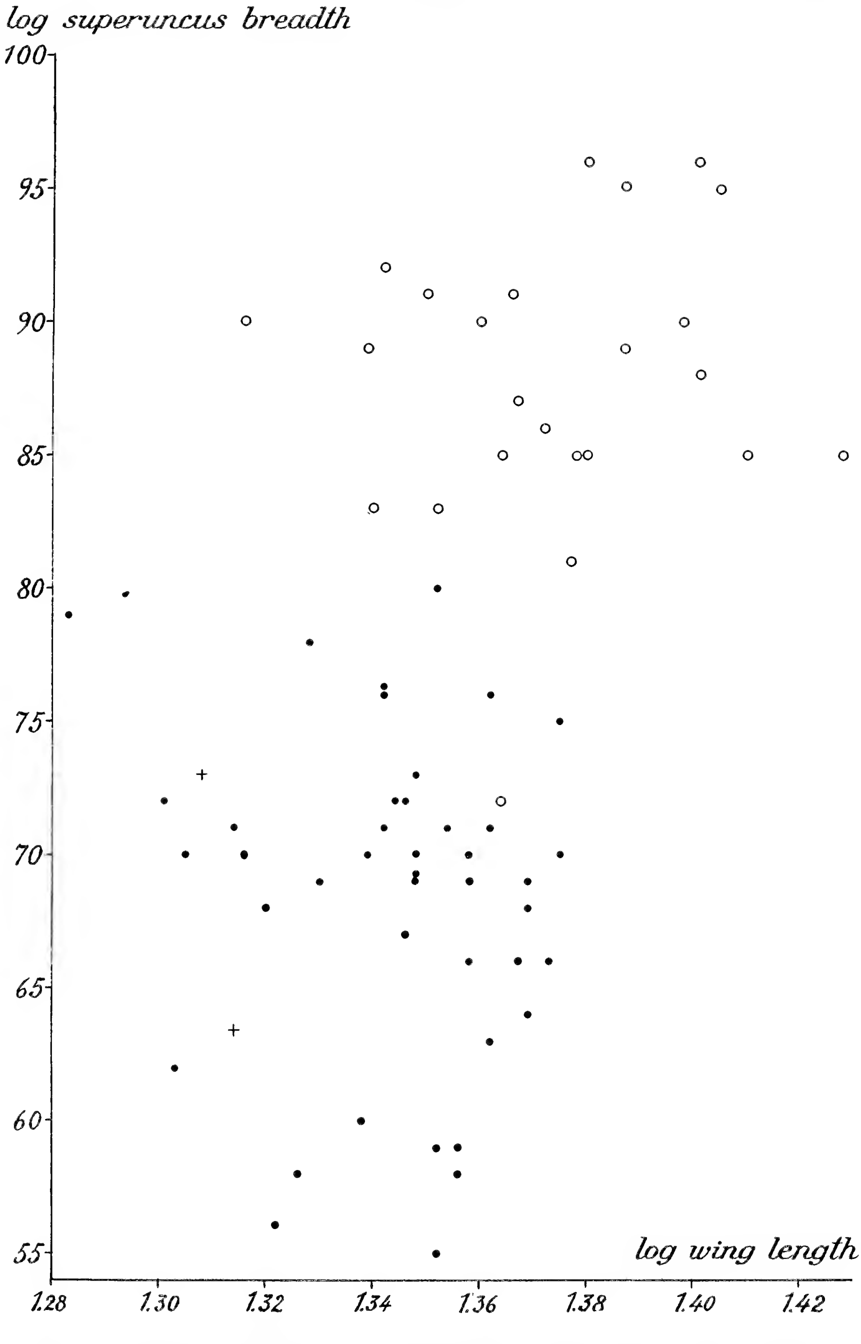


Fig. 5 Superuncus breadth of *C. phicomone* (open circles) and *C. nastes* (filled circles = Scandinavia, + North America) plotted against wing length.

the superuncus together with the uncus is pressed against the body of the female, just as the uncus in the genus *Pieris* according to Lorkovic (1947). To make possible the bending down of the superuncus during copulation a semicircular area laterally on the VIIIth tergit is less sclerotized than the rest (cf. fig. 2). This bending can be stated without studying any copulating pairs. In some specimens the superuncus is broken (cf. fig. 6), in some in addition kept between the two claspers.

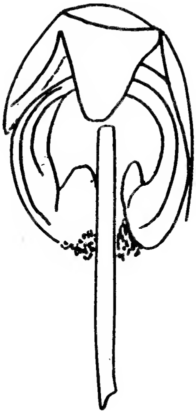


Fig. 6. *Colias interior* with superuncus broken during copulation.

The breadth of the superuncus of such specimens sometimes cannot be measured without maceration. A broken superuncus was found in all species where more than a few specimens were investigated, as shown in Table 4.

Only in very few species the superuncus is a straight process protruding from the VIIIth tergit. Also when unbroken the superuncus usually forms a bow downwards. This bow is present, even in its most pronounced form, in animals which have not copulated, as, for instance, in all the thirty *C. hecia* specimens investigated which in 1952 were caught at the beginning of the flying time on the northern side of the Lake Torne Trask.

To obtain a quantitative estimation of the variation of the form of the superuncus in lateral view, the angle of the distal part of the superuncus to the dorsal edge of the VIIIth tergum was measured. The result of this investigation is shown in Table 4. In general a broad superuncus is only slightly bent downwards while a narrow is bent more. The exceptions are rather few: *C. interior, montium,* and *phicomone.*

Species	n	$M_{\log x}$	$M_{\log y}$	r	P_r	b_x
A. Orange species						
C. hecla, Scandinavia	51	1.331	1.70	-0.18	0.3-0.2	-0.74
-"- , Siberia, Dudinska	4	1.355	1.67			
-"- , Baffin, Isl.	2	1.347	1.79			
-"- , Greenland	3	1.362	1.74			
C. hyperborea, N. Siberia	4		1.69			
C. eurytheme, N. America	6	1.456	1.76			
-"- , slightly orange Texas, Houston	6	1.313	1.61			
B. Yellow species						
a. hecla pattern						
C. palaeno, Europe	41	1.411	1.71	0.18	0.3-0.2	0.50
C. palaeno, Siberia	9	1.377	1.71	0.57	0.2-0.1	1.73
C. interior	2	1.311	1.67			
b. nastes pattern						
C. nastes, scandinavia	42	1.344	1.68	-0.09	0.6-0.5	-0.24
-"- , Siberia, Amur area	29	1.391	1.75	0.32	0.1-0.05	0.87
-"- , Altai, Sayan Mts.	12	1.379	1.67	0.35	0.3-0.2	0.86
-"- , N. America	2	1.311	1.68			
C. philodice, N. America	11	1.419	1.74			
C. montium, S. Kansu	9	1.370	1.77			

Table 1. Wing length (x), in mm, and breadth of superuncus (y), in an arbitrary scale, and their correlation in some Colias species with a slender superuncus. Logarithmic scale.

C. interior is in this character well separated from its allopatric sibling, *C. palaeno,* in having a rather straight but slender superuncus.

C. montium has a rather slender superuncus which is straight as is that of *cocandica.* In this respect another of the southern species, *C. phicomone,* is intermediate between *nastes* and *cocandica.* The superunus of *phicomone* is, however, rounded and not more or less pointed as it is in all other species with a slender superuncus except *C. interior, aurorina,* and *sagartia.*

By means of the two characteristics, *i.e.* the breadth and the form of the superuncus, it is possible to separate the two species *C. viluiensis* Mén. and *hyperborea* Gr. Gr. which live sympatrically in N.E. Siberia. Of *viluiensis* 7 specimens from the Verchojansk area, Lutsha near Yakutsk, Vilutsk and Vilui have been investigated. The four specimens of *hyperborea* were from Sib. pol., the Lena Valley

Species	n	$M_{\log x}$	$M_{\log y}$	Species	n	$M_{\log x}$	$M_{\log y}$
Orange species, hecla-pattern				Yellow species, nastes-pattern			
C. chrysotheme	5	1.350	1.89				
C. croceus, Europe	10	1.403	1.90	C. alpherahyi	1	1.436	2.02
-"- , Asia	11	1.429	1.89	C. christophi	1	1.369	1.86
C. eogene	8	1.368	1.87				
C. heos	12	1.474	1.99	C. cocandica	2	1.326	1.85
C. remanovi	2	1.446	1.91	C. phicomone	24	1.374	1.88
C. standingeri	6	1.395	1.83	C. sieversi	1	1.405	1.93
C. thisoa	2	1.417	1.90	C. sifanica	1	1.326	1.90
C. wiscotti	9	1.431	1.93				
C. viluensis	7	---	1.90				

Table 2. Wing length (x), in mm, and breadth of superuncus (y), in an arbitrary scale, in some Colias species with a broad superuncus. Logarithmic scale.

and Sredne Kolymsk.. The latter specimens all have a slender and strongly bent superuncus of the *hecla*-type, while all specimens of *viluiensis* have a straighter and broader superuncus. There is no overlap in any of the two characters; in the "angle-character" the gap is very wide.

In *Colias nastes* from Asia there is no similar correlation between the breadth and the shape of the superuncus. Among the 41 specimens investigated the coefficient of correlation is +0.093 which is far below significance ($0.8 > P > 0.7$).

Conditions are thus quite different in northern Asia as regards the *nastes*- and *hecla*-series of forms. In the *nastes*-series clines including characters of the genitalia reach the Amur area, Transbaikal, the Sayan Mts, and the Altai, and forms intermediate between arctic and Central Asiatic ones are present in North Western China and in the mountains of Central Europe. In the orange series of forms an overlap of a northern and a southern species is present between 65°-68° n. latitude and no intermediates have yet been found between these species.

Number of teeth near apex of aedeagus. In many groups of insects the number, shape, and position of the aedeagal teeth serve as good evidence to distinguish species. In the *Colias* species all the teeth are small, of a rather similar shape, situated near the apex. Variation in number is strong even within subspecies when compared with the differences occurring between species. Thus this character is without significance for the determination of individuals. A closer investigation of a material belonging to the group of species with a slender super-

	n	$M_{\log x}$	$M_{\log y}$
C. aurorina	6	1.449	1.80
C. sagartia	5	1.437	1.76
C. australis	8	1.384	1.74
C. hyale	27	1.373	1.79
C. erate	13	1.387	1.94
C. myrmidone	7	1.425	1.95
C. cunninghami	2	1.367	2.01
C. vautieri	2	1.327	1.83
P. imperialis	1	1.356	2.05

Table 3. Wing length (x), in mm, and breadth of superuncus (y), in an arbitrary scale, in some Colias species.

uncus, however, revealed some slight specific differences in the average number of teeth (cf. Table 5). The results of this investigation are:

C. nastes has on an average fewer teeth than *C. hecla* from the same locality (Scandinavian material $t = 2.45$; $0.02 > P > 0.01$, American material not differing significantly. There is a certain tendency of parallelism, both species having a lower number of teeth in Scandinavia than in North America. This tendency is not significant in any of the species, however. *C. palaeno* and *interior* both have a low number of teeth, while the number is fairly high in *C. meadi, philodice,* and *eurytheme.*

SPECIAL PART

The genus *Colias* may be parted in two genera: *Protocolias* (type *imperialis* Btlr.) and *Colias,* the latter in turn in two subgenera *Mesocolias* (type *vautieri* Guér.) and *Colias.* The descriptions of the genera, the subgenera and their various species may be given most easily in the form of a key.

1\. Small or medium-sized, orange butterflies with broad (0.40-0.45 mm) or very broad (0.5 mm), straight superunci. Superficial scales —if present—yellow and black, broad and flattened in the distal part. Apex of aedeogus without teeth.
Genus *Protocolias* and subgenus *Mesocolias* 2.

1'. Small to big, yellow, greenish or orange species with broad to slender (0.32 mm) superunci. Superficial scales in the black margin—if present—yellow, pointed, hairlike or broader. A number of teeth at apex of aedeagus
Subgenus *Colias* 3.

2\. Superuncus very broad and triangular. Pseudouncus short. Clasperhead with elongated tooth. Middle part of the clasper with a marked prong. Ventral arm of aedeagus broader in the distal end. Black and yellow superficial scales present.

Protocolias imperialis Btlr. (Pl. I:1)

2'. Superuncus broad. Tooth of clasperhead slightly bent upwards. Ventral lobe (v.l.) of inner side of the clasper (Klots 1929 a) more marked than in any other species of the genus. Distal part of ventral arm of aedeagus showing characteristic shape. Superficial scales absent.

Colias (*Mesocolias*) *vautieri* Guér. (Pl. I:2,3)

2". Superuncus very broad, genitalia small, claspers short (1.0-1.1 mm) but broad (0.6 mm). Distal part of ventral arm of aedeagus not broader than the proximal one. Superficial scales absent.

Colias (*Mesocolias*) *cunninghami* Btlr. (pl. I:4).

3\. Claspers caudally with a marked prong directed medially. Superuncus straight and fairly slender.

C. hyale L. (pl. I:5) and *australis* Ver.

3'. Claspers without any marked prong ....4.

4\. Claspers pointed in the middle part of the caudal edge (most easily seen from behind) ....5.

4'. Claspers not pointed in the middle part of the caudal edge 6.

5\. Superuncus straight, on an average 0.40-0.45 mm broad

C. erate Esp., *C. myrmidone* Esp. (Pl. I:6).

5'. Superuncus usually markedly bent downwards, 0.30-0.35 mm broad.

C. sagartia Led. (Pl. I:7) *C. aurorina* H. Sch. (Pl. I:8).

6\. Superuncus on an average less than 0.32 mm broad (cf. text fig. 3) usually strongly bent downwards (cf. Table 4) ....7.

6'. Superuncus on an average broader than 0.35 mm, usually straight ....13.

7\. Superuncus only slightly bent downwards ....8.

7'. Superuncus strongly bent downwards ....9.

8\. Superuncus in caudal view blunt-ended as in species with a broad superuncus. Inner side of clasper of *hecla*-type (cf. Pl. II:34)

C. montium Oberth. (Pl. I:9, 10).

8'. Superuncus in caudal view pointed. Inner side of clasper with well developed ventral lobe and ridged from its dorsal edge dorsocaudally towards the caudal part of the clasper (Fig. 14, 15)

C. interior Scudd. (Pl. I: 11-13, II: 14, 15).

9\. Ridge from dorsal edge of ventral lobe towards caudal part of the clasper present as in *C. interior.* Ventral lobe less well developed than in *C. interior* (cf. Fig. 16). Caudal edge of clasper often strongly bent inwards (most easily seen in caudal view).

C. palaeno L. (Pl. II:16-25).

C. christina Edw. (Pl. II:26-28).

C. palaeno: is most variable in all characters investigated except the breadth of superuncus (cf. the figures). One specimen from Abisko (42 specimens studied) completely lacks the ridge on the inner side of the clasper. Hence it cannot with certainty be separated from *C. nastes* or *hecla.* The limited material of *C. christina* appeared rather close to some specimens of *palaeno,* though it might be possible to separate the two species after examining a greater material.

9'. The caudal edge of the valva less strongly bent inwards ventrally. Inner side of clasper reminding of *hecla*-type (cf. fig. 34) ....10.

10\. Clasper (in lateral view) broadest rather ventrally ....11.

10'. Clasper broadest in the middle part ....12.

11\. Aedeagus on an average with a higher number of teeth at the distal end ....*C. hecla* Lef. (Pl. II:29-39).

Species, Population	Angle												Frequency of superuncus broken
	5-14	15-24	25-34	35-44	45-54	55-64	65-74	75-84	85-94	95-104	105-114	M	
Pop. of Table 1.													
C. hecla, Scand. Mts.						1	3	3	4	2		82	7/50
" , N. America				1	1	1	3		2			68	
C. hyperborea									3	1		93	
C. meadi					1			1	3	2	1	89	
C. eurytheme						1		2	2		1	85	7/17
C. palaeno, Scand. Mts.							2	1	4	1		85	14/56
" , Europe		1			1	5	4	3	4			69	14/56
" , Asia				1		1	1	1	2			72	14/56
" , N. America					1	4	2	1	2			69	14/56
C. interior [christina]			6	2	3							36	1/12
C. nastes, Scand. Mts.					2	1	3	6	8	1		80	4/25
" , Asia					2	2	1	4	17	4		85	7/41
" , N. America						1	1	1	1			75	
C. philodice							1	3	2	1		84	4/11
C. berylla				3								40	2/9
Pop. of Table 2.													
C. chrysotheme		2		1		2						40	
C. croceus, Europe		2	1									27	2/12
C. eogene		1	1		2	1						42	

11'. Aedeagus on an average with a lower number of teeth. Very similar to *C. hecla* ....*C. nastes* Bdv. (Pl. III:35-38).

12. Bigger, superuncus broader ....*C. eurytheme* Bdv. (Pl. III:39, 40).
C. philodice Gdt. (Pl. III:41).

12'. Smaller, superuncus slenderer. ....*C. meadi* Edw. (Pl. III:42, 43).

13. Superuncus bent downwards ....*C. phicomone* Esp. (Pl. III:44).

14. Superuncus diverging, very broad near the distal end. Clasper (in lateral view) broadest ventrally. ....*C. croceus* Fourcr. (Pl. III:45).

14'. Superuncus often with parallel or converging edges or clasper broadest in the middle part ....15.

15. Clasperhead more strongly marked, tooth strongly developed. Ventral arm of aedeagus broad in the distal part.
C. wiscotti Stgr. (Pl. III:46, 47)

C. marcopolo Gr. Grsh. probably also belongs here. No material has been available for investigation. Professor Sheljuzhko informs

C. heos		2	1	1	3	1						40	2/10
C. romanovi			1									30	
C. staudingeri			3									30	2/6
C. thisoa					2							50	
C. wiscotti	1	3	2	1		1						29	
C. viluensis		2	3	1								28	1/7
C. alpherakyi	1											10	
C. christophi			1									30	
C. cocandica			2									30	
C. phicomone				2	3	2	1	4	4			69	2/24
C. sieversi		1										20	
C. sifanica			1									30	
Pop. of Table 3.													
C. aurorina				2				2	1			66	
C. sagartia		1		1			1	2				58	
C. australis			3	1		1						38	3/8
C. hyale		2	2		2	2						40	4/30
C. erate	1		1									20	2/15
C. myrmidone		1	1			1						37	
C. cunninghami		1										20	
C. vautieri		1										25	1/3
P. imperialis	1											10	

Table 4. Angle (in degrees) of distal part of superuncus to dorsal edge of proximal part of VIIIth tergum.

that Avinov and Kusnezov both place *marcopolo* together with *wiscotti,* the latter as a subspecies. According to Sheljuzhko both forms fly together in the Pamir area and are probably different species in spite of a great similarity in the genitalia.

15'. Clasper head less strongly marked ....16.

16. A number of species remain which due to lack of sufficient material and/or great similarity could not be separated from each other:

Yellow species with *nastes*-pattern: *C. alpherakyi* Stgr. (Pl. III:48), *C. christophi* Gr.-Grsh. (Pl. IV:49), *C. cocandica* Ersch. (Pl. IV:50) (Specimen figured with triangular saccus; in a second specimen investigated the saccus is rounded as in all other species), *C. sieversi* Gr.-Grsh. (Pl. IV:51), *C. sifanica* Gr. Grsh. (Pl. IV:52). These Central Asiatic species together with *C. nastes, phicomone, montium* and others form one or—most probably—two polytypic species.

	n	2	3	4	5	6	7	8	9	10	11	12	M
C. hecla, N. Am.	8					5	1	2					6.6
" , Greenl.	3			1	1	1							5.0
" , Scand.	30			2	7	9	8	4					6.2
C. meadi	10					4	1	3	1			1	7.6
C. eurytheme	12				3	3	5		1				6.4
C. palaeno, N. Am.	10		1	1	5	2		1					5.2
" , Asia	8		1		1	6							5.5
" , Estonia	8		1		3		2	1	1				6.1
" , Scand.	21	1	2	7	2	3	1	3	1	1			5.4
C. interior	11			3	4	2	2						5.3
C. christina	1					1							6
C. nastes, N. Am.	6				1	4		1					6.2
" , Asia	5				1	3	1						6.0
" , Scand.	23		1	4	8	5	5						5.4
C. philodice	5				1	2	1				1		7.0

Table 5. Number of teeth near the apex of the aedeagus of Colias species with a slender superuncus.

Orange species with *hecla*-pattern: *C. chrysotheme* Esp. (Pl. IV:53), *C. eogene* Fldr. (Pl. IV:54, 55), *C. staudingeri* Alph. (Pl. IV:56), *C. thisoa* Mén. (Pl. IV:57), *C. viluiensis* Men., and *C. heos* (Pl. IV:58, 59). As in the previous group it is uncertain whether all these forms deserve each a specific status.

Orange species with *nastes*-pattern: *C. romanovi* Gr. Grsh. (Pl. IV:60).

This enumeration of *Colias* species is not complete.

DISCUSSION

The key given above does not show the phylogenetic relationships. These are, due to extensive introgressive hybridization, very difficult to find out. Suppose species A is closest related to the allopatric species B which has given rise to species C sympatric to A. Due to the introgressions A ➤ C or C ➤ A it is then possible that A and C are more similar in several characters than A-B or B-C. However, some characteristics, as for instance those on which the isolation between A and C depend, are likely to be of maximum difference in the case A-C.

Among the *Colias*-species investigated there exists a number of pairs of species within which the male genitalia are very similar: *C. eurytheme-philodice; C. hecla-nastes; C. aurorina-sagartia; C. myrmidone-erate; C. hyale-australis* and probably also *C. palaeno-christina* and *C. wiscotti-marcopolo*. Introgression has among these been established between *C. eurytheme-philodice* (Hovanitz 1949 a, b) and between *C. hecla* and *nastes*. Hybridization has been suggested between *C. sagartia* and *aurorina* (Lederer 1941). It is possible that pairs of a similar kind are present in Central Asia among the species figured from number

48 to number 58. Lederer (1941) mentions, among other suspected hybrids, specimens which have been supposed to be hybrids between *C. eogene* and *cocandica.* A number of species with different genitalia have been seen in copula (Lederer l.c.): *hyale* x *myrmidone, hyale* x *croceus, hyale* x *erate, croceus* x *erate,* and *hyale* x *phicomone.* The last cross gave rise to some larvae which died before the pupation. All these species have markedly different genitalia and are probably not very closely related. It therefore seems uncertain whether hybridization in these cases can give rise to introgression. If introgression occurs it must be possible to observe this fact also on the genitalia.

In all the pairs of sibling species first mentioned (*eurytheme-philodice* etc.), except *hyale-australis* and *palaeno-christina,* colors, and in most cases also patterns, are different. The first species is usually orange with a *hecla*-pattern, the second yellow with a *nastes*-pattern. Only *C. sagartia* has in addition a blue pigment which is present in some individuals of its orange sibling *aurorina.*

The common occurrence of differences in color and pattern between sibling species suggests that these colors are integrating part of the isolating mechanisms within the pairs. Sexual isolation of this kind has in the pair *Pieris napi-bryoniae* been established by Petersen, Tornblom and Bodin (1952). Males of both species are attracted by the white color of the *P. napi* female. The yellow female of *bryoniae* attracts the males solely by means of movements and odors. No releasing effect of any of the types of pattern was obtained neither in these pierids nor in similar experiments with the Silverwashed Fritillary (*A. paphia* L.) (Magnus 1954). Different color but probably not different pattern may therefore play a role for the sexual isolation between *Colias* species.

The geographical distribution of some subdivisions of the genus Colias may also be discussed. *Protocolias* and *Mesocolias* are entirely South American. The species of the subgenus *Colias* with a broad superuncus are all Palearctic, one group having penetrated even into the Ethiopian region. *Colias* with a slender superuncus are mainly distributed in North America and the northern Palearctic, only a few living further south in the latter region.

The distribution of the groups is to a great extent certainly the result of an evolution within different areas. It does not seem established that palearctic *Colias* have evolved from South American forms. They may as well have developed from primitive *Colias* in some other part of the world where they are now extinct.

The evolution of the superuncus. Among the two characteristics of the *Colias* genitalia, the superuncus and the pseudouncus, the latter is present in the genus *Anteos* as well as in *Catopsilia* and *Colias* (Klots 1929 a, b, Drosihn 1933). The superuncus, on the other hand, is very small and triangular in the *Anteos* species investigated (*menippe, clorinde,* Plate IV, figs. 61, 62) covering only the pseudouncus and the basal part of the uncus. A similar, though bigger superuncus is found in *Protocolias imperialis* and the genus *Phoebis* (Drosihn 1933). In the latter genus no pseudouncus is present. The *Catopsilia* and *Aphrissa* species have broad, straight and diverging superunci (cf. Plate IV, figs. 63, 64 and Drosihn 1933), rather similar to those of some *Colias* species. The triangular shape of the superuncus is probably primitive, as this shape is present in *Anteos* where the superuncus is comparatively small.

The superuncus has in the genus *Colias* (and probably also in *Catopsilia* and *Aphrissa*) taken over the function of the uncus of many other Lepidoptera (cf. Lorkovic 1947) to assist medially and dorsally in holding the female body during the copulation. The superuncus and the pseudouncus probably developed to support the uncus dorsally. As the superuncus became larger, it was placed directly against the female body, and thus the uncus instead changed to support the superuncus.

It has been suggested, for instance by Verity (1947), that *Colias* have developed from the Old World *Catopsilias*. The presence of the very primitive *Protocolias* with a triangular superuncus, a short pseudouncus, and the middle part of the clasper with a prong, makes this assumption rather unlikely. The triangular superuncus may be considered as a very pronouncedly convergent one (cf. fig. 2). The more or less parallel or divergent superunci of *Colias, Catopsilia* and *Aphrissa* may have evolved by means of parallel evolution towards more uncus-like conditions as discussed below in the case of *Colias.*

The *Catopsilias* and most *Colias* species have broad, straight, and unpointed superunci, characteristics which therefore may be considered primitive compared with those of *C. hecla, nastes* and *palaeno.* A similiar result is arrived at, if the problem is approached from another direction. As already mentioned the superuncus has in the genus *Colias* taken over the function of the uncus. The latter has had its function during so much longer a time that it may give a certain indication of what shape is most apt to give an optimal function. The uncus is slender, pointed, and rather straight. In the two first of these characteristics the uncus corresponds to the superuncus of the *hecla-nastes-palaeno*-type. Only it is even more pronounced then. The shape of the uncus on the other hand, is straighter in lateral view. The basal part of the superuncus is, however, situated more dorsally than the same part of the uncus (cf. textfig. 13). Only if the superuncus is bent downwards, it can be placed against the female body in the same place as the uncus of other Pierids.

The evolution of the superuncus thus seems to have converged with that of the uncus. There is, however, still a marked difference in shape between these two organs and for different reasons it is not likely that the convergence will become complete ever. As already mentioned the situation of the two organs is different. The pressure of the superuncus is supported by that of the uncus and probably also by that of the pseudouncus, and finally the claspers are in the genus *Colias* not built as in other genera.

SUMMARY

The male genitalia of a number of *Colias* species have been described. The genus is divided into one new genus and two subgenera of the genus *Colias*: The South American genus *Protocolias* (type *imperialis* Btlr.) and subgenus *Mesocolias* (type *vautieri* Guér.) and the mainly Holarctic subgenus *Colias*. The latter can be divided into a palearctic group with a broad straight superuncus and a nearctic and northern palearctic group with a slender superuncus which is bent downwards. Transitions between these two groups exist within the supraspecies *C. nastes*.

The evolution of the superuncus from a small beginning, as at present in the genus *Anteos*, via the broad superunci of the *Catopsilias* and some *Colias* into a slender superuncus has been discussed.

Several pairs of *Colias* species with identical or very similar genitalia exist. It is suggested that the similarity is combined with introgression. Several of the pairs include species of different colors. These colors may serve to isolate the species sexually from each other.

REFERENCES

DROSHIN, J. 1933. Über Art-und Rassenunterschiede der mannlichen Kopulationsapparate von Pieriden, 1-135. Stuttgart.

HOVANITZ, W. 1949a. Increased variability in populations following natural hybridization. In Jepsen, *et al. Genetics, Paleontology, and Evolution.* 339-355. Princeton.

HOVANITZ, W. 1949b. Interspecific matings between Colias eurytheme and Colias philodice in wild populations. *Evolution.* 3: 170-173.

KLOTS, A. B. 1929a. The genus Anteos Hubner (Lepidoptera, Pieridae). Bull. Brooklyn Ent. Soc. 24: 134-214.

——————, 1929b. The generic status of Catopsilia Hubner and Phoebis Hubner, with a discussion of the relationships of the species and the homologies of the male genitalia (Lepidoptera, Pieridae). *Bull. Brooklyn Ent. Soc.* 24: 203-214.

KUSNEZOV, N. J. 1915. Insectes Lépidopteres I in *Faune de la Russie* 1-337. Petrograd.

LEDERER, G. 1941. Die Naturgeschichte der Tagfalter. Stuttgart.

LORKOVIC, Z. 1928. Analyse des Speziesbegriffes und der Variabilitat der Spezies auf Grund von Untersuchungen einiger Lepidopteren. *Glasn. Soc. Scient. Nat. Croat.* 38: 1-64.

LORKOVIC, Z. 1947. Modes artificiels d'accouplement des papillons. *Glasn. Biol. Sekc. Ser.* II/B 1:86-98.

MAGNUS, D. 1954. Experimentelle Untersuchungen am Kaisermantel zur Analyse optischer Auslosungsreize. *Deutscher Entomologentag* in Hamburg 30. Juli bis 3. August 1953: 58-75.

PETERSEN, B., O. TORNBLOM, and N. -O. BODIN. 1952. Verhaltensstudien am Rapsweissling und Bergweissling (Pieris napi L. und Pieris bryoniae Ochs.) *Behaviour.* 4: 67-84.

WARREN, B. C. S. 1950. Speciation in the genus Colias: with special reference to C. hyale and C. australis. *Lambillionea.* 50: 90-98.

PLATES

a. lateral view
b. superuncus, dorsal view
c. caudal view
d. aedeagus, ventral or dorsal view
e. " , distal end in lateral view
f. clasper from inner side
g. saccus in ventral view
u. uncus
v.l. ventral lobe of the inner side of the clasper (Klots 1929 a)

PLATE I.

Fig. 1. *P. imperialis* (wrongly labelled Honolulu)
Fig. 2. C. *vautieri*, Ensenada
Fig. 3. C. *vautieri*, Ensenada
Fig. 4. C. *cunninghami*, Junin, Peru
Fig. 5. C. *hyale*, Oland, Sweden
Fig. 6. C. *myrmidone*, Germany
Fig. 7. C. *sagartia*, N.E. Persia
Fig. 8. C. *aurorina*, Armenia
Fig. 9. C. *montium*, Tatsienlou, Tibet
Fig. 10. C. *montium*, S. Kansu, China
Fig. 11. C. *interior*, Montreal, Canada
Fig. 12, 13. C. *interior*, Alaska Highway, mile 126, Beatton R. area, B.C.

PLATE II.

Fig. 14. C. *interior*, Alaska Highway, mile 90, Beatton R. area, B.C.
Fig. 15. C. *interior*, Alaska Highway, mile 90, Beatton R. area, B.C.
Fig. 16. C. *palaeno*, Alaska Highway, mile 450, Toal River, B.C.
Fig. 17. C. *palaeno*, Bjurfors, Sweden
Fig. 18. C. *palaeno*, Sweden
Fig. 19, 20. C. *palaeno*, Smaland, Sweden
Fig. 21. C. *palaeno*, Abisko, Sweden
Fig. 22, 23. C. *palaeno*, 10 miles South Burwash Landing, Y.T.
Fig. 24, 25. C. *palaeno*, Sweden
Fig. 26. C. *christina*, America borealis
Fig. 27. C. *christina*, Rocky Mts.
Fig. 28. C. *christina*, Am. bor.
Fig. 29. C. *hecla*, Nr. Haines Junction, Y.T., up Summit Cr. 6000'-7000' el.
Fig. 30. C. *hecla*, Bog. nr. Johnson's Crossing, Y. T.
Fig. 31. C. *hecla*, Dudinska, Siberia
Fig. 32. C. *hecla*, Sweden
Fig. 33. C. *hecla*, Kvikkjokk, Sweden
Fig. 34. C. *hecla*, 20 miles South Burwash Landing, Y. T.

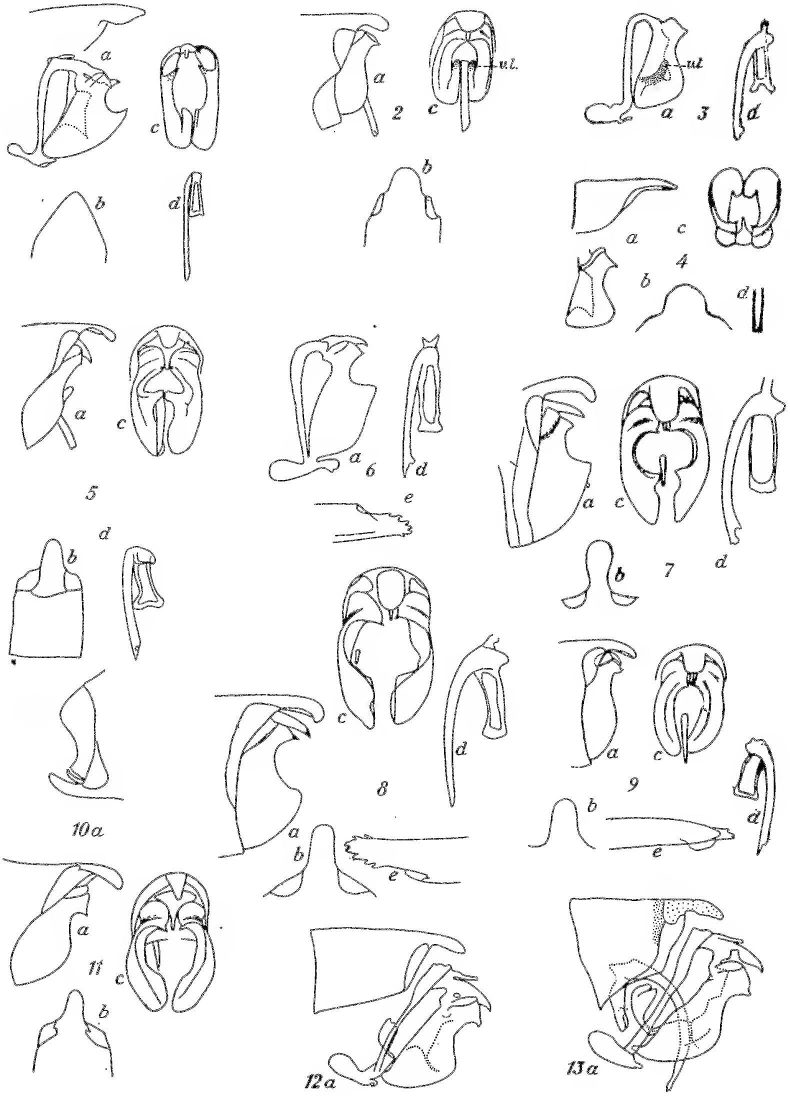
PLATE III.

Fig. 35. C. *nastes*, Nr Haines Junction, Y. T., up Summit Creek, 6000'-7000' el.
Fig. 36. C. *nastes*, Mt. Atabaska, Jasper N.P., Alberta, 7000'-8000' el.
Fig. 37, 38. C. *nastes*, Kvikkjokk, Swedish Lapland
Fig. 39. C. *eurytheme*, Texas
Fig. 40. C. *eurytheme*, Minnesota, U.S.A.
Fig. 41. C. *philodice*, Amer. bor.
Fig. 42, 43. C. *meadi*, Bow Pass, Jasper N. P., Alberta
Fig. 44. C. *phicomone*, Alps
Fig. 45. C. *croceus*, Tirol, Austria
Fig. 46. C. *wiscotti*, Turkestan
Fig. 47. C. *wiscotti separata*, Turkestan
Fig. 48. C. *alpherakyi*, Turkestan

PLATE IV.

Fig. 49. C. *christophi*, Turkestan
Fig. 50. C. *cocandica*, Turkestan
Fig. 51. C. *sieversi*, Turkestan
Fig. 52. C. *sifanica*
Fig. 53. C. *chrysotheme*
Fig. 54. C. *eogene*, Kisil Fast area
Fig. 55. C. *eogene*
Fig. 56. C. *staudingeri*, *Tian Shan*, Fu-Shu-Shan
Fig. 57. C. *thisoa*
Fig. 58. C. *heos*, N. Mongolia, long. 100°-110°, lat. 45°-50°
Fig. 59. C. *heos vespera*, S. Kansu, China
Fig. 60. C. *romanovi*, Turkestan
Fig. 61. *Anteos menippe*, Mattogrosso
Fig. 62. *A. clorinde*, Valles, Mex.
Fig. 63. *Catopsilia florella*, Syria
Fig. 64. C. *grandidieri*, Madagascar

PLATE I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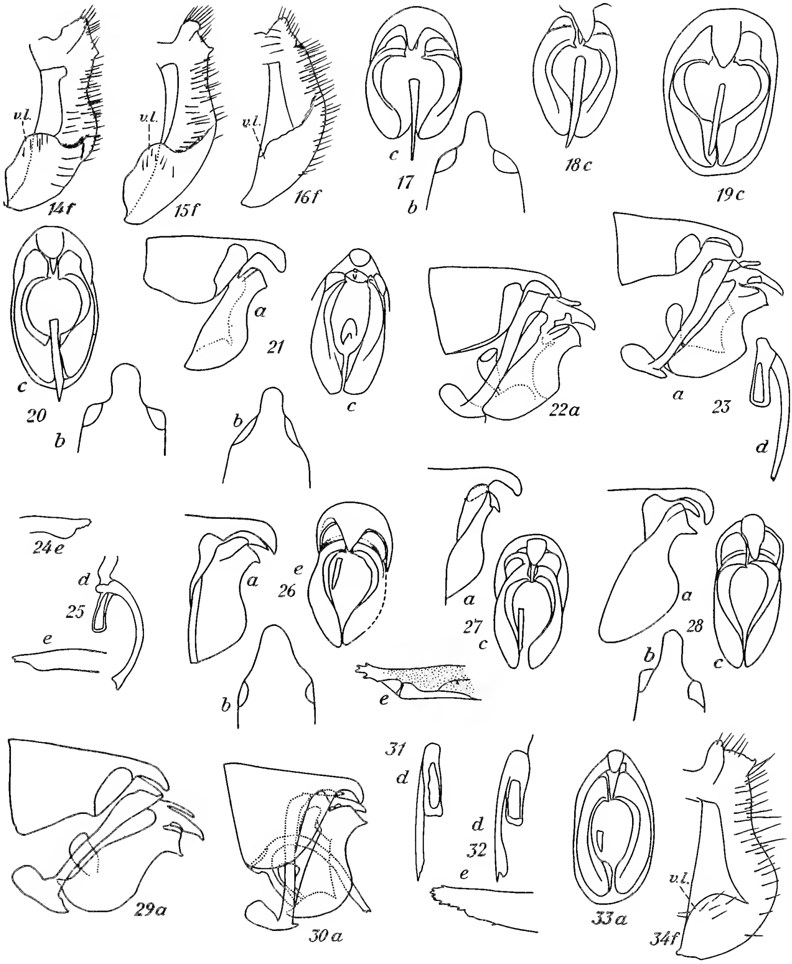
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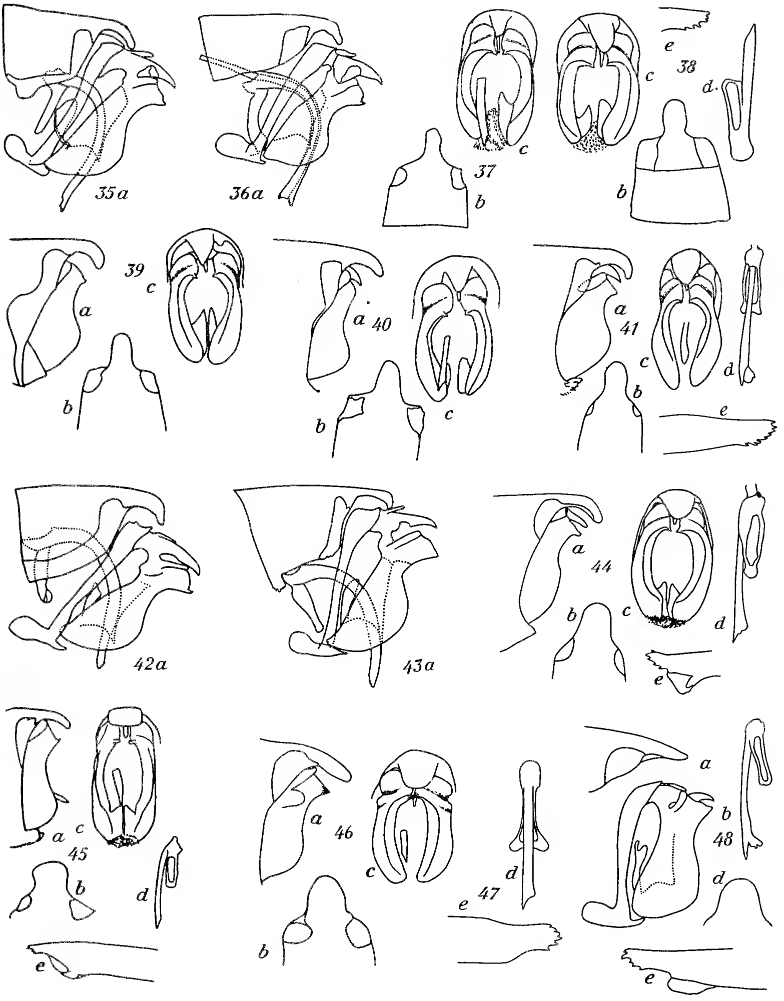
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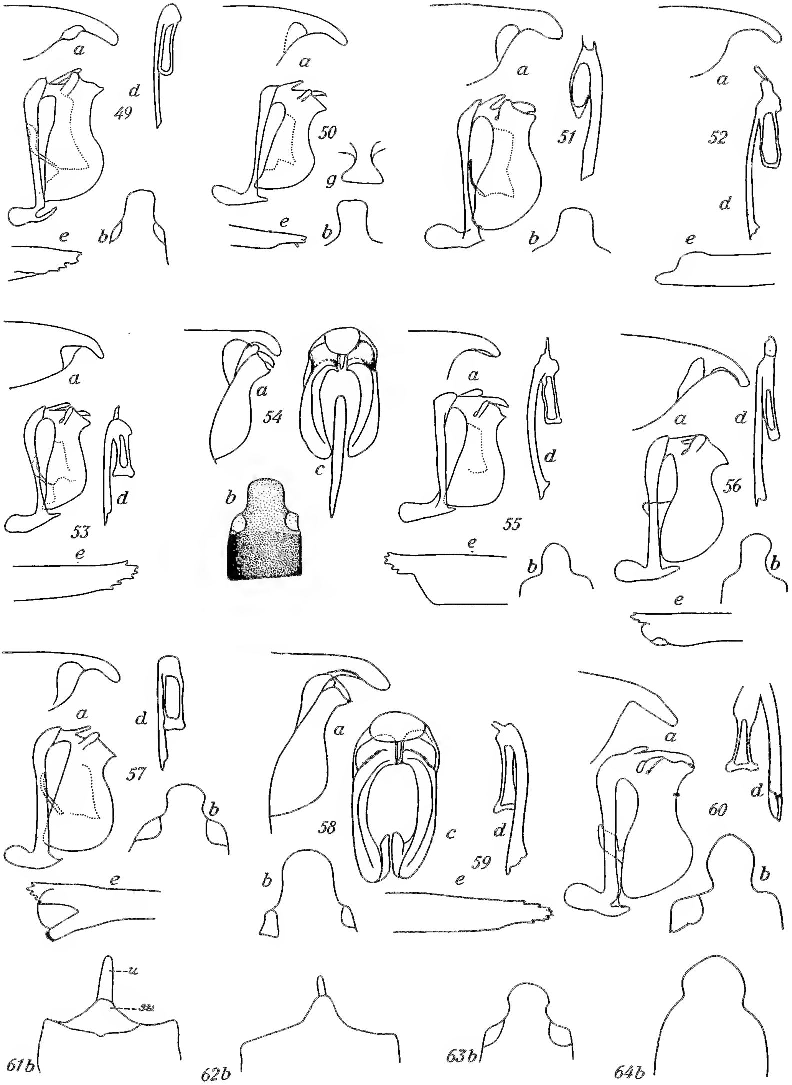
PLATE IV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62b
63b
64b

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THE EFFECT OF HYBRIDIZATION OF HOST-PLANT STRAINS ON GROWTH RATE AND MORTALITY OF PIERIS RAPAE[1]

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IT HAS BEEN PREVIOUSLY SHOWN (Hovanitz and Chang, 1962) that larvae of strains of *Pieris rapae* differ in their mortality rate, growth rate and final size dependent upon the plant which is supplied them for food. Slightly greater viability, greater rate of growth and increased size are characteristic results of feeding the larvae on kale *(Brassica oleracea* var. *acephala)* as compared with mustard *(Brassica nigra),* even though both plants are utilized by the species in the wild.

It is the purpose of this paper to report on the results of an experiment designed to compare these physiological factors in strains bred for several generations on each plant and then hybridized.

THE STRAINS

The strains of *Pieris rapae* used in these experiments were derived originally from two sources, both in the Los Angeles Basin of southern California. The first, here designated the kale strain, originated with wild females obtained in a cabbage field *(Brassica oleracea* var. *capitata)* in a truck crop growing area in western Orange County, near Huntington Beach. The other, here designated as the mustard strain, originated in the fields of the Los Angeles State and County Arboretum, where in the spring time *Pieris rapae* may be found in conjunction with black mustard *(Brassica nigra).* These have probably had no recent contact with cabbage since there are none grown commercially within nine miles of the area. Before testing in the experiments here described, the kale strain had passed through more than ten generations in the laboratory on kale and the mustard strain had passed through more than six generations in the laboratory on mustard.

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THE COMPARATIVE TESTS

Six comparative tests were run contemporaneously, consisting of twenty larvae each. These larvae were fed in petri dishes by daily changes of food, keeping each larvae well isolated from the others. It was especially important while they were small that the larvae were placed directly on top of the leaf of the plant. Of the six tests, two were of the parent strains; one of these was derived from kale and fed on kale during the experiment, while the other was derived from mustard and fed on mustard during the experiment. Four further sets were F_1 larvae from these two parent strains derived as follows:

One set consisted of F_1 larvae obtained by crossing a kale-strain female with a mustard-strain male and then by feeding the ensuing larvae on the food-plant of the mother (kale).

A second set consisted of larvae obtained by crossing a mustard-strain female with a kale-strain male and then feeding the ensuing F_1 larvae on the food plant of the mother (mustard).

A third set consisted of larvae obtained as in the manner of the first F_1 set above, but fed on the food plant of the father (mustard).

A fourth set consisted of larvae obtained in the manner of the second F_1 set above, but fed on the food plant of the father (kale).

MORTALITY

The mortality figures for the larvae were low in all the strains (table 1). The kale-strain parents had a mortality of ten percent, which compared well with the data previously obtained (Hovanitz and Chang, 1962). The mustard-strain parents had a mortality of thirty percent which also compared well with the previously recorded data.

The reciprocal F_1's behaved differently. When the kale-strain contributed the female parent and the mustard-strain contributed the male parent, the mortality of the F_1 larvae was twenty percent whether kale or mustard was used as food. On the other hand, when the mustard-strain contributed the female parent and the kale-strain contributed the male parent, the larvae had only a ten percent mortality when used on kale and zero percent mortality when bred on mustard. It is doubtful that these slight differences are significant for the N value of 20, though they may represent a real difference. It is possible that the hybrids show a greater viability as a result of their heterozygosity. Both parental strains have been considerably inbred during their maintenance in the laboratory. No reason can be given at this moment for the greater viability of the mustard female F_1's (10 and 0 percent) as compared with the reciprocal kale female F_1's (20 percent each).

LENGTH OF LARVAL PERIOD

The minimum length of life for the larvae from the egg to the adult for both of the parental strains was twenty-five days under the conditions of the experiment (table 1). *All four of the hybrid F_1 strains had a shorter larval length of life indicating a greater activity than the inbred parental strains.* The rate was speeded up to twenty-two days for the F_1 strains in which the female parent was derived from kale stock.

Type		Strain No.	No.	No. and %		Minimum days from egg to pupae
Parents	Kale-bred	5	20	2	10%	25
	Mustard-bred	6	20	6	30%	25
F_1 Kale ♀ x Mustard ♂	Kale-bred	2	20	4	20%	22
	Mustard-bred	1	20	4	20%	22
F_1 Mustard ♀ x Kale ♂	Kale-bred	4	20	2	10%	21
	Mustard-bred	3	20	0	0	23

Table 1. The comparative mortality and length of larval growth period of various strains of Pieris rapae.

For the F_1 stock in which the female parent was derived from mustard, the larvae bred on kale were speeded up to twenty-one days and those bred on mustard to twenty-three days. These data definitely indicate a significantly greater activity of the hybrid strains than the parental. However, there is no indication of any maternal effect on the inheritance of food-plant preference since the reciprocal crosses indicated the same general effects on mortality and growth rate whichever strain contributed the female parent.

GROWTH RATE AND MAXIMUM SIZE

The growth rate of the six sets of larvae was compared by measuring ten of the living larvae daily from the time of hatching from the egg to the time of pupation. The average of these ten measurements was plotted daily and curves drawn to illustrate their size increases (fig. 1). Differentiation between the curves occurred within the first few days but the first five days have been omitted in fig. 1, owing to the small size of the larvae. *On the fifth day, both parental strains had the smallest larvae while the two F_1 strains, in which the kale-strain female parent was used, had the largest larvae. The other two F_1 strains, in which the mustard-strain female parent was used, were intermediate.* During the entire growth period, nearly the same relationships held, with the exception of the kale-bred F_1 with a mustard-strain female

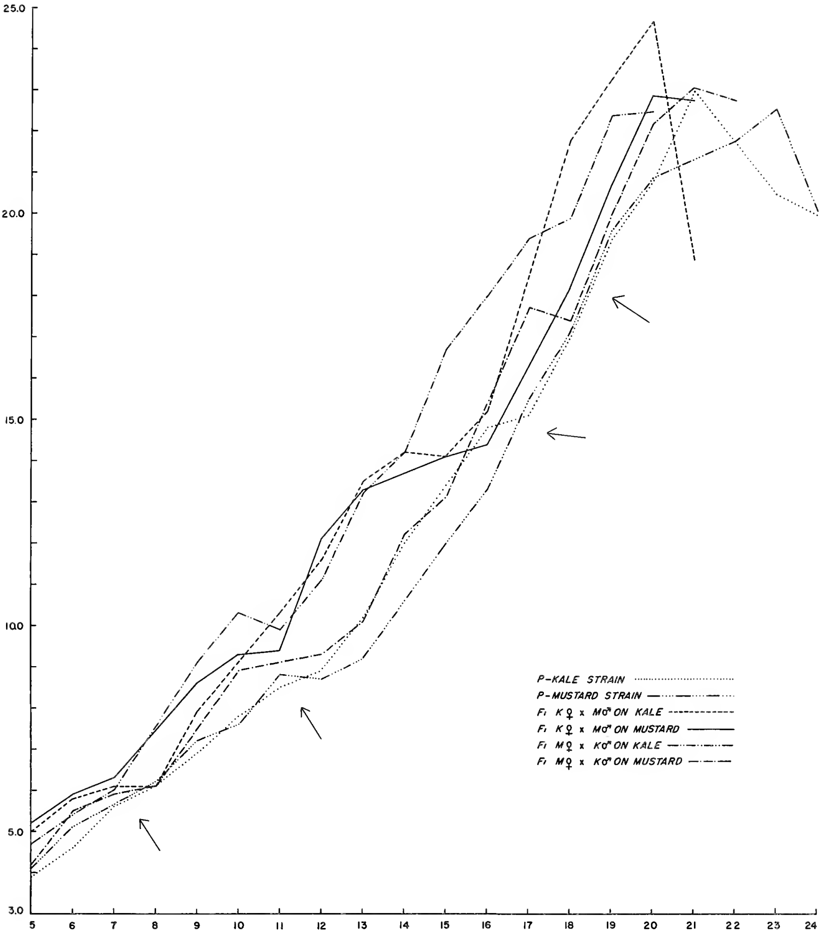

Fig. 1. Growth rates of larvae of six strains of *Pieris rapae* on kale and mustard. Vertical scale, length in mm.; horizontal scale, days after hatching from egg to pupation.

parent which for a time was faster than all the others. Of the two parental groups, the mustard-bred larvae were larger than the kale-bred at five days, but the kale-bred reached a maximum ahead of and larger than the mustard-bred. *Of the three groups on kale as compared with the three on mustard, the kale-bred group in each case reached a maximum size larger than or earlier than the comparable group on mustard. Of the parental as compared with the F_1 groups, the larvae of both F_1 hybrid groups consistently exceeded the larvae of the parental groups from the beginning to the end.*

The largest maximum size was attained by the F_1 group in which the female parent was derived from a kale-strain and in which the larvae were kale-bred. On the other hand, *the second largest maximum size was attained by the larvae of the F_1 group bred on mustard but which had a mustard-strain mother.*

It may be observed from the curves that at the periods of molting, sizes of the larvae are reduced. These periods are shown by the arrows (fig. 1). Because these reduction periods are delayed for the slower larvae, the older the larvae, the more difficult it is to compare the six groups on any one day.

SUMMARY AND CONCLUSIONS

1. Crosses were made between strains bred for many generations on kale and mustard.
2. The effect of hybridization between these host-selection strains has been to speed up development, to bring about increased sizes to the larvae, and to reduce mortality. These effects are probably due to the genetic effects of "hybrid vigor", in which the deleterious effects of inbreeding within the host-selected strains have been reduced by outcrossing.
3. These effects are greatest for the kale-strain than for the mustard-strain. This would tend to confirm our previous findings that kale is preferred as a food over mustard, even when mustard is utilized as the food for many generations.
4. The increased viability, increased growth rate and increased size of the larvae are greatest when the hybrid larvae are grown on the plant corresponding to the strain of the mother, rather than the father. For example, the F_1 hybrids where the mother was of the kale-strain grow larger and pupate sooner on kale than on mustard. Likewise, the F_1 hybrids where the mother was of the mustard-strain grow larger but not faster on mustard than on kale.

LITERATURE CITED

HOVANITZ, W. and VINCENT C. S. CHANG. 1962. The effect of various food plants on survival and growth rates of *Pieris* *J. Res. Lepid.,* 1(1): 21-42.

NOTICE

THE JOURNAL OF RESEARCH ON THE LEPIDOPTERA started publication in August, 1962. This fact makes it impossible for volume 1 to coincide with the calendar year, 1962 and still have four issues to the volume. The editor was confronted with the problem of two alternatives, (1) to extend the period for volume 1 to include the year 1963 and thus to have only four issues for the year 1962 and 1963, or (2) to have volume 1 completed early in 1963 by rapid issuance of the remaining numbers and then to issue the four numbers of volume 2 before the end of the year 1963. The second alternative has been selected, and therefore two more issues of the JOURNAL volume 1 will appear shortly, to be followed by four issues of volume 2 before the end of the year.

Orders received for the calendar year 1963 with no volume designation will be filled with volume 2 only; if volume 1 is desired, the year 1962 (volume 1) must be ordered. It is hoped that this explanation will help to solve the problems of institutional orders which have appeared.

Orders for individuals who subscribe before the fourth number of volume 1 appears, will have their subscriptions start with the first volume, and will be billed for volume 2 at the time of sending number 4 of volume 1.

In view of this rapid publication of papers, it is very likely that the editor will run short of manuscripts. It is urged that those who have good work to publish on the Lepidoptera will take advantage of this "chance of the lifetime" and send their MS to the editor.

It is suggested that subscribers and readers help the JOURNAL by becoming a member of THE LEPIDOPTERA FOUNDATION. See inside front cover.

Journal of Research on the Lepidoptera 1(2):163-168, 1963

1140 W. Orange Grove Ave., Arcadia, California, U.S.A.

CHANGE OF FOOD PLANT PREFERENCE BY LARVAE OF PIERIS RAPAE CONTROLLED BY STRAIN SELECTION, AND THE INHERITANCE OF THIS TRAIT[1]

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IT HAS BEEN SHOWN that larvae which have previously been fed on a particular food plant are more likely to select that kind of plant than if they had not previously been fed on it (Hovanitz and Chang, 1962 *a* and *b*). These data have shown that there was a shift in selection of mustard or of kale according to whether or not the larvae were from a kale or a mustard strain. Likewise, there was shown a greater selection for nasturtium by larvae previously fed on nasturtium, and indeed, by these same larvae, a greater selection for mustard over kale. This change in selection operates whether the larvae were fed on the changed food-plant for a long time (several generations) or a short time (part of the individual larval life).

In this paper, it is our purpose to test the effect of continued feeding of the larvae of *Pieris rapae* for many generations on mustard and kale by the process of isolating the strains so fed for many generations, then crossing the parental strains to get F_1 individuals and finally crossing the F_1 to get the F_2 segregation.

THE STRAINS

The strains of *Pieris rapae* used in these experiments were derived originally from two sources, both in the Los Angeles Basin of southern California. The first, here designated the kale strain, originated with wild females obtained in a cabbage field *(Brassica oleracea* var. *capitata)* in a truck crop growing area in western Orange County, near Huntington Beach. The other, here designated as the mustard strain, originated in the fields of the Los Angeles State and County Arboretum, where in the spring time *Pieris rapae* may be found in conjunction with black mustard *(Brassica nigra)*. These have probably had no recent contact with cabbage since there are none grown commercially within nine miles of the area. Before testing in the experiments here described, the kale strain had passed through more than ten generations in the labora-

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[1] Aided by a grant from the National Science Foundation, Washington, D. C.

tory on kale and the mustard strain had passed through more than six generations in the laboratory on mustard.

Larvae were selected from each and tested for their selection for a series of plants in the manner indicated in a previous paper (Hovanitz and Chang, 1962). The plants used in these tests were mustard *(Brassica nigra),* kale *(Brassica oleracea* var. *acephala),* nasturtium *(Tropaeolum majus),* Isomeris *(Isomeris arborea)* and Cleome *(Cleome lutea).*

STRAIN SELECTIONS

The tests were physically carried out in the manner indicated above. In order to be precise on the nature of any difference to be detected by these experiments, the tests were conducted in large numbers. Twenty-five larvae of each strain were used for twenty or forty trials each, giving a total of six hundred test times for each strain (table I). This was increased to six hundred sixty for the F_1 and nine hundred (with 45 individuals) for the F_2.

	mustard	kale	nasturtium	Isomeris	Cleome	none	no. of larvae	total test times
PARENTS								
On mustard	364 60.66%	119 19.83%	56 9.33%	18 3.0%	12 2.0%	31 5.16%	25	600
On kale	144 24.00%	354 59.0 %	50 8.33%	21 3.5%	15 2.5%	16 2.66%	25	600
F_1								
M ♀ x K ♂ (on mustard)	356 59.93%	141 21.36%	90 13.63%	23 3.48%	39 5.91%	11 1.67%	25	660
♀ ♂ (on kale)	328 49.68%	127 19.24%	109 16.51%	33 5.00%	36 5.45%	27 4.09%	25	660
F_2								
M ♀ x K ♂ (on mustard)	491 54.55%	145 16.11%	190 21.4 %	30 3.33%	42 4.66%	2 0.22%	45	900
K ♀ x M ♂ (on kale)	406 45.11%	146 16.22%	219 24.33%	79 8.77%	39 4.33%	11 1.22%	45	900

Table 1. The comparative mortality and length of larval growth period of various strains of *Pieris rapae.*

The differential selection of the plants by larvae of the two selected strains is clearly made apparent by the curve showing the percentage selection (fig. 1). The larvae from the mustard bred strain selected mustard sixty-one percent of the time as compared with kale twenty percent of the time. The kale strain larvae selected kale fifty-nine percent of the time as compared with mustard twenty-four percent of the time. The two strains show an almost complete reversal of their preferences with regard to these two plants, their preference being in the direction of the plant utilized as food for several generations.

The selection by larvae of these two strains for the other plants concerned was not significantly different. Nasturtium was selected nine percent of the time by the mustard strain and eight percent of the time by the kale strain. Isomeris was selected three percent of the time by each strain, and Cleome about two percent of the time. About five percent of the larvae of the mustard strain left test area with no selection as did about three percent of those of the kale strain. Thus, there is no difference observable between these two parental strains in their selection, except with regard to mustard and kale.

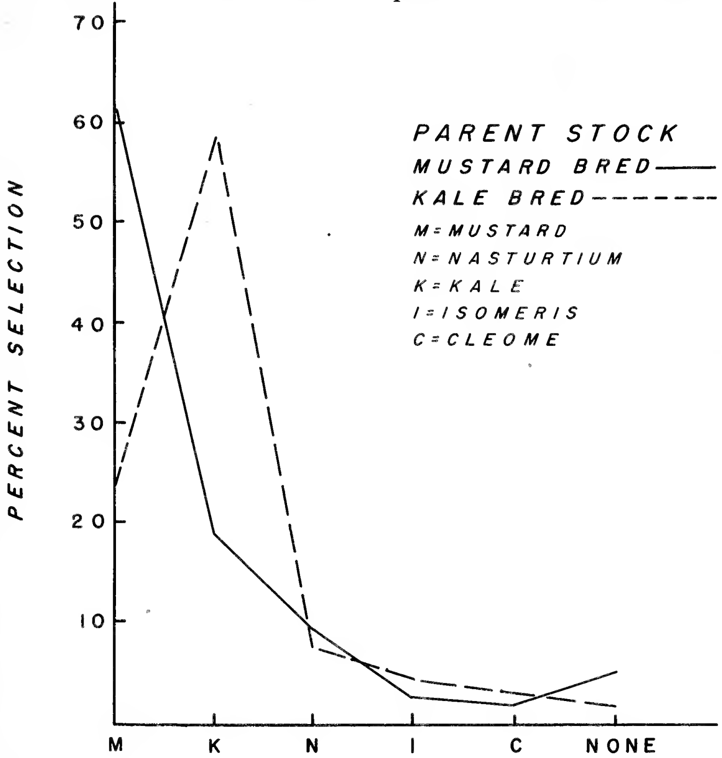

Fig. 1. Curves showing the percentage selection of various food plants by larvae of *Pieris rapae* from a kale and a mustard strain.

THE CROSSES

Adults of the two strains were crossed and the larvae tested for their preference toward a selection of plants. Since there was a possibility of a maternal influence on the inheritance of the food plant selectivity hinted at in a previous experiment, reciprocal crosses were

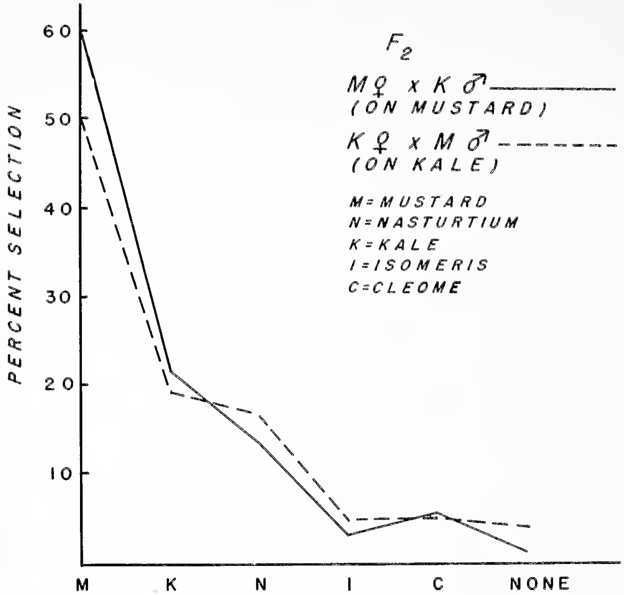

Fig. 2. Curves of the percentage selection of various food plants by larvae of *Pieris rapae* comparing the reciprocal F_1 of the strains shown in figure 1.

made, mustard strain female X kale strain male and vice versa. In each case, however, the larvae were bred on the plant of the female strain until tested. It is now known that it would also have been desirable to have had the reciprocal feeding tests made in addition, as can be seen below.

The F_1 larvae obtained, in which the female parent was from the mustard strain, showed little difference in selection of plants from the parent mustard strain except in an increase in selection of nasturtium and Cleome, neither plant of which was involved in this selection. The reciprocal F_1 larvae obtained from the cross of a kale strain female with a mustard strain male showed a much greater selection of mustard than the kale parent strain, and was more like that of either the mustard parent or of the reciprocal strain indicated (table 1, and fig. 2). In fact, the results of this cross would indicate that the genes for mustard selection are nearly completely dominant over those for kale selection. The cross would also indicate that they are transmitted at least through the male since a mustard strain male was used with a kale strain female and the larvae were bred on kale. The fact that the larvae were bred on kale may be the only reason that the selection was not higher toward mustard than is indicated. As with the reciprocal cross, there was a great increase in selection of nasturtium and Cleome following crossing. This was followed slightly by an increase toward Isomeris though this may not be significant. There is little doubt from these data that the selection of food plants is inherited, and that "mustard" is dominant over "kale" despite the fact that there is also superimposed upon this inheritance a selective propensity controlled by training during the life of the individual, as has been shown before.

The F_2 crosses were made in the same manner. F_2 larvae of each of the crosses indicated above were obtained and bred on the food plant of the mother (table 1). The tests on these larvae led to basically the same results as on the F_1 larvae with the exception that all percentages were reduced slightly and the percentages for nasturtium were raised greatly. Of significance too is the reduction of the larvae which made no selection at all. The reduction in selection of mustard and kale appears proportional and related to the increase in the selection of nasturtium (fig. 3).

DISCUSSION AND CONCLUSIONS

The data indicated in this paper appear to show that selection of genes for food plant preference occurs over a period of generations when strains are maintained isolated on particular food plants for many generations. These genes do not show maternal inheritance. In the crosses indicated in this paper, genes for selection of mustard over kale are apparently dominant over the reverse. This is indicated by the fact that in the F_1 of the cross kale strain X mustard strain or the reciprocal, selection is similar to that shown by the original mustard strain. The same results are shown for the F_2 but they are not so pronounced. Of great curiosity is the fact that in the F_1 there is an increase in selection for nasturtium, not one of the preferred plants of *Pieris rapae* (Hovanitz and Chang, 1962a). Feeding larvae on nasturtium has shown that there may be greater selection of this plant developed than would ordinarily be present. In the present case, however, no selection of this sort is involved and the increase is significant. This increase is even greater in the F_2 cross than in the F_1, there being a two and one half- to three-fold increase in selection of nasturtium in the F_2 as compared with the parental strains. A much slighter increase is also indicated for Isomeris and Cleome, and a decrease for the number of rejects, that is, those that make no selection. Reasons for this much greater selection for nasturtium and other plants following hybridization are not known nor can they even be guessed at intelligently at this time.

SUMMARY

1. Two food plant strains were developed by selection, one on kale *(Brassica oleracea)* and another on mustard *(Brassica nigra).*

2. When tested, each of these strains showed a much greater preference for their accustomed food plant than for any other tested. Those tested were mustard, kale, nasturtium, Isomeris and Cleome.

3. When these two strains are crossed, the F_1 hybrids showed a preferential selection most like the mustard parent strain. This indicates that the gene(s) for mustard is dominant over that for kale. There is

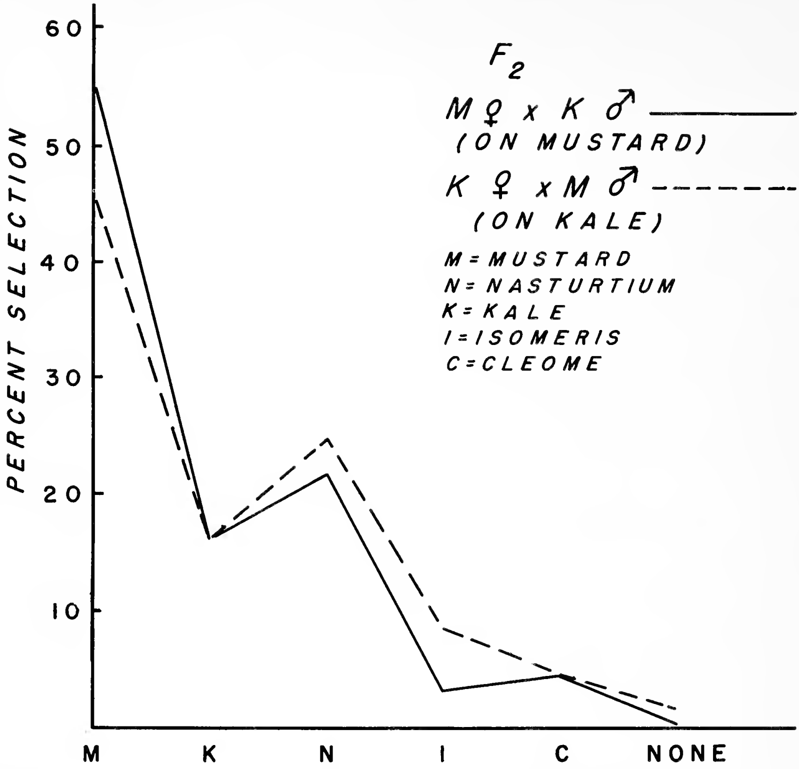

Fig. 3. Curves of the percentage selection of various food plants by larvae of *Pieris rapae* comparing the reciprocal F_2 of the strains shown in figures 1and 2.

also indicated a slight increase in selection of the other plants tested.

4. The F_2 of this cross showed results similar to the F_1, namely a selection in favor of mustard rather than kale whether or not the female parent had originally come from the mustard or the kale strain. Thus, maternal inheritance is not indicated here even though maternal effects were indicated on growth rate and mortality data in a previous paper.

5. As had been indicated, feeding the larvae even a short time on one particular food plant may influence it to have a preferential selection for that plant.

6. In the F_2 there is indicated a strongly increased preferential selection toward nasturtium which was not selected in any previous strain. This increase is also indicated slightly toward Isomeris and Cleome. No reason is advanced at this time for these results.

LITERATURE CITED

HOVANITZ, W. and VINCENT C. S. CHANG. 1962a. The effect of various food plants on survival and growth rates of *Pieris*. *J. Res. Lepid.* 1(1): 21-42.

——————— 1962b. The effect of hybridization of host-plant strains on growth rate and mortality of *Pieris rapae*. *J. Res. Lepid.* 1(2): this issue.

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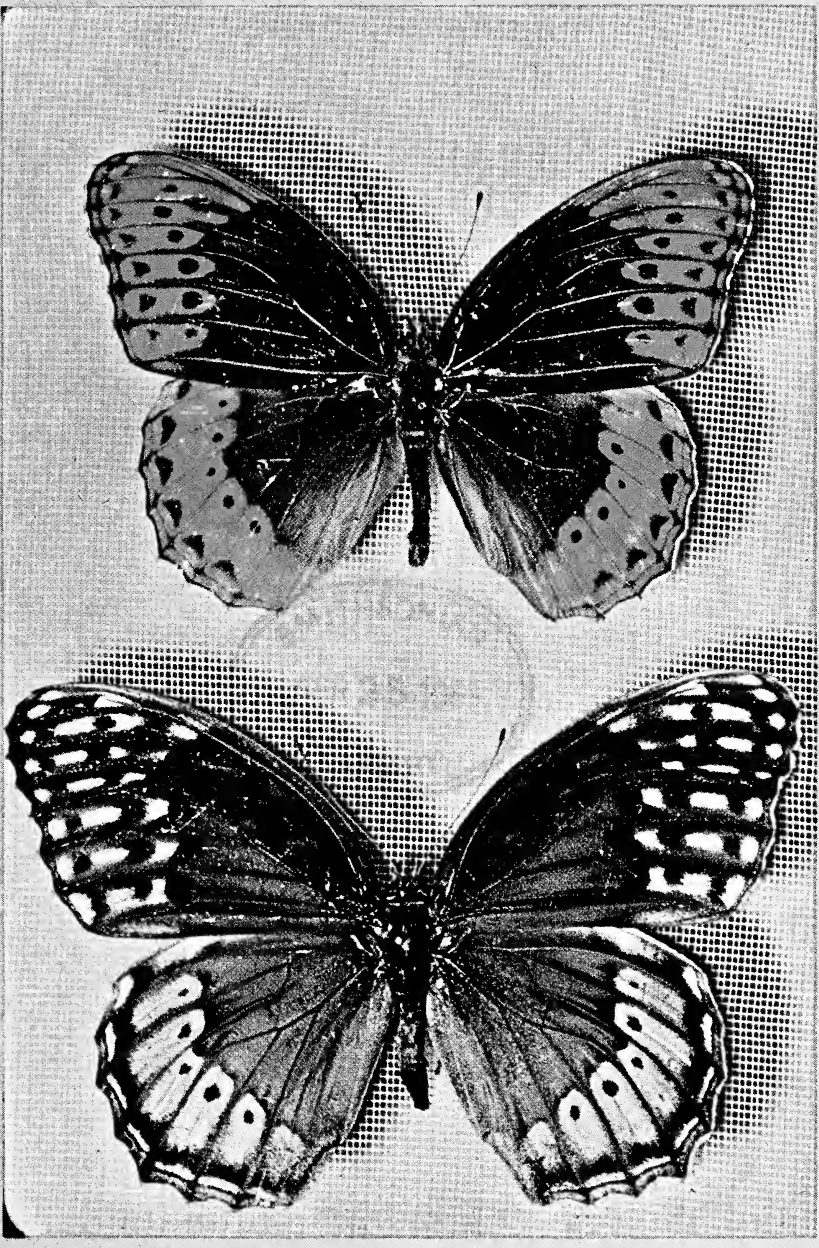

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Journal of Research on the Lepidoptera 1(3):169-182, 1963

1140 W. Orange Grove Ave., Arcadia, California, U.S.A.

SELECTION OF ALLYL ISOTHIOCYANATE BY LARVAE OF PIERIS RAPAE AND THE INHERITANCE OF THIS TRAIT[1]

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LARVAE WHICH HAVE PREVIOUSLY BEEN FED on a particular food plant are more likely to select that plant than if they had not previously been fed on it (Hovanitz and Chang, 1962*a* and *b*). It was shown that larvae which were fed on kale are more likely to select kale, and larvae which were fed on mustard are more likely to select mustard. Also, larvae which have previously been fed nasturtium have a higher selection on that plant than if they had not been fed on it. This change in food plant selection operates both if the adaptation comes over a period of several generations, or if only for a short time in the individual larval life. Later, it was shown that strains selected for several generations on each of two plants, kale and mustard, had strong selection for their respective food plants (Hovanitz and Chang, 1963*a* and *b*). Individuals from these two strains were then crossed to get the F_1 generation, and these were crossed to get the F_2 generation. The inheritance of this trait appears to be multifactorial but because of the nature of the testing, this point may be open to question.

The data to be presented in this paper were obtained in much the same manner as in the previously mentioned papers (Hovanitz and Chang, 1963*a* and *b*) with the exception that instead of testing the selection of the larvae for the plants themselves, they were tested for their selection of various concentrations of black mustard oil (allyl isothiocyanate). Tests were made on the parental larvae as well as the F_1 and the F_2.

THE STRAINS

The strains of *Pieris rapae* used in these experiments were derived from two original sources. The first, the kale strain, originated with wild females obtained in a cabbage field (*Brassica oleracea* var. *capitata*) in a truck crop growing area near Huntington Beach in Orange County, California. The other, the mustard strain, originated in the fields of the

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[1] Aided by a grant from the National Science Foundation.

Los Angeles State and County Arboretum where *P. rapae* is found on black mustard (*Brassica nigra*). Before testing in the experiments here described, the kale strain had passed through more than ten generations in the laboratory on kale (*Brassica oleracea* var. *acephala*) and the mustard strain had passed through more than six generations in the laboratory on black mustard.

EXPERIMENTAL SET-UP

The tests of the larvae were made in much the same manner as has previously been described (Hovanitz and Chang, 1962b) except that in place of the plants to be selected, at various points surrounding the flat, filter papers wetted with various solutions of allyl-isothiocyanate were placed. Preliminary tests had indicated that the larvae were attracted to dilutions of the mustard oil at 10^{-5} to 10^{-9} so the tests were made at these dilutions. Metal mosquito netting was cut in a circular arrangement to serve as a base for the filter paper. These discs of metal netting were placed on top of glass flasks partially buried in soil, secured to corks placed in the flasks and arranged in various parts of the flat according to the disposition shown in Figure 1. The filter paper was then set up top of the metal netting and wetted with distilled water solutions as shown. On one of these, distilled water only was placed so as to serve as a control for the others. To prevent the accumulation of mustard oil concentrations, the solutions were alternated around the flat. The set-up of the experiments is shown diagrammatically in Figure 1 and photographically in Figure 2. The larvae were set in the center of the flat and allowed to select any of the six test papers or to leave the flat without selection. It should be noted that the test papers were above the level of the larvae and therefore that the heavier-than-air mustard oils would drop down to their level. After each trial, the soil in the flat was mixed to prevent the origin of "trails." It should also be noted that it would be much easier for the larvae to leave the flat without any selection except for one factor, namely, that these larvae have a tendency to climb upwards when at all possible. Experience with lepidopterous larvae has shown that descent is usually made by means of dropping down on a silken thread, rather than by walking while ascent is made by walking. This accounts for the selection of the "water" alone just as frequently as they leave the flat without any selection at all.

The mustard oil used in these experiments was a natural product obtained from black mustard seed by compression and distillation. It is available commercially from the Fritsche Brothers firm. Allyl isothiocyanate is the principal component of the oil obtained from *Brassica nigra;* other mustard oils are found in other plants and all are esters of isothyocyanic acid. *Brassica nigra* seeds contain a glucoside, potassium myronate or sinigrin, which undergoes fermentation change due to the enzyme myrosin present in the seeds.

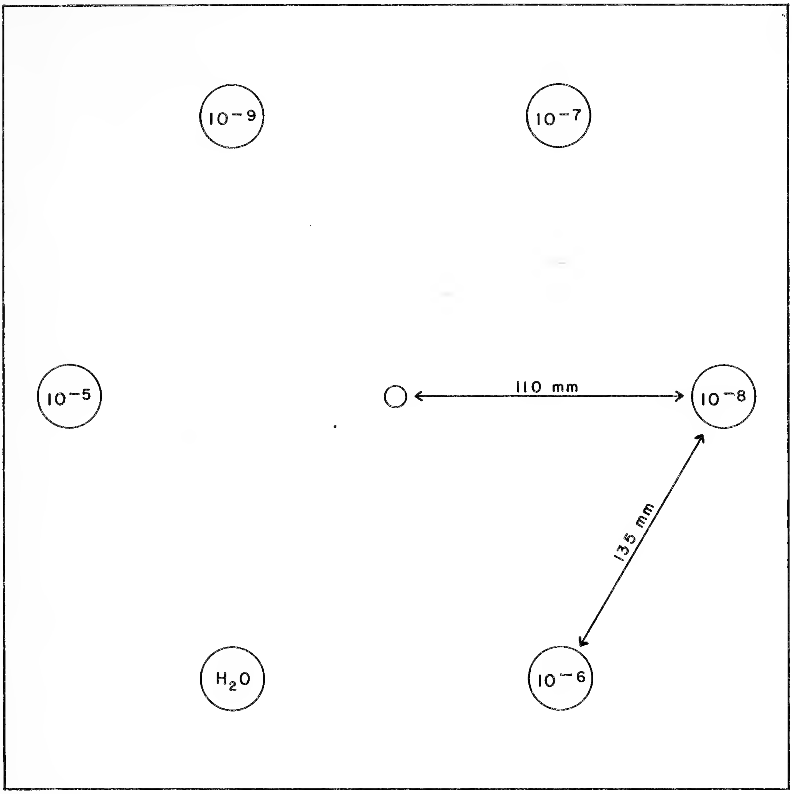


Fig. 1. The set-up for the larval tests. The larvae are placed in the center of the flat from where they are enabled to go in any direction toward one of the dilutions of mustard oil, or to leave the flat. The circles show the disposition of the filter papers which have upon them dilutions of mustard oil as indicated.

THE TEST SELECTIONS

Test selections were made by using a number of larvae for several times to get a combined sample. The number of individuals used depended in part on those available, but ranged from fifteen to forty-five giving a total number of tests from three hundred to nine hundred. These data are given in Table 1.

The parent strains were tested first. The mustard strain was tested with twenty-five larvae 20 or 40 times each giving a total of seven hundred trials. Of these, only nineteen or 2.7 percent made no selection and left the flat. Only twenty-four or 3.4 percent selected the filter paper with distilled water only on it. The others all selected the mustard oils, from a low of nearly 10 percent for the 10^{-9} to a high of nearly thirty percent for the 10^{-6}. These data are shown diagrammatically in Figure 3.

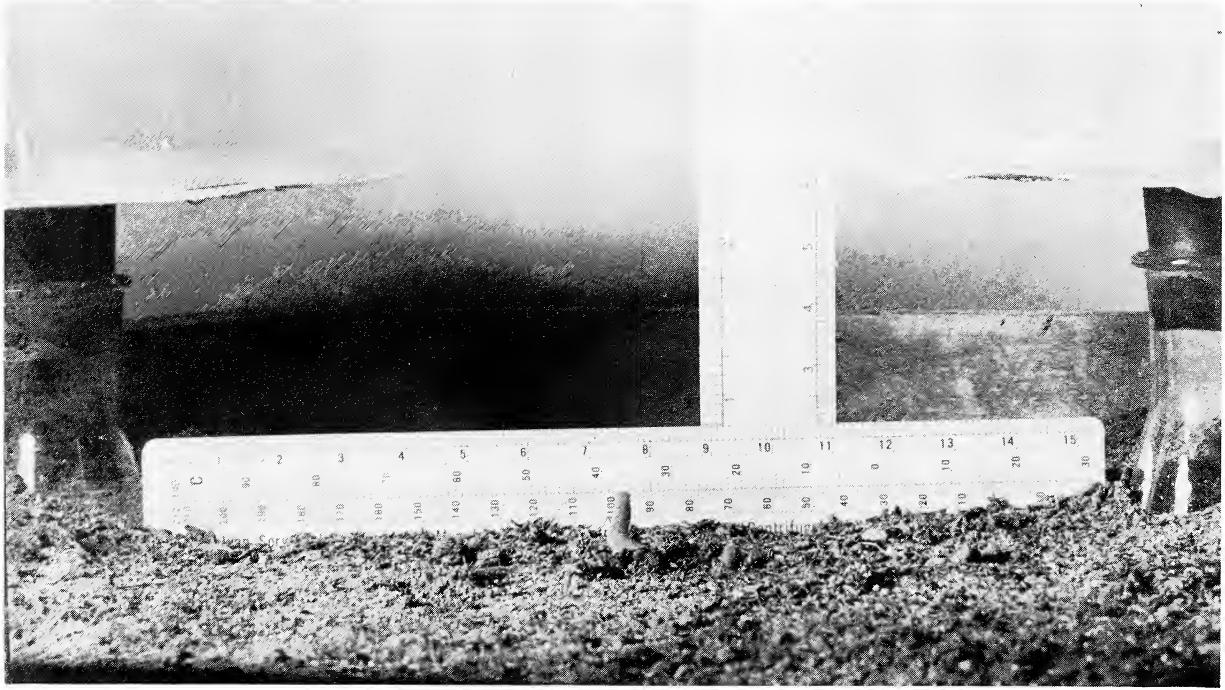


Fig. 2: Photograph showing the surface of the experimental flat, the flasks with filter paper upon them and a larva raising its foreparts. The rules are not present during an experiment and are indicated only for the purpose of illustrating the dimensions between the soil surface, the filter paper and the larvae.

TABLE 1 . The selection by larvae of different strains of *Pieris rapae* for different concentrations of allyl isothiothiocyanate (black mustard oil).

	10^{-5}		10^{-6}		10^{-7}		10^{-8}		10^{-9}		water		none		no. of larvae	total test times
PARENTS																
On mustard	109	15.57%	207	29.57%	141	20.14%	133	19.00%	67	9.57%	24	3.42%	19	2.7%	25	700
On kale	70	12.07%	88	15.17%	86	14.82%	198	34.13%	68	10.34%	19	3.27%	51	8.79%	25	580
F_1																
M♀ x K♂ (on mustard)	58	11.6 %	99	19.8 %	152	30.2 %	99	19.8%	57	11.4 %	28	5.6 %	7	1.4 %	25	500
K♀ x M♂ (on kale)	19	6.33%	55	18.33%	102	34.00%	69	23.0%	34	11.33%	11	3.66%	10	3.33%	15	300
F_2																
M♀ x K♂ (on mustard)	112	12.44%	211	23.44%	231	25.66%	187	20.77%	91	10.11%	42	4.66%	26	2.88%	45	900
K♀ x M♂ (on kale)	114	16.29%	146	20.86%	150	21.43%	124	17.71%	99	14.14%	41	5.86%	26	3.71%	35	700

The kale strain was also tested with twenty-five larvae for a total of five hundred eighty trials. The highest selection of these larvae was toward the concentration of 10^{-8}, larvae going to this concentration in thirty-four percent of the trials. This result is significantly different from the result for the kale larvae indicated above, in which the highest selection was toward the 10^{-6} concentration. These data can be compared diagrammatically in Figure 3. There is little doubt that the larvae of the kale-bred stock prefer the mustard oil at a lower concentration than do those of the mustard strain. It is probably not coincidental that the taste of the leaves of mustard is stronger than is that of kale (or cabbage) since the significant taste of these plants is due to allyl or other isothiocyanates. These data would seem to indicate (1) that the concentration of taste or smell-detectable mustard oils in the leaves of mustard is higher than that in kale, (2) that the larvae feeding on mustard have become adapted in some way to a higher concentration of these oils, and (3) that due to this adaptation, the "mustard" larvae have a greater selection of the higher concentration of mustard oil than the lower. It has been shown in another paper (Hovanitz and Chang, 1963b) that these two strains also select their own plants over the others when given a free choice. This preferred selection may be due wholly or in part to the difference in available allyl or other isothiocyanate in their leaves.

THE CROSSES

The crosses between the two food plant strains were carried out by making reciprocal hybrids. In the one case, the kale strain was used as the female parent and in the other case, the mustard strain. The hybrid larvae resulting from these crosses were fed on the food plant of the mother, since the mother was allowed to lay on its own preferred plant.

The selections made by the hybrid larvae in both crosses favored the concentration 10^{-7}, exactly half way between the selections made by the respective parent strains (Fig. 4). The frequency of selections for the kale female F_1 toward the 10^{-7} concentration was 34 percent as compared with 30 percent for the mustard female F_1.

Previous data have indicated that the immediate larval food plant eaten by the larvae had an effect on the food plant selections made by these larvae. If this held true for the selections of the mustard oils also, then the larvae of the kale female F_1, having been fed on kale during their life, and the larvae of the mustard female F_1, having been fed on mustard during their life, should have a preference for their respective plant. Data from Table 1 (Hovanitz and Chang, 1963b) indicate that this is so. Mustard female F_1 larvae selected mustard nearly 60 percent of the total selections as compared with nearly 50 percent selections for the kale female F_1 larval selections. It should follow, if our

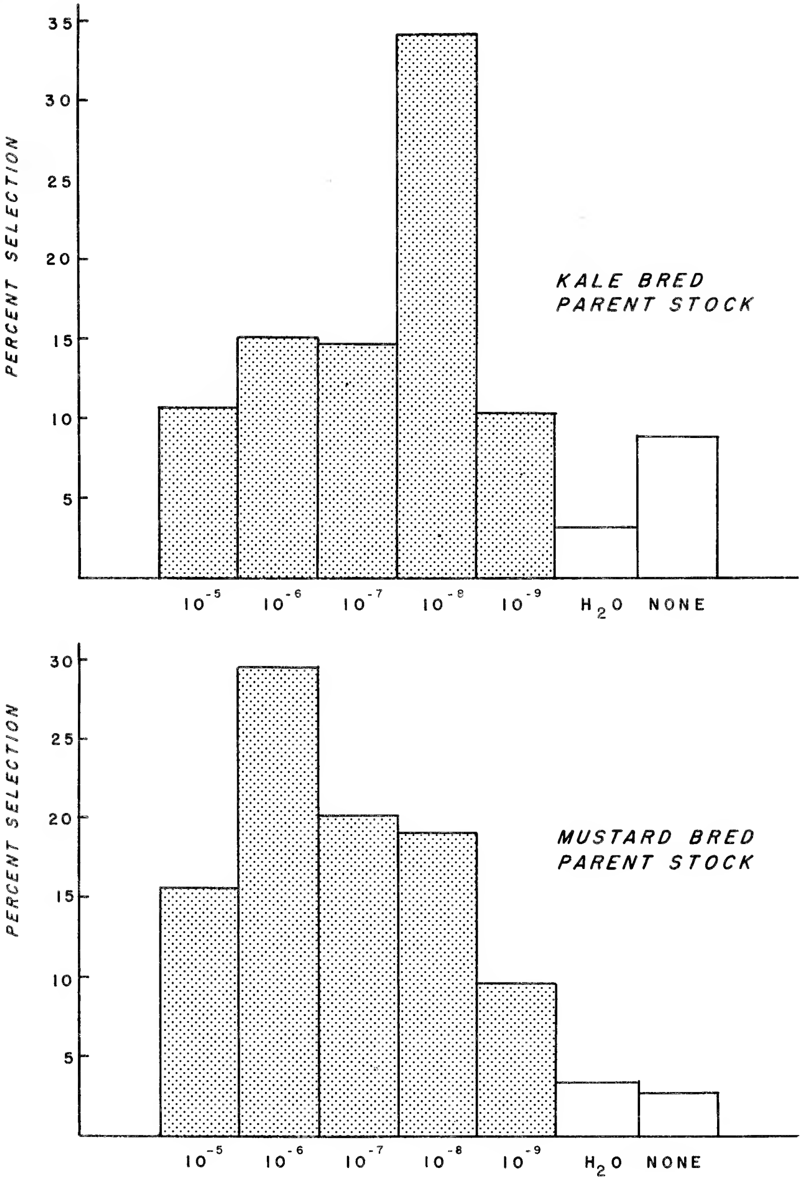


Fig. 3: Histograms illustrating the selections made by the larvae from the parental strains, comparing the kale and the mustard strains.

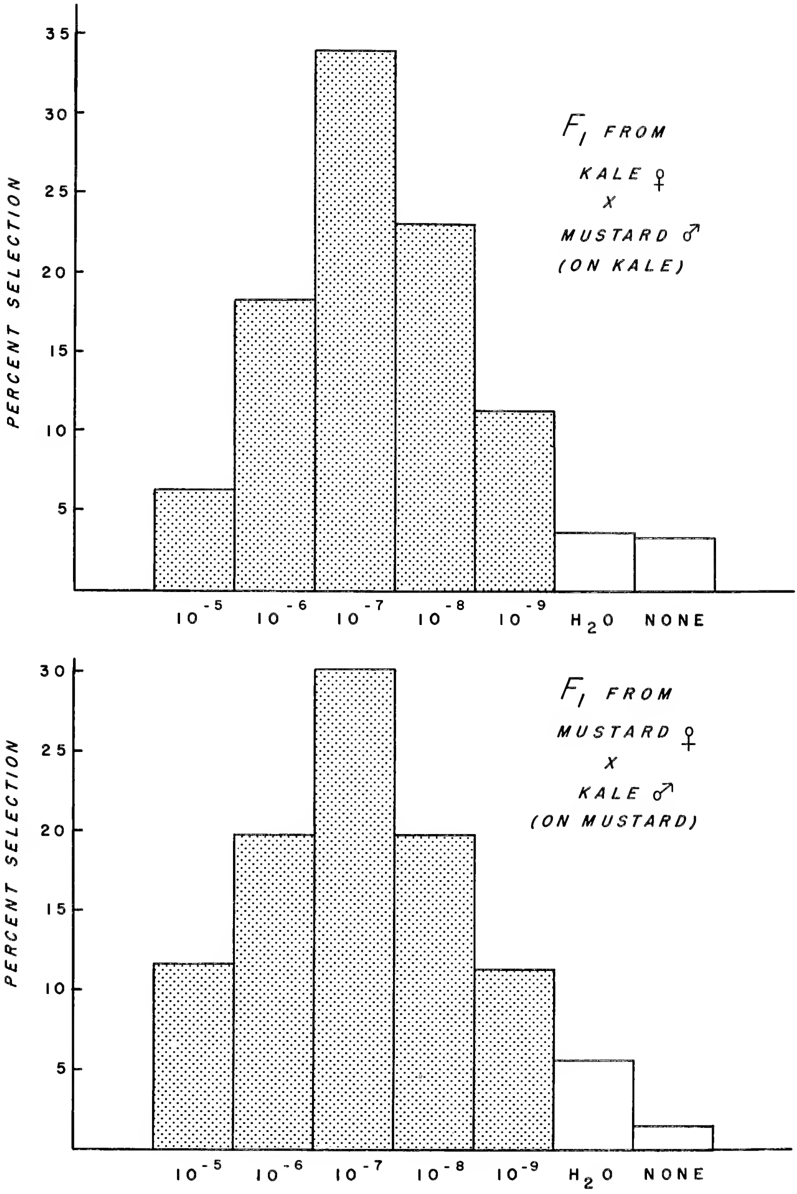


Fig. 4: Histograms illustrating the selections made by the F1 larvae from the reciprocal crosses between the kale and mustard strains.

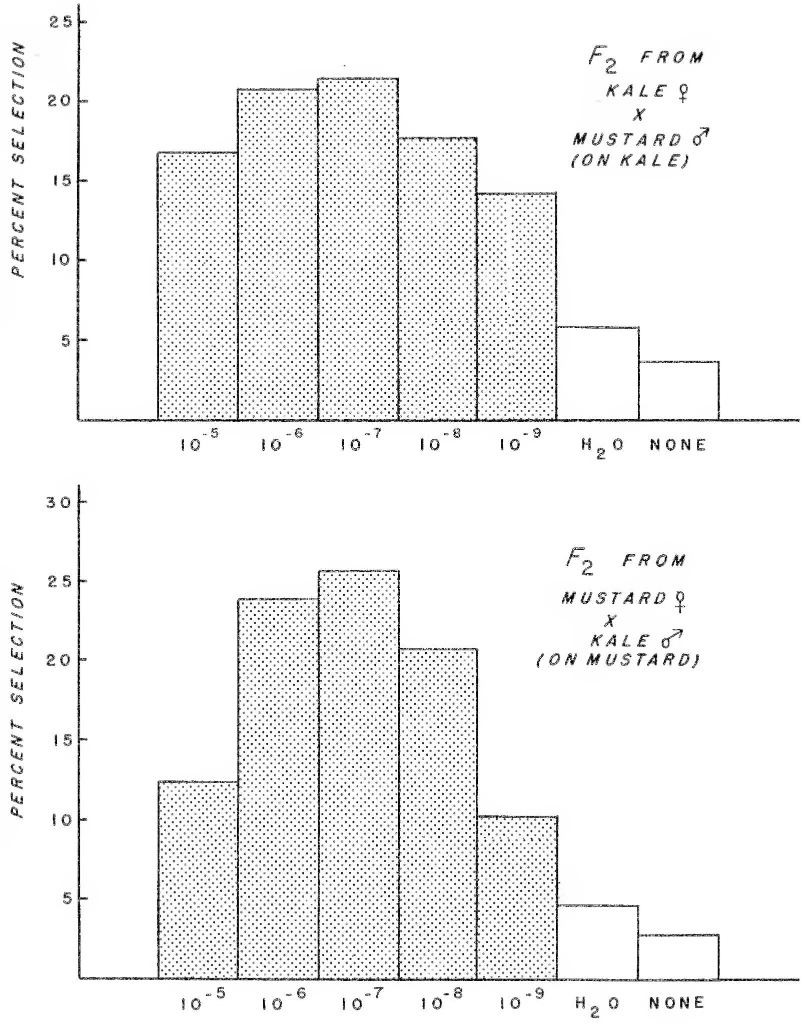


Fig. 5. Histograms illustrating the selections made by the F_2 larvae from the reciprocal crosses between the kale and the mustard strains.

assumptions are correct concerning the relationship between mustard oil concentration and food plant selectivity, that the mustard female F_1 larvae should select mustard oil concentrations at a higher level than the kale female F_1 larvae. That this is so can be seen by study of the histograms (Fig. 4) and the following calculations. Selections made by the mustard female F_1 larvae which are less than 10^{-7} (that is 10^{-5} or $^{-6}$) are 31.4 percent of the total as compared with 24.6 percent of the total for the kale female F_1 larvae. This shows that the larvae of the mustard female F_1 select a higher concentration of mustard oil than those of the kale female F_1 even though the modal class in both cases is at 10^{-7}. This difference is most probably attributed to the fact that the immediate F_1 larvae had been fed on the food plant of the mother, rather than that there was any genetic effect of maternal inheritance.

Two sets of F_2 have been bred, corresponding to the two sets of F_1. These two sets of F_1 are the reciprocal crosses mentioned above. The F_2 from the mustard female F_1 was continued on mustard for the food plant of the F_2 larvae, and the F_2 from the kale female F_1 was continued on kale. It would be expected, therefore, that each of these strains might diverge slightly in their selection according to the pattern of the larval foods. This result did not materialize.

The data indicate that the F_2 of both strains still have a selective propensity favoring the dilution, 10^{-7}, thus having the same modal class as the F_1 (Fig. 5). This is the expected genetic result for multiple factor inheritance. The second result expected for multiple factor inheritance is a wider range of variation in the F_2 than the F_1. This result is not shown by a wider range per se since no wider range of dilutions were used, but rather it is shown by a greater dispersion of the selections inside the range tested. This would give a greater standard deviation for the F_2 than for the corresponding F_1. The greater dispersion is very clear by study of the histograms, rearranged so that the mustard strains are on one page and the kale strains are on another (Figs. 6 and 7). The differences between the F_1 and the F_2 are striking. These results indicate clearly that the factors for food plant selection in *Pieris rapae* which have been separated in the two strains here tested are genetic and behave in a way comparable with polygenic inheritance. It also indicates that the populations of *Pieris rapae* existing in the wild are differentiated into genetically distinct populations, differing by genes which control the selection of food plants. These differences could account for a mechanism needed for species isolation (Hovanitz 1963c).

DISCUSSION AND CONCLUSIONS

The data indicated in this paper show that the strains which have been selected for particular food plant preferences over a period of several generations, and which when tested prefer the food plant upon which they have fed, also differ in their selection (preference) for various concentrations of mustard oil (allyl isothiocyanate). That these differences are genetic is apparent not only from the preceding data on food plant preferences but also on the data on mustard oil preferences introduced in this paper. Crossing of the two strains discussed here gives an F_1 which has a selection exactly intermediate between the two parental strains. The results are similar whether the kale strain contributes the maternal parent or whether the mustard strain contributes the maternal parent. There is, however, a greater selection of the higher concentrations in the strain fed on mustard than the one fed on kale.

The F_2 from these strains is similar to the F_1 except for the wider dispersion of the selections.

In the testing of these strains for food plant preferences, it was found that the larvae developed a preference for nasturtium in the F_1 and F_2. No reason can be deduced for this strange event based upon the present results unless it be that nasturtium emits at a concentration of mustard oil of the same attractive power as 10^{-7} allyl isothiocyanate or some other mustard oil of attractive significance. The odor of nasturtium does not seem to the human to be the same as that of allyl iosthiocyanate. However, it is possible that to the human, the odor of some other substance masks the odor of the attractive mustard oil, but that this odor does not do so in the larvae which are able to detect it.

Thorsteinsen (1953) has made the statement that larvae of the diamond-back moth, *Plutella maculipennis* (Cut.) are attracted to the odor of allyl isothiocyanate from a distance but are repelled by it when closeup so that they will not eat substances having this oil. Instead, they will eat substances with the corresponding glucoside, potassium myronate, but are not attracted to this substance from a distance. Since the glucoside is converted into the allyl isothiocyanate in the plant by a process of fermentation, it is probable that the attraction is really for the isothiocyanate not the glucoside, but that the isothiocyanate is produced slowly and in small quantities by the process of enzymatic fermentation. Indeed, Thorsteinson even indicates "in some experiments the addition of allyl mustard oils slightly increased feeding on media containing sinigrin." Wolfrom (1960) points out that "while the exact biological function of the plant glycosides is not established, it is probable that their formation provides the plant with a means of storing, in a harmless form, toxic and physiologically active materials which may be liberated by enzymes, in small quantities, when required." It seems not only possible but highly likely that the attraction differences noted by Thorsteinson are based upon the low concentration of allyl isothiocyanate rather than upon the presence of the glucoside sinigrin directly. Thorsteinson in fact admits this possibility in his comment, "On the other hand, it is possible that infinitesimal amounts of mustard oil vapor emanating from the leaves [by enzymatic action of myrosin on sinigrin] may stimulate the olfactory sense which is characteristically extremely sensitive in insects." Section in brackets not

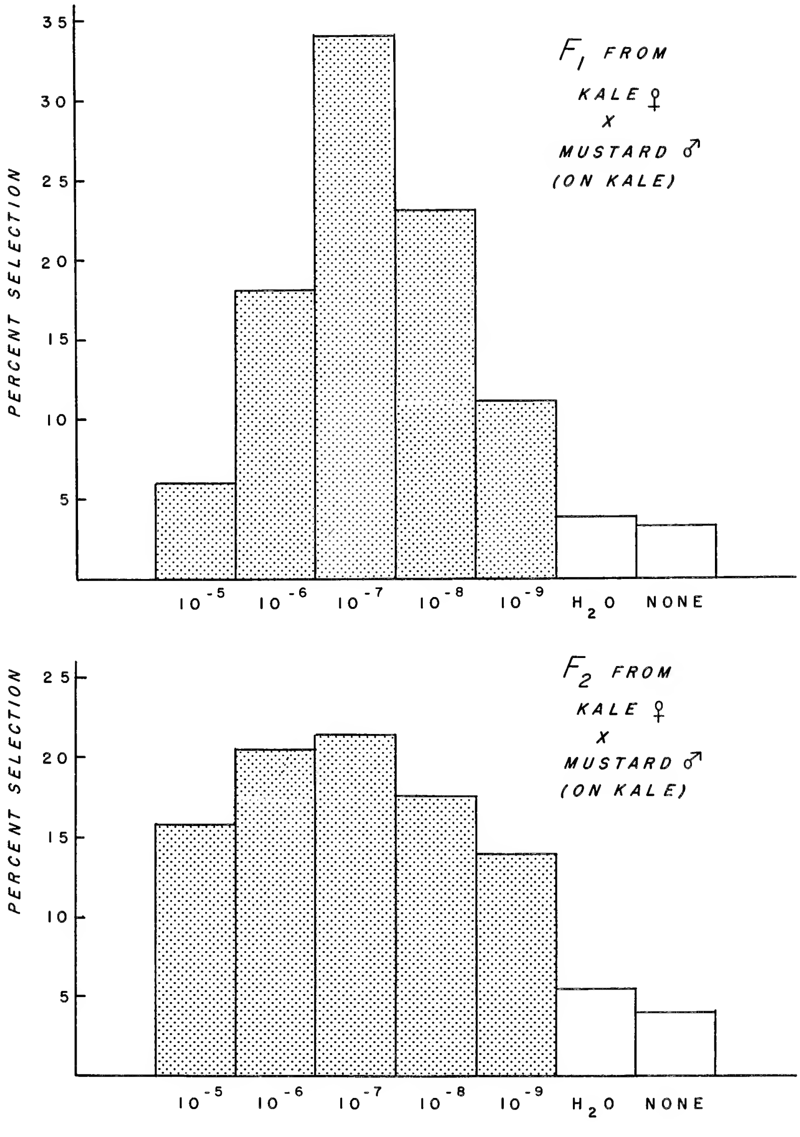
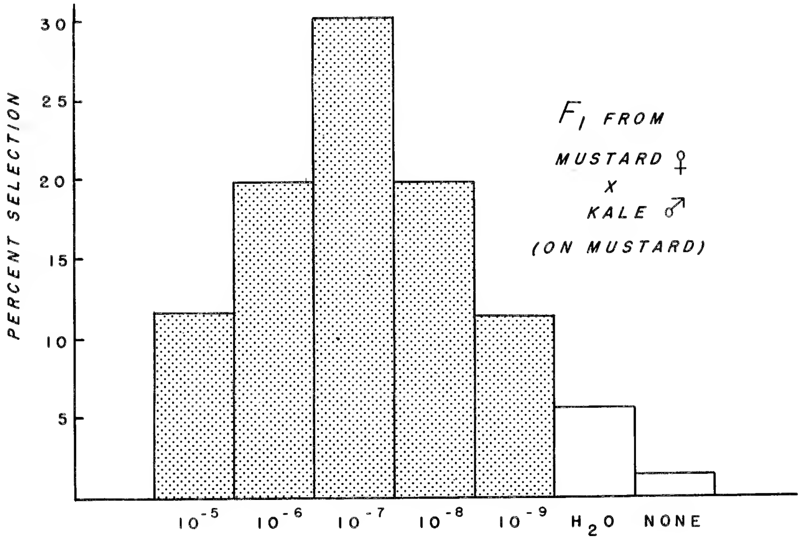


Fig 6. Histograms illustrating the selections made by the F_1 and F_2 larvae, comparing these larvae of the kale female crosses.



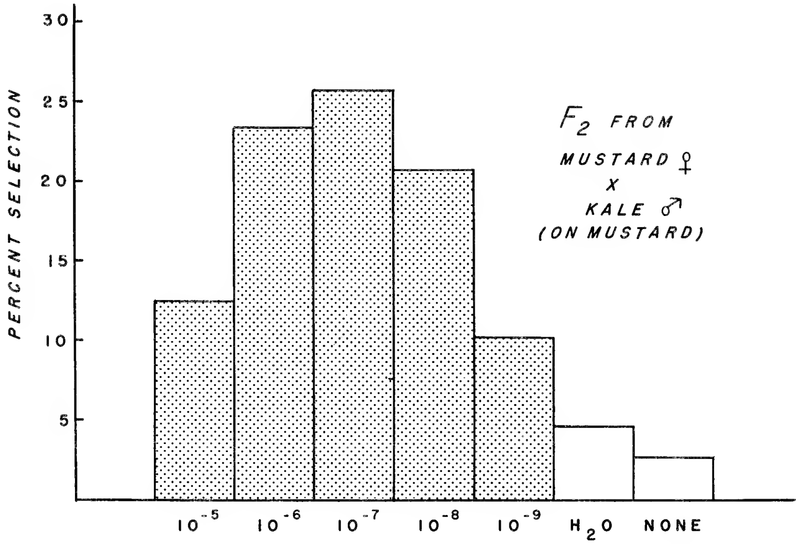


Fig. 7. Histograms illustrating the selections made by the F_1 and F_2 larvae, comparing these larvae of the mustard female crosses.

Thorsteinson's. Further testing of feeding responses of *Plutella* or *Pieris* larvae at a low mustard oil level are required to be certain of this differentiation. Presently published data of the present, or of other, authors are definitely not conclusive. Tests of this sort may be very difficult to make due to the high volatility of the mustard oil. There is no doubt that the use of the glucoside, rather than the oil, makes easier the maintenance of a low level of the oil vapor in the vicinity of the food. Our own data comparing the egg laying of the adults which are to be published later shows that the glucoside and mustard oil released from crushing seeds is more attractive than the mustard oil alone.

Verschaffelt (1910) was the first to study the relationship between the food plant choice of insects, plant odor and the chemistry of the relationship. He supposed that the larvae were attracted to the mustard oils present in the food plants but did not know whether the larvae differentiated between different oils or not. Dethier (1941) showed the selective effect of various odiferous oils toward lepidopterous larvae. Johansson (1951) showed that *Pieris brassicae* larvae preferred food plants to which they had already become accustomed by previous eating. This result has also been shown by us (Hovanitz and Chang 1962b and 1963a) on *Pieris rapae.*

LITERATURE CITED

DETHIER, V. G. 1941. Chemical factors determining choice of food plants by Papilio larvae. *Amer. Nat.* 75: 61-75.

HOVANITZ, WILLIAM and VINCENT C. S. CHANG. 1962a. The effect of various food plants on survival and growth rate of Pieris. *J. Res. Lepid.* 1 (1): 21-42.

————. 1962b. Three factors affecting larval choice of food plant. *J. Res. Lepid.* 1 (1): 51-62.

————. 1963a. The effect of hybridization of host-plant strains on growth rate and mortality of *Pieris rapae. J. Res. Lepid.* 1 (2): 157-161.

————. 1963b. Change of food plant preference by larvae of *Pieris rapae* controlled by strain selection, and the inheritance of this trait. *J. Res. Lepid.* 1 (2): 163-168.

————. 1963c. The relation of *Pieris virginiensis* Edw. to Pieris napi L. Species formation in Pieris? *J. Res. Lepid.* 1 (2): 124-134.

JOHANSSON, ARNE SEMB. 1951 The food plant preference of the larvae of *Pieris brassicae* L. *Norsk Ent. Tid. B.* VIII, 2.4-5: 187-195.

THORSTEINSON, A. J. 1953. The chemotactic responses that determine host specificity in an oligophagous insect (*Plutella maculipennis* (Curt.) Lepidoptera). *Canad. J. Zool.* 31: 52-72.

VERSCHAFFELT, E. 1910. The cause determining the selection of food in some herbivorous insects. *Proc. Acad. Sci. Amsterdam* 13(1): 536-542.

WOLFROM, M. L. 1960. Natural glycosides. *Encyclopaedia Britannica* 10: 448.

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BIOLOGY OF THE CEANOTHUS STEM-GALL MOTH, *PERIPLOCA CEANOTHIELLA* (Cosens)

WITH CONSIDERATION OF ITS CONTROL*

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THE STEM-GALL MOTH, *Periploca ceanothiella* (*Cosens*), has received but slight attention considering its importance as a pest of ornamentals on the genus *Ceanothus*. The genus *Ceanothus*, according to Van Rensselaer and McMinn (1942), comprises some 55 species native only to North America. Of these, some 44 species, and a number of horticultural varieties or selections, are grown in the Pacific Coast states. Many of them exhibit rather colorful bloom, ranging from the white flowers of *C. americanus* (New Jersey Tea) to the deep blue, lilac-like clusters of *C. thyrsiflorus* (Blue Blossom) and the pink of some selections. They occur mainly as shrubs and are used in landscape plantings and roadside beautification. Some, such as *C. gloriosus exaltatus* (Point Reyes Creeper) and *C. griseus horizontalis* (Carmel Creeper) are used as attractive groundcovers because of their low growing habit.

The distribution of the gall moth probably corresponds to the range of its host. Hodges (1962) in reviewing the genus *Periploca* mentions having examined specimens of *P. ceanothiella* collected in California, Kansas, New York, Ontario (Canada), and Texas. His review shifted this insect from the genus *Stagmatophora*, which it formerly occupied, to its present position in the genus *Periploca*.

DEVELOPMENT

This insect normally overwinters within its gall in some stage of larval development. Reference to Table 1 shows pupation to be barely under way in April and to continue, with moth emergence, throughout spring and early summer. Emergence, however, may begin as early as January from mature larvae brought in from outdoors and maintained under room temperatures.

The small, dark-colored moths (Fig. 1) begin egg laying within a few days following emergence. They deposit their small (0.5 mm) white

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TABLE 1. Status of overwintered *Periploca ceanothiella* galls.

PLACE & DATE 1962	Number of galls exam	PERCENT GALLS			
		With Larvae	With Pupae	With Parasites	Emerged
Arcadia					
April 9	88	87	2	11	0
May 18	64	60	21	15	4
June 7	142	23	44	19	14
July 26	104	2	6	3	89
Claremont					
April 25	85	52	28	18	2
May 16	80	28	22	11	39
June 14	76	19	26	15	40
La Canada					
April 17	66	94	0	6	0
May 22	70	62	4	19	15
Santa Barbara					
April 14	141	95	1	4	0

eggs on the underside of leaves, in leaf axils, and along the twigs. The eggs required 10 days for hatching under indoor temperatures of about 70° F. The newly hatched larvae move directly into the terminal growth where they penetrate the buds and inflorescences to cause the swellings or galls. Here the larva remains, feeding and growing on the inner tissue, until reaching full growth of 5 to 6.5 mm by the following spring or summer.

Before pupation begins, the larva cuts an exit hole partially through the side of the gall to leave only a thin film of bark which covers the entrance until time for the moth to emerge. This "window" or blocked entrance provides protection for the occupant against some enemies until it is ready to escape from the gall cavity. The pupation stage is spent within the gall and requires 24 days under room temperatures of about 70°F. Although the gall moths may emerge over a prolonged period of spring and summer, only one brood or annual generation was observed.

The pest has a stunting effect on the new growth. The galls may vary greatly in abundance, ranging from only an occasional gall to 20 or more per lineal foot of branch and twigs in heavy infestations. Some of the twigs may be killed outright from the injury. The most serious damage, however, was to the bloom. (Fig. 2). It was not unusual to see the flower clusters reduced to about 25% of their normal size, particularly where the gall larvae were present in the inflorescenses.

In no instance was more than one larva found per gall. In appearance, the gall is somewhat spindle-shaped and averaged about 13mm in length by 6mm diameter. (Fig. 3) This is about three times the diameter of the twig at point of junction with the gall.

PARASITES

The role of three naturally occurring ichneumonids in checking the stem gall is indicated in Table 1. All three, *Pristomerus baumhoferi* Cush., *Scambus aplopappi* (Ashm.), and *Apistephialtes nucicola* (Cush.), were observed mainly during the spring months. No hyperparasites were observed. Identifications were made by L. M. Walkley of the U.S. National Museum Staff. Muesebeck, Krombein, and Townes (1951) mention these ichneumonids as parasites of certain microlepidopterous larvae that tunnel in stems. Of the three parasites, *P. baumhoferi* was the most commonly encountered, and was the only one previously recorded as a parasite of this stem gall insect. The toll taken by the parasites ranged up to 19% of the gall-larvae. Only the mature larvae were attacked by the parasites.

NON-SUSCEPTIBILITY IN CEANOTHUS

Examination of Ceanothus collections at the Los Angeles State and County Arboretum in Arcadia, Rancho Santa Ana Botanic Garden at Claremont, and the Santa Barbara Botanic Garden at Santa Barbara (all southern California locations) showed varying degrees of non-susceptibility to the stem galls. It was an ideal way to check on this factor inasmuch as the Ceanothus species and varieties growing in each collection were equally exposed to the pest. The results presented in Table 2 would suggest the use of non-susceptible Ceanothus in plantings wherever practicable.

CHEMICAL CONTROL

Inasmuch as spraying of the Ceanothus with DDT had given little or no apparent control of this pest it was decided to test the systemic insecticide, dimethoate, for the purpose. A commercial formulation (Cygon) containing 43.5% dimethoate was mixed at the rate of one pint of this concentrate to 100 gallons of water and applied as a foliar spray to Ceanothus plantings in Arcadia on June 27, 1962. Examination made after one week following application showed that 92% of

TABLE 2. Occurrence of *Periploca ceanothiella* on various species, varieties and horticultural selections of *Ceanothus*.

HEAVY OCCURRENCE:

Ceanothus griseus
C. griseus horizontalis

MODERATE OCCURRENCE:

C. cyaneus
C. thyrsiflorus
C. 'Ray Hartman'
C. 'Marie Simon'

LIGHT OCCURRENCE:

C. arboreus
C. oliganthus
C. diversifolius
C. lemmonii
C. integerrimus
C. leucodermis
C. lobbianus
C. 'Treasure Island'
C. 'Sierra Blue'
C. 'Royal Blue'
C. 'Mountain Haze'
C. 'Mary Lake'
C. 'Concha'

NO OCCURRENCE:

C. americanus
C. parryi
C. papillosus
C. impressus
C. foliosus
C. insularis
C. cuneatus
C. ramulosus fascicularis
C. gloriosus
C. gloriosus exaltatus
C. rigidus albus
C. purpureus
C. prostratus
C. verrucosus
C. spinosus
C. jepsonii
C. masonii
C. megacarpus
C. greggi perplexus
C. 'Blue Cloud'
C. 'Lester Rowntree'

the gall larvae were killed. The spray, however, had no apparent effect on the mature gall larvae (which had ceased feeding), the pupae, or the parasites, *P. baumhoferi* and *A. nucicola;* adults of these normally emerged from galls collected from the treated areas. Effect of the treatment on *S. aplopappi* was not observed. The parasites developed only in the mature gall larvae, and therefore it is unlikely that they had had any contact with the insecticide. In addition to checking the stem gall infestation, the dimethoate also controlled the Ceanothus leaf miner, *Nepticula ceanothi* Braun, thrips, and an infestation of mites which were troublesome at the time. The spray used at this rate had no observable phytotoxic effect on the Ceanothus.

A similar application made on September 14, 1962 showed only 74% mortality of the gall larvae. This lower kill may have been due to the greater proportion of older, possibly more resistant, larvae at this time than at the June 27th spraying.

A soil drench of the dimethoate, made at six times the strength of the foliar spray, applied around the base of Ceanothus shrubs in Pasadena on July 11, 1962, resulted in 70% mortality of the gall larvae, but

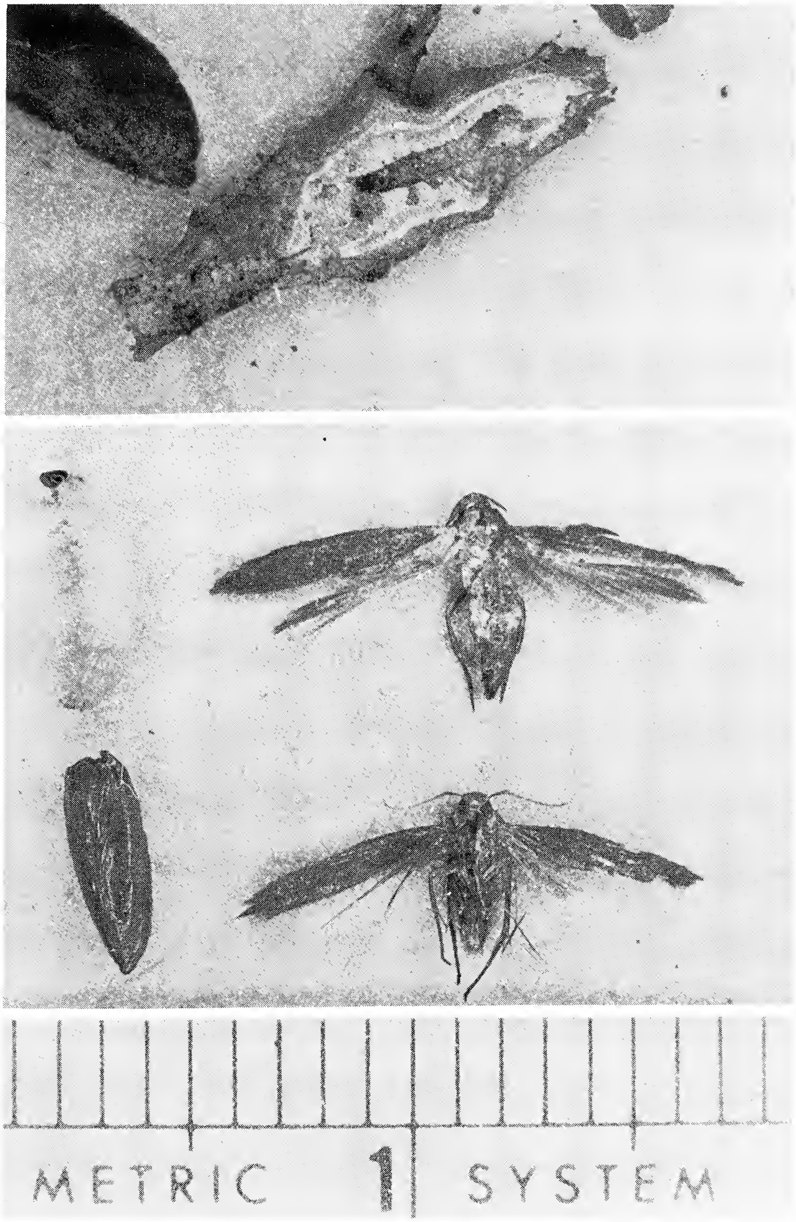

Fig. 1. The adult moth, *Periploca ceanothiella* (Cosens), at bottom right; larva and pupa at left; larva in cut gall at top.

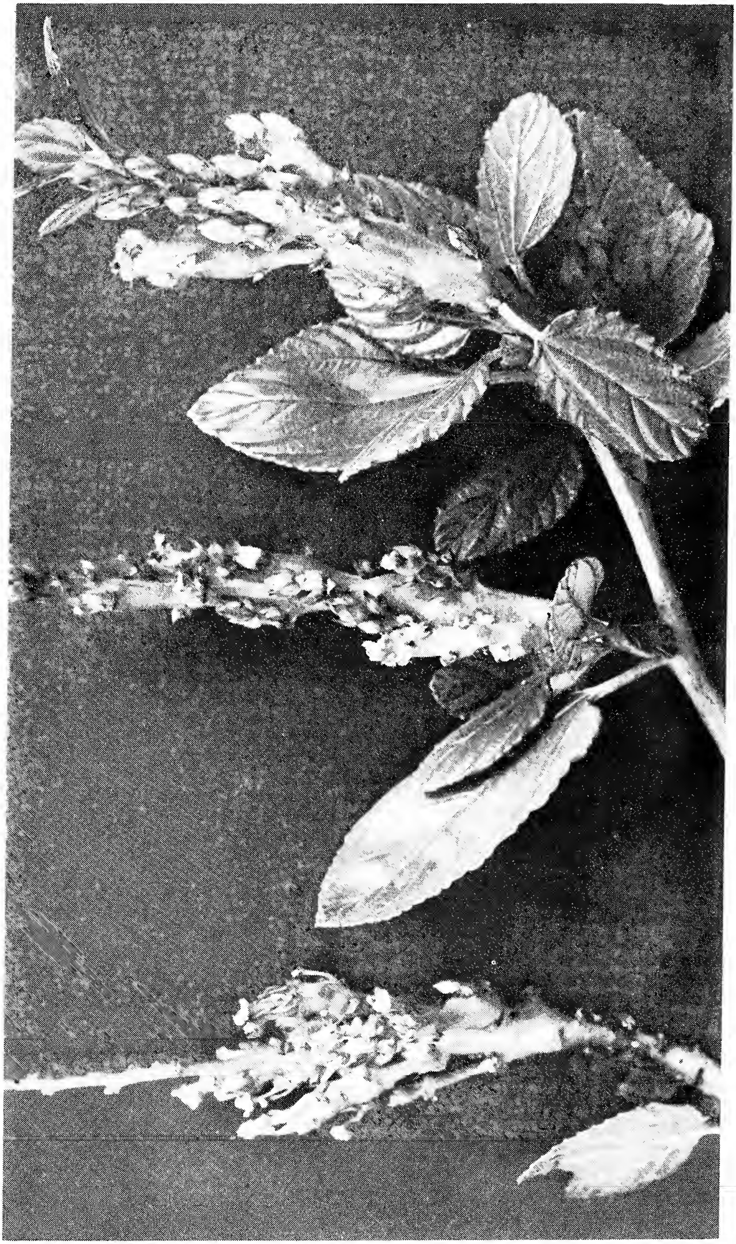

Fig. 2. Stem-galls caused by the larvae of *Periploca ceanothiella* C. on the stems of *Ceanothus thyrsiflorus*, showing swollen infloresecenses and almost complete destruction of the flowering buds.

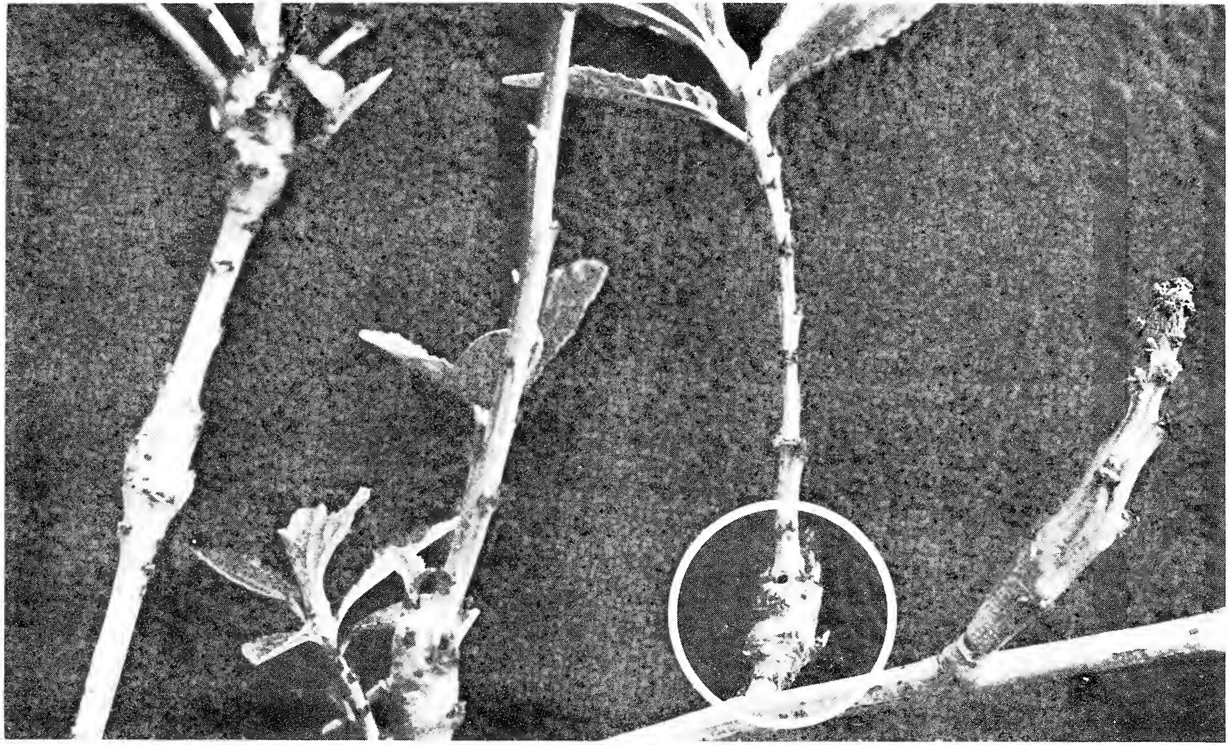

Fig. 3. Stem galls from which the moths have emerged; note the exit hole in the encircled gall. The twig at the right has been completely killed by the larvae. Note that the galls occur at the beginning of each period of stem growth, and that in the twig at the left, two different years' galls are shown.

caused burning and subsequent defoliation wherever the drench came in contact with the low-growing foliage. Examination of galls from untreated Ceanothus coinciding with observation on the treated shrubs, showed natural mortality of less than one percent, and of no significance.

Limited observations on Ceanothus growing in the wild showed the stem-galls to be less abundant than on Ceanothus grown under cultivation. This might indicate that irrigation and other care which these ornamentals received under cultivation makes them more attractive to this gall insect.

SUMMARY

The stem-gall moth, *Periploca ceanothiella* (Cosens), is a pest of ornamental shrubs in the genus *Ceanothus.* The moths emerge from the galls and lay their eggs throughout spring and early summer. There is but one generation or annual brood. Three naturally occurring ichneumonid parasites accounted for up to 19% mortality of the maturing gall larvae. No hyperparasites were observed. Examination of 40 species and varieties of Ceanothus growing in mixed collections at several southern California locations showed 2 with heavy occurrence of the galls, 4 with moderate occurrence, 13 with light occurrence, and 21 with no occurrence. This would suggest the planting of the more non-susceptible varieties to alleviate or avoid the problem where practicable. Dimethoate used as a foliar spray proved highly effective against the immature gall larvae, as well as the leaf miner, thrips, and mites, but had no apparent effect on the mature gall larvae and pupae, or the parasites. Limited observations indicated the galls to be more troublesome on Ceanothus growing under cultivation than in the wild.

REFERENCES CITED

VAN RENSSELAR, M., and H. E. McMINN. 1942. Ceanothus. *Gillick Press, Berkeley, California.* 308 pp.

MUESEBECK, C. F. W., K. V. KROMBEIN, and H. K. TOWNES. 1951. Hymenoptera North of Mexico Synoptic catalog. *Monograph No. 2, U. S. Department of Agriculture, Washington, D.C.* pp. 186, 188 and 387.

HODGES, R. W. 1962. A review of the genus Periploca with descriptions of nine new species. *Pan-Pacific Entomologist.* 38: 83-89.

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LARVAL FOOD-PLANT RECORDS FOR SIX WESTERN PAPILIOS

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REPORTED ON HERE are some of our recent observations on natural and laboratory foodplants used by *Papilio eurymedon* Lucas, *P. indra indra* Reakirt, *P. indra pergamus* Edwards, *P. bairdii* Edwards, *P. oregonius* Edwards, and *P. rudkini* Comstock. Some previously reported foodplants whose authenticity has been doubted are shown to be true larval foodplants, while several new plant records for these species are reported for northern Oregon and California populations.

1. *Papilio eurymedon.*

After a thorough review of available records, Brower (1958; 1962, *in litt.*) concluded that *Prunus* is not a foodplant of this species. The present authors (1962), however, recorded this plant as a possible foodplant for *P. eurymedon,* and several observations of *eurymedon* using *Prunus* seem to be worthy of publishing in view of the previous conflicting evidence.

While collecting in the vicinity of Frazier Park, Kern County, California, on June 30, 1962, the senior author observed what appeared to be a female *Papilio eurymedon* fluttering over a small bush of *Prunus ilicifolia.* This observation led to a search of the plant, which yielded one second-instar *Papilio* larva. This larva was brought back to the laboratory and was successfully reared on *Prunus lyoni.* It pupated on August 6 and on August 22, it produced a male *eurymedon.*

Noel McFarland (1962, *in litt.*) has also found *Prunus ilicifolia,* as well as *Rhamnus crocea,* to be foodplants of *Papilio eurymedon.* At Oak Pass in the Santa Monica Mountains of Southern California, he states: "*Prunus ilicifolia* . . . is the only plant I have ever found them on (beyond second instar) in the wild. I have often collected eggs and first instar larvae on *Rhamnus crocea.*"

At least in California, then, *Prunus ilicifolia* seems to be a natural and fully satisfactory foodplant for *Papilio eurymedon.*

2. *Papilio indra indra.*

In his *Butterflies of North America* (1897), Edwards stated that *Artemisia dracunculoides* (Compositae) was a foodplant of *P. indra* in Colorado. Kent Wilson (1961) apparently used this record in the most recent publication of foodplants for this species. However, in 1918 J. C. Hopfinger reported that he had never found *indra* larvae on *A. dracunculoides.* He did find black *Papilio* larvae (very probably *indra*) on an "umbelliferous species," on which he also found larvae of *P. zelicaon.* These black *"indra"* larvae would not accept *A. dracunculoides* when transferred to it.

As we reported in 1962, the foodplant of *P. indra* in the Sierra Nevada is *Pteryxia terebinthina* (formerly *Cymopterus terebinthinus*). There are many botanical records of this plant (Dr. Mildred Mathias, personal communication) for the area around Brewster, Washington, and the "umbelliferous" foodplant found by Hopfinger may well have been this species. Don Eff (1962, *in litt.*) reports the foodplant of *indra* in the Front Range of Colorado to be *Harbouria trachpleura* (Umbelliferae).

3. *Papilio indra pergamus.*

The first known foodplant of this subspecies of *indra* was found by Comstock (1928); this was *Tauschia parishii* (Umbelliferae) in the San Gabriel Mountains.

Fred Thorne (1962, *in litt.*) has found *pergamus* eggs and larvae on *Tauschia arguta* and *Lomatium lucidum* (Umbelliferae) on Tecate Peak, San Diego County, California.

4. *Papilio bairdii.*

Edwards (1893, 1898) found that carrot (*Daucus carota*) was somewhat acceptable to *bairdii* larvae, while the larvae "thrived" on fennel (*Foeniculum vulgare*). However, Brown (1957) states that these two plants are unacceptable to *bairdii.*

On July 27, 1962, the senior author collected 6 fifth-instar larvae and 2 fourth-instar larvae of *P. bairdii* on *Artemisia dracunculoides* (Compositae) at Barton Flats, San Bernardino County, California. In the laboratory, these larvae immediately accepted fennel when placed on this plant. Fennel and this *Artemisia* were eaten with no preference for either plant. These larvae pupated, and a male and female adult pair emerged on September 9, 1962.

5. *Papilio oregonius.*

On September 1, 1962, both authors collected larvae of *P. oregonius* at Heppner Junction (Gilliam County) along the Columbia River, Oregon. These larvae (1 second-instar, 2 fourth-instar, and 3 fifth instar larvae) were found on *Artemisia dracunculoides.* In the laboratory, they fed readily on fennel. It was of possible biochemical interest to note that the odors of crushed leaves of these plants were similar.

6. *Papilio rudkini.*

The natural foodplant of this species is *Thamnosma montana* (Rutaceae). But this *Papilio* has also been found on *Daucus carota* (Umbelliferae) in Yuma, Arizona (Bauer, 1955).

In April of 1962, the senior author collected ten larvae of *Papilio rudkini* on *Thamnosma montana* in Sentenac Canyon, San Diego County, California. These larvae were transferred to fennel in the laboratory, which was fairly acceptable to them (20% mortality). All refused to eat *Citrus,* which is very acceptable to *Papilio zelicaon.*

SUMMARY OF NATURAL AND LABORATORY FOODPLANTS RECORDED IN THIS PAPER

N=natural foodplant; L=acceptable as laboratory foodplant.

Papilio eurymedon	Rosaceae	
		Prunus ilicifolia (N)
		Prunus lyoni (L)
	Rhamnaceae	
		Rhamnus crocea (N)
Papilio indra indra	Umbelliferae	
		Pteryxia terebinthina (N)
		Harbouria trachpleura (N)

Previously-recorded *Artemisia dracunculoides* is dropped in this paper from the group of known foodplants of *P. indra indra.*

Papilio indra pergamus	Umbelliferae	
		Tauschia parishii (N)
		Tauschia arguta (N)
		Lomatium lucidum (N)
Papilio bairdii	Compositae	
		Artemisia dracunculoides (N)
	Umbelliferae	
		Daucus carota (L)
		Foeniculum vulgare (L)
Papilio oregonius	Compositae	
		Artemisia dramunculoides (N)
	Umbelliferae	
		Foeniculum vulgare (L)
Papilio rudkini	Rutaceae	
		Thamnosma montana (N)
	Umbelliferae	
		Daucus carota (N, but introduced plant)
		Foeniculum vulgare (L)

LITERATURE CITED

BAUER, DAVID L., 1955. Notes on the *Papilio machaon* complex in Arizona. *Lepid. News* 9: 7-10.

BROWER, LINCOLN P., 1958. Larval foodplant specificity in butterflies of the *Papilio glaucus* group. *Lepid. News* 12: 103-114.

BROWN, F. MARTIN, 1957. *Colorado Butterflies,* p. 215.

COMSTOCK, JOHN ADAMS, 1928. Records of the Lorquin Entomological Society. *Bull. Southern Cal. Acad. Sci.* 27: 73.

EDWARDS, WILLIAM H., 1893. Notes on a polymorphic Papilio. *Canad. Ent.* 25: 253-254.

————, 1897. *Butterflies of North America,* 3 vols.

————, 1898. Further observations on *Papilio bairdii* Edwards. *Canad. Ent.* 30: 11.

EMMEL, THOMAS C., & JOHN F. EMMEL, 1962. Ecological studies of Rhopalocera in a High Sierran community—Donner Pass, California. I. Butterfly associations and distributional factors. *Journ. Lepid. Soc.* 16: 23-44.

HOPFINGER, J. C., 1918. Notes on *Papilio indra* Reakirt. *Ent. News* 29: 354-5.

WILSON, KENT H., 1961. Family Papilionidae. pp. 30-50. *In* Ehrlich, Paul R. and Anne H., 1961. *How to Know the Butterflies,* Dubuque, Iowa: Brown, 262 pp.

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COLIAS PHILODICE IN CHIAPAS, MEXICO

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COLIAS PHILODICE GODART has the widest continuous range of any Coliad in North America. The species is found from the northern Arctic southward to the edge of desert areas in the Owens Valley of eastern California, the highlands of northern Arizona, and the Cochise and Rio Grande River valleys of New Mexico and Texas. In addition, three isolated populations of the species are known in the central mountains of Guatemala (Hovanitz, 1950a). The present note extends the known distribution of the species to include the republic of Mexico, and gives the frequency of white dimorphic females in the single population found.

The Mexican population of *C. philodice* was discovered in a long valley about 12.5 kilometers southeast (on Highway 190) from the plaza in San Cristobal de las Casas, central Chiapas. The valley is about a kilometer east of the highway at this point. The elevation above sea level is 7600-7700 feet, and the rolling mountains are covered with pine-oak forest, with grassy areas in the valleys.

At the time of our visit (March 26-29, 1959), these *Colias* were in full flight, and almost all specimens were fresh. The males were far more numerous than the females, but as every female seen was usually collected, the data given in Table 1 on relative abundance of the two female color phases may be considered fairly accurate considering the small number involved (for these dates). The frequency of white females in this locality is within the range of frequency (10 to 20%) found in the mountains of the western United States (Hovanitz, 1950b).

TABLE 1. Frequency of color phases of female *Colias philodice* in central Chiapas, Mexico.

Yellow Females	*White Females*	*Total*	*Per cent White* ± *S.E.*
11	2	13	15.38±10.0%

LITERATURE CITED

HOVANITZ, W. 1950a. The biology of Colias butterflies. I. The distribution of the North American species. *Wasmann J.. Biol.* 8: 49-75.

HOVANITZ, W. 1950b. The biology of Colias butterflies. II. Parallel geographical variation of dimorphic color phases in North American species. *Wasmann J. Biol.* 8: 197-219.

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NOTES ON THE EARLY STAGES OF TWO CALIFORNIA GEOMETRIDS

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AETHALOIDA PACKARDARIA

THIS MOTH WAS DESCRIBED by Hulst in 1888, as *Hemerophila packardaria.* He subsequently created two synonyms for the same insect, namely, *Selidosema lachrymosa* (1898, described from Los Angeles County), and *Selidosema homopteroides* (1901, from Oregon).

Aethaloida packardaria was pictured by McDunnough in 1920, on Plate VII, fig. ii of his Cleorini Studies.

In 1937 I published a description and illustration of the mature larva, from an example taken in Bouquet Canyon, Los Angeles County. This year (1962) I was able to obtain eggs and rear the species through to maturity, which will serve to supplement and amplify the former incomplete record.

Eggs were secured June 27 from captive females. *Ceanothus* and *Adenostoma* were supplied to them, and oviposition occurred in clusters on the tips of twigs. It was noted that the bases of the eggs in each cluster pointed outward.

EGG: 0.8 mm. high, x 0.6 mm. at the widest point. The form is subovoid, the base wider and the top tapering to a well rounded and smooth surface, with no discernible micropyle. The base tapers inward at the circumference and bears a circlet of pearl-like protrusions, about 20 in number, enclosing a granular depressed floor.

The surface of the egg above the circlet is finely granular, and does not bear ridges. The color, when first laid, is dull olive-green. Later it becomes darker.

Eggs laid June 27 hatched July 2 and 3, 1962. The illustration (fig. 1A), shows the egg in lateral aspect.

FIRST INSTAR LARVA: Length, 2 mm. Width of a typical body segment approximately 0.15 mm.

Head; width, 0.35 mm. Color, jet black except for a narrow transverse bar on the labrum, which is dull white. The ocelli are black, and the setae white.

The body is predominantly black. The thoracic segments taper from the widest next to the head to the third which grades into the 0.15

mm. wide first abdominal segment. The dorsum is solidly black. Laterally on each segment there is a large subtriangulate white spot on each side, which extends up over the dorso-lateral edge.

The legs are black, as are also the prolegs. There are rows of short white setae, the most prominent of which is in longitudinal alignment above the white spots.

The first instar larva is shown on figure 1B. No attempt has been made to accurately map the setae, but preserved larvae are available for this purpose.

SECOND INSTAR LARVA, observed July 7, '62. Length, 4.5 mm. Body width, 0.4 mm., as is also the head width.

Head, black, as in the first instar.

The body is a dull maroon over the dorsum. The white triangulate spots along the side persist as clumps of round spots in groups of approximately three, close together, or fusing with each other. There is a transverse line of round white dots on the front margin of the first segment.

The venter is dull maroon.

This batch of larvae did not thrive well, probably as a result of too quick drying of the food plant. Mature larvae were later beaten from *Adenostoma* and *Ceanothus,* and were carried through to maturity. My previous published description and illustration of the full grown larvae (1937) does not need to be repeated, but a drawing is here included on figure 1C.

PUPA: Length, 13.5 mm. Greatest width, 3 mm. Color, black on wing cases, thoracic and head portions; red-brown on the abdominal segments, with a darker shading on the segmental junctures, and the cauda.

Two black knobs protrude from the front of the head. The maxillae and antennae reach to the wing margins. The cremaster consists of a knobbed triangulate black element, from which arises a pair of relatively long recurved spikes, and along the sides, three short red-brown recurved hooklets. The spiracles are concolorous with the body, and relatively inconspicuous. The pupa is pictured on figure 1D.

BIBLIOGRAPHY

COMSTOCK, JOHN ADAMS. 1937. Miscellaneous Notes on Western Lepidoptera. *Aethaloida packardaria. Bull. So. Calif. Acad. Sci.* 36 (3): 41-124. Pl. 47.

HULST, G. D. 1888. Hemorophila packardaria. *Ent. Amer.* III: 217.

HULST, G. D. 1888. Hemerophila packardaria. *Ent. Amer.* III:217.

————————. 1898. *Selidosema lachrymosa. Can. Ent.* 30: 194.

————————. 1901. *Selidosema homopteroides. Jour. N. Y. Ent. Soc.* 8: 219.

McDUNNOUGH, J. H. 1920. Studies in North American Cleorini, (Geometridae) *Bull. Dept. of Agric. Canada.* 18: 37-38. Plate VII, fig. II.

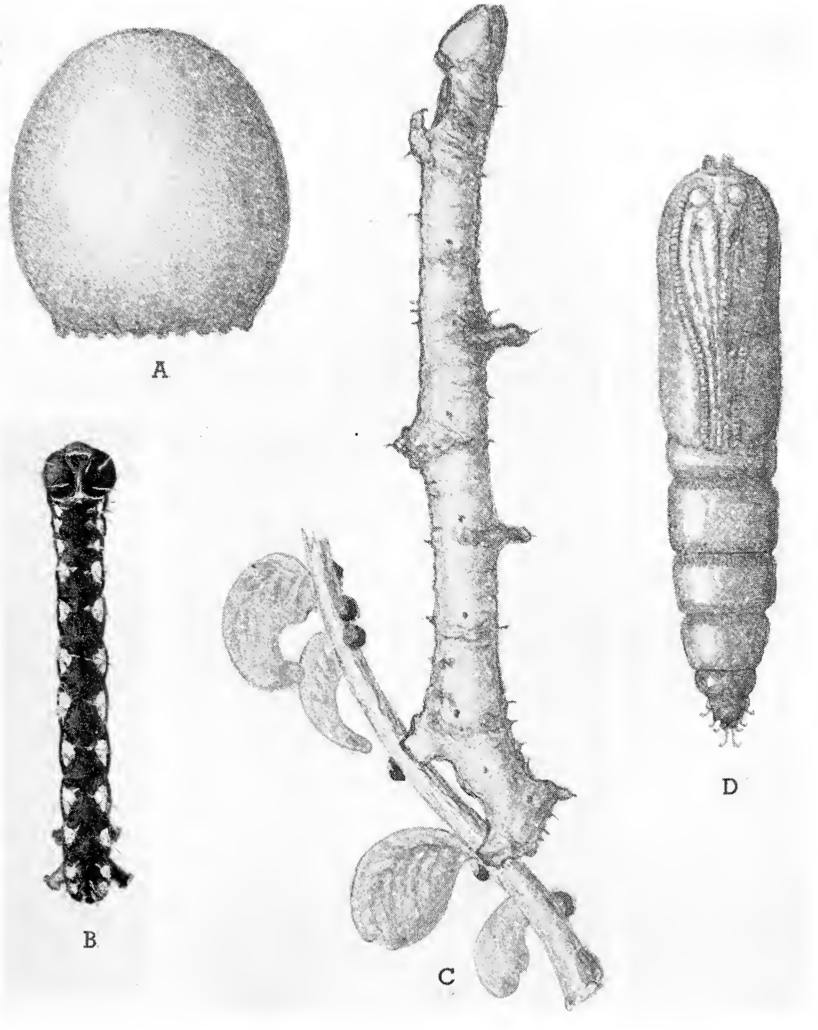

Fig. 1. Early stages of *Aethaloida packardaria* (Hulst). A. Egg, lateral aspect, enlarged × 50. B. First Instar larva, dorsal aspect, enlarged × 30. C. Mature larva, lateral aspect, enlarged × 3. D. Pupa, ventral aspect, enlarged × 5.

Reproduced from water color drawing by the author.

PROCHOERODES FORFICARIA

In 1956 I published notes on the larva and pupa of the geometrid moth, *Prochoeroides forficaria* (Guenée) from larvae obtained in Gila County, Arizona.

Dr. McDunnough's published comments on this species (1940) suggest that the Arizona specimens from which I described the larva and pupa are closer to form *catenulata* Grote, and that this "could very readily be considered a good species."

I have recently reared typical *P. forficaria* from material taken at Del Mar, and the following notes, with illustrations, give a more accurate analysis of the species designated

PROCHOERODES FORFICARIA

Eggs were laid April 10, 1962 in a rearing jar. They were laid on their sides, some singly, others in small bunches.

EGG: When first laid, bright green. Later they became dark, and prior to hatching were black. The form was an elongate oval, with about 16 ridges extending from base to micropyle. There were no horizontal ridges or lines. The micropyle was pitted.

