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TAXONOMIC NOTES ON *OENEIS UHLERI* REAKIRT (LEPIDOPTERA, SATYRIDAE)

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Oeneis uhleri uhleri Reakirt and the northern subspecies *uhleri varuna* Edwards generally are separated on the basis of the maculation on the upper side of the wings and the condition of the discal band on the under side of the hind wings. These criteria have served reasonably well when the material being examined has come from central Colorado or the provinces of Alberta and Saskatchewan. Recently I have had the opportunity to examine series from western Colorado and Wyoming. This material does not agree too well with either typical *uhleri* or *varuna*. While I have fairly well distributed series before me, I lack material from the two type localities.

Reakirt described *uhleri* in 1866 from material collected the previous year in August by James Ridings. In all probability Ridings' material was collected in the grassy parks that crown the Front Range west of Denver (Bergen Park, etc.). Edwards (1892–1897) greatly amplified Reakirt's description and set the basis for our present concept of the species. His studies were based on a series of 73 specimens collected by Theodore L. Mead in 1871. Mead's material was collected in the Front Range about 20 miles south of the assumed type locality. Edwards also had before him many more specimens collected by David Bruce during the period 1886 through 1891. Bruce's specimens came from the same general area as did Mead's. This country is rather dry ponderosa pine forest with much scattered open land that is grassy. It is in this grassy part of the forest that *uhleri* abounds in June and early July. A few fresh specimens are found in August that

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may represent a partial second brood or are just late-emerging insects. The same sort of country extends north and south from the type locality for at least 100 miles.

Edwards based his name *varuna* on material collected by Herbert K. Morrison in 1881 in the "Dacota Territory" at an elevation of about 1200 feet. I suspect that these specimens were taken somewhere in south central North Dakota, probably between Jamestown and Bismarck. He took about 100 *varuna*, of which Edwards received four males and three females. Later, Edwards (1892–1897) amplified his description with data from 33 males and five females taken by W. G. Wright in the foothills of several mountain ranges in eastern and central Montana. This is prairie country in the case of the types and foothill forest in the case of Wright's collection.

The material that has served as the basis for this study consists of seven series, four of *uhleri uhleri* and three of *uhleri varuna*. Throughout the following discussions these series are referred to by the locality from whence they came.

RAMPART RANGE: Sixteen males and two females collected by me near Woodland Park, Teller, County, Colorado, at 9500–9600 feet altitude between June 28 and July 4. The insects are common at this time in the deep grass on the south-facing slopes of the deep ravine through which the road climbs to the top of the range. The dominant tree in the area is the ponderosa pine, and there are a few Englemann spruce. The habitat is much the same as that at the assumed type locality west of Denver. The Rampart Range is the southward extension of the same peneplain upon which I believe Ridings collected the types.

HALL VALLEY: Twelve males and two females that I collected at the lower end of "Hall Valley" near the site of the now almost extinct town of Webster in Park County, Colorado. The material was taken on June 20 at 9600 feet altitude on the dry stream terrace at the bottom of the valley in a grassy patch amid quaking aspen, ponderosa pine, and Engelmann spruce. At the same time Lionel Higgins took a similar series that I have not been able to include, since it is in England. This locality is about 20 miles west and south of the assumed type locality. It was one of David Bruce's favorite collecting points from which he shipped many specimens to W. H. Edwards.

GOTHIC: Twenty-six males and four females collected by Walfried J. Reinthal of Norman, Oklahoma. The specimens were taken

between July 5 and 21 in the vicinity of the Biological Station of the Colorado Western State College. Reinthal described the habitat of the insects as the open grassy glades among the pines. These are the only *uhleri* that I have from the Pacific slope. They are somewhat different from the Atlantic slope material—larger and darker. It was this series that spurred me to make this study.

LARAMIE MOUNTAINS: Thirty-one males and 12 females collected by me in the Laramie Mountains, Albany County, Wyoming, on July 2 and 3. The precise locality of the collection is on the divide just southeast of Eagle Mountain. The insects were abundant in the deep grass of an open area containing a few scattered, venerable ponderosa pines and surrounded by second-growth lodgepole pine and aspen.

The above series are all *uhleri* rather than *varuna*. So far as I can tell, the Rampart Range and Hall Valley material is typical of the subspecies. The Gothic and Laramie Mountains series are somewhat atypical. All series were found in grassy openings in the forest and associated with ponderosa pine. The two atypical series came from areas that are wetter and cooler than the Front Range and the Gothic series from a country that has much more snow than any of the others.

LLOYDMINSTER, SASKATCHEWAN: Seventeen males and two females collected by Richard J. Fitch between May 28 and June 9 on "prairie," now in my collection.

CALGARY, ALBERTA: Fourteen males and six females collected by C. Garrett for Jean Gunder, in the collection of the American Museum of Natural History. The collecting dates range from June 11 to 27. This is prairie country.

DIDSBURY, ALBERTA: Forty-seven males and 24 females collected by C. Garrett for Jean Gunder, in the collection of the American Museum of Natural History. The collecting dates range from June 6 to 27. This is prairie country.

The three last-named series are *uhleri varuna*. They represent prairie strains similar to the types. Unfortunately I have not been able to examine a series of specimens that represent the forest strain such as Edwards received from Wright.

MACULATION

Edwards published (1892–1897) some data about the maculation of the upper side of both subspecies. From this he decided

that one of the criteria for the separation of *uhleri* from *varuna* is the greater development of ocelli on the upper side of *varuna*. On the basis of my studies it seems that the maximum number of ocelli that might occur on the upper side is 20. Edwards' data were based on one side of the insect, left or right. To determine how well my series compared with his I made similar counts. The results of his

TABLE 1

THE NUMBER OF OCELLI ON ONE SIDE (UPPER SURFACES) OF MALES

Series	*N*	Fore-wing	Hind Wing	Total	Per Cent
uhleri					
Edwards'	14	25	21	46	32.8 ± 4.0
Rampart Range	16	27	42	69	43.1 ± 3.9
Hall Valley	12	22	42	62	51.2 ± 4.6
Gothic	26	50	80	130	50.0 ± 3.1
Laramie Mts.	31	75	101	176	56.8 ± 3.4
All series	99	199	286	485	49.0 ± 1.5
varuna					
Dakota types	4	9	20	29	72.5 ± 7.1
Montana	33	123	146	269	81.5 ± 2.1
Lloydminster	17	59	77	136	80.0 ± 3.1
Calgary	14	56	59	115	82.3 ± 3.2
Didsbury	47	180	199	379	80.6 ± 1.8
All series	114	427	501	928	81.4 ± 1.2

and my counts form table 1, and the significance of the differences is given in table 2.

It is obvious that there is a difference in the degree to which the ocelli are developed on the two subspecies. But are these differences significant? It is possible to measure the differences in terms of the probability that such differences will occur in a homogeneous population. One way of stating this is the per cent of times such a difference may be expected to be equaled or exceeded in a homogeneous population. This per cent is often called the "level of confidence."

The level of confidence to be considered critical for subspecific differences among butterflies must be low in the face of evidence from accepted subspecies. It probably differs from family to family and from character to character. Statisticians generally consider a *t* of 3.0 significant when based on *SE* for laboratory experiments.