The average length of the egg was 0.9 mm. and the width, 0.5 mm.

There was considerable variation in size and form, some examples being elongate and somewhat less rounded at the ends.

The eggs hatched April 21 and 22, the larvae usually emerging from the side, leaving the remainder of the shell intact.

Not knowing the food plant, the following were tried; lettuce, dandelion, plantain, grass, fuschia, *Ceanothus* and *Cneridium,* none of which proved acceptable. They finally accepted willow.

FIRST INSTAR LARVA: Length, 4. mm. Width, 0.2 mm. Head width, 0.4 mm. The head is relatively large, and is mottled black and brown. Ocelli, black.

The body is cylindrical, elongate, and very narrow. The ground color is slaty gray. There is a broad longitudinal black band on the dorsum, with occasional darker spots on some of the segments. The lower lateral surface is a translucent gray-straw. The entire ventral surface is black. The single pair of prolegs, and anal prolegs, are dark on the lateral surfaces and lighter on the ventral surfaces. The setae are white, and very minute.

The first instar larva is illustrated on figure 2B.

In this phase the larvae were exceedingly active, dropping on a thread when touched.

Larva of 11 mm. in length, — head width, 1.55 mm.

The body is cylindrical, its entire surface being mottled red-brown. on the dorsum there are indefinite quadrate patches of darker brown, more clearly defined in the thoracic and caudal areas, but nowhere connected sufficiently to form an unbroken band. The true legs are yellow-brown, and the prolegs concolorous with the body. The latter are prominent and conspicuous.

MATURE LARVA: Noted on May 5, at the beginning of the final instar. Length of larva, 22 mm. Head width, 2.4 mm.

The body color is light wood brown, the head a shade lighter. The body is mottled with darker spots and dashes, and its surface is crossed transversely by numerous fine creases and ridges.

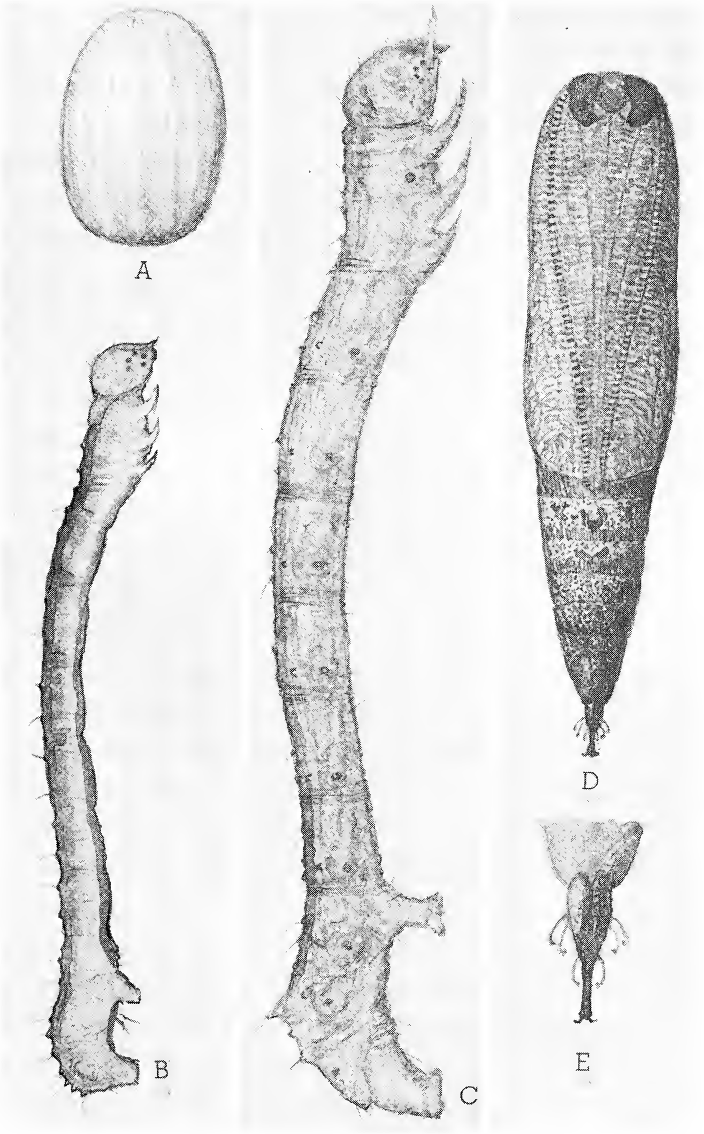

Fig. 2. Egg, larva and pupa of *Prochoerodes forficaria.* A. Egg, lateral aspect, enlarged × 40. B. First instar larva, lateral aspect, enlarged × 24. C. Mature larva, enlarged × 5. D. Pupa, ventral aspect, enlarged × 5. E. Cremaster, highly magnified.

Reproduced from water color drawing by the author.

Middorsally there is an indefinite longitudinal band of brown, nowhere clearly defined. Spiracularly there is a pinkish irregular band, enlarging around each spiracle, and contracting on the segmental junctures. Near each spiracle there are two or three round dots. The legs are slightly translucent, and the prolegs are concolorous with the body, or slightly tinged with yellow.

There are numerous small papillae scattered over the body, two pairs of which in the dorso-caudal area are slightly larger. All papillae bear short yellow-brown setae. This is the larval phase that is pictured on figure 2C.

On May 29, the larva measured 30 mm., the head width being 2.4 mm. as before. The chief difference in this prepupal stage is that there is less definite ornamentation, although the pinkish area following the spiracles is clearly defined, and the spiracles are more conspicuous, with dark rims and a surrounding rim of yellow.

In the final phase the larva becomes sluggish, and spends much time resting on a twig, or the midrib of a leaf, where it is ideally camouflaged. The first example pupated June 9, 1962.

PUPA: Length, 17 mm. Width through middle portion, 5 mm. The color is brown, with the eyes and terminal segments darker.

The antennae extend slightly beyond the wing margins. The wing cases and appendanges are overlaid with fine transverse brown lines and dashes. The dorsal surface, and the abdominal segments are heavily spotted with dark brown and black. The spiracles are concolorous with the body and are inconspicuous.

The cremaster is formed by a double ovoid extension, narrowing down to a clubbed shaft, which ends in two recurved tips that are arched latero-ventrally. Near the base of the shaft there are six small yellow-brown hooklets, three on each side. These arch medially. The pupa is illustrated on figure 2D and an enlarged figure of the cremaster on figure 2E.

The first imago emerged June 21, 1962.

In 1926 Stanley E. Flanders recorded the recovery of three species of parasites from larvae of *Prochoerodes forficaria,* namely, *Amblyteles caeruleus* (Cr.), *A. zebratus* (Cr.), and *Euplectrus* sp.

We have very little information on the range of *P. forficaria* but Dr. McDunnough's description of the southern British Columbia form *combinata* suggests that our typical species ranges northward through Oregon and perhaps Washington, where it grades into *combinata.*

We still need information as to its southern and eastern range.

BIBLIOGRAPHY

COMSTOCK, JOHN ADAMS. 1956. Scientific Notes. *Prochoerodes forficaria* Gn. Larva, Pupa. *Bull. So. Calif. Acad. Sci.* 55 (3): pp. 180-181.

FLANDERS, STANLEY E. 1926. Notes on Parasites at Saticoy, California During the Year 1925. *Pan. Pac. Ent.* 2 (7): pp. 157-158.

McDUNNOUGH, J. H. 1940. New North American Geometridae with Notes. 111. *Can. Ent.* 72 (5): pp. 90-103.

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GEOGRAPHICAL DISTRIBUTION AND VARIATION OF THE GENUS ARGYNNIS

III. ARGYNNIS DIANA

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The Diana fritillary, *Argynnis diana* Cramer, departs from the most usual color pattern for the genus as the pattern is developed in most species of the Nearctic and the Palearctic. The male and female both have the basal two-thirds of the wings a brownish black. This distribution of pigment is in part the reverse of the distribution for *Argynnis idalia,* in which the black pigment is primarily restricted to the outer half of the wings. It has already been pointed out (Hovanitz, 1963) that the distribution of this pigment for *idalia* is diametrically opposed to the ordinary tendencies in other members of the genus in which the black pigment is normally distributed in the area of the basal regions. This is the pattern arrangement for *Argynnis diana, A. cybele, A. leto, A. nokomis* and others in North America which show an extension of basal melanism. The remainder of the wings shows the usual pattern arrangement of black dots and black striping which is typical of the genus *Argynnis* in any part of the world. In the male, however, these black markings are greatly diminshed and restricted in most cases, especially on the hind wing, so that the outer one-third of the wings on the upper side are nearly a solid brownish-orange color. On the female this restriction of the black does not occur. It is in fact greatly extended so that not only is the outer margin all black, but the black-veined stripes are wide and extend from the basal black to the margin, and the black dots are large and converge to form black stripes running nearly from the anal margin to the inner margin at least on the fore wing. The part of the wings then remaining that would normally be a brown color in *Argynnis* is an irridescent blue. On the face of it, the female *diana* is a black butterfly with marginal and submarginal rows of blue spots. This dimorphism of the sexes of *A. diana* is the greatest expression in North American *Argynnis* of this type of variation. It is, however, nearly duplicated by some races of *Argynnis nokomis,* to which it may be closely related (fig. 1).

The under side of the wings also shows a very different aspect than the usual *Argynnis* pattern. This alteration of the pattern is more than the usual general suffusion of color over the wing but effects the pattern

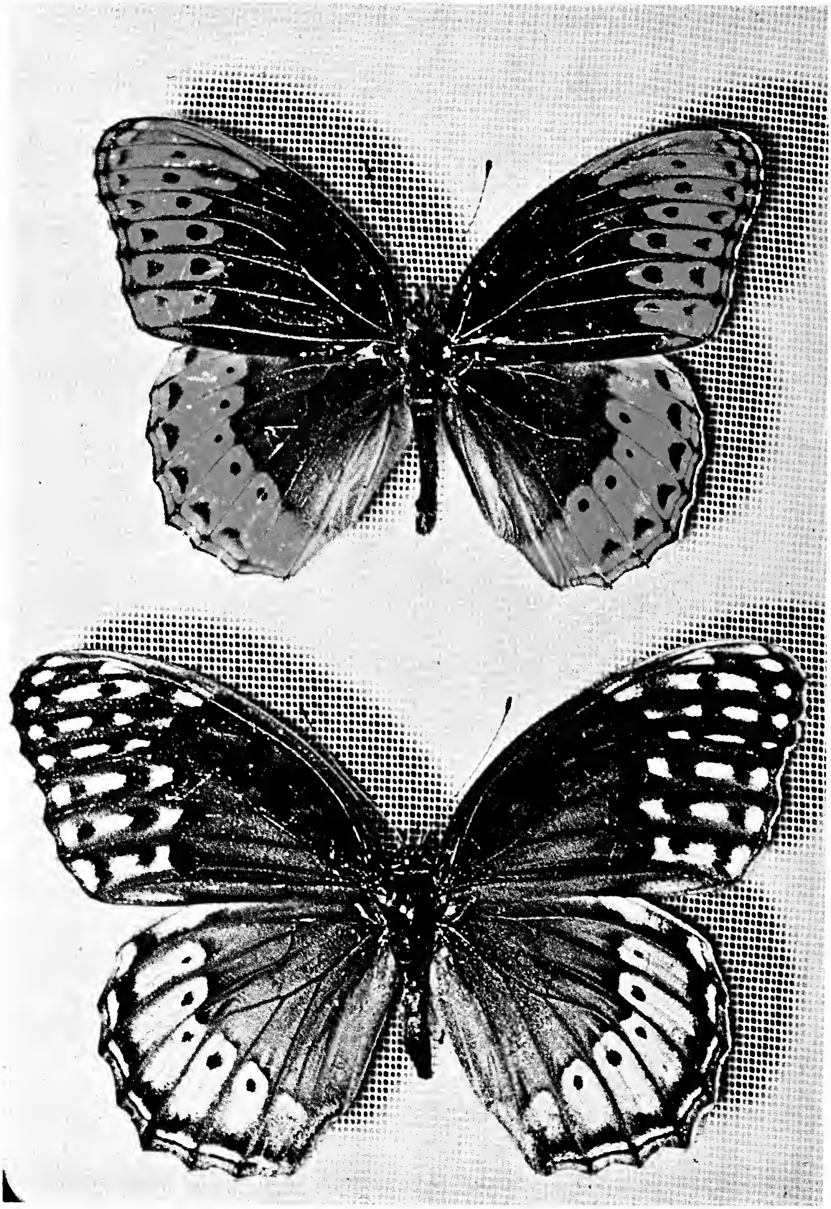

Fig. 1. *Argynnis diana,* upper side. Top, male; bottom, female. The blue is irridescent and may show only in certain directions of certain quality of light. (See fig. 2).

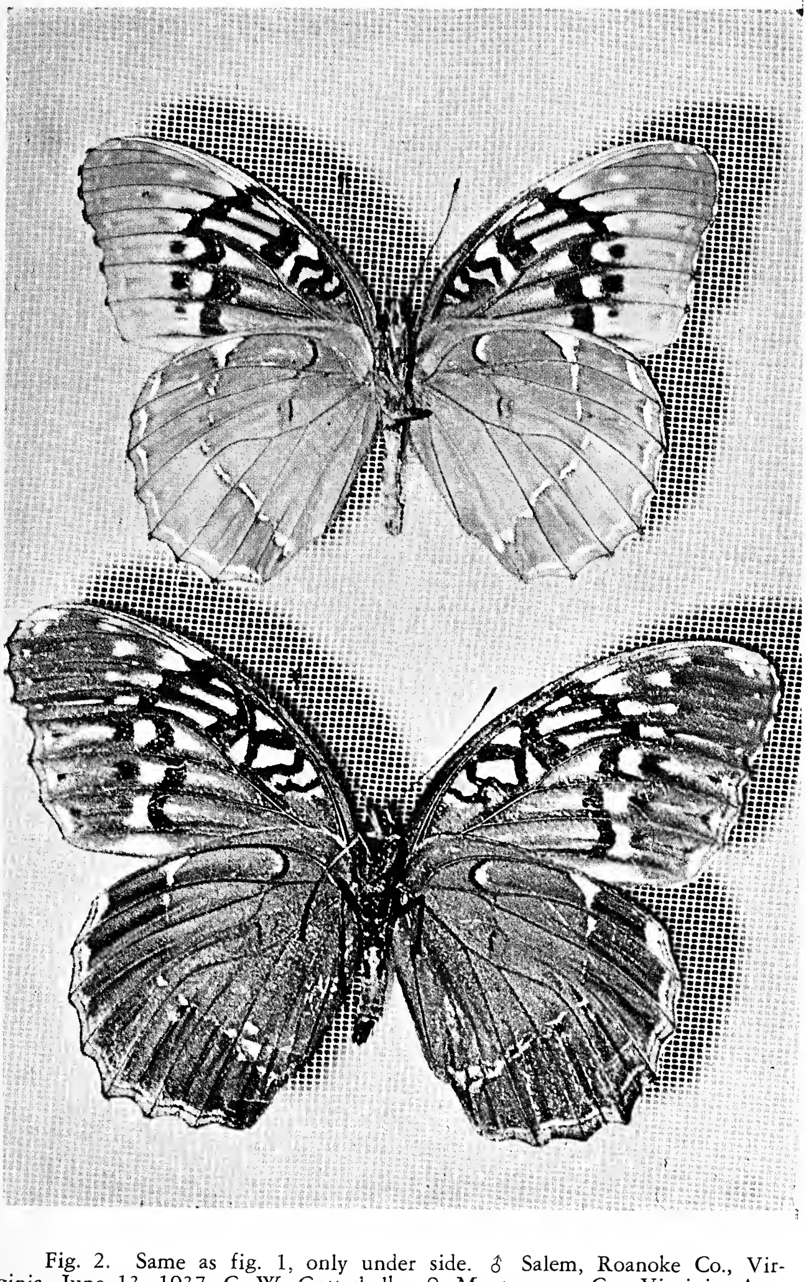

Fig. 2. Same as fig. 1, only under side. ♂ Salem, Roanoke Co., Virginia. June 13, 1937. C. W. Gottschalk. ♀ Montgomery Co., Virginia. Aug. 16, 1902. E. A. Smyth, Jr.

elements in such a way as to be most certainly of fundamental embryological nature. By this is meant the almost complete obliteration of the pattern elements on the underside of the hindwings in both the male and the female, with a slight degree of the same on the fore wings. In this development, *A. diana* is also most directly opposed to *A. idalia* in which the spots and pattern elements are well developed, even more so than in many other *Argynnis*. The pattern observed on the *diana* hind wing underside looks as though all markings had been wiped clean between the most marginal row of small spots and the usual *Argynnis* row of large silvery spots, substituting therefore, a uniform bluish black on the female, light brown in the male; likewise for the area from the base of the wing outward to the same row of spots nearly all markings of the usual *Argynnis* type appear to have been wiped clean except for a few minor points and substituting therefore a brownish-black on the female and light brown in the male. A small part of the central row of silvery spots of the usual *Argynnis* pattern remains, along with a small part of the cell spot and most marginal row in both the male and the female. The inner two-thirds of the fore wings on the under side in both sexes are similar to the usual *Argynnis* pattern. Interestingly enough, there is blue irridescence in this part of the wings of the male, even though the upper side of the male wings do not show it. (fig. 2)

A similar development of the pattern elements on the under side of *Argynnis* wings occurs in the groups related to *A. paphia, A. pandora, A. laodice, A. childreni,* etc. of Eurasia. These are the groups which have a distributional range through areas of higher rainfall, and thus more humid air, combined with higher summer temperatures. Some membrs of these groups also have a development of sexual dimorphism similar to that of *A. diana* and *A. nokomis,* even to the extent of having blue or bluish females while the male is the usual orange-brown color. More complete correlations between wing color, pattern type and insect size with climatic differences in various parts of the distributional range of *Argynnis* will come in a later issue.

The geographical distribution of *Argynnis diana* is a rather restricted one (fig. 3), hardly being more than 10° from the most northern part of its range to the most southern part and 15° from the most easterly to the most westerly part of its range. This area in miles is abou 1000 miles from east to west and three to four hundred miles from north to south. Actually, the present known distributional range is shaped somewhat like a triangle, with an acute angle in the far west in Arkansas. Except for a collection in western Pennsylvania which may be inaccurate, the species is known only as far north as southern West Virginia and central Virginia. The most southern localities are southern South Carolina and northern Georgia and an area of north-central Arkansas. There are records of the species from southern Illinois. It is likely that they may be found in southern Missouri, southern

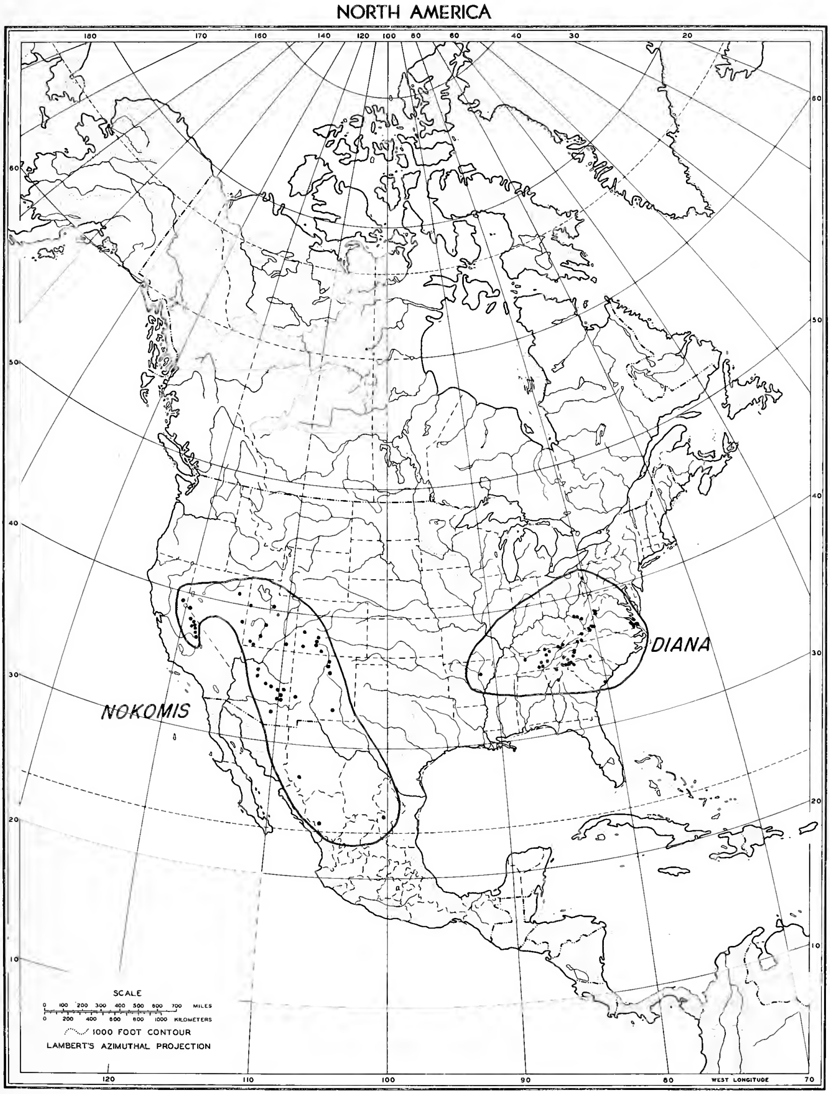

Fig. 3. Map showing the North American distribution of *Argynnis diana* and *A. nokomis*. Note the wide expanse of isolation between these two closely related butterflies; also the wide isolation between parts of the range of *A. nokomis*. Details on the geographical variation of *nokomis* will come in the next number in this series.

Indiana and southern Ohio in addition, though I have not seen specimens from these locations.

This species, despite its striking colors and size, is a relatively rare species due to the limited areas in which it lives. There is no evidence that at any time in the past the species was any less local than it is now, even though it is said that the deforestation of many parts of the east have contributed to its demise in many areas (Clark, 1951). The species exists in parts of North America away from the most heavily inhabited regions and therefore collectors have not had as much experience with it as with other species. Undoubtedly, the restricted habitat of the larvae contributes most to its own restricted range and the factors that are essential for larval environment are not known. Judging however from the habitats preferred by the adults and especially the females which is usually highly indicative, the species finds its home in areas of cold seepages and streams on the coastal plain, or in deep, damp, well wooded valleys or ravines, or on damp wooded mountain sides where there are cold streams (Clark, 1951). This corresponds to the habitat of *A. nokomis,* the western related species (fig. 1), which occurs in dry desert regions but only along cold streams where there is an abundance of boggy vegetation and locally a "wet-tropical" microhabitat as at Round Valley, Inyo County, California. This type of habitat is very local, not only in the desert regions of the west but also apparently in the east and is probably more responsible for the restriction of range of *diana* than the removal of the forest cover over extensive areas of the eastern parts of North America.

Clark (1951) gives the most complete description of the distribution, variation and habits of this species than has ever been given. The following is from his description:

"The first males to appear are smaller than those that emerge later, and the males from Highland County and from the higher latitudes in the mountains farther south are always small, resembling the earliest males from other regions.

"On the Coastal plain the males occasionally have on the under side of the hind wings at the end of the cell a conspicuous silver spot bordered inwardly and outwardly by black lines, corresponding to the silver spot in the same position in *S. cybele* though smaller, seldom reaching more than halfway across the cell, and the silver markings on the outer portion of the hind wings may be enlarged. Occasionally on the upper surface of the fore wings there are broad light dashes in the black ground color beyond the cell in the interspaces between veins 3 and 4, 4 and 5, 5 and 6, corresponding to the light dashes on the under side though with indefinite borders. So far as we have seen, these features are confined to males from the Coastal Virginia Plain. The majority of the males from the Coastal Plain, however, do not differ in any way from others from the mountains.

"Dr. Henry Skinner has pointed out that the males differ materially in the number and size of the black spots on the upper surface of the hind wings. We have seen males, both from the Coastal Plain and the mountains, with the light border of the hind wings almost immaculate. There is some variations in the size of the black spots on the fore wings, and veins 2, 3, and 4, may be narrowly or rather broadly infuscated. The contrast between the dark basal and light outer portions of the under surface of the hind wings is sometimes accentuated. These variations seem to bear no relation to locality.

"Dr. Skinner said that females from eastern Tennessee, western North Carolina, and southern Illinois are larger than those found in Virginia; but the females from the lower altitudes in southwestern Virginia appear to be quite as large as any from farther south. Dr. Skinner pointed out that the females vary a great deal in the degree of silver beneath and also in the band of large bluish or greenish spots on the hind wings above. In some specimens these spots are large, and in others they are confined to a small area around the black spots. The number and size of the cream-colored or white spots on the upper side of the fore wings is also quite variable."

It appears from my own observations as well as from those of others that there is quite a lot of variability in this species; most of these variations however appear to be individual rather than population in scope, with the exception of those that are directly related to the elevation differences described by Clark. Occasionally the blue irridescence has been changed to green. Statistical study of large samples seems to be called for to bring this variation out of the realm of guesswork.

The species flies over a long season, males coming out in the middle of June and females slightly later with a height of emergence in the middle of August and extending into September.

Most authors in discussing this species in handbooks comment on mimicry between this species and some other species which inhabit the same general geographical area. Ehrlich (1961) states "The female presumably mimics the distasteful *Aristolochia* swallowtail, *Battus philenor.*" Klots (1951) states "This is cited as a case of mimicry, the supposed model being the black and blue *Papilio philenor,* a swallowtail supposedly distasteful to birds." Scudder (1889) considers the female is a case of parastatic mimicry with *Basilarchia astyanax.* It is fortunate that most authors leave the case in doubt as most all situations of this sort are wild grasps at straws in the wind. The relationships in appearance of many butterflies in the same general geographical area, such as these three, *A. diana* in the east and *A. nokomis* in the southwest with *Papilio philenor* and *Basilarchia astyanax* are exceedingly interesting and deserve some intensive study. Too often these studies are superficial and involve some transference of a man's way of thinking to a butterfly or a bird. As purely a suggestion, it appears that a more satisfactory solution may be found in the physiological relationship of the butterfly with its physical environment, in which the colors are related in some way to light reflection from the butterfly's wings (U.V. light perhaps) which reflections are developed in the butterflies living in a warmer or more humid environment.

LITERATURE CITED

CLARK, A. H. 1951. The Butterflies of Virginia. *Smithsonian Misc. Collections,* 116(7): 1-95.

EHRLICH, PAUL and ANNE H. 1961. How to know the butterflies. *Brown, Dubuque, Iowa.*

HOVANITZ, WILLIAM. 1963. Geographical distribution and variation of the genus Argynnis. *J. Res. Lepid.* 1(2): 117-123.

KLOTS, A. H. 1951. Field guide to the butterflies. *Houghton Mifflin, Boston.*

SCUDDER, S. 1889. The Butterflies of the Eastern United States. *Cambridge, Mass.*

Journal of Research on the Lepidoptera 1(3):209-221, 1963

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THE GENERIC, SPECIFIC AND LOWER CATEGORY NAMES OF THE NEARCTIC BUTTERFLIES

PART 2 — *The Genus Colias*

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THE NAMES INCLUDED in this genus are presented in the same manner as were those of the genus *Pieris* in the first part of this series (*Jour. Res. Lepid.* 1(1):63-71, 1962).

W. Hovanitz has separated the members of the genus into specific groups as best he felt was possible in view of the extensive hybridization in the genus.

The genus *Zerene* Hübner, although considered a subgenus of *Colias* by some students, will be dealt with separately in a subsequent part.

The data for *chrysotheme* Esper has been listed under the *eurytheme* group purely as a convenient place in which to give this reference; should a relationship be established between *chrysotheme* and *eurytheme,* the former must, of course, be accorded priority.

The name *notatus* has been presented in the *philodice* group under the authorship of Megerle and also under the authorship of Clark and Clark because of its present uncertain nomenclatorial status.

LIST OF GENERIC NAMES USED OR AVAILABLE FOR COLIAS.

COLIAS Fabricus.

Type: *hyale* Linnaeus.

EURYMUS Horsfield.

Type: *hyale* Linnaeus.

COLIAS FABRICIUS. 1807 [before 19 Dec.][1] In K. Illiger. Magazin für Insektenkunde 6: 284, no. 24. Includes among others "*Pap . . . Hyale*" and "*P. Rhamni*" both considered to be of Linnaeus, 1758.

Type. *P[apilio]. D[anaus]. [Candidus] hyale* Linnaeus. 1758. Syst. Nat. 10th. Ed. 1: 469, no. 71.

Type Selection. 30 Sept. 1943. Opinions & Declarations Rendered by the International Commission on Zoological Nomenclature 2(13): 109-121. The type is declared to be *hyale* Linnaeus, 1758. This declaration invalidates the selection of "*Colias Rhamni,* Fab." (considered to be *rhamni* Linnaeus, 1758) by Latreille, 1810, Consid. Gén. Anim. Crust. Arach. Ins. : 440.

EURYMUS HORSFIELD. (Swainson Ms. name). 1829. [24 June][2]. Catal. Lepid. Ins. Contained Mus. Honor. East Indies Company (2): 134. Gives only "*Colias Hyale*" which is considered to be *hyale* Linnaeus, 1758. The name is a homonym of *Eurymus* Rafinesque, 1815[3].

Type. *P[apilio]. D[anaus]. [Candidus] hyale* Linnaeus. 1758. Syst. Nat. 10th. Ed. 1: 469, no. 71.

Type Selection. Horsfield. 1829 [24 June][2]. *Ibid.* (2): 134. "Mr. Swainson gives *Colias Hyale* as the type of this subgenus . . ."

LIST OF SPECIES AND LOWER CATEGORY NAMES USED OR AVAILABLE FOR COLIAS

1. COLIAS BEHRII W. H. EDWARDS.
   behrii W. H. Edwards.
   canescens (J. A. Comstock).
2. COLIAS BOOTHII CURTIS.
   boothii Curtis.
   chione Curtis.
3. COLIAS EURYTHEME BOISDUVAL.
   alba Strecker.
   alba Strecker.
   amphidusa Boisduval.
   ariadne W. H. Edwards.
   californiana Ménétriés
   chrysotheme (Esper).
   eurytheme Boisduval.
   flava Strecker.
   fumosa Strecker.
   intermedia Cockerell.
   keewaydin W. H. Edwards.
   pallida Cockerell.
   pallida Cockerell.
   pallida Cockerell.
   rudkini (Gunder).
   unicitrina (Gunder).
4. COLIAS GIGANTEA STRECKER.
   gigantea Strecker.
   harroweri Klots.
   marjorie Chermock & Chermock.
   mayi Chermock & Chermock.
   pelidneides Staudinger.
5. COLIAS HECLA LEFEBVRE.
   chrysothemoides Verity.
   glacialis M'Lachlan.
   hecla Lefebvre.
   hela Strecker.
   palamedes Hemming.
   pallida Skinner.
6. COLIAS MEADII W. H. EDWARDS.
   elis Strecker.
   meadii W. H. Edwards.
   medi (Gunder).
7. COLIAS NASTES BOISDUVAL.
   aliaska Bang-Haas.
   cocandicides Verity.
   gueneei Avinoff.
   harperi (Gunder).
   moina Strecker.
   nastes Boisduval.
   obscurata Verity.
   palliflava (McDunnough).
   rossii Guenee.
   streckeri Grum-Grshimailo.
   subarctica (McDunnough).
   thula Hovanitz.
8. COLIAS OCCIDENTALIS SCUDDER.
   alba Strecker.
   alberta Bowman.
   alexandra W. H. Edwards.
   astraea W. H. Edwards.
   barbara Henry Edwards.
   christina W. H. Edwards.
   chrysomelas Henry Edwards.
   edwardsii W. H. Edwards.
   emilia W. H. Edwards.
   harfordii Henry Edwards.
   hatui (Barnes & Benjamin).
   krauthii Klots.
   lambillioni Dufrane.
   martini (Gunder).
   occidentalis Scudder.
   pallida Cockerell.
   pallida Cockerell.
   pallidissima Bowman.
   shastae (Barnes & Benjamin).
   weaverae (Gunder).
9. COLIAS PALAENO (LINNAEUS).
   chippewa W. H. Edwards.
   helena W. H. Edwards.
   kohlsaati (Gunder).
   lapponica Staudinger.
   palaeno (Linnaeus).
   philomene (Hübner).
   werdandi Herrich-Schäffer.
10. COLIAS PELIDNE BOISDUVAL & LECONTE.
   interior Scudder.
   isni (Barnes & Benjamin).
   labradorensis Scudder.
   laurentina (Scudder).
   minisni Bean.
   mira Verity.
   moeschleri Grum-Grshimailo.
   nepi (Barnes & Benjamin).
   neri (Barnes & Benjamin).
   pelidne Boisduval & LeConte.
   skinneri Barnes.
   solivaga W. H. Edwards.
11. COLIAS PHILODICE GODART.
   alba Strecker.
   alba F. Chermock.
   albida (F. Chermock).
   albinic W. H. Edwards.
   anthyale (Hübner).

autumnalis Cockerell.
ehrmanni F. Chermock.
eriphyle W. H. Edwards.
europome (Haworth).
hagenii W. H. Edwards.
hybrida Strecker.
inversata Nakahara.
kootenai Cockle.
laurae (F. Chermock).
lutetincta Wolcott.
melanic W. H. Edwards.
melanic W. H. Edwards.
minor F. Chermock.
miscidice (Scudder).
nig Strecker.
nigricosta (F. Chermock).
nigridice (Scudder).
nigrina Strecker.
nigrofasciata Reiff.
notatus (Mergerle).
notatus (Clark & Clark).
pallidice (Scudder).
philodice Godart.
plicaduta Nakahara.
raritus (Gunder).
reducta Dufrane.
rothkei Reiff.
serrata (F. Chermock).
suffusa Cockerell.
virida Strecker.
vitabunda Hovanitz.

12. COLIAS SCUDDERII REAKIRT.

flavotincta Cockerell.
ruckesi Klots.
scudderii Reakirt.

1. COLIAS BEHRII W. H. EDWARDS.

behrii, Colias W. H. Edwards. Oct. 1866. Proc. Ent. Soc. Phila. 6 (pp. 201-208): 201. "From 2 ♂, 1 ♀, received from Dr. Behr, and taken among the Yo Semite mountains at an elevation of about 10,000 feet above the sea." No dates given. Spelled *behri* by J. A. Comstock, 20 May 1925, Bull. Sou. Calif. Acad. Sci. 24(1): 3.

canescens, Eurymus behri J. A. Comstock. 20 May 1925. Bull. Sou. Calif. Acad. Sci. 24(1): 3. "Type [♀], Tioga Pass, Yosemite, Calif., Aug. 4, 1922. Six paratypes [♀ ♀]. Same place and date. In the collection of the Southwest Museum."

2. COLIAS BOOTHII CURTIS.

chione, Colias Curtis. 1835. In J. Ross. Append. Narr. 2nd Voy. Search North-West Pass. (Nat. Hist. Sect.), pp. lxvi-lxvii, no. 11; plate A, fig. 6. ♂ & ♀ described. " . . . they were captured from the 14th of July to the 13th of August, 1830, and on the 19th were in a very wasted state; on the 14th of July, of the following year, one *Colias* only was taken." No locality nor series data given here.

boothii, Colias Curtis. 1835. In J. Ross. Append. Narr. 2nd. Voy. Search North-West Pass. (Nat. Hist. Sect.), pp. lxv-lxvi, no. 10; plate A, figs. 3-5. ♂ & ♀ described. No locality, series data nor dates given here. Spelled *boothi* by Verity, 1905-1911, Rhopal. Palaearctica, p. 238.

3. COLIAS EURYTHEME BOISDUVAL.

alba, Colias chrysotheme eurytheme Strecker. 1878 [Sept. - Oct.][4]. Butt. & Moths N. Amer., Compl. Syn. Catal., p. 83, no. 60b. Cites ♀ figures in W. H. Edwards, Butt. N. Amer. [I]: plate Colias III, figs. 5-6, 1869. No locality, series data nor dates given here.

alba, Colias chrysotheme keewaydin Strecker. 1878 [Sept. - Oct.][4]. Butt. & Moths N. Amer., Compl. Syn. Catal., p. 83, no. 60e. Cites ♀ figures in W. H. Edwards. Butt. N. Amer. [1]: plate Colias IV, figs. 8-9, 1869. No locality, series data nor dates given here.

amphidusa, Colias Boisduval. 1852 [Aug.][5] Ann. Soc. Ent. France. 2nd. Ser. 10(2): 286-287, no. 14. ♂ & ♀ described. "Du nord de la Californie." No series data nor dates given. Spelled *amphidona* by W. H. Edwards, 1869, Butt. N. Amer. [1]: [45].

ariadne, Colias W. H. Edwards. Jan. 1870. Trans. Amer. Ent. Soc. 3(?) sign. 2: 12-13. "1 ♂, 1 ♀, from the collection of Dr. Behr, and taken at Mokeluma Hills, California." No dates given.

californian, Colias edusa Ménétriés. Dec. 1855. Enum. Corp. Anim. Mus. Imper. Acad. Sci. Petropolitanae. Class. Ins. Ordo Lepid. (1): 80, under no. 253. "Ces caracteres indiques ci dessus se reproduisent constamment sur environs 6 males et 4 femelles, tous rapportes de la Nouvelle Californie par notre zele voyageur Wosnesensky." No dates given.

chrysotheme, Dan[*aus*]. *Can*[*didus*]. Esper. [1781][6]. Die Schmetterlinge 1(2) heft 3: 89-90, no. 131; plate 65, figs. 3-4. ♂ & ♀ described. No locality, series data nor dates given. Note: This name is included here only for convenience.

eurytheme, Colias Boisduval 1852 [Aug.][5]. Ann. Soc. Ent. France. 2nd. Ser. 10(2): 286, no. 13. "Commune dans toute la Californie. Elle habite aussi le Mexique et quelques parties des Etats-Unis." No sex, series data, nor dates given. Spelled *enegthenu* by W. H. Edwards, 1872, in F. V. Hayden, Prel. Rept. U. S. Geol. Surv. Mont. & Port. Adj. Terr. 5th. Rept. Progress, p. 466.

flava, Colias chrysotheme eurytheme Strecker. 1878 [Sept. - Oct.][4]. Butt. & Moths. N. Amer., Compl. Syn. Catal., p. 83, no. 60c. ♀ described. "Mus. Strecker." No locality, series data nor dates given.

fumosa, Colias eurytheme Strecker. 1900 [Mar. 9th - 13th][7]. Lepid., Rhopal. & Heter., Indig. & Exot. Suppl. No. 3: 19. "One ♀, Colorado . . .". No date given.

intermedia, Colias eurytheme Cockerell. Mar. 1888 [after 9th][8]. West Amer. Scientist 4(35): 41-43 (in pt.). ♀ described. "In this locality (Swift Creek, Custer Co., Colo[rado] . . .". No series data nor dates given.

keewaydin, Colias W. H. Edwards. [Sept. 1869, on or before 13th][9]. Butt. N. Amer. [I](4): [47]-[49]; plate (15), figs. 1-9. ♂ & ♀ described. "Found in the valley of the Mississippi from Nebraska and Illionis to Texas and westward to the Pacific, occupying much the same region as *Eurytheme,* but apparently less common and more local than that species. Also occasionally found in the Middle States and Canada." "There appear to be two broods during the year, the insects being most abundant early in the spring, in fact, before *Eurytheme* makes its appearance." No series data nor dates given.

pallida, Colias eurytheme Cockerell. Nov. 1887. West. Amer. Scientist 3(31): 217. ♀ described. " . . . near West Cliff, Custer Co., Colorado." No dates given.

pallida, Colias eurytheme intermedia Cockerell. Mar. 1888 [after 9th][8]. West. Amer. Scientist 4(35): 41-43 (in pt.). " . . . Whitish females occur of . . . *intermedia,* these may be called *pallida.*" No locality, series data nor dates given.

pallida, Colias eurytheme keewaydin Cockerell. Mar. 1888 [after 9th][8]. West. Amer. Scientist 4(35): 41-43 (in pt.). ". . . Whitish females occur of . . . *keewaydin* . . . these may be called *pallida.*" No locality, series data nor dates given.

rudkini, Eurymus eurytheme Gunder. 31 Dec. 1932. Can. Ent. 64(12): 277-278. "Holotype - ♀ . . . San Marino, Los Angeles Co., Calif., May 23, 1931. Type in Author's coll."

unicitrina, Eurymus eurytheme amphidusa Gunder. 8 May 1924. Ent. News 35(5): 158; plate 2, fig. J. "Holotype ♂, (Author's Coll.) Upland, Los Angeles County, California; August 2, 1921."

4. COLIAS GIGANTEA STRECKER.

gigantea, Colias pelidne Strecker. 1900 [Mar. 9th - 13th][7]. Lepid., Rhopal. & Heter., Indig. & Exot. Suppl. No. 3: 19. "Five ♂♂, 7 ♀♀, west coast Hudson Bay, above Fort York, Archdeacon Kirby." No dates given.

barroweri, Colias gigantea Klots. 22 Mar. 1940. Amer. Mus. Nov. No. 1054: 4-6. "Type Lot — All are from Clear Creek, vicinity Lower Green River Lake, Sublette Co., Wyo[ming]., alt. 8400 ft. Holotype male, three male and two female paratypes, August 3, 1935 . . .; allotype female, nine male and one female paratypes, July 16, 1939 . . ."

marjorie, Colias christina mayi Chermock & Chermock. 30 Apr. 1940. Can. Ent. 72(4): 82. "Holotype - ♀, June 26, 1933, Riding Mountains, Manitoba. Paratypes - 1-50, same locality." Page 81: " . . . holotypes will be deposited in Canadian National Collection . . ."

mayi, Colias christina Chermock & Chermock. 30 Apr. 1940. Can. Ent. 72(4): 81. "Holotype - ♂, July 1, 1933, Riding Mountains, Manitoba. Allotype - ♀, July 1, 1933, same locality. Paratypes - 1 to 150, same locality." Page 81: " . . . holotypes will be deposited in the Canadian National Collection and the allotypes in the Carnegie Museum."

pelidneides, Colias palaeno Staudinger. May 1901. In Staudinger & Rebel. Catal. Lepid. Palaearct. Faun. 3rd. Ed., p. 15, no. 86i. ♂ described. "Amer. bor. (Hudson Bay, Alaska)." No series data nor dates given.

5. **COLIAS HECLA LEFEBVRE.**

chrysothemoides, Colias hecla Verity. 1905-1911. Rhopal. Palaearctica; p. 356; p. xxxvii; plate LXXI, figs. 22-23; plate LXXI explanation page, figs. 22-23. "22 . . . ♂ (Territoire de Barren, 114°, 30' long. O., 67° 40' lat. N., Am. boréale)." "23 . . . ♀ ([same as 22])." Collection of British Museum. No series data nor dates given.

glacialis, Colias hecla M'Lachlan. 23 May 1878. Jour. Linnean Soc. (London), Zoology 14(74): 108. "Two ♂ and one ♀ from lat. 81° 45', August 12th, 1876, and one ♀ from Hales Sound, lat. 79° . . . also a much crippled ♂ . . . from Discovery Bay, July 18th, 1876 . . ."

hecla, Colias Lefebvre. 1836 [after 6 Apr.][10]. Ann. Soc. Ent. France 5(?): 383-387; plate 9, figs. 3-6. ♂ & ♀ described. " . . . l' Islande est la patrie . . .". No series data nor dates given.

hela, Colias Strecker. Sept. 1880. Bull. Brooklyn Ent. Soc. 3(5): 33-34. " . . . the present descriptions are from 1 ♂ and 2 ♀ ♀; a few more were taken, but these are all I have had the opportunity of examining. They were captured . . . a considerable distance above Fort Churchill on west coast of Hudson's Bay; . . .". No dates given.

palamedes, Colias hecla Hemming. May 1934. Stylops, Jour. axon. Ent. (5): 98, no. 17. A new name for *Colias hecla pallida* Skinner which he states is a homonym of *Colias erato pallida* Staudinger (1861, in Staud. & Wocke, Cat. Lepid. Europ., p. 3).

pallida, Colias hecla Skinner (Skinner & Mengel Ms. name). 1 Mar. 1892. Ent. News 3(3): 49; plate 2, fig. 4. ♀ figured. " . . . from Greenland." No date given. A homonym of *Colias erato pallida* Staudinger (1861, in Staud. & Wocke, Cat. Lepid. Europ., p. 3). Spelled *palida* by Holland, 1931, Butt. Book, rev. ed., p. 298.

6. **COLIAS MEADII W. H. EDWARDS.**

elis, Colias Strecker. 10 Mar. 1885. Proc. Acad. Nat. Sci. Phila. [37] (sign. 2): 24. Description concluded on page 25 (sign. 3): 7 Apr. 1885. "Taken . . . at an elevation of 10,000 feet, on the summit of "Kicking Horse Pass," in the Rocky Mountains, between Alberta Territory and British Columbia, at the boundary between the United States and the British possessions, about 300 miles north of Montana." "Capt. Geddes took about fifteen examples, all females . . ." No dates given.

meadii, Colias W. H. Edwards. Feb. 1871. Trans. Amer. Ent. Soc. 3(?) sign. 34: 267-268. ♂ & ♀ described. No locality, series data nor dates given. In his Butt. N. Amer. [1]: 59, 1868-1872, he says: "Taken in Colorado . . . in the month of July, 1871." He speaks of Mr. T. L. Mead taking 12 specimens on the "divide," 34 specimens on "Mt. Lincoln" and 1 specimen at "Kenosha House." Spelled *meadi* by Holland, 1931, Butt. Book, rev. ed., p. 297.

medi, Eurymus meadii Gunder. 30 June 1934. Can. Ent. 66(6): 125. "Holotype - ♀, . . . Beckenridge Peak (11,000 ft.), Empire County, Colorado, Aug. 8, 1919. Type in Author's coll."

7. **COLIAS NASTES BOISDUVAL.**

aliaska, Colias nastes Bang-Haas. 15 Aug. 1927. Horae Macrolepid. Reg. Palaearctica 1(3): 41. Figs. 24-25 on plate 5 were published later. "Habitat: Alaska: Ramport 8. Juli, . . ., 3 ♂ 2 ♀". Spelled *alaskae* by McDunnough, 1938, Mem. Sou. Calif. Acad. Sci. 1: 8, no. 52e.

cocandicides, Colias nastes rossii Verity. 1905-1911. Rhopal. Palaearctica; p. 355 (as *rossii*); p. xxxvii (as *cocandicides*); plate LXXI, figs. 7-9; plate LXXI explanation page, figs. 7-9 (as *rossii*). "7 . . . ♂ (Territoire de Barren, 114°, 30' long. 0., 67° 40' lat. N., Am. boréale)". "8 . . . ♀ ([same as 7])". "9 . . . ♂ . . . ([same as 7 & 8])". No series data nor dates given.

gueneei, Colias nastes Avinoff. 10 Dec. 1935. In Holland & Avinoff. Mem. Carnegie Mus. 12(2): sect. 5, sub-sect. 2: 13-14, no. 10; & page 32; plate 27, figs. 1, 11, 21-22, 25-27, 31-32. ♂ & ♀ described. Locality: Southampton Island. No series data nor dates given.

harperi, Eurymus nastes moina Gunder. 31 Dec. 1932. Can. Ent. 64(12): 278. "Holotype - ♀, . . .; Ft. Churchill, Manitoba, Can[ada]., July 19, 1932. Type in Author's coll."

moina, Colias Strecker. Sept. 1880. Bull. Brooklyn Ent. Soc. 3(5): 34. ♂ & ♀ described. "Described from a large number of examples mostly males." ["a considerable distance above Fort Churchill on West Coast of Hudson's Bay" . . .] (taken from Strecker's text of *hela*, p. 34).

nastes, Colias Boisduval. [1832][11]. Icon. Hist. Lépid. Nouv. Peu Connu (?): plate 8, figs. 4-5 (♂). Pages 245-246 published later (♂ & ♀). "Elle se trouve au Cap-Nord et en Islande. M. Sommer m'en a aussi envoyé plusieurs individus pris au Labrador." No series data nor dates given.

obscurata, Colias nastes streckeri Verity. 1905-1911. Rhopal. Palaearctica; pp. 354-355 (in pt.); p. xxxvi; plate LXXI, fig. 6; plate LXXI explanation page, fig. 6. "6 . . . ♂ . . . (Lake Louise, Alberta)". No date given.

palliflava, Eurymus nastes streckeri McDunnough. 25 July 1927. Can. Ent. 59(7): 153-154. ♂ described. " . . . higher slopes of Mt. McLean (above 6500 ft.) on July 12 . . .". ". . . type No. 2425 in the Canadian National Collection, Ottawa".

rossii, Colias nastes Guenée. 12 Oct. 1864. Ann. Soc. Ent. France. 4th. Ser. 4(2): 199-200. ♂ & ♀ described. " . . . trois individus . .". No locality nor dates given here. Spelled *rossi* by Holland, 1931, Butt. Book, rev. ed., p. 299.

streckeri, Colias nastes Grum-Grshimailo. 30 Apr. 1895. Horae Soc. Ent. Rossicae 29 (1-2): 290-291, no. 2. ♂ & ♀ described. "Specimen unum hujus varietatis sub nomine *"Colias Behrii?"* a lepidopterologo germanico D-re 0. Staudinger anno 1891, quattuor specimina, in provincia Alberta ad Laggan collecta, a lepidopterologo americano Dom. H. Strecker, cujus in honorem hanc forman nominavi, accepi".

subarctica, Eurymus nastes McDunnough. 1 Dec. 1928. Can. Ent. 60(11): 270-271. "Holotype. - ♂, Bernard Harbour, N. W. T., Aug. 9, 1915, . . . , No. 2863 in the National Collection, Ottawa. Allotype. - ♀, same data. Paratypes. - 4 ♂, 4 ♀, from same locality, taken on various dates early in August".

thula, Colias nastes Hovanitz. [1955, Mar. 9 - 11 Oct.][12]. Wasmann Jour. Biology 13(1): 1-8; figs. 1-2. "These collections [made in 1952 and 1953] of *Colias* consisted primarily of the species *C. nastes* (thirty-five specimens) . . .". "The specimens with which we are concerned here were collected at a camp located along this river [Meade River, northwestern part of Alaska Territory] at a point North 70° 45' by 156° 30' West". "Holotype male and Allotype female. Locality: Near the Mead River, Alaska Territory, Alaska, N 70° 45' x 156° 30' W. Date: Male July 13, 1952, and female July 11, 1952 . . . Depository: U . . . S . . . Nat. . . Mus. . ., Washington, D. C. Paratypes: One pair in the author's collection at the California Academy of Sciences, San Francisco, California. One pair each in the Canadian National Collection at the Department of Agriculture, Ottawa; the American Museum of Natural History, New York; and the British Museum of Natural History, London. These may be dated 1952 or 1953 . . . The remainder of the series are in the collection of the Allan Hancock Foundation".

8. COLIAS OCCIDENTALIS SCUDDER.

alba, Colias alexandra Strecker. 1878 [Sept. - Oct.][4]. Butt. & Moths N. Amer., Compl. Syn. Catal., p. 81, no. 55a. " . . . a white ♀ form of rare occurence". No. locality, series data nor dates given.

alberta, Colias eurytheme Bowman. 9 Mar. 1942. Can. Ent. 74(2): 25. "Holotype - ♂, Wembley, Al[ber]ta., June 24, 1925, in the author's collection. Allotype - ♀, Wembley, Alta., June 25, 1925, in the author's collection. Paratypes - 7 ♂, 2 ♀, Wembley, Alta., June 14-25, 1925; 1 ♂, 1 ♀, Beaver Lodge, Alta., June 29 and July 12, 1924; 1 ♂, Fort Vermilion, Alta., June 13, 1925; 1 ♀, Boswell, B. C., July 22, 1927; 2 ♀, Rolla, B. C., July 1 and 21, 1927. Paratypes in the Canadian National Collection and in the collection of the author."

alexandra, Colias W. H. Edwards. [1863, Mar.-May - 12 Oct.][13]. Proc. Ent. Soc. Phila. 2(1): 14-15. Figs. 1-3 on plate 11 may have been published later. "From Pike's Peak; in the Society's collection; 6 males, 1 female. The second female is from the collection of Mr. George Newman and was taken among the Rocky Mountains . . .". No dates given.

astraea, Colias W. H. Edwards. Feb. 1872. Trans. Amer. Ent. Soc. 4(?) sign. 8: 61. "From a single male taken near the Yellowstone Lake by the Hayden Expedition, in 1871". No date given.

barbara, Colias Henry Edwards. 5 Feb. 1877[14]. Pac. Coast Lepid. (24): 7-8 & 11. "Two females (Coll. Hy. Edw.), Santa Barbara, Baron v. Osten; Gilroy, J. Behrens". [Santa Barbara & Gilroy are both in California]. No dates given.

christina, Colias W. H. Edwards. [12 Oct. 1863][15]. Proc. Ent. Soc. Phila. 2(2): 79-80. ♂ & ♀ described. "Taken at the portage of Slave River . . .". No series data nor dates given.

chrysomelas, C[olias]. Henry Edwards. 5 Feb. 1877[14] Pac. Coast Lepid. (24): 8-9, 11. "Seven ♂, five ♀. Napa County, Cal[ifornia]. (Coll. Hy. Edw.)". No dates given. Spelled *chryomelas* by H. Edwards, *Ibid.*, p. 9.

edwardsii, Colias W. H. Edwards (Behr Ms. name). Jan. 1870. Trans. Amer. Ent. Soc. 3(?) sign. 2: 11. "1 ♂, 2 ♀, from the collection of Dr. Behr, taken at Virginia City, [Nevada] at high elevation . . .". No dates given. Spelled *edwardsi* by Barnes & Benjamin, 8 Dec. 1926, Bull. Sou. Calif. Acad. Sci. 25(3): 89, under 67a.

emilia, Colias W. H. Edwards. Jan. 1870. Trans. Amer. Ent. Soc. 3(?) sign. 2: 12. "From 1 ♂, 1 ♀, taken in Oregon . . . Collection of Dr. Behr". No dates given.

harfordii, C[olias]. Henry Edwards. 5 Feb. 1877[14]. Pac. Coast Lepid. (24): 9 & 11. "From seven males, (Coll. Hy. Edw.) Contra Costa Co. (Hy. Edw.). Havilah, Kern Co. (R. H. Stretch)". [Both localities in California]. Spelled *harfordi* by Holland, 1931, Butt. Book, rev. ed., p. 294, no. 5.

hatui, Eurymus alexandra edwardsi Barnes & Benjamin. 8 Dec. 1926. Bull. Sou. Calif. Acad. Sci. 25(3): 89, under no. 67a. "Type locality: Stockton, Utah. Number and sexes of types: Holotype ♀, VII-30-16; 1 ♀ Paratype, VII-5-3."

krauthii, Colias christina Klots. 24 Jan. 1935. American Mus. Nov. No. 767: 1-2. "Types. - Male holotype, allotype and thirty-one male and seven female paratypes, from twelve miles west of Custer, Black Hills, South Dakota, June 29, 1933; four male paratypes, vicinity of Custer, South Dakota, June 27, 1933, and five male and six female paratypes, Black Hills, South Dakota, July 1, 1931 . . .". "Holotype, allotype, and twelve male and five female paratypes are in the American Museum of Natural History; the remainder are in the author's collection."

lambillioni, Colias elis Dufrane. 28 Feb. 1947. Bull. & Ann. Soc. Ent. Belgique 83(1-2): 70. ♀ described. " . . . Canada, sans nom de localité precise . . .". No date given.

martini, Eurymus harfordii Gunder. 10 Sept. 1931. Bull. Sou. Calif. Acad. Sci. 30(2): 45. "Holotype ♀, . . . South side of Arrowhead Lake, San Bernardino Co., Calif. Sept. 2, 1931. Type in Author's coll."

occidentalis, Colias Scudder. Sept. 1862. Proc. Boston Soc. Nat. Hist. 9(?) sign. 7: 109-111; unnumb. fig. (p. 107). "2 ♂, 3 ♀. Gulf of Georgia (A. Agassiz); Fort Simpson, British America. (W. H. Edwards.)". No dates given.

pallida, C[olias]. alexandra Cockerell. May 1889. Entomologist 22(311): 128, under no. 2. Cites: " . . . (W. H. Edwards, Can. Ent., 1887, 229) . . .". Edwards speaks of two albino females sent by Bruce [from Colorado?]. No dates given.

pallida, C[olias]. christina Cockerell. May 1889. Entomologist 22(311): 128, under no. 2. Cites: " . . . (H. H. Lyman, Can. Ent., 1884, 6) . . .". Lyman speaks of two albino specimens of female. No dates given.

palidissima, Colias eurytheme alberta Bowman. 9 Mar. 1942. Can. Ent. 74(2): 25. "Holotype - ♀, Fort Vermilion, Al[ber]ta., July 15, 1925, in the author's collection. Paratypes - 2 ♀, same locality, June 9 and 15, 1925, in the Canadian National Collection and the collection of the author".

shastae, Eurymus occidentalis chrysomelas Barnes & Benjamin. 8 Dec. 1926. Bull. Sou. Calif. Acad. Sci. 25(3): 88, under no. 63a. "Albinic ♀ of *chrysomelas* . . .". "Type locality: Shasta Retreat, Siskiyou Co., Calif. Numbers and sexes of types: Holotype ♂ [in error], 1-7 July".

weaverae, Eurymus harfordii Gunder. 8 May 1924. Ent. News 35(5): 156-157; plate 2, fig. G. "Allotype [Holotype] ♀, (Author's Coll.) Warner Springs, San Diego County, California, July 3, 1949".

9. COLIAS PALAENO (LINNAEUS).

chippewa, Colias W. H. Edwards. [Aug. 1870][16]. Syn. N. Amer. Butt. (pp. 7-14): 8, no. 15. A new name for his own *Colias helena.* "Hab. - Great Slave Lake" [differs from that given for *helena*]. See his *helena* for data.

helena, Colias W. H. Edwards. [12 Oct. 1863][15]. Proc. Ent. Soc. Phila. 2(2): 80. ♂ & ♀ described. "From Mackenzie's River, . . .". No series data nor dates given. A homonym of *Colias helena* Herrich-Schäffer, 1844[17]. Syst. Bearbeit. Schmett. Europa 1(7): plate 45, figs. 206-207 (I have not seen this reference of Herrich-Schäffer).

kohlsaati, Eurymus chippewa Gunder. 10 Sept. 1931. Bull. Sou. Calif. Acad. Sci. 30(2): 45. "Holotype ♀, . . . Mt. McKinley Nat. Park, Alaska. July 14, 1930". "Type in Author's coll."

lapponica, Colias palaeno Staudinger. End Jan. 1871. In Staudinger & Wocke. Catal. Europ. Faun., p. 5, no. 58a. ♂ described. Cites figs. 403-4 (♀, *werdandi*) on plate 83 in Herrich-Schäffer. 1848[17], Syst. Bearbeit. Schmett. Europa 1(36). "Lap. Ross. s.". No series data nor dates given.

palaeno, Papilio [*Heliconius*] Linnaeus. 1761 [after 28 July][18]. Fauna Svecica. Ed. Alt., p. 272, no. 1014. "Habitat in Pteride rarissime Upsaliae, frequentior in Finlandia". No sex data, series data nor dates given.

philomene, [*Papilio*] Hübner. [1805][19]. Samm. Europ. Schmett. (Papiliones); no text; plate 117, figs. 602-603. Figs. 740-741 on plate 147 were published later.

werdandi, C[*olias*]. Herrich-Schäffer (Schönherr Ms. name). 1844[17]. Syst. Bearbeit. Schmett. Europa 1(3): plate 8, figs. 41-42; 1(7): 102 (published 1844); plate 83, figs. 403-404 (published 1848). No series data, no locality nor dates given. Homonym of *Colias werdandi* Zetterstedt, Insecta Lapponica, page 908, no. 2, [1839][20].

10. COLIAS PELIDNE BOISDUVAL & LECONTE.

interior, Colias Scudder. Sept. 1862. Proc. Boston Soc. Nat. Hist. 9(?) sign. 7: 108-109; 1 unnumb. text fig. (p. 107). "5 ♂, 1 ♀. Northern shore of Lake Superior (Prof. Agassiz); mouth Sasketchewan River, British America (S. H. Scudder.)". No dates given.

isni, Eurymus pelidne minisni Barnes & Benjamin. 8 Dec. 1926. Bull. Sou. Calif. Acad. Sci. 25(3): 89, under no. 69c. "Type locality: Laggan, Al[ber]ta. Number and sexes of types: Holotype ♀, 16-23 Aug."

labradorensis, Colias Scudder. Sept. 1862. Proc. Boston Soc. Nat. Hist. 9(?) sign. 7: 107-108; unnumb. fig. (p. 107). "8 ♂, 5 ♀. Caribou Island, Strait of Belle Isle, Labrador. (A. S. Packard, Jr.)". No dates given.

laurentina, Eurymus philodice Scudder. Mar. 1876. Proc. Boston Soc. Nat. Hist. 18(2): sign. 12: 189-190. " . . . Cape Breton Island" [from article title]. "Thirty-nine specimens were collected, of which ten were gynandromorphic females, eight pallid females, and the rest males". No dates given.

minisni, Colias elis Bean. Apr. 1895. Psyche, Jour. Ent. 7(228): 228. Intended to withdraw his Ms. name for what he considered the albinic female of *elis* Strecker.

mira, Colias pelidne Verity. 1905-1911. Rhopal. Palaearctica; p. 347; p. xxxiv; plate LXVIII, fig. 49; pl. LXVIII explanation page, fig. 49. "49 . . . ♂ . . . (Ravea, Labrador) [e coll. Elwes]". No date given.

moeschleri, Colias pelidne Grum-Grshimailo. 30 July 1894. Horae Soc. Ent. Rossicae 27 (3-4): 379, no. 1. 1 ♀ described. "Specimen unum e museo . . . Moeschleri, . . .; . . . alterum, in Labrador anno 1889 collectum, e museo lepidopterologi gemanici Dom. M. Wiskotti acceptum."

nepi, Eurymus interior Barnes & Benjamin. 8 Dec. 1926. Bull. Sou. Calif. Acad. Sci. 25(3): 89, under no. 65. "Type locality: Nepigon, Ontario. Number and sexes of types: Holotype ♀, and 1♀ Paratype both 8-15 July."

neri, Eurymus pelidne skinneri Barnes & Benjamin. 8 Dec. 1926. Bull. Sou. Calif. Acad. Sci. 25(3): 89, under no. 69b. "Type locality: Yellowstone Park, Wyo[ming]. Number and sexes of types: Holotype ♀ 8-15 July; 2 ♀ Paratypes, 8-15 July and no date; all being original type females of *skinneri* Barnes."

pelidne, C[olias]. Boisduval & LeConte. 1829. Hist. Gén. Icon. Lepid. Chen. l'Amer. Sept. 1(7): plate 21, figs. 4-5 (♀). Pp. 66-67 published in livrason 8. ♂ & ♀ described. "Elle habite le Groenland et l'Islande. M. Sommer, observateur trés-distingué, me l'a aussi envoyée comme venant du Labrador". No series data nor dates given.

skinneri, Colias pelidne Barnes. 1 Feb. 1897. Can. Ent. 29(2): 41-42. "Described from 15 males and 7 females - three of which are yellow, three white, and one intermediate — taken in Yellowstone National Park, and at Arangie, Idaho, in July".

solivaga, Colias W. H. Edwards (Henry Edwards Ms. name). 1877 [Feb. - 16 Apr.][21]. Trans. Amer. Ent. Soc. 6(?) signs. 1-6: 17, under no. 68. Gives a Henry Edwards Ms. name as a synonym of *interior* Scudder.

11. COLIAS PHILODICE GODART.

alba, Colias philodice Strecker. 1878 [Sept. - Oct.][4]. Butt. & Moths N. Amer., Compl. Syn. Catal., p. 82, no. 58a. Cites ♀ figures in W. H. Edwards, Butt. N. Amer. 2: plate Colias II, fig. 6 and plate III, figs. 5-6, 1876. No locality, series data nor dates given here.

alba, Colias philodice plicaduta F. Chermock. 28 Apr. 1927. Bull. Brooklyn Ent. Soc. 22(2): 119. "Holotype ♀. July 30, 1924; 2 paratypes August 17, 1925; 1 paratype August 16, 1925. N. S. Pittsburgh, P[ennsylvani]a."

albida, Eurymus philodice plicaduta F. Chermock. 15 Nov. 1928. Bull. Brooklyn Ent. Soc. 23(4): 173. A new name for his own *Colias philodice plicaduta alba* which he considered a homonym of *Colias philodice alba* Strecker, 1878. See his *alba* for data.

albinic, Colias philodice W. H. Edwards. [1884, after 12 Sept. - before 18 Feb. 1885][22]. Trans. Amer. Ent. Soc. 11(3-4): 264, under no. 68. Cites his own Butt. N. Amer. 2: plate Colias II, 1876. No locality, series data nor dates given here.

anthyale, Zerene Hübner. 1823 [1 Jan. - 20 Apr.][23]. Zütr. Samm. Exot Schmett. 2nd. 100: 21, no. 154. Figs. 307-308 on plate [54] were published earlier but without names. ♂ described. "Aus Pennsylvanien". No series data nor dates given.

autumnalis, Colias eurytheme eriphyle Cockerell. Mar. 1888 [after 9th][8]. West Amer. Scientist 4(35): 41-43 (in pt.). "On November 9, 1887, I caught a female specimen of the autumn brood of *eriphyle* in this locality" [(West Cliff, Custer Co., Colorado)].

ehrmanni, Colias philodice plicaduta F. Chermock. 28 Apr. 1927. Bull. Brooklyn Ent. Soc. 22(2): 118. "Holotype ♀. August 3, 1921. N. S. Pittsburgh, P[ennsylvani]a."

eriphyle, Colias W. H. Edwards. Apr. 1876. Trans. Amer. Ent. Soc. 5(?) sign. 26: 202-204. "Some thirty individuals of this species and of both sexes, were taken at Lake Labache, in British Columbia, . . . , and the whole series came into my possession". No dates given.

europome, P[apilio]. D[anaus]. C[andidus]. Haworth. 1803 [in or after July][18]. Lepid. Britannica (1): 13, no. 12. "Habitat in Anglia, rarissimo. D. Francillon et D. Swainson". "Descriptio (Ex exemplario Germanico)". No date given. A homonym of *europome* Esper [1777][13], Die Schmett. 1(1): plate 42, figs. 1-2 (I have not seen this reference of Esper).

hagenii, Colias W. H. Edwards. [1884, 19 Jan. - 20 Feb.][24]. Papilio 3(7-10): 160-161, no. 11; 3(7-10): 163-164. "From 20 ♂ 24 ♀ from various localities, from So. Colorado to Montana and Dacotah

(Bismarck)". No specific dates given. Spelled *hageni* by Holland, 1931, Butt. Book, rev. ed., p. 297, under no. 17.

hybrida, Colias philodice Strecker. 1878 [Sept. - Oct.][4]. Butt. & Moths N. Amer., Compl. Syn. Catal., p. 82, no. 58d. ♂ cited in W. H. Edwards, 1876, Butt. N. Amer. 2: plate Colias III. "Illinois, Georgia". No date given here.

inversata, Colias philodice Nakahara. 27 Jan. 1926. Bull. Brooklyn Ent. Soc. 20(5): 223. "Holotype: ♂, Midvale, Allegheny Co., P[ennsylvani]a., August 20, 1893 . . . Type in the Barnes Collection."

kootenai, Colias Cockle. 4 June 1910. Can. Ent. 42(6): 203-204. "Kalso and in Northern British Columbia" [from article title]. " . . . May 17 to 20, and fall brood to Oct. 9". No sex data nor series data given.

laurae, Eurymus eurytheme eriphyle F. Chermock. 9 Mar. 1929. Bull. Brooklyn Ent. Soc. 24(1): 21. ♀ described. "Holotype, VIII-1-1924: Edmondton, Alberta, Canada."

lutetincta, Colias philodice Wolcott. 11 Apr. 1893. Can. Ent. 25(4): 104, under no. 50. "I first met this form . . . in August, 1885, at Batavia, Ill[inoi]s . . . But have since taken it at different times at Grand Rapids, [Michigan] . . . and have collected in all about a dozen specimens, one of them a female".

maria, C[olias]. philodice W. H. Edwards (Grote Ms. name). 13 July 1885. Papilio 4(9-10): 171. Inadvertently describes a cyanide stained specimen.

melanic, Colias philodice W. H. Edwards. [1884, after 12 Sept. - before 18 Feb. 1885][22]. Trans. Amer. Ent. Soc. 11(3-4): 264, under no. 68. Cites [♀] in his Butt. N. Amer. 2: plate Colias III, 1876. No locality, series data nor dates given here.

minor, Colias philodice plicaduta F. Chermock. 28 Feb. 1927. Bull. Brooklyn Ent. Soc. 22(2): 118. "Holotype ♀. June 28, 1925. N. S. Pittsburgh, P[ennsylvani]a."

miscidice, E[urymus]. p[hilodice]. Scudder. 1 June 1889. Butt. East. U. S. & Canada 2(8): 1115. "Mr. F. G. Sanborn has shown me a very interesting suffused female of this species taken by Mr. John Osgood in Lynn, Mass[achusetts]., in August, 1863".

nig, Colias philodice Strecker. 1878 [Sept. - Oct.][4]. Butt. & Moths N. Amer., Compl. Syn. Catal., p. 82, no. 58b. ♂ from Montreal, Canada described; also cites W. H. Edwards, 1876, Butt. N. Amer. 2: plate Colias III, figs. 8-9 (copied from Glover's unpublished plate). No dates given.

nigricosta, Eurymus eurytheme eriphyle F. Chermock. 9 Mar. 1929. Bull. Brooklyn Ent. Soc. 24(1): 21. " . . . occurs in the female sex only". "Holotype, VIII-1-1924; Topoparatype, VIII-1-1924; Edmondton, Alberta, Canada".

nigridice, Eurymus phil[odice]. Scudder. 1 June 1889. Butt. East. U. S. & Canada 2(8): 1114. ♂ & ♀ described. Cites W. H. Edwards, 1876, Butt. N. Amer. 2: plate Colias III, figs. 8-9 (♂). Cites fig. 5 on Glover's unpublished plate I. Also cites other specimens which were not in his possession (one captured 29 July 1883).

nigrina, Colias philodice Strecker. 1900 [Mar. 9th - 13th][7]. Lepid., Rhopal. & Heter., Indig. & Exot. Suppl. No. 3: 19. Applies the name to what he formerly called *nig*. Here he cites 3 specimens: " . . . Bethlehem, P[ennsylvani]a. . . . Montreal, Can[ada] . . . Orillia, Can.". No dates given.

nigrofasciata, Colias philodice Reiff. 15 Jan. 1917. The Lepidopterist, Off. Bull. Bost. Ent. Club. 1(3): 22-23; plate 3, 1 unnumb. fig. ♀ described. " . . . was caught . . . during August, 1916 in Massachusetts, and it is now in the collection of the author".

notatus, Papilio Megerle. 28 Nov. 1803. Catalogus Insectorum Qua Viennae Austriae 28. Novembris 1803 Auctionis Lege Distrahuntur, p. ?, no. 436. "M. ex. Georg[ia] . . . 6". No dates given. I have not seen this reference, all data is from Clark & Clark.

notatus, Papilio Clark & Clark (Megerle Ms. name). 30 Apr. 1941. Proc. Ent. Soc. Washington 43(4): 81, no. 436; & page 83, no. 1. "M. ex Georg[ia]. . . 6". No dates given. Reprint Megerle's description.

pallidice, E[urymus]. p[hilodice]. Scudder. 1 June 1889. Butt. East. U. S. & Canada 2(8): 1115; pl. 7, fig. 6; pl. 7 explanation page, fig. 6. Page 1125 (published later). ♀ described. Cites W. H. Edwards, 1876, Butt. N. Amer. 2: plate Colias II, fig. 6 and plate Colias III, figs. 5-6. Also cites fig. 11 on Glover's unpublished plate 6. Data is general.

philodice, Colias Godart. 1819. In Godart & Latreille in Latreille. Encycl. Méth. 9(1): 87, no. 35 (named in French); 9(1): 100-101, no. 35. [♂] & ♀ described. "Elle se trouve dans l'Amérique septrentionale, particulierement dans la Virginie". No series data no dates given. Spelled *philodin* by W. H. Edwards, 1872, In Hayden, Prelim. Rept. U. S. Geol. Surv. Mont. & Port. Adj. Terr. 5th. Rept. Progress, p. 466.

plicaduta, Colias philodice Nakahara. 27 Jan. 1926. Bull. Brooklyn Ent. Soc. 20(5): 222-223. "Holotype: ♀, Ithaca, N. Y., July 30, 1923 . . . Paratopotype: ♀, July 16, 1924. Paratype: ♀, Lava, Sullivan Co., N. Y., "June." Holotype has been presented to the Barnes Collection, Decatur, Ill[inois]., and paratype is in the same collection. Paratopotype is retained in the collection of the writer".

raritus, Eurymus philodice Gunder. 30 July 1928. Can. Ent. 60(7): 163; plate A, figs. 2, 2a. "Data: Holotype ♀ . . . Scranton, P[ennsylvani]a. (bred . . .), July 8, 1927. In the Author's coll."

reducta, C[olias]. philodice anthyale Dufrane. 28 Feb. 1947. Bull & Ann. Soc. Ent. Belgique 83(1-2): 69. ♀ described. ". . . Temple, P[ennsylvani]a. . . ". No series data nor dates given.

rothkei, Colias philodice Reiff. 15 Aug. 1917. The Lepidopterist, Off. Bull. Bost. Ent. Club. 1(11): 84; plate 7, 1 unnumb. fig. "Collected August 27, 1905 in the Susquehana Valley, P[ennsylvani]a., . . . Type 1 male in Mr. Rothke's collection". Mentions another specimen (no status).

serrata, Eurymus philodice F. Chermock. 9 Mar. 1929. Bull. Brooklyn Ent. Soc. 24(1): 21. " . . . occurs in the male sex only . . .". "Holotype, VIII-8-1926; paratypes, No. 1, VIII-8-1926; Nos. 2, 3, 4, VII-10-1926; No. 5, VIII-12-1926; Rossgrove, near Aspinwall, P[ennsylvani]a."

suffusa, C[olias]. philodice Cockerell. Mar. 1889. Entomologist 22(310): 55. Cites: ". . . Massachusetts, Maynard, Butt. of New Eng., pl. VII, fig. 57c". No date given.

virida, Colias philodice Strecker. 1878 [Sept. - Oct.][4]. Butt. & Moths N. America, Compl. Syn. Cat., p. 82, no. 58c. ♂ described. "One example . . .". Type locality: [near Montreal, Canada]? No date given.

vitabunda, Colias chrysotheme Hovanitz. 30 July 1943. American Mus. Nov. No. 1240: 2, 3-4. "Holotype Female and Alotype Male. — McKinley National Park, Alaska, July 18 to August 9, 1930, . . ., J. D. Gunder Collection, in the American Museum Natural History. Paratypes. — Twelve males same data as above; eleven males same locality but July 29, 1931, . . .; for males July 15-20, 1931, . . . in Los Angeles Museum; ten while female same data as holotype; four white females July 20-30, 1931, . . . in Los Angeles Museum; one white female August 9, 1930, . . . in Los Angeles Museum".

12. COLIAS SCUDDERII REAKIRT.

flavotincta, Colias scudderi Cockerell. Apr. 1901. Psyche, Jour. Ent. 9(300): 186. Cites W. H. Edwards, Butt. N. Amer. [1]: plate 10, fig. 5 (♀) (part of illustrated series of *scudderii,* 1872).

ruckesi, Colias scudderi Klots. 2 Nov. 1937. Jour. New York Ent. Soc. 45(3-4): 324-326. "Holotype male, allotype female, nineteen male and one female paratypes, from Windsor Creek Canyon, west of Cowles, N. Mex., July 2, 1935, . . . Twenty-five male and nine female paratypes from the same locality, July 4, 1936, . . . All were taken in about middle Canadian Zone, at from 9000 to 9500 ft. altitude, in grassy meadows surrounded by forest, along the Forest Service trail about halfway between Cowles and the summit of Santa Fe Baldy Peak. Holotype, allotype, six male and two female paratypes deposited in the American Museum of Natural History; four male paratypes deposited in the U. S. National Museum; four male paratypes deposited in the Canadian National collection; the remainder of the paratypes at present in the author's collection."

scudderii, Colias Reakirt. [12 June 1865][25]. Proc. Ent. Soc. Phila. 4 (pp. 213-339): 217-218, no. 2. "Hab. — Rocky Mountains, Colorado Territory. (In my collection, ♂, and that of the Entomological Society. ♀.)". "This species was collected in August, 1864 . . .". Spelled *scudderi* by Holland, 1931, Butt. Book, rev. ed., p. 295, no. 10.

FOOTNOTES

[1] Vol. 6 title page date is qualified by indirect date data (certain names in Fabricius' article were mentioned in the Allgemeine Literatur-Zeitung, Halle [Jena] 2(303): cols. 1177-1181, 19 Dec. 1807).

[2] Pt. 2 title page date is qualified by indirect date data by A. S. Corbet, 28 Feb. 1939, Jour. So. Bibliog. Nat. Hist. 1(7): 96.

[3] Hemming. 1937. The Generic Names of the Holarctic Butterflies 1: 139, see no. 376.

[4] Work title page date is qualified by indirect date data on pages 39 & 48 in the Sept. & Oct. numbers of Vol. 3 of the Bull. Brooklyn Ent. Soc.

[5] Dos Passos. 1962. Jour. Lepid. Soc. 16(1): 45-46.

[6] Sherborn & Woodward. 1901. Ann. & Mag. Nat. Hist. Ser. 7. 7: 137-140.

[7] No. 3 title page date is qualified by the preface date and a Ms. date of receipt (13 Mar. 1900) written on a copy of No. 3 in the library of the Los Angeles County Museum.

[8] No. 35 title page date is qualified by the article signature date.

[9] The date Sept. 1869 (given for Pt. 4 as per footnote 16) is qualified by the receipt date of Pt. 4 (see Trans. Amer. Ent. Soc. 2: XVIII, 1868-9).

[10] Tome 5 title page date is qualified by a meeting date (see p. 383).

[11] Kirby. 1871. Syn. Catal. Diurn. Lepid., p. 494, no. 29a.

[12] Article received by publisher 9 Mar. 1955. No. 1 containing the article was received at the Allen Hancock Foundation Library (Univ. Sou. Calif.): 11 Oct. 1955.

[13] No. 1 title page date: Mar., Apr. & May 1863. No. 2 receipt date (see Proc. Ent. Soc. Phila., 2: 164).

[14] More actual publication date data is needed.

[15] Proc. Ent. Soc. Phila. 2: 164 (No. 2 receipt date is given). No. 2: pp. 61-162.

[16] Hemming. 1931. Proc. Ent. Soc. Lond. Ser. A. 6: 42-45. Pp. 7-14 of Synopsis were published with Butt. N. Amer., pt. 6.

[17] Hemming. 1937. Hubner 1: 579-589.

[18] Title page date is qualified by the preface date.

[19] Hemming. 1937. Hubner 1:146-324.

[20] Sherborn. 1922. Index Animalium, 2nd. Ser. Vol. A-B: cxxxi.

[21] Vol. 6 title page date is qualified by the date of signature 3 and the date of a letter of W. H. Edwards to H. Edwards (Henry Edwards correspondence in the Amer. Mus. Nat. Hist, N. Y.) dated 16 Apr. 1877 and stating he would mail a copy of the catalogue the next day.

[22] No. 2 (Vol. 11) of the Trans. Amer. Ent. Soc. was available 12 Sept. 1884 (see p. xxxvi, vol. 11). The issue date of the separate was 18 Feb. 1885 (see page 2 of separate).

[23] Hemming. 1937. Hubner 1: 451-487.

[24] Nos. 7-10 (v. 3) were not published before 19 Jan. 1884 (see indirect date data on page 193). No. 1 (v. 4) was published 20 Feb. 1884 (see p. 42, v. 4).

[25] Pp. 221-330 (Mar. & Apr. 1865) receipt date (see Proc. Ent. Soc. Phila., v. 4, p. xii).

Journal of Research on the Lepidoptera 1(3):223-235, 1963

1140 W. Orange Grove Ave., Arcadia, California, U.S.A.

A STANDARD METHOD FOR MOUNTING WHOLE ADULT LEPIDOPTERA ON SLIDES UTILIZING POLYSTYRENE PLASTIC

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COMPARATIVE MORPHOLOGICAL STUDIES of insects are greatly facilitated if the material is prepared and mounted in a way that permits its easy manipulation and rapid, yet detailed, examination. Mounting specimens dry, on pins, has been the method of preference of Lepidopterists virtually exclusively, but it does not permit detailed examination of integumentary features that are of great taxonomic importance. Attempts to interpret the relationships of higher categories in the lepidoptera entirely on the basis of structure externally visible on such specimens have, in many cases, led to errors and have confused the taxonomy of many groups.

Although most workers are willing to utilize slide mounts for limited parts of the body, especially the genitalia, they have not extended the treatment to the whole animal and prefer to keep their material in fluids, usually alcohol. While alcoholic specimens allow the greatest amount of freedom of examination, considerable time and patience is spent simply handling them—unstoppering vials, pouring alcohol, restoppering vials, etc. As a result, a worker may hesitate to make the innumerable comparisons and recomparisons requisite to phylogenetic analysis. Furthermore, since the specimen must be examined with relatively low power dissecting microscopes, many fine details, such as microchaetae and other minute sense organs, surface textures, striae, spicules, spiracular structure, etc., are not visible, or at least not clearly observable. Among the other disadvantages of alcoholic specimens are that they do not keep stains well, are subject to evaporation and destruction from drying and suffer damage due to repeated handling.

Slide mounts, on the other hand, permit very detailed observation and are very easily handled. Admittedly, they allow the specimen to be viewed only from a limited number of aspects, but if prepared in a careful manner, such as that described below, most of the integumentary anatomy is available for inspection. Slides may be stacked as high as 4 or 5 deep and the specimens readily compared by focusing up and down with a dissecting microscope or detailed drawings rapidly prepared for the same purpose with a microprojector. In addition, they may be permanently stained, are subject to destruction only by breaking, and may be handled indefinitely without wear. Even fairly large Lepidoptera (e.g., smaller *Catocala, Vanessa*) may be placed on slides but I do not recommend it for very large species (e.g., saturniids, sphingids).

The details of the method outlined below were worked out on noctuid moths of medium size with relatively simple genitalia. Yet I believe that most groups of Lepidoptera may be similarly treated, although, of course, certain groups may require special handling because of extremely small size or peculiar modifications, especially in the genitalia.

The general treatment below might be applied advantageously to many insect orders (especially Neuroptera, Trichoptera, Diptera, etc.). All stages of mosquitoes are beautifully accommodated and I have had promising results with Collembola, a group notoriously difficult to mount on slides. The latter usually shrivel badly in balsam and eventually deteriorate if placed in aqueous media, apart from being flattened or otherwise distorted.

THE USE OF POLYSTYRENE PLASTIC

Whole mounts of most insects require fairly thick preparations. Workers who have tried to make such preparations with the usual natural (Canada balsam, Euparal), synthetic (Permount, Diaphane), or mixed aqueous (PVA, Hoyer's) media find that there are certain difficulties: These media, when applied in large amounts take a very long time to·harden, specimens invariably move in them from their desired positions during the hardening period (even if the laborious and time consuming "layering" or "build-up" technique is used), and they change color or deteriorate after a time.

Polystyrene plastic[1] (hereafter referred to simply as "plastic"), however, primarily because of its setting qualities, is the ideal medium for holding dissected parts in their desired positions on slides. Because it gels evenly and rapidly throughout, any specimen, regardless of shape or center of gravity, may be orientated perfectly in any position. Further advantages of plastic over the media mentioned above are its greater transparency and resistance to discoloring, and its thorough hardness and permanency when finally cured. In addition, it has the desired qualities of being its own clearing agent and of slightly intensifying certain stains. It has one disadvantage at present; it cannot be dissolved gradually and without fragmenting after complete hardening by any agent I know and therefore a specimen cannot be removed once mounted. This is a serious drawback, however, only with scarce material which might need to be remounted for study from a different aspect. The methods described in this paper are intended primarily for morphological and phylogenetic studies where abundant material is available. In any case, since slides are rarely remade unless very poorly prepared

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[1] Known commercially by many trade names, this is the type used for embedding biological specimens and other items by hobbyists.

in the first place, the insolubility of plastic should not limit its use. Preparations on broken slides may be soaked off in cellosolve and glued onto new slides with a thin layer of plastic.

The steps involved in using plastic as a medium for thick microscope slide mounts are as follows:

1. The specimen, after dissection and dehydration in up to 95% ethanol (see directions below), is transferred to a mixture of 50% acetone and 50% uncatalyzed plastic (because of the difference in density between these components they do not mix readily—mixing may be accomplished by shaking them together in a vial for a few seconds). Since the acetone evaporates rapidly from the mixture, its container must be kept covered as much as possible. The mixture clears and completely dehydrates the specimen; the specimen should remain in it about fifteen minutes.

2. While the specimen is clearing, a slide is prepared to receive it in the following manner: Uncatalyzed plastic is dropped onto the slide and spread out over an area the size of the cover slip. Spreading is done with a glass rod (3mm. diameter), which has been previously dipped into catalyst. The rod is used to apply and thoroughly mix the catalyst into the plastic. The depth to which the rod is dipped determines the amount of catalyst picked up. I find that dipping it about 5mm. provides the right amount of catalyst to gel the thickest layer of plastic that can be spread over a 22mm. square area (size of standard, square cover slip) without running over. Enough plastic should be applied to just cover the thickest part of the specimen. If the specimen is very thick and the viscosity of the plastic is not enough for it to stand level with the specimen, more layers must be added.

3. The specimen is next transferred to the plastic on the slide and generally oriented.

4. The slide is then placed on a warming plate, previously heated to about 130°F. to accelerate the gelling of the plastic. While the preparation is on the plate, it is viewed with the low power of a dissecting microscope and the specimen appropriately oriented. The specimen is held in its desired position with dissecting needles until the plastic gels enough to firmly anchor it. At this temperature, gelling will begin rapidly and will be far enough advanced to hold the specimen in about 7-10 minutes[2]. Impending gelation can be noted by the cessation of movement in the plastic revealed by dust particles present in it.

5. The slide is allowed to remain on the warming plate about 15 minutes to ensure thorough gelation.

6. The preparation is then ready to receive a cover slip if the first layer of plastic was sufficient to cover the specimen. If not, more layers must be added in the same manner as the first.

7. Glass chips or other cover slip supports are unnecessary and should not be used since they hinder the settling of the cover slip on the slightly shrinking plastic, and may cause a broken preparation.

8. The cover slip is prepared by covering it with just enough catalyzed plastic (applied with glass rod as above) to spread over its entire area when inverted and placed on the specimen. When the cover slip is in place the whole preparation is returned to the warming plate for gelling. The heat also helps the plastic under the cover slip to spread. If too little plastic was applied, additional amounts may be added at the side of the cover slip until all the spaces are filled. Any excess plastic may be wiped off from around the edges or, if gelling has occurred, trimmed with a blade.

9. Complete hardening and curing of the whole preparation can be accomplished by leaving it overnight in an oven at about 100°F. or can be allowed to take place slowly at room temeprature.

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[2] This figure varies according to the formulation and age of the plastic. I find these times average but they may be longer especially for formulations designed for long shelf life.

STANDARD DISSECTION AND MOUNTING

Four slides are required to hold the various parts of the whole insect (fig. 1): 1. The main part of the body including the two halves of the head, thorax and abdomen are put on the first slide (the tegulae, antennae and basal portions of the right wings being dissected away—see below) (fig. 1:1); 2. A second slide holds the legs, basal portions of the right wings, antennae and tegulae (fig. 1:2); 3. The wings occupy a third slide (fig. 1:3); 4. The genitalia are put on a final slide (be they male (fig. 4b) or female (fig. 4a).

These main parts are dissected and mounted as follows:

Preliminary general dissection

The following instructions apply to specimens mounted on pins. Specimens in alcohol or otherwise preserved are excused from the impertinent steps.

1. The left pair of wings are broken off at their bases and the right pair cut off transversely with scissors beyond the end of the frenulum. The wings, with the data labels removed from the pin and a slide reference label, are set aside in a cellophane envelope.

2. The body of the insect, still on its pin, is wetted in 75% ethanol and then boiled in water for 5 minutes. This softens it and allows the pin to be removed easily.

3. The body is next transferred to a solution of 10% potassium hydroxide which is heated to near boiling in a small beaker or test tube suspended in a water bath. The specimen is left in the solution until thoroughly macerated (15 minutes).

4. After maceration, the body is transferred for dissection and cleaning to distilled water in a watch glass, preferably one with a slightly convex bottom.

5. Next the genitalia are removed. In the male this is done by severing the membrane between abdominal segments VII and VIII (or further cephalad to include special modifications on more proximal abdominal segments if present). The female is treated likewise, but by severing the membrane between segments VI and VII. The genitalia are rubbed clean of scales (I like to use a pointed applicator stick for this; others may prefer a fine camel's hair brush or like instrument) and transferred to clean distilled water.

6. The legs are now removed (coxae and trochanters should remain intact), rubbed clean of scales and transferred to clean water.

7. The body itself (head, thorax with bases of legs, and abdomen minus genitalia) is finally bisected with a sharp, single-edged razor blade. Great care must be taken at this step to insure as perfect a bisection as possible. The specimen is held ventral side up in the watch glass and a mid-ventral, longitudinal slit is made at the posterior end of the abdomen with scissors. The razor blade is then brought down on the mid-ventral line guided by this slit, the coxae and the two halves of the proboscis between which its edge is placed. The blade is first used to compress the body gently and then pressed firmly against the bottom of the watch glass and rocked to and fro to make the final cut. The slightly convex bottom of the watch glass helps to make a clean cut. After the halves of the body are separated, cleaned and rubbed free of scales, they join the other parts in distilled water.

8. Dehydration in 75% and 95% ethanol follows (if no aqueous stain is used—see "STAINING"). The female genitalia and phallus of the male genitalia go directly to 95% ethanol to harden their membranous parts. This is done in a special manner as described below.

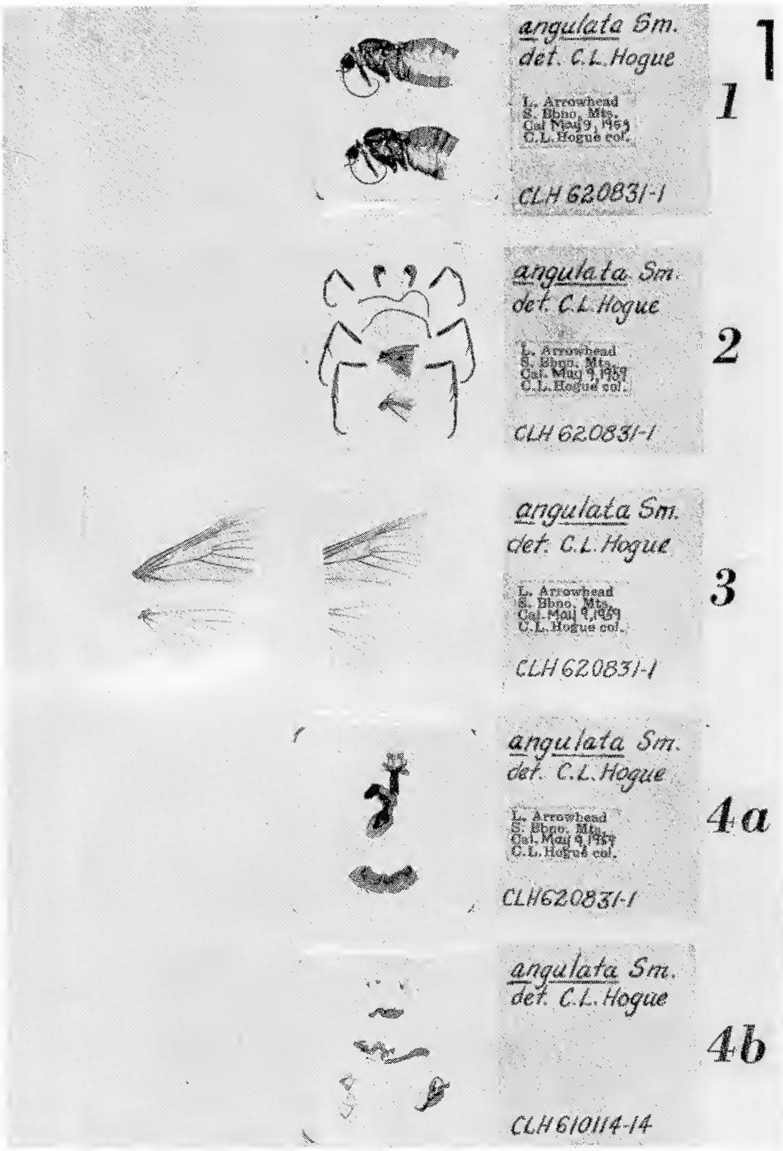
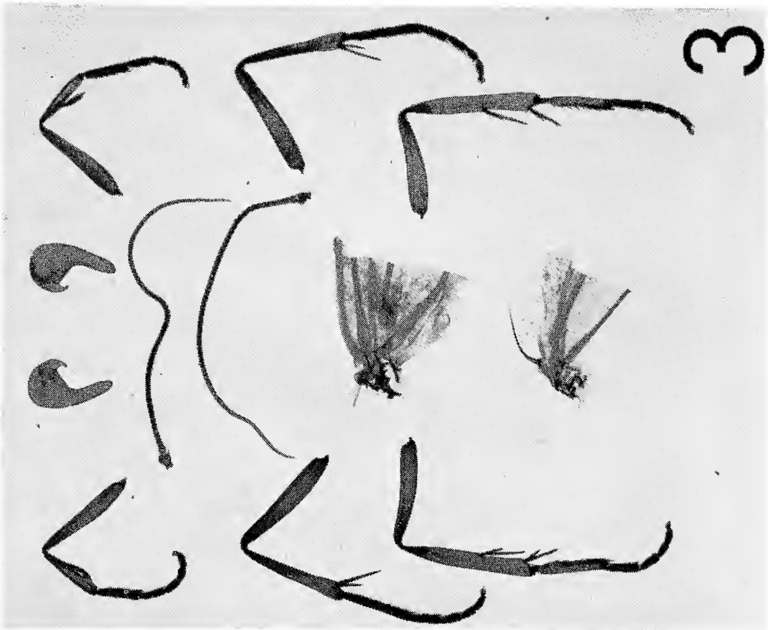


Fig. 1: Set of slides (*1 - 4*) holding a whole specimen (*4a* example a female; *4b* a male).



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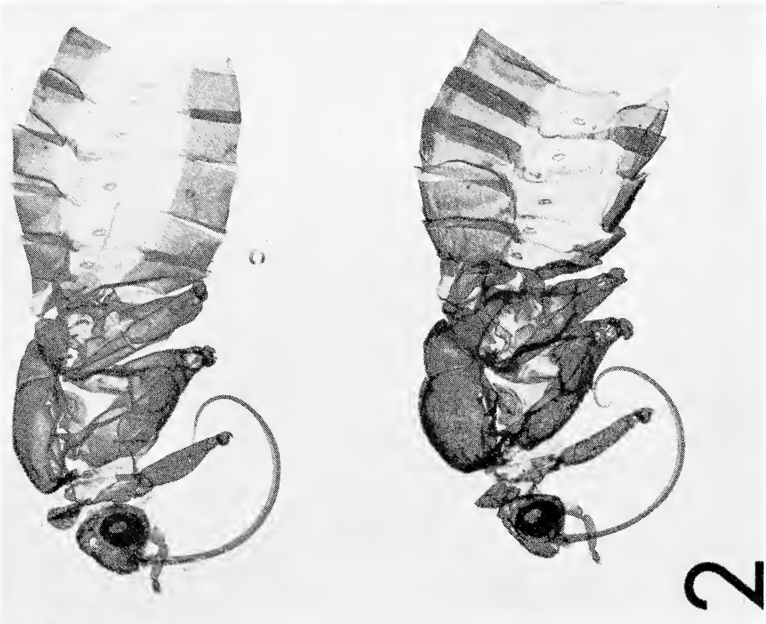

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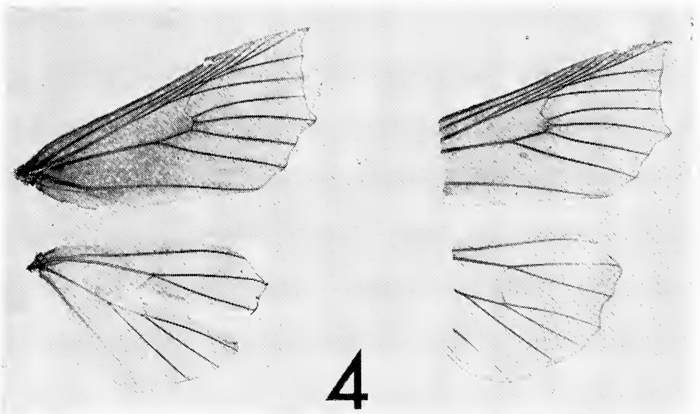

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Figs. 2-6: Close-up views of slides shown in fig. 1 to show detail of arrangement of parts. Fig. 2: Main body, bisected. Fig. 3: Miscellaneous parts. Fig. 4: Wings. Fig. 5: Female genitalia. Fig. 6: Male genitalia.

9. The wings, previously set aside in a cellophane envelope, are bleached for about 2 or 3 minutes (at least long enough for the veins to become well defined) in 5% sodium hypochlorite (full strength household bleach—Purex, Chlorox), washed in distilled water, and dehydrated by passage through 75% and 95% ethanol.

If it is desired that the veins be stained a totally different procedure is necessary:

After wetting in ethanol and soaking for 20-30 minutes in hydrogen peroxide (3%), the scales are carefully rubbed off with a blunt camel's hair brush. The denuded wings are then washed in distilled water and transferred to the stain. A long destaining period must follow in order to decolorize the membranes.

The dissected parts, now in 95% ethanol, are ready for fine, detailed dissection and cleaning (and staining with non-aqueous stains if desired—see "STAINING") before mounting in plastic on slides. I find that these two jobs are best done in the 95% ethanol; since the specimen has become fairly brittle, sclerites are easily separated and remaining unwanted scales easily flaked off.

Final dissection and mounting

The different parts are treated in various ways. Reference to the figures will clarify the descriptions (including terminology) of the fine points of dissection and orientation on the slide.

Slide 1: Main body (figs. 1:1;2)

The two halves of the main body of the specimen require only minor alteration before being transferred to the clearing mixture. The tegulae and antennae are removed and the bases of the right pair of wings are carefully dissected away with the axillary sclerites. These parts are mounted with the legs (see "Slide 2"). If the specimen is a noctuoid moth, the ventral portion of the second phragma is also cut away with fine scissors to allow an unobstructed inner view of the tympanal area. Similar special treatment may be necessary with other taxa.

The halves are mounted on the slide, one with its outer surface up and the other (the one with the cut phragma if noctuoid) with its inner surface up.

Slide 2: Legs, etc. (figs. 1:2;3)

The legs, bases of wings (with axillary sclerites), tegulae and antennae are all mounted together on the same slide since they are of about the same thickness and do not orient well if left attached to the main body. Usually these parts require no further dissection although sometimes one may desire to separate the components of the pretarsus or the antennae. Their orientation is best explained by the figures.

Slide 3: Wings (figs. 1:3;4)

No special treatment is needed for the wings. After dehydration they are simply mounted flat in the plastic (which also clears them). If too large to fit on a standard microscope slide, they may be accommodated by a large sized slide (2″ x 3″). If very large, they may have to be cut up into sections.

Slide 4: Genitalia — female (figs. 1:4a;5;7)

The following procedure is considerably modified from that usually employed by lepidopterists. The conventional procedure is to leave abdominal segment VII attached and to mount the entire undissected complex ventral side up or laterally on the slide. This, however, has the following undesirable features: (1) segment VII, still attached, obscures detailed viewing of the structures beneath, (2) if mounted with the ventral side up the venter of segment VIII is plainly visible but the pleura, which also may possess important characters, are not. Furthermore, only the ventral edges of the ovipositor lobes are in plain view; their profile, patterns of sclerotization and chaetotaxy are impossible to see. If mounted laterally, the reverse viewing difficulties are present. (3) The whole complex is cylindrical in general shape and rolls easily, making it hard to position in a standard way.

By mounting the female genitalia as described below, these difficulties are surmounted. The steps involved are as follows (fig. 7 shows them partly completed):

1. The genitalia have been freed from the remainder of the abdomen and cleaned of most of their scales (see above, "Preliminary general dissection").
2. Segment VII is removed by splitting it laterally and tearing it off. The tear should follow the line of the membrane between it and the following segment. Care must be taken not to damage the sclerites around the ostium bursae.

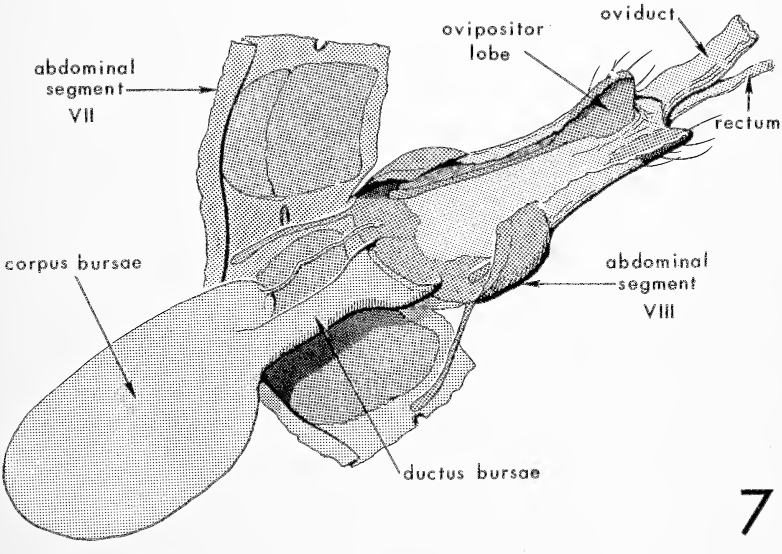


Fig. 7: Oblique dorsal view of female genitalia showing principal structures in state of partial dissection (diagrammatic).

3. Next, the genitalia proper are slit mid-dorsally, a cut being made first with scissors through segment VIII and continued by tearing caudad to the tip between the ovipositor lobes.

4. The genitalia are then opened up, the oviduct and rectum are pulled up and cut free, and the whole complex cleaned.

5. The bursa copulatrix is next inflated with water in much the same manner as the vesica of the male phallus (see below). The cannula is inserted into the ostium bursae and passed down the ductus bursae. The stream of water from the syringe cleans the corpus bursae internally and expands it into its full shape. Sometimes a tiny hole is needed to allow the escape of the fluid and debris. It is usually not necessary to go through a hardening process with the bursa copulatrix as is the case with the male phallus vesica since it generally holds its shape better than the latter.

6. Staining with aqueous stains follows if desired.

7. Preparatory to dehydration in 95% ethanol the genitalia are opened again and placed flat (inner surface down) in a stender. A small piece of glass (broken microscope slide) is placed over the opened portion (not over corpus bursae!) to hold it flat while the water is withdrawn from the vessel and replaced with 95% ethanol. The same may be done for segment VII, previously removed. It may be necessary, if not already done, to punch a small hole in the corpus bursae before adding the ethanol if the ductus bursae is so narrow that it would prevent the free exchange of liquids. Otherwise, the diffusion gradient—ethanol diffusing out faster than water diffusing in—may cause the collapse of the bursa.

8. Final cleaning may be carried out after dehydration. The preparation is then ready for clearing and mounting.

Slide 4: Genitalia – male (figs. 1:4b; 6; 8-10)

Lepidopterists disagree on dissection procedures and orientation of the male genitalia on slides. The majority prefer to leave all the elements intact and mount the complex ventrally with the valves spread open as widely as possible, the least troublesome method. Others also do not separate the parts but mount the whole complex laterally. Still others dissect various parts away, often only the phallus whose vesica may or may not be inflated and the main orientation is either ventral or lateral.

These variations may be dictated by either the whims of the investigator or the nature of the material, i.e., the positions of the characters of greatest significance. Too often it is the former. Obviously, the only scientific and rational approach to the problem is to dissect and mount many specimens in many ways, even keeping some unmounted in fluids. Yet when time is limited, and many comparisons are to be made, a single, standard method must be chosen. For this, I prefer to mount the main structure of the genitalia laterally, with one valve and other elements such as the juxta, anellus, etc. removed and mounted separately. Furthermore, I always inflate the vesica of the phallus; though this is a time consuming task, the results are well worth it.

Even apart from the conditions just mentioned, I believe that this procedure is superior to the undissected ventral mount for morphological study since there are generally better, undistorted viewing aspects for the majority of characters and additional characters are revealed. Specifically, (1) the uncus is natural in shape and position instead of being folded or angled if long, or viewed on end if short. Its entire profile is observable in plane view; (2) the tegumen is untwisted (otherwise usually resulting from the disturbed uncus); (3) the overall shape, lobes and spines etc. of the vesica are fully exposed, not compressed into the body of the phallus; (4) the anellus is not obscured by the juxta (and phallus too if left intact); (5) the valves (at least the one dissected away and usually also the one intact) lie completely flat so that their median structures are not distorted by foreshortening as is usually the case in a ventral mount.

The steps followed in dissecting the male genitalia are as follows:

1. The genitalia have been freed from the remainder of the abdomen and cleaned of most of their scales (see above, "Preliminary general dissection").

2. The phallus is removed by grasping it at the tip, i.e., posterior end protruding between juxta and anellus (fig. 8), and pulling gently to the rear (fig. 9). If the phallus does not so protrude, the forceps may need to be inserted a short distance into the canal inclosing it to gain a hold. If the phallus is withdrawn properly and carefully, the manica will turn wrong side out and the ductus ejaculatorius will pull out through the hole in it (fig. 9).

If staining with aqueous stains is desired at this point, the main portion of the genitalia should be set aside in distilled water. Otherwise, they may go directly into 95% ethanol.

3. The ductus ejaculatorius should now be snipped off with a pair of fine scissors a short distance from the aedeagus.

4. Next comes the preliminary inflation of the vesica. This is accomplished by first teasing as much as possible of the vesica out of the aedeagus with fine forceps and then inflating it with a hypodermic syringe filled with distilled water. I find that a 2cc. syringe tipped with a glass cannula (in preference to a regular hypodermic needle which does not permit the variety of sizes needed) best for this work. The cannula is inserted into the ductus ejaculatorius (fig. 10) and pressure applied until the vesica completely inflates and everts. It is usually necessary to crimp the ductus with forceps against the cannula at the point of insertion to prevent leakage and the phallus from coming free under the hydraulic pressure.

5. The vesica is next hardened to preserve its fully inflated shape (fig. 10). This step follows staining if aqueous stains are used. Several steps are necessary in this process:

a. The phallus is placed in clean distilled water in a watch glass.

b. A short length (1 cm.) of silk surgical suture (cardiovascular 5-0 or 6-0) is tied into a loose, simple knot and also put into the watch glass.

c. The hypodermic syringe is filled with 95% ethanol.

d. The cannula is inserted as above. This may be difficult since the alcohol rapidly diffuses out of the tip setting up a strong current which constantly carries the phallus away.

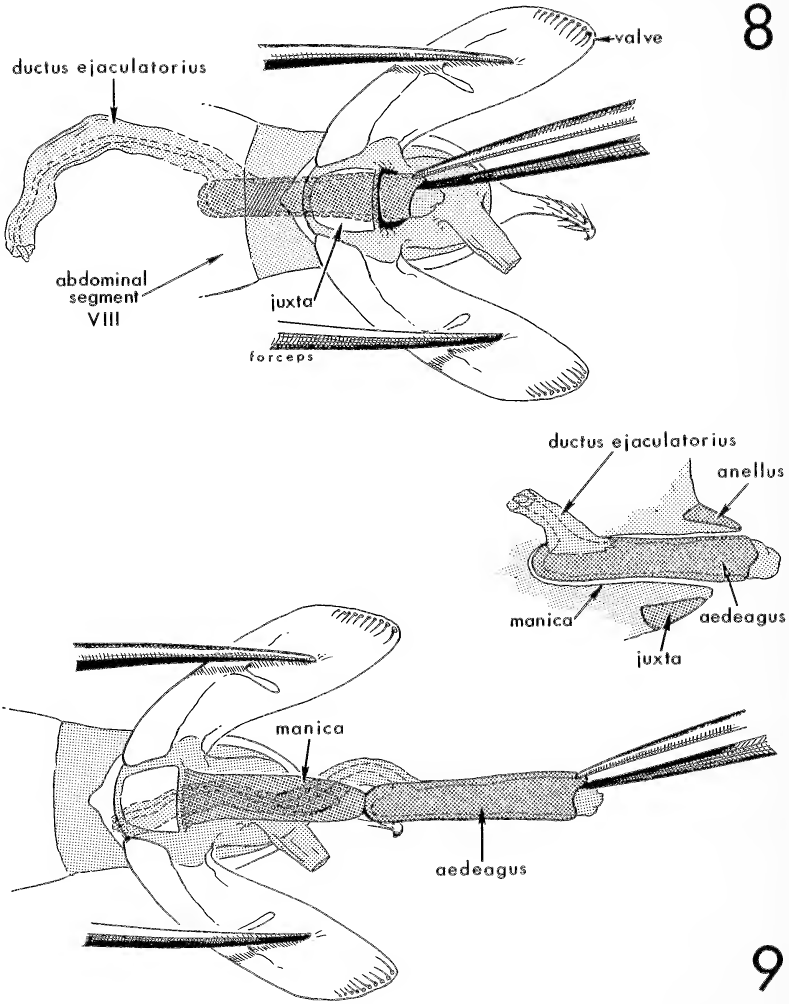
e. After the cannula is properly inserted the phallus is tied to it with the suturing thread (around the center of the aedeagus) by slipping the loose knot over it and drawing it tight with forceps (fig. 10). Some kind of clamp or modelling clay is useful at this point to hold the syringe while both hands are being used to tie the knot.

f. The water in the watch glass is now withdrawn and quickly replaced with 95% ethanol.

g. Pressure is exerted with the syringe and maintained for a short while (about 3 minutes usually suffices) until the vesica is thoroughly dehydrated and hardened. Leakage of the ethanol from the end of the vesica is prevented by clamping it with fine forceps (fig. 10).

h. The phallus is slipped off the cannula and the suturing thread untied and removed.

i. The phallus joins the rest of the genitalia in 95% ethanol.



Figs. 8-9: Ventral views of male genitalia showing principal parts and procedure for removal of phallus. Insert showing relationship of components of phallus complex in lateral, sectional view. (All figures diagrammatic).

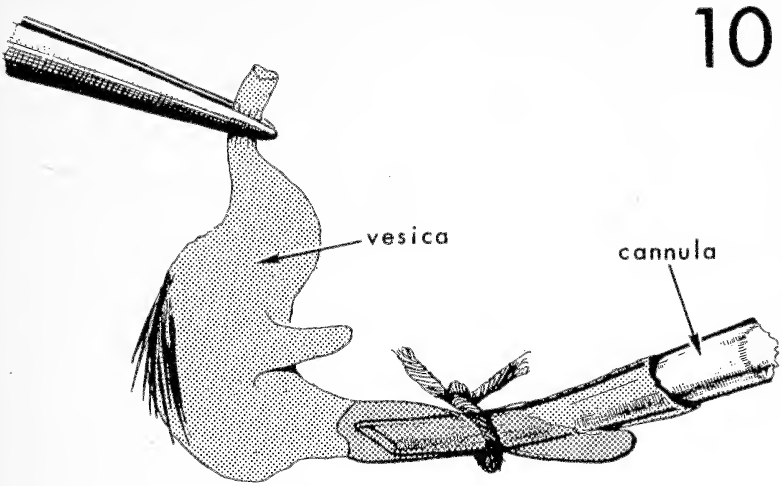


Fig. 10: Phallus of male genitalia properly prepared for inflation and hardening of vesica (diagrammatic).

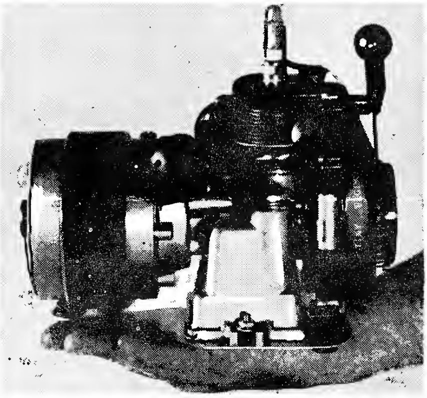
6. Further dissection, if desired (at least segment VII should be removed) and final cleaning may now be carried out in preparation of clearing and mounting.

STAINING

Only a few general remarks regarding stains will be made here. Each worker has personal preferences and many stains are in popular use, among them acid fuchsin, mercurochrome, and safranin. I have always found the first the most satisfactory. Acid fuchsin is taken up in the greatest amounts by the sclerotized parts of the integument leaving membranous parts clear. Thus sclerites are clearly defined and easily observed and drawn. Tiny sclerotic processes in membranes also show up very distinctly. I have not found the other stains mentioned to act in this manner.

Acid fuchsin is an aqueous stain, i.e., it is soluble in water and must be applied to a fully hydrated specimen. I usually apply it after preliminary dissection using a 5% solution diluted 1 drop to 10 ml. Overnight is usually long enough to leave the parts in the stain. If not enough stain is taken up in this time more is added until the specimen is deeply tinted. Staining is always followed by destaining in distilled water to clear the membranes and obtain the desired differentiation.

Non-aqueous stains may be applied to the specimens after they have been dehydrated in 95% or absolute ethanol.



Volume 1 *Number 3* *March, 1963*

THE JOURNAL OF RESEARCH ON THE LEPIDOPTERA

IN THIS ISSUE

SPECIAL NOTICE

The Journal is starting a series of short illustrated biographical sketches of past and present lepidopterists. In order to be wholly democratic and with no aim in mind of "honoring" anyone, all lepidopterists will be included. The only criterion will be a continued interest in the Lepidoptera, as shown by publication, collections, etc. The editor would appreciate receiving black and white prints of lepidopterists, together with a brief biographical sketch. This applies to lepidopterists of all countries. Authors sending manuscripts might send this material along with their articles.

THE JOURNAL
OF RESEARCH
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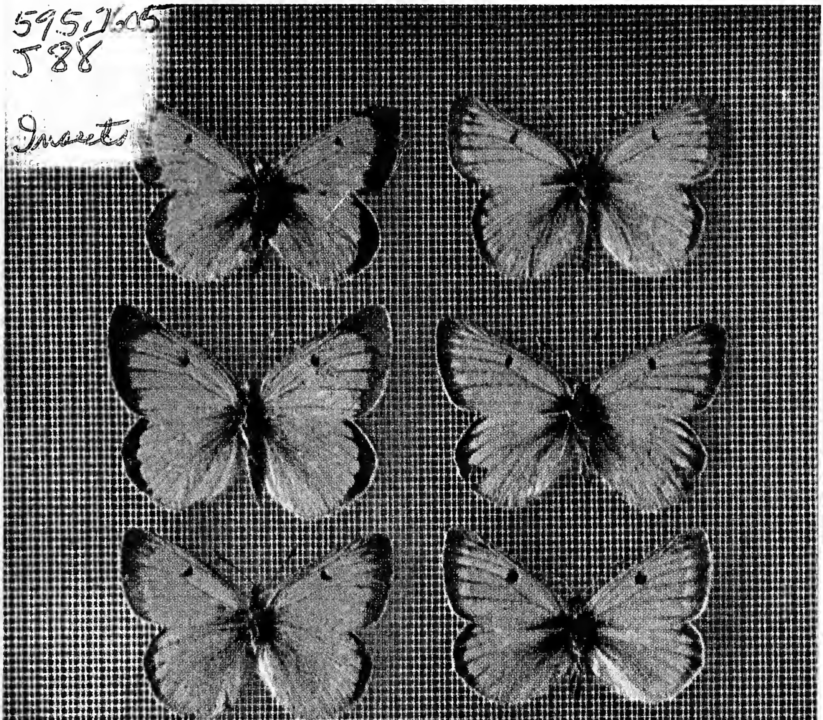

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THE PURPOSE OF THE JOURNAL is to combine in one source the work in this field for the aid of students of this group of insects in a way not at present available. THE JOURNAL will attempt to publish primarily only critical and complete papers of an analytical nature, though there will be a limited section devoted to shorter papers and notes. QUALITY WORK on any aspects of research on the Lepidoptera is invited. Analytical and well illustrated works are preferred, with a minimum of long description.

AUTHORS ARE REQUESTED to refer to the journal as an example of the form to be used in preparing their manuscripts. Illustrations should be of the best quality black and white, or line drawings and should be pre-arranged by the author to fit a reduced size of 4" x 6½." Footnotes should be avoided; bibliography should be as indicated. Tables should be set-up for page size as indicated. Manuscripts in good form and requiring little work by the editor will naturally appear first. Authors, who wish drawings made for them, may submit rough sketches and will be billed for the cost, which will be very negligible. Work to be done on research grants should so specify. When possible, tabular matter should be typed on good paper with a carbon ribbon in a form suitable for a one-third reduction and in a size to fit 4" x 6½."

THE JOURNAL is not a suitable place for continued changes of nomenclature; unless the author is himself analytically studying a group from its biological point of view and finds a change necessary, the editor must ask authors to refrain from any changes from the McDunnough Check List unless superseded by a monograph published since that date. Popular books are not to be considered as giving scientific credence to any name. It is rare that name changes need be made and preference is given to old names unless in the editor's opinion sufficient evidence is given to warrant such change.

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1140 W. Orange Grove Ave., Arcadia, California, U.S.A.

TECHNIQUES IN THE STUDY OF POPULATION STRUCTURE IN PHILOTES SONORENSIS

RUDOLPH H. T. MATTONI and MARVIN S. B. SEIGER

Life Sciences Department, North American Aviation, Downey, Calif. and Department of Biological Sciences, Purdue University, Lafayette, Ind.

THE HANDLING OF LIVING MATERIAL has always been an important factor in the design of biological experiments. This factor is especially critical in studying population structure under natural conditions. One of the most accurate techniques for determining parameters of population structure is that of capturing, marking, releasing and subsequent recapturing of individuals (Ford 1951). Such experiments would be biased if a behavioral response is elicited or differential viability imposed as a result of the technique employed.

We have developed a handling technique in sampling populations of the small Lycaenid butterfly, *Philotes sonorensis,* over a period of three collecting years. This routine appears to have little or no effect on the subsequent behavior of the butterfly. The purpose of this report is to describe and evaluate the technique.

Our objectives were to describe the distribution, numbers, and movements of adult individuals of *P. sonorensis* within a small circumscribed area in the Fish Canyon portion of the San Gabriel Canyon Wash near Los Angeles. These individuals were classified as to 8 male and 5 female spot pattern phenotypes. (Figure 1). Six stations, each 80 meters in diameter, were set up and sampled in 1955 and 1956. These were separated by distances ranging from 96 to 433 meters from the center of one area to the perimeter of another. The stations were destroyed by trenching operations in 1961 because of water requirements. New experimental sites were established in 1963 in other areas of the wash.

Sampling was done as weather permitted during the flight period in March. In 1955 a total of 809 specimens were captured 1126 times during 9 collecting days over a 21 day period. In 1956 there were 972 specimens captured 1226 times for 11 collecting days over a 29 day period. Sampling was done between 9 A.M. and 3 P.M., one hour being allotted to each station during each day. The order in which the stations were collected on consecutive days was ramdomized in order to minimize possible differential effects correlated with time

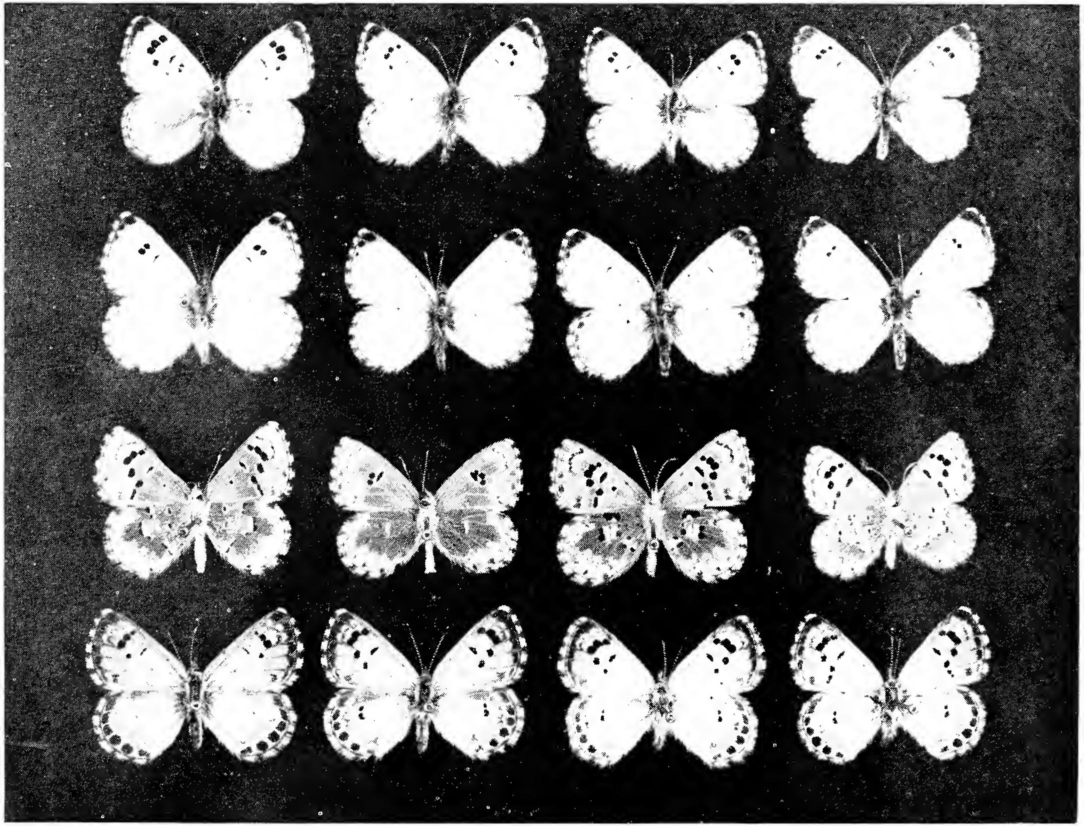
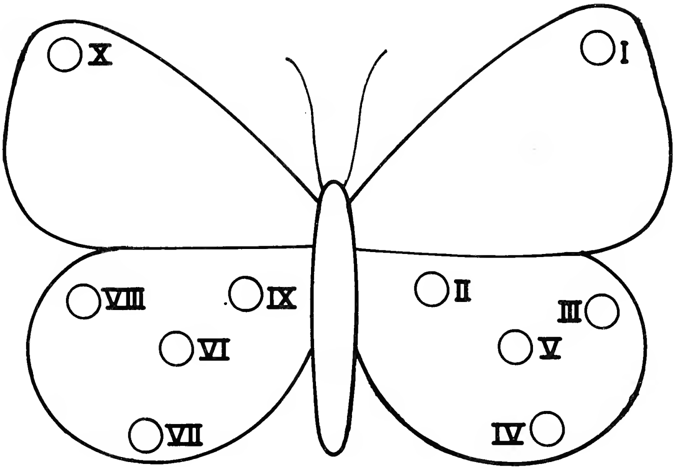


Fig. 1. Phenotypic classes found at San Gabriel which were recorded, the eight male types were classified according to the number and distribution of right forewing submarginal spots. Specimen 7 represents two classes; *comstocki,* which has the underside shown in specimen 10. Specimen 8 shows spotting assymmetry, classifiable as A on the right and D on the left side. Specimens 9 and 11 show two modal types of underside pattern, 12 the underside pattern of populations found outside the wash itself. Four female types were classified by the number of black spots found on the forewing cells of CUI and CU2. These range from 0 to 3 in specimens number 13 to 16 respectively. The female form of *comstocki* is not shown.

Fig. 2. (below) Photograph showing equipment described in the text. RHTM on right holding a specimen about to be placed in the recovery chamber on the portable desk. Vials with specimens can be seen in the compartment and the CO_2 tank behind. MSRS on left recording data.

Fig. 3. (above) Anaesthesis Tube.

of day. Each station was sampled for 30 minutes. This allowed 10 minutes for moving between stations and 20 minutes for handling. When a butterfly was caught it was removed from the net with a 1" x 4" shell vial and the vial was plugged with a cotton stopper. We avoided touching the specimens with anything other than the net and the vial. After the collecting period the vials of butterflies were assembled in the center of the collecting area. In all cases one of us (RHTM) classified and marked the specimens while the other (MSBS) recorded the data. This process took approximately 20 minutes per station. The equipment used is shown in Figure 2. This included a portable desk, carbon dioxide tank, and release carton. The compartment on the desk served to store vials in the shade. Each specimen was anesthetized in its vial by a 10 second exposure to CO_2 delivered at approximately 3 psi. The CO_2 was delivered from a small tank strapped to a pack frame for easy portability. A regulator maintained constant flow and pressure from the tank through the rubber tube to one of the glass tubes in a two hole rubber stopper inserted in the vial. The other glass tube in the stopper served as an exhaust to avoid excessive pressure in the vial (Figure 3). The anaesthetized butterfly was removed from the vial with flat bladed insect forceps and classified according to sex, forewing spot pattern and the area and date of previous capture if it had been a recaptured specimen. The specimen was then marked to indicate the date and area of capture. This was done by putting a dot of "Pactra" lacquer on the wing underside. The critical factor of this operation was maintaining a proper paint consistency. This was done by trial and error, using acetone as a diluent with a blunted dissecting needle. Six different colors were used to denote the six stations. These were applied to one of ten distinct underwing areas to denote the date of capture (Figure 4). The butterfly was then carefully laid on the bottom of a one gallon ice cream carton and allowed to recover. Recovery time varied, but seldom exceeded two minutes. The process was then repeated. After handling the last specimen, all the gear was assembled. Just prior to moving to the next station the carton was held upright, facing the sun, and was gently tapped so that the remaining specimens would fly off. If any specimen remained, the carton was inverted and vigorously tapped. If a specimen was not able to fly "normally" a distance of 10 feet, it was removed from the population and the event recorded. After the first day's collection, subsequent collecting within about 10 feet of the center of the station was avoided as a precaution again recapturing injured specimens, if any should exist. In 1955, 21 individuals including 10 recaptures, and in 1956, 37 individuals including 8 recaptures, were removed from the population. These figures are not wholly indicative of the effectiveness of the technique since about half of these represented specimens sampled for study.



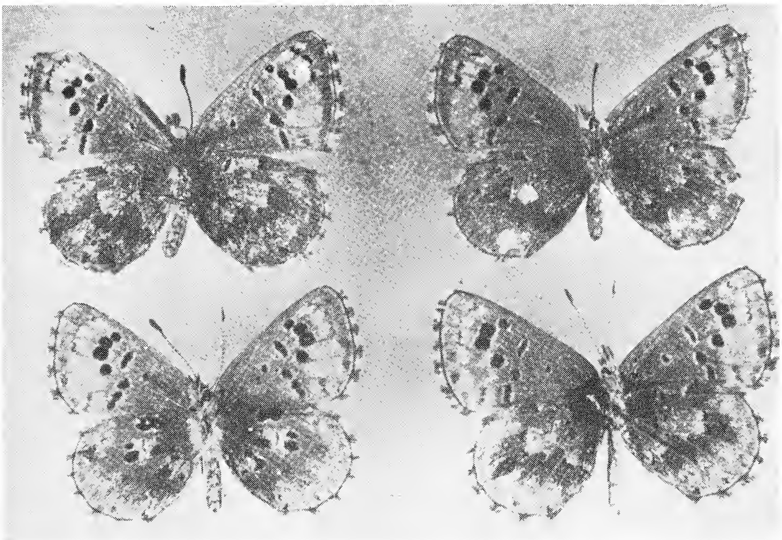


Fig. 4. Marking scheme on underwings to denote data of capture. The circles indicate the positions of the lacquer marks on the wings which correspond to the collecting day. (designated by Roman numerals).

Fig. 5. Recaptured specimens sampled on the last collecting day of 1955.

The distinctive feature of our technique is the use of CO_2 anaesthesis in the field. We feel that anaesthesis greatly decreases the probability of damage due to handling, especially when examining and marking such a small butterfly as *P. sonorensis*. The procedure was adopted because of its general acceptability in the laboratory for research in insect physiology and genetics. For example, Seiger (1953) studied the effects of different anaesthetics on the dipteran, *Drosophila mulleri*. He found no significant difference in fertility and fecundity between flies which had been given no anaesthesis and flies which had been anaesthetized with CO_2. The average quiescent period after anaesthesis was one minute. This was sufficient time to classify an individual for sex and wing pattern, determine if it had been recaptured, mark the lower wings, and allow the lacquer to dry. Following recovery, the individuals tended to remain quietly in the container, thus further minimizing damage. The lacquer fastens the scales to the wing membrane and dries so quickly that no more than ten losses were suffered by insects sticking to the container or themselves. In the laboratory, *P. sonorensis* could withstand CO_2 anaesthesis in excess of 10 minutes with no apparent ill effects, although under longer periods of exposure, partial paralysis would occur and eventually death ensue. There was no evidence for cumulative effect of repeated exposures of 10-30 seconds duration to CO_2. The possibility that abnormal behavior might result from anaesthesis has not been fully explored. In the first flight after anaesthesia, there appears to be a tendency for the butterflies to exhibit an escape behavior. After alighting once the behavior is not apparent. There appears to be no difference between the behavior of a butterfly in its first flight after anaesthesis and the behavior of a butterfly in flight after being captured in a net and released without anaesthesis. Although we feel that the advantages of anaesthesia far outweigh any possible disadvantages, we plan to determine whether there are any real effects of CO_2 on the behavior of *P. sonorensis* in future experiments.

We believe that the most important evidence of the negligible effect of our overall technique on behavior lies in the consistency of our data for two years with respect to the highly non-random pattern of movement. Another evidence was the remarkable behavior of 5 individuals in 1956. These moved away from their area of capture and subsequently returned. There are several reasons which indicate that viability effects are also negligible. Figure 5 shows four marked specimens sampled on the last day of 1955. These appear to be quite undamaged, that at the upper right having been followed for eleven days and caught four times. In the course of our studies, several insects flew the distance between the two farthest stations (433 meters), one flying a minimum of 819 meters. Lastly, because many specimens were captured more than once, it is possible to infer whether multiple handling had an additive effect on viability by comparing observed with expected values of multiple recaptures 0, 1, 2, 3 and 4 times.

Using a poisson distribution, the data for 1955 gives $\chi^2 = 23.7$ and $P = < .0001$ for 3 df; and for 1956, $\chi^2 = 5.4$ and $P = .12$ for 3 df. The highly significant departure from expected in 1955 is due entirely to an excess of specimens recaptured 3 and 4 times. The meaning of this departure is obscure, although it does not contradict the hypothesis of additive deleterious handling effects.

We found that the marking technique enabled us to distinguish individuals without confusion. The method can be compared to a punch card system in which each butterfly carries a recorded code on its wings, the color of the spot indicating the station where each capture took place and the position of the spot on he wing indicating the date of each capture. Thus the population size for each station can be determined for any given collecting day (Dowdeswell, Fisher and Ford 1949, Ford 1951), patterns of movement can be discerned and the life span of individuals can be calculated. These characteristics can be further quantified by correlation with maculation type and sex of the individuals. These data and conclusions are being prepared for publication in this journal.

For comparative information on field techniques in population study with Lepidoptera, the reader is referred to Abbot (1959), Ehrlich and Davidson (1960), Evans (1955), and Fales (1959); as well as those of Ford and his associates (op. cit.) We feel our technique has the least effect on viability and behavior differentials, particularly with reference to the use of anaesthesis; minimizing number of identifying marks on each individual; limiting individual contact to net, vial and forceps; and no more than 30 minute retention in the field. The last item, of course, is part of our experimental design. We feel that all such studies should take this factor into account, in spite of statistical difficulties in treating same day recaptures.

We gratefully acknowledge the contributions of Mr. Jack Roper of North American Aviation in providing the photographs for Figures 1, and 3, Dr. David Goodchild, CS & IRO for Figure 2, and Mr. Roy Pence, UCLA, for Figure 5.

SUMMARY

1. A method for anaesthetizing and marking individuals in order to determine population structure is described.

2. The benefits and possible disadvantages of the method are examined and some applications of the technique are mentioned.

REFERENCES

ABBOTT, W. 1959. Local Autecology and Behavior in *Pieris protodice.* Boisduval and LeConte with some comparisons to *Colias eurytheme* Boisduval. *Wasmann J Biol.* 17: 279-298.

DOWDESWELL, W. H., R. A. FISHER and E. B. FORD 1949. The Quantitative Study of Populations in the Lepidoptera. *Heredity.* 3: 67-84.

ERHLICH, P. R. & S. E. DAVIDSON 1960. Techniques for Capture — Recapture Studies of Lepidoptera populations. *Lep. News.* 14: 227-229.

EVANS, W. H. 955. Retrieving marked *Anthocharis reakertii. Lep. News.* 9: 118.

FORD, E. B. 1951. The Experimental Study of Evolution. *Australian and New Zealand Association for the Advancement of Science.* 28: 143-154.

FALES, J. H. 1959. A Field Study of the Flight Behavior of the Tiger Swallowtail Butterfly. *Ann. Ent. Soc. Amer.* 52: 486-487.

SEIGER, M. B. 1953. The Effect of X-Ray Dosage on Fertility, Fecundity and Incidence of Chromosomal Aberrations in *Drosophila mulleri.* Master's Thesis, University of Texas.

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1140 W. Orange Grove Ave., Arcadia, California, U.S.A.

EARLY STAGES OF A SOUTHERN CALIFORNIA GEOMETRID MOTH, DREPANULATRIX HULSTI HULSTI (DYAR)

JOHN ADAMS COMSTOCK

Del Mar, California

DR. DYAR, IN 1904, named *"Catopyrrha hulsti"* from a specimen contained in the Hulst collection under another name, without designating the locality of its origin. Dr. Rindge (1949) gave valuable data on the species, and its two subspecies, *D. carneolata* B. & McD. (1917) and *D. verdiaria* Grossbeck (1912) in his Revision of the Genus. He lists *D. carneolata* as an Arizona form of *Drepanulatrix hulsti,* and mentions California examples that seem indistinguishable from Arizona specimens.

He places *Drepanulatrix rindgearia* Sperry (1948) as a synonym of *D. hulsti.* He also notes that the early stages are unknown.

D. hulsti hulsti ranges throughout the greater portion of coastal California, wherever its food plant, *Ceanothus,* occurs.

It flies most abundantly from May to August, but has been reported as early as January, and late into September.

Eggs of this species were obtained this year (1962) in Del Mar, on several occasions, from May 25 to late August. For the most part these were laid singly on their sides. When first laid they were light green, with a pearly luster. Shortly they changed to cream or light tan, with contrasting dots and irregular tortuous bands of dark pink to salmon-red.

The characteristic from is ovoid, with a flattened base and rounded tip, but some approach a barrel-shaped form with flattened base. Our illustration (figure 1 A to C) shows the extremes of this variation, and also the early and late changes in markings.

Sculpture of the surface consists of longitudinal ridges, from 28 to 36 in number, running from the edge of the flattened base to the top. These ridges have 'pearled' edges, the pearls or raised points corresponding to the numerous horizontal lines crossing between the ridges. The raised pearls are small and relatively inconspicuous.

On the flattened base the ridges end abruptly, and within the circle formed by their terminations the surface is covered by numerous irregular hexagonal pits with raised walls, as shown in figure 1B.

There is considerable variation in the size of eggs, the average being 1 mm. tall by 0.6 mm. wide. Eggs laid May 25 hatched June 3. The larval egress was through one end, the remainder of the shell being left intact.

By comparison with the egg of *Drepanulatrix monicaria* it is larger, the number of ridges greater, and the salmon-red markings heavier.

FIRST INSTAR LARVA: Length, 3.75 mm. Head width, 0.4 mm. The head is wider than the first segment. The ground color is white with a heavy spotting of black dots on a brown base each side of the epicranial suture and the outer and upper two-thirds of each cheek. There are two raised papillae on the front. The mouth parts are brown, and the ocelli black on a white ground.

The first thoracic segment is narrower than the head, but wider than the remaining segments. The ground color of all body segments is white. There is a longitudinal middorsal irregular band of olive which is somewhat restricted at the segmental junctures. A narrow irregular dorso-lateral band parallels it. There are several rows of black papillae running generally in a longitudinal direction. The placement of these on the dorsal surface is shown in the illustration, (figure 1D). Each papillus is surrounded at its base by a white circlet, and mounts a black seta at its tip.

The legs are hyaline, with a tinge of light yellow. The single pair of prolegs and the anal prolegs are concolorous with the body.

LARVA OF 15 MM. LENGTH: Head width, 1.5 mm. Head, gray, spotted with black, the spotting heaviest on the margin of the crown and cheeks. The front is slightly less spotted. The mandibles and ocelli are black.

The body ground color is gray. Most of the segments are crossed transversely by five or six folds, on which are placed prominent black papillae bearing black setae. The entire surface of the body is heavily sprinkled with minute black and brown dots. These have a slight tendency to form longitudinal lines. The spots on the ventral surface are predominantly brown and are more definitely arranged in longitudinal lines.

The prolegs are concolorous with the body, and the true legs are less spotted and more hyaline.

MATURE LARVA: Length, 26 mm. Head width, 2.2 mm. Head; color, gray-brown, heavily spotted with minute brown dots. The front is finely ridged horizontally, with a line of six minute black dots running transversely near the lower edge. The labrum is darker, and is ridged longitudinally. The maxillae are dark brown, the ocelli black, and the antennae translucent.

Across the center of each cheek is a lunate black band, beginning near the epicranial suture, extending laterally, then arching inferiorly to end near the ocelli. The setae are brown, and arise from black papillae. The head is shown in front view on figure 1E.

BODY: Ground color, whitish gray, nearly obscured by numerous small brown and black dots. There is a suggestion of a double middorsal longitudinal brown stripe in the thoracic area. A poorly defined dark spiracular band, made up of dots, is present on some specimens. The spiracles have narrow black rims and cream colored centers. The legs

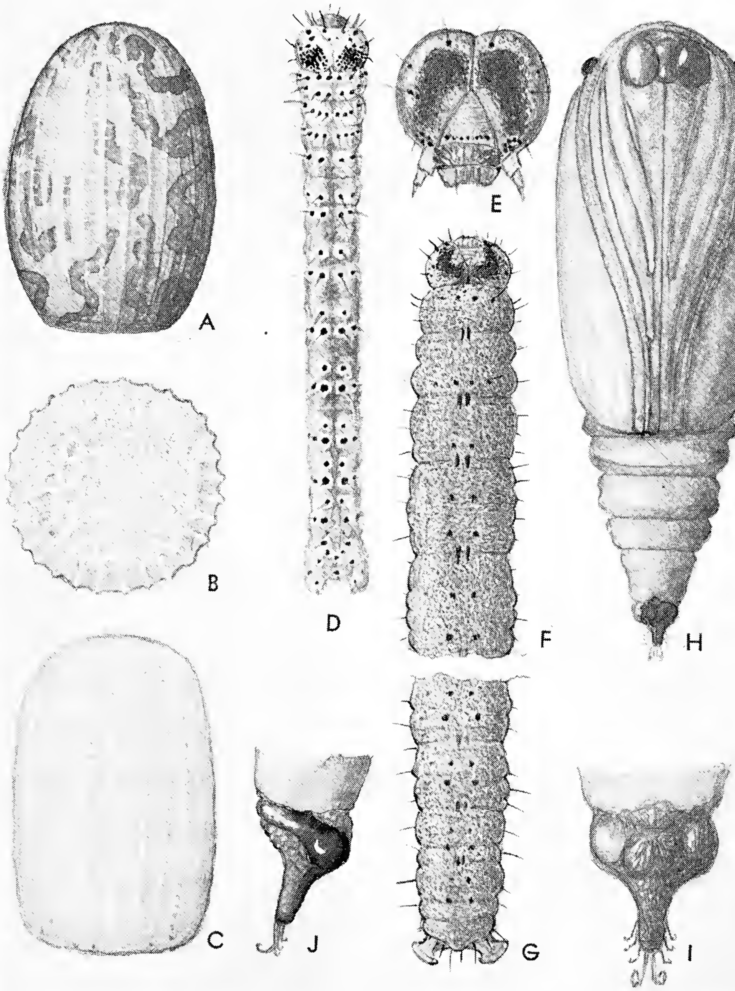

Figure 1

Early stages of *Drepanulatrix hulsti hulsti.* A. Egg, lateral aspect final color phase, enlarged X 40. B. Base of egg, enlarged X 40. C. Egg. elongate form, and early light phase, enlarged X 40. D. First instar larva, dorsal aspect, enlarged X 21. E. Head of mature larva, front view, enlarged X 10. F. and G. Mature larva, dorsal aspect, enlarged X 5.5. H. Pupa, ventral aspect, enlarged X 6. I and J. Cremaster, ventral and lateral aspects, enlarged X 14.

Reproduced from water color drawing by the author.

and prolegs are translucent, the latter being spotted with brown. The crochets are red-brown, apparently biordinal in alignment, and developed only along the lateral edge of the oval foot-pad, with short stubs only on the medial edge. The setae are light brown, relatively short, and arise from minute black papillae. (figure 1 F and 1 G).

Pupation occurred on the floor of the rearing jar, among leaves and debris, mixed with a few strands of silk.

PUPA: Length, 14 mm. Greatest width, through middle of wing cases, 4.2 mm.

The anterior two-thirds of the pupa is relatively wide and plump. The six terminal segments taper sharply to a distinctive cremaster, as will be noted on figure 1 H. An enlargement of the latter is pictured on figure 1 I.

The eyes are prominent, dark, and protruding. The cephalic end is evenly rounded. The antennae and maxillae extend to the margins of the wing cases. The spiracles are relatively small and nearly indistinguishable without a lens. There are no setae.

The color of the pupa is predominantly reddish brown, but the eyes and cremaster are black.

The cremaster is pear-shaped, with the stem end narrowed and elongated. Laterally it bears two globular bodies, one on each side, when viewed in ventral aspect. Portions of the surface are nodular. The tip bears several short spicules which arch dorsally. Two of these are longer, and recurve ventrally. These details can best be grasped by referring to the illustration on figure 1H.

The texture of the body surface of the pupa is predominantly smooth and glistening.

BIBLIOGRAPHY

BARNES, WILLIAM and J. McDUNNOUGH.,1917. *Contributions to the Lepidoptera.* 3 (4): Pl. 28, Figs. 5-6.

DYAR, HARRISON G. 1904. A few notes on the Hulst collection. *Proc. Ent. Soc. Wash.* 6: 226.

GROSSBECK, J. A. 1912. *Jour. N. Y. Ent. Soc.* 20: 285.

RINDGE, FREDERICK H. 1949. A revision of the Geometrid moths formerly assigned to Drepanulatrix. *Bull. Am. Mus. Nat. Hist.* 94 (5): 233-298.

SPERRY, JOHN L. 1948. Three apparently undescribed Geometrid moths from the southwest. *Bull. So. Calif. Acad. Sci.* 47 (1): 6-7.

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THE EFFECTIVENESS OF DIFFERENT ISOTHIOCYANATES ON ATTRACTING LARVAE OF PIERIS RAPAE

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THE EFFECTIVENESS OF BLACK MUSTARD OIL (allyl-isothiocyanate) on attracting larvae of *Pieris rapae* at various concentrations has already been described in this JOURNAL (Hovanitz and Chang, 1963). This mustard oil is the commonly used oil for condiments and is prepared by pressing from the seeds of black mustard (*Brassica nigra*). This oil is known also from various species of Cruciferous plants in addition to black mustard. Other mustard oils are known from a wide variety of plants, not all of them members of the family Cruciferae. This paper describes some experiments on the selection by *Pieris rapae* larvae on allyl-isothiocyanate produced by two different methods, and on three other isothiocyanates.

NATURALLY OCCURRING ISOTHIOCYANATES

Isothiocyanates (mustard oils) are naturally derived from glucosides which occur in a wide variety of the higher plants, belonging to a relatively small number of plant families (Kjaer, 1960). These glucosides are characterized by the ability to undergo enzymatic hydrolysis to isothiocyanates, hyrogen sulfate and D-glucose. The latter has invariably been encountered as the sugar moiety of the more than thirty individual compounds recorded thus far (Kjaer, 1960). According to this author, only nine glucosides of these thirty isothiocyanates have as yet been crystallized. The occurrence of more than one glucoside in a given plant species is most common; as many as eight individual glucosides have been distinguished in a single seed specimen. The compounds appear to be distributed over the entire plant; the glucosides are diffusely present in parenchymal tissues, especially in

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[1] *Aided by a grant from the National Science Foundation, Washington, D. C.*

the bark (Guignard, 1890, 1893). The embryo constitutes the site of accumulation in seeds. Little has been done to relate the variation in glucoside content as a function of the stage of growth, or of environmental factors such as climate, soil, etc. Stahmann, et al (1943) found that 2-phenylethylisothiocyanate, the aglucone of gluconosturtiin, to be the predominant mustard oil enzymatically liberated from the roots of *Brassica nigra,* whereas the seeds of this plant represent the classical source of the glucoside sinigrin which yields allyl isothiocyanate upon enzymatic fission. Delaveau (1958) has noticed considerable variation in the total and relative amounts of the individual glucosides in the plant *Alliaria officinalis* during its growth cycle. Considerable variation has been detected in quantitative and qualitative differences in glucoside content of various parts of a plant as well as in different lots of the same plant tissue.