This is a level of confidence of 0.27 per cent. My own studies of the statistics of variation among taxonomic units occurring in nature suggest that t must be 7.0 when PE is used and 4.72 when SE is used before it is really significant. This level of confidence is 0.02 per cent.

TABLE 2

SIGNIFICANCE OF THE DIFFERENCES ON THE UPPER SIDE, MALES

Series Pairs	Diff.	$S.D._d$	t	Level of Confidence
uhleri				
Edwards' *vs.* Rampart Range	10.3	5.6	1.84	6.6%
Edwards' *vs.* Hall Valley	18.4	6.1	3.02	0.3
Edwards' *vs.* Gothic	16.8	5.1	3.30	0.1
Edwards' *vs.* Laramie Mts.	24.3	4.9	4.96	0.006
Rampart Range *vs.* Hall Valley	8.1	6.0	1.35	17.7
Rampart Range *vs.* Gothic	6.5	5.0	1.30	19.4
Rampart Range *vs.* Laramie Mts	14.0	4.8	2.92	0.4
Hall Valley *vs.* Gothic	1.6	5.5	0.29	77.2
Hall Valley *vs.* Laramie Mts.	5.9	5.4	1.09	27.6
Gothic *vs.* Laramie Mts.	7.5	4.2	1.78	7.5
varuna				
North Dakota *vs.* Montana	9.0	7.4	1.21	22.6
North Dakota *vs.* Lloydminster	7.5	7.8	0.96	33.7
North Dakota *vs.* Calgary	9.7	7.8	1.24	21.5
North Dakota *vs.* Didsbury	8.1	7.3	1.11	26.7
Montana *vs.* Lloydminster	1.5	3.8	0.39	69.6
Montana *vs.* Calgary	0.7	3.8	0.18	85.7
Montana *vs.* Didsbury	0.9	2.8	0.32	74.9
Lloydminster *vs.* Calgary	2.2	4.5	0.49	62.4
Lloydminster *vs.* Didsbury	0.6	3.6	0.17	86.5
Calgary *vs.* Didsbury	1.6	3.7	0.43	66.7
All series of *uhleri vs. varuna*	32.4	1.9	17.0	1.0×10^{-12}

In table 2 it can be seen that when all of the *uhleri* taken together are compared with all of the *varuna* taken together t is 17.0, far in excess of 4.72, and that according to any standards the two subspecies are significantly different in maculation.

In the same table there appears a marked difference in t scores for the data established by Edwards and by me relating to typical *uhleri*. I believe this difference is false and is dependent upon different methods of counting ocelli. I suspect that Edwards

counted only true "eye-spots," while I included all spots, "eyed" or not. When differences in technique are eliminated by a comparison of only material studied by one of us, the t scores for the differences between the two subspecies are:

	DIFFERENCE	t
Edwards' data	47.8 ± 4.5	10.6
Brown's data	30.1 ± 2.2	13.7

In both cases t is so large that anyone should accept maculation as a valid character for separating the two subspecies.

Just as the data presented in table 2 point to the homogeneity of the series of *varuna,* they suggest that the series of *uhleri* studied represent four local variations of the subspecies, Edwards' series and my Rampart Range material being so much alike that they might well be considered one local population. A glance at Dice's map of biotic provinces (1943) shows that all the *varuna* samples came from the Saskatchewan biotic province and all the *uhleri* from the Coloradan. Since the former is rather uniform in climate and composed of rolling prairies and the latter is varied in climate and mountainous it is to be expected that more variation will be found among local populations from the latter than from the former.

DETAILS OF MACULATION

The preceding section suggests that an inquiry into the details of the maculation of the series grouped as *uhleri uhleri* may reveal significant differences among the populations sampled. The data gathered are best viewed first in a series of histograms that show the distribution of marks by interspace and by character, i.e., as ocelli, spots, and traces. In these histograms (fig. 1) the solid black areas represent the fractions caused by ocelli; the stippled areas, by spots; and the clear outlined areas, by traces. In each case the upper side is represented by the data plotted above zero; the under side, below zero. The histograms suggest that the under sides of the series studied are more different than the upper sides as given in tables 1 and 2. Further it is quite obvious that the under sides of both the Gothic and Laramie Mountains series are more ocellate than in either of the other series.

The numerical data on which the histograms were based were used to develop table 3.

These data suggest that the Gothic material is rather remote

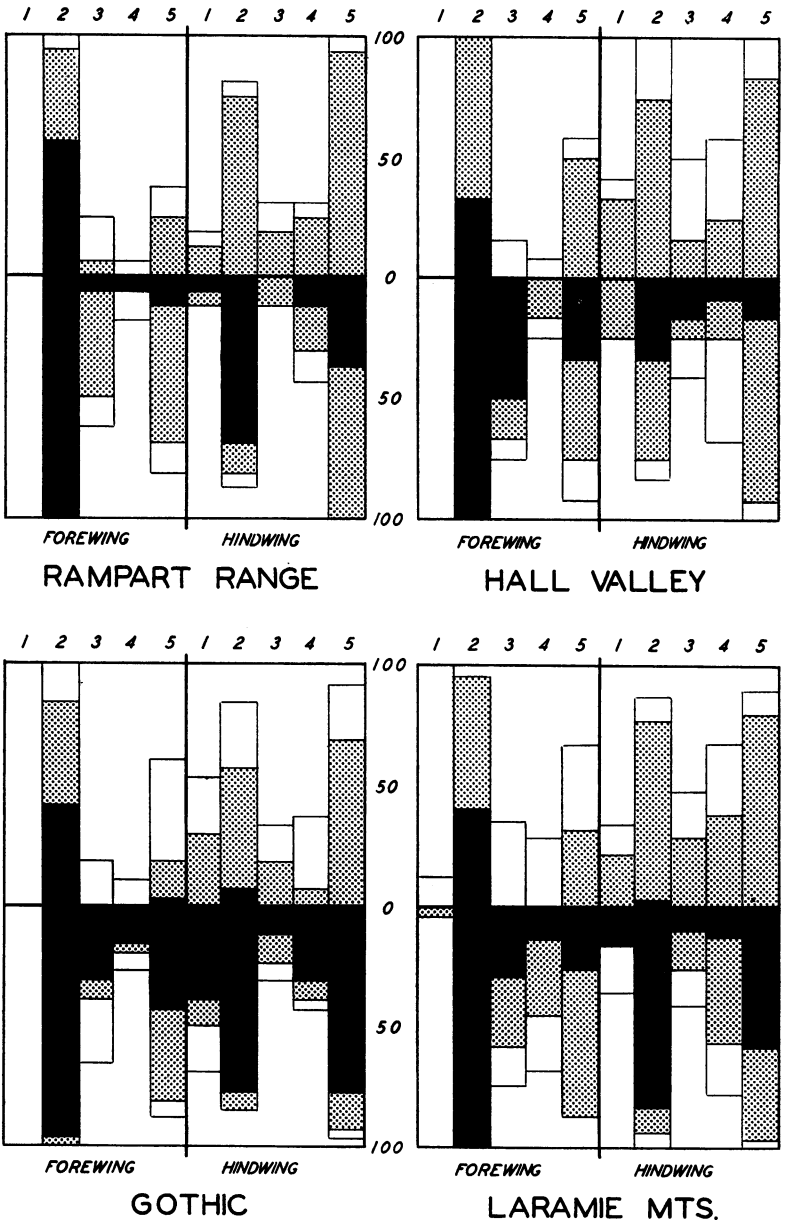


FIG. 1 Histograms of maculation. See text for explanation.

from the typical Front Range *uhleri* as represented by my series from Rampart Range and Hall Valley and that the difference

is much more evident on the hind wings than on the forewings. Although the differences found would satisfy an experimental biologist, I am not wholly satisfied that they represent a real subspecific difference.