A list of the known natural isothiocyanates and their parent glucosides in various plant genera and species which are known to be hosts of species of *Pieris* is given in table 1. In this table the plants are listed by families and genera. After each genus or species of plants is listed (1) the *Pieris* known to feed on it, (2) the mustard oil glucoside which has been isolated, or established as having been found, in that plant, (3) the aglycones (the mustard oils corresponding to the glucoside) and (4) the group of compounds to which it belongs.

Observation of this list does not seem to indicate any common denominator between the mustard oil, or glucoside, and the species of *Pieris* which is attracted to it, with a single exception. That is, sinigrin is present in most plants attracted by one or more species of *Pieris.* This, in itself, may mean little for sinigrin appears to be the most common mustard oil glucoside, and the earliest known. There are *Pieris* attracted by plants in which sinigrin is not known, for example, (1) *Lepidium,* which is a common food plant of *Pieris protodice* and *P. occidentalis,* (2) *Cleome* (and probably *Isomeris*), which is a common food plant of *P. protodice,* and *P. beckeri,* (3) *Tropaeolum,* a food plant of *Pieris rapae,* and (4) various *Resedaceae,* food plants of *Pieris daplidice.* In each of these plants indicated, there are some other mustard oil glucosides present, namely, glucotropaeolin and glucoraphanin for *Lepidium,* glucotropaeolin for *Tropaeolum,* gluconasturiin, glucobarbarian, and glucotropaeolin for the Resedaceae, and glucocapparin for *Cleome* (or *Isomeris,* Capparidaceae).

It seems likely that more than one mustard oil attracts *Pieris,* even of the same species. The possibility exists that there may be little specificity for the kind of mustard oil, so long as some one isothiocyanate is present in the proper concentration. Except for *Tropaeolum,* all listed food plants of *Pieris rapae* contain sinigrin in some part of the plant. Only glucotropaeolin is known from *Tropaeolum* itself, yet *Pieris rapae* survives on that plant after only a few generations of adaptation.

TESTS OF LARVAE OF PIERIS RAPAE TOWARD VARIOUS ISOTHIOCYANATES

The tests to be described here were made by subjecting larvae of *Pieris rapae* from our laboratory strain, grown for several generations on black mustard (*Brassica nigra*), to our testing device. This device has been described previously (Hovanitz and Chang, 1963). It consists essentially of a greenhouse flat, with filter paper moistened with dilutions of mustard oils, and spaced equally around the periphery of the flat. The larvae are set in the center and make their way to the side of the flat, being attracted to one or another of the mustard oils, at various concentrations.

For this experiment, tests were made of five different mustard oils in concentrations from 10^{-5} to 10^{-9}. These five were:

(1) benzyl-isothiocyanate: this is the aglycone of glucotropaeolin, found in Cruciferae: *Lepidium* sp., *Resedaceae,* and Tropaeolaceae: *Tropaeolum* sp. Synthetic origin.

(2) phenyl-isothiocyanate: there is no natural aglycone of this mustard oil listed by Kjaer. Synthetic origin.

(3) phenethyl-isothiocyanate: this is the aglycone of gluconasturtiin, found in *Barbarea, Brassica nigra. Brassica oleracea* and the *Resedaceae.* Synthetic origin.

(4) allyl-isothiocyanate: this is the algycone of sinigrin found in many plants. Commercial synthetic.

(5) same as above, only commercial natural product from *Brassica nigra* seeds.

Sources of the above mentioned mustard oils are described below.

General Procedure for the Preparation of Synthetic Mustard Oils

The following general procedure for the preparation of mustard oils from various amines was provided by Professor Henry Klostergaard of the San Fernando Valley State College. This method was used for the preparation of the phenethyl-, benzyl-, and methyl-isothiocyanates used in this paper. All procedures to be carried out at 0°C.

In a 2000 ml. Erlynmeyer flask, mix 0.07878 moles of the amine and enough absolute ethyl alcohol to make a 30% solution (by volume). To the above solution add 4.8 ml. CS_2 solution (0.03939 moles in a 1:1 solution with absolute alcohol). Wait 10 to 15 minutes, stirring often as there will be some heat evolved. Now add 100 ml. of the iodine solution (0.03939 moles or 10 gms. of iodine dissolved in 100 ml. absolute alcohol). The solution will start to clear up. Disregard any crystalliztion at this point. Shake until the brown color is gone and some yellow color appears. This is not stable so immediately go on to the next step. At this point add 25 ml. of the sodium solution (0.03939 moles or 0.9 gms. of sodium in 25 ml. absolute alcohol). The mixture will split and become homogeneous.

Now add another 100 ml. of the iodine solution as above. Some elementary sulfur will settle out (this is not soluble in ether). Now add 250 ml. acidifed water (1% HCL).

Next pour the solution into a separatory funnel and extract the mustard oil with ether. The mustard oil will appear in the ether phase or the top

TABLE 1. The occurrence of natural isothiocyanates and their parent glucosides in plant genera and species known to be hosts of species of Pieris (chemical data from Kjaer).

PLANT	INSECT	GLUCOSIDE	MUSTARD OIL	ISOTHIOCYANATE GROUP
CRUCIFERAE				
Alyssum	*Pieris rapae*	sinigrin	allyl isothiocyanate	unsaturated alkyl isothiocyanates
		glucoberteroin	5-Methylthiopentyl isothiocyanate	(λ)-Methylthioalkyl "
		glucoalyssin	5-Methylsulphinylpentyl isothiocyanate	"
		gluconapin	3-Butenyl isothiocyanate	unsaturated alkyl "
		glucobrassicanapin	4-Pentyl isothiocyanate	"
Arabis	*Pieris sisymbrii* *Euchloe* sp.	glucoarabin	9-Methylsulphinylnonyl isothiocyanate	(λ)-Methylthioalkyl "
		glucohirsutin	8-Methylsulphinyloctyl isothiocyanate	"
		glucocochlearin	(λ)-2-Butyl isothiocyanate	saturated alkyl isethiocyanates
		glucoputranjivin	isoPropyl isothiocyanate	"
		gluconapin	see above	
		sinigrin	see above	
Barbarea	*Pieris napi*	glucocapparin	Methyl isothiocyanate	"
		gluconasturtiin	2-Phenylethyl isothiocyanate	aromatic isothiocyanates
		glucobarbarin	2-Hydroxy-2-phenylethyl isothiocyanate	hydroxy-substituted "
		sinigrin	see above	
Brassica nigra	*P. rapae* *P. protodice* *P. occidentalis*	gluconasturtiin	see above	
		sinigrin	see above	
Brassica oleracea var. *capitata*	*P. rapae*	gluconasturtiin	see above	
Brassica oleracea vars.	*P. rapae*	glucorapiferum	2-Hydroxy-3-butenyl isothiocyanate	"

Brassica oleracea vars. cult.	*P. napi*	glucorapiferum	2-Hydroxy-3-butenyl isothyocyanate	
		gluconasturtiin	see above	
		glucobrassicanapin	see above	
		gluconapin	see above	
		sinigrin	see above	
		glucoiberin	3-Methylsulphinylpropyl isothiocyanate	(ω)-Methylthioalkyl isothiocyanates
		glucocheirolin	3-Methylsulphonylpropyl isothiocyanate	"
		glucoibervirin	3-Methylthiopropyl isothiocyanate	"
Dentaria	*Pieris napi*	not specific		
Lepidium	*P. protodice*	glucotropaeolin	benzyl isothiocyanate	aromatic isothiocyanates
	P. occidentalis	glucoraphanin	4-Methylsulphinyl-butyl isothiocyanate	(ω)-Methylthioalkyl isothiocyanates
		glucolepidiin	ethyl isothiocyanate	saturated alkyl isothiocyanate
		sinalbin	p-Hydroxybenzyl isothiocyanate	aromatic isothiocyanates
Raphanus	*P. rapae*	glucoraphanin	see above	
		sinigrin	see above	
Sisymbrium	*P. protodice*	glucoputranjivin	isopropyl isothiocyanate	saturated alkyl isothiocyanate
	P. occidentalis	gluco sisymbrin	2-Hydroxy-isopropyl isothiocyanate	Hydroxy-substituted "
	P. beckeri	glucocochlearin	(+)-2-Butyl-isothiocyanate	
		sinigrin	see above	
CAPPARIDACEAE				
Cleome also probably *Isomeris*	*P. protodice* *P. beckeri*	glucocapparin	methyl isothiocyanate	saturated alkyl isothiocyanate
RESEDACEAE				
	P. daplidice	gluconasturtiin	see above	
		glucobarbarin	2-Hydroxy-2-phenylethyl isothiocyanate	Hydroxy-substituted isothiocyanate
		glucotropaeolin	see above	
TROPAEOLACEAE				
Tropaeolum	*P. rapae*	glucotropaeolin	benzyl isothiocyanate	aromatic isothiocyanates

layer. Discard the lower layer. Add some 10% NaOH to the mustard oil and ether solution to take off the iodine and then discard the lower layer. Next wash the solution with an equal volume of distilled water. Discard the water layer. Now there is present an ether solution of the mustard oil. (Ice this solution immedately.) Vacuum distil this solution in a flash evaporator with the solution in the flask cooled by an ice-salt solution and successive flasks cooled by ether and dry ice. Keep the mustard oil and ether solution under vacuum for at least 1½ hours. The mustard oil will be left in the original flask. Remove it immediately and store at 0°C.

Caution

All the solutions involved in this preparation should be kept refrigerated at 0°C. until used. All work should be done under an adequate hood since the chemicals involved are highly toxic and odoriferous.

Tests of the larvae of *Pieris rapae* as indicated were made separately, utilizing the five dilutions of the mustard oils indicated. The actual dilutions may actually have been less than indicated because it appears that at the temperature used (about 20°C.), not all the mustard oil may have gone into solution. Each larva was tested twenty times, giving total test times ranging from 180 times for benzl-isothiocyanate to 680 times for phenyl-isothiocyanate.

The allyl-isothiocyanates differed in their response, according to their origin. One was derived from black mustard seeds by standard commercial techniques of compression, and fermentation. The other was synthetically prepared. In each case, the larvae selected the 10^{-6} dilution of mustard oil (22.1% for synthetic to 21.2% for natural) but the dispersal of the selections was different. For example, the dilution of 10^{-5} was selected by the larvae for the synthetic mustard oil 20.7% of the time, as compared with only 11.6% for the natural product. Dilutions of less than 10^{-7} are also different. For example, while the synthetic gave selections of 19.3% at 10^{-8}, the natural product gave 14%. At 10^{-9}, these were 15.2% for the synthetic as compared with 11.6% for the natural. An apparently significantly greater number of larvae left the flat without any selection at all with the natural (24.2%) as compared with the synthetic product (2.5%). This discrepancy was probably due to the human variation in carrying out the tests. The percentage is greater when the larvae are not allowed as long a selection period. This discrepancy would not affect the actual selections themselves.

Another effect is quite noticeable with these data, as well as with the data on the other mustard oils, namely, that the selections give a bimodal curve (see fig. 1). Such a bimodal curve was not clear with our previous testing though a trace of it might be detected (fig. 3, Hovanitz and Chang, 1963). The previous testing was made with the natural product which also shows a very poor bimodal curve (fig. 1). The synthetic product shows a more strongly indicated bimodality at 10^{-6} and at 10^{-8} (fig. 1). The reasons for the bimodal curve which is especially apparent for the synthetic allyl mustard oil are unknown.

Selections for benzyl-isothicoyanate are almost certainly negative,

TABLE 2. The selection by larvae of *Pieris rapae* for various concentrations of mustard oils.

	10^{-5}	10^{-6}	10^{-7}	10^{-8}	10^{-9}	distilled water	no selection	no. of larvae	total trials
Benzyl-isothio-cyanate	16 8.9%	15 8.3%	11 6.1%	15 8.3%	25 13.8%	17 9.4%	81 45%	9	180
Phenyl-isothio-cyanate	101 14.4%	127 18.7%	80 11.8%	118 17.4%	81 11.9%	83 12.2%	91 13.4%	34	680
Phenethyl-isothio-cyanate	60 15.0%	83 20.8%	48 13.5%	76 19%	65 18.8%	27 6.8%	25 6.3%	20	400
Allyl-isothio-cyanate (synthetic)	116 20.7%	124 22.1%	56 10.0%	108 19.3%	85 15.2%	57 10.2%	14 2.5%	28	560
Allyl-isothio-cyanate natural	58 11.6%	106 21.2%	54 10.8%	70 14%	58 11.6%	33 6.6%	121 24.2%	25	500

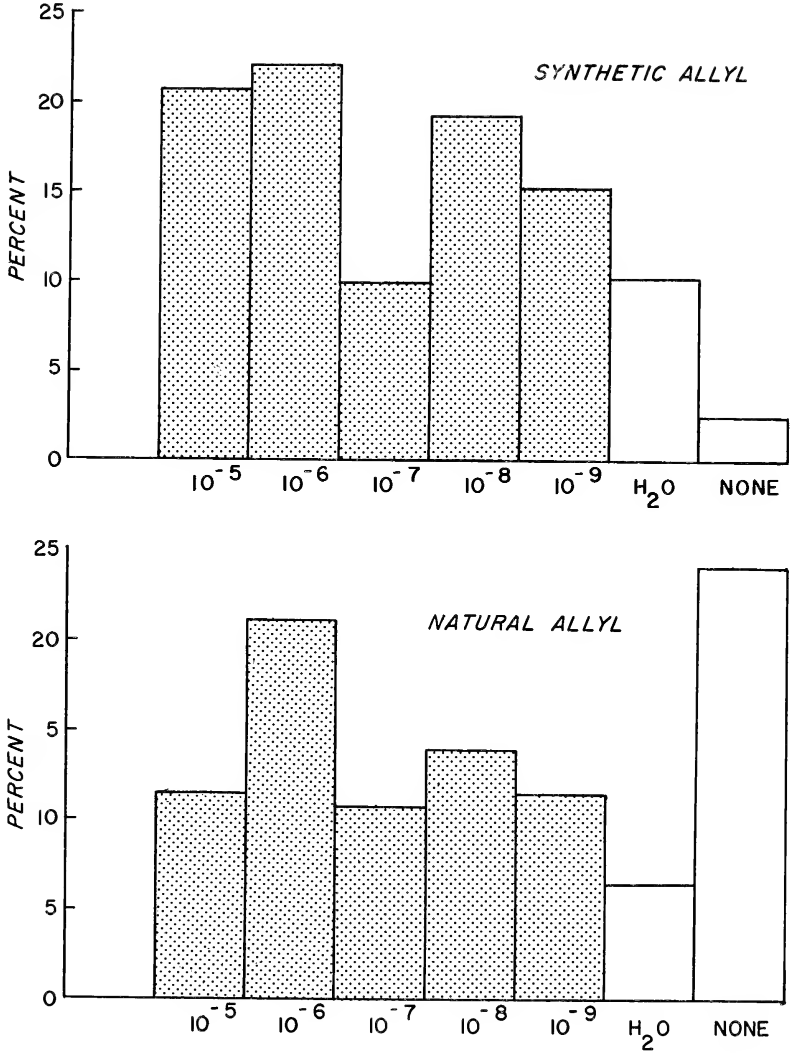

Fig. 1. Histograms illustrating the comparison between natural and snythetic mustard oils respecting their selection by larvae of *Pieris rapae*. Note the strong bimodality of the histogram showing the synthetic product as compared with the natural.

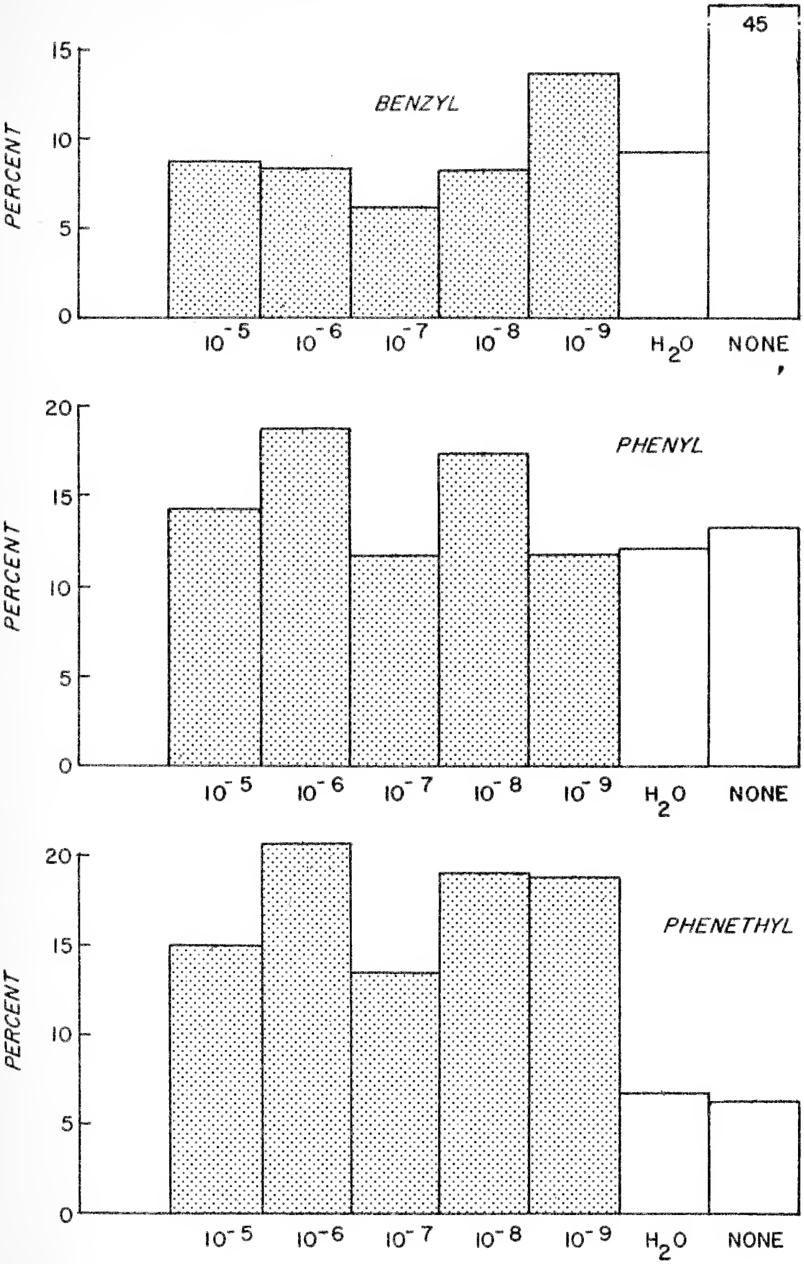

Fig. 2. Histograms illustrating the selections made by larvae of *Pieris rapae* for various dilutions of the mustard oils benzyl-isothiocyanate, phenyl-isothiocyanate and phenethyl-ioso-thiocyanate. Note the bimodality of two of the histograms and the nearly complete lack of selection indicated by the other.

not varying significantly from water alone (table 2 and fig. 2). This mustard oil also was the one in which dissolving in water appeared almost impossible and in which case the tests might very well have been conducted on water alone. Perhaps at a higher temperature, dissolving the mustard oil might have been accomplished but under the circumstances it does not seem as if this mustard oil could be of any influence on attracting *Pieris rapae* larvae to *Tropaeolum* species where it is found naturally.

Phenyl-isothiocyanate and phenethyl-isothiocyanate were about equally effective in attracting the larvae though there is a possibility that the phenyl mustard oil may be slightly less attractive than the phenethyl, since at each concentration the percent attraction was slightly less. However, the decrease possibly is not significant. The attraction of both of these mustard oils was not much different from that of allyl isothiocyanate (table 2 and fig. 2). This leads to the interesting possibility of the specificity between isothiocyanates in the generic sense and the Pieridae that are attracted to plants that contain the compounds. It is possible that the attraction is to the isothiocyanate part of the molecule and not to side chains. "When applied to the tongue, all mustard oils cause a sharp and burning sensation. Their odors, though mostly pungent, display characteristic individual differences which often are helpful in the detection and classification of mustard oils. Certain isothiocyanates, that undergo rapid intramolecular cyclization, give rise to a transient biting taste, followed by a sensation of bitterness. Like most synthetic mustard oils, those of natural origin show vesicant and frequently also lachrymatory properties," from Kjaer (1960). These same substances, however, when present in small concentration appear to give rise to the desirable condiment properties of the mustard oils and appear in turn account for the specificity of these oils to the larvae and adults of *Pieris.*

CONCLUSIONS AND SUMMARY

1. A list is given of the mustard oils which are known to occur in food plants of the Pieridae. These are derived from naturally-occurring glucosides which are also listed.

2. It seems evident from this list that more than one mustard oil attracts *Pieris,* since the evidence does not indicate that only one could be responsible.

3. Tests were made on the selection of larvae of *Pieris rapae* toward several mustard oils at various concentrations. These oils were either commercially obtained, or were synthetically compounded by us. The procedure used for synthetic compounding is described.

4. Synthetic and natural allyl mustard oils obtained commercially gave somewhat divergent testing results. The synthetic gave a bimodal curve with modes at 10^{-6} and 10^{-8} which were only slightly

or not at all apparent with the natural.

5. Other mustard oils tested were benzyl-isothiocyanate, phenyl-isothiocyanate and phenethyl-isothiocyanate.

6. Benzyl-isothicoyanate is the aglycone of glucotropaeolin, the glucoside of *Tropaeolum* sp. and some other plants. Its attraction power at the concentrations used is not different from that of distilled water. In view of the difficulties experienced in dissolving this substance, it is possible that none actually dissolved and that, therefore, the tests were actually on water alone.

7. Phenyl-isothiocyanate is not known to be natural occurring. Nevertheless, it had a selective effect on the larvae only slightly less effective than allyl- and phenethyl-isothiocyanates.

8. Phenethyl-isothiocyanate had an attractive power almost equivalent to that of the synthetic allyl-isothiocyanate. It is a naturally-occurring mustard oil, being the aglycone of gluconasturtiin which is found in *Nasturtium* and *Barbarea.*

9. It appears that more mustard oils than just allyl-isothiocyanate are attractive to *Pieris*. The experience with benzyl-isothiocyanate however indicates that not all are effective, at least not under the experimental conditions utilized.

LITERATURE CITED

DELAVEAU, P. 1958. Variations de la teneur en hétérosides à sénevol de l'*Alliaria officinalis* L. an coms de la végétation. *C. R. hebd. Séances Acad. Sci.*. 246: 1903.

GUIGNARD, L. 1890. Recherches sur la localisation des principes actifs des Crucifères. *J. Botanique* 4: 385.

———. 1893. Recherches sur la localisation des principes actifs chez les Capparidées, Tropéolées, Limnanthées, Résédacées. *J. Botanique* 7: 345.

HOVANITZ, W. and V. C. S. CHANG. 1963. Selection of allyl-isothiocyanate by larvae of *Pieris rapae* and the inheritance of this trait. *J. Res. Lepid.* 1(3): 169-182.

KJAER, ANDERS. 1960. Naturally derived isothiocyanates (mustard oils) and their parent glucosides. *Fortschritte d. Chem. org. Naturst.* 18: 122-176. Springer, Wien.

STAHMANN, M. A., K. P. LINK and P. C. WALKER, 1943. Mustard oils in crucifers and their relation to resistance to clubroot. *J. Agric. Res.* 67: 49.

Journal of Research on the Lepidoptera 1(4):261-274, 1963

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THE ORIGIN OF A SYMPATRIC SPECIES IN COLIAS THROUGH THE AID OF NATURAL HYBRIDIZATION

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I. INTRODUCTION

THE THEORETICAL SET UP for the origin of a new species in any biological group is the existence of two or more species in the same geographical area, which mix and reassort their combined gene combinations by the process of hybridization, F_1 intercrossing and back-crossing. There have been examples described in recent years in which crossing of this sort has served to blend together two existing species in a given area in such a way that both parental species cease existence as independent entities; this situation has been described generally as "subspecific intergradation" because of necessity the blending must be done on a geographical, or spatial, scale. Recent examples of this have been described by Sette (1962) involving the subspecies *macaria* and *laurina* of *Argynnis callippe,* and others by Hovanitz (1949).

In those cases in which natural hybridization of the two species has served only to permit gene (and character) interchange between the two original species, both of which maintain themselves as independent entities, but in which no new species is formed, the situation is described as one of introgressive hybridization. One of the most extensive cases of introgressive hybridization known is that existing between the species *Colias eurytheme* and *Colias philodice* (Hovanitz, 1943, 1944a, 1944b and 1948). Other cases which are less extensive are known in many other species of Colias.

Much more rare, possibly because the occurrence may be transient, is the situation in which two hybridizing species retain their separate existence, but out of the assorted gene pool arising by hybridization, there come a third species which maintains itself as a separate entity without the further necessity of hybridization. This is the situation to be analyzed in this paper.

It is almost axiomatic that *for closely related and interfertile species to exist in the same general area, and yet to maintain their separate identities, those two or more species must be separated in some way*

Fig. 1. North polar projection map showing the world distribution of *Colias hecla.*

by physiological or ecological isolation barriers for if this were not so, the genes of the two or more species would be blended together as in one gigantic melting pot. The isolation barriers for Colias appear to be such physiological and ecological ones rather than genetic ones since most species appear to be interfertile. Tied with these barriers is the selection for genes controlling adaptation for different habitats and different food plants of the larvae, which enable Colias to exist under a greater variety of conditions than would be possible were they all amalgamated into one species in a given geographical area.

Previous study has indicated that there is considerable natural hybridization in the genus Colias (Hovanitz, 1949, 1956). The species *Colias philodice* and *Colias eurytheme* have been shown to hybridize rather freely throughout all parts of their ranges where they are in

Fig. 2. North polar projection map showing the world distribution of *Colias nastes.*

contact, or where there is overlap of their habitats (Hovanitz, 1944a, 1944b). This is a classical example of *introgression, the reciprocal transfer of genes between two or more species in natural contact, but without the complete submergence of the identity of any.* Similar examples of natural hybridization have been described for the following species combinations of Colias:

Colias interior - C. christina
Colias hyale - C. erate - C. croceus
Colias christina - C. gigantea
Colias philodice - C. eurytheme
Colias hecla - C. nastes
Colias interior - C. philodice
Colias alexandra - C. philodice
Colias christina - C. philodice

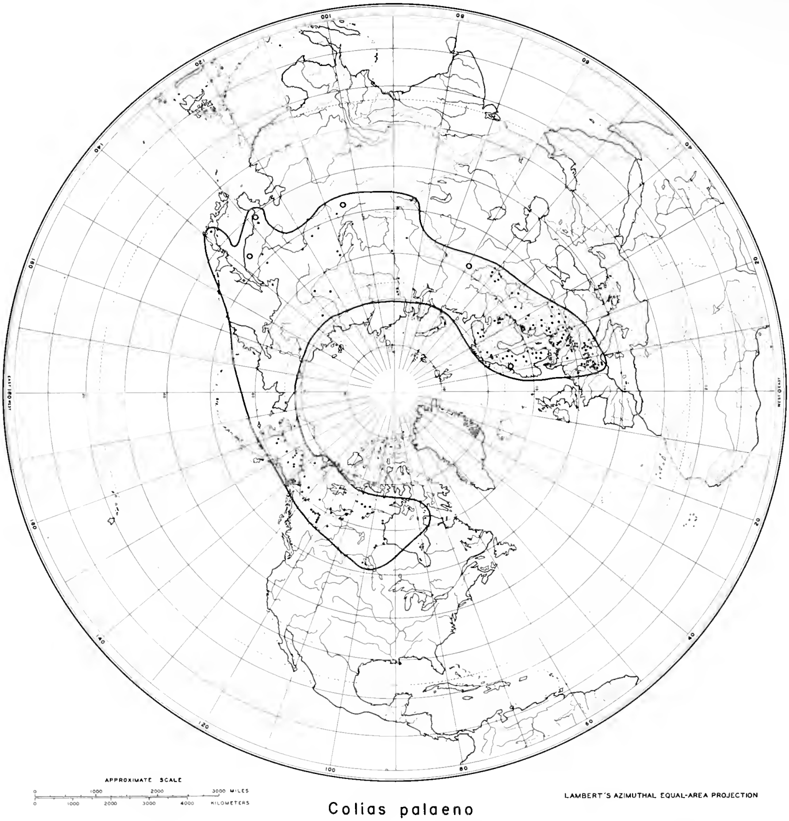

Fig. 3. North polar projection map showing the world distribution of *Colias palaeno.*

Without doubt a great number of additional combinations will be found, wherever any two or more of the species of this genus occur together. Species hybridization in the laboratory, or in the field, leadnig only to F_1 generation individuals, with no history of fertile backcrossing or of fertile F_2 production, would have no effect on altering the composition of natural populations. Such crosses therefore are only indicative of physical ability to mate, of F_1 to survive (though not of F_1 fertility), and to indicate something of the nature of genetic dominance of the many characters involved in the cross; however, they give no information at all on the evolutionary relationships between the parental species. Further testing must be done for this purpose by carrying the crosses through to the F_2 generation and backcross generations, and by study of the genetics of the natural populations themselves.

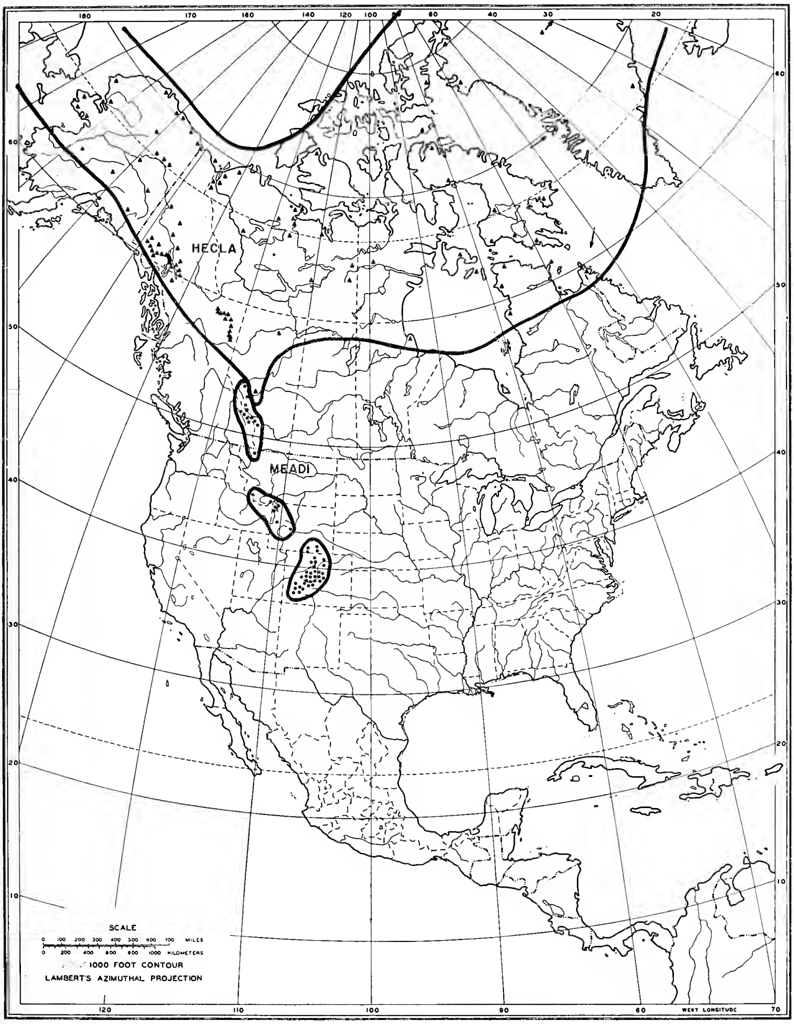

Fig. 4. Distribution of *Colias hecla* in North America, together with that of *Colias meadi.* The ranges of these two species do not overlap but are separated at their closest point by an altitudinal difference of 4000 feet. *Colias hecla* is found in the mountains and plains of the north and *Colias meadi* only in the mountains of the south.

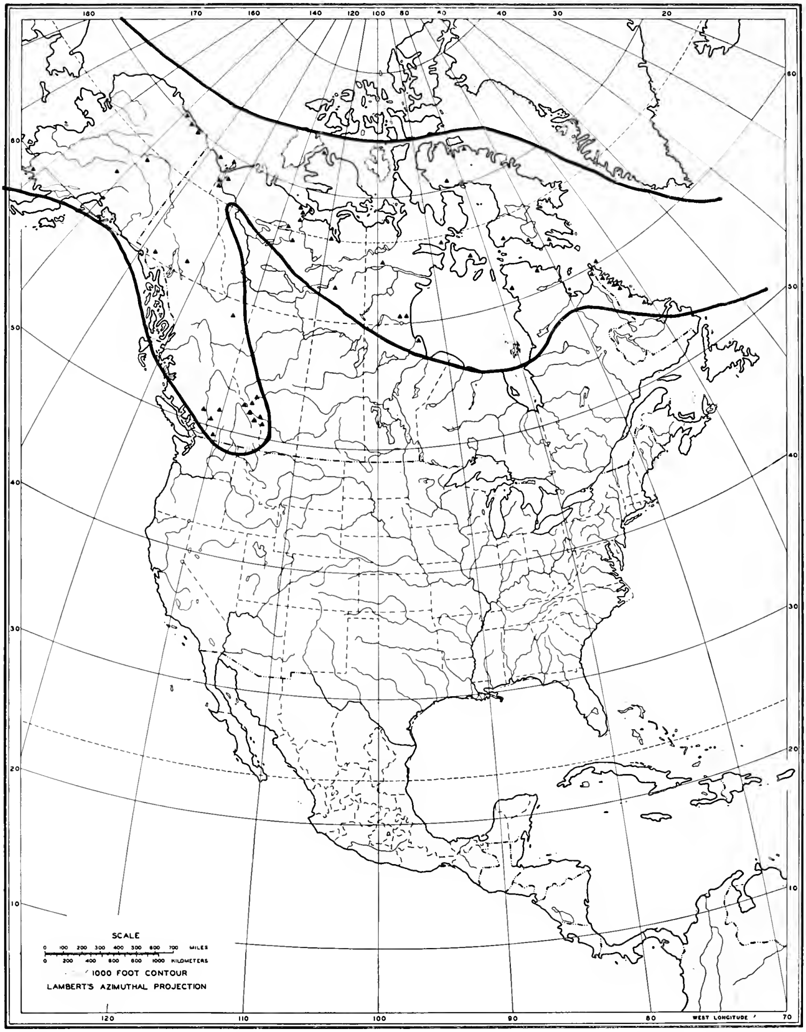

Fig. 5. Distribution of *Colias nastes* in North America. The species is found only in areas north of the tree line throughout the eastern and central parts of its range but occurs also far to the south in the western region of the Rocky Mountains in the alpine tundra.

It has been shown that *Colias hecla* and *Colias nastes* give all indications of hybridizing in the wild. These indications are as extensive as those which are known for *Colias eurytheme* and *Colias philodice* hybridizations, with the exception of a lack of the actual breeding experiments. In other words, the information is available by an analysis of wild populations, and character intergradation within the populations. It has been conjectured, in other publications, that these two species have hybridized in a certain area, namely the Canadian eastern arctic, in such a way and to such an extent, that a third species, *Colias boothi,* has originated as a result of such hybridization (Hovanitz, 1949). In the areas concerned, both parental species and the "intermediate" newly originated species all survive without the complete submergence of either parental species, or of the new species. The evidence indicates that on the fringes of the distributional area occupied by the "new species," intermediates are present in a way suggesting introgression only, rather than the independent existence of the new species. This "origin of a new species by hybridization" has been of theoretical significance in problems of evolution for many years; the present example is the first clear authenticated case of this type of origin which can be observed in action.

II. GEOGRAPHICAL RELATIONSHIPS BETWEEN *COLIAS HECLA, COLIAS NASTES* AND *COLIAS PALAENO*

The three most "northern" Colias in the world are *Colias hecla, Colias nastes* and *Colias palaeno,* the most northern of these three being first and *palaeno* being least northern. Although only the first two appear to be involved in the natural hybridization relationship, the third is considered here because of its frequent sympatric geographical distribution.

The world distributional ranges of these three species are shown in figures 1, 2, and 3. The North American ranges are shown in more detail in figures 4, 5 and 6. The latter three maps have been published previously (Hovanitz, 1951).

Colias hecla is distributed from northern Norway and Sweden across the arctic shores of Asia (fig. 1), across the Bering straits, across Alaska and northern Canada, throughout the Canadian arctic islands and around all coasts of Greenland. Southern extensions of range occur in several places around this circumpolar range. In Scandinavia, the species extends part way down the Sandinavian peninsula, but it does not appear in more southern European locations. In Asia, besides the coastal arctic locations, the species exists inland in the Verkhoyansk area and along the Lena river valley. Farther southwards, there is much material indicating the possibility of its existence in almost all ranges of central Asia including all the area from Hindukusch, Pamir and Karakorum across the Himalaya to Ladakh and mountains east and north. The ranges extending north and eastward from the Pamir to the Baikal and Transbaikal completes a circle of mountains around the Gobi desert where some form of *Colias hecla* appears to live. Dots marking the exact locations for this area on the map were omitted because of the difficulty in every case to be certain of the identifications between the *hecla* group of forms and a group related to *Colias meadi* of the mountains of North America. Both of these groups appear to be in the same areas of central Asia, though they are separated in North America into contiguous regions.

In North America, *Colias hecla* is found in Alaska in all areas except the parts southern and coastal of the main southern mountain masses. This includes the mountains and valleys of the interior, and the western and northern coastal plains. In the Rocky Mountains, the species is found as far south as the present location of the Alaska highway from Whitehorse to Ft. Nelson but there are no locations known south of this point in the mountains area. The species then extends southwards on the Rocky mountain piedmont and the valley of the tributaries of the Mackenzie River as far south as Nordegg (just west and south of Edmonton, Alberta). The range skirts the prairie country of central Canada near Lake Athabaska, eastward to Fort Churchill on the Hudson Bay. The species is found on the most northern part of the Ungava peninsula and the upper tip of Labrador, but not along the Labrador coast. The map (fig. 4) in addition to showing the distributional range of *C. hecla* also shows the range of *C. meadi,* the relationship of which to *C. hecla* is uncertain despite its close phenotypic appearance.

Colias nastes has a distributional range only slightly more "southern" than that of *Colias hecla.* Actually, the ecological requirements of *C. nastes,* besides a temperature generally below 50°F., are somewhat different from that for *C hecla* as will be seen later. Unlike *C. hecla, Colias nastes* does not exist on any part of Greenland or the most northern of the Canadian arctic islands. Thus, on its circumpolar range, there is a break of great proportions across the Atlantic which does not appear on the map for *C. hecla. Colias nastes* is found in Scandinava in the same general locations as *Colias hecla,* extending part way down the mountain range. From there, it extends across the European and the Asiatic coastal sections (presumably) across the Bering straits to Alaska, along the north coast of Alaska and Canada to Victoria Island and Baffin Island but not to the islands to the north. In the islands north of Europe and Asia, *C, nastes* is known in Novaya Zemlya and has been listed as having been taken in Spitzbergen. Southwards, the species as such is not known in Europe, unless *Colias phicomone* of the Alps and the Pyrenees should be considered the same species. There seems little reason for not so considering it, in view of the fact that they are so similar in most respects. However, if they were connected in their distributional range at some earlier time, as

Fig. 6. Distribution of the *Vaccinium*-feeding *Colias* of North America. These include *Colias palaeno* of the mountains and plains of the northwest, *Colias interior* of the plains in the southern part of the range as well as the Cascade and Appalachian Mountains, *Colias pelidne* of the eastern arctic and the northern Rocky Mountains, and *Colias behri* of the alpine regions of the Sierra Nevada.

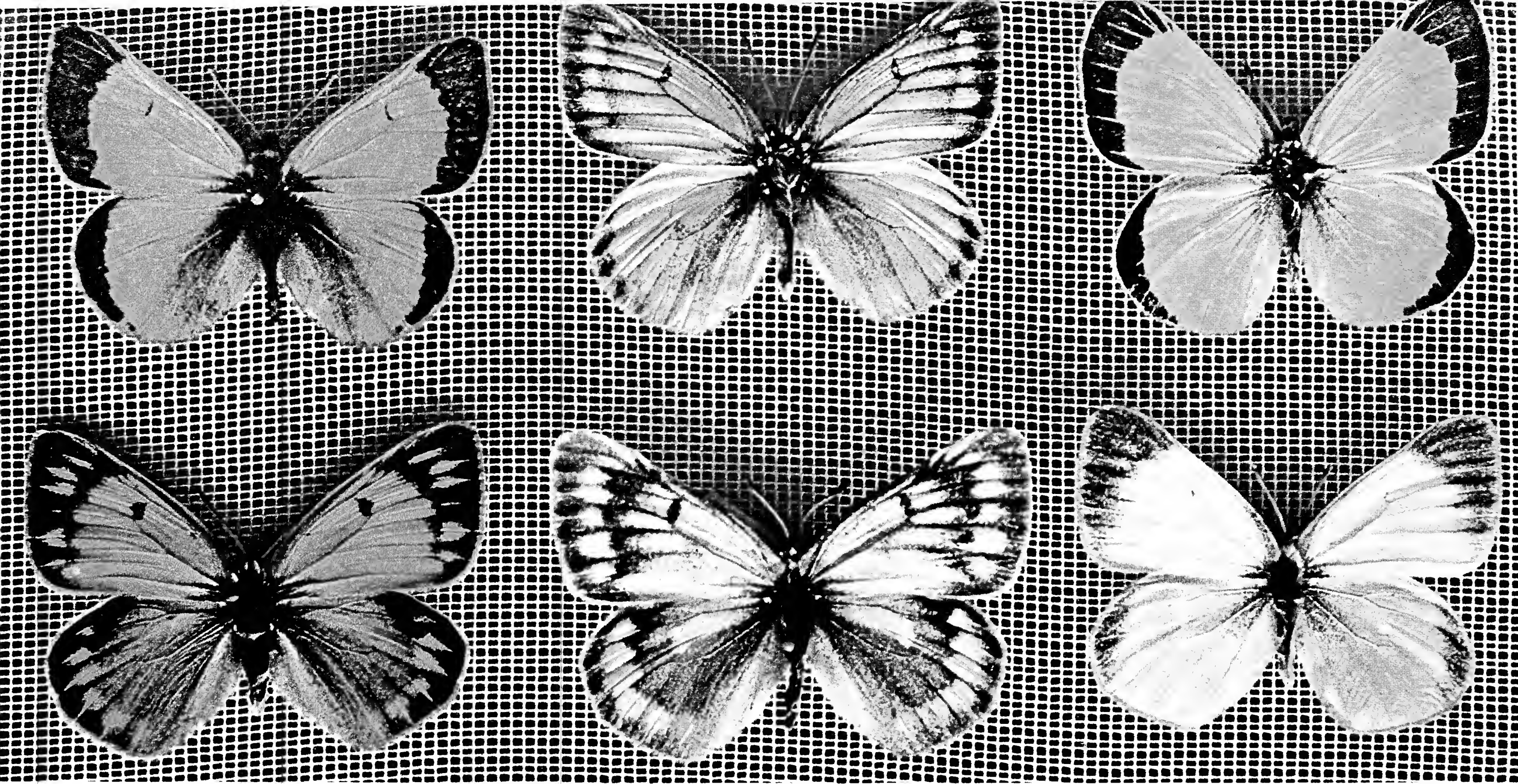

Fig. 7. LEFT: *Colias hecla* ♂ and ♀. Jebrentjakko, near Abisko, Sweden [Lapland], elev. 7-900 m. July 25-26, 1952. B. and W. Hovanitz.

CENTER: *Colias nastes* ♂. same as above hecla only July 17, 1952. ♀. Karsavaggejakk creek, near Abisko, Sweden [Lapland], 900 m. elev. July 29, 1952. B. and W. Hovanitz.

RIGHT: *Colias palaeno* ♂. Mile 691, Alaska Highway, near Rancheria, Yukon Territory. July 2, 1948. W. Hovanitz. *Colias palaeno* ♀. Alaska highway, 10 miles. South Burwash landing, Yukon Territory. July 1, 1948. W. Hovanitz.

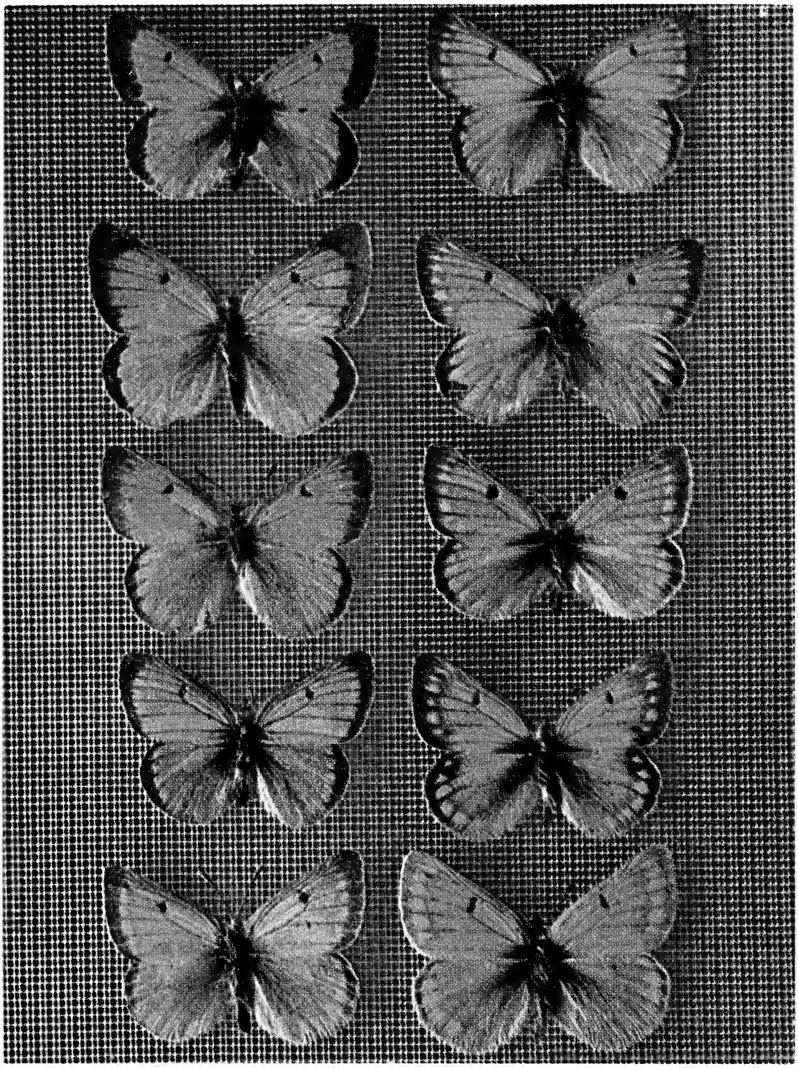

Fig. 8. Series of Colias, mostly identifiable as *Colias boothi,* showing by means of a graded series, nine steps in the border pattern transformation from the male (or *hecla*) pattern at the top left to the female (or *nastes*) pattern at the second to the bottom right. Grades are designated as 8 through 4 on the left column and 3 through 0 on the right column. The specimen on the bottom right does not enter the series but is shown to illustrate a weak pattern development on a grade 0 male. All specimens shown are males and all are from Coppermine, Northwest Territories, Canada, July 12-19, 1947, W. Hovanitz coll. except: (1) 2rd from top on right column: Repulse Bay, Northwest Territories, Canada. July 21, 1950. P. F. Bruggemann. (2) 5th from top (last one) in right column, Repulse Bay, July 15, 1950. P. F. Bruggemann.

during the Pleistocene ice age, many thousands of years of isolation since that time has brought differences between them and earned a species distinction. Southward in central Asia in the ring of mountains surrounding the Gobi desert, including the Himalayas there is a string of races all of which appear to be specifically related to *C. nastes;* the main form here is known as *C. cocandica.* The map for *C. nastes* therefore has quite a similarity to the map of *C. hecla.* It can be seen however that in the area of Asia west of Sakhalien Island, *C. nastes* occurs considerably south of the area of *C. hecla.*

In North America, *Colias nastes* occurs also farther south than *C. hecla.* The species extends southwards in the Rocky mountains from the mountains of Alaska and the Yukon Territory to the borders of the United States in British Columbia and Alberta. In Alberta, *C. nastes* occurs at an elevation of 7500 feet and up while *C. hecla* is found at about 3-4000 feet in the piedmont. In these areas, *C. nastes* is flying in late July and August while *C. hecla* at the lower elevations is flying in May. *C. nastes* does not extend into the lowland valley areas of the Mackenzie tributaries as does *C. hecla* but instead is found only to the north of the tree line from the mouth of the Mackenzie to the area of Ft. Churchill on the Hudson Bay. It is found on the Belcher islands in Hudson Bay. It is found in the northern part of the Ungava Peninsula and then southeastwards along the Labrador coast half way down. The fost northerly known locality is on the northern coast of Baffin island. These locations may be observed in relation to one another on the map (fig. 5).

Though *Colias palaeno* is not involved in the specific study here being analyzed, it was thought that it might be so involved and therefore, its geographical distribution is here given together with the two preceding species. This species has a generally more southern distributional range than either *Colias hecla* or *Colias nastes* as can be seen by study of the world map (fig. 3). The species is found in the Alps of Europe, in a number of locations in the territory intervening between the Alps and the Scandinavian mountains, and northwards and eastwards. It does not exist far south of Lake Baikal in central Asia but does extend southwards into Northern Korea, on the island of Hondo in Japan, Sakhalien Island, and Kamtchatka Peninsula. The species is not known on the islands north of Europe and Asia. In North America, the species is known in Alaska south of the Brooks range and north of the main southern ranges which skirt the coast. It reaches the coast of Northern America only at the mouth of the Mackenzie river but extends southwards along the route of the Alaska highway to a point just north of Ft. St. John and thence eastwards to the Riding Mountains of Manitoba and northwards to the tip of the Ungava Peninsula. Its range is limited southwards and eastwards by contact with *Colias pelidne* (also called *interior*). For details on this contact zone, the map of North America is more precise (fig. 6).

III. CHARACTERISTIC DIFFERENCES BETWEEN *COLIAS HECLA, COLIAS NASTES* AND *COLIAS PALAENO*

Colias hecla may be distinguished readily from *Colias nastes* by the fact that it is always orange in wing color (fig. 7), while *Colias nastes* is pale yellow. *Colias palaeno* is more generally a brighter lemon yellow (fig. 7).

A second character that separates *hecla* from *nastes* but not from *palaeno* is a male-female dimorphism of the pattern. The male pattern is a single solid band of black on the outer edges of the fore and hind wings. This appears on the wings of the males of both *hecla* and *palaeno* (fig. 7). The female pattern on the other hand differes from this in a way that might be described as a series of dots in the border band, or in what might be the band when it is all present. This is typically shown for the females of *hecla* and *nastes* on figure 7. The band of the female of *Colias palaeno* is so reduced that the dots show only slightly in that species. The male of *Colias nastes* differs from any other North American species of Colias in that it also shows a series of dots in the border band, much like the female. In some cases, it is very difficult to distinguish the males from the females by general appearances.

Other differences in habit, larval food plant and ecological preferences will be discussed later in this series.

Intergradation between *Colias nastes* and *Colias hecla* as would be caused by hybridization, the crossing of F_1 to obtain the F_2 segregation and backcrossing should give a series of intermediate products with all intergradations from the one parental type to the other. In addition there should be produced, if the genetic segregation truly assorts itself with slight effects of genetic linkage, into truly divergent types such as a fully orange male with the female border band, a type found nowhere under natural conditions in the ordinary range of the species. Another type of extreme divergence which would be found only under such conditions of gene assortment would be a yellow form with the typically male border pattern. All these types have been found in areas of presumed hybridization of these two species, *Colias hecla* and *Colias nastes.* A series of variations ranging from the male border band to the female border band in a series of nine steps (grades) is shown in figure 8. A similar graded series of nine steps for the orange pigment on the upper side of the wings is shown in figure 9. These series are to be used to illustrate the analysis of various populations of Colias from diverse regions in the arctic.

LITERATURE CITED (I, II, III)

HOVANITZ, WILLIAM. 1943. Hybridization and seasonal segregation in two races of a butterfly occurring together in two localities. *Biol. Bull.* 85: 44-51.

——— 1944a. The ecological significance of the color phases of *Colias chrysotheme* in North America. *Ecology* 25: 45-60.

——— 1944b. Genetic data on the two races of *Colias chrysotheme* in North America and on a white form occurring in each. *Genetics* 29: 1-30.

——— 1948. Ecological segregation of interfertile species of Colias. *Ecology* 29: 461-469.

——— 1949. Increased variability in populations following natural hybridization. In *"Genetics, Paleontology and Evolution,"* Princeton University Press, pp. 339-355.

——— 1951. The biology of Colias butterflies. I. The distribution of the North American species. *Wasmann J. Biol.* 8: 49.75.

——— 1956. Hybridization and species blending in the butterfly genus Colias. *Proc. XIV Int. Congr. Zool. Copenhagen,* 1953, p. 140.

SETTE, O. E. 1962. Variation in the silvering of *Argynnis* (*Speyeria*) *callippe* in the interior mountain area of southcentral California. *J. Res. Lepid.* 1(1): 3-20.

(to be continued)

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A METHOD FOR BREEDING PIERIS NAPI AND PIERIS BRYONIAE

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SINCE THE YEAR 1942 the author has bred *Pieris napi* L. and *Pieris bryoniae* Ochs. over a number of years. This breeding was carried out mainly in order to obtain information on the genetical, ecological, and taxonomical relationships between the two forms (cf. Petersen 1963, in press, and literature cited there). This paper will deal with the breeding methods used and some results obtained in this connection.

MATING

For copulation males and females were put together in cylindrical cages made of cotton net with a bottom of treetex. The cages were 2-4 dm high and had a diameter of 2-3 dm. In such a cage 2-4 females and a slightly larger number of males were placed. The cages were hung up in a window facing towards the south. Quite soon it was obvious that mating propensity was higher for *napi* in sunshine and for *bryoniae* in cloudy weather (cf. table 1). Mating propensity means in this case the frequency of mating of one sex compared with the same sex of the other species. The difference is statistically significant ($\chi^2 = 16.37$ with Yates' correction; $P < 0.001$). Müller and Kautz (1938 p. 15) state that sunshine is essential for the copulation of *bryoniae.* In nature *bryoniae,* like *napi,* copulates in sunshine. The experiments indicate only different ecological amplitudes for the copulation of the two species.

Matings under laboratory conditions were fairly easily obtained, not only by the author in Sweden, but also by Bowden and Easton in England (Bowden 1953, 1956, 1957, Bowden and Easton 1955). Entomologists in Central Europe, on the other hand, have had a number of difficulties in obtaining such matings. Some few experiments on hybridization have been reported by Fischer (1924, 1925) and Kautz (Müller and Kautz 1938 p. 159-161). The lack of success in many of the Central European experiments may be due to too high temperature during sunshine in Central Europe. The temperature in the windows used by the author, when the experiments were made in April and May, was usually about 24°-27°C. In the sunshine of Central European laboratories the temperature probably is higher, especially as the experiments usually are carried out during the summer months.

TABLE 1. Number of matings (f) of animals tested on mating propensity (m) under different conditions. Simplified from Petersen and Tenow, 1954, p. 182.

	sunshine		cloudy weather	
	f	m	f	m
napi	31	0.84	1	0.14
bryoniae	6	0.16	6	0.86
napi	22	0.76	2	0.29
bryoniae	7	0.24	5	0.71

TABLE 2. Survivals from growing *P. bryoniae* from Abisko, northern Sweden.

temperature	number of		
	eggs	larvae	pupae
4°	10	0	0
8°	10	3	0
13°	10	9	6
16°	10	10	9
20°	20	20	11
28°	10	7	0
32°	22	14	0
34°	5	0	0

EGG-LAYING

After copulation, the female was transferred into a cage with some flowers to feed on and leaves of a species of the family *Cruciferae* for egg-laying. *P. bryoniae* in nature lays the eggs almost exclusively on a single plant species, *Biscutella laevigata.* In one cage experiment a female preferred some other plants to *Biscutella,* about 80 eggs being laid on them and none on *Biscutella* (Petersen l.c.). Thus, every plant appropriate for the egg-laying of *napi* seems to be appropriate for *bryoniae.* However, most plants of families other than *Cruciferae* as well as some few species of this family are not eaten at all by the larvae.

TABLE 3. Results from breeding *P. napi* - *bryoniae* from four localities in Sweden. l. = number of newly hatched larvae, p. = number of pupae.

temp.	Scania			Uppsala			Murjek			Abisko		
	l.	p.	%	l.	p.	%	l.	p.	%	l.	p.	%
11°-12°	30	11	37				10	2	20	15	0	0
15°-16°	22	7	32	25	19	76				11	1	9
16°-17°	85	46	54	5	5	100	4	3	75	24	12	50
19°-20°	153	119	78	45	26	58	17	8	47	33	19	58
22°-23°	43	29	67				5	2	40	36	11	31
25°-26°	92	47	51	5	4	80						

STERILITY

In many broods of the species as well as of their hybrids, the eggs do not develop at all or only partly. Sterility appears with almost the same frequency in both types of crosses, 6 broods of 30 in the pure species, 6 of 28 in the hybrid crosses. Sterility is slightly more frequent among Bowden's F_1 hybrids and backcrosses, but the difference is not significant. The F_2 and F_3 crosses, on the other hand, have a significantly higher frequency of sterility, when compared with the F_1 crosses and back-crosses of Bowden ($x^2=5.94$ with Yates' correction, $0.02>P>0.01$).

TEMPERATURE

The influence of temperature on the breeding results was investigated in two series of experiments. In the first series, material from Abisko in northern Sweden was used. *P. bryoniae* flies here from 400 m up to 800 m in the subalpine and the lower parts of the alpine regions. The breeding results are shown in table 2. The optimal constant temperature for eggs and larvae was found to lie between 13° and 20° C. As the hibernating pupae require a rather low temperature the experiments were stopped at pupation.

In the second series, material from four Swedish localities was used (cf. table 3). The Abisko material developed fairly successfully from newly hatched larvae to pupation at 16° - 23° C. The material from Abisko was perhaps a little weaker than that in the experiment already described, as the eggs had to be sent by mail. The material from southern Sweden (Scania) developed at temperatures varying from 11° to 26° C. The adaptation to different climates is obviously not strong enough to show up in experiments on such a small scale, especially near the upper and lower limits of temperature.

DISEASES

A successful breeding is dependent, not only on appropriate food and temperature, but also on the health of the animals. Virus diseases often cause the blackening and death of the larvae. The cultures started first usually develop well, only some of the latest-developing larvae being affected. In later cultures the disease spreads like a pest, killing the larvae in great numbers. The results of table 3 may therefore better be expressed as different resistance to the disease at different temperatures, or perhaps as varying virulence of the virus, than as a direct effect of the temperature.

Most years, the larvae were kept in glass jars on cut leaves. As the disease seemed to spread more rapidly on wet leaves, it was decided to start breeding on living plants growing in flower pots. The results were promising in that the frequency of virus disease became very low. The fecundity of the animals, on the other hand, was not very high during this last year of more extensive breeding. It has been stated by several breeders of *Pieris napi* that it is impossible to breed many generations without crossing with fresh material taken in nature. The animals used belonged to the fourth generation in captivity and were unfortunately the only ones available at the time.

The best way of breeding *Pieris napi* has still to be investigated. Breeding at 20° C on a living plant of the family *Cruciferae,* which is easy to keep in flower pots, will probably give better results than any so far known. *Biscutella laevigata,* which grows as a weed in the gardens of Italy, will perhaps be the best food-plant for *P. bryoniae.*

LITERATURE CITED

BOWDEN, S. R. 1953. Timing of Imaginal Development in Male and Female Hybrid Pieridae. (Lep.) *Entomologist,* 86, No. 11: 255-264.

————, 1956. Hybrids within the European Pieris napi L. Species Group. (Lep., Pieridae). *Proc. South London Ent. Nat. Hist. Soc.,* 1954-55: 135-159.

————, 1957. Diapause in Female Hybrids: Pieris napi adalwinda and Related Subspecies (Lep.) *Entomologist,* 90, No. 1133: 247-254, 273-282.

BOWDEN, S. R. and N. T. EASTON. 1955. Diapause and Death: Further Observations on Imaginal Development in Pieris Hybrids (Lep.) *Entomologist,* 88, No. 1108: 174-178, 204-210.

FISCHER, E. 1924. Über die Zweibrütigkeit der P. bryoniae O. *Mitt. München. Ent. Ges.,* 14:8.

————. 1925. Neue Zuchtergebnisse bei Pieriden. *Mitt. Schweiz. Ent. Ges.,* 13.

MÜLLER, L. and H. KAUTZ. 1938. Pieris bryoniae O. and Pieris napi L. Wien. 1- 189.

PETERSEN, B. 1963. Breakdown of differentiation between Pieris napi L. and Pieris bryoniae Ochs. and its causes. *Zool. bidr. Uppsala,* 35: in press.

PETERSEN, B. and O. TENOW. 1954. Studien am Rapsweissling und Bergweissling (Pieris napi und Pieris bryoniae). Isolation und Paarungsbiologie. *Zool. bidr. Uppsala,* 30: 169-198.

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AN ANALYSIS OF THE NORTH AMERICAN SPECIES OF THE GENUS *CALLOPHRYS*

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INTRODUCTION

EXAMINATION OF CERTAIN SPECIMENS of Callophrys from montane habitats in California and Oregon indicate that these specimens belong to a cluster distinct from others so far described, and not fitting well with any known description of North American Callophrys. The purpose of this paper is to discuss certain characteristics of North American *Callophrys,* and to provide a name for the previously unrecognized series of populations. This name is needed for two forthcoming faunistic papers.

TAXONOMIC HISTORY OF *CALLOPHRYS*

Linnaeus (1758) described *P* (*apilio*) *P* (*lebeji*) *rubi* as follows: "Rubi. 154. P. P. alis dentato-subcaudatis; supra fuscis, subtus viridibus."

Billberg (1820) proposes the genus *Callophrys* with three groups, based on three tails, two tails and one tail. In the one-tailed group only *rubi* is listed.

Scudder (1875), selected *rubi* as the type of *Callophrys* as follows: "1820, Billb., Enum. Ins. 80: Vulcanus, rubi, and a Ms. species. Rubi may be taken as the type."

Until recently *Callophrys* has been limited to those few hairstreaks that matched *rubi* in every respect. The palaearctic names, besides *rubi* itself, include *borealis* Krul., *polaris* Möschl., *fervida* Stgr., *sibirica* Rühl and *suaveola* Stgr., omitting abberations that have been named. All of these have been considered both as full species and as subspecies or variants of *rubi.* Of these only *rubi,* as type of genus, will be mentioned further.

Ziegler (1960), combined the groups placed under *Mitoura* Scud., *Incisalia* Scud., *Sandia* Clench & Ehrlich, and *Callophrys* Billb., under the oldest name, *Callophrys,* as subgenera. This move had been presented in abbreviated form previously by Ehrlich and Clench (1960) in the paper describing *Sandia mcfarlandi.* Clench, in Ehrlich and Ehrlich (1961) used a similar arrangement but several genera are proposed for groups of hairstreaks outside the scope of this paper, which is concerned only with the members of the presently considered subgenus *Callophrys* as limited by Scudder's designation of *rubi* as the type.

THE AMERICAN SPECIES OF THE SUBGENUS *CALLOPHRYS*

All species of the subgenus *Callophrys* resemble one another very closely, and can be separated with any degree of assurance only by considerable effort. There always remain specimens the position of which is a matter of opinion in the light of present knowledge. There are two revisions of the group. Barnes and McDunnough (1923), grouped the species in a manner superior to previous treatments and described three subspecies. Clench (1944) revised the genus (as it was then considered) proposing one subspecies.

At present at least ten names are involved in the North American *Callophrys* (s. str.), and these have been regarded at one time or another as representing six distinct species. Characters that have been used to distinguish the various species have been color markings and wing shape. The male terminalia are exceedingly similar in all the named entities. This is not to say that differences may not exist, but so far they are not apparent. The present author has also dissected the female genitalia of the North American species and the European *rubi.* These studies have not resulted in any conclusions in time for the present paper.

An attempt has been made to examine all parts of the external surface of the body. Small differences may be detected in the palpi, antennae, facial hairs or tuft, and in wing shape, stigma and color markings. The results of these comparisons are given in Table 1.

It seems pertinent to include here a discussion of the problem of the identity of *dumetorum* Bdv. Boisduval (1852) writes (free translation from the original French) that "this Thecla resembles our *rubi* in every respect and is most likely only a local variety of that species." Close examination of *rubi* in comparison to specimens usually considered to represent *dumetorum* Bdv. shows a number of minor differences, but without doubt the two are closely related. Certain problems arise in deciding what would properly be considered as *dumetorum* Bdv. Clench (1955, op. cit, p. 220) gives a description of what he at that time regarded as *dumetorum.* The description suggests that he is describing the insect for which a new name will be proposed in this paper.

The Boisduval description could fit any of several named segregates. The figure by Oberthur (1913) shows a gray insect with overscaling of a cast of green not usual in the subgenus, and with a rather more complete macular band than one expects in insects that pass for *dumetorum* in collections. W. D. Field, of the Smithsonian Insitution, has kindly given me a detailed comparison of the insect figured by Oberthur, and which is usually regarded as the type of *dumetorum.* Whether or not this specimen is actually the one on which Boisduval based his description is not certain; this does not seem to be stated explicitly. Field informs me that Oberthur's figure is a faithful representation of the supposed type specimen. This specimen is a gray female with the fringes white or pale-tipped with a conspicuous macular band and no antennae.

This female specimen, by virtue of being illustrated by Oberthur, may need to be regarded as a lectotype, the illustration being one method of designation, as was suggested by Field (in litt). A possibility exists that it may indeed be the specimen described by Boisduval, but this point can not be settled in light of present knowledge.

Neither Boisduval's description nor Oberthur's illustration seem to fit exactly any presently known population of *Callophrys.* Either *dumetorum* was described from unusual specimen, or from some since unlocated population, or (most likely) neither the illustration nor the description are completely recognizable in relation to some well-known population. Of the specimens compared with the type, there seem to be fewer discrepancies with the lowland population most commonly considered to be *dumetorum,* except that the type is a gray female while the females of the lowland population tend to be brown or fulvous. However, gray females are not entirely unknown. The macular band is more than usually well-developed in the "type," but the band is variable in all species, and specimens from the foothills of the Sierra Nevada are known with complete macular band. The choice here made is to continue to use the name *dumetorum* for the cismontane lowland population of California, while retaining the option of changing this opinion should future findings make such a change desirable.

The exact locality where Lorquin collected his original specimen, subsequently named *dumetorum* by Boisduval, is partially in doubt, as is frequently the case with the Lorquin-Boisduval specimens. Species described in 1852 were from Lorquin's earlier collecting. In some of the descriptions there are phrases such as "Mountains of the Juba," suggesting that the specimens were taken near the mining operations along the Yuba River. A reading of Lorquin's adventures in California brings the same conclusion; that he was in the Sierran mining region prior to 1852. This is presumptive evidence, but certainly better than no inference at all. Specimens of *Callophrys* from the Sierra Nevada foothill localities relate to the populations from coastal and southern California rather than to those of the high Sierra Nevada. Here again the evidence favors use of the name *dumetorum* for the low elevation insects.

Should incontrovertible evidence subsequently be found, that this

Character	dumetorum auct.	apama	viridis
wing fringes	fuscous basally; pale tipped; not clear white	dark fuscous basally; pale tipped, dark scales mixed.	fuscous; the tips mixed pale and fuscous scales
fore wing apex	obtuse-angled	obtuse-angled	obtuse-angled
forewing, outer margin	oval in female; straighter in male and indented at Cu$_2$	oval in female; male slightly produced between Cu$_1$ and M$_3$	curved to M$_1$ or M$_2$; then nearly straight; tornus slightly incurved
hindwing, outer margin	crenate in spaces Cu$_1$, Cu$_2$ and 2nd A. (indentations shallow)	small crenation in space Cu$_2$; a deeper one in space 2nd A	hind wing appearing more than usually quadrate; crenations very slight
color of forewing costa below	fulvous, more marked in female	pale brown to dull fulvous; concolorous with other brown areas of wing	rich fulvous in both sexes
forewing below	invaded by gray or fulvous from anal margin to at least vein M$_1$	anal margin gray; disc invaded by rich fulvous at least to vein M$_1$	gray confined to anal cells only
vein-tips of hind wing below	vein tips and marginal line usually rusty-brown scaled	narrow but complete marginal line, outbrown, mesially black, inwardly white; vein tips dark	brown scales at vein-tips absent or nearly so
Macular band (lower surfaces of wings)	usually reduced to 3 spots; seldom complete; macules inwardly brown, then white	hindwing: complete, spots in Cu$_1$ & Cu$_2$ displaced out. Tricolored, 4-5 spots forewing	complete on both wings (though narrow) to reduced; mesial brown scaling reduced
shade of green below	grass green to golden green	rather dull green, brightened by admixture of fulvous scales	deep, frequently bluish, green.
scaling of labial palpi	black above, mixed black & white below; may have few green scales near base	hairs and scaling smooth; black above and below; white scales laterally	grizzled black and white throughout; third segment very pointed; scaling sparse, green scales basally
facial hairs (facial tuft)	erect or slightly proclinate; thicker laterally; black with green scales at bases	hairs markedly proclinate, thicker laterally; basal green scaling	erect or slightly proclinate; thicker laterally; black or gray; green scales at base
forewing stigma of male	small, ovate, usually gray and lighter than ground color	ovate to oval; gray, slightly lighter than ground	small, ovate, distinctly paler than ground color, or concolorous
antennal annuli (white rings)	usually 15 (seldom 16)	usually 15 (seldom 16)	14-17 (av. 16 in 34 specimens); antennae pale above (unique)
general facies as seen from above	male uniform fuscous with pale-tipped fringes; female brown with fulvous discs and pale-tipped fringes	male uniform dark fuscous; female same with very large fulvous discal areas	gray insect with nearly concolorous fringes; females usually gray (very seldom partly brown on disc)

TABLE 1

CHARACTER COMPARISON OF NORTH AMERICAN CALLOPHRYS (S.STR.)

affinis	sheridani	comstocki	lemberti n. sp.
basally fuscous; pale-tipped to white tipped	bases darker than wing; tips mixed white & fuscous	bases darker than wing; tips white, contrasting	basal scales mixed brown and gray; tips snow white (usually); occ. fuscous scales
approx. right-angled, tip rounded	acute, the forewing trigonate	rectangular; effect of short sharp tip	pointed, nearly as in sheridanii
curved to M_2, thence nearly straight to tornus	slight curve to M_1 or M_2, then straight to tornus or slightly concave	quite evenly curved, the curvature slight	curved to M_3 slightly indented between Cu_1 & Cu_2
quadrate, nearly rounded; crenations slight or obsolete	rounded; crenations scarcely visible	longest between M_3 & Cu_1; crenations evident but minute	rounded, crenations slight, between Cu_2 & 2nd A one is evident
gray to clay-colored, not contrasting	blackish; darker than rest of wing	dark in most males; concolorous to pale fulvous in females	narrowly brown or fulvous; contrasting
gray from anal margin to Cu_2; general wing surface green	dark gray to vein Cu_2	gray area extensive, to M_2(one female) on to across wing to costa (one male)	gray confined to anal cells; even here some green overscaling
slight brown at each vein-tip; terminal line not differentiated	spots at vein tips not evident; terminal line black	dark vein tips not evident; terminal line black, narrowly white inwardly	usually slight dark points at vein tips on both pairs of wings; approaches checkering
obsolete, or one spot in cell Cu_2	complete; straight; white; edged within and without by black	band complete but of separate spots; bowed out at cell Cu_2;macules white, black inwardly.	complete band to obsolete of discrete white spots black inwardly, narrow; obscure on forewing
uniform pale yellow-green	deep dark green scales mixed with dark gray scales about equally	deep dark green, the veins slightly contrasting dark	green scaling thin, uniform, bright pale green, the undercolor showing through
palpi slender and thin scaled; mixed black and gray all over	dark above; scaling below dense; mixed black and light gray (effect dark)	palpi slender, pointed; scaling sparse; dark above, mixed black & white below	palpi slightly darker above but mixed white and black scales throughout; third joint darker
facial hairs light gray, sparse, procumbent	dark, dense, slightly proclinate; underscaling prismatic, not green	tuft dense, coarse, black, proclinate; subscaling covered or obscure	hairs sparse, fine dark, sub-erect; green sub-scaling prominent
dark to black, sharply contrasting	stigma usually nearly concolorous with wing	small, slightly pale to concolorous and scarcely discernible	stigma small, subtriangular, concolorous to pale; seldom dark
17	av. 17 (16-18)	15-16	16 (17 on one specimen)
fulvous to bright rufous with dark terminal line & pale fringes	dark gray with black terminal line and white fringes; sexes alike in color	gray insect with dark terminal line and white fringes; sexes concolorous	mouse gray smooth-scaled insect with white fringes; females concolorous or dull brown (fuscous)

TABLE 1 (continued)

rubi	*Incisalia augustinus*	*Mitoura siva*	*Sandia mcfarlandi*
basally dark; tips with a few pale hairs	mixed brown & gray basally; tips sordid gray; dark at vein-tips (checkered)	forewings fuscous; hindwings pale-tipped	basally brown and fuscous mixed; tips white
tip quadrate, bluntly pointed	tip rectangular or nearly acute	rather acute	obtuse
rounded to M_3; thence nearly straight to tornus male indented at Cu_2	rather evenly curved but slightly flatter before tornus	quite evenly rounded slightly flattened before tornus	rounded
two well-marked crenations at cells Cu_2 and 2nd A.	at least a suggestion of a crenation between each pair of veins	tailed at Cu_1 & Cu_2; not crenate	tornal crenation evident, slight
broadly fulvous in female; narrowly so or gray in male	concolorous with wing	slightly fulvous, not greatly contrasting	lemon yellow to apricot
gray confined to anal cells	no contrast	fulvous invasion from anal margin almost to costa	yellow to apricot shade across entire wing
vein-tips brown; terminal line warm brown in female, less so in male	terminal line dark brown to black; veins not contrasting	complex pattern of black, white and rufous overscaling	terminal line black, invading vein tips
of small separated narrow white spots; nearly complete to obsolete	complete band of small round dark spots; dark basal shade	complete, irregular from inward out of bands of brown, black & white	narrow, complete, white flanked each side with black
grass green-suggests *dumetorum*	ground color pale vinaceous brown	smooth pale green scaling where other patterns are not evident	basically a luminous yellow-green
mostly dark with white scales on sides; green scales usually evident	mixed black & white scales; darker above	black above and at tips; basally, white overscaling	dark above and at tips; white scaling below and laterally; rather long
sparse, dark, mostly lateral; median green sub-scaling prominent	dense dark rich brown, procumbent; sub-scaling covered	very sparse, procumbent; iridescent underscaling very visible	hairs fine, short & erect; mixed black & white; subscaling dark
elongate-oval; androconia rather rough	very long oval, androconia small; black to pale	elongate-oval; dark to pale	elongate, about 3 times as long as wide
16	18	17, narrow and clear-cut	15-16; antennae very short, each segment short
gray with nearly concolorous fringes (male); dark brown with concolorous fringes (female)	dark brown with checkered fringes (male); female lighter richer brown	dark brown insect with fulvous on discs and two dark dots near hind wing tornus; female more fulvous	brown insect with fulvous discs & white fringes

TABLE 1 (continued)

position is untenable and that the population herinafter described as unrecognized is actually true *dumetorum,* the populations now con-considered as *dumetorum* and its variants must then become known as *perplexa* B. & McD., as the oldest available name definitely assigned to this coastal insect.

The notations in Table 1 are of necessity short. In some cases amplification is given in the species discussions. The characters used in Table 1 vary in the samples from the different populations, but the degrees of quality given are averages. In all cases the samples were adequate (twenty-five or more specimens) to large (fifty to one hundred specimens) except for *affinis* and *comstocki.* Of the latter, only four specimens were available for close study, and some fifteen specimens were examined in all.

For comparison, one species each of the subgenera *Incisalia, Mitoura* and *Sandia* (which contains a single species) are included and comparison will show that most of the characters used are specific rather than generic or subgeneric. The subgenus *Xamia* was excluded from lack of material, and the subgenus *Cyanophrys* because it enters our fauna only along the extreme southern border.

Clench (in Ehrlich & Ehrlich) defines *Callophrys* (s. lat.) and its subgenera primarily on genitalic characters. The subgenus *Callophrys* includes species with valvae not capped; the cornuti of the aedeagus slender, not spatulate; the scent-pad (stigma) well-developed, and the labial palpi about 1½ times as long as the vertical eye diameter. (This last character is shared with the other subgenera except for *sandia,* the palpi of which are about twice as long as the vertical diameter of the eye). The scales of the stigma are entire and with rounded ends and the hind wing is not tailed.

In addition may be mentioned the tornal "tab" of the hind wings, shared with *Incisalia;* the reduction of the hind wing marginal crenulations, restricted usually to the last three cells (much more extensive in *Incisalia*); the usually even green overscaling of the inferior surfaces, typical of the subgenus, and the complete lack of the thecla spot. The markings below are restricted to the submarginal band (macular band as frequently stated), which is often reduced or even absent, even in a single species. There is no other evident ornamentation.

In the following analyses of the species, only the original citation is given.

Callophrys rubi (L.)

Syst. Nat. 10th Ed. 1:483, No. 154:1758

Palaearctic. Range Europe and Asia. By some considered the only valid palaearctic species. Closely resembles *dumetorum* as considered here, but the green darker, the female less broadly fulvous, the wing fringes less contrasting, the stigma more elongate, and the under surface of the forewing not greatly invaded by gray or brown. In all specimens examined, the terminal line of the wings is much more evident.

Callophrys dumetorum (Bdv.)

Ann. Ent. Soc. France (2) 10:291:1852

A fuscous (male) or usually broadly fulvous (female) insect with pale-tipped but not white fringes; hind wing with three crenations, terminal line not strongly contrasting. Green below warm grading to yellowish green in southern specimens, nearly distinctive. Forewing deeply invaded by gray (male) or tan (some females) at least to vein M_1 and frequently (subspecies *perplexa*) to forewing costa. Veins of secondaries below dark tipped, the border usually clouded with brown scales. Whether or not this species is correctly identified as *dumetorum,* it is one of the distinctive entities of the subgenus. The invasion of the forewing by gray or brown seems diagnostic in its range. The subspecies *perplexa* B. & McD. (1923) is more yellowish-green below, the band reduced or obsolete (usually) and with the forewing invasion frequently extending to the costa. However, reduction of the macular band occurs in all populations of *dumetorum* (as well as in nearly all other populations of *Callophrys*) and this character must be used with caution. The macules of the band are bicolored, brown inwardly, outwardly white.

Callophrys apama (Edw.)

Papilio 2:137:1882

A very dark fuscous (male) or fuscous with broad fulvous discs (female) insect with fringes slightly pale-tipped, not notably contrasting. Green below rather dull but mixed with fulvous scales, giving a superficial appearance of being lighter than is really the case. Macular band (nominate *apama*) complete, the macules in spaces Cu_1 and Cu_2 displaced outwardly, the macules of the band tricolored, inwardly brown, mesially black and distally white. Facial tuft peculiar, sparse, rather light in color and the hairs markedly proclinate in all of the specimens examined. The name *homoperplexa* B. & McD. (op. cit., p. 68) was given to specimens such as those from Colorado, in which the macular band tends to become obsolete. The shade of green and the other characters remain similar.

Callophrys viridis (Edw.)

Though usually considered a synonym of *dumetorum, viridis* appears to be as distinct as most of the species, and was ressurected from synonomy by Clench (1944). It is a dark gray insect in both sexes when fresh (old specimens fade to a lighter gray), the fringes pale-

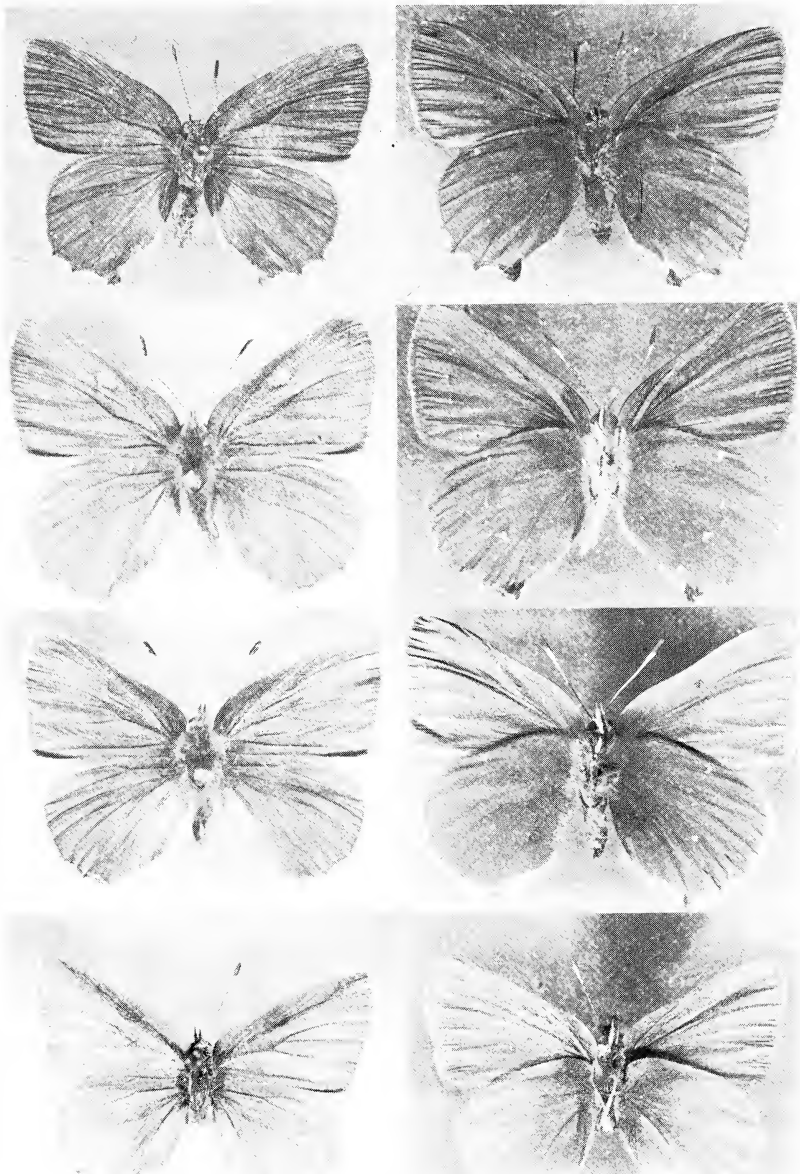

Fig. 1. *Callophrys.* Upper side to left; lower side to right. *Callophrys rubi* L. Near Hannover, Germany, 12:IV.52. G. Hesselbarth.

Callophrys dumetorum Bdv. El Portal, Mariposa Co., Calif. 16.IV.61, ca. 1200', J. W. Tilden.

Callophrys viridis Edw. Twin Peaks, San Francisco, Calif. 16.III.57, J. W. Tilden.

Callophrys affinis Edw. Dry Canyon, Salt Lake County, Utah 14.VII.49, J. C. Downey.

Photography by Jean Norton

tipped and usually contrasting, particularly on the hind wings. Occasional females in a long series are brown, very seldom fulvous, and normally females cannot be separated from males on color alone. The outlines of the wings are more quadrate than in other members of the subgenus; the crenations of the hind wings are discernible but small. The forewing below has the gray limited to the anal margin, not invading the disc. The green below is dark and frequently bluish, quite distinctive. The antennae are pale to whitish above, seemingly an unique character. The range in California is rather narrowly limited to the coast, from Santa Cruz County northward. Its range beyond California needs to be clarified. It flies very early in the year, late February to early April, and seldom leaves the vicinity of *Eriogonum* (usually *E. latifolium* Sm.) except to visit nearby flowers. It is partial to flowers of Umbelliferae. Its flight is low and easily overlooked. In spite of reports to the contrary, *viridis* seems to be the only species of the subgenus found in the immediate environs of San Francisco, and is also common in similar habitats in Marin County.

Callophrys affinis (Edw.)

Proc. Acad. Nat. Sci. Phila., 223:1862

A fulvous to bright rufous insect, with dark terminal line and usually dark contrasting stigma, the fringes pale-tipped to white, usually very contrasting. Below, uniformly pale yellow-green (nominate *affinis*), the macular band obsolete or represented by one or two minute macules only. This describes nominate material from Utah. North and west, specimens associated with this species are less fulvous above, more bluish-green below. *Washingtonia* Clench (1944) is based upon such specimens from Brewster, Washington.

Callophrys sheridanii (Edw.)

Field and Forest 3:48:1877

Whether this name is to be attributed to Edwards or to Carpenter may be a matter of opinion. A rather short badly written article with several misspellings and typographical errors, by Carpenter, states that Edwards is describing the species. It reads: "Thecla *sheridonii* (sic), new species, is named in honor of Lieut. Gen. P. H. Sheridan, U. S. Army, by W. H. Edwards, Coalberg, West Virginia, at the request of W. L. Carpenter, U. S. Army. Size and form . . . " Inasmuch as it is expressly stated that Edwards is writing the description and that it is at the request of Carpenter, the position is taken here that Edwards is the author of the name. However, the alternate opinion has also been expressed. In any case the present spelling is an emendation of an evident lapsus calami.

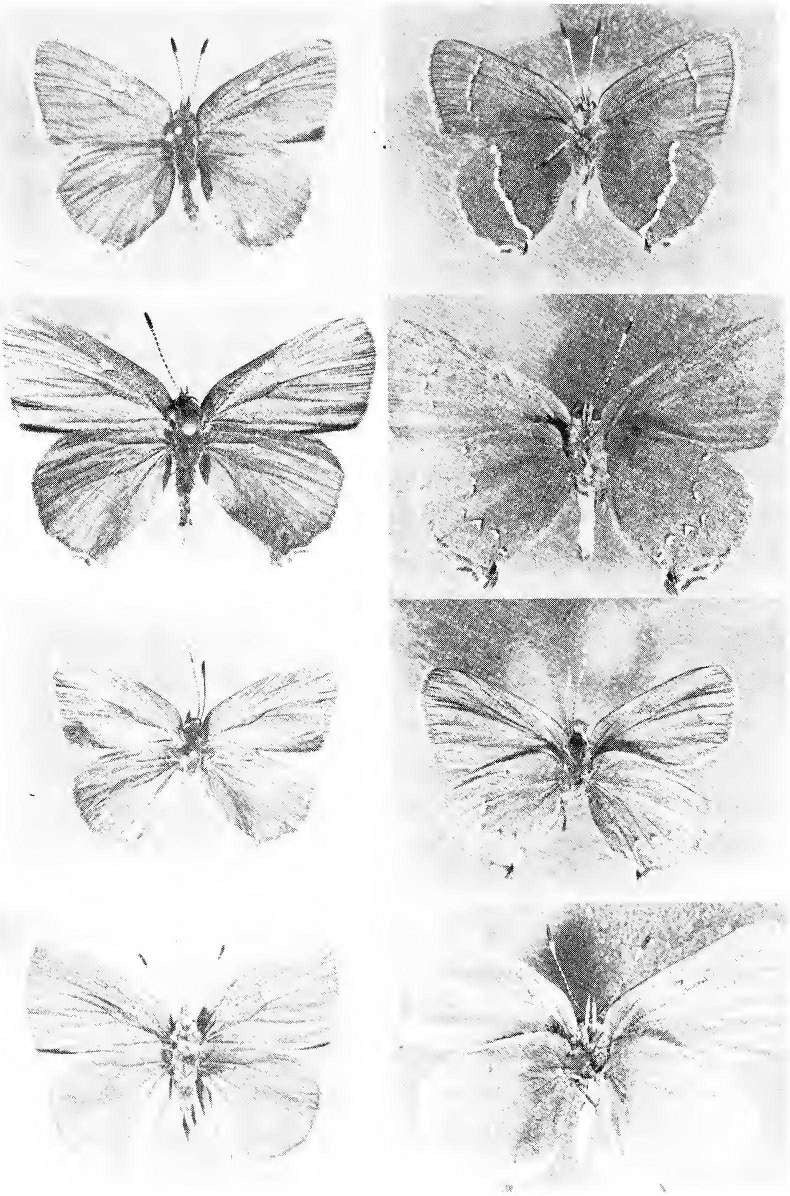

Fig. 2. *Callophrys.* Upper side to left; lower side to right.

Callophrys sheridanii Edw. Flagstaff Mt., Boulder Co., Colo. 17.IV.52, Don Eff.

Callophrys apama Edw. Strayhorse, Greenlee County, Ariz., 7.VII.58, 7800 ft., J. W. Tilden.

Callophrys comstocki Henne Providence Mts., San Bernardino Co., Calif. 2.IV. 50, Ray Hulbirt.

Callophrys lemberti Tilden, n. sp. West above Tioga Pass, Yosemite National Park, Calif. 8.VII.58 ca. 10500 ft., O. Shields.

Photography by Jean Norton

Sheridanii is the most divergent species in an otherwise closely related group. It is dark gray above in both sexes, with a black terminal line and white-tipped contrasting fringes. The stigma of the male is small, usually concolorous and not immediately evident. Below, the green is very dark and mixed almost evenly with black scales. The forewing is more acute than in the other species and the secondaries appear smaller and more evenly rounded. The facial tuft is unusually dense, erect and black, and most specimens show eighteen annuli in the antennae. The macular band is only slightly arcuate and is not usually broken into discrete macules. It is white mesially, faced on both edges with black. The name *neoperplexa* B. & McD. (Contrib. 5:671:-1923) was applied to specimens from Utah in which the macular band tends to become reduced or obsolete. The western range of *neoperplexa* remains to be established, but it appears to extend into eastern Oregon and eastern Washington.

Callophrys comstocki Henne

Bull. So. Calif. Acad. Sci. 39:71:1940

This species was described from the desert region of San Bernardino County, Calif. (Providence Mountains) and specimens are relatively scarce in collections. The precarious climate results in good populations of adults only in favorable years. *Comstocki* has been considered either a distinct species or a subspecies of *dumetorum.* Examination of the short series available to me for study, while not conclusive, indicates that *comstocki* is separable from other named segregates of the subgenus by characters at least equal to those defining most of the species. It is a gray insect in both sexes, the terminal line dark, the fringes white tipped and contrasting at least on the secondaries. The green below is dark, the veins slightly darker than the background color. The stigma is small, scarcely discernible and the facial tuft is dense, coarse, black and proclinate, almost concealing the underscaling. The vein tips are not dark on the hind wing below, but the terminal line there is black, nearly complete and inwardly bordered narrowly with white. The forewing is deeply invaded by gray, a character (almost the only one) it shares with *dumetorum.* The macular band is complete but of discrete macules, inwardly black, outwardly white, and the spot in cell Cu_2 is displaced outwardly.

Callophrys lemberti Tilden, n. sp.

A mouse-gray smoothly scaled species with pale or concolorous stigma and contrasting white-tipped fringes. Sexes similar, or females dull brown. Green of lower surfaces pale, the scaling thin, the ground color showing through. Macular band complete to obsolete, unusually narrow, of discrete macules.

Holotype male: Costa of forewing 13 mm.; costa upcurved to basal

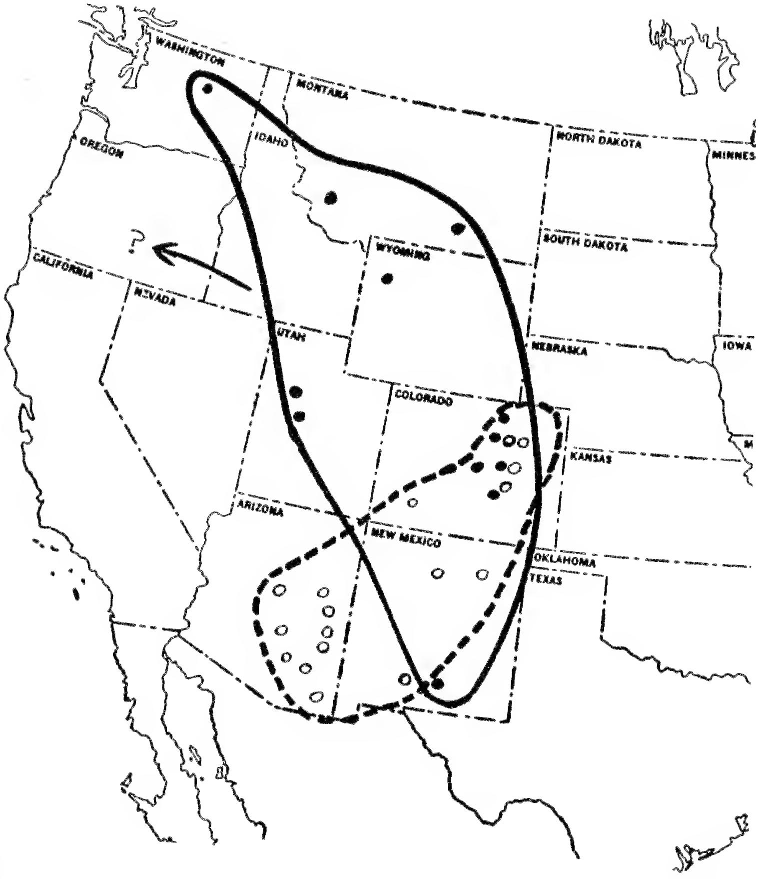

Fig. 3. Map showing distribution of *Callophrys apama* (°) and *C. sheridanii* (•).

third of cell, then straight to end of $R_2 + 3$, curved down thence to apex; outer margin of forewing curved to M_3, thence nearly straight to *2nd* A except for a slight indentation between Cu_1 and Cu_2; tornus diagonal, anal margin nearly straight. Hindwing: Rs=*2nd* A; $M_1 = Cu_1$, these the longest veins in this wing; two slight marginal crenations between Cu_1 and Cu_2 and between Cu_2 and *2nd* A; white annuli of antennae 16 as seen from lateral view; palpi dark above, grizzled black and white on sides and below, rather more blunt than usual in the subgenus but of no significance, since other specimens of the type series have palpi more pointed than in the holotype; facial area with gray, slightly proclinate hairs, the vestiture more dense laterally and with few irridescent green subscales showing through; body dark above, pale below; the legs annulated dark gray and white.

Upper wing surfaces gray (nearly mouse gray), the veins very slightly darker but not greatly contrasting; stigma nearly concolorous with wing; fringes of forewing concolorous at base, white at tips; fringes of hind wing concolorous gray mixed with golden brown scales at base, snow-white and contrasting at tips; tornal table downturned and dark.

Lower wing surfaces with smooth, pale, slightly yellowish green (nearly apple green) overscaling, which is thin, the gray ground color showing through between the individual scales, costa of forewing pale brown, moderately constrasting; anal area of forewing gray from margin to Cu_2, the gray not invading the disc; forewing with a slight suggestion of a macular band with macules in cells M_3, Cu_1 and Cu_2; fringes as on upper surface.

Secondaries with green overscaling over entire surfaces; macular band nearly complete but narrow, the macules narrowly black inwardly, outwardly and more widely (about ⅔) white; the macule in cell *3rd* A is a short dash; that in cell *2nd* A directed diagonally toward wing base; that in cell Cu_2 also diagonal but displaced towards wing margin by about one-half its own length; macule in cell Cu_1 lacking on right wing, indicated by four or five white scales on left wing; that in cell M_3 very faint, dull white and narrow; that in cell M_2 faintly indicated by a lack of green overscaling only; no macule in cell M_1; macule in cell Rs small but distinct; fringes nearly as on upper surface except for clusters of dark scales at vein tips, suggesting incomplete checkering; the tornal tab centrally black, narrowly faced on each side with white hairs; hairs of vannal margin gray at end of macular band, thence nearly white to base.

Allotype female: Forewing costa 13.5; wing shape and proportions essentially as in holotype male; white annuli of antennae 16 (an incomplete 17th on base of club); facial area with hairs sparse (as is frequent in female *Callophrys*); Body and legs as in holotype male.

Upper surfaces dull gray-brown, darker and very slightly more

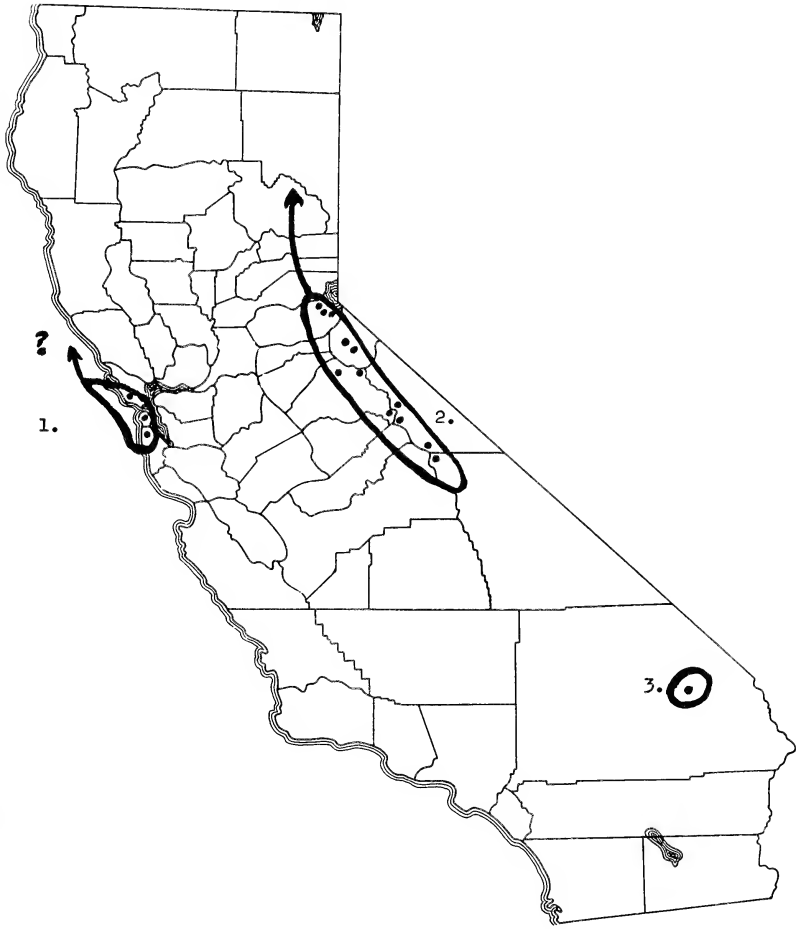

Fig. 4. Map showing distribution of *Callophrys viridis* (1), *lemberti* (2), and *comstocki* (3).

brownish than holotype male. Costa above with warm brown scales, some of which invade the wing nearly to vein Sc; fringes of forewings dark gray at base, white at tips, of hind wings brownish at base except for dark gray patches at vein tips, the fringe tips white; tab down-turned and dark, the fringes in the tornal area invaded by gray, the tips less contrasting.

Green overscaling of lower surfaces as in the male; forewing costa warm brown (nearly cinnamon); macular band indicated by two indistinct macules, in cells M_3 and Cu_1; fringes light gray at base, with darkenings at vein tips; fringe tips white; gray anal margin free of green overscaling not quite to Cu_2; macular band of hind wings very narrow, the spots small and white with the inward black scaling scarcely more than suggested, the band slightly bowed out but the macules not noticeably displaced; macules in cells M_2 and M_3 obsolete; fringes pale gray, distinctly dark at vein ends, appearing checkered; fringe tips white; a faint subterminal row of paler green scales before the fringes; tab and vannal margin as in holotype male.

Type material: Holotype male, West above Tioga Pass, Yosemite National Park, Calif., 9:VII.62, leg. Oakley Shields; allotype female, same locality, 10.VII.58, leg. Oakley Shields; seven designated paratypes as follows: 1 male 8.VII.58 (Shields); 2 males, + 1 ♀ 19.VII.52 (Tilden); 1 male 25.VI.61,, + 1 ♀ (Dirks); 1 male, 25.VI.62 (Dirks): All paratypes from same locality. Type locality: West above Tioga Pass, about 1 mile, where the Gaylor Lakes Trail reaches its highest point before dropping down to Gaylor Basin, thence southerly along the ridge to rock oucrops, about two to three hundred yards.

Type material distributed as follows: Holotype male and allotype female in the collections of the California Academy of Sciences; one male paratype in the collection of Oakley Shields, La Mesa, Calif., one male paratype in the collection of the Los Angeles County Museum; one female paratype in the collection of the Carnegie Museum, Pittsburgh, Penn.; one male paratype in the collections of the National Museum, Washington, D. C. The males are retained by the author because they have been dissected to examine the genitalia. Certain other specimens from the type locality are at hand but are in too poor condition to form paratypes.

Variation in the type series: In flown specimens the green appears very slightly darker; the macular band is never more complete or conspicuous than in the types. In three paratypes the macules of the band are smaller and in one specimen the band is very faint. One male paratype has the stigma very pale; in one other the stigma is slightly darker than the ground color.

Recognition characters for *Callophrys lemberti,* n. sp. are the smooth gray upper surfaces, nearly similar in both sexes; the very contrasting white-tipped fringes, particularly on the hind wings; the very narrow

Fig. 5. Map showing distribution of *Callophrys affinis.*

but frequently nearly complete macular band; the sub-checkered fringes of the hind wings below. It may be separated at a glance from *dumetorum* by the smooth gray upper surfaces and white fringes, and by the restriction of the gray of the lower surfaces of the hind wing to the anal margin. From *viridis* it may be separated by smaller size, more trigonate forewing and the pale green scaling below. From *comstocki* is may be known by the lack of contrast between ground color and the wing veins, especially on the lower surfaces of the hind wings, and by the more regular and narrower macular band and the contrasting brown coloration of the forewing costa. It bears no confusing resemblance to the remaining species. Specimens of *lemberti,* n. sp., collected long ago, tend to fade, the females particularly showing a sordid gray-brown above. The tendency of *Callophrys* specimens to fade is general.

Specimens from other localities than the type locality referred to *lemberti,* n. sp., are: 1 male, 1 female, west slope Mt. Dana, Yosemite National Park (Tilden); 1 male, 1 female, Warren Creek, Mono County, Calif. (Shields); 1 female, Mammoth Crest, Mono Co., Calif. (J. Powell); 2 males 1 female, Chipmunk Flat, Tuolumne County, Calif. (J. Powell); 2 males 1 female, the knobs just north of Sonora Pass, Stanislaus County, Calif. (Shields); 1 male 6 females, Ebbetts Pass, Alpine County, Calif. (J. Powell); 1 male 1 female, Leviathan Peak, Alpine County, Calif. (J. Powell); 1 male, Echo Lakes Area, Eldorado County, Calif. (Dirks); another male from Echo Lakes, without collector label; 1 female, Mt. Tallac, Eldorado County, Calif. (F. X. Williams, 1909); 1 male, Tamarack Lake, Eldorado County, Calif. (no collector label); 1 male, Crater Lake National Park, Klamath County, Oregon (D. Huntzinger); 1 male, west slope Mt. Thielson, Klamath County, Oregon (Shields), 26 specimens in all extending from the Central Sierra Nevada to nearly central Oregon. In addition there are several apparently conspecific specimens too worn to use for reference.

The species is named in honor of an early collector in the Tuolumne Meadows and Tioga Pass sections of what is now Yosemite National Park.

Thanks are due the following individuals and institutions for the loan of material: Ernst Dornfeld, Corvallis, Oregon; David Huntzinger, Mt. Timpanogos Cave National Monument, Utah; C. Don MacNeill, California Academy of Sciences, San Francisco, Calif.; E. J. Newcomer, Yakima, Washington; Jerry Powell, California Insect Survey, University of California, Berkeley, Calif.; Oakley Shields, La Mesa, Calif., and Fred Thorne, El Cajon, Calif.

Special thanks are due Paddy McHenry, Burbank, Calif., for providing certain references not otherwise available.

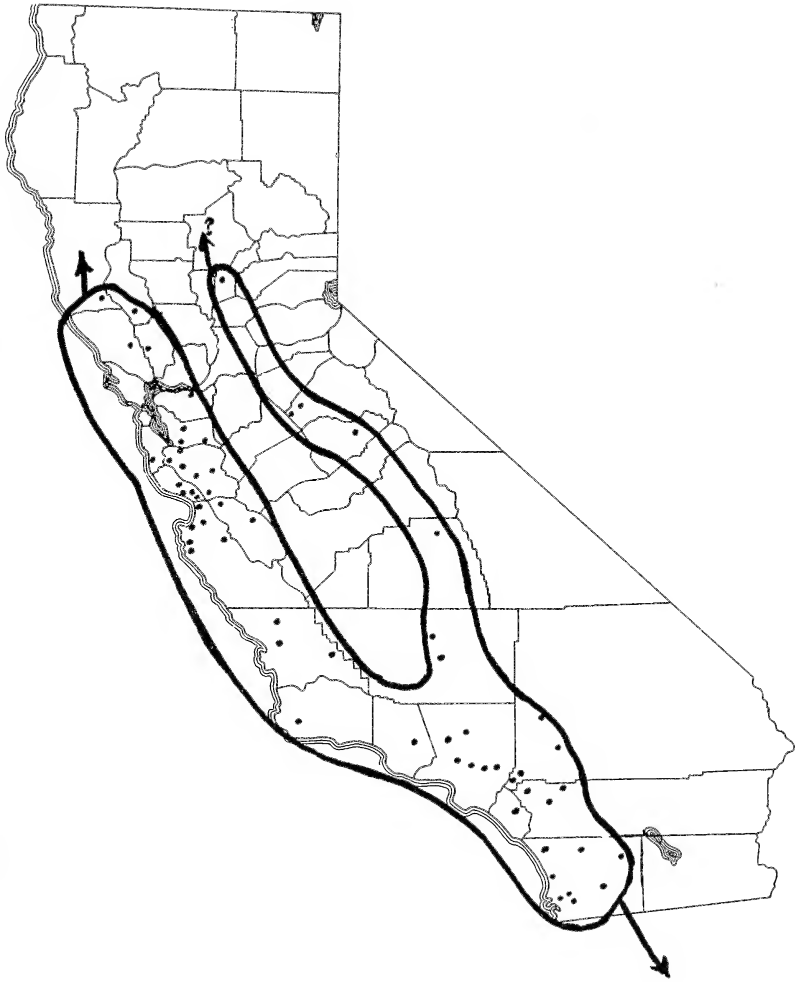

Fig. 6. Map showing distribution of *Callophrys dumetorum.*

SUMMARY

The species of *Callophrys* Billberg, s. str., are compared by use of certain minor characters mostly previously unused. An unrecognized species, *C. lemberti,* n. sp., is described. Specimens other than those of the type series are referred to this new name and the range as now known is given, being from the central Sierra Nevada of California to Mt. Thielson, Oregon.

REFERENCES

BARNES, W., & J. McDUNNOUGH 1923. *Contrib. Nat. Hist. Lepid. North America.* 5:64.

BILLBERG, C. J. 1820. *Enumeratio insectorum in Museo Billberg, p.* 80.

BOISDUVAL, JEAN A. 1852. *Lepidopteres de California. Ann. Soc. Ent. France,* (2) 10:291.

CLENCH, H. 1944. *Notes on lycaenid butterflies.* a. The genus *Callophrys* in North America. *Bull. Mus. Comp.* uoo. 94:217-229.

CLENCH, H., in EHRLICH, P. R., & ANNE H. EHRLICH. 1961. *How to know the Butterflies,* 200-211.

EHRLICH, P. R. & H. CLENCH. 1960. A new subgenus and species of *Callophrys* (s. l.) from the southwestern United States. *Ent. News* 71:137-141.

EDWARDS, W. H. 1862. *Proc. Acad. Nat. Sci.,* Philadelphia, p. 223.

————————. (in CARPENTER, W. L.) 1877. *Field & Forest,* 3:48.

————————. 1882. *Papilio* 2:137.

HENNE, C. 1940. *Bull. So. Calif. Acad. Sci.,* 39:71.

LINNEAEUS, C. 1758. *Systema Naturae,* 10*th* Ed., 1.483.

OBERTHUR, C. 1913. *Etudes Lep. Comp.,* Fasc. IX (Partie l*re*) Pl. CCXXXVI, fig·1926.

SCUDDER, S. 1875. *Proc. Am. Acad. Arts & Sci., Boston,* 10:132, no. 202.

ZIEGLER, J. B. 1960. Preliminary redefinition of North American Hairstreak genera. *J. Lep. Soc.,* 14:19-23.

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NOTICE

MEETING: Western Section, Lepidopterists Society

Place: Santa Barbara Museum of Natural History,
Santa Barbara, Calif.

WHEN: August 24-25, 1963.

Papers: Over ten papers and demonstrations have already been received; there is time for more to be received. Send to the Editor of this Journal.

IN ADDITION: THE LEPIDOPTERA FOUNDATION, its aims and purposes will be discussed.

THE JOURNAL OF RESEARCH ON THE LEPIDOPTERA

Volume 1 *Number* 4 *May,* 1963

IN THIS ISSUE

BIOGRAPHICAL SKETCHES

A number of these have been received but we need more. The space where these could go is lost at the end of papers unless authors send in their photos and sketches. We hope to start this feature in volume 2.

THE JOURNAL OF RESEARCH ON THE LEPIDOPTERA

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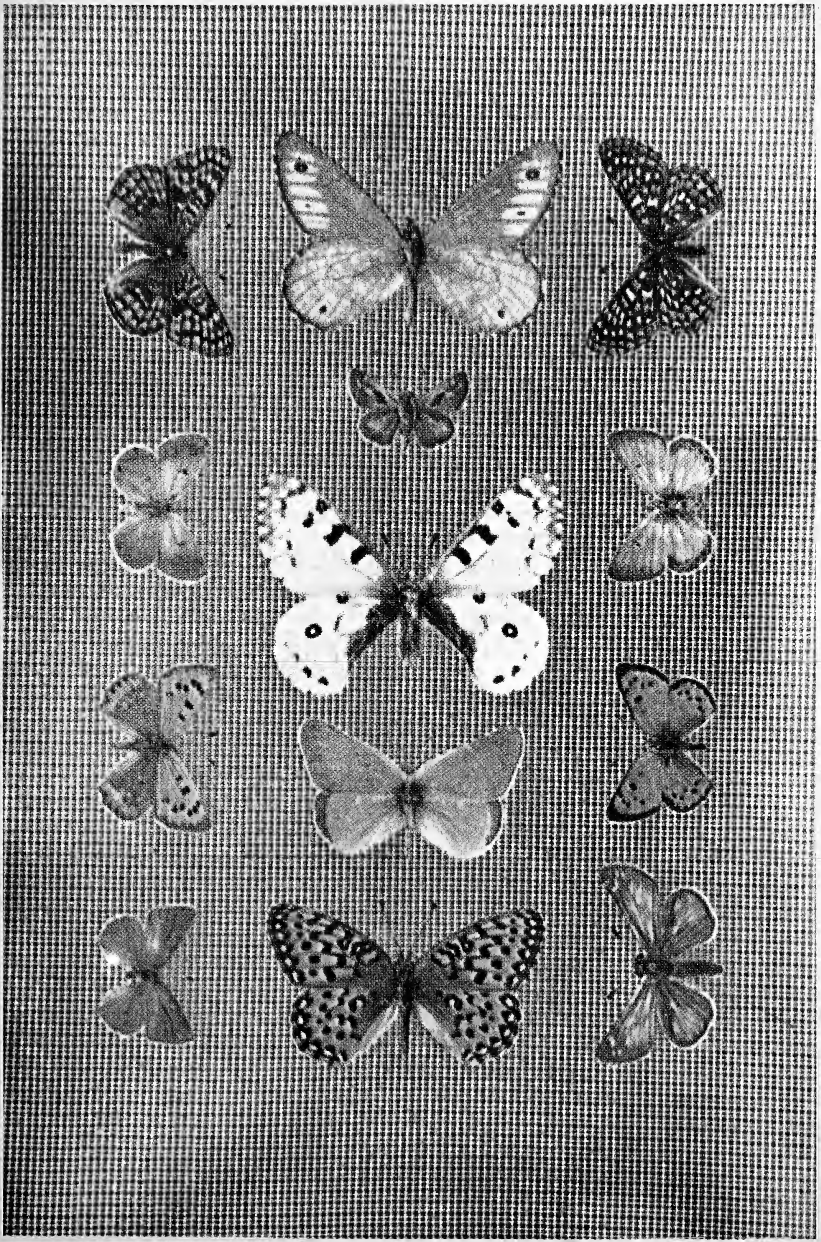

Volume 2 *Number 1* *July, 1963*

THE JOURNAL OF RESEARCH ON THE LEPIDOPTERA

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THE PURPOSE OF THE JOURNAL is to combine in one source the work in this field for the aid of students of this group of insects in a way not at present available. THE JOURNAL will attempt to publish primarily only critical and complete papers of an analytical nature, though there will be a limited section devoted to shorter papers and notes. QUALITY WORK on any aspects of research on the Lepidoptera is invited. Analytical and well illustrated works are preferred, with a minimum of long description.

AUTHORS ARE REQUESTED to refer to the journal as an example of the form to be used in preparing their manuscripts. Illustrations should be of the best quality black and white, or line drawings and should be pre-arranged by the author to fit a reduced size of 4" x 6½." Footnotes should be avoided; bibliography should be as indicated. Tables should be set-up for page size as indicated. Manuscripts in good form and requiring little work by the editor will naturally appear first. Authors, who wish drawings made for them, may submit rough sketches and will be billed for the cost, which will be very negligible. Work to be done on research grants should so specify. When possible, tabular matter should be typed on good paper with a carbon ribbon in a form suitable for a one-third reduction and in a size to fit 4" x 6½."

THE JOURNAL is not a suitable place for continued changes of nomenclature; unless the author is himself analytically studying a group from its biological point of view and finds a change necessary, the editor must ask authors to refrain from any changes from the McDunnough Check List unless superseded by a monograph published since that date. Popular books are not to be considered as giving scientific credence to any name. It is rare that name changes need be made and preference is given to old names unless in the editor's opinion sufficient evidence is given to warrant such change.

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Journal of Research on the Lepidoptera 2(1):1-96
1140 W. Orange Grove Ave., Arcadia, California, U.S.A.

YOSEMITE BUTTERFLIES

An Ecological Survey of the Butterflies of the Yosemite Sector of the Sierra Nevada, California

JOHN S. GARTH
Allan Hancock Foundation
University of Southern Californa
Los Angeles, California
and
J. W. TILDEN
San Jose State College
San Jose, California

July, 1963

FOREWORD

Organized interpretation of the chief features of National Parks had its beginning in Yosemite National Park in 1920. Suitable guide leaflets and bulletins found a useful place in the educational program. At first printed material covered wide fields of nature study. But with more visitors have come many with specialized backgrounds and they seek help. Whereas, the first bulletins attempted coverage of all insects found, we now come to one dealing only with butterflies. The senior author graduated from the Yosemite School of Field Natural History with the Class of 1933 and made his first contribution to the subject by publishing a list of the Butterflies of the Boundary Hill Research Reserve (Bull. Southern California Academy of Sciences, 33, Sept.-Dec., 1934, pp. 131-135). He widened his studies to the Butterflies of Yosemite National Park in the fifties and herewith is a paper that emphasizes where each butterfly is found and what plant its larvae feed upon. Colored plates give the amateur a chance to identify species found and the text places zonal locations and ecology. Other national parks that have profited by the senior author's field work are Grand Canyon, Glacier, and Grand Teton. Crater Lake and Lassen have profited similarly from the field work of the junior author.—Harold C. Bryant.

The original costs of this publication were underwritten by the Lepidoptera Foundation and the Journal of Research on the Lepidoptera and the separate issue is made available as a public service to visitors of the Yosemite National Park and adjacent areas.

William Hovanitz, Founder, The Lepidoptera Foundation
Editor, The Journal of Research on the Lepidoptera

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ALLAN HANCOCK FOUNDATION CONTRIBUTION Number 248.

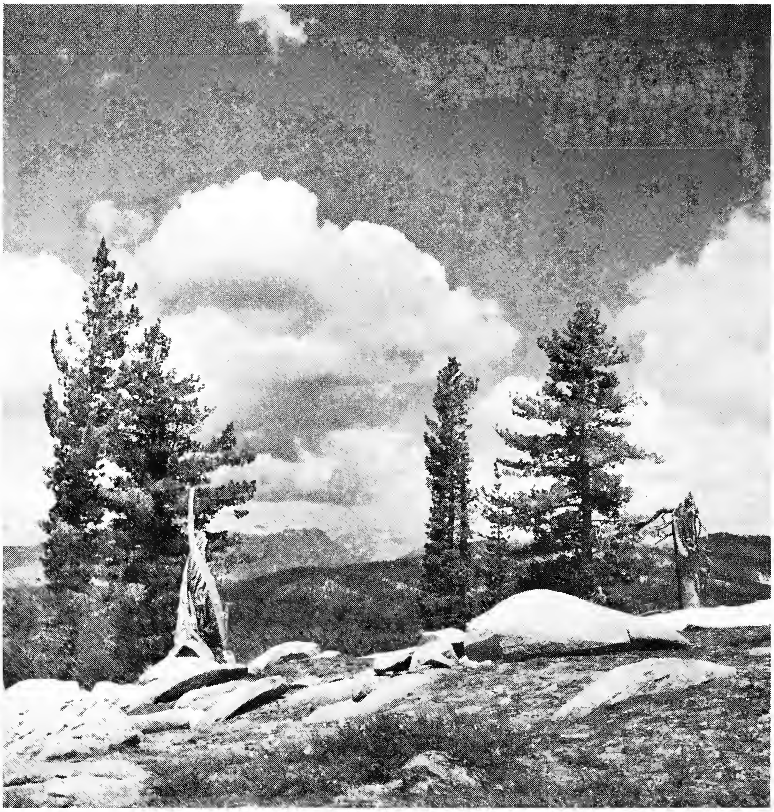
CONTENTS

HISTORICAL NOTE

The authors are indebted to Mrs. Mary V. Hood, Park Historian, Yosemite National Park, for calling their attention to an early record of butterfly collecting by John Muir, as recorded by W. F. Badè in *Life and Letters of John Muir,* 1924:

> Muir to Mrs. Ezra S. Carr, August 13, 1871. "I suppose you have seen Mr. King, who kindly carried some [butter]flies for Mr. Edwards . . . I collected most of them upon Mount Hoffman, but was so busy in assisting Reilly that I could not do much in butterflies." (*Op. cit.,* Vol. I, p. 292).
>
> Henry Edwards to John Muir, August 25, 1871. "In the small box that you sent me [through Mrs. Carr] are four species new to my collection and two of these are new to science . . . All the specimens are rare, and are different from those found in the Valley. The two new species are the bright crimson copper one from Cathedral Peak, and one of the small bluish butterflies. There is a pair of greenish yellow ones, very rare and interesting. The species was described from a pair only which were taken by the Geological Survey at the headwaters of the Tuolumne River, and strange to say, no others have turned up until you found it now . . . It is really very singular that the remove of a few miles from the Yosemite should produce species so very different from those of the Valley itself, and at the same time so characteristic in their forms." (*Op. cit.,* pp. 263-264).

Of the butterflies mentioned, the bright crimson copper is probably The Lustrous Copper, *Lycaena cupreus* (Edw.), while the greenish yellow ones are undoubtedly Behr's Sulphur, *Colias behrii* Edw. It should be noted, however, that the author is W. H. Edwards in each case. Both species are illustrated on color plate III.



Frontispiece. Boundary Ridge, el. 9,000 ft., Research Reserve. Western White Pine and sparse ground cover of herbs and grasses. Hudsonian life zone elements weakly present. Rocky outcrop association. *Papilio zelicaon* flies to the summit, while *Euchloe creusa hyantis* and *E. ausonides coloradensis* keep to the leeward of the ridge.—Neva Snell.

INTRODUCTION

The Yosemite National Park embraces 1,189 square miles of the most diversified territory to be found in the Sierra Nevada. From the edge of the San Joaquin Valley at near sea level it extends to the crest of the Sierran divide, culminating in Mt. Conness, Mt. Dana, and Mt. Lyell, each over 13,000 feet in elevation. Between these extremes occurs a wide range of climatic conditions, giving rise to a wealth of plant and animal life scarcely to be duplicated elsewhere on the North American continent. The vertebrate fauna has been thoroughly investigated by Grinnell and Storer (1924), who recorded 97 species of mammals, 231 of birds, and 34 of reptiles and amphibians in "Animal Life in the Yosemite," their Yosemite sector extending beyond park boundaries to include part of the San Joaquin Valley and of the Mono Basin as well.

The larger host of invertebrates, and of insects in particular, have long demanded similar investigation. The butterflies are an ideal group with which to begin this study. They are diurnal, or daylight fliers, and so lend themselves to easy observation, as distinguished from moths, of which most are nocturnal or crepuscular in flight. They are also for the most part conspicuous, and therefore likely to attract the attention of even the casual park visitor. Again, their number as species found in a given area roughly approximates the number of bird species, if only those actually residing (*i.e.,* nesting) in that region be enumerated. Thus the butterflies constitute a natural group of insects small enough to be encompassed by the amateur naturalist in a season, yet sufficiently diversified to entice the professional entomologist to return year after year to resolve the problems of habit and habitat that they present.

Like the many other natural attractions of our National Parks, butterflies enjoy the protection of far-sighted legislation and are held in trust for future generations as part of America's outdoor heritage. Their unauthorized removal is contrary to park regulations; however, the advanced researcher who can establish his connection with a public museum or other scientific institution, such as a university, may qualify for one of two types of collecting permits, and should consult the Park Naturalist, with offices in the Yosemite Museum, regarding his eligibility for this consideration.

THE LEPIDOPTERIST'S YOSEMITE

The territory now included in Yosemite National Park has been known to butterfly enthusiasts since the days of the gold rush of '49. The pioneer entomologist, Pierre Lorquin (for whom Lorquin's Admiral is named), followed the mother lode to Placerville, and from thence crossed the Sierra. His exact route is not known, but if he crossed by Tioga Pass, el. 9,941 ft., it is quite possible that the "Great Salt Lake" above which he discovered the Irene Fritillary (*Argynnis atlantis irene*) was Mono Lake, and not the Great Salt Lake of Utah. Indeed, had type localities been designated as carefully then as now, we might find that many of our California butterflies were first observed by a naturalist somewhere in the Yosemite region. The hermit Lembert (whose name is memorialized in Lembert's Dome) for many years supplied the entomological world with specimens of Behr's Sulphur (*Colias behrii*) from his hideaway in Tuolumne Meadows, and it was not until the Tioga Road opened to tourist travel in 1915 that his secret source of this rarity was discovered.

The entire northern section of the park and much of the southeastern part is still traversable by foot or horseback only, and is virgin territory for the lepidopterist. For many years following its establishment in 1925 the Yosemite Field School (short title for Yosemite School of Field Natural History) conducted annual summer excursions into this hinterland under the capable leadership of former Park Naturalist C. A. "Bert" Harwell. Begun as a six-day circuit of the established Hi-Sierra Camps, this "back-country trip" developed into an independent pack caravan that lost itself among the glaciers for a ten-day to two-week period and seldom returned without a contribution to the natural history of the park. During the 1933 to 1937 period the Field School included among its members a number of students of insects whose training and experience made it possible to observe and record much valuable information concerning the habits of rarely encountered species, particularly in connection with the annual surveys of Boundary Hill Research Reserve, instigated in 1933 by Joseph S. Dixon, field biologist, National Park Service. Sections on butterflies in the Research Reserve Reports were written in 1933 by John S. Garth and Fred C. Ziesenhenne, in 1934 by Janet Mabry and Edmund D. Godwin, in 1935 by Theodore H. Eaton, Jr., and in 1937 by Robert Godwin, Frances Cramer, and Verlin Baysinger. The 1936 report, by R. Paul Allen and Carsten Aherns, noted succinctly: "Rain for six days, no butterflies." These reports are on file at the Yosemite Museum, where they constitute an important supplement to the published report of Garth (1935a).

It was as a resurvey after an absence of 23 years from Yosemite that the senior author undertook the present assignment at the request of Chief Park Naturalist Douglass H. Hubbard, the intervening years having been enriched with similar experiences at Grand Canyon, Glacier, and Grand Teton national parks. Desirous of extending the earlier coverage of the park, he began his observations in 1956 in the vicinity of Mather, including the lower Tuolumne, Hetch-Hetchy, and Aspen valleys. In the same year the junior author, whose Yosemite experience also dates from the late 1920's, began under park auspices an ecological study of the area adjacent to Tioga Pass, including a transect from Pilot Peak to Mt. Dana (Tilden, 1959). Since both investigators were limited to brief visits to the area at critical periods, they were fortunate to find in Oakley Shields a summer resident whose activities spanned the entire season at Tuolumne Meadows, where his father, Allan Shields, was a seasonal naturalist. By combining records over the succeeding 7-year period it has been possible to present a fairly consistent picture of the situation in the park's high country, its western approaches, and of the Mono Basin to the east, although the coverage of some areas is less complete than might have been desired.

THE SURROUNDING NATIONAL FORESTS

The visitor driving to and from Yosemite Valley commonly arrives by one of three routes from the west and leaves by another. These are California State Highways 41 via Coarsegold and Wawona, 140 via Mariposa and El Portal (the All-Year Highway), and 120 via Groveland and Buck Meadows. For many miles he travels through wooded foothills of the Sierra and Stanislaus National Forests, where opportunities for observing butterflies are equal to those within the National Park, while collecting is unrestricted. If visiting Tuolumne Meadows, he may wish to leave the Park by its eastern entrance, traveling through Inyo National Forest from Tioga Pass to Lee Vining, there joining U. S. Highway 395. Should he seek an area comparable to the Park's high country he will find it at Saddlebag Lake, accessible by road from Tioga Lake, and adjacent to the Hoover Wildlife Preserve and the Hall Primitive Area. Other east-slope mountain lakes accessible from Highway 395 are Lundy Lake, the Virginia Lakes, and the June Lake circuit.

During the years 1950-1958 the junior writer spent considerable time in the Mono Lake region, obtaining many records later verified and extended by Oakley Shields. In 1958 the senior writer established temporary residence at June Lake and from this base made one-day trips to Gem Lake, Saddlebag Lake, and the Virginia Lakes basin. In 1957 and again in 1959 Oakley Shields crossed the Sierran Divide at Donohue Pass and proceeded southeastward via Agnew Pass to Agnew Meadows. In the spring of 1961 particular effort was made by Park Naturalist Keith Trexler to explore the western foothills, where the season begins from six weeks to two months earlier than in Yosemite Valley. The results of these extra-limital investigations were to add a number of species that rarely, if ever, occur within Park boundaries, but which deserve consideration in any account of the butterflies of the Yosemite region, which includes the encircling National Forest lands as well. It is the authors' hope that the inclusion of these localities outside the Park will serve to entice the butterfly enthusiast away from the few crowded centers and into the less frequented but no less rewarding byways.

YOSEMITE FOOT-TRAILS

While some of the most spectacular butterflies, including the Leto Fritillary (*Argynnis cybele leto*) and the California Sister (*Limenitis bredowii californica*), fly within the confines of Yosemite Valley, the lepidopterist seeking the rarities for which the Park is famous must be willing to do some strenuous hiking. The valley walls rise perpendicularly three thousand feet and more, but once their summit is gained a large expanse of comparatively level country is accessible by means of foot-trails that wind through alpine meadows fragrant with wildflowers. Over 700 miles of such trails traverse the territory within Park boundaries, making the Yosemite a veritable entomologist's paradise.

Leaving the north side of the valley floor by the Yosemite Falls trail, a two-hour climb, best accomplished in the early morning, places one in a position to select either the Eagle Peak, Yosemite Creek, or North Dome trails for a day among the Parnassians (*Parnassius clodius baldur* and *P. phoebis behrii*). Likewise, the ascent to Glacier Point by the Ledge or Four-Mile trails allows the entomologist a choice of either the Pohono or Glacier Point trails that parallel the south rim of the valley and along which the Nivalis Copper (*Lycaena nivalis*) is certain to be encountered. The "high country," reached either via Lake Tenaya or Lake Merced, is the habitat of the Ivallda Arctic (*Oeneis chryxus ivallda*), Malcolm's Checker-Spot (*Melitaea damoetas malcolmi*), and the Lustrous Copper (*Lycaena cupreus*). It was the privilege of the senior writer, as a member of the Yosemite Field School class of 1933, to cover over 200 miles of trail outside of Yosemite Valley, climbing Mt. Lyell, el. 13,090, Mt. Kuna, el. 12,956, and Mt. Dana, el. 13,050 feet, on successive days, and in 1958, exactly 25 years later, to retrace a portion of this itinerary, from Tuolumne Meadows to Merced Lake via Vogelsang Pass, with Oakley Shields. (And aside from the trail's being steeper and the butterflies more elusive, things were much as he remembered them!) Generally speaking, June is the month for exploring the Yosemite Valley, July for the valley's rim, and August for the glacier country.

LIFE ZONES

The incline from El Portal on the west to the Sierra Crest at the eastern park boundary may be subdivided into five regions or life zones, each supporting a distinctive flora and fauna. These zones, in ascending order, are Upper Sonoran, Transition, Canadian, Hudsonian, and Arctic-Alpine. A sixth zone, the Lower Sonoran, occurs a few miles west in the San Joaquin Valley. Thus within the greater Yosemite region is to be found every life zone recognized in temperate North America with the exception of the Subtropical, found only in Florida and southern Texas. In many cases the zones merge imperceptibly, as when a forest predominantly of Jeffrey Pine and Incense Cedar, typically Transition, gives way to one of Red Fir and Quaking Aspen, typically Canadian. In others the line of demarcation may be startlingly abrupt, as when the south slope of a chaparral-clothed ridge (Upper Sonoran) gives way to an open evergreen glade (Transition) on the opposite-facing north slope at the same elevation. While the subject of life zones has been exhaustively treated elsewhere, it may be said that of the factors that determine life zones temperature is the single most important, and that temperature is regulated by latitude, altitude, direction of prevailing winds, proximity to bodies of water, ascending currents of warm air from desert regions, descending drafts of cold air from mountain tops or glaciers, character of substrate, and pattern of drainage.

BUTTERFLIES AS LIFE-ZONE INDICATORS

Plants and animals may be divided into two groups with respect to life zones: those that range over a wide territory and those that adhere closely to a single zone. The former are called cosmopolites because of their unrestricted movement; the latter are called indicators, because their presence is considered sufficient to establish the presence of the zone. (See Grinnell and Hall, 1919). Thus the Cony (*Ochotona*) of the rock slides is an indicator of Hudsonian Zone; the Sierra Nevada Rosy Finch (*Leucosticte*) of the snow banks is an indicator of Arctic-Alpine Zone; and the Chamise (*Adenostoma*) of the chaparral is an indicator of Upper Sonoran Zone. On the assumption that the most permanent indicators are those most to be relied upon, plants and animals might be arranged, in descending order of reliability, in the following order: trees and shrubs, herbs and forbs, mammals, reptiles and amphibians, and birds. In attempting to place insects in such a scale consideration need be given to their dependence on a particular host plant in the larval stage, their normal flight range as adults, and their migratory habits. Thus the insect combines the fixity of the plant, the mobility of the mammal or reptile, though to a resricted degree, and the periodic wanderings of the bird, although less perfectly developed. The insects might with some justification be ranked between

Figure 1. Profile of the YOSEMITE REGION showing life zones and biotic provinces, together with a list of the butterfly species most closely restricted to them.

CALIFORNIAN PROVINCE

UPPER SONORAN ZONE

Coenonympha t. californica
Cercyonis silvestris
Argynnis c. inornata
Euphydryas c. chalcedona
Euphydryas e. rubicunda
Melitaea leanira
Apodemia m. tuolumnensis
Habrodais grunus
Strymon auretorum
Strymon adenostomatis
Callophrys d. windi
Callophrys dumetorum
Callophrys iroides
Lycaena a. arota
Lycaena gorgon
Philotes speciosa
Pieris napi venosa
Epargyreus clarus
Thorybes pylades
Heliopetes ericetorum
Erynnis z. funeralis

TRANSITION ZONE

Argynnis c. leto
Argynnis z. zerene
Argynnis hydaspe
Callophrys johnsoni
Callophrys nelsoni
Everes amyntula
Colias o. chrysomelas
Thorybes diversus
Hesperia h. yosemite
Amblyscirtes vialis

CANADIAN ZONE

Argynnis irene
Boloria epithore
Euphydryas c. sierra
Melitaea hoffmanni
Lycaeides a. anna
Plebejus saepiolus
Plebejus lupini
Anthocharis s. stella
Pyrgus ruralis
Erynnis p. lilius
Hesperia harpalus, blend

HUDSONIAN ZONE

Callophrys lemberti
Lycaena mariposa
Lycaena nivalis
Philotes b. battoides
Plebejus g. podarce
Glaucopsyche l. columbia
Colias behrii
Thorybes m. nevada
Polites s. tecumseh

ARCTIC-ALPINE ZONE

Oeneis c. ivallda
Euphydryas e. nubigena
Melitaea d. malcolmi
Lycaena cupreus
Lycaena p. hypophlaeas
Plebejus s. comstocki
Pieris o. calyce
Parnassius p. behrii
Hesperia miriamae

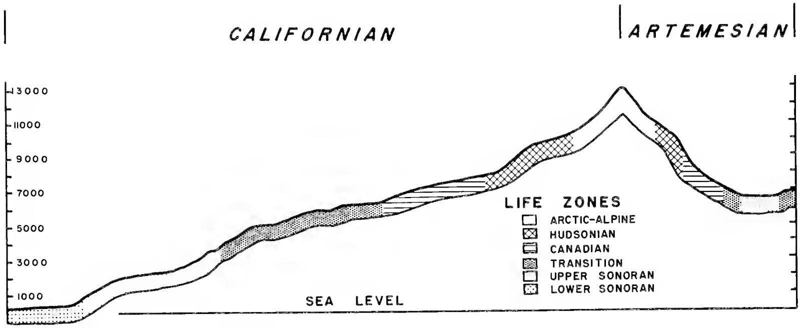
ARTEMESIAN PROVINCE

CANADIAN-HUDSONIAN

Cercyonis oeta
Argynnis z. malcolmi
Lycaena heteronea
Lycaena rubidus
Lycaena editha
Hemiargus isolus
Thorybes m. nevada
Hesperia nevada

TRANSITION-UPPER SONORAN

Coenonympha t. mono
Cercyonis p. ariane
Danaus g. strigosus
Argynnis n. apacheana
Argynnis c. nevadensis
Euphydryas e. monoensis
Melitaea acastus
Limenitis w. nevadae
Apodemia m. mormo
Strymon dryope
Lycaena a. virginiensis
Everes comyntas
Leptotes marina
Philotes b. glaucon
Pieris beckeri
Colias p. hagenii
Hesperia harpalus



the plants and the vertebrates, possessing greater reliability as indicators than the mammals, birds, and reptiles on which much of the ecological work of the past has been done, their importance in this respect having but lately been recognized.

The first attempts at zonal analysis of California butterflies were of necessity incomplete and therefore inconclusive. Based upon the record, in some cases, of but a single specimen, and without knowledge, in many instances, of the larval food plant, the assignment of the species to a given life zone was made without knowledge of its status within that zone, whether as resident or vagrant. The pioneer work of Comstock and Dammers in the 1930's made known the life histories of most of the butterfly species of the southern half of the state, while workers of a younger generation, among whom may be mentioned Don MacNeill, John Burns, G. and R. Bohart, Noel McFarland, Paul Opler, Tom and John Emmel, and Oakley Shields, have defined the range of species and subspecies within the entire state with exactness. Thus the life zone normally inhabited by a butterfly of the Yosemite region can be stated with more assurance than was possible a quarter-century ago. A brief characterization of life zones follows:

Upper Sonoran Zone: The chaparral or "elfin forest" that clothes the foothills from 1,500 to 4,000 feet (occasionally lower) constitutes the Upper Sonoran Zone. It is characterized by a great variety of shrubby plants, many of which exhibit remarkable adaptations for conserving moisture, including anastomosing root systems that check soil erosion. Digger Pine, California Buckeye, Poison Oak, and Chamise (*Adenostoma*) are typical species, as is Interior Live Oak of the included Foothill Woodland community. The Chalcedon Checker-Spot (*Euphydryas c. chalcedona*), California Ringlet (*Coenonympha tullia californica*), and Sylvan Satyr (*Cercyonis silvestris*) seldom stray beyond the confines of this life zone.

Transition Zone: Between the Austral zones (Lower and Upper Sonoran) and the Boreal zones (Canadian, Hudsonian, and Arctic-Alpine) lies a broad intermediate area known as Transition Zone. Its coniferous forest contains the trees of greatest commercial value: Big Tree, Yellow Pine, Jeffrey Pine, Sugar Pine, Incense Cedar, White Fir, and Douglas Fir. Azalea, Nuttall Dogwood, and Black Cottonwood fringe its streams; Black Oak and Golden Cup Oak clothe its valley floors and mountainsides, respectively. The Leto, Hydaspe, and Zerene fritillaries (*Argynnis cybele leto, A. hydaspe,* and *A. z. zerene*) represent its considerable butterfly population. Transition Zone extends from 4,000 (or less in some localities) to 7,000 feet, merging imperceptibly into Canadian Zone along its upper border.

Canadian Zone: Red Fir replaces White Fir in the open forest and Quaking Aspen displaces Azalea and Black Cottonwood along the water courses. A secondary chaparral, reminiscent of Upper Sonoran Zone, but composed of matted Snow Brush (*Ceanothus*), Chinquapin

(*Castanopsis*), and Huckleberry Oak (*Quercus vaccinifolia*), covers the steeper slopes. The Western Banded Elfin (*Callophrys eryphon*), Sierra Checker-Spot (*Euphydryas chalcedona sierra*), and Western Meadow Fritillary (*Boloria epithore*) are good butterfly indicators. Canadian Zone extends from 7,000 to 9,000 feet (or less in some localities), with Lodgepole Pine invading from its upper margin.

Hudsonian Zone: At about the 8,500 foot level Lodgepole Pine appears, to be joined at the 9,000 foot level by Mountain Hemlock to form the Hudsonian forest, discontinuous because of the tremendous rock slides and glacial cirques. Tuolumne Meadows, at 8,600 feet, is pure Hudsonian and here are found Behr's Sulphur (*Colias behrii*), the Podarce Blue (*Plebejus glandon podarce*), and the Mariposa Copper (*Lycaena mariposa*). The upper limits of Hudsonian Zone are defined by timberline at approximately 11,000 feet.

Arctic-Alpine Zone: The Alpine Willow, stunted to a height of a few inches, and the Sierra Nevada Rosy Finch inhabit the bleak talus slides and snow banks above timber line. The zone is characterized by perennial herbs with small tops and large root systems. The heathers, *Bryanthus* and *Cassiope,* and Alpine Sorrel (*Rumex*) cling to meager patches of damp soil. The Ivallda Arctic (*Oeneis chryxus ivallda*), Malcolm's Checker-Spot (*Melitaea damoetas malcolmi*), and the tiny Yosemite Blue (*Plebejus shasta comstocki*) fly from 11,000 feet (occasionally less) to the tops of Mt. Dana and Mt. Lyell. Recently Miriam's Skipper (*Hesperia miriamae*) has been added to the strictly Arctic-Alpine list.

It should be remembered that it was in California, and particularly on the west slope of the Sierra Nevada, that most of the detailed work on life zones, including the delineation of indicator species, was done. It is also on the west slope of the Sierra Nevada and Cascade ranges that life zones attain their optimum development, occurring in regular succession from west to east in response to moderate gradients of slope and a comparatively mild, ocean-controlled climate. Elsewhere life zones are likely to occur haphazardly, with extreme local conditions often overriding the effects of latitude and altitude, which elsewhere are the principal factors governing temperature, on which the life-zone concept was originally based. One of these, the humidity factor, was taken into consideration by Grinnell, Storer, and Dixon in both the Yosemite and Lassen sectors, which included an arid region east of the Sierra divide. Their concept of a trans-montane fauna conditioned by high aridity as opposed to a cis-montane fauna conditioned by high humidity leads us to the principle of replacement of one set of zonal indicators by another whenever certain natural boundaries are transgressed. This is better expressed within the context of a more recent ecologic concept, that of the Biotic Province.

BIOTIC PROVINCES

The replacement of one set of indicator species by another can be so complete that we may question whether we are dealing with the same life zone in two widely separated regions, or even in adjacent regions, when each indicator species has been replaced by a different but closely related species or subspecies. The solution to this predicament is found in the concept of the Biotic Province, originated by Vestal (1914) and developed by Dice (1943), who divided the North American continent into 28 biotic provinces, of which 14 occur in states west of the Rockies, 7 in California. These are geographical areas, permanent and mutually exclusive, and containing within their confines vertical bands that Dice calls, not life zones, but life belts. In such a system the principle of replacement need not be considered, for by definition no life belt extends beyond its province, although similar life belts may occur in adjacent provinces.

In the Yosemite region, as has been mentioned, all life zones are represented from Lower Sonoran (in the San Joaquin Valley) to Arctic-Alpine, with a correspondingly wide spectrum of plant and animal life. Park boundaries are drawn, however, in such a manner that the eastern boundary coincides with the crest of the Sierra Nevada, thus limiting the park proper to one biotic province, the Californian. If we extend the Yosemite sector eastward to include the eastern slope of the Sierra (as did Grinnell and Storer in extending their Yosemite sector to the shore of Mono Lake), we will have added another biotic province, the Artemesian, and with it the replacement species of that province, potentially doubling the list of species for zones above 6,500 feet. No more than this could be accomplished by combining the species lists from two different parks, the one completely Californian, the other Artemesian. Furthermore, such an extension is necessary in order to compare the butterfly faunas of Yosemite and Lassen, whose boundaries stop at the Sierran Crest, with those of Glacier and Rocky Mountain, whose boundaries include territory on both sides of the Continental Divide.

An unexpected dividend for the biologist of this meeting of faunas along the border of two biotic provinces is the opportunity of studying natural hybridization. Perhaps no better experimental material has been provided by nature for this purpose than the butterflies known as Admirals (genus *Limenitis*). These are found throughout North America and are known as allopatric, or replacement, species. Opportunity to observe natural hybridization between Californian *L. lorquini* and Artemesian *L. weidemeyerii nevadae* occurs where their ranges meet on the west shore of Mono Lake. A similar opportunity to observe natural hybridization between Montanian *L. lorquini burrisoni* and Saskatchewan *L. arthemis rubrofasciata* occurs on the east side of Glacier Park, at Many Glacier. Whether the fact that they hybridize readily reduces the *Limenitis* complex to a single polymorphic species is a debatable question; however, it should be noted that the interbreeding is limited to a narrow buffer zone and does not extend to entire populations, and that wherever it occurs both parent species are present, as would be required to perpetuate the hybrid, which is presumed to be sterile.

PLANT COMMUNITIES

A more subtle ecologic division than either life zone or biotic province has long been sought by entomologists attempting to define more closely the habitats of insect species. This has at last been provided in the system of plant communities developed by Munz and Keck (1949, 1950). Of the 28 California plant communities recognized by these authors, at least 16 (plus two of our own designation) occur in the greater Yosemite region. Here an attempt is made to list in sequence the plant communities that one might encounter in crossing the Sierra Nevada from San Joaquin Valley to Mono Lake, with a side trip into Yosemite Valley:

1. Valley Grasslands (on leaving the Valley).
2. Foothill Woodland (as around Cathay).
3. Chaparral (the familiar "elfin forest").
4. Coastal Sage Scrub (formerly California Sagebrush Association, includes Honey Sage Scrub, occurs sporadically).
5. Oak Woodland (including Golden Cup Oak lands; as Yosemite Valley).
6. Mixed Evergreen Forest (Laurel-Madroño association; as Yosemite Valley walls).
7. Yellow Pine Forest (monotypic, with an understory of "Mountain Misery").
8. Mixed Forest (non-pure Douglas Fir, Yellow Pine, and broadleaf trees below pure conifers). Our designation; probably an ecotone.
9. White Fir-Cedar Forest (on cut-over land, as at Mather). Our designation; a successional sub-climax or post-climax community.
10. Red Fir Forest (as between Tamarack Flat and Smoky Jack).
11. Lodgepole Pine Forest (as Tuolumne Meadows).
12. Subalpine Forest (often with Mountain Hemlock and White-Bark Pine; as Tioga Pass).
13. Alpine Fell-Fields ("rock gardens" above timber line; as Gaylor Lakes).
14. Juniper Woodland (eastern declivity; as below Tioga Pass).
15. Piñon-Juniper Woodland (lower down; as around Lee Vining).
16. Sagebrush Scrub (Great Basin Sage, *Artemesia tridentata*).
17. Shadscale Scrub (the Salt-Bush type of scrub).
18. Alkali Sink (as around Mono Lake).

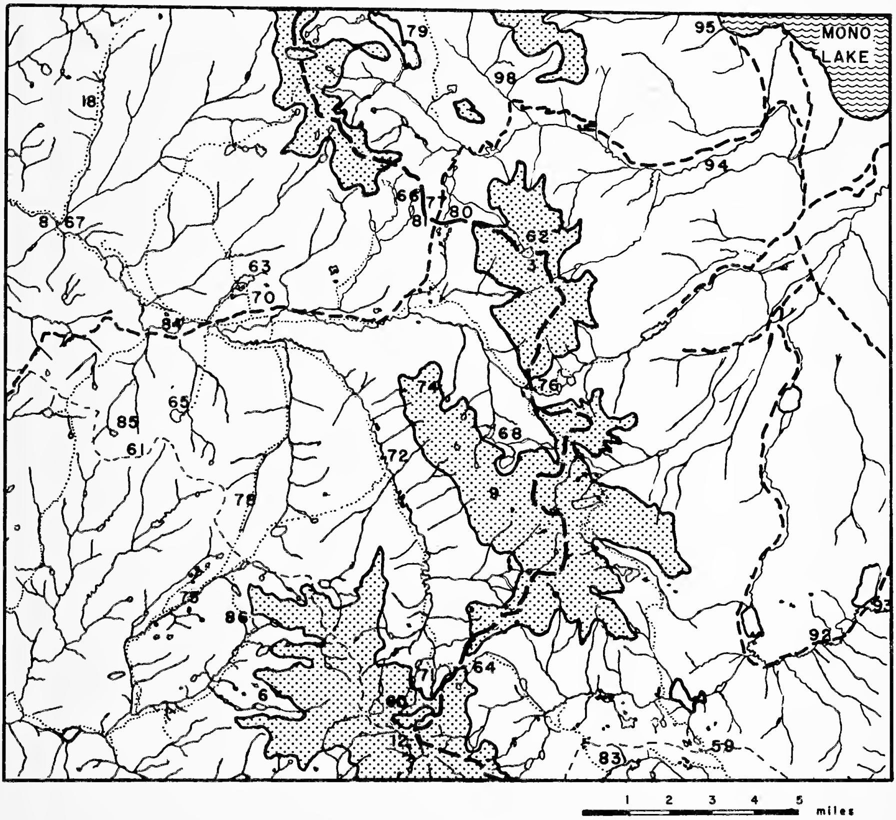


Figure 2. Map showing the YOSEMITE high country, indicating roads --------, trails.........., streams ______________, areas over 11,000 feet in elevation and collecting localities:

1933-1934 : 3, Mt. Dana; 6, Florence Lake; 8, Glen Aulin; 9, Kuna Crest; 12, Mt Lyell; 18, Coldwater Canyon.

1956-1962: 59, Agnew Pass; 60, Bert L.; 61, Cockscomb Pk.; 62, Mt. Dana, N. slope; 63, Dog L.; 64, Donohue Pass; 65, Elizabeth L.; 66, Gaylor L.; 67, Glen Aulin; 68, Helen L.; 70, Lembert Dome; 71, Lyell Base Camp; 72, Lyell Fork Meadow; 74, Mammoth Pk.; 75, Merced R.; 76, Mono Pass; 77, Pilot Pk.; 78, Rafferty Ck. Tr.; 79, Saddlebag 80, Tioga Pass; 81, NW above Tioga Pass; 83, Thousand Island L.; 84, Tuolumne Meadow; 85, Unicorn Pk.; 86, Vogelsang Pass.

East slope , 1956-1962: 92, Gull L.; 93, June L.; 94, LeeVining Cr.; 95, Mono L.; 98, Warren Ck.

> [One of us (Tilden) suggests the presence of still another east-slope brush community, consisting of *Cercocarpus, Purshia,* and desert *Prunus,* not provided for in the system proposed by Munz and Keck.]

It will be noted that by far the greater number of plant communities (13 as against 5) are found on the western slope, which has the greatest extent both in distance and in elevation. It will further be seen that as one progresses beyond 13, which represents the Sierran crest, the plant communities are entirely different from those before 13, yet they occupy corresponding altitudinal belts and life zones in reverse order. This difference in plant life is paralleled by a difference in animal life, including the insects, and is evidence that each slope lies in a different biotic province, where relative humidity, rather than temperature difference based on altitude, is the controlling factor. Perhaps no better example could be given of the need for both systems (life zones and biotic provinces).

FOOD PLANTS

The lepidopterist who pursues his interest seriously becomes increasingly aware of the dependence of insects on plants. For not only do butterflies as adults seek flowers for nectar, but as caterpillars they depend on vegetation for sustenance. Many are highly selective in their choice of plant food, adhering to one kind and rejecting all others. More frequently, however, any one of a group of related plants will serve: witness the predilection of the Whites for mustards, or of the Sulphurs, for legumes. The lepidopterist soon learns to equate these butterfly preferences with plant groups possessing certain structural resemblances, particularly as regards their flowers, and recognized by botanists as plant families. A list of thirty-eight common plant families and one hundred eleven of their genera on which butterflies of the Yosemite region are known or believed to feed as larvae is presented with the hope that it will lead to further investigation.

Occasionally, and for no apparent reason, a butterfly will be found to feed upon a plant quite unrelated to those usually preferred by its group. Thus *Colias behrii* is known to be a *Vaccinium* feeder, whereas most *Colias* species prefer legumes. But as Hovanitz (1950) has shown, the *Vaccinium*-feeding habit is shared by several *Colias* species in other parts of the world. Since it is highly improbable that such a choice of food plant would have been made independently by each of them, this food habit becomes a clear indication of relationship, setting the *Vaccinium* feeders apart from others of their genus. When one of the Whites, *Neophasia menapia,* forsakes the mustards usual to its group for the needles of a pine tree, we may be certain that it is not temporarily off its diet, but that it is following a behavior pattern as old as the genus itself, and perhaps responsible for its segregation.

Often a butterfly named for the plant believed to be its host has proven to feed upon another. The hair-streak, *Strymon adenostomatis,* was found to feed on Mountain Mahogany (*Cercocarpus*), and not on Chamise (*Adenostoma*), as its given name would imply. (It should have been called *"cercocarpivorous"*!) Indeed, the question as to whether the Blues, *Plebejus acmon* and *P. lupini,* deserve specific distinction may ultimately rest upon whether they feed exclusively on Lupine (*Lupinus*) and on Buckwheat (*Eriogonum*), respectively, or indiscriminately on both.

Yosemite butterflies for which the larval food plant is either unknown or in need of confirmation are the following:

Unknown

Melitaea damoetas malcolmi
Melitaea hoffmanni
Callophrys doudoroffi windi
Callophrys lemberti
Lycaena nivalis
Plebejus glandon podarce
Plebejus shasta comstocki
Lycaeides argyrognomon anna
Thorybes mexicana nevada
Thorybes diversus
Erynnis persius
Erynnis propertius
Polites sonora

Needing Confirmation

Callophrys nelsoni (*Libocedrus*?)
Lycaena rubidus (*Rumex*?)
Lycaena phlaeas hypophlaeas (*Rumex*?)
Plebejus lupini (*Eriogonum*?)
Philotes speciosa (*Eriogonum* in Yosemite?)
Colias zerene (*Amorpha* not found in Yosemite)
Parnassius clodius baldur (for *Vaccinium* only)
Pyrgus ruralis (for *Potentilla* = *Horkelia* only)
Erynnis pacuvius lilius (*Ceanothus*?)

A documented observation of oviposition (egg laying) of any of these species, with positive identification of the plant of choice, or better still, the rearing of any of them from egg to adult would be an important contribution to the natural history of the Yosemite region.

SOME PLANTS ON WHICH YOSEMITE BUTTERFLIES FEED AS LARVAE

In the left hand column of the list (Table 1) that follows, host plants are listed alphabetically by family and genus. (To have listed plants by species would have prolonged the list unduly.) In the middle column the common name of the plant is given. In the right hand column butterfly species known or believed to feed on that plant are listed alphabetically by genus and species. (Subgenera are omitted, as are subspecies, where more than one occurs in Yosemite, unless each is known to have a different food plant.) The symbols o, l, and r indicate that the butterfly has been seen to ovipost on, the larvae have been taken from, or the insect reared to maturity on that plant by one of us. Otherwise, names of host plants have been taken from the literature, carefully culled to eliminate genera not known to occur in the Sierra Nevada. Butterfly species feeding on more than one plant are starred*.

Grasses (POACEAE=GRAMINACEAE) and Sedges (CYPERACEAE) are not listed because detailed information concerning the genera involved is lacking. Known to be grass feeders are all the SATYRIDAE and, of the HESPERIIDAE, the subfamily Hesperiinae. It is believed that when this information becomes available, it will be shown that butterflies exhibit as marked a preference for certain of the monocotyledonous grasses and sedges as they do for certain of the dicotyledonous plants.

THE GEOLOGICAL BACKGROUND

The landscape of the Yosemite region has been moulded by many forces, but by far the most impressive of these has been glaciation. The work of glaciers may be observed in the U-shaped gorges of the Tuolumne and Merced rivers, in the hanging valleys of Little Yosemite and Bridal Veil Creek, in the polished domes and erratic boulders, in the glacial lakes (called tarns) and cirques, and in the minaret summits of Cathedral and Unicorn peaks. Less evident, but no less genuine, are the effects of glaciation on the flora and fauna, including the butterflies. For as the glaciers retreated, the cold-adapted species followed them northward and to the mountain tops, where small glaciers continue to exist on the shaded slopes of Lyell, Maclure, Dana, and Conness. Thus the entire upper tier of life zones, the Canadian, Hudsonian, and Arctic-Alpine, is inhabited by butterfly species whose nearest relatives fly either on other isolated mountain tops in temperature regions or at near sea level in Canada, Hudson Bay, or the Arctic regions, as these zonal names imply. This discontinuous "boreo-alpine" distribution is as much a consequence of Pleistocene glaciation as the polished granite over which one walks along the Merced Lake trail, or the lateral moraines that rim the montane meadows.

A second consequence of Yosemite's geological history is that those butterflies that now fly above timberline, and in particular the grass-feeding Satyridae, such as The Ivallda Arctic (*Oeneis chryxus ivallda*) and Riding's Satyr (*Eumenis ridingsii*), and Hesperiinae, such as the newly found Miriam's Skipper (*Hesperia miriamae*), having no trees but only barren rock on which to alight, have come to resemble exactly the color, shade, and texture of the particular rock found in their restricted habitat, whether it be sedimentary or metamorphic. (See Hovanitz, 1940). In order that the lepidopterist may better appreciate these earthen pigments that provide the backdrop for the Yosemite landscape and constitute the palette from which the colors of Yosemite's alpine butterflies (Plate III) have been selected, although without design on the insect's part, the following quotation by Francois E. Matthes, father of Sierran geology, is given. The italics are the authors'.

> "Next to the broad belt on the lower slope of the Sierra Nevada, the masses of metamorphic rocks situated near the crest of the range are the most extensive. They make up the bulk of Mount Dana, Mount Gibbs, and Parker Peak, as well as the jumble of mountains north of Tioga Pass, whose central summit is Mount Warren. These mountains, in consequence of their composition, are variously tinted in subdued *yellows, browns, reds,* and *purples* and by contrast with the *pale-gray* peaks of granite near by appear somber, as if overcast by perpetual shadows. The metamorphic rocks in this crest region, however, differ appreciably in character as well as in structure from those in the lower belt. There is but little slate among them, schist, quartzite, and volcanic rocks being predominant; and the folding is less deep and less complex. These facts are readily observed on and about Mount Dana, which is capped by gently flexed beds of volcanic origin."
>
> —Matthes, 1930, p. 26.

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REGARDING NAMES USED IN THIS PAPER

Since the publication of "Butterflies of California" (Comstock, 1927), no comparable book on California butterflies has appeared. The excellent color plates make this a most useful reference, but time and the activities of butterfly students have brought about many changes. Additional species have been found to occur in California; numerous subspecies have been described; and many revisionary works have appeared. Among these may be mentioned those on Ringlets (Davenport, 1941; Brown, 1955), on Fritillaries (dos Passos and

Fig. 3. Mt. Lyell, el. 13,900 ft., from tree-line at about 11,000 ft. (Upper Lyell Base Camp). Arctic-Alpine life zone, Alpine Fell-Fields, with montane meadow and rock garden associations. Habitat of *Lycaena phlaeas hypophlaeas, Euphydryas editha nubigena, Melitaea damoetas malcolmi,* and *Oeneis chryxus ivallda.*—Joseph S. Dixon.

Grey, 1947), on Checker-Spots (Gunder, 1929; Bauer, 1961), on Metal-Marks (Opler and Powell, 1961), on Hair-Streaks (Ziegler, 1960; Clench, 1961), on Coppers (Klots, 1936; Clench, 1961), on Blues (Nabokov, 1949; Downey, 1961), and on Skippers (Lindsey, Bell, and Williams, 1931; Lindsey, 1942). As a result, only a fraction of our California butterflies continue to bear the generic and specific names by which they were known as recently as 1927.

Following the publication of "Check List of Lepidoptera of Canada and the United States of America" (McDunnough, 1938), incorporating changes recommended in "Generic Names of Holarctic Butterflies" (Hemming, 1934), together with the findings of many other workers, no similar standard of reference has been advanced. Publication of a new check list by C. F. dos Passos is believed imminent, and changes made since 1938 will be reflected therein. Many of these will have been anticipated in "A Field Guide to the Butterflies" (Klots, 1951), but this admirable little book treats only the eastern species. Still other modifications appear in "How to Know the Butterflies" (Ehrlich and Ehrlich, 1961).

In deciding what names to use in this article, the authors have tried to steer a moderate course, adopting many names now accepted by common usage, but avoiding some of the more recent innovations until these shall have met with general approval. The sequence and arrangement of genera and families follows as closely as possible what we are led to believe will be the arrangement of the forthcoming check list already referred to. The more advanced student as well as the professional should be able to make use of that publication in conjunction with this one, which is intended primarily as a field guide, and not primarily as a contribution to the systematic literature.

The authors' departure from a strict interpretation of the Rules of Zoological Nomenclature in designating the western subspecies of *Atlides halesus* as *estesi* Clench rather than as *corcorani* Gunder is deliberate. For while it is conceded that Gunder's name is the older of the two, it was applied, not to the entire race, but to a single aberrant individual. We believe that intent should be given due weight in such matters, and it was certainly not Gunder's intent to define the western subspecies, whereas it was Clench's. The same logic is followed in attributing *Lycaeides melissa inyoensis* to Nabokov, and not to Gunder.

ACCOUNT OF SPECIES OF THE YOSEMITE REGION

SATYRIDAE

1a. *Coenonympha tullia californica* West. & Hew. **Pl. I, fig. c**

b. *Coenonympha tullia mono* Burdick **Pl. IV, fig. a**

THE CALIFORNIA RINGLET and THE MONO RINGLET are the two races of this widespread species found in the Yosemite region, the former flying in the western foothills, the latter on the sage-brush flats of Mono Basin. Weak fliers, they keep close to the grasses on which the larvae feed. Following the studies of Davenport (1941) and Brown (1954, 1955), all North American ringlets except the rare Hayden's Ringlet, *Coenonympha haydenii* (Edw.), of Wyoming and adjacent states are considered subspecies of the Eurasian *C. tullia* (Müller), although Burdick (personal communication) was inclined to regard his *mono* as a derivative of the Great Basin-Rocky Mountain *C. t. ochracea* Edw., which he appeared to regard as a distinct species.

Life Zones: Upper Sonoran (Transition). Plant Communities: Valley Grasslands, Foothill Woodland; Sagebrush Scrub, Marsh. Host Plants: POACEAE (Grasses).

2. *Cercyonis pegala ariane* (Bdv.)

It is with some hestitation that the name THE ARIANE SATYR is applied to specimens from Mono Lake, because it is BARON'S SATYR, *Cercyonis pegala baroni* (Edw.), that occurs in a similar situation in northeastern California and southeastern Oregon.

Life Zones: Upper Sonoran. Plant Communities: Piñon-Juniper Woodland, Marsh, and Montane Meadow. Host Plants: POACEAE (Grasses).

3. *Cercyonis silvestris* (Edw.) **Pl. I, fig. e**

THE SYLVAN SATYR is a creature of the chaparral forest that clothes the foothills. A lover of shade, it seeks to lure the pursuer ever deeper into the undergrowth. Its favorite haunts are groves of Manzanita, Scrub Oak, and Mountain Mahogany, interspersed with an occasional Digger Pine.

Life Zones: Upper Sonoran (Transition). Plant Communities: Foothill Woodland, Chaparral. Host Plants: POACEAE (Grasses).

4. *Cercyonis oeta* (Bdv.) **Pl. IV, fig. c**

THE LEAST SATYR was not encountered in Yosemite Park during the 1933-1934 period, although it was known to inhabit the dry eastern slope of the Sierra Nevada. Since that time, however, it has been found on several occasions in the Tioga Pass region, but always within sight of the Sierran Divide.

Life Zones: Transition, Canadian, Hudsonian (Arctic-Alpine). Plant Communities: Juniper Woodland, Piñon-Juniper Woodland, Sagebrush Scrub (Alpine Fell-Fields). Host Plants: POACEAE (Grasses).

5. ***Oeneis chryxus ivallda*** **(Mead)** **Pl. III, fig. b**

THE IVALLDA ARCTIC inhabits the bleak, wind-swept summits that culminate in Mt. Lyell, Mt. Dana, and Mt. Conness. They may be encountered in a boulder-strewn clearing between stands of Mountain Hemlock, as near Vogelsang Camp, on barren ridges, as the crest above Tioga Pass crossed by the Gaylor Lakes trail, or on the moraines just east of Tioga Pass. Edmund Godwin reported "many seen at 12,000 feet on Matterhorn" in 1934. Erratic fliers, extremely difficult to capture, the Arctics have a habit of leaning with the wind when alighting, their mottled wings resembling a patch of lichen. According to Hovanitz (1940), the gray forms are found on granite, the brown forms on sedimentary rock. The line of contact between the two formations passes through the Yosemite sector and is a conspicuous feature of Sierran geology. Because of the inaccessibility of its habitat, the IVALLDA ARCTIC presents the ultimate challange to the energetic lepidopterist.

Life Zones: Arctic-Alpine (Hudsonian). Plant Communities: Alpine Fell-Fields, Subalpine Forest (Glacial Moraine). Host Plants: POACEAE (Grasses).

DANAIDAE

6. ***Danaus (Danaus) plexippus*** **(Linn.)**

THE MONARCH is common in Yosemite Valley and throughout the lower elevations of the park. Various species of Milkweed grow along the Merced River at Old Village, at Mirror Lake, and at the fork in the road to the Giant Yellow Pine, as well as along the higher trails that follow the canyon rim. It also occurs on the eastern Sierra slope, at Mono Lake, and has been found at Upper Lyell Base Camp (Shields). The banded larvae are easily discernible, but the waxy green chrysalids defy detection.

Life Zones: Unrestricted below Hudsonian. Host Plants: ASCLEPIADACEAE: *Asclepias* (True Milkweeds).

7. ***Danaus (Tasitia) gilippus strigosus*** **(Bates)**

THE STRIATED QUEEN in another milkweed feeder that occurs in Yosemite territory only on the dry east side of the Sierra Nevada, in the vicinity of Mono Lake. It may be distinguished from *Danaus (Tasitia) gilippus berenice* (Cram.) of the southeastern United States by the scattered white scales along the wing veins. Both are subspecies of the tropical *D. (T.) gilippus* (Cram.), ranging northward from Brazil.

Life Zones: Sonoran, both Lower and Upper (= Austral). Plant Communities: Many. Host Plants: ASCLEPIADACEAE: *Asclepias* (True Milkweed), and several other milkweed genera.

NYMPHALIDAE

8. *Argynnis* (*Semnopsyche*) *cybele leto* Behr

THE LETO FRITILLARY is the handsomest butterfly of the Yosemite Valley and the species most certain to attract the attention of the park visitor in the late summer season. From the thistles at Mirror Lake, which they visit for nectar, the butterflies may be traced to the sequestered meadow near Camp 9. Here the velvet-brown females deposit their eggs among the dried grasses, while the ruddy males hover above them, for *leto* is one of the two California fritillaries in which the sexes differ in color, the other being the following *apacheana.*

Life Zones: Transition. Plant Communities: Poplar Woodland (Black Cottonwood). Host Plants: VIOLACEAE: *Viola* (Violet).

9. *Argynnis* (*Speyeria*) *nokomis apacheana* Skin.

Pl. IV, fig. k

THE APACHE FRITILLARY, athough of another species, may be considered the eastern Sierran counterpart of The Leto Fritillary of the western Sierra. Even more spectacular than *leto,* it flies in the well watered meadows of the Owens River drainage, and has been found recently at Gull Lake and Mono Lake. The females emerge a full two weeks later than the males, and so dissimilar are the sexes in color that they might be mistaken for different species. The under side of the male is illustrated in color.

Life Zones: Upper Sonoran (Transition). Plant Communities: Wet Meadow, Marsh. Host Plants: VIOLACEAE: *Viola* (Violet).

10a. *Argynnis* (*Speyeria*) *zerene zerene* Bdv. Pl. I, fig. b
b. *Argynnis* (*Speyeria*) *zerene malcolmi* Comst.

THE ZERENE FRITILLARY is common along Highway 41 from Chinquapin to Wawona, in the Mariposa and Tuolumne Big Tree groves, and at Mather and Hetch-Hetchy summit. Every patch of thistle will bear investigation, for this fritillary is highly susceptible to its lure. Its Sierran east-slope counterpart, MALCOLM'S FRITILLARY, is found along the road from Highway 395 to Mammoth, and at Warren Creek on the Tioga Road. Its first choice for nectar is *Monardella,* a dwarf mint.

Life Zones: Transition, Canadian. Plant Communities: Yellow Pine, White Fir (Red Fir), Mixed Coniferous forests for *A. z. zerene,* Sagebrush Scrub, Jeffrey Pine Forest, Piñon-Juniper, and Juniper Woodland for *A. z. malcolmi.* Host Plants: VIOLACEAE: *Viola* (Violet).

11a. *Argynnis* (*Speyeria*) *callippe inornata* Edw.
b. *Argynnis* (*Speyeria*) *callippe nevadensis* Edw. Pl. IV, fig. b

THE PLAIN FRITILLARY flies in the western foothills of the Yosemite region in the late spring. It has been found at Fish Camp,

Fig. 4. Research Reserve, el. 8,700 ft. Open slope with Western White Pine predominant; Lodgepole Pine and Red Fir also present, with understory of Manzanita and Huckleberry Oak. Canadian life zone. *Philotes battoides* and *P. shasta comstockii* hover over the dwarf buckwheat and sparse grasses *ruralis* may be seen here.—Neva Snell.

at Briceburg, and at Indian Flat, below El Portal. THE NEVADA FRITILLARY, its eastern Sierran counterpart, flies in the Mono Lake region in early summer. It has been found at the summit above Crowley Lake on Balsam Root (*Balsamorhiza*), a large-leaved composite. The Great Basin races of *callippe* tend to be green and silvered below, the races of the western foothills brown and unsilvered.

Life Zones: Upper Sonoran (lower Transition). Plant Communities: (Chaparral) Foothill Woodland, Yellow Pine and Mixed Forest for *A. c. inornata;* Sagebrush, Piñon-Juniper Woodland, Jeffrey Pine Forest openings, Juniper Woodland for *A. c. nevadensis.* Host Plants: VIOLACEAE: *Viola* (Violet).

12. *Argynnis (Speyeria) egleis* Behr
Syn. *Argynnis (Speyeria) montivaga* Behr

THE EGLEIS FRITILLARY, known for many years as THE MOUNTAIN VAGABOND, is a species of uniformly small size characterized by a slight thickening of the veins of the primaries. It flies with The Arge Fritillary at Tioga Pass and is common at all elevations above 6,000 feet, preferring the minted slopes, whereas *A. mormonia arge* prefers the meadows. On the west slope of Mt. Dana it fairly swarms in the late afternoon sunlight.

Life Zones: upper Transition, Canadian, Hudsonian (Arctic-Alpine). Plant Communities: Openings in Mixed Coniferous, White and Red Fir, and Lodgepole Pine Forests (Alpine Fell-Fields). Host Plants: VIOLACEAE: *Viola* (Violet).

13. *Argynnis (Speyeria) atlantis irene* Bdv. **Pl. II, fig. h**

THE IRENE FRITILLARY of Yosemite, as determined for the earlier survey by Dr. J. McDunnough, is a dark race, some specimens of which are strongly suggestive of The Hydaspe Fritillary. *Irene,* however, is found at elevations well above those at which *hyaspe* occurs, and for this reason should not be confused with it. One of us (Tilden) has taken it also on the Sonora Pass Road, between Strawberry and the Clark Fork Road. In Yosemite it is something of a rarity.

Life Zones: upper Transition, Canadian. Plant Communities: Yellow Pine-Sugar Pine, White Fir and Red Fir Forests. Host Plants: VIOLACEAE: *Viola* (Violet).

14. *Argynnis (Speyeria) hydaspe* Bdv.

THE HYDASPE FRITILLARY first appears in Yosemite Valley about the Fourth of July, flying rapidly across the valley floor but pausing over the *Monardella* of the talus slopes. It is completely unsilvered and the creamy spots on the under side give a "checker-board" effect quite different from the purplish shades and frequent light silvering of the somewhat similar but usually larger *zerene.*

Life Zones: Transition, lower Canadian. Plant Communities: Yellow Pine, Mixed Coniferous, and White Fir Forests. Host Plants: VIOLACEAE: *Viola* (Violet).

15. *Argynnis (Speyeria) mormonia arge* Stkr. **Pl. III, fig. 1**

The Sierran race of THE MORMON FRITILLARY flies with THE EGLEIS FRITILLARY throughout the park. Males lack the enlarged veins of the forewing; females are more finely marked than those of *egleis;* otherwise the two species are indistinguishable, and particularly so when on the wing. The active males range widely, but the females will be found near moist meadows. The Rocky Mountain race of *A.* (*S.*) *mormonia* is *eurynome* Edw.

Life Zones: Canadian, Hudsonian (Arctic-Alpine). Plant Communities: Sub-alpine Meadows; Alpine Fell-Fields, Meadow and Grassland. Host Plants: VIOLACEAE: *Viloa* (Violet).

16. *Boloria (Clossiana) epithore* (Edw.) **Pl. II, fig. d**

THE WESTERN MEADOW FRITILLARY favors small, open glades beneath fir trees. Along Yosemite Creek it is particularly abundant in mid-July. There is also a colony on Dana Trail, where it passes through a marsh before rising sharply onto the slope of the mountain. The under side of the secondaries resembles *Boloria* (*C.*) *toddi* (Holl.), a widely ranging eastern species; however, in *epithore* the outer margin of the primaries is rounded, whereas in *toddi* it appears square-cut.

Life Zones: Canadian (Hudsonian). Plant Communities: White and Red Fir Forest; Bogs and Marshes. Host Plants: VIOLACEAE: *Viola* (Violet).

17a. *Euphydryas chalcedona chalcedona* (Dbldy. & Hew.)
b. *Euphydryas chalcedona sierra* (Wgt.)

THE CHALCEDON CHECKER-SPOT ranges throughout the foothills of the western portion of the state, being replaced in the Sierran highlands by THE SIERRA CHECKER-SPOT, now recognized, through the work of J. D. Gunder (1929), as a subspecies, or geographical race. Typical *chalcedona* may be found abundantly among the chaparral-clothed foothills, whereas race *sierra* prefers the wooded glades of the evergreen belt. A variety of food plants is acceptable to the voracious larvae.

Life Zones: Upper Sonoran for *E. c. chalcedona;* Canadian for *E. c. sierra.* Plant Communities: Foothill Woodland, Chaparral for *E. c. chalcedona;* Fir Forest for *E. c. sierra.* Host Plants: SCROPHULARIACEAE: *Scrophularia* (Bee Plant); *Pentstemon* (Pentstemon); *Castilleja* (Paint Brush); *Mimulus* (Monkey Flower); and *Diplacus* (Sticky Monkey Flower) for *E. c. chalcedona;* BORAGINACEAE: *Mertensia ciliata* var. *stomatechoides* (Mertensia), for *E. c. sierra,* according to Davenport and Dethier (1937). CAPRIFOLIACEAE: *Symphoricarpos albus* (Snow Berry) for *E. c. chalcedona.*

18a. *Euphydryas editha rubicunda* (Hy. Edw.) **Pl. I, fig. d**
b. *Euphydryas editha nubigena* (Behr) **Pl. III, fig. c**
c. *Euphydryas editha monoensis* Gund. **Pl. IV, fig. f**

THE RUDDY CHECKER-SPOT flies in the western Sierra from

Tulare to Sierra counties, its "lowland" counterpart of the eastern Sierra being THE MONO CHECKER-SPOT. As suggested by Comstock (1927), and confirmed by Gunder (1929), THE CLOUD-BORN CHECKER-SPOT, *E. nubigena,* has proven to be a delicately marked dwarf form that has adapted itself to alpine areas. All are subspecies of the widely ranging *Euphydryas editha* Bdv., each with a well defined and mutually exclusive range of its own.

Life Zones: Upper Sonoran, Transition for *E. e. rubicunda* and *E. e. monoensis;* Hudsonian, Arctic-Alpine for *E. e. nubigena.* Plant Communities: Foothill Woodland for *E. e. rubicunda;* Piñon-Juniper Woodland for *E. e. monoensis;* Alpine Fell-Fields for *E. e. nubigena.* Host Plants: PLANTAGINACEAE: *Plantago* (Plantain).

19. ***Melitaea (Chlosyne) damoetas malcolmi*** **Comst.**

Pl. III, fig. a

MALCOLM'S CHECKER-SPOT was described from the then only known colony at Red Lake, el. 11,000 ft., above the Mammoth Lakes Basin, where it flies on a precipitous talus slide. It is now known to fly in the Yosemite region and throughout the central Sierra at corresponding elevations. Perhaps the most intimate knowledge of the species is possessed by Oakley Shields, who has combed the high country for isolated colonies. The most accessible of these is located above Upper Gaylor Lake near an abandoned stone cabin reached by a fisherman's trail from Tioga Pass.

Life Zones: upper Hudsonian, Arctic-Alpine. Plant Communities: Alpine Fell-Fields. Host Plants: Not known. Possibly COMPOSITAE: *Aster* (Aster).

20. *Melitaea (Chlosyne) acastus* Edw.

THE ACASTUS CHECKER-SPOT is a Great Basin flier, found sparingly around Mono Lake. The few records from late June and early July suggest an earlier flight season.

Life Zones: Upper Sonoran. Plant Communities: Sagebrush Scrub, Meadowland. Host Plants: COMPOSITAE: *Aster* (Aster).

21a. *Melitaea (Chlosyne) palla palla* Bdv. **Pl. II, fig. j**
b. *Melitaea (Chlosyne) palla whitneyi* Behr

THE NORTHERN CHECKER-SPOT ranges widely throughout the Sierra Nevada and Cascade chains as well as the Rockies. It is replaced at higher elevations in the southern Sierra by WHITNEY'S CHECKER-SPOT, a darker and ruddier form. Whether *whitneyi* actually occurs in the Yosemite region is a matter for further investigation. None were encountered in the course of the present survey.

Life Zones: Upper Sonoran, Transition, Canadian for *M. (C.) p. palla;* Hudsonian for *M. (C.) palla whitneyi.* Plant Communities: Foothill Woodland, Chaparral, Mixed Evergreen Forest. Host Plants: COMPOSITAE: *Aster* (Aster).

22. ***Melitaea (Chlosyne) hoffmanni*** **Behr** **Pl. II, fig. 1**

HOFFMANN'S CHECKER-SPOT was the most abundant butterfly on the Research Reserve in 1933. They fairly swarmed over *Monardella,* the nectar seeming to intoxicate, or at least render them oblivious to the observer's presence. In 1956 but a few were seen on a north-facing slope along the Tioga Road opposite the White Wolf turnoff.

Life Zones: Canadian. Plant Communities: Openings in Fir Forest. Host Plants: Not known.

23. ***Melitaea (Chlosyne) leanira*** **F. & F.**

THE LEANIRA CHECKER-SPOT invades the western portions of the park from the foothills east of the San Joaquin Valley, where it properly inhabits the chaparral. It is common at Indian Flat, below El Portal.

Life Zones: Upper Sonoran (Transition). Plant Communities: California Sagebrush Scrub (also called Coastal Sage Scrub), Foothill Woodland. Host Plants: SCROPHULARIACEAE: *Castilleja* (Indian Paint Brush), *Cordylanthus tenuis* (Bird's Beak).

24a. ***Phyciodes (Phyciodes) campestris campestris*** **(Behr)**
b. ***Phyciodes (Phyciodes) campestris montana*** **(Behr)**

THE FIELD CRESCENT is found about moist places at lower elevations, as on the floor of Yosemite Valley, or at Mather, just outside the park. Higher up it grades imperceptibly into THE MOUNTAIN CRESCENT, in which the tawny ground color has all but obliterated the submarginal row of spots on the secondaries. Although heretofore treated as a distinct species, on the basis of Yosemite specimens the present authors prefer to consider *montana* but an altitudinal race of *campestris.* Specimens from Mono Lake are clearly intermediate.

Life Zones: Upper Sonoran, Transition for *P. (P.) c. campestris;* Canadian, lower Hudsonian for *P. (P.) c. montana.* Plant Communities: Several. Wet Meadowland, Roadside Associations. Host Plants: COMPOSITAE: *Aster* (Aster).

25. ***Phyciodes (Phyciodes) mylitta*** **(Edw.)** **Pl. II, fig. c**

THE MYLITTA CRESCENT frequents the streamside and moist meadows, often in association with the following species, *Polygonia satyrus* (Edw.). It can be recognized by the bright yellow-brown ground color. California specimens are typical, that is to say, darker, whereas Rocky Mountain specimens incline toward the lighter races *Phyciodes (P.) mylitta pallida* Edw. and *thebais* (G. & E.).

Life Zones: Upper Sonoran, Transition, Canadian. Plant Communities: Several, as is frequent with wide-ranging species. Host Plants: COMPOSITAE: *Carduus* (Italian Thistle), *Cirsium* (Native Thistle), and *Silybum* (Milk Thistle).

26. ***Polygonia satyrus*** **(Edw.)**

THE SATYR is a streamside flier that alights on the trunks of

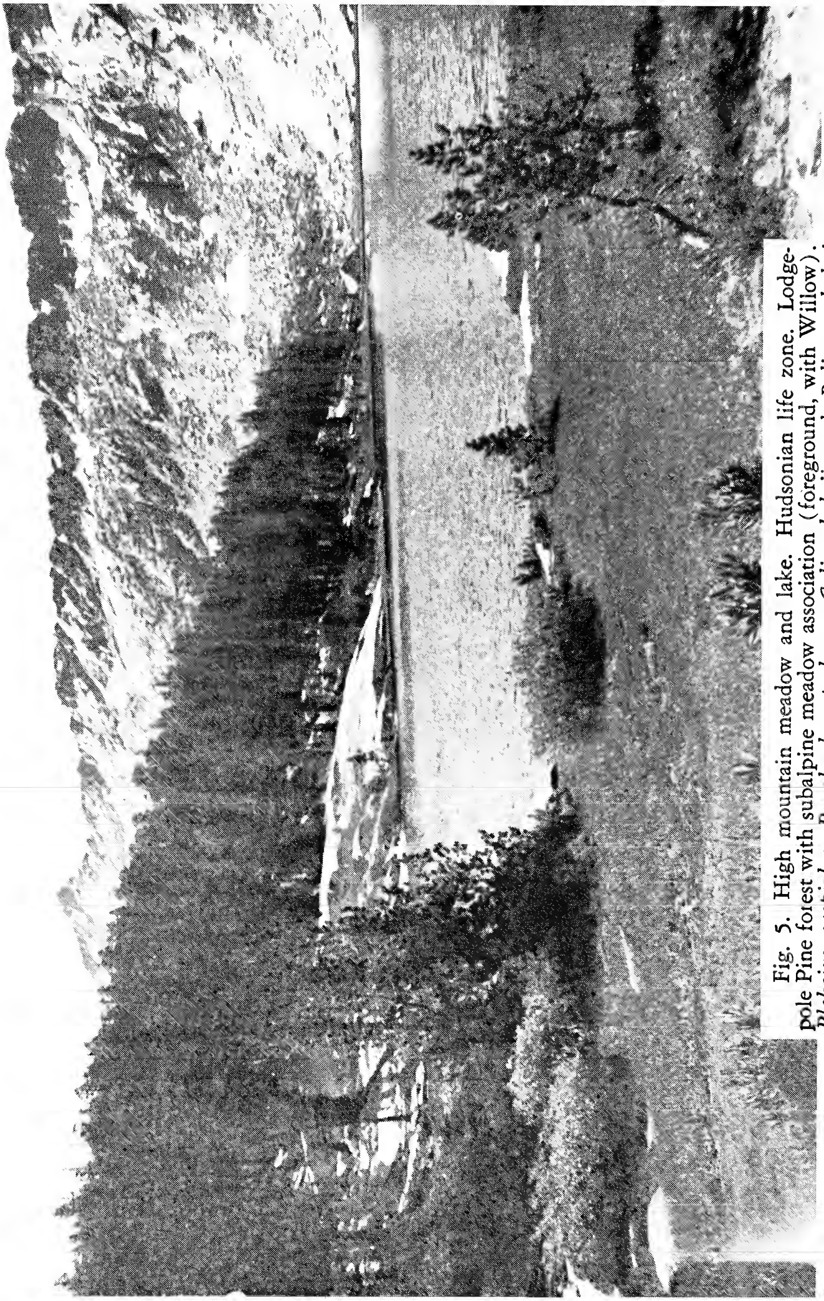


Fig. 5. High mountain meadow and lake. Hudsonian life zone. Lodgepole Pine forest with subalpine meadow association (foreground, with Willow). *Plebejus saepiolus*, *P. glandon podarce*, *Colias behrii*, and *Polites sabuleti tecumseh* fly here, as does *Argynnis mormonia arge* in late season.—Joseph S. Dixon.

Alder, Willow, and Cottonwood, to blend indistinguishably with the mottled bark.

Life Zones: Upper Sonoran, Transition. Plant Communities: Foothill Woodland, Mixed Coniferous Forest, and others. Riparian Association. Host Plants: URTICACEAE: *Urtica* (Nettle).

27. ***Polygonia faunus rusticus*** (Edw.)

THE RUSTIC ANGLE-WING occurs principally north of Yosemite, but may be looked for wherever Azalea grows. Its inclusion in the Yosemite fauna is based on an early record of Dr. E. O. Essig. The specimen was seen by the senior author at the Yosemite Museum in 1933.

Life Zones: Transition. Plant Communities: Several. Moist Woodland, Riparian associations. Host Plants: ERICACEAE: *Rhododendron* (Azalea); SAXIFRAGACEAE: *Ribes* (Currant, Gooseberry); BETULACEAE: *Alnus* (Alder); SALICACEAE: *Salix* (Willow).

28. ***Polygonia zephyrus*** (Edw.) **Pl. II, fig. k**

THE ZEPHYR replaces THE SATYR (*Polygonia satyrus*) as the common Angle-Wing of the Canadian and Hudsonian zones, its pale gray underside serving as a distinguishing feature. Yosemite Creek in mid-July is a typical situation for the species. Its food plant, *Ribes,* is a common shrub in the Subalpine Forest.

Life Zones: Transition (upper), Canadian, Hudsonian. Plant Communities: Fir Forest, Lodgepole Pine Forest, Subalpine Forest. Host Plants: ERICACEAE: *Rhododendron* (Azalea); SAXIFRAGACEAE: *Ribes* (Currant, Gooseberry).

29. ***Nymphalis californica*** (Bdv.)

THE CALIFORNIA TORTOISE-SHELL appears in outbreak numbers every few years throughout the Sierra. The June flights observed by the senior author in General Grant (now Sequoia-Kings Canyon) National Park in 1922, in the San Bernardino Mountains in 1931, and in Yosemite in 1933 were all in a northerly or northwesterly direction, roughly paralleling the axis of the Sierra. However, former Park Naturalist C. A. Harwell, while on a glacier-measuring survey, reported a return flight on October 4, 1933, in which myriads of the insects passed through the highest mountain passes, all heading south. The duration of the spring flight is but a few days. It begins at dawn and lasts until after sundown. At times the greatest density of the insects appears to be at tree-top level; again they come so near the ground that they may be knocked down with a hat. A few weeks later the *Ceanothus* is matted with webs of the gregarious larvae. Complete defoliation over large areas results. The investigation of such an outbreak was the first professional assignment of Dr. H. C. Bryant, co-founder of the Yosemite Field School. Observations by Edwards and Behr before 1900 in the Mill Valley section are mentioned by C. B. Williams in his monograph on butterfly migration. One of us (Tilden) has observed this phenomenon in Yosemite as recently as 1961. The explanation seems to be that the CALIFORNIA TORTOISE-SHELL is a swarming species which, like the lemming, has cycles of abundance followed by a drastic reduction in the population, due to causes as yet not fully understood.

Life Zones: Unrestricted in flight, although the food plant does not occur above Canadian. Host Plants: RHAMNACEAE: *Ceanothus,* particularly *C. cordulatus* (Snow-Bush), and other smooth-leaved species.

30. *Nymphalis milberti furcillata* (Say)

MILBERT'S TORTOISE-SHELL has an inward urge to fly upward, and has been seen at the very summit of Mt. Lyell, el. 13,090 ft., the highest point in Yosemite. Form *subpallida* (Ckll.) flies with normal individuals, although not commonly. The subspecific designation *furcillata* (Say) is considered applicable to all western specimens south of Oregon.

Life Zones: Transition, Canadian, straying higher. Host Plants: URTICACEAE: *Urtica* (Nettle).

31. *Nymphalis antiopa* (Linn.)

THE MOURNING CLOAK is one of the world's most widespread butterflies, occurring in Europe, northern Asia, and Japan. In England it is called The Camberwell Beauty.

Life Zones: Unrestricted. Host Plants: SALICACEAE: *Salix* (Willow); *Populus* (Poplar, Cottonwood); ULMACEAE: *Ulmus* (Elm).

32. *Vanessa atalanta* (Linn.)

THE ALDERMAN or THE RED ADMIRAL is found in Europe and Japan, as well as in North America. Few butterflies are easier to recognize by sight.

Life Zones: Upper Sonoran, Transition. Host Plants: URTICACEAE: *Urtica* (Nettle), *Boehmeria* (False Nettle), *Parietaria* (Pellitory).

33. *Vanessa virginiensis* (Dru.)

THE VIRGINIA LADY is widely distributed throughout North America and may be recognized by the large eye-spots on the under surface of the hind wings.

Life Zones: Upper Sonoran, Transition, Canadian. Host Plants: COMPOSITAE: *Gnaphalium* (Cudweed; Everlasting), *Anaphalis* (Everlasting, *Antennaria* (Everlasting), *Artemesia heterophylla* (Mugwort).

34. *Vanessa cardui* (Linn.)

THE PAINTED LADY or THE THISTLE BUTTERFLY is probably the most cosmopolitan of butterflies. Native to the Northern Hemisphere, it has been introduced elsewhere.

Life Zones: Unrestricted. Host Plants: BORAGINACEAE: *Amsinckia* (Fiddle-Neck), *Crypantha* (Nievitas); COMPOSITAE: *Carduus* (Italian Thistle), *Cirsium* (Native Thistle), *Silybum* (Milk Thistle).

35. *Vanessa carye* (Hbn.)

THE WEST COAST LADY is restricted to the western United

States, where it is more common in back yards and vacant lots than in the out-of-doors.

Life Zones: Unrestricted. Host Plants: MALVACEAE: *Malva* (Mallow), *Lavatera* (Tree Mallow), *Sida* (Alkali Mallow), *sidalcea* (Checkerbloom, Wild Hollyhock), *Sphaeralcea* (=*Malvastrum*) (Apricot Mallow, Bush Mallow).

36. *Precis orithya evarete* (Cram.)
Syn. *Junonia coenia* Hbn.

THE BUCKEYE may be recognized by the brightly colored eyespots on all wings. The aggressive males have been known to select a perch and defend a "territory".

Life Zones: Upper Sonoran, Transition, (lower Canadian). Host Plants: PLANTAGINACEAE: *Plantago* (Plantain); SCROPHULARIACEAE: *Mimulus* (Monkey Flower).

37. *Limenitis* (*Limenitis*) *weidemeyerii nevadae* (B. & B.)
Pl. IV, fig. h

THE NEVADA ADMIRAL is a Great Basin race of the Rocky Mountain Weidemeyer's Admiral, *Limenitis* (*L.*) *weidemeyerii* (Edw.), found at Mono Lake on the eastern side of the Sierra Nevada. At Lee Vining, where its range overlaps that of the following species, *L.* (*L.*) *lorquini* Bdv., the hybrid *L.* (*L.*) *fridayi* (Gund.) occurs. Since the blend is an even one, in which the characteristics of neither species predominate, we would prefer to indicate it as *L. w. nevadae* × *L. lorquini*, rather than as a form of the above.

Life Zones: Upper Sonoran, Transition. Plant Communities: Several. Aspen Grove, Willow Thicket, Riparian Associations. Host Plants: SALICACEAE: *Populus* (Aspen, Cottonwood), *Salix* (Willow).

38. *Limenitis* (*Limenitis*) *lorquini* Bdv. Pl. II, fig. b

LORQUIN'S ADMIRAL adheres to the riparian association throughout three life zones, seldom straying from the willows and poplars of the stream bed. On the wing it is sometimes confused with the following species, but the manner of flight is quite different.

Life Zones: Upper Sonoran, Transition, Canadan. Plant Communities: Several. Aspen Grove, Willow Thicket and Riparian Associations. Host Plants: SALICACEAE: *Salix* (Willow), *Populus* (Aspens and Cottonwoods). ROSACEAE: *Prunus* (Choke-cherry).

39. *Limenitis* (*Adelpha*) *bredowii californica* (Butl.)
Pl. I, fig. g

THE CALIFORNIA SISTER flies with the foregoing species, which it superficially resembles, but from which it may be told on the wing by the habit of alternating a few rapid beats with a glide in which the wings are held slightly below the horizontal level. Unlike LORQUIN'S ADMIRAL, however, THE CALIFORNIA SISTER forsakes the stream margins for the hot canyon walls and the Golden Cup Oak association. No other insect is so likely to attract the attention of the park visitor.

Life Zones: Upper Sonoran, Transition, Canadian. Plant Communities: Oak Woodland, Mixed Evergreen Forest. Host Plants: FAGACEAE: *Quercus* (Oak), especially *Quercus chrysolepis* (Golden Cup Oak, Maul Oak).

40a. ***Apodemia mormo mormo*** **(F. & F.)**
b. ***Apodemia mormo tuolumnensis*** **Opler & Powell**

THE MORMON METAL-MARK is found at higher elevations and on the east Sierran slope. THE TUOLUMNE METAL-MARK is known only from Pate Valley in the Grand Canyon of the Tuolumne, the type locality. It is "a Sierran population characterized by a great extent of orange on the upper side together with reduction of white spots and dark under side. So far as is known it is restricted to a population along a four mile area of the Pate Valley Trail from about 4500' to 7000'. It is likely a segregate from *virgulti,* its nearest geographic relative, which probably occurs in scattered colonies through the lower foothills to the west." (Opler and Powell, 1961) BEHR'S METAL-MARK, *Apodemia mormo virgulti* (Behr), is the near relative.

Life Zones: Upper Sonoran (Transition) for *A. m. tuolumnensis;* to Hudsonian for *A. m. mormo.* Plant Communities: Chaparral for *A. m. tuolumnensis;* Sagebrush Scrub and Piñon-Juniper Woodland for *A. m. mormo.* Host Plants: POLYGONACEAE: *Eriogonum* (Buckwheat), perennial species only.

LYCAENIDAE

41. ***Habrodais grunus*** **(Bdv.)** **Pl. I, fig. h**

BOISDUVAL'S HAIR-STREAK is noted for its crepuscular habits. A party of the Yosemite Field School, on its way to the Research Reserve, discovered it flying at Columbia Point before 5 a.m. in semi-darkness. It continues to hover above the live oaks after the last rays of sunlight have left the canyon walls.

Life Zones: Transition (Canadian). Plant Communities: Oak Woodland, Chaparral. Host Plants: FAGACEAE: *Quercus chrysolepis* (Golden Cup Oak, Maul Oak); *Castanopsis* (Chinquapin) suspected.

42. ***Atlides halesus estesi*** **Clench**

THE GREAT BLUE HAIR-STREAK displays a metallic blue of dazzling luster on the superior surfaces. Rarely encountered north of Tehachapi, it has been found several times in Yosemite since the capture by a small boy of the specimen recorded by Garth (1935). The worn condition of Yosemite specimens suggests flight from lower elevations, perhaps outside the park.

Life Zones: Upper Sonoran (Transition, Canadian). Plant Communities: Foothill Woodland. Host Plants: LORANTHACEAE: *Phoradendron* (Mistletoe), male flowers only.

43. ***Strymon (Strymon) melinus pudica*** **(Hy. Edw.)**

THE COMMON HAIR-STREAK flies in the Museum garden and throughout the lower elevations of the park. It is the western race *pudica,* the only race that flies in California.

Life Zones: Upper Sonoran (Transition). Plant Communities: Several. Host Plants: BORAGINACEAE: *Cynoglossum* (Hound's Tongue). LEGUMINOSAE: *Astragalus* (Loco Weed, Rattle Weed), *Hosackia* (=*Lotus*), *Lupinus* (Lupine). MALVACEAE: *Malva* (Mallow). POLYGONACEAE: *Polygonum* (Knot Weed). GUTTIFERAE: *Hypericum* (St. John's Wort). LABIATAE: *Hyptis* (Bee Sage).

44. ***Strymon* (*Satyrium*) *fuliginosum semiluna* (Klots)** **Pl. IV, fig. j**

THE SEMI-LUNATE GOSSAMER WING is an early season flier at Mono Lake. Like *Melitaea* (*Chlosyne*) *acastus,* it has been found in late June, but is probably on the wing a month earlier.

Life Zones: Upper Sonoran. Plant Communities: Sagebrush Scrub. Host Plants: LEGUMINOSAE: *Lupinus* (Lupine).

45. ***Strymon* (*Satyrium*) *behrii*** (Edw.) **Pl. IV, fig. g**

BEHR'S HAIR-STREAK is characteristic of the dry eastern slopes of the Sierra Nevada. An isolated colony also exists on the desert slope of the San Bernardino Mountains, in southern California..

Life Zones: Upper Sonoran. Plant Communities: Sagebrush Scrub. Host Plants: LEGUMINOSAE: *Lupinus* (Lupine), *Lotus* (=*Hosackia*), *Astragalus* (Loco Weed, Rattle Weed). ROSACEAE: *Purshia tridentata* (Antelope Brush, Bitter Brush), reported (1963).

46. ***Strymon* (*Satyrium*) *auretorum*** (Bdv.) **Pl. I, fig. k**

THE GOLDEN HAIR-STREAK may now be reported authoritatively from the Yosemite region on the strength of specimens found during the present survey along Hetch-Hetchy Road north of Mather. When compared with specimens of The Nut-Brown Hair-Streak, *Strymon* (*Satyrium*) *auretorum spadix* (Hy. Edw.), from Crystal Lake in the San Gabriel Mountains of southern California, they proved to be noticeably different in hue and marking. Specimens were attracted to Syringa, *Philadelphus Lewisii* var. *californicus,* to the fragrant blooms of which the Theclinae are partial.

Life Zones: Upper Sonoran. Plant Communities: Chaparral. Host Plants: FAGACEAE: *Quercus* (Oak), especially *Q. Douglassii* (Blue Oak) in the Sierra foothills.

47. ***Strymon* (*Satyrium*) *saepium* (Bdv.)**

THE HEDGE-ROW HAIR-STREAK is abundant on the blossoms of the Buckeye, *Aesculus californicus,* in the late afternoon, where it flies with *Strymon* (*Satyrium*) *auretorum* and *Euphydryas chalcedona.*

Life Zones: Upper Sonoran. Plant Communities: Chaparral (west slope); Sagebrush Scrub (east slope). Host Plants: RHAMNACEAE: *Ceanothus,* especially *C. cuneatus* (Buck Brush). ROSACEAE: *Cercocarpus* (Mountain Mahogany).

48. ***Strymon* (*Satyrium*) *adenostomatis* (Hy. Edw.)**

THE GRAY HAIR-STREAK occurs in the western foothills near Jerseydale and along the road to Hetch-Hetchy, above Mather.

Life Zones: Upper Sonoran. Plant Communities: Chaparral. Host

Plants: ROSACEAE: *Cercocarpus,* especially *C. betuloides* (Hard Tack, Mountain Mahogany). Not *Adenostoma* (Chamise Bush), as its name would imply.

49. *Strymon (Satyrium) sylvinus* (Bdv.)

THE SYLVAN HAIR-STREAK is found about the willows of the stream bed, rather than in forest glades, as the name might suggest. Specimens from Mono Lake show no great tendency toward race *desertorum* (Grin.), which occurs from Kern County north through Owens Valley.

Life Zones: Upper Sonoran (lower Transition). Plant Communities: Several. Riparian Association. Host Plants: SALICACEAE: *Salix* (Willow).

50. *Strymon (Satyrium) californica* (Edw.)

THE CALIFORNIA HAIR-STREAK is partial to the flowers of Pink Pussy-Paws, *Spraguea umbellata,* from which it may be plucked with fingers or with forceps. It is also attracted to Yerba Santa, *Eriodictyon californicum,* when it visits the nature garden behind the Yosemite Museum.

Life Zones: Upper Sonoran (lower Transition) on west slope; Upper Sonoran and High (arid) Transition on east slope. Plant Communities: Chaparral, Oak Woodland (west slope); Sagebrush Scrub, Juniper Woodland (east slope). Host Plants: RHAMNACEAE: *Ceanothus cuneatus* (Buck Brush). ROSACEAE: *Cercocarpus* (Mountain Mahogany). Possibly FAGACEAE: *Quercus* (Oak).

51. *Strymon (Satyrium) dryope* (Edw.)

THE DRYOPE HAIR-STREAK was encountered playing about sage at Mono Lake.

Life Zones: Upper Sonoran. Plant Communities: Sagebrush Scrub (east slope); Chaparral, Foothill Woodland (coastal California). Riparian Association. Host Plants: SALICACEAE: *Salix* (Willow).

52. *Callophrys (Callophrys) dumetorum* (Bdv.)

THE BRAMBLE HAIR-STREAK is the green hair-streak of moderate elevations on the western slope of the Sierra Nevada. At high elevations, and on the eastern slope, it is replaced by the following species.

Life Zones: Upper Sonoran. Plant Communities: Chaparral. Host Plants: POLYGONACEAE: *Eriogonum* (Buckwheat), especially *E. nudum.*

53. *Callophrys (Callophrys) lemberti* Tilden **Pl. III, fig. k**

LEMBERT'S HAIR-STREAK is the greenish hair-streak of the higher elevations of the park. Its relationships appear to be with *Callophrys (C.) sheridani* Edw. of the Rocky Mountains, in which the band of white across the under side of the secondaries is more or less continuous. Discovered during the course of this survey, it has been named in honor of the pioneer resident of Tuolumne Meadows, John Batiste Lembert.

Life Zones: Hudsonian, Arctic-Alpine. Plant Communities: Alpine Fell-Fields. Associated with "rock garden" *Eriogonum, E. ovalifolium.* Host Plants: Unknown.

54. ***Callophrys (Mitoura) spinetorum*** **(Hew.)**

THE THICKET HAIR-STREAK is a highly prized find that may be recognized by the bold white line across the under side of the secondaries. Its dull bluish upper side distinguishes it from the following *Callophrys (Mitoura) johnsoni* (Skin.).

Life Zones: Transition, Canadian. Plant Communities: Mixed Coniferous Forest, White Fir Forest, Red Fir Forest. Host Plants: LORANTHACEAE: *Arceuthobium* (Dwarf Mistletoe), a genus occurring on conifers.

55. ***Callophrys (Mitoura) johnsoni*** **(Skin.)** **Pl. I, fig. l**

JOHNSON'S HAIR-STREAK, a close relative of *Callophrys (Mitoura) spinetorum,* may be told from the latter by means of its brownish upper side. The species is a prize over all of its range, but occurs more frequently in the Yuba Pass-Gold Lake area of Sierra County, California, and in the Pacific Northwest.

Life Zones: Transition, Canadian. Plant Communities: Coniferous Forest. Host Plants: LORANTHACEAE: *Arceuthobium Douglassii* (Dwarf Pine Mistletoe).

56. ***Callophrys (Mitoura) nelsoni*** **(Bdv.)** **Pl. I, fig. i**

NELSON'S HAIR-STREAK, like The California Hair-Streak, occurs in the nature garden behind the Yosemite Museum. Both swarm over the pink clusters of *Spraguea* (Pussy Paws) and may be picked off by forceps. They may also be found at Jerseydale, at the junction of Highway 120 with Hetch-Hetchy Road, and on the warm road-shoulders above Tamarack Flat.

Life Zones: Transition, Canadian. Plant Communities: Mixed Coniferous Forest. Host Plants: PINACEAE: *Libocedrus decurrens* (Incense Cedar), probably.

57. ***Callophrys (Incisalia) doudoroffi windi*** **(Clench)** **Pl. I, fig. j**

WIND'S ELFIN was encountered at a damp spot in the trail near Indian Flat, where it was flying with the following species. It differs from normal *doudoroffi* of the Monterey Coast in being much lighter and less heavily banded below. Males are slaty gray above and brown beneath; females are quite golden in color. The form has not been illustrated previously.

Life Zones: Upper Sonoran. Plant Communities: Chaparral. Host Plants: Not known. Perhaps CRASSULACEAE: *Sedum* (Stonecrop), as for the related *C. (I.) fotis.*

58. ***Callophrys (Incisalia) iroides*** **(Bdv.)**

THE WESTERN ELFIN is one of the first butterflies to emerge in the spring. March finds it on the wing in the foothills of the San Joaquin Valley. It is a very plain, brown elfin. The larvae are probably bud-feeders, like those of *Celastrina argiolus echo* (Edw.).

Life Zones: Upper Sonoran (lower Transition), occasionally to Canadian. Plant Communities: Chaparral, and the chaparral-like understory of coniferous forests. Host Plants: CONVOLVULACEAE: *Cuscuta* (Dodder). RHAMNACEAE: *Ceanothus* (Buck Brush, Wild Lilac). ERICACEAE: *Arbutus* (Madroño), *Arctostaphylos* (Manzanita), *Vaccinium* (Bilberry). Perhaps CRASSULACEAE: *Sedum* (Stonecrop).

59. *Callophrys* (*Incisalia*) *eryphon* (Bdv.)

THE WESTERN BANDED ELFIN clings quite constantly to the coniferous forest. Never common, its discovery gives cause for comment.

Life Zones: Transition, Canadian, lower Hudsonian. Plant Communities: Yellow Pine, Red Fir, and Lodgepole Pine Forest. Host Plants: PINACEAE: *Pinus ponderosa* (Yellow Pine), *P. contorta Murrayana* (Lodgepole Pine).

60a. *Lycaena* (*Tharsalea*) *arota arota* (Bdv.)

b. *Lycaena* (*Tharsalea*) *arota virginiensis* (Edw.)

THE AROTA COPPER and THE NEVADA COPPER occupy the western and eastern slopes of the Sierra Nevada, respectively. The former was found in Pate Valley by Edmund Godwin on California Laurel, *Umbellularia californica;* the latter occurs at Mono Lake and at Bodie where specimens seem almost indistinguishable from those from Virginia City, Nevada, the type locality.

Life Zones: Upper Sonoran, Transition. Plant Communities: Mixed Evergreen Forest (west slope); Juniper Woodland, Sagebrush Scrub (east slope). Host Plants: SAXIFRAGACEAE: *Ribes* (Currant), *Grossularia* (Gooseberry). The overwintering eggs are deposited at the bases of thorns.

61. *Lycaena* (*Lycaena*) *gorgon* (Bdv.)

THE GORGON COPPER flies in the foothills surrounding the western approaches to the park. Single brooded, it is on the wing during late spring and early summer, when it may be expected to occur as a vagrant within the park boundaries.

Life Zones: Upper Sonoran. Plant Communities: Foothill Woodland, Chaparral. Host Plants: POLYGONACEAE: *Eriogonum* (Buckwheat), especially *E. nudum.*

62. *Lycaena* (*Lycaena*) *heteronea* Bdv.

THE VARIED BLUE is common on the east slope of the Sierra Nevada. It has been found west of the divide in the sagebrush zone above the subalpine forest between Tioga Pass Checking Station and the summit of Gaylor Lakes Trail. It is also sometimes common below Tuolumne Meadows on the way to Return Creek, below Glen Aulin.

Life Zones: Hudsonian (in Yosemite). Plant Communities: Sagebrush Scrub, often where mixed with Pine Forest or Juniper Woodland.

Host Plants: POLYGONACEAE: *Eriogonum* (Buckwheat). Associated with *E. umbellatum* (Sulphur Flower).

63. *Lycaena* (*Lycaena*) *xanthoides* (Bdv.)

THE GREAT COPPER flies in the foothills throughout the state and is distinguished by its large size and dull coloration.

Life Zones: Upper Sonoran (lower Transition). Plant Communities: Chaparral, Foothill Woodland, Yellow Pine Forest clearings. Meadow and open Streamside. Host Plants: POLYGONACEAE: *Rumex hymenosepalus* (Dock).

64. ***Lycaena (Lycaena) rubidus*** **(Behr)** **Pl. IV, fig. d**

THE RUDDY COPPER, earlier suspected of flying in the Yosemite region (Garth, 1935), occurs in the sagebrush region of the Gaylor Lakes Trail mentioned under the preceding *Lycaena (L.) heteronea,* and on the east Sierran slope as well.

Life Zones: Upper Sonoran to Hudsonian (Arctic-Alpine). Plant Communities: Sagebrush Scrub, openings in Subalpine Forest, and Alpine Fell-Fields. Host Plants:. POLYGONACEAE: *Rumex* (Dock), probably.

65. ***Lycaena (Lycaena) editha*** **(Mead)**

EDITH'S COPPER is a creature of the higher elevations of the eastern portion of the park, where it flies in company with *Lycaena mariposa, L. rubidus,* and *L. heteronea.* It resembles a compact model of *Lycaena xanthoides,* and might be called (with tongue in cheek), "The Small Great Copper."

Life Zones: Hudsonian, Arctic-Alpine. Plant Communities: Subalpine Forest openings, Subalpine Meadow, Alpine Fell-Fields. Host Plants: POLGONACEAE: *Rumex paucifolius* (Alpine Dock). ROSACEAE: *Potentilla tenuiloba, Horkelia fusca* (Cinquefoil).

66. ***Lycaena (Lycaena) mariposa*** **Reak.**

REAKIRT'S COPPER frequents small meadows of the southern exposure as far as timber line, but does not fly above. It was encountered by the senior author at 10,600 feet while crossing the Lyell Fork of the Tuolumne River preparatory to an ascent of Kuna Crest.

Life Zones: Hudsonian. Plant Communities: Openings in Subalpine Forest. Host Plants: POLYGONACEAE: *Polygonum Douglassii* (Buckwheat); can be raised on *Rumex* (Dock).

67. ***Lycaena (Lycaena) nivalis*** **(Bdv.)** **Pl. II, fig. f**

THE NIVALIS COPPER, known for many years only from a small colony at Glacier Point, flies generally throughout the park at elevations of 7,000 feet and above. It resembles The Purplish Copper, *Lycaena (L.) helloides,* but has an immaculate under side.

Life Zones: Canadian, Hudsonian. Plant Communities: Rocky Outcrops and Alpine Fell-Fields. Host Plant: Unknown. POLYGONACEAE: *Eriogonum* (Buckwheat) suspected.

68. ***Lycaena (Lycaena) helloides*** **(Bdv.)**

THE PURPLISH COPPER is believed to be primarily a dweller of the lowlands, but occasional specimens have been found at higher elevations. It lacks the luster of the preceding *Lycaena (L.) nivalis* and has a faintly dotted under side.

Life Zones: Upper Sonoran (Transition). Plant Communities: Forest openings. Moist situations, rocky outcrops. Host Plants: POLYGONACEAE: *Rumex acetosella* (Sheep Sorrel), *Polygonum aviculare* (Knotweed), *Oxytheca.* ONAGRACEAE: *Gayophytum.*

69. *Lycaena* (*Lycaena*) *phlaeas hypophlaeas* (Bdv.)
Pl. III, fig. h

The Sierran form of THE AMERICAN COPPER, first reported from the Yosemite region by Garth (1935b), has been established as the typical *Lycaena* (*L.*) *phlaeas hypophlaeas*. Although the glacial tarn on the north face of Mt. Maclure known locally as Bert Lake in honor of former park naturalist C. A. "Bert" Harwell was revisited by Oakley Shields, no additional specimens were found there. The north slope of Mt. Dana, however, yielded a limited number, found on a steep slope on which footing was precarious. Characterized by its small size, subdued brassy color, and bluish spots above the orange submarginal band of the secondaries, the Yosemite form appears closer to the Arctic race *feildeni* M'Lachlan than to the eastern race, to which the name *americana* Morris is now applied.

Life Zones: Arctic-Alpine. Plant Communities: Alpine Fell-Fields Host Plants: POLYGONACEAE: *Rumex* (Dock), especially *R. acetosella,* for the eastern subspecies.

70. *Lycaena* (*Lycaena*) *cupreus* (Edw.) **Pl. III, fig. j**

THE LUSTROUS COPPER is the most intense bit of color on the wing in Yosemite. Its fiery dress enlivens the mountain meadows. Only *Lycaena* (*L.*) *snowi* (Edw.) of the Rockies, considered by Klots (1936) and by Brown (1955) to be a subspecies of *cupreus,* rivals it in brilliance. It flies over *Spraguea umbellata* (=*Calyptridium umbellatum*) (Pink Pussy Paws) on rock slides not far from retreating snow.

Life Zones: Hudsonian, Arctic-Alpine. Plant Communities: Alpine Fell-Fields. Host Plants: Unknown.

71. *Lepotes marina* (Reak.)

THE MARINE BLUE, an Austral species, has been encountered by us only in the Mono Lake area.

Life Zones: Lower Sonoran, Upper Sonoran. Plant Communities: Several over its wide range. Host Plants: LEGUMINOSAE: *Medicago* (Alfalfa), *Astragalus* (Loco Weed, Rattle-Weed), *Lathyrus* (Sweet Pea).

72. *Brephidium exilis* (Bdv.)

THE PYGMY BLUE, until found at Mono Lake in the final year of this study, was recorded as present in the Yosemite region on the strength of a single female specimen obtained by Oakley Shields at Saddlebag Lake. It is the smallest of North American butterflies, with a wing expanse of .65 in.

Life Zones: Unrestricted. Plant Communities: Alkali Sink, Salt Marsh. Host Plants: CHENOPODIACEAE: *Atriplex* (Salt Bush), *Chenopodium* (Lamb's Quarters).

73. *Hemiargus* (*Echinargus*) *isolus* (Reak.) **Pl. IV, fig. e**

REAKIRT'S BLUE is an ubiquitous species, never common, but occurring over a wide territory and to a considerable elevation in the

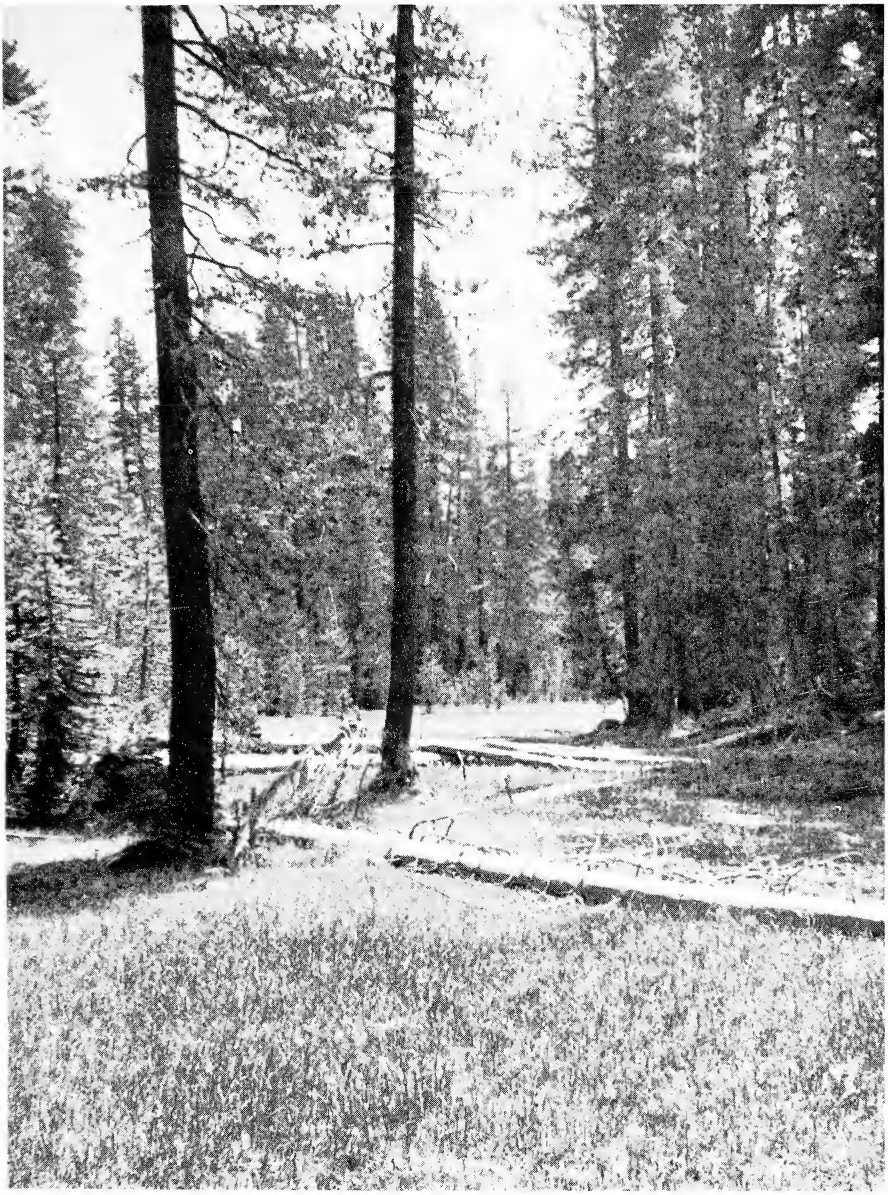


Fig. 6. Moist meadow surrounded by Lodgepole Pine and Red Fir forest. Canadian Zone. Research Reserve, el. 8,000 ft. *Anthocharis sara stella, Plejus saepiolus, Polygonia zephyrus, Precis orythya evarete,* and *Pyrgus ruralis* may be seen here.—Neva Snell.

drier eastern portions of the Sierra Nevada, at least in the 1958 season. A row of black dots encircled with white on the underside of the primaries is a distinguishing feature.

Life Zones: Unrestricted. Plant Communities: (Among others) Sagebrush Scrub. Host Plants: LEGUMINOSAE: *Astragalus* (Rattle Weed, Loco Weed), *Hosackia* (= *Lotus*), *Trifolium* (Clover).

74. *Lycaeides argyrognomon anna* (Edw.) Pl. II, fig. i

THE ANNA BLUE occurs at higher elevations in the western portion of the park, being found in the upper tier of timbered zones. It is always associated with lupine.

Life Zones: Canadian, Hudsonian. Plant Communities: Fir Forest openings. Host Plants: Undetermined. Probably LEGUMINOSAE: *Lupinus* (Lupine).

75. *Lycaeides melissa inyoensis* Nab. Pl. IV, figs. i and l

THE INYO BLUE is the name to be given to the race formerly recognized by most Californian lepidopterists as *lotis* (Lint.). According to Nabokov (1949), true *lotis* is a race of the foregoing *Lycaeides argyrognomon* restricted to peat bogs of Mendocino County. THE INYO BLUE flies in the eastern portion of the Yosemite region.

Life Zones: Unrestricted. Plant Communities: Several, including Freshwater Marsh, Alkali Sink, Meadowland, Marsh, Cultivated Field, Fence-Row, and Roadside Associations. Host Plants: LEGUMINOSAE: *Astragalus* (Loco Weed, Rattle Weed), *Hosackia* (= *Lotus*), *Lupinus* (Lupine), *Medicago* (Alfalfa), *Glycyrrhiza lepidota* (Liquorice), at Lone Pine.

76. *Plebejus* (*Agriades*) *glandon podarce* (F. & F.) Pl. III, fig. g

THE GRAY BLUE is perhaps the most characteristic butterfly of the Sierran sub-alpine meadow. It is common at Tioga Pass, where at times it fairly swarms, always in association with *Dodecatheon alpinum* (Shooting Star). As soon as the sun's rays leave the mountain valleys, it settles upon the grasses and sedges and may be picked by hand or by forceps. A cross on each fore-wing serves to distinguish the species.

Life Zones: Upper Canadian, Hudsonian (Arctic-Alpine). Plant Communities: Sub-alpine Meadow, Alpine Fell-Fields. Host Plants: Unknown. PRIMULACEAE: *Gregoria* for European *P. glandon,* to which *Primula* (Primrose) and *Dodecatheon* (Shooting Star) are related.

77. *Plebejus* (*Plebejus*) *saepiolus* (Bdv.)

THE GREENISH BLUE flies with the foregoing species, *Plebejus* (*A.*) *glandon podarce,* and in equal abundance. *P.* (*P.*) *saepiolus,* however, descends to lower elevations, as at Glacier Point and Aspen Valley. As with the former species, only the male wears the color indicated by the common name, the female being drab brown. The commonest blue in the park at higher elevations, and the one with the longest flight season, it has two broods, the first tending to oviposit on clover, the second on *Hosackia.*

Life Zones: Canadian, Hudsonian (Arctic-Alpine). Plant Communities: Subalpine Meadow, Alpine Fell-Fields. Host Plants: LEGUMINOSAE: *Trifolium* (Clover), *Hosackia* (= *Lotus*).

78a. ***Plebejus* (*Icaricia*) *icarioides icarioides* (Bdv.)**
b. ***Plebejus* (*Icaricia*) *icarioides helios* (Edw.)**

BOISDUVAL'S BLUE is a widely distributed species, having been subdivided into numerous geographical races. The Yosemite form is close to the nominate form; the name *helios* Edw. is here applied to specimens from Mono Lake. Because of its relatively large size and uniform markings, as well as its solid blue coloration, this species may be confused with *Lycaena* (*L.*) *heteronea* Bdv. when on the wing.

Life Zones: (Upper Sonoran), Transition, Canadian. Plant Communities: Coastal Sage Scrub, Chaparral, Foothill Woodland, Yellow Pine and Mixed Coniferous Forest openings for *P. i. icarioides;* Sagebrush Scrub, Pinon-Juniper Woodland, Juniper Woodland, Jeffrey Pine Forest openings for *P. i. helios.* Host Plants: LEGUMINOSAE: *Lupinus* (Lupine), perennial species only.

79. ***Plebejus* (*Icaricia*) *shasta comstocki* (Fox) Pl. III, fig. e**

THE YOSEMITE BLUE is the name given this insect in Comstock's "Butterflies of California," although by virtue of its Latin name it might be called Comstock's Blue instead. Its metropolis is above timber line, but isolated colonies occur above 7,000 feet, as at Glacier Point. It flies over dwarf lupine and yellow buckwheat, *Eriogonum incanum,* but has not been observed to oviposit on either. The long flight season suggests two broods. The Rocky Mountain *Plebejus* (*Icaricia*) *shasta minnehaha* (Scud.) flies only above tree line and often above 12,000 feet.

Life Zones: Hudsonian, Arctic-Alpine. Plant Communities: Subalpine Forest openings, Alpine Fell-Fields. Host Plants: Unknown. LEGUMINOSAE: *Lupinus* (Alpine Lupine) suspected.

80. ***Plebejus* (*Icaricia*) *acmon* (West. & Hew.)**

THE ACMON BLUE may be found throughout the Sierra Nevada at almost any elevation. It occasionally flies in company with the following *Plebejus* (*I.*) *lupini.* From this circumstance, plus a possible different host plant, it has been suggested that the two are distinct species, and they are tentatively so considered here.

Life Zones: Upper Sonoran, Transition, Canadian (Hudsonian. Plant Communities: Many. Host Plants: LEGUMINOSAE: *Astragalus* (Loco Weed, Rattle Weed), *Hosackia* (= *Lotus*), *Lupinus* (Lupine). POLYGONACEAE: *Eriogonum* (Buckwheat).

81. ***Plebejus* (*Icaricia*) *lupini* (Bdv.)**

THE LUPINE BLUE may be distinguished from *Plebejus* (*I.*) *acmon* by the purplish luster of both sexes. The two are sometimes found together, as at Smoky Jack Camp. Specimens from 11,000 feet are visibly smaller than those from moderate elevations; those from Lee Vining are visibly larger.

Life Zones: Canadian, Hudsonian, High Arid Transition. Plant Communities: Not determined. Subalpine Forest, Alpine Fell-Fields, Juniper Woodland, Sagebrush Scrub, among others. Host Plants: Apparently unknown, as distinct from *P. (I.) acmon. Eriogonum* (Buckwheat) association noted.

82. *Everes comyntas* (Godt.)

THE EASTERN TAILED BLUE is the species represented on the east side of the Sierra Nevada, although it is not known to which of several subspecies the Mono Lake population should be assigned.

Life Zones: Upper Sonoran (Hudsonian). Plant Communities: Not determined. Freshwater Marsh, Moist Meadow associations. Host Plants: LEGUMINOSAE: *Trifolium* (Clover), *Vicia* (Vetch), *Astragalus* (Loco Weed, Rattle Weed).

83. *Everes amyntula* (Bdv.)

THE WESTERN TAILED BLUE has been seen in Yosemite Park by one of us (Garth). It was flying over a tall, succulent lupine in the vicinity of a white fir grove at Hetch-Hetchy summit. It occurs in the foothills west of the park.

Life Zones: Transition (Canadian). Plant Communities: Yellow Pine Forest openings. Host Plants: LEGUMINOSAE: *Astragalus* (Loco Weed, Rattle Weed), *Lathyrus* (Sweet Pea), *Vicia* (Vetch).

84. *Philotes enoptes* (Bdv.)

THE DOTTED BLUE, as found at Glacier Point, is typical. Specimens found at Research Reserve show mixed characters, but are separable from the following species.

Life Zones: Transition, Canadian (Hudsonian). Plant Communities: Understory of several. Host Plants: POLYGONACEAE: *Eriogonum* (Buckwheat) of the *latifolium* group. The eggs are concealed in the flower head, on which the larvae feed.

85a. *Philotes battoides battoides* (Behr)

b. *Philotes battoides glaucon* (Edw.)

THE SQUARE-SPOTTED BLUE of Yosemite is an inhabitant of the Alpine Fell-Fields, appearing very early in the year for so high an altitude. It also flies atop Research Ridge (Boundary Hill), keeping well within the few acres marked by the presence of weak Hudsonian elements. It flies over *Eriogonum incanum,* a yellow buckwheat, and *Astragalus bolanderi,* a straggly legume. Specimens found within the park represent the typical form. Specimens found at Mono Lake are referred to THE GLAUCON BLUE, a subspecies.

Life Zones: Hudsonian for *P. b. battoides;* Upper Sonoran, Arid Transition for *P. b. glaucon.* Plant Communities: Rock Garden for *P. b. battoides;* Juniper Woodland, Sagebrush Scrub for *P. b. glaucon.* Host Plants: POLYGONACEAE: *Eriogonum* (Buckwheat).

86. *Philotes speciosa* (Hy. Edw.)

THE SMALL BLUE is typically a desert insect, found around dry lake beds (playas) in the Mojave Desert. Occasional specimens occur in the Central Valley region of California, and one of us (Garth) has found it at Hume Lake in Sequoia-Kings Canyon National Park. The

Mariposa and Briceburg specimens collected by G. and R. Bohart may represent an undescribed subspecies. Both specimens are larger, with wider margins in the male, and with the hind wings less spotted below, than normal specimens from the desert. In the absence of sufficient material, description must wait.

Life Zones: Lower Sonoran in the Mojave Desert; Upper Sonoran (Transition) in the western Sierra Nevada. Plant Communities: Not determined. Stream Bed Association. Host Plants: POLYGONACEAE: *Eriogonum* (Buckwheat) in San Diego County; *Oxytheca perfoliata* in the Mojave Desert; in the Sierra unknown.

87. *Phaedrotes piasus* (Bdv.)

THE ARROWHEAD BLUE, while not common in the Yosemite region, occurs in the western foothills, the middle elevations, and on the eastern slope at Mono Lake.

Life Zones: Upper Sonoran, Transition, Canadian. Plant Communities: Several. Host Plants: LEGUMINOSAE: *Lupinus* (Lupine).

88a. *Glaucopsyche lygdamus behrii* (Edw.)
b. *Glaucopsyche lygdamus columbia* (Skin.)

BEHR'S BLUE flies in the early spring in the western foothills. At higher elevations it is replaced by THE COLUMBIA BLUE, a montane subspecies found in cooler parts of most of the United States and Canada. It is not common in the Tioga Pass region, nor indeed anywhere, its colonies being widely scattered.

Life Zones: Upper Sonoran for *G. l. behrii;* Canadian, Hudsonian for *G. l. columbia.* Plant Communities: Foothill Woodland, Chaparral for *G. l. behrii;* Subalpine Forest, Alpine Fell-Fields for *G. l. columbia.* Host Plants: LEGUMINOSAE: *Lotus* (= *Hosackia*), *Astragalus* (Loco Weed, Rattle Weed), *Lathyrus* (Sweet Pea), *Lupinus* (Lupine), *Vicia* (Vetch).

89. *Celastrina argiolus echo* (Edw.)

THE ECHO BLUE is the western representative of a highly polymorphic species, now recognized as having Old World affinities. One of the earliest butterflies to emerge in the spring, it follows the season's advance to higher altitudes, occurring through three life zones. Male and female are strikingly dissimilar in pattern.

Life Zones: Upper Sonoran, Transition, Canadian. Plant Communities: Many. Host Plants: LEGUMINOSAE: *Hosackia* (= *Lotus*), *Lupinus* (Lupine); RHAMNACEAE: *Ceanothus* (Lilac), *Spiraea* (Spirea); SAPINDACEAE: *Aesculus* (Buckeye); ERICACEAE: *Arctostaphylos* (Manzanita); FAGACEAE: *Quercus* (Oak); CORNACEAE: *Cornus* (Dogwood). In many instances, only the flower buds are fed upon.

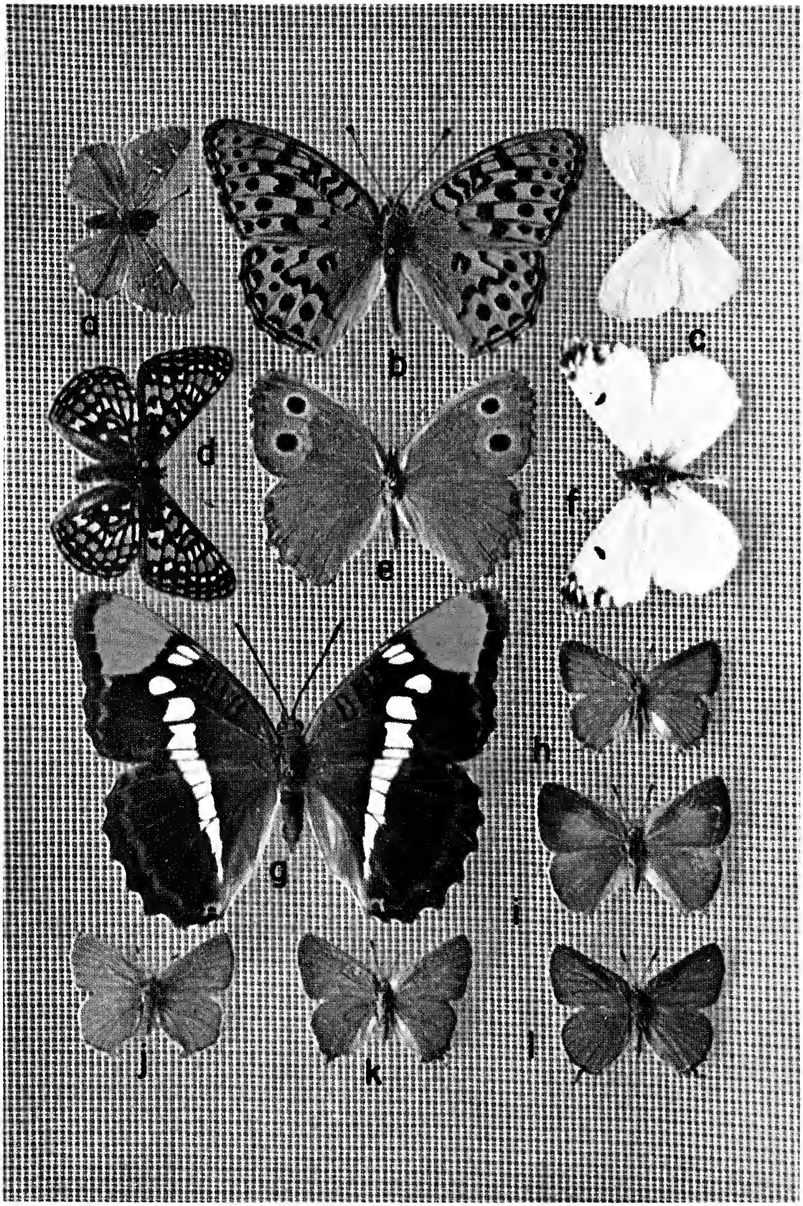


PLATE I

PLATE I

THE WESTERN FOOTHILLS

a. Thorbes diversus ♂
Aspen Valley, J.S.G.
b. Argynnis z. zerene ♂
Mather, J.S.G.
c. Coenonympha t. californica ♂
Jerseydale, J.S.G.
d. Euphydryas e. rubicunda ♂
Indian Flat, J.W.T.
e. Cercyonis sylvestris ♀
Hetch-Hetchy, J.S.G.
f. Anthocharis lanceolata ♂
Yosemite Valley, Paul Allen
g. Limenitis b. californica ♀
Hetch-Hetchy, J.S.G.
h. Habrodais grunus ♀
Hetch-Hetchy, J.S.G.
i. Callophrys nelsoni ♀
Hetch-Hetchy, J. S.G.
j. Callophrys d. windi ♀
Indian Flat, J.W. T.
k. Strymon auretorum ♀
Hetch-Hetchy, J S.G.
l. Callophrys johnsoni ♂
Jerseydale, A.O.S.

PLATE II

THE WESTERN MID-ELEVATIONS

a. Anthocharis s. stella ♀
White Wolf, J.S.G.
b. Limenitis lorquini ♂
Aspen Valley, J.S.G.
c. Phyciodes mylitta ♀
Yosemite Creek, J.S.G.
d. Boloria epithore ♀
Tioga Road, J.S.G.
e. Parnassius c. baldur ♂
White Wolf, J.S.G.
f. Lycaena nivalis ♀
Research Reserve, J.S.G.
g. Hesperia harpalus ♂
Yosemite Creek, J.S.G.
h. Argynnis a. irene ♂
Aspen Valley, J.S.G.
i. Lycaeides a. anna ♂
Aspen Valley, J.S.G.
j. Melitaea palla ♂
White Wolf, J.S.G.
k. Polygonia zephyrus ♀
Tuolumne Grove, J.S.G.
l. Melitaea hoffmanni ♀
White Wolf, J.S.G.

PLATE III

THE HIGH COUNTRY

a. Melitaea d. malcolmi ♂
Gaylor Lakes, J.S.G..
b. Oeneis c. ivallda ♂
Glacier Lodge, J.S.G.
c. Euphydryas e. nubigena ♀
Rafferty Creek, J.S.G.
d. Polites s. tecumseh ♂
Upper Gaylor Lake, J.S.G.
e. Plebejus s. comstocki ♂
Yosemite Park, J.S.G.
f. Parnassius p. behri ♂
Gaylor Lakes, J.S.G.
g. Plebejus g. podarce ♂
Research Reserve, J.S.G.
h. Lycaena p. hypophlaeas ♀
N. slope, Mt. Dana, A.O.S.
i. Colias behri ♂
Tioga Pass, J.S.G.
j. Lycaena cupreus ♂
Lembert Dome, J.S.G.
k. Callophrys lemberti (paratype) ♂
Tioga Pass, J.W.T.
l. Argynnis m. arge ♀
Tioga Pass, J.S.G.
m. Hesperia miriamae ♀
Unicorn Peak, A.O.S.

PLATE IV

THE MONO BASIN

a. Coenonympha t. mono ♂
W of LeeVining, A.O.S.
b. Argynnis c. nevadensis ♂
near Mammoth, J.S.G.
c. Cercyonis oeta ♂
June Lake, J.S.G.
d. Lycaena rubidus ♂
Virginia Lakes, J.S.G.
e. Hemiargus isolus ♀
Rafferty Cr., J.S.G.
f. Euphydryas e. monoensis ♂
Mono Lake, A.O.S.
g. Strymon behrii ♀
Mammoth, J.S.G.
h. Limenitis w. nevadae ♂
Mono Lake, J.S.G.
i. Lycaeides m. inyoensis ♂
Mono Lake, J.W.T.
j. Strymon f. semiluna ♂
Mono Lake, A.O.S.
k. Argynnis n. apacheana ♂
Round Valley, J.S.G.
l. Lycaeides m. inyoensis ♀
Lone Pine, J.W.T.

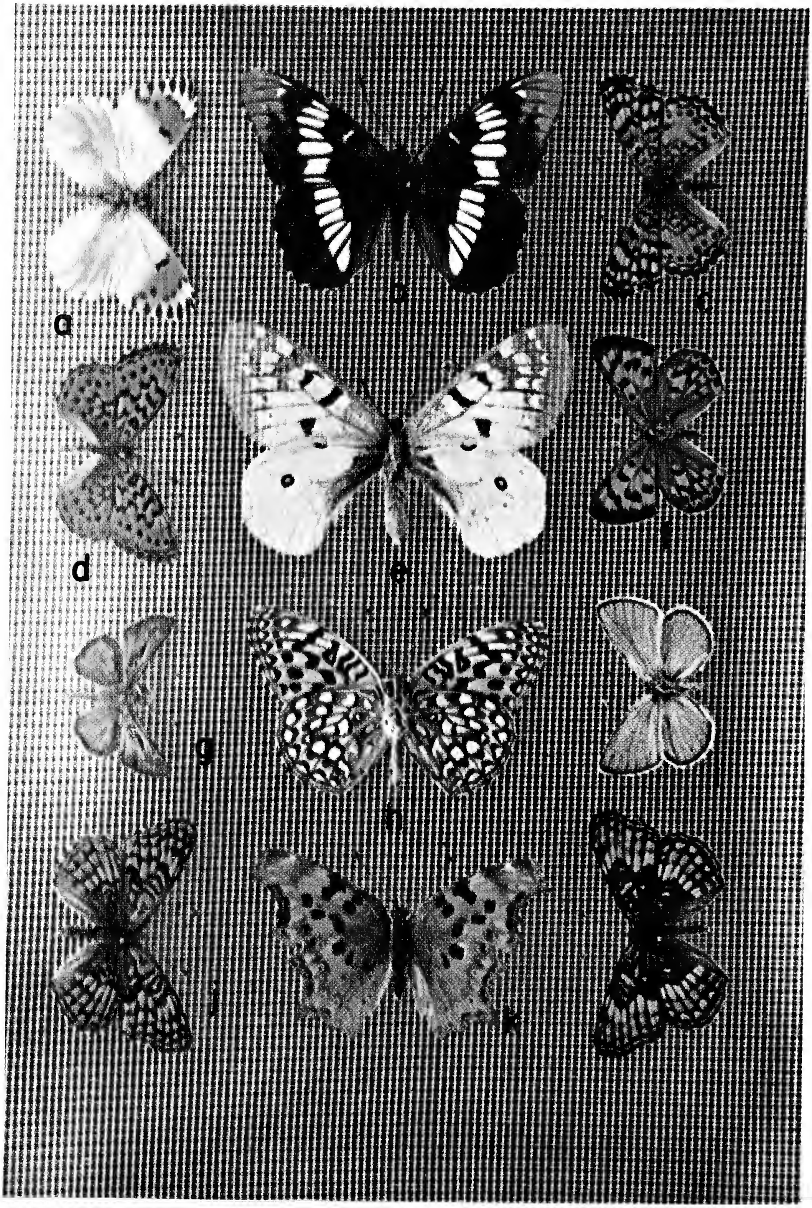


PLATE II

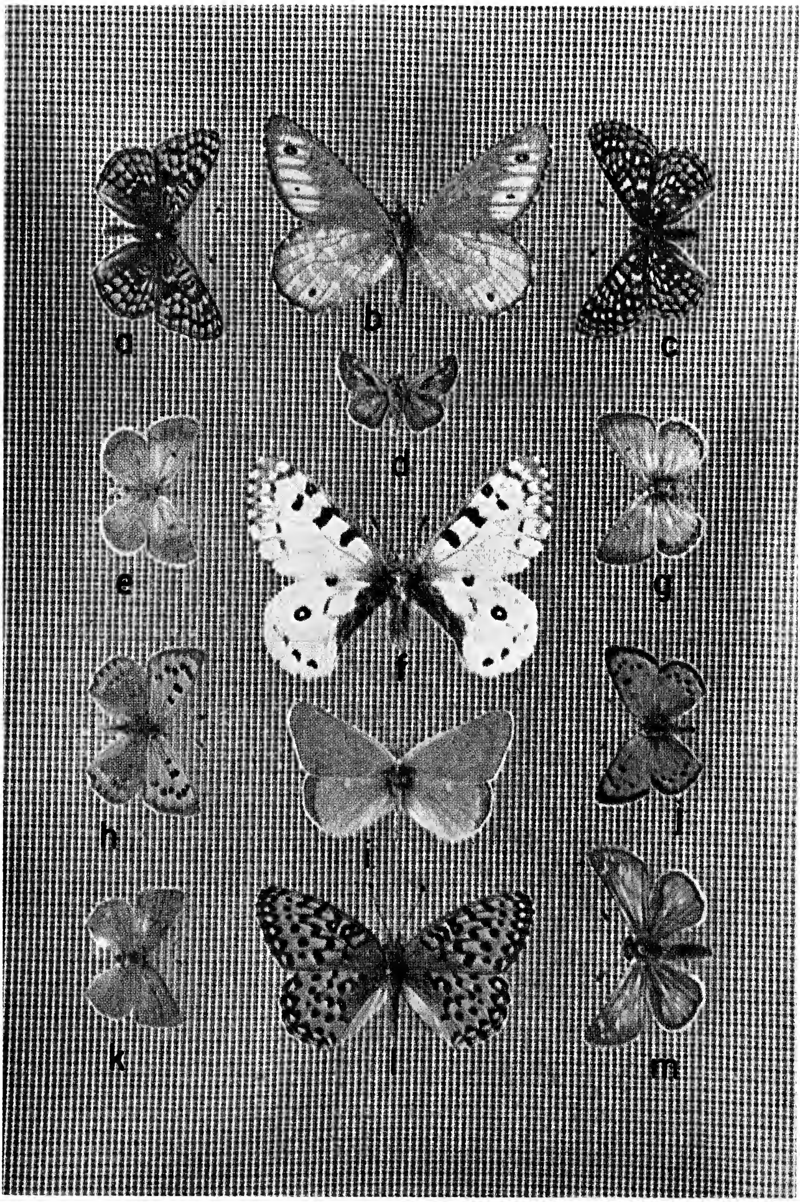


PLATE III

PIERIDAE

90a. *Anthocharis* (*Anthocharis*) *sara sara* Lucas
Anthocharis (*Anthocharis*) *sara reakirtii* Edw., *gen. vern.*
b. *Anthocharis* (*Anthocharis*) *sara stella* Edw. **Pl. II, fig. a**

THE SARA ORANGE-TIP and its overwintering form, REAKIRT'S ORANGE-TIP, occur in the western lowlands at Briceburg and El Portal. THE STELLAR ORANGE-TIP is the high-altitude race found in California, race *julia* Edw. being from Colorado and race *flora* Wgt. from Oregon and north. Females of this form are yellowed, unlike those of the lowland forms, in which females are white like the males.

Life Zones: Upper Sonoran, lower Transition for *A. sara sara;* upper Transition, Canadian for *A. s. stella.* Plant Communities: Valley Grasslands, Foothill Woodland, Chaparral, Yellow Pine Forest for *A. s. sara;* White Fir Forest, Red Fir Forest for *A. s. stella.* Forest openings and Riparian Association. Host Plants: CRUCIFERAE: *Arabis* (Rock Cress), *Brassica* (Mustard), *Sisymbrium* (Hedge Mustard).

91. *Anthocharis* (*Falcapica*) *lanceolata* Lucas **Pl. I, fig. f**

THE LANCEOLATE MARBLE (formerly called Boisduval's Marble when authorship was attributed to him) is an early flier, to be sought from mid-May to mid-June. It seeks the vertical walls of Yosemite Valley and may be seen on the precipitous talus slopes near Bridal Veil Falls. Yosemite specimens are almost gray enough beneath to match race *australis* (Grin.) from southern California.

Life Zones: Upper Sonoran, Transition. Plant Communities: Chaparral, Foothill Woodland, Mixed Evergreen Forest. Rocky Outcrop and Cliffside Associations. Host Plants: CRUCIFERAE, especially *Arabis perfoliata* (Rock Cress).

92. *Euchloe creusa hyantis* (Edw.)

EDWARDS' MARBLE may be separated from the following Colorado Marble by the heavy green marbling of the under side of the secondaries against a background of dead white, *Euchloe ausonides coloradensis* having less green and of a decidedly yellowish cast against a pearly white ground color. The green of both species is an effect produced by yellow scales laid over black, as examination with a hand lens will demonstrate. The black bar at the end of the cell is wide in *creusa.*

Life Zones: Upper Sonoran, Transition, Canadian. Plant Communities: Chaparral, Foothill Woodland, Mixed Evergreen Forest, White Fir Forest. Host Plants: CRUCIFERAE: *Arabis* (Rock Cress), *Streptanthus* (Jewel Flower).

93. *Euchloe ausonides coloradensis* (Hy. Edw.)

THE COLORADO MARBLE is the common *Euchloe* of the Research Reserve, where approximately four specimens were found for every one of *E. creusa hyantis.* Both fly to the mountain tops and may be seen in good numbers by the observer who stations himself in such

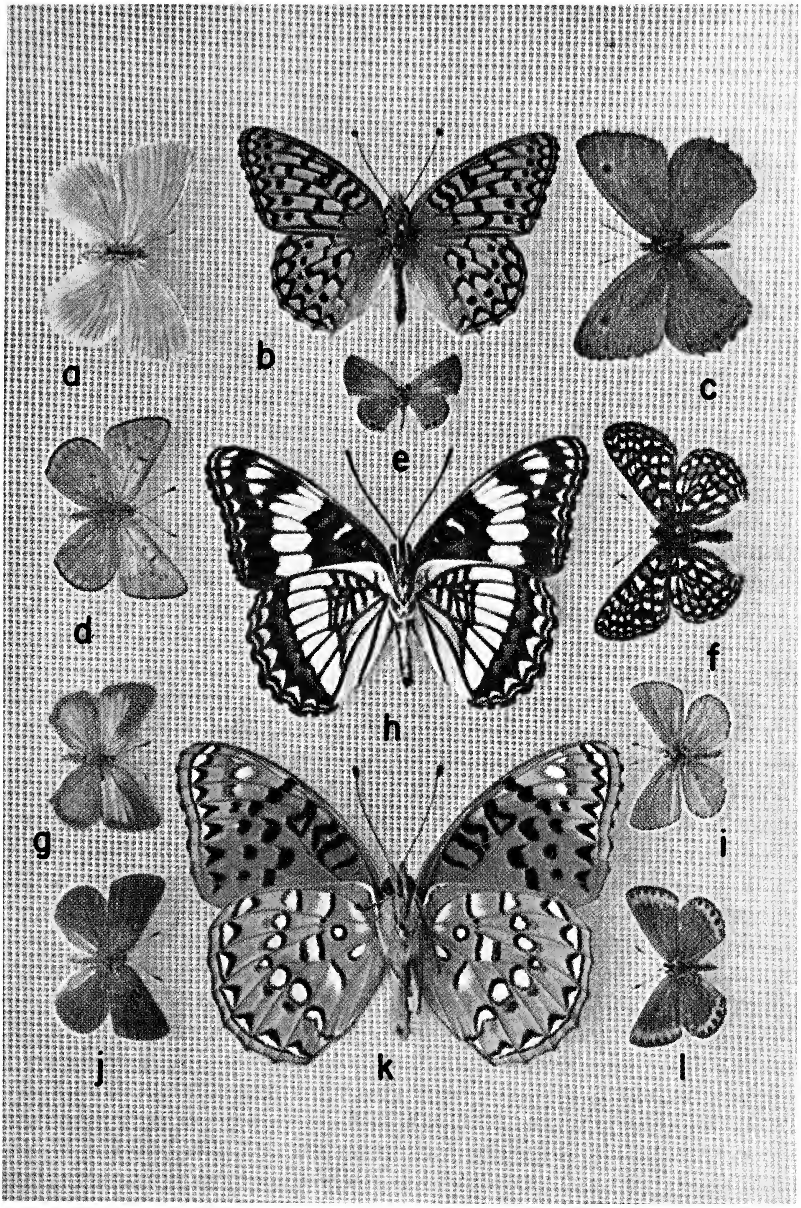


PLATE IV

a situation. Like Behr's Parnassian, *Parnassius phoebus behrii* Edw., it belongs to the Great Basin fauna. The black bar at the end of the cell is narrow.

Life Zones: Canadian, Hudsonian. Plant Communities: Coniferous Forest openings. Host Plants: CRUCIFERAE: *Arabis* (Rock Cress), *Erysimum* (Wall Flower), *Sisymbrium* (Hedge Mustard).

94. *Colias eurytheme* Bdv.

THE CLOUDED SULPHUR is partial to grassy meadows and to cultivated areas, where it substitutes introduced alfalfa for indigenous *Astragalus* for its food plant. The summer form, *amphidusa* Bdv., is larger and more orange. Both have two forms of the female, normal and albinic, but only one form of the male.

Life Zones: Unrestricted. Plant Communities: Immaterial, if legumes be present. Host Plants: LEGUMINOSAE: *Astragalus* (Loco Weed, Rattle Weed), *Hosackia* (= *Lotus*), *Medicago* (Alfalfa), *Melilotus* (Sweet Clover), *Trifolium* (Clover), *Vicia* (Vetch).

95. *Colias philodice hagenii* Edw.

HAGEN'S SULPHUR is a Great Basin race of a widely ranging North American species found otherwise mostly east of the Rocky Mountains. According to Hovanitz (1943, 1950), it does not occur west of the Sierra-Cascade Divide Triple-brooded at Mono Lake, it may be recognized by its yellow, rather than orange, coloration.

Life Zones: Upper Sonoran, Transition. Plant Communities: Moist Meadows. Host Plants: LEGUMINOSAE: *Trifolium* (Clover).

96. *Colias occidentalis chrysomelas* Hy. Edw.

THE GOLDEN SULPHUR is the largest member of its genus occurring in California. An early flier, it is considered a rarity, having been seen by but one of us (Tilden) in the vicinity of Mather on June 30, 1962, in the course of this survey.

Life Zones: Transition. Plant Communities: Associated with coniferous forest at moderate elevations. Host Plants: LEGUMINOSAE: (Legumes).

97. *Colias behrii Edw.* **Pl. III, fig. i**

BEHR'S SULPHUR is the only greenish sulphur butterfly of the Sierra Nevada. Until the opening of the Tioga Road in 1915 it was considered a great rarity because of the extreme inaccessibility of its habitat, the Tuolumne Meadows. John Batiste Lembert, who homesteaded the Soda Springs quarter section in 1885, found that there was a demand for these butterflies and for a dozen years supplied them in quantity to universities and museums. The secret of their haunts he shared with the Indians, who in turn refused to divulge it to outsiders.

We now know that *Colias behrii* has as its metropolis the Tuolumne Meadows, that smaller colonies are present in adjacent subalpine meadows, and that it has been found to the south at Rock Creek and Mineral King. Its occurrence is tied closely to the distribution of Dwarf Bilberry, on which the larvae exclusively feed. Form ♀ *canescens*

PLATE V

a. Erynnis pacuvius lilias ♂
Chowchilla Mtn. J.W.T.
b. Argynnis zerene malcolmi ♂
Mammoth Lakes, J.W. Friday
c. Lycaena gorgon ♀
Lebec, J.S.G.
d. Everes amyntula ♂
Yucaipa, J.S.G.
e. Papilio indra ♂
Tioga Pass, A.O.S.
f. Callophrys iroides ♂
Grant Nat'l Park J.S.G.
g. Strymon saepium ♀
Hetch-Hetchy, J.S.G.
h. Lycaena editha ♀
Tioga Pass, J.S.G.
i. Philotes battoides glaucon ♂
Mono Lake. A.O.S.
j. Brephidium exilis ♂
Long Beach, J.S.G.
k. Philotes battoides battoides ♂
Research Reserve, J.S.G.
l. Pieris occidentalis calyce ♀
W of Tioga Pass, A.O.S.
m. Danaus plexippus ♂
Mather, J.S.G.
n. Euchloe creusa lotta ♀
Darwin, R.P. Allen
o. Polites sonora ♀
Aspen Valley, J.S.G.
p. Vanessa carye ♂
Topanga Canyon, J.S.G.
q. Vanessa cardui ♀
Grant Nat'l Park, J.S.G.
r. Polites sonora ♂
Bridal Veil Creek, J.S.G.
s. Lycaena heteronea ♀
Gem Lake, J.S.G.
t. Callophrys iroides ♂
Mammoth Lakes, J.S.G.
u. Phaedrotes piasus ♂
Tujunga, J.S.G.
v. Plebejus icarioides helios ♀
Warren Creek, J.S.G.

PLATE VI

a. Thorbes pylades ♂
Jersydale, J.W.T.
b. Pyrgus ruralis ♂
Boulder Creek, J.W.T.
c. Ochlodes agricola ♂
Hetch-Hetchy, J.S.G.
d. Amblyscirtes vialis ♂
Flagstaff, Ariz., K. Roever
e. Argynnis atlantis irene ♂
Aspen Valley, J.S.G.
f. Leptotes marina ♀
Long Beach, J.S.G.
g. Vanessa virginiensis ♀
Santa Cruz Mtns., J.S.G.
h. Strymon melinus pudica ♂
Long Beach, J.S.G.
i. Nymphalis milberti ♀
Yucaipa, J.S.G.
j. Lycaena arota virginiensis ♀
Mono Lake, A.O.S.
k. Pieris napi venosa ♂
Briceburg, K.T.
l. Papilio eurymedon ♂
Idyllwild, J.S.G.
m. Plebejus saepiolus ♂
Research Reserve, J.S.G.
n. Colias eurytheme ♂
Mather, J.S.G.
o. Argynnis cybele leto ♀
Strawberry, J.S.G.
p. Argynnis callippe inornata ♀
Jerseydale, A.O.S.

PLATE V

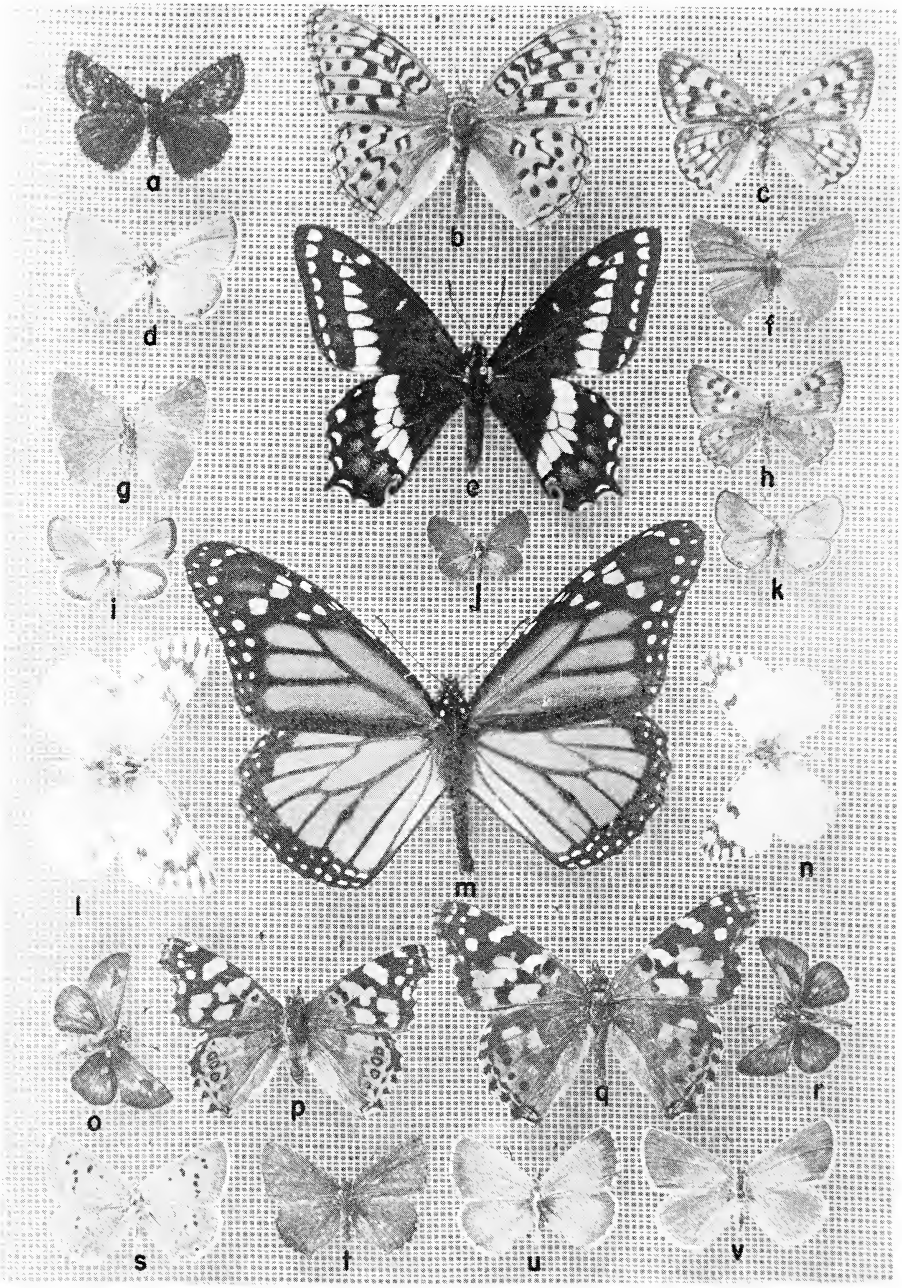
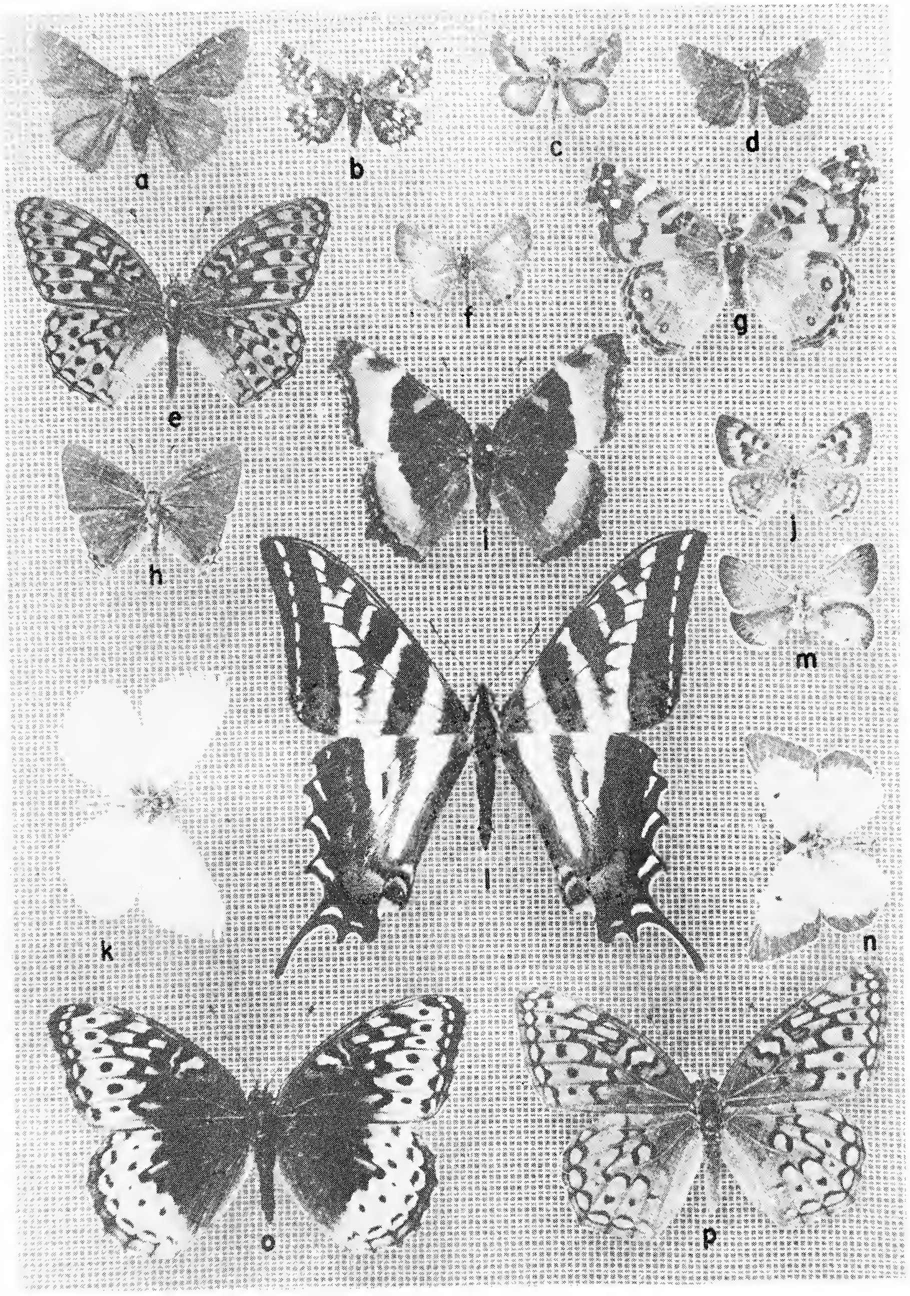


PLATE VI



Comst., although relegated to synonymy by McDunnough (1938), we find to be a valid albinic form that may be recognized on the wing.

Life Zones: Hudsonian (Arctic-Alpine). Plant Communities: Subalpine Meadows; basin areas of Subalpine Forest; moister parts of Alpine Fell-Fields. Host Plants: ERICACEAE: *Vaccinium caespitosum* (Dwarf Bilberry).

98. *Colias (Zerene) eurydice* Bdv.

THE CALIFORNIA DOG-FACE or FLYING PANSY, as it is sometimes called, must be a vagrant in the Yosemite region, for Hall (1912) does not record its food plant, False Indigo or Lead Bush, as occurring in the park. It is abundant in the foothills of southern California, and has been selected as the State butterfly. The male bears the figure of a dog's head on the forewing; the female is pure sulphur yellow.

Life Zones: Upper Sonoran, lower Transition. Plant Communities: Not determined for the Yosemite region. Host Plants: LEGUMINOSAE: *Amorpha californica* (False Indigo).

99. *Nathalis iole* Bdv.

THE DAINTY YELLOW is likely to be encountered in the least expected places, from sea level to 9,000 feet, and from early spring to early winter. There are no set rules of behavior for this diminutive sulphur, which has followed the Filaree into many an improbable situation.

Life Zones: Unrestricted. Plant Communities: Ubiquitous. Host Plants: GERANIACEAE: *Erodium* (Filaree). COMPOSITAE: *Helenium* (Sneezeweed), *Dyssodia* (None). CARYOPHYLLACEAE: *Stellaria* (Chickweed).

100. *Neophasia menapia tau* (Scud.)

THE PINE WHITE reaches the peak of its flight in August. The adults are high fliers, seldom descending from the tree tops. Although not abundant in 1933, they were seen by the hundreds in 1928 along the Big Oak Flat road by one of us (Garth). The larvae are of special interest to forest entomologists, having been known to defoliate pine trees over large areas. Resurrected from synonymy, the name *tau* is now applied to the western form.

Life Zones: Transition, Canadian. Plant Communities: Yellow Pine Forest, Jeffrey Pine Forest (east slope); occasionally Lodgepole Pine Forest. Host Plants: PINACEAE: *Pinus ponderosa* (Yellow Pine), *P. contorta Murrayana* (Lodgepole Pine); also, according to the observation of one of us (Tilden), *Pseudotsuga taxifolia* (Douglas

101. *Pieris (Pontia) beckerii* Edw.

BECKER'S WHITE prefers an arid environment and is encountered east of the Sierra Nevada from the Mojave Desert north through Owens Valley to Mono Lake. The green-margined veins of the under side suggest one of the Marbles, and where it flies with *Anthocharis*

PLATE VII

a. Epargyreus clarus ♀
Lagunitas, E.C. VanDyke
b. Hesperia juba ♂
Mather, J.W.T.
c. Ochlodes sylvanoides ♂
Virginia Lakes, J.S.G.
d. Erynnis propertius ♂
Yosemite Creek, J.S.G.
e. Glaucopsyche lygdamus columbia ♂
White Wolf, J.S.G.
f. Cercyonis pegala ariane ♀
Round Valley, J.S.G.
g. Argynnis egleis ♂
Yosemite Creek, J.S.G.
h. Plebejus i. icarioides ♀
Aspen Valley, J.S.G.
i. Euchloe creusa lotta ♀
Mono Lake, A.O.S.
j. Philotes speciosa ♂
Mojave Desert, J.S.G.
k. Heliopetes ericetorum ♂
Switzer-land, J.S.G.
l. Apodemia m. mormo ♂
Mono Lake, A.O.S.
m. Papilio rutulus ♂
Idyllwild, J.S.G.
n. Precis orithya evarete ♂
Grant Nat'l Park, J.S.G.
o. Plebejus lupini ♂
W. of Tioga Pass, A.O.S.
p. Nymphalis californica ♀
Idyllwild, J.S.G.
q. Colias eurytheme form alba ♀
Big Bear Lake, J.S.G.
r. Lycaenopsis argiolus echo ♀
Yucaipa, J.S.G.
s. Lycaena a. arota ♀
Gold Creek, J.W.T.
t. Lycaena xanthoides ♀
Mather, J.S.G.
u. Callophrys spinetorum ♂
Idyllwild, J.S.G.
v. Strymon adenostematis ♀
Hetch-Hetchy, J.S.G.

PLATE VIII

a. Erynnis tristis ♂
Redwood City, J.. W. T.
b. Thorbes mexicana nevada ♂
Tioga Pass, A.O.S.
c. Pyrgus communis ♂
Los Angeles, J.S.G.
d. Nathalis iole ♂
Warren Creek, A.O.S.
e. Pieris sisymbrii ♂
Research Reserve, J.S.G.
f. Ochlodes agricola ♂
El Portal
g. Strymon dryope ♂
Mono Lake. A.O.S.
h. Papilio zelicaon ♀
Mather, J.S.G.
i. Strymon californica ♂
Hetch-Hetchy
j. Lycaena helloides ♂
Mather, J.S.G.
k. Lycaena nivalis ♀
Glacier Point, J.D. Gunder
l. Melitaea leanira ♂
m. Colias (Zerene) eurydice ♂
Santa Ana R., J.S.G.
n. Phyciodes c. campestris ♂
Mather , J.S.G.
o. Argynnis mormonia arge ♂
Hetch-Hetchy, J.S.G.
p. Plebejus acmon ♂
Hetch-Hetchy
q. Philotes enoptes ♀
Research Reserve, J.S.G.
r. Polygonia satyrus ♂
Mono Lake, A.O.S.

PLATE VII

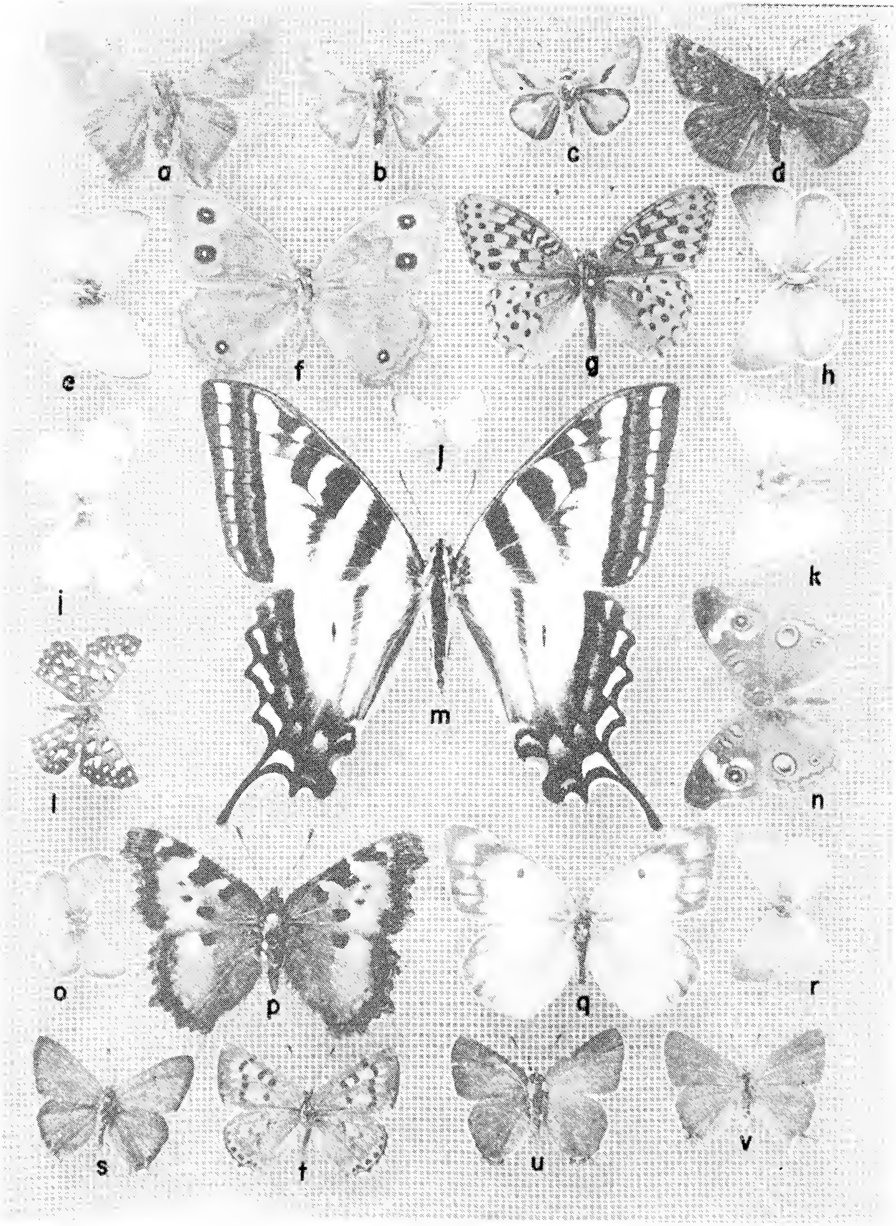
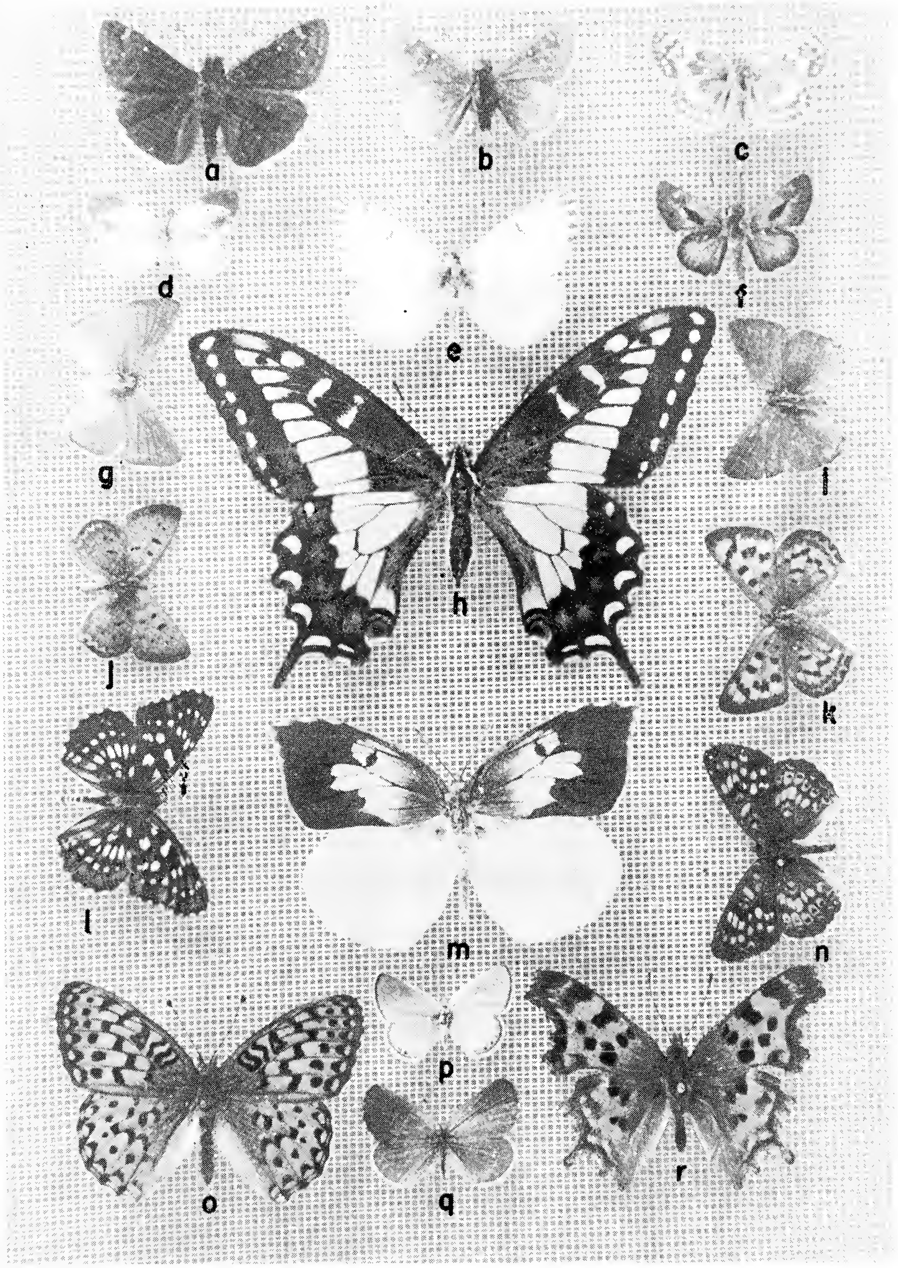


PLATE VIII



lanceolata australis Grin. in some of the desert canyons the two are not always distinguishable when on the wing.

Life Zones: Upper Sonoran, Transition. Plant Communities: Sagebrush Scrub, Shadscale Scrub, Piñon-Juniper and Juniper Woodland. Host Plants: CAPPARIDACEAE: *Isomeris arborea* (Bladder Pod). CRUCIFERAE: *Brassica nigra* (Mustard), *Sisymbrium altissimum* (Hedge Mustard), *Stanleya pinnata* (Desert Plume, Prince's Plume).

102. ***Pieris* (*Pontia*) *sisymbrii*** Bdv.

THE CALIFORNIA WHITE is an early flier in the western foothills, where it may be found at Briceburg and El Portal in mid-March. At higher elevations it flies in mid-summer with the following *Pieris* (*Pontia*) *occidentalis calyce,* these two being the only whites then on the wing. While *Sisymbrium,* from which it takes its scientific name, grows abundantly in the meadows of Research Reserve, the species exhibits a marked preference for *Caulanthus* and *Streptanthus* when these are available, according to Hovanitz (personal communication).

Life Zones: Unlimited. Plant Communities: The entire gamut from west to east. Host Plants: CRUCIFERAE: *Arabis* (Rock Cress), *Caulanthus* (Rock Cabbage), *Sisymbrium* (Hedge Mustard), *Streptanthus* (Jewel Flower).

103. ***Pieris* (*Pontia*) *protodice*** Bdv. & Lec.

THE COMMON WHITE appears limited to the lower tier of life zones in Yosemite. Those seen above Transition Zone are believed to have wandered upward because of their worn condition.

Life Zones: Upper Sonoran, Transition (Canadian). Plant Communities: Many. Host Plants: CAPPARIDACEAE: *Cleome lutea* (Bee Plant). CRUCIFERAE: *Brassica nigra* (Mustrad), *Raphanus* (Radish), *Lepidium densiflorum* (Pepper Grass), *Sisymbrium altissimum* (Hedge Mustard), the first and two last at Mono Lake on the authority of W. Hovanitz.

104a. ***Pieris* (*Pontia*) *occidentalis occidentalis*** Reak.
b. ***Pieris* (*Pontia*) *occidentalis calyce*** Edw.

THE WESTERN WHITE occurs throughout the park, its altitudinal form, EDWARD'S WHITE; at higher elevations only, although a small, dark form resembling *P. o. calyce* may be found in early spring in the western foothills. What one finds in the high country in August is *calyce,* freshly emerged (It is the only brood at higher elevations), plus worn second-brood *P. o. occidentalis* that have invaded from lower levels. L. G. Higgins of England recently (1953) associated *calyce* Edw. with the European *callidice* Esper as subspecies of *P.* (*Pontia*) *occidenalis,* which has been shown by Hovanitz (1963) to be specifically distinct from the preceding *P.* (*Pontia*) *protodice.*

Life Zones: Unrestricted for *P. o. occidentalis;* Canadian, Hudsonian for *P. o. calyce.* Plant Communities: Many for *P. o. occidentalis;* Alpine

Fell-Fields for *P. o. calyce*. Host Plants: CRUCIFERAE: *Arabis* (Rock Cress), *Lepidium densiflorum* (Pepper Grass), *Sisymbrium altissimum* (Hedge Mustard), the last two in the Mono Lake area, according to Hovanitz (personal communication).

105. ***Pieris* (*Pieris*) *napi venosa*** Scud.

THE VEINED WHITE is found in the foothills adjacent to Yosemite National Park on the San Joaquin Valley side from mid-March to mid-May, when it appears on the floor of Yosemite Valley. More lightly marked than typical *venosa,* this foothill population is not referable to any other named subspecies.

Life Zones: Upper Sonoran, Transition. Plant Communities: Foothill Woodland, Chaparral, Mixed Coniferous Forest. Riparian and Cool Woodland associations. Host Plants: CRUCIFERAE: *Barbarea* (Winter Cress), *Brassica* (Mustard), *Dentaria* (Milk Maids), *Raphanus* (Radish).

106. ***Pieris* (*Pieris*) *rapae*** **(Linn.)**

THE CABBAGE WHITE was introduced from Europe into Quebec, Canada, in 1858, reaching California about 1883. It now occupies not only cultivated areas, but has expanded into wild lands as well.

Life Zones: Unrestricted. Plant Communities: Many, as would be expected of a highly adaptable immigrant. Host Plants: CRUCIFERAE: *Brassica* (Mustard), *Radicula* (Yellow Cress), the latter around Cathay.

PAPILIONIDAE

107. ***Papilio zelicaon*** Luc.

THE ANISE SWALLOWTAIL is a "hill-topper" species, choosing the most exposed situations for its flight. Usually only the males disport themselves in this way, six being found at the very summit of Research Ridge. It is partial to the blossoms of the Western Wallflower, *Erysimum asperum.* Although readily confused with *Papilio bairdii brucei* Edw., which occurs in the region of the Mono Craters east of the Sierra Nevada, *P. zelicaon* has less yellow on the abdomen than does *P. brucei.*

Life Zones: Unrestricted. Plant Communities: Chaparral, Foothill Woodland, openings in Coniferous Forest. Host Plants: UMBELLIFERAE: *Daucus* (Wild Carrot), *Foeniculum vulgare* (Fennel, Anise), *Heracleum lanatum* (Cow Parsnip).

108. ***Papilio indra*** Reak.

THE INDRA SWALLOWTAIL has been seen also at the summit of Research Ridge. An erratic flier, it has proven most elusive, and Yosemite records are few. These include the floor of Yosemite Valley, the summit of Yosemite Falls, northwest above Tioga Pass, and Mono Lake. On the west bank of Yosemite Creek it flies with *Parnassius phoebus behrii* Edw. on dry slopes in association with Juniper, *Sedum,* and *Sanicula.*

Life Zones: Transition, Canadian, Hudsonian. Plant Communities: Juniper Woodland. Host Plants: UMBELLIFERAE: *Pteryxia* (= *Cymopterus*) *terebrinthina* in the Sierra Nevada (Emmel and Emmel, 1963).

109. *Papilio rutulus* Luc.

THE WESTERN TIGER SWALLOWTAIL is a species that transcends zonal limits in its adherence to the stream-bank association. It occurs at El Portal on the Merced River, thence through the Yosemite Valley and its tributary streams well into Canadian Zone. One of us (Tilden) has even observed it in Subalpine Forest at Tioga Pass.

Life Zones: Unrestricted. Plant Communities: Willow, Cottonwood, and Aspen groves, Riparian Association. Host Plants: SALICACEAE: *Populus* (Cottonwood), *Salix* (Willow). BETULACEAE: *Alnus* (Alder). ROSACEAE: *Prunus* (Choke-Cherry).

110. *Papilio multicaudatus* Kby.
Syn. *Papilio daunus* Bdv.

THE TWO-TAILED SWALLOWTAIL has been known to inhabit the Yosemite region since 1930, when B. A. Thaxter and Edna Banta, Yosemite Field School members, wrote: "Among the swallowtails found here we took *Papilio daunus,* the largest western species, a bright yellow butterfly with black markings and two tails on each hind wing." Their brief report, "Some Butterflies and Moths of the Yosemite Valley Region," is on file at the Yosemite Museum, but their two specimens are without accompanying data. For information on exact locality and date we are indebted to Oakley Shields, who twice encountered it in August at Jerseydale, where it came to thistles.

Life Zones: Upper Sonoran, Transition. Plant Communities: All at moderate elevations. Host Plants: SALICACEAE: *Populus* (Cottonwood), *Salix* (Willow). LAURACEAE: *Umbellularia* (Laurel). OLEACEAE: *Fraxinus* (Ash). ROSACEAE: *Amelanchier* (Service Berry), *Prunus* (= *Cerasus*) (Choke-Cherry). RUTACEAE: *Ptelea* (Hop Tree).

111a. *Papilio eurymedon eurymedon* Luc.
b. *Papilio eurymedon albanus* F. & F.

THE PALE SWALLOWTAIL is more frequently encountered on dry hillsides than is the nearly related and equally abundant *Papilio rutulus.* While the food plant adheres strictly to the lower zones, the strong wings of the butterfly carry it to the tops of the highest peaks. A form or possible subspecies occurring at the higher altitudes, smaller in size and darker in color, is known as *P. e. albanus* F. & F.

Life Zones: Upper Sonoran, Transition, straying higher. Plant Communities: Chaparral, Foothill Woodland, and the chaparral-like under story of most Coniferous Forests. Host Plants: RHAMNACEAE: *Rhamnus* (= *Frangula*) *californicus* (Coffee Berry), *R. crocea* (Red Berry), *Ceanothus* (Snow Bush).

112. ***Parnassius clodius baldur*** **Edw.** **Pl. II, fig. e**

THE BALDUR PARNASSIAN flies to the very rim of the precipitous walls of Yosemite Valley, but does not descend into the valley itself. In the Research Reserve it was particularly abundant, flying over thickets of *Castanea* (Chinquapin) and *Holodiscus* (Ocean Spray), and pausing occasionally to sip nectar from yellow *Senecio*, a composite. While the fir belt generally defines its habitat, it occasionally strays higher among Lodgepole Pine and Mountain Hemlock. A few individuals are without the black-margined secondaries and suggest the parent species, *P. clodius* Mén.

Life Zones: (upper Transition), Canadian, lower Hudsonian (Arctic-Alpine). Plant Communities: Red Fir Forest; Lodgepole Pine Forest; exceptionally, Alpine Fell- Fields. Host Plants: CRASSULACEAE: *Sedum* (Stonecrop). ERICACEAE: *Vaccinium* (Bilberry). SAXIFRAGACEAE: *Saxifraga* (Saxifrage).

113. ***Parnassius phoebus behrii*** **Edw.** **Pl. III, fig. f**

BEHR'S PARNASSIAN is well established on the eastern slope of the Sierra Nevada, as befits its affinities with the Great Basin fauna. The arid eastern exposures of many ridges west of the Sierran divide, with the persistent association of Juniper and *Sedum* (Stonecrop), have served to lure this butterfly westward through Tioga Pass to Yosemite Creek: It also flies in the *Potentilla fruticosa* zone of the Alpine Rock Garden sub-association of the Alpine Fell-Fields. The larvae and pupae of *P. s. behrii* were first described from specimens secured by the senior author and Edmund Godwin at Rock Creek Lake.

Life Zones: Canadian, Hudsonian, Arctic-Alpine. Plant Communities: Juniper Woodland, Alpine Fell-Fields. Host Plants CRASSULACEAE: *Rhodiola rosea* (Western Roseroot), *Sedum obtusatum*, *S. stenopetalum* (Stonecrop). SAXIFRAGACEAE: *Saxifraga* (Saxifrage).

HESPERIIDAE

114. ***Epargyreus clarus*** **(Cram.)**

Syn. *Epargyreus tityrus* (Fabr.)

THE SILVER-SPOTTED SKIPPER is a widely distributed species recognizable by its large size and the conspicuous silvery spot on the under side of each hind wing. It frequents the flowers of California Buckeye, *Aesculus californica*, a well known tree of the western foothills, and is favored by plantings of Locust as an ornamental.

Life Zones: Upper Sonoran. Plant Communities: Foothill Woodland, Yellow Pine Forest. Host Plants: LEGUMINOSAE: *Robinia* (Introduced Black Locust), and other legumes.

115. ***Thorybes pylades*** **(Scud.)**

THE NORTHERN DUSKY-WING is the low-elevation species of this genus in California. It is larger but has smaller spots on the forewing than the following *Thorybes mexicana nevada*, and the male has a costal fold.

Life Zones: Upper Sonoran. Plant Communities: Chaparral, Foothill Woodland, (Yellow Pine Forest). Host Plants: LEGUMINOSAE: *Trifolium* (Clover), and other legumes.

116. ***Thorybes mexicana nevada*** **Scud.**

THE NEVADA DUSKY-WING is the alpine and subalpine *Thorybes* of the Sierra Nevada, flying to 11,000 feet. Smaller and with larger spots than the preceding *T. pylades,* the male has no costal fold and the spots are outlined with a dark rim.

Life Zones: Canadian, Hudsonian, Arctic-Alpine. Plant Communities: Alpine Fell-Fields, Subalpine Forest (Glacial Moraine). Host Plants: Unknown. LEGUMINOSAE: *Amorpha californica* (False Indigo) for the parent species, according to Comstock and Dammers (1933).

117. ***Thorybes diversus*** **Bell** **Pl. I, fig. a**

BELL'S DUSKY-WING is easily confused with The Northern Dusky-Wing, *Thorybes pylades,* being of similar size, but lacks the costal fold in the male. A denizen of grassy openings in the forest belt, it shuns the broad, open meadows.

Life Zones: Transition. Plant Communities: Openings in several types of Forest. Host Plants: Not known.

118. ***Pyrgus ruralis*** **(Bdv.)**

THE TWO-BANDED SKIPPER prefers openings in the forest rather than damp meadows, and is best distinguished by its darker color, even checkering, and montane habitat. Flying close to the ground, it is inconspicuous and easily overlooked.

Life Zones: Canadian. Plant Communities: Openings in Red Fir and Lodgepole Pine Forest. Host Plants: MALVACEAE: *Sidalcea* (Checkerbloom, Wild Hollyhock). ROSACEAE: *Potentilla* (Cinquefoil) suggested.

119. ***Pyrgus communis*** **(Grote)**

THE COMMON CHECKERED SKIPPER is abundant at low elevations, often near habitations where introduced mallow grows. It may be recognized by the conspicuous flight habit, bluish-gray and white checkered pattern, and proximity to human dwellings.

Life Zones: Upper Sonoran, Transition. Plant Communities: Several. Favors weedy growth around cultivated areas. Host Plants: MALVACEAE: especially *Malva* (Mallow) and *Sidalcea* (Checkerbloom). The larvae draw the leaves together with silken threads.

120. ***Heliopetes ericetorum*** **(Bdv.)**

THE LARGE WHITE SKIPPER is a rapid flier, difficult to capture, and hence a rarity. The female is more heavily marked than the male and resembles the foregoing *Pyrgus communis.*

Life Zones: Upper Sonoran (lower Transition). Plant Communities: Chaparral, Foothill Woodland, "Mountain Misery" (*Chamae-*

batia foliosa) belt of cut-over stands of Yellow Pine Forest. Host Plants: AMARANTHACEAE: *Amaranthus* (Pigweed). MALVACEAE: *Malvastrum* (Apricot Mallow).

121. *Erynnis persius* (Scud.)

THE PERSIUS DUSKYWING is a small, dark insect with few contrasting markings. Long misidentified in the west, it has been shown by Burns (unpublished doctoral dissertation) to be common to California at moderate elevations.

Life Zones: (Upper Sonoran) Transition, Canadian. Plant Communities: (Foothill Woodland), Yellow Pine and Fir Forests, both White and Red. Host Plants: Best regarded as unknown. Early records are untrustworthy.

122. *Erynnis pacuvius lilius* (Dyar)

DYAR'S DUSKYWING, as identified by John Burns, is common at intermediate elevations. Gin Flat, Crane Flat, and similar locations are its usual haunts. One of us (Tilden) found it common on Cowchilla Mountain, outside the park, in June, 1954.

Life Zones: (upper Transition) Canadian. Plant Communities: Chaparral-like understory of montane forests. Host Plants: Unknown. RHAMNACEAE: *Ceanothus* (Snow Bush, Wild Lilac) for Colorado *pacuvius,* as reported by Donald Eff (personal communication).

123. *Erynnis propertius* (Scud. & Burg.)

THE PROPERTIUS DUSKWING is the largest and commonest of our Duskywings. The front wings have few spots and present a slightly "grizzled" appearance, rather than a solid black effect. It frequents edges and openings in the forest at moderate elevations.

Life Zones: (Upper Sonoran) Transition, Canadian. Plant Communities: Chaparral, Foothill Woodland, Yellow Pine and other Coniferous Forests. Host Plants: FAGACEAE: *Quercus* (Oak), especially Live Oaks of various species.

124. *Erynnis zarucco funeralis* (Scud. & Burg.)

THE FUNEREAL DUSKYWING is the most easily recognized of our Duskywings. The front wing is pointed and the fringes of the hind wing are white. There is an indistinct brownish patch on the outer third of the forewing that is lacking in the following *Erynnis tristis;* the males also have a tibial tuft.

Life Zones: (Lower Sonoran) Upper Sonoran. Plant Communiities: Valley Grasslands, Foothill Woodland (Chaparral). Host Plants: LEGUMINOSAE: *Hosackia* (= *Lotus*) *scoparia, Medicago* (Alfalfa), and other legumes.

125. *Erynnis tristis* (Bdv.)

THE SAD DUSKYWING may be expected to occur in the oak woodlands and foothills, although it has not yet been found in the Yosemite region. Slightly smaller than the preceding *Erynnis z. fun-*

eralis, and with the forewing not noticeably pointed, it lacks the brown patch on the forewing and the tibial tuft.

Life Zones: Upper Sonoran. Plant Communities: Foothill Woodland, Oak Woodland. Host Plants. FAGACEAE: *Quercus* (Oak).

126a. ***Hesperia harpalus harpalus*** **(Edw.)** **Pl. II, fig. g**
b. ***Hesperia harpalus yosemite*** **Leuss.**

THE HARPALUS SKIPPER is the characteristic *Hesperia* of the eastern declivity of the Sierra Nevada and the adjacent Great Basin area surrounding Mono Lake. It is rather pale above, and shows well developed silver spots below, especially in the females. THE YOSEMITE SKIPPER is the subspecies that occurs on the western slope of the Sierra. It is smaller and more brightly colored than normal *harpalus* and the spotting of the under sides of the hind wings tends to be small or to disappear. At high elevations there occurs a "blend-zone" form that is intermediate. The literature treats the Great Basin form as *H. idaho* (Edw.), but there seems no reason for retaining this name.

Life Zones: Transition, Canadian. Of the "blend-zone" population: Hudsonian (Arctic-Alpine). Plant Communities: Not noticeably selective. Host Plants: POACEAE: (Grasses).

127. ***Hesperia miriamae*** **MacNeill** **Pl. III, fig. m**

MIRIAM'S SKIPPER is the most alpine of our skippers, being found entirely above tree line on Mono Pass and on the summits of the higher peaks, such as Unicorn. It is a small, dark species, with large, irregular spots on the under surface of the hind wings. But recently described (MacNeill, 1959), it is still a rarity, and will continue to be so due to the inaccessibility of its habitat.

Life Zones: Arctic-Alpine. Plant Communities: Alpine Fell-Fields. Host Plants: POACEAE (Grasses), presumptively. Actually, unknown.

128. ***Hesperia nevada*** **(Scud.)**

THE NEVADA SKIPPER is a Great Basin species found on the eastern Sierra slope from Mono Lake to elevated areas above Tioga Pass. A small species with irregular macular bands on the under side of the hind wings, it frequents open rocky areas at high elevations.

Life Zones: Arid Transition, Canadian, Hudsonian. Plant Communities: Juniper Woodland, Subalpine Forest, Alpine Fell-Fields. Host Plants: POACEAE: Grasses.

129. ***Hesperia juba*** **(Scud.)**

THE YUBA SKIPPER is not limited by elevation, being found sparingly across the Sierra crest from the western foothills to the Great Basin. A large species of powerful flight, it may be recognized by the fuscous border of the front wing, which is *sharply limited* and does not grade into the rufous ground color. The under side of the wings is greenish brown to dark brown and the spots are large and usually white.

Life Zones: Unlimited. Plant Communities: Apparently not restricted. Ubiquitous. Host Plants: POACEAE: (Grasses), probably.

130. *Ochlodes sylvanoides* (Bdv.)

THE WOODLAND SKIPPER is one of the commonest skippers, ranging across the mountains from the western foothills to the Great Basin and eastward to Colorado. It is a moderate-sized, orange-brown species, with the stigma of the male touching the dusky border of the wing. An unwary species, it may be found fairly swarming on roadside flowers. The Mono Lake population is slightly paler, but differs from Colorado *napa* Edw., a subspecies with which it has been confused.

Life Zones: Upper Sonoran, Transition (Canadian). Plant Communities: Several. Not restricted within its life zones. Host Plants: POACEAE: (Grasses).