TABLE 3

SIGNIFICANCE OF DIFFERENCES IN PER CENT OF OCELLI ON UNDER SIDE OF *uhleri uhleri* SERIES

Series Pairs	Diff.	$S.E._d$	t	Level of Confidence
Both wings				
Gothic *vs.* Rampart Range	17.0	4.6	3.69	0.02%
Gothic *vs.* Hall Valley	19.2	4.7	4.08	0.01
Gothic *vs.* Laramie Mts.	7.2	4.1	1.75	8.0
Laramie Mts. *vs.* Rampart Range	9.8	4.3	2.28	2.3
Laramie Mts. *vs.* Hall Valley	12.6	4.4	2.86	0.42
Forewings				
Gothic *vs.* Rampart Range	11.9	6.4	1.85	6.3
Gothic *vs.* Hall Valley	5.5	6.9	0.80	42.4
Gothic *vs.* Laramie Mts.	3.3	5.7	0.58	56.2
Laramie Mts. *vs.* Rampart Range	8.6	6.1	1.41	15.9
Laramie Mts. *vs.* Hall Valley	2.2	6.7	0.33	74.1
Hind wings				
Gothic *vs.* Rampart Range	21.9	6.5	3.37	0.08
Gothic *vs.* Hall Valley	34.0	6.0	5.67	*ca.* 3.6×10^{-4}
Gothic *vs.* Laramie Mts.	10.8	5.9	1.83	6.7
Laramie Mts. *vs.* Rampart Range	11.1	6.2	1.79	7.3
Laramie Mts. *vs.* Hall Valley	23.2	5.6	4.14	0.01

Perhaps a similar study of the three samples of *uhleri varuna* will shed some light on the question. Table 2 shows that these series represent a reasonably homogeneous population. Data drawn from the under sides of the wings of these insects are presented in table 4, and comparisons of the most divergent sets of data compose table 5.

It is evident that the numbers of ocelli and spots taken together are as uniform as might be expected from series drawn from a homogeneous population. When the total numbers were used as in table 2 the largest t score found was 0.49. Such a t score is expected to be exceeded or equaled by 62.4 per cent of the samples drawn

from a single population. So far as the details of the maculation are concerned, the greatest t score in table 5 is 2.89. Such a score is equaled or exceeded 0.39 per cent of the time by samples drawn from the same population. Thus the individual components of the pattern are about 100 to 150 times as variable as the pattern taken as a whole. This supports the conclusion drawn from the

TABLE 4

FREQUENCIES FOUND FOR OCELLI AND SPOTS ON UNDER SIDE OF THE *varuna* SERIES

	Lloydminster	Calgary	Didsbury
Ocelli on both wings	39.4 ± 3.8	51.4 ± 4.2	51.3 ± 2.3
Spots on both wings	33.5 ± 3.6	22.2 ± 3.5	22.8 ± 1.9
Ocelli and spots on both wings	36.4 ± 2.6	37.8 ± 2.9	37.0 ± 1.6
Ocelli on forewings	41.2 ± 5.4	51.4 ± 6.0	47.2 ± 3.3
Spots on forewings	31.8 ± 5.1	22.8 ± 5.0	21.2 ± 2.7
Ocelli and spots on forewings	36.4 ± 3.7	37.2 ± 4.1	34.3 ± 2.2
Ocelli on hind wings	37.7 ± 5.2	51.4 ± 6.0	55.3 ± 4.2
Spots on hind wings	35.3 ± 5.2	21.4 ± 4.9	24.2 ± 2.8
Ocelli and spots on hind wings	36.4 ± 3.7	36.4 ± 4.1	39.8 ± 1.8

TABLE 5

COMPARISONS OF THE MOST DIVERGENT SERIES OF *varuna*

Item	Series Pair	Diff.	$S.E._d$	t	Level of Confidence
Ocelli on both wings	Lloydminster *vs.* Calgary	12.0	5.7	2.11	3.5%
Spots on both wings	Lloydminster *vs.* Calgary	11.3	5.0	2.26	2.5
Ocelli and spots on both wings	Lloydminster *vs.* Calgary	1.4	3.9	0.36	71.9
Ocelli on forewings	Lloydminster *vs.* Calgary	10.2	8.1	1.26	21.2
Spots on forewings	Lloydminster *vs.* Didsbury	10.6	5.8	1.83	6.7
Ocelli and spots on forewings	Calgary *vs.* Didsbury	2.9	4.7	0.62	53.5
Ocelli on hind wings	Lloydminster *vs.* Didsbury	17.6	6.1	2.89	0.39
Spots on hind wings	Lloydminster *vs.* Calgary	13.9	7.2	1.93	5.4
Ocelli and spots on hind wings	Lloydminster *vs.* Didsbury	3.4	4.1	0.83	40.7

pattern as a whole that *u. uhleri* as represented by the four series is more variable than *u. varuna*. This variability expressed as the range of t scores is given in table 6.

Before conclusions about the maculation are given, it might be well to discuss for a moment the importance of the t scores.

In this and the foregoing section I have used with each per cent its standard error. The *t* scores therefore are the differences expressed as multiples of the standard error and these have been translated to "levels of confidence" for one degree of freedom. For this I have used Pearl (1940, appendix 4, table B).

While subspeciation of *Heliconius charitonius* Linné was being studied, it became evident to me that significant *t* scores for that species are 7.00 or greater when the probable error is used as the

TABLE 6

RANGES OF *t* SCORES FOUND IN COMPARISON OF COMPONENTS OF MACULATION OF *uhleri* AND *varuna* MALES

	u. uhleri	*u. varuna*
Ocelli on underside of both wings	1.75–4.08	0.02–2.11
Spots on under side of both wings	0.25–4.38	0.15–2.26
Ocelli and spots on under side of both wings	0.49–2.93	0.19–0.36
Ocelli on under side of forewings	0.80-1.86	0.62–1.26
Spots on under side of forewings	0.44–3.22	0.22–1.83
Ocelli and spots on under side of forewings	0.06–1.64	0.18–0.62
Ocelli on under side of hind wings	1.79-5.67	0.58–2.89
Spots on under side of hind wings	0.44–3.00	0.32–1.93
Ocelli and spots on under side of hind wings	0.47–2.39	0.00–0.83

divisor of the difference. The same degree of difference is expressed by a *t* score of 4.72 when the standard error is used as the divisor. The chance that either of these scores will be equaled or exceeded in a single population is about 0.02 per cent. Such a minute chance seems from empirical data to represent the possibility that a group of random specimens from one good subspecies will resemble another equally good subspecies.

If we accept this same *t* score as being significant for *uhleri*, then *u. uhleri* and *u. varuna* are valid subspecies statistically as well as in the eyes of taxonomists. The Gothic strain of *uhleri uhleri* approaches significant differences from the typical Rampart Range-Hall Valley strains more frequently than does the Laramie Mountain strain.

In order to accept the Gothic strain as a subspecies different from the typical Front Range *uhleri*, the *t* score that represents a significant difference must be lowered to a level below that accepted by experimental biologists if we take into consideration all of the variables. If on the other hand we are willing to accept

a single feature of the maculation as being of subspecific significance, then to accept the Gothic strain as different from the more typical strains we must set t at 3.50 for the threshold of significance. This has a level of confidence of 0.05 per cent, one case among 2000. Considering the work that has been done by taxonomists with the genus *Oeneis* in an empirical manner, I doubt that segregation on the basis that t equals 3.50 would be acceptable.

Summing up the findings about the maculation we find: (1) the differences between *u. uhleri* and *u. varuna* are highly signifi-

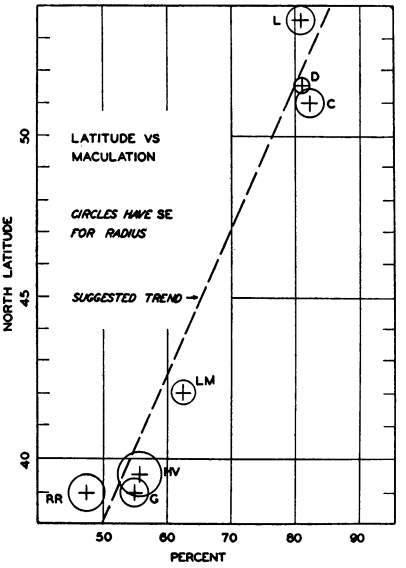


FIG. 2. Maculation cline.

cant; (2) *u. varuna* is much less variable than *u. uhleri;* (3) the Gothic strain of *u. uhleri* may be a weakly defined subspecies.

DISCAL BAND ON UNDER SIDE OF HIND WINGS

The material before me bears out Edwards' contention that the band on the under side of the hind wings is more prominent on *varuna* than on *uhleri*. However, the separation of the two subspecies on this basis is not so sharp as he would lead one to suppose. The band varies so much from specimen to specimen that it alone is not a safe criterion for subspecies.

To analyze the situation, I classified the under sides of the hind wings of the specimens according to five categories: uniformly

graded from the light margin to the darker base; poorly divided, the outer margin of the discal band ill defined and the inner margin not discernible; well divided, the outer margin of the band well defined but no inner margin evident, thus the wing divided into a lighter outer portion and a darker inner part; fair band, with the outer margin well defined and the inner one ill defined; and good

TABLE 7

CONDITION OF THE DISCAL BAND ON THE UNDER SIDE OF THE HIND WINGS

Series	*N*	No Division	Divided	Banded
uhleri uhleri				
Rampart Range	16	75.0 ± 8.3	18.7 ± 9.7	6.2 ± 6.0
Hall Valley	12	83.3 ± 10.8	8.3 ± 8.0	8.3 ± 8.0
Rampart Range and Hall Valley	28	78.6 ± 7.8	14.3 ± 6.6	7.1 ± 4.9
Gothic	26	46.1 ± 9.6	23.1 ± 8.1	30.8 ± 8.9
Laramie Mts.	31	6.5 ± 4.4	54.9 ± 9.0	38.8 ± 8.7
uhleri varuna				
Calgary	14	21.4 ± 11.0	71.4 ± 12.1	7.2 ± 6.9
Didsbury	47	25.5 ± 6.4	44.7 ± 7.3	29.8 ± 6.7
Lloydminster	17	11.8 ± 7.8	5.9 ± 5.7	82.3 ± 9.3

TABLE 8

CHI-SQUARE FOR COMPARISON FOR VARIOUS PAIRS OF DATA RELATING TO CONDITION OF BAND ON UNDER SIDE OF HIND WING

Pair	Chi-square	Interpretation
uhleri vs. varuna	1.6575	Not significant
Gothic *vs.* Hall Valley and Rampart Range	6.8845	Not significant
Laramie Mts. *vs.* Hall Valley and Rampart Range	33.5933	Highly significant
Laramie Mts. *vs.* Gothic	12.8694	Approaches significance
Calgary *vs.* Didsbury	3.8269	Not significant
Lloydminster *vs.* Calgary	18.6699	Probably significant
Lloydminster *vs.* Didsbury	14.4044	Approaches significance

band, with both margins of the band well defined. The samples were too small for the five divisions to be maintained. Thus in table 7 the first category is reported as "no division," the second and third combined as "divided," and the fourth and fifth as "banded." The female series were too small to warrant reporting.

I hope in time to gather enough females to make a similar study of them.

It will be noted that the Hall Valley and Rampart Range series have been pooled. There was no significance to the differences found between these series. In all other cases there are significant differences. This suggests that the condition of the discal band on the under side of the hind wings is too sensitive for use as a subspecific character, except in broad terms. This is borne out by the Chi-square test noted in table 8, which also shows that the condition of this band may be of considerable use in the study of the micro-races that compose an acceptable subspecies.

Since I have used three categories of condition, there are two degrees of freedom in the statistics. For experimental work under controlled conditions when the 1 per cent level of confidence is considered significant, Chi-square is 9.210 for two degrees of freedom and P equal to 0.01. If we maintain the same standard of probability, namely, P equals 0.0002, as for the t scores, which have the same distribution as do Chi-square, then the threshold of significance is not reached until Chi-square is about 20.0, with two degrees of freedom. For those who believe that I am too conservative, the data in table 8 will allow them to interpret my findings to their satisfaction.

COLOR

The color of the upper side of the males varies from light reddish brown to ocher. The lightest-colored series is that from Calgary and the darkest is the Gothic material. From the specimens in my own collection I suspect that the color tends to fade rather perceptibly even when the insects are stored out of light and only occasionally exposed to diffuse light while being studied. In spite of this there seems to be a definite difference in the color of northern as opposed to southern material.

In order to estimate this variation I arranged each series examined in an ascending order of color density in horizontal rows. The various series were so pinned out that insects in the horizontal rows with the same color were one beneath the other. In this way the entire collection fell into 14 perceptible color categories. I made no attempt to name these slight differences in color. The visual arrangement was then transferred to a chart showing the per cent of each series that fell into each of the 14 color categories. From that information table 9 was constructed, indicating the

lightest-colored category, the range of the middle half of the series, and the darkest category represented by each series studied. The sequence in which the series are reported is from the lightest to the darkest. Edwards recognized the darkest of the specimens found among *uhleri* as variety *obscura*. These fall into color categories 12, 13, and 14. He makes no mention of the source of the dark specimens. If the types come from the western slope of the Continental Divide in Colorado that name is available for the Gothic material should it be deemed wise to recognize that material as a subspecies.