131. *Ochlodes agricola* (Bdv.)

THE FARMER flies from May in the western foothills to July at higher elevations, but is absent from the east side of the Sierra Nevada. It frequents streamsides, openings in lush woodlands, and overgrown roadsides. Smaller and darker than the preceding *Ochlodes sylvanoides,* it shows pale translucent spots in the forewing, at the end of the stigma in the male, and near the end of the cell in the female. It is seldom found in wet meadows or dry fields.

Life Zones: Upper Sonoran, Transition. Plant Communities: Openings in Forests. Riparian and Roadside Associations. Host Plants: POACEAE: (Grasses).

132a. ***Polites sabuleti sabuleti*** **(Bdv.)**
b. ***Polites sabuleti tecumseh*** **(Grin.)** **Pl. III, fig. d**

THE SANDHILL SKIPPER is found in the Yosemite area, in one form or another, entirely across the Sierran crest, from the western foothills to the Great Basin. About the size of The Woodland Skipper, *Polites s. sabuleti* has the under surface of the hind wings tan, the spots yellowish and extending onto the wing veins, which are also yellow. At higher elevations it is replaced by THE TECUMSEH SKIPPER, which fairly swarms in the subalpine meadows adjacent to Tioga Pass. It is much smaller, darker, brighter, and more greenish than normal *Polites sabuleti.* Its flight season, July to September, is long for an alpine species, perhaps indicating two broods.

Life Zones: Upper Sonoran, Transition for *P. sabuleti;* Canadian, Hudsonian, Arctic-Alpine for *P. s. tecumseh.* Plant Communities: Not restrictive for *P. sabuleti;* Subalpine Meadow, Alpine Meadow and Grassland for *P. s. tecumseh.* Host Plants: CYPERACEAE: *Carex filifolia* (Sedge). Also recorded as LEGUMINOSAE: *Trifolium monanthum* (Clover). The latter, if correct, is a departure from the food preferences of this group, which are characterized as feeding on Monocotyledons.

133. *Polites sonora* (Scud.)

THE SONORAN SKIPPER is the usual mid-summer skipper of intermediate elevations in Yosemite National Park. Resembling the Woodland Skipper, *Ochlodes sylvanoides,* in size and appearance, it is a darker, more olivaceous rufous, with a thicker, more complex stigma. Below, the hind wings are olivaceous tan with a light basal spot and a band of light spots across the wing. A somewhat lighter phase occurs in the higher portions of the Great Basin, as at Mono Lake.

Life Zones: Arid Transition, Canadian, Hudsonian. Plant Communities: Meadowlands, Freshwater Marsh, Alkali Sink; openings in forests of several kinds. Host Plants: Unknown.

134. *Amblyscirtes vialis* (Edw.)

THE ROADSIDE SKIPPER is a widely distributed species, found in the cooler parts of the United States and southern Canada from California to Maine. In the Yosemite region it is a rarity. A dull dun-colored species, of small size, with a few small specks near the tip of the forewing, purplish gray shades on the under surface, and checkered fringes, it frequents cool, moist spots, such as meadow edges and forest clearings, at elevations of from 4,000 to 7,000 feet.

Life Zones: Transition, Canadian. Plant Communities: Not known for the Yosemite region. Host Plants: POACEAE: (Grasses) in the eastern United States; has not been reared in the west.

LITERATURE CITED

BADE, WILLIAM F. 1924. The life and letters of John Muir. In two volumes. Vol. I: vii 399 pp. Houghton Mifflin, Boston & New York.

BAUER, DAVID L. 1961. Tribe Melitaeini, Checker Spots, Crescents, and Patch Butterflies, pp. 127-146. *In*: Ehrlich, Paul R., and Anne H. How to know the Butterflies. 262 pp. Wm. C. Brown, Dubuque, Iowa.

BROWN, F. MARTIN. 1954. Colorado Butterflies. Part I. Satyridae. *Proc. Denver Mus. Nat. Hist.,* No. 3: 1-32.

——— 1955. Studies of Nearctic *Coenonympha tullia* (Rhopalocera, Satyridae.) *Coenonympha tullia inornata* Edw. *Bull. Amer. Mus. Nat. Hist.,* 105 (4): 363-409.

CLENCH, HARRY. 1961. Tribe Theclini, Hairstreaks, pp. 177-220. Tribe Lycaenini, The Coppers, pp. 220-228. *In*:Ehrlich, Paul R., and Anne H. How to know the Butterflies. 262 pp. Wm. C. Brown, Dubuque, Iowa.

COMSTOCK, JOHN A. 1927. Butterflies of California. 334 pp., 63 pls. Author, Los Angeles.

DAVENPORT, DEMOREST. 1941. The butterflies of the satyrid genus *Coenonympha. Bull. Mus. Comp. Zool., Harvard,* 87(4): 215-349, pls. 1-10.

DICE, LEE R. 1943. The biotic provinces of North America. vii + 78 pp., 1 map Univ. Michigan Press, Ann Arbor.

DOS PASSOS, C. F., and L. P. GREY. 1947. Systematic catalogue of *Speyeria* (Lepidoptera, Nymphalidae) with designations of types and fixations of type localities. *Amer. Mus. Novitates,* No. 1370: 1-30.

DOWNEY, JOHN C. 1961. Tribe Plebejini, The Blues, pp. 228-242. *In*: Ehrlich and Ehrlich. How to Know the Butterflies. 262 pp. Wm. C. Brown, Dubuque, Iowa.

EMMEL, THOMAS C., and JOHN F. EMMEL. 1962. Ecological studies of Rhopalocera in a High Sierran community—Donner Pass, California. I. Butterfuly associations and distributional factors. *J. Lepid. Soc.,* 16: 23-44.

——— 1963. Larval food-plant records for six western Papilios. *J. Res. Lepid.,* 1(3): 191-193.

ERIKSEN, C. H. 1962. Further evidence of the distribution of some boreal Lepidoptera in the Sierra Nevada. *J. Res. Lepid.,* 1(1): 89-93. /

EHRLICH, PAUL R., and ANNE H. EHRLICH. 1961. How to know the butterflies. vi+ 262 pp., 524 figs. Wm. C. Brown, Dubuque, Iowa.

GARTH, JOHN S. 1935a. Butterflies of the Boundary Hill Research Reserve, Yosetmite National Park, California. *Bull. Sou. Calif. Acad. Sci.,* 33: 131-135.

——— 1935b. Butterflies of Yosemite National Park. *Ibid.,* 34: 37-75.

GRINNELL, JOSEPH, and HARVEY M. HALL. 1919. Life-zone indicators in California. *Proc. Calif. Acad. Sci.,* 9(2): 37-67.

———, and TRACY T. STORER. 1924. Animal life in the Yosemite. xviii + 752 pp., 62 pls., 65 figs. Univ. Calif. Press, Berkeley.

GUNDER, JEAN D. 1929. The genus *Euphydryas* Scud. of Boreal America (Lepidoptera, Nymphalidae). *Pan-Pac. Ent.,* 6(1): 1-8, pls. 1-12, maps 2.

HALL, HARVEY M., and CARLOTTA C. HALL. 1912. A Yosemite flora. vii + 282 pp. Paul Elder, San Francisco.

HEMMING, FRANCIS. 1934. Generic names of Holarctic butterflies. 184 pp. British Museum (Natural History), London.

HIGGINS, L. G. 1953. Butterfly collecting in U.S.A. *Entomologist,* 86(9): 207-210.

HOVANITZ, WILLIAM 1940. Ecological color variation in a butterfly and the problem of "protective coloration." *Ecol.,* 21(3): 371-380.

———. 1943. Hybridization and seasonal segregation in two races of a butterfly occurring together in two localities. *Biol. Bull.* 85: 44-51.

———. 1950. The biology of *Colias* butterflies. I. The distribution of the North American species. *Wasmann J. Biol.,* 8(1): 49-75.

———. 1963. Evidence for the species distinction of *Pieris protodice* and *Pieris occidentalis. J. Res. Lepid.* 2: in press.

KLOTS, ALEXANDER B. 1936. The interrelationships of the species of the genus *Lycaena* Fabricius (Lepidoptera, Lycaenidae). *Bull. Brooklyn Ent. Soc.,* 31(4): 154-170.

———. 1951. A field guide to the butterflies of North America, east of the Great Plains. xvi + 349 pp., 40 pls., 9 figs. Houghton Mifflin, Boston.

LINDSEY, ARTHUR W. 1942. A preliminary revision of *Hesperia. Denison Univ. Bull., Jour. Sci. Labs.,* 37: 1-50, pls. 1-6.

———, E. L. BELL, and R. C. WILLIAMS. 1931. Hesperioidea of North America. *Ibid.,* 26: 1-142.

MATTHES, FRANCOIS E. 1930. Geologic History of the Yosemite Valley. *Geol. Surv. Professional Paper* 160: 1-137, 52 pls.

MacNEILL, C. DON. 1959. A new species of *Hesperia* from California (Lepidoptera: Hesperiidae). *Wasmann J. Biol.,* 17(1): 89-94.

McDUNNOUGH, J. 1938. Check list of the Lepidoptera of Canada and the United States of America. Part I. Macrolepidoptera. *Mem. Sou. Calif. Acad. Sci.,* 1: 1-275.

MUNZ, PHILIP A., and DAVID D. KECK. 1949. California plant communities. *El Aliso,* 2(1): 87-105. 1950. (Same title)—Supplement. *Ibid.,* 2(3): 199-202.

NABOKOV, VLADIMIR. 1949. The Nearctic members of the genus *Lycaeides* Hbl. *Bull. Mus. Comp. Zool.,* Harvard, 101: 479-541.

OPLER, PAUL, and JERRY A. POWELL. 1961. Taxonomic and distributional studies on the western components of the *Apodemia mormo* complex (Riodinidae). *J. Lepid. Soc.,* 15(3): 145-171.

TILDEN, J. W.. 1959. The butterfly associations of Tioga Pass. *Wasmann J. Biol.,* 17(2): 249-271.

VESTAL, A. G. 1914. Internal relations of terrestrial associations. *Amer. Nat.,* 48: 413-445.

WILLIAMS, C. B. 1930. The migration of butterflies. Oliver and Boyd, Edinburgh.

ZIEGLER, J. BENJAMIN. 1960. Preliminary contribution to a redefinition of the genera of North American hairstreaks (Lycaenidae) north of Mexico. *J. Lepid. Soc.,* 14: 19-23.

YOSEMITE BUTTERFLY RECORDS

The documented records on which the textual material rests have been segregated from the body of the article (Appendix I) because of its length; however these localities are of great importance to specialists interested in the specific locations where these species may be found.

West-slope records precede east-slope records and are separated from them by a period. Each locality is followed by all subsequent records from that locality, first by the same observer, then by other observers. Localities are separated by a semi-colon. Apart from these intended departures an exact chronology is maintained.

Following the abbreviated locality and date (day, MONTH, and year), the initials of the responsible observer are given. These are John S. Garth (JSG), Edmund D. Godwin (EDG), Allan Oakley Shields (AOS), J. Wilson Tilden (JWT), and Keith Trexler (KT). Others who contributed an occasional record are named with the appropriate citation.

LOCALITIES AND ABBREVIATIONS

To conserve space in the body of the list a standard set of abbreviations has been adopted, (Appendix II) following the practice established by entomological reports of a similar nature (Garth, 1935b): Localities represented extend from Briceburg and Buck Meadows at the western approaches to Yosemite National Park to Mono Lake at the eastern Gateway, and from Conway Summit on the north to Deadmans Summit on the south along U. S. Highway 395. (A few localities, such as Cathay and Oakhurst on the west side and Bridgeport and Casa Diablo Hot Springs on the east side, transcend even these limits.) Some are in the National Park, some are in the surrounding National Forests, while some are outside of either. Localities outside Yosemite National Park are identified by National Forest (NF), of if outside the National Forest, by California County (Co.). Each locality is characterized by Life Zone and Plant Community; the division into west slope and east slope suffices to indicate the Biotic Province. Elevations (7214, 10,500) are in feet and are taken from U. S. D. I. Geological Survey Topographical Maps of Yosemite (1948) or of adjacent Quadrangles. These are accurate to the nearest 100-foot contour except in the case of mountain peaks, lake levels, or places of habitation, where precise figures (BM) can be given.

APPENDIX I

SOME PLANTS ON WHICH YOSEMITE BUTTERFLIES FEED AS LARVAE

o = oviposition observed; 1 = larva taken from; r = reared to adult on plant named; ? = doubtful record; * = feeding on more than one plant

AMARANTHACEAE

Amaranthus	Pigweed	*Heliopetes ericetorum	

ASCLEPIADACEAE

Asclepias	Milkweed	Danaus plexippus Danaus g. strigosus	o, 1, r

BETULACEAE

Alnus	Alder	*Papilio rutulus *Polygonia f. rusticus	1, r

BORAGINACEAE

Amsinckia	Fiddle-Neck	*Vanessa cardui	1, r
Cryptantha	Nievitas	*Vanessa cardui	1, r
Cynoglossum	Hound's Tongue	*Strymon melinus	
Mertensia	Mertensia	Euphydryas c. sierra	

CAPPARIDACEAE

Cleome	Bee Plant	*Pieris protodice	o, 1, r
Isomeris	Bladder Pod	*Pieris beckeri	o, 1, r

CAPRIFOLIACEAE

Symphoricarpus	Snow Berry	*Euphydryas chalcedona	o, 1, r

CARYOPHYLLACEAE

Stellaria	Chickweed	*Nathalis iole	

CHENOPODIACEAE

Atriplex	Salt Bush	*Brephidium exilis	
Chenopodium	Lamb's Quarters	*Brephidium exilis	r

COMPOSITAE

Anaphalis	Everlasting	*Vanessa virginiensis	1
Antennaria	Everlasting	*Vanessa virginiensis	1
Artemesia	Mugwort	*Vanessa virginiensis	
Aster	Aster	*Melitaea acastus ?Melitaea d. malcolmi Phyciodes campestris	
Carduus	Thistle	*Phyciodes mylitta *Vanessa cardui	o, 1, r o, 1, r

Cirsium	Thistle	*Phyciodes mylitta	o, 1, r
		*Vanessa cardui	o, 1, r
Dyssodia	(none)	*Nathalis iole	
Gnaphalium	Cud Weed, Everlasting	*Vanessa virginiensis	1
Helenium	Sneeze Weed	*Nathalis iole	
Silybum	Milk Thistle	*Phyciodes mylitta	
CONVOLVULACEAE			
Cuscuta	Dodder	*?Callophrys iroides	
CORNACEAE			
Cornus	Dogwood	*Celastrina argiolus	1, r
CRASSULACEAE			
Rhodiola	Roseroot	*Parnassius p. behrii	1
Sedum	Stonecrop	*Parnassius c. baldur	
		*Parnassius p. behrii	1
CRUCIFERAE			
Arabis	Rock Cress	Anthocharis lanceolata	o
		*Anthocharis sara	o, 1, r
		*Euchloe ausonides	o, 1, r
		*Euchloe creusa	
		*Pieris occidentalis	
		*Pieris protodice	
		*Pieris sisymbrii	
Barbarea	Winter Cress	*Pieris napi	
Brassica	Mustard	*Anthocharis sara	o
		*Pieris beckeri	
		*Pieris napi	
		*Pieris protodice	o, 1, r
		*Pieris rapae	o, 1, r
Caulanthus	Rock Cabbage	*Pieris sisymbrii	o, 1, r
Dentaria	Milk Maids	*Pieris napi	o, 1, r
Erysimum	Wall Flower	*Euchloe ausonides	
Lepidium	Pepper Grass	*Pieris occidentalis	o, 1
		*Pieris protodice	o, 1
Radicula	Water Cress	*Pieris rapae	
Raphanus	Radish	*Pieris napi	
		*Pieris protodice	o
Sisymbrium	Hedge Mustard	*Anthocharis sara	o
		*Euchloe ausonides	o, 1
		*Pieris beckeri	
		*Pieris occidentalis	
		*Pieris protodice	o
		*Pieris sisymbrii	
Stanleya	Desert Plume, Prince's Plume	*Pieris beckeri	1, r
Streptanthus	Jewel Flower	*Euchloe creusa	
		*Pieris sisymbrii	
Thlaspi	Penny Cress	*Pieris protodice	

ERICACEAE			
Arbutus	Madroño	**Callophrys iroides*	
Arctostaphylos	Manzanita	**Callophrys iroides*	
		**Celastrina argiolus*	1, r
Rhododendron	Azalea	**Polygonia f. rusticus*	
		**Polygonia zephyrus*	
Vaccinium	Bilberry, Huckleberry	**Callophrys iroides*	
		Colias behrii	o, 1,
		*?*Parnassius c. baldur*	
FAGACEAE			
Quercus	Oak	*Limenitis b. californica*	
		**Celastrina argiolus*	r
		Erynnis propertius	r
		Erynnis tristis	
		Habrodais grunus	
		?*Strymon auretorum*	
		*?*Strymon californica*	
GERANIACEAE			
Erodium	Filaree	**Nathalis iole*	
GUTTIFERAE			
Hypericum	St. John's Wort	**Strymon melinus*	
LABIATAE			
Hyptis	Bee Sage	**Strymon melinus*	
LAURACEAE			
Umbellularia	Laurel	*?*Papilio multicaudatus*	
LEGUMINOSAE			
Amorpha	False Indigo	*Colias eurydice*	o, 1
		Thorybes mexicana	
Astragalus	Loco Weed, Rattle Weed	**Colias eurytheme*	o, 1
		**Everes amyntula*	
		**Everes comyntas*	
		**Glaucopsyche lygdamus*	
		**Hemiargus isolus*	
		**Lycaeides melissa*	o
		**Plebejus acmon*	
		**Strymon behrii*	
		**Strymon melinus*	
Dalea	(Includes Smoke Tree)	**Leptotes marina*	
Glycyrrhiza	Liquorice	**Lycaeides melissa*	
Hosackia		*?*Celastrina argiolus*	
(= *Lotus*)		**Colias eurytheme*	o, 1, r
		*?*Erynnis z. funeralis*	
		**Glaucopsyche lygdamus*	
		**Hemiargus isolus*	
		**Lycaeides melissa*	
		**Plebejus acmon*	o

		*Plebejus saepiolus	o (2nd brood)
		*Strymon behrii	
		*Strymon melinus	o, 1, r
Lathyrus	Sweet Pea	*Everes amyntula	
		*Glaucopsyche lygdamus	
Lupinus	Lupine	*?Celastrina argiolus	
		*Glaucopsyche lygdamus	
		?Lycaeides a. anna	
		*Lycaeides melissa	
		Phaedrotes piasus	
		Plebejus icarioides	o, 1
		Strymon fuliginosum	
		*Strymon melinus	o, 1, r
Medicago	Alfalfa	*Colias eurytheme	o, 1, r
		*Erynnis z. funeralis	
		*Leptotes marina	
		*Lycaeides melissa	
Melilotus	Sweet Clover	*Colias eurytheme	o
Robinia	Black Locust	Epargyreus clarus	
Thermopsis	False Lupine	*Colias eurytheme	
Trifolium	Clover	Colias philodice hageni	o, 1, r
		*Colias eurytheme	o
		*Everes comyntas	
		*Hemiargus isolus	
		*Plebejus saepiolus	o (1st brood)
		?Polites sabuleti	
		Thorybes pylades	
Vicia	Vetch	*Colias eurytheme	o, 1
		*Everes amyntula	o
		*Everes comyntas	
		*Glaucopsyche lygdamus	
LORANTHACEAE			
Arceuthobium	Dwarf Mistletoe	Callophrys johnsoni	
		Callophrys spinetorum	1, r
Phoradendron	Mistletoe	Atlides halesus	1, r
MALVACEAE			
Lavatera	Tree Mallow	*Vanessa carye	
Malva	Mallow	*Strymon melinus	r
		*Vanessa carye	o, 1, r
		*Pyrgus communis	1, r
Malvastrum	Apricot Mallow	*Heliopetes ericetorum	
Sida	Alkali Mallow	*Vanessa carye	
Sidalcea	Checkerbloom, Wild Hollyhock	*Pyrgus communis	
		*?Pyrgus ruralis	
		*Vanessa carye	o, 1, r
Sphaeralcea	Bush Mallow, Apricot Mallow	*Vanessa carye	
ONAGRACEAE			
Gayophytum		*Lycaena helloides	

OLEACEAE			
Fraxinus	Ash	*Papilio multicaudatus	
PINACEAE			
Libocedrus	Incense Cedar	Callophrys nelsoni, probably	
Pinus	Pine	Callophrys eryphon	
		*Neophasia menapia	
Pseudotsuga	Douglas Fir	*Neophasia menapia	
PLANTAGINACEAE			
Plantago	Plantain	Euphydryas editha	o, l, r
		*Precis o. evarete	o, l, r
POLYGONACEAE			
Eriogonum	Buckwheat	Apodemia mormo	
		Callophrys dumentorum	o
		?Callophrys lemberti	
		Lycaena gorgon	o
		Lycaena heteronea	
		?Lycaena nivalis	
		Philotes battoides	
		Philotes enoptes	o
		*Plebejus acmon	
		?Plebejus lupini	
Oxytheca	(none)	*Lycaena helloides	
		Philotes speciosa	
Polygonum	Knot Weed	*Lycaena helloides	
		*Lycaena mariposa	
		*Strymon melinus	
Rumex	Dock, Sorrel	*Lycaena editha	o
		*Lycaena helloides	o
		*Lycaena mariposa	
		?Lycaena p. hypophlaeas	
		?Lycaena rubidus	
		Lycaena xanthoides	o
RHAMNACEAE			
Ceanothus	Snow Bush	*Callophrys iroides	l, r
		*Celastrina argiolus	l, r
		Erynnis pacuvis	
		*Papilio eurymedon	
		Nymphalis californica	l
		Strymon californica	l, r
		Strymon saepium	l, r
Rhamnus (= Frangula)	Cascara, Buckthorn, Coffee Berry	*Papilio eurymedon	l, r
ROSACEAE			
Amelanchier	Service Berry	*Papilio multicaudatus	
Cercocarpus	Mountain Mahogany	Strymon adenostomatis	l, r
		Strymon californica	l, r
		Strymon saepium	

Potentilla (= *Horkelia*)	Cinquefoil	**Lycaena editha*	
		*?*Pyrgus ruralis*	
Prunus (= *Cerasus*)	Choke Cherry	**Limenitis lorquini*	1
		**Papilio multicaudatus*	
		**Papilio rutulus*	1, r
Purshia	Antelope Bush	*Strymon fuliginosum*	
Spiraea	Spirea	**Celastrina argiolus*	
RUTACEAE			
Ptelea	Hop Tree	**Papilio multicaudatus*	
SALICACEAE			
Populus	Poplar	**Limenitis lorquini*	1
		**Limenitis w. nevadae*	
		**Nymphalis antiopa*	o, 1, r
		**Papilio multicaudatus*	
		**Papilio rutulus*	o, 1, r
Salix	Willow	**Limenitis lorquini*	
		**Limenitis w. nevadae*	
		**Nymphalis antiopa*	o, 1, r
		**Papilio multicaudatus*	
		**Papilio rutulus*	
		*?*Polygonia f. rusticus*	
		Strymon dryope	1, r
		Strymon sylvinus	1, r
SAPINDACEAE			
Aesculus	Horse Chestnut (includes Buckeye)	**Celastrina argiolus*	1, r
SAXIFRAGACEAE			
Glossularia	Gooseberry	**Lycaena arota*	o, 1, r
		**Polygonia f. rusticus*	
		**Polygonia zephyrus*	
Ribes	Currant	**Lycaena arota*	
Saxigraga	Saxifrage	**Parnassius c. baldur*	
		**Parnassius p. behrii*	
SCROPHULARIACEAE			
Castilleja	Paint Brush	**Melitaea acastus*	
		**Melitaea leanira*	
Cordylanthus	Bird's Beak	**Melitaea leanira*	
Diplacus	Sticky Monkey Flower	**Euphydryas chalcedona*	o, 1, r
Mimulus	Monkey Flower	**Euphydryas chalcedona*	
		**Precis o. evarete*	
Penstemon	Penstemon	**Euphydryas chalcedona*	
Scrophularia	Figwort, Bee Plant	**Euphydryas chalcedona*	o, 1, r

ULMACEAE			
Ulmus	Elm	*Nymphalis antiopa	o, 1, r
UMBELLIFERAE			
Daucus	Wild Carrot	*Papilio zelicaon	1, r
Foeniculum	Fennel, Anise	*Papilio zelicaon	o, 1, r
Heracleum	Cow Parsnip	*Papilio zelicaon	1, r
Pteryxia		Papilio indra	
URTICACEAE			
Boehmeria	False Nettle	*Vanessa atalanta	
Parietaria	Pellitory	*Vanessa atalanta	
Urtica	Nettle	Nymphalis milberti	
		Polygonia satyrus	1, r
		*Vanessa atalanta	1, r
VIOLACEAE			
Viola	Violet	Argynnis (all) Boloria epithore	

THREE ANOMALOUS SITUATIONS

While the regularity of zonal progression and the exclusiveness of biotic provinces have been emphasized, certain irregularities occur that are of sufficient interest to the lepidopterist to warrant considration. The first of these may be found at Tioga Pass, where the loosely consolidated moraines provide a situation duplicating the alpine rock garden. Within a few feet of these moraines may be seen flying the Arctic-Alpine butterflies, *Oeneis chryxus ivallda* and *Euphydryas editha nubigena,* species that normally occur above timber line, a thousand or more feet higher. The explanation is believed to be found in drainage, both of air that funnels through the pass and cools the ground sufficiently to permit the growth of Alpine Willow, and of water that enables these slightly elevated rock piles to become snow-free with the first rays of summer sun, and to flower a month before the Alpine Fell-Fields above.

A second paradoxical situation occurs at timberline, as along the Gaylor Lakes trail above Tioga Pass, where at an approximate elevation of 10,500 feet may be found Artemesian species that normally occur at Mono Lake, 4,000 feet below. *Cercyonis oeta, Lycaena rubidus, L. heteronea,* and *Hemiargus isolus* are found in a sage-brush environment much like Mono Lake, but with *Artemesia rotbrockii,* rather than *A. tridentata,* as the sage, and with *Eriogonum latifolium* and *Aplopappus* sp. as the plant associates. The butterflies are not "fly-ups" from below, but appear to be permanently established on these brushy summits. Here the tie to a plant community, the Sagebrush Scrub, seems stronger than the restriction to a particular life zone or altitudinal belt. Thus one may, after observing "Arctic-Alpine" butterflies at Tioga Pass, nominally Hudsonian, ascend a thousand feet and observe "Upper Sonoran" butterflies flying at tree-line!

While normally the Sierran Crest divides the Californian biotic province from the Artemesian, a series of lesser crests to the westward support Western Juniper on their eastern slopes, and with it the Juniper-Woodland butterflies, *Parnassius phoebus behrii, Euchloe ausonides coloradensis,* and *Hesperia nevada.* It is therefore not necessary to travel to the eastern slope of the Sierra Nevada to observe Great Basin butterflies; many of these have infiltrated the mountain passes and may be found in favored situations as far west as Yosemite Creek, well within the central portion of the park.

APPENDIX II

YOSEMITE RECORDS

SATYRIDAE

1a. Coenonympha tullia californica West. & Hew. El Portal 28-VI-33 (JSG); Mather 12-VII-56 (JSG), 14-V-61 (JWT); Crane Flat 18-VIII-57 (JWT); Jerseydale 30-V-59 and 11-VI-61 (JWT), 26-VI-59 (JSG), 30-VIII-60 (AOS); Briceburg 21-III-61 (KT); Cliff House 9-VI-61 (JWT).

b. Coenonympha tullia mono Burdick Mono Lake 3 to 5-VII-38 and 23-VI-62 (JWT), 30-VI-58 and 12-VI-62 (AOS); W of Lee Vining 26 to 28-VI-61 (AOS, common).

2. Cercyonis pegala ariane (Bdv.) Mono Lake 17-VII-57 (JWT), 16 to 20-VII-58 and 13-VII-60 (AOS); 10 miles E of Mono Lake 24-VII-59 (AOS).

3. Cercyonis silvestris (Edw.) El Portal 28-VI-33 (JSG), 10-VI-61 (JWT); Pate 23-VII-34 (EDG); Benson 24-VII-34 (EDG); Hetch-Hetchy 13 to 15-VII-56 (JSG); Indian Flat 30-V-59 (JWT, seen), 10-VI-61 (JWT); Jerseydale 26-VI-59 (JSG), 11-VI-61 (JWT); Cathay 11-VI-61 (JWT).

4. Cercyonis oeta(Bdv.) Tioga Pass 19-VIII-52 (JWT); Crest W of Tioga Pass 6-VIII-57, 31-VII to 20-VIII-58 and 23 to 28-VII-60 (AOS); Upper Gaylor Lakes 1-VIII-58 (JSG), 20-VIII-58 (AOS); Pilot Peak 31-VIII-58 (JWT). Bodie 18-VII-57 (AOS); June Lake 14 to 22-VIII-57 (JSG); Mono Lake 6-VII-58 (AOS), 23-VI-62 (JWT); Warren Creek 21 to 28-VII-58, 11-VIII-60 and 26-VI-61 (AOS); Agnew Pass and Thousand Island Lake 5-VIII-59 (AOS).

5. Oeneis chryxus ivallda (Mead) Dana, W slope 7-VII-31 (JWT); Florence 5-VIII-33 (JSG); Lyell 6-VIII-33 (JSG); Dana 8-VIII-33 (JSG); Slide 1-VIII-34 (EDG); Pilot Peak 16-VIII-52 and 18-VII-57 (JWT); Crest W of Tioga Pass 12 to 15-VII-57 and 9-VII to 19-VIII-58 (AOS); Tioga Pass 10-VII-58 (AOS); Helen Lake 18 to 29-VII-58 (AOS); Cockscomb 26-VII-58 (AOS); Dana, N slope 31-VII-58 (AOS); Upper Gaylor Lake 1-VIII-58 (JSG); Vogelsang Pass 3-VIII-58 (JSG); Bert Lake 9-VIII-58 (AOS); Unicorn 12-VIII-58 (AOS).

DANAIDAE

6. Danaus (Danaus) plexippus (Linn.) Camp 9, Yosemite Valley, 23-VII-33 (JSG); Yosemite Creek 7-VII-56 (JSG); Mather 11 and12-VII-56 (JSG); Crane Flat 19-VII-57 (JWT); Darrah, Jerseydale, and Indian Flat 29 and 30-V-59 (JWT, seen); Jerseydale and Cathay 11-VI-61 (JWT). Mono Lake 30-VI-41 (JSG, seen), 23-VI-62 (JWT).

7. Danaus (Tasitia) gilippus strigosus (Bates) Mono Lake 30-VI-30 (JWT, seen); 16-VII-58 (AOS).

NYMPHALIDAE

8. Argynnis (Semnopsyche) cybele leto Behr Camp 9, Yosemite Valley, 23-VII to 2-VIII-33 (JSG).

9. Argynnis (Speyeria) nokomis apacheana Skin. Mono Lake 13-VIII-50 and 15-VIII-51 (JWT), 22 to 26-VIII-57, 25-VIII-58, and 4-VIII-60 (AOS); Gull Lake 14 to 28-VIII-57 (JSG), 2-IX-58 (JWT).

10 a. Argynnis (Speyeria) zerene zerene Bdv. Wawona 20-VII-33 (JSG); Jerseydale 21 to 24-VI-56, 19-VI-58, and 9 to 13-VI-62 (AOS); Mather 11 to 15-VII-56 (JSG); Hetch-Hetchy Summit 13-VII-56 (JSG); Aspen

Valley 14-VII-56 (JSG); Yosemite Creek Trail 17-VII-56 (JSG); Crane Flat 19-VIII-57 (JWT).

b. Argynnis (Speyeria) zerene malcolmi Comst. Agnew Pass 13-VIII-57 and 5-VIII-59 (AOS); Mono Lake 26-VIII-57 (AOS); Lundy 20-VII-58 (AOS); Warren Creek 28-VIII-58 (AOS); Casa Diablo 2-IX-58 (JWT).

11a. Argynnis (Speyeria) callippe inornata Edw. Jerseydale 21-VI-56, 23-VI-57, 5-VII-60, 21 to 23-VI-61 and 9 to 13-VI-62 (AOS); El Portal 30-V-58 (JWT); Oakhurst, Madera County, 24-VI-62 (JWT).

b. Argynnis (Speyeria) callippe nevadensis Edw. Mono Lake 15-VII-38, 30-VI-50 and 23-VI-62 (JWT), 7-VII-58 (AOS); Above Crowley Lake 29-VI-41 (JSG); Bodie 18-VII-57 (AOS); 5 miles N of Mono Lake 28-VI-61 (AOS).

12. Argynnis (Speyeria) egleis Bdv. Eagle Peak 1-VII-33 (JSG); Reserve 16-VII-33 (JSG); Dana 8-VIII-33 (JSG); Pate 23-VII-34 (EDG); Yosemite Creek 9-VII-56 (JSG); Mather 12-VII-56 (JSG); Hetch-Hetchy Summit 13-VII-56 (JSG); Smoky Jack 4-VII-57 (JWT); Gin Flat 12 to 19-VII-57 (JWT); Lembert Dome 24-VII-57 (AOS); Crest W of Tioga Pass 6-VIII-57, 19-VIII-58, 1-VIII-59 and 14-VIIto 2-VIII-60 (AOS); Crane Flat 18-VIII-57 (JWT); Pilot Peak 30 to 31-VIII-58 (JWT); Unicorn 27-VII-59 (AOS); Glen Aulin 25-VII-60 (AOS). June Lake 14-VIII-57 (JSG); Lundy 20-VII-58 (AOS); Warren Creek 21-VII-58 (AOS).

13. Argynnis (Speyeria) atlantis irene Bdv. Coldwater 3-VIII-34 (EDG); Tenaya 4-VIII-34 (EDG); Aspen 14-VII-56 (JSG); 5 miles W of Lower Ottoway Lake 19-VIII-61 (AOS).

14. Argynnis (Speyeria) hydaspe Bdv. Camp 19, Yosemite Valley 5-VII-33 (JSG); Ledge 9-VII-33 (JSG); Glen Aulin 10-VIII-33 (JSG); Pate 23-VII-34 (EDG); Buck Meadow 4-VII-54 (JWT); Crane Flat 4-VII-54 (JWT); Jerseydale 28-VI-56, 15 to 16-VI-58, 18-VI and 4-VII-60 (AOS), 26-VI-59 (JSG); Mather 12-VII-56 (JSG); Hetch-Hetchy Summit 13 to 17-VII-56 (JSG).

15. Argynnis (Speyeria) mormonia arge Stkr. Tioga Pass 13-VIII-29 (JSG), 14-VII-31, 12 to 13-VIII-50, and 16-VIII-57 (JWT), 4-VIII-57, 19-VIII-58 and 1-VIII-59 (AOS); Dana 8-VIII-33 (JSG); Coldwater 3-VIII-34 (EDG); Crane Flat 19-VII to 19-VIII-57 (JWT); Tuolumne Meadows 18-VII to 14-VIII-57 and 3-IX-58 (JWT), 15 to 21-VIII-58 (AOS); Pilot Peak 15-VIII-57 and 3-VIII-58 (JWT); Dana, W slope 16-VIII-57 and 30-VIII-58 (JWT); Lyell Fork 10-VIII-58 and 3-VIII-59 (AOS); Gaylor Lakes 31-VIII to 3-IX-58 (JWT); Elizabeth Lake 27-VII-59 (AOS). Warren Creek 11-VIII-60 (AOS).

16. Boloria (Clossiana) epithore (Edw.) Tioga Pass 7-VII-31 (JWT); Eagle Peak 1-VII-33 (JSG); Ledge 9-VII-33 (JSG); Reserve 16-VII-33 and 7 to 10-VII-56 (JSG); Yosemite Creek 7 to 17-VII-56 (JSG); White Wolf 10-VII-56 and 24-VI-59 (JSG); Aspen Valley 14-VII-56 (JSG); Crane Flat 19-VII-57 and 10-VI-61 (JWT), 24-VI-61 (AOS, abundant); Tenaya 11-VII-58 (AOS); Badger Pass 23-VI-59 (JSG); Glacier Point 23-VI-59 (JSG); Tamarack 24-VI-59 (JSG).

17a. Euphydryas chalcedona chalcedona (Dbldy. & Hew.) El Portal 28-VI-33 (JSG), 14-V-61 (JWT); Glacier 9-VII-33 (JSG); Jerseydale 16 to 19-VI-57, 15 to 19-VI-58 and 9 to 13-VI-62 (AOS); Darrah and Jerseydale 30-V-59 (JWT); Indian Flat 30-V-59 and 14-V-61 (JWT).

b. Euphydryas chalcedona sierra (Wgt.) Return Creek 11-VII-31 (JWT); Eagle Peak 1-VII-33 (JSG); Reserve 14-VII-33 (JSG).

18a. Euphydryas editha rubicunda Hy. Edw. El Portal 8-V-32 (R. G. Wind), 14-V-61 (JWT); Jerseydale 15 to 18-VI-58 and 9 to 13-VI-62 (AOS);Indian Flat 30-V-59, 27-V-60 and 13-V-61 (JWT).

b. Euphydryas editha nubigena (Behr) Tioga Pass 7-VII-31, 19-VII-52 and 18-VII-57 (JWT), 29-VII-56, 8 to 13-VII-57, 9-VII to 24-VIII-58, 20 to 23-VII-60 and 25-VI-61 (AOS), 1-VIII-58 (JSG); Pilot Peak 18-VII to 15-VIII-57 (JWT); Helen Lake 18 to 29-VII-58 (AOS); Gaylor Lakes Trail 19-VII-58 (JWT); Dana, W slope 20-VII-58 (JWT); Rafferty Creek 3-VIII-58 (JSG); Vogelsang Lake 3-VIII-58 (JSG).

c. Euphydryas editha monoensis Gund. Mono Lake, near Lee Vining 4-VII-28 and 30-VI-50 (JWT); 19-VI-54 (JSG), 30-VI to 16-VII-58, 13-VII-60 and 26 to 27-VI-61 (AOS).

19. Melitaea (Chlosyne) damoetas malcolmi Comst. Dana, W slope 17-VII-31 (JWT); Lyell 6-VIII-33 (JSG); Dana 8-VIII-33 (JSG); Pilot Peak 16-VIII-52 and 18-VII-57 (JWT); Upper Gaylor Lake 31-VII-57 and 9 to 19-VII-58 (AOS), 1-VIII-58 (JSG); Crest W of Tioga Pass 9-VIIto 31-VII-58, 14-VIIto 2-VIII-60 and 25-VI-61 (AOS); Helen Lake 18-VII-58 (AOS); Dana, N slope 31-VII to 24-VIII-58 and 6 to 8-VIII-60 (AOS); Bert Lake 9-VIII-58 (AOS). East above Saddlebag Lake 28-VII-58 (AOS).

20. Melitaea (Chlosyne) acastus Edw. Mono Lake 5-VII-38 and 30-VI-50 (JWT), 30-VI-41 (JSG), 30-VI-58 (AOS).

21a. Melitaea (Chlosyne) palla palla Bdv. Eagle Peak 1-VII-33 (JSG); Ledge, Glacier 9-VII-33 (JSG); Reserve 16-VII-33 (JSG); Yosemite Creek 7 to 17-VII-56 (JSG); White Wolf 10-VII-56 (JSG); Indian Flat 30-V-59, 27-V-60 and 13-V-61 (JWT); El Portal 14-V-61 (JWT); Jerseydale 21-VI-61 (AOS).

22. Melitaea (Chlosyne) hoffmanni Behr Reserve 14 to 18-VII-33 (JSG); Pate 23-VII-34 (EDG); Benson 24-VII-34 (EDG); White Wolf 10-VII-56 (JSG).

23. Melitaea (Chlosyne) leanira F. & F. Ledge 9-VII-33 (JSG); Tamarack Flat 3-VIII-54 (JWT); Darrah 30-V-57 (JWT); Indian Flat 30-V-59 and 13-V to 10-VI-61 (JWT); El Portal 14-V-61 (JWT); Jerseydale 22-VI-61 (AOS).

24a. Phyciodes (Phyciodes) campestris campestris (Behr) Museum 5-VII-33 (JSG); Mather 12-VII-56 (JSG), 10-VI-61 and 30-VI-62 (JWT); Hetch-Hetchy 13-VII-56 (JSG); Jerseydale 23-VI-61 (AOS).

b. Phyciodes (Phyciodes) campestris montana (Behr) Reserve 16-VII-33 (JSG); Dana 8-VIII-33 (JSG); Coldwater 3-VIII-34 (EDG); Tamarack Flat 3-VII-54 (JWT); Aspen Valley 14-VII-56 (JSG); below Helen Lake 19-VII-60 (AOS). Thousand Island Lake 4-VIII-59 (AOS).

c. Phyciodes (Phyciodes) campestris,intermediate form Mono Lake 30-VI-41 and 19-VI-54 (JSG), 17-VII-57 and 23-VI-62 (JWT), 30-VI to 20-VII-58, 13-VII-60, 26 to 27-VI-61 and 12-VI-62 (AOS); Huntoon Public Camp, Bridgeport 19-VI-54 (JSG); June Lake 14 to 29-VIII-57 (JSG); Warren Creek 21 and 28-VII-58 (AOS); W of Lee Vining 26 to 27-VI-61 (AOS).

25. Phyciodes (Phyciodes) mylitta (Edw.) Museum 5-VII-33 (JSG); Benson 24-VII-34 (EDG); Yosemite Creek 9-VII-56 (JSG); Aspen Valley 14-VII-56 (JSG); Crane Flat 18-VIII-57 (JWT), 24-VI-59 (JSG); Tioga Pass 1-IX-57 (AOS); Tenaya 11-VII-58 (AOS); Glacier Point 23-VI-59 (JSG); Jerseydale 26-VI-59 (JSG), 30-VIII-60 (AOS); El Portal 21-III-61 (KT),

14-V-61 (JWT);Yosemite Valley 19-IV-61 (KT); Indian Flat 13-V-61 (JWT); Mather 10-VI-61 (JWT); Warren Creek 11-VIII-60 (AOS).

26. Polygonia satyrus (Edw.) Museum 5-VII-33 (JSG). Mono Lake 20-VI to25-VIII-58 and 27-VI-61 (AOS).
27. Polygonia faunus rusticus (Edw.) "Yosemite" VI-26 (E. O. Essig). Specimen in Yosemite Museum in 1933.
28. Polygonia zephyrus (Edw.) Reserve 14-VII-33 (JSG); Yosemite Creek 9-VII-56 (JSG); Aspen Valley 14-VII-56 (JSG); Jerseydale 17-VII-56 and 16-VI-58 (AOS); Dana, W slope 20-VII-58 (JWT); Tioga Pass 20-VIII-58 (AOS); Upper Gaylor Lake 20-VIII-58 (AOS); Dana, N slope 31-VII to 24-VIII-58 and 8-VIII-60 (AOS); Badger Pass 23-VI-59 (JSG); Tuolumne Grove 24-VI-59 (JSG). Mono Lake 30-VI-41 (JSG).
29. Nymphalis californica (Bdv.) Yosemite Valley 24-VI to 5-VII-33 (JSG); Ledge 9-VII-33 (JSG); Darrah, Jerseydale, and Indian Flat 30-V-59 (JWT); Bridal Veil Creek 23-VI-59 (JSG); White Wolf 24-VI-59 (JSG); Cliff House 9-VI-61 (JWT); Crane Flat, Gin Flat, and Mather 10-VI-61 (JWT) (outbreak numbers); El Portal 10-VI-61 (JWT); Jerseydale and Cathay 11-VI-61 (JWT). Donohue Pass 4-VIII-59 (AOS).
30. Nymphalis milberti furcillata (Say) Lyell 6-VIII-33 (JSG); Tioga Pass 8-VIIto 6-VIII-57, 1-VIII-58, and 25-VI-61 (AOS); Crest W of Tioga Pass 1 to 19-VIII-58 (AOS); Lyell Base Camp 9-VIII-58 (AOS); Dana, N slope 24-VIII-58 (AOS). Mono Lake 30-VI-41 (JSG), 26-VI-61 (AOS); Warren Creek 29-VIII-57 (AOS); Agnew Meadows 9-VIII-58 (AOS).
31. Nymphalis antiopa (Linn.) Research Reserve 8-VII-56 (JSG, seen). Mono Lake 30-VI-41 (JSG, seen).
32. Vanessa atalanta (Linn.) "Yosemite" VI-26 (E. O. Essig).
33. Vanessa virginiensis (Dru.) Research Reserve 14 to 18-VII-33 and 10-VII-56 (JSG); Yosemite Creek Trail 9-VII-56 (JSG); Mather 10-VI-61 (JWT).
34. Vanessa cardui (Linn.) Research Reserve 14 to 18-VII-33 (JSG); Yosemite Creek Trail 9-VII-56 (JSG).
35. Vanessa carye (Hbn.) Research Reserve 14 to 18-VII-33 (JSG); Hetch-Hetchy 12-VII-56 (JSG). Huntoon Public Camp, Bridgeport 19-VI-54 (JSG).
36. Precis orithya evarete (Cram.) Ledge Trail 9-VII-33 (JSG); Research Reserve 14 to 19-VII-33 and 8 to 10-VII-56 (JSG); Yosemite Creek Trail 9-VII-56 (JSG); Mather 11 and 12-VII-56 (JSG), 10-VI-61 (JWT); Jerseydale 17-VI-60 (AOS); El Portal 4-IV-61 (KT); Indian Flat 13-V-61 (JWT); Cathay 11-VI-61 (JWT). Mono Lake 13-VII-60 (AOS).
37. Limenitis (Limenitis) weidemeyerii nevadae (B. & B.) Mono Lake 30-VI-41 (JSG), 30-VI-50 (JWT), 30-VI to 20 -VII-58 and 26-VI-61 (AOS). Limenitis (L.) weidemeyerii nevadae X Limenitis (L.) lorquini (Hybrid) Mono Lake 17-VIII-51 (JWT), 19-VI-54 (JSG), 7 to 20-VII-58, 25-VII-59 and 27-VI-61 (AOS).
38. Limenitis (Limenitis) lorquini Bdv. Yosemite Valley VII-33 (JSG); Pate Valley 23-VII-34 (EDG); Aspen Valley 14-VII-56 (JSG); Jerseydale 16-VI-58 (AOS); Darrah and Jerseydale 30-V-59 (JWT, seen); Indian Flat 30-V-59 (seen) and 13-V-61 (JWT); Cliff House 9-VI-61 (JWT); Mather 10-VI-61 (JWT). Mono Lake 30-VI-58 (AOS).
39. Limenitis (Adelpha) bredowii californica (Butl.) Museum 5-VII-33 (JSG); Camp 9, Meadow 23-VII-33 (JSG); Mather 12 to 15-VII-56 (JSG),

10-VI-61 (JWT); Hetch-Hetchy 13 to 15-VII-56 (JSG); Aspen Valley 14-VII-56 (JSG); Crane Flat 24-VI-59 (JSG); Jerseydale 26-VI-59 (JSG), 11-VI-61 (JWT), 9 to 13-VI-62 (AOS); Darrah, Jerseydale, and Indian Flat 30-V-59 (JWT); El Portal 14-V-61 (JWT); Cliff House 9-VI-61 (JWT).

RIODINIDAE

40a. *Apodemia mormo mormo* F. & F. Little Yosemite 3-VIII-33 (JSG). Mono Lake 22 to 26-VIII-57 and 20-VII-58 (AOS); June Lake 22-VIII-57 (JSG); Conway Pass, N of Mono Lake 21-VIII-60 (JWT).

b. *Apodemia mormo tuolumnensis* Opler & Powell Pate Valley 23-VII-34 (EDG, as *A. m. virgulti*).

LYCAENIDAE

41. *Habrodais grunus* (Bdv.) Columbia Point 14-VII-33 (JSG); Pohono Trail 23-VII-33 (JSG); Benson 24-VII-34 (EDG); Hetch-Hetchy 13-VII-56 (JSG); Jerseydale 21 to 23-VI-61 (AOS).

42. *Atlides halesus estesi* Clench Museum 5-VIII-34 (collector unknown); Yosemite Creek Trail 9-VII-56 (JSG).

43. *Strymon (Strymon) melinus pudica* (Hy. Edw.) Museum 8-VII-33 (JSG); Mather 12-VII-56 (JSG); Darrah 29-V-59 (JWT).

44. *Strymon (Satyrium) fuliginosum semiluna* (Klots) Mono Lake 30-VI-50 (JWT), 30-VI-58 (AOS).

45. *Strymon (Satyrium) behrii* (Edw.) Mono Lake 30-VI-50 and 23-VI-62 (JWT), 30-VI to 20-VII-58 and 27-VI-61 (AOS); W of Lee Vining 18-VII-57 and 24-VI-58 (AOS); Bodie 18-VII-57 (AOS); Mono Craters 23-VII-57 (AOS); Warren Creek 26-VI-61 (AOS). 5 miles N of Mono Lake 28-VI-61 (AOS).

46. *Strymon (Satyrium) auretorum* (Bdv.) El Portal 28-VI-33 (JSG), 10-VI-61 (JWT); Briceburg and Mariposa 26-VI-54 (JWT); Hetch-Hetchy Road 13 to 15-VII-56 (JSG); Jerseydale 21 and 22-VI-58 (AOS); Darrah 29-V-59 (JWT); Cathay 11-VI-61 (JWT).

47. *Strymon (Satyrium) saepium* (Bdv.) El Portal 28-VI-33 (JSG); Pate 23-VII-34 (EDG); Hetch-Hetchy Road 13-VII-56 (JSG); Gin Flat 17-VIII-57 (JWT); Jerseydale 21 and 22-VI-58 (AOS); Darrah and Indian Flat 30-V-59 (JWT); Cathay 28-V-60 and 11-VI-61 (JWT); Cliff House 9-VI-61 (JWT), Warren Creek 28-VII and 28-VIII-58 (AOS); Gull Lake 2-IX-61 (JWT).

48. *Strymon (Satyrium) adenostomatis* (Hy. Edw.) Mariposa 26-VI-54 (JWT); Jerseydale 21 and 22-VI-58 (AOS); Darrah 29-V-59 (JWT).

49. *Strymon (Satyrium) sylvinus* (Bdv.) Museum 8-VII-33 (JSG); Bear Creek Lodge 26-VI-54 (JWT); Hetch-Hetchy Road 13-VII-56 (JSG); Jerseydale 21-VI-61 (AOS). Mono Lake 5-VII-38 (JWT).

50. *Strymon (Satyrium) californica* (Edw.) Old Village 12-VI-32 (JWT); Museum 5-VII-33 (JSG); Pate 23-VII-34 (EDG); Big Oak Flat Road 2-VII-54 (JWT); Mirror Lake 2-VII-54 (JWT); Tamarack Flat 4-VII-54 (JWT); Hetch-Hetchy Road 13 to 15-VII-56 (JSG); Mather 15-VII-56 (JSG); Jerseydale 15 to 22-VI-58, 17-VI-60 and 21 to 23-VI-61 (AOS); Darrah 30-V-59 (JWT); El Portal 14-V and 10-VI-61 (JWT); Cathay 11-VI-61 (JWT). Mono Lake 5-VII-38, 30-VI-50, 17-VII-57, and 23-VI-62 (JWT), 30-VI-58 and 27-VI-61 (AOS); Lee Vining 24-VI-58 (AOS); Warren Creek 21-VII-58 (AOS); 5 miles N of Mono

Lake 28-VI-61 (AOS).

51. Strymon (Satyrium) dryope (Edw.) Mono Lake 20-VII-58 and 4-VIII-60 (AOS); Bridgeport 15-VIII-52 (JWT).

52. Callophrys (Callophrys) dumetorum (Bdv.) Briceburg 21-III-61 (KT); El Portal 16-IV-61 (JWT); Mather 14-V-61 (JWT).

53. Callophrys (Callophrys) lemberti Tilden Reserve 16-VII-33 (JSG); Pilot Peak 19-VII and 16-VIII-52 (JWT); White Wolf 10-VII-56 (JSG); Crest W of Tioga Pass 9-VII-58 and 25-VI-61 (AOS), 20-VII-58 (JWT); Tioga Pass 10-VII-58 (AOS). Warren Creek 12-VI-62 (AOS).

54. Callophrys (Mitoura) spinetorum (Hew.) Tamarack Flat 4-VII-54 (JWT); Jerseydale 18-VI-57 and 27-VIIto 3-VIII-62 (AOS); Tioga Road 24-VI-59 (JSG).

55. Callophrys (Mitoura) johnsoni (Skin.) Jerseydale 27 and 28-VII-56, 9-VIII-56 and 27-VII-62 (AOS).

56. Callophrys (Mitoura) nelsoni (Bdv.) Museum 5-VII-33 (JSG); Reserve 14 to 18-VII-33 (JSG); Hetch-Hetchy 13-VII-56 (JSG); Jerseydale 30-V-59, 27-V-60, and 11-VI-61 (JWT), 26-VI-59 (JSG), 9 to 13-VI-62 (AOS); Crane Flat 24-VI-59 (JSG); Highway 120 and Hetch-Hetchy Road 14-V-61 (JWT); Cliff House 9-VI-61 (JWT); Mather 10-VI-61 (JWT).

57. Callophrys (Incisalia) doudoroffi windi (Clench) Indian Flat 16-IV-61 (JWT).

58. Callophrys (Incisalia) iroides (Bdv.) Ledge 9-VII-33 (JSG); Crane Flat 3-VII-54 (JWT); Jerseydale 19-VI-58 and 21 to 23-VI-61 (AOS), 29-V-59 (JWT); Darrah 29-V-59 (JWT); Glacier Point 23-VI-59 (JSG); El Portal 4-IV-61 (KT); Mather 10-VI-61 (JWT).

59. Callophrys(Incisalia)eryphon (Bdv.) Reserve 9 to 14-VII-33 (JSG); Tamarack Flat 4-VII-54 (JWT); Smoky Jack 4-VII-54 (JWT); Mather 12-VII-56 (JSG), 10-VI-61 (JWT); Jerseydale 16-VI-58 (AOS), 29-V-59 (JWT); Tenaya Canyon 11-VII-58 (AOS). Mono Lake 27-VI-61 (AOS).

60a. Lycaena (Tharsalea) arota arota (Bdv.) Museum 8-VII-33 (JSG); Pate 23-VII-34 (EDG); Jerseydale 29-VI to 27-VII-56, 1-VIII-58, 24-VIII-60, 23-VI-61 and 28-VII-62 (AOS).

b. Lycaena (Tharsalea) arota virginiensis (Edw.) Mono Lake 17-VII-57 (JWT), 26-VIII-57, 7 to 20-VII-58 and 13-VII-60 (AOS).

61. Lycaena (Lycaena) gorgon (Bdv.) Darrah 29-V-59 (JWT); Indian Flat 30-V-59 and 13-V to 10-VI-61 (JWT); El Portal 14-V-61 (JWT).

62. Lycaena (Lycaena) heteronea Bdv. Lyell Base Camp 26-VII-57 (AOS); Tioga Pass 4-VIII-57 (AOS); Merced Lake Trail 4-VIII-58 (AOS); Gaylor Lakes Trail 3-IX-58 (JWT); Dana, N slope 8-VIII-60 (AOS). Warren Creek 7-VIII-57 and 21-VII to 28-VIII-58 (AOS); Lundy 20-VII-58 (AOS); Mono Lake 13-VII-60 (AOS). Thousand Island Lake 4-VIII-59 (AOS).

63. Lycaena (Lycaena) xanthoides (Bdv.) Mather 11 and 12-VII-56 (JSG), 30-VI-62 (JWT); Hetch-Hetchy 13-VII-56 (JSG); Aspen Valley 14-VII-56 (JSG).

64. Lycaena (Lycaena) rubidus (Behr) Mono Lake 27-VII-37 (JWT), 30-VI-41 (JSG), 30-VI to 7-VII-58 and 27-VI-61 (AOS); Gaylor Lakes Trail 16-VIII-52 (JWT); Warren Creek 7 to 29-VIII-57, 21-VII to 28-VIII-58 and 11-VIII-60 (AOS); Agnew Pass 5-VIII-59 (AOS); W of Lee Vining 28-VI-61 (AOS).

65. Lycaena (Lycaena) editha (Mead) Kuna 7-VIII-33 (JSG); Dana 8-VIII-33 (JSG); Kerrick 27-VII-34 (EDG); Snow Lake 29-VII-34 (EDG); Tamarack Flat 4-VII-54 (JWT); Tioga Pass 16 to 17-VII-57 (JWT), 14-VII to 24-VIII-58 and 14-VIII-60 (AOS); Gin Flat and Crane Flat 19-VII-57 (JWT); Rafferty Creek 21-VII-57 (AOS); Tioga Meadow 15-VIII-57 (JWT); Pilot Peak 15-VIII-57 and 31-VIII-58 (JWT); Dana, W slope 17-VIII-57 and 20-VIII-58 (JWT); Tuolumne Meadows 15 to 21-VIII-58 (AOS), 3-IX-58 (JWT); Gaylor Lakes Trail 30-VIII to 3-IX-58 (JWT); Lyell Base Camp 3-VIII-59 (AOS); below Agnew Pass 5-VIII-59 (AOS). Mono Lake 30-VI-41 (JSG); Bodie 18-VII-57 (AOS); Warren Creek 21-VII-58 (AOS).
66. Lycaena (Lycaena) mariposa Reak. Kuna 7-VIII-33 (JSG); Slide 29-VII-34 (EDG); Dana, W slope 13-VIII-50, 15-VIII-51, 16-VIII-57 and 30-VIII-58 (JWT); Lyell Base Camp Trail 26-VII-57 and 10-VIII-58 (AOS); Tioga Pass 4-VIII-57, 20-VIII-58 and 1-VIII-59 (AOS); Pilot Peak 15-VIII-57 (JWT); Elizabeth Lake 27-VII to 22-VIII-58 and 27-VII-59 (AOS); Merced Lake Trail 4-VIII-58 (AOS). Agnew Meadow 13-VIII-57 (AOS).
67. Lycaena (Lycaena) nivalis (Bdv.) Tioga Pass 14-VII-31 (JWT), 20-VIII-58 (AOS); Glacier 9-VII-33 (JSG); Reserve 14-VII-33 (JSG); Kuna 7-VIII-33 (JSG); Benson 24-VII-34 (EDG); Kerrick 27-VII-34 (EDG); Gaylor Lakes Trail 15-VIII-51, 6-VIII-53 and 19-VII to 3-IX-58 (JWT); Smoky Jack 3-VII-54 (JWT); Yosemite Creek Trail 9-VII-56 (JSG); Dog Lake Trail 19-VII-56 (JSG); Rafferty Creek Trail 21-VII-57 and 24-VII-58 (AOS); 3-VIII-58 (JSG); Tenaya Canyon 11-VII-58 (AOS); Crest W of Tioga Pass 4 to 18-VIII-57, 20-VIII-58 and 20 to 23-VII-60 (AOS); Lyell Fork Meadows 10-VIII-58 and 3-VIII-59 (AOS); Dana, N slope 24-VIII-58 (AOS). Warren Creek 21-VII-58 (AOS).
68. Lycaena (Lycaena) helloides (Bdv.) El Portal 28-VI-33 (JSG); Mather 12-VII-56 (JSG). Mono Lake 5-VII-38 (JWT).
69. Lycaena (Lycaena) phlaeas hypophlaeas (Bdv.) Lyell 6-VIII-33 (JSG); Dana, N slope 6 to 13-VIII-60 (AOS).
70. Lycaena (Lycaena) cupreus (Edw.) Tioga Pass 7-VII-31, 13-VIII-50, 15-VIII-51, 16-VII to 16-VIII-52, 6-VIII-53, and 18-VII to 16-VIII-57 (JWT), 7 to 15-VII-57, 9-VII to 24-VIII-58, 15-VII-60 and 25-VI-61 (AOS); Kuna 7-VIII-33 (JSG); Dana 8-VIII-33 (JSG); Snow Lake 29-VII-34 (EDG); Dog Lake Trail 19-VII-56 (JSG); Pilot Peak 18-VII to 15-VIII-57 (JWT); Cockscomb Peak 26-VI-58 (AOS); Tuolumne Meadows 4-VII-58 (AOS); Crest W of Tioga Pass 9-VII to 1-VIII-58 (AOS); Helen Lake 18 to 29-VII-58 (AOS); Elizabeth Lake 27-VII-58 (AOS); Upper Gaylor Lake 1-VIII-58 (JSG); Rafferty Creek Trail 3-VIII-58 (AOS).
71. Leptotes marina (Reak.) Mono Lake 30-VI-41 (JSG), 30-VI-50 (JWT, seen) and 23-VI-62 (JWT).
72. Brephidium exilis (Bdv.) E above Saddlebag Lake 28-VII-58 (AOS); Mono Lake 23-VI-62 (JWT).
73. Hemiargus (Echinargus) isolus (Reak.) Tioga Pass 9-VII to 7-VIII-58 (AOS); Crest W of Tioga Pass 9-VII-58 (AOS); Upper Gaylor Lake 14-VII-58 (AOS); Rafferty Creek Trail 3-VIII-58 (JSG, AOS); Vogelsang Lake 3-VIII-58 (JSG, AOS); Gaylor Lakes Trail 31-VIII to 3-IX-58 (JWT); Tuolumne Meadows 3-IX-58 (JWT). Mono Lake 20-VII-58 (AOS); Lee Vining 24-VII-58 (AOS); Warren Creek 28-VII-

58 (AOS).

74. Lycaeides argyrognomon anna (Edw.) Conness Creek 11-VII-31 (JWT); Dana 8-VIII-33 (JSG); Kerrick 27-VII-34 (EDG); Coldwater 3-VIII-34 (EDG); Tenaya 4-VIII-34 (EDG); Crane Flat 2-VII-54 and 19-VII-57 (JWT); Hetch-Hetchy Summit 13-VII-56 (JSG); Aspen Valley 14-VII-56 (JSG); Gin Flat 19-VII-57 (JWT); Tuolumne Meadows 14-VIII-57 (JWT); Badger Pass 23-VI-59 (JSG).

75. Lycaeides melissa inyoensis Nab. Reserve 16-VII-33 (JSG); Benson 24-VII-34 (EDG); Helen Lake 18-VII-58 (AOS); Cockscomb Peak 26-VII-58 (AOS); Upper Lyell Base Camp 10-VIII-58 and 3-VIII-59 (AOS). Mono Lake 20-VII-58 (AOS), 23-VI-62 (JWT); E above Saddlebag Lake 28-VII-58 (AOS); Warren Creek 11-VIII-60 and 26-VI-61 (AOS); Conway Summit 23-VI-62 (JWT).

76. Plebejus (Agriades) glandon podarce (F. & F.) Tioga Pass 7-VII-31, 13 and 14-VIII-50, 15-VIII-51, 16-VIII-52, 6 and 7-VIII-53, and 16-VIII-57 (JWT), 1 to 24-VIII-58 and 23-VII-60 (AOS); Eagle Peak 1-VII-33 (JSG); Reserve 18-VII-33 and 10-VII-56 (JSG); Kuna 7-VIII-33 (JSG); Kerrick 27-VII-34 (EDG); Tuolumne Meadows 16-VII-57 (JWT); Dana, W slope 17-VIII-57 and 30-VIII-58 (JWT); Elizabeth Lake 27-VII-58 (AOS); Helen Lake 29-VII-58 (AOS); Upper Gaylor Lake 1-VIII-58 (JSG); Bert Lake 9-VIII-58 (AOS); Unicorn Peak 23-VIII-58 (AOS); Bridal Veil 23-VI-59 (JSG); White Wolf 24-VI-59 (JSG); Dana, N slope 8-VIII-60 (AOS).

77. Plebejus (Plebejus) saepiolus (Bdv.) Glacier 9-VII-33 (JSG); Reserve 17-VII-33 (JSG); Florence 5-VIII-33 (JSG); Pate 23-VII-34 (EDG); Tioga Pass 15-VIII-51, 6-VIII-53 and 16 to 18-VIII-57 (JWT), 9-VII to 24-VIII-58 and 13 to 15-VII-60 (AOS); Crane Flat 3-VII-54 and 19-VII-57 (JWT); Hetch-Hetchy Summit 13-VII-56 (JSG); Aspen Valley 14-VII-56 (JSG); Tuolumne Meadows 18-VII-57 (JWT); Gin Flat 19-VII-57 (JWT); Dana, W slope 17-VIII-57 and 20-VII to 30-VIII-58 (JWT); Crest W of Tioga Pass 9-VII to 20-VIII-58 (AOS); Helen Lake 18-VII-58 and 19-VII-60 (AOS); Rafferty Creek Trail 3-VIII-58 (JSG, AOS); Gaylor Lakes Trail 31-VIII to 3-IX-58 (JWT); Bridal Veil and Badger Pass 23-VI-59 (JSG); White Wolf, Tioga Road, and Crane Flat 24-VI-59 (JSG). Mono Lake 5-VII-38, 30-VI-50 and 14-VIII-57 (JWT), 30-VI-41 (JSG), 13-VII-60 (AOS).

78a. Plebejus (Icaricia) icarioides icarioides (Bdv.) Glacier 9-VII-33 (JSG); Aspen Valley 14-VII-56 (JSG); below Vogelsang Pass 3-VIII-58 (AOS); Badger Pass 23-VI-59 (JSG); Crane Flat 24-VI-59 (JSG); Jerseydale 29 to 30-V-59 and 11-VI-61 (JWT), 26-VI-59 (JSG), 9 to 13-VI-62 (AOS); Indian Flat 13-V-61 to 10-VI-61 (JWT); Mather 10-VI-61 and 30-VI-62 (JWT).

b. Plebejus (Icaricia) icarioides helios Edw. Mono Lake 4-VII-38 and 23-VI-62 (JWT), 30-VI-41 and 19-VI-54 (JSG), 7 to 20-VII-58 and 26 to 27-VI-61 (AOS); Conway Pass, N of Mono Lake 30-VI-50 and 23-VI-52 (JWT); Huntoon Public Camp, Bridgeport 19-VI-54 (JSG); Bodie 28-VII-57 (AOS); Agnew Pass and Donohue Pass 4-VIII-59 (AOS); Warren Creek 11-VIII-60 (AOS); W of Lee Vining 26-VI-61 (AOS); 5 mi N of Mono Lake 28-VI-61 (AOS).

79. Plebejus (Icaricia) shasta comstocki Fox Reserve 16-VII-33 (JSG); Kuna 7-VII-33 (JSG); Kerrick 27-VII-34 (EDG); Slide Creek 29-VII-34 (EDG); Tioga Pass 13-VIII-50, 15-VIII-52, 5 to 6-VIII-53, and 16-VIII-57 (JWT), 15-VII-57, 14-VII to 20-VIII-58 and 15 to 20-VII-

60 (AOS); Pilot Peak 15-VII-57 and 19-VII to 31-VIII-58 (JWT); Gin Flat 17-VIII-57 (JWT); Dana, W slope 17-VIII-57 and 30-VIII-58 (JWT); Upper Gaylor Lake 14 to 19-VII-58 (AOS); Helen Lake 18-VII-58 (AOS); Upper Lyell Base Camp 9-VIII-58 (AOS); Crest W of Tioga Pass 19 to 20-VIII-58 (AOS); Dana, N slope 24-VIII-58 and 8-VIII-60 (AOS); Gaylor Lakes Trail 3-IX-58 (JWT). Bodie 18-VII-57 (AOS); Lundy 20-VII-58 (AOS); Donohue Pass 4 to 6-VIII-59 (AOS); Warren Creek 11-VIII-60 (AOS).

80. Plebejus (Icaricia) acmon (West. & Hew.) Reserve 14-VII-33 (JSG); Pohono 25-VII-33 (JSG); Kerrick 27-VII-34 (EDG); Coldwater 3-VIII-34 (EDG); Smoky Jack 4-VII-54 (JWT); Mather 11 to 13-VII-56 (JSG); Hetch-Hetchy Summit 13-VII-56 (JSG); Gin Flat 17-VIII-57 (JWT); Tenaya Canyon 11-VII-58 (AOS); Tuolumne Meadows 3-IX-58 (JWT); Jerseydale 30-V-59, 27-V-60 and 11-VI-61 (JWT), 26-VI-59 (JSG); Indian Flat 30-V-59, 27-V-60 and 14-V to 10-VI-61 (JWT); Briceburg 21-III-61 (KT); El Portal 21-III-61 (KT), 14-V-61 (JWT); Cliff House 9-VI-61 (JWT); Mather 10-VI-61 (JWT); Cathay 11-VI-61 (JWT). Mono Lake 30-VI-41 (JSG), 30-VI to 7-VII-58 and 12-VI-62 (AOS); Huntoon Public Camp, Bridgeport 19-VI-54 (JSG); Warren Creek 11-VIII-60 and 26-VI-61 (AOS).
81. Plebejus (Icaricia) lupini (Bdv.) Eagle Peak 1-VII-33 (JSG); Dana, W slope 16-VIII-52, 6-VIII-53 and 20-VII-58 (JWT); Smoky Jack 3 to 4-VII-54 (JWT); Crest W of Tioga Pass 12-VII-57, 4-VII to 19-VIII-58, 15 to 23-VII-60 and 25-VI-61 (AOS); Upper Gaylor Lake 14-to 19-VII-58 (AOS); Helen Lake 18-VII-58 (AOS); Dana, N slope 24-VIII-58 (AOS). Lee Vining 3 to 5-VII-38 (JWT); E above Saddlebag Lake 28-VII-58 (AOS); Below Conway Summit 23-VI-62 (JWT).
82. Everes comyntas (Godt.) Mono Lake 5-VII-38, 30-VI-50 and 23-VI-62 (JWT), 26-VI-61 and 12-VI-62 (AOS); E above Saddlebag Lake 28-VII-58 (AOS).
83. Everes amyntula Bdv. Hetch-Hetchy Summit 13-VII-56 (JSG, seen); Jerseydale 30-V-59 (JWT).
84. Philotes enoptes (Bdv.) Yosemite Valley 17-VI-32 (JWT); Ledge 9-VII-33 (JSG); Reserve 16-VII-33 and 7-VII-56 (JSG); Tioga Pass 16-VII-52 (JWT), 12-VII-57, 9-VII to 14-VIII-58 and 14 to 23-VII-60 (AOS); Smoky Jack 4-VII-54 (JWT); Big Oak Flat Road 5-VII-54 (JWT); Tenaya Canyon 11-VII-58 (AOS). E above Saddlebag Lake 28-VII-58 (AOS).

85a. Philotes battoides battoides (Behr) Reserve 15 to 16-VII-33 and 7-VII-56 (JSG); Slide Creek 29-VII-34 (EDG); Gaylor Lakes Trail 16-VIII-52, 6-VIII-53 and 3-IX-58 (JWT); Mt. Hoffman 14-VII-57 (AOS); Pilot Peak 18-VII-57 and 31-VIII-58 (JWT); Crest W of Tioga Pass 19-VII to 1-VIII-58, 14 to 15-VII-60, 25-VI-61 and 8-VIII-62 (AOS); Helen Lake 18 to 29-VII-58 (AOS); Cockscomb Peak 26-VII-58 (AOS); Vogelsang 23-VII-58 (JWT); Vogelsang Pass 3-VIII-58 (AOS).

b. Philotes battoides glaucon (Bdv.) Mono Lake 5-VII-38 and 23-VI-62 (JWT), 30-VI-41 (JSG), 30-VI-58 and 26 to 27-VI-61 (AOS); Warren Creek 21-VII-58 (AOS); Conway Summit 23-VI-62 (JWT).

86. Philotes speciosa (Hy. Edw.) Mariposa 30-V-32 (G. & R. Bohart); Briceburg 3-VI-38 (R. M. Bohart).
87. Phaedrotes piasus (Bdv.) Eagle Peak 1-VII-33 (JSG); Reserve 9 to 14-VII-34 (EDG ?); Jerseydale 9 to 13-VI-62 (AOS); Mather 30-VI-62 (JWT). Mono Lake 30-VI-41 (JSG).

88a. *Glaucopsyche lygdamus behrii*(Edw.) Indian Flat 16 to 17-IV-61 (JWT); El Portal 17-IV-61 (JWT).

b. *Glaucopsyche lygdamus columbia* (Skin.) Eagle Peak 1-VII-33 (JSG); Reserve 9 to 14-VII-34 (EDG?); Tioga Pass 16-VIII-52 (JWT); Crane Flat and Tamarack Flat 3-VII-54 (JWT); White Wolf 10-VII-56 (JSG); Tenaya Canyon 11-VII-58 (AOS); Upper Gaylor Lake 19-VII-58 (JWT); Dana, W slope 20-VII-58 (JWT); Below Vogelsang Pass 3-VIII-58 (AOS); Badger Pass 23-VI-59 (JSG). E above Saddlebag Lake 28-VII-58 (AOS).

89. *Celastrina argiolus echo* (Edw.) El Portal 28-VI-33 (JSG); Glacier 9-VII-33 (JSG); Reserve 14 to 18-VII-33 and 7-VII-56 (JSG); Crane Flat 3-VII-54 (JWT); Mather 12-VII-56 (JSG), 14-V-61 (JWT); Aspen Valley 14-VII-56 (JSG); Darrah, Jerseydale, and Indian Flat 29 to 30-V-59 and 10-VI-61 (JWT); Badger Pass and Bridal Veil 23-VI-59 (JSG); Tamarack 24-VI-59 (JSG); Briceburg and El Portal 21-III-61 (KT).

PIERIDAE

90a. *Anthocharis (Anthocharis) sara sara* Luc. Indian Flat 13-V-61 (JWT); El Portal 14-V-61 (JWT).

Anthocharis (Anthocharis) sara reakirtii Edw., *gen. vern.* Briceburg 21-III-61 (KT), 16-VI-61 (JWT); El Portal 21-III and 4-IV-61 (KT), 14-IV-62 (JWT); Indian Flat 17-IV-61 (JWT).

b. *Anthocharis (Anthocharis) sara stella* Edw. Eagle Peak 1-VII-33 (JSG); Reserve 16 to 17-VII-33 (JSG); White Wolf 10-VII-56 (JSG).

91. *Anthocharis (Falcapica) lanceolata* Luc. Eagle Peak 1-VII-33 (JSG); Ledge 9-VII-33 (JSG); Yosemite Valley 14-V-59 (R. Paul Allen); Jerseydale 9 to 13-VI-62 (AOS).

92. *Euchloe creusa hyantis* (Edw.) Eagle Peak 1-VII-33 (JSG); Glacier 9-VII-33 (JSG); Reserve 16-VII-33 (JSG); Ostrander 4-VII-34 (EDG); El Portal 16-IV and 14-V-61, and 14-IV-62 (JWT, common); Indian Flat 17-IV-61 (JWT); Mather 14-V-61 (JWT).

93. *Euchloe ausonides coloradensis* (Hy. Edw.) Reserve 16 and 17-VII-33 (JSG); Tamarack Flat 3-VII-54 (JWT). Mono Lake 30-VI-58 (AOS).

94. *Colias eurytheme* Bdv. Ledge 9-VII-33 (JSG); Reserve 16-VII-33 and 7 to 11-VII-56 (JSG); Camp 9, Yosemite Valley 23-VII-33 (JSG); Crane Flat 3-VII-54, 18-VIII-57, and 10-VI-61 (JWT); Mather 11 to 12-VII-56 (JSG), 14-V and 10-VI-61 (JWT); Hetch-Hetchy 13-VII-56 (JSG); Aspen Valley 14-VII-56 (JSG); Gaylor Lakes Trail 19-VII-58 (JWT); Dana, W slope 30-VIII-58 (JWT); Briceburg 21-III-61 (KT); El Portal 21-III-61 (KT), 14-V-61 (JWT); Yosemite Valley 19-IV-61 (KT); Indian Flat 13-V-61 (JWT); Jerseydale 11-VI-61 (JWT).

95. *Colias philodice hagenii* Edw. Mono Lake 30-VI-41 (JSG); 18-VII-57 and 30-VI-58 (AOS).

96. *Colias occidentalis chrysomelas* Hy. Edw. "Yosemite" VI-26 (E. O. Essig).

97. *Colias behrii* Edw. Tioga Pass 13-VIII-29 and 1 to 3-VIII-56 (JSG), 14-VII-31, 13-VIII-50 and 16-VIII-57 (JWT), 4-VIII-57 and 14-VII to 19-VIII-58 (AOS); Florence 5-VIII-33 (JSG); Kuna 7-VIII-33 (JSG); Kerrick 27-VII-34 (EDG); Snow Lake 29-VII-34 (EDG); Tuolumne

Meadows 15-VIII-57 (JWT); Pilot Peak 15 to 18-VIII-57 (JWT); Upper Gaylor Lake 19-VII to 20-VIII-58 (AOS); Helen Lake 29-VII-58 (AOS); Crest W of Tioga Pass 31-VII-58 (AOS); Rafferty Creek Trail 3-VIII-58 (AOS, JSG); Merced Lake Trail 4-VIII-58 (AOS); Lyell Base Camp 10-VIII-58 (AOS); Elizabeth Lake 23-VIII-58 (AOS). E of Donohue Pass 4 to 6-VIII-59 (AOS).

98. *Colias (Zerene) eurydice* Bdv. "Yosemite" VI-26 (E. O. Essig or P.J. Woolf).

99. *Nathalis iole* Bdv. "Yosemite" VI-26 (P. J. Woolf). Warren Creek 20, 21 and 28-VII-58 (AOS).

100. *Neophasia menapia tau* (Scud.) Big Oak Flat Road VIII-28 (JSG, seen); Little Yosemite Valley 3-VIII-33 (JSG); Pate 23-VII-34 (EDG); Buck Meadow 4-VII-54 (JWT); Unicorn Peak 27-VII-59 (AOS). Deadman's Summit 20-IX-56 (JWT); June Lake 21-VIII-57 (JSG).

101. *Pieris (Pontia) beckeri* Edw. Mono Lake 5-VII-38, 30-VI-50, 15-VIII-53 and 23-VI-62 (JWT), 26 and 27-VI-61 (AOS).

102. *Pieris (Pontia) sisymbrii* Bdv. Eagle Peak 1-VII-33 (JSG); Reserve 16-VII-33 and 7-VII-56 (JSG); Dana, W slope 19-VII-52, 16-VIII-53 and 20-VII-58 (JWT); Upper Gaylor Lake 4 to 8-VII-57, 9 to 19-VII-58 and 25-VI-61 (AOS); Crest W of Tioga Pass 9-VII-58 (AOS); Tioga Pass 10-VII-58 (AOS); Briceburg and El Portal 21-III-61 (KT); El Portal 14-IV-62 (JWT).

103. *Pieris (Pontia) protodice* Bdv. & Lec. El Portal 28-VII-33 (JSG); Yosemite Creek Trail 9 to 17-VII-56 (JSG).

104a. *Pieris (Pontia) occidentalis occidentalis* Reak. Crest W of Tioga Pass 18 to 20-VIII-57 and 19 to 20-VIII-58 (AOS).

b. *Pieris (Pontia) occidentalis calyce* Edw. Pilot Peak 18-VIII-52, 15-VIII-57, and 20-VII-58 (JWT); Crest W of Tioga Pass 8-VII-57 and 9-VII-58 (AOS); Upper Gaylor Lake 9-VII-58 (AOS), 1-VIII-58 (JSG); Vogelsang Camp 3-VIII-58 (JSG). Warren Creek 29-VIII-57 (AOS).

105. *Pieris (Pieris) napi venosa* Scud. Yosemite Valley 14-V-59 (R. P. Allen); Briceburg 21-III-61 (KT); El Portal 14-IV-61 (JWT); Jerseydale 22-VI-61 (AOS).

106. *Pieris (Pieris) rapae* (Linn.) Pate 23-VII-34 (EDG); Indian Flat 30-V-59 (JWT, seen).

PAPILIONIDAE

107. *Papilio zelicaon* Luc. Reserve 16-VII-33 (JSG); Mather 15-VII-56 (JSG); Jerseydale 16-VI-57 and 4-VIII-62 (AOS); Crest W of Tioga Pass 9-VII-58 (AOS); Upper Gaylor Lake 19-VII-58 (AOS); El Portal 4-IV-61 (KT).

108. *Papilio indra* Reak. Yosemite Valley 17-VI-32 (JWT); Reserve 18-VII-33 (A. Carthew); Crest W. of Tioga Pass 25-VI-61 (AOS). Mono Lake 23-VI-62 (JWT). Mammoth Peak 16-VII-60 (AOS).

109. *Papilio rutulus* Luc. Camp 19, Yosemite Valley 26-VI-33 (JSG); Pate 23-VII-34 (EDG); Yosemite Creek Trail 9-VII-56 (JSG); Hetch-Hetchy 13-VII-56 (JSG); Darrah, Jerseydale, and Indian Flat 29 to 30-V-59 (JWT). Mono Lake 30-VI-41 (JSG, seen), 27-VI-61 and 12-VI-62 (AOS); W of Lee Vining 27-VI-61 (AOS); Below Conway Summit 23-VI-62 (JWT).

110. *Papilio multicaudatus* Kby. Jerseydale 7-VIII-56 and 2-VIII-57 (AOS).

111a. Papilio eurymedon eurymedon Luc. Ledge 9-VII-33 (JSG); Pate 23-VII-34 (EDG); Mather 12-VII-56 (JSG); Hetch-Hetchy 13-VII-56 (JSG); Jerseydale 16-VI-57, 16-VI-58, 21-VI-61 and 13-VI-62 (AOS); Darrah, Jerseydale, and Indian Flat 29 to 30-V-59 (JWT).

b. Papilio eurymedon albanus F. & F. Research Reserve 10-VII-56 (JSG).

112. Parnassius clodius baldur Edw. Tioga Pass 7-VII-31 (JWT); Eagle Peak 1-VII-33 (JSG); Glacier 9-VII-33 (JSG); Dana 8-VIII-33(JSG); Slide 29-VII-34 (EDG); Gin Flat 4-VII-54 (JWT, seen); Jerseydale 23-VI-56, 21-VI-57, 16 to 18-VI-58 and 22-VI-61 (AOS); Yosemite Creek 7-VII-56 (JSG); White Wolf 10-VII-56 (JSG); Crest W of Tioga Pass 12-VII to 18-VIII-57, 28-VII to 19-VIII-58 and 4 to 20-VII-60 (AOS); Pilot Peak 18-VII-57 and 31-VIII-58 (JWT); Rafferty Creek 21-VII-57 (AOS); Tenaya Canyon 11-VII-58 (AOS); Lewis Creek Trail 3-VIII-58 (JSG); Dana, W slope 30-VIII-58 (JWT).

113. Parnassius phoebus behrii Edw.
Reserve 14-VII-33 (JSG); Dana 8-VIII-33 (JSG); Pilot Peak 13 to 14-VIII-52, 18-VII to 15-VIII-57 and 31-VIII-58 (JWT); Upper Gaylor Lake 31-VII to 20-VIII-57 and 31-VII to 20-VIII-58 (AOS), 19-VII-58 (JWT), 1-VIII-58 (JSG); Helen Lake 18-VII-58 (AOS); Dana, W slope 20-VII-58 (JWT); Crest W of Tioga Pass 19-VIII-58 (AOS); Dana, N slope 24-VIII-58 (AOS). E of Saddlebag Lake 28-VII-58 (AOS).

114. Epargyreus clarus (Cram.) Coulterville Road VI-26 (D. D. MacLean); Indian Flat 30-V-59 (JWT, seen).

115. Thorybes pylades (Scud.) Fish Camp 18-VI-57 (JWT); Jerseydale 30-V-59 (JWT); Indian Flat 13-V-61 (JWT).

116. Thorybes mexicana nevada Scud. Tioga Pass 7-VII-31, 16-VIII-52 and 18-VII-57 (JWT); 8-VII-57, 26-VI to 19-VII-58, 14-VII-60 and 25-VI-61 (AOS); Reserve 16-VII-33 (JSG); Tamarack 3-VII-54 (JWT); Pilot Peak 18-VII-57 and 31-VIII-58 (JWT); Dana, W slope 17-VIII-57 and 20-VII-58 (JWT); Gaylor Lakes Trail 9-VII-58 (JWT); Crest W of Tioga Pass 9-VII-58 (AOS); Upper Gaylor Lake 14 to 19-VII-58 (AOS), 1-VIII-58 (JSG); Helen Lake 18 to 29-VII-58 (AOS); Gin Flat and Crane Flat 10-VI-61 (JWT).

117. Thorybes diversus Bell Aspen 14-VII-56 (JSG); Jerseydale 16-VI-57 and 16-VI-58 (AOS); Mather 10-VI-61 and 30-VI-62 (JWT).

118. Pyrgus ruralis (Bdv.) Reserve 15-VII-33 and 10-VII-56 (JSG); Tamarack 3-VII-54 (JWT); Tenaya 11-VII-58 (AOS, seen): Lyell Fork Meadows 7-VIII-58 (AOS).

119. Pyrgus communis (Grote) "Yosemite" VI-26 (P. J. Woolf); Aspen Valley 14-VII-56 (JSG); El Portal 16-IV, 14-V and 10-VI-61 (JWT); Indian Flat 15-IV, 14-V and 11-VI-61 (JWT).

120. Heliopetes ericetorum (Bdv.) Jerseydale 16-VI-58 (AOS); El Portal 14-V-61 (JWT, seen); Highway 120 and Hetch-Hetchy Road 14-V-61 (JWT).

121. Erynnis persius (Scud.) Reserve 15-VII-33 (JSG, as afranius); Chowchilla Mt. 26-VI-54 (JWT); Aspen Valley 14-VII-56 (JSG); Mather 15-VII-56 (JSG); Badger Pass 23-VI-59 (JSG); Indian Flat 17-IV-61 (JWT); Jerseydale 21 to 23-VI-61 (AOS).

122. Erynnis pacuvius lilius (Dyar) Chowchilla Mt. 26-VI-54 (JWT, common); Tamarack Flat 3-VII-54 (JWT); Crane Flat 24- VI-59 (JSG).

123. Erynnis propertius (Scud. & Burg.) Ledge 9-VII-33 (JSG); Reserve

16-VII-33 (JSG); Crane Flat 3-VII-54 (JWT); Yosemite Creek 9-VII-56 (JSG); Mather 12-VII-56 (JSG), 10-VI-61 (JWT); Hetch-Hetchy Summit 13-VII-56 (JSG); Badger Pass 23-VI-59 (JSG); Briceburg 21-III-61 (KT); El Portal 21-III-61 (KT), 14-V-61 (JWT); Yosemite Valley 19-IV-61 (KT); Indian Flat 13-V and 10-VI-61 (JWT); Jerseydale 17-VI-60, 21-VI-61 and 4 to 13-VI-62 (AOS).

124. Erynnis zarucco funeralis (Scud. & Burg.) Coulterville Road VI-26 (D. D. MacLean).

125. Erynnis tristis (Bdv.) No Yosemite record.

126a. Hesperia harpalus harpalus (Edw.) Mono Lake 17-VII to 26-VIII-57, 30-VI to 20-VII-58 and 26-VI-61 (AOS), 26-VIII-57 and 20-VII-58 (JWT); Bodie 18-VII-57 (AOS); Lee Vining 24-VI-58 (AOS); Warren Creek 26-VI-61 (AOS).

Hesperia harpalus (Edw.), "blend zone" form Eagle Peak 1-VII-33 (JSG); Reserve 16-VII-33 (JSG); Yosemite Creek 9 to 17-VII-56 (JSG); Rafferty Creek 21-VII-57, 24-VII to 3-VIII-58 (AOS); Dana, W slope 16-VIII-57 and 30-VIII-58 (JWT); Crest W of Tioga Pass 18 to 20-VIII-57, 20-VIII-58 and 20 to 28-VII-60 (AOS); Merced Lake Trail 4-VIII-58 (AOS); Unicorn Peak 12-VIII-58 and 27-VII-59 (AOS); Gaylor Lakes Trail and Pilot Peak 31-VIII-58 (JWT); Tuolumne Meadows 3-IX-58 (JWT); Cold Canyon 25-VII-60 (AOS); Dana, N slope 8-VIII-60 (AOS).

b. Hesperia harpalus yosemite Leuss. Big Oak Flat Road, near entrance to Tuolumne Grove 2-IX-29 (J. Strohbeen and A. E. Dodge, the type series); Carl Inn 11-VII-31 (JWT); Wawona 27-VIII-46 (JWT); Smoky Jack 4-VII-54 (JWT); Jerseydale 1-VIII-57 (AOS).

127. Hesperia miriamae MacNeill Mono Pass, Inyo County VIII-56, VIII-57 and VIII-58 (Don MacNeill, the type series); Unicorn Peak 26-VII, 12 and 23-VIII-58, and 27-VII-59 (AOS); Cockscomb Peak 26-VII-58 (AOS); Dana, N slope 31-VII-58 and 8-VIII-60 (AOS).

128. Hesperia nevada (Scud.) Mono Lake 26-VI-61 (AOS); Warren Creek 26-VI-61 and 12-VI-62 (AOS).

129. Hesperia juba (Scud.) "Yosemite" VI-26 (collector unknown); Old Village 17-VI-32 (McQuesten); Mather 10-VI-61 (JWT). Mono Lake 27-VI-61 (AOS).

130. Ochlodes sylvanoides (Bdv.) Yosemite Valley VII-33 (JSG); Pate Valley 23-VII-34 (EDG); Hetch-Hetchy 13-VII-56 (JSG); Crane Flat 18-VIII-57 (JWT); Mather 4-IX-57 (JWT); Jerseydale 2-IX-58 (AOS). Mono Lake 14 and 15-VIII-51 and 13 to 15-VIII-52 (JWT).

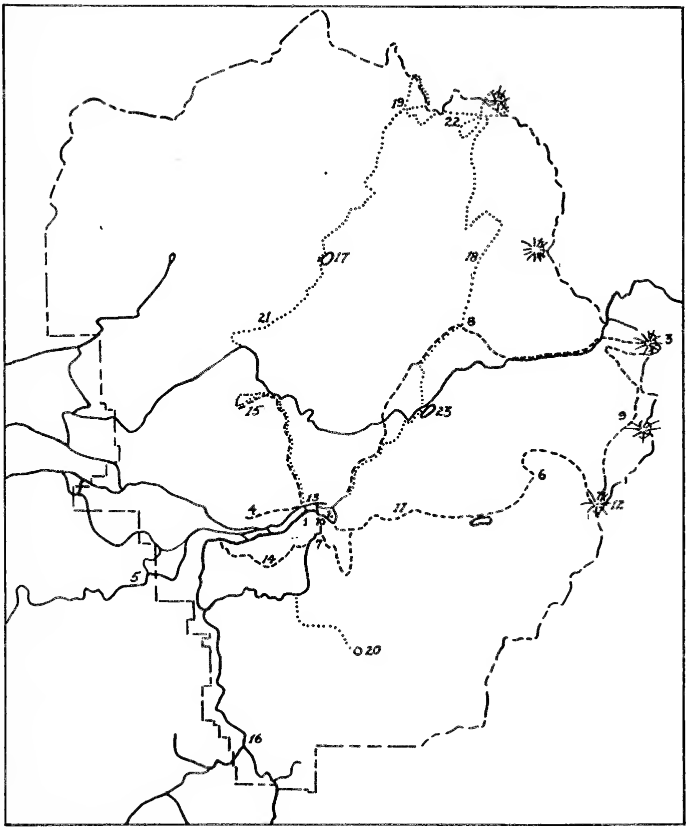
131. Ochlodes agricola (Bdv.) Darrah 29-V-59 (JWT); Indian Flat 30-V-59 (JWT); El Portal 14-V-61 (JWT).

132a. Polites sabuleti sabuleti (Bdv.) Bridgeport 14-VIII-50 and 16-VIII-51 (JWT); Mono Lake 23-VI-62 (JWT).

b. Polites sabuleti tecumseh Grin. Tioga Pass 7-VII-31, 13-VIII-50, 15-VIII-51, 18-VIII-52 and 18-VII to 16-VIII-57 (JWT), 14-VII to 7-VIII-58 (AOS); Reserve 17-VII-33 and 10-VII-56 (JSG); Kuna 7-VIII-33 (JSG); Kerrick 27-VII-34 (EDG); Snow Lake 29-VII-34 (EDG); Tuolumne Meadows 15-VIII-57 and 3-IX-58 (JWT), 15-VIII-58 (AOS); Gin Flat 17-VII-57 (JWT); Rafferty Creek 24-VII-58 (AOS), 3-VIII-58 (JSG); Upper Gaylor Lake 1-VIII-58 (JSG); Upper Lyell Base Camp 9-VIII-58 (AOS); Elizabeth Lake 12-VIII-58 (AOS); Dana, W slope 30-VIII-58 (JWT); Pilot Peak 31-VIII-58 (JWT).

133. Polites sonora (Scud.) Ledge 9-VII-33 (JSG); Reserve 17-VII-33 (JSG); Tioga Pass 16-VIII-52 (JWT); Aspen Valley 14-VII-56 (JSG); Crane Flat 18 and 19-VII-57 (JWT); Gin Flat 19-VII-57 (JWT); Tuolumne Meadows 14-VIII-57 and 3-IX-58 (JWT), 15 to 21-VIII-58 (AOS); Bridal Veil 23-VI-59 (JSG); Mather 10-VI-61 and 30-VI-62 (JWT). Mono Lake 4-VII-33, 5-VII-38, 30-VI-50 to 13-VIII-50 and 15-VIII-51 (JWT), 15-VIII-57, 30-VI-58 and 27-VI-61 (AOS); Bodie 18-VII-57 (AOS); Warren Creek 11-VIII-60 (AOS); W of Lee Vining 26-VI-61 (AOS).

134. Amblyscirtes vialis (Edw.) Yosemite Valley, Meadow near Ahwahnee Hotel 17-VI-32 (JWT); Jerseydale 17-VI-57, 22-VI-61 and 9 to 13-VI-62 (AOS).



YOSEMITE PARK

1933 Localities: 1—Camp 19; 2—Camp 9; 3—Mt. Dana; 4—Eagle Pk.; 5—El Portal; 6—Florence L.; 7—Glacier Pt.; 8—Glen Aulin; 9—Mt. Kuna; 10—Ledge Tr.; 11—Little Yosemite; 12—Mt. Lyell; 13—Museum; 14—Pohono Tr.; 15—Research Reserve; 16—Wawona.

1934 Localities: 17—Benson L.; 18—Coldwater Can.; 19—Kerrick Pass; 20—Ostrander L.; 21—Pate Valley; 22—Slide Can.; 23—Tenaya L.

Key

——— Auto Rd. - - - - Trails Covered 1933 . . . . Trails Covered 1934

APPENDIX III

YOSEMITE LOCALITIES

West-slope localities visited by John S. Garth in 1933 (See Map 1):

1. Camp 19: Yosemite School of Field Natural History headquarters near Sentinel Bridge, floor of Yosemite Valley (3960). Transition Zone; Meadow Association.
2. Camp 9: Meadow near Camp Curry in Yosemite Valley (4000), a favorite haunt of *Argynnis cybele leto*. Transition Zone; Black Cottonwood; Meadow Association.
3. Dana: Trail from Tuolumne Meadows (8600) to top of Mt. Dana (13, 050). Hudsonian, Arctic-Alpine Zone; Subalpine Forest; Alpine Fell-Fields.
4. Eagle: Trail from top of Yosemite Falls (6525) to summit of Eagle Pk. Canadian Zone; Red Fir Forest; Moist Meadow; Riparian Association.
5. El Portal: Highway 140 near El Portal (1919) on the Merced River; short distance up Coulterville Road. Upper Sonoran Zone; Chaparral; Stream.
6. Florence: Lake above Lewis Creek Trail (10, 500). Hudsonian Zone, in close proximity to Arctic-Alpine. Subalpine Forest; Montane Meadows.
7. Glacier: Trail from Glacier Point (7214) to top of Nevada Falls (5910). Canadian Fir Forest replaced by Upper Sonoran Chaparral after fire.
8. Glen Aulin: High Sierra Camp on Tuolumne River at confluence of Conness Creek (7850). Canadian Zone; Transition elements (*A. hydaspe*).
9. Kuna: From Lyell Base Camp (10, 600) to summit of Kuna Crest (12, 000), down Dana Fork to Tuolumne Meadows (8600). Hudsonian, Arctic-Alpine Zone; cirques, tarns, snow banks, talus slopes, alpine meadows.
10. Ledge: Short trail from Camp Curry (4000) to Glacier Point (7214). Transition, Canadian Zone; steep cliffs, talus slopes, springs, stream.
11. Little Yosemite: Hanging Valley above Nevada Falls (5910) on Merced Lake Trail. Transition Zone; Jeffrey Pine, White Fir, Western Juniper.
12. Lyell: From Vogelsang Lake (10, 500) to summit of Mt. Lyell (13, 090). Hudsonian, Arctic-Alpine Zone; glaciers, tarns, Alpine rock gardens.
13. Museum: Garden along diverted stream behind Yosemite Museum (4000).
14. Pohono: Trail from Glacier Point (7214) over Sentinel Dome (8117) to Inspiration Point (5391). Canadian and Transition Zone; stream, meadow.
15. Reserve: Boundary Hill Research Reserve, a 25-square-mile area bounded by the Tioga Road, Yosemite Creek, Cascade Creek, and the north rim of Yosemite Valley. (6525 - 9200). Canadian Zone with weak Hudsonian atop Research Ridge; Red Fir Forest; Lodgepole Pine; Western Juniper.
16. Wawona: Highway 41 (Wawona Road) from Chinquapin (6266) to Wawona (4096). Transition Zone; Dry Hillside; *Monardella* and *Erysimum*.

West-slope localities visited by Edmund D. Godwin in 1934 (See Map 1):

17. Benson: Trail from Pate Valley (4500) over Pleasant Ridge (8000) to Pleasant Valley (7000) and Benson Lake (8000). Transition, Canadian Zone; Upper Sonoran influence (*Cercyonis silvestris*, *Coenonympha*).
18. Coldwater: Trail from Virginia Creek (8500) to Glen Aulin (7800) along Coldwater Canyon. Canadian Zone; Red Fir Forest; Riparian Assoc.
19. Kerrick: Trail from Benson Lake (8000) through Seavey Pass (9100) to Kerrick Canyon (8900), thence to Kerrick Meadows (9400). Canadian to Hudsonian Zone; Red Fir, Lodgepole Pine Forest; Montane Meadow.

20. *Ostrander*: Trail from Glacier Point Road (7100) to Ostrander Lake (8500). Canadian to Hudsonian Zone border (*Tsuga mertensiana*).
21. *Pate*: Trail from Harden Lake (7575) down north-facing granite slope to Pate Valley (4500). Canadian to Transition Zone; Upper Sonoran influence from opposite exposure. *Monardella* and *Umbellularia*.
22. *Slide*: Trail from Kerrick Meadows (9400) to Snow Lake (10, 200) to Slide Canyon (10, 000). Hudsonian Zone; Subalpine Meadow Association (*Colias behrii*).
23. *Tenaya*: McGee Lake Trail from Glen Aulin (7850) on the Tuolumne River to Tenaya Lake (8141). Canadian Zone; Red Fir; Lodgepole Pine.

Western Foothill localities visited from 1956 to 1962, mostly outside Yosemite National Park:

24. *Bear Creek Lodge*: On Highway 140 between Midpines (2477) and Briceburg (1186). Transition Zone; Yellow Pine Forest; Riparian Association.
25. *Big Oak Flat Road*: Highway 120, the part between Groveland (2846) and Carlon (4624) within Stanislaus N F. Upper Sonoran, Transition Zone.
26. *Briceburg*: Mariposa Co., on Highway 140 in Merced River Bottom (1186). Upper Sonoran Zone; Chaparral and Coastal Sage Scrub.
27. *Buck Meadows*: Stanislaus N F, on Highway 120 (3006). Transition Zone; Yellow Pine Forest with "Mountain Misery" (*Chamaebatia*) understory.
28. *Carl Inn*: Stanislaus N F, at juncture of Hetch-Hetchy Road to Mather and Old Tioga Road (4718). Transition Zone; Mixed Forest, cut over.
29. *Cathay*: Mariposa Co., on Highway 140; Upper Sonoran; Oak Woodland.
30. *Chowchilla Mtn.*: Sierra N F, W of Fish Camp (4982) on Chowchilla Mtn. Road, near Bear Wallow turnoff. Canadian Zone; Red Fir Forest.
31. *Cliff House*: Stanislaus N F, on Highway 120 N Fork, Tuolumne River, crossing. Transition Zone; Yellow Pine Forest; Yerba Santa.
32. *Darrah*: Mariposa Co. (3400). Upper Sonoran, Transition Zone; Chaparral; Coastal Sage Scrub; Yellow Pine, Mixed Forest; Riparian Assoc.
33. *El Portal*: Yosemite N P, on Highway 140 in Merced River Bottom (1919). Upper Sonoran Zone; Chaparral, Coastal Sage Scrub; Riparian Assoc.
34. *Groveland*: Stanislaus N F, on Highway 120 (2846). Transition and Upper Sonoran Zone; Yellow Pine Forest; Mixed Forest; Chaparral.
35. *Highway 120 and Hetch-Hetchy Road*: Juncture, Big Oak Flat Road and Mather Road (4624). Upper Sonoran, Transition; Oak Wood; Yellow Pine.
36. *Indian Flat*: Sierra N F, on Highway 140 in the Merced River bottom (1553). Upper Sonoran Zone; Coastal Sage Scrub, Chaparral; Yellow Pine.
37. *Jerseydale*: Sierra N F, (3800). Transition Zone; Yellow Pine, Mixed Forest; *Chamaebatia*, *Monardella* (*Argynnis hydaspe*); some Meadowland.
38. *Mariposa*: Mariposa Co., on Highway 140 (2046). Upper Sonoran, Transition Zone; Chaparral, Coastal Sage Scrub; Mixed Forest; Riparian Assoc.
39. *Mather*: Stanislaus N F (4522), on Hetch-Hetchy Road. Transition Zone; Yellow Pine, Mixed and White Fir Forest; Montane Meadow; Riparian. Includes Carnegie Experimental Garden (Hog Ranch) 1 mi NE of Mather.
40. *Oakhurst*: Madera Co., on Highway 41. Upper Sonoran Zone; Foothill Woodland; Oak and Digger Pine with *Ceanothus* and grass (*Coenonympha*).

West-Slope Mid-Elevation Localities visited from 1956 to 1962, all within Yosemite National Park:

41. *Aspen Valley*: On Old Tioga Road above turnoff from Mather Road at Carl Inn (6390). Canadian Zone; Red Fir Forest; Montane Meadow; lupine.

42. Badger Pass: Meadow beside Badger Pass Ski Lodge on Glacier Point Road (7300). Canadian Zone; Red Fir Forest; Wet Meadow Association.
43. Bridal Veil: Public Camp on Bridal Veil Creek where crossed by Glacier Point Road (7000). Canadian Zone; Red Fir Forest; Riparian Assoc.
44. Crane Flat: On Highway 120 where it becomes the Tioga Road (6192). Transition Zone; Mixed Forest; Montane Meadow. Also roadside above.
45. Gin Flat: On Tioga Road above Crane Flat (7036). Canadian Zone; Montane Meadow.
46. Glacier Point: Road to, with maximum elevation 7800 feet. Canadian Zone; openings in Red Fir Forest; Montane Meadow; Riparian Assoc.
47. Hetch-Hetchy: Road from Mather (4522) to Hetch-Hetchy Reservoir (3796). Upper Sonoran Zone; Digger Pine; Manzanita. Summit (5027) Transition Zone; White Fir Forest; Streamside Association; lupine.
48. Mirror Lake: Floor of Yosemite Valley (4082). Transition Zone; Black Oak, White Fir, Incense Cedar, Cottonwood, Ceanothus, Coffee Berry.
49. Old Village: Yosemite Valley floor (3964). Transition Zone; Riparian.
50. Research Reserve: Meadow in Blue Jay Creek (7900). Canadian Zone; Red Fir, Lodgepole Pine. Research Ridge (8700) Dry Hillside Assoc.
51. Smoky Jack: Public Camp on Tioga Road above Gin Flat. Canadian Zone; Red Fir Forest; Montane Chaparral.
52. Tamarack Flat: Meadow above Tamarack Public Camp on Tioga Road (6390). Upper Canadian Zone; Red Fir; Lodgepole Pine; Ceanothus.
53. Tioga Road: North-facing slope 1 mi W of White Wolf turnoff (8000) and first summit beyond White Wolf (8090). Canadian Zone; Red Fir Forest.
54. Tuolumne Grove: On Highway 120 W of Crane Flat (5500-6000). Transition Zone; Mixed Forest; Big Tree; Riparian Assoc. Polygonia zephyrus.
55. White Wolf: One mi N of Tioga Road (8090). Canadian Zone; Red Fir Forest; Montane Meadow Assoc. Plebejus saepiolus, P. glandon podarce.
56. Wawona: Open forest between Wawona Lodge (4096) and the turnoff to Giant Forest (4350). Transition Zone; Yellow Pine Forest.
57. Yosemite Creek: Trail S from Public Camp on Tioga Road (7200). Canadian Zone; Riparian and Wet Meadow; Western Juniper on drier slopes.
58. Yosemite Valley: Floor of Valley (4000). Transition Zone; Mixed Forest; Riparian Association. Includes Meadow near Ahwahnee Hotel. A. vialis.

High Country localities visited since 1956 (those near Tioga Pass since 1929):

59. Agnew Pass: Inyo N F (9946). Hudsonian Zone; open sage slope.
60. Bert Lake: N slope of Mt. Maclure (11,700); Arctic-Alpine; rock gardens.
61. Cockscomb Peak: Cathedral Range (11,000); Arctic-Alpine; White-Bark Pine; gradual slope; Spraguea in gravelly areas. Hesperia miriamae.
62. Dana, N slope: (11,000-13,050). Arctic-Alpine; rockslides, flowers, grass. Lycaena p. hypophlaeas. Dana, W slope: From Tioga Pass (9941) to timber line (11,000). Hudsonian to Arctic-Alpine; Subalpine Forest; Alpine Fell-Fields.
63. Dog Lake Trail: From Tuolumne Meadows (8600) to Dog Lake (9240). Hudsonian Zone; Subalpine Forest; talus slides; rock gardens. Lycaena cupreus.
64. Donohue Pass: Inyo N F (11,100). Arctic-Alpine; meadows, exposed rock.
65. Elizabeth Lake: Cathedral Range (9500). Hudsonian Zone; Lodgepole Pine; meadows, willows, heather. Lycaena mariposa, Polites s. tecumseh.
66. Gaylor Lakes: Above Tioga Pass Checking Sta. (10,500). Arctic-Alpine; Alpine Fell-Fields. Includes Upper Gaylor Lake. Melitaea d. malcolmi.
67. Glen Aulin: On Tuolumne River (7850). Canadian Zone; Jeffrey Pine; arid slope.

68. Helen Lake: E of Kuna Crest (10,896). Arctic-Alpine; White-Bark Pine.
69. Hoffmann, Mt.: W of May Lake (10,921). As above; flowers in gravel.
70. Lembert Dome: N of Tuolumne Meadows (9400). Hudsonian; forested.
71. Lyell Base Camps: Head of Lyell Fork (11,000). Arctic-Alpine; treeline.
72. Lyell Fork Meadows: (9000). Hudsonian; Lodgepole Pine; willow stream.
73. Ottoway Lake: Clark Range (8000). Canadian Zone; Red Fir Forest.
74. Mammoth Peak: N end, Kuna Crest (12,225). Arctic-Alpine; exposed.
75. Merced Lake Trail: From Merced Lake (7100) to Tuolumne Pass (10,100) via Fletcher Creek. Canadian to Hudsonian; Coniferous Forest; Meadows.
76. Mono Pass: Inyo N F (10599). S of Tioga Pass, between Mt. Gibbs and Mt. Lewis. Arctic-Alpine; Alpine Fell-Fields. Hesperia miriamae.
77. Pilot Peak: NW above Tioga Pass via Gaylor Lakes Trail (11,100). Hudsonian, Arctic-Alpine; Subalpine Forest, Alpine Fell-Fields. (See 81).
78. Rafferty Creek: (8600-10,100). Hudsonian; Lodgepole Pine; Riparian.
79. Saddlebag Lake: Inyo N F (10,050). Upper Hudsonian and Arctic-Alpine; few trees, willows, grasses, some rock. Includes E above (10,500).
80. Tioga Meadow: (9941). Montane Meadow E of Tioga Pass Checking Sta.
Tioga Pass: (9941). Hudsonian Zone; Subalpine Forest; Glacial Moraine.
81. Tioga Pass, NW above: (10,500-11,000). Tree-line Association; rock gardens. Parnassius p. behrii, Pieris o. calyce, Oeneis c. ivallda.
82. Tenaya Canyon: (4,000-8,000, average 6,000). Canadian Zone; stream bed choked with firs, aspen, willows; exposed slopes (Philotes enoptes).
83. Thousand Island Lake: Inyo N F (9850). Hudsonian; Lodgepole Pine; sage.
84. Tuolumne Meadows: On Tioga Road (8600). Hudsonian; Lodgepole Pine. extensive meadows. Site of Lembert Homestead; metropolis of C. behrii.
85. Unicorn Peak: Cathedral Range (10,849). Arctic-Alpine; boulder jumble.
86. Vogelsang: Trail from Vogelsang Camp (10,100) to Vogelsang Pass (10,400) and below. Hudsonian, Arctic-Alpine; Subalpine Forest; Alpine Fell-Fields.

East-slope localities visited during survey; mostly Mono Basin; all outside Yosemite National Park:

87. Bodie: 11 mi E of Highway 395 (8369). Pinyon; Great Basin Sage; Meadow.
88. Bridgeport: On Highway 395 (6743). Willow Thicket; Riparian Association.
89. Casa Diablo Hot Springs: Inyo N F, on Highway 395 (7198). Transition; Great Basin Sage Brush in Jeffrey Pine Forest; sparse Streamside Assoc.
90. Conway Pass: On Highway 395 N of Mono Lake, 200 ft. below Summit (8136). Great Basin Scrub (Desert Peach, Chrysothamnus, Purshia); Montane Meadow; Aspen Grove.
91. Deadman Summit: Inyo N F, on Highway 395 (7734 or 8168). Transition; Jeffrey Pine Forest; Purshia, Artemesia, Chrysothamnus, Eriogonum.
92. Gull Lake: Inyo N F (7600), on June Lake circuit. Moist Montane Meadow; Willow Thicket; Brownie Thistle (Cirsium acaulescens). A. n. apacheana.
93. June Lake: Inyo N F (7716). Junction of Highway 395 and June Lake Road. Transition; Jeffrey Pine Forest; Great Basin Sage. Neophasia menapia.
94. Lee Vining Creek: Inyo N F (7000). Above turnoff to last campground on Tioga Pass Road. Dry Hillside; Manzanita; Ceanothus, Bitter Cherry.
95. Mono Lake: (6419). Many associations in close proximity: Freshwater Marsh, Salt Sink Margin, Willow Thicket, Aspen Grove, Moist Meadow.
96. Mammoth: Inyo N F (7900). On Highway 395, about 2-3 mi below. Transition; Jeffrey Pine Forest; Great Basin Sage Brush; Great Basin Scrub.
97. Lundy: Inyo N F (7766). Sage, Aspen, Willow. Collecting to 8700 feet.
98. Warren Creek: Inyo N F (9000-9500). N fork of Lee Vining Creek above Tioga Road crossing. Canadian Zone; willowed stream, sage-aspen slope.

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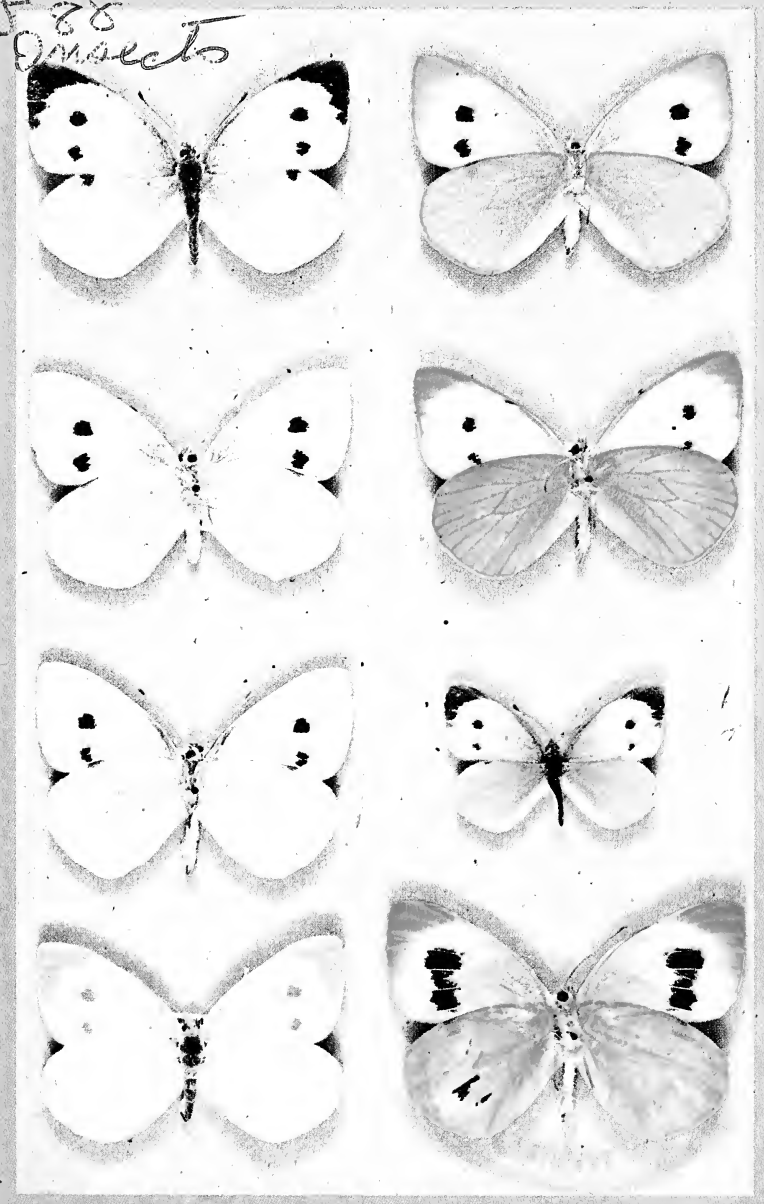

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THE PURPOSE OF THE JOURNAL is to combine in one source the work in this field for the aid of students of this group of insects in a way not at present available. THE JOURNAL will attempt to publish primarily only critical and complete papers of an analytical nature, though there will be a limited section devoted to shorter papers and notes. QUALITY WORK on any aspects of research on the Lepidoptera is invited. Analytical and well illustrated works are preferred, with a minimum of long description.

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QUANTITATIVE ANALYSIS OF CERTAIN WING AND GENITALIA CHARACTERS OF PIERIS IN WESTERN NORTH AMERICA

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ALL SPECIES OF *Pieris* which occur in western North America were named in the nineteenth century at which time wing coloration and pattern were the most obvious characteristics used for identification. Great variations are present between various species of the genus *Pieris* with respect to these characters. Such variations have contributed to disagreement concerning the number of species which occur in North America. Some authors list seven species: *P. rapae, P. napi, P. virginiensis, P. sisymbrii, P. beckeri, P. protodice* and *P. occidentalis* (Klots 1932, McDunnough 1939). Abbott et al (1960) in a statistical study utilized six morphological characters which included the length and the width of the front wing, the length of the hind wing, body length and the degrees of melanization of the upper and lower sides of the wings of the specimens. They found that there is a continuous variation in wing sizes, color and marking between *P. protodice, P. occidentalis* and *P. sisymbrii.* Such variations were found associated with geographical location and climate. They suggested that *P. protodice, P. occidentalis* and *P. sisymbrii* were a single species. Klots (1961) in his latest *Pieris* list, cited only six species, excluding *P. occidentalis.* Hovanitz (1962) combined the distribution of *P. occidentalis* and *P. protodice* in a geographical study because of uncertainty of how to separate them. Evidence for considering them as separate species is given in this paper. Hovanitz (1963) also indicated that *P. napi* and *P. virginiensis* ought to be considered as a single species at the present time for nomenclatural purposes pending more complete evidence of their possible sympatric distribution. Since *P. virginiensis* occurs only in the region east of the Rocky Mountains in North America, it is excluded from consideration in this paper. In the present paper, mainly morphological characters are studied, which are intended to aid in the elucidation of the biological relationships between these various species of *Pieris.*

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[1] *This work was supplementary to work aided by a grant from the National Science Foundation.*

MATERIALS AND METHODS

Five hundred specimens have been studied from the collections gathered by William Hovanitz and the author throughout the region in recent years. Despite this fact, this study is not intended of an exhaustive geographical study.

The wing characters used in this study include: (1) wing color and pattern, of which the detailed description will not be given; however, the most important characters are outlined in the text, and (2) wing venation, which is relatively uniform in the genus *Pieris.* Differences have been found in the length of the R_3, and in the location of R_2 in respect of M_2 and (3) the androconial scales which are the scent scales found with the black scales in the dot on or near the discal vein on the male fore wings.

The characters used for the male genitalia include (1) the uncus, (2) the juxta, (3) the saccus and (4) the penis. For the female genitalia, only the signum bursa has been used; this is a chitinized structure on the corpus bursa.

The overall size of the insects influences the size of their internal structures. To make this size difference of negligible influence, the simple ratio: the length of the left front wing against the length of a particular structure has been used for aiding in the elimination of such possible differences.

$$\text{Ratio} = \frac{\text{the length of a given structure}}{\text{the length of left front wing}} \times 100$$

The terminology of structural parts employed here has been adapted from Klots (1931). The color terms whenever used in the text follow the "Dictionary of Color" by Maerz and Paul (1930).

I. *P. rapae* and *P. napi*

Color and pattern (fig. 1a): *P. rapae* and *P. napi* are different from other species by lacking a dot on the discal vein of the fore wings. Most samples of *P. rapae* and *P. napi* are easily separated, except the all-white forms of both species.

Venation: The mean ratio (table 1) between the length of the left fore wing and the length of the discal cell are statistically different for these two species. The probability that the difference might be due to chance alone is less than 0.001 when the degree of freedom is 45 (as tested by "*t*"). The histogram (fig. 3) shows however that the range of ratios is continuous from one species to another. In actual fact, however, no overlap has been observed in the investigation between these two species though it may occur when the sample size is larger.

Location of the discal cell, and method of measuring venation are illustrated in fig. 2.

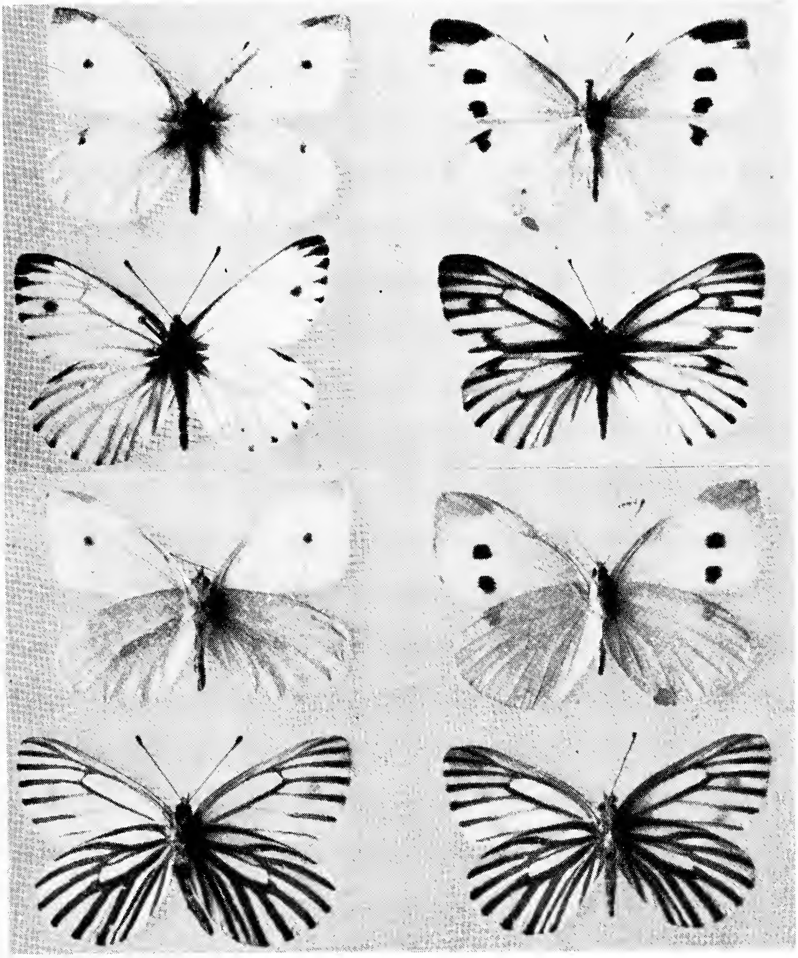


Fig. 1a. *Pieris rapae* and *Pieris napi*. Male on left, female on right. Upper four are upper side;lower four are lower side.

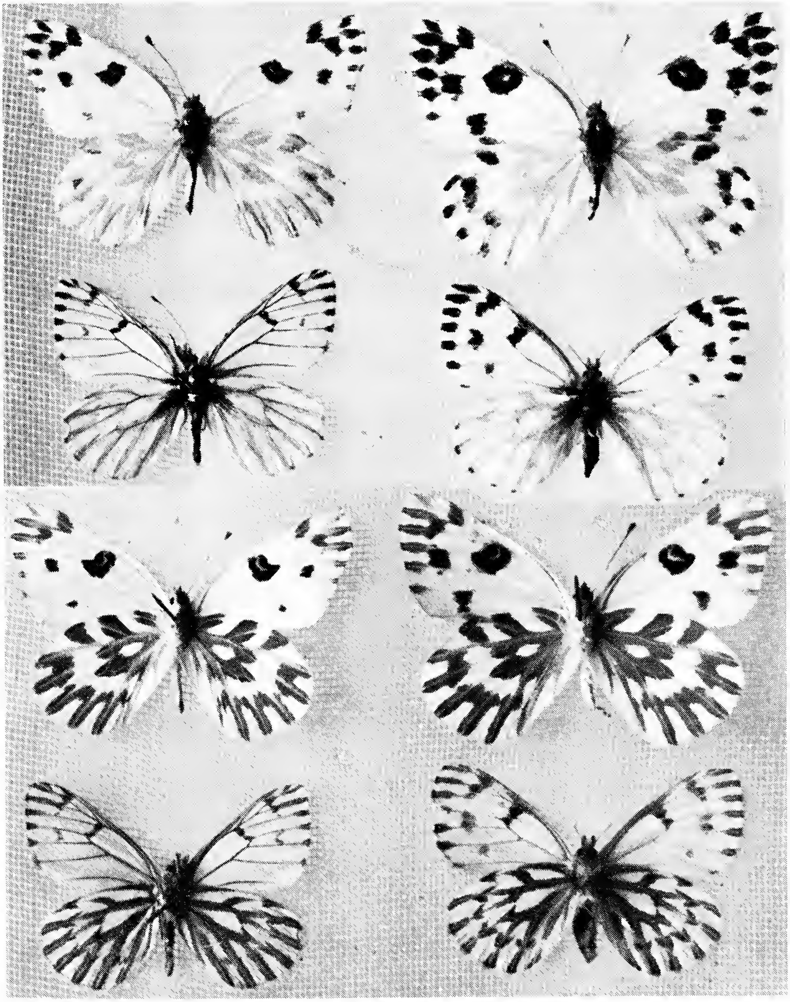


Fig. 1b. *Pieris beckeri* and *Pieris sisymbrii*. Male on left, female on right. Upper four are upper side, lower four are lower side.

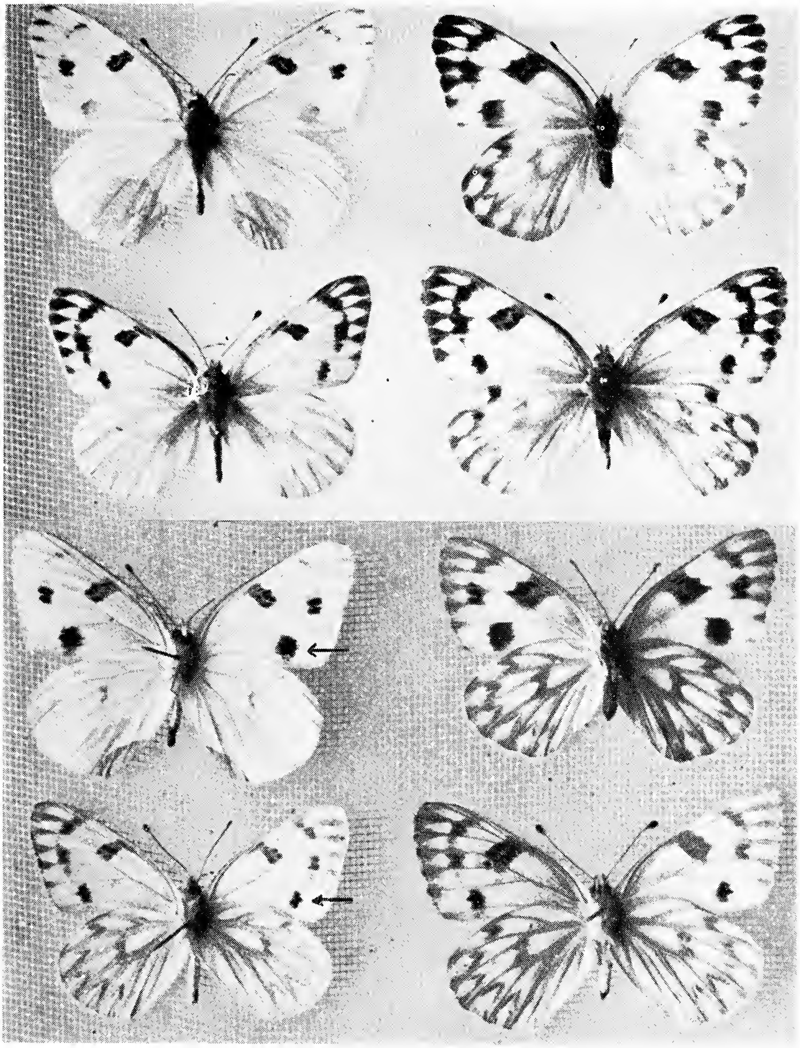


Fig. 1c. *Pieris protodice* and *Pieris occidentalis.* Male on left, female on right. Upper four are upper side, lower four are lower side.

Table 1 Ratios between length of discal cell and length of front wing

Species	No.	Mean length front wing	Mean length discal cell	Ratio	S. D.	S. E.	t	Probability
P. rapae	25	23.18 mm	12.44 mm	53.66	1.85	0.37	12.24	0.001
P. napi	20	21.79 mm	13.10 mm	60.15	1.65	0.37		

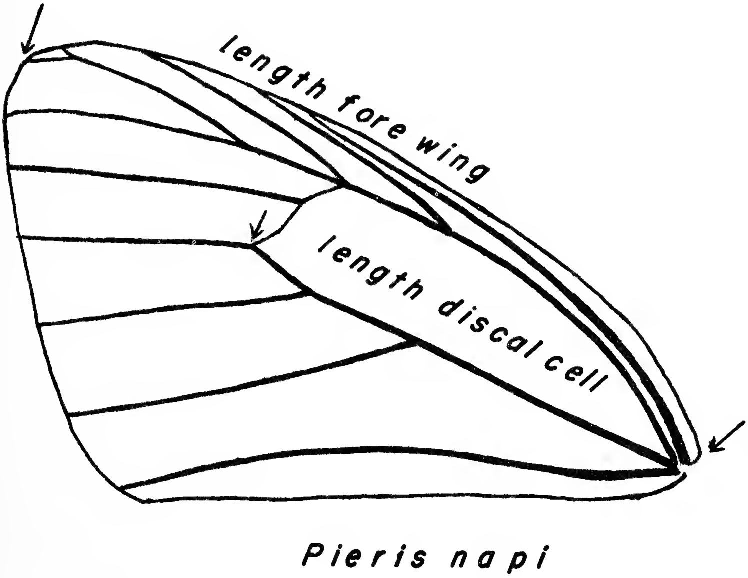
Table 2 Ratios between width of androconia and length of front wing

Species	No.	Mean length front wing	Mean width androconial stalk	Ratio	S. D.	S. E.	t	Probability
P. rapae	20	23.43 mm	0.12 mm	0.50	0.07	0.016	19.39	0.001
P. napi	20	23.55 mm	0.27 mm	1.14	0.13	0.029		

S. D. = Standard deviation; S. E. = Standard error

Androconia (fig. 4, 5, table 2): Both *P. rapae* and *P. napi* have androconial scales with broadened tops and two lobes. A difference is found on the width of the scale's stalk which for *P. rapae* is narrower than *P. napi*. The probability as shown by the "*t*" test that the difference between the mean ratio of these two species is due to chance alone is less than 0.001 for a degree of freedom of 40. The histogram (fig. 5) shows that there is a wide gap between the ratios. This is one of the characters that can be used to separate the all white forms of a *P. rapae* and *P. napi.*

Male genitalia: (1) the uncus (figs. 6, 7, table 3) is more slender and less curved at the ventral side for *P. rapae* and *P. napi* than for the other four species in the genus *Pieris.* The ratios: the length of the uncus against the length of the fore wing range from 2.07 to 2.84 for *P. rapae,* and from 2.69 to 3.05 for P. *napi.* The probability that this difference might be due to chance alone is 0.025 for a degrees of freedom of 18 as tested by *t:*



Pieris napi

Fig. 2. Location of discal cell and points of measurement

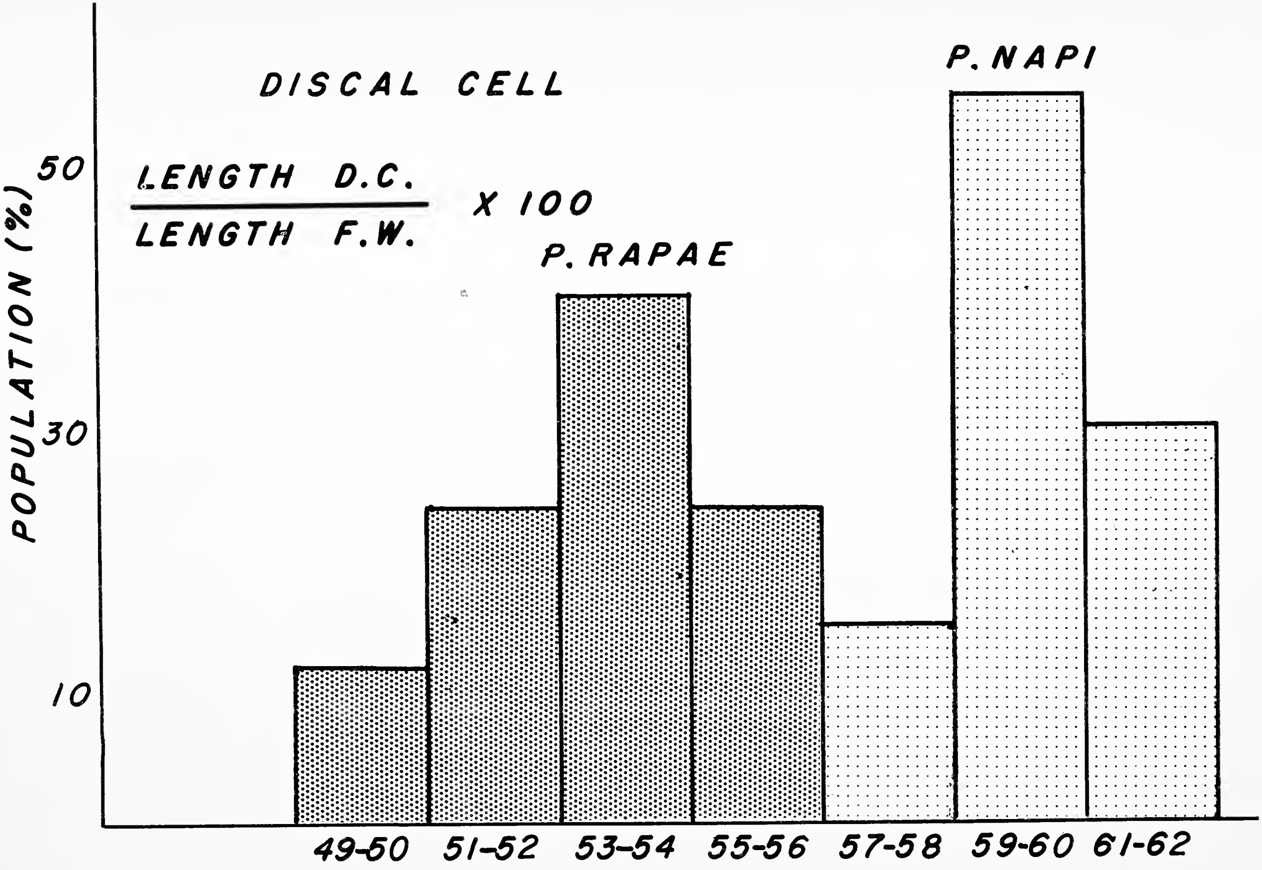


Fig. 3. Histogram illustrating the differences in ratios distribution between *P. rapae* and *P. napi*

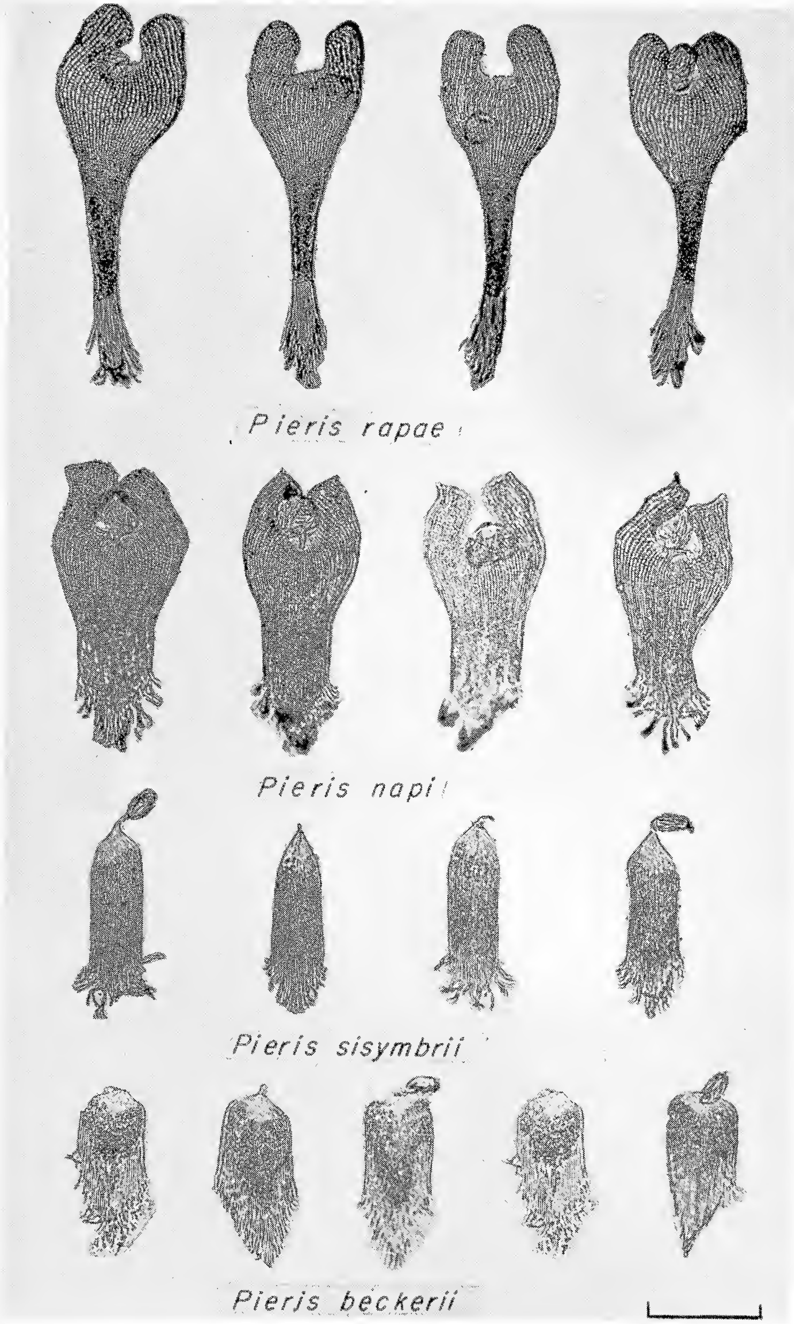


Fig. 4. Androconial scales (400x)

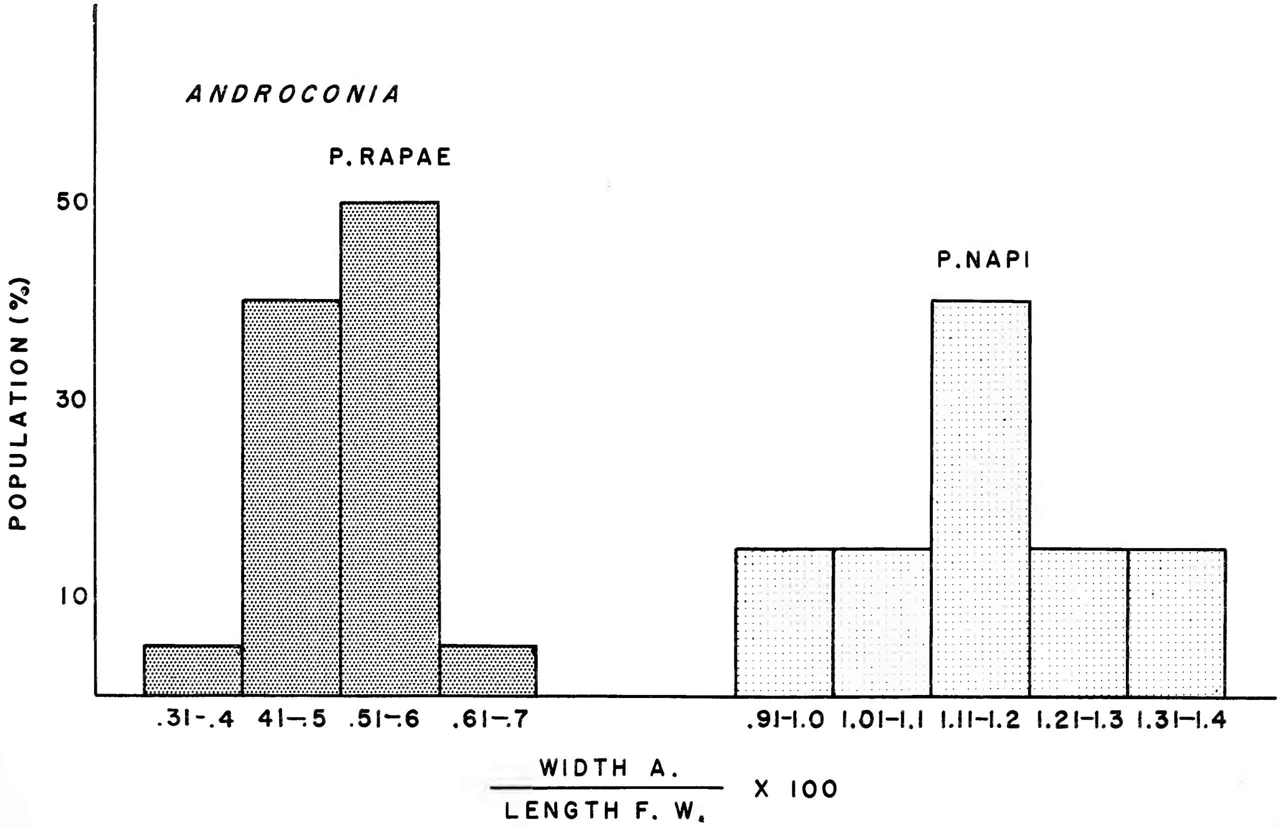


Fig. 5. Histogram illustrating the differences in ratios distribution between *P. rapae* and *P. napi*

Table 3 Ratios between length of various genital structures and length of front wing

Uncus

Species	No.	Mean length of uncus	Mean length of front wing	Mean of ratio	S. D.	S. E.	t	Probability
rapae	10	0.59 mm	22.6 mm	2.61	0.18	0.05	2.5	0.025
napi	8	0.70 mm	24.8 mm	2.81	0.12	0.04		
sisymbrii	11	0.55 mm	20.34 mm	2.71	0.23	0.07	3.54	0.005
beckeri	9	0.54 mm	24.18 mm	2.25	0.33	0.11		
protodice	37	0.48 mm	22.5 mm	2.12	0.22	0.04	1.38	0.2 +
occidentalis	25	0.56 mm	23.4 mm	2.40	0.22	0.04		

(2) The juxta (fig. 7) is quite different in shape between *P. rapae* and *P. napi.* The lower end of the juxta of *P. rapae* is triangular; however, in *P. napi,* this structure is reduced in size and not hollowed out.

(3) The saccus and penis (fig 8, table 4) show no significant differences between *P. rapae* and *P. napi.*

Signum bursa (fig. 8): This structure is again a good character to separate *P. rapae* and *P. napi.* The signum bursa of *P. rapae* is like a pair of kidneys; the central part is less toothed. In *P. napi,* it has a long unchitinized tail which is so distinctive that there is nò problem in separating this species from others in the genus *Pieris.*

The samples of *P. rapae* came from *(1)* Arcadia, Los Angeles County, California (5 individuals), *(2)* Newport Beach, Orange Co., Calif. (5), *(3)* Riverside, Riverside Co. Calif. (5), (4) Bishop, Inyo Co. Calif. (5), *(5)* Klamath Falls, Klamath Co. Oregon (5), and (6) Satus Creek, Yakima Co. Washington (5). The samples of *P. napi* came from *(1)* Lopez Canyon, San Luis Obispo Co. Calif. (5), (2) Berkeley, Calif. (1), (3) Utah (1), (4) Hurricane Ridge, Olympic National Park, Wash. (10), (6) British Columbia (2), (7) Yukon Territory (6), and (8) Alaska (3).