TABLE 9

COLOR CATEGORIES

Series	Lightest	Mid 50%	Darkest
Calgary	1	2.8– 5.2	6
Didsbury	1	3.0– 6.0	7
Lloydminster	1	3.3– 5.7	9
Hall Valley	3	3.5– 5.7	8
Laramie Mts.	3	3.8– 8.0	14
Rampart Range	3	4.3– 8.3	11
Gothic	3	8.8–11.5	14

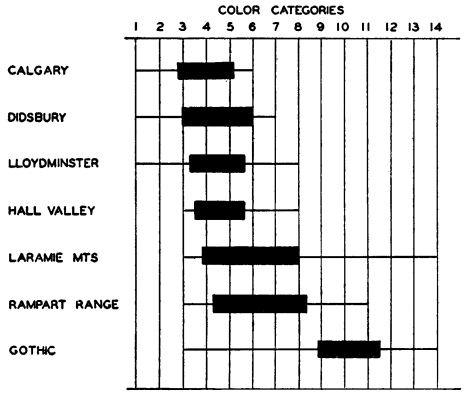


FIG. 3. Bar graphs of color intensity.

It is obvious from figure 3, which is a graphic presentation of table 9, that the Gothic material stands apart from all other series studied. I have applied the Chi-square test to the data from this series and all other *u. uhleri* combined. To eliminate some of the errors of judgment in placing specimens in color categories,

I have grouped the categories in pairs. Thus for this computation there were six categories. This means that the statistics have five degrees of freedom. Chi-square for this comparison is 36.2258. The 1 per cent level for the five degrees of freedom has a Chi-square of 15.086. Since the level I am using has a Chi-square a little more than double that at the 1 per cent level, I believe it can

TABLE 10

PARAMETERS OF THE LENGTH OF THE LEFT FOREWING

Series	N	Mean ± *P.E.*	*S.E.*	*V*
Males				
uhleri uhleri				
Rampart Range	16	22.92 ± 0.20	1.15	5.0
Hall Valley	12	22.61 ± 0.13	0.65	2.9
Gothic	26	24.54 ± 0.16	1.15	4.7
Laramie Mts.	31	22.56 ± 0.14	1.13	5.0
All series	85	23.17 ± 0.10	1.43	6.2
uhlier varuna				
Lloydminster	17	19.98 ± 0.15	0.86	4.3
Calgary	14	20.99 ± 0.16	0.86	4.1
Didsbury	47	21.41 ± 0.09	0.89	4.4
All series	78	20.99 ± 0.08	1.06	5.1
Females				
uhleri uhleri				
Rampart Range	2	22.5	—	—
Hall Valley	2	22.9	—	—
Gothic	4	25.0	—	—
Laramie Mts	12	23.83 ± 0.32	1.58	6.6
All Series	20	23.84 ± 0.24	1.58	6.6
uhleri varuna				
Lloydminster	2	22.3	—	—
Calgary	6	23.10 ± 0.43	1.42	6.1
Didsbury	24	23.00 ± 0.14	1.02	4.4
All series	32	23.00 ± 0.13	1.07	4.7

be said that the Gothic series is significantly darker than the rest of the *uhleri uhleri* used in this study.

SIZE

With the seven series under consideration before me it is apparent that the insects from Gothic, Colorado, are considerably larger than those from elsewhere. Likewise, the Lloydminster

specimens seem to be definitely smaller than the others. These visual impressions are confirmed by actual measurements. The means and parameters for the various series are presented in table 10. My measure of size is the greatest radius of the left forewing.

When the various series of *uhleri uhleri* are studied it is evident that the Gothic series stands well apart from the others. In a test of the differences, *t* (based on *P.E.*, therefore significant only if over 7.0) for combinations of the three series, Rampart Range, Hall Valley, and Laramie Mountains, falls betweeen 0.26 and 1.50, which is not significant. When the Gothic series is compared with the other three the *t* score lies between 6.23 and 9.62. On this basis I consider it proper to say that the Gothic insects are significantly larger than other *uhleri uhleri* studied. The inadequate female series bear this out.

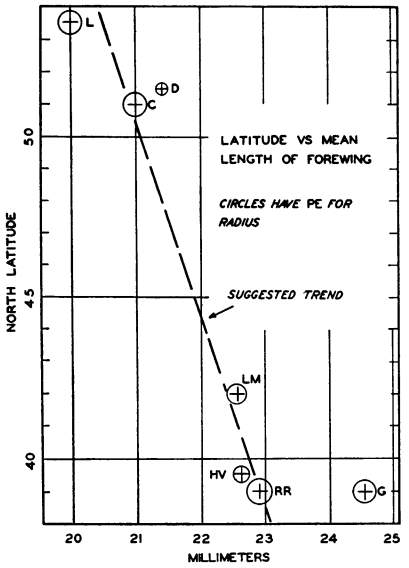


FIG. 4. Size cline.

A similar examination of the series of *uhleri varuna* reveals that while the Didsbury-Calgary comparison yields a *t* score of 2.33, comparisons with the Lloydminster series yield scores of 4.59 and 7.94. This suggests that the Lloydminster material may be significantly smaller than the insects from the northwestern part of the subspecies range.

The coefficients of variation (V) are a little lower than generally met with among butterflies for this measure and suggest that since this species is conservative, variation in size may be of some taxonomic importance.

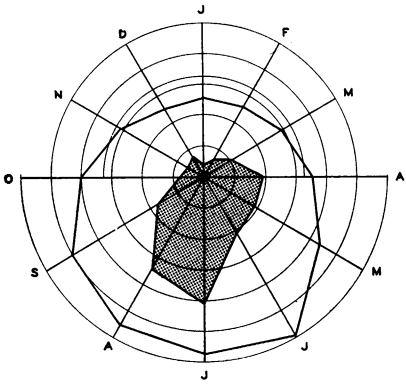
When the two subspecies are compared, the data from the various series taken in pairs yield t scores ranging from 6.78 to 20.73, which are certainly significant. If the material I have studied truly represents each subspecies, it can safely be said that *varuna* is a smaller subspecies than *uhleri*. Of this I am not certain. A definite north-south cline in size (fig. 4) seems to be demonstrable by the series studied, provided the Gothic series is omitted. It is possible that the cline is controlled by temperature and that the apparent difference in size of the two subspecies is physiological rather than genetic.

CLIMATOLOGY

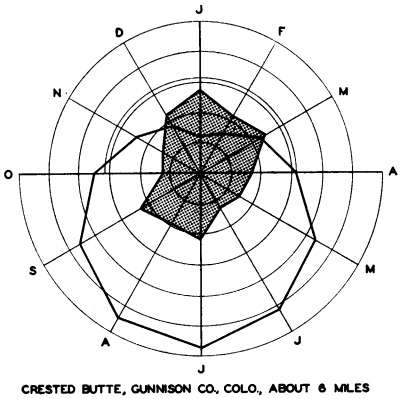
Figure 5 shows five climatographs, based on data collected by the United States Weather Bureau, that apply to stations for *Oeneis uhleri*. The Weather Bureau station of Auldhurst in Teller County, Colorado, is about a mile from the area where I collected the Rampart Range series. I suspect that the slopes where I collected are a little more favored with moisture and a little cooler than Auldhurst. The Gothic series was collected in an area some 6 or 7 miles north of the Crested Butte station. At the collecting station the precipitation may be a little higher and the temperature a little lower than at Crested Butte. In both cases the climatographs would be little different if data were available from the exact collecting stations.