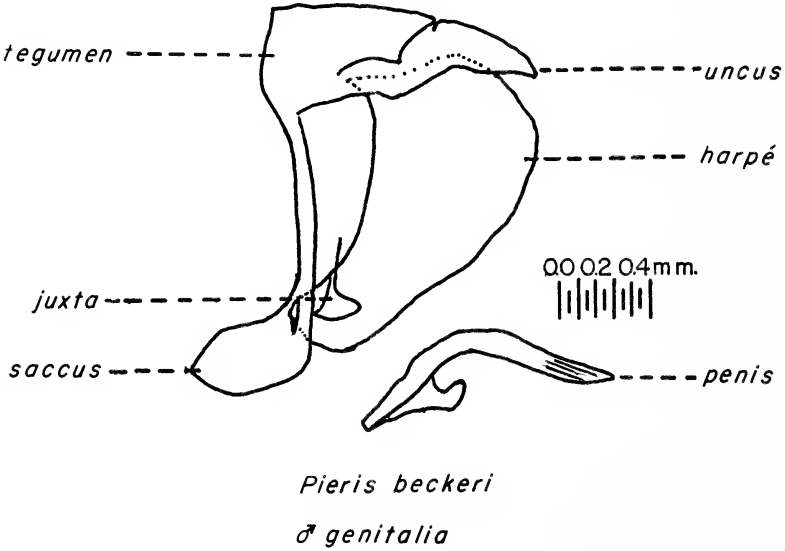


Fig. 6. The lateral view of male genitalia

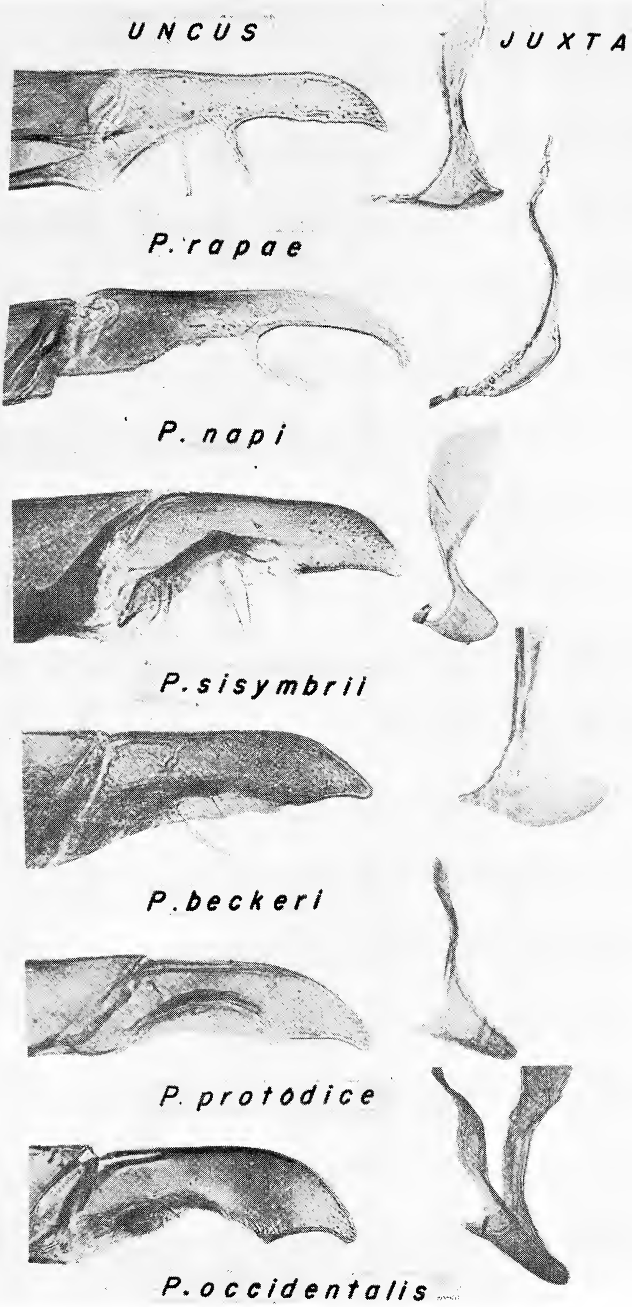


Fig. 7. Male genital structures

Table 4 Ratios between length of various genital structures and length of front wing

Saccus

Species	No.	Mean length of saccus	Mean length of front wing	Mean of ratio	S. D.	S. E.	t	Probability
rapae	9	0.51 mm	22.59 mm	2.26	0.27	0.09	1.38	0.2 +
napi	7	0.51	24.8	2.08	0.19	0.07		
sisymbrii	8	0.48	20.98	2.30	0.28	0.10	0.94	0.2 +
beckeri	8	0.51	23.7	2.17	0.24	0.09		
protodice	53	0.62	22.96	2.68	0.31	0.04	12.2	0.001
occidentalis	30	0.81	23.54	3.45	0.19	0.04		

Table 5 Ratio between length of R_3 and length of front wing

Species	No.	Mean length front wing	Mean length R_3	Ratio	S. D.	S. E.	t	Probability
P. sisymbrii	12	20.73 mm	0.89 mm	4.16	1.10	0.32	7.83	0.001
P. beckeri	12	24.82 mm	0.36 mm	1.42	0.50	0.14		
P. sisymbrii	12	20.73 mm	0.89 mm	4.16	1.10	0.32	7.86	0.001
P. protodice	34	22.79 mm	0.27 mm	1.17	1.10	0.19		

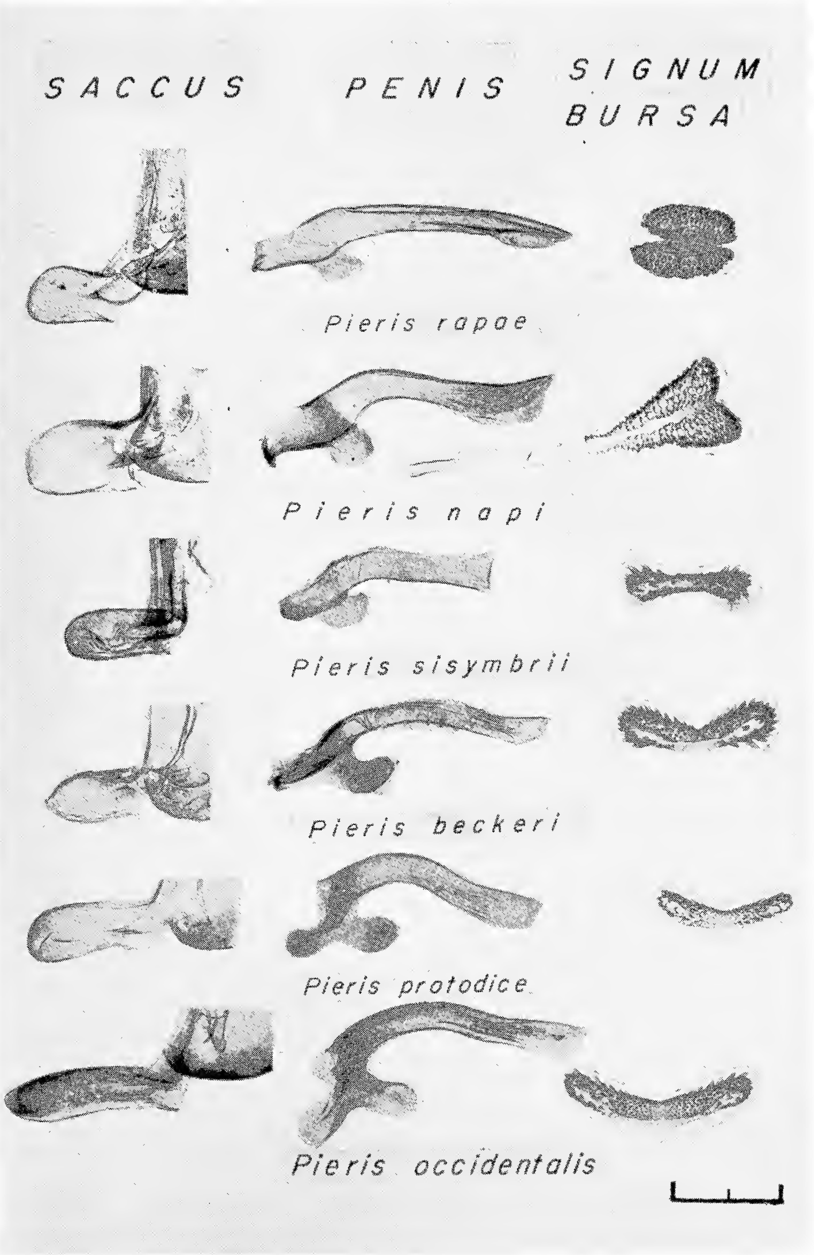


Fig. 8. Male and female genital structures

II. *P. sisymbrii* and *P. beckeri*

1. Color and pattern (fig. 1b): These two species are easily separated by the color and the pattern on the wings. *P. beckeri* has the intensified moss green color and *P. sisymbrii* has the biskra data color along the vein on the underside of the wings.

2. Venation (fig. 9, table 5): The length of R_3 between *P. sisymbrii* and *P. beckeri* differs. The ratio of fore wing length over R_3 for *P. sisymbrii* ranges from 2.34 to 5.88; for *P. beckeri* ranges from 0.95 to 2.62. The probability that the mean for the two populations could have been drawn by chance from the same population is less than 0.001 when degrees of freedom is 24 as tested by *t*.

3. Androconia (fig. 4): The scent scales of *P. sisymbrii* and *P. beckeri* are similar but unlike *P. rapae* and *P. napi.* The tiny, lobeless scales of *P. sisymbrii* are nearly parallel at the lateral border, and the roots are limited to the base. The scales of *P. beckeri* are usually irregular shaped and the roots are often occupied half the length of the scale.

4. Uncus (fig. 7, table 3): The uncus of *P. beckeri* and *P. sisymbrii* have hairy processes at the ventral side, particularly in *P. sisymbrii.* The actual length of the uncus in the two is much the same, but the ratio is different (probability 0.005; d.f. 20) due to the constant smaller size of wing length in *P. sisymbrii.*

5. Juxta (fig. 7): The juxta of *P. beckeri* and *P. sisymbrii* are similar except the apex is slightly curved upward in *P. beckeri.*

6. Saccus (fig. 8, table 4): There is little difference in shape or size with respect to this structure.

7. Penis (fig. 8): The shape of the penis in *P. sisymbrii* and *P. beckeri* is like the penis of *P. rapae* and *P. napi.* However, it is distinctly different from the penis of *P. protodice* and *P. occidentalis.* The basal protuberance of the penis of *P. beckeri* and *P. sisymbrii* is insignificant. But it rises abruptly for *P. protodice* and *P. occidentalis.*

8. Signum bursa (fig. 8, table 6): The signum bursa of *P. sisymbrii* and *P. beckeri* is stick-shaped, with large, heavily chitinized teeth. The difference between the ratios is probably caused by chance error due to the extremely small sample of *P. sisymbrii* examined, rather than to a real difference.

The samples of *P. sisymbrii* came from (*1*) Kelso Valley, Kern Co. Calif. (2), (*2*) Roads End, Tulare Co. Calif. (1), (*3*) King's Canyon, Fresno Co. Calif. (2), (*4*)Hurricane Ridge, Olympic National Park, Wash. (6), and (*5*) Whitehorse, Yukon Territory (1). The samples of *P. beckeri* came from (*1*) Long Valley, Mono Co. Calif. (1), (*2*) Mono Lake, Mono Co. Calif. (2), (*3*) Gardnerville, Douglas Co. Nevada (2), (*4*) Minden, Douglas Co. Nevada (2), (*5*) Doyle, Lassen Co., Calif. (2), and (*6*) Satus Creek, Yakima Co. Wash. (3).

Table 6 Ratios between length of various genital structures and length of front wing

Signum bursa

Species	No.	Mean length of signum bursa	Mean length of front wing	Mean of ratio	S. D.	S. E.	t	Probability
sisymbrii	2	0.75 mm	22.8 mm	3.28	0.05	0.032	3.86	0.01
beckeri	6	0.76	26.87	2.84	0.14	0.057		
protodice	35	0.74	23.32	3.18	0.195	0.03	14.4	0.001
occidentalis	25	0.96	24.0	4.03	0.25	0.05		

Table 7 Ratios between width of tornus dot and length of front wing

Species	No.	Mean length front wing	Mean width tornus dot	Ratio	S. D.	S. E.	t	Probability
P. protodice	32	22.80 mm	2.83 mm	12.38	1.33	0.23	18.48	0.001
P. occidentalis	28	22.53	1.41	6.28	1.22	0.23		

III. *P. protodice* and *P. occidentalis*

1. Color and pattern (fig. 1c, table 7): The color and pattern of these two species are many times undistinguishable, especially in comparison between the high temperature form of *P. occidentalis* and the low temperature form of *P. protodice.* The primary difference in the pattern, besides the gross one of more extensive black pigment on *P. occidentalis* males than on *P. protodice* males, is in the size and shape of the dot in the tornus area near the inner margin on the underside of the fore wings. The dot on *P. protodice* is large, square shaped and not clearly outlined, part of the dot being sometimes submerged on the uppersides. The dot of *P. occidentalis* is small, relatively clearly outlined, usually not submerged. The ratios for the width of the tornus dot range from 8.73 to 15.38 for *P. protodice;* and from 3.95 to 8.51 for *P. occidentalis.* The probability that this difference is due to chance alone is less than 0.001 for the degrees of freedom of 60 by the *t* test.

2. Venation (fig 9, 10, table 5): The R_3 veins of *P protodice* and *P. occidentalis* are quite short, sometimes being completely missing. The mean ratios of wing length over R_3 length between the two species do not show much difference. (1.17 for *P. protodice*; and 1.15 for *P. occidentalis*). However, the difference is significant between *P. protodice* and *P. sisymbrii* in comparing the ratios despite the similarities in their wing color and pattern. The mean ratio for *P. sismybrii* is 4.16; and for *P. protodice* it is 1.17. That the difference as indicated might be due to chance is less than 1/1000 for the degrees of freedom of 46 by the *t* test.

In *P. protodice,* the intersection of R_2, R_s+M_1 (point "A") is usually above point "B" where M_2 joins that vein; however, point "A" is usually on or below point "B" in *P. occidentalis.* The distance between point "A" and point "B" is measured and plotted on the diagram (fig. 11) against the ratio obtained from the width of the tornus dot to the length of the fore wing. When point "A" is above point "B" the measurement is given a "+" sign. When point "A" is below point "B" the measurement is given a "—" sign. The diagram (fig. 11) shows that *P. protodice* and *P. occidentalis* are well separated by these two characters. Few exceptional dots on the diagram as the measurements between point "A" and point "B" having a "—" sign for *P. protodice* or vice versa for *P. occidentalis* are from the specimens collected at the overlap zone of these two species.

The width of tornus dot and the location of R_2 in respect of M_2 are two pirmary characters used in the investigation to separate the two species.

3. Androconia: Thirty-five specimens of male *P. protodice* and twenty-eight specimens of male *P. occidentalis* from ten different localities were checked, but no androconial scales have ever been found. Similar results were also observed by Bernardi (1947).

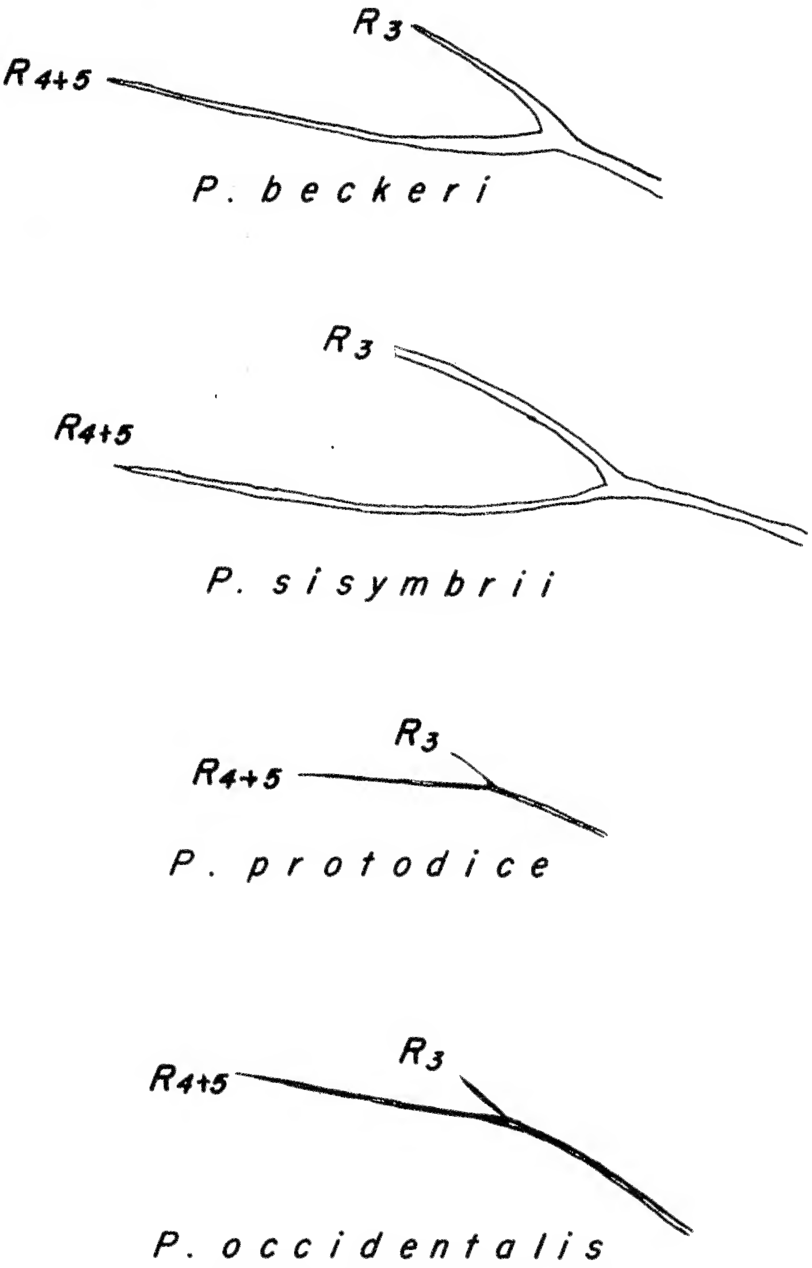


Fig. 9. Venations showing the differences in the length of R_3

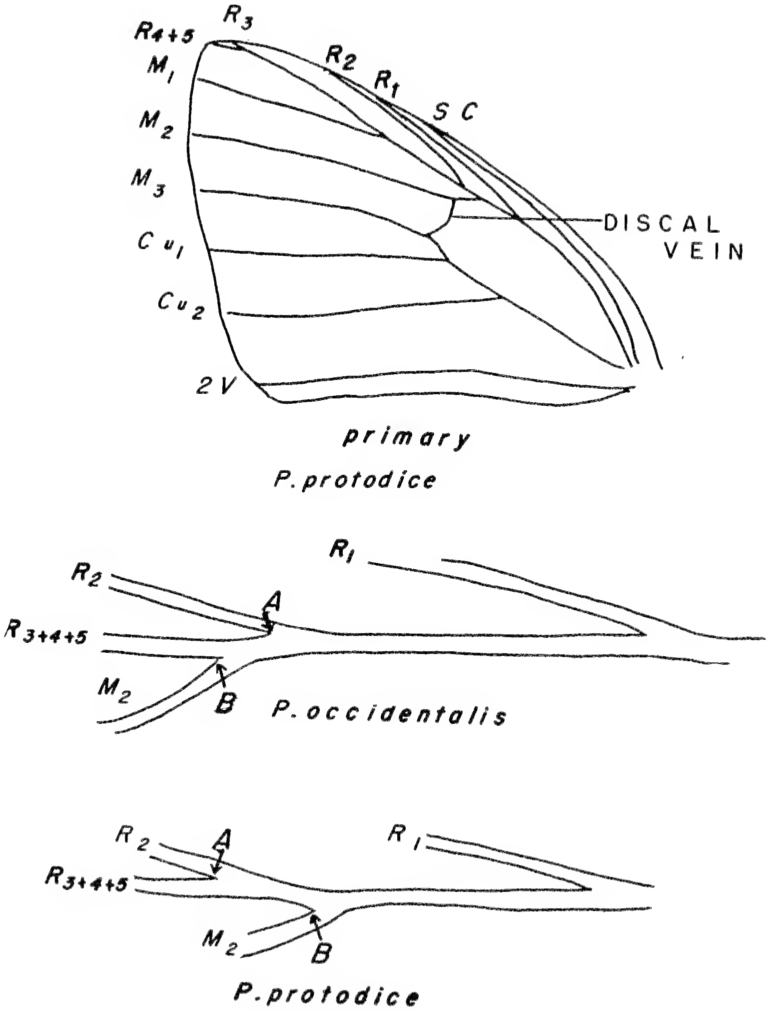


Fig. 10. Venations showing the left fore wing and the differences in the location of point "A" in respect to point "B" between *P. protodice* and *P. occidentalis*

4. Male genitalia: (1) Uncus and juxta (fig. 7, table 3): No difference is found between *P. protodice* and *P. occidentalis* in respect to these two characters.

(2) Saccus (fig. 8, 12, table 4): The length of saccus is statistically different between *P. protodice* and *P. occidentalis.* The mean ratio (length of fore wing over length of saccus) for *P. protodice* is 2.68; for *P. occidentalis* it is 3.45. The probability is less than 0.001 that the difference may be due to chance when the degrees of freedom is 83 as shown by the *t* test.

The scatter diagram (fig. 12), which shows each individual ratio of these two species against its own wing length, shows that overlap is present in this character despite the difference in mean ratio. This may be due to the variation in wing size caused by geographical and climatical difference. In cooler areas, the butterfly is usually smaller and in warmer areas, larger. If some specimens of *P. occidentalis* are from the extreme southern locations and some specimens of *P. protodice* from the extreme north, the gap in ratio between these two populations is reduced, and overlap occurs. This point is demonstrated by fig. 14. If the specimens of *P. protodice* and *P. occidentalis* are from the same locality and collected at the same time, these two species are usually separable.

(3) Penis (fig. 8): The penis of *P. protodice* and *P. occidentalis* is strongly curved at the basal part and this difference makes these two species easily distinguishable from other species in the genus *Pieris.* The penis size in P. *protodice* is smaller than in *P. occidentalis.*

5. Signum bursa (fig. 8, table 6): The signum bursa of *P. protodice* and *P. occidentalis* is similar to *P. sisymbrii,* but with smaller teeth and less chitinization. The length of signum bursa in *P. protodice* is shorter than the one in *P. occidentalis.* The mean ratio (length of fore wing over length of signum bursa) for *P. protodice* is 3.18 and for *P. occidentalis* is 4.03. The probability that this difference is due to chance alone is less than 0.001 when the degrees of freedom is 60 by the *t* test. The scatter diagram (fig. 13) for individual ratios shows that there is no overlap present between these two species with respect to this character.

The mean ratio of each population at a given locality for *P. protodice* and *P. occidentalis* is also plotted on a diagram (fig. 14) which shows that the ratios of the specimens from northern localities such as Alaska are larger than the ratios of the specimens from southern localities. The differences in ratios for the specimens from various southern localities are not significant. This is porbably due to the closeness in distance between the localities and to similarities in environment. This diagram illustrates however that the ratio is not everywhere unchanged. The ratio gradually increases in the more northern

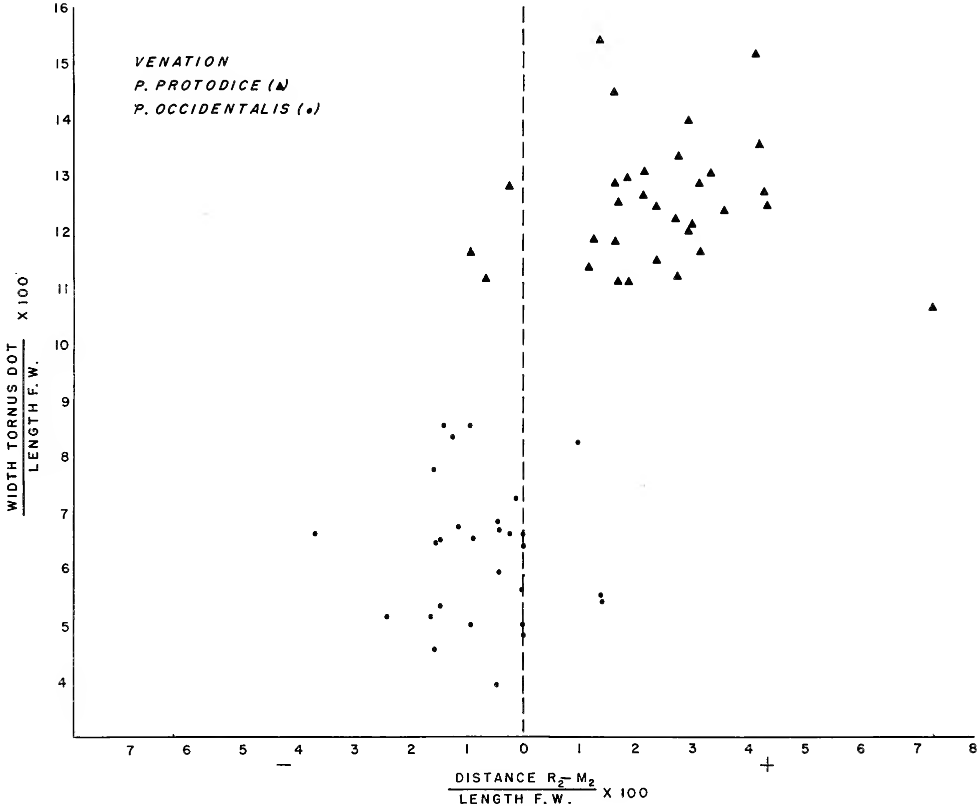


Fig. 11. The measurements between point "A" and point "B" (see fig. 10) plotted against the ratios obtained from the width of the tornus dot to the length of the fore wing

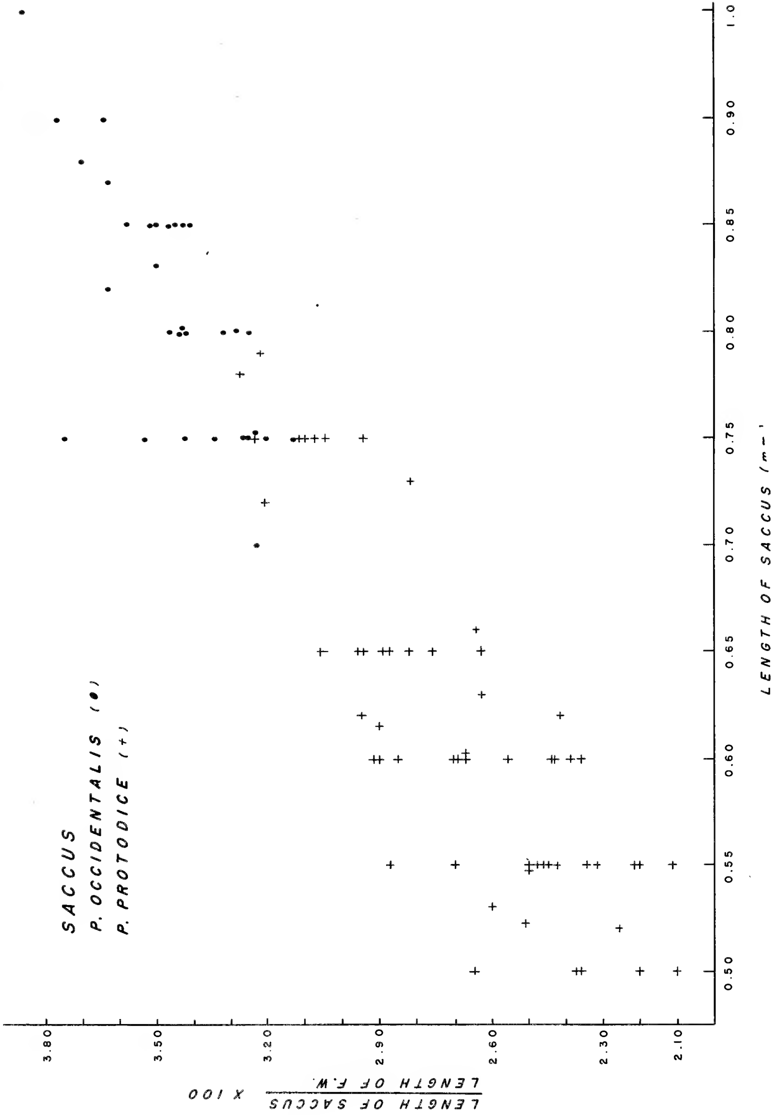


Fig. 12. Scatter diagram showing the individual ratio of saccus length to the length of fore wing plotted against the individual saccus length in *P. protodice* and *P. occidentalis*

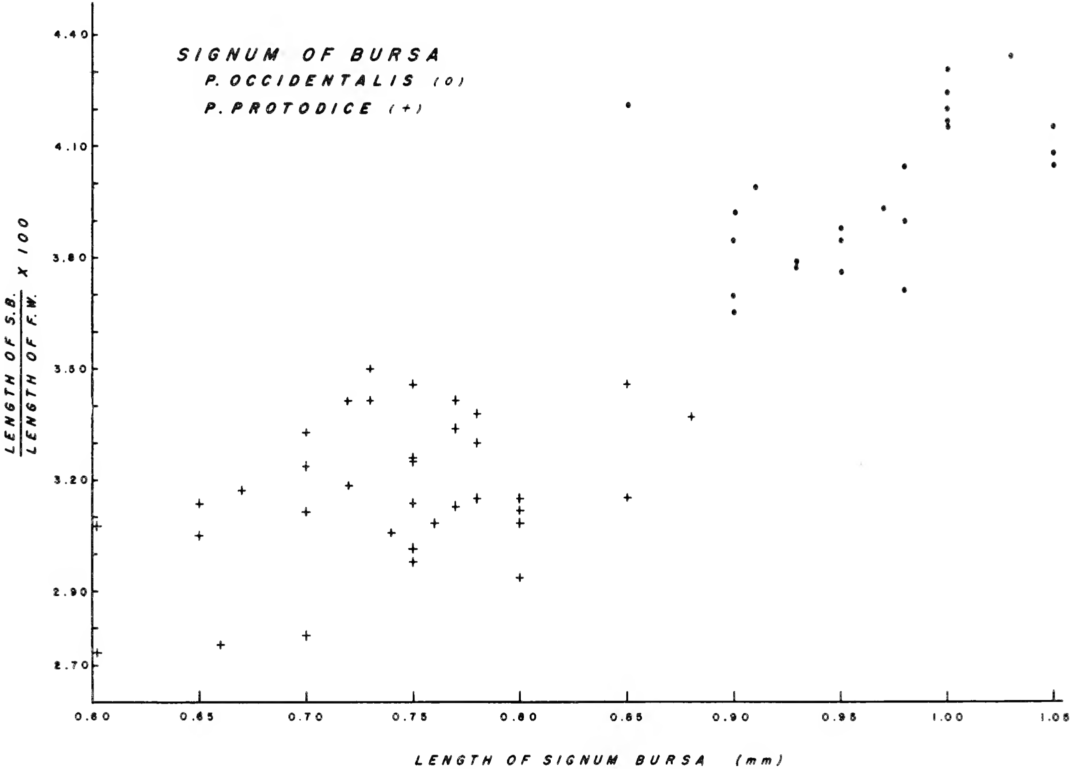


Fig. 13. Scatter diagram showing the individual ratio of the length of signum bursa to the length of fore wing plotted against the individual length of signum bursa in *P. protodice* and *P. occidentalis*

Fig. 14 Scatter diagram showing the mean ratio of the length of signum bursa to the length of fore wing in each locality plotted against the mean length of signum bursa

localities. The ratios of two species may overlap at different localities though they do not do so at the same location.

The samples of *P. protodice* came from (*1*) Laguna Canyon, Orange Co. Calif. (11), (*2*) Moorpark, Ventura Co. Calif. (4), (*3*) Independence, Inyo Co. Calif. (2), (*4*) Big Pine, Inyo Co. Calif. (2), (*5*) Mammoth Lake, Mono Co. Calif. (1), (*6*) Mono Lake, Mono Co. Calif. (4), (*7*) Coleville, Mono Co. Calif. (5), (*8*) Gardnerville Douglas Co. Nevada (1), (*9*) Minden, Douglas Co. Nevada (1), and (*10*) Doyle, Lassen Co. Calif. (4). The samples of *P. occidentalis* came from (*1*) Long Valley, Mono Co. Calif. (1), (*2*) Mammoth Creek, Mono Co. Calif. (2), (*3*) Mono Lake, Mono Co. Calif. (2), (*4*) Coleville, Mono Co. Calif. (1), (*5*) Gardnerville, Douglas Co. Nevada (11), (*6*) Doyle, Lassen Co. Calif. (3), (*7*)Klamath Falls, Klamath Co. Oregon (4), (*8*) Satus Creek, Yakima Co. Washington (2), (*9*) British Columbia (1), and (*10*) Alaska (1).

GEOGRAPHICAL DISTRIBUTION OF *P. PROTODICE* AND *P. OCCIDENTALIS*

The geographical distribution of all species in the genus *Pieris* in North America except *P. protodice* and *P. occidentalis* is thoroughly investigated by Hovanitz (1962) (fig. 15). The data here presented are mostly gained by extensive search throughout the range of *P. protodice* and *P. occidentalis* in West Coast conducted by William Hovanitz in the summer of 1962. *P. protodice* is most abundant in the south, from the southern tip of Baja California northwards, gradually reducing its population and being replaced by *P. occidentalis.* The northern border of *P. protodice* is still unclear. At present this species is only in California and Nevada southwards. There is no record in Oregon and northward. *P. occidentalis* extends from central Alaska along the Rocky Mountains and the Cascade Mountains southwards into the Sierra Nevada Mountains (and the Rocky Mountains). The most southern locality known from our data at present in the Pacific coast area is Long Valley, Mono Co., Calif. It is very likely this species may be found at more southern places on high Sierra Nevada Mountains.

P. occidentalis and *P. protodice* overlap from Long Valley, Mono Co. Calif. northward to Doyle, Lassen Co., Calif. Further investigation may extend the overlap zone more northward even to Washington.

The habitats of these two species are very similar; both like sunny, open, grassland. *P. protodice* prefers warmer temperatures and semidesert conditions. It feeds on *Brassica nigra, Caulanthus* sp., *Lepidium densiflorum, Sisymbrium altissimum, Cleome lutea,* and *Thelypodium lasiophyllum. P. occidentalis* prefers relatively cool temperatures. It is usally found at places relatively moist, as near a lake, ditch or farm land. The food plants of *P. occidentalis* are nearly the same as for

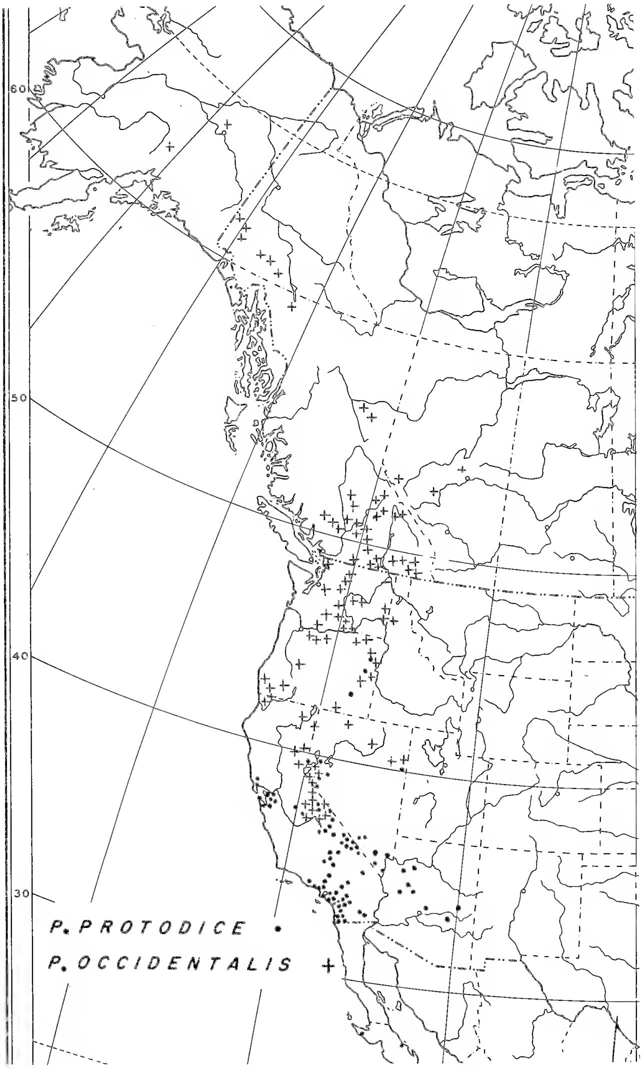


Fig. 15. Map showing the distribution of *P. protodice* and *P. occidentalis* in western North America

P. protodice except that *Cleome lutea* has not yet been recorded.

P. protodice and *P. occidentalis* are found flying together in the overlap zone. The males of these two species at a particular locality are usually separable by the marking and color on the wings, in which *P. protodice* is less darkly marked than *P. occidentalis.*

DISCUSSION AND CONCLUSIONS

The present data indicates some clear structural differences between the six species of *Pieris. P. rapae* and *P. napi* are similar in many characters, such as uncus, saccus, and the color and pattern on the wings, but they also can be distinguished by their differences in pattern and the signum bursa, juxta and androconial scales. *P. sisymbrii* and *P. beckeri* are similar in their uncus, saccus, androconial scales and signum bursa, but can usually be distinguished by wing pattern and venation. *P. protodice* and *P. occidentalis* can be distinguished by wing pattern, wing venation, structural differences in the length of saccus and signum bursa only in a statistical study. These two species also differ in their geographical distribution pattern, but overlap greatly in a sympatric area.

P. sisymbrii differs in many characters from *P. protodice,* such as wing venation, genital structures and others. The most significant difference is the presence of androconial scales, which are absent in *P. protodice* and *P. occidentalis.*

The results serve to show that *P. protodice* and *P. occidentalis* are sympatric species, an uncertainty which led Hovanitz (1962) to combine their geographical distributions into one map. The other species of the genus *Pieris* in Western North America are *P. rapae, P. napi. P. sisymbrii,* and *P. beckeri.* It is always possible that even these may be found at some time in the future to be subdivided into cryptic species by some characters not yet discovered.

ACKNOWLEDGEMENT

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LITERATURE CITED

ASAKAWA, F. 1961. Morphological observation on the androconia in the butterflies. (Ja) *New Ent.* 10(2): 7-15.

ABBOTT, W., L. S. DILLON, and R. R. SHRODE. 1960. Geographic variation in *Pieris protodice* Boisduval and Leconte (Lepidoptera: Pieridae). *Wasmann J. Biology* 18: 103-127.

BERNARDI, G. 1947. Revision de la classification des especes holarctiques des genus *Pieris* Schr. et Pontia Fabr. (Pep., Pieridae). *Miscellanea Entomologica,* Paris 44: 65-80.

HOVANITZ, W. 1962. The distribution of the species of the genus *Pieris* in North America. *J. Res. Lepid.* 1(1): 78-83.

————. 1963. The relation of *Pieris virginiensis* Edw. to *Pieris napi* L. Species formation in *Pieris? J. Res. Lepid.* 1(2): 124-134.

JACKSON, R. A. 1946. Causes for seasonal variation in the number of Lepidoptera. *Proc. & Trans. S. London Ent. & Nat. Hist. Soc.* 1945-46: 43-51.

KLOTS, A. B. 1931. A generic revision of the Pieridae (Lepidoptera) together with a study of the male genitalia. *Entomologica Americana* 7 (new series) (3): 139-204; (4): 205-243.

KLOTS, A. B. 1961. Family Pieridae. In *"How to know the butterflies"* edited by Ehrlich, P. R. and A. H. Ehrlich. Wm. C. Brown Co. Dubuque, Iowa.

MAERZ, A. and M. R. PAUL. 1930. A dictionary of color. 1st Ed. McGraw-Hill Book Co. New York.

MARIANI, M. 1937. Anatomia e fisiologia degli organi genitali femminili delle *Pieris* Schrk. (Lepidoptera, Pieridae). *Festschrift für Prof. Dr. Embrik Strand.* 3: 434-450.

McDUNNOUGH, J. 1939. Check list of the Lepidoptera of Canada and the United States of America. *Mem. So. Calif. Acad. Sci.* 11(1): 1-171.

McHENRY, P. 1962. The generic, specific and lower category names of the Nearctic Butterflies. Pat I. The genus Pieris. *J. Res. Lepid* 1(1): 63-71.

OKANO, M. 1951. Comparative morphology of the male genitalia of Japanese Pieridae. *Ann. Report Gakougei Fac. Iwate Univ.* 2: 38-46.

PETERSON, B. 1963. The genitalia of some colias species. *J. Res. Lepid.* 1(2): 135-156.

QUERCI, O. 1936. Notes on *Pontia protodice* Boisduval and Leconte (Lep: Pieridae). *Trans. Amer. Ent. Soc.* 62: 37-47.

TUXEN, S. L. (editor). 1956. Taxonomist's glossary of genitalia in insects. Ejnar Munksgaard, Copenhagen.

WARREN, B. C. S. 1961. The androconial scales and their bearing on the question of speciation in the genus *Pieris,* (Lepidoptera.) *Ent. Tidskr.* 82(3/4): 121-148.

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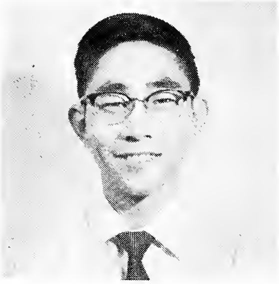

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GENETIC AND ENVIRONMENTAL VARIATION IN *PIERIS BRASSICAE*

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INTRODUCTION

THE PRINCIPAL FORM OF VARIATION in *Pieris brassicae* L. consists of either a reduction or expansion in the amount of black present. In certain local populations the variation is constant and marked enough to be designated as a race, such as *P. brassicae cheiranthi* in the Canary Islands. Marked variation in color, however, is exceedingly rare and, until now, only some half dozen specimens were known.

In 1950 a stock of *P. brassicae* originating from Cambridge was established at the Unit of Insect Physiology and has been continuously bred ever since. This stock has already been reported on (David & Gardiner 1951; David 1957). In 1959 another stock, originating from Oxford, was established as a separate culture and was also continuously brooded under the same conditions as the Cambridge stock.

Until 1960 the amount of variation noticed in the Cambridge stock was small, and confined to known variation in the black markings. This has already been briefly reported on (David & Gardiner 1961).

During the past three years, however, two color varieties have appeared, as well as the previously unknown albino form; known varieties also seem to have been more common, although this could well be due to more careful observation (fig. 1).

The opportunity was taken to determine the genetics of these varieties and also to examine the combination of two pairs of allelomorphs to produce a double recessive. It is believed that this is the first time such a cross has been done with a butterfly.

From time to time specimens considerably smaller than the normal size turn up in various species of butterflies. In the case of *P. brassicae* specimens of between 40-50 mm. wing span are referable to ab. *minor* Ksienschopolsky. According to Frohawk (1934) normal wild caught specimens vary from 63 mm. in the male to 76 mm. in the female. In the continuously brooded culture kept at the Unit of Insect Physiology the size is 55-63 mm. in the male and 54-65 mm. in the female (David & Gardiner 1961).

Occasional specimens of ab. *minor* were noted in the Cambridge stock. At times entire batches have been on the small side. Specimens bred from these were normal. It occurred to the author that ab. *minor* might be an effect of starvation rather than a genetic effect. This has been investigated as will be described.

DESCRIPTIVE

Pieris brassicae L. ab. _coerulea_ ab. nov.

The normal cream and green coloration on the underside of the wings is replaced by a pale blue color. On the upper side, the white areas of the wings have a pure white appearance and are rather thinly scaled; in normal specimens they are creamy white or off white in color.

Larvae and pupae normal. The majority of the adults of this variety fail to eclose properly. Some specimens may emerge with striped scales, especially on the hind wing, which gives them a translucent blue color, deeper in shade than normally formed *coerulea.*

Holotype ♂, Allotype ♀: Two specimens selected from the F_1 generation obtained by the pairing of two ab. *coerulea* which emerged from a continuous brooded culture kept in the Laboratory since 1950. In the author's collection.

Paratypes: Five pairs also selected from the F_1. Two pairs have been deposited in the Rothschild-Cockayne-Kettlewell collection at Tring, two pairs are in the author's colletion, and one pair in the collection of Mr. H. Douglas Bessemer.

Type locality: The original stock from which this aberration arose was collected in the vicinity of Cambridge, England, in 1950.

Synonyms. ab *pallida.* Graham-Smith & Graham-Smith
ab. *anthrax.* Graham-Smith & Graham-Smith

Graham-Smith and Graham-Smith (1930) after describing *anthrax* state "Perhaps a specimen exhibited by Leeds (1909) with undersides of the hind wings a very distinct blue . . . are examples of this aberration."

Under *pallida* they state "A very marked example from Monk's Wood, Hunts., is figured by Frohawk (1914, pl. 3, fig. 20)."

The specimen figured by Frohawk (1914) is stated by him to have been taken by Mr. H. A. Leeds in Monk's Wood in 1906 and there can be little doubt that it was this specimen that was exhibited by Leeds at the Annual Exhibition of the South London Entomological and Natural History Society in 1909.

Mr. A. L. Goodson has compared the present variety with the *anthrax* and *pallida* in the R.-C.-K. collection at Tring and it in no way resembles either of them nor, in the author's opinion, does it bear any resemblance to the illustrations of *anthrax* and *pallida* in the paper by Graham-Smith and Graham-Smith (1930).

Mr. H. Douglas Bessemer, who has the original Leeds specimen in his collection, very kindly invited the author to visit him and examine it. There is no doubt that it is the same as the present variety and was wrongly identified by Graham-Smith and Graham-Smith.

Pieris brassicae L. ab. *jauni* ab. nov.

In May 1961 it was noticed that the underside of some butterflies being reared in the Laboratory was different in color to normal specimens, being a pale straw color compared to the normal greenish-yellow. The difference is more striking in freshly emerged living specimens than in dead set ones. The larvae are normal but the prepupae and pupae are a golden-yellow without any trace of the normal green. The pupae are also without the normal black speckling. Unlike some other color varieties the butterflies eclose normally.

Holotype ♂, Allotype ♀: Two specimens selected from the culture in May 1961. In the author's collection.

Paratypes: Two pairs similarly selected. In the author's collection.

Type locality: The original stock from which this aberration arose was collected at Oxford, England, in August 1959.

Pieris brassicae ab. *albinensis* Gardiner

This variety has already been described (Gardiner 1962). It is a simple recessive and is noted here since it was used with *coerulea* to obtain the double recessive.

EXPERIMENTAL

Most insects were bred according to methods already described (David & Gardiner 1952; David 1957) with the exception that when a single pair of butterflies was being paired a small nylon covered cage measuring 1 x 1 x 1½ feet was used instead of a large cage. A percentage of the larvae were also reared in 2 lb. jam jars at the rate of about 20 per jar. This enabled an accurate check to be kept on mortality. This was generally done with the F_1 broods, the larger numbers of the F_2 being reared in cages. No difficulties were encountered with either pairing or oviposition nor, apart from the F_1 of ab. *jauni,* was there any appreciable mortality of the larvae. Due to limitations of time, space and food, it was only possible to rear a small percentage of the total ova obtained. Since a single fertile *brassicae* was found to lay over 500 ova, the potential F_2 was some 125,000 individuals, an impossible number to rear.

ab. *coerulea*

In November 1962 a female emerged in the Cambridge stock. She was paired to a normal male from the same batch and the resulting ova were reared to give an F_1 of normal insects. These were crossed and a selection of the resultant ova reared.

The F_2 produced 347 normal and 116 *coerulea* butterflies, a ratio of 2.99 : 1, a very good agreement with the expected 3 : 1 ratio for a simple recessive. The majority of the *coerulea* however failed to eclose normally and remained stuck by the wing tips to the pupal case.

While this brood was being reared, further *coerulea* emerged from a batch of the stock Cambridge butterflies. Two pairings were obtained and all the F_1 and subsequent generations were *coerulea.* This aberration is therefore a recessive. It's extreme rarity under natural conditions can be explained by the difficulty the butterflies have in getting free of the pupal case.

The blue color is due to an absence of the normal yellow pigments and is present normally in the wing-membrane. This can be shown faintly by rubbing off the scales of a normal *brassicae* between finger and thumb. A very similar appearance to *coerulea* can also be produced by immersing a normal *brassicae* in the bleaching agent sold, under the name of 'Parazone.' The question of the chemistry of this and other color forms of *brassicae* is at present under investigation by a colleague of the present author and will be dealt with in a later paper.

The failure to eclose is more marked in the males than the females. In the first two generations only about two per cent of the specimens could be described as immaculate. About 50 per cent fail to clear the pupal case and are stuck by one or both fore wing tips; others get clear but one or more wings fail to expand. In many instances there is extensive stripping of the scales, especially of the hind wing, which then has a deep blue translucent appearance.

After several generations the percentage of normal eclosions rises to about 80 per cent. This is similar to the trend that occurred in *albinensis* (Gardiner 1962). Since 1961 *albinensis* has been passed through a further ten or twelve generations and the percentage failing to eclose normally is now negligible, and there seems little doubt that *coerulea* will eventually reach this stage.

While failure to eclose is a semi-lethal factor linked, initially, with *coerulea* it is also partially controlled by the temperature at which eclosion takes place. Two experiments were done on this, using the F_2 generation of the pure line in the first and *albinensis* in the second.

A cage of *coerulea* pupae was kept at 20°C. until 12 normal (5.7%) and 198 crippled specimens had emerged. The remaining pupae were than transferred to 12.5°C. and at this temperature 38 normal (27.0%) and 103 crippled specimens emerged.

In the second experiment *albinensis* was used, half the pupae being at 25°C. and half at 12.5°. At 25°C. 15 normal (30.0%) and 35 crippled emerged while at 12.5°C. 28 normal (58.4%) and 20 crippled emerged.

These results clearly show that failure to eclose is more marked at higher temperatures.

ab *jauni*

These were noted in May 1961 in a stock obtained from Oxford which had been bred for a number of generations in the Laboratory.

A pair of these butterflies was mated and 100 of the ova reared. In this generation the mortality, mainly granulosis virus, was 76%. The 14 adults obtained were all of the variety. These were paired at random and 100 F_2 ova reared to produce 97 butterflies, also of the variety.

After the F_1 males had paired with their sisters they were paired with normal females and a percentage of the ova laid were reared to produce all normal butterflies. These were mated at random to produce the F_2 of which a percentage of the total ova laid were reared, with little mortality. This generation produced 100 normal and 34 ab *jauni* butterflies. This is a 3 : 1 ratio.

This variety seems to be due to the lack of the normal greenish colored pigment. It segregates as a simple recessive and breeds true. It is of interest as being one of the few known instances in the butterflies in which a single gene manifests its effect not only in the adult but also in the earlier stages.

ab *minor*

About 200 final instar larvae, which had been kept well supplied with food during their earlier stages, were allowed to feed normally for 3 days and were then starved. About half died, the remainder wandered around their cage and eventually pupated. Normally, at 20°C, the final instar larvae feeds for 5 days before pupation (David & Gardiner, 1962).

The majority of the pupae produced butterflies, all ab *minor*, the smallest specimens having a wing span of 37 mm. male, 38 mm. female.

As a control siblings to the starved larvae were kept and allowed to feed normally and pupate when ready. These all produced normal sized butterflies.

Eggs obtained by the pairing of several of these *minor* were reared and an adequate supply of food was given throughout their life. Normal size specimens were produced.

It is evident from this result that ab *minor* can be produced by a condition of the external environment, starvation, on the larvae. Nevertheless the size of *brassicae* is, at least in some instances, genetically controlled. This will be dealt with more fully in the discussion.

ab *nigroviridescens*

About a hundred prepupae of the Cambridge stock were put in a desicator containing water to give 100% R.H. and kept at 20°C. One reasonable specimen of *nigroviridescens* Rocci emerged and two partially crippled adults intermediate between normal and *nigroviridescens*.

No breeding was done from these nor have any similar specimens ever been noted in the Cambridge stock. It is considered probable, however, that the *nigroviridescens* produced was a result of the saturated humidity of the environment.

ab *coerulea/albinensis*

The cross between *coerulea* and *albinensis* was performed both ways. One brood, *coerulea* ♂ X *albinensis* ♀ being reared by the author and the brood from the reciprocal cross being reared by Mr. C. F. Rivers of the Agricultural Research Council's Virus Research Unit.

In both crosses the butterflies used were from a pure bred line of the respective recessive.

In both crosses the several hundred individuals of the F_1 were all normal *brassicae.*

The F_2 of both crosses gave a ratio very close to 9 : 3 : 3 : 1 as is to be expected from the independent assortment of two pairs of allelomorphs. The back-cross was also performed to give a 1 : 1 : 1 : 1 ratio. The numbers involved are shown in Table 1.

These results show that linkage, which has not yet been shown to occur in butterflies (Ford 1946) is not present. Since *brassicae* has a relatively large number, 15, of chromosomes (Lorković, 1941) this is perhaps not very surprising. It would have been more interesting to have crossed *coerulea* with *jauni,* since both involve a change in the same pigment, unlike *albinensis* which is caused by an absence of black. Unfortunately by the time *coerulea* appeared the *jauni* form had been lost.

Cross	normal	coerulea	albinensis	albinensis coerulea
coerulea ♂ X albinensis ♀	921	295	304	97
albinensis ♂ X coerulea ♀	695	233	227	76
coerulea/albinensis X double heterozygote	97	96	92	95

Table 1. The numbers of butterflies reared in the F_2 of the double recessive cross and the F_1 of the back-cross.

As might be expected the majority of the double recessives failed to eclose normally but, like their respective grandparents, the percentage of normal eclosions rises with continual breeding.

Homeosis

This is extremely rare in butterflies. In *brassicae* specimens are known in which the fore wing black markings are duplicated on one side of the hind wing. According to Ford (1946) there is no definite evidence of its nature in butterflies but it has been shown to be genetic in *Drosophila.*

During the course of hybridising Cambridge stock *brassicae* with race *cheiranthi* from the Canary Islands, three homeotic specimens turned up in one brood of some 300 individuals, all the progeny of one pairing.

The male parent was an F_3 from a back-cross of an F_1 *brassicae/cheiranthi* hybrid to *cheiranthi,* while the female was an *albinensis* extracted in the F_2 of an *albinensis* crossed to the F_1 *brassicae/cheiranthi* hybrid. The *cheiranthi* used for the back-cross and the F_1 *brassicae/cheiranthi* hybrids had the same father.

All the homeotics were male with the black markings on the fore wing underside partially replicated on the hind wing of one side only.

One male was mated to his sister and sib pairing was continued to the F_3, some 300 individuals being reared in each generation. No more homeotic specimens were produced.

This is of course a negative result, but it shows that homeosis is not caused by a single recessive allelomorph. The most likely explanation of its occurrence, in this instance, is an upset in the genetic compatability due to a slight variation between the parent genes.

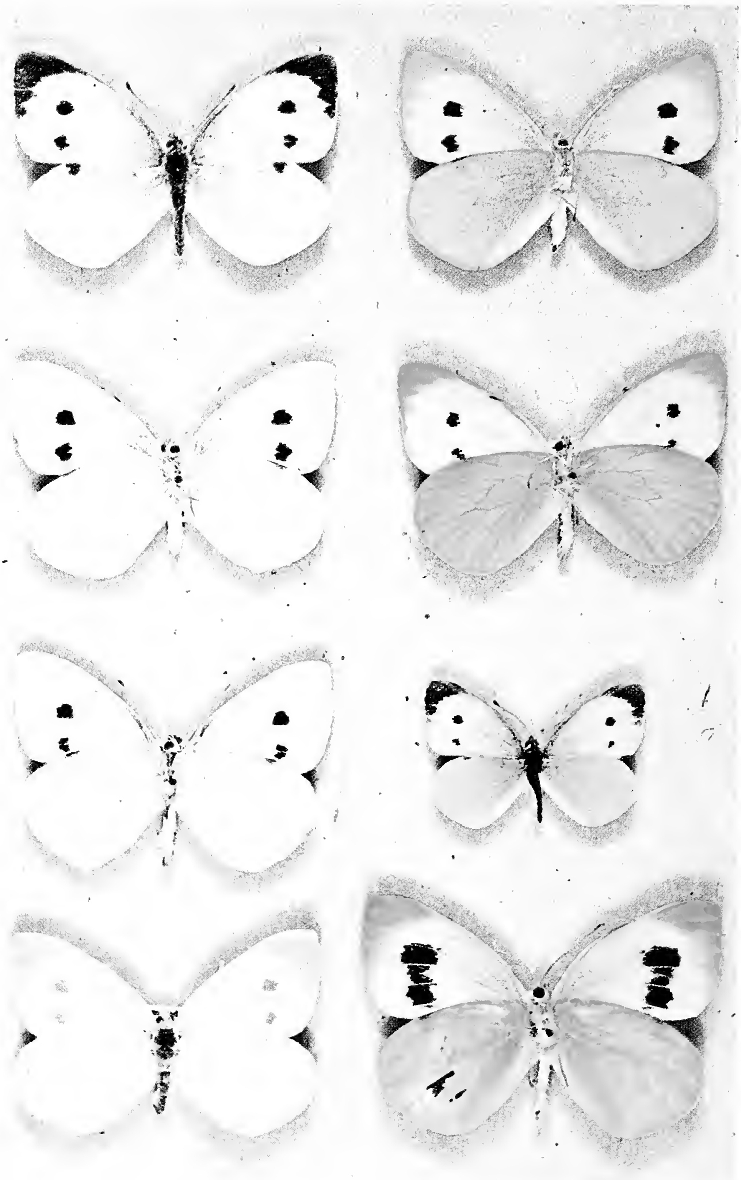
DISCUSSION

The continuously brooded stock of *brassicae* kept at the Unit of Insect Physiology is now thirteen years old and provides a unique opportunity for the study of variation in a butterfly. The numbers produced have varied from a few dozen to a thousand or more per week.

In addition to a number of known aberrations two new ones, *jauni* and *albinensis,* have been produced. A third, *coerulea,* was only previously known from two examples, both taken over fifty years ago.

As was to be expected, changes in the color of the wings, *coerulea* and *jauni,* are recessives. It is probable that the yellow form ab *flava* Kane is also recessive and its extreme rarity is, like *coerulea,* due to failure to eclose normally.

The failure to eclose of *coerulea* and *albinensis* appears to be due to the wings sticking to the pupal case. Indeed scales can be seen to be left behind in the pupal cases from which specimens have succeeded in getting free. It is however a disability which is overcome by con-



Left side, from top down. ab *coerulea* ♀ allotype (upperside). ♀ paratype (underside L). ♂ holotype (underside). ♀ *coerulea/albinensis* (upperside) L. Right side. Typical *brassicae* ♀ (underside). ab *jauni* ♂ holotype (underside). ab *minor* ♀ (upperside). ♂ *brassicae/cheiranthi* hybrid underside showing homeosis.

tinued breeding. This failure to eclose, however, again occurs if *albinensis,* from a normally emerging stock is crossed to typical *brassicae* and extracted again in the F_2. The effect is mechanical, more marked in the males than in the females and is affected by temperature. It might be that it is a genetic effect and it would be interesting to breed from the crippled specimens if this were possible. Since only perfect images are used for breeding, there is a very strong selection towards normality and only recessive genes producing crippling are rapidly eliminated for butterflies which cannot fly are unable to mate or oviposit.

Although *minor* can be produced by starvation the size of *brassicae* is also genetically controlled. From time to time small backward larvae are found in stocks of *brassicae.* Attempts to breed these have so far been unsuccessful. Usually the larvae die. Two or three have been brought to pupation, the pupae being comparable in size to *minor,* but no adults emerged.

In 1951 the wing span of the Cambridge stock *brassicae* was 53 mm. ♂ and 58 mm. ♀ (David & Gardiner, 1952). By 1960 however this had risen to 58.5 mm. in the male, while the females had decreased to 57.9 mm. (David & Gardiner, 1961).

The continuous inbreeding of the Cambridge stock has produced specimens with virtually no size difference between the sexes. This is smaller, especially in the female than the respective male and female sizes of 63 mm. and 76 mm. given by Frohawk (1934). It would appear that Frohawk had some unusually large female specimens before him. The author now believes that this figure may be a misprint in Frohawk's book. A 76 mm. *brassicae* would be a giant specimen. Wild specimens caught in 1943 from the author's collection being 58 mm. and 63 mm, while F_1 bred examples from a freshly caught wild female in 1957 are 58 mm. in both sexes.

The Cambridge stock is therefore not significantly different in size to some wild populations, but both it and wild populations vary in size over a period of years.

In *P. brassicae* race *cheiranthi* the males are 60-65 mm. and the females 65-70 mm. (12 examples measured), but the wings are also broader so that the butterfly looks even larger. If these are crossed to Cambridge stock *brassicae* the F_1 insects are intermediate in size and in the F_2 a range of sizes are produced. Size in this instance is clearly under genetic control.

The Cambridge stock *brassicae* are on the whole lighter and with less black than wild populations. The varieties that have turned up, *reducta* Fritsch, *colliurensis* Gelin and intermediates, are all those with a reduction of black.

The author has in his collection a female series from heavily marked with a trace of *fasciata* Kiefer to extreme *colliurensis,* in which the remaining spot is very feint.

The evidence from this and also from hybrid crosses to *cheiranthi* (which will be dealt with fully in a subsequent paper) clearly shows that a multifactorial effect is involved in the degree of black on the wings.

SUMMARY

Two new varieties of *Pieris brassicae* L., *coerulea* and *jauni* are named and shown to be recessive in character.

The failure to eclose in early broods of *coerulea* and *albinensis* is shown to be partly influenced by temperature.

The double recessive *coerulea/albinensis* has been reared and the two allelomorphs concerned shown not to be linked.

Ab. *nigroviridescens* is considered to be probably produced by saturated humidity.

The small form, *minor,* can be produced by starvation. Nevertheless size in *brassicae* is also genetically controlled.

The size of *brassicae,* both bred and wild, shows variation over a period of years. It is also believed that Frohawk's figure of 76 mm. for the female wing span is a misprint.

Homeosis is shown not to be due to a simple recessive gene.

The Cambridge stock of *brassicae* shows a tendency for reduction in the amount of black on the wings. The evidence is that this is multifactorial.

REFERENCES

DAVID, W.A.L. 1957. Breeding *Pieris brassicae* L. and *Apanteles glomeratus* L. as experimental insects. U. *Pflkrankh.* 64: 572-477.

DAVID, W. A. L., GARDINER, B.O.C. 1952. Laboratory breeding of *Pieris brassicae* L. and *Apantless glomeratus* L. *Proc. R. ent. Soc. Lond* (A) 27: 54-56.

——— 1961. The mating behaviour of *Pieris brassicae* (L.) in a laboratory culture. *Bull. ent. Res.* 52: 256-280.

——— 1962. Observations on the larvae and pupae of *Pieris brassicae* (L.) in a laboratory culture. *Bull. ent. Res.* 53: 417-436.

FORD, E. B. 1946. Butterflies. Collins, London.

FROHAWK, F. W. 1914. A Natural History of the British butterfies.

——— 1934. The complete book of British butterflies. Ward, Locke, London.

GARDINER, B.O.C. 1962. An albino form of *Pieris brassicae* Linnaeus (Lep., Pieridae). *Ent. Gaz.* 13: 97-100.

GRAHAM-SMITH, G. S., GRAHAM-SMITH, W. 1930. *Pieris brassicae,* L., with special reference to aberrations from Aberdeenshire. *Ent. Rec. & J. Var.* 42: 1-7.

LORKOVIC, Z. 1941. Die Chromosomenzahlen in der Spermatogenese de Tagfalter. *Chromosoma* 2: 1511-191.

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TYPE LOCALITIES OF THE MEGATHYMIDAE

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IT IS NOT POSSIBLE for a person to make a careful systematic or ecological study of any group of lepidoptera unless the type localities of all of the known species and subspecies are well known. In recent years this information has been carefully presented in the original descriptions, however some of our earlier authors were not as careful and we have to do considerable research in order to associate a present habitat with their findings.

In working with the Megathymidae I have found that there are several cases where no specific type locality was given or else the locality was entirely too general. With that in mind this paper presents a list of these localities (Table 1) with the hope that it will make it easier for future workers to have the type localities at hand while they are doing research on this particular group of lepidoptera.

REFERENCES

BARNES, WILLIAM, & JAMES H. McDUNNOUGH, 1912. A review of the Megathymidae. *Contrib. Nat. Hist. Lepid. No. Amer.* 1: 1-28, pps.

BASSETT, ANNA S., 1938. Some Georgia records of John Abbot, Naturalist. *Auk* 55: 244-254.

BELL, ERNEST L., 1938a. The Hesperioidea. *Bull. Cheyenne Mountain Mus.,* 1: 1-35.

——— 1938b. A new genus and five new species of Neotropical Hesperiidae. *Amer. Mus. Novitates,* no. 1013: 1-11, figs. 1-6.

BUTLER, ANDREW G., & HERBERT DRUCE, 1872. Descriptions of new genera and species of lepidoptera from Costa Rica. *Cistula Enet.* 1: 95-118.

DOW, ROBERT P., 1914. John Abbot of Georgia. *Journ. New York Ent. Soc.* 22: 65-72.

Thanks are expressed to the National Science Foundation for research grants making my work on the Megathymidae possible.

EDWARDS, W. H., 1882. Description of species of butterflies taken in Arizona by Jacob Doll, 1881. *Papilio* 2: 19-29.

FREEMAN, H. A., 1943. Notes on and redescriptions of *Megathymus yuccae* (Bdv. & LeC.) and its sub species. *Ent News* 54: 211-217.

——— 1950. Notes on *Megathymus,* with description of a new species. *Field & Lab.* 18: 144-146.

——— 1952a. Notes on *Megathymus yuccae* (Bdv. & LeC.), with description of a new subspecies. *Field & Lab.* 20: 29-33.

——— 1952b. Two new species of *Megathymus. Amer. Mus. Novitates* no. 1953: 1-9, figs. 1-13.

——— 1955. Four new species of *Megathymus. Amer. Mus. Novitates,* no. 1711: 1-20, figs. 1-34.

——— 1958. A revision of the genera of the Megathymidae, with the description of three new genera. *Lepid. News.* 12: 81-92.

——— 1960. Notes on *Agathymus* in Texas, and the description of a new species from Mexico (Megathymidae). *Journ. Lepid. Soc.* 14: 58-62.

——— 1962. A new species of *Agathymus* from Texas. *Amer. Mus. Novitates,* no. 2097, 1-7, figs. 1-6.

HARBISON, CHARLES F., 1957. A new species of *Megathymus* from Baja California, Mexico. *Trans. San Diego Soc. Nat. Hist.* 12: 231-262, pls. 18-21.

HOLLAND, W. J., 1930. New species and varieties of North American butterflies. *Ann. Carnegie Mus.* 19: 155-160.

MURRAY-AARON, E., 1942. Herbert Morrison in Mexico. *Ent. News* 53: 142-143.

POLING, OTHO C., 1902. A new *Megathymus* from Arizona. *Ent. News* 13: 97-98, 1 pl.

RILEY, CHAS. V., 1876. Notes on the Yucca Borer, *Megathymus yuccae* (Bdv. & LeC.). *Trans. Acad. Sci. St. Louis* 3: 323-343, figs. 25-31.

——— 1877. Additional notes on *Megathymus yuccae. Trans. Acad. Sci. St. Louis* 3: 566-568.

SKINNER, HENRY, 1895. A new *AEgiale* (*Megathymus*). *Can. Ent.* 27: 179.

——— 1911. The larger Boreal American Hesperiidae including *Eudamus, Erycides, Pyrrhopyge* and *Megathymus. Trans. Amer. Ent. Soc.* 37: 169-209-, pl. 10.

STALLINGS, DON B., & J. R. TURNER, 1954. Notes on *Megathymus neumoegeni,* with description of a new species. *Lepid. News* 8: 77-87.

——— 1956a. Description of a new subspecies of the *Megathymus yuccae* (Bdv. & LeC.) complex. *Bull. So. Calif. Acad. Sci.* 55: 150-152, pl. 3.

——— 1956b. Notes on *Megathymus ursus,* with description of a related new species. *Lepid. News* 10: 1-8.

——— 1957. Four new species of *Megathymus. Ent. News* 68: 1-17.

——— 1958. A review of the Megathymidae of Mexico, with a synopsis of the classification of the family. *Lepid News* 11: 113-137, 8 pls.

——— 1960. A new species of *Agathymus* and a new subspecies of *Megathymus. Ent. News* 71: 109-115.

——— 1961. A new subspecies of *Agathymus mariae* from Mexico. *Journ. Lepid Soc.* 15: 19-22.

STRECKER, HERMAN, 1871. Description of a new species of *AEgiale* and notes on some other species of North American Lepidoptera. *Proc. Acad. Nat. Sci. Philadelphia* 1876: 148-153.

Skipper from Arizona. *Bull. So. Calif. Acad. Sci.* 53: 75-87, pl. 2.

TINKHAM, ERNEST R., 1954. The biology and description of a new Giant Skipper from Arizona. *Bull. So. Calif. Acad. Sci.* 53: GE-RG, *pl.* B. ....

TABLE 1

AEGIALE Felder

1. hesperiaris (Walker), vic. Mexico City, D. F., Mexico

AGATHYMUS Freeman

1. neumoegeni (Edwards), approx. 9 mi. S. Prescott, Ariz.
2. carlsbadensis (Stallings and Turner), Guadeloupe Mtns., Carlsbad Cavern National Park, N. M., on the Mesa at the head of Yucca Canyon, elevation 5470 feet, pH 7.9.
3. florenceae (Stallings and Turner). Davis Mtns., Scenic Drive, Texas, elev. 6200 ft., pH 5.9.
4. judithae (Stallings and Turner), Hueco Mtns., approx. 8 mi. E. Hueco, Texas, el. 5300 ft., pH 7.3.
5. diabloensis Freeman, Diablo Mtns., approx. 5 mi. W. Victoria Canyon, Texas, el. 5700 ft., pH 7.4.
6. mcalpinei (Freeman), 5.1 mi. N. Marathon, Texas, flats near foothills of Glass Mtns., elev. 4300 ft., pH 7.4.
7. chisoensis (Freeman), Chisos Basin, Texas, elev. 5400ft. pH 5.2.
8. juliae (Stallings and Turner), north of Zarca, Durango, Mexico, on highway 45 at Klm. 1317, elev. 6300 ft.
9. hoffmanni (Freeman), Valle de Mexico, Mexico.
10. evansi (Freeman), Ramsey Canyon, Arizona.
11. belli (Freeman), La Bequilla, Durango, Mexico.
12. aryxna (Dyar), The accepted type of this species is figured in the Biologia Cent. Amer. Lep. Het. III, pl. 69, fig. 4. It represents very well the maculation of the specimens found in the Santa Rita Mtns., Santa Catalina Mtns., on down towards Nogales, Ariz. Murray-Aaron (Ent. News 53: 143) states that he and Morrison collected around Nogales and on down to Hermosillo, Sonora, Mexico. The specimen is labelled N. Sonora, Mexico, Morrison, indicating that the specimen was collected in the general vicinity south of Nogales, Sonora, since Hermosillo is in the central part of the state. We do not know whether the specimen in question was collected on that trip or another that Morrison made by himself; the dates of their collecting trip has been lost. There is some question as to the status of drucei, which was named from fig. 3 in the Biologia by Skinner. One specimen from the Chiricahua Mtns. and one from Ramsey Canyon, Huachuca Mtns., Ariz. are identical with the figure of drucei. Specimens from those two areas deviate slightly from those from the Santa Rita and Santa Catalina Mtns. I would like to indicate the type locality of aryxna as being the western slopes of the Patagonia Mtns., S. E. of Nogales, Sonora, Mexico.
13. baueri (Stallings and Turner), Verde Hot Springs, Yavapai county, Arizona, elev. 4000 ft.
14. freemani Stallings and Turner, nr. Bagdad, Yavapai county, Arizona, elev. 5000 ft.

15. fieldi Freeman, Guadalajara, Mexico, Jalisco Highway, 15, klm. 724, elev. 4400 ft.
16. mariae (Barnes and Benjamin), Franklin Mtns., El Paso, Texas, approx. elev. 3900 ft., pH 8.4.
17. micheneri Stallings, Turner and Stallings, approx. 15 mi. S. Allende, Coahuila, Mexico, elev. 1300 ft., pH 7.0.
18. stephensi (Skinner), Mason Valley (La Puerta), San Diego county, Calif.
19. comstocki (Harbison), 2 mi. N.E. San Simon, Baja Calif., Mex.
20. remingtoni (Stallings and Turner), mountains S. of Jacala, Hidalgo, Mexico, on highway 85, klm. 250, elev. 6000 ft.
21. estelleae (Stallings and Turner), plains 56 mi. S.E. Reynosa, Mexico, near General Bravo, Nuevo Leon, elev. 400 ft. pH 7.3.
22. polingi (Skinner), Baboquivari Mtns., Pima county, Arizona
23. alliae (Stallings and Turner), 15 mi. W. Cameron, Arizona, along canyon of Little Colorado R., elev. 5000 ft.
24. indecisa (Butler and Druce), Costa Rica
25. rethon (Dyar), Sierra de Guerrero, Mexico

TURNERINA Freeman

1. mejicanus (Bell), Guanacevi, Durango, Mexico
2. hazelae (Stallings and Turner), near Chilpancingo, Guerrero, Mexico, highway 95, klm. 235, elev. 2300 ft.

MEGATHYMUS Scudder

1. yuccae (Boisduval and LeConte)
   a. yuccae (Boisduval and LeConte), Aiken county, South Carolina is here designated type locality as it is the nearest place to Abbot's home in Scriven county, Georgia where he is known to have collected, and where Yucca grows. Yucca smalliana and Y. flaccida.
   b. buchholzi Freeman, Jupiter, Florida. Yucca gloriosa
   c. stallingsi Freeman, Caldwell, Kansas. pH 6.1, Yucca arkansana.
   d. wilsonorum Stallings and Turner, Victoria, Tamalipas, Mexico. Yucca treculeana and Y. carnerosana.
   e. coloradensis Riley, vicinity of Colorado Springs, Colo. Yucca glauca.
   f. navajo Skinner, Ft. Wingate, Zuni Mtns., New Mexico. Yucca baccata.
   g. arizonae Tinkham, Mountain View, Pima county, Arizona. Yucca elata and Y. Thornberi.
   h. martini Stallings and Turner, Little Rock, Los Angeles county, Calif. Yucca brevifolia.
   i. browni Stallings and Turner, Salina, Utah. Yucca harrimaniae.
2. cofaqui (Strecker), The allotype was collected at Boca Grande, Florida which is here designated as the type locality. The exact locality of origin of the holotype is believed to

be somewhere in northern Florida near Georgia, collected by Morrison. Yucca aloifolia.

3. harrisi Freeman, Stone Mountain, Georgia. Yucca filamentosa.
4. streckeri (Skinner), Type locality here designated at Petrified Forest area, Arizona as photos of the type agrees best with mat erial from that area. Yucca Standleyi, probably.
5. texanus, Barnes and McDunnough
    a. texanus Barnes and McDunnough, 2♂♂, 2♀♀ collected by Jacob Boll at Dallas and San Antonio, Texas. To this collector Dallas was North Texas and San Antonio was South Texas. Kerrville, Texas is here designated at the type locality by reason of being the nearest known place to the above where texanus may be found. Yucca glauca, associate.

    b. leussleri Holland, Sand Hills near Valentine, Nebraska. Yucca glauca, probable.
6. ursus Poling, Santa Catalina Mtns., west of Redington, Pima county, Arizona, pH 6.1. Yucca Schottii.
7. violae Stallings and Turner, Carlsbad Cavern National Park, New Mexico, elev. 4700 ft., pH 7.5, Yucca Torreyi.
8. beulahae Stallings and Turner, near Ixmiquilpan, Hidalgo, Mexico, highway 85, klm. 176, elev, 5700 ft. Agave ? near Schottii.

STALLINGSIA Freeman

1. smithi (Druce), Amula, Guerrero, Mexico, approx. 3000 ft. Manfreda maculata, probable.
2. maculosus (Freeman), 2 mi. S. Kingville, Texas, elev. 100 ft., pH 7.0. Manfred maculosa.

BIOGRAPHICAL SKETCHES

FREEMAN, HUGH AVERY

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Born: Conway, Arkansas, Oct. 7, 1912

Married: 1939, 3 children

A. B. : Hendrix College, 1936

M. S. : Southern Methodist University, 1938

Teacher: High school Texas, 1938-48

Instructor: Biology, Southern Methodist University, 1948-51

Teacher: High school, Dallas, 1951

Interests: Started collecting lepidoptera in 1928

Began specializing in the hesperioidea in 1938. In 1942 started intensive study of the Megathymidae, which is still going on. Also interested in the study of metal marks and hairstreaks. Has published 44 articles on lepidoptera, most of which were upon the hesperioidea.

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THE DISTRIBUTION OF AN ENDEMIC BUTTERFLY LYCAENA HERMES

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ONE OF THE MOST INTERESTING of the endemic butterflies is *Lycaena hermes* (Edw.). Its known range extends fifty miles north of the Mexican border almost to Fallbrook, San Diego County, California, and south of the border almost one hundred miles to a point eighteen miles south of Santo Tomas, Baja, California, Mexico. In San Diego County it ranges inland to Pine alley, about forty miles from the Pacific Ocean.

Older literature and check-lists tended to overstate the range, i. e., California and Nevada, whereas all recently published information understates the range. In the light of present knowledge, the area occupied may be as large as the state of Connecticut. However, within this range its distribution is limited to pockets where the larval food plant occurs, so that the total area where the insect acually flies is probably not more than a fraction of one percent of the maximum area. Such limited distribution within a given range is not unique with endemics, being a common occurence among plants and animals.

Colonies of the Hermes Copper are closely confined to the vicinity of the host plant, *Rhamnus crocea* Nutt. Extensive collecting for over thirty years has failed to produce specimens beyond a short distance from the larval food plant. There is no observable tendency to migrate, to "hilltop," or otherwise to stray from these colonies, although there must be some inter-colony movement, probably by the males. Populations within the known range therefore depend on the distribution of the host plant, and there is certainly nothing novel about this among insects.

It is very difficult to analyse the complex factors which determine why a certain plant has been successful in a given spot, and why it has been able to out-compete all other plants for this particular place in the sun. In the case of *Rhamnus crocea*, the only consistent requirement seems to be a well drained soil of better than average depth, yet not deep enough to support trees. Such soils occur along canyon bottoms and on hillsides with a northern exposure; therefore, it is in these situations that *hemes* is generally found.

A notable point about *hermes* is that the host plant extends well beyond the range of this insect. *Rhamnus crocea,* in one form or another, extends to Mt. Diablo in the coastal ranges of California; along the foothills of the Sierra Nevada; on the Channel (Santa Barbara) Islands; and even into the Mojave Desert. Yet within its range in San Diego County, *hermes* tolerates greater climatic extremes than it would encounter in some of the contiguous coastal areas open to colonization, and in insular areas which might have been available at one time.

Freezing winters with snow are normal in Pine Valley at an elevation of 3800 feet, while summer temperatures of 105°F. are not uncommon in some of the foothill localities. To borrow an appropriate sentence from Hovanitz (1963), said of the distribution of *Argynnis idalia,* "The biological reasons for this restricted distributional range are not known." Biologists will appreciate how often this same conclusion must be drawn.

Nelson (1921) recognized a San Diegan Faunal District in northwestern Baja California which roughly corresponds with the area occupied by *hermes* in that Mexican state, but did not define the northern limits of this life zone in Southern California. A few species of plants appear to be restricted to about the area inhabited by *hermes,* but there is little to suggest, at least north of the border, that the area should be segregated from the Upper and Lower Sonoran life zones usually assigned to it. Nor has northwestern Baja California been shown to be an originator of new species, since the coastal fauna shows a close affinity to that of coastal Southern California, and the mountain fauna is simply an extension of the southern Sierran with the exception of a few instrusions (Rindge, 1948; Powell, 1958; Patterson and Powell, 1959; Truxal, 1960).

L. hermes is in a good state of balance in its environment. The season of emergence for the adults is very dependable, as is their presence every year in their select habitats. There is no wide fluctuation in numbers from year to year, although the current prolonged drought has reduced the populations in common with nearly all Lepidoptera. It would be difficult to believe that it is not autochthonous. Fossil evidence of insect distribution is so limited that it will probably never be known whether *hermes* ranged over a wider territory than now. It is an insect which seems to exhibit stability due to long occupation of its present habitat, yet it is difficult in the light of other biological evidence to view the present range as a refugium of some sort.

Concerning the genus *Lycaena,* Clench (1961) has stated, "A curious and possibly quite ancient genus, strongly developed in both the Palaearctic and the Nearctic regions, with a small handful of outliers — one in Guatemala, one in South Africa and several, most perplexing, in New Zealand." Perhaps this offers a clue, yet careful studies by Klots (1936) and Freeman (1936) have indicated that *hermes* has affinities with other North American members of the genus. Klots says, "Evidently *hermes* is, structurally at least, far closer to *gorgon* and *heteronea* than to its tailed Nearctic congeners." Freeman placed *hermes* in his *xanthoides* group on the basis of the genitalia, together with *dione, rubidus,* and *editha.*

Another interesting thing about *hermes* is the use of a species of Rhamnaceae as the larval host. Most congeners feed on Polygonaceae (*Eriogonum, Rumex, Polygonum*); some of Rosaceae (*Potentilla*); some on Saxifragaceae (*Ribes*); and some on Ericaceae (*Vaccinium*), but this use of a Rhamnaceous plant is believed to be unique for the genus (Davenport and Dethier, 1937). The commonest source of nectar for the imagines is *Eriogonum fasciculatum* Benth., one of the Polygonaceae, and this plant is almost invariably present. Could this in some ancient time have served as the larval host?

One might reason that the failure of *hermes* to invade large areas which appear to be open to colonization might be due to prior occupation of particular ecological niches by another species (competitive exclusion). The unusual food plant which is not used in other areas by any member of the genus would seem to rule this out. Or, if one wishes to consider *hermes* as the victim of some complex predator-parasite relationship which grew up around one of the congeners and favored it over *hermes, Lycaena* (*Tharsalea*) *arota* would be the most logical candidate. This species appears to be at the extreme southern limit of its range in San Diego County as evidenced by the few specimens ever taken. Since it feeds on *Ribes,* there is no direct competition, and the hypothesis becomes even more dubious from the fact that *hermes* lives sympatrically, or at least there are zones of contact along watercourses with *Lycaena helloides* and *L. xanthoides.* These should reasonably be expected to furnish whatever environmental pressures that *arota* might.

There is rather general belief that *hermes* is in a last ditch struggle for survival in San Diego County. This isn't true! Colonies have survived in areas that have been overrun with houses for many years; in areas being grazed by livestock; in areas being farmed (avocado orchards); and in areas which have been burned-over with some frequency. The map, Fig. 1, shows the wide distribution of known colonies which should ensure survival for the foreseeable future. This map should not be regarded as a complete record of distribution, since accessibility by road has been the main factor in locating colonies.

The insect has been beautifully illustrated in Comstock's "Butterflies of California" and his poetic description of the butterfly in nature is worth repeating. He says, "It is a fascinating little sprite as it darts about in the sunlight, or sports is showy colors while balanced on a tuft of wild buckwheat." As for the flight period, my earliest record is May 20, 1934, and the latest is July 20 at Alpine by George Field. Records from several hundred captures show peak flight about June 20, but the best time to collect males is about June 10, and for the females about June 20. Field captures show a large preponderance of males (85%), but this a probably a false indication of the actual sex ratio because of the more retiring habits of the females, and because of their tendency to flee directly from the place of disturbance so that they are quickly lost to sight. However, the percentage of females increases late in the flight period in common with many butterflies. The males practice territorialism, but are not very aggresive about it. They will patrol a section of flyway, or watch it from a vantage point, often on the host plant, but from any suitable perch. Both sexes visit flowers avidly, and the blossoms of *Eriogonum fasciculatum* supply the bulk of nectar.

The species is single-brooded and spends about two-thirds of its life in the egg stage. It aestivates and hibernates in the ovum, and the hatching of one egg was observed under field conditions on March 16. Mature larvae were recovered by beating the host plant on May 24 near Lyons Peak, where the season is delayed due to elevation. The egg, mature larva, and pupa have been illustrated by Comstock and Dammers (1935). Females oviposit readily in captivity, but unless the ova are kept on a living plant, they fail to hatch. The reason for this is not known, but may simply be dessication. Nothing in this life history sets *hermes* apart in any remarkable way from other members of the genus, although several are multivoltine.

As a generalization, most endemics are univoltine (consider the alpine relicts) but there are numerous exceptions. A good example is *Strymon avalona* Wright, another interesting endemic, which is confined to Santa Catalina Island off the southern California coast despite the fact that its food plant, *Hosackia* (*Lotus*) *argophylla* Gray, is more widespread. This insect has a succession of broods. The biological reasons for its restricted distributional range are not known, but are easier to deal with than is the case with *hermes,* since insular, alpine, acid bog, or other types of endemism offer the biologist some solace during the brief instant in evolutionary time that he is around to observe distribution.

Populations of the Hermes Copper in each colony are not great, probably numbering in the hundreds. Six sample counts taken at random from field notes for 1955 to 1959 show the capture of 69 specimens in 405 minutes, about 6 minutes per catch. Any day in which 50 specimens are taken can be regarded as exceptional. It is entirely fair to regard the insect as "not uncommon" as expressed by Clench (1961) — in fact, it falls comfortably into Clark's (1932) standard of "abundant" (where fifteen or more can be taken in an average day).

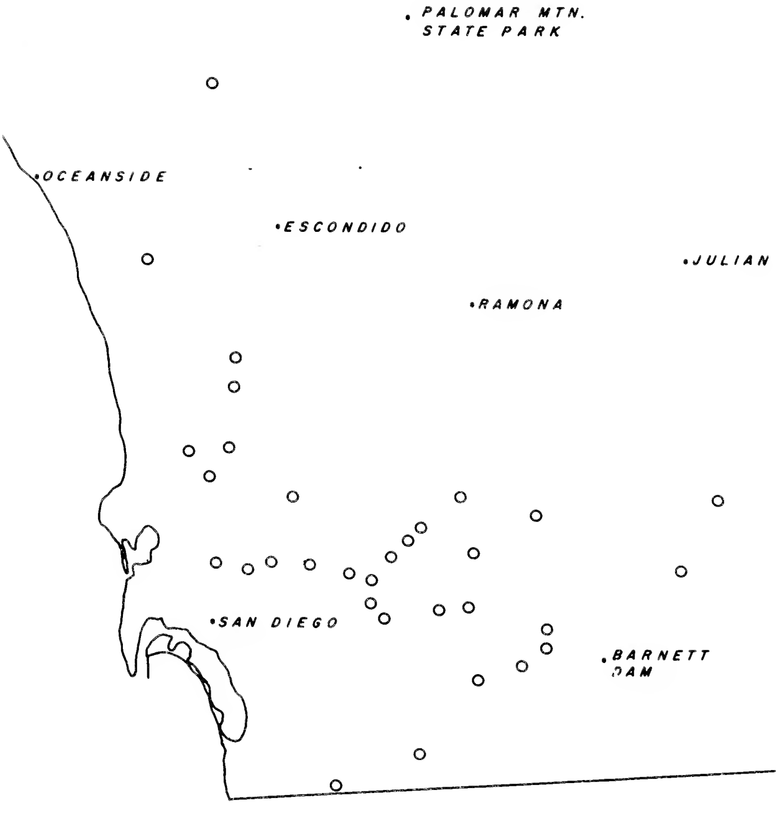

Fig. 1. Map showing the distribution of *Lycaena hermes* in San Diego county, California.

It has been stated previously that there must be some inter-colony movement. The basis for this is that differences among the populations are not readily observable, if indeed any exist. It must be admitted that no effort has been made to compare adequate series from different colonies to see if any segregation is evident. This would be an interesting study, but until it is made, it seems best to assume that gene flow throughout the entire range is adequate to prevent segregation.

If this is true, then the gene pool has some magnitude. Nevertheless, it seems likely that *hermes* is a conservative species, homozygous for many of its characters, variability being restricted by a close adaptation to a narrow environment. Barriers to spread appear to be intrinsic, that is, because of the inherited behavior patterns, the imagines "choose to remain" within very limited areas despite their ability to fly elsewhere, and presumably, to occupy larger territories (see Ehrlich, 1961). The chromosome number has not been published yet (N=24 for most species of the genus (Maeki and Remington, 1960) but this information is expected to be available soon.

Perhaps the distinctive facies and unusual food plant of *hermes* represent a genetic breakthrough which will result in time in a more widespread and successful species. Only time will tell whether the insect has retreated into a final refugium, the nature of which is not too evident, or whether it has the genetic resources eventually to expand its habitats.

That such expansion is possible has been demonstrated in a spectacular way by *Paratrytone melane melane* (Edw.) which was not recorded from San Diego County prior to 1941. Wright (1930) said, "Further collecting in wooded areas of the county may produce this species." Gunder (1930), in his now classic checklist of the butterflies of Los Angeles County wrote, "Never seemingly abundant in one locality, but may be had, several at a time each year." Rindge (1948) recorded this insect from southern Lower California, but this is now regarded as a distinct and undescribed sub-species (Mac Neill, 1962).

I first encountered this skipper on July 20, 1941, when two specimens were collected near El Cajon, California. Visits to the same spot July 23, 24, 25 and August 2 and 3 resulted in fifteen more specimens, and show my interest in what I thought was a once-in-a-lifetime chance. Other collectors also reported finding this species for the first time in San Diego that year. On October 5, 1941, a specimen was taken in the desert at Mason Valley, San Diego County. Since then, quite contrary to my expectations, this insect has become one of the very common skippers in my garden, flying from February to December. Powell (1958) records it from northwestern Baja, California in what I believe to be a further extension of this same population explosion.

This is an example of an insect which suddenly expanded into and occupied contiguous areas which are evidently well suited to it. It is not the purpose of this article to discuss this interesting phenomenon, but simply to point out that extensions of range are possible, and that it may be the privilege of the lepidopterist to see it happen in his own yard.

SUMMARY

The known range of *Lycaena hermes* (Edw.) extends from fifty miles north of the Mexican border in San Diego County to one hundred miles south of the border in Baja California. The insect occurs in colonies around the foodplant *Rhamnus crocea,* but has failed to invade other areas that appear suitable for reasons that are not known. The life history and field behavior are not unusual. The species is believed to be autochthonous and conservative, perhaps in a final refugium, but spread to other areas is possible, as has been demonstrated by *Paratrytone melane* (Edw.)

REFERENCES

BROWN, F. MARTIN 1962. Notes about the types of some species of butterflies described by William Henry Edwards. *Ent. News.* 73 (10): 265-268 (pg. 267).

CLARK, AUSTIN H. 1932. Butterflies of the District of Columbia. *Smithsonian Inst. U. S. Nat. Mus. Bull. 157, Wash. D. C.* (pg. 25).

CLENCH, HARRY K. 1961. In, *How to know the butterflies. Ehrlich and Ehrlich. Brown Co., Dubuque, Iowa* (pg. 22).

COMSTOCK, JOHN A. 1927. Butterflies of California. *Los Angeles, Calif.* (pg. 172 and Pl 51, Figs. 9-11).

COMSTOCK, JOHN A. and CHARLES M. DAMMERS 1935. Notes on the early stages of three butterflies and six moths from California. *Bull. So. Calif. Acad. Sci.* 34 (2); 120-141. (pp. 124-126).

DAVENPORT, D and V. G. DETHIER 1937. Bibliography of the described life histories of Rhopalocera of America north of Mexico 1889-1937. *Ent. Amer.* 17 (New series) (4); 155-196. (pp. 174-175).

DRAUDT, Dr. M. 1924. In Seitz, Macrolepidoptera of the world Vol. 5. American Rhopalocera. *Stuttgart, Germany.* (p. 812).

EDWARDS, WILLIAM HENRY 1870. Description of new species of Lepidoptera found within the United States. *Trans. Amer. Ent. Soc.* 3:21 original description of *Chrysophanus hermes.*)

EHRLICH, PAUL R. 1961. Instrinsic barriers to dispersal in checkerspot butterfly. *Science* 134, No. 3472: 108-109.

FREEMAN, T. N. 1936. Notes on the specific grouping of the genus Lycaena (Lepidoptera). *Can. Ent.* 68: 277-279.

GUNDER, J. D. 1930. Butterflies of Los Angeles County, California. *Bull. So. Calif. Acad. Sci.* 29 (2): 1-59 (on page 58).

HOLLAND, W. J. 1931. Butterfly Book (Revised ed.), *Doubleday and Co.. New York.* (on page 247).

HOVANITZ, WILLIAM 1963. Geographical distribution and variation of the genus Argynnis. *J. Res. Lepid.* 1 (2): 117-123 (on page 123).

JEPSON, WILLIS LINN 1925. Manual of the flowering plants of California. *Univ. of Calif. Press, Berkeley, Calif.* (on pages 614-615).

KLOTS, ALEXANDER B. 1936. The interrelationship of the species of the genus Lycaena Fabricius (Lepid., Lycaenidae), *Bull. Brooklyn Ent. Soc.* 31 (4): 154-171. (on page 164).

MacNEILL, C. DON 1962. A preliminary report of the Hesperiidae of Baja California. *Proc. Calif. Acad. Sci.*, 4th series, 30 (5): 91-116.

MAEKI, KODO and CHARLES L. REMINGTON 1960. Studies of the chromosomes of North American Rhopalocera, Part 3. *J. Lep. Soc.* 14 (2): 127-147.

MUNZ, PHILIP A. 1935. Manual of Southern California Botany, *Claremont Colleges, Claremont, Calif.* (on page 299).

NELSON, EDWARD W. 1921. Lower California and its natural resources. *Mem. Nat. Acad. Sci., Wash., D. C.* 16: 1-194. (on page 118).

PATTERSON, DONALD and JERRY A. POWELL 1959. Lepidoptera collecting in the Sierra San Pedro Martir, Baja California *J. Lep. Soc.* 13: 229-235.

POWELL, JERRY A. 1958. Additions to the knowledge of the butterfly fauna of Baja California Norte. *Lep. News* 12: 26-32.

RINDGE, FREDERICK H. 1948. Contributions toward a knowledge of the insect fauna of Lower California. No. 8 Lepidoptera; Rhopalocera. *Proc. Calif. Acad. Sci.*, 24: 289-311.

TILDEN, J. W. 1955. A revision of Tharsalea Scud. (s. str.) with description of a new subspecies (Lepid., Lyc.) *Bull. So. Calif. Acad. Sci.* 54 (2): 67-77.

TRUXALL, FRED S. 1960. Symposium: Biogeography of Baja California and adjacent seas. The entomofauna with special reference to its origins and affinities. *Syst. Zoo.* 9 (1-4): 165-170.

WRIGHT, WILLIAM GREENWOOD 1906. Butterflies of the West Coast. Second ed. *San Bernardino, Calif.*

WRIGHT, WILLIAM S. 1930. Annotated list of the butterflies of San Diego County, California. *Trans. San Diego Soc. Nat. Hist.* 6 (1): 1-40 (on pages 25, 26 and 40).

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CALLOPHRYS (LYCAENIDAE) FROM THE PACIFIC NORTHWEST

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OVER TWO YEARS AGO Mr. E. J. Newcomer, of Yakima, Washington, sent for examination and identification a series of *Callophrys* (*Callophrys*) taken near his home. He subsequently augmented this lot by other specimens, some of which were also taken locally while others were from farther afield in the state. More recently Mr. David L. Bauer, of Bijou, California, has sent for study additional specimens of this subgenus from both Washington and Oregon. The present paper is concerned chiefly with this assembled material. My best thanks are due both these gentlemen for the opportunity to study and report on this now sizable and instructive collection from a region whence before *Callophrys* had been all but unknown.

Callophrys is in several ways a very difficult subgenus. Problems of discriminating species occur in several regions, notably (but by no means exclusively) that under discussion in this paper. An even greater problem exists in the group as a whole: the correct association in polytypic species of the various named entities. Six species are currently recognized (Clench, 1961) in the subgenus (*dumetorum* Boisduval, *comstocki* Henne, *apama* Edwards, *affinis* Edwards, *viridis* Edwards and *sheridanii* Edwards), a number which is probably too large. On the other hand, we know that there must be at least two species for two occur sympatrically in many places: *sheridanii* and *apama* in Colorado; *sheridanii* and *affinis* in the Yellowstone area and near Brewster, Washington, *sheridanii* and *dumetorum* near Yakima, Washington; *viridis* and *dumetorum* in the San Francisco Bay area. But throughout their known ranges *apama* and *affinis* do not; nor do *affinis* and *dumetorum; apama* and *dumetorum; sheridanii* and *viridis;* or *affinis* and *viridis.*

It is tempting, and it may possibly be correct, to associate *sheridanii* and *viridis* as one species; *dumetorum, comstocki* (which is sympatric with no other), *apama* and *affinis* as another. This arrangement would satisfy nicely the conditions of sympatry, but it creates other problems; and besides, it is sheer speculation.

The traditional method of resolving such difficulties is by study of the male genitalia. Barnes and Benjamin (1923), the first authors to revise the group, did not make use of these structures nor did I in my revision of some years ago (Clench, 1944). The present occasion seemed an excellent opportunity to fill this long-standing desideratum. Preparations were accordingly made of all of the major and most of the minor entities, usually of several individuals each, and these preparations subjected to study. Preliminary examination failed to disclose any qualitative differences but did reveal the existence of considerable variation in relative lengths of different structures. A series of measurements was then made and these carefully and elaborately analyzed individually, paired in correlations, as ratios and by other more esoteric means, which it is pointless to describe as the results of the whole inquiry were thoroughly, discouragingly negative: the male genitalia of *Callophrys* s.s. show considerable individual variability but give no evidence whatever of variation useful for discriminating species. We are still where we were before.

Three species of *Callophrys* s.s. are now known from the Pacific Northwest, one here recorded for the first time. They epitomize the difficulties noted just above and it would be fatuous to presume that the results here given represent the final word on the solution of those difficulties. Decisions on relationships had to be made and I have tried to make them as accurately as possible.

Callophrys (*Callophrys*) *affinis washingtonia* Clench

Known from Alta Lake (type locality) and Brewster, Washington and from Summerland, Osoyoos, Penticton and Keremeos, British Columbia, the latter records in the Canadian National collection.

Size rather large (about as in *dumetorum perplexa* or *apama*); ground color above greyish with a distinct brownish tinge and in the female with some discal fulvous (occasionally in the male as well); underside apple green, a little less yellowish than in nominate *affinis* but decidely yellower than other members of the genus; on the forewing the green extends posteriorly to about CU_2, thus covering most of the wing; postmedian spot row completely absent or at most represented by faint, hardly visible traces. Base of fore wing costa below pale grey.

Callophrys (*Callophrys*) *dumetorum* Boisduval

When Mr. Newcomer sent his first series of *Callophrys* he wrote that he was interested to learn whether they represented one species or two, for some were immaculate below like *affinis,* others well marked, more or less as in *sheridanii.* Study showed that all of this variability actually was comprised in the one new subspecies of *sheridanii* described below. There was a surprise for us both, however, that came to light only when the specimens were being studied after spreading: a single fresh male of *dumetorum* from Satus Creek, 2000 ft., Yakima Co., Washington, taken in 16 May 1960. When I wrote to him about this discovery and described its differentiating characters, Mr. Newcomer checked through his material and found an additional specimen from the same locality taken 16 May 1959. Returning to the same area in the spring of 1961 he was able to take several additional specimens most of which he sent on for study: Kussdhi Creek, off Satus Creek, 2000 ft., Yakima Co., 24 May 1961 (1 female), and 2 June 1961 (1 male); Ski area near Satus Pass, 3700 ft., Klickitat Co., 2 June 1961 (1 female). In the material sent by Mr. Bauer were two males of this species from Shelton, Mason Co., Washington, 2 May 1958. All these specimens represent a considerable northward extension of the known range of *dumetorum* (cf. Clench, 1961: 210).

Three regional lists relating to the area under consideration in this paper have had to be ignored: Bowman (1919) on Alberta; Blackmore (1927) on British Columbia; and Leighton (1946) on Washington state. Each lists *dumetorum* and no other *Callophrys* s. s. (except Leighton, who also lists *dumetorum perplexa* and *sheridanii*), misdeterminations (partial or complete) rather typical of the trouble these butterflies have given to systematists.

Males [Description refers only to Washington material.] are uniform grey above with a very slight brownish cast. Females above are largely dark fulvous, shading to brownish fuscous in the basal third of both wings, along costa, termen and (more broadly) apex of fore wing as well as very narrowly along termen of hind wing. The fringe is greyish white (markedly duller than the fringe of either *affinis* or *dumetorum*), darker basad. On the under surface of both sexes the inner marginal grey of fore wing extends costad usually to M_3; the postmedian line of this wing is tolerably well developed from Cu_2 to M_1 or R_4, but often rather faint, occasionally even obsolete (though a trace of the dark basal part of the line usually persists). The postmedian line of the hind wing is highly variable in its expression, ranging from nearly complete (bars in all interspaces from Sc to inner margin) to nearly absent (slight whitish bars in Sc - Rs and Cu_1 - Cu_2); base of fore wing costa below usually fulvous. Size rather small: about the same as *s. sheridanii.*

The subspecies of *dumetorum* have never been worked out adequately. Even the range of the species is imperfectly known. For the present these Washington specimens seem best left under nominate *dumetorum* with which they agree far more closely than with *d. perplexa* Barnes and Benjamin from the lowlands of southern California.

Callophrys (*Callophrys*) *sheridanii neoperplexa* Barnes and Benjamin

The upper surfaces of both sexes are uniform grey with no tinge of brownish or fulvous. Base of fore wing costa below pale grey. Under surface green, on fore wing extending posteriorly to Cu_2; postmedian lines well developed on both wings, usually more or less continuous (the component white bars conjoined), but rather thin and lacking the black basal edging characteristic of *s. sheridanii.* Size small.

In the Pacific Northwest known only from Brewester, Washington where the late J. C. Hopfinger used to take it rather frequently. Until the receipt of Mr. Newcomer's material it was not realized just how unusual this record is. See the discussion below.

Callophrys (*Callophrys*) *sheridanii newcomeri* new subspecies

The upper surfaces of both sexes are uniform grey, unrelieved by any brownish tint or fulvous, much as in the other *sheridanii* subspecies. Base of fore wing costa below, pale grey. It differs chiefly in the strong tendency to reduction of the postmedian line of the underside, continuing the trend away from *s. sheridanii* that is evident in *s. neoperplexa* Barnes and Benjamin. This is especially marked on the fore wing where most specimens show either no trace of the line at all or only a few faint bars; occasionally it may be fully present but is then only faintly developed. In only one specimen, a female from Ft. Simcoe, is it fully present and strongly developed. The row on the hind wing is rarely completely absent (a female from Mill Creek), but almost always lacks several bars at least, especially those in Rs - M_1 and M_3 - Cu_1. On the fore wing upper side of the Mill Creek series there is a definite, though faint, pale grey patch, strong at cell-end and fading rapidly distad.

Holotype, male, and 5 male *paratypes,* all Mill Creek, 1800 ft., Yakima Co., Washington, 29 March 1961 (E. J. Newcomer) the holotype including male genitalia slide C-791; 5 male and 7 female *paratypes,* Ft. Simcoe, 1200 ft., Yakima Co., Washington, 6 April 1960 (E. J. Newcomer).

Holotype and most of the paratypes, C. M. Ent. type series no. 478. Some paratypes are being returned to Mr Newcomer.

Remarks. In addition to the type series, the following material has been seen: Mt. Spokane, 5000 ft., Spokane Co., Washington, 27 June 1960 (E. J. Newcomer), 3 males and 2 females; Blue Mts., 4800 ft., Columbia Co., Washington, 17 June 1961 (E. J. Newcomer), 2 males; Lonerock, Gilliam Co., Oregon, 7 June 1961 (D. L. Bauer), 2 males and 2 females (doubtfully typical).

The Canadian National Collection has specimens from Waterton Lakes Park, Alberta, and from Okanagan Landing and Vernon, British Columbia, all of which I believe are referable to *newcomeri,* though I saw them but briefly while on a visit in 1956 and made only a few notes on their peculiarities.

The Oregon population and the four from Washington all show a certain amount of independent differentiation. The greatest departure is found in the Lonerock series where females show a definite fulvous tinge above, unique in the species, and the under surface (which is more uniform in appearance than in any of the Washington populations) has the postmedian line on both wings practically obsolete save for the portion posterior to Cu_1 on the hind wing. Should these differences hold true in a larger series it may be advisable to separate this under another subspecific name.

The fresh series of males from Mill Creek shows a faint, small, pale discal patch on the fore wing above as noted above; this also occurs in some of the males from Ft. Simcoe, though more weakly. The Mill Creek series also averages somewhat larger than the others.

The specimens from Mt. Spokane are somewhat smaller, tend to be somewhat darker below and have the postmedian line of the fore wing below absent completely.

Several points concerning *sheridanii* in the Northwest merit further discussion. These points may be grouped under two broad headings: *geographic variation* and *climatic adaptation.*

Geographic variation. The differences between *sheridanii* populations from place to place are of a rather unusual nature. The most conspicuous aspect of this is the isolated occurrence of *s. neoperplexa* at Brewster, Washington, remote from the nearest other populations of that subspecies in southwestern Montana and with much of the intervening area occupied, apparently by *s. newcomeri* (see fig. 1). It is not yet known whether this Brewster *neoperplexa* represents an enclave entirely cut off from other *neoperplexa* populations or a peninsula-like intrusion, perhaps along river valleys.

The population of *newcomeri* at Lonerock, Oregon, differs more from any of the Washington populations than these do from each other, rather surprizing in view of its close geographic proximity. Lonerock and Ft. Simcoe, for example, are much closer than Ft. Simcoe is to Mt. Spokane; and both Lonerock and the Blue Mts. locality in Columbia Co., Washington, are on the same (northwest) slope of the same mountain range. In addition to its greater differentiation, the Lonerock series also seems less individually variable. Again it should be pointed out that the small size of the series makes these observations tentative and uncertain.

In Washington the known populations of *newcomeri* show a definite but rather low level of interpopulation differentiation as already discussed; and within each population a rather high level of individual variability. The interpopulational differences seem to bear little relation to the geographic distances separating the populations, the Mill Creek and Ft. Simcoe populations, for example, being only a little less different from one another than either is from the Mt. Spokane series.

There is evident here a definite hierarchy of differentiation: the greatest, that between *newcomeri* and *neoperplexa;* next, in *newcomeri,* between the Washington populations collectively and the one population from Oregon; and finally, the slight differentiation between the Washington populations. In a general way this hierarchy undoubtedly reflects the past history of the species in this region and it is a temptation to draw on it as well as on some of the other data on variation given above in speculation on the past events that may have led to the situation as it is today. Until larger series can be obtained, however, the data basic to such speculation would be far too shaky. My repeated emphasis of this point is in no way intended as a slight to the much appreciated efforts of Mr. Newcomer and Mr. Bauer: their collections are by no means small as series go in *Callophrys* and, further, they were not collecting with statistical needs in mind. Statistics is a notoriously avaricious taskmaster.

Climatic adaptation. The various factors which together make up what we call climate exert a strong control over the distribution of Lepidoptera as they do for many other groups of organisms. Indeed, we may imagine the range of a species of butterfly or moth as an area bounded by not one but a number of lines, each one representing a limiting value, for that species, of some particular climatic factor. Such a notion, evidently, is a great oversimplification but the principle is valid and useful.

We may touch on the problem only briefly and incompletely here in connection with *C. sheridanii*. Two types of climatic responses may be discerned: (1) responses to particular factors singly, and (2) responses to two or more jointly (correlated responses). The data used are weather bureau mean figures as recorded, for example, in *Climate and Man* (U.S.D.A. Yearbook of Agriculture, 1941). On no account is it to be imagined that the insects are necessarily responding directly to these variables as such. It is merely that they appear to function as indices more or less closely correlated with whatever factors may actually be responsible, factors which themselves may be quite inaccessible for analysis over a large area.

Three variables were selected for study: mean January temperature, mean July temperature, and mean annual precipitation. Values of these were tabulated for all the known *sheridanii* localities for which they were available, as given in Table 1. By inspection we may establish the approximate limits for each of these:

mean January: all records fall between 14° and 32°F
mean July: all records fall between 57° and 76° F
ann. precip.: all records fall between 10 and 25 inches

The map (fig. 1) shows the results of applying these limits over the northern part of the range of *sheridanii*: all the shaded areas lie outside them and hence are presumably unavailable to *sheridanii*.

Obviously these three factors are not sufficient to account for the whole of the present range of the species. A large part of Montana (east of the mountains) and of South Dakota, for example, fall within these limits, yet *sheridanii* does not occur there. It is quite probable that variables other than these three are, at least in part, responsible. Yet without extending observation beyond them the distributional limits of *sheridanii* could be approximated still more closely by the use of correlated responses.

TABLE 1

Mean temperature (° F) for July and January and mean annual precipatation (inches) for localities where Callophrys (Callophrys) sheridanii has been taken.

Station		Locality	mean Jan.	mean Jul.	mean ann. precip.
1	Wash.:	Ft. Simcoe	28.4	75.2	12.29
2		Blue Mts. (Columbia Co.)	28(ca.)	68(ca.)	?
3		Mt. Spokane, 5000 ft.	17.2	58.7	22(ca.)[1]
4		Brewster	27.6	73.8	10.66
5	Oregon:	Lonerock	31.7	62.0	15.44[2]
6	Mont.:	Dillon	24.4	65.1	16.67
7		Ennis	21.7	64.5	10.69
8		Polaris	20(ca.)	62(ca.)	?[3]
9	Wyo.:	Centennial	21.5	61.4	16.91
10	Colo.:	Boulder Co.	28(ca.)	71(ca.)	?[3]
11		Red Feather L., 8400 ft.	15.0	57.9	?[4]
12		Ft. Collins	26.0	68.9	15.20
13	Utah:	Stockton	25.5(ca.)	72.3(ca.)	12.90[5]
14	N. Mex.:	Cloudcroft	30.1	59.7	24.58[2]

1. Temperature values are those of Spokane reduced equally by a lapse rate of 1° F/300 ft. Precipatation estimated from regional values.

2. Spots for Lonerock, Oregon, and Cloudcroft, New Mexico, are omitted from the graph. They fall so far outside the pattern of the remaining localities that I strongly suspect them of not representing the particular localities where the sheridanii were actually taken. There is no error in the values themselves which were kindly confirmed for me by Mr. T. L. Long, National Weather Records Center, Asheville, North Carolina. Needless to say, this is a common problem in mountainous country where small differences in elevation or exposure can exert major changes in the climatic picture.

3. Estimated values.

4. Temperature values are those of Ft. Collins reduced as described in note 1.

5. All values are interpolated from those of two adjacent bracketing localities.

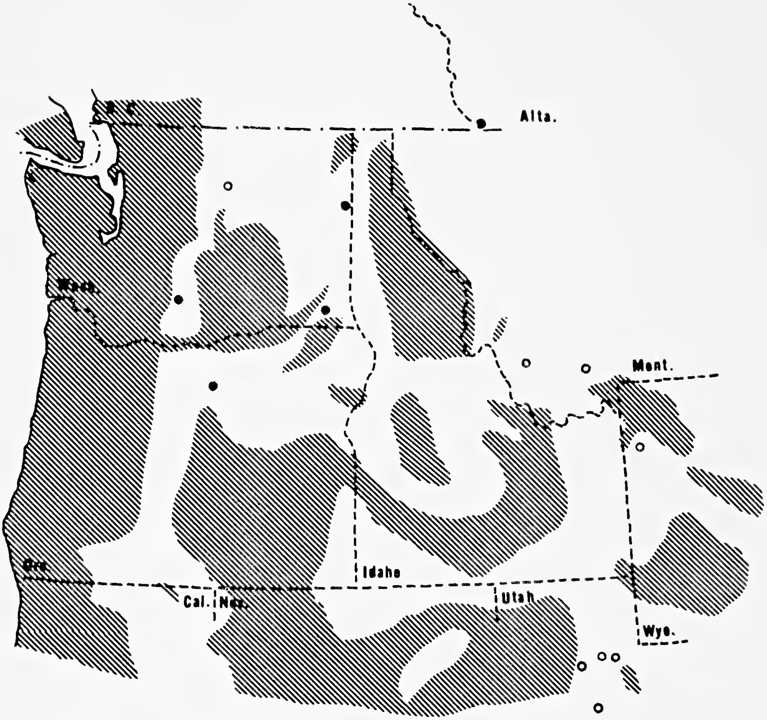

Fig. 1. Map of a portion of the range of *C.* (*Callophrys*) *sheridanii* showing localities of subspecies *neoperplexa* (open circles) and subspecies *newcomeri* (solid circles). Excluded areas (shaded) have one or more of the following: (1) mean January temperatures below 14°F or above 32°; (2) mean July temperatures below 57° or above 76°; (3) mean annual precipitation below 10 or above 25 inches.

The method of correlated responses makes use of a well known fact that organisms seldom respond to these or other climatic factors singly, but that tolerance to one is usually in some way related to the value of the other. This can be seen in the accompanying graph of *sheridanii* localities (fig. 2), plotted for values of mean January and mean July temperatures. When mean July temperature is below, for example, 60° F, then *sheridanii* will occur in such localities only if mean January temperature is somewhere between, roughly, 14° - 22°; but when mean July temperature exceeds 70° it occurs in localities where the mean January temperature is above about 24°. Thus for any given July temperature the range of tolerance to January temperatures is much less than the range applicable to the species over its whole range and conversely.

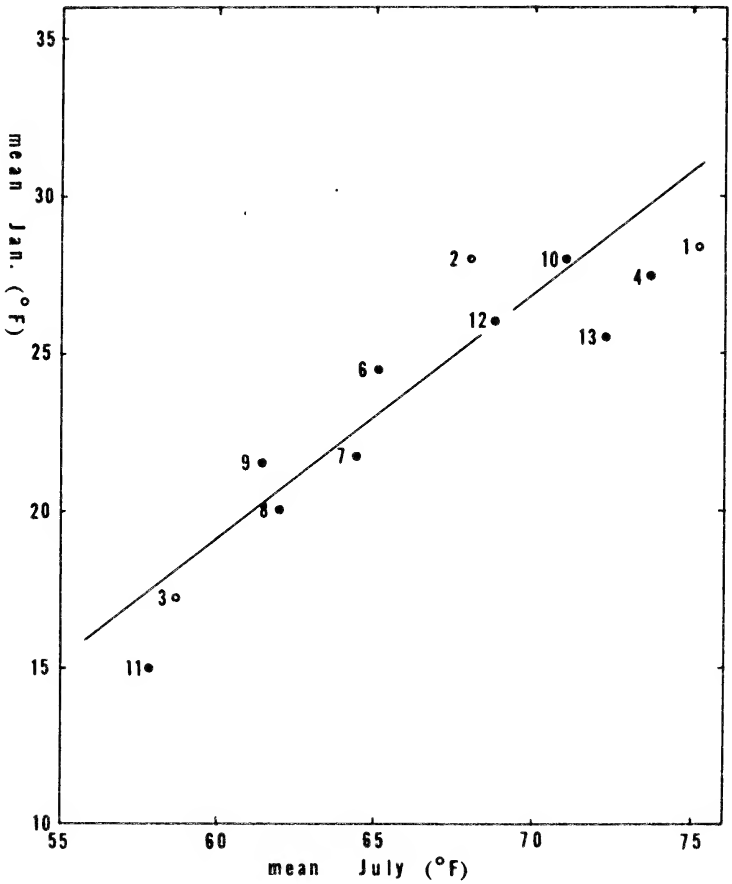

Fig. 2. Graph of known localities of C. (*Callophrys*) *sheridanii* (numbered as in table 1) according to their mean January and mean July temperatures.

Similar plots (mean January against mean July) have been constructed for several other Norther American lycaenids [*Callophrys* (*Incisalia*); *Lycaena thoe*], all of which show patterns generally similar to that of *sheridanii*. In all, for example, the correlation is rectilinear, occupying a band of more or less uniform breadth, though this breadth, the slope of the band, and its position vary from one species to another. In those species with a sufficient number of locality points (*sheridanii* is not one of them) a further, rather paradoxical, effect is noted: the upper limit of temperature tolerance is set by a January threshold, the lower limit by a July threshold. In other words, such species can extend into warm areas only to a point where increasing winter temperatures form a barrier; and can extend into cold areas only so far as summer temperatures continue to be sufficiently warm. Neither the heat of summer nor the cold of winter seems to be relevant. This may well be true of *sheridanii* but the available data are insufficient to demonstrate it.

There will be, then, within the limits set by the particular factors singly, additional "excluded areas" in this two dimensional manifold whose July and January means lie outside this band of correlated temperature responses. These, when added to the other excluded areas (as shown on the map, fig. 1), would still further restrict the territory available to the species. This has not been done for *sheridanii* because the number of locality points available is not sufficient to permit a reliable determination either of the central regression line or the breadth of the band. Inspection, however, shows that much of the above-mentioned areas of Montana and South Dakota would thereby be excluded. This, parenthetically, suggests that the correlated response to summer and winter mean temperatures is a major impediment to the eastward spread of *sheridanii*.

REFERENCES

BARNES, WILLIAM and FOSTER H. BENJAMIN, 1923. Notes and new species. *Contrib. Nat. Hist. Lejid. N. America* 5 : 62-96 [*Callophrys*, pp. 64-69].

BLACKMORE, E. H. 1927. Check list of the Macrolepidoptera of British Columbia, *Victoria*: *E. H. Banfield*. 47 pp.

BOWMAN, KENNETH 1919. Annotated check-list of the Macrolepidoptera of Alberta. *Red Deer*: *Alberta Nat. Hist. Soc.*, 16 pp.

CLENCH, HARRY K. 1944. Notes on lycaenid butterflies. a. The genus Callophrys in North America. *Bull. Mus. Comp. Zool.* 94: 217-229.

———— 1961. Tribe Theclini *in* Paul R. and Anne H. Ehrlich, *How to know the butterflies* (Dubuque, Iowa: W. C. Brown Co.): 177-220 [*Callophrys* (*Callophrys*), p.p. 209-210].

LEIGHTON, BEN V. 1946. The butterflies of Washington. *Univ. Washington Publ. Biol.* 9: 47-63.

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EUPHYES DUKESI

A Review of Knowledge of its Distribution in Time and Space and its Habitat

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Euphyes dukesi Lindsey,[1] has been reported from Alabama, Virginia, Ohio, Michigan, and Louisiana. This paper reports its occurrence in Mississippi and North Carolina and in a new section of Louisiana, gives notes on its habitat and on its known distribution in time and space.

The finding of *E. dukesi* in Mississippi suggested the desirability of reviewing available information on all the known occurrences. In the course of the review, valuable unpublished information on its occurrence in North Carolina, Virginia, Louisiana, Michigan, and Ohio was obtained and is here presented. It is hoped that this review will stimulate search for additional occurrences, especially in the wide gaps that separate the known occurrences.

ALABAMA

Euphyes dukesi was described by Lindsey (1923) from a type series of four specimens from Mobile Co., Alabama, that were taken by W. C. Dukes of Mobile. Bell (1926) gave additional data on the type locality and reported having taken specimens on *Hibiscus* flowers one mile from Union Station, Mobile, in a marsh with waist- to shoulder-high grass. Lindsey, Bell, and Williams (1931) reported that it was collected in considerable numbers in 1925 by Dr. Van Aller and Mr. Lading (sic)[2] of Mobile and by Bell during a short collecting trip near that city. It was on the wing from 24 August to 11 October. Holland (1931) figured a ♂, referred to in his text (p. 388) as "type" and on his plate (plate LIV, fig. 26) as "paratype" and stated: "It occurs in southern Alabama and probably elsewhere along the Gulf." Klots (1951) figured a pair from Mobile, Ala. Evans (1955) recorded that 2 ♂ ♂ and 1 ♀ from Alabama were in the British Museum. Clench (in litt) reported that the only two specimens of *dukesi* in the Carnegie Museum are the two ♂ paratypes mentioned by Lindsey (1923) as being in his collection.

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[1] This species was formerly placed in the genus *Atrytone* Scud. 1872. Evans (1955 noted that the type species of *Atrytone* is *arogos* B. & LeC. 1833. He included *Atrytone* only *arogos* and *logan*. He also noted that the type species of *Euphyes* Scud. 1872 is *vestris* Bdv. He included in *Euphyes* the remaining species of North American skippers formerly lumped with *arogos* and *logan* under *Atrytone*. The validity of the separation of the species formerly so lumped into the two groups into which Evans divided them, and hence the validity of the change of the generic name for *dukesi* from *Atrytone* to *Euphyes* appears to be concurred in by all of those with whom the author corresponded in collecting the information summarized in this paper.

[2] Henry Peter Löding, author of *Catalogue of Beetles of Alabama*. Ala. Geol. Surv., Monograph 11, 1945, 172 pp.

VIRGINIA

Clark (1932) did not list *dukesi* as possible for the vicinity of the District of Columbia. Clark and Clark (1951) described the area in Norfolk and Princess Anne Counties from which they had *dukesi* records based on their own work and that of Otto Buchholz. They concluded that, in this area, *dukesi* has one brood that flies between 12 June and 16 July. Martin and Truxal (1955) reported that the Los Angeles County Museum collection included *dukesi* taken in Virginia in August. Rindge checked the American Museum of Natural History series and reported (in Litt) that there were 35 ♂♂ and 26 ♀♀. Virginia specimens from the Buchholz collection include both ♂♂ and ♀♀ taken in June for which the localities are given as "Norfolk Co.," "Pr. Anne Co.," and "Suffolk." Suffolk, Va., is in Nansemond Co. A ♂, probably collected by Buchholz, that came to us from C. F. dos Passos, is labelled "Pecaty Road, vic. Hickory, Va. Norfolk Co., 26 VI 40" Charles V. Covell, Jr. reported (in litt) that he had not taken *dukesi* in his collecting in the Norfolk area. Col. S. S. Nicolay reported (in litt) that he had taken specimens in Virginia in all months, May through August, is convinced that, in this area, *dukesi* is double brooded, and estimated that the first brood is out between 25 May and 5 July and the second between 20 August and 15 September. He thought that it may be possible for it to be found as late as October. Col. Nicolay provided the following notes on collecting *dukesi* in Virginia: "A fair number of specimens were taken in the period 4-15 July 1951. The location of the habitat is the difficult factor; once the habitat is located, they are not particularly difficult to capture. North Landing, Princess Anne Co., a locality mentioned by Clark and Clark (1951), is actually a bridge crossing a canal. *Dukesi* is found abundantly in the few yards of marsh on either side of the bridge and along the banks of a small stream that empties into the canal at the bridge, but it is not found 100 yards away from the bridge on either side, nor in any of the fields a block away. *Dukesi* was also found in other spots in and around the Dismal Swamp area of Princess Anne and Norfolk Counties. Each locality is actually a spot since the insects never wander away from their chosen ground. One can collect in a field or along a trail within a stone's throw of the deep swamp habitat of *dukesi* and not find a single stray. They were not found more than a few yards from standing water. The best collecting method is to work the edges of small roads that cut through the gum swamps. The ♂♂ in search of ♀♀ will fly along the edge of the road for a few yards before turning back into the tall swamp grass from whence they came. This grass grows under the trees of the swamp, not out in the open. They are fond of pickerel weed (*Pondeteria cordata*) and at times were found swarming around clumps of its spired blue flower along the edges of small bodies of water. The specimens taken in July 1951 were quite well worn, especially the ♂♂, with an occasional ♀ appearing fresh. On 25 August 1951, at the same localities, freshly emerged specimens were found in large numbers, particularly ♂♂. These relations have been found to exist in each of the five seasons during which observations have been made."

OHIO

References to the occurrence of *dukesi* in Ohio were found in Freeman (1942), Harris (1950), Klots (1951), and Pliske (1958 "1957"), but no detailed published account has been located. The earliest record of *dukesi* from Ohio that was found is of a ♂ taken on 10 July 1940, at Sylvania by Donald Eff given in Freeman (1942). Sylvania is 11 miles northwest of Toledo, in Lucas Co., close to the Michigan border. Eff described (in litt) the locality as "in the Oak Openings in northwest Ohio, an acid, quicksand base, area of about 140 square miles set in the midst of rich farming land. Before canals were dug and the water level was higher, it was a combination of swamps and higher sandy knolls. Much of the land in the northeast corner of Indiana and southeast Michigan would fall in the same general category." The occurrence of *dukesi* in Ohio was apparently not known to Macy and Shepard (1941). F. S. Badger of Kokomo, Ind., described (in litt) his experiences collecting *dukesi* in Ohio on 7 July 1957 as "one of the most fantastic experiences I have had in this section of the country. Homer Price took me to the old disused bed of the Miami Canal on a blistering hot sticky day. Equipped with knee-high rubber boots, we followed the canal to an area where it was over-grown with wide-bladed sedges from bank to bank. Sloshing around in water 6 to 12 inches deep, we started seeing ♂♂ flying all over the place. The canal was pretty well shaded by trees and was only about 12 to 15 feet wide. There were some sedges in the adjoining woods in one area and here, particularly, *dukesi* abounded. It had been our intention to take only a half dozen specimens but the skipper was so abundant that I ended up with 36 ♂♂ and 1 ♀ in about 90 minutes of collecting. The only other butterflies were common dark skippers, a few worn *Strymon falacer*, and worn *Speyeria cybele*." One ♂ collected by Badger on 7 July 1957, now in our collection, is labelled: "Miami Canal, Paulding Co., Ohio." Mr. Badger not only sent us the foregoing account but also asked Mr. Homer F. Price of Payne, Ohio to provide additional information. Mr. Price gave (in litt) the following records and comments:

" (a) Marie DeLarme Creek, Carryall Township, Paulding Co., Ohio: 29 June 1955 ♀, 4 July 1955 3 ♂ ♂, 30 June 1956 ♂, 8 July 1956 ♂, the sedges are nearly shoulder-high some years at this station, low ground along the creek. A small colony; in some seasons none are seen.

" (b) Miami Canal, Defiance Township, Defiance Co., Ohio: 8 July 1956 ♂. Very wet woods along the canal, the sedges were rather short, none were seen in the canal, which was dry.

" (c) Miami Canal at Charloe, Brown Township, Paulding Co., Ohio: 14 July 1950 ♂ ♀, 16 July 1950 2 o o, 23 July 1950 2 ♂ ♂ 30 July 1950 ♀, 25 August 1950 ♂ (worn, latest record), 2 July 1959 3 ♂ ♂ 1 ♀ (fresh). The species is quite common some seasons in and along the canal where the sedges are of normal size. They occur at rather open spots where there is a little sunshine. Many specimens have been collected at this station.

"I am of the opinion that this species is more plentiful in this area than is generally believed. Recently I have collected *dukesi* at various stations along the canal from the Defiance County line south to the Putnam County line. This area has a low gradient, having been a part of the Black Swamp. The soil is a very heavy clay. I have been of the opinion that *dukesi* probably appeared first in western Ohio near the southern terminus of the Miami Canal at Cincinnati and extended its range northward along the canal. Hot weather, mud and water, mosquitoes and deer flies, probably cause some collectors to remain at home during early July when *dukesi* should be searched for. It appears that we have only one brood here. They seem to like shade - but not deep shade."

Badger gave (in litt) the following additional Charloe records from specimens now in his collection that were taken by Price: 15 July 1951 2 ♂ ♂, 22 July 1951 ♀, 21 July 1954 ♀, and 4 July 1955 ♂. Badger has included *dukesi* on his preliminary manuscript list of Indiana butterflies on the basis of its known occurrence in Ohio within a few miles of the Indiana border. Price also mentioned that he had correspondence with Chermock and had provided material for study in connection with the possibility that the Ohio and Alabama populations might be subspecifically different. Covell stated (in litt) that his collection contained a ♂ obtained from Frank Chermock labelled "Chasloe, Pauling Co., Ohio, 15 July 1957" taken by Price.

LOUISIANA

Lambremont (1954) described the single speciment known to him from Louisiana, taken by him, as constituting a possible westward range extension. His specimen, a ♂, Tulane University #2064, was taken 11½ miles west of Oak Grove, West Carroll Parish, on 19 June 1950. This locality is near the Boeuf River about 20 miles west of the Mississippi River, and more than 200 miles north of the Gulf of Mexico. Harris (1950) gave the range of *dukesi* as: "known from southern Louisiana, southern Alabama (Mobile), southeastern Virginia, and Ohio." Harris wrote (in litt) that the information on *dukesi* given in his 1950 report was written by A. H. Clark and has kindly provided a copy of Clark's letter of 13 July 1950 to him, reading in part: "I am returning the manuscript . . . I have added . . . in brackets . . . *A. dukesi* which certainly occur (s) in Georgia." Harris commented, with regard to Clark's reference to "southern Louisiana" that he assumed that Clark knew of records. It seems unlikely that Clark on 13 July 1950 would have known of Lambremont's 19 June 1950 record. The reference by Clark is almost certainly to a previously unpublished occurrence discovered by William D. Field which Mr. Field has described (in litt) as follows: "I took a series of *dukesi* near a drainage ditch in what had once been a swamp near Camp Plauche, Jefferson Parish, La., on May 15, 1944. This swamp had been well-drained but had a good flora resembling a woods with only a light amount of undergrowth. The details of the latter escape me except for the catbrier (*Smilax*). Camp Plauche was right next to the town of Harahan, less than a mile from the Mississippi River. This series was sent to Austin Clark for the museum. However, at present there is only a single male in the collection." Harahan is on the north (left) bank just a little upstream from New Orleans.

MICHIGAN

Pliske (1958 "1957") described the occurrence of *dukesi* at Ann Arbor, Michigan. He reported 2 ♂♂ taken by Arthur Slater and himself on 21 July 1956 in a small marsh on the north side of the Huron River about one mile east of Ann Arbor, Washtenaw Co., Mich.; a second ♂ taken at the same locality the following day; and a ♀ taken on 13 July 1957. A second locality, ½ mile east of the first, yielded a ♀ on 27 July 1956 and a ♂ on 15 July 1957. Both marshes were dominated by the lake-margin sedge (*Carex lacustris*) characterized by broad blades, 1 cm. or more in width, spreading in a criss-cross manner. On 28 July a ♀ was observed ovipositing on the underside of a sedge leaf about 1½ feet above the ground. The eggs were collected by W. H. Wagner and were described by Pliske. Pliske's account refers to the Ann Arbor colony as the fourth to have been discovered, actually, although not known to him, it was the sixth, the fourth and fifth having been the two Louisiana occurrences. Wagner has provided (in litt) additional data on the Michigan occurrence of *dukesi* as follows: Subsequent to the development of the data reported by Pliske, a battered ♂ that had been taken by Sherman Moore on 28 July 1952 at Highland Park, Oakland Co., Michigan was found in the University of Michigan collection in the *E dion* series. Wagner notes that the thoroughly urbanized region of Highland Park in Detroit is wholly unsuited to the occurrence of *dukesi* and that the specimen must be a stray. Wagner having visited the North Landing, Virginia, locality with Clark and also the Ann Arbor, Michigan locality, compared them as follows: "The habitat there (North Landing) was very different from the Michigan one: deep, shady swamp, the butterflies rather slow flying among grasses and sedges. Here the species reminds me more of *dion.* It flies with the latter as well as *A. logan, P. viator, E. conspicua,* and *P. massasoit.*"

MISSISSIPPI

Mather and Mather (1958) regarded *E. dukesi* as of probable occurrence in Mississippi. This was proved correct when I took a ♂ on 4 October 1959 about 4 miles north of Clinton, Hinds Co. The locality is on the north side of the Kickapoo Road bridge over Bogue Chitto Creek, Sec. 33, T 7 N, R 1 W. The specimen was taken at about 3 p.m., feeding on flowers of *Eupatorium* (*Conoclinum*) *coelestinum* that were growing in a marshy area within a few feet of a pool of essentially stagnant water in the creek bed. This locality is about 200 miles north of the Gulf of Mexico. A comparison of the three males at hand reveals that the Mississippi specimen is more like the Virginia one than the Ohio one especially in that it has less yellow hair on the hindwing above and less bright yellow on the hindwing below. The separation of the black areas of the stigma on the forewing above is most distinct in the Virginia specimen, slightly less distinct in the Ohio specimen, and still less distinct in the Mississippi specimen. At the same locality on the same date, the first Mississippi specimen of *Poanes viator* was taken. A second *viator* was taken there on 11 October 1959 by M. & E. Roshore but no additional specimens of either species have been found on numerous subsequent visits.

NORTH CAROLINA

Nicolay reported (in litt) the taking of *dukesi* on 6 June 1960 at a locality about 7 miles southeast of New Bern, Craven Co., in a small swamp located along the Neuse River. Based on his observations in Virginia he regarded the locality as a typical *dukesi* habitat. Specimens of both sexes were taken, the condition of the ♂ ♂ suggested that they had been on the wing for about a week, the ♀ ♀ were quite fresh.

SUMMARY AND DISCUSSION

The geographical distribution of the localities at which *E. dukesi* has been found to occur is shown by figure 1; also shown are the wide areas between the Great Lakes, the Middle Atlantic Coast, and the Gulf States from which the insect is not yet known. Nicolay reported (in litt) that he did not find *dukesi* during the two years (1947-49) that he collected in the Pensaçola, Fla., area. Zeiger reported (in litt) the taking of a series of 17 ♂♂ and 5 ♀♀ of *P. viator* on 23 May 1962 among giant cutgrass, in brackish water, along the edge of the Suwanee River, near its mouth. He will visit this locality again and check for the occurrence of *E. dukesi.* Neither Lambremont (1954) nor Mather and Mather (1958) found it in coastal Louisiana or Mississippi. Freeman (1951) did not report it from Texas. Harris reported (in litt) that he felt certain that it will be found in swamps in Georgia such as those of the Altamaha River, the Okefenokee, and other suitable localities. He also indicated that Buchholz, whose records of *dukesi* from Virginia were cited by Clark and Clark (1951) and who had many Georgia records, apparently had no records of *dukesi* from Georgia. Roever (in litt) reported that he had never collected in the type of marsh in Tennessee in which *dukesi* might be expected to occur but regarded the open marsh around Reelfoot Lake in northwest Tennessee and the spring-fed gum swamps in the Hatchie River bottom near Viedo, 4-5 miles southeast of Mercer, Madison Co., as likely areas.

E. dukesi appears to be single brooded in Ohio and Michigan and double-brooded in Virginia and the Gulf states; the months of record for the seven states in which it is known to occur are shown in table 1.

E dukesi appears to be a swamp butterfly, but while the Ohio and Michigan occurrences are apparently closely connected with sedges, the Virginia occurrence is in the gum (*Nyssa aquatica*) swamps, which as Clark and Clark (1951, p. 8) pointed out, lie west of the sedge marshes that, in turn lie behind the sand dunes of the Virginia coast. Until more complete knowledge of the distribution of *dukesi* becomes available, it would seem prudent to describe its distribution as: northeast and southeast Louisiana, central Mississippi, southwestern Alabama; eastern North Carolina, southeastern Virginia; northwestern Ohio, and southeastern Michigan, rather than in terms that imply its occurrence in the large regions between these areas of known occurrence.

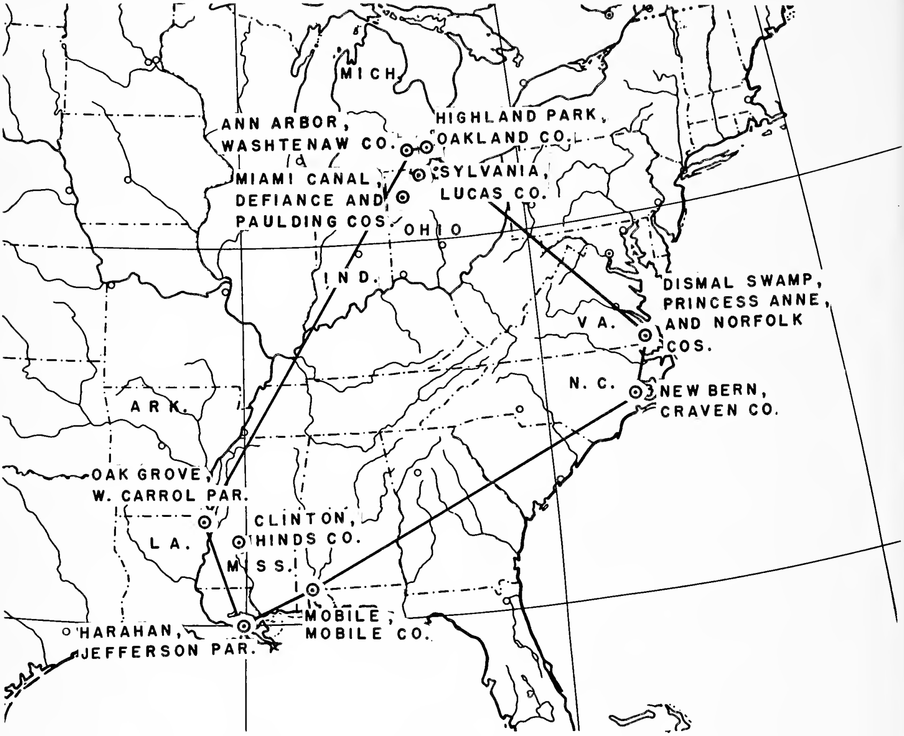

Fig. 1. Map showing the locations where Euphyes dukesi has been found.

	MAY	JUN	JUL	AUG	SEP	OCT
MICHIGAN			X			
OHIO		X	X	X		
VIRGINIA	X	X	X	X	(a)	(b)
NORTH CAROLINA		X				
ALABAMA				X	X	X
MISSISSIPPI						X
LOUISIANA	X	X				

(a) Probable (b) Possible

TABLE 1. The monthly occurrence of Euphyes dukesi at various localities in the eastern United States.

ACKNOWLEDGEMENTS

The principal value of this paper derives from the data provided by Col. S. S. Nicolay, Cherry Point, N. C.; Mr. William D. Field, Washington, D. C.; Mr. F. S. Badger, Kokomo, Ind.; Mr. Homer F. Price, Payne, Ohio; Mr. Lucien Harris, Jr., Atlanta, Ga.; Mr. Charles V. Covell, Jr., Norfolk, Va.; Dr. Frederick H. Rindge, New York, N. Y.; Mr. Charles F. Zeiger, Jacksonville, Florida; Mr. Harry K. Clench, Pittsburg, Penn.; Mr. Kilian Roever, Tucson, Ariz.; Dr. Warren H. Wagner, Ann Arbor, Mich; Mr. Donald Eff, Boulder, Colo.; Mr. H. A. Freeman, Garland, Texas; Mr. John M. Burns, Middletown, Conn.; and their kind permission to publish them; their cooperation is deeply appreciated.

REFERENCES

BELL, E. L. 1926. Notes of some Hesperiidae from Alabama, *Jour.* N. Y. *Ent. Soc.,* 34: 269-271.

CLARK, AUSTIN H. 1932. The Butterflies of the District of Columbia and vicinity. *Smithson. Inst., Bull. U. S. Nat. Mus.,* 157, 337 pp.

CLARK, AUSTIN H. and LEILA F. CLARK 1951. The butterflies of Virginia. *Smithson. Misc. Coll.,* 116 (7): 1-239.

EVANS, W. H. 1955. A Catalogue of the American Hesperiidae, Part IV. *British Museum (London)*, 499 pp.

FREEMAN, H. A. 1942. Notes on some North American Hesperiidae with the description of a new race of *Polites verna* (Edwards) (Lepidoptera) (Rhopalocera). *Ent. News,* 53: 103-106.

———— 1951. Ecological and sytsematic study of the Hesperiidea of Texas. *Southern Methodist Univ. Studies,* No. 6: 1-67.

HARRIS, LUCIEN JR. 1950. The butterflies of Georgia. *Bull. Georgia Soc. Naturalists,* 5: 29 pp.

HOLLAND, WILLIAM J. 1931. The Butterfly Book (revised edition). *Doubleday & Co., Garden City, N. Y.,* 424 pp.

KLOTS, ALEXANDER B. 1951. A Field Guide to the Butterflies. *Houghton Mifflin Co., Boston,* 349 pp.

LAMBREMONT, EDWARD N. 1954. The butterflies and skippers of Louisiana. *Tulane Stud. Zool.,* 1: 125-164.

LINDSEY, A. W. 1923. New North American Hesperiidae. *Ent. News,* 34: 209-210.

————, ERNEST L. BELL and R. C. WILLIAMS, JR. 1931. The Hesperioidea of North America. *Jour. Sci. Lab. Denison Univ.* 26: 1-142.

MACY, RALPH W. and HAROLD H. SHEPARD 1941. Butterflies. *Univ. of Minnesota Press, Minneapolis,* 247 pp.

MARTIN, LLOYD M. and FRED S. TRUXAL 1955. A list of North American Lepidoptera in the Los Angeles County Museum, Part 1 - Butterflies. *Los Angeles Museum, Science Series,* No. 18: 1-35.

MATHER, BRYANT and KATHARINE MATHER 1958. The butterflies of Mississippi. *Tulane Stud. Zool.* 6: 63-109.

PLISKE, THOMAS E. 1958 "1957". Notes on Atrytone dukesii (sic), a rare species new to southern Michigan (Hesperiidae). *Lepid. News,* 11: 42.

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1140 W. Orange Grove Ave., Arcadia, California, U.S.A.

THE COMPLETE LIFE HISTORY OF STAPHYLUS HAYHURSTI

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THIS OBSCURE LITTLE SKIPPER is one of those species that are easily overlooked by the non-observant collector. It inhabits a wide range in the eastern United States extending at least as far as Pennsylvania and Nebraska and south to Florida and Texas, being replaced in southern Texas by the closely related *Staphylus mazans* Reakirt. Host plants include *Chenopodium* and *Alternanthera* and the species is rather localized to areas where these weeds grow. One of the peculiarities of *hayhursti* is the moth like habit of spreading the wings out flat against the surface upon which it alights. It is strongly attracted to certain flowers and at times I have found a dozen or more specimens clustered about a bed of Spearmint flowers (*Mentha spicata*) *during late July* in a good local. Sweet Clover (Melilotus) also seems to have a particular attraction for the species. In rural areas the best collecting spots for *hayhursti* will be associated with moist rather shady habitat. An idea spot is a small creek running through a wooded area or the weedy edges beside an old railroad track. In urban areas it is drawn to vacant lots grown up in weeds where an ample supply of the host plants can be found growing. There are two distinct broods produced each year in Missouri and probably at least three further south. In a normal year you can find *hayhursti* from the third week in May to the end of the third week in June and again from mid July until the end of August. The larvae produced by the second brood normally hibernate in the third instar in this area. An occasional third brood specimen is produced but these are very rare.

From time to time scattered bits of information on the early stages of this species have appeared but as far as I can ascertain there has been no complete life history published on this butterfly. In May of 1962 I was able to obtain 49 ova from a worn female placed on potted Lambs Quarters and covered with a bag of Nylon netting. From these eggs 21 adults were reared and the larvae were carefully observed and recorded in detail. Since Edwards' description of *hayhursti* in 1870 was based on material from "Missouri" this description should approximate topotypical specimens. The illustrations which accompany this description were drawn by William H. Howe.

OVA: Eggs were obtained from 25 to 28 May. The eggs were laid singly usually beneath the leaves with a few placed above and a few others on the stems. The ova is very small, less than 1 mm. in diameter and has a flattened circular appearance. The color is a deep orange brown with a raised cream colored pattern of irregular ridges. The six largest radiating out from the top center to the sides. Under low power magnifaction the egg has the appearance of a white star on an orange background.

FIRST INSTAR LARVA: The first emergence occurred on 1 June. The newly hatched larva is translucent light orange, abdominal segments 8, 9 and 10 are dull brown dorsally. The head and prothoracic shield are shiny black. After the first day of feeding the body assumes a pale green color with orange edges. The first meal is a hole eaten through the top of a leaf. The second day a small tent about one eighth inch square is made near the tip of a leaf by cutting three sides and folding the severed section to the top of the leaf and fastening it with a few threads of silk.

SECOND INSTAR LARVA: Body dark green, abdominal segments 9 and 10 pale orange brown, abdomen translucent orange yellow. Head and prothoracic shield clear black. The larvae leave the tent a short distance and feed during the day on top of the leaves, eating holes through the leaves. The larvae are very agile and when disturbed they rapidly retreat to the tent.

THIRD INSTAR LARVA: Body pale watery green with no visible markings, thickly covered with short white setae, a few longer hairs on the last segment. Abdominal segments 8, 9 and 10 are creamy yellow with a pale brown tone dorsally. The neck is a slightly paler green than the body. Due to the translucence of the body the edges of the abdomen appear to be pale yellow. The prothoracic shield has a pale green dorsal area shading into deep purple at the sides. Head deep purple and thickly covered with short white setae, face deeply cleft vertically at the epicranial suture. Mandibles are a contrasting shade of reddish purple.

FOURTH INSTAR LARVA: Body medium green covered with short white setae, abdominal segments 8, 9 and 10 slightly paler, section 10 with a few longer hairs. The neck is slightly paler and the prothoracic shield is visible only as two pale brown subdorsal spots. The head is deep purple, almost black and thickly covered with medium length white hair. The growth rate is greatly accelerated in this instar.

FINAL INSTAR LARVA: Length of fully grown larvae, 20-23 mm. Body ground color is a deep green with a rosy overcast, intersegmental folds pinkish green. Legs cream color with the rest of the abdomen and the prolegs deep green. The body is thickly covered with fine white hair, some slightly longer on the last segment. The spiracles are pale creamy white and slightly raised. The skin is quite translucent, the heart visible as a deep green mid dorsal line. In this instar the prothoracic shield has turned to a very pale brown color. Head deep purple almost black, thickly covered with white hair and deeply cleft vertically at the epicranial suture. The tent in the final instar consists of an entire leaf folded together and pupation occurs in the tent with the addition of a very thin lining of silk and a silken pad to which the cremaster is attached.

PUPA: First pupation occurred 27 June. Length of pupae 13-17 mm., width at widest point of wing cases 3.5 mm. The pupa case is thickly dusted with a white powdery bloom. Abdomen pale orange brown, the wing cases and thorax light olive brown. Spiracles dark brown and noticeably raised. The abdomen and head are thickly covered with short orange bristles. Cremaster dark brown consisting of a single sharp point. Adults emerged from the 10th to 16th of July, males and females emerging at the same time. All specimens were quite large and the measurements for the larvae and pupae given should compare closely with those of wild specimens. The time spent in each instar was quite constant, usually five days elapsing between moults.

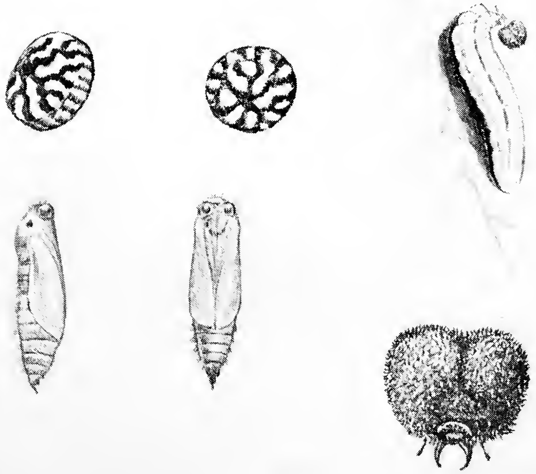

Fig. 1. Early stages of Staphylus hayhursti. Ova, pupa, mature larva and enlarged front view of the head.

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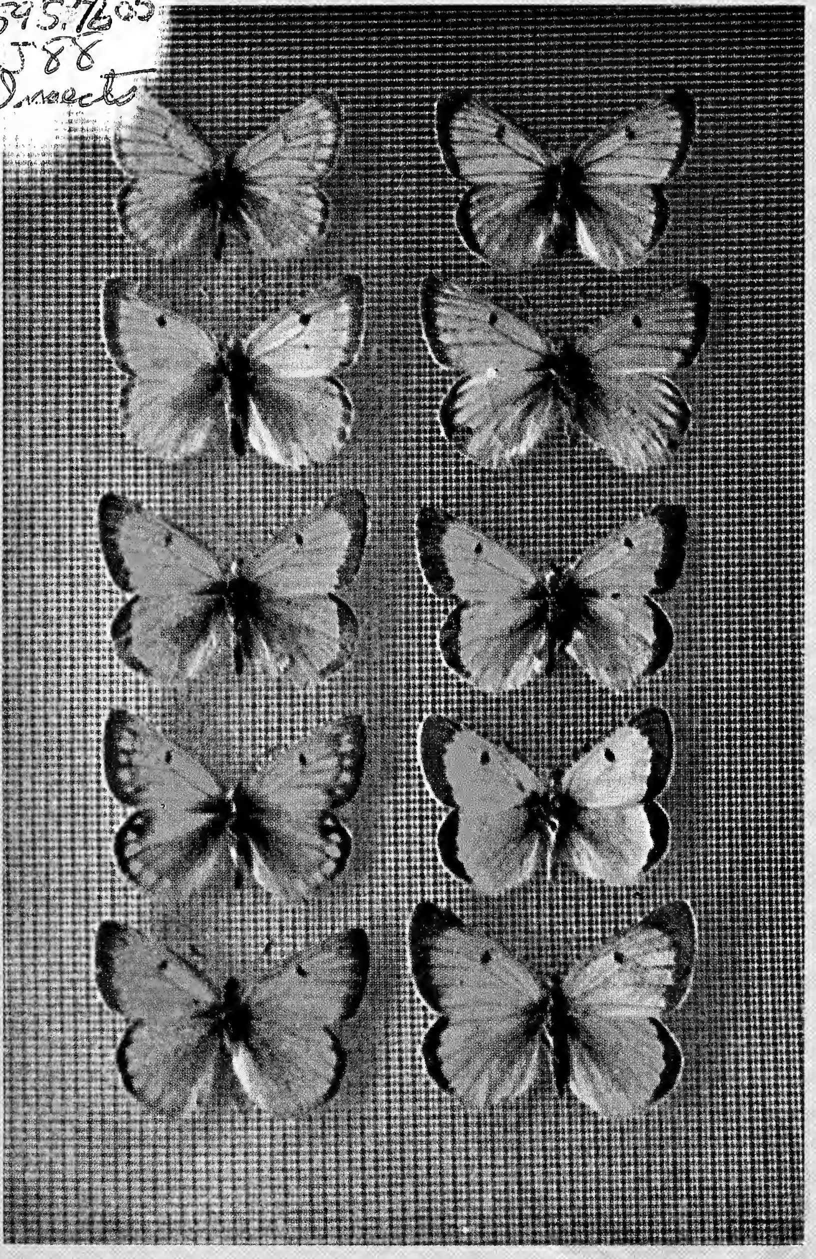

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AFFINITIES AND DISTRIBUTION OF ANTILLEAN ITHOMIIDAE[1]

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THE FAMILY ITHOMIIDAE, a characteristic component of the lepidopterous fauna of the American humid tropics, is represented in the Antilles only by two species, both members of the genus *Hymenitis*. One species is found on Cuba, the other occurs on Jamaica and Hispanola (fig. 1), and their affinities are with Central American species It is surprising that no other species have reached the islands since the lands surrounding the Caribbean support a rich ithomine fauna: it is puzzling to find *Hymenitis,* a genus of frail sun-shunning species, on the Greater Antilles instead of any of the sturdy sun-loving genera. That no ithomine is found on any of the Lesser Antilles is probably because no precisely suitable ecologies are available on those islands.