The estimated conditions at the Eagle Mountain collecting area in the Laramie Mountains of Wyoming are at best an educated guess. The climatograph is based on data from Marshall, Albany County, Wyoming, some 16 miles to the west-northwest and on the high rolling ground outside the range. The Marshall pattern was followed, with appropriate changes in temperature based on a temperature-altitude gradient and some knowledge of air drainage, and the precipitation was increased according to the best estimates of the United States Weather Bureau and my own estimates from the vegetation.

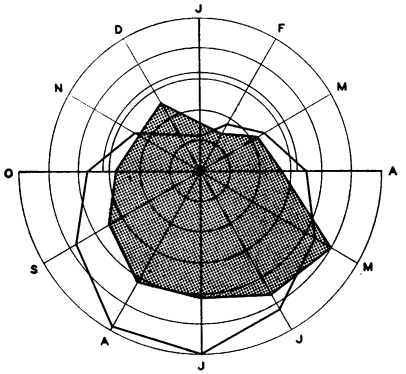
Calgary, Alberta, and Bismarck, North Dakota, are so situated that the diagrams are applicable for some distance from the



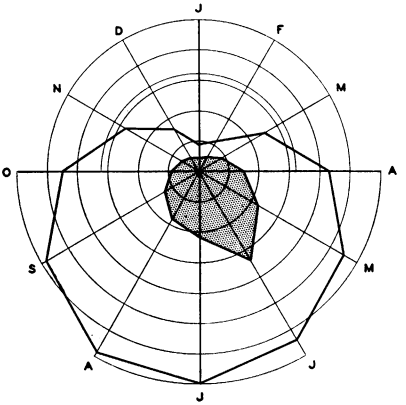
AULDHURST, TELLER CO., COLO., 1 MILE SW RAMPART RANGE



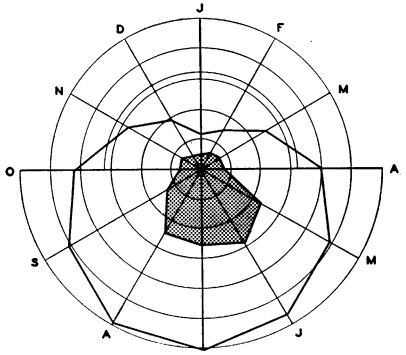
CRESTED BUTTE, GUNNISON CO. COLO., ABOUT 6 MILES OF COLLECTED AREA AT GOTHIC



ESTIMATED CONDITIONS AT "LARAMIE MTS." ALBANY CO., WYO



BISMARCK, N.D.



CALGARY, ALTA.

EXPLANATION OF CLIMATOGRAPHS

RADIAL LINES REPRESENT MONTHS
CONCENTRIC CIRCLES REPRESENT 1 INCH OF PRECIPITATION OR 10°F.
HALF CIRCLE FROM O TO A REPRESENTS 32°F.
STIPPLED POLYGON REPRESENTS MEAN MONTHLY PRECIPITATION DATA
CLEAR POLYGON REPRESENTS MEAN MONTHLY TEMPERATURE DATA

FIG. 5. Climatographs.

weather station. Thus they probably fit more closely than any others the conditions prevailing at the collecting grounds.

Each of the three subspecies appears to have rather characteristic climatic requirements. In one case (*u. reinthali*) winter moisture is in excess of summer. This is the reverse of conditions at the stations for *u. uhleri* and *u. varuna*, where summer moisture is greatly in excess. Longer and warmer summers seem to be the rule for *O. u. varuna* in spite of the fact that its range is far to the north of that of *u. uhleri*, the collecting stations of which all have short summers.

SUMMARY AND CONCLUSIONS

The summary of data presented in the body of the discussion are given in table 11.

TABLE 11

SUMMARY OF *Oenis uhleri* STRAINS

	uhleri uhleri				*uhleri varuna*				
	R.R.	H.V.	G.	L.M.	N.D.	M.	C.	D.	L.
Habitat									
Prairie					x		x	x	x
Woodland	x	x	x	x		x			
Size	22.9	22.6	24.5	22.6	—	—	21.0	21.4	20.0
Color, mean category	6.3	4.6	10.3	5.9	—	—	4.0	4.5	4.5
Discal band on under hind wing[a]									
Graded	75%	83%	46%					26%	
Divided				54%			71%	45	
Banded			31	39				40	82%
Maculation									
Less than 60%	x	x	x	x					
More than 70%					x	x	x	x	x

[a] Only those per cents significantly different from 0 are given.

After much consideration I believe that the Gothic strain of *u. uhleri* is sufficiently distinctive to warrent subspecific recognition. The strain involved is darker and larger than any other known strain of the species. It is intermediate to typical *uhleri* and *varuna* in maculation and condition of the band on the under side of the hind wings. It is separated from the other strains of *uhleri* by a mountain barrier that is broached by passes lying 1000

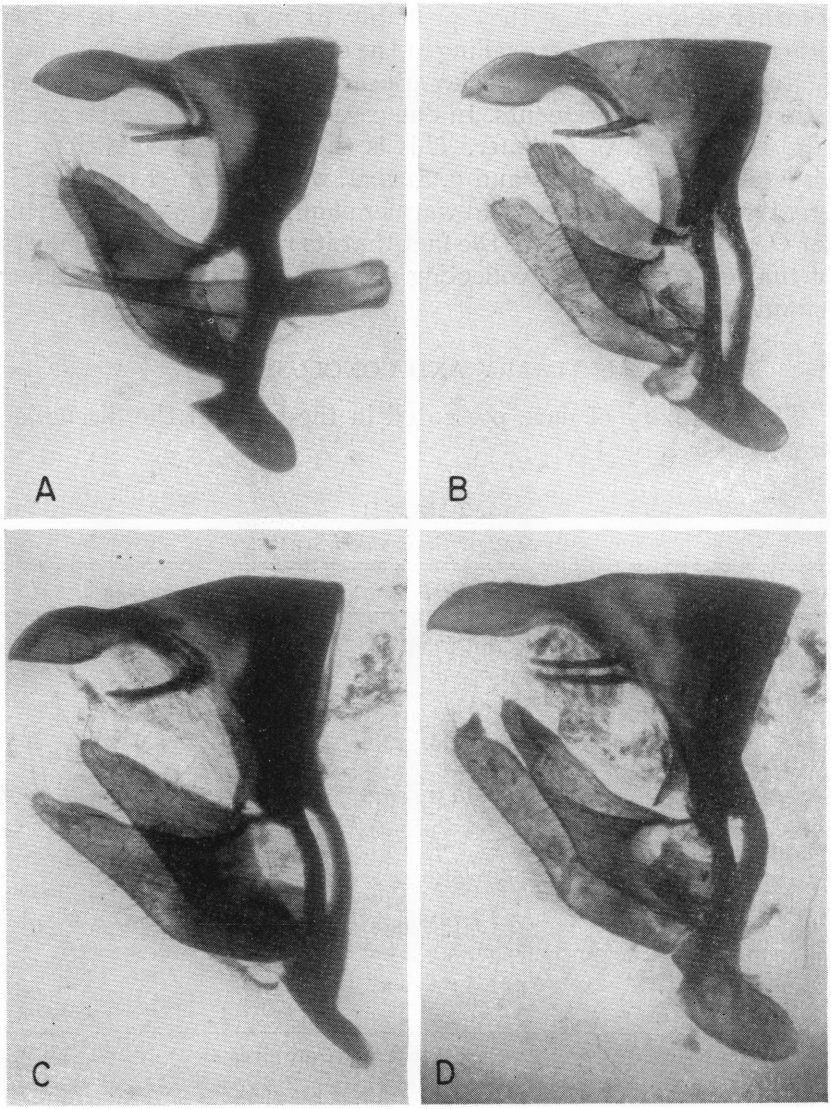


FIG. 6. Male genitalia of *Oeneis uhleri*. A, B. *O. uhleri varuna* Edwards. A. Lloydminster, Saskatchewan, Canada, June 3, 1949 (R. J. Fitch). B. Didsbury, Alberta, Canada, June 11 (C. Garrett). C. *O. uhleri uhleri* Reakirt, Rampart Range, Teller County, Colorado, June 28, 1949 (F. M. Brown). D. *O. uhleri reinthali* Brown, Gothic, Gunnison County, Colorado, July 5, 1949 (W. J. Reinthal).

to 2000 feet above the normal limit of the species—10,000 feet. It is the only strain thus far discovered on the Pacific slope of the Continental Divide.

It is likely that the initial segregation took place at the latest during the Sangamon interglacial epoch and that differentiation took place during the long period of complete isolation that coincided with the alpine glaciation of the Continental Divide in Colorado during the Wisconsin glacial epoch. It is probable that this strain has been segregated from the true *u. uhleri* for at least 60,000 years.

The Laramie Mountains strain, while somewhat different from typical *u. uhleri* and approaching *u. varuna* in regard to the under side of the hind wings, is not sufficiently distinctive to warrant subspecific recognition. It too is an isolated strain. In this case the isolation is much more recent, probably not longer ago than 10,000 years. Throughout the Wisconsin epoch and the post-Pleistocene pluvial period the barrier that now separates this strain from strains in the southern Rocky Mountains in Colorado did not exist. An aerial reconnaissance of the Laramie Range made in 1951 satisfied me that the range is now completely separated from the normal range of *u. uhleri* by a low, dry area sufficiently wide to prevent interchange between the Laramie Mountains strain and strains in the northern part of the southern Rocky Mountains.

Among the *varuna* strains it would be very much worth while to investigate those inhabiting the low, wooded mountain ranges in eastern and central Montana. The material collected there by Wright and studied by Edwards has the habitat of *u. uhleri*, not that of *u. varuna*. It is possible that this material is *u. uhleri*, superficially resembling *u. varuna*.

I have found no constant genitalic differences among the various strains studied (see fig. 6).

Extended correspondence and discussion with Cyril F. dos Passos, a recognized authority on *Oeneis*, played a large part in convincing me that the variety of *uhleri* from the Pacific slope of Colorado should be named. At his suggestion I am doing so and naming the subspecies in honor of the man who brought it to my attention.

Oeneis uhleri reinthali, new subspecies

This subspecies is more closely related to *u. uhleri* than to *u.*

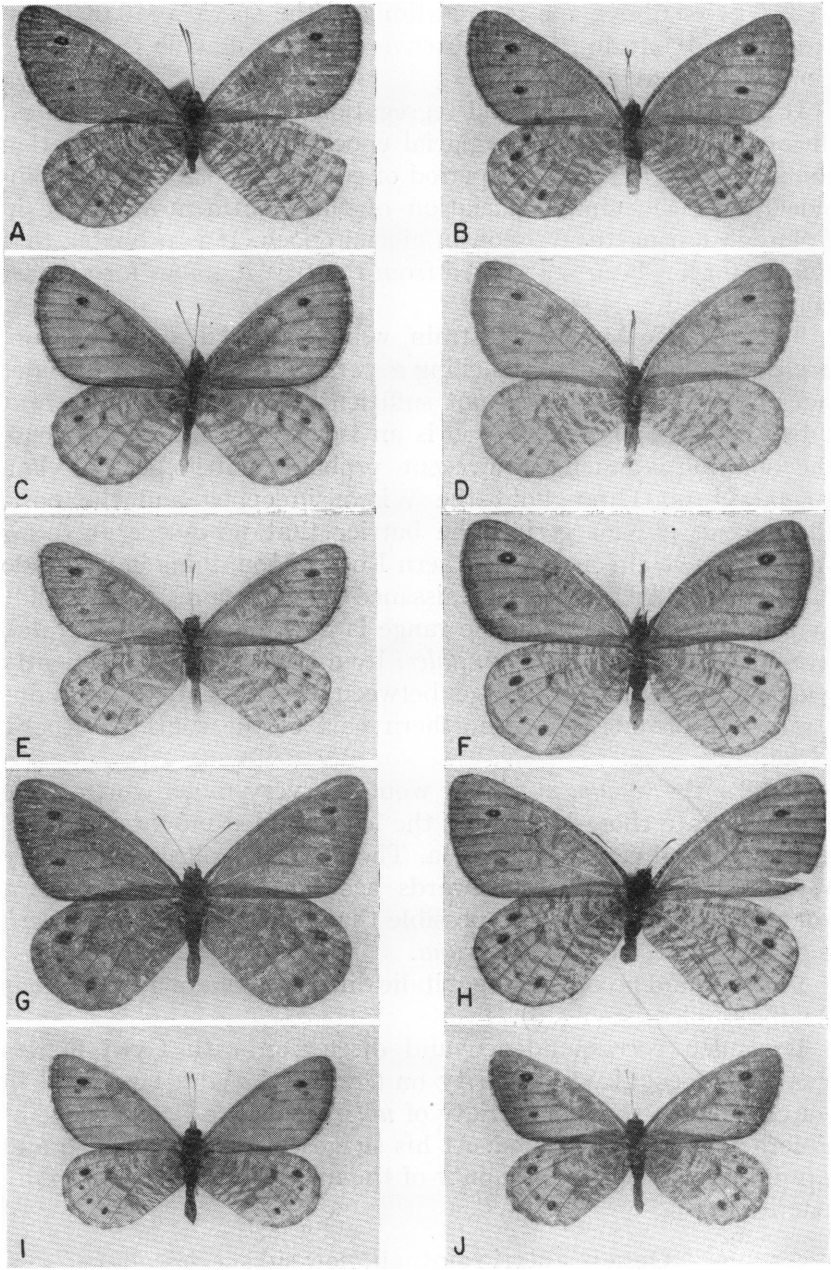


FIG. 7. Upper sides of *Oeneis uhleri* (see opposite page).

varuna. It differs from the former in size and color and from the latter in maculation.

MALES: Upper side is dull reddish brown, as dark as, or darker than, the female figured by W. H. Edwards (1892–1897, *Chionobas* III, fig. 3). The basal two-thirds or more of the cell is soft velvety gray. The veins are lined with diffuse grayish scales. There is a reasonably well-defined grayish brown vadum. The fringe is light with dark wedges at the termini of the veins. The costal margin of the forewing is speckled with dark and light scales, especially towards the base of the wing. On the forewings there almost always is a moderately large, not sharply defined black spot in R-M_1 about midway from the end of the cell to the edge of the wing. There is rarely more than a tiny cluster of white scales in this spot. Usually there is a similar spot in Cu_1-Cu_2 and occasionally a tiny one in M_1-M_2. Occasionally all spots are reduced to mere traces. The hind wings are a little lighter in color than the forewings and translucent enough to reveal the irrorate pattern on the under side. The submarginal series of dark spots is much more fully developed than on *u. uhleri*. Spots Cu_1-Cu_2 and M_1-M_2 rarely are absent. Spot R-M_1 is present about half of the time and spots in M_2-M_3 and M_3-Cu_1 are, about one-third of the time. Occasionally there is a spot in Cu_2-A.