In order to explore the zoogeographic implications of the Antillean ithomines, it is first necessary to review the systematics and phylogeny of these insects.

SYSTEMATICS

[*Hymenitis* Anonymous, 1807; column 1180. Type of genus, *Papilio polymnia* Linne, 1758, by designation of Hemming, 1934]

Hymenitis Hübner, 1816: 8. Type of genus, *Hymenitis diaphane*: Hübner, 1816, designated by Scudder, 1875.

=*Greta* Hemming, 1934: 28. Type of genus, *Hymenitis diaphane*: Hübner, by original designation.

Hemming's discovery (1934) that *Hymenitis* first appeared in print in 1807, nine years prior to the "Verzeichniss," would seem to reduce the Hübner name to homonymy. By selecting *Papilio polymnia* as type of *Hymenitis* Anonymous, Hemming made the name an absolute synonym for *Mechanitis* Fabricius, 1807; *Greta* was proposed to replace *Hymenitis* Hübner. Hemming's actions were justified under a strict interpretation of the International Code, which provides for the invalidity of anonymous publications only if issued after 1951.

The 1807 article was an unsigned review of a manuscript by Hübner circulated for the information of his colleagues. The anonymous

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[1] This study was conducted with the support of National Science Foundation grant GB-510.

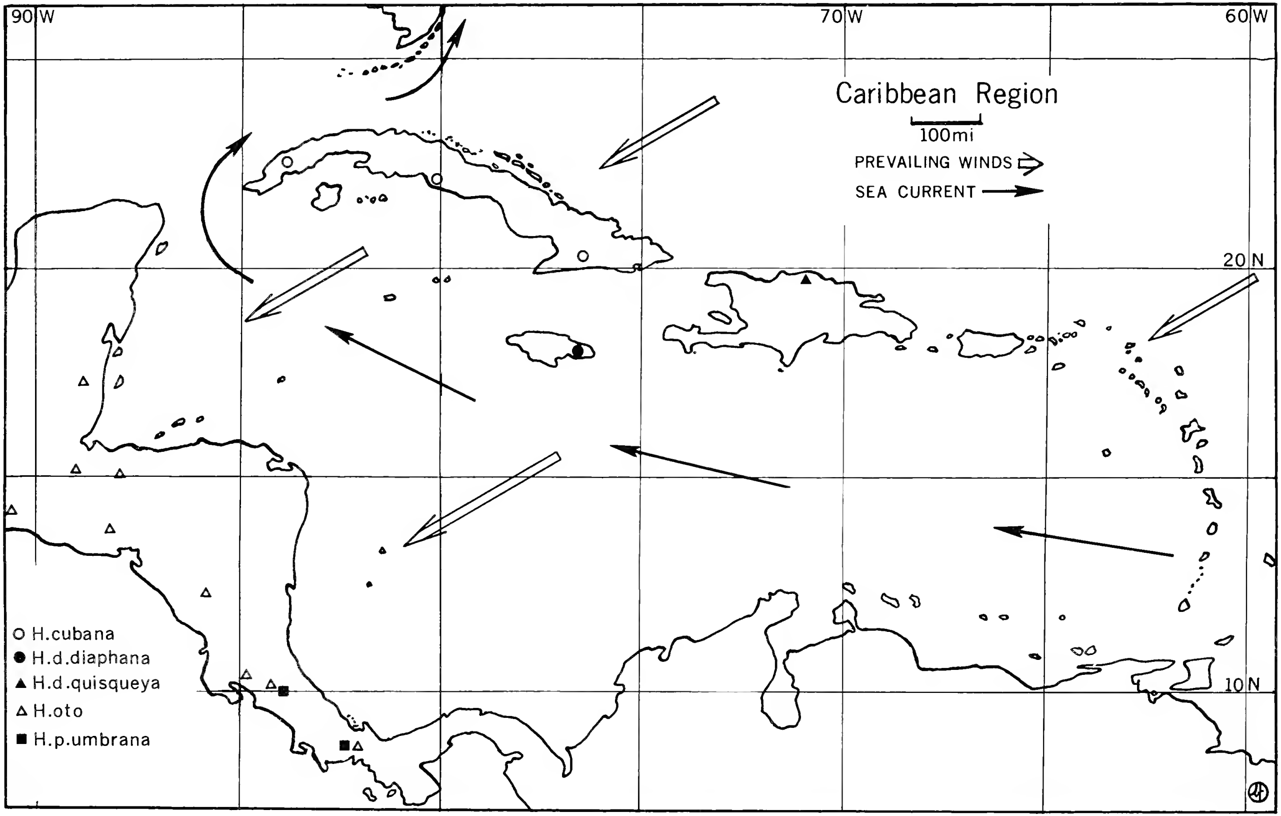

Fig. 1. Map of the Carribbean region showing distribution of the Antillean ithomines and related species.

reviewer saw fit to publish the contents of the Hübner manuscript, but with some unauthorized alterations: some of the proposed generic names were replaced, others were juggled. One of the names juggled was *Hymenitis* and the reviewer used it for insects other than those Hübner intended.

The two objections to accepting the validity of this publication are that the generic name *Hymenitis* has no author, and that the unsigned article was malicious and "scooped" Hübner in a manner which today would be condemned as being unethical.

Hemming avers that the review was in fact written by Illiger, the editor of the journal, but there is no proof of authorship in the article itself. At most, Illiger as editor was responsible for permitting an unsigned review to appear, but responsibility and authorship are not the same things. *Hymenitis* Anonymous was the illegitimate offspring of a mother (the editor), but no father (author) was willing to claim it. Proving that Illiger was the author of the review would not purge it either of anonymity or of unethical intent. In my opinion, the first legitimate publication of *Hymenitis* as a generic name was by Hübner, 1816. Hemming could have cleared the situation best by requesting that the 1807 article be suppressed.

HYMENITIS CUBANA

Hymenitis cubana Herrich-Schäffer, 1862: 118. (Cuba).

Figs. 2 and 7

Gundlach (1881) recorded the larval food plant as *galan* (the local name for a member of the genus *Cestrum,* family Solanaceae) and observed that the insect flies slowly and is nearly invisible in the forest shadows. He reported *cubana* from the mountains at each end of the island and said it seemed to be absent from the central Trinidad range; it since has been captured in the central mountains.

Specimens exmined, 6 ♂, 12 ♀:

Cuba: Sierra Maestra, Oriente, 1000 feet, 1 ♂, 2 ♀ (M.C.Z.)[2]. Loma del Gato, Cobra Range, Oriente, 3000 feet, 2 ♂, 4 ♀ (M.C.Z.). Turquino River, Oriente, 1 ♀ (M.C.Z.). Buenos Aires, Trinidad Mts., 2500-3500 feet, 1 ♂ (M.C.Z.). No station (Oriente, *fide* Bates, 1935), 2 ♂, 5 ♀ (M.C.Z.).

HYMENITIS DIAPHANA

Heretofore known only from Jamaica, a second subspecies from Hispanola is described below. *H. diaphana* is easily distinguished from *H. cubana* because in the former the black marginal band of the forewing follows the wing contour at the apex, while in the latter the black margin is wider and heavier at the apex in males and in females fills

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[2] The following abbreviations are used to indicate museum collections: A.M.N.H., American Museum of Natural History, New York; C.M., Carnegie Museum, Pittsburgh; M.C.Z., Museum of Comparative Zoology, Cambridge.

the entire area beyond the white postdiscal band. Despite these external differences (figs. 2 and 3) the male genitalia of the two species are similar (figs. 7 and 10), though *diaphana* has the saccus, penis and uncus shorter and a different armature at the apex of the valve.

Hymenitis diaphana diaphana (Drury), 1773: 13; pl. 7, fig. 3. (Jamaica).

Figs. 3 and 10

Drury's figure accurately depicts a male and there can be little doubt of the correct identification. Avinoff and Shoumatoff (1948) comment that *diaphana* is "extremely localized, restricted sometimes to a stretch of land a half-mile across. In such places it is very abundant. It never emerges into the bright sunlight from its dense humid habitat." It is found only in the Blue Mountains of eastern Jamaica at about 3000 feet above sea level.


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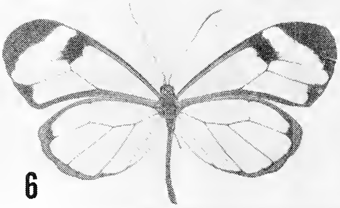
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Fig. 2. *Hymenitis cubana,* a male from the Trinidad range, Cuba.

Fig. 3. *H. d. diaphana,* a male from Corn Puss Gap, Blue Mountains, Jamaica.

Fig. 4. *H. d. quisqueya* new subspecies, holotype male from Mt. Diego de Ocampo, Dominican Republic.

Fig. 5. *H. polissena umbrana,* a male from Cachi, near Mt. Irazu, Costa Rica.

Fig. 6. *H oto,* a male from Mt. Irazu, Costa Rica.

Specimens examined, 74 ♂, 45 ♀:

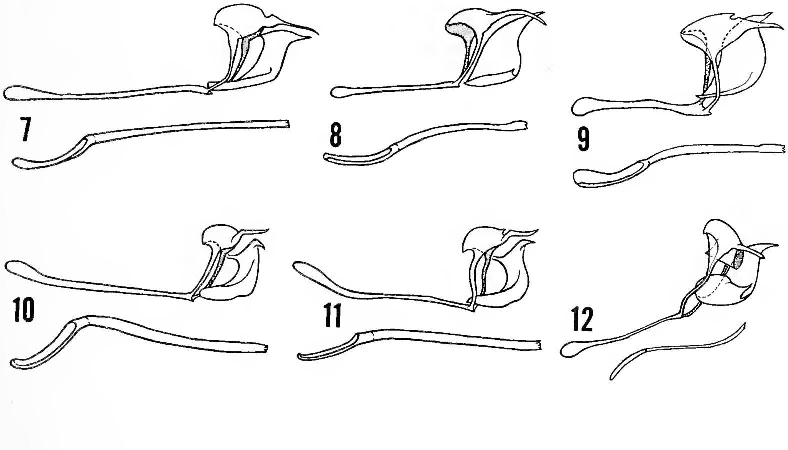
Jamaica: Corn Puss Gap, 37 ♂, 10 ♀ (C. M., M.C.Z.). Cuna Cuna Pass, 31 ♂, 34 ♀ (C.M., M.C.Z.). Fish Brook, 1 ♂, 1 ♀ (C.M.). Moore Town, 2 ♂ (C.M., M.C.Z.). John Crow Hill, 1 ♂ (C.M.). No station, 2 ♂ (A.M.N.H., M.C.Z.).

Hymenitis diaphana quisqueya new subspecies

Figs. 4 and 11

Three males taken by Darlington in the mountains of northwestern Dominican Republic between 3000 and 4000 feet above sea level in July represent an undescribed subspecies and extend the known range of the species to one more island of the Greater Antilles. It is possible that *diaphana* may eventually be found on Puerto Rico.

The Dominican subspecies is similar to *H. d. diaphana* of Jamaica but the following differences are noted in males: The dark discocellular bar of the forewing is narrower and the white costal spot and white scaling on the base of M_1 is only half to two thirds the width of the same markings in *H. d. diaphana.* The black marginal scaling is a little bit wider between M_3 and CU_1 of the forewing and between M_3 and CU_2 of the hindwing, so that this band gives the impression of being of a more uniform width than is true of the Jamaica subspecies. On the underside all dark markings are yellowish brown and appear to be paler than the reddish brown present on *H. d. diaphana.*



Figs. 7 to 12. Male genitalia in lateral view, the left valve removed and the dissected penis below. Fig. 7, *H. cubana.* Fig. 8, *H. oto.* Fig 9, *H. morgane.* Fig. 10, *H. d. diaphana.* Fig. 11, *H. d. quisqueya* new subspecies, paratype. Fig. 12, *H. polissena umbrana.*

The male genitalia do not differ.

Holotype ♂ and two ♂ paratypes: Mt. Diego de Ocampo, Dominican Republic, 3-4000 feet, July 1938, Darlington. Holotype and one paratype in Museum of Comparative Zoology; one paratype in Carnegie Museum (male genitalia number 1172J).

The ancient indian name for Hispanola is said to have been Quisquey.

PHYLOGENY

The coloring and pattern of the wings are difficult to use to associate ithomine subspecies correctly (Fox, 1956) and for that reason must be used with caution to analyze phylogenies. As in many other genera of this family, the wings of *Hymenitis* are mostly transparent and the markings are reduced to the dark marginal bands on both wings, the discocellular band of the forewing and some white scaling beyond the forewing discal cell and faint white spots against the marginal bands. That so many transparent ithomines look so much alike is not part of the "mimicry" phenomenon: transparency is a protective adaption of the species that live within the shadows of the dense forests.

Study of the Ithomiidae demands close attention to morphologic detail both for correct identification and for phylogenetic analysis. The venation of the hindwings suffices to define most of the genera, but to evaluate the relationships among species of a genus, the male genitalia usually are more useful than wing pattern.

Hymenitis diaphana and *H. cubana* differ from all other members of the genus by the extraordinary length of both the penis and the saccus (figs. 7, 10 and 11). These two species share a simply formed triangular valve with two other species, both Central American, *H. oto* (fig. 8) and *H. morgane* (fig. 9). All other *Hymenitis* species have the sacculus of the valve greatly enlarged and produced posteriorward as a prominent projection which may be quite complex in some. *H. polissena umbrana* Haensch has this development of the sacculus present in a less complex form (fig. 12), and in this respect connects the *diaphana* group with the rest of the genus.

The pattern of *H. cubana,* although so strongly reduced, has one pecularity of interest: the black marginal band of the forewing is exceedingly thin in Cu_1-Cu_2, but wide at the anal angle and above Cu_1 and in females the marginal color fills most of the wing apex beyond the white transverse band. This arrangement of the marginal coloring occurs in only one other species of *Hymenitis,* Central American *oto.* Because of the similarities between *cubana* and *oto* with respect both to male genitalia and to pattern, it is evident that these two species are closely related. Because of certain structural features present in *cubana* and not in *oto* — the length of the penis and saccus in males, and the unique shape of the forewing, which is produced to angles at M_3 and at the apex — *oto* must be the more primitive. This by no means indicates that *cubana* necessarily evolved from *oto;* it indicates only that the two species were derived from common stock and that *cubana* has become the more specialized, perhaps because its limited geographic range would favor the establishment and preservation of mutations better than the wide range of *oto*.

The residual black markings of *diaphana* are narrowed to a degree matched only by *polissena* of Costa Rica and western Panama (*H. p. umbrana*) and western Eucador (*H. p. polissena*). Superficially the two species look exactly alike,.but in *diaphana* the discocellular veins of the fore wing are displaced distad so that the discal cell is about two thirds of the wing length, while in *polissena* and all other *Hymenitis* the discal cell is only about one half the wing length. Despite the almost exact duplication of pattern between *diaphana* and *polissena,* which certainly cannot be mimicry, the male genitalia differ markedly Not only is the shape of the valve in *polissena* (fig. 12) more complex, but the penis is of an entirely different shape, being slender, poorly sclerotized and deeply sinuate. *H. polissena* and *diaphana* are not nearly as closely related to each other as are *cubana* and *oto.* The male genitalia of *morgane* (an exclusively Mexican species) are similar to those of *diaphana,* but the patterns on the wings differ greatly.

ZOOGEOGRAPHIC CONSIDERATIONS

The vertebrate fauna of the Greater Antilles seems in general to be related to and derived from the Central American fauna, according to Darlington (1957) and Brown (study in preparation) finds that the butterfly fauna of Jamaica is similarly related; the Antillean Ithomiidae fall into the same pattern. The zoogeographic problem is to ascertain how the fauna of the Antilles got there from Central America and to explain why the South American species are so poorly represented.

For many years it was believed that the Greater Antilles had been physically continuous with Central America until well into Tertiary time and that the existing Antillean fauna was derived, at least in part, from relicts marooned on what became islands when the seas intruded. Schuchert (1935) held this view.

It is no longer believed that when a faunal relationship is shown between two areas separated by seas, such a relationship automatically demonstrates the former existence of a land connection. Simpson (1940, 1953), Darlington (1957) and others have demolished most of the bridges erected by earlier zoogeographers, and only a few such connections are now acceptable. Speculation involving continents drifting about has been put forward in various forms, but continental drift has been used chiefly as a plausible (?) substitute for intercontinental land bridges which otherwise would have had to be discarded.

Animal distribution is generally explained without resort to "Lost Atlantis" or to continental drift. Matthew's theory (1915) of holarctic distribution accounts adequately for the presence of living faunae on all continents and islands; within the framework of Matthew's theory, rafting accounts for much of the dispersal to islands. The term "rafting" may be taken in a general sense, comprising transportation by literal rafts, by aerial means and by "hitch hiking."

Rafts of flotsam, formed in flooded rivers and drifting out to sea, carry many animals. Should such a raft happen to find its way to an island, the surviving individuals could disembark and establish themselves in a new habitat. Transportation by aerial means is well known for spiders and occurs in many other groups, especially for small, light weight arthropods. The power of flight combined with air currents may carry somewhat larger species for great distances. Hitch hiking is usual for arthropods with parasitic or semiparasitic habits.

The hazards involved in rafting by any means are such that the chances of a successful journey — one leading to a new colony of the species — are small indeed, and the hazards are especially great in the flotsam rafts. Flotsam rafts normally break apart at the mouth of the river and at sea they are likely to be well doused by salt water even if no storm is encountered. Should rafted individuals survive exposure and the vagaries of wind and current happen to put them ashore, the landing must be made at or very near a suitable ecological situation. It has been pointed out that, despite the poor probabilities, a succesful trip need occur but once during a very long period of time and it is not difficult to demonstrate mathematically that fortuitous if improbable conditions might pertain occasionally. If the animal being rafted is physiologically able to survive exposure to salt water, or if its habits are such that it may travel in some protected part of the raft, there is a better chance of a successful journey. Presumably most mammals, for example, need only to cling to the flotsam until a landing is made and during the trip they would face a greater hazard from starvation or exposure to sun than from salt water; the larvae of wood-boring insects might be transported safely within their burrows. Conversely, animals without physiological protection against exposure and without habits that would place them in a protected situation *en route,* have a lessend probability for survival.

Transportation by flotsam rafts appears to be out of the question for *Hymenitis*. Salt water would destroy eggs, larvae, pupae or adults and none of these stages is passed in a protected place. Because *Hymenitis* requires a very specific ecological situation, one which is not present near the Antillean coasts, no mathematical calculation of the chances of survival for a long enough time to reach an island has any bearing. If not destroyed by the sea, these insects would still face an overland journey of many miles in order to reach forests 3000 feet above sea level. Furthermore, it seems implausible that ocean currents or the winds (fig. 1) could give much assistance to transporting Central American butterflies to the Antilles.

Aerial transportation also is unlikely in the case of *Hymenitis*, though it cannot be ruled out as a mode of dispersal for other butterflies. Unlike most groups, *Hymenitis* remains within the cover of dense forest and does not seek the sun or open places; the reaction to the least breeze is to drop to the ground and cling. It is conceivable that a hurricane could transport adults, provided the wind were strong enough to suck the insects out of the forest, but not only is the direction of winds toward, not from Central America, but it is hard to imagine that such wind force would not also crush and kill the insects.

If rafting by any method could serve to distribute *Hymenitis* or the other ithomines, one would expect on the Greater Antilles to find representatives of the rich fauna of Colombia, Venezuela and the Guianas rather than of the reduced fauna of Central America, since all factors of wind and current are favorable to rafting from the northern coast of South America but unfavorable to rafting from Central America. Of all the ithomines, *Hymenitis* and other groups with similar habits are the most unlikely to be rafted. If rafting occurred, why are the sun-loving *Mechanitis, Melinaea, Tithorea* and *Hypothyris* not present on on the Antilles?

Darlington (1957) comments, "It might be supposed that the Gulf Stream would prevent drift from reaching the West Indies from Central America and might favor drift transport from South America in spite of the greater distance. But this plausible idea is not supported by facts." I must agree with his view on this matter, but for a reason different than he expressed it. For Ithomiidae there are no facts to support drift (rafting) by any method.

The Greater Antilles stand within the continental shelf, separated from Central America only by shallow seas, and the possibility cannot be dismissed that the two present land areas were once continuous. Such a connection would not be "Lost Atlantis" bridging the deep seas and while there is little evidence to support the connection, there is no geologic evidence against it. Darlington (1957) assumed that the Greater Antilles were formed by oceanic volcanoes because volcanic rocks and marine limestones are present. Woodring (1954), however, commended that, "It is quite evident on ordinary geological grounds that a considerable part of the Caribbean Sea was land during the Cretaceous and that at least some of this land was still land during the Eocene." F. M. Brown (private communication) states that current geologic and oceanographic investigations, partly conducted by private industry and not yet published, are yielding data which seem to indicate that the Greater Antilles were indeed once connected with Central America. At present, the entire question should be regarded without prejudice as on open one.

Schuchert (1935) thought that the Greater Antilles were connected by dry land with Central America along what is now the Nicaraguan swell — a high, wide hump of the sea floor running from Puerto Rico, Hispanola and Jamaica to Honduras and Nicaragua — and by a similar connection between Yucatan and western Cuba. He suggested that the entire island group was part of the Central American mass as recently as the Oligocene and that duuring Miocene time Jamaica, Hispanola and Puerto Rico were connected sporadically with the continent but that Cuba remained insular. Perhaps Schuchert was right.

Proponents of rafting have a second line of defense: the belief that only the geography and climates of late Pliocene and of Pleistocene times exerted significant influence on the distribution of modern faunae. This belief is based on study of vertebrates, and nothing in the present paper is intended as contradictory to the conclusions of students of that phylum. The enviably full fossil record has permitted mamalogists to reconstruct a reasonably complete picture of mammalian evolution during the Tertiary. Oligocene time, for example, need not be considered in connection with the distribution of most mammals, since modern mammal species were not yet in existence.

Zoogeographers working with invertebrates, particularly with groups like Lepidoptera for which there is almost no significant fossil record, must rely upon principles of evolution and zoogeography developed by mammalogists. "The fundamentals of invertebrate distribution are substantially the same as those affecting vertebrates . . . The salient difference is timing" (Miskimen, 1961). Jeannel (1949) pointed out that, "the antiquity of insects becomes evident when compared with that of vertebrate groups. The Tertiary and Quaternary lasted for 30 million years[3] and comprised the entire evolution of the placental mammals; but at the beginning of the Tertiary, most insect genera already existed much as they do today." According to Vandel (1949), "The most evolved orders of insects (Lepidoptera, Diptera, Hymenoptera) made their appearance during the Mesozoic epoch. At the beginning of the Tertiary, the living entomological fauna [of the world] was definitely constituted and thereafter underwent no important alteration." To evaluate insect distribution it is necessary to consider events of the entire Tertiary, not just the effects of recent glaciations.

There is no doubt that the insect fauna of the north temperate zone was profoundly affected by Pleistocene glaciation: the extent of influence of glaciation on tropical and subtropical faunae is less clear and in many regions may have been negligible. In all situations there is a basic difference between the effect of the Pleistocene upon mammals and its effect upon insects: mammals were evolving, insects had already evolved modern genera and species. Recent glaciation superimposed certain geographic adjustments on pre-existing distributional patterns of insects, but created the distributional patterns of modern mammals.

[3] Today we know the time estimate should be much longer.

The Ithomiidae is one of the most primitive families of the Nymphaloidea (Fox, 1956) and must be of considerable antiquity. The fact that one genus (*Tellervo*) is found in the East Indies while the rest are neotropical suggests that the family must have been in existence at the opening of the Tertiary. Even though *Hymenitis* is one of the more specialized genera of the family, it probably was in existence in Oligocene time. Thus if Schuchert's connection between the Greater Antilles and Central America during Oligocene or Miocene actually existed, it would have provided a distributional route to the Greater Antilles for these butterflies.

An objection to land route distribution — the same objection that arises to rafting — is the question of why only certain *Hymenitis* species are found on the islands. This is a question which cannot be answered definitely, no matter which method of dispersal is postulated, but it is easier to imagine that *Hymenitis* managed to survive while other genera became extinct than it is to imagine that *Hymenitis* alone of all the ithomines managed to beat the odds and find its way to the islands from Central America.

SUMMARY

1. The only Ithomiidae found on the Antilles are *Hymenitis cubana* on Cuba, *H. d. diaphana* on Jamaica and *H. d. quisqueya* (herein described) on Hispanola.

2. The affinities of these Antillean ithomines are with certain Central American *Hymenitis*. All are transparent-winged inhabitants of the humid forests, shunning sunlight and open situations; all are found from 1000 to 7000 feet above sea level.

3. Distribution by rafting is unlikely because of the direction of sea and air currents and because of the habits and fragility of *Hymenitis*. If rafting ever distributed ithomines, the fauna of Venezuela and the Guinas and the hardier sun-loving should be represented on the islands.

4. Alternatively, these ithomines may have reached the Antilles during early Tertiary time if, as Schuchert and others thought, the islands once were continuous with Central America.

REFERENCES CITED

ANONYMOUS, 1807. Allg. Lit. Zeitg., Halle [Jena], 2. [*fide* Hemming, 1934]

AVINOFF, A. and N. SHOUMATOFF, 1946. An annotated list of the butterflies of Jamaica. *Ann. Carnegie Mus.,* 30: 263-295.

BATES, M., 1935. The butterflies of Cuba. *Bull. Mus. Comp. Zool.,* 78: 65-258.

DARLINGTON, P. J., JR., 1957. Zoogeography: the geographical distribution of animals. John Wiley & Sons, Inc., New York.

DRURY, D., 1773. Illustrations of natural history, 2. London.

FOX, R. M., 1956. A monograph of the Ithomiidae. Part I. *Bull. Amer. Mus. Nat. Hist.,* 111: 7-76.

GUNDLACH, J., 1881. Contribucion a la entomologia Cubana. Havana.

HEMMING, F., 1934. The generic names of the holarctic butterflies. British Museum (Natural History), London.

HERRICH-SCHAEFFER, G. A., 1862. Schmetterlinge aus Cuba. *Corresp.-Blatt zoo.-min. Ver. Regensburg,* 16: 118-120.

HÜBNER, J., 1816-1826. Verzeichniss bekannter Schmetterlinge. Augsburg.

JEANNEL, R., 1949. Les Insectes Fossiles. *in* P.-P. Grassé, *Traité de Zoologie,* 9: 18-85. Masson et Cie, Paris.

MATTHEW, W. D., 1915. Climate and evolution. Reprint 1939, New York Academy of Sciences.

MISKIMEN, G. W., 1961. Zoogeography of the coleopterous family Chauliognathidae. *Syst. Zool.,* 10: 140-153.

SCHUCHERT, C., 1935. Historical geology of the Antillean-Caribbean region. John Wiley & Sons, Inc., New York.

SIMPSON, G. G., 1940. Mammals and land bridges. *Jour. Washington Acad. Sci.,* 30: 137-163.

——— 1953. Evolution and geography. Oregon State System of Higher Education, Eugene, Oregon.

WOODRING, W. P., 1954. Caribbean land and sea. *Bull. Geol. Soc. Amer.,* 65: 720-730.

VANDEL, A., 1949. Généralitiés sur les Arthropodes. *in* P.-P. Grassé, *Traité de Zoologie,* 6: 79-158.

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OVIPOSITIONAL PREFERENCE TESTS WITH PIERIS

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Los Angeles State College, Los Angeles, California

PREVIOUS REPORTS BY US (Hovanitz and Chang, 1962, 1963) have described the results of larval selections of various food plants. The present paper continues this series of reports by describing the selections made by the female adults on various food plants for the purpose of egg laying. A similar type of study has been made by Takata (1961) using *Pieris rapae crucivora,* though with somewhat different results. This study will be mentioned below.

METHOD

The ovipositional tests were made in marquisette-covered cages, 18″ x 18″ x 24″ tall. The plants used in each test were living, potted plants grown in the glass house. In any given test, the plants selected were all of about the same size and were relatively small so as to fit in the dimensions of the cage size without severe crowding. The differing shapes, growing habits and leaf sizes of the plants used were variables which could not be controlled. There is no doubt that these factors might have some influence on egg laying of the adult females.

The females were placed in the cages with the respective plants and allowed to mate and to oviposit. The eggs were counted periodically for the totals indicated in the tables. The females used in each cage varied in number from five to fifteen but the average was between five and ten. These were fed honey and water solution in the mornings during the course of each test.

RELATIONSHIP BETWEEN OVIPOSITIONAL PREFERENCE OF THE FEMALE AND THE FOOD PLANT STRAIN OF ITS LARVA

A relationship is apparent between the ovipositional preference of the adult female and the food plant eaten by its larva. This relationship may be seen in table 1 in which strain A, *Pieris napi,* laid more eggs on its ancestral food plant *Dentaria* than on any of the other plants

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[1] Aided by a grant from the National Science Foundation, Washington, D.C.

Table 1. Ovipositional selections by adults of *Pieris*

A Species	Mustard	Kale	Nasturtium	Dentaria	Isomeris	Total	Natural food plant
napi	82 31.66%	43 16.6%	28 10.81%	105 40.54%	1 0.38%	259	Dentaria
B Species	Mustard	Kale	Nasturtium	Lepidium	Isomeris	Total	Natural food plant
protodice	305 23.55	12 0.92	6 0.46	536 41.31	436 33.67	1295	Lepidium
C Species	Mustard	Kale	Nasturtium		Isomeris	Total	Natural food plant
protodice	417 67.58	41 6.64	3 0.49		156 25.28	617	Mustard

Table 2. Ovipositional selections by adults of *Pieris protodice*
Strain C from wild (Laguna Canyon on mustard), C → D 2 generations on Kale
↘ E 2 generations on mustard

Species	Mustard	Kale	Nasturtium	Isomeris	Total	Natural food plant
C protodice	417 67.58%	41 6.64%	3 0.49%	156 25.28%	617	mustard
D protodice	190 26.39	210 29.17	23 3.19	297 41.25	720	
E protodice	378 60.87	43 6.93	1 0.16	199 32.05	621	

tested. Over forty percent were laid on *Dentaria*, about thirty-two percent on black mustard (*Brassica nigra*), about seventeen percent on kale and less than one percent on Isomeris, out of a total of 259.

This relationship is further apparent in the data of strain B, *Pieris protodice* (table 1). A strain of this species from Mono Lake, Calif. where the native food plant is *Lepidium,* laid forty-one percent on *Lepidium,* about twenty-four percent on mustard, about one percent on kale and thirty-four percent on Isomeris, out of a total of 1295. The high percentage on *Isomeris* is interesting in view of the fact that Isomeris does not exist in Mono Lake area.

Another strain of *Pieris protodice* from Laguna Canyon, Orange county, Calif., strain C, where the food plant is black mustard, gave different results. Females of this strain laid nearly sixty-eight percent of their eggs on black mustard, seven percent on kale, less than one percent on nasturtium and twenty-five percent on Isomeris. Unfortunately, there was no Lepidium available for testing with these females.

The two tests with *Pieris protodice* show a quantitative relationship between the selection by the females and the odor of the plants selected. Excluding naturtium, the plants may be arranged in the order Isomeris, *Lepidium,* mustard and kale in the direction from strong odor to weak odor. Females with *Lepidium* ancestry show a higher selection for plants with a stronger odor, and plants with a mustard ancestry show selections favoring a decreased odor requirement. In Table 1, strain B (Lepidium ancestry) shows a selection toward Isomeris of 33 compared with 25 for strain C (mustard ancestry). Likewise, strain B shows only one percent toward kale as compared with seven percent for strain C. The increase in selection of the mustard strain toward mustard (68 percent as compared with 23 percent) is therefore not the whole picture, as comparable changes occur also with the other plants.

CHANGE OF OVIPOSITIONAL PREFERENCES BY FOOD PLANT CHANGES OF THE LARVAE

Changing the food plants fed the larvae has the direct effect of changing the plants selected by the adult females for egg laying. Table 2 shows the effect of splitting strain C (table 1) into two strains, one fed on kale (D) and the other fed on mustard (E). These were grown for two generations on the respective food plants.

The results indicate an increased selection for kale by the kale strain, 29 percent as compared with 7 percent. The strain kept on mustard (E) did not vary greatly from the selections made by the original parents strain (C).

Table 3. Ovipositional selections by *Pieris rapae*, parent strains, F_1 and F_2. Larvae always fed on food plant of female parent. Parent strains, 10 or more generations on a particular plant.

	Mustard	Kale	Nasturtium	Cleome	Isomeris	Total
Parents						
mustard-strain	1080 86.81%	24 1.92%	38 3.05%	80 6.43%	22 1.70%	1244
Kale-strain	125 18.65	433 64.62	70 10.4	28 4.1	14 2.08	670
F_1						
M ♀ xK ♂	467 34.92	346 25.87	471 35.22	12 0.89	41 3.06	1337
K ♀ x M ♂	263 23.88	328 29.61	466 42.32	35 3.17	11 0.99	1101
F_2						
M ♀ x K ♂	969 47.57	644 31.60	344 16.40		90 4.42	2037
K ♀ x M ♂	567 29.50	783 40.70	486 25.29		86 4.47	1922

Table 4. Ovipositional selections by *P. rapae* reared on *Isomeris* for a given number of generations, 1961 tests.

Generation	Mustard	Kale	Isomeris	Nasturtium	Total
Second	148 47.20%	91 29.1%	1 3.2 %	73 23.3 %	313
Fourth	237 54.50	91 20.0	162 23.9	10 1.6	500

A similar relationship has been found with *Pieris rapae* (Table 3). A strain kept for 10 or more generations on mustard in the laboratory was compared with a strain grown an equal length of time on kale. The mustard bred strain showed a selection of 87 percent on mustard as compared with a selection by the kale strain of only 19 percent on that plant; the kale strain adults selected kale 65 percent of the time as compared with only 2 percent on kale from the mustard strain.

Pieris rapae, which have been switched over from kale or mustard to Isomeris, also show an increased preference for the latter plant but the selections take a lot longer period of time to become effective. It has previously been shown that larvae of *Pieris rapae* grown on kale for the first time have a high mortality rate approaching the lethal condition. However, after a number of generations they are able to survive satisfactorily on the new food plant. Ovipositional tests (Table 4) of *Pieris rapae* reared on Isomeris show that adults from the second generation of larvae fed on Isomeris show little change in their selection. Most eggs are still laid on mustard with a high proportion on kale and nasturtium. In the fourth generation however, there are 24 percent of the eggs laid on Isomeris and a corresponding drop in those laid on nasturtium. A more complete series of tests of this sort is shown in Table 5 which will be discussed below.

GENETIC CHANGE OF OVIPOSITIONAL PREFERENCES AS SHOWN BY INTERSTRAIN CROSSES

The genetic significance of the changes in ovipositional preferences as created by larval feeding habits are shown by crosses involving parent strains, one of which has been adapted to kale and the other to mustard (Table 3). The parent strains have been grown for ten or more generations on their respective food plants and show a high ovipositional selection for their own larval food plants (fig. 1).

The F_1 of the cross kale-strain female X mustard-strain male was grown on kale and the reciprocal cross was grown on mustard. Ovipositional preferences in the first of these two crosses indicate that the F_1 adults, even though fed on kale as larvae, did not select kale to the extent of the kale parental strain. There was a drop in selection of kale from 65 percent to 30 percent. The increase appears to have all gone to the selection of nasturtium (fig. 2).

In the reciprocal cross, the F_1 larvae were grown on mustard. The adults from these larvae dropped in their selection of mustard from 87 perecent to 35 percent. The increase in this case was not only toward nasturtium but also toward kale.

It is clear from these crosses that the genes for the inheritance of food plant preferences by the adult for ovipositional purposes is transmitted through the male as well as through the female. Indications

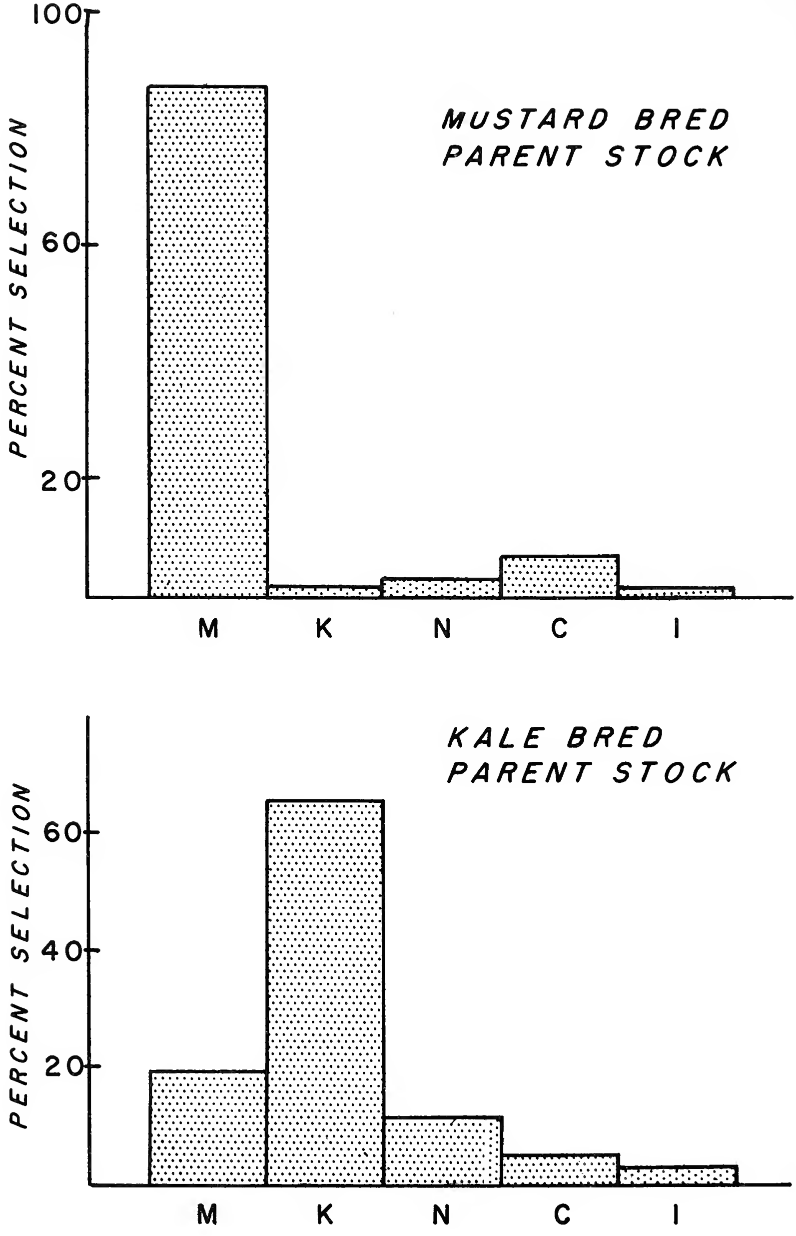

Fig. 1. Oviposition selection by females of *Pieris rapae* for the plant on which the strain has been maintained for more than 10 generations.

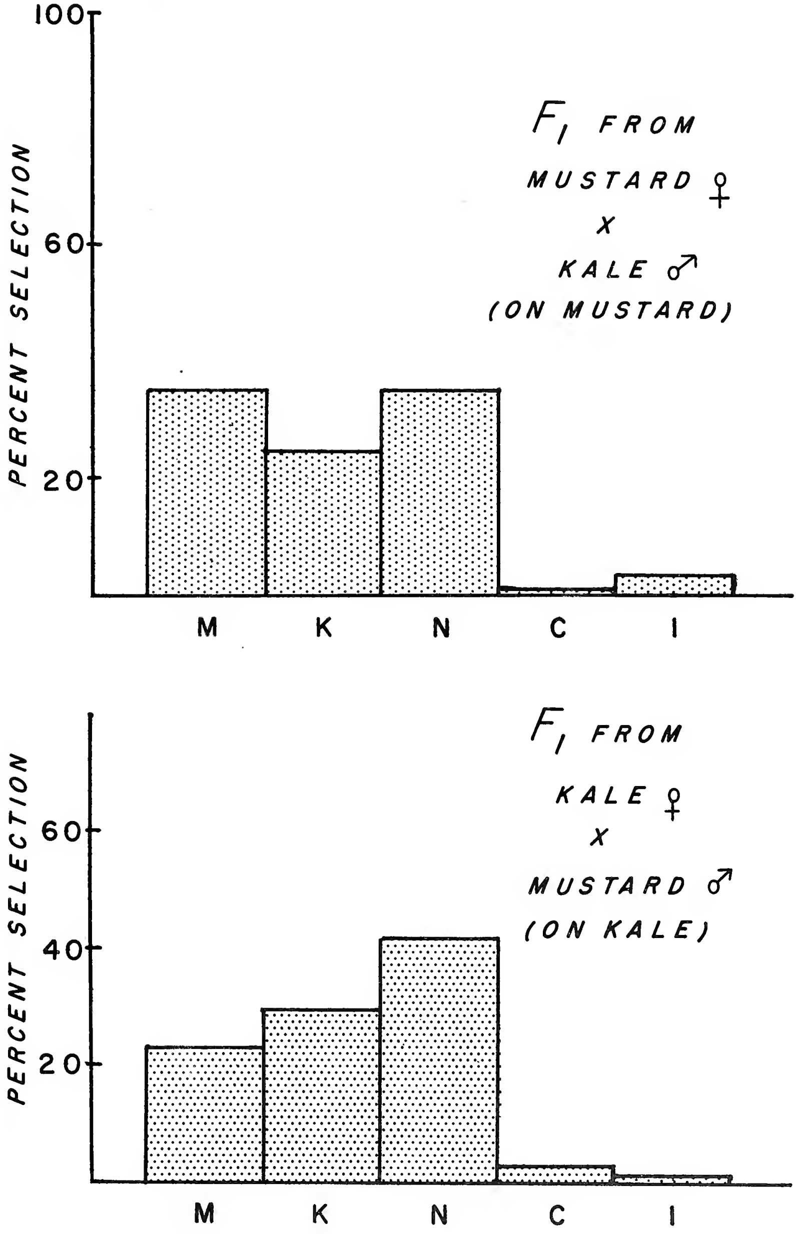

Fig. 2. Oviposition selection by females of *Pieris rapae* produced by crossing mustard and kale strains to obtain the F_1.

Table 5. Ovipositional selections by adults of P. rapae grown on nasturtium for a given number of generations. (former plant, kale)

Generation	Mustard		Kale		Nasturtium		Isomeris		Total
1	546	36.27%	662	43.98%	297	19.73%	0	0	1505
3	100	8.31	555	46.09	463	38.45	86	7.14 %	1204
5	97	26.50	106	28.96	163	44.53	0	0	366
7	186	32.12	113	19.51	194	33.50	86	14.85	579
8	16	17.02	16	17.02	35	37.23	27	28.72	94

Table 6. Ovipositional selections by adults of P. rapae grown on Isomeris for a given number of generations. (former plant, kale)

Generation	Mustard		Kale		Nasturtium		Isomeris		Total
1	330	45.70%	299	41.41%	61	8.44 %	32	4.43 %	722
3	55	28.94	108	56.84	5	2.63	22	11.57	190
5	333	34.43	481	49.74	77	7.90	76	7.85	967
7	237	26.93	307	34.88	47	5.34	289	32.84	880
9	76	30.27	90	35.80	17	6.77	68	27.09	251
11	192	26.32	363	49.59	38	5.15	139	18.99	732

Table 7. Ovipositional selections by adults of *P. rapae* grown on kale for a given number of generations. (former plant, kale)

Generation	Mustard		Kale		Nasturtium		Isomeris		Total
1	340	42.55 %	389	48.88%	40	5.04 %	27	3.39 %	796
3	204	18.08	778	68.79	95	8.42	53	4.70	1128
5	402	19.97	1397	69.39	152	7.55	62	3.07	2013
7	91	27.00	208	61.72	30	8.90	8	2.37	337
8	100	36.90	102	37.63	31	11.44	38	14.02	271
9	128	18.57	299	43.40	109	15.82	153	22.21	689
10	341	41.13	375	45.23	45	5.40	68	8.20	829
12	627	23.92	1574	60.07	54	2.06	367	14.00	2622

Table 8. Ovipositional preference of *P. protodice* females from Palm Springs (area of *Isomeris*).

Mustard		Kale		Nasturtium		Isomeris		Total
142	41.16%	1	0.29%	0	0	202	58.55%	345

that these traits may be maternally inherited are therefore not wholly if at all true.

The F_2 of the mustard female F_1 and the reciprocal shows a somewhat similiar selection pattern as the F_1, with the exception that the selection of nasturtium has been reduced in favor of both mustard and kale (fig. 3).

RATE OF CHANGE OF OVIPOSITIONAL PREFERENCES OVER A PERIOD OF SEVERAL GENERATIONS

The rate of change of ovipositional preferences during the course of several generations has been studied in three series, one in which the larvae have been bred on nasturtium, one on Isomeris and one on kale. These data are indicated in tables 5, 6 and 7.

Nasturtium is not a normal food plant of *Pieris rapae,* but colonies of the insect have become adapted to the plant both in Europe and in the United States. Larvae from a strain previously fed on kale were transferred to nasturtium and maintained on that plant for eight generations. Adults from some of these generations were tested for their preferences toward kale, mustard, nasturtium and Isomeris. The normal selection of kale strain adults to Isomeris is about 10 percent (Table 3). The first generation after the larvae were fed nasturtium, the selection went up to 20 percent, the third generation 38 percent, the fifth generation 45 percent, the seventh generation 34 percent and the eighth generation 37 percent. The lack of any change above 34 percent may mean that this is the best possible selection that can be obtained after any amount of selection.

It is significant that during the course of these selections for nasturtium, selection for kale went progressively down and that at the same time selection for Isomeris went progressively up. As has been previously pointed out, this result may be due to the stronger odoriferous substances present in nasturtium and Isomeris, absent in kale.

Isomeris is not known to be a wild food plant for *Pieris rapae* anywhere. Larvae are, however, able to survive on this plant, especially after conditioning. Larvae from a strain fed previously on kale were trensferred to Isomeris and maintained on this plant for eleven generations. The normal selection of kale strain adults to Isomeris is about 2 percent (Table 3). The first generation of adults from larvae fed on Isomeris selected this plant 4 percent of the time, the third generation 12 percent of the time, the fifth generation 8 percent of the time, the seventh generation 32 percent of the time, the ninth generation 27 percent of the time and the eleventh generation 19 percent of the time (fig 5). A significant increase is apparent, though the variation is somewhat great, and this increase is additive for several generations. It is of interest that the selection of Isomeris, though

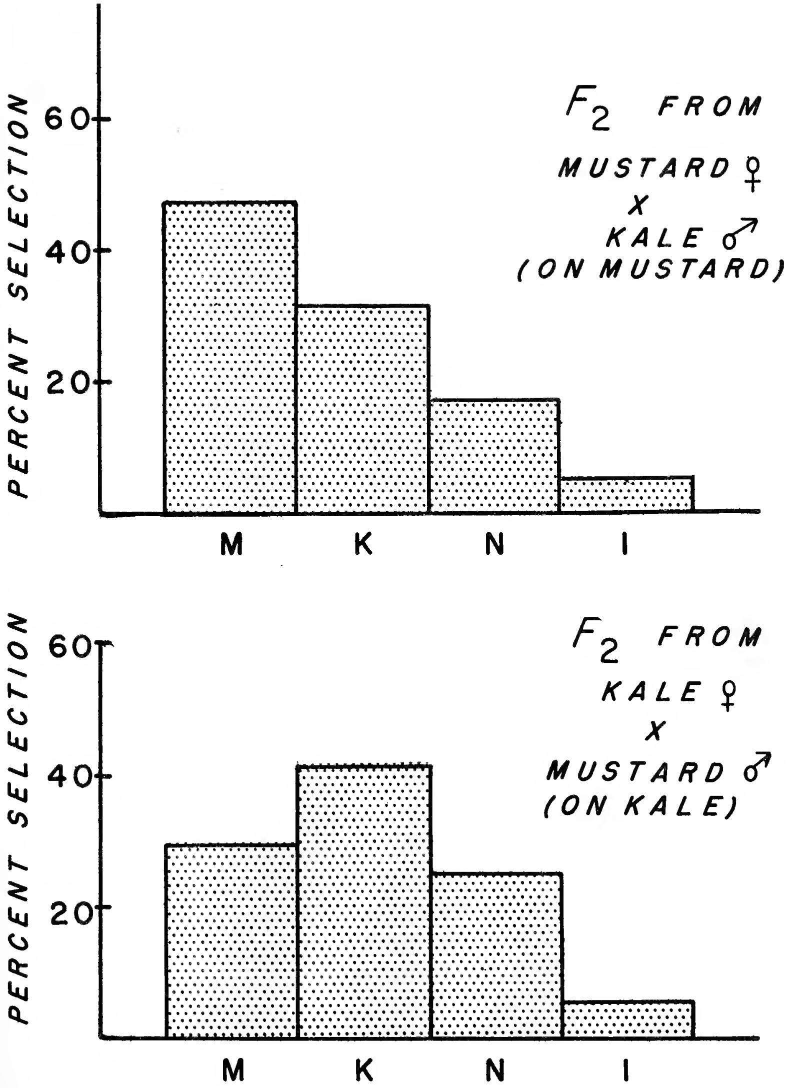

Fig. 3. Oviposition selection by females of *Pieris rapae* produced by crossing the F_1 individuals indicated in fig. 2.

increased, is never greater than that for kale and only comes close to duplicating the selections for mustard.

Strains grown on kale for twelve generations, after originating from wild individuals growing on mustard, were tested in the third experiment. A mustard strain selected kale about two percent of the time. After one generation on kale, the selection of kale was 48 percent, after three generations 69 percent, five generations 69 percent, seven generations 62 percent, eight generations 38 percent, nine generations 43 percent, ten generations 45 percent and twelve generations 60 percent (fig. 6). Again there is no doubt of the increased rate of selection of the larval food plant by the adults for the first few generations though there are somewhat erratic results thereafter due to unknown causes. In fact after three generations the selections of kale were as good as is expected in a strain kept permanently on kale (Table 3).

This experiment indicates that adaptation to kale is much faster than to plants such as Isomeris and nasturtium, and is also much more effective.

ADDENDUM

The following data were made available after the previous portion of this paper was written. Adults of *Pieris protodice* were collected in the vicinity of Palm Springs, in an area typical of the Coachella desert. As a result it cannot be anticipated that the cruciferous plants typical of coastal California were present. Instead, the bushes of Isomeris are the most abundant plants of this group. These females were allowed to oviposit in tests as the preceding, with the result that Isomeris was the plant most commonly selected (59 percent) with mustard in abundance (41 percent) (Table 8). These data compare with *P. protodice* selections in an area where mustard is the wild food plant as follows: Isomeris 25 percent instead of 59 percent, and mustard 67 percent instead of 41 percent.

DISCUSSION AND CONCLUSIONS

These results of ovipositional experiments illustrate the same events as have been shown previously for *larval* selections of food plants, namely that previous exposure to a plant is correlated with the selection of that plant by the particular insect. This increase of selection occurs not only in the first generation of exposure, but also after subsequent generations of exposure. It is easier to change the selection of Pieris toward kale than it is toward Isomeris or nasturtium. This is true both with respect to the speed with which the change is made as well as in the extent to which the change occurs.

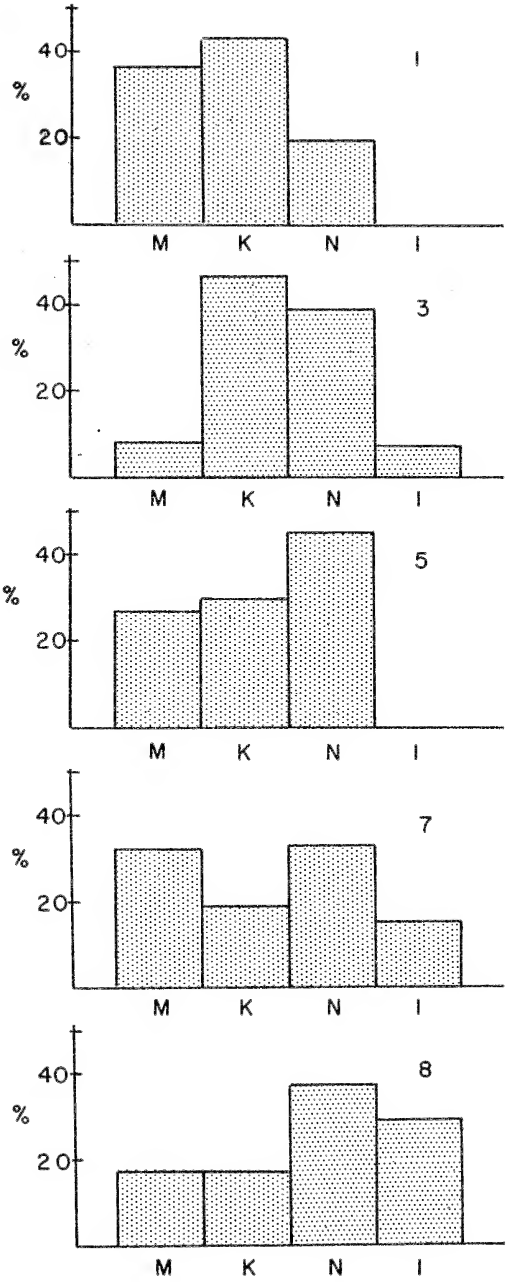

Fig. 4. The change in ovipositional selection by adults of *Pieris rapae* after 8 generations of growing on nasturtium.

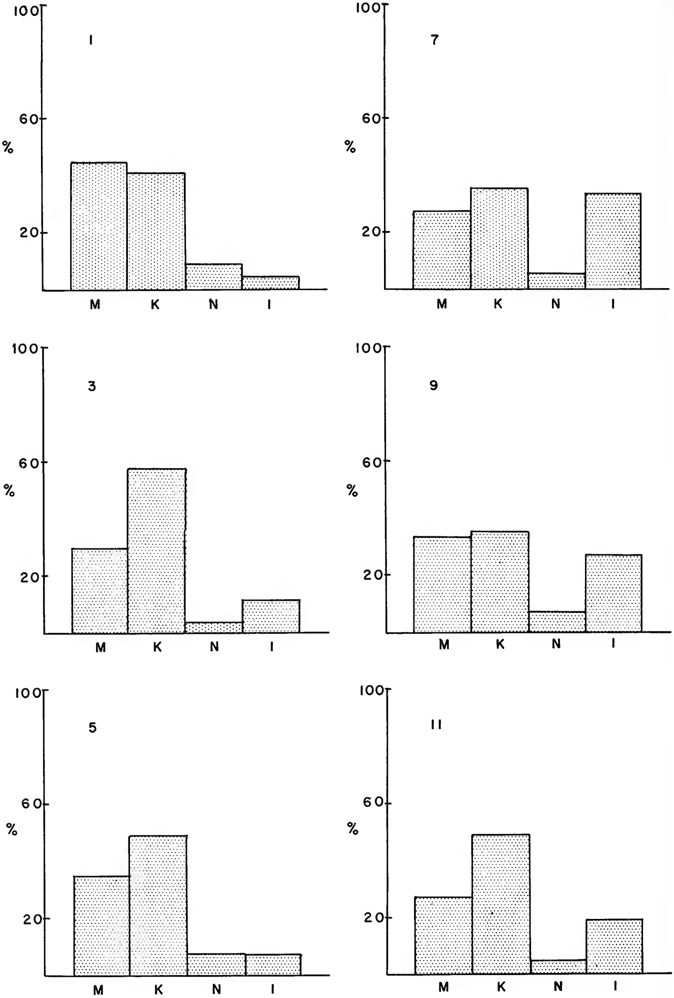

Fig. 5. The change in ovipositional selection by adults of *Pieris rapae* after eleven generations of growing on Isomeris.

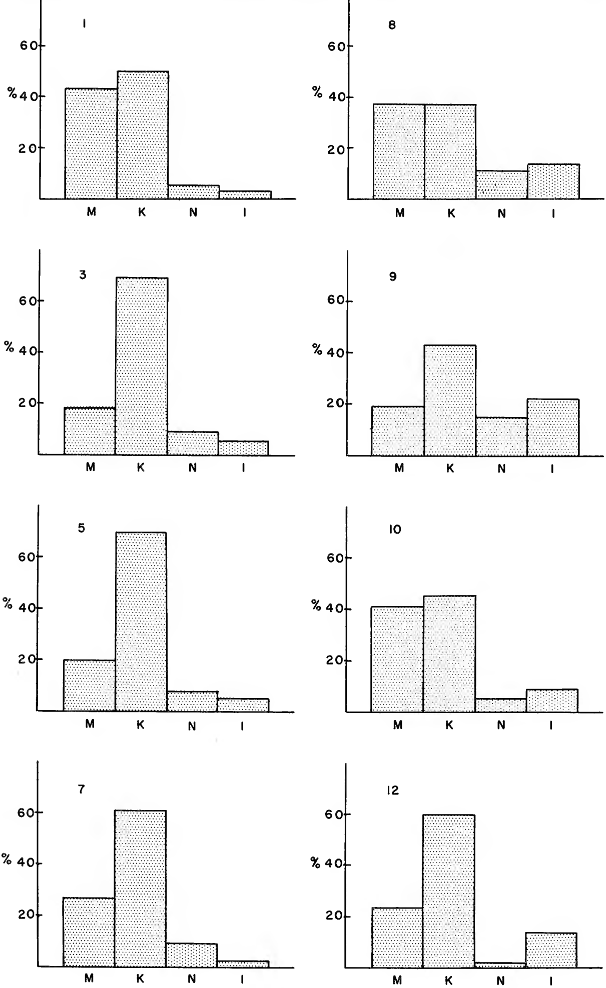

Fig. 6. The change in ovipositional selection by adults of *Pieris rapae* after twelve generations of growing on kale.

The heredity of the food plant selections has been tested by both F_1 and F_2 crosses. The results indicate that the F_1 selections are intermediate between the parental selections and that the F_2 is also, but the latter tends to match the food plant on which the F_2 larvae are fed. An unknown cause accounts for a heavy increase in selection of nasturtium in the F_1 which is not so apparent in the F_2. The gene or genes for the food plant specificities is clearly carried both by the males as well as by the females and there is no sign of maternal inheritance, except a psuedo-maternal effect which is imposed upon the progeny by the food directly eaten by them.

These results are directly opposed to those of Takata (1961) in which he says: "If the larvae were reared with cabbage for successively many generations, the emerged butterflies tended more and more to avoid cabbage as their ovipositing plant, as the successive life on cabbage was lengthened . . . The direction of the change was quite inverse to that of the larval food preference, which was shown by that the larvae preferred the host plant on which they and their ancestors had been fed." No reason can be given for the difference between his results and ours, nor is their any clue as to what it might be with the one exception: In our own experiments, more than two plants were available both for larval selections as well as for adult selections. It was possible in our experiments therefore for the adults to select some plant other than the two being tested in case neither of the original two were satisfactory. As an example of this phenomenon, in the F_1 of the mustard-kale strain crosses, the greatest proportion of the adults selected nasturtium rather than either mustard or kale. Had nasturtium not been available, the adults would have had to choose between two plants neither of which was preferred. Something of this sort might explain the results of Takata.

LITERATURE CITED

HOVANITZ, W. and V.C.S. CHANG. 1962. Three factors affecting larval choice of food plant. *J. Res. Lepid.* 1(1): 51-61.

———— 1962. The effect of various food plants on survival and growth rate of Pieris. *J. Res. Lepid.* 1(1): 21-42.

———— 1963. Change of food plant preference by larvae of Pieris rapae controlled by strain selection, and the inheritance of this trait. *J. Res. Lepid.* 1(2): 163-168.

———— 1963. The effect of hybridization of host-plant strains on growth rate and mortality of Pieris rapae. *J. Res. Lepid.* 1(2): 157-162.

TAKATA, N. 1961. Studies on the host preference of common cabbage butterfly, *Pieris rapae crucivora* (Boisduval). XII. Successive rearing of the cabbage butterfly larva with certain host plants and its effect on the ovipositional preference of the adult. *Jap. J. Ecology* 11: 147-154.

Journal of Research on the Lepidoptera 2(3)201-203, 1963

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NOTES ON THE EARLY STAGES OF DREPANULATRIX MONICARIA (GUENEE) (GEOMETRIDAE)

JOHN ADAMS COMSTOCK
Del Mar, California

THE LIFE HISTORY of this moth has been treated at some length by Dr. Frederick H. Rindge in his classic "Revision of the Genus" in 1949. No illustrations were included other than of the genitalia.

I have recently reared this species, and made drawings of the egg, first instar larva, final instar larva and pupa. The brief notes accompanying these drawings will serve to supplement, and in a few particulars to amplify Dr. Rindge's text.

A gravid female of *Drepanulatrix monicaria* was captured on May 22, 1962, in Del Mar, California. Numerous eggs were laid May 23 and 24. These were laid singly on their sides. They hatched June 3 and 4.

EGG: The egg is ovoid, the base flattened and the top regularly rounded. It is 0.75 mm. high by 0.50 mm. wide on the average.

The accompanying drawing, (figure 1A) shows it in an upright posture on which I base the measurement of height and width, but Dr. Ridge gives its measurement in relation to the normal prone position, hence the disparity in our terms.

I could detect no "flattening" of viable eggs, nor any that were "wedge shaped."

When first laid, the color was a glistening greenish white. Subsequently it changed to mottled and streaked reddish orange of varying intensities. The surface is covered with longitudinal ridges, approximately 24 in number. Each ridge carries a line of minute pearl-like nodules along its edge. Between the ridges there are transverse lines or low ridges. The base is covered by irregular hexagonal cells with raised walls. The longitudinal ridges seem to fuse into a slightly pitted surface over the rounded top, but no regular micropyle could be detected.

The egg is very similar to that of *Drepanulatrix hulsti*, but is smaller.

The young larvae exit from one end, the remainder of the shell being left intact.

The recorded food plants for this species are *Ceanothus thyrsiflorus* Eschs., *C. macrocarpus* Nutt., *C. spinosus* Nutt., and *C. sorediatus* Hooker & Arnott. Our young larvae readily accepted the first named plant.

FIRST INSTAR LARVA: Length, 3 mm.

Head width, 0.30 to 0.33 mm. Color, glistening yellow, with a narrow dark margin on the edge of the posterior juncture with the first body segment. Ocelli, black. There is no spotting on any portion. Setae, short and colorless to white.

Body; ground color, light yellow-green, with a wide middorsal band which is olive-green on the first two segments, shading into red-brown caudally.

The first segment is narrower than the head and wider than the second segment. The light green on this segment is slightly tinged with yellow. The black papillae on the body are relatively smaller than those on *Drepanulatrix hulsti,* but occupy much the same positions. They are narrowly encircled at their bases by white, in strong contract to the wide white circlets on *D. hulsti.*

The setae are black. A substigmatal band is usually present.

The first larval instar is shown in dorsal aspect on figure 1B.

FINAL INSTAR: This is given in detail by Dr. Rindge in his Revision. The wide variation in color and markings is particularly noteworthy. No two examples are exactly alike. The color ranges from a smoky gray (almost black and heavily spotted) to a rich spotted green. Two dark examples have a discontinuous middorsal line of burnt orange. The green and tan examples lack this, or show only slight suggestions of it. All types are sprinkled with either light or dark spots. The specimen I selected was probably in the early phase of the final instar and not fully grown as it measured only 13 mm. It is pictured in lateral aspect on figure 1C. In this example the head was yellow and the body green, with white spots.

PUPA: Length, 10 mm. Greatest width, 3 mm. Head well rounded. Eyes not prominent. Antennae and maxillae extending to wing margins. Abdomen tapering to cremaster,—the latter ending in a large papillus which bears four recurved hooklets each side of the median line. Two of these, centrally placed, are relatively long. All arch laterally.

The color of the chrysalis is deep brown, with a slight tinge of green on the wing cases in newly formed pupae. The surface texture is glistening.

The pupa is shown in figure 1D. An enlarged figure of the cremaster is included on figure 1E.

The first imago emerged July 23, 1962.

This moth ranges along the Pacific coast from southern Alaska to the Mexican border, and perhaps into northern Baja California.

Dr. Rindge recorded three parasites, i.e. *Chaetophlepsis* sp., *Patelloa* sp., and *Apanteles* sp.

REFERENCES

RINDGE, FREDERICK H. 1949. A Rev. of the Geometr. Moths formerly assigned to Drepanulatrix. Lepidoptera. *Bull. Am. Mus. Nat. Hist.* 94: (59) pp. 233-298. Egg, larva, pupa, food pl.

McFARLAND, NOEL. 1959. In litt. 1/21/'59. Food pl.

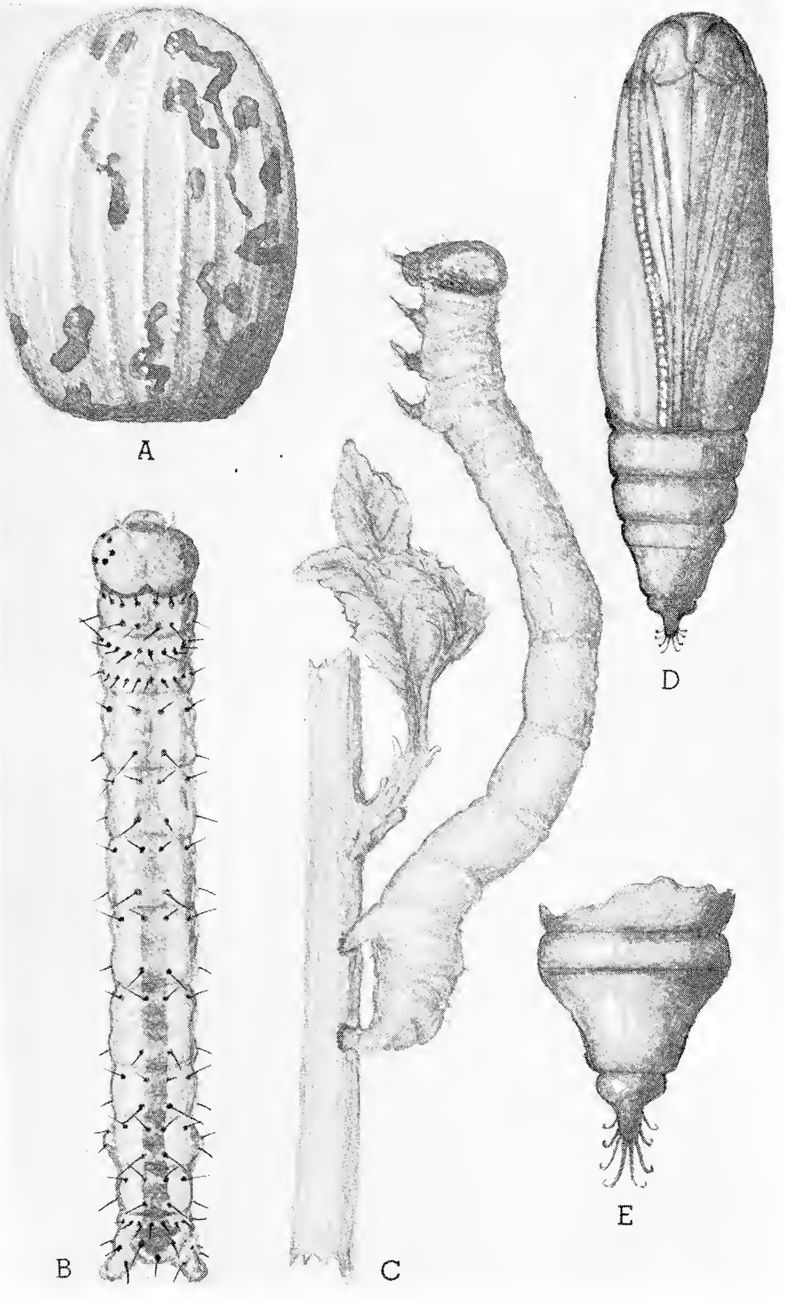

FIGURE 1. Early stages of *Drepenulatrix monicaria* (Guenée) *A. Egg*, enlarged X 90. B. First instar larva, enlarged X 40. C. Mature larva on twig of *Ceanothus*, enlarged X 10. D. Pupa, ventral aspect, enlarged X 10. E. Cremaster, enlarged X 20.

Reproduced from water color drawing by the author.

BIOGRAPHICAL SKETCHES

COMSTOCK, JOHN ADAMS

[1373 Crest Road, Del Mar, California]

Born: Evanston, Illinois, Jan. 30, 1883. Son of John Adams Comstock, descendent of William Comstock, from England, 1637, and Nellie Hurd, daughter of Judge Harvey B. Hurd, one of the founders of Northwestern University.

M. A. (Hon.): Occidental College, 1924

D. O. : College of Osteopathic Phys. and Surg., 1945

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M. D. : California College of Medicine, 1962

D. Sc. : California College of Medicine, 1962

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Selected List of Past Positions: Secretary, Chicago Entom. Soc., 1898-1903

Recorder, Entom. Soc., Chicago Acad. Sci., 1903-04

Taught Anatomy and Embryology, Coll. Phys. Surg., 1915-1920

Assist. and Dir. Southwest Museum, 1920-1926

Editor, Publ. Sou. Calif. Acad. Sci., 1921-62

Act. and Assist. Dir. L. A. Co. Museum, 1928-38

Director Science, L. A. Co. Museum, 1939-48. Retired 1948

President Fellows, San Diego Soc. Nat. Hist. 1958; Lepid. Soc., 1962

Member, Board of Directors, Nat. Hist. Mus. San Diego, 1957

Interests: Butterflies of California (book, 1927)

Geneology (book "History and Geneology of the Comstock family in America," 1949)

Life Histories of Lepidoptera

Publications: 194+ papers mostly illustrated life histories, 1902-1963

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THE ORIGIN OF A SYMPATRIC SPECIES IN COLIAS THROUGH THE AID OF NATURAL HYBRIDIZATION

WILLIAM HOVANITZ

[*continued from volume 1, page 274*]

IV POPULATION ANALYSES FROM SIGNIFICANT REGIONS

Analysis of the variation of *Colias hecla, Colias nastes* and *Colias boothi* (where present) has been made at a large number of stations throughout arctic North America and at one station in northern Sweden. The North American stations are shown on the map (fig. 10) drawn for this purpose. Many of the stations shown are taken from the map drawn for the "Northern Insect Survey" of the Canadian Government and made available for this use by Dr. T. N. Freeman.

In addition to the localities which are taken from that map, some stations are shown which represent samples made by others. There are included a sample from the Meade River, Alaska made available by Dr. John Garth, a sample from Coppermine, Northwest Territories, collected by the author in 1947, a sample from Danske Island in the Hudson Bay made available by the Danish National Museum, Copenhagen, and a sample from Coral Harbour, Southampton Island, collected by Dr. G. M. Sutton and made available by the Carneigie Museum, Pittsburgh.

The analyses of the populations has been made by the two characters indicated in section III in this series, namely, by applying a numerical value to the grade of border pattern displayed by each specimen, and also by applying a numerical value to the grade or orange pigmentation displayed by each specimen. These two values for each specimen are then plotted on a scatter diagram, which gives a fair idea, on perusal, of the condition of the variation of the three species in any one locality. As the females all show the same border pattern for both species, this sex was rated by color only. These diagrams are indicated as figures 11 through 42. The method of grading the insects is described in section III and is illustrated in color in figures 8 and 9.

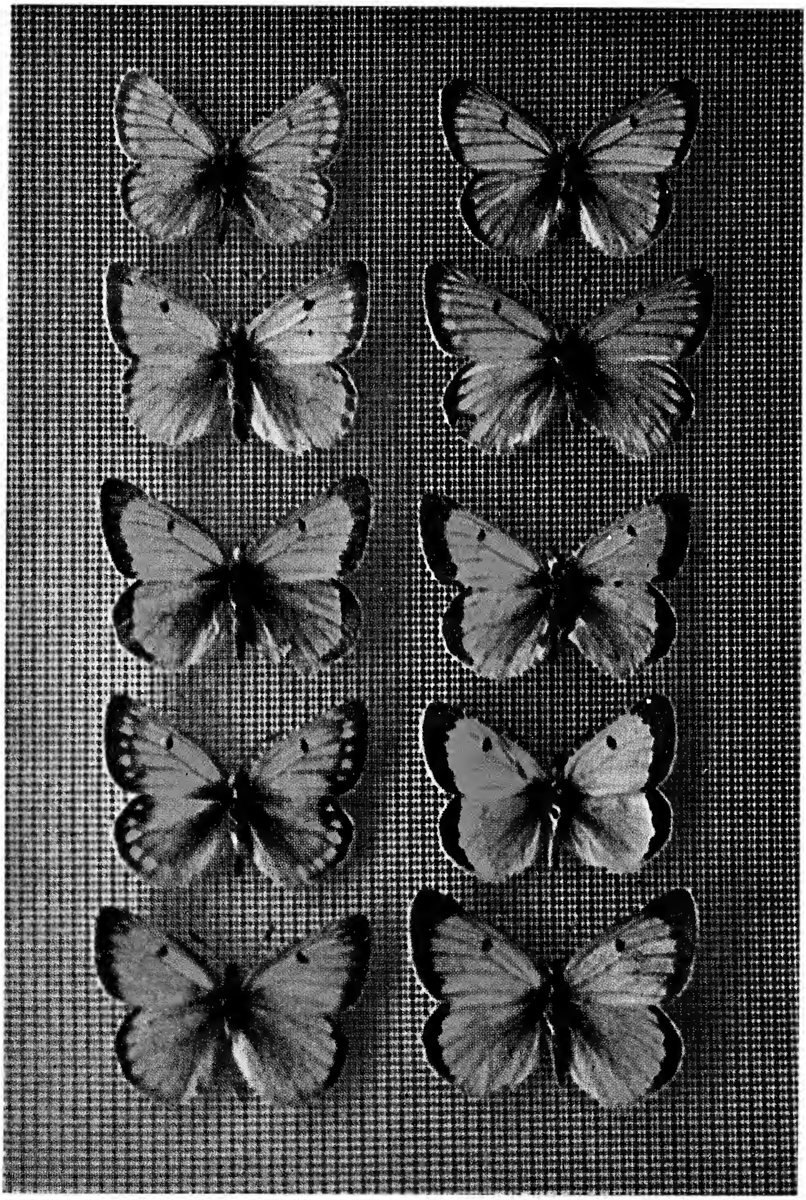


Fig. 9. Series of Colias, mostly identifiable as *C. boothi,* showing by means of a graded series, nine steps in the orange color development on the fore wings of the male from the yellow at the top left to the full orange at the second to the bottom right. Grades are designated as 0 through 4 on the left column and 5 through 9 on the right column. The specimen on the bottom right does not enter the series but is shown to illustrate a variation in which the fore wings are orange and the hind wings yellow. All specimens shown are males. All are from Coppermine, Northwest Territories, Canada, July 12-19, 1947, W. Hovanitz coll. except (1) grade 0, top on left column, Repulse Bay, Northwest Territories, Canada, Aug. 2, 1950. P. F. Bruggemann, (2) Grade 8, fourth from top on right column, Repulse Bay, N. W. T., Canada, July 27, 1950. J. E. H. Martin.

Fig. 10. Map showing locations where samples of *Colias hecla*, *Colias nastes* and *Colias boothi* have been analyzed.

DANSKE

BORDER

ORANGE	0	1	2	3	4	5	6	7	8
8									
7	1								
6			1		1				
5	1								
4					3	1			
3				1					
2		1							
1									
0	7								

♂ ♀

COPPERMINE

BORDER

ORANGE	0	1	2	3	4	5	6	7	8
8									
7		1						2	1
6			3		3		1	1	
5					3	2	1	1	1
4									1
3			1		1		1		
2	1			1			1	1	
1					1				
0									

♂ ♀

Figs. 11-42. Diagrams illustrating the range of variation in the populations of Colias which have been graded for two characters.

♂	ORANGE								
BORDER	0	1	2	3	4	5	6	7	8
0	3							1	
1									
2									
3						1	1		
4									
5									
6									
7							1		1
8							2	5	13
♀	7					1	3	3	7

BATHURST INLET

♂	ORANGE								
BORDER	0	1	2	3	4	5	6	7	8
0	1							1	
1									
2			1						
3					1				
4									
5									
6						1			
7									
8									8
♀								1	

COPPERMINE

♂	ORANGE								
BORDER	0	1	2	3	4	5	6	7	8
0	35	17			1		1		
1									
2									
3		1							
4					1				
5									
6									
7									
8									
♀	7	9	3	2	3	2			

CORAL HARBOUR

♂	ORANGE								
BORDER	0	1	2	3	4	5	6	7	8
0	55								
1									
2	1								
3	1								
4									
5									
6									
7									
8									
♀	10								

FORT CHIMO

ORANGE

♂	0	1	2	3	4	5	6	7	8
0	30	12		2	2		1	1	
1	1	3	3	2	2	3	1	2	
2			1	1	2	6	1		
3		1	1	3		1	1		
4		1			1				
5	1								
6		1			1				
7									
8							1	40	7
♀	6	4	5	3	4	1	2	3	3

BORDER

SPENCE BAY

ORANGE

♂	0	1	2	3	4	5	6	7	8
0	112	26	3	2	2	2			
1	5	1	1	1	3	2	3	1	
2	3		1	1	2	3			
3	1	1	1		1	1	1		
4	1								
5	1	1					1		
6		1							
7									
8									15
♀	32	11	6	7	3	3	2	2	5

BORDER

CORAL HARBOUR

♂ BORDER \ ORANGE	0	1	2	3	4	5	6	7	8
0									
1									
2	2								
3	4								
4	5			1					
5	4								
6	5								
7	5								
♀ 8								3	

MEADE RIVER

♂ BORDER \ ORANGE	0	1	2	3	4	5	6	7	8
0	14	8		2					
1					1				
2	1				1				
3				2	1				
4		1		3	2				
5			1		1	1			
6	1								
7									
♀ 8								3	1

CORAL HARBOUR

♂	ORANGE								
BORDER	0	1	2	3	4	5	6	7	8
0	18								
1	1								
2									
3									
4									
5									
6									
7									
8									
♀	4								

REINDEER DEPOT

♂	ORANGE								
BORDER	0	1	2	3	4	5	6	7	8
0	87		1						
1	6	1							
2	4								
3	1								
4	3								
5	1								
6	1								
7									
8								6	
♀	34						1	4	

PORT HARRISON

♂	ORANGE								
BORDER	0	1	2	3	4	5	6	7	8
0	13								
1									
2									
3									
4									
5	1								
6	1								
7	1								
8							1		3
♀	5								

HOLMAN, VICTORIA IS.

♂	ORANGE								
BORDER	0	1	2	3	4	5	6	7	8
0	27	1							
1	8	1							
2	2								
3	2								
4	1								
5	4								
6	1								
7	2								
8								—6—	
♀	11	1							

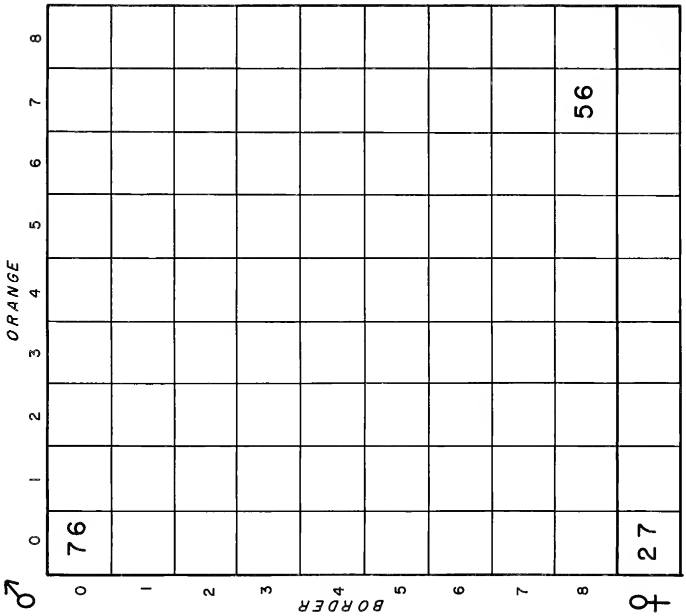
CAMBRIDGE BAY

♂	ORANGE								
BORDER	0	1	2	3	4	5	6	7	8
0	2								
1									
2	1								
3	1								
4	2								
5									
6	1								
7									
8									
♀									

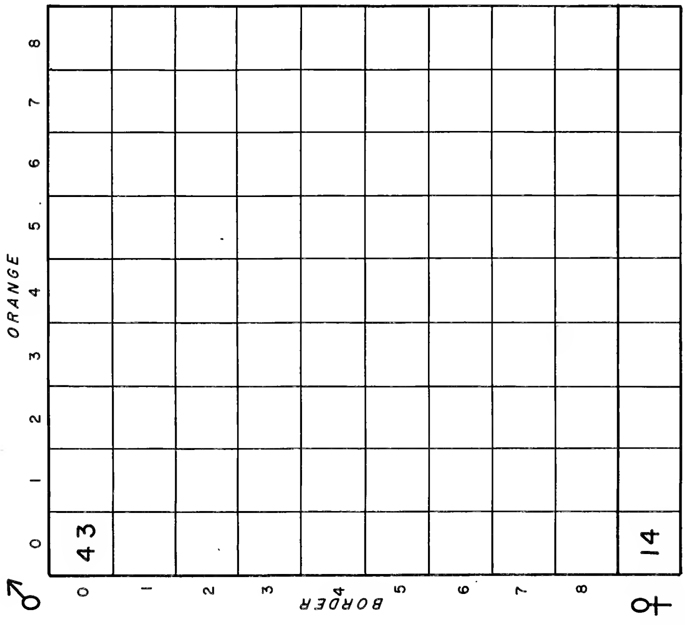
PAYNE BAY

♂	ORANGE								
BORDER	0	1	2	3	4	5	6	7	8
0	9								
1									
2									
3									
4									
5									
6									
7									1
8								2	17
♀	1							1	8

FIRTH RIVER



HERSCHEL ISL.



CHURCHILL

ORANGE

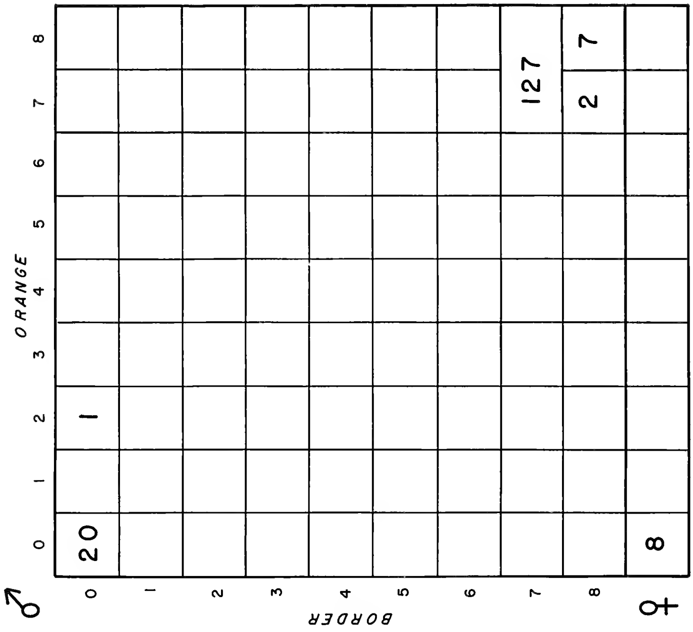
♂ BORDER	0	1	2	3	4	5	6	7	8
0	24						1		
1						2		4	3
2							2	1	2
3								2	1
4									1
5						1			
6							2	7	4
7				2			2	9	5
8			1				1	5	57
♀		1		1	1	4	2	6	10

CHESTERFIELD

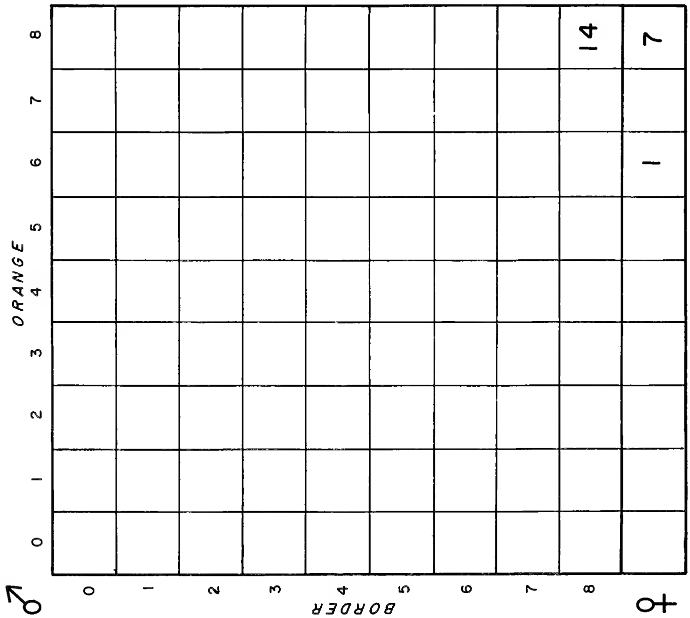
ORANGE

♂ BORDER	0	1	2	3	4	5	6	7	8
0	81	1		1	1	1		1	
1	1	1							
2									
3								1	
4								1	
5									
6									3
7								1	5
8						1		3	57
♀	28	1	1	1	2	2	1	5	26

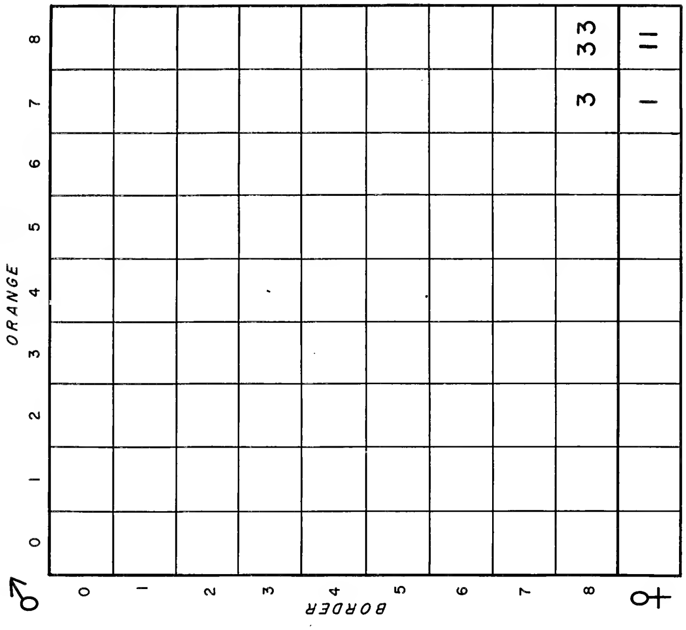
ESKIMO PT.



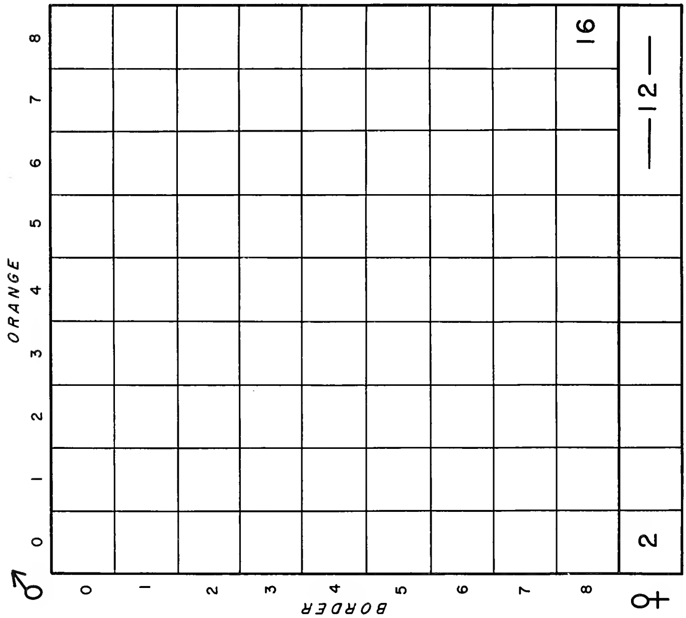
FROBISHER BAY



MUSKOX LAKE



CLYDE, BAFFIN ISLAND



KIDLURT

ORANGE

♂	0	1	2	3	4	5	6	7	8	♀
8									83	9
7										16
6										5
5										2
4										
3										
2										
1										
0										

BORDER

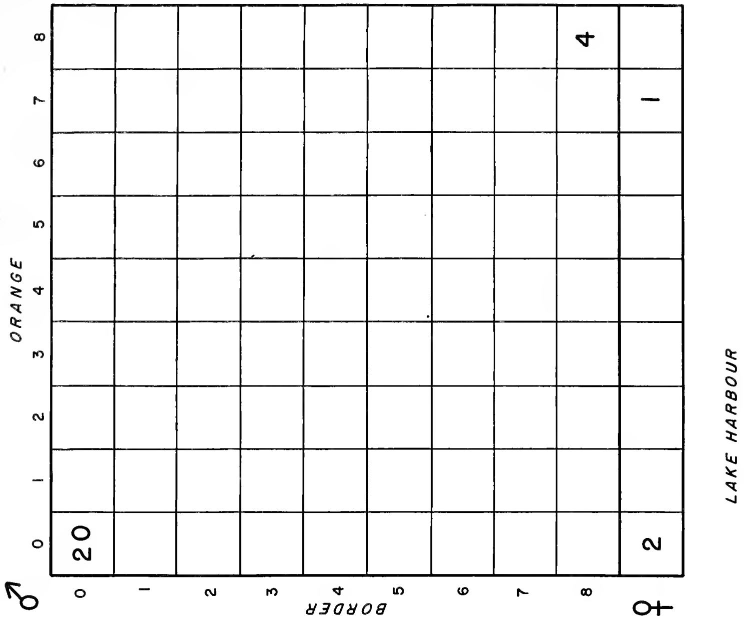
ELLESMERE

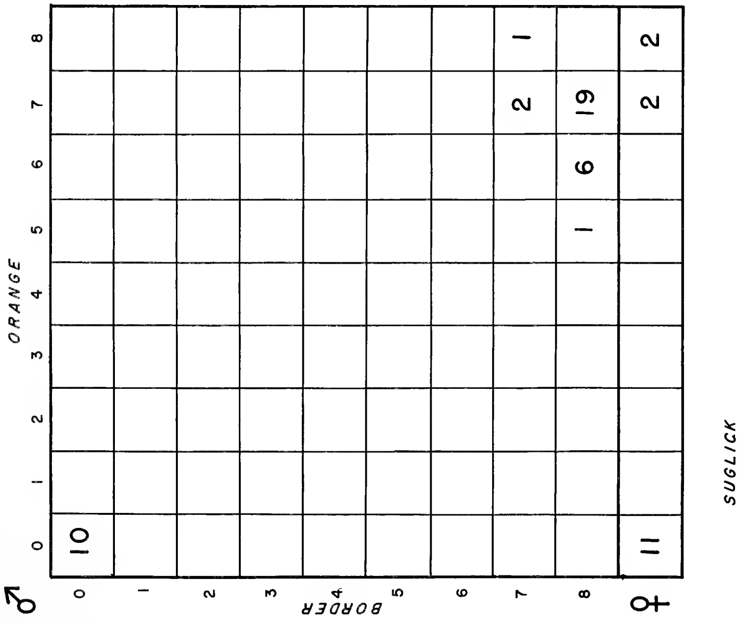
ORANGE

♂	0	1	2	3	4	5	6	7	8	♀
8									16	7
7									5	12
6									1	3
5										1
4		1								2
3										
2										
1										
0										

BORDER

PELLY BAY


ORANGE
0
1
2
3
4
5
6
7
8
BORDER
0
1
2
3
4
5
6
7
8
♂
♀
20
2
4
1
LAKE HARBOUR


ORANGE
0
1
2
3
4
5
6
7
8
BORDER
0
1
2
3
4
5
6
7
8
♂
♀
10
11
1
2
19
6
1
2
2
SUGLICK

ORANGE

♂ BORDER	0	1	2	3	4	5	6	7	8
0									
1									1
2									
3								1	
4								1	
5									
6								1	2
7				1				4	5
8								2	3
♀					2	1	1	3	3

PADLEI

ORANGE

♂ BORDER	0	1	2	3	4	5	6	7	8
0	45	2					1		1
1									1
2						1			1
3									1
4								2	1
5									3
6									4
7						1	1	4	11
8						1		1	2
♀	3	2		1		5	5	4	1

BAKER LAKE

♂	ORANGE								
BORDER	0	1	2	3	4	5	6	7	8
0	114	2	1	2	1	1	2	1	
1	1	2	1	2	2	5	5	3	1
2		4	2	7	7	5	4	2	
3			3	9	5	5	3	3	
4			4	1	4	3		1	
5		1	2	1	2	2	1		
6		2	4	3	2	2	1		
7			2	2	1		1	1	
8								12	45
♀	38	13	14	8	13	10	6	5	19

REPULSE BAY

♂	ORANGE								
BORDER	0	1	2	3	4	5	6	7	8
0									1
1									
2								1	
3									
4									
5									
6									
7								1	
8									
♀							1		

KEEWATIN

BIOGRAPHICAL SKETCHES

TILDEN, JAMES WILSON

[125 Cedar Lane, San Jose, Calif.]

Born: Philo, Calif. , 1904

Married: 1943, 3 children

A. B. : San Jose State College, 1942

M. A., PhD.: Stanford University, 1948

Associate Editor: Lepid. News, 1959

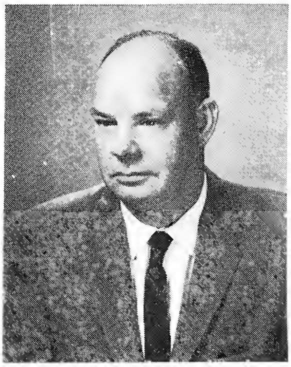
Professor of Entomology: San Jose State College, 1948-.

Consultant: Santa Clara County Health Department. 1955-59

Contributor to many scientific journals

Interests: Ecology, Distribution and Migration of Lepidoptera, especially Hesperiidae and Lycaenidae.

Teaching: Advanced General Entomology, Biological Control, Forest Entomology.



Journal of Research on the Lepidoptera 2(3):225-228, 1963

1140 W. Orange Grove Ave., Arcadia, California, U.S.A.

A RUBBER STAMP METHOD FOR PRODUCING SPECIMEN LABELS

PHILLIP A. ADAMS
Orange State College, Fullerton, California

THE METHOD DESCRIBED BELOW has proved a speedy and convenient means of producing insect labels, and appears equally adaptable for labels of larger size. Anyone capable of lettering neatly with a crow-quill pen should have little difficulty in mastering the technique. Some practice probably will be required before best results consistently are obtained. These directions are the result of much experimentation, and should be followed meticulously. Brand names of several materials are given because other brands have not proved so satisfactory; substitutions should be avoided.

In view of modern advances in techniques of reproduction, preparation of the mold by hand engraving may appear retrogressive. However, this method offers several advantages. No expensive equipment is required, and all the materials are easily obtainable. There is no necessity for setting up or distributing type, nor is there a press to clean. The equipment may be taken into the field. Most important, the method is extremely rapid. Maximum efficiency is attained for series of eight to fifty labels.

Ross scratchboard makes an ideal mold for insect labels. The thinness of the plaster surface limits the stamp to low relief; consequently letters must be made small and close together. For larger lettering, as is used in bird and mammal labels, where deeper engraving is required, thin tablets of plaster of paris are satisfactory. Wax is not suitable as a mold, since the shavings clog the impressions of the letters.

Lettering is cut with a dissecting needle, shortened to 8 mm and resharpened. The needle should be held vertically, and gentle, even pressure used. Letters with closed loops must be executed with particular care to prevent the centers of the loops from breaking out. Because of the low relief in stamps with fine lettering, blank spaces tend to print as smudges. If spaces cannot be avoided, lines should be ruled through them (fig. 1). Engraving these labels is so rapid that a separate mold easily may be made for each date, thus eliminating the necessity of annotating individual labels with pen.

Letters need not be cut deeply to print well. Avoid cutting through the plaster coating of the scratchboard to the paper beneath;

if this occurs, the rubber often pulls up flakes of plaster as it is separated from the mold. This sticking may be prevented by treating the scratchboard with silicone mold-release, or with polypropylene glycol (hydraulic brake fluid). Ordinarily such treatment is not necessary, unless the board has been coated with ink, but it greatly improves the working qualities of the scratchboard.

Make a frame by cutting in a piece of thin, waxed cardboard, a rectangular opening large enough to allow a space of at least 4 mm surrounding the engraved label, when the frame is placed over the label. This frame will depress the face of the stamp surrounding the label, so that only the portion included in the opening will print. Using the frame as a guide, incise a border no farther than 1 mm from the lettering, and slightly deeper (fig. 1). The space between this border and the cardboard frame is then filled with parallel engraved lines (fig. 2). This border area supports the face of the stamp, preventing smudging, and allowing more pressure to be used in printing, without wearing down the letters so rapidly. The wider it is, the better will be the quality of the labels. The printed border is trimmed away from the finished labels.

A stamp handle is made by cementing a rectangle of glass or metal, 10 x 30 mm, to the end of a large cork (fig. 5). Over this is placed a 20 x 70 mm strip of wire gauze, the ends of which are bent back and taped to the sides of the cork.

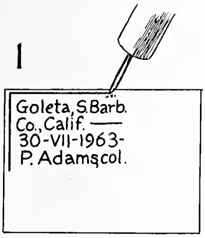
To make the stamp, a small pellet of Eberhard Faber kneaded rubber is laid over the mold (fig. 3). The cardboard frame is steadied with the left hand while the stamp handle is pressed down firmly into the rubber, and removed with a slight rocking motion. This should result in a thin layer of rubber on the face of the stamp handle, extending about 3 mm beyond the impression of the frame, and bearing a perfect impression of the mold (fig. 4). If too much rubber has been used, the edges should be pressed down to prevent their printing.

The stamp pad is a piece of one fourth inch foam neoprene, such as is used in skin diver's wet suits, covered with a tough piece of plastic film, taped in place. After each use, the plastic is stripped off and discarded. Rigid surfaces, such as with glass, are not suitable for ink plates, since they do not ink the stamp evenly, and their lack of resilience causes the stamp to wear down rapidly. Cloth stamp pads are too coarse for insect labels, and cannot be used with oil ink.

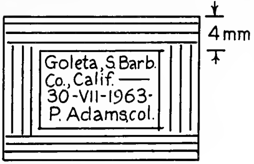
The ink is spread with a brayer made from a piece of coat-hanger wire, with a 40 mm length of tygon plastic or smooth rubber tubing for a roller. The tubing may be discarded after each use. If shaped as shown in figure 6, the brayer may be set down without the inked roller touching the surface.

Either ordinary printers ink or oil linoleum block-printing ink may be used. It should be spread out quite thin, and frequently rolled. If allowed to become tacky, the ink pulls rubber from the face of the stamp.

1



2



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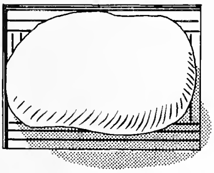
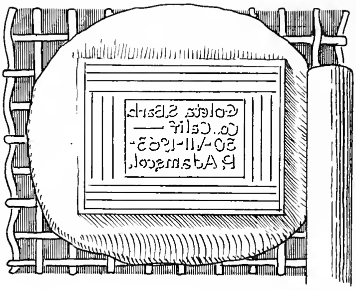
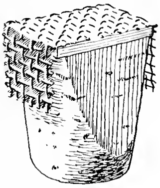


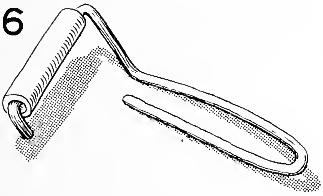
4



5



6



7

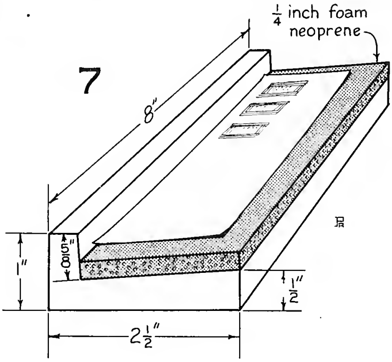


Fig. 1. Incising the inner border around the label, using a cardboard frame as a guide. Fig. 2. The completed label mold, engraved in scratchboard. Note wide engraved border. Fig. 3. Cardboard frame and kneaded rubber pellet in position over mold. Fig. 4. The stamp, formed for forcing the rubber into the mold with the stamp handle. Edges of rubber being pressed down to prevent smudging. Fig. 5. The stamp handle. Wire gauze is held in place with a few turns of tape. Fig. 6. Brayer. Fig. 7. Printing pad with guide for aligning labels.

When inking and printing, hold the cork gently between the thumb and third finger, with the index finger on the top of the cork. Touch the stamp to the inked surface, release the thumb and third finger, and press lightly with the index finger. Print with the same motion. Very little pressure is required; delicate handling produces clean impressions and prevents premature deterioration of the stamp. Two labels usually can be printed each time the stamp is inked.

Any medium weight paper may be used, so long as the surface is smooth. For very small lettering, a coated paper, such as is used to line insect boxes, is ideal. A sheet of foam neoprene under the paper results in better impressions and prolongs the life of the stamp. Straight rows of labels may be produced using a margin guide as shown in figure 7. With this device printing is slightly more difficult, but cutting out the labels is greatly facilitated.

After about fifty impressions, a kneaded rubber stamp usually will require renewal. Remove the ink with scrap paper, peel off the rubber, reshape it, and take another impression from the mold. Discard the rubber when it absorbs so much ink as to lose its springiness, or becomes sticky.

Permanent stamps can be made with a variety of materials. Silicone rubber has been used with good success. The mold should be lubricated with green soap or silicone before engraving. A long curing time — twenty-four hours or more — may be required. If difficulty is experienced peeling the silicone from the mold, the scratchboard can be dissolved in hot potassium hydroxide solution. Kneaded rubber is much easier to use. Results with permanent stamps have not been sufficiently better to make the extra trouble and delay seem worth while.

Mr. Richard Fall, of Bio Metal Associates, has given encouragement and valuable suggestions, and has kindly assisted in procuring materials used in developing the technique. I am gratefuly to R. B. Cowles for his comments on the manuscript.

Journal of Research on the Lepidoptera 2(3):229-239, 1963

1140 W. Orange Grove Ave., Arcadia, California, U.S.A.

GENERIC OR SUBGENERIC NAMES CLOSELY RELATED TO ARGYNNIS

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1032 E. Santa Anita Ave., Burbank, California

A REVIEW WAS MADE of the generic and subgeneric names that have been applied over the world to the Argynnid butterflies as an incidental to preparing a list of the generic and specific names that have been used for the Neartic Argynnids. This paper is a summary of that study.

The names are listed in alphabetical order. Synonyms (where the types are the same) are listed alphabetically but under the names having priority. As no study of the biological relationships of this group of insects has been made, no attempt has been made to indicate preferential use of the names as genera, subgenera, or if the names should be used at all.

Various authors have dealt at length with the generic arrangements for this group of butterflies, for example Reuss (1926, [1927]): Warren (1944, 1955); Dos Passos and Grey (1945); and Warren, Dos Passos and Grey (1946). These authors should be consulted for biological diagnosis of certain species and for definitions and subjective analyses of the genera.

Dos Passos and Grey (1945) associated the genus *Euptioeta* Doubleday (1848) with the Argynnid butterflies but Warren, Dos Passos and Grey (1946) dropped this generic name from that consideration.

A chronological history of the names of generic (or subgeneric) rank proposed for the Argynnid butterflies is summarized as follows:

1758. Linnaeus (1758) applied the name *Papilio* to all butterflies. Argynnids were given this name from 1758 through the first part of the 1800's.

1777. Scopoli erected the name *Argyreus* for a group of assorted butterflies which included some Argynnids.

[1806]. Hübner erected the name *Dryas* for *paphia* Linnaeus in an "unpublished" work.

1807. Fabricius erected the name *Argynnis* which has been the most generally accepted name for the species of this group since its origin.

[1819]. Hübner recognized *Argynnis* Fabricius and erected four additional generic names for some of the Argynnids: *Acidalia, Argyronome, Brenthis* and *Issoria.* Recognition of these names was slow and much confusion was caused since no type species were originally designated. The name *Brenthis* appears to have been generally misused.

1820. Billberg essentially applied the name *Argyrea* to the Argynnid butterflies. Little or no use has been made of this name.

1851. Nordman erected the name *Damora* in connection with describing a new species. Very little use has been made of this name also.

1872 and 1875. Scudder erected the names *Speyeria* and *Semnopysche* for certain Nearctic species. These names have only recently been resurrected by Dos Passos and Grey for generic (*Speyeria*) and subgeneric (*Semnopysche*) use. Editorial policy in one journal has aided in the popularization of the name *Speyeria* as a generic name.

1900. Moore in his "Lepidoptera Indica" erected the names *Boloria* and *Rathora.* Reuss helped to put the name *Boloria* to common use.

1920 to 1928. Reuss erected the following names for Argynnid genera or subgenera: *Eudaphne, Eudryas, Clossiana, Fabriciana, Kükenthaliella, Mimargyra, Mesoacidalia, Mesodryas, Neoacidalia, Proacidalia, Proclossiana, Prodryas, Profabriciana, Prokükenthaliella, Protodryas, Pseudorathora,* and *Yramea.* These names included some homonyms and synonyms.

1942. Warren erected the name *Pandoriana* in connection with his studies.

1943. Hemming proposed *Childrena* to replace *Eudryas* Reuss which was preoccupied.

1944. Bryk erected the name *Chilargynnis* for *cytheris* Drury apparently being unaware of Reuss' *Yramea* with the same type.

The use of these names varies greatly depending upon (1) the preference by specialists for large or small genera, or (2) whether the group as a whole is considered a subfamily or a genus. At the one extreme, each species of the group might be considered under a different generic name and the group then is called *Argynninae;* at the other extreme, all species of the group might be considered under one generic name and the group is then called *Argynnis.*

LIST OF NAMES USED FOR GENERIC OR SUBGENERIC PURPOSES

- ARGYNNIS FABRICIUS.
  - Type: paphia Fabricius = paphia Linnaeus.
  - ARGYREA BILLBERG.
    - Type: paphia Billberg = paphia Linnaeus.
  - DRYAS HÜBNER (in Tentamen).
    - Type: paphia Hübner = paphia Linnaeus.
  - MESODRYAS REUSS.
    - Type: paphia Linnaeus.
- ARGYREUS SCOPOLI.
  - Type: niphe L. = hyperbius Johansson [Linnaeus ?].
  - ACIDALIA HÜBNER.
    - Type: niphe L. = hyperbius Johansson [Linnaeus ?].
  - MIMARGYRA REUSS.
    - Type: hyperbius Johansson [Linnaeus ?]. Later named niphe by Linnaeus.
- ARGYRONOME HÜBNER.
  - Type: laodice Pallas.
  - EUDAPHNE REUSS.
    - Type: laodice Pallas.
- BOLORIA MOORE.
  - Type: pales Schiffermüller [Denis and Schiffermüller].
- BRENTHIS HÜBNER.
  - Type: hecate Wien. Verz. [Denis and Schiffermüller].
- CHILDRENA HEMMING.
  - Type: childreni G. Gray.
  - EUDRYAS REUSS.
    - Type: childreni G. Gray.
- CLOSSIANA REUSS.
  - Type: selene [Denis and Schiffermüller].
- DAMORA NORDMANN.
  - Type: paulina Nordmann = sagana Dbdy. and Hew.
- FABRICIANA REUSS.
  - Type: niobe Linnaeus.
- ISSORIA HÜBNER.
  - Type: lathonia Linnaeus.
  - RATHORA MOORE.
    - Type: lathonia Linnaeus.
- KÜKENTHALIELLA REUSS.
  - Type: gemmata Butler.
- MESOACIDALIA REUSS.
  - Type: aglaia L. = charlotta Haworth.
- NEOACIDALIA REUSS.
  - Type: cybele Cramer [Fabricius].
- PANDORIANA WARREN.
  - Type: maja Cramer = pandora Schiffermüller [Denis and Schiffermüller].
- PROACIDALIA REUSS.
  - Type: clara Blanchard.
- PROCLOSSIANA REUSS.
  - Type: aphirape Hübner = eunomia Esper.

PROFABRICIANA REUSS.
Type: *jainadeva* Moore.
PROKÜKENTHALIELLA REUSS.
Type: *excelsior* Butler.
PROTODRYAS REUSS.
Type: *kamala* Moore.
PRODRYAS REUSS.
Type: *kamala* Moore.
PSEUDORATHORA REUSS.
Type: *isaeea* Doubleday (*Nomen nudum*) = *issaea* Moore.
SEMNOPYSCHE SCUDDER.
Type: *diana* Cramer.
SPEYERIA SCUDDER.
Type: *idalia* Drury.
YRAMEA REUSS.
Type: cytheris Drury.
CHILARGYNNIS BRYK.
Type: *cytheris* Drury.

DATA FOR THE NAMES

ARGYNNIS FABRICIUS. 1807 [before 19 Dec.][1]. In K. Illiger. Magazin für Insektenkunde 6: 283, no. 19. Includes among others "*Pap. Paphia*" which is considered to be of Linnaeus.

Type. *P*[*apilio*]. *N*[*ymphalis*]. [*Phaleratus*] *paphia* Linnaeus. 1758. Syst. Nat. 10th. Ed. 1: 481, no. 138.

Type Selection. Latreille. 1810. Consid, Gen. Anim. Crust. Arach. Ins., p. 440. Says in a section devoted to types of genera, after having established that Argynne = *Argynnis*: "Argynne. *Argynnis paphia*, Fab.; ejusd., *melitaea cinxia*". As used by Latreille *paphia* Fab. is considered to be *paphia* Linnaeus.

Note. Hemming. 1958. Official List of Generic Names in Zoology. 1st. Install.: 69, no. 609. *Argynnis* is included on Official List and has preference over *Argyreus* Scopoli.

ARGYREA BILLBERG. 1820. Enumeratio Insectorum in Museo Gust. Joh. Billberg; p. 77. Includes among others "*paphia*" which is considered to be of Linnaeus.

Type. *P*[*apilio*]. *N*[*ymphalis*]. [*Phaleratus*] *paphia* Linnaeus. 1758. Syst. Nat. 10th. Ed. 1: 481, no. 138.

Type Selection. Hemming. Sept. 1933. Entomologist 66 (844): 197. Says of *Argyrea*: "Type = *Argyrea paphia* Linn."

DRYAS HÜBNER. [1806][2]. Tentamen Deter. Digest. Demon. Singul. Stirp. Lepidopterorum; p. [1], no. IV of Tribus 1 listed under Phalanx 1.

Type. *P*[*apilio*]. *N*[*ymphalis*]. [*Phaleratus*] *paphia* Linnaeus. 1758. Syst. Nat. 10th. Ed. 1: 481, no. 138.

Type Selection. Hübner. As above. Says: "IV. Dryades - *Dryas Paphia*." The *paphia* of Hübner is considered to be *paphia* Linnaeus, 1758. Since only *paphia* is included by Hübner, it becomes the type of the genus.

Note. Hemming. 1958. Official Index Reject. and Invalid Works Zool. Nomen. 1st. Install.: p. 4, no. 14. Hübner's "Tentamen" is included as a rejected work based on Opinion 97 of the Internat. Comm. Zool. Nomenclat.

Note. The name Dryas was later validly published by Hübner and P. N. P. iulia Fabricius was selected by Hemming as its type species.

MESODRYAS REUSS. 25 Jan. 1927. Deutsch. Ent. Zeitschr. (Berliner Ent. Zeit. und Deutsche Ent. Zeit. Wieder.). Jahrg. 1926 (5): 434-435 (in part). Proposes a new name for Dryas Hübner [1806][2] as used in the "Tentamen" (which has been ruled invalid by the Internat. Comm. Zool. Nomen.).

Type. P[apilio]. N[ymphalis]. [Phaleratus] paphia Linnaeus. 1758. Syst. Nat. 10th. Ed. 1: 481, no. 138.

Type Selection. Reuss. As above. Says: "...Mesodryas T. Rss., Type paphia L..."

ARGYREUS SCOPOLI. 1777. Introd. Hist. Natur.; pp. 431-432, no. 171. Includes among others no. 208 (= P. N. [P.] niphe Linnaeus, 1767.

Type. P[apilio]. N[ymphalis]. [Phaleratus] niphe Linnaeus. 1767. Syst. Nat. 12th. Ed. 1(2): 785, no. 208. (= Papilio N. hyperbius Johansson [or Linnaeus ?], 1763 [after 23 June][3]. Amoenitates Academicae 6: 408-409, no. 75).

Type Selection. Reuss. 8 July 1928. Internat. Ent. Zeitschr. 22 (14): 146. Says of Argyreus: "...Die erstgenannte Art ist hyperbius L. (= niphe L., Syst. Nat., ed. xii, Nr. 208) = Type***)."

Note. Linnaeus proposed niphe as a new name for hyperbius for some undetermined reason.

Note. Hemming. 1958. Official List of Generic Names in Zoology. 1st. Install.: p. 101. no. 758. Argyreus is included on Official List but does not have preference over Argynnis Fabricius.

ACIDALIA HÜBNER. [1819][4]. Verz. Bekannt. Schmett. (2): 31, no. 3. Includes "A[cidalia]. Niphe Linn. Syst. 308..."

Type. P[apilio]. N[ymphalis]. [Phaleratus] niphe Linnaeus. 1767. Syst. Nat. 12th. Ed. 1 (2): 785, no. 208. (= Papilio N. hyperbius Johansson [or Linnaeus ?], 1763 [after 23 June][3]. Amoenitates Academicae 6: 408-409, no. 75).

Type Selection. Scudder. 1875 [Apr.][5]. Proc. American Acad. Arts and Sci. 10 (art. v): 101, no. 12. Says of Acidalia: "Niphe may therefore be taken as the type."

Note. Linnaeus proposed niphe as a new name for hyperbius for some undetermined reason.

MIMARGYRA REUSS. Apr. 1922. Archiv für Naturgesch. 87a (11): 221-222. Considers Mimargyra as a subgenus of Dryas as used by Hübner in his "Tentamen" [1806].

Type. Papilio N[ymphalis]. hyperbius Johansson [or Linnaeus ?], 1763 [after 23 June][3]. Amoenitates Academicae 6: 408-409, no. 75.

Type Selection. Reuss. As above. Says: "Mimargyra m., subgen. nov., Type: hyperbius Joh..."

Note. Linnaeus proposed P. N. [P.] niphe (1767, Syst. Nat. 1 (2): 785, no. 208) as a new name for hyperbius.

ARGYRONOME HÜBNER. [1819][4]. Verz. Bekannt. Schmett. (2): 32, no. 6. Includes among others "265. A[rgyronome]. Laodice Pall. Iter. 1. 61."

Type. *Papilio Nymph[alis]*. *Phaleratus laodice* Pallas. 1771. Reise Verch. Provinzen Russischen Reichs 1: 470, no. 61.

Type Selection. Scudder. 1875 [Apr.][5]. Proc. American Acad. Arts and Sci. 10(art. v): 120, no. 120. Says of *Argyronome*: "Should *Laodice* prove generically distinct from the species of the *Dryas* and *Argynnis*, this name may be reserved for it..."

Note. Fruhstorfer. [14 May 1912][5a]. In Seitz. Die Gross-Schmetter. der Erde. 2nd. Abteil. 9(127): 514. Spells name as *Argyronoma*.

EUDAPHNE REUSS. Apr. 1922. Archiv für Naturgesch. 87a(1): 220-221 (in part). Considers *Eudaphne* as a subgenus of *Dryas* as used by Hübner in his "Tentamen" of [1806][2].

Type. *Papilio Nymph[alis]*. *Phaleratus laodice* Pallas. 1771. Reise Verch. Provinzen Russischen Reichs 1: 470, no. 61.

Type Selection. Reuss. As above. Says: "*Eudaphne*, m. subgen. nov., Type: *laodice* Pall..."

BOLORIA MOORE. 10 Apr. 1900. Lepidoptera Indica 4(pp. 177-248): 243-244 (and pp. 245-254); plates 375-378).

Type. *P[apilio]*. *pales* [Denis and Schiffermüller]. 1775 [8 Dec.][4]. Ankünd. Syst. Werkes Schmett. Wienergegend; p. 177, no. 8 of K (pp. 176-178).

Type Selection. Moore. As above. Says of *Boloria*: "Type. - *B. Pales*, Schiff."

BRENTHIS HÜBNER. [1819][4]. Verz. Bekannt. Schmett. (2): 30, no. 2. Includes among others "234. *Brenthis Hecate* Schiff. Verz. L. 4."

Type. *P[apilio]*. *hecate* [Denis and Schiffermüller]. 1775 [8 Dec.][4]. Ankünd. Syst. Werkes Schmett. Wienergegend; p. 179, no. 4 of L (pp. 178-179).

Type Selection. Scudder. 1872 [June][6]. Syst. Rev. Some Amer. Butt., pp. 24-25. Says of *Brenthis*: "Type *Papilio Hecate* Wien. Verz."

CHILDRENA HEMMING. 15 Feb. 1943. Proc. Royal Ent. Soc. London. Ser. B. 12 (2): 30. Proposes a new name for *Eudryas* Reuss which is preoccupied.

Type. *Argynnis childreni* G. Gray. 1831 [Feb.][7]. In J. Gray. Zool. Misc. 1 (1): 31.

Type Selection. Hemming. As above. Says of *Childrena*: "Type *Argynnis childreni* Gray, 1831."

EUDRYAS REUSS. 22 Oct. 1926. Internat. Ent. Zeitschr. 20(28): 253.

Type. *Argynnis childreni* G. Gray. 1831 [Feb.][7]. In J. Gray. Zool. Misc. 1 (1): 31.

Type Selection. Reuss. As above. Says: "...die neue Gattung: *Eudryas* T. Rss., Typ *childreni*." The name *childreni* is of Gray as per a later Reuss reference.

Note. *Eudryas* Reuss is a homonym of *Eudryas* Boisduval. [10 Apr. 1836][8]. Hist. Nat. Ins. Spec. Gen. Lepid. Plates (Livrs. 1-2): p. 4 (explanation of plates); plate 14 (10b), fig. 9. Hemming proposed *Childrena* as a new name.

CLOSSIANA REUSS. 30 Oct. 1920. Entomolog. Mitteilungen 9(10-12): 192 (foot-note).

Type. *P[apilio]*. *selene* [Denis and Schiffermüller]. 1775 [8 Dec.][4]. Ankünd. Syst. Werkes Schmett. Wienergegend; p. 321, no. 11 of K (pp. 176-178).

Type Selection. Reuss. As above. Says: "Clossiana m., Type: selene." In a later reference he says "selene Schiff."

DAMORA NORDMANN. 1851. Bull. Soc. Imper. Nat. Moscou 24 (pt. 2, no. 4): 439-442; plate 11, figs. 1-2.

Type. Damora paulina Nordmann. As above. Pages 440-442; plate 11, figs. 1-2. (= Argynnis sagana Doubleday and Hewitson. [4 Oct. 1847][9]. Genera Diur. Lepid. 1(12): plate 21, fig. 1. Text on page 175, no. 18 was published later.

Type Selection. Nordmann. As above. Gives only "Damora paulina", a new species which is considered to be a synonym of Argynnis sagana Doubleday and Hewitson.

FABRICIANA REUSS. 30 Oct. 1920. Entomolog. Mitteilungen. 9(10-12): 192 (foot-note).

Type. P[apilio]. N[ymphalis]. [Phaleratus] niobe Linnaeus. 1758. Syst. Nat. 10th. Ed. 1: 481-482, no. 143.

Type Selection. Reuss. As above. Says: "Fabriciana m., Type: niobe". The name niobe is of Linnaeus as per a later Reuss reference.

Note. Hemming. 1958. Official List of Generic Names in Zoology. 1st. Install.: 172, no. 1244. Fabriciana is included on Official List.

ISSORIA HÜBNER. [1819][4]. Verz. Bekannt. Schmett. (2): 31, no. 2. Includes among others "251. I[ssoria]. Lathonia Linn. [1767] Syst. Pap. 213." which is in turn P. N. [P.] lathonia Linnaeus, 1758.

Type. P[apilio]. N[ymphalis]. [Phaleratus] lathonia Linnaeus. 1758. Syst. Nat. 10th. Ed. 1: 481, no. 141.

Type Selection. Scudder. 1875 [Apr.][5]. Proc. American Acad. Arts and Sci. 10 (art. v): 198, no. 577. Says (in part) of Issoria: "1850. Steph., Cat. Brit. Lep. 14: uses it for Lathonia only. In which he is followed by Kirby (1858), and this therefore becomes the type.

RATHORA MOORE. 10 Apr. 1900. Lepidoptera Indica 4 (pp. 177-248): 241 (and pp. 242-243; plate 375).

Type. P[apilio]. N[ymphalis]. [Phaleratus] lathonia Linnaeus. 1758. Syst. Nat. 10th. Ed. 1: 481, no. 141.

Type Selection. Moore. As above. Says of Rathora: "Type. - R. Lathonia, Linn."

KÜKENTHALIELLA REUSS. 1 Apr. 1921. Societas Entomologica 36 (4): 16.

Type. Argynnis gemmata Butler. Jan. 1881. Ann. and Mag. Nat. Hist. Ser. 5. 7 (37): 32, no. 1; plate 4, fig. 1.

Type Selection. Reuss. As above. Says: "...and Kükenthaliella m. (= Boloria part.), Type gemmata Btlr."

MESOACIDALIA REUSS. 10 Apr. 1926. Deutsche Ent. Zeitschr. (Berliner Ent. Zeit. und Deutsche Ent. Zeit. Wieder.). Jahrg. 1926 (1): 69, subgenus no. 2 of genus no. VI (Acidalia Hübner).

Type. P[apilio]. N[ymphalis]. [Phaleratus] aglaja Linnaeus. 1758. Syst. Nat. 10th. 1: 481, no. 140. (= P. N. P. charlotta Haworth. 1803 [in or after July][10]). (I have not seen this reference of Haworth).

Type Selection. Reuss. As above. Indicates the type when he says: "*2. Subg. Mesoacidalia T. Rss., aglaia L."

Note. Hemming. 14 Nov. 1942. Proc. Ent. Soc. London, Ser. B. 11(11): 155-160. Shows that the oldest name available for what Linnaeus called P. N. [P.] aglaja (1758, Syst. Nat. 10th. Ed. 1: 481, no. 140) is P. N. P. charlotta Haworth since the name aglaja is a homonym of P. H. aglaja Linnaeus (1758. Syst. Nat. 10th. Ed. 1: 465, no. 44).

NEOACIDALIA REUSS. 10 Apr. 1926. Deutsche Ent. Zeitschr. (Berliner Ent. Zeit. und Deutsche Ent. Zeit. Wieder.). Jahrg. 1926 (1): 69, gives as a synonym of genus no. VI (Acidalia Hübner).

Type. P[apilio]. N[ymphalis]. P[haleratus]. cybele Fabricius. 1775 [17 Apr.][4]. Syst. Ent.; p. 516, no. 311.

Type Selection. Reuss. As above. Says: "VI. Acidalia Hbn., cybele Cram. (nur Pfeilduftschuppen)." The "cybele Cram." of Reuss is considered to be cybele Fabricius as Fabricius is the author of the name; Cramer never used the name.

PANDORIANA WARREN. Nov. 1942. Entomologist: 75(954): 245-246.

Type. Pap[ilio]. Nymph[alis]. Phalerat[us]. maja Cramer. [1776][4]. Uitland. Kapellen Voorkom. Drei Waereld-Deelen Asia, Africa en America 1 (8): 153. The text; p. 35, no. B-C; and figures B-C on plate 25 were published earlier without a complete name. (= P[apilio]. pandora [Denis and Schiffermüller]. 1775 [8 Dec.][4]. Ankünd. Syst. Werkes Schmetter. Wienergegend; p. 176, no. 1 of K (pp. 176-178).)

Type Selection. Warren. As above. Says: "Genus Pandoriana gen. nov., type Papilio maja Cramer (= pandora Schiffermüller)".

Note. Hemming. 1958. Official List of Generic Names in Zoology. 1st. Install.: 177, no. 1270. Pandoriana is included on Official List.

Note. The maja of Cramer and pandora [Denis and Schiffermüller] are considered to indicate the same species.

PROACIDALIA REUSS. 10 Apr. 1926. Deutsche Ent. Zeitschr. (Berliner Ent. Zeit. und Deutsche Ent. Zeit. Wieder.). Jahrg. 1926 (1): 69, subgenus no. 3 of Genus VI (Acidalia Hübner).

Type. Argynnis clara Blanchard. 1844. In Jacquemont. Voy. dans Inde 4: 20, no. 14; plate 2, figs. 2-3. (I have not seen this work of Blanchard).

Type Selection. Reuss. As above. Says: "*3. Subg. Proacidalia T. Rss., clara Blanch." Since Reuss gives only clara, it becomes the type.

PROCLOSSIANA REUSS. 10 Apr. 1926. Deutsche Ent. Zeitschr. (Berliner Ent. Zeit. und Deutsche Ent. Zeit. Wieder.). Jahrg. 1926 (1): 69, subgenus no. 1 of genus no. V (Clossiana Reuss).

Type. [Papilio] aphirape Hübner. [24 Dec. 1799]-[13 Apr. 1800][11]. Samm. Europäischer Schmetter. (Papiliones): plate 5, figs. 23-25. Text on page 8, no. 1 was published later. (= Pap. Nimph. Phal. eunomia Esper. [1799][12]. Die Schmetterlinge. Suppl. Theils 1 (?): 94, no. 212. Plate 110 (? publication date) contains fig. 5 which is lalelled "N. Phaler. Eunomia.").

Type Selection. Reuss. As above. Says: "*1. Subg. Proclossiana T. Rss., aphirape Hbn."

Note. The name aphirape Hübner is considered to be a synonym of eunomia Esper. Hübner in his aphirape text cites eunomia as a synonym. Dates of publication: eunomia (text): [1799][12]; eunomia (figure): ?; aphirape (figure): [24 Dec. 1799]-[13 Apr. 1800][11]; aphirape (text): [21 Nov. 1805]-[31 Dec. 1805][11].

PROFABRICIANA REUSS. 10 Apr. 1926. Deutsche Ent. Zeitschr. (Berliner Ent. Zeit. und Deutsche Ent. Zeit. Wieder.). Jahrg. 1926 (1): 70; given as an unnumbered subgenus of genus no. VII (Fabriciana Reuss).

Type. *Argynnis jainadeva* Moore. [Nov. 1864][13]. In Lang. Ent. Mon. Mag. 1 (6): 131.

Type Selection. Reuss. As above. Says: "Subg. *Profabriciana* T. Rss., *jainadeva* Moore." Since Reuss gave only *jainadeva*, it becomes the type.

PROKÜKENTHALIELLA REUSS. 25 Jan. 1927. Deutsche Ent. Zeitschr. (Berliner Ent. Zeit. und Deutsche Ent. Zeit. Wieder.). Jahrg. 1926 (5): 435.

Type. *Argynnis excelsior* Butler. 1 Apr. 1886. Proc. Zool. Soc. London for 1895 (4): 729-730, no. 42.

Type Selection. Reuss. As above. Says: "... *Prokükenthaliella* T. Rss., subg. nov., Typ *excelsior* Butl..."

PROTODRYAS REUSS. 8 July 1928. Internat. Ent. Zeitschr. Guben 22(14): 146. Proposes *Protodryas* to replace *Prodryas* Reuss which is a preoccupied name.

Type. *Argynnis kamala* Moore. 1857 [after 7 Dec.][14]. In Horsfield and Moore. Catal. Lepid. Ins. Mus. Hon. East-India Co. 1: 156-157, no. 324.

Type Selection. Reuss. As above. Says: "... *Protodryas* T. Rss. gen. nov., Typ *kamala* Moore..."

PRODRYAS REUSS. 10 Apr. 1926. Deutsche Ent. Zeitschr. (Berliner Ent. Zeit. und Deutsche Ent. Zeit. Wieder.). Jahrg. 1926 (1): 66; subgenus no. 1 of genus no. I (*Dryas* Hübner).

Type. *Argynnis kamala* Moore. 1857 [after 7 Dec.][14]. In Horsfield and Moore. Catal. Lepid. Ins. Mus. Hon. East-India Co. 1: 156-157, no. 324.

Type Selection. Reuss. As above. Says: "*1. Subg. *Prodryas* T. Rss., *kamala* Moore."

Note. *Prodryas* Reuss is a homonym of *Prodryas* (fossil) Scudder. 3 May 1878. Bull. U. S. Geol. and Geogr. Surv., 4(2): 520. Reuss later proposed the name *Protodryas* to replace his *Prodryas*.

PSEUDORATHORA REUSS. 10 Apr. 1926. Deutsche Ent. Zeitschr. (Berliner Ent. Zeit. und Deutsche Ent. Zeit. Wieder.). Jahrg. 1926 (1): 68, subgenus no. 1 of genus no. III (*Rathora* Moore).

Type. *Argynnis issaea* (*Nomen nudum*) Doubleday (G. Gray Ms. name). [2 June 1848][9]. In Doubleday and Hewitson. Genera Diur. Lepid. 1(20): 174, no. 3. (= *Argynnis issaea* Moore (G. Gray Ms. name). 1857 [after 7 Dec.][14]. In Horsfield and Moore. Catal. Lepid. Ins. Mus. Hon. East-India Co. 1: 156, no. 323).

Type Selection. Reuss. As above. Says: "*1. Subg. *Pseudorathora* T. Rss., *isaeea* Dbldy., *isaeoides* T. Rss. Ztrlgb." Note: Reuss probably intended to nominate *isaeea*! as the type species but did not do so. If no type has subsequently been named, I will here designate "*isaeea* Dbldy.", used by Reuss, as the type of the genus *Pseudorathora* Reuss but noting the identity of the species in accord with the data presented in the following note.

Note. The name *Argynnis issaea* has an involved history. It was apparently first used as a *Nomen nudum* by G. Gray in his Lepid. Nepal. p. 11, 1846. It was later used as a *Nomen nudum* (G. Gray Ms. name) by Doubleday in *Genera Diur. Lepid.* 1: 174, no. 3. Moore (in Horsfield and Moore. Lepid. Ins. Mus. Hon. East-India Co. 1: 156, no. 323) would appear to be the author since he applies the name to Kollar's description of *lathonia* Linnaeus (not Linnaeus) in Hugel's Kaschm. 4: 440, 1848. Reuss misspelt the name as *isaeea.* (I have not seen the works of Gray and Kollar).

SEMNOPYSCHE SCUDDER. 1875 [Feb. - 6 Mar.][15]. Bull. Buffalo Soc. Nat. Sci. 2 (4) signs. 30-34: 238, no. 52; pp. 258-259, no. 44.

Type. *Pap[ilio]. Nymph[alis]. Phaler[atus] diana* Cramer. [1777][4]. Uitland. Kapell. Voorkom. Drie Waereld-Deelen Asia, Africa en America 2(16): 148. Described and figured earlier, without a name, on page 4, figs. D-E and on plate 98, figs. D-E in Vol. 2, pt. 9.

Type Selection. Scudder. As above. Says of *Semnopysche*: "Type: *Papilio Diana* Cram."

SPEYERIA SCUDDER. 1872 [June][6]. Syst. Rev. Some Amer. Butt., p. 23.

Type. *Nym[phalis]. Phal[eratus]. idalia* Drury. [1773][4]. Illust. Nat. Hist. 1: [1] in Index. Described and figured earlier (without a name) on page 25, figs. 1-3 and plate 13, figs. 1-3.

Type Selection. Scudder. As above. Says of Speyeria: "Type *Papilio Idalia* Drury."

YRAMEA REUSS. 30 Oct. 1920. Entomolog. Mitteilungen 9(10-12): 192 (foot note).

Type. *Nym[phalis]. Ph[aleratus]. cytheris* Drury. [1773][4]. Illust. Nat. Hist. 2: 7, figs. 3-4; plate 4, figs. 3-4; p. [1] in Index.

Type Selection. Reuss. As above. Says: "1) *Yramea* m., nov. gen., Type: *cytheris* Drury (1773)."

CHILARGYNNIS BRYK. 6 Nov. 1944. Archiv für Zoologi 36a(3): 8-9 (9-10, in part).

Type. *Nym[phalis]. Ph[aleratus]. cytheris* Drury. [1773][4]. Illust. Nat. Hist. 2: 7, figs. 3-4; plate 4, figs. 3-4; p. [1] in Index.

Type Selection. Bryk. As above. Says: "Genus *Chilargynnis* m. (gen. nov.). Typus generis: *Nymph. Ph. cytheris* Drury, 1773."

FOOTNOTES

1. Vol. 6 title page date is qualified by indirect date data (certain names in Fabricius' article were mentioned in the Allgemeine Literatur-Zeitung, Halle [Jena] 2(303): cols. 1177-1181, 19 Dec. 1807).
2. Hemming. 1958. Official Index Reject. and Invalid Workes in Zool. Nomencl. 1st. Install.: p. 4, no. 14.
3. Vol. 6 title page signature is qualified by article date.
4. Hemming. 1958. Official List Works Approv. Avail. Zool. Nomencl. 1st. Install.: p. 4, no. 15 (dates for Hübner's Verz. Bek. Schmett.); p. 7, no. 30 (dates for Vols. 1-3, Drury's Illust. Nat. Hist.); p. 9, no. 34 (date for Fabricius' Syst. Ent.); p. 9, no. 37 (date for [Denis' and Schiffermüller's] Ankünd. Syst. Werkes Schmett. Wienergegend); pp. 9-10, no. 38 (dates for Cramer's and Stoll's Uitlandsche Kapelen).

5. Vol. 10 title page signature date is qualified by date of receipt given for article in Psyche, Jour. Ent. 2(33-34): 9, no. 716, 1883.
5a. Griffin. 1936. Trans. R. Ent. Soc. Lond. 85: 243-279.
6. Work title page date is qualified by date of a review in June 1872 number of Amer. Nat. 6: 354-359.
7. Sherborn. 1922. Index Animalium, 2nd. Ser. Vol. A-B: cxxxi.
8. Scudder. 1899. Psyche, Jour. Ent. 8: 153-154.
9. Hemming. 1936-1943. Jour. Soc. Bibliog. Nat. Hist. 1: 335-464.
10. Work title page signature date is qualified by the preface date (p. xxx).
11. Hemming. 1937. Hübner 1: 146-324.
12. Sherborn and Woodward. 1901. Ann. and Mag. Nat. Hist. Ser. 7. 7: 137-140.
13. I have not seen the wrappers for Vol. 1 which apparently gave the dates and numbers for each respective number. On the basis of the plan for later volumes I have established this date.
14. Vol. 1 title page date is qualified by the preface date (p. v).
15. Vol. 2 title page signature date is qualified by the date of signatures 30-34 and the date of receipt of a copy of the article (ex Cambridge Ent. Club, copy now in my library).

LIST OF REFERENCES

Dos Passos, Cyril Franklin and Lionel Paul Grey.
1945. A genitalic survey of Argynninae (Lepidoptera, Nymphalidae). American Mus. Novitates (1296): 1-29; figs. 1-54.

Doubleday, Edward.
1848. In Doubleday, Hewitson and Westwood (in part). The Genera of Diurnal Lepidoptera... 1: 168-170 (Euptioeta).

Linnaeus, Carolus.
1758. Syst. Nat. 10th. Ed. 1: 458-488, no. 203 (Papilio).

Reuss, F. A. Theodore.
1926. Systematischer Überblick der Dryadinae T. Rss., mit einigen Neubeschreibungen. Deutsche Ent. Zeitschr. Jahrg. 1926: 65-70.
[1927]. Über Funktion der Sexualarmaturen bei Lepidopteren (Rhop.) und die resultierende Weiterentwicklung meines versuchten natürlichen Systems der Dryadinae T. R. Ibid. Jahrg. 1926: 431-440.

Warren, Brisbane Charles Somerville.
1944. Review of the classification of the Argynnidi: with a systematic revision of the genus Boloria (Lepidoptera; Nymphalidae). Trans. R. Ent. Soc. Lond. 94: 1-153; plates 1-68; text figs. 1-14.
1955. A review of the classification of the Subfamily Argynninae (Lepidoptera: Nymphalidae). Part 2. Definition of the Asiatic genera. Ibid. 105: 381-391; plates 1-4, each with an explanation page.

Warren, Brisbane C. S., Cyril F. Dos Passos and Lionel P. Grey.
1946. Supplementary notes on the classification of Argynninae (Lepidoptera: Nymphalidae). Proc. R. Ent. Soc. Lond. (B) 15: 71-73.

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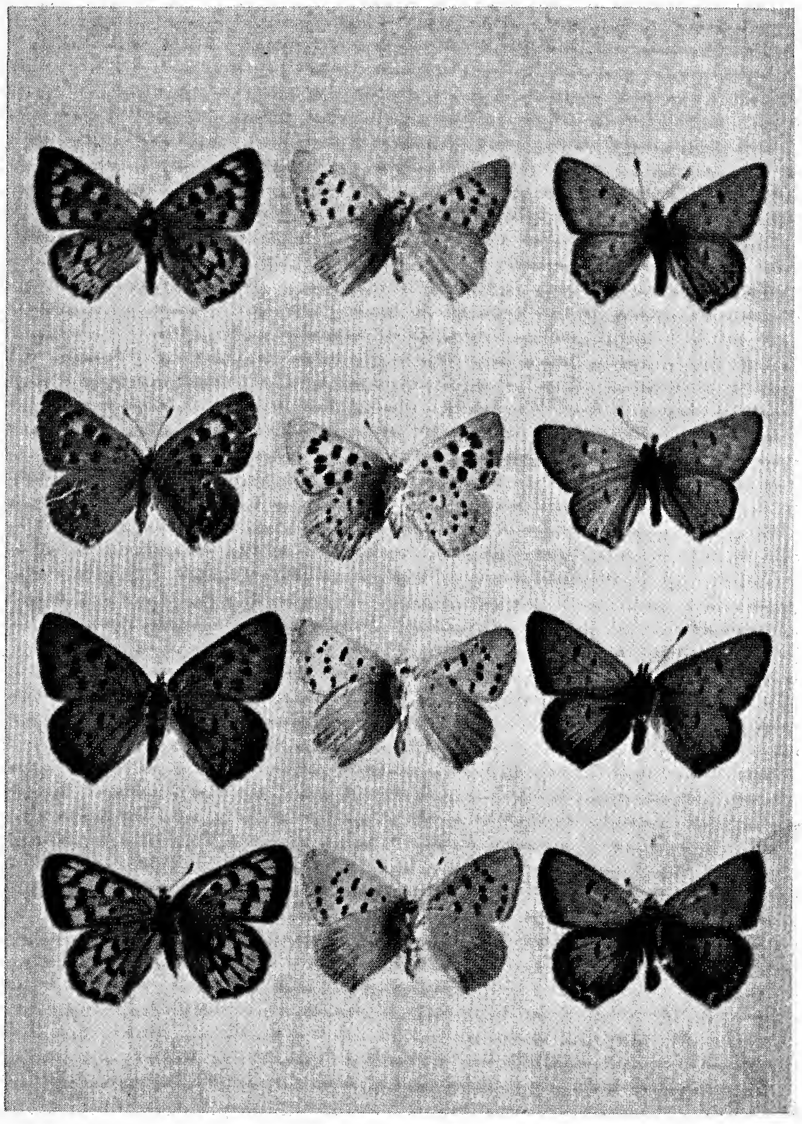

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1140 W. Orange Grove Ave., Arcadia, California, U.S.A.

EVIDENCE FOR LACK OF TERRITORIALITY IN TWO SPECIES OF HAMADRYAS (NYMPHALIDAE)

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A TERRITORY AS DEFINED BY KENDEIGH (1961) "is any area defended against intruders." Today, it is a well known fact that many animals have well established territories for either their entire lives or else for only brief periods during their lives, e.g., during the breeding season or at feeding times. This behavior pattern frequently has been reported for vertebrates — birds (Hinde, 1956), mammals (Seton, 1909, 1925-28), amphibians (Sexton, 1960), fish (Hasler and Wisby, 1958), turtles (Cagle, 1944); some invertebrates — snails (Edelstam and Palmer, 1950), wood ants (Elton, 1932), dragonflies (Jacobs, 1955). In regards to butterflies, it is known that many species *(Phyciodes tharos, Precis coenia, Lycaena phleas, Danaus plexippus,* several angle wings of the genus *Polygonia)* are pugnacious, chasing any moving object that gets within close range (Klots, 1951). It even has been recorded (Klots, 1951) that males of *Lethe sp.* adopt favorite perches on tree trunks which they resume day after day, darting out occasionally in order to drive away other males. If this is the case, it can be said that these species exhibit territoriality. However, there is no experimental evidence to support this idea which is based solely on field observations.

Closely related to territoriality, is the subject of home range— "that area regularly traversed by an individual in search of food, mates and caring for young" (Kendeigh, 1961). The few experiments undertaken with butterflies (Dowdeswell, Fisher and Ford, 1940, 1949; Evans, 1955; Abbott, 1959; Faler, 1959; Ehrlich, 1961) show that some species of butterflies do not wander very much during the course of their lives but rather are sedentary and tend to remain in relatively small areas. In other words, they have small home ranges.

The present paper sheds a little light on these two areas of behavior regarding two nymphalids, *Hamadryas februa gudula* Fruhstorfer and *Hamadryas guatamalena guatamalena* Bates.

While engaged in collecting butterflies in the Tuxtla Mountains, Veracruz, Mexico (summer, 1962), I became aware that there were fairly large populations of both *Hamadryas februa* and *Hamadryas guatamalena* in a small (two acres) tract of land given over to the cultivation of coffee. These butterflies were a conspicuous part of the landscape for whenever any moving object entered the immediate area, individuals which previously were resting on the trees, darted out, making the peculiar clicking noises that are so characteristic for the group (Ehrlich & Ehrlich, 1961). After a few seconds of rapid zig-zag motions, they again usually took up resting positions on either the same trees or else on others in the same general vicinity.

The attitudes of rest for these two species are quite interesting. Individuals rest head downward on the trunk or larger limbs with their wings stretched out horizontally and held flat against the bark. In this position, individuals are very much indiscernable for the somber color patterns of the dorsal side of the wings blend in perfectly with the bark and its lichen encrustations. Trees of the species *Inga spuria* Humb. & Bonpl. (Leguminosae) which has been planted for their value as shade trees in coffee culture were the tallest in the area and were most often used for resting.

After collecting in this area for several days, I noticed that many of the *I. spuria* trees habitually seemed to have one or more individuals of *H. februa* and *H. guatamalena* resting on them. A good friend of mine (and an ardent butterfly collector, also) remarked that he had observed this same type of phenomenon throughout Mexico and parts of Central America and that he thought that individuals rested repeatedly on certain apparently "favored" trees and defended these positions against all intruders. If this were the case, both species exhibited territoriality. This had to be determined.

In this same tract were numerous orange trees. These (the larger trees in particular) served as excellent feeding stations for both species of *Hamadryas* as well as for several species of *Prepona, Smyrna, Anaea* and *Caligo.* Termites being numerous in the area, frequently made excavations into the bark and sap wood of these trees and consequently caused sap to ooze out from the burrowings. This sap combined with moisture (either from heavy morning dew or from rainwater) gave off a strong acrid odor which was quite noticeable to me for a distance of a meter or more. Apparently this fermenting sap was highly prized by the above mentioned butterflies for at such times (when conditions were favorable for production of good quantities of sap and for the fermentation thereof), large numbers of them were seen feeding on the material. Because of the high population densities of *Hamadryas* in the area, it was a common everyday sight to see several individuals of each species feeding simultaneously on these trees. When a new arrival tried to join the feeding association, it usually was chased away. However, sometimes it was able to force its way into the group and thus take up a feeding position. It had to be determined whether territorialism was being exhibited here, that is, whether or not the same individuals were feeding at the stations day after day.

In an attempt to get some quantitative data concerning the above phenomena, three simple capture-recapture experiments were performed.

EXPERIMENT I: RESTING HABITS OF HAMADRYAS FEBRUA GUDULA FRUHST.