Under side of the forewing is whitish to very pale pinkish brown, boldly striated with dark scales basad of the end of the cell and close to the margin in the apex, leaving a much less striated band in which are found the submarginal spots. Spots M_1-M_2 and Cu_1-Cu_2 are rarely absent and generally ocellate.

FIG. 7. Upper sides of *Oeneis uhleri*. A-F. *O. uhleri uhleri* Reakirt. A. Male, Rampart Range Road, Teller County, Colorado, 9600 feet, June 28, 1949 F. M. Brown). B. Female, same data as for male A. C. Male, Hall Valley, Park County, Colorado, 9600 feet, June 20, 1950 (F. M. Brown). D. Female, same data as for male C. E. Male, southeast of Eagle Mountain, Laramie Mountains, Albany County, Wyoming, 7500 feet, July 2, 1951 (F. M. Brown). F. Female, Palmer Canyon, Laramie Mountains, Albany County, Wyoming, 6000 feet, July 1, 1951 (F. M. Brown). G–H. *O. uhleri reinthali* Brown. G. Holotype male, near Gothic, Gunnison County, Colorado, July 16, 1949 (W. J. Reinthal). H. Allotype female, near Gothic, Gunnison County, Colorado, July 12, 1949 (W. J. Reinthal). I-J. *O. uhleri varuna* Edwards. I. Male Lloydminster, Saskatchewan, May 28, 1949 (R. J. Fitch). J. Female, Lloydminster, Saskatchewan, June 6, 1949 (R. J. Fitch).

All specimens in the collection of F. M. Brown except the holotype and allotype of *O. uhleri reinthali* Brown, which are in the collection of the American Museum of Natural History.

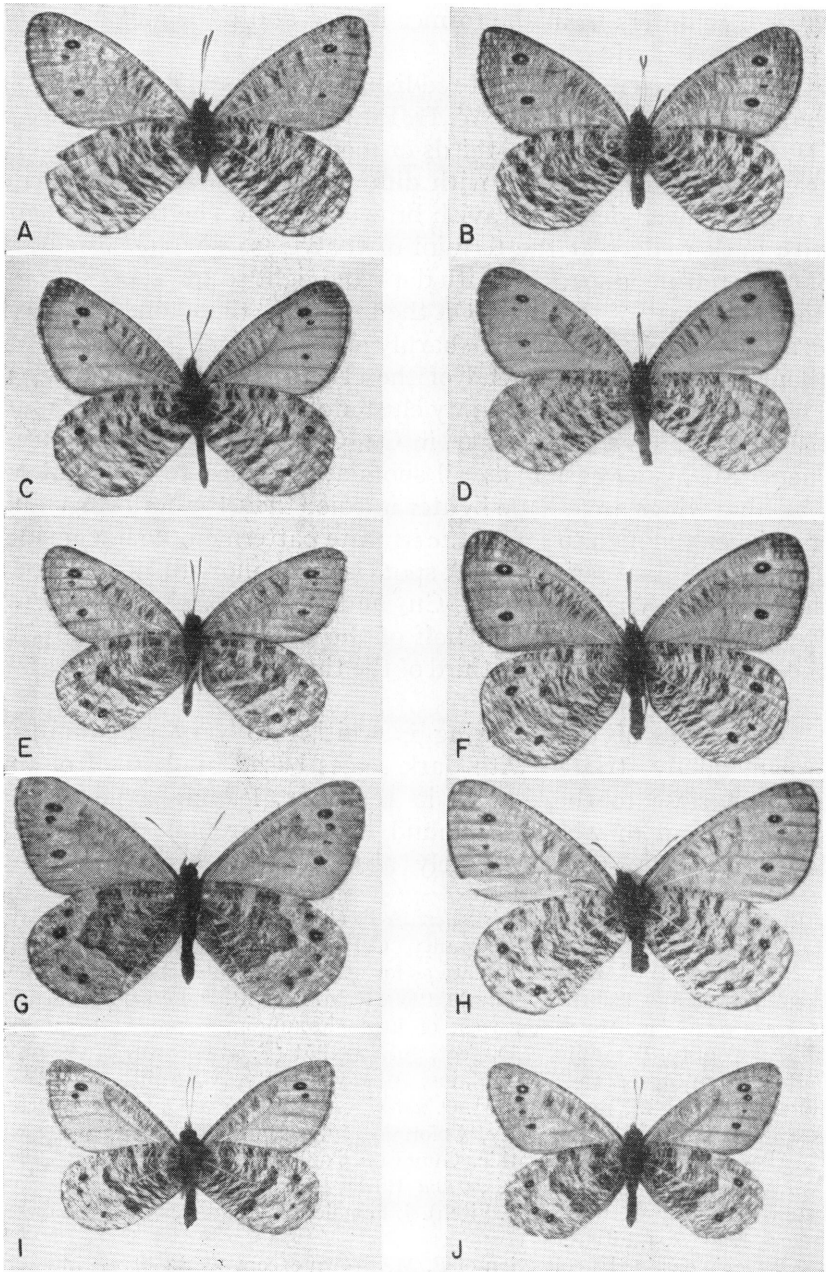


FIG. 8. Under sides of specimens shown in figure 7.

Spot M_2-M_3 is generally present, and M_3-Cu_1 is often so. The hind wings are irrorate, often with a sharply defined basal area outwardly edged with a broad zone of almost white scales and deeply indented with whitish from the coastal margin around the base of R_s. A definite dark discal band is not uncommon. The submarginal spots usually are ocellate and occur with about the same frequency as on the upper side.

FEMALES: A little lighter in color than the males, with the characteristic difference in wing shape and lacking the soft grayish scaling in the cell on the upper side of the forewing. The maculation is a little bolder and more fully developed than on the males.

GREATEST RADIUS OF LEFT FOREWING: Males, 24.54 ± 1.15 mm.; females, 25.0 mm.

TYPES: Holotype, male, near Gothic, Colorado, July 16, 1949, collected by W. J. Reinthal, for whom the subspecies is named. The specimen bears my study number 21. Allotype, female, near Gothic, Colorado, July 12, 1949, collected by W. J. Reinthal. This specimen bears my study number 4. Paratypes, 25 males and three females taken in same vicinity as holotype and allotype between July 5 and 21, 1949, by W. J. Reinthal. Holotype and allotype deposited in the American Museum of Natural History; paratypes in the collection of W. J. Reinthal, Terrell, Texas.

In addition to the type series of *u. reinthali* I have recently seen eight specimens from various localities in the La Plata and San Juan Mountains of southwestern Colorado in the collection of Bernard Rotger of Pagosa Springs, Colorado, and a long series in the United States National Museum from Silverton, Colorado, collected by Barnes.

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