Three trees which, after several daily inspections proved to be fairly constant resting places for *H. februa,* were selected and marked, each with a distinct and different color. The trees were situated in a triangular pattern and were approximately 10 meters apart. All butterflies on these trees were captured, marked using the 1-2-4-7 system of Ehrlich & Davidson (1960), and immediately released. At the same hour on the following day, the trees were inspected and all butterflies found resting upon them were captured, checked and released. Any new, unmarked individuals were marked. All other trees within a distance of 20 meters in all directions were checked, also. It should be mentioned here that when approaching the trees, considerable caution was exercised so that the butterflies were caused the least amount of disturbance. This same procedure was followed for 11 consecutive days.

The results of this experiment proved to be rather interesting. Of 24 individuals (20 ♂ ♂, 4 ♀ ♀) of *H. februa* marked during the 11 days of the experiment, only 5 specimens were recaptured on the same trees from which they were taken originally. Of these 5, only 3 were captured more than once on the original tree. Of these same 24 individuals, only 9 were recaptured on nearby trees. Thus, it appears that most individuals do not regularly frequent the same trees or even other similar trees in the nearby area, and that there is a constant influx of new individuals from other surrounding areas.

EXPERIMENT II: RESTING HABITS OF HAMADRYAS GUATAMALENA GUATAMALENA BATES

Two *I. spuria* trees which seemed to be visited frequently by members of *H. guatamalena* were selected. All butterflies found resting on them were captured, marked and released. The following day the trees were inspected and all individuals found upon them were checked. All new, unmarked specimens were marked and released. Again, all other trees within a distance of approximately 20 yards were checked. This procedure continued for 7 consecutive days.

Of 9 individuals (7♂♂, 2♀♀) of *H. guatamalena* marked, none were recaptured on the trees from which they were taken originally. Of these 9, only 2 were recaptured in the immediate vicinity. Thus, it appears that *H. guatamalena* also does not habitually frequent the same resting spots but that new individuals enter the area from adjacent habitats.

EXPERIMENT III: FEEDING HABITS OF H. FEBRUA AND H. GUATAMALENA.

As mentioned previously, several of the Citrus trees in the study area served as excellent feeding stations for both species of HAMADRYAS. In an attempt to determine if feeding territories existed for the species, two highly productive trees situated about 10 meters apart were marked with different colors and all specimens of HAMADRYAS found on them were marked with corresponding colors. The same procedure of checking was followed here.

After 7 consecutive days of checking, the following results were obtained. Of a total of 15 individuals (5♂♂, 3♀♀ of *H. februa* and 3♂♂, 4♀♀ of *H. guatamalena*) marked, none were recaptured on the marked trees or on any other trees in the general vicinity. Thus, it appears that no evidence exists for the presence of feeding territories in either species.

DISCUSSION

It appears from the three simple capture-recapture studies described above, that there is no evidence for territoriality in either *Hamadryas februa* or *H. guatamalena,* two species of nymphalids which upon first observations, appear to be rather sedentary in their habits; it appears that these species do not frequent the same rest spots daily nor do they have preferred feeding places. From field observations, it appears that the resting spots are gotten on a "first come, first serve" basis and that the more aggressive individuals usually gain control of the desired spots. These same individuals in turn retain their positions until driven off by intruders or until intrinsically motivated to go elsewhere. Therefore, I think that it is better to say that these 2 species are very pugnacious.

One might argue that since these positions are defended, their exists at least a sort of "transient territoriality." However, close field observations do not bear this out; after the departure of an intruder, individuals may or may not return to the same spots. Indeed, it appears that there is an equal chance of them selecting other resting areas. Therefore, I do not believe that one can say that these species have even "transient territories."

It is interesting to speculate on the "whereabouts" of the marked individuals. Only on one occasion was a marked specimen recovered outside of the study area. This recovery was made 6 days subsequent to the termination of the three experiments. The insect, a male specimen of *H. februa,* was feeding on the exuding sap of an orange tree which was growing in a cow pasture approximately 100 yards from the original study area. It seems improbable that the marked individuals were injured during the actual marking process for no evidence for this was observed. That this marking technique can be employed with even smaller species of nymphalids without any apparent ill-effects to the specimens, was shown by Ehrlich & Davidson (1960) in their work with the checkerspot *Euphydryas editha* Boisduval. To be sure, the question of predation does arise here: were the marked individuals more susceptible to attacks by such things as lizards or birds? I believe that this question can be answered in the negative for as mentioned above, individuals of both species do not fly a great deal but spend a large amount of their time resting with their wings expanded horizontally and held flat against the bark. In such positions, the small artificial marks on the undersurfaces are completely invisible. Furthermore, flights when made, are of short duration and of such a rapid nature as to cause little chance of the markings becoming detected by predators. Therefore, I think that it is highly probable that marked individuals simply wandered off to surrounding areas and became widely dispersed amongst the multitude of other individuals. I think, then, that it is safe to conclude that these two species do not have small home ranges. An interesting future experiment would be to enlarge the study area and to determine the actual dispersion distances.

In conclusion, it seems that there is no evidence for territoriality in either *Hamadryas februa* or *Hamadryas guatamalena.*

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LITERATURE CITED

ABBOTT, W. 1959. Local autecology and behavior in *Pieris protodice* Boisduval & Leconte with some comparisons to *Colias eurytheme* Boisduval (Lepidoptera: Pieridae). *Was. J. Biol.* 17: 279-298.

CAGLE, F. R. 1944. Home range, homing behavior, and migration in turtles. *Misc. Publ. Mus. Zool., Univ. Michigan,* 61: 1-34.

DOWDESWELL, W. H., R. A. FISHER, & E. B. FORD. 1940. The quantitative study of populations in the lepidoptera. I. *Polyommatus icarus* Rott. *Ann. Eugenics* 10: 123-136.

————. 1949. The quantitative study of populations in the lepidoptera. II. *Maniola jurtina* L. *Heredity* 3: 67-84.

EDELSTAM, C. and C. PALMER. 1950. Homing behavior in gastropodes. *Oikos* 2: 259-270.

EHRLICH, P. 1961. Intrinsic barriers to dispersal in checkerspot butterfly. *Science,* 134, no. 3472: 108-109.

EHRLICH, P. & A. H. 1961. How to know the butterflies. Wm. C. Brown Pub. Co., Dubuque, Iowa, 262 pp.

EHRLICH, P. R. & S. E. DAVIDSON, 1960. Techniques for capture-recapture studies of lepidoptera populations. *Journ. Lep. Soc.* 14: 227-229.

ELTON, C. 1932. Territory among wood ants (*Formica rufa* L.) at Picket Hill. *J. An. Ecol.* 1: 69-76.

EVANS, W. H. 1955. Retrieving marked *Anthocaris reakertii. Lep. News* 9:118.

FALES, J. H. 1959. A field study of the flight behavior of the Tiger Swallowtail Butterfly. *Ann. Ent. Soc. Am.* 52: 486-487.

HASLER, A. D. and W. J. WISBY. 1958. The return of displaced large-mouth bass and green sunfish to a "home" area. *Ecol.* 39: 289-293.

HINDE, R. A. 1956. The biological significance of the territories of birds. *Ibis* 98: 340-369.

JACOBS, M. E. 1955. Studies on territorialism and sexual selection in dragonflies. *Ecol.* 36: 566-586.

KENDEIGH, S. C. 1961. Animal ecology. Prentice-Hall, Inc., Englewood Cliffs, N. J., 468 pp.

KLOTS, A. B. 1951. A field guide to the butterflies of North America, east of the Great Plains. Houghton Mifflin Company, Boston, Mass., 349 pp.

SETON, E. T. 1909. Life histories of northern animals. Charles Scribner's Sons, New York, N. Y., 2 vols.

————. 1925-28. Lives of game animals. Doubleday, Doran Col, New York, N. Y., 4 vols.

SEXTON, O. J. 1960. Some aspects of the behavior and of the territory of a dendrobatid frog, *Prostherapis trintatis. Ecol.* 41 (1): 107-115.

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1140 W. Orange Grove Ave., Arcadia, California, U.S.A.

A SYNOPSIS OF THE WEST INDIAN LYCAENIDAE, WITH REMARKS ON THEIR ZOOGEOGRAPHY

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THE BASIC REFERENCE for students of the Antillean Lycaenidae is the thorough revision of Comstock & Huntington (1943). The particular strength of this work is in the detail at species and subspecies level, in the very large amount of material so profitably studied that few major subsequent distributional discoveries have been or are likely to be made, and in the meticulous and extremely perceptive study of the older literature that underlies the whole work, resulting in a stability of species nomenclature that many a better known area might well envy.

Problems of higher classification in the family, however, were almost completely passed over. Reason for this is not hard to discover: the problems involved so far transcended the boundaries of the West Indies that to resolve them would have necessitated an effort out of all proportion to the study and very likely would have greatly postponed or even completely stopped its appearance.

Subsequent work by others now has made considerable progress in reducing that hiatus. Of particular significance is the revision of some of the blues by Nabokov (1945), who brought an intimate knowledge of palearctic as well as nearctic groups to bear on the neotropical fauna, where this knowledge was peculiarly valuable. Much later my own work on the reclassification of the North American hairstreaks (Clench, 1961) touched on many West Indian groups and indicated that the male genitalia in particular could be of major assistance in determining their relationships.

Some time ago Mr. F. Martin Brown asked if I would go over the Jamaican hairstreaks for him in order to bring their generic classification into line with the North American revision. This took more time than at first expected, particularly in the collateral examination of mainland species, but when the task was done it was evident that a very little additional work would extend the results from just one island to the whole West Indian region. In view of the many changes indicated by Nabokov's work and of an unpublished survey of my own of *Leptotes* (world-wide), prepared by a fortunate coincidence for quite another purpose, it seemed opportune to combine all this into a synoptic list, herewith presented (Table I).

TABLE 1

SYNOPSIS OF THE WEST INDIAN LYCAENIDAE

family LYCAENIDAE
subfamily STRYMONINAE
tribe EUMAEINI

Eumaeus Hübner 1819
1. atala Poey 1832 (Cuba, Bahamas*)
a. florida Rober 1926(Florida)
=grayi Comstock and Huntington 1943

tribe STRYMONINI

Chlorostrymon Clench 1961
2. maesites Herrich-Schäffer (Florida, Bahamas, Cuba, Jamaica, Puerto Rico [not yet taken on Hispaniola but should occur])
a. clenchi Comstock and Huntington 1943 (Dominica)
3. simaethis Drury 1770 (Cuba, Hispaniola, Puerto Rico, Virgin Islands, St. Kitts, Dominica, St. Vincent)
a. jago Comstock and Huntington 1943 (Jamaica)
Other subspecies in Central and South America
Calycopis Scudder 1876
4. beon Cramer 1780 (Hispaniola). Status uncertain
Nesiostrymon new genus (see note no. 1)
5. celida Lucas 1957 (Cuba)
a. shoumatoffi Comstock and Huntington 1943 (Jamaica)
b. aibonito Comstock and Huntington 1943 (Puerto Rico)
[not recorded from Hispaniola but probably occurs there]
Callophrys Billberg 1820 ("see note no. 2")
subgenus Cyanophrys Clench 1961
6. crethona Hewitson 1873 (Jamaica)
Pseudolycaena Wallengren 1859 (see note no. 3)
7. marsyas Linnaeus 1758 (South America)
a. cybele Godman and Salvin 1896 (St. Vincent)
Another subspecies in South America
Heterosmaitia new genus (see note no. 4)
8. bourkei Kaye 1924 (Jamaica)
Allosmaitia new genus (see note no. 5)
9. coelebs Herrich-Schaffer 1862 (Cuba)
10. fidena Hewitson 1867 (Hispaniola, Puerto Rico)
*11. piplea Godman and Salvin 1896 (St. Vincent, Grenada, Dominica)
Strymon Hübner 1818
12. acis Drury 1770 (Antigua Dominica *)
a. mars Fabricius 1777 (Puerto Rico,*Virgin Is., St. Kitts)
b. petioni Comstock and Huntington 1943 (Hispaniola)
c. casasi Comstock and Huntington (Cuba)
Carpenter and Lewis (1943) report two subspecies from the Cayman Is., one from Grand Cayman and one from Little Cayman and Cayman Brac. The identity of neither is known to me.
d. armouri Clench 1943 (Bahamas)
e. subspecies ? (Caicos Islands: Rindge 1955)

f. gossei Comstock and Huntington 1943 (Jamaica)
g. bartrami Comstock and Huntington 1943 (Florida)
13. martialis Herrich-Schaffer 1864 (Florida; Bahamas; Cuba; Jamaica; Little Cayman, Cayman Islands)
14. rufofusca Hewitson 1877 (St. Vincent; [Central America])
15. bubastus Cramer 1780 [South America, including Trinidad]
a. ponce Comstock and Hintington 1943 (Puerto Rico; Virgin Islands; St. Kitts; Antigua; Dominica; St. Lucia; St. Vincent; Grenada)
16. columella Fabricius 1793 (Hispaniola)
a. modesta Maynard 1873 (Florida; Dry Tortugas *)
b. cybira Hewitson 1874 (Jamaica; Cuba; Bahamas*, Grand Cayman, Cayman Islands *)
c. arecibo Comstock and Huntington 1943 (Puerto Rico)
Other subspecies in Central America and related islands.
* 17. antigua Comstock and Huntington 1943 (Antigua, Virgin Islands)
* 18. toussainti Comstock and Huntington 1943 (Hispaniola)
* 19. cristophei Comstock and Huntington 1943 (Hispaniola)
* 20. limenia Hewitson 1868 (Cuba; Jamaica; Hispaniola; Puerto Rico)
21. bazochii Godart 1822 [Central and South America]
a. gundlachianus Bates 1935 (Cuba; Jamaica; Hispaniola)
Electrostrymon Clench 1961 (see note no. 6)
22. pan Drury 1773.(Jamaica)
23. angelia Hewitson 1874 (Cuba)
a. pantoni Comstock and Huntington 1943 (Jamaica)
b. dowi Clench 1941 (Bahamas)
c. boyeri Comstock and Huntington 1943 (Hispaniola; Puerto Rico; Virgin Islands -St. Croix, 4. v. 1941, leg. Beatty: 2 males, Carnegie Museum)
24. angerona Godman and Salvin 1896 (St. Kitts; St. Vincent; Dominica)
* 25. dominicana Lathy 1904 (Dominica)

subfamily PLEBEJINAE
tribe CATOCHRYSOPINI

Leptotes Scudder 1876 (see note no. 7)
(a) cassius group
26. cassius Cramer 1775 ([South America]; possibly Martinique)
a. catilina Fabricius 1793 (Virgin Islands; St. Kitts)
b. theonus Lucas 1857 (Florida; Bahamas; Cuba; Grand Cayman, Little Cayman and Cayman Brac, Cayman Islands;*Jamaica; Hispaniola; Puerto Rico)
c. chadwicki Comstock and Huntington 1943 (Dominica; Gaudeloupe)
Other subspecies in Central America.
(b) marina group
?27. marina Reakirt 1868 (Puerto Rico, probably as casual or misidentified theonus; [Central America])
28. perkinsae Kaye 1931 (Jamaica)

tribe PLEBEJINI (see note no. 8)

- Hemiargus Hübner 1818
  - subgenus Hemiargus Hübner 1818
    - 29. ceraunus Fabricius 1793 (Jamaica; Hispaniola; Navassa)
      - a. filenus Poey 1832 (Cuba; Bahamas; Grand Cayman, Cayman Islands *)
      - b. antibubastus Hübner 1818 (Florida; Georgia; etc.)
      - Other subspecies in Central America, south to Costa Rica.
    - 30. hanno Stoll 1790 [South America, north to Costa Rica]
      - a. watsoni Comstock and Huntington 1943 (Hispaniola; Puerto Rico; Virgin Islands; St. Kitts; Antigua; Guadeloupe; Dominica; Martinique; St. Lucia; Grenada; Barbados)
      - Other subspecies in South America.
  - subgenus Echinargus Nabokov 1945
    - 31. isola Reakirt 1866 (Puerto Rico, probably casual; [Mexico])
      - Other subspecies on the mainland, from western United States to Costa Rica.
  - subgenus Cyclargus Nabokov 1945 (see note no. 9)
    - 32. dominica Moschler 1886 (Jamaica)
    - 33. ammon Lucas 1857 (Cuba; Bahamas; Grand Cayman, Cayman Islands)
    - 34. woodruffi Comstock and Huntington 1943 (Puerto Rico; Virgin Islands; St. Kitts)
    - 35. erembis Nabokov 1948 (Little Cayman Island, Cayman Brac, Cayman Islands)
    - 36. thomasi Clench 1941 (Bahamas)
      - a. bahamensis Clench 1943 (Crooked Island, Bahamas, where it appears to be constant)
      - b. bethune-bakeri Comstock and Huntington 1943 (Florida)

      - c. noeli Comstock and Huntington 1943 (Hispaniola; Mona Island)
- Pseudochrysops Nabokov 1945
  - 37. bornoi Comstock and Huntington 1943 (Hispaniola; Puerto Rico [casual?])

subfamily BREPHIDIINAE

- Brephidium Scudder 1876 (see note no. 10)
  - 38. exilis Boisduval 1852 [western United States through Central America]
    - a. isophthalma Herrich-Schaffer 1862 (Bahamas; Cuba; Hispaniola; Jamaica; Grand Cayman, Cayman Islands)
      - =thompsoni Carpenter and Lewis 1943

  - * 39. barbouri Clench 1943 (Bahamas) Status uncertain
  - 40. pseudofea Morrison 1873 (Florida; Georgia; northern Bahamas)

All taxonomic changes and additions are provided in a series of notes referring to this list (Table I). The format of the list needs but few remarks. References are not given but may be obtained readily from Comstock & Huntington (1943) or some other work listed at the end. Distributions are complete so far as I know them. Species with an asterisk preceding their number have not been examined genitalically; all others have. An asterisk immediately following a locality indicates that the taxonomic status of the form in question is uncertain on the island.

Bates (1935: 188) remarked concerning the West Indian Lycaenidae, "The family at present, then, is of almost no use to . . . the zoögeographer," a remark which was certainly true enough when it was written. Comstock & Huntington's work made a considerable improvement, but left continental relationships, as before, quite uncertain. Nabokov's work and the present reclassification of the hairstreaks have both paid particular attention to these continental affinities, and as a result there are few forms whose relationship to mainland species or groups is still doubtful. The time, in other words, has come for a zoogeographic assessment of the group. For a number of reasons it has been impossible to attempt a "complete" analysis of Antillean lycaenid zoogeography. Instead, I have selected certain aspects of the problem for study and presentation here, and these may be found at the conclusion of the paper.

I. Nesiostrymon, new genus

Type species: *Thecla celida* Lucas 1857
(ssp. *shoumatoffi* Comstock & Huntington 1943)

Hind wing tailed. Male fore wing with a diffuse scent patch, its scales peripherally intermixed with ground color scales. Frons with appressed scales only, lacking any erect, bristle-like scales. Eyes with sparse, short hair. Male genitalia (fig. 3): the whole genital ring dorso-ventrally attenuate, due apparently to the ring being inclined (dorsal part to the rear) more than usual, relative to the body axis; falces of normal size, the fore arm straight with a slight, short, gradual apical constriction; an abrupt angle at the elbow; vinculum slender, sides subparallel for much of its length; saccus long, tapering, slender, with a rounded, slightly inflated tip; valvae short (considerably shorter, even, than the fore arm of the falx), completely fused with only a slight apical notch to indicate the division, broadest half-way from base. Penis long and slender, as usual, apically upcurving, with a single, simple exserted, acuminate cornutus, lightly sclerotized; no ventral terminal keel or ventral (or other exterior) teeth.

Remarks. Clearly related to *Ministrymon* Clench (*leda* Edwards, *clytie* Edwards) and to *Tmolus* Hübner (*echion* Linnaeus, *azia* Hewitson), although well differentiated from both. It may be distinguished from these two by the lack of bristly scaling on the frons, the more inclined genital ring and the consequent attenuation of this ring dorso-ventrally, and in the very short, completely fused valvae. With both it shares the single, simple acuminate cornutus, lack of ventral keel on penis tip, the very long saccus and the rather angular form of the falces.

The brilliant blue above is more like *Tmolus* (*echion*) than *Ministrymon,* as is the slightly more rounded wing shape and the diffuse scent patch.

The mainland (Mexico) species *tera* Hewitson is quite possibly congeneric but has not yet been examined critically.

II. Callophrys (Cyanophrys) crethona Hewitson

The genitalia of this species (fig. 1) indicate quite conclusively that it is a true *Cyanophrys.* Like the pattern, however, they suggest that *crethona* is more different from continental members of the subgenus than most of the latter are from each other, thus implying a relatively great age to the separation of *crethona.* Comstock & Huntington (1943: 123) state, however, that it is closely related to an undescribed species from Mt. Roraima, Brasil, a species I have not seen.

III. Pseudolycaena Wallengren 1859

Type species: *Papilio marsyas* Linnaeus 1758

Hind wing tailed, and with a tornal cleft. No scent patches. Frons with appressed scales only, lacking any erect bristle-like scaling. Eyes with sparse, short hair. Male genitalia (fig. 2): large, lateral hair pencils present, and a dorsal chitinous piece of undetermined shape attached to anterior border of tegumen; vinculum with posterior "shoulder" projection, vinculum strut prominent, strongly curved into this projection; falces rather strongly and evenly curved; saccus eight to ten times as long as width at middle, the sides subparallel, apex short, tapered, blunt; valvae rather short, broad, with lateral denticulate wings, pointed apex, slight dorso-lateral tooth, mesial borders divergent from before the middle. Penis with tip flared, definitely upturned, with two terminal cornuti, the longer one with small, obscure, apical teeth; terminal part of penis shaft with several short, external, longitudinal rows of small teeth.

Remarks. Structurally the genus is allied to *Atlides* Hübner (*halesus* Cramer) and *Arcas* Hübner (*imperialis* Cramer), particularly the former. All three of these genera share such significant characters as the extremely long, slender saccus, compact valvae, apically flared and upturned penis, special structural attachments on the anterior vinculum associated with the lateral hair pencils; and all three have the curious and interesting tornal cleft on the hind wing, as first pointed out by Godman & Salvin (1887: 15).

So far as I know the genus is monotypic, the sole species, *marsyas* Linn., with a Central American subspecies (*damo* Druce), a South American (nominate *marsyas*) and the still little known Lesser Antillean subspecies, *cybele* Godm. & Salv.

Fig. 1. *Callophrys* (*Cyanophrys*) *crethona* Hewitson, male genitalia (slide C-705). Penis on left. This and the succeeding genitalia drawings were made from mounts prepared as follows: first the penis was removed; then the vinculum was cut through on the right side and the structures opened out so that the inner sufaces are uppermost. Drawings were made to show the complete structures of the left side only (though usually both valvae are drawn). Uncus, tegumen and falx are to the top right; saccus and valvae to the left. This somewhat unorthodox procedure permits showing the structures with a minimum amount of distortion.

Fig. 2. *Pseudolycaena m. marsyas* Linnaeus, male genitalia (slide C-822). Penis below, the central part of the shaft omitted, but with a scale to indicate true relative length.

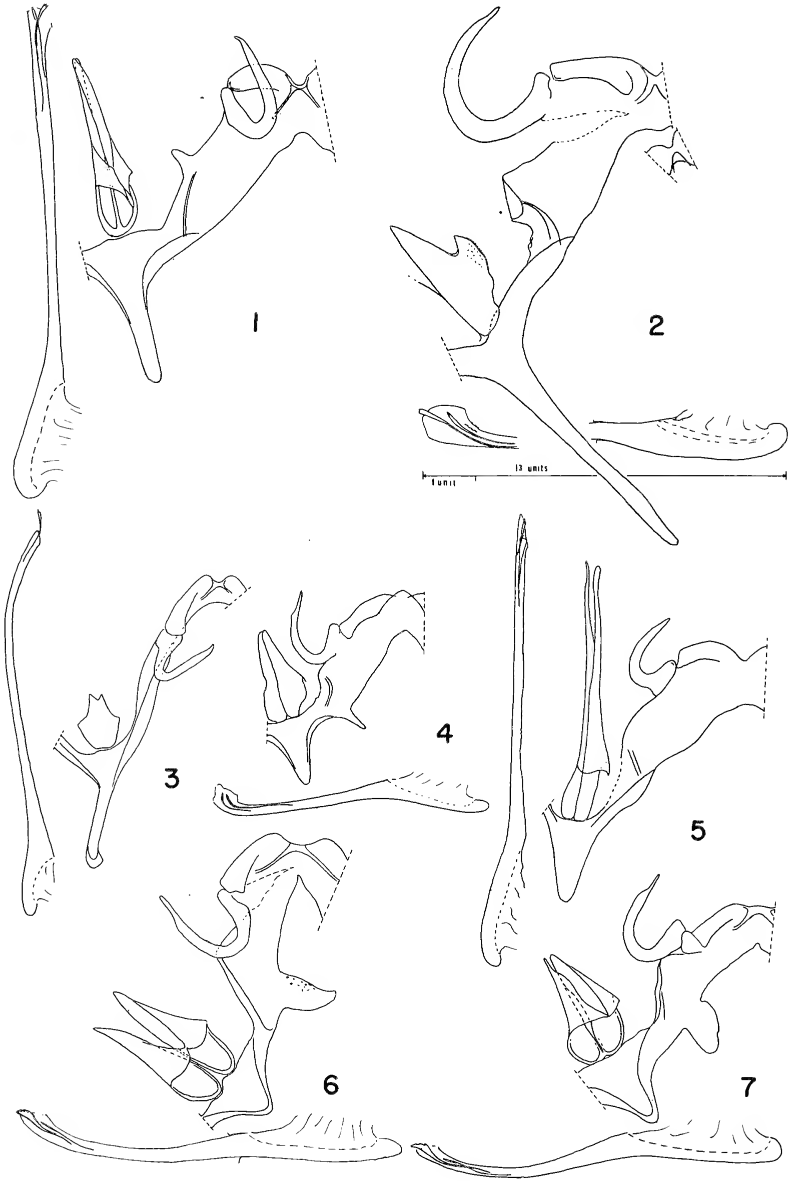
Fig. 3. *Nesiostrymon celida shoumatoffi* Comstock & Huntington, male genitalia (slide C-708). Penis on left.

Fig. 4. *Heterosmaitia oppia* Godman & Salvin, male genitalia (slide C-823). Penis below.

Fig. 5. *Allosmaitia coelebs* Herrich-Schäffer, male genitalia (slide C-829). Penis on left.

Fig. 6. *Heterosmaitia bourkei* Kaye, male genitalia (slide C-709). Penis below.

Fig. 7. *Heterosmaitia brescia* Hewitson (?), male genitalia (slide C-826). Penis below.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IV. Heterosmaitia, new genus

Type species: *Thecla bourkei* Kaye 1924 (Jamaica)

Hind wing tailed; males with androconial apparatus variable (see below). Frons bristled to variable degree. Male genitalia (Figs. 4, 6, 7): falces with tips prominently and abruptly constricted; vinculum with anterior triangular projection (associated with the paired lateral eversible scale tufts or coremata); saccus short, twice or less than twice as long as width at middle; valvae of normal length, simple, mesial edges smooth; penis without ventral keel or ventral teeth, more or less upturned apically, with two terminal cornuti. Males all with a tornal red spot on hind wing above.

Remarks. The genus is mostly developed on the mainland, principally in Central America. Investigation of potential relatives or possible members is still incomplete, but studied members may be grouped as follows:

1. *oppia* group

Eyes with dense, long hairs. Frons with dense, erect, long bristles in the median dark area; male fore wing without scent pad; hind wing with a dark glandular patch at origin of Rs, with a few long, erect, specialized scales from it near its posterior border; associated with this is a flat-lying, heavy fringe of dark scales arising on the inner margin of the fore wing below, directed anteriorly; around this fringe the wing scaling is modified to form a large opalescent-iridescent patch in Cu_2-2A below cell, with a patch of dark ochraceous mealy scales in the center. Male genitalia (fig. 4): anterior triangular process of vinculum small, close to saccus; valvae ventrally contiguous to near their tips; penis strongly upturned apically; cornuti subequal in thickness, with few or no apical teeth.

Includes only the Central American *oppia* Godman & Salvin.

2. *bourkei* group

Eyes with short, sparse hairs. Frons with bristles sparse, slight; male with scent pad on fore wing at cell-end; no specialized scaling on fore wing below or hind wing above. Male genitalia: anterior triangular process of vinculum large, farther from saccus (more or less mid-lateral); mesial edges of valvae divergent from before the middle; penis slightly upturned apically; one cornutus apically much thicker than the other with many apical teeth.

Subgroup A. Saccus much less than half as long as valva; larger cornutus with apical expanded part short, the expansion abrupt; penis slightly upturned (fig. 6). Subterminal line of fore wing below rather well developed; fuscous border of male fore wing above covers about half the cell-end-to-apex distance.

Includes *bourkei* Kaye (Jamaica) and at least two Central American species, one of which has been tentatively identified as *guadala* Schaus.

Subgroup B. Saccus much more than half as long as valva; large cornutus with apical expansion gradual and rather long; penis not at all upturned (fig. 7). Subterminal line of fore wing below very faint; fuscous border of male fore wing above covers about 1/3 the cell-end-to-apex distance.

Includes several apparently distinct species ranging from Mexico to South America, including one tentatively identified as *brescia* Hewitson. No West Indian species are known.

V. Allosmaitia, new genus

Type species: *Thecla coelebs* Herrich-Schäffer 1862 (Cuba)

Hind wing tailed. Eyes with rather long, dense hairs. Frons sparsely bristled. Male without scent pad on fore wing but on hind wing with a tuft of long, dark hairs arising from a small modified patch in the angle between Sc and the costal border of the cell; associated with this there is on the fore wing below a small, shining patch of modified scales on the inner marginal area, near which vein 2A is slightly enlarged and scaleless. Male genitalia (fig. 5): no triangular process on anterior border of vinculum; falces with gradually tapering tips; valvae exceeding long and slender, the result of a greatly attentuated and produced terminal region, the mesial border serrate terminally; penis apically very slightly and gradually upturned, with two cornuti, one of which is distally enlarged, spatulate, and provided with a flat terminal edge armed with a row of low teeth; saccus moderate in length. Male above with no red spot at tornus. Fore wing of male with fuscous border extending basad to cell-end.

Remarks. Clearly allied to the preceding genus, *Heterosmaitia*, differing most notably in the long tuft of hairs on the hind wing androconial patch, the absence of an anterior process on the vinculum, the extraordinarily produced valvae, the spatulate, truncate cornutus, as well as in the absence of a tornal red spot on the male hind wing above.

Includes the following species: *pion* Godman & Salvin (Central America), *coelebs* Herrich-Schäffer (Cuba), *fidena* Hewitson (Hispaniola, Puerto Rico). In addition, the following species probably also belong but no specimens have been available for study: *piplea* Godman & Salvin (=*subobscura* Lathy ?) (St. Vincent, Grenada, Dominica), *panchaea* Hewitson (=*scoteia* Hewitson ?) (Amazonas, Minas Geraes).

VI. Electrostrymon Clench 1961

The West Indian species (save *dominicana* Lathy, which I have not seen) are, according to both pattern and genitalia, more closely interrelated than any is to *endymion* of the mainland, the type species and the only mainland species I have so far investigated.

VII. Leptotes Scudder 1876

This genus is holotropical in distribution, being known in the Old World chiefly under the name *Syntarucus* Butler 1900. The American species divide neatly, according to male genital characters, into three groups and additional, co-equal, groups occur in the Old World. None of these groups would seem to warrant being called even a subgenus. The three American groups are:

(1) The *cassius* group. This includes only *cassius* (with all its subspecies) and a still undescribed species from the Colombian Andes.

(2) The *marina* group. Comprises *marina* Reakirt, *perkinsae* Kaye and perhaps *parrhasioides* Wallengren from the Galapagos Islands. This group is also represented by a number of species in Africa, Madagascar and associated islands.

(3) The *callanga* group. This is perhaps the most primitive group in the genus, and includes *callanga* Dyar, from the Peruvian Andes, and most surprisingly *webbianus* Brullé of the Canary Islands.

VIII. Tribe PLEBEJINI

The classification here is essentially that of Nabokov (1945), with his subfamily Plebejinae demoted to a tribe, his relevant genera demoted to subgenera under *Hemiargus,* except for *Pseudochrysops,* which is distinct enough in every way to be accorded full generic status.

IX. Subgenus Cyclargus

Nabokov groups these five species into two "superspecies": (1) comprising *dominica* and *ammon;* (2) comprising *thomasi, woodruffi, erembis.* Interesting confirmation exists in the sympatry (more or less) of *ammon* and *thomasi* in the Bahamas; and Nabokov suggests that *erembis* may eventually be found in Cuba, sympatric there with *ammon.*

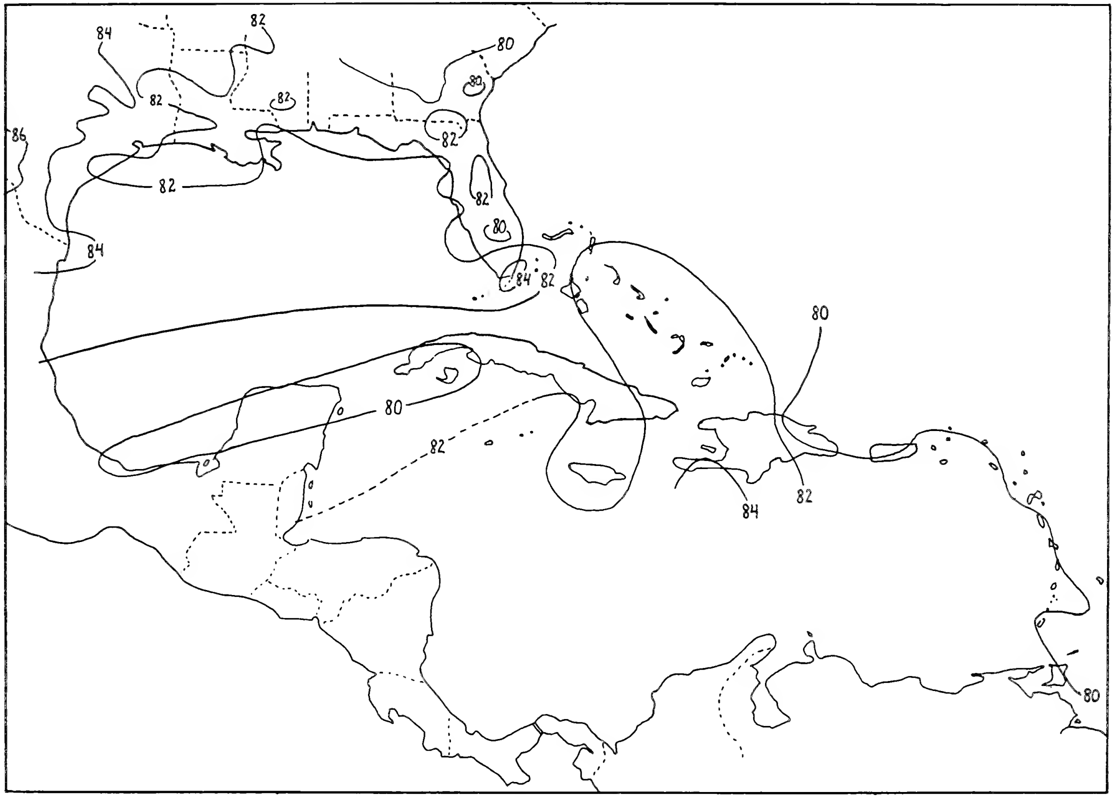

Fig. 8. Present-day mean July temperatures (°F) in the West Indies.

X. Brephidium Scudder 1870

Carpenter & Lewis (1943: 392) described *Brephidium isophthalma thompsoni* in comparison with *pseudofea* Morr., under the mistaken, but then prevalent, opinion that is was nominate *isophthalma*. It is not distinguishable from other Antillean populations of *isophthalma*.

Brephidium barbouri Clench was described as a distinct species, but later was synonymized by Gillham (1955). In view of Gillham's attitude towards subspecies, ând of the subtle and minute species differences in the male genitalia of *Brephidium* which he may not have been able to appreciate, as well as of the differences given in the original description, his action must be restudied. Rindge's remarks (1955: 14) are interesting in this connection.

ZOOGEOGRAPHICAL CONSIDERATIONS

The general pattern of lycaenid distribution in the Antilles is essentially similar to that shown by most other groups of animals (cf. Darlington, 1957: 510). In brief, they constitute a depauperate fauna of distinctly Central American aspect; they can be entirely accounted for under an assumption of waif dispersal across water gaps similar to those occurring today; the most striking endemics of the region occur in Jamaica and Hispaniola; and despite the frequent development of endemic subspecies in the different islands or island groups the insular region as a whole presents a rather uniform, cohesive, facies. In contrast to some animal groups, however, the lycaenids of both southern Florida and the Lesser Antilles contain such a sizable and unmistakable West Indian component that for purposes of discussion these areas must be considered integral, if peripheral, parts of the Antillean region.

The following discussion is not intended to be a full analysis of West Indian lycaenid zoogeography. I have simply singled out for discussion a few points that seem especially clear or particularly interesting with emphasis on processes and events in the hope and belief that these are of the most interest and value to others.

1. *Late Pleistocene climatic changes*

If there is one event that stands out more than any other as the most important architect of the present distribution pattern of lycaenids in the West Indies, that event would have to be the last (Wisconsin) glaciation of the Pleistocene. It is well known, though still too little appreciated by some zoogeographers, that during the times of glacial advance temperatures dropped considerably not just at the ice front but the world over. The actual amount of the drop undoubtedly varied to some extent from place to place but it was on the order of approximately 9° Fahrenheit (Flint, 1947: 455). Antillean lycaenids demonstrate such a temperature drop quite unmistakably, and even indicate certain of its details. Since summer temperatures in the West Indies (fig. 8) are very little zoned there is no direct evidence in the lycaenids whether or not these temperatures were affected by Wisconsin cooling[3]

[3] Though a certain amount of indirect evidence suggests that they probably were.

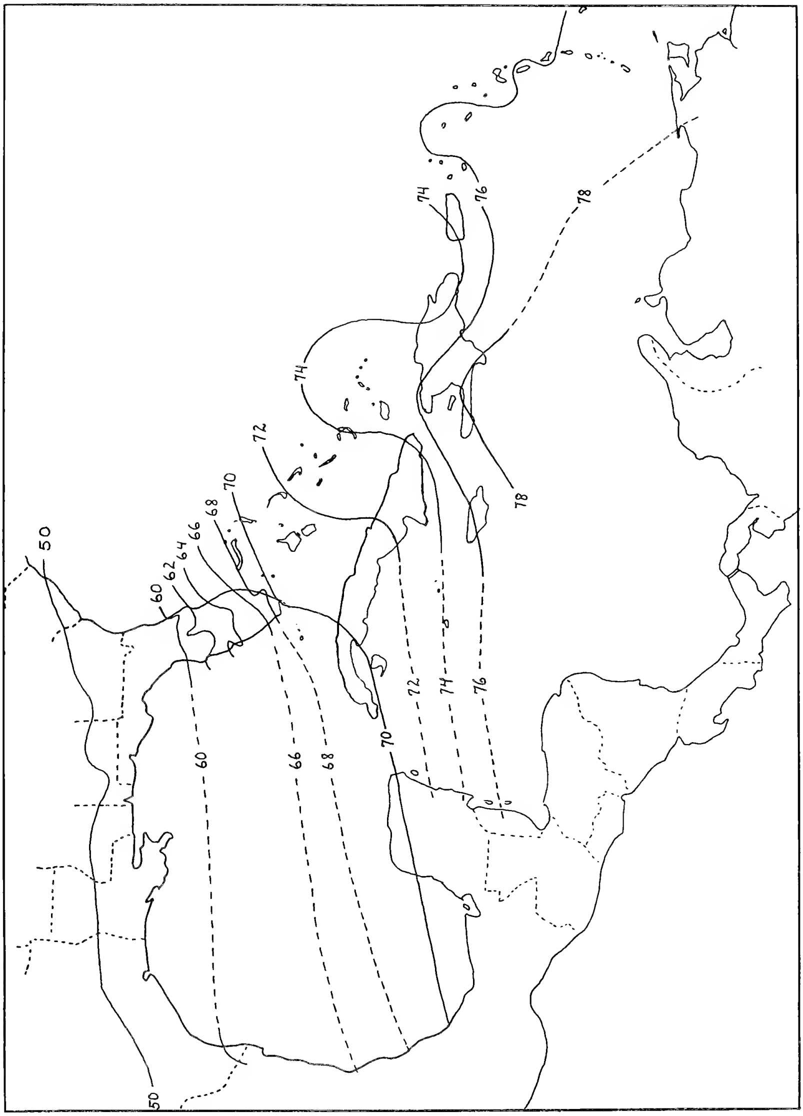

Fig. 9. Present-day mean January temperatures (°F) in the West Indies.

but there is definite indication that winter temperatures were lowered. The amount of winter (January) mean temperature reduction that best fits the present distributional evidence is approximately 8° F. Interestingly only a very slight modification of the present January isotherm contours (fig. 9) is required: a uniform reduction would almost suffice. The needed modification is a slight shift to the east of the "warm zone" which now lies over western Hispaniola, and of the cooler zone which occurs just to the east over northeastern Hispaniola and western Puerto Rico, so that the first would lie squarely over Hispaniola and the second directly over Puerto Rico.

The evidence that leads to these conclusions consists of three parts: (1) evidence for the reduction and its amount; (2) evidence for the slight eastward zonal shift; and (3) evidence for the time when this happened.

The reduction and its amount. Let us begin with the Antillean element in peninsular Florida, which is clear-cut, of obvious derivation (Cuba or the Bahamas) and, most importantly, is "open ended" — the northern limits of the ranges are determined by the direct interaction of the organisms and the environment, rather than being imposed by an island shore.

Florida's Antillean lycaenids may be divided into three groups according to their relationships to their nearest relatives in the islands:

Ia. Undifferentiated. *Chlorostrymon maesites, Strymon martialis, Leptotes cassius theonus.*
Ib. Subspecifically distinct. *Eumaeus atala, Strymon acis, S. columella, Hemiargus thomasi, H. ceraunus.*
Ic. Specifically distinct. Only *Brephidium pseudofea* (whose probably postglacial invasion of the northern Bahamas may be ignored for present purposes).

On the basis of their tolerance to January mean temperatures in Florida they also divide into three groups but differently assorted:

IIa. Northern boundary coincides more or less with 65° isotherm: *E. atala, C. maesites, S. acis, S. martialis, S. columella.*
IIb. Northern boundary coincides more or less with 62° isotherm: *L. cassius, H. thomasi.*
IIc. Northern boundary farther north than 60° isotherm: *H. ceraunus, B. pseudofea.*

The hypothesis which best explains the above facts is that at some past time conditions in Florida were measurably cooler than now; that during this cooler time and because of it the greater part of the Antillean element was absent; and that subsequently conditions warmed to about their present state, permitting the island forms to invade the peninsula and establish themselves, creating the present fauna. Important in this connection is the degree of differentiation of these invaders. This is discussed more fully below and all that need be said here is that with the exception of *pseudofea* (Ic above) they show a fairly consistent degree of differentiation ("slight" subspecies to undifferentiated) of a small order of magnitude. This argues for a nearly simultaneous entry into Florida not very long ago (as opposed, for example, to random arrival and establishment at intervals over a long period of time.)

A drop of twenty degrees would be required to completely eliminate all the West Indian species now in Florida because of the considerably more cool tolerant group IIc above. Such a reduction is patently absurd for it would also have eliminated virtually all the lycaenids in the islands too. A much more realistic 8° would suffice to lower the mean January temperature of warmest Florida from its 70° to 62°, probably sufficient to wipe out all but the rebellious IIc species and further south not too severe for survival on some islands. Taking into consideration the distinct possibility that some species, particularly those of group IIb, may have become adapted in Florida to somewhat cooler conditions than they could tolerate when they first arrived (for several reasons more likely on the mainland than in the islands), a more conservative 6° might be suggested. The higher figure, however, is preferable because of what apparently happened in the islands: a drop of only 6° would be insufficient to explain the pattern of survival which is indicated there (discussed more fully below). Nonetheless this reasoning suggests that in the absence of the stronger selection pressures of the mainland the minimum tolerance of Antillean lycaenids was about 66° mean January temperature.

The eastward zonal shift. A reduction of 8° in the present Antillean January isotherm of 74° would bring it down to the suggested critical value of 66°, and this isotherm may be imagined as roughly dividing the insular region into two areas: a northern one which in Wisconsin time had winter temperatures below the critical value; and a southern one which had temperatures above this value and hence presumably could have served as a refuge area during that glaciation.

An island which today harbors one or more endemic full species can be presumed to have maintained at least those species through Wisconsin times. Jamaica has five such endemics, Hispaniola three, Cuba three (including *E. atala* which, though not endemic, must have survived the glaciation there). Puerto Rico and the Bahamas have none. There are also several significant endemics in the Lesser Antilles, but distributional knowledge is insufficient to discuss them in detail. It is legitimate to conclude from this that Jamaica, Hispaniola, and the Lesser Antilles must have had adequate winter temperatures during Wisconsin time while Puerto Rico and the Bahamas did not. Cuba, on this basis, probably had adequate conditions but only marginally so.

The present January isotherm of 74° (hypothetical Wisconsin 66°) comes close to dividing the Antilles in just that way. It passes barely through southernmost Cuba, consistent with the marginal conditions just suggested; Jamaica and the Lesser Antilles lie wholly below it and Hispaniola nearly so, in harmony with the conditions suggested by their relatively large number of endemics.

But as it stands it is not perfect. Marginal conditions, according to the present configuration of the isotherm, should have prevailed in the southern Bahamas and in Puerto Rico, whereas there is no evidence that any lycaenids survived in either. Adjustment of the configuration to conform with the endemics (and lack thereof) is, however, minor: push it southward where it intersects the Bahamas[4] and nudge it a little to the east where it crosses Hispaniola and back again over Puerto Rico. The results are shown in fig. 10.

The time it happened. The best source of information on this point is the degree of differentiation that has taken place between the forms in Florida and their nearest insular relatives (see groups Ia, Ib, above). The maximum differentiation is shown by the members of Ib, all of which are "slight" subspecies of insular species. This degree of divergence is typical of what is imputed to post-Wisconsin effects in many groups of animals (not just lycaenids, or even just butterflies), and in places where glacial influence is more directly ascribed to the differentiation. Little more need be said: by their degree of divergence, the concordance of several forms, and their presence in a place where conditions were appropriate, they indicate arrival in Florida, either from Cuba or the Bahamas, closely following the warming temperatures that accompanied recession of the Wisconsin ice sheet far to the north.

As to the undifferentiated species in group Ia, there are two explanations. They might be late arrivals and accordingly have had too little time to become differentiated; or they might have arrived with the others but because of a much lower evolution rate have simply failed to diverge. I incline to the latter possibility for a number of reasons:

First, these same species show similar effects among the islands: no divergence between islands where other species have become postglacially divergent, sometimes (e.g. *C. maesites*) showing subspecies only where a separate glacial refuge can be invoked.

Second, when the temperatures were warming at the end of Wisconsin time the northerly islands must have presented a sort of ecological vacuum extremely receptive to immigrants from the south. Since then, however, it is likely that the hypothesized "closed association" or "closed community" effect has become operative. This hypothesis

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[4] A little push only; a very few butterflies, *Eurema chamberlaini* Butler being the most conspicuous, seem to have been able to persist in these islands during the Wisconsin.

Fig. 10. Assumed mean conditions for January during Wisconcin glacial maximum. Line represents approximate position of 66°F isotherm (position and configuration based on present day January isotherm of 74° with modifications: see text). Shaded areas represent presumed refugia during Wisconsin time.

(cf. Weaver & Clements, 1938: 171) holds that in a climatically stable situation communities so adequately fill the available niches that they tend to impede the establishment of immigrants from without. It is, of course, not an absolute condition but a tendency. It must, however, become increasingly effective with decreasing distance from the prospective source of the immigrant. Between the West Indian islands, for example, it seems probable that movement between adjacent islands is sufficiently frequent that those forms capable of becoming established have already done so long ago while those incapable continue to fail.

Third, statistically it is more logical to expect a variety of evolution rates in a group than a single rate. There is no reason whatever to expect a form to subspeciate simply because it has the chance. Florida's Antillean lycaenids present an entirely reasonable pattern of some low rates, some higher rates (time has been insufficient to distinguish clearly between "high" and "not so high" rates, however).

Resumé. It would be well to recapitulate the events discussed above, putting them in chronological order.

(1) The advance of the Wisconsin ice sheet was accompanied all over the world by a marked drop in temperature. In the West Indies the effect was to reduce mean January temperatures by about 8°F., the effect, if any, on summer temperatures being indeterminate.

(2) The result of this was to extirpate completely the Antillean lycaenids in Florida (except *Brephidium pseudofea*), the Bahamas and Puerto Rico, and most of them in Cuba. Survival was possible on a large scale only in Jamaica, Hispaniola and in the Lesser Antilles (the latter discussed below).

(3) When the Wisconsin sheet retreated, some 12,000 years ago, conditions returned to approximately their present state and concurrently many species that had been confined to the three or four refugia just mentioned spread out rapidly, occupying all islands (more or less) capable of supporting them.

(4) Since that time certain of these species have evolved, or have continued to evolve, producing subspecific differentiation among the islands. Others with a slower evolution rate have remained visibly undifferentiated.

It may be of interest to summarize the probable or possible lycaenid faunal composition of the four principal refugia at the height of the Wisconsin glaciation. The evidence allocating a particular species to one or another refugium is various. Endemic full species are, of course, immediately assignable. But assignment of others is based on the most likely refugium, granted the foregoing sequence of events. Species that today show among the islands subspecies of about equal divergence one from another (e.g., the subspecies of *E. angelia*) are assumed to have spread out from a single refugium. Those such as *S. acis* that show two groups of subspecies suggest double refugia with subspeciation already in progress between them during Wisconsin time.

1. Cuba. *E. atala, A. coelebs* and *H. ammon* are endemic there or nearly so, and apparently survived the Wisconsin there. A total of three species.

2. Jamacia. *C. crethona, H. bourkei, E. pan, L. perkinsae* and *H. dominica* are all endemic full species and must have survived the Wisconsin *in situ*; in addition the following were likely: *S. acis* (ancestor of sspp. *bartrami, casasi, gossei, armouri*), *S. martialis, S. columella* (ancestor of sspp. *modesta, cybira*), *L. cassius theonus, H. ceraunus* (ancestor of sspp. *filenus, ceraunus, antibubastus*), *B. exilis isophthalma.* A total of 11 species listed.

3. Hispaniola. *S. cristophei, S. toussainti, P. bornoi* are all endemic there today. Additionally the following were likely: *A. fidena, S. acis* ancestor of sspp. *acis, mars, petioni*) *S. columella* (ancestor of sspp. *columella, arecibo*), *S. limenia, E. angelia, H. thomasi.* A total of nine species listed.

4. Lesser Antilles. *A. piplea, S. antigua, E. angerona, E. dominica* are all endemic there today. The following were likely in addition: *P. marsyas cybele, S. bubastus ponce, L. cassius catilina, L. cassius chadwicki, H. hanno watsoni, H. woodruffi.* A total of nine species listed, one of them in two subspecies.

The following species were undoubtedly present on one or more of these refugia but the particular one (or ones) cannot now be deducted from available data: *N. celida; S. bazochii; C. maesites* (ssp. *clenchi* probably was present in the Lesser Antilles but the refugium of *m. maesites* cannot be determined); *C. simaethis* (ssp. *jago* was probably present in the Jamaica refugium but the refugium of *s. simaethis* is not determinable.

In concluding this subject it may be of interest to add some observations on three related matters.

First, the Wisconsin extirpation of the Antillean lycaenids in Florida, the Bahamas, Puerto Rico and at least partially in Cuba, does not imply that these areas were without Lycaenidae during the glaciation. Florida, to judge by availability and systematic relations today, must have had a sizeable number of species; but which of these, if any, might have invaded the islands themselves is not known, nor is it ever likely to be since they have now all disappeared. From this last I should guess that the putative transient boreal element could not have been particularly large in the islands, or some would surely have managed somehow to survive into the present. A few species in other butterfly families, however, suggest just such a history. *Phyciodes phaon* Edwards (Nymphalidae) is a possible example.

Second, although it cannot be invoked in explanation of any known lycaenid distribution, the matter of altitudinal range deserves brief notice since it is definitely involved in the distribution of certain other butterflies. A species adapted to conditions found above an elevation of roughly 2000-2500 feet or so could have survived the suggested glacial temperature drop more or less in place simply by moving downward. Such groups of species as *Calisto* (Satyridae), *Atlantea* (Nymphalidae),*Dismorphia* (Pieridae) and *Hymenitis* (Ithomiidae) probably owe their preservation through the Wisconsin glaciation to this factor.

Third, there are several groups of related species in the islands whose affinities suggest that they arose within the island area by a process analogous to that which has produced the now observable subspecies in many species. The Antillean species of *Electrostrymon* form one such group; the subgenus *Cyclargus* another; the Antillean *Allosmaitia* probably yet another. Each of these groups suggests dispersal through the islands from a refugium (or original beachhead of establishment in the islands) closely following a glacial recession. The degree of divergence in these instances and the subsequent history of several of the component species imply forcibly that a glaciation older than the Wisconsin was responsible, perhaps the next earlier (Illinoian).

2. *Mainland colonization from the islands*

Under this heading I propose to unite the discussions of three different examples, all of which share the possibility that they have colonized the Central American mainland from the islands. This seems to be a novel idea: at least I know of no prior suggestion of it in any group. It is hard to tell though whether this is due to the probable rarity of the phenomenon or to such preoccupation with the many problems associated with invasion from the mainland that the idea of a reverse colonization simply never occurred to anyone. In any case there are three instances in the lycaenids where this seems to be indicated. Parenthetically it may be noted that of roughly 20 successful migrations between islands and mainland (other than Florida) needed to account for the Antillean Lycaenidae, three (15%) are of this abinsular type, the remaining 17 being more conventional adinsular colonizations. If the lycaenids represent a fair zoogeographic sampling of the island fauna, 15% is quite large enough to make abinsular colonizations worth looking for in other groups.

1. *Strymon columella.* This species does not occur in South America but it is present in Central America (including Baja California and some of the offshore Pacific islands) where it ranges north into southern United States, and it occurs on all the major islands and island groups of the Greater Antilles. There are several related species in the West Indies (*antigua, toussainti, cristophei, limenia*), while in South America occur still other allied species. This pattern suggests that there was an early colonization of the Antilles, probably from South America, followed by speciation within the islands that resulted eventually in the formation of *columella.* Then, most likely during the Wisconsin, the latter crossed over into Central America. With

the recession of the Wisconsin sheet, in addition to spreading out from its island refugia it also spread, in Central America, to Baja California and to some of the islands off the West Coast.

The remaining two examples are even more unusual in that they show definite evidence of having come originally from Africa. So far I am aware these two, the *Leptotes marina* group and *Brephidium,* are the only New World Lycaenidae to which an African origin can be attributed. It has been suggested that *Zizula cyna* Edw. (purely continental from southern United States south to Brazil and Bolivia) is such an African derivative but fuller investigation does not support the contention. *Z. cyna* is a distinct New World species; its closest ally, the polytypic *Z. gaika* Trimen, ranges from Africa to Australia. Comparison of *cyna* with various *gaika* populations show a distinctly greater resemblance to those from eastern Asiatic localities than to those of Africa. The only conclusion possible on this evidence is that *cyna* was derived from Asia *via* the Bering Strait route and not from Africa.

2. *Leptotes marina* group. As pointed out above (note no. 7) this group consists of a number of species in Africa, Madagascar and several of the islands in the western Indian Ocean as well as the three New World species, *perkinsae* (Jamaica), *marina* (Central America) and probably *parrhasioides* Wallengren (Galapagos Islands).[5] The *marina* group occurs nowhere else but related groups also occur in Africa. The presence of members of the group on so many remote oceanic islands is dramatic evidence of a considerable propensity for colonizing across large water distances so it would be by no means impossible for a hypothetical "*marina* group ancestor" to have made the long voyage from Africa to the New World. The real question is the site of its landfall. On the face of it South America would appear to be the best answer by far; it is nearest to Africa and it is the largest available target for a random trajectory to hit. The evidence against this possibility, however, is to me persuasive though admittedly tenuous.

First, the present distribution of the New World members of the group is distinctly northern tropical, almost subtropical. Only *parrhasioides* is truly equatorial (in latitude but not in climate).

Second, for some unknown reason the tropics generally are not very favorable for the Plebejinae. This is least true in the East Indies, most true in the New World. It is therefore distinctly possible that a form of this subfamily arriving in eastern South America would be poorly equipped *a priori* to compete and establish itself there. In the West

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[5] Comstock & Huntington (1943:95) cite *marina* from Chile and the Galapagos. It is hard to question the accuracy of such meticulous observers but it is even harder to accept these records. Either mislabelling or misdetermination would seem to be involved here.

Indies, on the other hand, conditions appear to be much more favorable to the subfamily. *Leptotes, Hemiargus* and *Pseudochrysops* flourish there and together make up a larger percentage of the lycaenid fauna than in any other tropical area in the Americas.

Third, comparison with *Brephidium* (which presents at least one additional type of evidence) shows a strongly similar pattern in many respects, and each thereby lends support to the other.

The tentative conclusion is that the ancester of the New World members of the *marina* group crossed from Africa to the West Indian region where it became established; that from there it successfully invaded the Central American mainland; and then spread from there to the Galapagos. It is impossible, at least with the information available now, to guess when this might have happened. Diversification of the group in the New World has left no tangible clues to evolution rates. One might say that if evolution rates in the group were more or less typical, then the Atlantic crossing might have been made in mid-Pleistocene or thereabouts but that is completely without documentation.

3. *Brephidium.* There are many points of similarity to the *marina* group in the distribution pattern of this genus, and just enough differences that, if they share a similar history, one tends to complement the other in evidence. There are three known species of *Brephidium* (omitting *B. barbouri* because of insufficient information):

B. pseudofea Morr., confined to Florida and Georgia with a single recently discovered colony (Rindge, 1952: 13) in the northern Bahamas.

B. exilis Bdv., widespread in the New World with these known and very distinct subspecies: nominate *exilis* from Oregon and Nebraska (probably not overwintering) south so far as now known to eastern Texas and on the Pacific Coast to southern Baja California and to Mazatlàn (Sinaloa, Mexico) at least; a still undescribed subspecies from coastal Yucatan; probably one or more other subspecies down to northern Venezuela, the limit of the known continental distribution of the species; *e. isophthalma* from the West Indies.

B. metophis Wallengren in South Africa, chiefly in the western Cape Province and western Orange Free State, more or less sympatric there with the related monotypic genus *Oraidium* (*barberae* Trimen). See Swanepoel (1953: 80-81) for information on these two species.

No other members of the genus and no other closely related genera are known anywhere.

The northern range of *exilis* on the mainland and its nearly complete absence from South America implies a northerly source, further supported by the presence of ssp. *isophthalma* in the Greater Antilles. The distinctness and the presence in Florida of *pseudofea* constitute strong presumptive evidence that it is there a survivor of an earlier invasion from the islands, again implying a longer occupancy by the genus in the Antilles than on the mainland, where only one species is known.

These points lead to the conclusion that an ancestral *Brephidium* crossed from Africa to the West Indies and became established there; then later spread to Florida to form *pseudofea;* and still later crossed to the mainland to give rise to the several subspecies of *exilis* now known there.

We are in a somewhat better position in *Brephidium* than in the *marina* group to date these events, however roughly. The presence of *isophthalma* on several Greater Antillean islands without apparent subspeciation is evidence that the evolution rate of *exilis* is rather low, requiring more than post-Wisconsin time to produce visible subspeciation. We are, therefore, led to conclude that the invasion of the mainland, where several distinct subspecies now occur (all different from the insular subspecies as well), preceded the Wisconsin; and that the origin of Floridian *pseudofea* must be much older still. The whole New World history of the genus could have been written since the onset of the Pleistocene, and may well have been, but it could easily have been even older.

In passing it may be noted that this suggestion of an African origin of New World *Brephidium* carries with it the likelihood that at the time of the Atlantic crossing *Brephidium* in Africa enjoyed a wider, or at least considerably different, range than it does now. Possibly it was then an inhabitant of the savanna regions of the interior of Upper Guinea.

3. *The Lesser Antilles fauna*

Our knowledge of the lycaenids of this curious chain of islands appears to be still fragmentary, but there are two points at least which warrant brief remarks and for which the distributional evidence seems adequate.

Mention has already been made of the likelihood that the Lesser Antilles served as a Wisconsin refugium. This refugium, however, appears to have functioned much less as a source of postglacial spreading than either of the other two primary refugia, Jamaica and Hispaniola. These facts are relevant: (1) the Virgin Islands are faunistically a part of the Lesser Antilles (cf. Comstock & Huntington, 1943: 121); (2) of the 12 lycaenid species regularly occurring in Puerto Rico, the first "port of call" for a potentially expanding Lesser Antillean refuge fauna, three (*C. maesites, C. simaethis, N. celida*) must be omitted for uncertainty of origin; three (*S. bubastus, H. hanno, H. woodruffi*) are clearly derived from the Lesser Antilles in postglacial times while the remaining nine are apparently derived from Hispaniola; (3) St. Kitts shares most, perhaps all, of its fauna with the Virgin Islands, but the remaining Lesser Antilles do not do so to the same extent. These three points suggest that the failure to expand postglacially may be more apparent than real. The problem would be neatly solved by making the assumption that the Virgin Islands shared Puerto Rico's low temperatures during Wisconsin times and were therefore not inhabited; that when recession of the Wisconsin sheet began, invasion of Puerto Rico started from Hispaniola while simultaneously the Virgin Islands were being invaded from St. Kitts. This would explain not only the predominantly Hispaniolan character of the Puerto Rican fauna and the Lesser Antillean character of the Virgin Islands fauna but also the apparent failure of the Lesser Antillean refuge fauna to disperse; for under this hypothesis it would not have lacked capacity to disperse but simply did not have the opportunity to spread so far because of the opposing expansion of the Hispaniolan refuge elements.

Strikingly apparent is another aspect of this Lesser Antillean fauna: its integral relation to, and derivation from, the fauna of the Greater Antilles. Fourteen species are known from the islands, from the Virgin Islands to Grenada inclusive. Of this number one remains an enigma as to its origin (*S. rufofusca*); one is indeterminate and could have reached the Lesser Antilles from either the north or the south (*C. simaethis*); three are of unquestionable South American origin (*P. marsyas, S. bubastus, H. hanno*), and *L. c. cassius* may also have invaded the islands from South America as far as Martininque (only a single male is known from the island). The remaining nine species are of obvious Antillean derivation: *A piplea, S. acis, S. antigua, E. angelia, E. angerona, E. dominicana* (probably), *C. maesites, H. woodruffi, L. cassius* (sspp. *catalina* and *chadwicki*). Counting only those of reasonably assured origin shows that the Lesser Antillean fauna is about 75% Greater Antillean in origin, 25% South American.

4. *The age of the Antillean lycaenid fauna*

Throughout the preceding discussion attempt has been made wherever possible to apply some sort of age estimate to the events set forth. By extending analogous reasoning as well to species not specifically discussed we reach an interesting conclusion concerning the age of the lycaenid fauna now in the Antilles. At least two glaciations are required for certain species groups (*Brephidium, Electrostrymon, Cyclargus*); no member of the fauna is so remote systematically from its nearest continental ally that the differentiation could not have occurred since the onset of the Pleistocene. One may conclude from this that early Pleistocene, more or less, is the most likely time for the initiation of events that culminated in today's fauna. If evolution rates were substantially less than is here estimated, then of course this time would need to be pushed back accordingly.

In brief there is no firm evidence of the time this fauna first began to invade the islands, but contributing data in the form of systematic affinities and suggested or implied evolution rates in "typical" lines lead to the conclusion that early Pleistocene is the most likely time.

BIBLIOGRAPHY

BATES, M., 1935. The butterflies of Cuba. *Bull. Mus. Comp. Zool.* 78: 63-258, 23 figs.

CARPENTER, G. D. H., and C. B. LEWIS, 1943. A collection of Lepidoptera (Rhopalocera) from the Cayman Islands. *Ann. Carnegie Mus.* 29: 371-396, 9 figs.

CLENCH, H. K., 1961. Theclini (pp. 177-219) *in* P. R. and A. H. Ehrlich, *How to know the butterflies.* Dubuque, Iowa (W. C. Brown), [8] + 262 pp., 525 figs.

COMSTOCK, W. P. and E. I. HUNTINGTON, 1943. Lycaenidae of the Antilles (Lepidoptera, Rhopalocera). *Ann. New York Acad. Sci.* 45: 49-130, 2 text figs., 1 plate.

DARLINGTON, P. J., 1957. Zoogeography: the geographic distribution of animals. New York (Wiley), xi, 675 pp., 80 figs.

FLINT, R. F., 1947. Glacial geology and the Pleistocene epoch. New York (Wiley), ix, 589 pp., 88 text figs., 6 plates.

GILLHAM, N. W., 1955. *Brephidium barbouri* Clench a synonym of *Brephidium exilis isophthalma* (Herrich-Schäffer) (Lepidoptera: Lycaenidae). *Psyche* 62: 34.

GODMAN, F. D., and O. SALVIN, 1879-1901. Insecta, Lepidoptera-Rhopalocera, *in Biologia Centrali-Americana.* Vol. 1 (1879-1886, 1901). xlvi, 487 pp.; vol. 2 (1887-1901), 782 pp.; vol. 3, 112 plates.

NABOKOV, V., 1945. Notes on neotropical Plebejinae (Lycaenidae, Lepidoptera). *Psyche* 52: 1-61, 1 text fig., 8 plates.

RINDGE, F. H., 1952. The butterflies of the Bahama Islands, British West Indies (Lepidoptera). *Am. Mus. Novit.* #1563, 18 pp.

———— 1955. The butterflies of the Van Voast-American Museum of Natural History Expedition to the Bahama Islands, British West Indies. *Am. Mus. Novit.* #1715, 20 pp., 8 figs.

SWANEPOEL, D. A., 1953. Butterflies of South Africa. Cape Town (M. Miller), 320 pp., 8 halftone, 17 colored plates.

WEAVER, J. E., and F. E. CLEMENTS, 1938. Plant Ecology (2nd Edition). New York (McGraw-Hill), xxii, 601 pp., 271 text figs., frontispece.

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THE SYNONYMY, VARIABILITY AND BIOLOGY OF *LYCAENA NIVALIS*

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Lycaena nivalis Bdv. is a very interesting species in several ways. (1) Its synonymy has been somewhat confused; (2) it is quite variable, which may explain the confusion of names; and (3) its life history was described more than 50 years ago in the Canadian Entomologist, but this fact has gone unrecognized, again because of confusion of names.

L. nivalis, and its subspecies *browni* Dos Passos, occurs, according to Clench (1961), "from southern British Columbia south to Colorado, Utah and the middle Sierras of California." Llewellyn Jones (1951) says it is found in British Columbia in the Southern Interior and the Kootenays, in other words, the entire area between the Fraser River and Alberta north to about latitude 52°. In Washington the writer has taken it in Okanogan, Yakima and Klickitat Counties, and it is particularly abundant in Yakima County. Leighton (1946) records it from Leavenworth, which is in Chelan County, and it should also occur in the intervening Kittitas County and perhaps elsewhere in the state.

In Oregon the writer has taken it on Mt. Ashland, Jackson County; at Tombstone and Lost Prairies, Linn County, which are just west of the Cascade summit at Santiam Pass; in the Ochoco and Maury Mountains, Crook County; and in the Warner Mountains, Lake County. In California he collected it years ago just north of Lake Tahoe and more recently just west of Ebbet Pass, Stanislaus County, and in the Warner Mountains, Modoc County. Comstock (1927) says it occurs "at high elevations throughout the Sierras." Brown (1957) records the species from northern and western Wyoming and northern Utah, and the subspecies *browni* from southern Idaho, northwestern Colorado and southeastern Wyoming. The writer has taken it at Aspen Grove, Utah County, Utah.

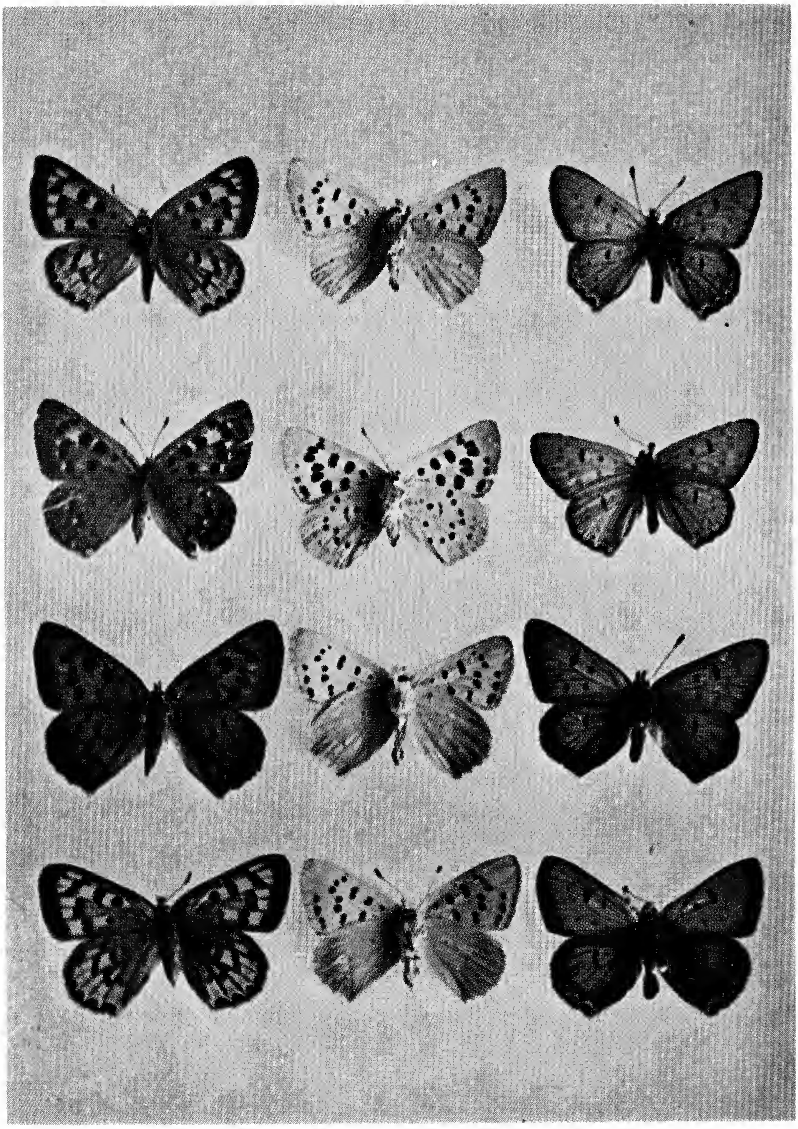

Fig. 1. *Lycaena* from Oregon and Washington.
a. Typical *Lycaena nivalis*. Maury Mts., Crook Co., Oregon. b. Similar but females melanic, and black spots below more pronounced. Camas Creek, Warner Mts., Oregon. c. Typical *L. n. browni*. Bear Canyon, Yakima Co., Wash. d. Similar below, but colors more intense; females with very little melanism. Cascade Mts., Oregon.

SYNONYMY

Edwards (1877) listed *nivalis* as a synonym of *mariposa* and *ianthe* as a synonym of *zeroe,* and this synonymy was followed by Dyar (1902). Barnes & McDunnough (1917) listed *zeroe* as a synonym of *mariposa* and *ianthe* as a synonym of *nivalis,* and this synonymy has been used by Comstock (1927) and Holland (1931). Holland's original Butterfly Book (1904) did not recognize *nivalis, ianthe* or *zeroe* at all. Wright (1907) figured what is certainly *nivalis* but called it *zeroe.*

The writer has referred to the original descriptions of *ianthe, nivalis* and *zeroe*[1], and it is difficult to see how some of this synonymy came about. Edwards (1871), in describing *ianthe,* says in part: "Underside pale buff much powdered at base with grey; primaries have a marginal series of rounded brown spots, obsolete apically, suffused near inner angle with fulvous; a median tortuous row of brown spots or points; a bar on arc, a large round spot below cell. Secondaries have a marginal series of orange crenations, obsolete toward outer angle; a medium row of black dots; an obsolete discal streak; a point in cell and another below." This certainly describes *nivalis,* so that Barnes & McDunnough were correct in making *ianthe* synonymous with that species.

Boisduval's (1869) description of *nivalis* is in Latin and French, and it may be translated into English about as follows:

> Upper side of wings darkly fulvous, middle lunules black, shot with iridescent purple; posterior marginal band fulvous; fore wings below pale ochraceous with black spots; hind wings pale, lunules ferruginous.
>
> It looks something like our *hiere* but is very small. The fore wings of the male are a smoky fawn with a beautiful violet reflection. Each wing is marked in the middle with a blackish lunule and with several obsolescent spots faintly visible; below there is a small crenelated band at the margin of ferruginous fawn, bordered behind by black lunules. Below, the fore wings are yellow-ochre, very pale, with black spots as in our species; the secondaries are rosy-yellow, a little glaucous at the base, with some small black spots scarcely indicated, and a series of marginal, obsolete fawn-colored lunules. The female is a clear yellow-fawn, spotted as in other species of the group. Below, it does not differ from the male. This species is very distinct, and similar to *helloides.* It is found in the Sierras.

Nivalis, meaning "belonging to the snow," is an appropriate name for the species, as it occurs only in areas where there is considerable, and sometimes very heavy, snowfall.

Boisduval's (1869) description of *zeroe,* again in Latin and French, may be Anglicized as follows:

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[1] *The latter two courtesy of F. Martin Brown.*

Wings darkly fuscous, with purple iridescence, middle unules marginally dark fuscous; fore wings with black spots. Fore wings below ochraceous with black spots; hind wings cinereous with thin black spots.

Something like our *hiere* but smaller and in size similar to the preceding. The fore wings of the male are of a brownish tinge washed with fawn and with a violet reflection, and a small discoidal, blackish lunule at the edge; the wings above are marked with black spots; below in the anal angle is a small area with a trace of fawn lunules. The hind wings above are pale yellow-ochre, with black spots; below ashy gray with black spots in the lunules, transversely arranged; on the hind edge there is a series of sagittate whitish spots cut with black. The female is a lively yellowish fawn, spotted with black as in other species. This pretty species inhabits the high mountains of the Utah border in June and July.

The description of *zeroe* follows that of *nivalis* in Boisduval's paper, so that his statement that *zeroe* "se rapproche par la taille de l'espèce précédente" is comparing the *size* of the two. And it is obvious that this description of *zeroe* would fit *mariposa* quite well, as the secondaries of the latter are certainly "ashy gray" below. One cannot help wondering if imperfect translation of these descriptions caused Edwards to list *nivalis* as a synonym of *mariposa*, and Wright to figure *nivalis* and call it *zeroe*.

In view of the above information the present synonymy appears to be correct.

VARIABILITY

The genus *Lycaena* includes a number of species that are quite variable as attested by the names given to subspecies as well as the names that have become synonyms. *L. nivalis* is no exception and its variability may well be due to its occurrence under widely differing climatic conditions. This is made possible by the distribution of its major food plant, *Polygonum douglasii*, in both the Transition and Boreal Zones, at elevations of at least between 2,000 and 7,500 feet, and where annual precipitation ranges from about 15 inches to 60 inches or more.

Brown (1957) reports that in Colorado *nivalis* frequents sage-brush flats and is rarely found along streams. In Oregon the writer has taken it at 7,000 feet on the slopes of Mt. Ashland; in a lush meadow at 4,000 feet in Linn County; in rather dry yellow-pine areas at 5,000 to 6,000 feet in the Ochoco and Maury Mountains in Crook County; and in somewhat similar areas at 6,000 to 7,500 feet in the Warner Mountains in Lake County. In Washington it may be found in canyons at relatively low elevations and also on mountain slopes and in high meadows. So variability is probably inevitable.

Material from Tombstone and Lost Prairies has a very intense coloration, the yellow and pink of the under side being brilliant, and the fawn color of the upper side of the females in very sharp contrast to the fuscous spots and margins. The same coloration occurs on material from Mt. Ashland, where precipitation would be at least 40 inches, and to a considerable extent on material from Harts Pass in northern Washington where the precipitation is high.

Specimens from the Ochoco and Maury Mountains, on the other hand, have a much less intense coloration, the ground color beneath, even in fresh specimens, being a washed-out light cream, with a tinge of pinkish on the secondaries, but no evidence of yellow. The color of the males above is somewhat less intense, and the females have a considerable smoky suffusion above. Here the spring rainfall is light and the annual not over 20 inches. Material from the Warner Mountains is similar to that from the Ochocos, except that the females are more melanic. Precipitation there is probably 20 to 25 inches.

Specimens from Satus Pass and Bear Canyon have rather contrasting yellow and pink coloration below, not as intense as on specimens from the Oregon Cascades, but much brighter than on the Ochoco material. Satus Pass females have perhaps less smoky suffusion, on the whole, than those from Bear Canyon. It should be pointed out that in the areas where intense coloration occurs, there would be less sunlight than in the areas where the colors beneath are less intense, and this may be a factor in determining the intensity of the colors.

Mean temperatures have been examined, particularly those of May and June, which might be expected to have the most effect. The highest temperatures occur in the southern part of the area and they decrease to the north. This does not match up with the difference in the coloration. And, as can be seen in the table, elevation is probably not a factor.

Lacking experimental data, no explanation is evident for the color variations found in *nivalis,* other than those suggested here.

SUMMARY OF VARIETIES

There are four rather distinct varieties of *nivalis* in the area under discussion:

1. Typical *nivalis,* mostly pinkish below with some black spots on the secondaries; the females with much yellow or

orange above. Sierra Nevadas, California, and Ochoco and Maury Mountains, Oregon. Fig. 1a.

2. Similar, but females very melanic above and black spots on secondaries below more pronounced. Warner Mountains, Oregon. Fig. 1b.

3. Typical *browni,* females with some orange above to very melanic; contrasting pink and yellow below and black spots on secondaries much reduced or absent. Utah to Washington. Fig. 1c.

4. Similar below, but colors much more intense, the pink contrasting strongly with the yellow; black spots reduced or obsolete; the females above with very little melanism, the orange ground color contrasting greatly with the fuscous spots and margins. Cascade Mountains of Oregon, specifically Linn and Jackson Counties. Fig. 1d.

The writer is not a taxonomist, but if *browni* is a valid subspecies, it would seem that this Cascade Mountain variety could legitimately be named as another subspecies, particularly as the conditions under which it occurs are very different from those elsewhere.

LIFE HISTORY

The writer described the early stages of *nivalis* more than 50 years ago (Newcomer, 1911). Unfortunately, for identification of the species, he had access only to the color plates of West Coast butterflies issued by Wright (1907) after the plates of his book on the same subject had been destroyed in the San Francisco earthquake and fire of 1906. And since Wright figured *nivalis* and called it *zeroe,* this writer described the early stages as those of *zeroe.* Adults were collected at the time and were later given to the California Academy of Sciences in San Francisco. Dr. C. Don MacNeill, Assistant Curator, has very kindly looked these up and he writes about them as follows: "I find a short series of your specimens of both *L. nivalis* and *L. mariposa* from the Lake Tahoe region. Of your material of *L. nivalis* one male and one female each bear an additional hand-penned label stating 'zeroe.' . . . . All of your material of *L. mariposa* came from 5-Lakes[2] and none of the specimens bear a 'zeroe' label."

Later writers, not realizing the misidentification, have consistently said that the early stages of *nivalis* were unknown.

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[2] *These lakes are at an elevation of 7500 feet, while Deerpark, where nivalis was taken, is at 6500 feet. Both are just south of the Squaw Valley ski area.*

Brown (1957) has indicated the range of the subspecies *browni* to be southeastern Wyoming, northwestern Colorado and across southern Idaho; and in a later paper (1961) he has extended this range to include Washington. In the original description, DosPassos (1938) mentioned Wyoming, Utah, Idaho and the Methow Valley in Washington. Typical *nivalis* occurs in California and up into Oregon.

The subspecies *browni* occurring in Yakima County, Washington, differs from those collected elsewhere in that the upper side of the females is usually entirely or almost entirely darkened by a smoky suffusion that obscures the normal yellowish fawn ground color. (Since the original description says "females are very melanic on the upper side," it may be assumed that this smokiness occurs elsewhere.) Brown, in his 1961 paper, surmised that this might be due to greater humidity in this area.

A study of the Weather Bureau's climatological data indicates that humidity does apparently affect the coloration but not in the way suggested by Brown. From available weather records and with some interpolation, the approximate precipitation in inches at some of the localities where *nivalis* occurs may be given (Table 1). Most of the precipitation in all of these localities would be in the form of snow and hence, in addition to the annual, records are given for April to June, as that would be the time when larvae and pupae would be present and the precipitation then would come mostly as rain.

TABLE 1

Locality	Elevation	Precipitation in Inches			
		April	May	June	Annual
Lakeview, Lake Co., Oreg.	4800	1.2	1.5	1.4	14
Ochoco Mts., Crook Co., Oreg.	5000	1.2	2.4	1.5	19
Tombstone Prairie, Linn Co., Oreg.	4000	3.5	4.3	1.0	90
Satus Pass, Klickitat Co., Wash.	3700	2.2	1.2	0.2	26
Bear Canyon, Yakima Co., Wash.	3000	1.0	0.8	1.2	19
Methow Valley (Winthrop), Okanogan Co., Wash.	3200	0.7	1.0	1.3	14
Harts Pass, Okanogan Co., Wash.	5500	6.0	4.0	3.0	85

The writer found females of *nivalis* (*zeroe*) ovipositing on *Polygonum douglasii* at Deerpark, near Lake Tahoe, California, in July 1909. He took them to Palo Alto and the eggs hatched the following February. Since *douglasii* was not available there, he tried related plants and succeeded in rearing some of the larvae on a species of *Rumex*. The young larvae ate pits in the leaves of this plant but older ones devoured the leaves entirely.

Since the Canadian Entomologist is generally available in libraries, it will not be necessary to repeat the rather long description of the early stages here. A brief summary should suffice for those who do not have access to the original descriptions.

Egg—Diameter, 0.85 mm. Depressed spheroid, ornamented with deep, polygonal pits; color pale bluish.

Larva—Four instars; newly hatched a little over 1 mm. in length; full-grown, 17 mm. Slug-shaped, brownish yellow when first hatched; later becoming pale green with a dorsal line of rose or claret color; a narrow whitish line on each side of it; cervical shield sunken on full-grown larvae, in the shape of a double diamond; dorsal and lateral hairs brownish; dorsum covered with small, white, hairless tubercles. Head dark brown.

Pupa—Length 10.5 - 11 mm. Rather stout, but longer for its breadth than usual with lycaenid chrysalids. Color at first very pale yellowish-green with a pinkish dorsal stripe; later pale straw-yellow with some brown spots. Hairs, resembling miniature trumpets, scattered thickly on dorsum of head and more sparingly on thorax and abdomen, appearing like minute tacks stuck into the skin.

In July, 1962, the writer saw a female *nivalis* ovipositing on a small, more or less dried-up plant near Satus Pass, Washington. This plant proved to be *Polygonum douglasii*,[3] an annual. The area in Bear Canyon, west of Yakima, Washington, where *nivalis* is particularly abundant, was immediately examined, and plants of *P. douglasii* were found. This species occurs from British Columbia to the mountains of southern California and east to the Rocky Mountains. It is sometimes the dominant annual in high, open prairies. Later, it was found growing wherever *nivalis* was flying in Washington and Oregon, and it is, as previously mentioned, probably the major food plant of the species.

[3] Determined from Abrams "Illustrated Flora of the Pacific States," vol. II, Stanford Univ. Press, Stanford, Calif., 1944.

The adults of *nivalis* frequent the flowers of yarrow (*Achillea millefolium*), woolly-sunflower (*Eriophyllum lanatum*), spiraea, and occasionally others in the vicinity of the larval food plant.

Females were collected alive and put in plastic ice-cream cups with the food plant; and eggs were deposited on the plant and also on the sides of the containers. These eggs were kept over winter outdoors but they did not hatch. Probably this was due either to lack of moisture or to too much cold. The winter temperature got as low as —3°F. In the natural habitat the wintering eggs would almost always be covered with snow during the cold weather and would therefore not be subject to temperatures much below freezing. Probably the eggs could be carried through successfully in a refrigerator.

Thus we see that this single-brooded species passes about eight months of its life in the egg stage which is subjected to the heat of summer,—and the eggs would often be on or near dry ground in full sunlight,—the cold of autumn and the "refrigeration" of winter. They would also be subjected to considerable extremes of moisture during that time. And when the snow has gone, the newly hatched larvae must seek out the seedling plants sprouting from seeds produced by the plants on which oviposition occurred. And yet the species is successful and is quite common at times.

REFERENCES

BARNES, WILLIAM & McDUNNOUGH, J. 1917. Check List of Lepidoptera, *Herald Press, Decatur, Ill.* p. 15.

BOISDUVAL, J. B. A. 1869. Lepidopteres de la Californie. *Ann. Soc. Ent. Belgique,* 12:44-45.

BROWN, F. MARTIN. 1957. Colorado Butterflies. *Proc. Denver Mus. Nat. Hist., Denver.* p. 157.

———— 1961. A note about *Lycaena nivalis browni* (Lycaenidae). *Journ. Lepid. Soc.* 15:107-8.

CLENCH, HARRY K. 1961. Tripe Lycaenini. In Ehrlich & Ehrlich, How to Know the Butterflies. *Brown, Dubuque, Iowa.* p. 226.

COMSTOCK, J. A. 1927. Butterflies of California. *Los Angeles,* p. 174.

DOS PASSOS, CYRIL F. 1938. Some New Subspecies of North American Lycaenidae. Can. Ent. 70:45.

DYAR, HARRISON G. 1902. A List of North American Lepidoptera. *Bull. 52, U. S. N. M.* p. 41.

EDWARDS, W. H. 1871. *Trans. Am. Ent. Soc.* 3:211.

———— 1877. Catalogue of the Lepidoptera of America North of Mexico. Part 1, Diurnals. *Am. Ent. Soc.* p. 43.

HOLLAND, W. J. 1904. The Butterfly Book. *Doubleday Page & Co., New York.* pp. 251-5.

———— 1931. The Butterfly Book (revised). *Doubleday & Co., Garden N. Y.* p. 249.

LEIGHTON, BEN V. 1946. The Butterflies of Washington. *Univ. Wash. Publ. in Biology.* 9:47-63.

LLEWELLYN JONES, J. R. J. 1951. An Annotated Check List of the Macrolepidoptera of British Columbia. *Occ. paper no. 1, The Ent. Soc. of B. C.* p. 20.

NEWCOMER, E. J. 1911. The Life Histories of Two Lycaenid Butterflies. *Can. Ent.* 43:83-88.

WRIGHT, W. G. 1907. Colored Plates of the Butterflies of the West Coast. *San Bernardino, Calif.* Plate XXVIII, no. 346.

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COMPARISON OF THE SELECTIVE EFFECT OF TWO MUSTARD OILS AND THEIR GLUCOSIDES TO PIERIS LARVAE

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THE EFFECTIVENESS OF VARIOUS MUSTARD OILS (isothiocyanates) on attracting larvae of *Pieris rapae* has been shown previously (Hovanitz, Chang and Honch, 1963b, and Hovanitz and Chang, 1963a). In this paper, some data are presented to compare the effectiveness of two of these mustard oils with their corresponding glucosides. The combinations of mustard oils and glucosides being considered are allyl isothiocyanate with sinigrin, and benzyl isothiocyanate with glucotropaeolin. The naturally known occurrence of the substances in plants is indicated in Table 1 of the before mentioned paper (Hov., Chang and Honch, 1963b).

THE STRAINS AND EXPERIMENTAL SET-UP

The two strains of *Pieris rapae* used in these experiments are the same as used in previous experiments. The first, the kale strain, has been maintained ten or more generations on kale and the second, the mustard strain, has been maintained for more than ten generations on mustard.

The experimental set-up for these tests has been the same as for those tests previously made (Hovanitz and Chang, 1963a).

ATTRACTION OF GLUCOSIDES

The glucoside, glucotropaelum, is known to occur naturally in a wide variety of plants, some natural food plants of *Pieris rapae* and others not.

Previously published results of tests on the mustard oils corresponding to these glucosides have indicated that larvae of *Pieris rapae* bred on mustard have no more selection for benzyl isothiocyanate than for distilled water, where the dilutions have

This work was done with the aid of a grant from the National Science Foundation.

TABLE 1. Attraction of glucosides of various concentrations to Pieris rapae larvae

	Test	10^{-3}		10^{-4}		10^{-5}		10^{-6}		10^{-7}		10^{-8}		10^{-9}		Water		None		Total
glucoside: glucotropaeolum larvae: mustard-strain	1					34	11.33	37	12.33	61	20.33	49	16.33	56	18.67	24	8.00	39	13.00	300
	2					66	20.63	44	13.75	51	15.94	51	15.94	49	15.31	34	10.62	25	7.81	320
	3					38	15.83	37	15.41	45	18.75	37	15.42	33	13.75	32	13.33	18	7.50	240
	Total					138	16.05	118	13.75	157	18.25	137	15.93	138	16.04	90	10.46	82	9.53	860
glucoside: glucotropaeolum larvae: kale-strain	1					20	10.00	50	25.00	34	17.00	27	13.50	32	16.00	12	6.00	25	12.50	200
	2					24	15.00	27	16.87	22	13.75	25	15.62	37	23.12	13	8.12	12	7.50	160
	3					36	22.50	28	17.50	22	13.75	24	15.00	13	8.12	14	8.75	23	14.37	160
	Total					80	15.38	105	20.19	78	15.00	76	14.62	82	15.76	39	7.50	60	11.53	520
glucoside: sinigrin larvae: mustard-strain	1					48	17.14	19	6.78	47	16.78	42	15.00	48	17.14	19	6.78	57	20.36	280
	2					38	11.87	54	16.87	52	16.25	63	19.69	47	14.69	40	12.50	26	8.12	320
	Total					86	14.33	73	12.17	99	16.50	105	17.50	95	15.83	59	9.83	83	13.83	600
	3	81	13.50	97	16.16	102	17.00	98	16.35	84	14.00					69	11.50	69	11.50	600
glucoside: sinigrin larvae: kale-strain	1					35	13.46	44	16.92	40	15.38	40	15.38	25	9.61	32	12.31	44	16.92	260
	2					14	10.00	23	16.43	34	24.28	26	18.57	18	12.86	12	8.57	13	9.28	140
	3					77	24.06	44	13.75	48	15.00	51	15.94	39	12.19	21	6.56	40	12.50	320
	Total					126	17.50	111	15.41	122	16.94	117	16.25	82	11.38	65	9.03	97	13.47	720

ranged from 10^{-5} to 10^{-9}. On the other hand, similar larvae tested for allyl isothiocyanate showed a strong selection for this mustard oil at a concentration of 10^{-6} (Hovanitz, Chang and Honch 1963b). Larvae bred on kale tested in the same way showed a decided preference for a more dilute concentration, 10^{-8} (Hovanitz and Chang 1963a).

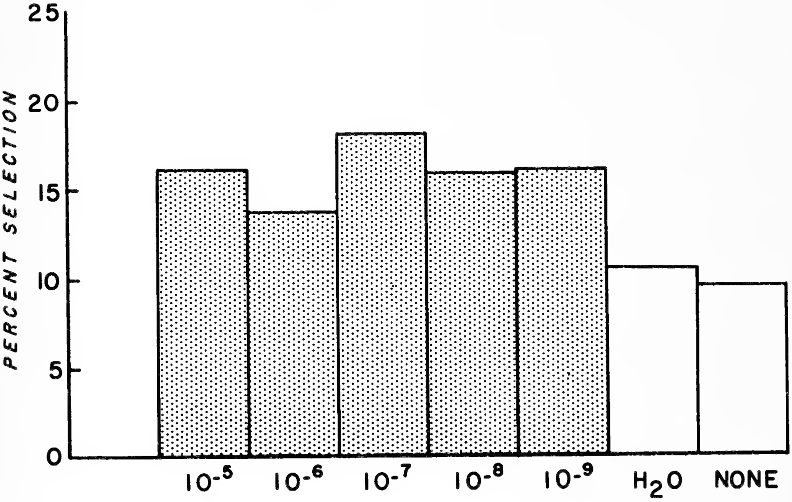
Tests of larvae bred on kale, and other tests of larvae bred on mustard, were made on the two glucosides (Table 1). These tests have indicated that both glucosides have some selective influence on the larvae but that the selection is not very much greater than that on water alone.

Glucotropaeolum tested with mustard-strain larvae at concentrations of 10^{-5} to 10^{-9} and distilled water showed an average selection of 18 percent for a concentration of 10^{-7} as compared with water at 10 percent (Fig. 1). The other concentrations were not much different at 13 to 16 percent. This compares with no apparent selection for the corresponding mustard oil, benzyl-isothiocyanate.

Glucotropaeolum, tested again with kale-strain larvae at the same concentrations, showed the highest rate of selection, 20 percent, at 10^{-6} as compared with water at 7.5 percent and other concentrations at 15 percent (Fig. 2). This indicates a positive selection for the glucoside, whereas no selection was indicated for the corresponding mustard oil, benzyl isothiocyanate.

Sinigrin, the glucoside of allyl-isothiocyanate, was tested with mustard-strain larvae at concentrations of 10^{-5} to 10^{-9} and distilled water in a series of two tests and at concentrations of 10^{-3} to 10^{-7} in a third. The average of the first two tests indicate a high selection of 17.5 percent at a concentration of 10^{-8} as compared with water at ten percent though other concentrations were not greatly different, at 12 to 16.5 percent (Fig. 3). It is possible that there is little significant effect of change of concentration.

The same tests were made over to see if a higher concentration of sinigrin had a greater influence on selection. Concentrations were arranged from 10^{-3} to 10^{-7} (Fig. 5). The highest selection, in this series, 17 percent, was at 10^{-5}, with other concentrations ranging from 13.5 to 16 percent, compared with water alone at 11.5 percent. There seems to be little difference in selection at the different concentrations except that water is selected less than the glucoside sinigrin. These results differ



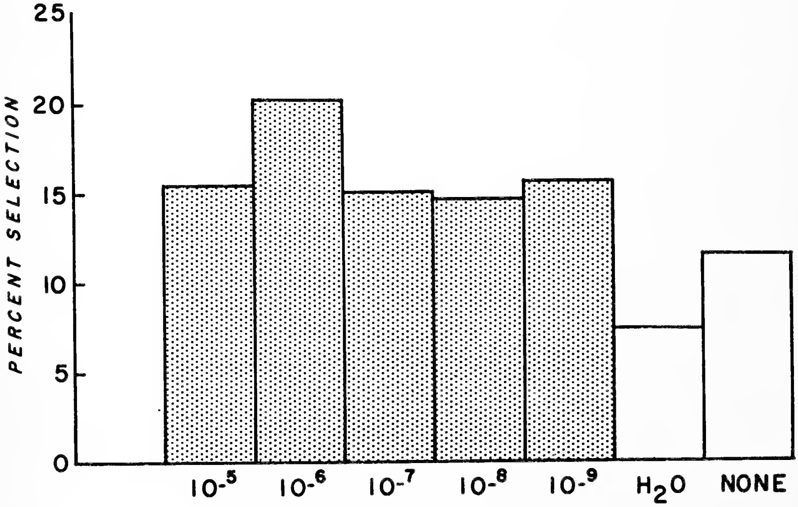
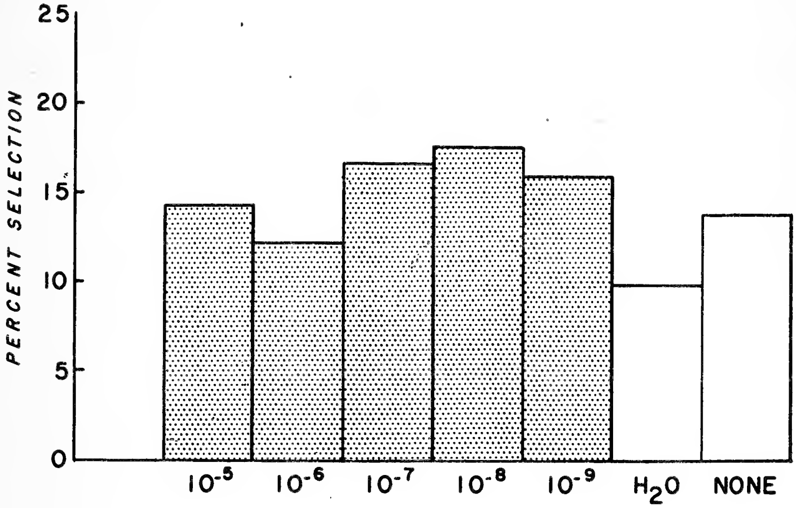


Fig. 1. The percent selections by larvae of *Pieris rapae* of a standard bred strain tested for attraction to various dilutions of glucotropaeolum.

Fig. 2. Similar selections by larvae from kale bred strains of *Pieris rapae* tested to glucotropaeolum.



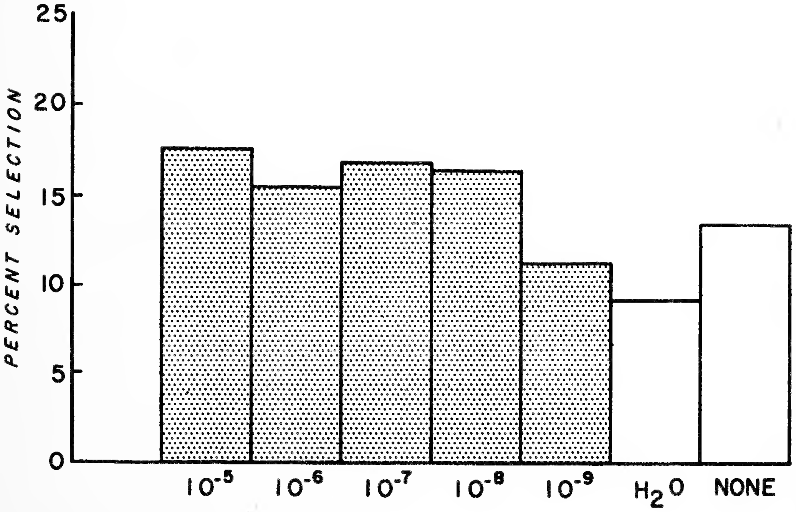


Fig. 3. The percent selection by larvae of mustard strain *Pieris rapae* tested for attraction to various dilutions of sinigrin.

Fig. 4. Similar selections by larvae of kale strain *Pieris rapae* to sinigrin.

markedly from the selection data of mustard-strain larvae for allyl-mustard oil, with a high selection of 30 percent at 10^{-6} (Hovanitz and Chang, 1963b).

Sinigrin was also tested with larvae from the kale strain (Fig. 4). The concentration of -0^{-5} led to selections of 17.5 percent followed closely by 17 percent at 10^{-7}. This corresponded to water at 9 percent, and a range of 11 to 16 percent for the other concentrations. These results also differ markedly from the selection data of kale strain larvae for allyl-mustard oil, with a high selection of 34 percent at 10^{-8} (Hovanitz and Chang 1963a).

CONCLUSIONS AND DISCUSSION

The results of these experiments lead to the following conclusions:

1. Glucotropaeolum is more effective in attracting larvae of *Pieris rapae* than its corresponding oil, benzyl-isothiocyanate. However, the oil has no apparent attractive influence at all and the glucoside has only a slight effect.
2. There is little difference in selection between the various concentrations of the glucoside.

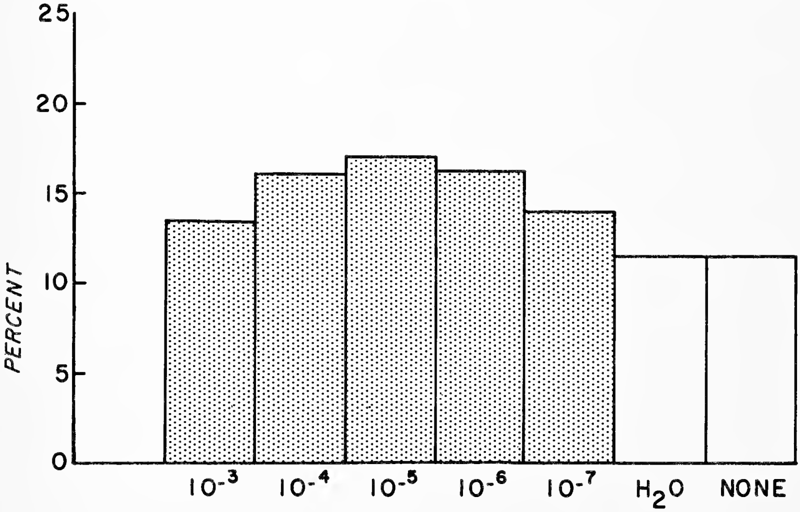


Fig. 5. The percent selections by larvae of mustard strain *Pieris rapae* tested for attraction to various dilutions of sinigrin.

3. There is little difference in selections made by the larvae toward glucotropaeolum depending on whether they were from the mustard strain or the kale strain, though it is possibly significant that a higher selection may occur toward a concentration of 10^{-7} for the mustard strain larvae as compared with a concentration of 10^{-6} for kale strain larvae.

4. Sinigrin is less effective in attracting larvae of *Pieris rapae* than its corresponding oil, allyl isothiocyanate.

5. There is little difference in selection between the various concentrations of the glucoside.

6. There is little difference in selections made by the larvae toward sinigrin depending on whether they were from the mustard strain or the kale strain. It is possibly significant that a higher selection may occur for a higer concentration of sinigrin for the mustard-strain larvae. This result is opposed to the selection data obtained for the same strains tested for allyl mustard oil (Hovanitz and Chang, 1963a).

Interpretation of these results may depend finally upon future experiments which would differentiate the ability of the larvae to perceive odors from a distance. The experimental set-up for these tests has been based upon the ability of the larvae to react to odors from a distance of over 100 mm. If the attraction of larvae to the glucoside sinigrin is really based upon attraction to the allyl mustard oil vapors emanating from sinigrin by hydrolysis, then there may be very little difference in the total amount of the mustard oil present at any time and this could conceiveably account for the almost lack of selective differentiation between various concentrations of sinigrin, unlike that of the mustard oil itself. If the mustard oil emanating from the sinigrin were restricted by the speed of the reaction of hydrolysis, then the oil vapors would possibly be dissipated quickly in the air and not carry far enough to attract the larvae differentially. On the other hand, selections made close at hand, within a few millimeters, might serve to bring about such a differentiation.

The lack of any clear-cut selective differences under the conditions of these experiments is strange in view of the great effectiveness of larval selections of different food plants from the same distances. It is possible that the plants have a means to store the mustard oils obtained by enzymatic hydrolysis of sinigrin in greater concentrations that is possible where the sinigrin is directly exposed to the air. It is difficult experimentally to control the concentration of mustard oils for experimental purposes because of their great volatility.

LITERATURE CITED

HOVANITZ, W. and V. C. S. CHANG, 1963. a. Selection of allyl isothiocyanate by larvae of *Pieris rapae* and the inheritance of this trait. *J. Res. Lepid.* 1 (3): 169-182.

HOVANITZ, W., V. C. S. CHANG and G. HONCH, 1963. b. The effectiveness of different isothiocyanates on attracting larvae of *Pieris rapae.* *J. Res. Lepid.* 1 (4): 249-259.

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THE *ANNAPHILA ASTROLOGA* COMPLEX
WITH DESCRIPTIONS OF THREE NEW SPECIES

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THE SPECIES-COMPLEX presently known as *Annaphila astrologa* Barnes and McDunnough has had a long and confused history. This paper is an attempt to clarify the status of the several entities now bearing the name *A. astrologa* B. & McD.

The original type specimens to which Barnes and McDunnough (1918) applied the name *A. astrologa* were three females, from various non-specific locations in Arizona. When Rindge and Smith (1952) revised the whole genus *Annaphila, astrologa* was further described, including the picturing of the genitalia of the adult male and female, based on an extended series. While other species were treated in great detail, the authors noted that more specimen data in the species *astrologa* might alter their opinion.

This author discovered that it was possible to separate out from this long series of presumed *astrologa* several segrates all of which seemingly fit the description of *astrologa*. Two of these were collected together in various locations of Los Angeles, Orange and Riverside Counties of southern California. A third, unlike either of the two others, but related to those above, was collected in the Kern River basin of the Sierra Nevada Mountains.

Through the cooperative assistance of Lloyd Martin of the Los Angeles County Museum, E. A. Todd of the United States National Museum (USNM), Frederick Rindge of the American Museum of Natural History, and Jerry Powell of the University of California, Berkeley (UCB), the bulk of the material used in the Rindge-Smith study was reassembled and restudied with the intent of clarifying the status of these forms.

This work now being completed, the writer is led to the following conclusions: (1) that the original series used in the description of *astrologa* by Barnes and McDunnough included two species, (2) that the revision of Rindge and Smith (1952) failed to make this distinction, and working on this dual-as-one thesis, they placed two additional species under the name *astrologa*.

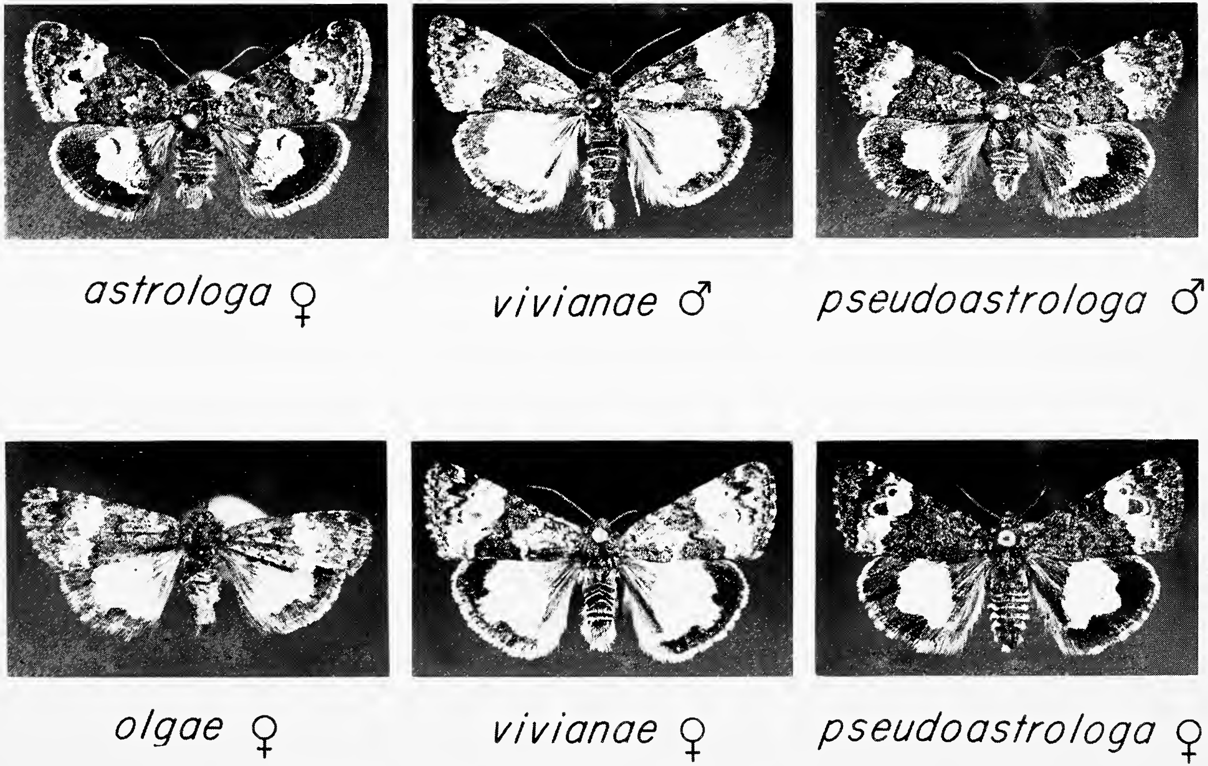


Fig. 1. Upperside facies of *Anaphila astrologa*, *A. vivianae*, *A. pseudoastrologa*, and *A. olgae* as indicated.

The initial task of the author was to establish which of the four species was to be called *astrologa.* In the original series of three specimens, two are con-specific, the third distinct, as noted above. One of the former had been used by Barnes and McDunnough (1918) to illustrate *astrologa.* In addition, con-specific material from California was used by Rindge and Smith to illustrate the male genitalia. Thus these two originals are designated the type series of *astrologa,* with the TYPE specimen so labled in the USNM collection. This example most closely agrees with the original description. The example illustrated in this paper (Fig. 1, 2) is from California, as are the specimens used in the drawings of the genitalia (Fig. 3, 4).

Annaphila astrologa B. & McD. (modified description) (fig. 1, 2, 3, 4).

Wing expanse: 17-20 mm. *Head - Vertex*: Black, few gray and whitish hair-like scales. *Front*: Black, with triangular tuft of long hair-like scales. *Antennae*: Black, with whitish scales at segment ends. *Palpi*: Mostly white. *Thorax*: Mostly black, few lighter scales (dorsal). Lighter ventrad, overlain with lighter hair-like scales of legs. *Abdomen - dorsal*: black, white rings at intersegmental area; *ventral*: same, with longer intersegmental hair-like scales giving a lighter aspect. *Wings - Fore wing upper*: Ground color black, with scattered lighter scales giving frosted aspect to base and sub-occipital areas. Basal area black, strongly frosted with light scales from base to basal line. Basal line whitish to basal dash, which is also whitish, indistinct. T. A. line white, "W" shaped, accented basally, distad at radius, and Cu area, mesad in medial and anal margin areas. Orbicular indistinct, oval, gray on black, often absent. Claviform absent. Median line broad, black, sub-parallel to T. A. line. Reniform outlined in white, kidney shaped, gray-cream in center. Connected to costa by white patch width of reniform, distad fusing with anterior end of T. P. line white, thin, penciled into a script "B" on distad end of Reniform, broader posteriad to anal margin. More clearly penciled than in *pseudoastrologa.* Area between T. P. line and S. T. line outlined in black, frosted with white scales. S. T. Line white, incomplete, broadest at apical end—faintest at Cu-2. Fringes black except at vein ends, which are white. *Hind wing upper*: ground color orange ventrally, bordered in black. Basal area 1/5 black, often overlain with long orange hairs, giving striated appearance. Discal spot usually present as lunule or spot (black). Outer 2/5 of wing is black band, broadest as rucurved hook in area of m-1. Fringes mostly white, black at tips of veins, often 1 mm dark band in area of anal veins. *Fore wing lower*: basal area to median line orange . Often a black area bordered by orange basally and distally. Median line black, well-marked, often spreading. Widest at costa. Reniform a black dash, often a black lunule. In field of orange, area between t. p. line and s. t. line a black band, broadest costad. Tip white. Fringes black, white at vein ends. *Hind wing lower*: basal area orange to t. a. line, t. a. line black, more an arc than above, occasionally incomplete. Discal spot black, lunule, central area orange to outer margin, outer margin as above. Fringes as above.

Type: Lectotype, female, Arizona (collector unknown), (no date), the specimen used is the one Barnes and McDunnough labeled "Type " and pictured in their publication in Contr.

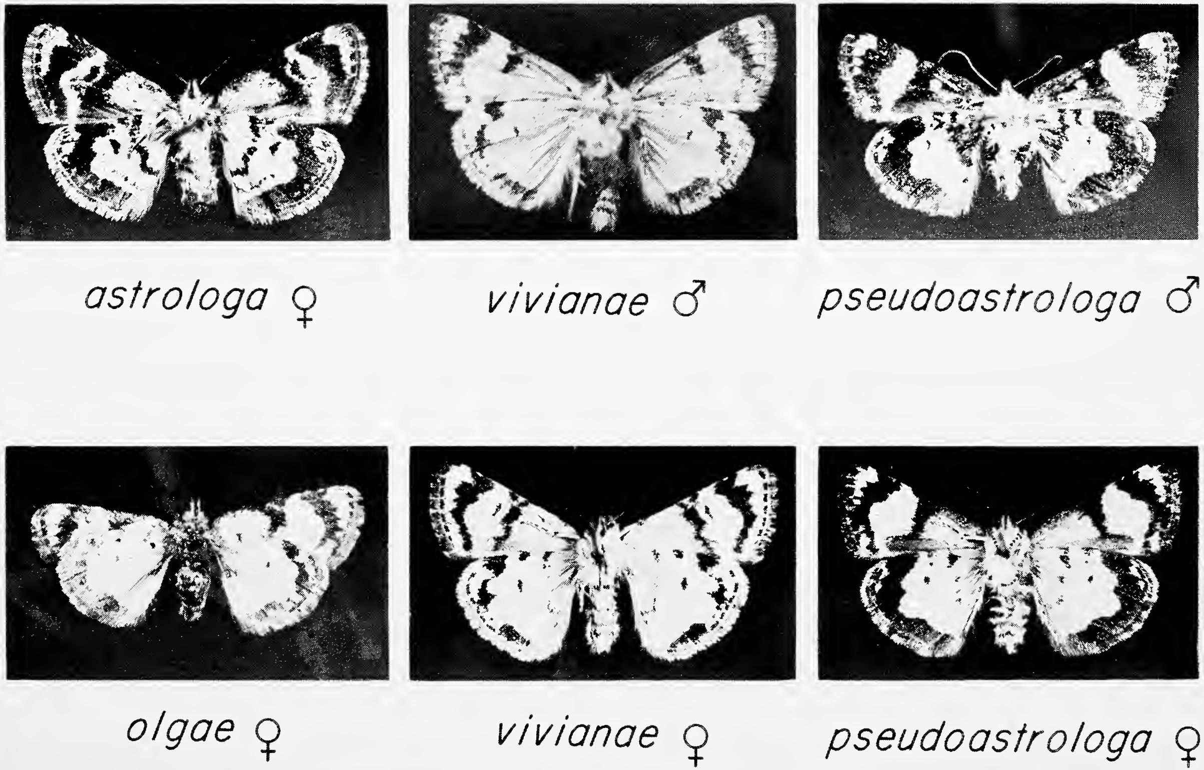


Fig. 2. Underside facies of *Anaphila* species as indicated.

Nat. Hist. Lepidoptera of N. America, Vol. 4, No. 2, Pl. 19, Fig 11. This is noted, as the B. & McD. series had as one of the three specimens the type of*Annaphila olgae,* sp. nov., as defined in this work.

Early stages: Will be discussed in a subsequent paper.
Foodplant: Emmenthalia penduliflora (Whispering Bells) California foodplant.
Type Locality: Reddington, Arizona.

Range: Southern Arizona; southern California, coastal to San Francisco, Mojave basin, west side. Not known from the Sierra Nevada range. This author believes that the California population, at least, is only on the wing in March and April. The flowering of growth cycle of the foodplant (dead in the summer months) precludes normal flight at the noted month of July.

Remarks: Rindge & Smith note that more material was needed to clarify exact relationship in this area. The male genitalia is noted as variable; in fact, it is very constant, the median spine in the valve serving as a differentiating character between *astrologa* and *pseudoastrologa.* It also appears that Rindge & Smith pictured the female genitalia of *pseudoastrologa* for *astrologa,* the differentiation here being the markedly stronger sclerotization of the ductus bursae of astrologa, and its larger size and elongated posterior cross section. With regard to maculation, *astrologa* is best separated by its more definitely penciled design, and presence of a black reniform spot on the underside of the fore wing. The latter is often present in *vivianae,* but the larger size and lighter total aspect of *vivianae* definitely separate these species; the conflict is likely to be with *pseudoastrologa,* with which it shares locality in California.

Male genitalia: Figure 3. *Valves*: symmetrical, complex, elongate, narrow, with costal projection, larger anal projection, tip curved, pointed (no ventro-medial projection, as in *pseudoastrologa*). *Tegumen*: elongate, tapering posteriad to base of uncus. *Uncus*: elongate, tapering posteriad, tip rounded. *Phallus*: (expanded). *Aedeagus*: sclerotized base 2 mm long, group of 12-15 secondary cornuti on ventral surface. *Vesica*: armed with several dozen primary cornuti longer than the secondary group, and separable into larger basal group (and more numerous filliform distal group).

Female genitalia: Figure 4. *Segment 8*: A transverse ring, most heavily sclerotized dorsally, less completely ventrad. *Ovipositor lobes*: subtriangular, scattered setae throughout. *Ductus bursae*: strongly sclerotized, more so than any of the other species of the complex, 1.5 mm long. Posterior end twice as wide as anterior end. *Corpus bursae*: 2 mm long, surface with numerous sub-equal small spines.

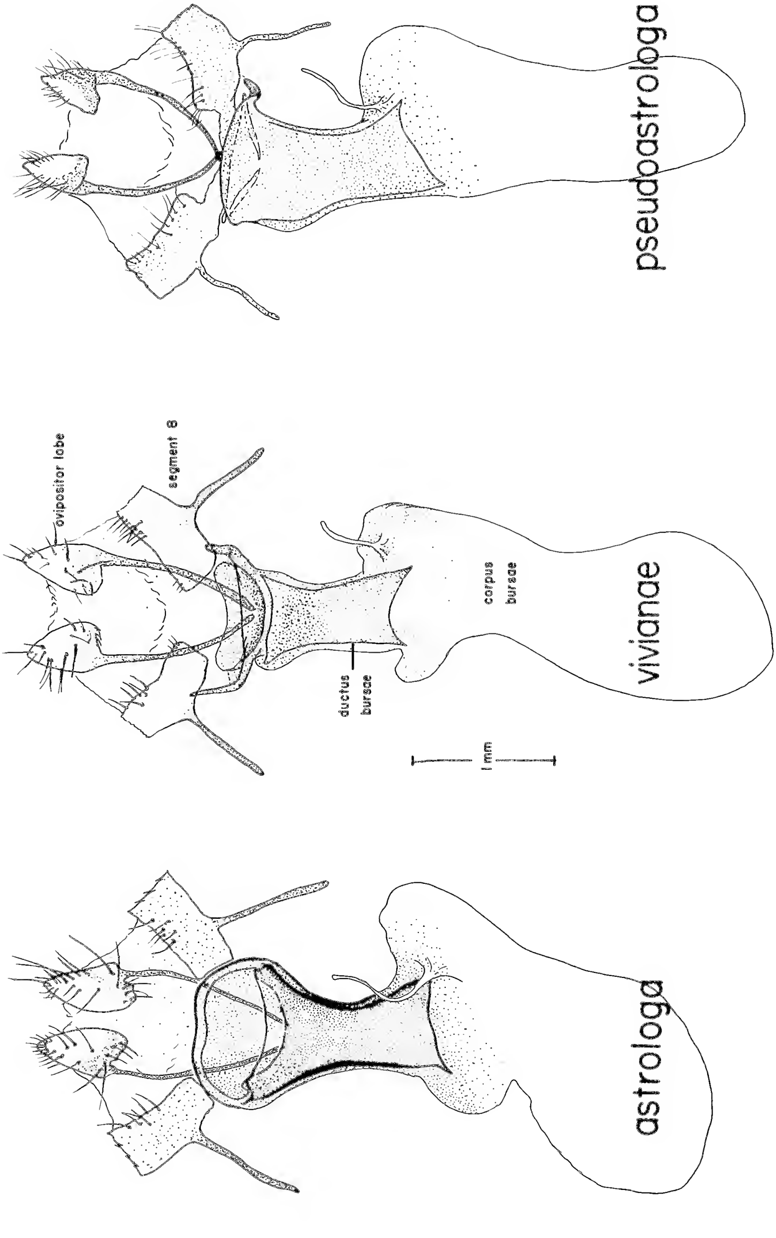


Fig. 3. Female genitalia of *Anaphila* species as indicated.

Annaphila olgae sp. nov. (fig. 3, 4).

The third specimen of the original B. & McD. series is unlike any other *Annaphila* known to this writer, and is here named *Annaphila olgae* sp. nov., in honor of my mother-in-law, Mrs. Olga Cornibe Presco, of South Pasadena, California. While the writer does not generally approve the naming of single specimens, it is felt that this particular case ought not to be left untreated. It does not appear to be a malformed individual, nor other than a representative example of its kind. Further, it is part of the original series of the basic species examined (Fig. 1, 2).

Male (unknown). *Female*: *Head* - *Vertex*: black, shaped as astrologa; *front*: black; *antennae*: missing; *palpi*: mostly white. *Thorax* - *Dorsal*: mostly rubbed in holotype, few scales left dark. *Ventral*: light tan, darker than any of the other species. *Abdomen* - *Dorsal*: a dark brown, under scope some lighter scales at segment boundaries; rubbed somewhat. *Ventral*: lighter than dorsum, but again darker in overall aspect than the others of the group. *Wing span*: 16.5 mm (as mounted). *Wings* - *Fore wing upper*: overall most like *pseudoastrologa*, but with ground color brown where *pseudoastrologa* is black. Only exceptions noted. *Basal area*: much rubbed, but under scope no evidence of light scales as in either *astrologa* or *vivianae*. *Reniform*: elliptical, rather than lunar, as in the others. *Hind wing upper*: most like *vivianae*, with basal band and basal area lighter even than *vivianae*. Brown again replaces black areas of other species. *Discal spot*: absent. *Distal band*: brown, least wide in m-cu area. *Fringes*: brown, white at vein ends. *Genitalia*: not known; type specimen not dissected.

Type: Fig. 1, 2. Holotype, female, Arizona (collector unknown) (not date). The third of the three specimens in the type of series of *astrologa*, as defined by Barnes and McDunnough. *Early stages*: unknown. *Foodplant*: unknown, but probably an annual in the family Hydrophyllaceae. *Type locality*: southern Arizona. *Range*: unknown. *Remarks*: this species is now known by the type alone. Since the specimen is one loaned by the USNM for this work, it has been returned. Kodachrome slides, with index to actual size, are available at the Los Angeles County Museum. It is believed that as the Tucson-Globe area is investigated with respect to the genus *Annaphila*, *olgae* may be taken in this area.

Annaphila pseudoastrologa sp. nov. (fig. 1, 2, 3, 4).

A third species, not part of the original series but included by Rindge and Smith, is here designated *Annaphila pseudoastrologa* sp. nov. Its California range is much the same as *astrologa* and its appearance very closely resembles that of *astrologa* B. & McD. It is of interest that in the areas where both occur together, examination of the foodplants growing in intimate contact may often yield the separate species, each from its chosen plant. The author has worked out the life cycles of both *astrologa* and *pseudoastrologa*, but these will be treated in detail in a subsequent paper.

Annaphila pseudoastrologa n. sp.

Wing expanse 19-24 mm. Male (& Female alike). *Head* - *Vertex*: black. Under scope few gray and orange-brown scales. *Front*: black, with triangular tuft of long, hair-like scales. *Antennae*: gross aspect black, with medial end of each segment black, distal and white, giving ringed appear-

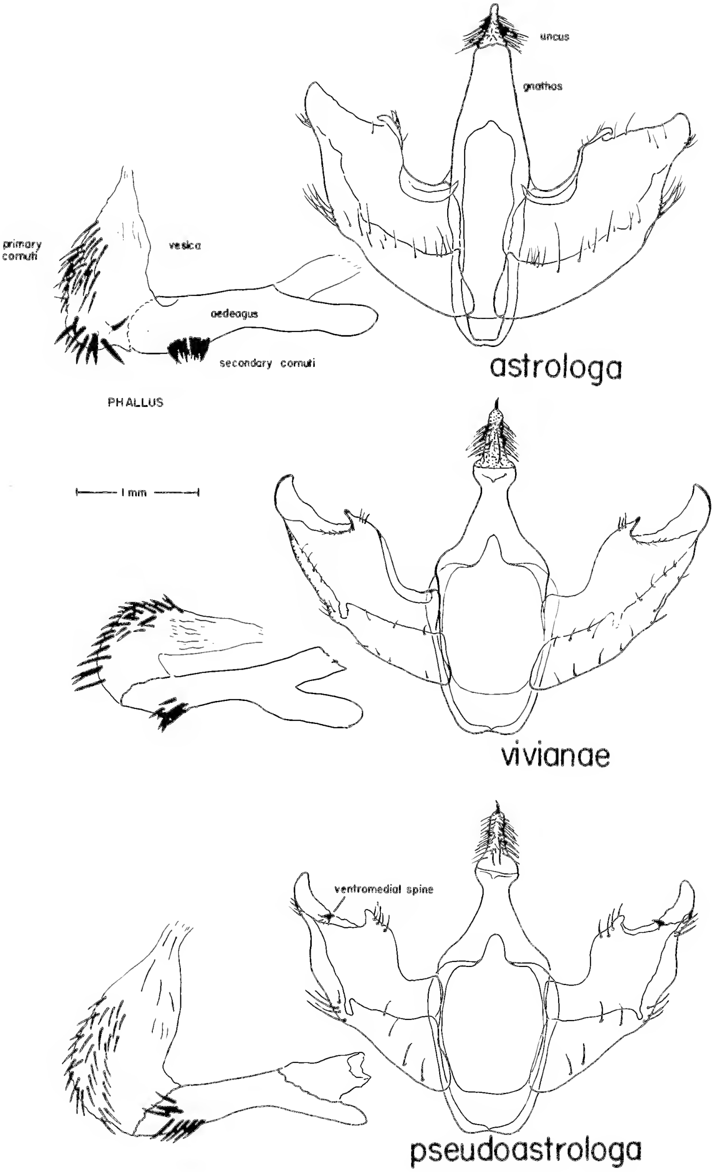


Fig. 4. Male genitalia of *Anaphila* species as indicated.

ance. *Palpi*: mostly white, with scattering of black, giving a light gray aspect, longer and lighter than *astrologa. Thorax - Dorsal*: black throughout. *Ventral*: white, especially so due to light hair-like scales on femurae. *Abdomen - Dorsal*: black cephalad, with white ring scales on caudal margin, these longer and more profuse than on *astrologa. Lateral*: transition between dorsum and ventrum. *Ventral:* caudal margin scales hair-like, overlying the anterior darker scales of next posterior segment, giving the whole surface a whitish aspect. *Legs* - Segments dark mesad, with distal light ring, scales hair-like. *Wings* - wing expanse 19-24 mm. *Upper surface fore-wing*: ground color gray-black. *Basal line*: black, extending from costa to posterior edge of radius. *T. A. line*: black, delineated by the grayish-black mesal area to basal line; zigzag distad on negative veins, mesad on positive veins. *Orbicular*: outlined in black, round, center often gray-black, causing whole area to be indistinct. *Claviform*: indistinct, often faintly outlined in black. *Median Line*: Indistinct to absent; always most prominent at anal margin. *Reinform*: White, suboval, lightly tinted gray central portion, always less so than *astrologa;* attached to costa by white patch terminating at t.p. line. *T.p. line*: white, blending to costal patch anteriad reniform; a light penciled line forming a script "B," touching reniform upper, central, and lower distal points; becomes broadened between cubitus and anal margin. *S.t. line*: at apex, a light dash; indistinct to absent posteriad r-2 vein. *Fringes*: black, often lighter at vein ends. *Upper surface hind wing*: *General pattern*: 1/3 area centrally orange, border black, costal, distal and anal margins more pronounced than basal margin. *Basal area*: scales hairlike, mostly black. *T.a. line*: indistinct, always the margin of bordering band, blending to ochrous center; always thinnest near end of a-1 vein. *Discal spot*: usually absent; when present a dot, rarely a fain dash. *Discal-anal border*: black, with outline of mesal edge distinctly less recurved than in *astrologa;* usually less wide than in *astrologa. Fringes*: mostly dark, white at vein ends; occasionally light anteriad m-1. *Lower Surface fore wing*: ground color orange; orange to medial line. *Median line*: black; variable as to width and degree of spreading mesad and distad into orange field; question mark-shaped, complete from costa to anal margin; some specimens show costal black dash marginal scales to median line. *Reniform* absent. *T.p. line*: black band, curved distad from costa to anal margin, broadest at costa: fused to distal margin between m-2 to cu-2 veins. *Tip*: white, edged in black. *Fringes*: black, white at vein ends. *Lower surface hind wing*: ground color concolorous ochre and black with fore wing. *T. a. line*: black, variable from complete to discontinuous line, often variably fused mesad into basal area. *Discal spot*: faint to absent in lighter specimens; a few black scales when present; always less than in *astrologa* and fainter than in *vivianae. Marginal band*: typical for all the complex; black, similar to *astrologa*, but never penciled as sharply as *in astrologa. Tip*: white-yellow twin patch of scales, edged in black. *Hind wing lower surface*: tip - fringes black and white, variable, mostly white near apex. *Holotype*: Male (Fig. 1) above Seminole Hot Springs, Coll. F. P. Sala, Santa Monica Mts., L. A. Co., Calif. March 9, 1957. *Allotype*: Female (Fig. 1) above Seminole Hot Springs, Coll. F. P. Sala, Santa Monica Mts., L. A. County, Calif. March 10, 1958. *Early Stage*: Will be discussed in a subsequent paper. *Foodplant*: *Phacelia parryi* Torr. and *P. minor* Harvy. *Type locality*: upper Latego Canyon, Santa Monica Mountains, Los Angeles (above Seminole Hot Springs) County, Calif. *Range*: southern California. The Santa Monica coastal mountain ranges. The intermediate ranges of the San Gabriels, the San Bernardino and Santa Rosa ranges, and into the desert ranges, wherever the annual foodplants, *Phacelia parryi* Torr. and *Phacelia minor* Harvy. The known northern limit thus far is southern Ventura County on the Pacific Coast, and the San Gabriels on the western margin of the Mojave. This is subject to change with further investigation. It does not appear to fly with *vivianae* in the southern edge of the Sierras, however. *Early Stages*: Life cycle will be detailed in a subsequent publication. On wing from late March through April, depending on location and altitude, and yearly climatic situation. *Remarks*: The holotype and allotype of *pseudoastrologa* have been deposited in the Los Angeles County Museum along with several paratypes. A pair of paratypes have also been placed in the collections of the USNM, Yale University, Cornell University, UCB, and the Neidhoefer collection, and the collection of William Bauer. *A. pseudoastrologa* is distinguished from all other species of this group by: *Gross aspect*: lack of white scaling on basal upper fore wing. Lack of median spot on hind wing upper and/or lower side; generally larger (20-23 mm wing span). *Genitalia* (male): median spine in ventromedial spine near apex of valve. *Genitalia* (female): incomplete segment 8, ductus bursae not so sclerotized as *astrologa. Genitalia*: male, Fig. 3, *Valves*: similar to *astrologa*, but with prominent ventromedial spine (fig. 4 "spine") near apex of valve. *Tegumen*: elongate, tapering, constricted anteriad uncus, broadened at tip. *Uncus*: broad at base, constricted to 1/2 basal width through posterior three quarters of length; tip pointed. *Phalus* (expanded): aedeagus similar to *astrologa*, secondary spines (cornuti) larger and fewer in number (6-8). *Vesica*: primary spines (cornuti) sub-equal throughout; long, filliform. *Genitalia* (female, fig. 4): *Segment 8* incomplete ring, less sclerotized throughout than in *astrologa. Ovipositor lobes* triangular, rounded at corners, half as wide at base as length. *Ductus bursae* well sclerotized, slightly tapering from maximum width at posterior opening, less than 1.5 mm long; sclerotization less than in *astrologa. Corpus bursae* gross aspect much like *astrologa*.

Annaphila vivianae sp. nov. (fig. 1, 2, 3, 4).

A fourth species from the Kern River basin of Kern County, California is yet again unlike any of those previously discussed, being the most spectacular of the group. This insect is here named *Annaphila vivianae* sp. nov., in honor of my wife, Mrs. Vivian P. Sala. Thus far, the known range of *vivianae* is restricted to Kern Canyon area of the Kern River. None of the other species of the *astrologa* complex has yet been taken from the southern tip of the Sierra foothill area. The life cycle of *vivianae* is also complete, and will be discussed later with the others.

Annaphila vivianae (original description)

Wing expanse 19-24 mm. Male and female alike. *Head - Vertex*: black, with liberal sprinkling of light scales. *Front*: black and white. *Antennae*: gross aspect black, medial end of segments ringed with white, under scope. *Thorax - Dorsal*: black and white, giving a dusty gray aspect gross. *Ventral*: white, more so than for any other members of this group. *Abdomen - Dorsal*: black, with white fringe covering inter-segmental area. *Ventral*: same, with longer fringe scales giving gross aspect a whiter tone. *Legs*: black-white banded. *Wings - Upper surface forewing*: ground color mostly white, black band across the orbicular area. White in basal area due to gross suffusion of basal area to T. A. line, and extensive widening of reniform and T. P. line. *Basal line*: white, extending from costa to medium. *T. A. line*: white, approximately .5 mm. wide, penciled finely in black mesad, extending from costa to anal margin. *Basal area*: white. *Orbicular*: indistinct to absent; when present outlined in light scales. *Claviform*: absent. *Reniform*: white, lunar, often without brown-gray lunule in center; strongly fused with white at costa. *T. P. line*: fused to reniform (white) at costa, "B" marking finely penciled, fused to reniform lower distal margin, fused out to S. T. line to anal margin. *S. T. line*: white, finely penciled to cu 1 fused to anal margin. *Area between T. P. line and S. T. line*: black. *Apex*: black, strongly overlain with white, frosted. Fringes: black, more strongly outlined in white at vein ends. *Hind wing upper surface*: pale orange, lighter than any other of the group; banded distally in black, mesally brown-black. Band broken at distal end basal margin. Orange area covering ¾ surface (more than any of other species). *Basal area*: basal band narrow, weak, long hairlike scales. *T. A. line*: faint, marks border of orange-yellow certer. *Discal spot*: usually absent, very faint dash on strongly marked specimen. *Distal band*: black, least wide in area from m-2 to cu-2. *Fringes*: white, occasionally few dark scales between veins, (lighter than any other species of the group). *Fore wing lower surface*: ground color orange. *Costa*: orange. *Median line*: represented by dark spot on costal margin, quadrate black spot in area of radial to medial veins. Area between T. P. line and S. T. line a black band from costa to cu-2. Tip white, veins delineated with darker scales. Fringes dark, white at vein ends. *Hind wing lower surface*: ground color orange. Discal spot faint, black. Outer margin band incomplete, starting at costal tip, broken at r-1 area, again at m-1 area to cu-1 continuing to inner margin. Apical tip white, veins darker, fringes white, darker at vein ends.

Male Genitalia: (Fig. 3) *Valves*: as per *astrologa*. *Gnathos*: as per *pseudoastrologa* (restricted caudad). *Uncus*: as per *pseudoastrologa*. *Phallus* (expanded): aedeagus sclerotized base 2 mm. lg. group of 6 to 8 secondary cornuti. *Vesica*: armed with several dozen primary cornuti subequal and strongly sclerotized. *Female Genitalia* (Fig. 4): *Segment 8*: incomplete ring. *Ovipositor lobes*: trangular, rounded, most nearly like *astrologa*. *Ductus bursae*: well sclerotized throughout, less than *astrologa* approx. 1 mm long, 0.6 mm. wide; less taper than either *astrologa* or *pseudoastrologa*. *Corpus burae*: like *astrologa* and *pseudoastrologa*.

Type holotype male: (Fig. 1, 2) Lower Kern Canyon, Kern County, California, March 12, 1956. Coll. Vivian Sala; deposited in Los Angeles County Museum collection. *Alotype female*: (Fig. 1, 2): Lower Kern Canyon, Kern County, California. March 2, 1960. Coll. F. P. Sala; deposited in Los Angeles County Museum collection. *Early stages*: Will be discussed in subsequent paper. *Foodplant*: *P. cicutaria*. *Type locality*: Kern Canyon, Kern County, California. *Range*: Southern tip of Sierra Nevada Mountains-Kern River drainage area canyons. The range may be extended to the north on the western slope of the Sierra, wherever *P. cicutaria* occurs in favored localities. Flight is restricted to a 3-4 week period usually beginning in the middle of March and completed by the second week in April, varying with the termination of winter rains.

Remarks:A. vivianae is one of the spectacular species. It is distinguished from all other *Annaphila* by the whitish suffusion over the normally black areas, and in the predominance of orange on the undersides of the wings. The known range is restricted (thus far) to the southern Sierra mountain range and *vivianae* does not with the other species of the *astrologa* group. In the Rindge-Smith material was-one specimen probably from the Havilah, Kern County, California area, probably a Henry Edwards specimen. *A. vivianae* may be the originating stock species. In habit and early stages, *viviane* is most like *pseudoastrologa*. With respect to sequencing of appearance of the *Annaphila* species of the Kern

Canyon area, it is an earlier flier than are either *astrologa* or *pseudoastrologa* are in their areas.

This species is named for my wonderful wife, Mrs. Vivian Presco Sala, who collected the holotype.

Evaluation of the several separating characters of the species lead me to believe that *A. vivianae* might be the forerunner of the group, *pseudoastrologa* and *olgae* being the most closely related, and *astrologa* possibly the latest derivative.

A. pseudoastrologa has the widest range in southern California following the range of its foodplants (*Phacelia parryi* Torr. and *P. minor* Harvy). It has been taken along the Pacific Coastal plain as high as 5,000 ft. in the coastal and intermediate ranges, and occasionally in the desert mountains of southern California and the Arizona types. *A. olgae* is known only from the type, and its data is only "So. Arizona, poling" (no date). It does carry a Poling label, and thus might be from the Tucson area of Arizona.

The rearing of the three species noted has thus far indicated a marked constancy of maculation and gross structure for each species. Thus, differences not in accord with these, and from ecologically separable areas as well, are suspect. Several specimens in the series evaluated as *astrologa* by Rindge and Smith from this southern California area do not fit any of the four species discussed in this paper. These have been separated from the *astrologa* series, and while the Rindge-Smith label has been left on the pin, it has been folded and noted as not agreeing with the descriptions listed. Two specimens so noted are from "western San Diego County, California." They are quite worn and indefinite as to collected location data. It was deemed inadvisable to use these as the basis for description of species. These will be held pending acquisition of additional material. One specimen from eastern San Diego is again different, being markedly more extensive in areas of black intruding on the orange areas. It most closely resembles *pseudoastrologa* and possibly is a race thereof. It has been set aside for future determination.

It is appropriate to discuss the California habitat of these species and some of the adaptations of *Annaphila* in general to this type of environment:

All *Annaphila* thus far reared by this writer (8 species) have indicated an annual life cycle and a pupal diapause, with no layover in the pupal stage beyond one year. Thus, in general, a species can be assumed to be restricted to those areas where the foodplant, an annual, is able to grow from seed each year.

It is the nature, in general, for the annual foodplants to be restricted to canyon slope areas, and to grow most profusely where the ground is often naturally disturbed (silt-flooding or slope slippage). These plants are clustered in chosen locations and found not at all elsewhere.

The various California mountain ranges, within which these foodplant locations are found, are strongly separated one from another ecologically. Add to this the local nature of the flight patterns of *Annaphila,* and the probability of transfer of the adults from one location to another is small indeed.

Degrees of isolation can be noted. The Sierra flora and accompanying *Annaphila* are strongly divergent from all the other coastal and intermediate southern California ranges. *A. vivianae* is not known to occur with any other of the *astrologa* complex species.

Further, the several coastal and intermediate ranges are now ecological islands as well. *A. astrologa* and *pseudoastrologa* fly together in the Santa Monica and the San Gabriel Mountain ranges, and thus these two are sympatric.

Acknowledgments

In addition to the aforementioned assistance in loaning of the materials used in this work, the assistance of Dr. Leland R. Brown, of the Department of Entomology of the University of California, and the Department of Entomology of the Los Angeles County Museum is gratefully noted.

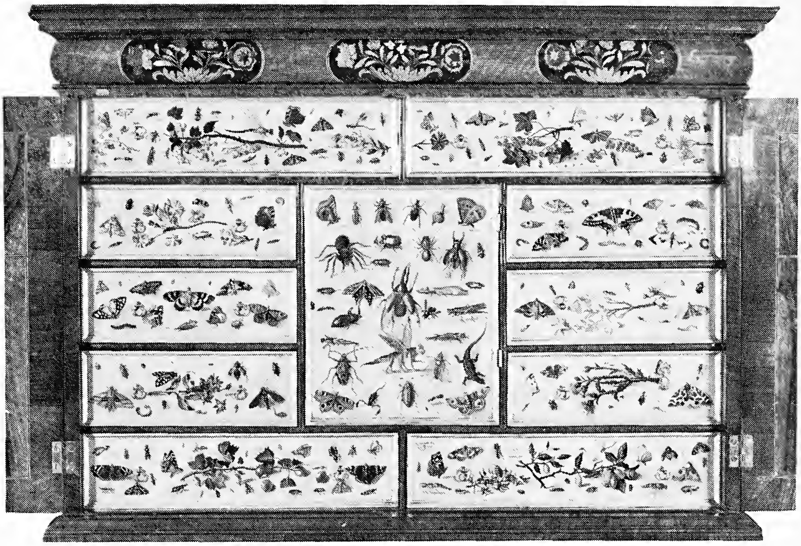
Finally, the author is most grateful to Dr. Charles L. Hogue of the Los Angeles County Museum, who unselfishly assisted in the preparation of the illustrations and suggested the method for preparation of the genitalia.

Literature Cited

BARNES, W. and J. McDUNNOUGH. 1918. Original Description of *Annaphila astrologa. Cont. Nat. Hist. Lepid. No. America,* 4(2):

JEPSON, W. L. 1925. Manual of Flowering Plants. California School Book Depository.

RINDGE, F. H. and C. I. SMITH. 1952. A Review of the Genus *Annaphila* Grote (Lepidoptera, Philadelphia). *Bull. Amer. Mus. Nat. Hist.* 98(3):191-256.



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1140 W. Orange Grove Ave., Arcadia, California, U.S.A.

COLLECTING OF ANNAPHILA SPILA
WITH NOTES ON THE "CRIMSON-WINGED" GROUP OF THE GENUS

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University of California,
Davis, California

THE LARGEST SERIES TO DATE of *Annaphila spila* Rindge & Smith was collected in the spring of 1961, at which time a series of over forty specimens was taken in a sheltered draw and along a creek just below Monticello Dam in Solano County, California. In this area, erogeny is magnificently pronounced, with some of the strata almost perpendicular, and as a result, the hillside habitat of *spila* proved very difficult collecting. The area is predominantly chaperral with a scattering of *Pinus sabiniana* and various species of *Quercus* dotting the hillsides.

The flight time is relative to the morning temperature and seemed to begin around 10:00 A.M.; no specimens of *spila* were collected or seen after 4:00 P.M., even though the temperature still seemed favorable for their flight. Moderate breezes were blowing, and in combination with the temperature may have had some bearing on the termination of the diurnal flight. However, the breezes were also evident around 12:30 P.M., at the peak of flight. The reasons for the terminations of the diurnal flight of *spila* as well as other species of *Annaphila* still remains unknown. Specimens of *A. decia* Grote, *A. depicta* Grote, and *A. divinula* Grote were collected in the same area until 5:00 P.M., and probably could have been collected later in the day as well.

The adults of *spila* were found to frequent the flowers of a small number of plant species, predominantly *Monardella breweri.* The adults were also collected on *Gilia* sp., *Erodium* sp., and *Psycocarpos* sp. Occasionally they were seen hovering around *Cercus occidentalis,* but none were observed either alighting on the leaves or feeding on the flowers. One specimen was collected around 12:30 P.M., while apparently drinking water from a damp, sandy spot along a stream.

The "crimson-winged" group in the genus *Annaphila* is comprised of *superba* Henery Edwards, *spila* Rindge & Smith, and *evansi* Rindge & Smith. *A. superba* may be readily distinguished from both *spila* and *evansi* by the reniform being centrally of ground color, outlined in white, and connected to the costa by a white patch above the anterodistal margin of the reniform; by the ventral surface of the primaries possessing a complete median cross line or band. *A. spila* and *evansi* are more closely related to each other than either is to *superba,* as is readily seen by the maculation of the dorsal surfaces of the primaries; the transverse ridge across the top of the frons; the female and male genitalia. Neither *spila* nor *evansi* display a white outlined reniform; however in freshly emerged specimens a faint gray outlining of the reniform may be seen; nor do they display complete median cross lines on the ventral surface of the primaries as does *superba. A. spila* has a dot on the ventral surface of the primaries in place of the band present in *superba,* and *evansi* lacks both of these characters.

As may be seen by the relationship in the genitalia of these species, it seems plausable to assume they arose from a common ancester, and that *superba* is evolving as a discrete unit while *spila* and *evansi* are evolving as another more closely associated unit. The "crimson-winged" group is most probably an offshoot of the "*astrologa-ida*" group. The female genitalia of *superba* show a similarity to the female genitalia of *ida* Rindge & Smith, but the genitalia of the males do not show this as well.

In the "Revision of the genus *Annaphila*" (Rindge & Smith, 1952), the new species *spila* was based on very few specimens of which only one was a male. A female was chosen as the type and the description was drawn from this sex. I was not sure of the justification of including the allotype male in the type series, as it was collected in an entirely different geographical area which is separated from the type locality by the great interior valley of California. Further study has proved the populations from the coast ranges to be conspecific with those of the foothills of the Sierra-Nevada, just as Rindge and Smith suspected.

In the original description of *spila,* it was stated that this is an obscurely marked species. I find this not to be so in every instance; but it must be kept in mind that Rindge & Smith had very few specimens. The species of *Annaphila* are very easily rubbed, and this probably accounts for *spila* being described as an obscurely marked species. However, in comparison with *superba,* both *spila* and *evansi* in excellent condition are more obscurely marked; but in fresh specimens one can readily see the cross lines of the primaries which are light gray to white in both sexes.

LITERATURE CITED

RINDGE, F. H. and SMITH, C. I. 1952. A revision of the genus *Annaphila* Grote (Lepidoptera, Phalaenidae). *Bull., Amer. Mus. Nat. Hist.* 98(3): 57 pp., 8 plates.

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